TILAPIINE FISHES
of the genera *SAROTHERODON*, *OREOCHROMIS* and *DANAKILIA*

ETHELWYNN TREWAVAS

The tilapias are cichlid fishes of Africa and the Levant that have become dispersed throughout the warm countries of the world for fish-farming. This book describes forty-one recognized species that have the habit of carrying the eggs and embryos for safety in the mouth of one or both parents. Substrate-spawning species, belonging to the now restricted genus *Tilapia*, are not treated.

Of the mouth-brooding species, three genera are included, but one of them, *Danakilia*, comprises a single species that does not grow to a size suitable for fish-farming. The other two, *Sarotherodon*, with nine species, and *Oreochromis*, with thirty-one, are distinguished primarily by their breeding habits and their biogeography, supported by structural features. Each species is described, with its diagnostic features emphasized and illustrated, and to this is added a summary of what is known of the ecology and behaviour. Conclusions on relationships involve assessment of parallel and convergent evolution.

The tilapias, unlike the majority of fishes, subsist as adults almost entirely on vegetable food, and for *Sarotherodon* and *Oreochromis* this comprises microscopic organisms found in the algal growths covering submerged surfaces of plants and rocks, in the plankton and in organic detritus. Within this range, specialization is reflected in diversity of the structures concerned with feeding.

Danakilia is endemic in the warm, alkaline waters of the Danakil Depression, between the Ethiopian Highlands and the Red Sea. It is particularly interesting because of its resemblance to a recently discovered cichlid of Iran, from which it is separated by the whole Arabian Peninsula, where no cichlids are found today.

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Preface and acknowledgments

This review is the result of study of African cichlid species extending over many years. It began in 1928 when as assistant to Dr C. Tate Regan I collaborated with him in describing some of the species of *Haplochromis* of Lake Victoria and went on to describe, under his guidance, the big collection of Lake Malawi fishes made by Dr Cuthbert Christy at Tate Regan's instigation.

Every taxonomic study of the Cichlidae is based on Regan's broad classification of the family as well as his detailed work on species. In 1920 he improved on Boulenger's classification of 1899 and 1915 by separating on osteological grounds the *Tilapia* group from *Haplochromis* and others that had been confused with it; and divided *Tilapia* into four subgenera, one of which, *Sarotherodon*, (now divided into three genera) is the main subject of this review. *Neotilapia*, which Regan made a monotypic genus, is here somewhat doubtfully regarded as a subgenus of *Oreochromis.*

When I became responsible for the care of freshwater fishes at the British Museum (Natural History), many of the questions that were being asked by fishery biologists working in Africa were concerned with the tilapias. In 1938–9 I had the good fortune to take part in a survey of the fishes and fisheries of Lake Malawi (Nyasa), sponsored by the Colonial Development Fund. To my two colleagues on this survey, Dr Kate Ricardo-Bertram and Mr H. J. H. Borley, I am extremely grateful for enabling me to concentrate on the taxonomic work involved. It was my first practical demonstration of the need to combine museum and field studies, and I have since been able to visit other parts of Africa to try to find answers to the problems raised by studies of small samples in the Museum.

In 1947 I spent two months in Nigeria, again with the support of the Colonial Development Fund. In 1965 a grant from the Ministry of Overseas Development enabled me to travel for four months, spending most of that time in Tanzania and Zambia and shorter periods in Uganda, Kenya, Malawi and Jordan. In 1970 I joined an expedition to West Cameroons organized by Professor J. Green and Dr S. A. Corbet of Westfield College, University of London, and supported by grants from the Royal Society, London University and the Godman Exploration Fund. This journey ended in a short visit to Ghana.

On these visits I have had the invaluable cooperation of members of the fisheries departments and others, who, with the support of their respective governments took care of the logistic details, making my brief visits maximally productive. To these I have pleasure in acknowledging my great indebtedness and gratitude. I must mention: Captain W. B. Dowson (Nigeria, 1947); Dr R. G. Bailey (Tanzania, 1965); Mr M. J. Mann and Mr R. L. Welcomme (Uganda, 1965); Mr M. A. E. Mortimer and the following members of his staff at the Zambian Fisheries Research Institute (1965): Mr Graham Bell-Cross, Mr T. G. Carey, Mr Colin Tait, who escorted me respectively to Lake Mweru, River Kafue and the Luangwa Valley, giving me at the same time the benefit of their expert local knowledge; Mr David Eccles and Mr R. G. Kirk and their staff (Malawi, 1965). In Cameroons we received invaluable help from the Helminthological Research Institute at Kumba for which I am most grateful to Dr Brian Duke (Director), Mr Peter Moore (who lent us his house while he was on leave) and especially to Dr Henry Disney, who personally made collections with us and drove us to the places we wished to visit. In Ghana I was welcomed to his department by Professor Ewer at the University of Ghana and was accompanied to some of the coastal lagoons by Mr Walter Pople, who has an unrivalled knowledge of the ecology of those lagoons. I was also able to accompany Mr S. A. Whyte on a visit to the remarkable Ashanti lake Bosumtwi, the ecology of whose fishes he has ably described in the publication listed here among the references.

From Amman, Mr Paul Spangle (who was then, under the auspices of the U.S.A.I.D. program, advising the Jordanian Government on tourism) took me with him to the oasis of Asraq, where Abu Gozi kindly caught for us with his cast-net samples of the fishes inhabiting the pools.

A very useful visit was paid to Israel in 1961. There Dr Lev Fishelson demonstrated to me that what had appeared in the Museum to be one species in fact comprised two, *O. niloticus* and *O. aureus.* On this visit, which was planned as a holiday, I received the greatest kindness from the late Dr H. Steinitz, the late Professor G. Haas, and from Drs H. and Tamara Mendelsohn, Dr Adam Ben-Tuvia and his wife Sheila.

On all these visits we found the local fishermen friendly and happy to share with us their intimate knowledge of the fishes and their habits. It was with their help that we were able to take the first steps towards the recognition of the four closely related species of subgenus *Nyasalapia* in Lake Malawi, for which they had special names, at least at some stages of the life-history. At Lake Barombi-Mbo in Cameroons there was one small village, whose chief was very anxious to keep control of the little crater-lake, with which the life of the village was intimately bound. Nevertheless he and the villagers, who knew the seventeen species of fishes inhabiting the lake (eleven of them endemic cichlids), caught for us specimens of all of them and corrected our limited museum knowledge. No doubt we owed much of this good will to the fact that we were introduced by Dr Henry Disney and by Mr Ekome, the latter the laboratory superintendent at the Helminthological Institute and a respected resident of Kumba. It is to be hoped that the lake and village will be allowed to retain their integrity.

On a recent visit to Kenya I received valuable help and hospitality from Mr René Haller, Mr J. D. Balarin and Mr I. S. N. Parker.

I have further benefited by correspondence with many people interested in fish and fisheries of Africa, and by discussions with them during their visits to the Museum. Many of them have already been named, but I must mention Dr R. Jubb, now of Grahamstown; the late Mr H. Copley of Kenya; Dr Malcolm Coe, formerly of Nairobi University and now at Oxford; Dr M. Bruton of Rhodes University, Grahamstown; Mr D. Tweddle (Malawi); Professor H. M. Peters of Tübingen; Dr A. I. Payne, formerly of Njala University, Sierra Leone; Dr Karel Liem (M.C.Z., Harvard University); my colleagues Dr P. J. P. Whitehead (formerly of Kenya), Dr P. H. Greenwood (formerly of Uganda), Dr D. R. Rollinson, and latterly Dr Lynne Parenti.

Dr Thys van den Audenaerde has generously communicated to me the results of his journeys in West Africa and sent me prints of his colour photographs of species that I have not seen alive.

Very special thanks are due to Dr Rosemary Lowe-McConnell. Her many publications on tilapias are referred to in their proper places and listed in the bibliography. In addition I have enjoyed many discussions with her on matters tilapiine and she has spared time to read through the typescript, adding valuable suggestions as well as making corrections in detail. She was also my invaluable companion in Kenya in 1981.

Dr Brendan McAndrew (University of Stirling) has given generously of his time to explain to me the nature of the evidence and the techniques used in exploring cell-chemistry, as well as the basis of the assumption that the enzymes directly express an important part of the genome.

Since my official retirement from the staff of the British Museum (Natural History) in 1961 I have had the privilege of continuing to work on the collections there and to use all the facilities of the Museum, including photography, radiography, scanning electron micrography and microscopic technology. Radiographs were also made for me by Dr D. Cohen (USNM), Mrs Eugenie Böhlke (ANSP) and Dr M. H. Hobdell then of Kings College, University of London, to whom I offer my sincere thanks.

Finally our colleague Gordon Howes has lent his combined artistic and scientific skills to improving some of the illustrations, and Mrs Myra Givans prepared the script for publication.

Type specimens of many species are in the BMNH and I have also been able to see, either on visits or on loan, types and other important specimens in several museums, for which I am grateful to the following colleagues responsible for their care (for explanation of the abbreviations see p. 40): Professor M. Poll and Dr Thys van den Audenaerde (MRAC); Dr P.

Kähsbauer (NHMW); Dr W. Klausewitz (Senck. Mus.); the late Dr James Böhlke and Mrs Böhlke (ANSP); Drs L. Schultz, E. Lachner, S. Weitzman (USNM); Dr Donn E. Rosen (AMNH); Dr W. N. Eschmeyer and Mr W. I. Follet (CAS); Dr M. L. Bauchot, Dr Th. Monod and the late Dr L. Bertin (MNHN); Dr E. Tortonese (Mus. Civ. G. Doria, Genoa); Dr K. Deckert (ZMB) and Dr M. Boeseman (RMNH); and Mrs Myvanwy Dick (MCZ).

Illustrations signed D.W.O. are by naturalist and illustrator Denys Ovenden.

Scope and policy of this review

Ecology

This review is primarily taxonomic, and although what is known of the natural history of each species is recorded no general summary of these matters is added. Such general accounts have been published in the book edited by Pullin & Lowe-McConnell (1982), especially the articles by Philippart & Ruwet (pp. 15–59) and Lowe-McConnell (pp. 83–113). Several aspects are dealt with by Fryer & Iles (1972) and Lowe-McConnell (1975). These books use the same original sources as I have, and although I have not always quoted them in addition, they are well worth consulting for an overall view of behaviour and ecology.

Zoogeography and the fisheries

The use in Africa of the tilapias for fish farming and stocking lakes and dams has confused their value as indicators of the history of the waters of the continent. The major part of the material on which this review is based was collected before these widespread introductions were made, so that the paragraphs headed 'Natural distribution' can in most cases be relied on. The paragraphs on 'Dispersal by man' are less complete and this aspect of the 'unnatural history' of the tilapias is constantly changing. Introductions have sometimes been started under careful supervision, but have fallen into other hands. In Israel the native *Oreochromis niloticus* can now no longer be recognized, and to get a pure strain experimenters have imported stock of the species from Ghana. In Kenya in the 1930s the areas of *O. spilurus spilurus* and *O. s. niger* were fairly well-marked, although stocking of farm dams had been going on since the nineteen-twenties. It is now difficult to find a stream in whose system both subspecies, as well as *Tilapia 'zillii'*, have not been introduced. Some of the short rivers south of the Sabaki seem to contain only *O. s. spilurus*, with three anal spines; but even in one of these there was, in 1981, an admixture of individuals with four anal spines below a dam, possibly indicating inclusion of *O. s. niger*. The Great Ruaha, tributary of the Rufigi in Tanzania, is believed to have had quite other connections in the geologically recent past, but its tilapias can now tell us little about that. The Lower and Middle Zambezi once held different but related species of *Oreochromis*, *O. mossambicus* and *O. mortimeri*, but stocking has now confused them and they have probably hybridized.

Among other introductions, Lake Victoria, which once contained only two endemic species of *Oreochromis* and no *Tilapia*, now has *Tilapia zillii* (and *rendalli*?), *Oreochromis leucostictus* and *O. niloticus*. These *Oreochromis* came originally by accident with *T. zillii* from Lake Albert, but the situation may now have been further confused by the addition of stock of the Lake Turkana subspecies of *O. niloticus* (I. S. C. Parker, pers. commn).

One of the uses of the present review is therefore to record the distribution of the genera and species of the mouth-brooding tilapias before interference by man. It may also help those interested to identify the species now in their waters, but the fishes themselves have sometimes failed to distinguish their new neighbours and have interbred with them.

The probably harmful results of indiscriminate introductions, through hybridization and competition are illustrated by Daget & Moreau (1981). See pp. 451–452 herein. A bibliography of the most important cultured tilapias is that of Schoenen, 1982.

Phylogeny

The generic and subgeneric groupings adopted are indications of the position taken with regard to relationships. With the accounts of the species or groups of species conclusions or suggestions on relationships are offered; but pp. 32–37, on parallelisms or convergences and the overlapping of numerical characters give sufficient reasons for the absence of cladograms.

In listing the 'distinguishing characters' for each species my aim has been to assist the reader in distinguishing a species both from its nearest relatives and from its sympatric or neighbouring congeners. The needs of fish farmers receiving tilapias of unknown origin have also been borne in mind, but history during previous captivity may add difficulties here.

Taxonomic innovations

In this work the ranking of some taxa has been revised, namely: the former subgenera *Sarotherodon*, *Oreochromis* and *Danakilia* have been raised to the rank of full genera. One new species and five new subspecies have been named. These are:

Sarotherodon melanotheron paludinosus subsp. n. (p. 64)
Oreochromis niloticus filoa subsp. n. (p. 167)
Oreochromis niloticus baringoensis subsp. n. (p. 177)
Oreochromis niloticus sugutae subsp. n. (p. 179)
Oreochromis macrochir mweruensis subsp. n. (p. 438)
Oreochromis malagarasi sp. n. (p. 426)
Oreochromis (*Vallicola*) subgen. n. (pp. 27 & 29).

Contents

Introduction

The use in the title of the word 'tilapiine' implies the recognition of a Subfamily (Tilapiinae) or a Tribe (Tilapiini). The time is not ripe for the definition of subfamilies within the Cichlidae. This will involve consideration of the very diverse members of the Family in India, Sri Lanka, Madagascar, and Central and South America, as well as, for example, the Tanganyika genera. We may tentatively recognize a Tribe, Tilapiini, although its limits are not easily defined. It is an exclusively African and Levantine assemblage, including *Tilapia*, *Sarotherodon*, *Oreochromis*, *Danakilia*, *Iranocichla*, *Tristramella*, *Pelmatochromis*, *Pterochromis*, the endemic genera of Barombi Mbo and probably some specialized genera of rapids (*Steatocranus*, *Gobiochromis*).

The Tribe Tilapiini is basically distinguished from the Haplochromini by the structure of the apophysis on the base of the skull for the articulation of the upper pharyngeal bones. In Tilapiini its facets are formed from the parasphenoid alone (Fig. 1 & 2), whereas in *Haplochromis* and related genera the basioccipital forms up to one half of each facet. This feature and its significance were first noticed by Regan (1920), who by this means was able to purge the unnatural assemblage included in *Tilapia* by Boulenger (1899, 1915) (who was himself dissatisfied with it) of many unrelated species that had been included only because of their bi- and tri-cuspid teeth. That this condition of the apophysis is plesiomorphic within Cichlidae is hypothesized from its occurrence in *Etroplus*, the endemic genera of Madagascar and all Neotropical genera except *Cichla*, whether the pharyngeal teeth are slender or enlarged. Moreover it characterizes related outgroups, e.g. Labridae and Embiotocidae (Liem & Greenwood, 1981). For application of the criterion of the pharyngeal apophysis in other cichlid genera see Greenwood (1978).

The three tilapiine genera *Tilapia*, *Sarotherodon* and *Oreochromis* were formerly included in the broad genus *Tilapia* (Trewavas, 1966*a* & *b*; Thys, 1968*b*) and may still conveniently be known as 'the tilapias'. Of the other tilapiine genera the least specialized is *Pelmatochromis*

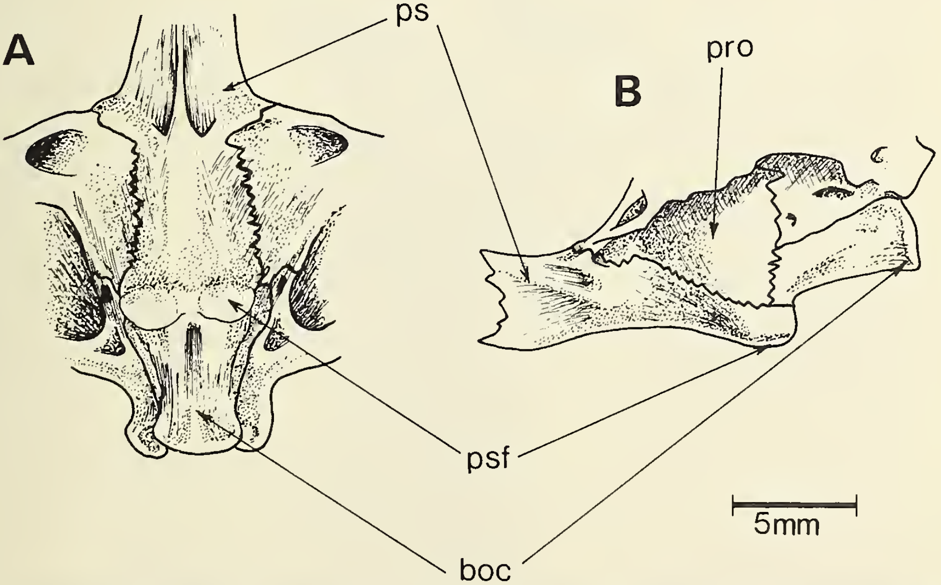

Fig. 1 *Oreochromis shiranus.* A, posterior part of base of skull, showing part of the parasphenoid with the apophysis for the upper pharyngeal bones, the prootic and the basioccipital; B, lateral view of the same. After Greenwood, 1978, fig. 2. boc = basioccipital; pro = prootic; ps = parasphenoid; psf = facet on parasphenoid for articulation of upper pharyngeal. Drawn by Gordon Howes.

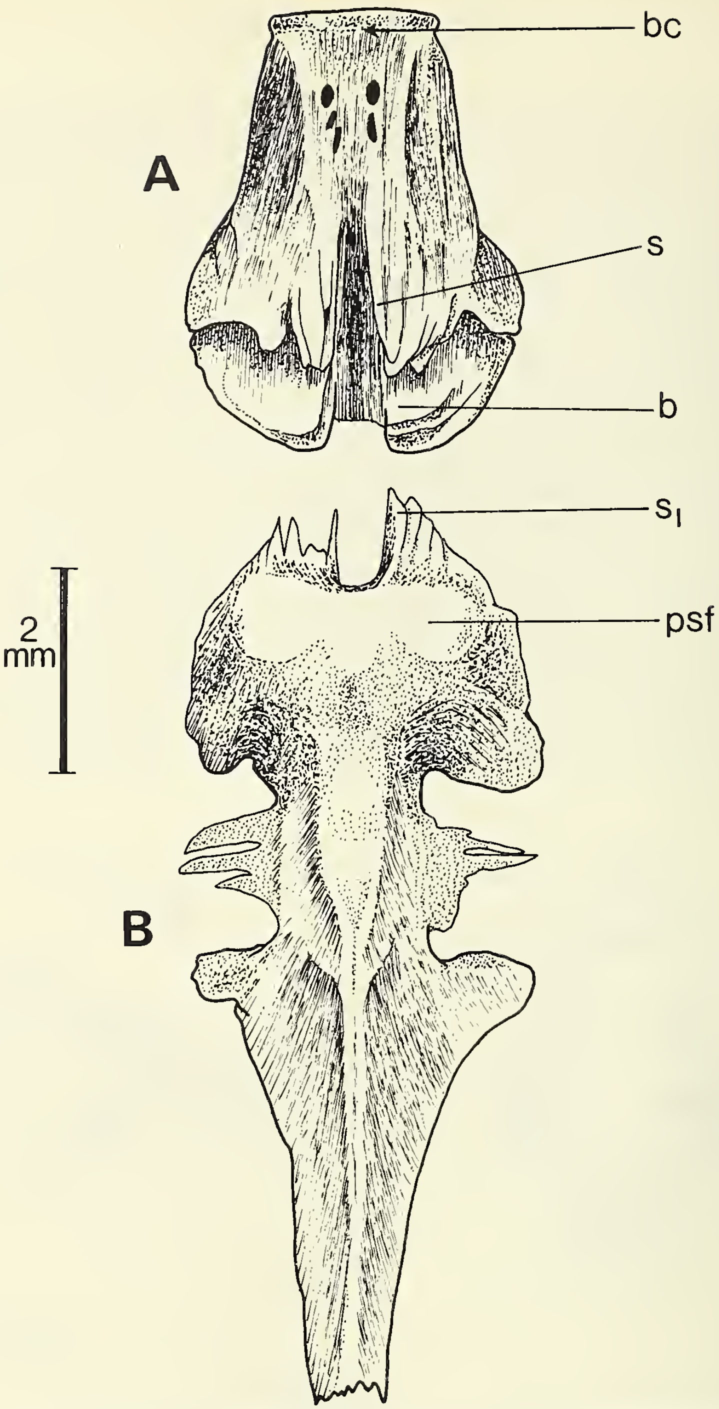

Fig. 2 *Oreochromis mossambicus.* A, the basioccipital; B, part of the parasphenoid disarticulated to show the pharyngeal apophysis involving only the parasphenoid, and the interdigitating union of the two bones, b is a stout lamina of the basioccipital lying dorsally to the posterior end of the parasphenoid, *s* and s_1 the interdigitating laminae that meet in a suture behind the apophysis. After Greenwood, 1978, fig. 3. Drawn by Gordon Howes.

Steindachner (as restricted by Thys, 1968*c*). The species have retained certain characters that are primitive in Cichlidae, namely low numbers of vertebrae (26 or 27) and of scales in the lateral line series (27 or 28) and only four lateral line openings in the preorbital bone (see p. 9). The dentition is suited for the seizure of small invertebrates, the most usual source of food for freshwater fishes, and in the absence of any evidence of mouth-brooding they are assumed to be substrate-brooders. An important difference between *Pelmatochromis* and the basic species of *Tilapia* is in the diet, which in *Tilapia* is mainly vegetarian in the adult, and in the structural features, especially of dentition and intestine, associated with this diet. Thys (1968*b*) has proposed to make *Pelmatochromis* a subgenus of *Tilapia* and to include in it one of the herbivorous *Tilapia* (*T. busumana*), a decision that I have disputed (Trewavas, 1973*a*).

Thys's classification differs from that adopted here (Table 1) partly in the rank given to the groups, but also in the different emphasis placed on the nature of the dentition. The apparent weighting in the present scheme of the arming of the jaws with unicuspid teeth in *Pelmatochromis* and bi- and tricuspid teeth in *Tilapia* depends not merely on the shape of the teeth, but on the fact that all the interrelated species placed in *Tilapia*, *Sarotherodon* and *Oreochromis* have notched teeth throughout life (excluding the secondary condition in some mature males) and all three species of *Pelmatochromis* have curved, conical teeth. Thys considered this difference to be less than trenchant, instancing the unicuspid posterior premaxillary teeth in *T. busumana* and the presence of some bicuspid teeth in young *Pelmatochromis*. But I have examined young *P. buettikoferi* and found the teeth to be unicuspid in the smallest sizes (28 mm SL), and among about 80 specimens of *P. nigrofasciatus* only in those of 22–38 mm SL did I find some notched outer teeth. Above this size they are simple or shouldered. I have seen no young *P. ocellifer*.

Table 1. Classification of the tilapias (Tilapiini) with notched teeth (other than specialized rheophil genera).

Genus	Subgenus	Type species	Breeding habit
Tilapia A. Smith	Three to six subgenera	*Tilapia sparrmanii* A. Smith	Substrate spawners and guarders
Tristramella Trewavas	—	*Chromis sacer* Günther	Biparental mouth-brooders
Danakilia Thys	—	*Tilapia franchettii* Vinciguerra	Mouth-brooders (details unknown)
Sarotherodon Rüppell	—	*Sarotherodon melanotheron* Rüppell	Paternal, biparental or maternal mouth-brooders
Oreochromis Günther	*Oreochromis* Günther	*Oreochromis hunteri* Günther	Arena spawners and maternal mouth-brooders
	Alcolapia Thys	*Tilapia grahami* Boulenger (=*O. (A.) alcalicus grahami)*	Arena spawners and maternal mouth-brooders
	Vallicola nov.	*Tilapia amphimelas* Hilgendorf (=*O. (V.) amphimelas)*	Probably as *Oreochromis*
	Nyasalapia Thys	*Chromis squamipinnis* Günther (=*O. (Ny.) squamipinnis)*	Arena spawners and maternal mouth-brooders
	Neotilapia Regan	*Chromis tanganicae* Günther (=*O. (Ne.) tanganicae*)	Maternal mouth-brooder (details unknown)

In adults of all three species the teeth are uncompromisingly unicuspid (cf. Trewavas, 1973*a*, figs 1A & 9).

Nevertheless, *Pelmatochromis*, especially *P. nigrofasciatus* (Pellegrin), may be representative of the ancestral group from which *Tilapia* diverged by an ancient dichotomy based on diet.

Regan (1920) and Trewavas (1966*c*) included *Sarotherodon* in *Tilapia* as a subgenus, comprising *Oreochromis* as well as *Sarotherodon* of the present classification. Thys (1968*b*) recognized seven subgenera of mouth-brooding tilapias, *Sarotherodon*, *Oreochromis*, *Alcolapia*, *Neotilapia*, *Nyasalapia*, *Loruwiala* and *Danakilia*, and in 1971 he added *Nilotilapia*. *Sarotherodon* was given the rank of genus by Trewavas (1973*a*; 1980; 1982*b*, but not the addendum), who then included all Thys's mouth-brooding subgenera within it. Later (Trewavas, 1981; 1982*a*; 1982*b*, addendum) I became convinced that this was unsound and proposed the present classification, with *Sarotherodon* and *Oreochromis* as separate genera. This expresses the view that, although *Sarotherodon* and *Oreochromis* probably arose from substrate-brooding *Tilapia*, they may have come from different species. It follows the lead given by the studies of reproductive behaviour and development published by H. M. Peters and his pupils from Tübingen (see p. 13 footnote), and is supported by geographical and anatomical features, which, though supplying few trenchant differences, have a cumulative value.

The relationship of *Danakilia* became clear only on the discovery by Coad (1982) of *Iranocichla*, which showed that, although a mouth-brooder, its origin was independent of that of either *Sarotherodon* or *Oreochromis* (see p. 503).

The evidence that *Sarotherodon* and *Oreochromis* stemmed from one or more substrate-brooding species of the genus *Tilapia* or from a shared common ancestor depends on the resemblances between the three genera.

Resemblances between *Tilapia, Sarotherodon* and *Oreochromis*

1. Apophysis on the base of the skull and its facets for articulation of the upper pharyngeal jaws formed from the parasphenoid alone.
2. Caudal skeleton with five distinct hypurals and two epurals.
3. Preorbital (lacrimal) bone with five openings of the lateral line system. Exceptions with only four are deemed to be secondary reductions.
4. Ventral vertebral apophyses (here named *spondylophysial apophyses*) for the attachment of the swimbladder and fibres of the retractor muscles of the upper pharyngeals present on the third vertebra, united below the dorsal aorta and usually produced into a spine.
5. Pigmentation. A black spot, known as the tilapia-mark, at the junction of spinous and soft parts of the dorsal fin, surrounded by a clear or yellow zone, present usually in the young, in some species also in the adult.
6. Scales cycloid, though often with a fringe of minute cilia in the young.
7. Diet in adults predominantly vegetarian, the food varying in coarseness from macrophytes to phytoplankton or even bacteria, with concomitant structural features, namely:
    a. teeth of jaws with notched crowns.
    b. pharyngeal teeth slender, fine, not enlarged (except in *Tilapia buttikoferi*) or flattened.
    c. intestine long, in adults from seven to fourteen times the standard length.
    d. general body shape rather deep, with long pectoral fin.
8. One long chromosome in a haploid complement of 22 has been recognized as a tilapia-marker (K. W. Thompson, 1976; Kornfield *et al*., 1980; and see p. 12).

Of these characters numbers 1 and 2 are plesiomorphic for Cichlidae. Numbers 3 and 4 are derived (or apomorphic) within Cichlidae, but are shared with many other African cichlids, including other tilapiines and many haplochromines. Number 5 is of limited diagnostic value, but seems to be confined to the tilapiines. Number 6 is probably the plesiomorphic state in the family Cichlidae, though not in the Percomorphs; if so, the more prominently ctenoid scales

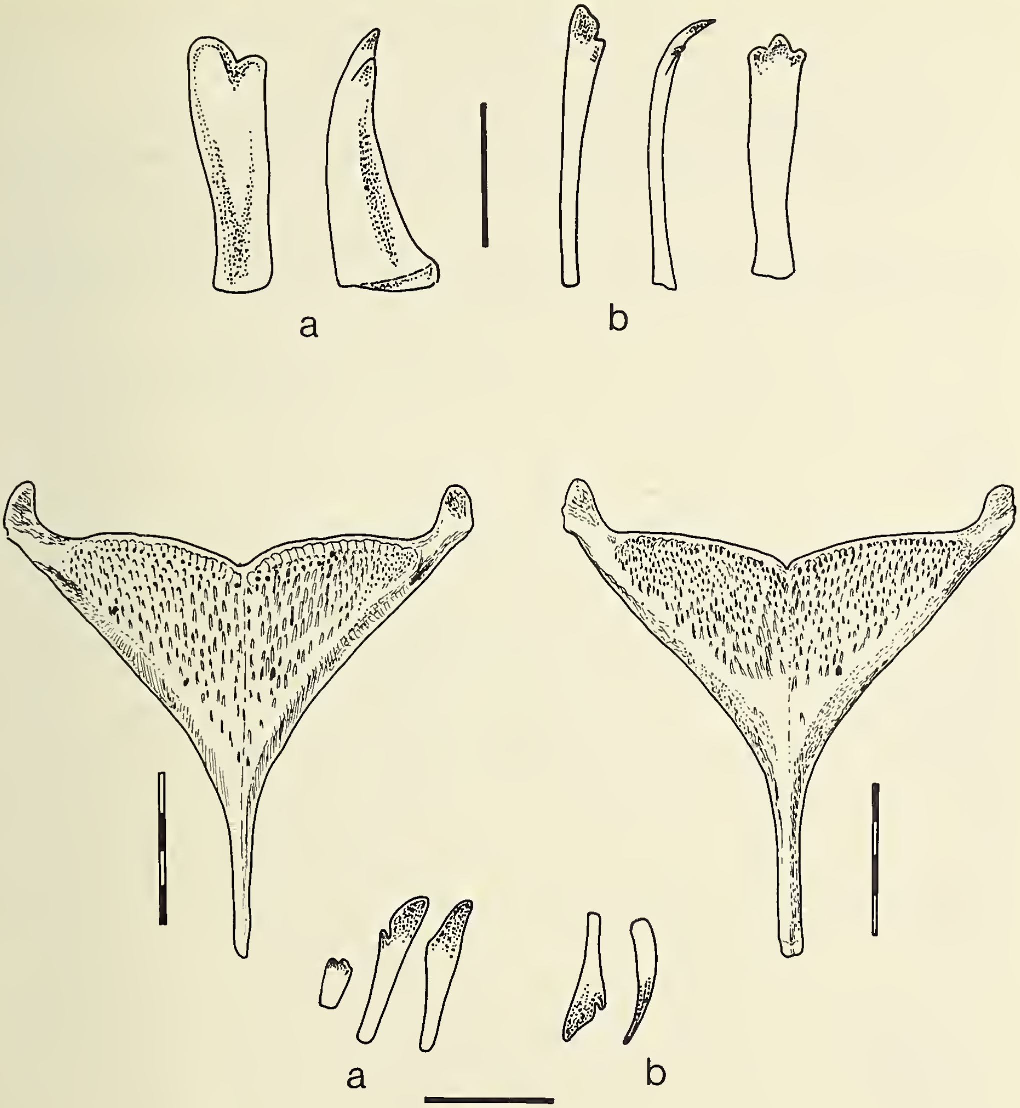

Fig. 3 Above, teeth from the outermost row of the jaw of: a, *Tilapia rendalli* 140 mm SL; b, *Oreochromis karongae* 164 mm SL. Below, *Tilapia mariae,* lower pharyngeal bones of, left, a fish of 117 mm SL; right one of 104 mm SL; and teeth from the jaws of: a, a fish of 155 mm SL (one inner and two outer); b, one of 88 mm SL (two views of the same tooth).

of *Lamprologus* and many haplochromines must be considered a derived (or secondarily derived?) condition. Number 7 a vegetarian diet, is not found in *Etroplus* nor is it known in the Madagascan genera and it is rare among Neotropical species. Some African, non-tilapiine lineages, include species feeding on epiphytic or epilithic algae, e.g. *'Haplochromis' similis* Regan, *Neochromis nigricans* (Boulenger) and notably in the rock-fishes of Lakes Malawi and Tanganyika. The diet and concomitant structures distinguish *Tilapia*, *Sarotherodon* and *Oreochromis* from *Pelmatochromis. Tristramella*, *Danakilia* and *Iranocichla* are vegetarian, but include species with enlarged pharyngeal teeth. Character number 8 seems diagnostic of the three genera under discussion in contrast to others in which it has been investigated, but its full significance can only be assessed following karyological investigations on a wider scale.

The following paragraphs are expansions of the above brief statements

1. The importance of the pharyngeal apophysis on the skull has been discussed on p. 1.
2. The caudal skeleton was described by Vandewalle (1973) in 108 cichlid species assigned

Table 2. Frequencies of vertebral numbers in samples of the species of *Tilapia*, *Sarotherodon*, *Oreochromis* and *Danakilia*. The data include some from Daget (1960*a*), Daget & Iltis (1965) and Loubens (1965).

Vertebrae	26	27	28	29	30	31	32	33	34
Genus *Tilapia*									
guinasana	17								
sparrmanii	2	22	8						
ruweti	1	27	4						
baloni		3	17	1					
busumana	1	25	2						
buttikoferi			7						
discolor		2	8						
guineensis		2	36	1					
kottae			2						
camerunensis			6						
cameronensis			2						
nyongana		1	3						
margaritacea	1	29							
dageti			6						
louka			5						
zillii		5	33	2					
rendalli			1	31	1				
'*rendalli*' (Dongwenna)				5	9				
mariae			3	9					
brevimanus				2					
cabrae			1	18	1				
Genus *Sarotherodon*									
S. m. melanotheron	10	25	1						
S. m. leonensis		6	4						
S. m. heudelotii		2	10	3					
S. mvogoi			3	2					
S. lohbergeri				4					
S. linnellii				15					
S. caroli				3	1				
S. steinbachi				7	8	1			
S. galilaeus		2	5	19	12	1			
S. tournieri			2						
S. occidentalis				5	3				
S. caudomarginatus					1	4			
Genus *Oreochromis*									
Subgen. *Oreochromis*									
O. niloticus niloticus					7	47	5		
O. n. cancellatus					2	15	1		
O. n. filoa	1		3	7	6				
O. n. vulcani					2	20	6		

Vertebrae	26	27	28	29	30	31	32	33	34
O. n. baringoensis				(1)	4	6			
O. n. sugutae				3	6	1			
O. n. eduardianus				2	9	2			
O. esculentus					2	2			
O. aureus (Jordan Valley)		1	11	79	29	1			
O. aureus (elsewhere, excl. Ain Feshka				6	33	5			
O. hunteri						2	3	15	1
O. pangani							1	2	2
O. jipe							1	2	
O. s. spilurus			3	33	4				
O. s. spilurus (Buffalo Springs)				8	3				
O. s. niger				9	23	1			
O. s. percivali			5	1					
O. korogwe				15	3				
O. u. hornorum				8	18				
O. u. urolepis				8	9				
O. placidus				14	13	1			
O. s. shiranus					7				
O. s. chilwae				3	17				
O. mossambicus			3	2	17	1			
O. mortimeri				5	14	(3)			
O. andersonii					1	16	2		
Subgen. ?									
O. leucostictus		4	14	5					
Subgen. *Alcolapia*									
O. alcalicus		21	32	3	1				
Subgen. *Vallicola*									
O. amphimelas					8	15	2		
Subgen. *Nyasalapia*									
O. angolensis				3					
O. lepidurus			3						
O. variabilis				1	4	1			
O. upembae				8	1				
O. malagarisi				3	6				
O. rukwaensis				6					
O. m. macrochir				1	12				
O. m. mweruensis					3	2	1		
O. salinicola					2				
O. karomo				8					
O. karongae						1	6	1	
O. squamipinnis (or *saka*)						3	8		
O. lidole (Lake Malawi)						1	3		
O. lidole (Chungruru)						3			
O. chungruruensis					2				
Subgen. *Neotilapia*									
O. tanganicae					1	10			
Genus ?									
O. schwebischi		1	9	1					
Genus *Danakilia*									
D. franchettii		5							

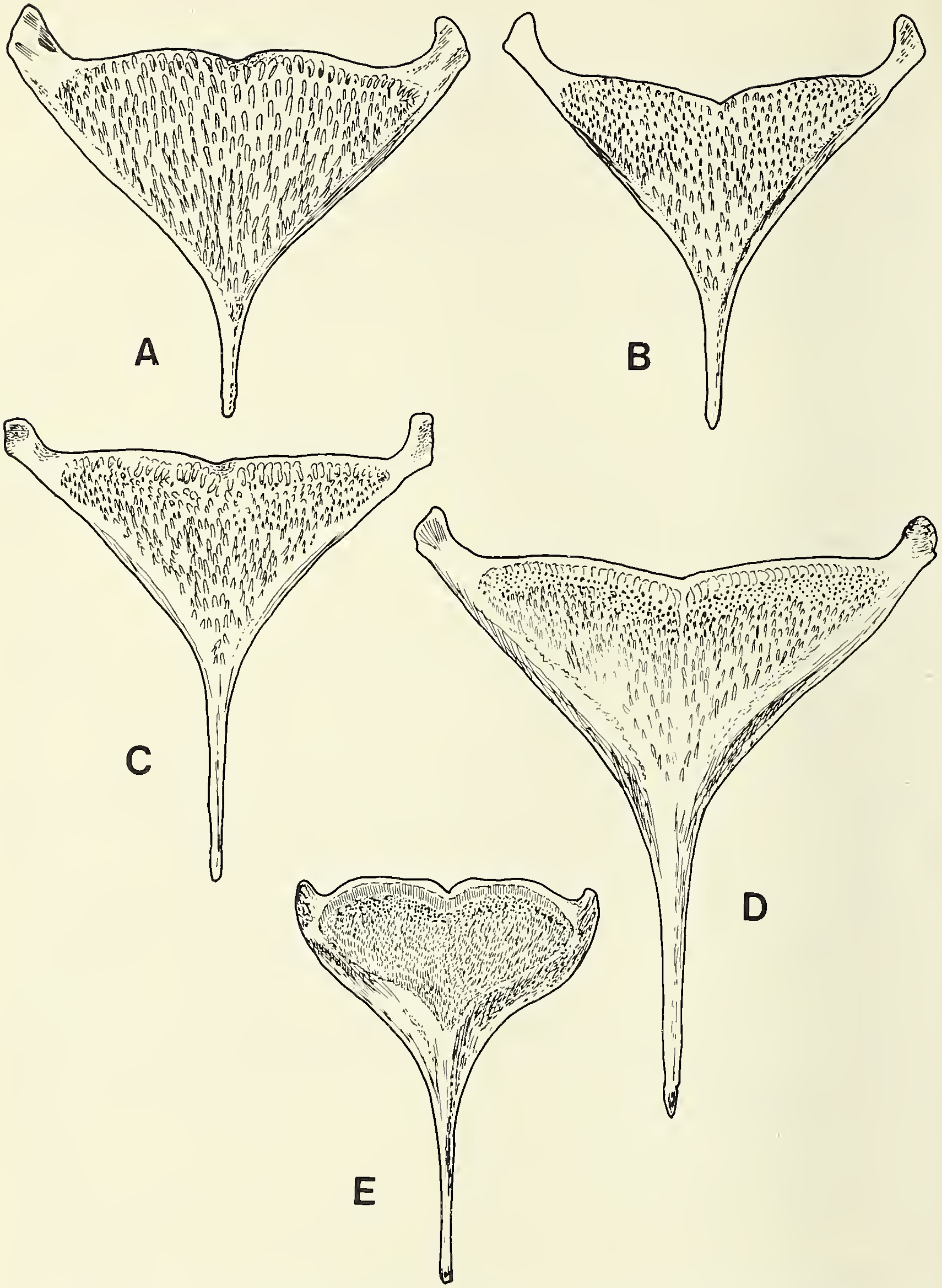

Fig. 4 Lower pharyngeal bones of: A, *Tilapia rendalli*; B, *T. cabrae*; C, *Oreochromis aureus*; D, *O. mossambicus*; E, *Sarotherodon galilaeus*.

to 88 genera. He found five distinct hypurals and usually two epurals in *Etroplus*, in the endemic genera of Madagascar, in the twenty-one Neotropical species examined, including *Cichla*, and in *Hemichromis*, as well as in four species of *Tilapia*, one of *Sarotherodon* and four *Oreochromis*. I have found the same pattern in dry skeletons and, or, radiographs of all tilapias examined for this purpose, namely:

> Eight species of *Tilapia*, two of which were also seen by Vandewalle. In each species 1–11 individuals were examined.
>
> Eight species of *Sarotherodon*, one of which was also seen by Vandewalle. The highest number of individuals examined was 33 in *S. galilaeus*. Among the 27 specimens of *S. melanotheron*, radiographs of two showed hypurals 1 and 2 fused or very closely apposed.
>
> Fourteen species of *O. (Oreochromis)* two of which were also seen by Vandewalle.
>
> Eight species of *O. (Nyasalapia)* one of which was also seen by Vandewalle.
>
> *O. (Vallicola) amphimelas*
> *O. (Alcolapia) alcalicus*
> *O. (Neotilapia) tanganicae*
> *Danakilia franchettii*
> *Iranocichla hormuzensis*

Two species of *Pelmatochromis*, *P. buettikoferi* and *P. nigrofasciatus* also have five hypurals and so has *Tristramella sacra*. The same condition prevails among the haplochromines of Lake Victoria (Greenwood, pers. commn). Modifications of the pattern by fusions of two or more hypurals were found by Vandewalle mainly in some of the genera of Lake Tanganyika.

3. *Lateral line system.* This system has been described fully for the tilapias by Peters (1973) and some comparative details have been given by Cichocki (1976). The detail most useful for our present purpose is the number of neuromasts and canal openings carried by the preorbital (lacrimal) bone. In the tilapiine species used by Peters (*Tilapia tholloni*, *T. zillii*, *T. mariae*, *Sarotherodon galilaeus*, *S. melanotheron*, *Oreochromis niloticus* and *O. mossambicus*) the normal number of openings is five, serving four neuromasts (see Fig. 16). Peters also figures (*op. cit.*, fig. 3b–d) in some small, aquarium bred individuals exceptional bones with two, four or six openings, but except in two species and some individuals of another as described below (p. 167) I have found as he did that in *Tilapia*, *Sarotherodon* and *Oreochromis* five is the standard number. The fifth opening carries the canal to the second infraorbital bone. In some cases the dermal branch-canals divide distally, giving groups of minute openings. Each group represents one opening in the bony canal and is counted as one.

In *Tristramella*, *Danakilia* and *Steatocranus* and in the four specialized genera of Lake Barombi Mbo, Cameroun (Trewavas *et al.*, 1972) as well as in most haplochromines and in *Tylochromis*, *Ptychochromis* and *Chromidotilapia* (*C. guntheri*, *C. kingsleyae*) there are also five openings. This is therefore a widespread African state of the character, but in Cichlidae I would consider it derived on the following grounds.

There are four openings (and probably three neuromasts) in *Etroplus* (India), in *Paretroplus* and *Paratilapia* (Madagascar) and in the New World genera examined by Cichocki (1976: 98, figs. 1.24–26) for this character. Dr S. O. Kullander (pers. commn) also informs me that this is true of all the Neotropical cichlids, about 220 species, examined by him. Among African genera not confined to the Great Lakes I have found only four openings in *Nanochromis*, *Hemichromis*, *Pseudocrenilabrus*, *Pelmatochromis* (two species), *Pterochromis*, and *Thysia*; some species of *Pelvicachromis* are variable. These have retained also the primitive character of low vertebral numbers. Moreover, Peters (*op. cit.*, p. 121 ff) demonstrated that in the ontogeny of the tilapias the hindmost is the last of the four neuromasts to be enclosed in the bone.

There is more variation among the Tanganyika genera (Greenwood, pers. commn) but they have not yet been fully investigated for this character.

The presence of only four openings in certain specialized species of *Oreochromis* is therefore interpreted as a derived reversal (pp. 29 and 403, below), i.e. secondarily derived.

4. *Spondylophysial apophyses.* In most species of *Tilapia*, *Sarotherodon* and *Oreochromis* the

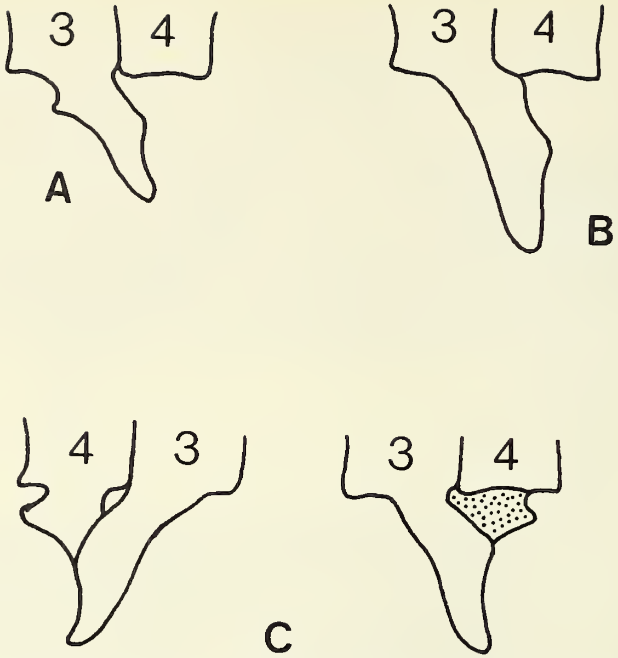

Fig. 5 Diagrammatic sketch of the inferior vertebral apophyses (spondylophysial apophyses) supporting the anterior end of the swimbladder. A and B, the typical condition, drawn from skeletons of *Sarotherodon melanotheron heudeloti* (A) and *S. galilaeus* (B). C, an exceptional condition drawn from a skeleton of *S. melanotheron nigripinnis*; the asymmetry of right and left sides is shown by the convention used by Steinitz & Ben Tuvia (1960), the additional element of the right side being shown on the left by shading. The ordinal numbers of the vertebrae are indicated.

spine produced from fused right and left apophyses is long, a feature possibly associated with the deep body and buoyancy requirements of a browsing fish. Tough fibres of the swimbladder coat are firmly attached to it. Exceptionally the fourth vertebra or the second may contribute a small part to the base of the spine (Fig. 5), but the main part is formed from the third.

Little information can be offered on intraspecific variation in this feature because it cannot be seen in radiographs or alizarin preparations. In all skeletons of *Tilapia* examined the apophysis bearing a spine is based on the third vertebra, but in one of *T. zillii* a bony bridge unites the spine with the fourth on one side only; in two of *T. buttikoferi* a small buttress from the fourth supports the base of the spine; in one of four skeletons of *Sarotherodon melanotheron* the fourth vertebra is involved on the right side only (Fig. 5). In two of three specimens of *O. amphimelas* a buttress from the second supports the third apophysis on one or both sides. The third vertebra alone is involved in the following (one specimen examined unless otherwise stated): *Tilapia rendalli*, *T. sparrmanii*, *T. busumana* (2), *T. guineensis*, *T. buttikoferi*, *T. mariae*, *T. cabrae*, *T. brevimanus; Sarotherodon melanotheron* (3 of 4 skeletons), *S. galilaeus* (8 of 9 skeletons reported by Steinitz & Ben-Tuvia, 1960); *Oreochromis n. niloticus* (2), *O. n. eduardianus*, *O. jipe*, *O. andersonii*, *O. mossambicus*, *O. shiranus* (3), O. (*Nyasalapia*) *squamipinnis*, *O.* (*Ny.*) *variabilis*; *O.* (*Neotilapia*) *tanganicae* (2); *O.* (*Alcolapia*) *alcalicus* (3); *O.* (*Vallicola*) *amphimelas* (one of three, see above).

Among the species of *Sarotherodon*, *S. steinbachi* has no spine, but the arch formed by the union of the apophyses of the third vertebra is thickened and receives a buttress from the fourth, a derived condition related to the massive pharyngeal jaws and their muscles. A similar condition is found, among several variants, in *Iranocichla* (Coad, 1982), another species with enlarged pharyngeals.

In *Danakilia* (one specimen) the bases of the fused apophyses arise from the whole length of the third vertebra and parts of the second and fourth. In *Iranocichla hormuzensis* the fourth vertebra is involved in 14 out of 20 apophyses (ten specimens, right and left apophysis each scoring one) Coad (1982); and in *Tristramella* Steinitz & Ben-Tuvia (1960) found the fourth vertebra again the main contributor to the spine. In both these genera there may be contributions from the second to the fifth vertebrae.

Among cichlids in general there is much diversity. In the haplochromines of Lakes Victoria and Malawi and the rivers the third vertebra is the usual one involved. Absence of the apophyses or their reduction in size and situation on the fourth or fifth vertebra are in some haplochromines associated with an elongate body-shape and increased numbers of vertebrae (e.g. *Serranochromis*, *Rhamphochromis*).

In Central and South America, spondylophysial apophyses on the third vertebra uniting to form a spine are found in *Geophagus brasiliensis*, *G. surinamensis* and *G. jurupari* and in *Symphysodon* and *Pterophyllum*, all of which have specializations and geography distancing them from tilapiines. In *Acara* and *Cichlasoma* the apophyses are poorly developed often do not meet, rarely form a spine and may be on the third or fourth vertebra. In *Crenicichla*, elongate and predacious species, there are no *enlarged* apophyses in this part of the column. In *Cichla* they are very short, on the third vertebra and do not meet.

Etroplus has no spondylophysial apophyses, but the centra of the anterior vertebrae are strengthened. In a skeleton of *Paretroplus polyactis* the apophyses are short, not united, on the fourth vertebra; in one of *Paratilapia polleni* similar short apophyses are on the third vertebra. It may be recalled that the swimbladder of *Etroplus* extends into the otic region (Dehadrai, 1959); skeletal evidence points to the probability that this is also so in the Madagascar genera (see also Cichocki, 1976).

Within the family Cichlidae, therefore, the union of right and left spondylophysial apophyses and their continuation as a spine does not seem to be a plesiomorphic character-state, but an apomorphy developed several times independently, perhaps in relation to a rather deep, compressed body-form. What the three genera under discussion have in common is its relative constancy. The interpretation by Steinitz & Ben-Tuvia (1960) of divergence from this state in *Tristramella* as a secondary condition derivable from that of *Tilapia* is on this view open to doubt.

5. *Pigmentation.* The tilapia-mark on the dorsal fin often persists in the adult in genus *Tilapia*, in which it is under emotional control (Voss, 1977). In *Sarotherodon* and *Oreochromis* it is usually present in the young, but disappears at sizes of 50–100 mm SL. It is one of the distinguishing marks between the sister-species *Sarotherodon linnellii* and *S. caroli*, being present in young of the former, absent in the latter.

The tilapia-mark is found also in *Steatocranus irvinei* (Trewavas) and *Stomatepia mariae* (Holly), both here regarded as Tilapiini, but in these it is not ringed and so is not thrown into such prominence. A typical ringed tilapia-mark is present in young *Danakilia franchettii*. In *Pelmatochromis buettikoferi* Steindachner, a possibly homologous mark in the young 'moves' to the dorsum, below the fin, in older fishes.

Other features of the pigmentation are not peculiar to these genera. In common with many other fishes there is an opercular spot, where intense pigment, partly melanin and partly yellow or red, is combined with iridophores to give deep peacock colours and metallic gold. It is used with spread opercula in frontal aggressive display.

The basic melanin pattern of the trunk is common also in the haplochromines and some Neotropical species. It consists of two longitudinal bands, a mid-lateral and a more dorsal one roughly parallel to the upper lateral line, and a varying number of vertical bars, one of which is often represented by a blotch on the top of the caudal peduncle, the blotch that gave its name to *O. spilurus*.

These markings and in some species an oblique black bar crossing the eye are under nervous or hormonal control and serve as marks of expression and signals. This aspect of the pattern has been discussed by Seitz (1949), Baerends & Baerends van Roon (1950), Neil (1964), Voss

& Ruwet (1966), Lanzing & Bower (1974) and other authors. Voss (1977) published an informative illustrated account and Fryer & Iles (1972) devoted a chapter (ch. 7) to it in other genera. Vertical bars are characteristic of the young and often express fear in adults. They are considered to be protective by breaking up the outline of the body.

In addition to their role as 'language' there are species-specific manifestations of the elements of the pattern. The longitudinal stripes are rarely continuous, but are represented by blotches at the intersections with the vertical bars. The complete pattern is frequently preserved in *Tilapia zillii*, but the related *T. rendalli* and *T. guineensis* more often emphasize the vertical bars and the most conspicuous pattern in *T. tholloni* consists of two longitudinal series of black blotches. *T. mariae* displays vertical bars in the young and a series of lateral blotches in the adult. A typical manifestation in females and non-breeding males of *Oreochromis mossambicus* is shown in Fig. 100 (upper). In *O. karomo*, *O. malagarasi* and *O. upembae* a mid-lateral series of five large blotches is emphasized and there are smaller mid-lateral blotches in *O. urolepis*, *O. andersonii*, often in *O. niloticus* and others. Vertical bars similar to those of the young are present facultatively in adults of the Malawi species-flock of subgenus *O.* (*Nyasalapia*) and also in certain phases of *Sarotherodon galilaeus* and some populations of *S. melanotheron* (Fig. 000).

Baerends & Baerends van Roon (1950) and Lanzing & Bower (1974) distinguish two systems, respectively of large and small melanophores, but their respective schemes do not seem to correspond and their relation to the behaviour patterns is not clear.

6. *Scales.* More comparative work is needed on these, both within the Tilapiini and in other Cichlidae. Although the scales of smaller haplochromines have a ctenoid edge, those of large species like *Serranochromis* and *Sargochromis* become cycloid. Within the tilapiines the circuli are parallel to the edge in the tilapias, but conform to a more gothic pattern in *Pelmatochromis*.

The surface of the scales in *O. mossambicus* has been studied with the aid of the electron scanning microscope by Lanzing & Higginbottom (1974). The circuli in the rostral field, where they are divided by radial interruptions, carry minute spinules which are revealed at a magnification of × 160 and over. The comparative value of this feature has not been explored, either within the Cichlidae or more widely.

The process of calcification has been described by Lanzing & Wright (1976).

7. Further notes on trophic structures follow with the generic characters (pp. 15–18).

8. A chromosomal tilapia-marker in the form of a very long chromosome was found by K. W. Thompson (1976) in two species of *Tilapia* (*T. sparrmanii* A. Smith and *T. mariae* Blgr), and two of *Oreochromis* (*O. aureus* and *O. mossambicus*); whereas in two African haplochromines (*Astatotilapia burtoni* (Günther) and *Melanochromis auratus* (Blgr) there is no such outstanding chromosome. Kornfield *et al.* (1980) also found the long marker chromosome in *Tilapia zillii*, *Sarotherodon galilaeus* and *Oreochromis aureus*, but not in *Tristramella* nor in *Astatotilapia flaviijosephi* (Lortet).

K. W. Thompson (1979) reported on the karyotypes of 41 species of Neotropical Cichlidae. The commonest diploid number was 48, which Thompson considered the basic number for teleost fishes. Deviations from this number were considered to be the result of inversions or fusions. Kornfield *et al.* (1980) found the basic number in their *Tilapia*, *Sarotherodon* and *Oreochromis* to be 44 and considered that any reports to the contrary (e.g. Badr & El-Dib, 1977) were mistaken. Jalabert *et al.* (1971) found the same number (44) in *O. niloticus* and *O. macrochir*.

The basis for distinguishing *Tilapia, Sarotherodon* and *Oreochromis* as genera

These may be considered under four headings: reproduction and development; feeding; structural characters not obviously contingent upon either function; and biogeography.

1. Reproduction and development

The species of *Tilapia* are substrate brooders, those of *Sarotherodon* and *Oreochromis* are mouth-brooders*. The concomitant differences in structure and behaviour were described by Baerends & Baerends van Roon (1950) and Lowe-McConnell (1959). The researches and insights of members of the school of behavioural physiology at Tübingen led by H. M. Peters† have shown that mouth-brooding has evolved in cichlids from substrate-brooding in different ways and that the tilapias have developed two types of mouth-brooding syndrome, which may be designated the nuclear family and arena-spawning. Figure 35 of Heinrich (1967*a*) shows many of the behavioural contrasts, Bauer has analysed the instinctual part played by the young in mouth-brooding, and developmental studies by Peters (1965*a*) and Peters & Berns (1979*a* & *b*, 1982) as well as a number of field and laboratory studies by others have added greatly to the understanding of the bearing of these differences upon relationships.

The characteristics of the three breeding syndromes are:

(*a*) *Tilapia*, in common with many other cichlids, lays eggs which adhere to the substrate and are guarded by both parents until the young are able to fend for themselves. The eggs of *Sarotherodon* have only a vestigial adhesive layer and those of *Oreochromis* have none; in both genera they are held in the mouth of one or both parents until the young are free-swimming and in *Oreochromis* after this at night and in case of danger. Both genera are ovophil mouth-brooders (Peters & Berns, 1978; 1982).

(*b*) In *Tilapia* there is no or minimal sexual dimorphism or dichromatism (a size difference between mating partners has been claimed for *Tilapia mariae* by Townsend, 1979). *Sarotherodon* resembles *Tilapia* in this respect, but in *Oreochromis* males have distinctive and conspicuous breeding colours, are generally bigger than females and in some species have enlarged jaws and unicuspid teeth when mature; other males have a tassel-like appendage on the genital papilla.

(*c*) In *Tilapia* there is a long period of pair-bonding before spawning and after spawning the partners are held together by the devotion of both to the care of the young (Lamprecht, 1973; Wickler, 1976). In *Sarotherodon* there is evidence, at least for some species that the pair swim together for some days before spawning (pp. 55 & 109; McAndrew, pers. commn), but this is not continued after the eggs are safely in the mouth or mouths.

(*d*) The studied species of *Tilapia* and *Sarotherodon* are monogamous, at least for one brood. In *Oreochromis* both polygny and polyandry are practised.

(*e*) The eggs vary in size within a species and even within a single clutch, but there is an average size characteristic of each species. In *Tilapia* eggs are relatively small, long diameter from 1·1–2·0 mm in *T. zillii* (Lowe-McConnell, 1955), to 2·7 mm (average 2·1 mm, Whyte, 1975) in *T. discolor*; in *Sarotherodon galilaeus*, the range is 2·8–3·0 mm (Lowe-McConnell, loc. cit.) in *S. linnellii* up to 5·5 mm (Trewavas *et al.*, 1972); in *Oreochromis* there is a similar range, from 2·8–4·3 mm in *O. niloticus* (the smaller extreme in precociously breeding individuals), to about 5·2 mm in *O. karomo* (Lowe-McConnell). The numbers of eggs increase with the size of fish and bear an inverse relation to the size of egg. The maximum numbers are highest in *Tilapia*, followed by large specimens of *Sarotherodon galilaeus* and are lowest in *Oreochromis*. In both *Sarotherodon* and *Oreochromis* some species have very large yolks and correspondingly few eggs (Fig. 6; for details of fecundity see text and also Peters, 1963*b*; Welcomme, 1967*a*; Payne & Collinson, 1983).

(*f*) In *Tilapia* the parental roles of the sexes are similar, but most of the fanning is done by the female and most of the coping with intruders by the male. In *Sarotherodon* the eggs and

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*Although preserved specimens of *Tilapia discolor* have been found with eggs in the mouth (Trewavas & Irvine *in* Irvine, 1947; Thys, 1970) this species has been shown by Whyte (1975) to be a typical substrate-brooder, assiduous in transporting eggs or young to a safe hiding-place.

†Peters, 1959; 1961*a* & *b*; 1965*a* & *b*; 1971; Peters & Brestowsky, 1961; Kraft & Peters, 1963; Fishelson & Heinrich, 1963; Dambach, 1963; Fishelson, 1966; Heinrich, 1967*a*; Brestowsky, 1968; Bauer, 1968; Goedel, 1974; Peters & Berns, 1978; 1979*a* & *b*; 1982.

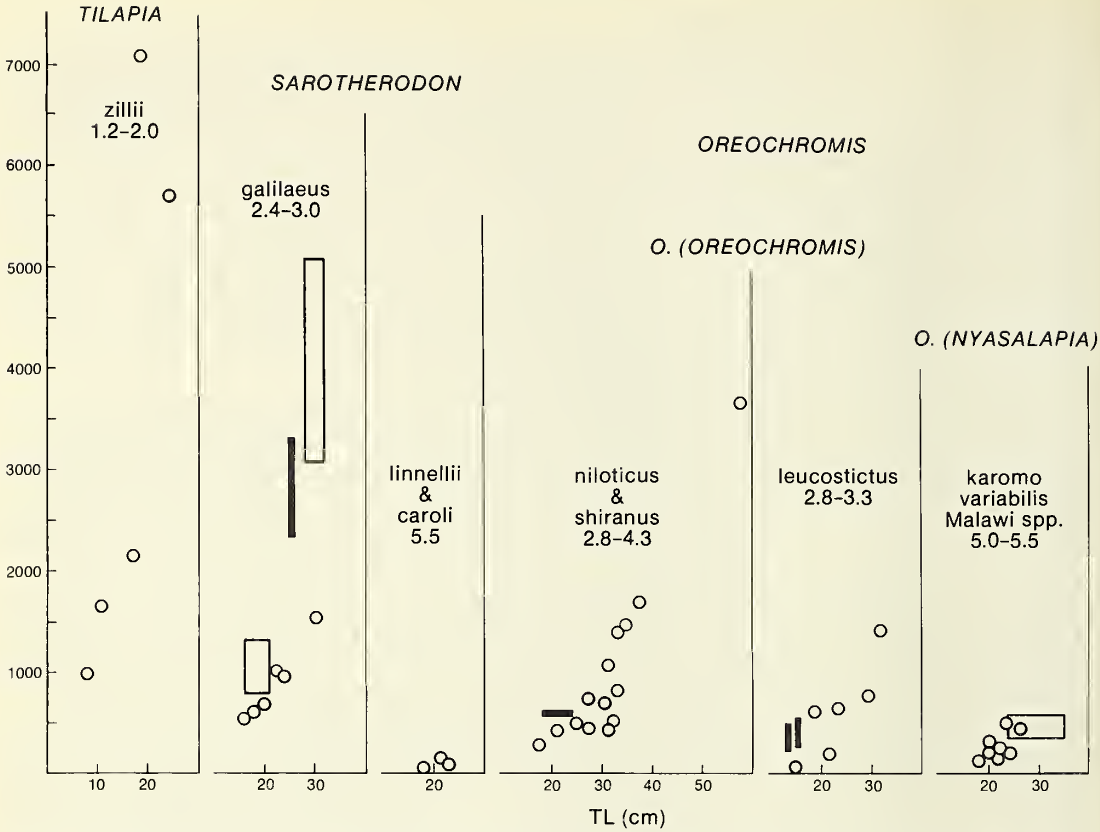

Fig. 6 Numbers of ripe ovarian eggs counted in species of *Tilapia*, *Sarotherodon* and *Oreochromis*. Rectangles and bars represent data given in ranges of both total length and numbers of eggs. Data from Lowe-McConnell (1955), Ben-Tuvia (1960), Welcomme (1967*a*) and Trewavas *et al.* (1972). Numbers below specific names give the range of long diameter of the eggs in mm. Ordinate: numbers of eggs.

embryos are brooded in the mouth of one or both parents. In *Oreochromis* they are taken into the maternal mouth, where they remain for a period of 7 to 17 days according to the species and the temperature. After this the young may be taken back into the mouth at night or at times of danger.

(*g*) In *Tilapia*, when the eggs hatch, the parents take the larvae to one of several prepared pits, where the larvae adhere for a few days to the surface by the secretion from three pairs of glands on the top of the head. In *Sarotherodon* and *Oreochromis* the eggs hatch in the parental mouth. In *Sarotherodon* the larval adhesive glands are vestigial but may produce a little secretion (Peters & Berns, 1978; 1982). In *Oreochromis* (where known) they are further regressed or absent.

(*h*) In *Tilapia* the substrate-adhering larvae wave their well-vascularized tails to secure ventilation of the developing tissues ('wriggler phase'). In *Sarotherodon* and *Oreochromis* respiration is at first dependent on the parent's respiratory movements and later on the network of vessels covering the yolk-sac, possibly fanned by the larval pectoral fins (Fishelson, 1966: 649). The caudal vessels are less developed than those of *Tilapia*. Specifically the *vena caudalis inferior* in *Tilapia* larvae is well developed and is supplied by a network of capillaries in the finfold; the *vena caudalis profunda* develops in parallel with it. In *Sarotherodon* and *Oreochromis* the finfold network is less developed and soon degenerates, at which time the *vena caudalis inferior* takes part in the formation of the *vena caudalis profunda* (Fishelson, 1966: 576–586).

(*i*) The newly released larvae of some species of *Oreochromis* (exemplified by *O. niloticus*) exhibit a contact reaction to the brooding parent that for two or three weeks has the effect under natural conditions, of causing the young to take refuge in the parental mouth. Such weak and infrequent contacts as are made by the larvae of *Tilapia* (represented by *T. tholloni*) are not directed to entering the parent and are followed immediately by flight to the bottom, the usual fear-reaction of *Tilapia* larvae. The genetic basis of this behaviour was demonstrated by Peters & Brestowski (1961) in artificially produced hybrids between *T. tholloni* (♀) and *O. mossambicus* (♂). *In Sarotherodon melanotheron* the young were observed not to enter the parental mouth after being released, but experiments by Bauer (1968: 33 & fig. 10) with extraorally reared embryos and surrogate parents (models) have shown that the contact behaviour, though weaker than in *O. niloticus*, develops and reaches a maximum at the same time after spawning as in *O. niloticus*. Because the yolk is so much bigger in *S. melanotheron* the genetically determined sensitive period for initiating the reaction comes and passes while the embryo is still passive in the parental mouth. Thus the manifestation of this instinct in mouth-brooders, but not its presence or absence, is dependent on the size of the egg. In *O.* (*Nyasalapia*) *squamipinnis*, however, a large egg and a strong contact-reaction are evidently not incompatible (Berns, Chave & Peters, 1978).

(*j*) Fishelson (1966, see especially fig. 166) determined the time of a number of developmental events in *T. tholloni*, *O. niloticus* and *S. melanotheron* ('*macrocephala*'), species with respectively small, medium and large eggs. Of fourteen events, twelve developed at times in the order of size of eggs and so do not necessarily qualify as intergeneric differences. In the other two the event came later in *T. tholloni*; *O. niloticus* and *S. melanotheron* kept a time-relationship corresponding to their egg sizes. These two events were the resorption of the blood-vessels of the finfold and the appearance of the intersegmental vessels, at least the former of which is associated with the respiratory function of the finfold (see (*h*) above).

(*k*) The relative weight of the ripe testes is lower in *Tilapia* and *Sarotherodon* than in *Oreochromis*. This ratio has been described quantitatively by Peters (1971) for a few species and is in agreement with qualitative observations by Loubens (1965) on *O. schwebischi*, and by myself on the Malawi species, *O. urolepis* and *S. melanotheron*; but needs further quantitative observations on more species. It is probably associated with the long periods of sexual readiness undergone by the arena-spawning males, in contrast to the more punctuated sexual activities of both sexes in the monogamous species.

(*l*) Interbreeding experiments and observations support the generic divisions adopted as far as they go. Wohlfahrt & Hulata (1981) have given a summary of these up to date and they are referred to below with the accounts of the species involved. No crosses between species of *Oreochromis* and *Sarotherodon* nor between either of these and *Tilapia* have been reported except by artificial fertilization (Peters & Brestovsky, 1961; Heinrich, 1967*a*; Bauer, 1968; Fishelson, in prep.), and this fact and the results support the generic division. On the other hand, *Oreochromis (O.) niloticus* and *O. (Nyasalapia) macrochir* have hybridized freely when introduced together into a large lake (p. 451), and this may be held to support the inclusion of both subgenera in the genus *Oreochromis*. Nevertheless the results of this involuntary experiment indicate limited compatibility, both genetic and ecological (Daget & Moreau, 1981 & see p. 451 below).

2. Food and trophic adaptations

(*a*) Many species of *Tilapia* consume macrophytes, a habit culminating in *T. rendalli*, which grows to a bigger size than most *Tilapia*, and whose voracious tearing of the newly flooded grasses in the Lufira River is vividly described by Ruwet (1963*a*). In others, e.g. *T. mariae*, the usual diet is the periphyton clothing the submerged parts of plants such as *Potamogeton* and *Naias*.

It is the exception to find *Tilapia* subsisting mainly on phytoplankton, as do populations of *T. kottae* and *T. mariae* in the extremely eutrophic Lake Barombi Kotto.

Species of *Sarotherodon* and *Oreochromis* rarely eat macrophytes (but Daget, 1954, considers *O. niloticus* an unsuitable inhabitant of rice-fields). Many use epiphytic growths, some epilithic algae, and others feed almost entirely on phytoplankton.

Most species of the three genera include organic detritus in the diet.

(*b*) Dentition. The teeth of the jaws and pharynx are typically coarser in *Tilapia* than in *Sarotherodon* or *Oreochromis.* Even in *T. mariae* and *T. cabrae*, whose teeth are fine and slender in small fishes they become relatively coarse in individuals that grow to a good size. In *Oreochromis n. niloticus* and *O. pangani girigan*, however, the teeth of both jaws and pharynx are nearly as coarse as in *T. zillii.* A large *O. niloticus* from the Lower Nile has a few anterior teeth of the upper pharyngeals tricuspid, the third cusp being a brown-tipped shoulder as often in *T. zillii* and *T. rendalli.* In genus *Sarotherodon* the teeth of both jaws and pharynx are fine in all the species.

(*c*) The median length of the lower pharyngeal bone in *Tilapia* is 21·5–30·4% length of head, and is less than 29 in all but two species. Ranges in *Sarotherodon* and *Oreochromis* are shown in Table 3.

Table 3. Proportions as generic and subgeneric characters

A. Depth of Preorbital Bone as % length of head

Genus or Subgenus	Depth preorbital	Range of minima	Range of maxima	Exceptions
Sarotherodon	19·0–33·0	19·0–28·0	26·0–33·0	*S. lohbergeri* 17·5–24·0 *S. linnellii* 17·5–24·5
'*O.*' *schwebischi*	20·0–29·5	—	—	—
O. (Oreochromis)	16·0–27·5	16·0–20·5	21·0–27·5	*O. urolepis* 20·0–28·5
O. (Alcolapia)	17·0–24·0	—	—	—
O. (Vallicola)	12·5–16·5	—	—	—
O. (Nyasalapia)	18·0–27·0	18·0–21·0	22·0–27·0	—
O. (Neotilapia)	24·5–30·5	—	—	—

B. Length of Lower Pharyngeal Bone as % length of head

Genus or Subgenus	Range	Range of minima	Range of maxima	Mean or Range of means	Exceptions
Sarotherodon	31·6–43·5	31·6–37·2	37·0–43·5	34·0–38·3	*S. steinbachi*, 40·0–49·5
'*O.*' *schwebischi*	35·5–40·0	—	—	38·3	
O. (Oreochromis)	25·6–36·6	25·6–33·0	30·3–36·6	27·7–34·5	*O. aureus*, one specimen 23·8 *O. esculentus* 30–38
O. (Alcolapia)	29·2–36·5	—	—	31·3	One specimen 27·3
O. (Vallicola)	29·1–32·1	—	—	30·84	
O. (Nyasalapia)					
excl. L. Malawi	31·5–40·0	31·5–34·5	33·0–40·0	33·5–36·5	
Lake Malawi	34·5–44·0				
O. (Neotilapia)	35·0–40·5	—	—	37·46	

The shortest pharyngeal bones of mouth-brooders are in *O. aureus*, *O. korogwe*, *O. pangani girigan*, *O. p. pangani* and *O. niloticus*, all members of subgenus *Oreochromis*, but only in the first two (where enough specimens were examined) is the mean less than 29% (see Table 119). The ratio of length of blade to length of dentigerous area depends partly on the overall length of the bone and partly on the extent of the dentigerous area. Neither of these ratios is a reliable guide to interspecific relationship as may be seen by comparing members of pairs or groups of sister species with each other, especially *O. (O.) pangani* with *O. (O.) jipe* (Fig. 124) and *O. (Ny.) lidole* with *O. (Ny.) karongae* (Fig. 168).

If *Sarotherodon* has retained more vestiges of the reproductive structures and behaviour of *Tilapia* than has *Oreochromis*, it has diverged from *Tilapia* more markedly in the dentition, especially of the pharynx. It is in the subgenus *Oreochromis*, notably *O. niloticus*, that we find a pharyngeal dentition most like that of *Tilapia*.

(*d*) The lower gill-rakers of the first arch in *Tilapia* number 6–12, except in subgenus *Pelmatolapia* (*T. mariae*, *T. brevimanus* and *T. cabrae*) in which they are 12–16(17). In *Sarotherodon* and *Oreochromis* there are 13–28, except in *O. (A.) alcalicus* (9–14) and *O. (V.) amphimelas* (12–16), both species of special habitats.

(*e*) The width of the head and the interorbital width in terms of the standard length or length of head vary considerably among the species. Peters (1961*a*) examined these parameters in several species of substrate-brooding and mouth-brooding tilapias. Figure 7 is based on the histogram of fig. 2 of Peters and seems to show a broader head in the mouth-brooders. The scattergram of Peters' fig. 4 takes account of allometry and shows an almost complete separation between the two groups in the ratio interorbital width to width of head at the opercula. Goedel (1974) also gave measurements showing a wider neurocranium in *O. niloticus* than in *T. tholloni*.

However, measurements from *Tilapia mariae*, a species not used by Peters, give a range of interorbital width from 13·1–16·6% SL (N=22, mean 13·73). This is the modal class for Peters'

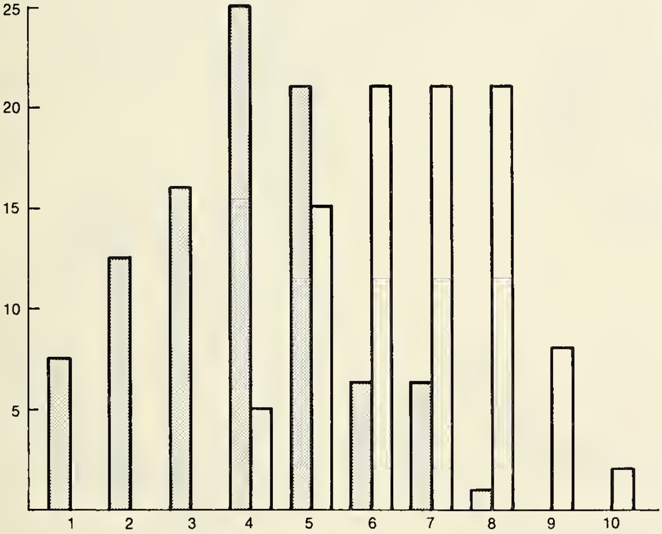

Fig. 7 Frequencies of occurrence of classes of interorbital width of substrate-brooders (*Tilapia*: white) and mouth-brooders (*Sarotherodon* and *Oreochromis*: dark). Highest values on left, lowest on right. The interorbital width is expressed as %SL. After Peters, 1961*a*, fig. 2, with quotients converted to percentages.

Classes:

1. 17.3–19.6 3. 14.7–15.9 5. 12.5–13.4 7. 10.8–11.5 9. 9.6–10.1
2. 16.1–17.2 4. 13.5–14.6 6. 11.6–12.4 8. 10.2–10.7 10. 9.1–9.5

mouth-brooders. Further, the ratio in *Oreochromis jipe*, among others, compares better with *Tilapia zillii* than with some other mouth-brooders.

This character, therefore, is useless for generic diagnosis and all that can be claimed is that wider neurocrania are found in some mouth-brooders than in any *Tilapia*. In the former it may be viewed as indicating a broad buccopharynx, an advantage in a method of feeding that involves passing large quantities of water through the mouth, as well as for accommodating young of an unusually large size, especially in *O. (Nyasalapia) lidole.*

Summary of trophic adaptations

The long lower pharyngeal bone, the long array of gill-rakers and the broad skull are all measures of the big buccopharynx of *Sarotherodon* and *Oreochromis* (Fig. 8). This may well be an advantage to a fish whose habits require the passage of large quantities of water through the mouth, as well as for buccal incubation. It is noticeable that the most extreme values of these parameters are characteristic of the most specialized plankton feeders. Note especially the long, narrow pharyngeal bone in *Sarotherodon caroli* and *O. (Nyasalapia) lidole* (Figs 33 & 168), both species also with very weak jaw-dentition, and *O. lidole* with a very broad interorbital space. In these the pharyngeal teeth are very fine and cover a small area of the bone. They have no need for preparation of the food before it is passed into the stomach.

It is noticeable too that in all these trophic adaptations *Tilapia mariae* approaches or overlaps *Sarotherodon* and *Oreochromis*, especially those species that use epiphytic growths. In its

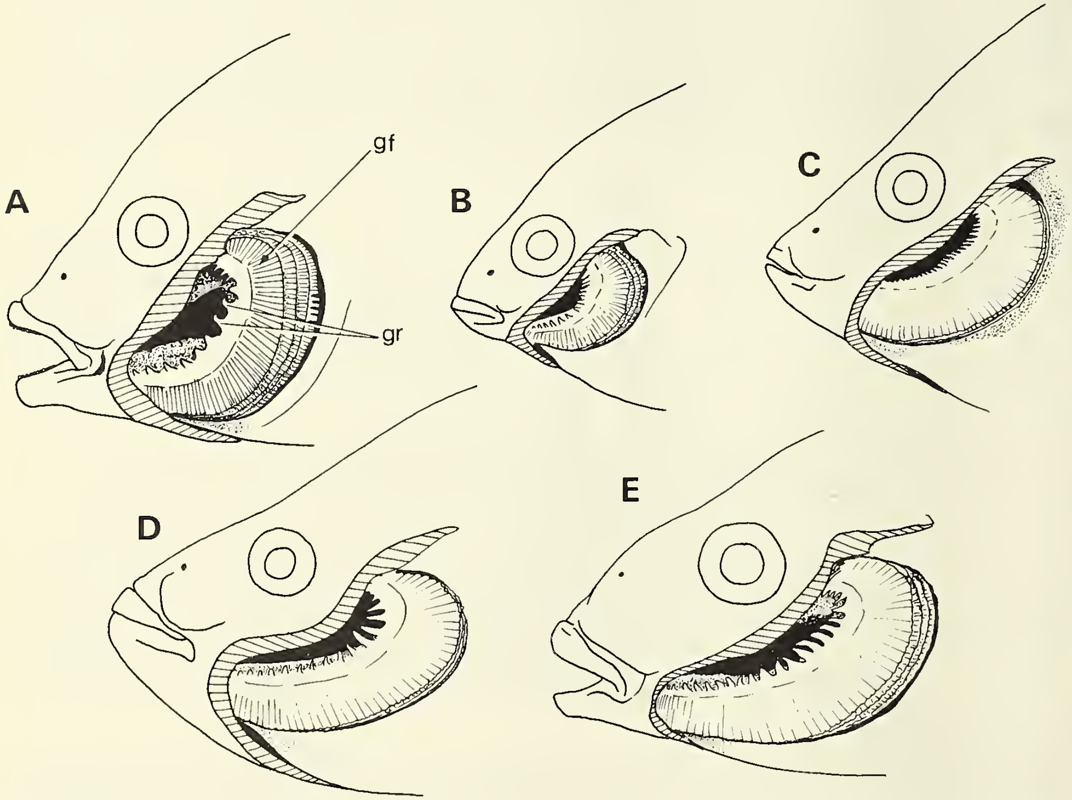

Fig. 8 Heads, with gill-cover cut away to show the first gill-arch: A, *Tilapia rendalli*; B. *T. mariae*; C. *Sarotherodon galilaeus*; D, *Oreochromis (Oreochromis) pangani*; E. *Oreochromis (Nyasalapia) squamipinnis.* Gill-filaments diagrammatic; gf = gill filament; gr = gill-raker. Figs A & E after Bertram, Borley & Trewavas, 1942.

reproductive structures and habits it remains a substrate-brooder, and the shape of the buccopharynx is more tilapia-like than mouth-brooder-like (Fig. 8).

3. Other structural characters

(*a*) *Numbers of vertebrae and lateral line scales.* In the tilapias low numbers of vertebrae are considered primitive (although sometimes secondarily reduced). In the related genera *Pelmatochromis* and *Pterochromis*, among fifteen specimens in which they have been counted the total numbers of vertebrae are 26 (f.11) or 27 (f.4). Table 2 shows the range in *Tilapia* to be 26–30, in *Sarotherodon* 26–31, and in *Oreochromis* (26)27–34. The mode of modes in *Tilapia* is 28, in *Sarotherodon* 29, and in *Oreochromis* 30. See further on p. 33.

The numbers of scales in the lateral line series are generally one or two higher than the vertebrae.

(*b*) *Ossification of the ethmoid* (Fig. 9). As in related genera, the ethmoid cartilage is generally well covered in bone in *Tilapia*; not only the lateral ethmoid, but also the supraethmoid meets the vomer in a paired sutural union, leaving only a narrow cartilaginous surface between. In all *Sarotherodon* and *Oreochromis* examined for this feature (fourteen species) the supraethmoid is free from the vomer. There are, however, some individuals and perhaps two species of *Tilapia* (*T. rendalli* and *T. tholloni*) in which the supraethmoid also ends freely (Trewavas, 1973*a*; Goedel, 1974, figs 6 & 17).

This free condition of the anterior end of the supraethmoid is uncommon in Cichlidae, but it is also present in the species of *Perissodus* (Liem & Stewart, 1976) and in *Haplotaxodon microlepis* of Lake Tanganyika (as has been demonstrated to me by Dr Melanie Stiassny). These genera appear to have no close phyletic relationship with the tilapias and since they are not microphagous the functional explanation suggested by Trewavas (*loc. cit.*) cannot be applied to them. The free ethmoid is a derived (apomorph) character and although its sporadic appearance in *Tilapia* may be held to support the relationship between *Tilapia*, *Sarotherodon* and *Oreochromis*, its presence in the Tanganyika genera named must be regarded as an example of convergence. Its constant presence throughout *Sarotherodon* and *Oreochromis*, however, adds to the characters pointing to their interrelationship.

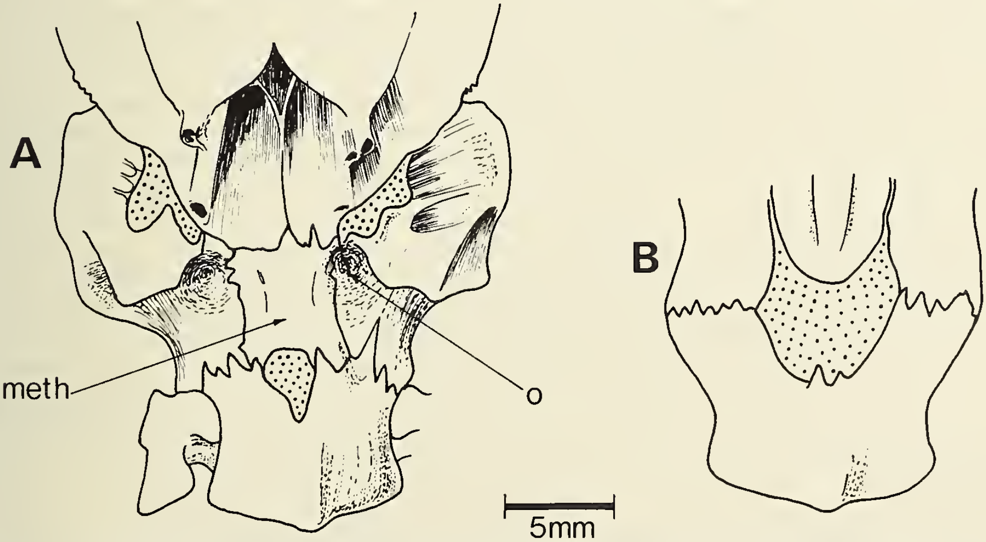

Fig. 9 Dorsal view of ethmoid region in: A, *Tilapia zillii* of 205 mm SL; B, *Oreochromis shiranus* of *ca.* 250 mm SL. meth = supraethmoid; o = olfactory foramen. Cartilage stippled.

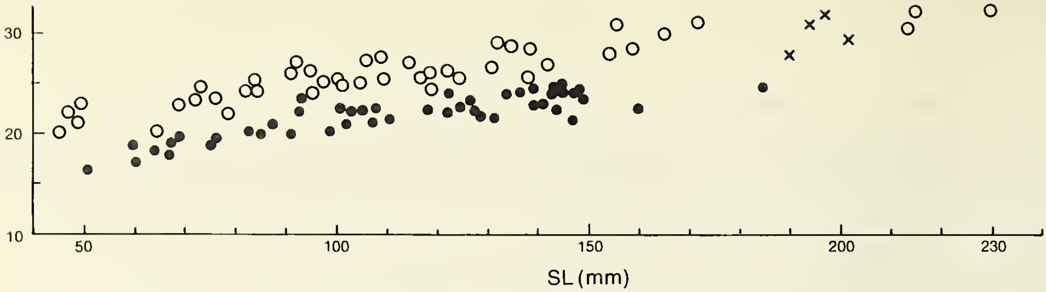

Fig. 10 Depth of preorbital bone as % length of head in: *Sarotherodon melanotheron* (○); *S. linnellii* with *S. caroli* (●); *S. mvogoi* (×). Although the values for *S. melanotheron* are very high, those for *S. linnellii* and *S. caroli* are similar to *O. mossambicus* and *O. mortimeri* (cf. Fig. 13, also Fig. 47).

(*c*) *Depth of preorbital bone* (Fig. 10 & Table 3). This, expressed as % length of head, varies in all three genera and is positively allometric with the standard length and length of head. The ratio is, however, consistently high in the species of *Sarotherodon,* with the exception of two species of the crater-lake Barombi Mbo, both of which have long heads. In the nominate subgenus of *Oreochromis* it is generally lower, but large specimens of *O. urolepis* rival *Sarotherodon* in the relative depth of the bone (Fig. 47), and there is no significant difference between its depth in *Sarotherodon* and subgenus *Nyasalapia* or *Alcolapia.* Subgenus *Vallicola (O. amphimelas)* has an exceptionally narrow preorbital. In *O. schwebischi* and *O. (Neotilapia) tanganicae* the bone is so deep as to be one of the factors suggesting relationship to *Sarotherodon* (p. 24).

Because of the allometry this measurement is better appreciated in scatter diagrams, which are found in the text. Especially in *Danakilia franchettii,* which remains small, the unusual depth of the preorbital can be seen only by comparison with specimens of other species at the same size (Fig. 188). It is one of the characters showing the relationship of this species to *Iranocichla hormuzensis.*

(*d*) *Chromosomes.* The presence of a distinctive long chromosome in all three genera has been noted on pp. 4, 12. Kornfield *et al.* (1980) compared the chromosomes of *Tilapia zillii, Sarotherodon galilaeus* and *Oreochromis aureus* and found no significant differences between them in gross morphology. In their material, however, all the chromosomes of *O. aureus* and *S. galilaeus* contained centromeric heterochromatin, whereas in *T. zillii* ten to twelve chromosomes were without it. So far, this is only an interspecific difference.

(*e*) *Cell chemistry.* The method of electrophoresis has been used to study allozymes and other proteins of tilapias. Most studies up to 1980 were summarized by Avtalion (1982). Avtalion himself, with Mires (1976) and with other collaborators (1975) as well as Herzberg (1978; see p. 198) have found markers to distinguish *Oreochromis niloticus* and *O. aureus* and their hybrids. Intergeneric studies were pioneered by Chen & Tsuyuki (1971), who used two species of *Tilapia* (*T. zillii* and *T. rendalli*) and two of *Oreochromis* (*O. urolepis hornorum* and *O. mossambicus*). The two species of each genus are, on other grounds, considered to be closely related, so the fact that these authors were able to characterize the pairs is not necessarily significant at the generic level. Similarly, Iles & Howlett (1968) and Basasibakwi (1975) each reported on *T. zillii* and one species of *Oreochromis.* Baron (1975) typed the serum proteins of *Tilapia zillii* and three species of *Oreochromis, O. mossambicus, O. niloticus* and *O. macrochir.* He was somewhat critical of the significance of his own results because his samples were taken from populations with a long history of captivity, and the results with *O. mossambicus* were not in agreement with those of other authors.

Badawi (1971) studied serum proteins of the four tilapias of the Nile delta, *T. zillii, S. galilaeus, O. niloticus* and *O. aureus.* The protein fractions were labelled 1 to 7. *T. zillii* had none of no. 7, in contrast to all three mouth-brooders, and most of the protein of *T. zillii* was present in fractions 4, 5 and 6, whereas in the three mouth-brooders it was in fractions 3, 6 and 7. The mobility of the proteins, however, was approximately equal in *T. zillii* and *S. galilaeus* (distance migrated 95 and 90 mm respectively) and less than in *O. niloticus* (120 mm) and *O. aureus* (118 mm).

Kornfield *et al.* (1980) measured the allozymic similarities at 21 loci between the cichlid species of the Sea of Galilee. The resultant phenogram showed a high degree of similarity between *O. aureus* and *S. galilaeus*, with *T. zillii* more distant from both. The two species of *Tristramella* were also closely similar between themselves and equally dissimilar from the *Tilapia* and the two mouth-brooders. As would be expected, *Astatotilapia flaviijosephi* had a low index of similarity with the five tilapiines.

McAndrew & Majumdar (1983) have reported on the alleles at twenty-two variable loci in proteins from muscle, liver and eye tissues in good samples of nine tilapiine species, *Tilapia zillii*, *Sarotherodon galilaeus* and seven species of *Oreochromis*. Their most surprising result was that *O. jipe* diverged more from the other *Oreochromis* than did *S. galilaeus* or even *T. zillii*. This is so much in conflict with the evidence of morphology and biogeography that some unknown explanation must be sought and, as the population sampled had been for some time in captivity (McAndrew, pers. commn), I prefer to leave it out of consideration in trying to determine the relevance of the results to phylogeny. The other species of the Pangani system were not represented.

One of the 22 enzymes tested was adenosine deaminase of muscle. This was so variable in mobility among the species that I omit it also as evidence above the species level.

The remaining 21 enzymes (or enzyme fractions; some are dimeric), tested in one *Tilapia*, one *Sarotherodon* and six *Oreochromis* give the following results:

All the species have uniform mobilities at five loci (alcohol dehydrogenase, α-glycerophosphate dehydrogenase, malic enzyme 1, phosphoglucomutase, esterase-1). *T. zillii* has unique alleles at six of the 21 loci, *S. galilaeus* at five. The six species of *Oreochromis* are remarkably uniform, *O. mossambicus*, *O. andersonii* and *O. aureus* having each two unique alleles among 21 loci, *O. niloticus* only one and *O. spilurus* and *O. macrochir* none. They agree with each other at 13 loci and there is greater or less departure from uniformity at 8.

Further, *T. zillii* and *S. galilaeus* differ from each other in the alleles of 13 of the 21 loci and agree in 8. Of the 13 proteins that are uniform in *Oreochromis* 10 are also uniform with them in *S. galilaeus*, 6 in *T. zillii*.

The results on this part of the basic chemistry are therefore consistent with the conclusions based on morphology, ethology and biogeography, namely that *Tilapia*, *Sarotherodon* and *Oreochromis* form characterisable groups*. The strength of the argument is in the relative uniformity shown by the species of *Oreochromis*. The weakness is in the use of only one species each of *Tilapia* and *Sarotherodon*. What is needed is a parallel study of several species of *Tilapia* and *Sarotherodon* and more standardization of techniques. (See Rollinson, 1980. Systematics Ass. Special vol. **16** : 123–146.)

(*f*) Blood cells. Badawi & Said (1971) studied the blood of the four species of the Nile delta mentioned above. Their *Tilapia zillii* had smaller and more numerous red cells than either the two *Oreochromis* or *S. galilaeus*. *T. zillii* and *S. galilaeus* differed in the amount of haemoglobin present, but this is known to be variable in individual vertebrates.

As with the chemical results, the significance of these for taxonomy can be assessed only after wider studies.

4. Biogeography

Figures 11 and 12 show the distribution of *Sarotherodon* and the two main subgenera of *Oreochromis*, *Sarotherodon* inhabits the brackish and fresh waters of West Africa from the Zaire

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*Dr McAndrew (pers. commn) has expressed these results in phenograms made according to the various formulae current in this discipline, but the position of *S. galilaeus* is less well defined, appearing closer to one or another of the species of *Oreochromis* than is the impression derived from my cruder analysis. I am grateful to Dr McAndrew for letting me see a prepublication copy of his papers with Majumdar (1983 & unpublished).

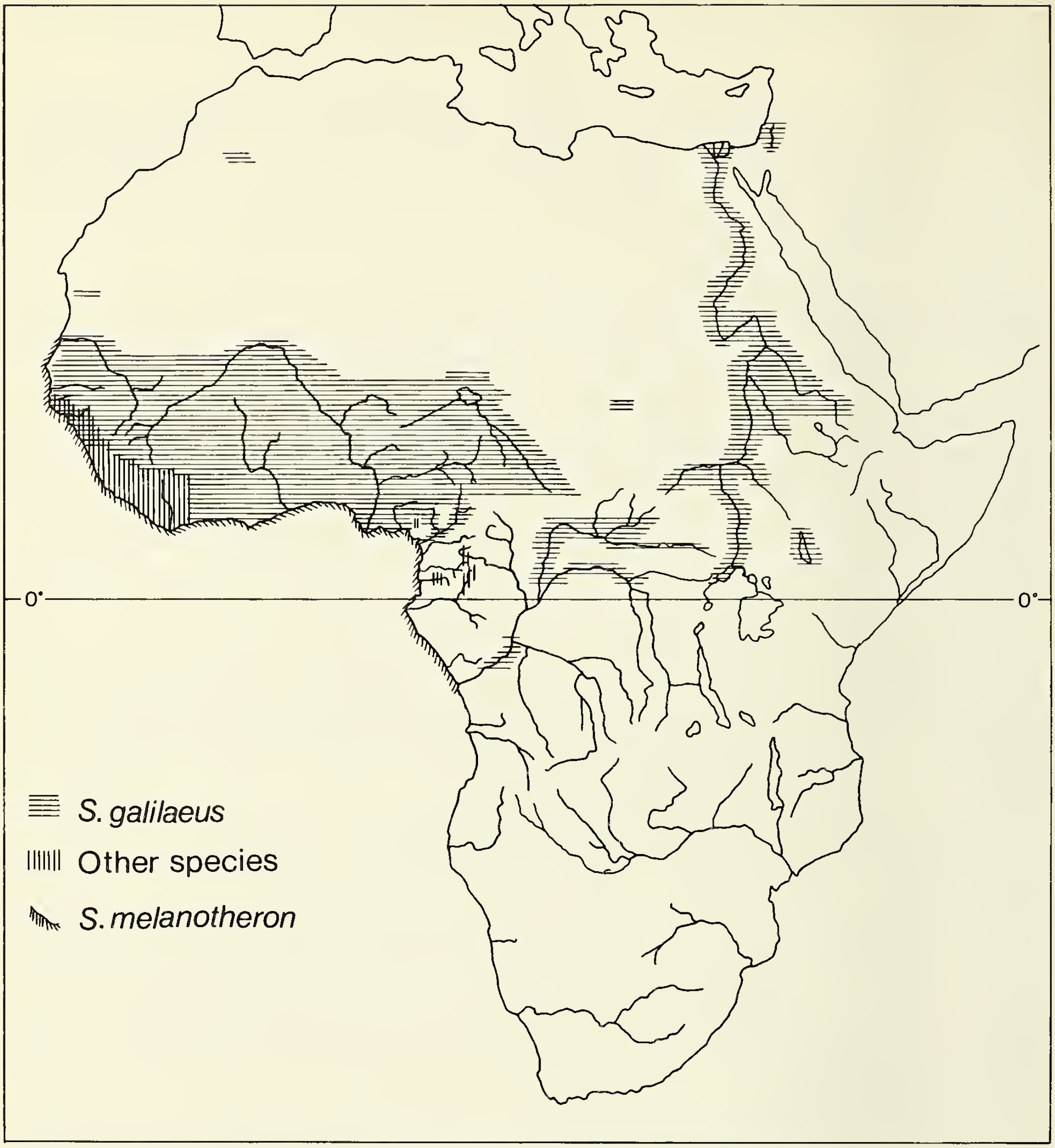

Fig. 11 Area of distribution of genus *Sarotherodon.*

to Senegal with a relic population in the Draa, south of the Atlas Mountains, one species extending to the Nile system and the Jordan Valley. *Oreochromis* is characteristic of the rivers and lakes of East and Central Africa, its range extending to the western rivers only in Angola and the Soudanian region. The area common to *Oreochromis* and *Sarotherodon* is the Soudanian (including Lake Chad), the Nile and the Levant (including the Jordan Valley). The distribution of *Tilapia* coincides with that of *Sarotherodon* and in addition with *Oreochromis* in the Zambezi basin and southwards. But north of the Zambezi there is no record of native *Tilapia* in the rivers flowing to the Indian Ocean. *Tilapia* and *Sarotherodon* are alike in being represented in the Nile and the Levant each by a single species, *T. zillii* and *S. galilaeus.* It is as if this had been a peripheral area for both genera during the Upper Pleistocene, when the Sahara presented no

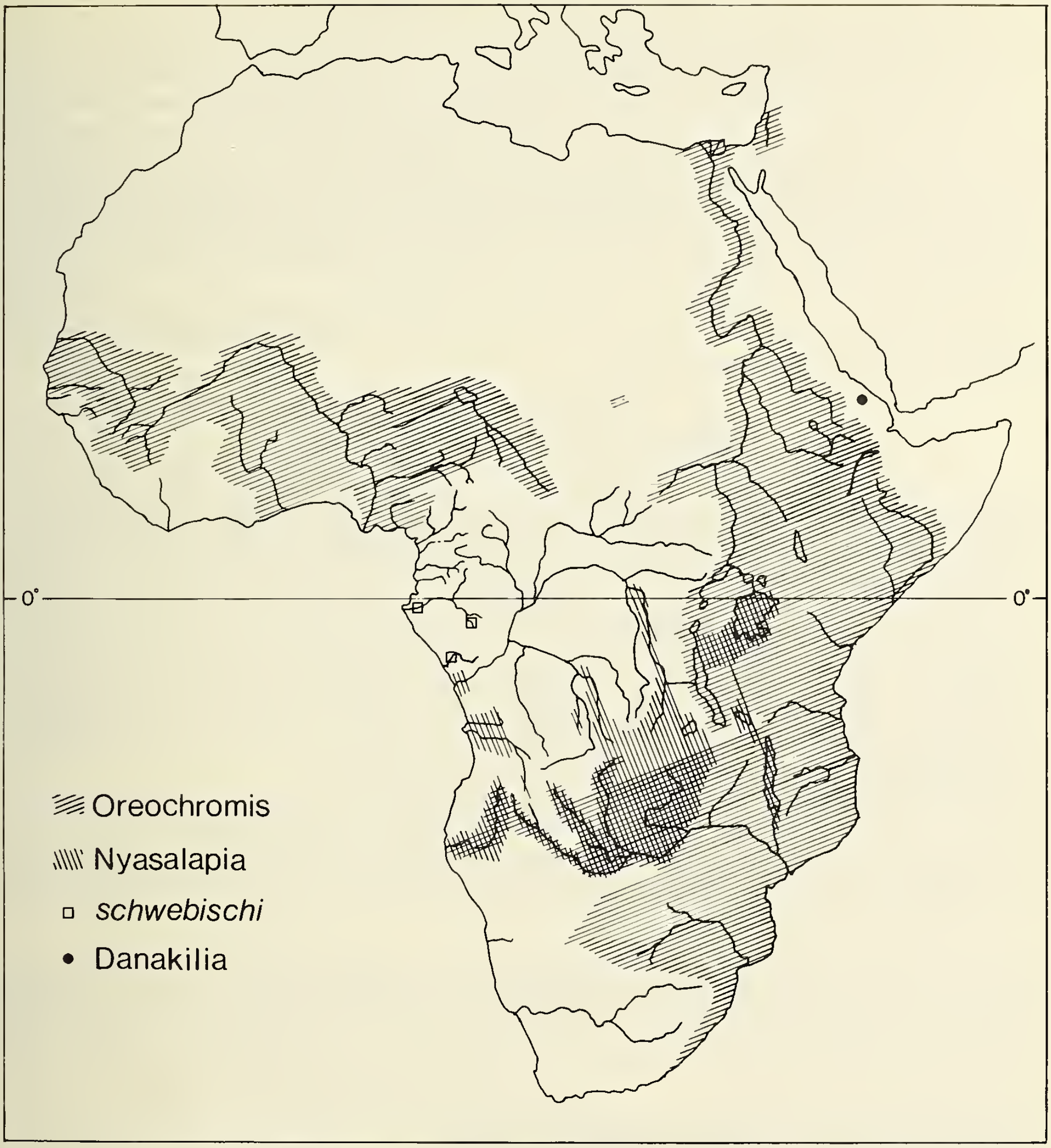

Fig. 12 Areas of distribution of subgenera *Oreochromis* and *Nyasalapia.*

barrier to the spread of aquatic organisms (see Beadle, 1974). The same favourable period may have allowed the westward spread of the two species of *Oreochromis*, *O. niloticus* and *O. aureus.* This is a possible explanation of the overlap of the areas of the three genera and subsumes that *Sarotherodon* originated in the West and *Oreochromis* in the East and that their overlap is secondary. See also Thys, 1963 & 1971: 205.

The position of *'O.' schwebischi* and *Neotilapia tanganicae*

For a species to be placed in one of the genera *Sarotherodon* or *Oreochromis* as now defined, it should satisfy the criteria of morphological similarity, reproductive category and geographical conformity. Two species fail this compound test.

O. (Neotilapia) tanganicae is confined to Lake Tanganyika, the origin of whose fauna was probably the ancient Central Basin of the Congo, where neither *Sarotherodon* nor *Oreochromis* is now found. *O. (Oreochromis) niloticus* is believed to have entered the lake only in quaternary times, and *O. (Nyasalapia)*, with species at the very threshold of the lake in the Malagarazi delta, still does not enter it. In body-form, deep preorbital bone and long pharyngeal *N. tanganicae* resembles *Sarotherodon galilaeus*, but the small size of the scales of the belly is a feature of *Oreochromis*. Except that it is a maternal mouth-brooder its breeding habits are unknown.

The possibility that *schwebischi* is more closely related to *Sarotherodon galilaeus* than to *Oreochromis* is put forward on pp. 35–36, where it is suggested that its *Oreochromis*–like breeding syndrome may be a parallel development.

Genus *SAROTHERODON* Rüppell

Sparus (part); Linnaeus, 1758: 282.

Sarotherodon Rüppell, 1852: 21. Type species by monotypy *Sarotherodon melanotheron* Rüppell, *loc. cit.*; Günther, 1862: 293; Trewavas *et al.*, 1972: 43; Trewavas, 1974: 408; 1981*a*: 12; 1981*b*: 42; 1982*a*: 79; 1982*b*, addendum: 11–12.

Sarotherodon (part); Trewavas, 1973*a*: 20; 1978: 181 & 121; 1978*a*: 181; 1978*b*: 127; 1980: 1; 1982*b*: 3; all articles in Pullin & Lowe-McConnell, 1982.

Chromis (part); Günther, 1862: 270–273.

Melanogenes Bleeker in Günther, 1862: 272; Bleeker, 1863: 36. Type species by page priority *M. macrocephalus* Bleeker, 1863: 36 = *S. melanotheron.*

Tilapia (part); Boulenger, 1899: 105; Pellegrin, 1904: 307 (271, sep. pag.); Boulenger, 1915: 138; and many authors following this, culminating in the argument of Peters, 1979.

Tilapia (Sarotherodon) (part); Regan, 1920: 38.

Tilapia (Sarotherodon) and group III–J of 'Section III: *Sarotherodon*'; Thys, 1968*b*: xxxviii–xxxix.

Boulenger evidently considered *Sarotherodon melanotheron* to be a *nomen nudum* and placed it in the synonymy of *Tilapia macrocephala* (Bleeker), but Regan recognized its validity in using *Sarotherodon* as a subgeneric name.

ETYMOLOGY: Greek, *sarothron* a brush and *odous* a tooth. *Melanogenes*, from Greek *melas* black and *genys* chin or cheek. *Tilapia* is the attempt by its author, A. Smith (1840), to spell the Bushman name for 'fish'. The root is *apia*, pronounced épia, preceded by a click rendered *Til* (see Smith, A. (Ed. Kirby), 1939).

Distinguishing characters

1. Scales of belly not much smaller than flank scales.
2. Male genital papilla small and simple.
3. Weight of ripe testes relative to body weight very low, comparable to that of *Tilapia* and lower than that of *Oreochromis.*
4. Breeding habits (known in five species). Sexual dimorphism and dichromatism minimal or lacking. Eggs and young brooded by both parents or the male, and, in two species, by the female with no male brooding reported. A pair bond formed for short periods before spawning. Eggs with vestigial adhesive layer but not adhering firmly to substrate. Embryos with vestigial adhesive glands on the head known in two (or three?) species (Peters, 1965; Peters & Berns, 1978), and less regressed than in *Oreochromis.*
5. Outermost teeth bicuspid (unicuspid in mature males of *S. linnellii*).
6. Preorbital bone deep, at 100–200 mm SL 20–32% length of head, up to 33% in one species, (Figs 10 & 47), with five lateral-line openings.

7. Anal spines III.
8. Lower pharyngeal bone long, 31·6–49·5% length of head; pharyngeal teeth very fine; toothed area in adults shorter than the anterior blade, except in *S. steinbachi* (Fig. 29).
9. Lower gill-rakers 14–27. Microbranchiospines present, at least in adults.
10. Jaws not becoming enlarged in mature male and female.

CONTAINED SPECIES AND DISTRIBUTION. Ten species, two with five subspecies each. They are listed in Table 2 and described on pp. 41–138. The type species is confined in nature to brackish water.

West Africa from the Zaire to Senegal and one species also in rivers Adrar and Draa; in the Nile system including Lakes Albert and Turkana, and in the Levant, including the Jordan Valley (Fig. 11).

Genus *OREOCHROMIS* Günther

Chromis (part) Cuvier, 1817: 266 (*non* Cuvier, 1814*a* & *b*); *idem*, 1829: 266; Günther, 1862: 267.
Chromys (part) Castelnau, 1861: 12 (variant spelling of *Chromis* Cuvier). No type species.
Oreochromis Günther, 1889: 70. Type species by monotypy *Oreochromis hunteri* Günther, *loc. cit.*; *idem*, 1894: 89; Trewavas, 1981*a* & *b*; 1982*a* & *b in*, Pullin & Lowe-McConnell (eds): 11–12.
Tilapia (part) Boulenger, 1899*a*: 105; Pellegrin, 1904: 307, Boulenger, 1915: 138 and many authors following this, culminating in the argument of Peters, 1979.
Tilapia (Sarotherodon) (part); Regan, 1920: 38; Trewavas, 1966*c*: 394.
Tilapia (Oreochromis); Thys, 1968*b*: xxxvi.
Sarotherodon (part); Trewavas, 1973*a* & *b*; 1976; 1978; 1980.
Sarotherodon (Oreochromis); Trewavas, 1982*b in*, Pullin & Lowe-McConnell (eds): 3–13 (not the addendum).
See also the subgenera.

ETYMOLOGY. Greek *oros*, *oreos* = mountain and *Chromis*. The type species inhabits a crater-lake on the slopes of Kilimanjaro.

Four subgenera.

Distinguishing characters

The whole genus is distinguished from *Sarotherodon* by states of characters 1–4 (see p. 24) as listed for that genus, namely:

1. Scales of belly smaller, often much smaller than flank scales (Figs 110 & 127).
2. Genital papilla of male and female well developed.
3. Weight of ripe testes relative to body weight higher than known in *Sarotherodon*, although quantitative data are available for only two species (Peters, 1971).
4. Maternal mouth-brooders, usually with marked sexual dimorphism and dichromatism at breeding time. Male constructs and defends a mating territory in an arena with other males, where they are visited by females. No pair-bond. Where known, both polygyny and polyandry are practised. A T-position characterizes the mating behaviour (see Fig. 172). Brooding females withdraw to nursery areas where topography permits remote from the mating areas. Eggs without an adhesive layer. Where known (three species), larval adhesive glands more regressed than in *Sarotherodon*.

With the exception of 1, which is not a trenchant character, these distinctions are all concerned with the breeding pattern, which is still undescribed in the two monotypic subgenera *Neotilapia* and *Vallicola*. For the evidence that arena-spawning (the lek system) is general in the other three subgenera see the summary on pp. 26–27, as well as the accounts of the species.

For further comparisons with *Sarotherodon* see the definitions of subgenera and Table 3.

Distribution. East and Central Africa, the Nile and the Levant, with two species extending to West Africa, and one each in the Lower Zaire and the Angolan Province of Angola. Two Zambezi species extend their distribution to the Cunene River in southern Angola.

'O.' schwebischi, doubtfully placed here, is endemic to the Ogowe and Chiloango systems (p. 489).

Evidence of the breeding pattern of *Oreochromis*

The essential, correlated elements of the arena-spawning syndrome are six and are the same as in some birds (Crooke, 1965; Wilson, 1977) and also in *Astatotilapia desfontainesii* (Kirchshofer, 1953) and probably other haplochromines. These are:

1. Sexual dimorphism. In addition to the shape of the genital papilla of the sexes, external differences include one or more of the following: elongation of the soft dorsal and anal fins of males (not unique to this breeding pattern); elongation of the jaws and simplification of the jaw teeth, not only by wear (many species of subgenus *Oreochromis*); prolongation of the genital papilla of males into tubercles and filaments (subgenus *Nyasalapia*).
2. Sexual dichromatism, from a more intense iridescence in the breeding male to conspicuous red, blue or black colouring with white or bright orange or red borders to dorsal and caudal fins. The female remains inconspicuously coloured.
3. Arena-spawning. Males establish territories grouped in an arena. Females visit them there and mating occurs in the centre of a territory.
4. Polygamy. No pair-bond is formed. Males mate with several females successively and females may mate with several males for the fertilization of one clutch. Polyandry has been less often recorded than polygyny.
5. Maternal mouth-brooding.
6. Separate nursery areas. The female takes the brood away from the mating area. According to the topographical situation she may rejoin the school of non-breeding individuals or seek well-oxygenated waters inshore, often in the shelter of marginal vegetation or in shallow pools.
7. A possible seventh concomitant of this syndrome is the relative size of the testes, which, where known, is greater in this genus than in *Sarotherodon* or *Tilapia*; but the only quantitative research on this ratio in tilapiines involved very few species (Peters, 1971).

The whole breeding pattern is not often observed in aquarium studies and in Nature can only be seen in clear, shallow water and by good fortune. But a spawning arena may be identified when a net operated in one place, or at places of similar depth, catches predominantly males in breeding livery. A nursery area similarly yields many brooding females and at certain seasons these may be the only members of a given species caught in traps set in the reeds. Such experiences count as positive evidence of arena-spawning.

If, in an aquarium, one or more males are able to establish each his territory on the bottom and the other inhabitants form a school near the surface, from which an occasional female descends to mate with a male, this counts as circumstantial evidence of arena-spawning.

The whole syndrome has been observed directly in *O. mossambicus*, *O. alcalicus*, *O. variabilis*, *O. macrochir*, *O. karomo* and *O. squamipinnis*. Some elements have been recorded for most other species. In this context conspicuously coloured territorial males and maternal mouth-brooding are together strong indication of arena-spawning. The tabulated data (p. 27), show that such evidence has been obtained from the majority of species. Only seven species have so far failed to supply this minimum of evidence, and of these only *O. (Neotilapia) tanganicae* has other structural evidence throwing doubt on its purtenance to genus *Oreochromis*.

For details of breeding patterns and authorities supplying them see the sections on 'Breeding' under the separate species.

The evidence for arena-spawning in the species of *Oreochromis* from observation of the elements of the syndrome. The heads of the columns signify: sexual dimorphism, sexual dichromatism, arena spawning, polygamy (polygyny and possibly polyandry), maternal mouth-brooding, separate nursery areas.

Species	Dimorph.	Dichrom.	Arena	Polygamy	♀ brooder	Sep. nursery
niloticus	+	+	+	+	+	+
aureus	+	+	≈	+	+	+
leucostictus	+	+	+	+	+	+
esculentus	+	+	+	+	+	+
spilurus	+	+	+	—	+	+
urolepis	+	+	+	—	+	—
korogwe	+	+	—	—	+	—
mossambicus	+	+	+	+	+	+
mortimeri	+	+	—	—	+	—
placidus	+	+	—	—	—	—
shiranus	+	+	≈	—	+	+
pangani	+	+	—	—	+	—
jipe	+	+	—	—	+	—
hunteri	—	+	—	—	—	—
andersonii	+	+	—	—	+	—
alcalicus	+	+	+	+	+	join school
amphimelas	—	+	—	—	+	—
variabilis	+	+	+	+	+	+
upembae	+	+	—	—	—	—
malagarasi	+	—	—	—	—	—
karomo	+	+	+	+	+	+
rukwaensis	+	+	+	—	+	+
macrochir	+	+	+	+	+	+
angolensis	+	+	—	—	—	—
lepidurus	+	—	—	—	—	—
squamipinnis	+	+	+	—	+	+
saka	+	+	+	—	+	+
lidole	+	+	+	—	+	+
karongae	+	+	—	—	+	—
tanganicae	—	—	—	—	+	—
schwebischi	+	+	≈	—	+	—

Circumstantial evidence is indicated by ≈. A dash signifies 'not reported'.

Subgenera of *Oreochromis*

1. *Oreochromis* Günther, 1889: 70. Type species by monotypy, *Oreochromis hunteri* Günther, *loc. cit.* Including *Nilotilapia* Thys, 1971: 204; no type species named, here designated *Labrus niloticus* Linnaeus = *Oreochromis niloticus* (by virtual tautomy).
2. *Alcolapia* Thys, 1968*b*: xxxv. Type species, by original designation, *Tilapia grahami* Boulenger, 1912*b*: 519 = *O. (Alcolapia) alcalicus grahami.*
3. *Vallicola* nov. Type species *Tilapia amphimelas* Hilgendorf, 1905: 405 = *O. (Vallicola) amphimelas.*

4. *Nyasalapia* Thys, 1968*b*: xxxv. Type species, by original designation, *Chromis squamipinnis* Günther, 1864: 311 = *O. (Nyasalapia) squamipinnis.* Including *Loruwiala* Thys, 1968*b*: xxxvi, type species, by original designation, *Tilapia macrochir* Boulenger, 1912*a*: 139.
5. *Neotilapia* Regan, 1920: 38. Type species, by original designation, *Chromis tanganicae* Günther, 1893*b*: 630 = *O. (Neotilapia) tanganicae.*

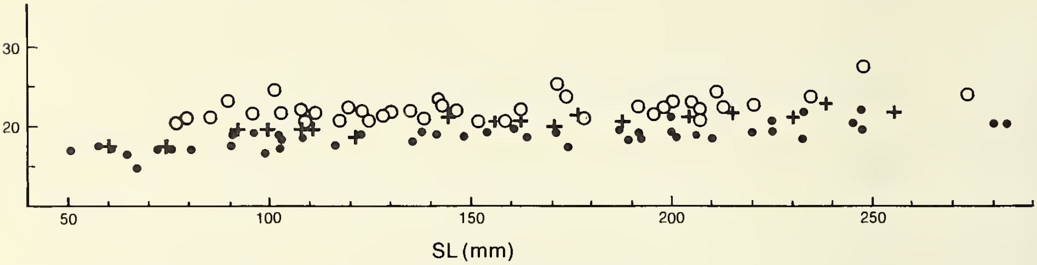

Fig. 13 Depth of preorbital bone as % length of head in: *Oreochromis mossambicus* with *O. mortimeri* (○); *O. niloticus* (●); *O. aureus* (+). See also Figs 81 & 132.

Distinguishing characters of the subgenera of *Oreochromis*

Subgenus *Oreochromis*

1. Outermost teeth bicuspid in the young and in adult females, but in mature males of several species becoming unicuspid by wear or replacement. (Some or all teeth of outermost row replaced by tricuspids in large fishes of some populations of *O. niloticus*).
2. Preorbital bone of moderate depth, at 100–200 mm SL 18–25% length of head in most species, but 18–23% in others; not scaly (Figs 13, 72 & 81).
3. Preorbital bone with five lateral line openings (exception see p. 167).
4. Anal spines III, III–IV, IV, IV–V or IV–VI.
5. Scales of belly smaller, in some species much smaller, than those of flanks; transition between the two sizes gradual or abrupt.
6. Pharyngeal teeth ranging from relatively coarse, with the length of the lower dentigerous area approximately equal to that of the blade or a little longer, to very fine on a reduced dentigerous area. See also p. 16 and Table 119.
7. Microbranchiospines present except in some individuals of *O. spilurus percivali.*
8. Lower gill-rakers 14–27 (13–16 in *O. s. percivali*).
9. Jaws in mature fishes of some species becoming greatly enlarged, especially in males.
10. Male genital papilla simple or with a distal notch, not tasselled.
11. Breeding characters as for the genus (pp. 25–27).
12. Length of pectoral fin, in fishes over 80 mm SL, 29·0–44·5% SL, rarely less than 30%. Maximum not less than 37% in any species.

Contained species and distribution. Fifteen species, one with seven subspecies, one with three, and four with two. They are listed in Table 2 and described on pages 139–374.

The generic position of '*O.*' *schwebischi,* which inhabits the Ogowe system, the Chiloango and Niari Kouilou (Fig. 12) is doubtful (pp. 35–36 & 489).

Absent from the Guinean Forest zone from the Corubal River to southern Cameroun and from the rivers Zaire, Bengo and Quanza; a limited penetration into the Lower Niger and Volta from the Soudanian belt. Except in the Nile and the Levant no known trace of this subgenus north of the Sahara, but two nilotic species extend in the Soudanian belt to the Chad basin, the rivers Niger and Volta, and the western rivers from Senegal to the Gambia. The majority of species are in the eastward-flowing rivers, the type species and its relatives inhabiting small lakes on the slopes of Kilimanjaro and the Pangani River, which drains one of the lakes to the Indian

Ocean. *Oreochromis niloticus* extends its area into Lakes Edward/George and Kivu as well as, probably secondarily, into Lake Tanganyika, and has subspecies in Ethiopian waters and Lake Baringo. Lake Victoria harbours an endemic species. A species of the Zambezi extends to the Okavango and the Cunene system and there is a species in Lakes Malawi and Chilwa.

Subgenus *Alcolapia*

1. Outermost teeth normally bicuspid and inner tricuspid, but both outermost and inmost may be unicuspid in bigger fishes, the former at least partly by wear.
2. Depth of preorbital bone 19–24% length of head at 95–130 mm SL; bone not scaly (Figs 131 & 132).
3. Preorbital bone with four lateral line openings.
4. Anal spines III, rarely II.
5. Scales of chest and belly very small, with some naked patches.
6. Pharyngeal bone with small teeth and long blade.
7. Microbranchiospines absent.
8. Lower gill-rakers 9–14.
9. Jaws not becoming greatly enlarged in mature males.
10. Genital papilla simple, but conspicuous.
11. Breeding habits basically as in subgenus *Oreochromis,* but nest in favourable circumstances more elaborate.
12. Pectoral fin short, 24·4–27·8% SL in fishes of 94–127 mm SL.

Contained species and distribution. A single species, with two subspecies, not known to exceed 130 mm SL, though rumoured to reach a total length of about 22 cm (SL about 150 mm).

Lakes Natron and Magadi in the eastern Rift Valley; introduced into Lake Nakuru. See pages 375–391 and Table 2.

Subgenus *Vallicola* nov.

1. Teeth very small, becoming unicuspid in mature males from no great size and in larger females.
2. Preorbital bone scaly, narrow, its depth 12·5–17·0% length of head in fishes of 82–270 mm.
3. Preorbital bone with four lateral-line openings.
4. Anal spines III.
5. Scales of nape, dorsum and belly very small, the transition from flank to belly scales abrupt, along a curve from base of pectoral fin to vent.
6. Length of lower pharyngeal bone 29–32% length of head; teeth very fine, dentigerous area in adults only about one third of the median length of the bone.
7. Microbranchiospines absent.
8. Lower gill-rakers 12–16.
9. Jaws not becoming enlarged in mature fishes.
10. Male genital papilla simple.
11. Breeding habits unknown, but probably a maternal mouth-brooder.
12. Pectoral fin short, (22·0) 26·4–32·3% SL in fishes of 80–270 mm SL.

Contained species and distribution. A single species, inhabiting Lakes Manyara, Eyasi, Kitangiri and Singida in Tanzania. See Table 2, and pages 375–404.

Subgenus *Nyasalapia*

1. Outermost teeth bicuspid in the young, several with an admixture of tricuspids in adults, in one species (*O. karomo*) all tricuspid in adults, in males of *O. angolensis* some posterior unicuspid.

2. Preorbital bone not scaly, its depth not exceeding 27·0% length of head at 100–200 mm SL, up to 27·7% above this size.
3. Preorbital bone with five lateral-line openings.
4. Anal spines III.
5. Scales of belly smaller than flank scales, transition gradual or rather abrupt.
6. Pharyngeal teeth very fine and anterior blade of lower pharyngeal bone longer than the dentigerous area.
7. Microbranchiospines present.
8. Lower gill-rakers 17–26 (15–18 in *O. salinicola*).
9. Jaws not becoming greatly enlarged in mature fishes.
10. Genital papilla tasselled in mature males, except in *O. salinicola.*
11. Breeding habits as in *O. (Oreochromis)*, but nest, where known (7 or 8 species), with a central, raised platform.
12. Length of pectoral fin 35·0–44·5% SL, except in *O. salinicola* (27·8–32·1%).

CONTAINED SPECIES AND DISTRIBUTION. Fifteen species in Central Africa and in western rivers from the Cunene to the lower Zaire (Fig. 12). Listed in Table 2 and described on pages 405–488.

Subgenus *Neotilapia*

1. Teeth all with long, slender shafts, in 8–10 close-set rows, the outermost bicuspid in the young, all tricuspid in fishes of SL above about 100 mm SL. Jaws not produced forwards.
2. Preorbital bone not scaly, its depth at 100–200 mm SL 24–29% length of head, up to 30% above this size.
3. Preorbital bone with five lateral-line openings.
4. Anal spines III.
5. Scales of belly very small; an abrupt transition between these and the flank scales.
6. Lower pharyngeal teeth fine and close-set, in a heart-shaped area that is shorter than the anterior blade.
7. Microbranchiospines present.
8. Lower gill-rakers 22–26.
9. Jaws not becoming enlarged, except possibly in very large males.
10. Male genital papilla small and simple.
11. A maternal mouth-brooder, bringing eggs to reedy places for brooding. Breeding habits otherwise unknown.
12. Length of pectoral fin 38·0–44·3% SL.

CONTAINED SPECIES AND DISTRIBUTION. A single species, abundant in the peripheral zone of Lake Tanganyika, to which it is endemic. Described on pages 496–502.

Comments on the subgenera of *Oreochromis*

Except for *Vallicola*, the subgenera of *Oreochromis* recognized here were also recognized by Thys (1968*b*) as subgenera in his 'Section III, *Sarotherodon*' of the comprehensive genus *Tilapia*, and following him by Ruwet (1976). In addition, Thys proposed the subgenus *Loruwiala* for *O. macrochir* and other tasselled species. As already pointed out (Trewavas, 1973*b*), the tasselled genital papilla on which *Loruwiala* was defined also characterizes *Nyasalapia* Thys, to which *O. macrochir* is related and there is no need for both names.

In 1968*b* Thys defined a group comprising *O. niloticus* and its subspecies, and in 1971 proposed a subgenus *Nilotilapia*, doubtless intended for *O. niloticus* and its subspecies, and possibly also for his unnamed 'Group III–G' of 1968*b*. I have included *O. niloticus* in subgenus *Oreochromis*.

Oreochromis niloticus differs from typical species of *Oreochromis*, including the sympatric *O. aureus*, in not having a bright red or orange margin to the dorsal fin in the breeding male. In the nominate subspecies there is said to be little sexual dichromatism, the male being only a little brighter than the female at breeding time (Heinrich, 1967*a*; El Zarka *et al.*, 1970), but in some large males the red flush may be very distinctive. In *O. n. eduardianus*, moreover, the male develops extensive melanic areas, and in *O. n. vulcani* and probably other subspecies he becomes very dark and iridescent at breeding time. The breeding behaviour appears to be essentially as in other species of *Oreochromis*.

In Ethiopian waters, and Lakes Turkana and Baringo *O. niloticus* is not accompanied by any other species of *Oreochromis*; but in West Africa, the lower Nile and the Levant *O. aureus* is also present. The absence of *O. aureus* from the Nile above the delta leaves it isolated from all species of *Oreochromis* except *O. niloticus*. It resembles the more typical species in having a bright red or orange margin to the dorsal fin in the breeding male, but like *O. niloticus* its preorbital bone is relatively narrow and there is no enlargement of the jaws in mature fishes. It does not show any special resemblance to either of the species that Thys placed with it in his 'Group III–G' (*O. esculentus* and *O. leucostictus*), and it is questionable whether it is a sister-species of *O. n. niloticus* or an isolated representative of the more typical species of subgenus *Oreochromis* (see p. 139).

Of Thys's Group III–G, *O. esculentus* is probably related to *O. niloticus*, which it resembles in colour, but it is much more distinct from *O. niloticus* than are the subspecies of the latter in Ethiopia and Lakes Turkana and Baringo. This is in line with the well-known fact that the present native fish fauna of Lake Victoria is not a nilotic one, unlike that of Lakes Albert and Turkana. See also p. 172, below, and Whitehead, 1962*b*.

The relationship of *O. leucostictus* of Lakes Edward/George and Albert is not clear. It has not the bright red margin to the dorsal fin common in *Oreochromis** and its vertebral numbers are low.

Oreochromis alcalicus has been allotted the subgeneric name *Alcolapia* Thys because its relationships are unclear. They are discussed with the account of the species (p. 403). Thys included *O. amphimelas* with *O. alcalicus* in *Alcolapia*, but I have treated it as a separate subgenus for reasons stated (p. 377). Features common to the two species, but believed to be responses to the hot alkaline waters of the environment, are detailed on p. 33.

Although the Central African species of the subgenus *Nyasalapia* show in their jaws and dentition other signs of interrelationship, the possession of a bifid tassel of tubercles and filaments on the male genital papilla is the only character linking *O. angolensis* and *O. lepidurus* to them. Occasional individuals of the subgenus *Oreochromis* have a papilla with a distal notch (see Fig. 91), but no species of *Oreochromis* other than those here included in *Nyasalapia* has

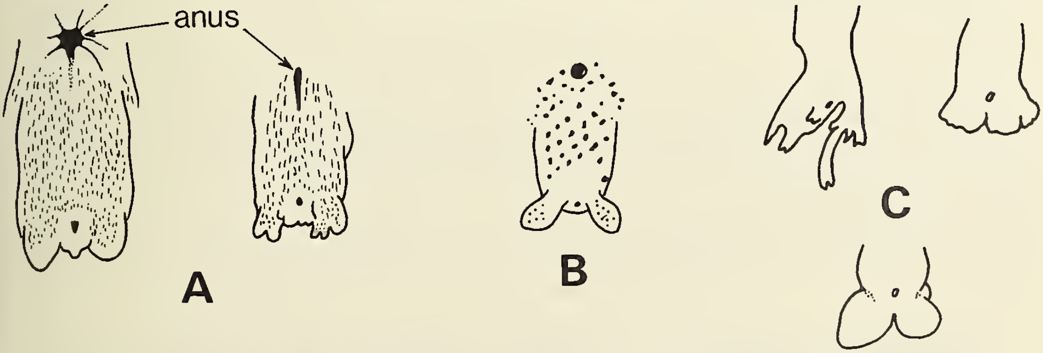

Fig. 14 Genital papilla of male; A, *Tilapia sparrmanii* (two individuals of 150 & 112 mm SL); B. *T. margaritacea* (one fish of 92 mm SL); C, *Oreochromis (Nyasalapia) malagarasi* (three fishes of 180–187 mm SL).

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*But cf. fig. 263 in Staek, 1965, of a male in full breeding colours, which has a conspicuous red margin of the dorsal.

an elongate tassel. Within *Nyasalapia* the tassel develops only in well-grown males and *O. salinicola,* included in the subgenus mainly because of its geographical position, does not grow big enough to develop one. Among the substrate brooders, two males of *Tilapia sparrmanii* and one of *T. margaritacea* have been found with structures similar to the incipient stages of the tassels in *Nyasalapia* (compare Figs 14 & 171). Whether this is parallelism or an indication of the group of *Tilapia* from which the subgenus *Nyasalapia* was derived is an open question (see p. 37). The area of distribution occupied by *T. sparrmanii* includes the whole of that of *O. (Ny.) macrochir.*

Subgenus *Neotilapia* remains monotypic. The resemblance in dentition between *O. (Ne.) tanganicae* and *O. (Ny.) karomo,* which caused Thys to unite them subgenerically, being outweighed by important differences and dismissed as parallelism or even convergence (p. 488).

Genus *DANAKILIA* Thys van den Audenaerde

Tilapia (part); Vinciguerra, 1931 : 105.

Tilapia (*Danakilia*) Thys, 1968*b*: xxxv. Type species by original designation *Tilapia franchettii* Vinciguerra, 1931: 105.

ETYMOLOGY: Danakil, the name of the territory and the people of the type locality.

Distinguishing characters

1. Teeth of jaws all tricuspid.
2. Depth of preorbital at sizes below 84 mm SL (longer than which the species is not known to grow) 20·5–26·3% length of head. Eye small, diameter 21–22% length of head at 69–74 mm SL.
3. Preorbital bone with five lateral-line openings.
4. Anal spines III.
5. Scales of chest and belly small, not imbricating, but contiguous.
6. Lower pharyngeal teeth in a heart-shaped area, fine and close-set in young; those of posterior row compressed, then about four rows of bevelled teeth of which those of a middle group became enlarged and flattened in adults.
7. (a) Lower gill-rakers 10–12. (b) Microbranchiospines absent.
8. Jaws not becoming greatly enlarged.
9. Male genital papilla simple.
10. Testes weights not recorded.
11. Breeding habits unknown, but large eggs (long diameter about 3·5 mm) bespeak a mouth-brooder.

These characters are listed for comparison in the same order as those of the subgenera of *Oreochromis* (p. 28). The order of importance for generic relationships is, 11, 2, 7, 3, 1. Character 11 excludes it from *Tilapia*; 2 and 7(a) relate it to *Iranocichla* Coad, 1982; and 1 is unique within Tilapiini, the tricuspid teeth being of a different shape from those of other tilapiine species (compare Figs 176, 183 & 187).

CONTAINED SPECIES AND DISTRIBUTION. Endemic to Lake Afrera (Giulietti) and neighbouring swamps in the Danakil desert. A single species (p. 503).

Parallel modifications in populations of thermal and alkaline waters

In East Africa, where rift valleys and volcanoes are manifestations of tectonic instability, there are many places where hot alkaline springs emerge to form pools, streams, swamps or lakes. Where the conditions become tolerable to fish life, that is, where the water temperature sinks below 40°C and evaporation has not yet made the waters too saline, there are often populations of tilapiine cichlids. These may be clearly isolated populations of a local species or they may have become so much modified in their special environment that it is not obvious from which species they have been derived.

Of the first group are:

(i) *Oreochromis niloticus filoa* of the hot springs near Addis Ababa (p. 167).

(ii) *Oreochromis n. sugutae*, living at Karpedo, between Lakes Baringo and Turkana (p. 179).

(iii) The population of *O. n. vulcani* inhabiting a stream entering Lake Turkana near Loyengalani (p. 176), but not sufficiently isolated to have developed any peculiarity other than that of precocious breeding.

(iv) A population of *O. leucostictus* in a pool in a small tributary of the Semliki River at the foot of Mount Ruwenzori (p. 221).

(v) The population of *O. aureus* of the pools at Ain Feshkha on the shore of the Dead Sea.

(vi) *O. spilurus percivali* (p. 260) of a pool fed by hot springs near the south bank of the Northern Uaso Ngiro.

Of the second group are:

(vii) *O. salinicola* of the saline springs at Mwashia, Shaba (p. 454).

(viii) *O. alcalicus alcalicus* and *O. a. grahami* of Lakes Natron and Magadi (p. 375).

(ix) *O. amphimelas*, of which the type locality is in the Lake Manyara basin (inhabited by the most affected population of the species) and which is also native to other lakes of this part of the rift system (p. 391).

(x) *Danakilia franchettii* of Lake Afrera in the Danakil Depression near the shore of the Red Sea (p. 503).

These populations have in common:

1. Small size of sexual maturity and low maximum size.
2. Low numbers of vertebrae compared with the putative parent species (but not in populations iii, iv and vii).
3. Low numbers of dorsal fin-rays (not demonstrated for populations ii (?), iii, iv and vii).

Members of the second group also have in common:

4. Low numbers of gill-rakers.
5. Absence of microbranchiospines, but not in *O. salinicola*.
6. Very small, thin scales (which may be non-imbricating) on chest and belly and in some also on nape.

Details of these characters are given under the respective species and (vertebrae) in Table 2.

The question arises as to how far these features are responses to the environment or are evidences of relationship.

1. It is a well-known capacity of tilapias, often deplored by fish-culturists, to reproduce at a small size in confined waters, irrespective of their thermal quality. This capacity and its survival value have been discussed by Iles (1971, 1973), Fryer & Iles (1969; 1972: 362 ff: Lowe-McConnell, 1975: 205; several authors in Pullin & Lowe-McConnell, 1982). It is probably a response to stress, acting through the hormones (cf. Noakes & Leatherland, 1977), and within the genera under consideration it has no bearing on relationships.

2. The range of vertebrae throughout *Sarotherodon*, *Oreochromis* and *Danakilia* is 26–34 (Table 2) and not all the species with low numbers are inhabitants of thermal waters. In *S. melanotheron* the range of 26–28 (mode 27) is probably due to the retention of a plesiomorphic character-state. The same may be true of *S. tournieri*, *O. leucostictus* and *'O.' schwebischi*.

The influence of temperature at an early stage of development on the number of metameres and therefore of vertebrae is well documented (see Lindsey, 1961; Garside, 1966; & references therein). It evidently operates through growth-rate, which is faster at high temperatures. Not only are the populations of thermal waters characterized by low vertebral numbers, but also differences in mean vertebral numbers characterize related populations of lower and higher altitudes that provide higher and lower temperatures. Examples are *Oreochromis aureus* of the Jordan Valley contrasted with populations of the same species at and above sea-level (Table 48); *O. s. spilurus* and *O. s. niger* respectively of low and higher altitudes; and *O. mortimeri* of the Middle Zambezi in contrast to the related *O. andersonii* of the plateau (see Table 2).

In passing, it may be noted that the units of metameric variation do not correspond with the vertebral units, as is illustrated by the frequent presence as an anomaly among the caudal vertebrae of many fishes of a single centrum with two neural and haemal spines. In other words, though acting on the metameres, the variation is independent of metameric arrangement.

Among the populations of thermal waters, the significance of the low vertebral number (27) in *Danakilia franchettii* must be judged by comparison with its nearest relative, *Iranocichla hormuzensis* Coad, 1982 (see p. 503), which has 28–30 (mode 29). The streams of south-western Iran in which this species lives are saline and the air temperature there is high throughout the year, but *D. franchettii* clearly lives at the extreme tolerable levels of both temperature and salinity and this is probably the direct cause of the difference in vertebral numbers, which therefore does not diminish the evidence for the mutual relationship of the two species.

The wide ranges of vertebral numbers in *O. alcalicus* (27–30, mode 28) and *O. n. filoa* (26–30) indicate instability. It is suggested that *O. alcalicus* may be related to *O. variabilis*, which has 29–31 vertebrae (mode 30); and *O. n. filoa* is of course to be compared with *O. n. cancellatus*, in which the mode is 31.

O. amphimelas seems at first sight to be exceptional in having a rather high number of vertebrae (mode 31) and we can only regard it as reduced if we compare it with *O. hunteri*, *O. pangani* and *O. jipe*, a relationship that is at least geographically possible. But *O. esculentus*, with which it has hybridized easily, has the same modal number (31).

That the vertebral numbers in *O. aureus* are environmentally influenced is well demonstrated by the parallel effect on this species and *Tilapia zillii* at Ain Feshkha (Chervinski, 1968; & see Table 49, herein).

The small sample of *O. n. sugutae* shows a lower mode and mean than the neighbouring populations of Lakes Baringo and Turkana, and *O. s. percivali* has a lower mean than in *O. s. spilurus* (Table 2).

3. In some of these examples we find low numbers of dorsal rays, especially of spines: *D. franchettii* XII–XIV (c.f. XIV–XVI in *Iranocichla*), *O. alcalicus* IX–XIII, *O. amphimelas* XII–XIV (XV), in contrast to a modal XVI or XVII in other species.

4. The lower gill-raker numbers, 9–14 in *O. alcalicus*, 12–16 in *O. amphimelas*, contrast with the rarity of the lowest numbers (13, 14) in the other species. *O. salinicola*, with a low gill-raker count of 15–18 contrasts with its putative relatives, *O. macrochir* and *O. upembae*, (20–25); and *O. s. percivali* (13–16) with *O. s. spilurus* (15–19). The low numbers in *Danakilia*, however, are very close to those of its relative, *Iranocichla*.

5. That microbranchiospines are absent in *O. alcalicus*, *O. amphimelas* and *D. franchettii* and reduced in *O. s. percivali* can hardly be a coincidence, but it is difficult to suggest a functional explanation in the absence of any knowledge of the function of these structures in the species that possess them. Microbranchiospines sometimes appear late in ontogeny and some of the species lacking them remain small. But they are absent also in large *O. amphimelas* of Lake Kitangiri and the specimens of *Iranocichla* that possess them are as small as those of *D. franchettii* that lack them.

6. The small size of the scales of chest and belly was considered by Thys (1971: 204) to characterize *Oreochromis* in contrast to *Sarotherodon*. In the latter they are only a little smaller than the flank scales and there is a smooth gradient from one to the other.

There is, however, much variation within genus *Oreochromis*. The thoracic scales are always much smaller than the flank scales. In the type species, *O. hunteri*, there is an abrupt change to the very small scales of the belly, but this is not universal in the genus. In *O. spilurus*, for example, there is an even gradation and the belly scales are only a little smaller. In *O. (Nyasalapia) lidole* there is an abrupt transition to very small belly scales, and the contrast is usually noticeable in *O. squamipinnis* and *O. saka* (Fig. 164). In *O. (Neotilapia) tanganicae* the transition is rapid and the contrast marked. In these examples we do not find correlated ecological conditions, neither is the condition indicative of special degrees of relationship.

Greenwood (1979) used the nature of the thoracic squamation to define haplochromine genera, considering the lack of ecological correlation to indicate a phyletic explanation.

In other cichlid genera very small scales of chest, belly and nape often characterize species inhabiting rapids or living among rocks. In these the scales are usually non-imbricating and the areas may even be scaleless or include naked patches. Such squamation is found among the 'mbuna' of Lake Malawi, which are small fishes inhabiting rocky places, and in the species of *Steatocranus*, which frequent rapids.

Among the populations of thermal waters, *O. alcalicus*, *O. amphimelas* and *Danakilia franchettii* have the scales of chest, belly and nape reduced in various degrees. Unlike the small scales of such species as *O. lidole* and *O. tanganicae* these small scales are usually non-imbricate and in some cases there are naked patches. In this specialization *D. franchettii* is less extreme than its relative *Iranocichla hormuzensis* (p. 503), although in temperature and salinity its environment is more extreme. *Iranocichla hormuzensis* inhabits pools and backwaters of shallow, stony streams and feeds largely on epilithic algae. This brings it into line with the rheophil and lithophil species mentioned above and suggests that the epilithic feeding habit may be a factor responsible for the reduced squamation.

In sum, there is good reason to believe that the shared characters listed are mostly responses to the shared special features of the environment, and we must look to other characters for indications of relationship.

Further examples of parallelism and convergence

Parallelisms that may be interpreted as responses to similar special environments have been detailed in the preceding section. Others can be seen as indications of a basic similarity of the genome in *Sarotherodon* and *Oreochromis*.

The first two are examples of parallel functional complexes, the others of parallelisms in single features.

1. Parallel trophic structures associated with a diet of phytoplankton find their extreme expression in *Sarotherodon linnellii* and *S. caroli* (pp. 84–93) on the one hand, and *O. (Nyasalapia) lidole* (pp. 457ff.) on the other. The systems involve small jaw teeth in narrow bands and very fine pharyngeal teeth on a reduced area of the lower bone relative to the size of the blade. In Lake Barombi-Mbo (Kumba) *S. linnellii* and *S. caroli* represent two stages in this reduction (Fig. 33), and probably the small *Myaka myaka* Trewavas is the end stage of the same series (Trewavas *et al.*, 1972). In Lake Malawi *O. (Ny.) lidole* is an end-term of a similar series, whose less specialized members are *O. squamipinnis* and *O. saka*. *O. lidole* itself becomes more extreme in the crater-lake Chungruru (p. 465).

Both these parallel forms are characterized by a big head, and the parallel is especially close when the population of *O. lidole* in the crater-lake Chungruru is compared with the *linnellii-caroli* pair. It is noteworthy that the relative size of the head increases with the growth of the fish, the reverse of the usual allometry. This supports the view that it is a growth phenomenon associated with poor nutrition as in the well-known 'hunger-form' of carp (Wunder, 1949). It results in a large food-gathering apparatus supporting a small, lean body.

2. The same type of mating system has apparently evolved in a species of *Sarotherodon* and in *Oreochromis*, resulting here in an indecisive placing of '*O.*' or '*S.*' *schwebischi*. If the genera are to be defined on the mating system this species conforms to *Oreochromis*, but comparison of immature *schwebischi* with *Sarotherodon galilaeus* reveals a resemblance which is very close

indeed. It involves a small mouth, long pharyngeal bone of identical shape and dentition, a deep preorbital bone and an emarginate caudal fin. The general likeness is apparent in comparing Pl. IX of Thys, 1964, with Fig. 37 (p. 99). The malanin pattern of the body consists of facultative vertical bars, the persistent juvenile bars. Traces of the common tilapiine pattern of two horizontal stripes or series of spots (blotches) as in most *Oreochromis* are not found in our examples of *schwebischi* and very rarely in *S. galilaeus**. The dentigerous area of the lower pharyngeal is enlarged in both species by an apparent backward growth of the tooth-plate, the teeth are of the same slender shape and the size of the ventral scales is undiminished. Yet the mature male *schwebischi* presents a very different appearance, with darker colouring, a scarlet dorsal margin, simplified jaw teeth and enlarged jaws giving a concave upper profile (Fig. 179), all features of the eastern species of the subgenus *Oreochromis* and unknown in *S. galilaeus.*

The geographical position supports the inclusion of *schwebischi* in *Sarotherodon* rather than *O. (Oreochromis)* (Fig. 12), which is separated from it by the whole basin of the Zaire. With the exception of the brackish water species *O. (Ny.) lepidurus*, *schwebischi* is surrounded by species of *Sarotherodon*—*S. melanotheron* in brackish water, *S. mvogoi* to the north-east, *S. g. sanagaensis* in Cameroun, and *S. g. boulengeri* in the Lower Zaire. The two last are here (pp. 120 & 122) placed as subspecies of *S. galilaeus*, with which they agree in the modal number of vertebrae (29, versus 28 in *schwebischi*), but no mature specimens are available and if the sexes prove to be dimorphic or dichromatic this would point to a nearer relationship with *schwebischi*. Thys has suggested that *schwebischi* may be related to subgenus *Nyasalapia*, but no genital tassel has been reported. If it is more closely related to *S. galilaeus* its breeding pattern is a parallelism with *Oreochromis.*

It is not impossible that arena-spawning has developed independently in the subgenera *Oreochromis* and *Nyasalapia*. They are recognized as divergent subgenera by the enlargement of the jaws in mature males of several species of *O. (Oreochromis)* and the tasselled male genital papilla of *O. (Nyasalapia)*, differences supported by their different but overlapping geographical distributions.

Arena-spawning is practised also in haplochromines, e.g. *Astatotilapia desfontainesi*, for which it was beautifully reported by Kirchshofer (1953). Between these and *Oreochromis* the concept of convergence is more appropriate than parallelism. Even more remarkably, as Loiselle & Barlow (1978) have pointed out, the *Oreochromis* breeding syndrome is almost identical with the 'lek' system in some birds. One may adapt a comment on arena-spawning in birds by Crook (1965: 212) thus;

> The emergence of the typical (arena) behaviour depends on, firstly, the presence of territorial/courtship display in social groups not connected with the *nursery* site selection, secondly, the performance of incubation and *guarding* by the females, thirdly, loose pair-bonding permitting polygamy and promiscuity, fourthly, food availability such that the females working alone can rear a brood (possibly of diminished size) and which enables the male to spend little time in feeding. Lastly, the remarkable display structures of the males render them a risk at the *nursery areas* thereby favouring their separation from them.

This is a word-for-word copy from Crook, except the italicized words, which in his statement are respectively 'nest', 'nest construction' and 'cryptic nests', the word 'nest' having a different connotation for birds from that of its loose use for the mating territory in cichlids. The 'food availability' is provided by the large egg-yolks, although this is not a feature confined to arena spawners (c.f. *Sarotherodon melanotheron*). Large eggs also result in a numerically smaller brood. Moreover, both sexes during breeding utilize fat that was stored among the viscera prior to breeding.

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*Among many young preserved *S. galilaeus* examined, with juvenile vertical bands, some between 30 and 50 mm SL have two or three bands emphasized at the level of the mid-lateral longitudinal stripe.

Among birds this far from universal behaviour is said to have evolved independently in seven lineages (Wilson, 1975: 25).

The 'nest' with a central raised mating platform, characteristic of subgenus *Nyasalapia*, has been described also in the Malawian *'Haplochromis' heterodon* Trewavas by Fryer & Iles (1972, fig. 155).

The advantages of this mating system to the species have been well perceived by Kirchshofer (1953: 307) and by Ruwet (1962).

3. Development of broad bands of tricuspid teeth with long, slender shafts and curved crowns in *O. (Nyasalapia) karomo* (pp. 482–488), and *O. (Neotilapia) tanganicae* (pp. 496–502). As between these two the shape of the jaws is quite different (Figs. 175 & 185); in *O. karomo* they are prolonged forwards, in *O. tanganicae* they remain short but transversely broadened. The contrasting characters of the two species, indicating different relationships, are summarized on page 488. Similar tricuspid teeth characterize the unrelated genera *Petrotilapia* and *Petrochromis.*

The tricuspid outer teeth of *Danakilia franchettii* are accompanied by still more contrasting characters and themselves are a different shape from those of *O. karomo* and *O. tanganicae*, being short and not sharply curved (Fig. 187).

4. Expanded gill-rakers in breeding females have been found in *O. (Alcolapia) alcalicus*, *O. (Vallicola) amphimelas* and *O. (Oreochromis) mossambicus* (Fig. 135). They are known also in *Serranochromis robustus jallae* (Trewavas, 1964, fig. 5) and *Pseudocrenilabrus multicolor* (Reinboth, 1956, fig. 7). In the non-tilapiines this is obviously convergence and it may be convergence or parallelism between the subgenera of *Oreochromis.* But it may be a temporary condition in the females, associated with mouth-brooding, and is possibly commoner than observations have revealed.

5. A complicated genital papilla. Within the genus *Oreochromis* the presence of a tasselled genital papilla has been taken as a sign of relationship, and the subgenus *Nyasalapia* has been defined on it. Two individuals of *Tilapia sparrmanii* and one of *T. margaritacea* have been found to possess a bifid male papilla very similar to the condition of that in individuals ripening at the same small size in *Nyasalapia.* This may be more than parallelism and raises the question of the possible origin of *Nyasalapia* from an ancestral *Tilapia sparrmanii* (see p. 31).

6. Increased numbers of vertebrae. Table 2 shows a wide range of vertebral numbers in each of the genera *Tilapia*, *Sarotherodon*, *Oreochromis*, with increasing modes in that order. The facts seem to support the view that two factors are at work, a genetic factor making for increased numbers in some phyla (e.g. *T. sparrmanii*, *T. baloni*, *T. rendalli; S. melanotheron*, *S. galilaeus*, *S. caudomarginatus*) and the factor of temperature, making for decreased numbers in thermal or lowland waters (p. 33).

Terms, abbreviations and methods of measurement

Figs 15 & 16

Standard length (SL) is the length from the anterior end of the upper lip to the base of the caudal fin. '150 + 40 mm' means SL 150 mm and length of caudal fin from base to tip of middle rays 40 mm. *Total length* (TL) is the sum of these two plus any projecting part of the lower jaw; this is the measurement used in fishery statistics, but rarely in taxonomy. TL is usually expressed in cm, SL in mm.

Depth of body is the greatest depth, excluding fins.

Length of head (*L. head*) is measured from the anterior edge of the upper lip to the most posterior part of the bony opercular edge, with calliper points on both places, i.e. it is not a projection.

Length of snout (*L. snout*) is measured in the same way to the anterior edge of the orbit.

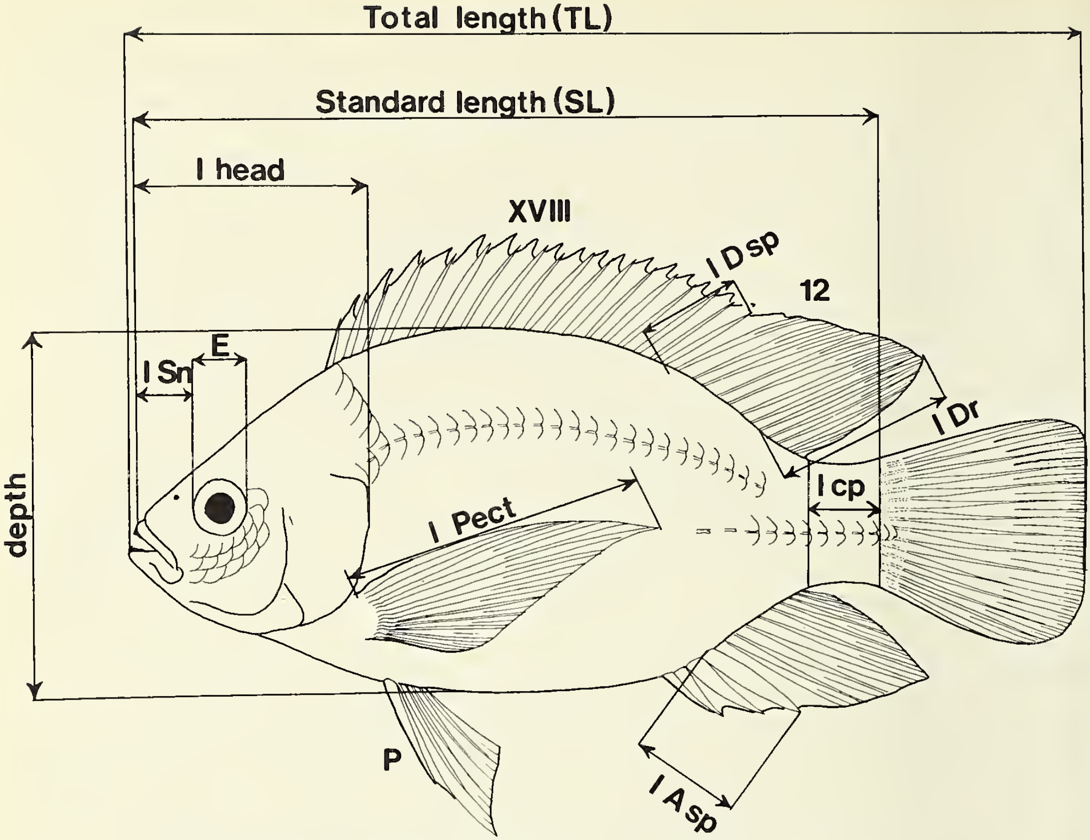

Fig. 15 Outline drawing of *Oreochromis* to show methods of measurement.

Diameter of eye (*eye*) is the horizontal diameter of the iris.

Depth of preorbital bone (*D. preorb.*) (*lacrymal*) is measured from the middle of the orbital edge of the bone to its oral edge along a line continuing the radius of the orbit.

Interorbital width (*interorb.*) is the least width of the roof of the skull between the eyes. The calipers press on the skinny orbital rim so that little but the bone is measured.

Length of lower jaw (*lower jaw*) is measured from the lip at the mandibular symphysis to the posterior edge of the jaw, above the retroarticular.

Caudal peduncle (*caud. ped.*). Its length is the horizontal distance from the end of the base of the dorsal fin to the base of the caudal. Its depth is the least depth.

Lower pharyngeal bone (*lower phar.*; *phar.*). Its width is the greatest width from right to left. Its length and the length of its dentigerous area are measured in the median sagittal line.

The *teeth* of the outermost row of the upper jaw are counted (for speed) on one side and this number is doubled to give the whole.

The *gill-raker* count is that of the outer series of the anterior arch. If the whole series is recorded it is in three sections, epibranchial + angle + ceratobranchial (and hypobranchial if included); thus: 3 + 1 + 15. The raker at the angle is not so easily determined as in some families of fishes and there may occasionally be two or none at the hinge. If only the cerato- hypo- branchial series (*lower gill-rakers*) is given the one at the angle is omitted.

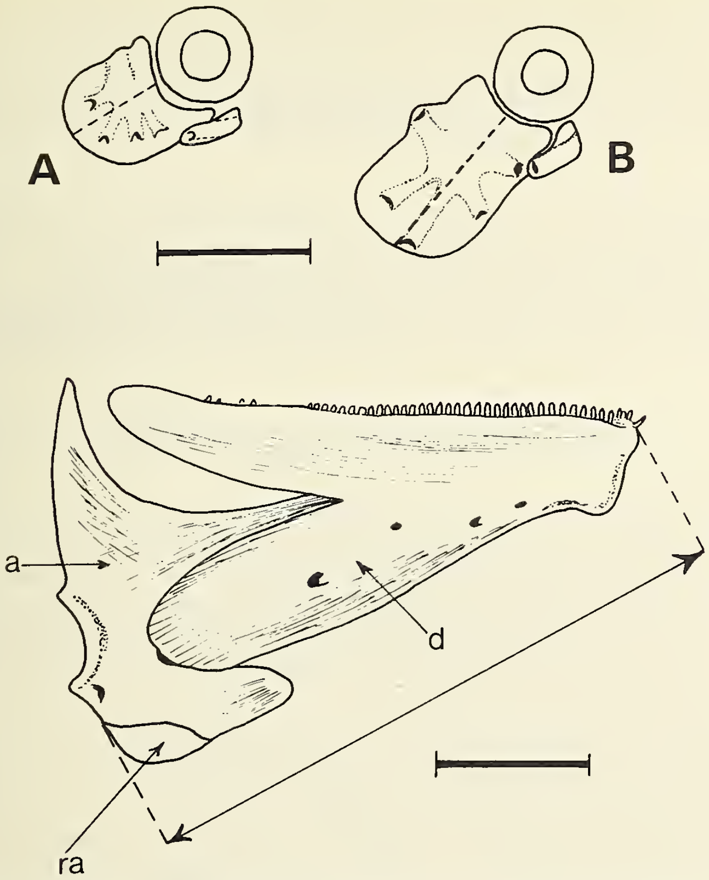

Fig. 16 Above, outline of eye, preorbital (lachrymal) bone and 2nd infraorbital of : A. *Oreochromis niloticus cancellatus*; B. *O. urolepis*. The broken line shows the measurement 'depth of preorbital bone'. Scale = 20 mm. Below, lateral view of lower jaw of *O. n. niloticus* to show the measurement 'length of lower jaw'. Scale = 10 mm. a = anguloarticular; d = dentary; ra = retroarticular.

Microbranchiospines (Gosse, 1956) are present on the outer faces of the second, third and fourth branchial arches except where noted.

'Scales in the lateral line series' are counted first along the upper lateral line, then the lower lateral line starting with the scale next behind the oblique row downwards and forwards from the last upper lateral line scale. This gives one or two more than the mid-lateral series and is the count used also by Regan, Boulenger, Greenwood and Thys van den Audenaerde. The number of scales between bases of pectoral and pelvic fins is sometimes given as an indication of the size and number of scales on the chest, but the smallest scales are usually anterior to this.

Fin ray counts The fin-ray notation is the usual one. The last dorsal or anal ray is counted if it is distinct to the base and the penultimate compares well in size with the one before it. It usually has no endoskeletal support. The pectoral rays are constant in range within these genera (13–15) and are not mentioned. The principal caudal rays are 16 in the Cichlidae and are also not mentioned. The pelvic rays have the standard percoid count of I spine and 5 soft rays.

Nest. This term is used for the pit excavated for mating. It is not comparable to a bird's nest, which is the home of the young until they are independent. In the maternal mouth-brooding species it is the mating territory excavated and defended by the male. Mating takes place in the centre of it, in some species on a special mound or platform. The eggs are immediately removed by the brooding parent. A less important pit is also prepared by one or both partners in the paternal or biparental brooding species, but of these we have little detailed information.

Frequency. f.

Sep. pag. = *separate pagination.* Used where a separately published article has the pages numbered independently of those of the same article in a serial publication (e.g. Pellegrin, 1904).

Means are sometimes given without standard deviations, but readers will appreciate that samples are often too small for differences to be statistically significant. It is hoped that they may be a guide. No means are given for samples smaller than 5, or for allometric characters.

Abbreviations of names of institutions

Albany Mus.	Albany Museum, Grahamstown, South Africa
AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences, Philadelphia
BMNH	British Museum (Natural History), London
CAS (SU)	Stanford University Collection, California Academy of Sciences
Mus. Genoa	Museo Civico di Storia Naturale Giacomo Doria, Genoa
Mus. Lyon	Musée d'Histoire Naturelle, Lyon
MNHN	Muséum National d'Histoire Naturelle, Paris
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium
NHMW	Naturhistorisches Museum, Vienna
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden
SAM	South African Museum, Cape Town
Senck. Mus.	Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt am Main
USNM	United States National Museum, Washington DC
ZMB	Zoologisches Museum der Humboldt Universität, Berlin
ZMH	Zoologisches Museum der Universität Hamburg
Thys	I have abbreviated the name of Dr Thys van den Audenaerde as he himself does.

In the lists of 'Material examined' the four-part register numbers (year, month, day, number of specimen) refer to the collections of the British Museum (Natural History).

Genus *SAROTHERODON* – I

Sarotherodon melanotheron
Sarotherodon mvogoi

Sarotherodon melanotheron Rüppell

Sarotherodon melanotheron Rüppell, 1852:21 (Gold Coast = Ghana)
For synonymy see the subspecies.

Distinguishing characters

Vertebrae 26–29, usually 27 or 28. Scales in lateral line series 27–30, mode 28 or 29 in different populations.

Lower gill-rakers 12–19 (12–16 in *S. m. nigripinnis*, (13) 14–19 in other subspecies).

Preorbital bone deep (Fig. 10):
at SL 45–80 mm less than diameter of eye, 20·0–26·5% length of head.
at SL 80–100 mm approximately equal to diameter of eye.
at SL 100–130 mm greater than eye, 24·5–27·5% length of head.
at SL 135–216 mm greater than eye, 28–31% length of head.
at SL 230 mm 32·5% length of head.

Mouth very small, lower jaw 27–34% length of head, exceptionally 36 or 36·5. Teeth very small, with slender shafts and spoon-shaped crowns, in 3–6 rows, the outermost bicuspid, the inner tricuspid; 50–106 in outer row of upper jaw.

Lower pharyngeal bone narrow (width 26·5–34·0% length of head), its blade equal to median length of toothed area in young, up to 2·2 times in adult; teeth slender and crowded, but less numerous and on a lighter bone than in *S. galilaeus*.

Caudal slightly emarginate.

Eggs large, up to 4·0 (4·5) mm long diameter, yellow or orange-coloured, brooded in mouth of male (where habits are known).

General colour pale nacreous blue on lower flanks to orange or metallic golden yellow on the back. Patches of intense black in patterns variable within a characteristic range for each population, but absent in some individuals, in the young and perhaps in some populations.

No sexual dimorphism, except that the head may be larger in males than in females (Tables 7 & 13). Sexual dichromatism, where known, confined to the operculum, which is metallic gold in mature males, transparent, appearing mauve from the red gills showing through it in females.

Natural distribution

Brackish estuaries and lagoons, rarely in neighbouring fresh or salt water, from Senegal to Zaire.

Subspecies

Sarotherodon m. melanotheron Rüppel, 1853. Brackish lagoons and estuaries along the coast of Ivory Coast to Cameroon.

Melanic areas in adult usually present on lower parts of head, on the cleithrum and on apices of caudal and soft dorsal fins, the caudal marks extending along the dorsal and ventral edges of the fin; no vertical bars on the flanks in adults, but occasional irregular and asymmetrical spots probably representing such bars; a median spot or transverse bar on the nape rather constant.

Length of head 34·9–39·8% SL in females, 35·8–42·7% in males, but overlap considerable (Table 7). Vertebrae 26–28, mode 27 (Table 4). Soft dorsal rays 10–12, a weak mode at 11 (Table 6). Lower gill-rakers 13–19, mode 16. Lower pharyngeal with fine crowded teeth and long blade.

Sarotherodon m. heudelotii (Dumeril, 1859), Senegal to Guinée, in brackish water.

Melanin pattern in adult not including extensive black patches on lower parts of head nor black tips to caudal and soft dorsal fins. Sometimes traces of black bars on flanks, but these usually not well developed.

Length of head 34–38% SL at SL 90 mm or more; no sexual dimorphism detected. Vertebrae 27–29, mode 28. Soft dorsal rays 11–13, mode 12 (Tables 4–6). Lower gill-rakers 15–18 (19), usually 16 or 17 (Tables 4 & 5). Lower pharyngeal teeth a little coarser and on a slightly more gibbous bone than in other subspecies (Fig. 20A & B).

Sarotherodon m. leonensis (Thys van den Audenaerde, 1971), salt and brackish water in coastal region of Sierra Leone and Lake Piso, Liberia, at the latter locality caught in fresh water close to its contact with brackish.

Melanin pattern in mature fishes including black patches on lower parts of head, 4–7 vertical bars of irregular shape on the flanks and a bar on base of caudal; one to four black spots on basal part of dorsal fin, sometimes bounded with white like a tilapia-mark; no conspicuous black tips at corners of caudal fin.

Length of head 32–39% SL, not sexually dimorphic (Table 12). Vertebrae 27 or 28, mode 27. Soft dorsal rays 11–14, mode 12, Lower gill-rakers 15–19, mode 16 (Tables 4 & 5). Lower pharyngeal as in *S. m. melanotheron.*

Sarotherodon m. paludinosus subsp. n., pools in a swampy area at Sangalkam and freshwater holes at Hann, both localities near Dakar.

Melanin pattern in adults (up to 96 mm SL) strongly expressed, including variable patches on lower parts of head and 4–7 vertical bands of irregular shape on the flanks.

Length of head 38–41% SL (Fig. 19 & Table 12). Vertebrae 26 or 27. Soft dorsal rays 11 or 12 in equal numbers. Lower gill-rakers 14–17, usually 15 or 16 (Tables 4 & 5). Dentigerous area of lower pharyngeal with more rounded lobes than in other subspecies.

Sarotherodon m. nigripinnis (Guichenot *in* Duméril, 1859), brackish and neighbouring fresh waters along the coast from Rio Muni to Zaire.

Melanic areas variable from total absence to total coverage of head, body and fins, the latter only in adults of southern populations of Chiloango and Zaire.

Table 4. *Sarotherodon melanotheron.* Summary of some meristic characters, using the data in Tables 5 and 6. The sample from Mouri Lagoon is omitted. The figures for *S. m. paludinosus* are from Sangalkam fishes only.

	Vertebrae				Total dorsal rays				Lower gill-rakers			
	N	Range	Mode	Mean	N	Range	Mode	Mean	N	Range	Mode	Mean
S. m. heudelotii	44	27–29	28	27·93	39	26–28	27	27·36	38	15–19	16	16·66
S. m. paludinosus	5	26–27	27	26·8	20	26–27	26	26·35	20	14–17	15=16	15·57
S. m. leonensis	10	27–28	27	27·4	25	26–29	28	27·4	23	15–19	16	16·52
S. m. melanotheron	56	26–28	27	26·95	43	25–29	27	26·72	47	13–19	16	15·98
S. m. nigripinnis	19	26–28	28	27·53	83	24–27	26	25·92	125	12–17	15	14·59

Table 5. *Sarotherodon melanotheron.* Frequencies of meristic characters in samples of populations and subspecies. For localities see text.

	Vertebrae				Scales in 1.1. series				Anal soft rays					Gill-rakers (lower)							
	26	27	28	29	27	28	29	30	7	8	9	10	11	12	13	14	15	16	17	18	19
S. m. heudelotii																					
'St Louis		6	15	1		3	13	2			14	6						8	9	1	
Lag. Gandjole			10		1		2	3			7						2	2	2	1	
La Sine		2	3			1	4				5						1	3	1		
Lake Retba			3	4		1	3	3			4	3						2	1	3	1
S. m. paludinosus	1	4			1	11	8			5	9	2				2½	6½	7	4		
S. m. leonensis		6	4		4	10	4			1	13	6	1				4	8	7	3	1
S. m. leonensis (Thys)					4	12	9	2	3	21	6					1	4	5	17	1	2
S. m. melanotheron																					
Ivory Coast (Daget & Iltis)	1	10	7				[27–30]														
Ghana and Nigeria	10	27	1		4	13	6			5	19	3			1	7	9	13	10	6	1
Mouri		6								5	1						1	3	1		
S. m. nigripinnis																					
BMNH	1	3	3		2	11	6			17	4			1	2	11	8	1			
Thys, 1964					5	82	17		3	46	3			2	3	24	22	1			
Thys, 1966					2	6				6	2			1	3	1	1	1			
Daget & Stauch, 1968		4	8														[13–15]				
Roman (Rio Muni)										24	10					3	15	9	6		
Roman (*aequatorialis*)										6	4				1	6	3				

Table 6. *Sarotherodon melanotheron.* Frequencies of dorsal fin-ray numbers in samples of populations and subspecies. Lower mean numbers of soft rays and totals by Thys reflect different policies in counting the last ray.

	Dorsal spines				Dorsal soft rays						Dorsal totals					
	XIV	XV	XVI	XVII	9	10	11	12	13	14	24	25	26	27	28	29
S. m. heudelotii																
'St Louis'		11	9				3	17					2	10	8	
Lag. Gadjole		3	4				3	3	1					5	2	
La Sine		2	3				1	4						3	2	
Lake Retba		2	5				1	6					1	1	5	
S. m. paludinosus	2	18					10	10					13	7		
S. m. leonensis		14	11				7	13	4	1			4	9	10	2
S. m. leonensis (Thys)		20	10				20	10					13	14	3	
S. m. melanotheron																
Ivory Coast (Daget & Iltis)		[XV–XVI]					[10–12]									
Ghana and Nigeria	1	22	18	2		7	19	17				2	12	26	2	1
Mouri		5	1			1	4	1					5	1		
S. m. nigripinnis																
BMNH		12	8	2	1	7	11	4				2	11	10		
Thys, 1964	1	33	18		1	28	23				1	14	34	3		
Thys, 1966		4	4			5	3					1	7			
Roman (Rio Muni)		33	17	2		27	24	1								
Roman (*aequatorialis*)		5	5		1	4	5									

Length of head 35·2–40·2% SL. No sexual dimorphism detected. Vertebrae 26–28, mode 27 (Tables 4 & 5). Soft dorsal rays 9–12, mode 10 or 11 (according to different observers). Lower gill-rakers 12–17, mode 15 (Tables 4 & 5). Lower pharyngeal as in *S. m. melanotheron.*

Discussion

The subspecies are not so well defined that one could be sure of the provenance of a specimen in isolation. This, however is characteristic of subspecies. Neither is it possible to trace a cline in the long series of populations represented. Although as might be expected, the mean number of vertebrae is highest in the most northern population, it is not significantly different from that of the most southerly subspecies.

The *pigment pattern* was the feature that impressed Thys in his field studies (pers. comm. and c.f. his definition of '*Tilapia leonensis*'). This, though sometimes characterizing populations, is also very variable within a population.

Elements that can be detected in most populations are the vertical bars, a feature shared with *S. galilaeus.* Unlike the juvenile vertical bars of most species of *Sarotherodon*, they are irregular in outline, depending on which and how many pigmented scales compose them. In some cases only one or a few scales on a flank are pigmented, a pattern which is recognized as a reduction of the fasciated one only because of intermediate conditions. A black bar immediately behind the cleithrum may be present without the others.

Rare in *S. galilaeus* but characteristic of populations of *S. melanotheron* from Sierra Leone to Zaire is the presence of intense black patches on the lower jaw, throat, branchiostegal membrane, lower parts of operculum, pre- and interoperculum that have given the species the name of 'black-chinned tilapia' among aquarists. In the samples here included in *S. m. heudelotii* this is poorly developed although the lower jaw and parts of the branchiostegal membrane may show traces of pigment. In populations in which it is developed it seems to increase with sexual maturity and may involve all the lower half of the head, even in localities where maturity comes at a small size (e.g. at Cape Coast Castle Lagoon; see p. 54). In Chiloango and the Zaire the black may spread to the whole head and even cover the body and fins.

A pigment feature characteristic of mature *S. m. leonensis*, but not observed in the Gulf of Guinea, is the presence of up to four black blotches, sometimes bordered with white like a tilapia-mark, on the basal part of the dorsal fin. Vaguer blotches in the same place have also been noted in the populations near Dakar, and one may ask whether the individuals concerned were too small or immature for valid comparison with those from Sierra Leone.

In contrast to the blurred subspecific distinctions, the species is well characterized by its low numbers of vertebrae, deep preorbital bone, paternal brooding habit and vestigial pair-bonding, as well as, in nature, its strong preference for brackish water.

Sarotherodon melanotheron melanotheron Rüppel

Sarotherodon melanotheron Rüppel, 1852:21 (Goldküste = Ghana); Günther, 1862:273 (from Rüppel); Trewavas, 1973*a*: 23; Sydenham, 1977:984 (Lower Ogun River, Nigeria).

Tilapia (Sarotherodon) melanotheron; Thys van den Audenaerde, 1968*b*:xxxviii; *idem*, 1971:213 (Ivory Coast to Kribi, Cameroun).

Tilapia melanotheron; Barlow & Green, 1968 (behaviour).

Chromis microcephalus Günther, 1862:272 ('West Africa' & 'Ashantee'; partly ex Bleeker).

Melanogenes microcephalus Bleeker, 1863:37, pl. 6, fig. 1. (Ashantee).

Tilapia microcephala; Boulenger, 1899*a*:114; Schreitmüller, 1920:209, fig.

Melanogenes macrocephalus Bleeker *in* Günther, 1862:273; Bleeker, 1863:36; pl. 6, fig. 2 (Ashantee).

Chromis macrocephalus; Günther (ex Bleeker), 1862:273.

Tilapia macrocephala; Boulenger, 1899*a*:115; *idem*,, 1915:176, fig. 113; Pellegrin, 1904:316 (Ivory Coast); *idem*, 1920*a*:121 (Ivory Coast); 1923:284; Arnold & Ahl, 1936:516; Aronson, 1945:403; *idem*, 1948:33; *idem*, 1949:133; *idem*, 1951:1; *idem*, 1956:146 (aquarium stock, photos); *idem*, 1957:278, 285, 289, 290–1, 294–5 (reproductive behaviour); *idem*, 1958 (function of mouth-brooding); Aronson & Holz-Tucker, 1947:572; 1949:88 (hormones & reproduction); Jakowska, 1950 (spermatogenesis); Shaw, 1950:62; 1951, 449 (extra-oral embryonic survival); Shaw & Aronson, 1954:379 ff. (parental care, development); Shaw, 1956:152 (development, figs.); Boeseman, 1963:28, pl. 5, fig. 4 (syntypes, restriction); Dambach, 1963 (development & behaviour of young); Kraft & Peters, 1963 (egg & oogenesis); Fujita *et al.* 1966 (temperature tolerance); Burchard *in* Reed *et al.*, 1967:142, fig. 168.

Tilapia heudelotii (part, not of Duméril); Pellegrin, 1904:314 (Kotonou); Boulenger, 1915:175 (specimens 22, 39, 40 only); Irvine & Trewavas *in* Irvine, 1947:275, fig. 181 (Gold Coast = Ghana); Daget, 1951:1149 (Ivory Coast); Sterba, 1962:741 (fig. 936?); Gras, 1961:583 (Dahomey); Boeseman, 1963:29, pl. 5, fig. 3 (syntype of *C. microcephalus* and Nigerian specimens); Thys van den Audenaerde, 1966:30; Heinrich, 1967*b* (courting & spawning); Daget & Durand, 1968 (Ivory Coast).

Tilapia heudelotii macrocephala; Bauchot & Blanc, 1961:98 (Ghana); Daget, 1962*a*:157; Daget & Iltis, 1965:268, fig. 169 (Ivory Coast); Heinrich, 1967*a*:686 ff. (aquarium stock, reproductive behaviour, hybrids); Bauer, 1968:22 ff. (contact behaviour, hybrids); Sterba, 1962:742, fig.; *idem*, 1970:577, pl. 246 (aquarium).

Notes on the synonyms

Sarotherodon melanotheron was proposed by Rüppell as a new binomen, the proposal being accompanied by a definition of the genus, which validates both names according to the International Code. The binomen was used by Günther (1862), who recognized the similarity to his

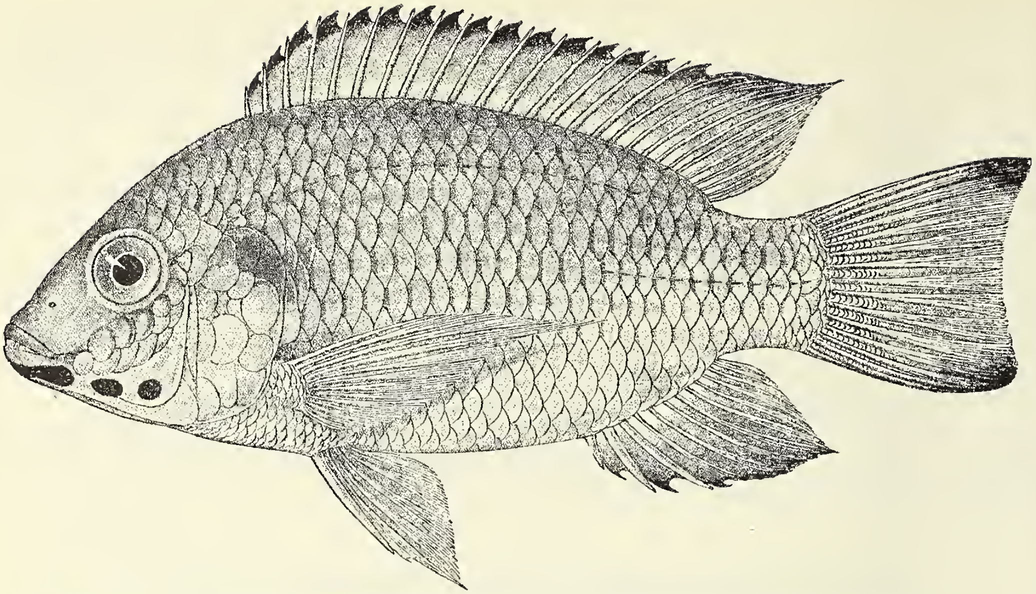

Fig. 17 *Sarotherodon m. melanotheron,* 122 mm SL, Lagos. From Boulenger, 1915, fig. 113.

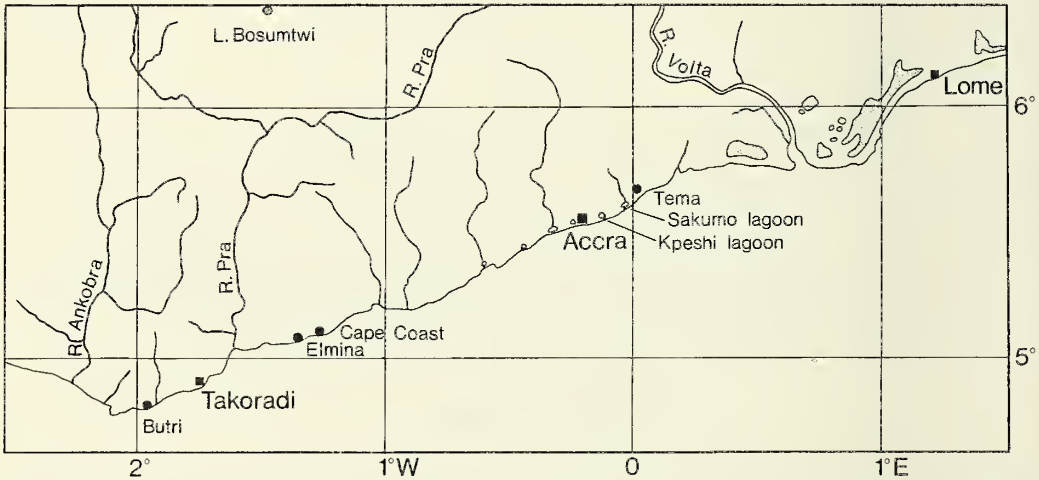

Fig. 18 Part of the coast of Ghana to show probable type locality (Butri) of *Melanogenes macrocephala,* and *M. microcephala* of Bleeker, and other collecting localities.

Chromis microcephalus. Boulenger, in his revisions of 1899 and 1915, placed *S. melanotheron* in the synonymy of the later *T. macrocephala* (Bleeker), dismissing it wrongly as a *nomen nudum,* and he was joined in this action by Pellegrin (1904). Regan, however, used *Sarotherodon* for a subgenus (1921).

I follow *Thys* (1968*b*) in adhering to the law of priority, and use *melanotheron* for the superspecies and for the subspecies found from Ivory Coast to Cameroun. The syntypes are still preserved in the Senckenberg Museum.

Boeseman (1963) pointed out that although the name *S. melanotheron* was validly proposed, Rüppell's description was too brief for certain identification. On examining the types in the

Senckenberg Museum, Thys was able to confirm that this species is identical with *Chromis microcephalus* and according to his views (and mine) also with *Melanogenes macrocephalus.* I have also seen one of the syntypes and agree with Thys.

The question as to whether or not Bleeker's specimen of *C. microcephalus* (a female), and the two syntypes of *M. macrocephalus* (males) represent distinct species or subspecies has been discussed by Boeseman (1963). Both were collected in Ghana ('Côte d'Or') by H. S. Pel. Apart from their sex, the only significant difference between them is in the relative size of the head, that of the syntypes of *M. macrocephalus* being respectively 41·5 and 38·6% SL (40·8 and 40% according to Boeseman), that of Bleeker's specimen of *M. microcephalus* 37·3% (33·3%, Dr Boeseman). Dr Boeseman considered some evidence, in a personal communication to him from me, that in this species the biggest heads were found in males, but did not consider it sufficent to warrant assigning all Bleeker's three specimens to the same subspecies. He regarded Bleeker's specimen of *M. microcephalus*, and the two BMNH specimens described with it by Günther, as at least subspecifically distinct from *M. macrocephalus* under the earlier name *heudelotii*, whose holotype came from Senegal. More recently I have obtained further evidence that, especially in Ghana, the relative mean size of the head is greater in males than in females, although in one population females too may have bigger than average heads (Table 7).

The exact locality of Pel's collections is unknown. A biographical memoir of this collector was published by Holthuis (1968), from which we learn that Pel went to the Gold Coast (Ghana) in 1840 as Kommandant of the trading-post or fort at Elmina. In 1843 he was promoted Resident and stationed at Accra. During his stay in Ghana, from 1840 to 1850, he spent periods in his official capacity at Accra, Elmina and Butri. The zoological collections made at Butri and the neighbouring Dabo Krom were his most important, according to Holthuis. The River Butri enters the sea amid mangroves and Pel found there marine and brackish-water fishes. This may have been the type locality of one or both of *S. macrocephalus* and *microcephalus*, though even if both were collected near Butri they may have come from separate lagoons.

During a short visit to Ghana in 1970 I visited Cape Coast Castle with Mr Walter Pople of the University of Ghana and examined cast-net catches of fishermen in a lagoon close to the castle. At this time the movements of the marine currents had enclosed a small lagoon separated from the sea by a steep mound of loose gravel. The fishes were abundant and all much smaller than the types in Leiden, though sexually mature. The head measured 35·1–38·0% SL in nine females, 38·2–42·7% in nine males (Table 7).

At Kpeshi, a closed lagoon a few km east of Accra, a sample of four males likewise showed a higher, though overlapping range for the length of head compared with that of thirteen females (Table 7).

Later I received for identification from Mr K. N. Eyeson six specimens from Mouri, a lagoon about four miles from Cape Coast Castle. These comprised three females and three males of 107 to 122 mm SL, the head in the females being 39 to 39·8% SL, in the males 38·5 to 41%. Thus, in this sample, the ratio in males corresponds to that of the same sex in other localities, that of the females is higher. In pigmentation and meristic numbers these fishes resemble typical populations of the Gulf of Guinea. Whether, as seems likely, the big heads are a growth phenomenon dependent on the ecological conditions of Mouri Lagoon or the result of a genetic factor developed during isolation, is unknown.

The types of *macrocephalus* and *microcephalus* thus fall into line with the sex-linked differences in head-length within populations in Ghana. If alternatively the syntypes of *M. macrocephalus* are male representatives of a population like that of Mouri Lagoon, in which both sexes may have big heads, I would still not consider this alone to amount to a subspecific distinction.

I have therefore (as has Thys) regarded both of Bleeker's and Günther's names as synonyms of *S. m. melanotheron.* (*S. m. paludinosus*, p. 64, is another big-headed population, but has other peculiarities that have induced me to name it.)

Boeseman (1963), who designated a lectotype for *macrocephalus*, refrained from doing so for *microcephalus*. This name was first published by Günther, and only partly ex Bleeker and partly on two specimens in the BMNH with the vague locality label 'West Africa'. Examination of the latter does not provide enough information to fix their subspecific identity, any pigment that they may once have possessed having now faded.

Irvine & Trewavas (*in* Irvine, 1947) followed Boulenger in ignoring the name *melanotheron* and used the next senior name of the superspecies, *Tilapia heudelotii*, to include all the populations from Senegal to Zaire. Other authors (Daget, 1962*a*; Daget & Iltis, 1965; Heinrich, 1967; Bauer, 1968) have used the trinomen *T. heudelotii macrocephala* for the Gulf of Guinea population and for aquarium stock probably derived from it. Bauer's arguments for this usage would have been correct but for the validity of *S. melanotheron*, announced by Thys in the same year.

TYPES. Syntypes of *S. melanotheron*: Senckenberg Museum nos 1316, 5411, 5412, respectively 90, 84·5 and 81 mm SL.

Syntypes of *C. microcephalus*: RMNH 4831, 118 mm SL, here designated lectotype, and BMNH 1855.9.19.281, 2 specimens of 139·5 and 99·5 mm SL respectively.

Syntypes of *M. macrocephalus*: RMNH 4916 b, 136 mm SL (lectotype, Boeseman, 1963) and 4916 a, 132 mm SL, both males from 'Côte d'Or'.

Distinguishing characters

See pp. 41–42. Thys (1966) expressed doubt as to the value of the gill-raker count as a distinguishing character, noting that his lower numbers for *S. m. nigripinnis* came from small specimens. But I find no correlation between size and number of gill-rakers at least from 50 mm SL upwards, and Tables 4 & 5 support the validity of this distinction.

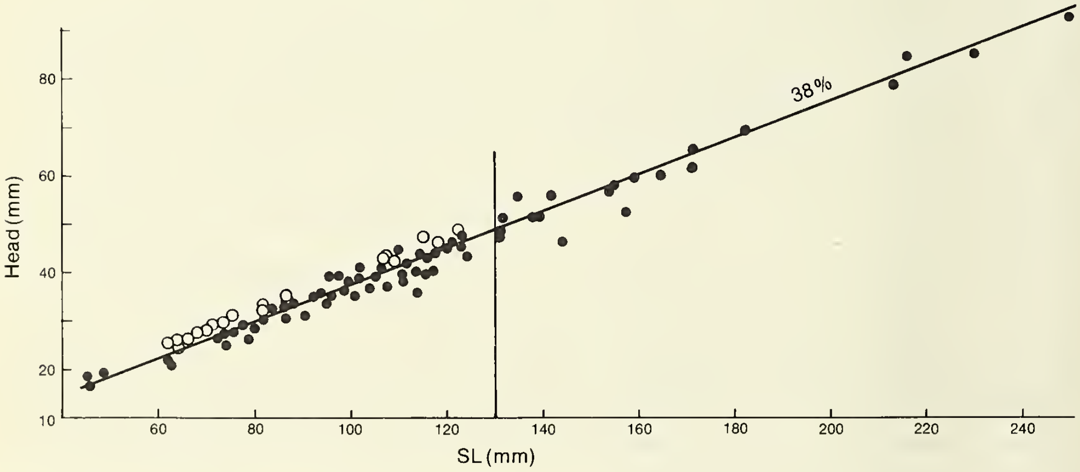

Fig. 19 *Sarotherodon melanotheron*. Relation between length of head and SL. The oblique line is at 38%. In juveniles the ratio may be above or below this value regardless of sex. From SL 130 mm upwards 20 specimens have been measured. Of these only 5, all males, including the syntypes of *Melanogenes macrocephalus*, have a ratio above 38%; those with 38% or less comprise 7 males, 7 females and 1 unsexed. The open circles represent the sample from the pools at Sangalkam, near Dakar (*S. m. paludinosus*, 62–86 mm SL) and that from Mouri Lagoon, Ghana (107–122 mm SL). For small specimens the head in these is not unusually big, but it is exceptional that it is above 38% in all specimens of both sexes in both samples. The sample from Cape Coast Lagoon (see text & Table 7) is not plotted on the graph. If it were, its males would be above the 38% line with the Sangalkam fishes and all its females below the line.

Table 7. *Sarotherodon m. melanotheron*, size of head in males and females of samples from localities in Ghana and Nigeria.

					Mean	
Locality etc.	Sex	N	SL(mm)	Head % SL	♀	♂
Mouri	♀	3	107·5–122·0	39·0–39·8	39·6	
	♂	3	107·0–115·0	38·5–41·0		39·9
Cape Coast	♀	9	50·5–88·0	35·1–38·0	36·5	
	♂	9	50·5–77·0	38·2–42·7		39·7
Kpeshi	♀	13	66·5–115·5	34·9–37·8	36·37	
	♂	4	66–108	37·1–40·1		38·66
Danfa	♀	1	83·5	38·0	38·0	
	♂	2	91, 95	37·8, 39·0		38·4
C. microcephalus lectotype	♀	1	118	37·0	37·0	
C. macrocephalus syntypes	♂	2	132, 135	38·6, 41·5		40·05
S. melanotheron syntype	♂	1	84·2	38·0		38·0
Ancobra River	♀	4	100–111	35·0–38·0	36·35	
Weija	♀	1	158	36·1	36·1	
	♂	1	159	38·3		38·3
Lagos	♀	11	80·6–121·5	35·5–39·7	37·1	
	♂	18	84·0–164·5	35·8–42·1		38·2

All localities. Mean of 43 females: 36·84. Mean of 41 males: 38·83.

Description

Based on 26 specimens of SL 84–220 mm, including one of the syntypes of *S. melanotheron*, the syntypes of *Melanogenes macrocephalus* and *Chromis microcephalus* and 20 other specimens from coastal lagoons and estuaries of Ghana and Nigeria, with meristic characters also from additional specimens.

For proportions and meristic numbers see Table 4–6 and 8.

Because of the variation in head length I have calculated the depth of the preorbital and the interorbital width also as % SL. They are respectively 9–12 and 12–14·5.

Teeth in 3–6 series, 46–100 in outer row of upper jaw; outermost bicuspid, with slender shafts and spoon-shaped crowns; inner tricuspid.

Gill-rakers (2–3)+(0–2)+(13–19), mode on lower part of arch 16 (Table 4). Microbranchiospines present on outer sides of arches 2–4 in fishes over 30 mm SL.

Lower pharyngeal bone long and narrow, its length 31·5–36·0% length of head, width 26·0–30·5; blade 1·2–2·2 times the median length of the toothed area, increasing in relative length with the size of the fish; teeth slender, crowded posteriorly, sparse anteriorly (Figs 20 & 21).

Scales in 2 series on cheek, rarely with 2 or 3 additional scales; 3 or 3½ between origin of dorsal and lateral line, 3–4 (5) between bases of pectoral and pelvic fins; not very small on chest and belly.

Dorsal XV 10–12, XVI 10–12 or XVII 11–12; among 45 specimens the commonest combinations are XV 12 (f. 13) and XVI 11 (f. 17) (Tables 4 & 6). Pelvic produced to a short, white filament.

Genital papilla small, subconical or leaf-shaped in the male, a short funnel with scalloped edge in the mature female.

Table 8. *Sarotherodon melanotheron.* Proportions in samples of *S. m. melanotheron*, sorted according to size-ranges, and in *S. m. nigripinnis.* The size-groups are chosen, as far as the available material permits, for ease of comparison with the other subspecies (Tables 11 & 12.).

	S. m. melanotheron			*S. m. nigripinnis*
N	8	17	1	12
SL(mm)	84–110	114·5–171·5	216	72–123
Proportions as % SL				
Depth	38·0–48·6	37·0–47·5	45·0	41·3–44·3
L. head	37·0–40·5	36·0–41·5	39·0	35·2–40·2
L. pect. fin	40.0–50·0	39·0–47·7	42·0	37·0–44·7
L. caud. ped.	11.0–12·4	10·0–13·7	10·6	11·6–14·4
D. caud. ped.	15·0–18·0	15·0–18·0	17·5	16·3–18·0
Caud. ped.l/d	0·6–0·85	0·6–0·85	0·6	0·7–0·9
Proportions as % l. head				
L. snout	37·5–38·7	35·0–43·3	38·0	32·0–38·5
Eye	21·0–27·5	19·0–24·0	18·0	21·5–25·9
D. preorb.	24·2–27·1	24·6–31·0	31·0	22·2–27·0
Interorb.	30·5–37·0	34·6–40·3	37·2	29·5–37·0
Lower jaw	29·6–34·0	28·8–33·3	31·5	29·5–32·8

COLORATION. (1) Observed at Lagos. General colour a pale opaline blue, with a darker or golden-yellow spot at the base of each scale; scales of two or three dorsal rows marked with iridescent orange colour. Operculum of mature female transparent, appearing purple from the red gills showing through: cheek, operculum and part of suboperculum of mature male a metallic gold colour. Lower lip pale, often white in mature fishes. Individually variable intense black markings on lower jaw, branchiostegal membrane, lower parts of head, above eye, on nape, on cleithrum from its upper end to below pectoral base, sometimes on upper lip and often one or two small spots on flank. These markings not necessarily symetrical, more intense and extensive in mature individuals, but variable even in these; absent in juveniles. Dorsal and anal fins with vague markings and greenish iridescence; in mature fishes soft dorsal and anal fins often with narrow black margin and tips; corners of caudal often intense black, the rest of the fin translucent, colourless or mauve. Pectoral colourless. Pelvics dusky with white leading edge and short filament.

Tilapia-mark conspicuous in young but vanishing at about 50 mm SL.

In older individuals there is more scattered melanin, giving a soiled appearance to the whole colour-scheme.

(2) In aquaria much variation has been observed in the melanin pattern of the trunk. In a photograph with Shaw's article of 1956 some individuals have the broken vertical bands common in more western populations and others a mid-lateral horizontal series of contiguous blotches. Schreitmüller (1920) records that in his aquarium specimens, probably of this subspecies, vertical bands appeared at higher temperatures, but these may have been the juvenile bars, which are under physiological and emotional control.

The origin of these aquarium specimens is unknown and in most cases they were kept in fresh water. The photo by Marcuse in Sterba (1970, pl. 246) shows typical markings.

Ecology

Food

Williams (1962) reported the stomach-contents in the Lagos area as sand, mud, benthic diatoms

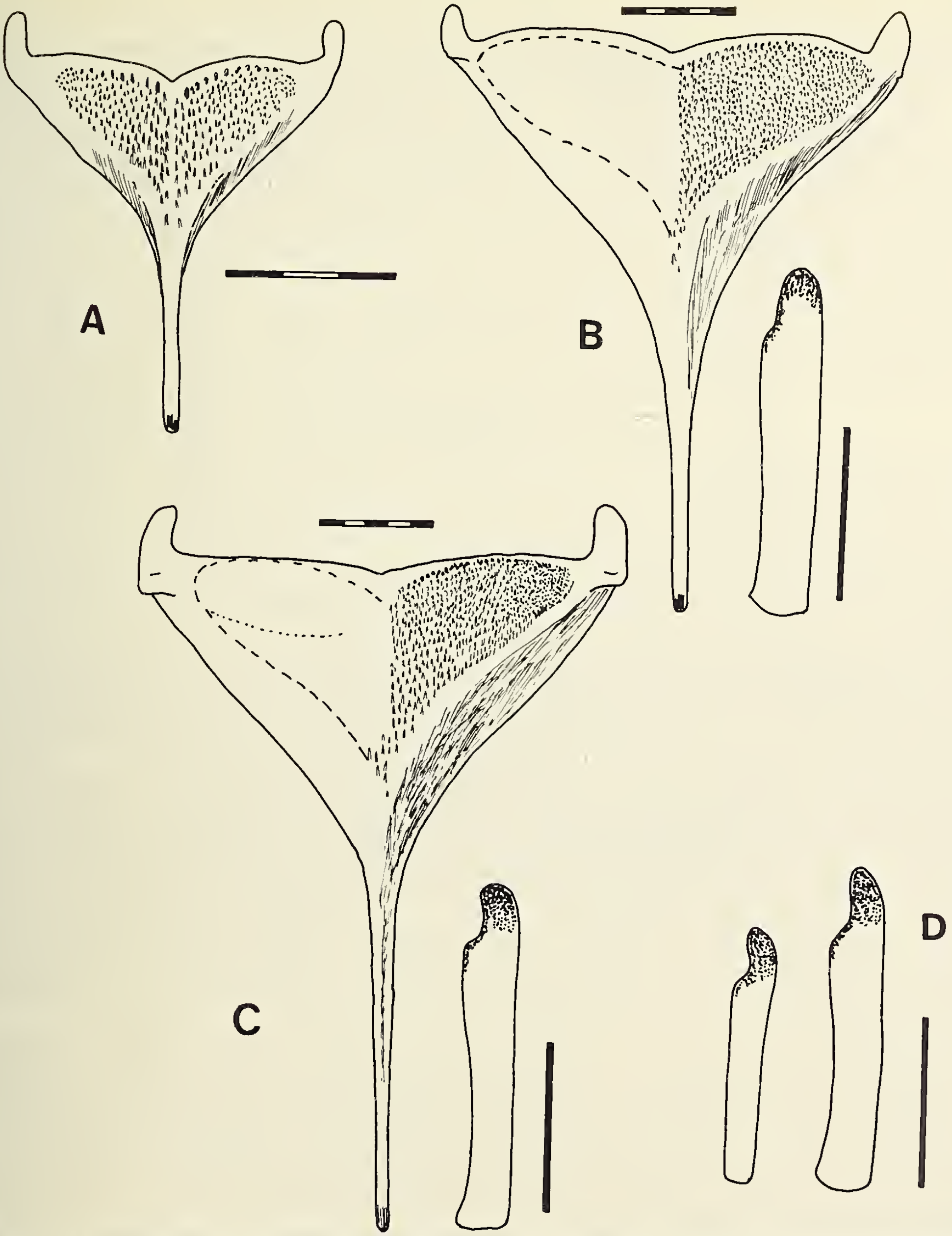

Fig. 20 Pharyngeal bones of *Sarotherodon melanotheron*: A, juvenile of 49 mm SL from St. Louis, Senegal; B, adult of 213 mm SL from St Louis with isolated posterior tooth; C, adult of 220 mm SL from Lekki Lagoon, Nigeria with isolated posterior tooth; D, isolated posterior teeth from, left, fishes of 160 mm SL from Weija, right, 142 mm SL from Maka. Scales are in mm.

and filamentous algae, from which it may be concluded that *S. m. melanotheron* is an aufwuchs and detritus feeder.

In Sakumo Lagoon, 20 km east of Accra, Pauly (1976) found the stomachs of adults to contain the fine fraction of the bottom mud, comprising inorganic granules of 50–100 μ diameter, pennate diatoms and organic detritus. From this it may be inferred that coarser granules are rejected

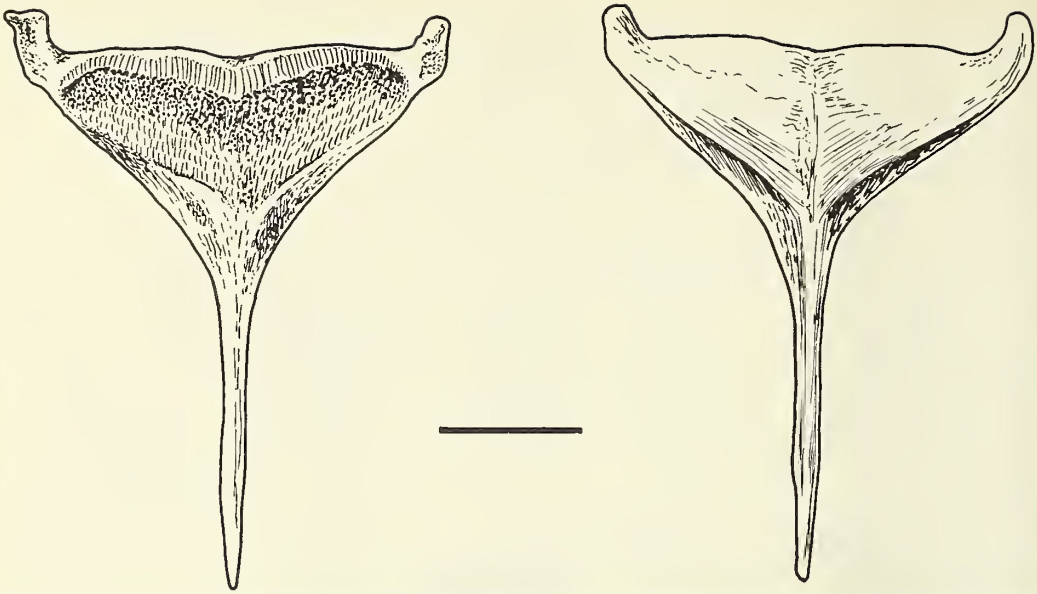

Fig. 21 Pharyngeal bone of *Sarotherodon melanotheron* from Weija, Ghana of 160 mm SL. Scale = 5 mm.

in the mouth and pharynx. Pauly also recorded that feeding in the lagoon is nocturnal, with intermittent daytime feeding. This may be to elude predatory birds, to whom the fishes would be dangerously visible in the clear, shallow waters of this lagoon. (cf. also *S. galilaeus multifasciatus* in Lake Bosumtwi, p. 116).

Captain W. B. Dowson (*in litt.*, 1947) observed fishes of this species near Lagos browsing on the surfaces of submerged plants. When the water surface was completely undisturbed they swam in schools, breaking the surface with their open mouths and making a sucking noise. This phenomenon has been observed in other fishes, sometimes with an expressed doubt as to whether they are feeding or compensating a lack of oxygen in the stagnant water. Near Lagos, although the water surface may be smooth on a windless day there is continual tidal motion and in such shallow waters oxygen cannot be lacking. In such conditions phytoplankton would be more than usually concentrated at the surface, and this too must be added to the probable food sources for *S. melanotheron.*

As with other species, juveniles have been found to be more carnivorous. Pauly (1976) found the main food of fry of 2·5 cm TL in Sakumo Lagoon to be harpacticoid copepods, with subsidiary amounts of phytoplankton, benthic diatoms and miscellaneous zooplankton. At 4 cm TL copepods were only occasionally present and above 4 cm the adult regime was adopted. In this connection it is interesting to note that the large columnar mucus-cells of the pharyngeal pads develop only when the young reach 3·5–4·0 cm (Shaw & Aronson, 1954), after which the mucus-trap mechanism is required for feeding.

Salinity tolerance

In nature this species is confined to brackish lagoons and estuaries, and is abundant in the mangrove zone. A report of its occurrence in Lake Chad has not been confirmed.

Near Accra a pond, Nungwa Pond, in the course of a river, was dammed to make a reservoir. In 1949, while it was still a pond (and probably brackish) specimens of *S. melanotheron* were sent to the BMNH, and in 1960 further specimens were received from ‘Nungwa Reservoir’. But in 1970 it was no longer found there. Its place had been taken by *S. galilaeus* in the now completely fresh water.

Williams (1962) tested the tolerance of the species at Lagos, (*a*) by gradual transfer from fresh water to sea-water at a chloride concentration of 37·5‰, with no mortality; (*b*) by direct transfer from brackish to fresh water on the one hand and salt water on the other. On transferring to a concentration of 30·7‰ the mortality was 50%.

This demonstrates a very wide tolerance in circumstances that might occur naturally, but it is wider than the range at which the fish 'chooses' to live. Lagos Lagoon is always brackish at its seaward end, but in the wet season the flooded rivers extend the freshwater zone seawards. Williams netted samples at different seasons at six stations from Tarkwe on the sea to Isheri, about 11 km upstream from the mouth of the Ogun River. At Tarkwe and Isheri the catches included no *S. melanotheron* at any season. At the two intermediate stations, Onikan and Ikoyi, this species was abundant except in August and September, when the water was at its lowest salinity and catches were smaller. At Ikoyi they were also small in May, a dry month. From Ikorodu, 11 km up the lagoon from Lagos, near the mouth of the Ogun, there is movement down to the more saline localities in the flood season and a reverse migration in January, February and March, when the lower parts of the lagoon become more saline.

The town of Lagos lies at the brackish to sea-water end of the lagoon. Mangrove grows in suitable places and extends some miles along the lagoon. To avoid standing water in the town, a network of open 'antimalarial drains' was constructed and in these the characteristic fish species were (in 1947) *Periophthalmus papilio* and other gobioids, *Aplocheilichthys spilauchena* (Bleeker), *Hemichromis fasciatus* Peters, *Tilapia guineensis* (Bleeker), and *S. melanotheron*; these controlled both weeds and insect larvae. During a journey along Lagos Lagoon eastwards the species that are no longer found when mangrove gives way to grass are *P. papilio*, *A. spilauchena* and *S. melanotheron*. The lagoon is connected by a narrow strait with Lekki Lagoon, where the water was (in 1947) quite fresh. *S. melanotheron* is there replaced by *S. galilaeus* and there is a typical freshwater fauna, including mormyrids. Here we caught a single specimen of *S. melanotheron*, the largest in our records, a male with reduced testes.

The presence of this large individual among freshwater species is reminiscent of the migrations of adult tunny and other marine fishes in the non-reproductive phase to northern Atlantic waters far from suitable breeding grounds, and indeed of the migration of birds. It shows too how the populations of brackish lagoons may communicate even through fresh waters, for movement from Lekki Lagoon along the waterways parallel to the coast in either direction would bring the wanderer back into brackish water.

Experimental work by Shaw & Aronson (1954) showed that *S. melanotheron* (as '*T. macrocephala*') can live, breed and produce viable offspring in freshwater aquaria, as long as the embryos are allowed to develop normally in the parental mouth. When the developing eggs were removed from the mouth, however, it was only in sea-water dilutions of 20–80% (optimum 40%) that a good survival rate was obtained. Brestowsky (1968) succeeded in rearing embryos of this species in fresh water by providing sufficient water movement, but it remains significant that the less adequate methods of Shaw & Aronson were more successful in saline than in fresh water. It seems questionable if a susceptibility that can rarely be tested in nature, where the embryos normally develop in the mouth, can control the distribution of the species. But Aronson (1949) found the survival of eggs in the mouth in his freshwater aquaria so far from 100% that he devoted some space to telling how the parents deal with decaying eggs. Possibly even for mouth-protected embryos there is an optimum salinity.

Temperature tolerence

The air temperature in the Gulf of Guinea is fairly uniform and high—22–32°C. Schreitmüller recorded for this species (probably this subspecies) in aquaria that water temperatures of 17–19°C were tolerated, but that no breeding occurred below 20–23°. Bauer (1968) found 27°C a satisfactory temperature for his experimental animals.

Breeding

Information on reproduction, breeding behaviour and development in this species is unusually complete, thanks to the researches of Schreitmüller (1920), Asch (1939), Aronson (1945, 1949, 1951, 1957), Jakowska (1950), Aronson & Holz-Tucker (1950), Shaw & Aronson (1954), Peters (1959, 1963*a* & *b*, 1965*a*), Dambach (1963), Kraft & Peters (1963), Fishelson (1966), Heinrich (1967*a* & *b*), Bauer (1968), Barlow & Green (1968, 1969, 1970), Pauly (1976) and Peters & Berns (1978). Reference should be made to these for quantitive accounts of the behaviour. For the comparative significance see also p. 13. The following is a qualitative summary of the results, supplemented by a few field observations.

Spawning occurs throughout the year, but with diminished frequency in periods of heavy rain. Aronson (1957) attributes this to reduced illumination brought about by cloudy skies and silt-laden water, but reduced salinity at such times is a factor worth consideration.

The conspicuous black patches on the lower parts of the head, on the nape and pectoral girdle as well as on the vertical fins develop in both sexes as they reach maturity. Barlow & Green showed that a given fish can control their intensity and extent to some degree, though not their position, and that they tend to be darker in the smaller of a mated pair regardless of sex. Schreitmüller (1920) also observed that they were more intense in breeding fishes.

The sexes are distinguished externally by the genital papilla and by the metallic gold colour of the operculum in the male (see p. 50).

The male is normally the brooding parent, a fact already recognized in 1920 by Schreitmüller, who described the breeding of this species under the name *T. microcephala**. In the antimalarial channels at Lagos immature fishes, mature males and females and brooding males were caught in the same cast-net. The channels were about 1·6 m wide, the depth of the water fluctuated with the tides and it is possible that the sexes are less segregated here than they would be in a more spacious environment. Pauly (1976) does not report any segregation in Sakumo Lagoon, however. As far as could be judged from several samples of 25 to 160 individuals examined by me at Lagos the sex-ratio is approximately 1 : 1, a result also obtained by Pauly (1976).

Size of maturity. From the antimalarial drains at Lagos the smallest ripe female measured by me was 69 mm SL, the smallest brooding male 78 mm. During a visit to Cape Coast Lagoon, Ghana, in 1970 I preserved 31 individuals (17 male, 13 female, one immature unsexed) from a cast-net catch. They were all small, 51–88 mm SL; most had developing or mature gonads, and all except three of the smallest had extensive patches of intense black on the lower parts of the head and above the pectoral and white lower lip, features associated with sexual maturity. Seven of those preserved had pouched gular regions and these were all males, one of them with testes thick-walled and flabby, apparently spent, but none was carrying eggs in the pouch. They had probably been brooding and had abandoned the brood in the net. Of the ten unpouched males only two were over 60 mm in SL (67 and 68 mm). Of the thirteen females none had a pouched throat. Ovarian eggs varied from 0·5 mm diameter at 52 mm SL to 2·5 mm at 88 mm SL. The latter were very loosely attached to the ovarian wall. The smallest female recorded as 'ripe' was only 53·5 mm in SL. This was a very small lagoon.

In aquaria breeding may occur at a still smaller size. Shaw & Aronson (1954, pl. 35, fig. 1) published a photograph of a brooding male, which, if the caption is correct, measured only 35 mm SL.

Barlow & Green (1968) stated that where there is a marked discrepancy in size most of the courting is done by the smaller partner. But they later (1969) concluded that some of the supposed courting movements were better interpreted as appeasement gestures, and would naturally be exhibited more by the smaller partner. Other detailed reports of pairing (Shaw & Aronson, 1954; Heinrich, 1967*a*) record that the initiative in courtship, pit digging and mating activities

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*As pointed out to me by Peters (pers. commn) some doubt surrounds the specific identity of Schreitmüller's fishes and of the sex of the brooder.

is taken by the female (Barlow & Green suggest that the experimenters may have placed a smaller female with a bigger male, following the analogy of many other cichlids; or they may have done so less deliberately because in a given environment females mature at a smaller size than males). Eventually a male is stimulated to react in a mainly passive manner and a pair-bond is established. The bond is shown to be progressively firm (Heinrich), though always less so than in the substrate brooders. As it becomes established the male takes an increasing part in defending and digging the pit, which is a simple, shallow saucer. Aronson (1949) stated that the differences between the sexes in courtship behaviour are quantitative only, progressing to equality as the time for the spawning act approaches.

Dowson (unpublished, 1947) observed the mating pits in shallow water close inshore in Lagos Lagoon. They were close together and varied from 10 to 40 cm in diameter. In aquaria (Aronson, 1949 & 1956) a pair may make 1–3 nests of $13\cdot 2 \times 11\cdot 8$ cm with an average depth of $2\cdot 6$ cm.

The spawning act in aquaria occupied only a few minutes. The eggs were shed in a few large batches, each batch fertilized by the male as it was shed, but not taken into the mouth until all were laid. In aquaria a male may behave atypically and delay picking up the eggs or leave them in the pit, a result, as Heinrich believed, of excessive passivity on the part of the male in courtship, or of some other circumstance resulting in weak pair-bonding or its absence; or his mouth may be too small to hold them all. In the latter case the female may pick up the abandoned eggs, usually after a delay of some minutes, and incubate them (Aronson, 1949; Heinrich, 1967*a*:728). Asch (1939) observed an incubating male of this superspecies engage in a spawning act with a second female and add her eggs to the already advanced embryos in his mouth, churning both broods about together. (Asch used the name *T. dolloi* and may have had either *S. m. melanotheron* or *S. m. nigripinnis*). If such behaviour is common it emphasizes the weakness or brevity of the pair-bond and the contrast with the substrate spawners.

At Lagos I examined on one occasion 97 females and 72 males. Eighteen of the males were brooding eggs or embryos, but not a single female was doing so, nor did I find one in examining several other catches. Dissection of these males revealed small testes (cf. Peters, 1971); stomach and intestines were empty except in three, where there was a small quantity of the usual dark green mud, probably residual from the last feed before incubating.

In the search for factors influencing spawning in *S. melanotheron* and the nature of the sexual roles, Aronson & Holz-Tucker (1950) tested female pairs and found that courting resembling that in normal pairs resulted in spawning on the part of one of the pair. As for picking up the eggs, which of course were unfertilized, this was more likely to be done by the non-laying partner than by the layer. Aronson & Holz-Tucker drew from this the lesson that even in a teleost fish sexual behaviour may be influenced by social conditions.

Although such behaviour is unlikely to occur in nature, this and other experimentally induced anomalies show that the sex of the brooding partner is not in itself the most important factor separating the reproductive behaviour of *S. melanotheron* from that of the maternal mouthbrooders that practice arena-spawning. Heinrich has made the point that it is more significant that a pair-bond is formed between the parent fishes, that sexual dimorphism is minimal and that no T-stand is taken by the partners during fertilization.

Aronson (1948:39) reported that the eggs may occasionally be eaten by a parent, especially by the female, but Pauly (1976) found no evidence that this occurs in nature. Although eggs or larvae were found occasionally in the stomachs of males, they never showed any sign of digestion and were probably swallowed in the panic at capture. No eggs or larvae were found by him in the stomachs of females.

The delay in picking up the eggs exposes them to egg-robbing predators. An example of this danger was observed by me at Lagos. A pair were evidently in the early stages of courting, the female passing over a scarcely perceptible mating pit and the male standing by. A more active interest was taken in her by a small crab that repeatedly nudged the female's protruding genital papilla, impatient, no doubt, for a meal of fresh caviare. The pair were disturbed by a fishing operation before spawning could take place.

Table 9. *Sarotherodon melanotheron*, length of egg in aquarium stock. From Fishelson (1966).

Number of clutches examined	Length of egg
1	2·7–3·0
3	3·4–3·6
2	3·5–3·7
3	3·7–3·9
1	4·0–4·1

The eggs are orange coloured and large. Aronson reports a long diameter of 2·0–3·5 mm and a width of 1·5–2·5 mm. Fishelson (1966) gives a length-range of 2·7–4·1 mm, but not all in one female (Table 9). Peters' lengths are 2·0–4·5 mm (1963, fig. 5), given with a warning, that the smallest eggs were from females of a smaller size than would be likely to be mature in nature. Eggs in the mouth of a male examined by me at Lagos measured approximately 3·5×2·5 mm. Other brooding males held embryos of various sizes with reduced yolk.

Peters (1963*b*) found that in this species the number of eggs bore an inverse relation to the average weight of an egg. The number ranged from 200 from a female of body weight 20 g to 860 from one of 140 g; the average weight of the 860 eggs was low (10 mg), and two larger females had fewer (resp. 400 and 480) and heavier (resp. 21 and 20 mg) eggs.

A few, 'doubtless functionless' adhesive threads are present on the egg surface (Kraft & Peters, 1963:473).

The young are released after varying periods in the mouth, approximately fifteen days (Shaw, 1956). The size at release is 9·2–11·5 mm. Developmental stages have been described by Shaw & Aronson (1954), and Bauer devised an apparatus (1968, fig. 1) to keep the eggs in motion and to permit extraoral development.

Rudimentary, functionless and evanescent adhesive organs were described on the head of fourth day embryos by Peters (1965*a* & *b*) and Peters & Berns (1978). They are less regressed than in the maternal mouth-brooders, *Oreochromis niloticus* and *O. mossambicus* and may even exude a little secretion giving a mucous reaction.

When the young are released they have no 'contact reaction' to the parents such as mediates the return to the mouth in case of disturbance or at night in, e.g. *O. niloticus* or *O. esculentus*. Bauer demonstrated that the genetically determined phase of maximal contact reaction in *S. melanotheron* arrives and passes when the embryo is still yolk-laden, and normally resident in the mouth. The extraorally developed embryos made ineffective leaps in the direction of the surrogate parent, beginning not earlier than the ninth day after spawning and ending on the fourteenth day. This shows that the difference in this element of behaviour between *S. melanotheron* and the maternal mouth-brooders is a matter of relative timing rather than a presence or absence phenomenon.

As with other mouth-brooders, the newly released young have a schooling reaction with each other and form a family school for an unknown period (Dambach, 1963). At this stage they act together to flee from a source of potential danger, but this is the result of visual communication and not, as Fryer & Iles (1972:174–5) supposed, of the emission of a fright substance. Fryer & Iles misunderstood a sentence of Noble (1939).

Hybrids

Professor H. M. Peters has artificially fertilized eggs of *S. melanotheron* (aquarium stock) with sperm from *O. niloticus*. F_1 hybrids of both sexes were obtained and twelve of them, 4 males and 8 females of 82–98 mm SL, were deposited in the BMNH, where I examined them.

Table 10. Comparison of meristic data from wild samples of two subspecies of *S. melanotheron*, and samples of *O. niloticus* from Israel, with those from hybrids between the two species.

Vertebrae	26	27	28	29	30	31	32
S. m. melanotheron	10	31	1				
S. m. heudelotii			10	3			
Hybrids				4	8		
O. niloticus (Israel)					7	27	1
Dorsal spines	XIV	XV	XVI	XVII	XVIII		
S. m. melanotheron		23	13				
S. m. heudelotii	2	13	11				
Hybrids			6	6			
O. niloticus (Israel)			6	17	1		
Total dorsal rays	25	26	27	28	29	30	31
S. m. melanotheron	2	19	15				
S. m. heudelotii	1	3	10	10			
Hybrids					11	1	
O. niloticus (Israel)					2	17	5

They resemble *O. niloticus* in the most contrasting proportion, the depth of the preorbital bone, which in *S. melanotheron* of this size measures 22–25·5% length of head, in *O. niloticus* 15·0–19·0, in the hybrids 17·0–20·0. In numbers of scales, vertebrae and dorsal fin-rays they are intermediate (Table 10).

The object of this and other crosses effected at Tübingen and reported by Peters (1965*a* & *b*), Bauer (1968), and Heinrich (1967*a*) was to test the genetic basis of behavioural characters. With *O. niloticus* hybrids were obtained in both directions, and when *O. niloticus* was the male parent Bauer was able to obtain an F_2 generation and to backcross the F_1 with both parents. With *O. mossambicus* ♂ and *S. melanotheron* ♀ the hybrids were all female; attempts at the reverse cross were unsuccessful. With *Tilapia tholloni* hybrids were obtained when the male parent was *S. melanotheron*; the reverse cross resulted in high mortality among the embryos.

This species has not, to my knowledge, been used to produce hybrids for fish culture.

Distribution

Natural distribution Lagoons and estuaries from Ivory Coast to southern Cameroon.

Thys (1966) found it difficult to establish a boundary between this subspecies and *S. m. nigripinnis*. In including a fish of 158 mm SL from Souélaba (3°48′N), he pointed out that in colouring it resembled the populations of the Gulf of Guinea but that its gill-raker number (17) was higher than in any of his more southern specimens. It is in fact modal for *S. m. melanotheron* (see Table 5). Later (1968*a*) Thys included Kribi in southern Cameroon (and by implication also Souélaba) in the range for *S. m. melanotheron*, and until statistical evidence is available for Cameroonian populations this may be accepted as the probable southern limit.

Dispersal by man. This is a favourite aquarium fish and even the stock used for experimental work has been derived from the aquarium trade. Sterba (1962:742 & 1970:577) gives 1907 as the earliest year of its importation to Europe, but there have possibly been other introductions. The aquarium stock on which Aronson's experiments were performed had been in the New York Museum since 1936, and Aronson (1956) believed that it had been imported to America in the 1920s from European dealers. From it stock has been sent back to Europe for similar purposes (Bauer, 1968:23).

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
Senckenberg Mus. 5411 (one of the syntypes)	84·5	'Goldküste' (Ghana)	Mus. Basel
RMNH 4831 (lectotype of *C. microcephalus*)	118	'Cote d'Or' (Ghana)	Pel
BMNH 1855.9.19.281 (paralectotypes of *C. microcephalus*)	139·5, 99·5	'West Africa'	Haslar collection
RMNH 4916 (lectotype & paralectotype of *M. macrocephalus*)	135, 132	'Cote d'Or'	Pel
1911.5.31.53	114	Sekondi Lagoon, Ghana	W. P. Lowe
1930.3.24.27–35 (11 fishes)	68–94	Accra	F. R. Irvine
1932.2.27.15–16 1944.2.9.32–33	38·5–135	Lagoons near Accra	F. R. Irvine
1882.6.22.24–27	100–111	Ancobra River, Ghana	Capts Burton & Cameron
1949.10.20.103–4	84, 90	Nungwa pond, nr Accra	M. Noel-Buxton
1960.1.6.25–27	101–131	Nungwa Reservoir, nr Accra	J. D. Thomas
1973.5.14.1143–1145	83–95	Danfa Pond, nr Accra	S. A. Whyte
1973.5.14.1146–1177	74·5–88	Cape Coast Lagoon, Ghana	E. Trewavas
1973.5.14.1178–1194	66·5–116	Kpeshi Lagoon, nr Accra	E. Trewavas
1972.2.18.17–22	107–122	Mouri Lagoon, c. 4 miles from Cape Coast	K. N. Eyeson
1949.10.20.105–106	152–159	Weija, Dhensu R., Ghana	M. Noel-Buxton
1949.2.23.7	171·5	Tano creeks, Ghana	G. W. Coulter
1944.2.9.28–31	47–51	Lagoons, Prampram, Ghana	F. R. Irvine
1962.7.12.1 (ref. specimen for behaviour studies)	64	Accra	G. P. Baerends
1962.9.18.143	75	Takoradi (Atlantide Sta. 71)	J. Nielsen
1977.3.21.57	71	Sakumo Lagoon, E. of Accra	R. Lubbock
1908.7.22.1–2	57, 71	'West Africa'	E. Reichert
1933.3.10.12	250	'West Africa'	Zool.Soc.Lond.
1933.3.10.2	249	'West Africa'	Zool.Soc. Lond.

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1953.4.28.265	216	Lekki Lagoon, southern Nigeria	E. Trewavas
1953.4.28.257–264	94–165	Onikan ponds, Lagos	E. Trewavas
1908.10.21.1–8 1908.12.9.21–40	48–71	Lagos Lagoon	G. E. Bruce
1908.12.9.11–20	80–118	Lagos Lagoon	G. E. Bruce
1910.10.25.24–43 (82 fishes)	17–40	Lagos	G. E. Bruce
1956.9.6.40	114	Ikoyi, Lagos	Williams
1959.8.18.151–154	99–125	Agboyi, nr Lagos	P. I. R. Maclaren
1959.8.18.191–2	92, 110	Lagos Lagoon	P. I. R. Maclaren
1945.7.9.5–6	70, 79	Lagos Lagoon	W. B. Dowson
1933.10.4.20	55	Niger delta	J. P. Arnold
1913.3.12.11	45	Sapelle, Niger	J. P. Arnold
1968.10.8.2	129	Lagos Lagoon	S. Fagade
1909.3.30.30	73	Cross River (Bende Distr.)	W. A. C. Cockburn
1946.5.1.8–10	70–72	Aquarium specimens	L. Aronson
1969.7.14.1	52·5	Aquarium specimen	R. Setterington

Sarotherodon melanotheron heudelotii (Duméril)

Tilapia heudelotii Duméril, 1859:254 (Senegal); Günther, 1862:270; Boulenger, 1899*a*:118; Pellegrin, 1904:314 (part, with redescription of types of *T. heudelotii* & *T. rangii*); *idem*, 1908*b*:97, fig. 14 (Senegal & Casamance Rivers); Boulenger, 1915:173 (specimens 1–20 only & fig. 111); Arnold & Ahl, 1936:515 (not the fig.); Daget, 1948:46 (Senegal only); *idem* 1951:1149 (Senegal & Guinée); Sterba, 1962: fig. 938 (?) (aquarium); ? Springer & Finucane, 1963:317 (intro. into Florida); ? Finucane & Rinckey, 1964 (feral in Florida).

Tilapia heudelotii heudelotii; Daget, 1962*a*:156, fig. 49; Daget & Iltis, 1965:270 (Senegal to Guinée); Bauer, 1968:24; Daget, 1969:1115 (Senegal R.).

Tilapia (Sarotherodon) heudelotii; Thys van den Audenaerde, 1968*b*:xxxvii; *idem*, 1971:213.

Tilapia rangii Duméril, 1859:255 (Gorée); Boulenger, 1899*a*:126.

Tilapia multifasciata (*non* Günther); Pellegrin, 1941:189 (Bay of Bolama).

Tilapia multifasciata macrostoma Pellegrin, 1941:189 (B. of Bolama).

TYPES. Holotype: 96+22 mm, from Senegal, coll. Heudelot MNHN 9371.

Holotype of *T. rangii*: 90+20 mm, from 'Gorée', coll. Rang. MNHN 9374.

Holotype of *T. multifasciata macrostoma*: 185+50 mm, from Bulama (=Boulam or Bolama), an island-studded estuary, Guinea Bissau, collected on the *Sylvana* expedition in 1913 (st. 88). MNHN 1941.80.

Distinguishing characters

See p. 42 and Tables 4–6 & 11.

Description

Based on the holotype and nineteen specimens from near St Louis, Senegal, and from La Sine. Some smaller fishes are used for meristic characters. A sample from Lake Retba, near Dakar, agrees with these in proportions, and its meristic numbers are listed separately in Tables 5 and 6, and are included in Table 4.

Table 11. *Sarotherodon melanotheron.* Proportions in samples of *S. m. heudelotii* and two samples from Hann, near Dakar, collected at different times, one having a big head and so resembling *S. m. paludinosus*, the other resembling *S. m. heudelotii* in this feature.

	St Louis & La Sine		L. Retba	Hann	
N	3	11+5	7	3	2
SL(mm)	154–230	72·5–104·0	101·5–116·0	89–127	73, 95·6
Proportions as % SL					
Depth	46–49	41–50	39–43	41–43	—
L. head	36·3–37·0	33·5–37·7	34–37	35–36	40, 40·8
L. pect. fin	41–46	33·5–43·0	34·5–38	37–41	39, 39
L. caud. ped.	10·0–12·5	10–14	11·6–15	12·0–12·5	—
D. caud. ped.	15·7–18·2	15·0–16·8	14–15	15·5–16·5	—
Caud.ped.l/d	0·5–0·8	0·56–0·97	0·85–1·05	0·7–0·8	—
Proportions as % l. head					
L. snout	38·5–40·0	32·2–38·0	37–39	35–36	—
Eye	18·5–21·5	23·0–27·5	20·5–23	22–25	27·6, 23·9
D. preorb.	28·0–32·5	22·6–25·5	25–28	22·0–26·5	23·9, 26·3
Interorb.	35–37	27·7–34·0	28–31	32·5–38·0	29·7, 30
Lower jaw	27–30	27·5–34(36)	28·5–34·5	29–31	31, 28

The main features are those of the species, listed on p. 41. See p. 42, and Tables 4 to 6 and Fig. 20A & B.

The strong positive allometry of the preorbital bone is plain from Table 11. In the biggest available fish (230 mm SL; Fig. 22) it reaches the unique ratio of 32·5% length of head (12% SL). In smaller fishes the bone is equal to that in other subspecies at comparable sizes.

Scales on cheek in 2–3 rows; in the samples from 'St. Louis' 2 rows with occasionally 1–3 additional scales; in Lakes Gandjole and Retba usually three rows. Scales from origin of dorsal to lateral line 3, 3½ or 4, usually 3 or 3½. For lateral line see Table 5.

Of the 27–29 vertebrae, 12–14, usually 13, are caudal.

COLORATION. The collection from St Louis, registered in BMNH in 1900, includes young with traces of the juvenile vertical bars, adults with no markings except a small spot above the pectorals (one of these was the model for Fig. 22), and one of 154 mm SL with traces of the irregular vertical bars on the right flank (possibly faded on the left).

From the lagoon of Gandjole, fishes of 90–105 mm SL have the irregular vertical bars well represented, including a dense streak partly on the cleithrum. The anterior bars do not always reach the dorsum, one or two posterior are on the dorsal part of the caudal peduncle. There are no dark patches on the lower part of the head. Five of this sample were females; one gonad examined was 'starting'.

A photograph by Thys of a freshly caught fish of about 180 mm SL from Marsassoum, Casamance River, shows no black markings on the flanks or head. The general colour is pale nacreous blue, back a little darker, lower parts of head and belly white, nape, top of head and snout purple; fins transparent mauve, shading to pinkish on the dorsal lappets and edge of soft fin; lower lip white; a grey bar across iris, whose pupillary rim is gold.

Six fishes of 101–116 mm SL from Lake Retba were also females with active gonads (eggs up to 3 mm long). The lower lip (as in most sexually mature fishes of the species) was white, the lower jaw variably pigmented, and a little dark pigment on operculum and cheek. A dark bar on the cleithrum and 2–4 flank bars, the latter represented each by a few dark scales. A little dark pigment on the caudal; basal part of dorsal fin with variable dark blotches, but these with vaguer outlines than the blotches in *S. m. leonensis*.

These observations suggest that both the size of maturity and the pigmentation may be influenced by the environment.

Pellegrin described as the distinctive colour-features of '*Tilpia multifasciata macrostoma*' a submarginal dark bar on the caudal fin. This mark is still on the type and although it is present on both sides it has such a regular outline that it appears artificial, as though a band had lain across the fin preventing it from fading. This might easily have happened between 1913, when the fish was collected, and 1941, when Pellegrin's description was published, especially when we remember that the Paris collections were at this time kept on open shelves to be viewed. Mme Bauchot and Dr Daget both agree that the bar appears to be artificial. The only other pigmentation of this fish is a smudge on the lower jaw and one dark scale in the middle of the left flank.

Ecology

Salinity tolerance

The description of the localities of capture (p. 62) illustrates the essentially brackish water preference of this, as of other, subspecies. It has been reported from the sea (Cadenat, 1946), but in the flood seasons the salinity of the coastal waters is reduced by outflow from the rivers. The long estuary of the Gambia is mentioned on page 63; 32 km above the limit of the mangrove, at McCarthy Island, there is a typical freshwater fauna, and *S. melanotheron* is no longer found. Nor do collections from Kaidi, where the Senegal River is fresh, include this species. In the lower part of the Senegal River six fresh water localities harbour *Oreochromis niloticus*, *O. aureus*, *S. galilaeus*, and *Tilapia zillii*; in two brackish localities *S. melanotheron* and *T. guineensis* occur together.

The representatives of *S. melanotheron* in two freshwater localities near Dakar, Sangalkam and Hann, have certain peculiarities that have led me to describe them under a separate subspecific name (p. 64), but this is not so of samples from the saline Lake Retba, also near Dakar. These latter have neither the big head nor the low meristic numbers that characterize the freshwater populations and I have included them with *S. m. heudelotii*.

The holotype of *Tilapia multifasciata macrostoma* together with some specimens that Pellegrin included in '*T. multifasciata*' are examples of *S. melanotheron* (see under 'Coloration', above). They were collected in the Bay of Bulama, into which the rivers Corubal and Geba discharge.

Temperature tolerance

No data are available for populations in their natural environment. Springer & Finucane (1963) report of stock (possibly of this subspecies) that had become feral in Florida. It showed considerable resistance to cold, part of the population even surviving an exceptional cold period when the water-temperature fell to about 10°C.

Breeding

The only record of breeding is that of Cadenat (1946 & 1950) who caught a brooding male in the sea off Senegal. No measurement of fully ripe eggs is available, but ovarian eggs reach at least 3 mm in long diameter.

Distribution

NATURAL DISTRIBUTION. In lagoons and estuaries, and occasionally in the sea from Senegal to Guinée. In most of this area the coastal plain is broad and very low, and estuarine conditions extend far inland. Some of the lagoons and 'marigots' are connected with the rivers only in flood times, and in these the salinity fluctuates, sometimes becoming very high by evaporation. *S. m. heudelotii* inhabits such waters together with *Tilapia guineensis.*

Gandjole is a lagoon connected seasonally with the Senegal River and becoming very saline in the dry season.

The populations near Dakar inhabit waters of diverse quality. Lake Retba is a closed, warm, saline lake, described by Thys (letter of 13.1.69) as 'soapy' (a soda lake?). It lies about 40 km NE of Dakar and approximately 800 m from the sea. The seven fishes that I examined were collected by Thys in 1966, all females with active gonads and rather well expressed pigment patterns. Unlike the freshwater populations near Dakar, they do not seem to provide any characters that would exclude them from *S. m. heudelotii.*

La Sine is described by Thys (letter of 13.1.1969) as 'the dead end of a sea-arm, near Kaolack;

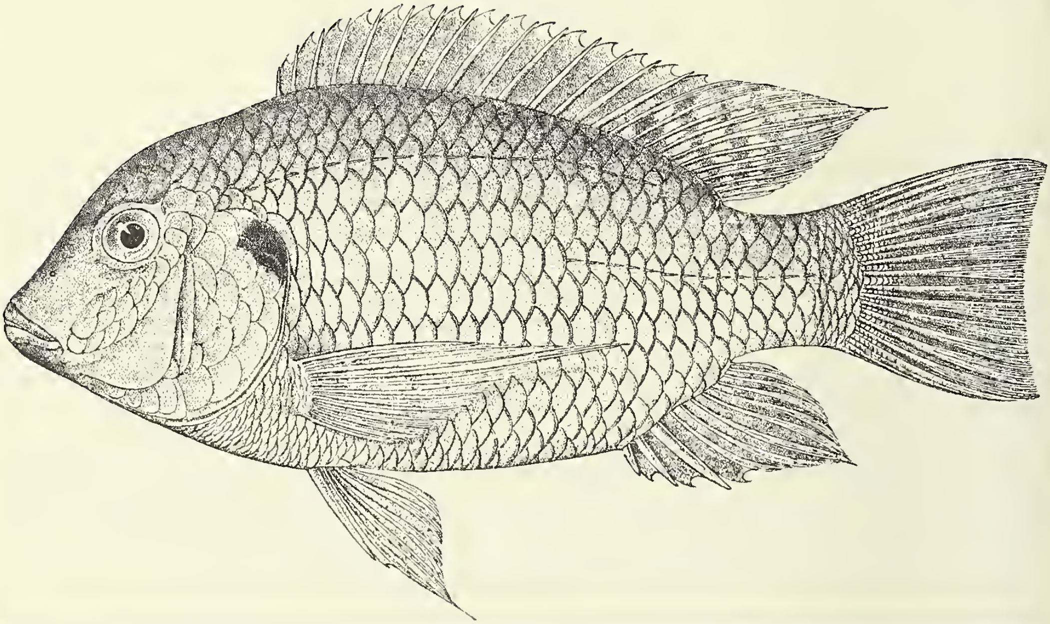


Fig. 22 Above, *Sarotherodon melanotheron heudelotii* from St Louis, Senegal, 230 mm S:L. From Boulenger, 1915, fig. 111. Below, *S. m. paludinosus,* holotype, 82 mm SL. (Photograph, BMNH).

water as sea-water or even more concentrated by evaporation'. It is far inland, its marine connection with the Saloum River being an estuary north of the Gambia. The Gambia itself is bordered by mangrove to a point 80 miles (128 km) upstream (Reeve, 1912), and from this point we have three young *S. melanotheron*. The Casamance River (Kasamansa) also has a long estuary and Thys has collected *S. m. heudelotii* from near Marsassoum.

I can find no reason for excluding the type of '*Tilapia multifasciata macrostoma*' from *S. m. heudelotii*. It was collected in the Bay of Bulama, Guinea Bissau, into which the rivers Corubal and Geba discharge. I have seen no specimens from the coast of Guinée, and farther south we have other subspecies.

DISPERSAL BY MAN. No records of the introduction of this subspecies outside its natural distribution, but it is possible that it may have contributed to aquarium stocks, including that which has become feral in Florida (Springer & Finucane, 1963).

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
MNHN 9371 (Holotype of *T. heudelotii*)	96 (100 in 1903)	Senegal	Heudelot
MNHN 9374 (holotype of *T. rangii*)	90	'Gorée'	Rang
MNHN 1941–80 (holotype of *T. multifasciata macrostoma*)	183	Bulama, Guinea Bissau	Comte Jean de Polignac, *Sylvana* Expedition, Feb.–June, 1913
1900.6.28.204–213 1900.6.28.214–223	62–230	St Louis, Senegal	Delhez
1978.3.13.16–31	28–38	St Louis, delta of Senegal R.	D. Dorfman
1978.3.13.32–36	32·5–48	Daouling, nr Senegal R.	D. Dorfman
MRAC 156720–38 (7 specimens)	90–105	Lagune de Gandjole 10 km S St Louis, Senegal	D. F. E. Thys van den Audenaerde, 1966
MRAC 156323–46 (7 specimens)	101·5–117·5	Lake Retba (saline) c. 40 km from Dakar	D. F. E. Thys van den Audenaerde, 1966
1957.2.18.2–4	43–74·5	Gambia R., 80 miles upstream from Bathurst	Midwinter
MRAC 156446.462	82–104, 138	La Sine, Senegal 16°24′W 14°26′N	D. F. E. Thys van den Audenaerde, 1966
Subspecies doubtful, introduced in Florida			
1970.3.19.1–14	30–191	Florida	Finucane & Buntz, State of Florida, Game & Fish Commission

Sarotherodon melanotheron paludinosus subsp. n.

TYPES. Holotype: male, 82+22 mm, from Sangalkam, near Dakar; coll. H. M. Peters. BMNH 1968.5.20.1.

Paratypes: four fishes, 64.5+16 to 75.5+20 mm, with same data as holotype. BMNH 1968.5.20.2–5.

Distinguishing characters

See p. 42; Tables 4–6, 12 & 13; Figs 19, 22 & 23.

Distribution

Pools in a swampy region at Sangalkam, about 25 km east of Dakar, and freshwater holes at Hann, a short distance south of Dakar. These waters were not connected with the sea, at least at the time when the collections were made.

Discussion

Thys (1971) has suggested that the populations near Dakar might take the name *Tilapia rangii* Duméril. Although the type of *T. rangii*, said to have been collected at Gorée, may well have come from the mainland, as Thys suggests, it has neither the pigmentation nor the morphological peculiarities of the fishes of Sangalkam and Hann, and I cannot distinguish it from *Sarotherodon m. heudelotii.* Hence I have proposed a new name for these freshwater populations, whose peculiarities Thys also recognized. Samples from another lake near Dakar, Lake Retba, where the water is saline, are also in my view indistinguishable from *S. m. heudelotii.*

How permanent the special features of these populations may be remains to be seen, but they are now much more distinctive than those of the freshwater population named *Tilapia aequatorialis* by Roman, which both Thys and I have synonymized with *S. m. nigripinnis* (p. 68). In contrast to the big-headed population of Mouri Lagoon (p. 47), the big head is only one of the distinguishing features of *S. m. paludinosus.*

From Hann I have seen very few fishes. The two with big heads (Table 10) were collected by Thys, but three others collected by Professor Peters have smaller heads (34·8–36·2% SL). Other characters in both samples are not conclusive. The lower gill-rakers are 16–18 in both samples, dorsal rays XV 11 or XV 12. The pharyngeal teeth in one with a big head resemble those of the Sangalkam fishes, in one with a small head those of *S. m. heudelotii*, but the latter is a bigger fish (127 mm SL) and comparison is not satisfactory.

None of these fishes has the basal blotches on the dorsal fin developed as typically as in *S. m. leonensis*, although several had active gonads. There is, however, a tilapia-mark in some Sangalkam specimens at a size (up to 82 mm SL) at which I have not seen it in *S. m. melanotheron*, and in some of these there are further dusky markings on the base of the dorsal fin.

Altogether, the definition of these freshwater populations as subspecies is unsatisfactory, and naming them can only call attention to the desirability of studying them ecologically and in bigger samples, and especially of comparing them with each other and with that of the not very distant saline Lake Retba.

At Sangalkam the ovary of a 65 mm SL fish is 'starting' and at 70 mm the testes are at about the same stage.

Fig. 23 Lower pharyngeal bone of *Sarotherodon m. paludinosus,* 82 mm SL. Median length of bone 10·4 mm.

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1968.5.20.1–5 (holotype and paratypes)	64·5–82	Marigot de Sangalkam 25 km E of Dakar	H. M. Peters
University of Tübingen (15 fishes)	62–85·5	Marigot de Sangalkam	H. M. Peters
University of Tübingen (3 fishes)	89–127	Hann, 10–15 km from Dakar, in fresh pools	H. M. Peters
MRAC (2 fishes)	73, 96	Hann, south of Dakar	D. F. E. Thys van den Audenaerde

Sarotherodon melanotheron leonensis (Thys van den Audenaerde)

Tilapia macrocephala (part ?): Boulenger, 1916*a*:328 (Sierra Leone).
Tilapia (Sarotherodon) leonensis Thys van den Audenaerde, 1971:205 fig. 1 (Sierra Leone and western Liberia).
Sarotherodon melanotheron; Mayland 1978:fig on p 307.

TYPES. Holotype: male, 207 mm TL, from Grafton Bridge, Sierra Leone, coll. Thys van den Audenaerde, 1966. MRAC 169989.

Paratypes: 44 fishes, 70–210 mm TL from salt and brackish water in Sierra Leone. MRAC 169990–170002 and 170028–170037; and 4 specimens from Lake Piso, Liberia, in fresh water near its contact with brackish. Coll. Thys. 1966.

Table 12. *Sarotherodon melanotheron*. Proportions in samples of *S. m. paludinosus* and *S. m. leonensis*. The figures in the last column are taken from Thys (1971). As was his custom, Thys probably used only about ten of his types for these measurements.

	S. m. paludinosus Sangalkam	*S. m. leonensis* Sierra Leone		(Thys)
N	15	9	7	45(?)
SL(mm)	65·0–85·5	69–106	115–171	46–144
Proportions as % SL				
Depth	37·0–41·5	39·0–48·5	42·0–51·5	41·3–54·0
L. head	38·0–40·7	34·4–37·7	(32)37·0–39·0	33·6–38·5
L. pect. fin	40·0–46·0	37·0–45·0	40·3–42·5	37·9–44·7
L. caud ped.	12·4–14·0	11·3–12·7	10·0–13·0	—
D. caud. ped.	14·0–15·5	16·0–18·0	16·0–18·0	—
Caud. ped.l/d	0·7–1·0	0·6–0·8	0·6–0·75	—
Proportions as % l. head				
L. snout	32–35	33–41	38–42	—
Eye	23–27	23·0–29·5	20·5–25·5	20·4–28·3
D. preorb.	20·0–25·5	22·0–27·5	26–29	24·1–27·5
Interorb.	25–32	31–35	33·0–36·5	31·4–38·5
Lower jaw	28–32	27–31	29·5–32·0	—

Table 13. *Sarotherodon m. heudelotii*, *S. m. paludinosus* and *S. m. leonensis*. Relative length of head in males and females of available samples. No sexual dimorphism is apparent, but in *S. m. paludinosus* the mean length of the head in both sexes is greater than in the other two subspecies.

Subsp. & locality	Sex	N	SL(mm)	Head % SL	Mean Female	 Male
S. m. heudelotii						
St Louis	♀	3	154–230	36·3–37·0		
	♀	1	87	34·0	36·05	
La Sine	♀	4	81·6–138·0	35·0–37·3	36·20	
	♂	2	92·2–104·0	35·7–37·0		36·35
Gandjole	♀	5	92·5–105·0	36·0–37·7	36·64	
	♂	2	90·0–96·0	36·0–36·5		36·25
L. Retba	♀	6	101·0–117·5	34·0–37·2	34·98	
Bulama (type of *T. m. macrostoma*)	?	1	183	36·6		
S. m. paludinosus						
Sangalkam	♀	6	64·5–82·0	38·0–40·3	38·78	
	♂	8	66·0–85·5	37·7–40·7		39·76
Hann	♀	1	95·6	40·8		
	♂	1	73·0	40·0		
S. m. leonensis	♀	7	69·0–144·0	32·0–37·9	35·3	
	♂	7	85·0–171·0	36·7–39·0		37·78

All samples except *S. paludinosus*
25 females: Range 32·0–37·9% Mean 37·14
11 males: Range 36·0–39·0% Mean 37·24

S. m. paludinosus
7 females: Range 38·0–40·8% Mean 39·79
9 males: Range 37·7–40·7% Mean 39·79

Distinguishing characters

Only the pigment pattern distinguishes this population (see p. 42 and more fully below), the distinctive features being a narrow black bar at the caudal base and, in mature fishes, 1–3 black blotches on the basal part of the soft dorsal fin, sometimes bordered with white like a tilapia-mark. Yellow centres on the scales, and yellow edges of dorsal and caudal fins are present, but may not be peculiar to this subspecies.

Description

For proportions and meristic characters see Tables 4 to 6, 12 & 13.

The teeth of the jaws are as in other subspecies, in up to six rows in specimens examined by me, 7–8 according to Thys. In the biggest seen by me, a male of 171 mm SL, many outer teeth have the crowns worn to a single cusp and a female of 91 mm also has many worn teeth.

The pharyngeal bone is as in *S. melanotheron*, its length about 35–37·5% length of head, the blade 1·5 times the median length of the toothed area at 79 mm SL, up to twice as long in the paratypes.

Two rows of scales on the cheek, 3 or 3½ between origin of dorsal and lateral line, 4–6 between bases of pectoral and pelvic fins. For lateral line scales see Table 5.

In a male of 171 mm SL the tip of the soft dorsal reaches a vertical two-fifths of the length of the caudal beyond its base. In smaller fishes, both male and female, it is less prolonged.

The pelvic fin ends in a short white filament, reaching the anus or genital papilla. Caudal slightly emarginate.

Size: the biggest examined is a male 171 + 42·5 mm to end of middle caudal rays.

Coloration. Thys (1971) describes the life-colours as including yellow centres of the scales of the flank. In the middle of the flanks the centres are bigger than the surrounding dark parts, but dorsally the dark parts are more extensive. The margins of dorsal and caudal fins are also yellow. In preserved fishes the extreme edges of these fins are black or dusky, but the intense black tips so frequent in *S. m. melanotheron*, are not found in *S. m. leonensis*.

Thys describes the eye as black, but I find only the upper part of the iris black, as in other subspecies (and many other fishes, a device protecting the eye from excess light from above). Pigmentation of the lower parts of the head is variable and may be quite extensive in mature fishes. On the flanks a dark vertical streak partly on the cleithrum is usually present, and the irregular dark vertical bars are variously represented, sometimes by only a few isolated dark-edged scales. A more consistent and characteristic feature of mature fishes is a dark streak at the caudal base.

A tilapia-mark is present or absent in young preserved fishes. A similar mark may appear in sexually mature fishes and may be accompanied by one to three additional black marks of the same kind behind it on the soft dorsal. In the material in the BMNH such conspicuous markings are present in males of 171, 142, 103 and 85 mm SL; the 142 mm fish has also three blotches on the spinous dorsal, but these are not outlined in white; in a male of 115 mm SL a dark blotch on the soft fin is only vaguely outlined; three females of 91, 84 and 69 mm SL have each only one blotch, in the position of a tilapia-mark. In all these fishes, if the gonad was preserved it was in some stage of activity. Mayland's figure (1978:307) is probably from this population.

Ecology

Salinity tolerance

The localities of capture were mostly in tidal reaches of rivers in the mangrove zone or just above it, but also 'at Bonthe, in sea', 'in a tidal pool on the beach at Goderich' as well as 'a stream at Goderich in fresh water' and 'at the mouth of a rivulet entering Lake Piso, Liberia, in fresh water at the contact zone of fresh and brackish'. It is therefore never far from brackish water.

Breeding

Females with active gonads ('starting') have been found at Goderich at 69 mm SL and males at about 85 mm SL. Thys gives the length of the eggs (presumably ovarian) as approx. 2·5–3·5 mm.

Distribution

Brackish water and neighbouring salt and fresh waters of Sierra Leone and western Liberia.

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1915.5.19.19	142	Maka, Sierra Leone	N. W. Thomas
1915.8.12.54	144	Murray Town, Sierra Leone	W. P. Lowe
1958.9.18.189–201 (20 fishes)	18–78·5	Bonthe (in sea) Sierra Leone	T. S. Jones
1968.4.10.3–11	69–106	Freshwater stream at Goderich, Sierra Leone	Bromhall
1981.8.17.75–95	73–171	Lower reaches of streams on Freetown Peninsula, Sierra Leone	A. I. Payne

Sarotherodon melanotheron nigripinnis (Guichenot)

Tilapia nigripinnis Guichenot *in* Duméril, 1859:254, pl.xxii fig. 2,2a (Gabon): Günther, 1862:270 (copied); Boulenger, 1899*a*: 315 (one syntype redescribed); Pellegrin, 1904:315 (syntypes redescribed); *idem*, 1915:504 (Gabon); Blanc, 1962:224; Thys van den Audenaerde, 1968*a*:229 (types); *idem* 1968*b*:xxxviii (Rio Muni to Zaire); *idem*, 1971:213; Roman, 1971:230, fig. 100 (Rio Muni).

Tilapia dolloi Boulenger, 1899*c*:123 pl.xlv fig. 5 'Lake Obeke, Upper Congo', but see Thys, 1964 & below): *idem* 1901*b*:467 ('Obeke', Gabon & Benito R.); *idem*, 1912:25; *idem*, 1915:184, fig. 119 (as before, Landana & Chiloango); Pellegrin, 1904:332 (copied); *idem*, 1915:504 (Gabon); Arnold & Ahl, 1936: 512; ? Asch, 1939:54 (paternal mouth-brooding); Sterba, 1959: pl. 162 middle.

Tilapia heudelotii dolloi; Thys van den Audenaerde, 1964:117, pl.vi (Lower Zaire); Daget & Iltis, 1965:270; Daget & Stauch, 1968:42 (Coastal region of Congo).

Tilapia heudeloti(i); Boulenger, 1915:173 (specimen no. 38 only, Gabon); Pellegrin, 1928*c*:9, 39 (Banana, Bula Bemba); Sterba, 1962:741, fig. 936 (?); Thys van den Audenaerde, 1966:30, fig. 3, pl.IV (Gabon).

Tilapia aequatorialis Roman, 1971:232, fig. 101 and col. pl. on p. 35 (Rio Muni, in fresh water).

TYPES. Syntypes: 2 specimens of 70 and 71 mm SL, Gabon, coll. Aubrey-Lecomte. MNHN A 9396.

Syntypes of *T. dolloi*: 3 specimens of 109,145 and 153 mm TL, MRAC 1085–1087, and 2 of 95 and 111 mm SL, BMNH 1899.11.27.80–81, all from 'Lake Obeke' (see below), coll. P. Delhez.

Holotype of *T. aequatorialis*: 89 mm SL, from the Miyogo R., affl. of Monyoga, Rio Muni; paratypes: 7 of 45–85 mm SL with the same data and 2 of 57 and 74 mm SL from Bolondo, Rio Muni. The two last are MRAC 164.709,710.

Distinguishing characters

See p. 42 and Tables 4–6 & 8. The numbers of dorsal and anal fin-rays are in lower but overlapping ranges compared with *S. m. melanotheron*, and the mean number of gill-rakers is significantly lower. In Tables 5 & 6 data from Thys (1964 & 1966) have been incorporated. In 1966 Thys expressed doubt as to the value of the gill-raker count, but I have found it lower than in the other subspecies irrespective of size of fish.

Proportions of 16 specimens of 80–142 mm SL show no significant differences from the ranges given in Table 8 for *S. m. melanotheron*. Five mature fishes (one male and four females) from Pointe Noire have big heads, measuring 38–39·5% SL. In the others the range is 35–40·2, and Thys (1964 & 1966) gives a range 34–38·8 for his samples from Zaire and Gabon.

In the southern populations the black markings become more extensive with growth and some individuals may become black all over, (Thys 1964 & 1966).

Description

See 'Distinguishing characters' above, and Tables 4–6 & 8.

The largest specimen recorded measures 232 mm TL (about 180 mm SL), and was collected at Apomande in the region of the estuary of the Ogowe by M. Loubens (Thys, 1966:35).

COLORATION. A description of the distribution of black pigment in a sample of nine preserved fishes from Chiloango Town will illustrate the variability of this feature.

Of six males, one has dark bases on all the scales below the upper lateral line nearly down to the belly; dark pigment also covers the chest, head, pelvic fins and the vertical fins. The other five have dark bars of the '*multifasciata*' type, i.e. more intense on the middle and lower parts of the flanks by reason of very black bases of one to ten scales in each bar; two of them have no black markings on head and shoulder; the others have variable amounts of black pigment on lower jaw, sub-operculum, operculum, interoperculum, behind cleithrum, and on nape; the fins are dusky, but not black.

The two nearly ripe females have a general dark brown colour, no vertical bars, much black pigment on lower parts of head and gill-cover, behind cleithrum, and on the flank above the pectoral base; pelvics and vertical fins are darkly dusky, chest intense white, in one with a black patch in front of the pelvics.

The five mature specimens (both sexes) from Pointe Noire have the body pigment restricted to a few isolated black spots on the scales and a blotch above the pectoral base.

There is evidence, therefore, that in the populations of the Zaire and Chiloango estuaries the dark pigment extends over body and fins in mature fishes, especially females; but that at Pointe Noire, Gabon and Rio Muni totally dark individuals are not found (Thys, 1966 & the present study), although individual variation is wide. Although the corners of the caudal fin may be a little more densely pigmented than the rest of the fin, the sharp contrast of black corners and black upper edge of the fin seen in some *S. m. melanotheron* does not characterize *S. m. nigripinnis*. Roman (1971) states that the specimens determined by him as *S. nigripinnis* have black markings on the chin and at the corners of the caudal, but the photographed fish (fig. 100) has only a small smudge on the lower jaw, and the tips of the caudal lobes are pale. In his '*T. aequatorialis*' such markings are said to be absent.

Distribution

In brackish water from southern Rio Muni to the estuary of the Zaire, and in one or two neighbouring freshwater localities.

The doubts expressed by Thys (1964:18) concerning the provenance of the types of *T. dolloi* seem fully justified. 'Lake Obeke' was mapped by Boulenger (1901) in the Central Basin of the Zaire (Congo) whereas no examples of this species have subsequently been reported above the brackish water of the long estuary.

Specimens in USNM recorded by Fowler (1919) as *T. heudelotii* from River Quanza, Angola, belong in part to *Tilapia cabrae*, part to *T. guineensis* (see Trewavas, 1973*b*). The specimen from Souelaba, Cameroon, tentatively included by Thys (1966) in this subspecies, was later (Thys, 1968*b* & 1971) considered to be within the range, both geographical and meristic, of the nominate subspecies.

Two large specimens recorded by Thys (1966:36, pl. IV) were said to come from fresh water, a lagoon (Fernan Vaz) south of the Ogowe; but this is a coastal lagoon and possibly, like the big specimen from Lekki Lagoon (p. 53) they may have been only temporary residents in this water.

The population distinguished by Roman (1971) as *T. aequatorialis* inhabited the fresh water of the Miyogo River, affluent of the Monyoge. Neither of these rivers is marked on the map in Roman's book. *T. aequatorialis* is described as differing from the *S. nigripinnis* of Rio Muni by its deeper body and caudal peduncle, and by a lower but overlapping range of gill-raker numbers. The body proportions are, however, within the range for the subspecies, and Table 5 shows that this is also true of the gill-raker count, which is the same as that given by Daget & Stauch (1968) for their Congo sample. Thys (1968*b*) has also synonymized *T. aequatorialis* with *T. nigripinnis*.

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
MNHN 9396 (syntypes of *T. nigripinnis*)	71, 70	Gabon	Aubrey-Lecomte
1899.11.27.80–81 (two of the syntypes of *T. dolloi*)	95, 111	'Obeke' (?)	Delhez
1889.3.2.7	112	Sette Cama, Gabon	Gerrard
1900.2.17.120	80·5	Benito R., 15 miles from mouth	G. L. Bates
1905.5.12.8–10	48–98	Landana, Congo	Jackson
1912.4.1.536–545 (545 skel.)	67–123	nr Chiloango Town	W. J. Ansorge
1930.10.2.2	45·5	Etembwe R., nr Cape San Juan Rio Muni	H. Meinken
1979.5.22.15–19	133–142	Pointe Noire	P. J. P. Whitehead

Sarotherodon mvogoi (Thys)

Tilapia heudelotii (part, *non* Duméril); Boulenger, 1915:173 (Efayong & Akonolinga only); Pellegrin 1929*b*:360 (Akonolinga).

Tilapia heudelotii dolloi (part, *non* Boulenger); Thys van den Audenaerde, 1964:120 (Nyong R. only).

Tilapia mvogoi Thys van den Audenaerde, 1965:382 (Akonolinga, Nyong R.); *idem* 1966:20, pl. II & fig. 2 (Nyong & Ja Rivers); Trewavas, 1969:272 (Ivindo & Ntem Rivers).

Tilapia (Sarotherodon) mvogoi; Thys van den Audenaerde, 1968*b*:xxxix; *idem*, 1971:215.

TYPES. Holotype: 193 + 64 mm from Akonolinga, Nyong R., Cameroon, coll. Thys. MRAC 152666.

Paratypes: 33 specimens of total lengths 154–257 mm (SL 116–193 mm) from Akonolinga, coll. L. Mvogo. MRAC 152667–89.

Distinguishing characters

A freshwater *Sarotherodon* with a simple male genital papilla, and a lower pharyngeal bone with fine, crowded teeth and a long blade. In adults the profile of the head is decurved and the

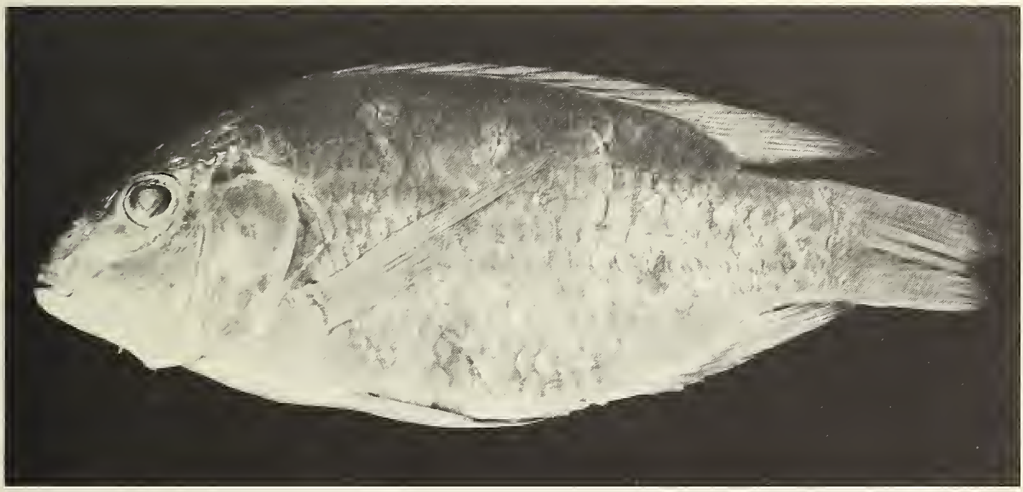


Fig. 24 *Sarotherodon mvogoi* from the Ja River, 197 mm SL. (Photograph, BMNH).

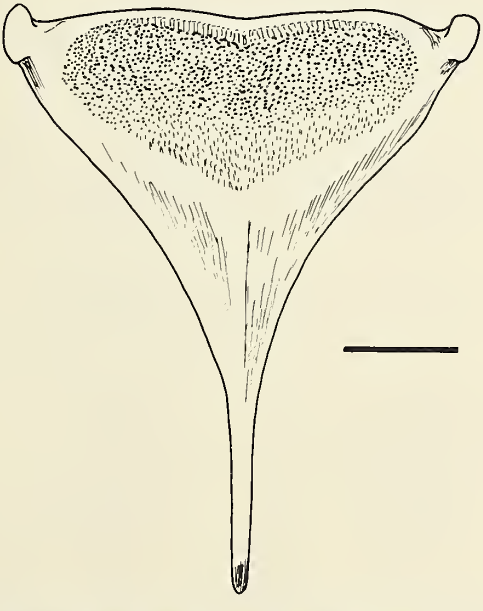


Fig. 25 *Sarotherodon mvogoi* pharyngeal bone of a specimen 194 mm SL, Ja River. (The teeth are much more numerous than the dots representing them.) Scale = 5 mm.

preorbital bone is very deep, reaching 32% length of head at *ca* 200 mm SL. This makes the snout measurement also long, up to 43·5% length of head. The mouth is small, the lower jaw not reaching 30% length of head. There are 19–24 gill-rakers on the lower part of the first arch, 28 or 29 vertebrae, 27–30 scales in the lateral line series, and a total of 24–27 dorsal rays. The colour in life (Thys, 1966) is silver-grey, darker on the back, whitish below with series of pink spots along the flanks, one to each scale.

The small genital papilla and small mouth of males distinguish it from *S. schwebischi*, and the higher number of gill-rakers from *S. melanotheron.* The latter has a straight profile and is found only in or near brackish water. *S. galilaeus* has a straight profile, a deeper body, and higher ranges of scales in the lateral line series and of total dorsal rays (Tables 21–24). *O. (Ny.) macrochir* (which has been introduced for pisciculture into these river-systems) has a narrower preorbital bone (Table 16), and a tasselled male genital papilla.

In West Africa *S. occidentalis* resembles *S. mvogoi* in the decurved profile and deep preorbital bone, but it has 30–32 scales in the lateral line series and higher numbers of dorsal fin-rays (29–31), as well as a higher though overlapping range of gill-raker numbers (22–27 lower).

Description

The proportions and some meristic characters of adults are set out in Tables 14 and 15, and some further details under the heading 'Distinguishing characters' above. See also Fig. 9, and the following supplementary notes.

The decurved profile is characteristic of adults, but a young fish of 65·5 mm from Akonolinga has a straighter profile. In this fish the preorbital bone measures about 23·5% length of head in accordance with its usual allometric trend and corresponding to the lowest value given by Thys. Five still smaller fishes from Nyabessam, Ntem River, also have straight profiles, preorbital depths of 21·5–22·5% length of head and 18 or 19 gill-rakers. Their assignment to *S. mvogoi* rather than to *S. melanotheron* is therefore provisional, resting mainly on the distance of Nyabessan from the sea.

Table 14. Proportions and some meristic numbers in *S. mvogoi.*

	Thys, 1966	R. Ja	R. Ivindo
SL(mm)	116–193	194, 197	190, 202
As % SL			
Depth	39·3–47·2	43, 44	41·5, 41·5
L. head	34·7–37·7	33·6, 35·2	37·7, 39·5
L. pect. fin	36·1–42·7	36·5, 41·3	35·5, 40·5
Longest dorsal spine	11·2–15·0	11·6, 12·2	10·5, 12·5
L. caudal ped.		11·0, 11·7	12·0, 13·5
D. caudal ped.	—	15·2, 15·7	14·5, 14·5
As % length head			
L. snout	38–44	43·0, 43·5	40·5, 42·5
Eye	18·2–24·7	19·6, 18·2	21·3, 20·3
D. preorbital	23·0–28·7	31·0, 32·1	28·0, 29·6
Interorb.	34·4–39·6	39·6, 37·6	36·1, 35·0
Lower jaw	23·7–29·4	28·5, 28·0	27·8, 25·6
L. phar.	36·4–40·3	39·0 (1 fish)	36·2 (1 fish)
W. phar.	30 (holotype)	30·5 (1 fish)	30 (1 fish)
Vertebrae	—		28 (2 fishes)
Gill-rakers	(2–5)+(0–1)+(20–24)	(3–4)+1+(19, 22)	(2–3)+1+(22, 22)

Table 15. Frequencies of dorsal fin-rays and scales in the lateral line series in samples of *S. movogi.*

Dorsal fin	XIV 12	XV 9	XV 10	XV 11	XV 12	XVI 10	XVI 11
Nyong R. (Thys)	1	1	3	14	4	1	
Ja R.							2
Ivindo R.				1	1		

Totals	24	25	26	27
Nyong R.	1	2	17	4
Ja R.				2
Ivindo R.			1	1

Scales lat. line series	27	28	29	30
Nyong R. (Thys)	1	12	11	
Ja R.		1	1	
Ivindo R.				2

Teeth in 2–5 series (Thys), 4–6 in the Ja and Ivindo specimens, from 85 (*ca* 125 mm SL) to 110 in the outer row of the upper jaw, with slender shafts and spoon-shaped crowns; outer all bicuspid, inner tricuspid.

Pharyngeal teeth (Fig. 25) very slender and crowded, the toothed area with moderately rounded lobes and a short apex. Blade 1·65 times the median length of the toothed area (in a fish of 65·5 mm SL), to 1·95 times (in an adult of 190 mm); already a little longer in the young Ntem specimens.

There are 2 rows of scales on the cheek, rarely a few scales of a third row; 27–29 (Nyong, Ntem and Ja) or 30 (Ivindo) in the lateral line series; 3, 3½ or 4 between origin of dorsal and lateral line, 2–4 between bases of pectoral and pelvic fins. Scales of chest only a little smaller than the flank scales above them.

Table 16. *Oreochromis (Ny.) macrochir* (for comparison with *S. mvogoi*, Tables 14 & 15): depth of preorbital bone and number of scales in the lateral line series.

	SL(mm)	preorb. % head	scales lat. line
Lake Mweru	121	20·0	31
Lake Mweru	132	21·3	32
Lake Mweru	138	20·3	32
Lake Mweru	177	22·8	32
Lake Mweru	193	22·0	32
Thys, 1964	95–260	20·0–23·9	(30) 31–33

For dorsal fin-rays see Table 15. Anal III 8–9 (10). Tips of dorsal soft rays reaching vertical of $\frac{1}{4}$ to $\frac{2}{3}$ length of caudal, anal not quite so far. Pelvic extremity reaching vent or nearly. Caudal slightly emarginate with rounded corners.

Genital papilla short and leaf-shaped in male, truncate in female.

COLORATION. See p. 72. The young Ntem fishes still have a tilapia-mark and traces of 5 or 6 juvenile vertical bars on the body. The 65·5 mm fish from the Nyong River is dark all over body and fins, not merely from preservation, as shown by the abundant melanophores. Thys reports the vertical fins as uniform grey, the pelvics paler and the pectoral transparent.

Ecology

Nothing is reported.

Distribution

Rivers Nyong and Ntem, Cameroon; upper Ja (Congo system); Ivindo River (northern tributary of Ogowe). In fresh water.

Discussion

Thys (1966:90–91) has discussed the past and present relations of the upper parts of the Nyong, Ntem, Ja and Ivindo Rivers, sources of all of which are in the high swampy lands. River-capture and reversal of flow have characterized the history of these waters and the faunistic unity of the region is well illustrated by the distribution of *S. mvogoi.* Although the populations are now isolated, the few specimens available do not support any division into subspecies.

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1909.7.9.83–84	194, 197	Ja R. at Efayong	G. L. Bates
1913.10.29.27	66·5	Nyong R. at Akonolinga	G. L. Bates
1969.4.15.2–3	190, 202	Ivindo R., 'Lac' Koubebe between Nzam & Bende	coll. J. Mbote; pres. J. Gery
CAS(SU) 15689	49–56	Ntem R. at Nyabessam	

Genus *SAROTHERODON* – II
The species of the crater-lake Barombi-Mbo, West Cameroon

Sarotherodon lohbergeri ***Sarotherodon linnellii***
Sarotherodon steinbachi ***Sarotherodon caroli***

The species described here are four of eleven endemic cichlids (see Trewavas *et al.*, 1972) of the small lake Barombi-Mbo (=Kumba Lake). This is a nearly circular crater-lake in the Mount Cameroon complex at 9°22′ E, 4°38′N about 56 km NNE of Mount Cameroon itself. Its diameter is about 2·5 km, its maximum depth 111 m, and it must be young geologically speaking, lying as it does in a still active volcanic complex. An eruption occurred on a flank of Mount Cameroon in 1959.

Sarotherodon linnellii was first described from the lake ('Elephant Lake') by Lönnberg in 1903, and others almost certainly from the same lake by Holly in 1930, who then had only three species, *S. lohbergeri*, *S. caroli* and *Stomatepia mariae*, whose locality was given simply as 'Kamerun'. They have since been found only in Barombi-Mbo, except that young of one of them (*S. lohbergeri*) were collected in a pool in the present outlet system of the lake (p. 78).

The lake is believed to have formerly discharged into the Meme system, to which its feeder stream then probably belonged. The Tilapiini now present in the Meme are *Tilapia camerunensis* Lönnberg, *T. kottae* Lönnberg, *T. mariae* Boulenger, *Sarotherodon galilaeus* (Linn.) and, in brackish water, *S. melanotheron* Rüppell. It is to *S. galilaeus*, and possibly to *S. melanotheron*, that the four species assigned to *Sarotherodon* are probably related, while the ancestry of the others is more doubtful. At least ten, probably also the eleventh, of the endemics are mouth-brooders, to judge from the size of the eggs and in some cases from more direct evidence. Three of the *Sarotherodon* are known to be biparental mouth-brooders. The habits of the other (*S. caroli*) are still unknown. Where ripe eggs are known they are olive-green and large, and in one at least there are vestigial adhesive threads. These features relate them to *Sarotherodon* rather than the arena-spawning *Oreochromis*.

The species here included in *Sarotherodon* are microphagous, but those excluded have adopted, one may say phylogenetically reverted to, the habit of feeding on small invertebrates or even small fishes, with a greater or less development of appropriate trophic structures.

Structurally, a peculiarity shared by most of the Barombi-Mbo cichlids is a relatively large head (or small trunk). The lake is very poor in planktonic organisms and the slope of its floor is steep, features that provide poor pastures for fishes dependent on phytoplankton or detritus; and it is perhaps not too fanciful to see in the unusual proportions either emphasis on the food-gathering apparatus, or the inability to maintain more than a small body. The maximum size of all the Barombi-Mbo cichlids is low, only the exceptional *S. linnellii* reaching a Standard Length of 185 mm, also a reflexion of poor food supply.

Sarotherodon lohbergeri (Holly)

Tilapia lohbergeri Holly, 1930:203. pl. 2, fig. 10 (Cameroon); Trewavas, 1962:171, fig. 7 (Lake Barombi-Mbo, Cameroon).
Tilapia (Sarotherodon) lohbergeri; Thys van den Audenaerde, 1968*b*:xxxviii.
Sarotherodon lohbergeri; Trewavas *et al.*, 1972:48, 80, figs 4, 5, 27.

TYPE. Holotype: 89+23 mm, coll. Haberer in 'Kamerun' NHMW 13951.

Distinguishing characters

A *Sarotherodon* of small size (up to 106 mm SL), with 29 vertebrae and 30–31 scales in the lateral line series. Teeth of jaws in 4–7 series, movable, with slender shafts and broad, curved crowns. Pharyngeal teeth slender, crowded, unicuspid; lower pharyngeal bone 36–39% length of head, broad, with apophyses extending a little behind the toothed plate; median length of blade as long as or longer than that of toothed area. Gill-rakers 14–18 on lower part. Pectoral fin 31·0–36·3% SL. No colour differences between the sexes. Eggs 4·5 mm in long diameter, green, brooded by both parents (Peters, pers. commn).

Silvery grey, with a mid-lateral black stripe extending from operculum to caudal base, interrupted on anterior part of caudal peduncle. Mature fishes of both sexes with variable black areas on lower jaw and lower parts of head. No tilapia-mark.

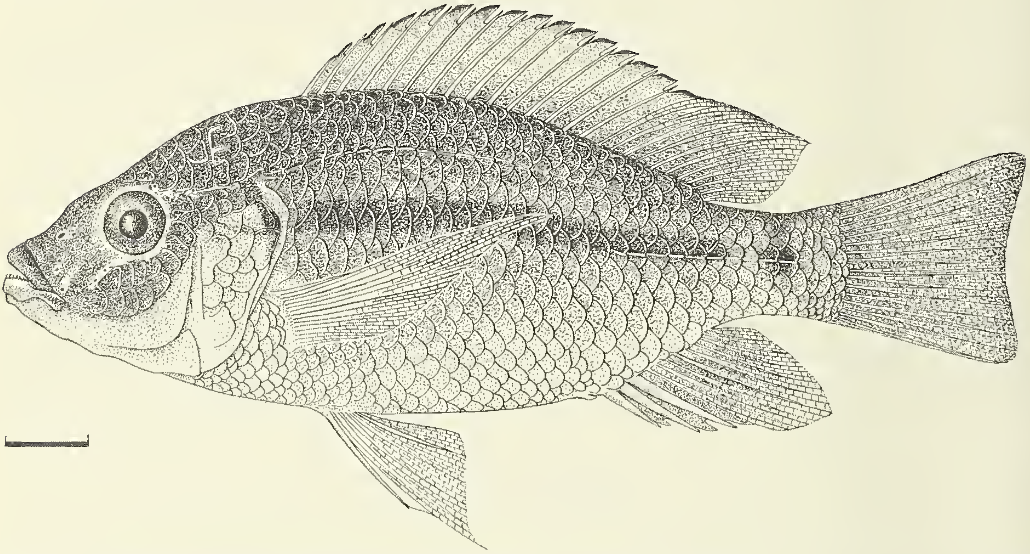


Fig. 26 *Sarotherodon lohbergeri*. From Trewavas *et al.*, 1972: fig. 4. Scale = 10 mm. Drawn by Sharon Chambers.

Table 17. *Sarotherodon lohbergeri*: proportions and meristic characters.

N	21			
SL(mm)	48–102	Dorsal	XV 11	4
As % SL			XVI 10	1
Depth	37·0–45·0		XVI 11	14
L. head	33·0–38·4		XVI 12	1
L. pect. fin	31·0–36·3		XVII 11	1
L. caud. ped.	13·2–14·5			
Caud. peduncle l/d	1·0–1·06	Dorsal totals	26	5
As % length head			27	14
L. snout	32·0–42·0		28	2
Eye	20·6–28·2			
D. preorb.	17·8–23·9	Anal	III 8	2
Interorb.	29·4–35·0		9	17
Lower jaw	26·5–31·7		10	2

Description

Based on 21 specimens of 48·0–101·5 mm SL, all (including the holotype?) from Barombi-Mbo. Additional details from freshly caught and living fishes, including young.

Proportions and main meristic characters in Table 17. Some other details in 'Distinguishing characters', above.

Upper profile of head straight from occiput to tip of snout or a convexity before the eye. Jaws meeting evenly or lower slightly projecting.

Teeth very movable with very slender shafts, 50–80 in outermost row of upper jaw, and 4–7 rows in adults. Outer with a lateral notch in the broad, curved crown, in some individuals a few lateral tricuspid; inner all tricuspid. Already 3–4 rows in young of 27–34 mm SL.

Gill-rakers short, (2–4) + (0–1) + (14–18) on the first arch. Microbranchiospines present.

Lower pharyngeal: see above under 'Distinguishing characters' and Fig. 27. Length 36·0–38·5%, width 27·5–32·5% length of head.

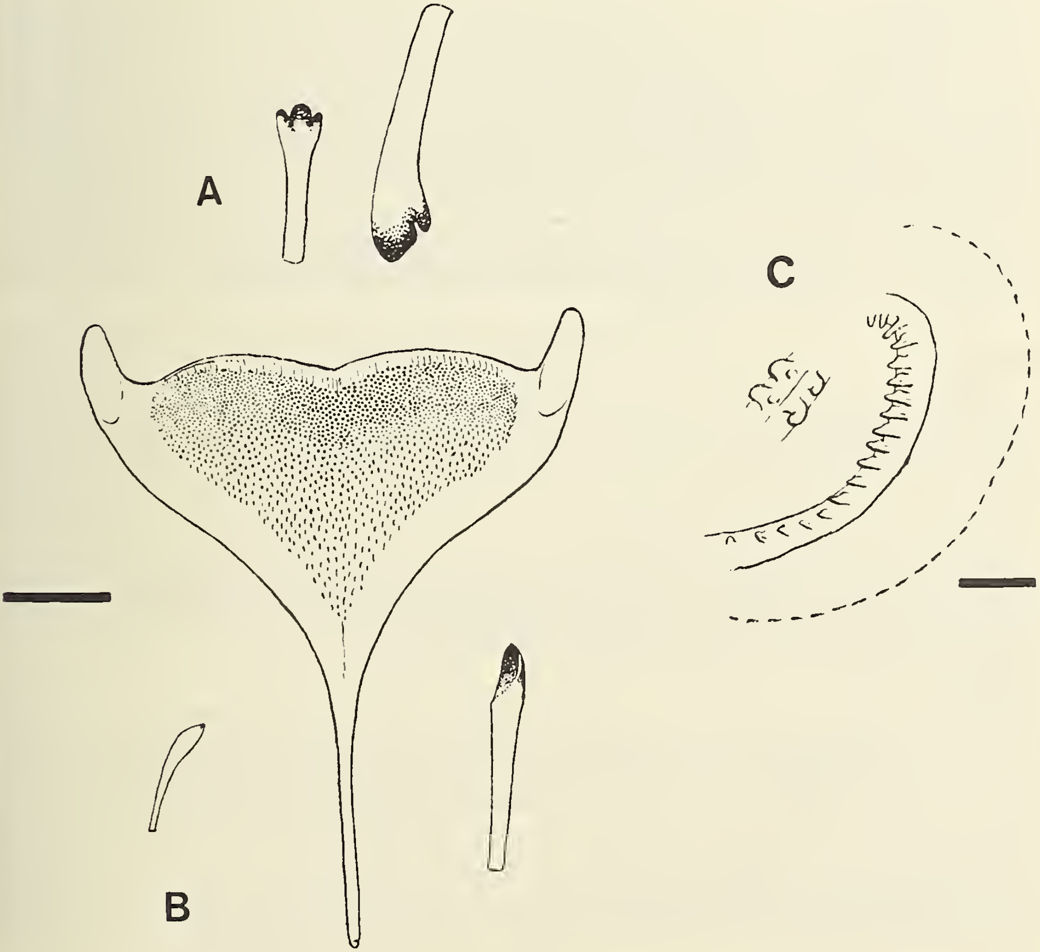


Fig. 27 *Sarotherodon lohbergeri*: A, teeth from an inner and the outermost row of the jaw; B, lower pharyngeal bone, and anterior and posterior teeth from it; C, the first gill-arch, with part of it enlarged to show the rakers of both series. Scales = 3 mm. From Trewavas *et al.*, 1972; fig. 5.

Two rows of scales on cheek; 30–31 (32) in the lateral line series, 3–4 from origin of dorsal to lateral line, 3½–4½ between bases of pectoral and pelvic fins; 15 or 16 around caudal peduncle.

Tips of dorsal and anal fins reaching to end of caudal peduncle or slightly beyond. Caudal slightly emarginate. Pectoral extending to above vent; pelvic not reaching vent.

Genital papilla small and leaf shaped in male; a short funnel in females that have laid eggs.

COLORATION. See above. The mid-lateral black stripe is usually, but not always present; it was not seen in the living young of 30 mm SL, though in some of them it appeared after death. The young have pearly bodies, and pelvic and anterior part of anal fins are tinged with vermilion or orange. There is no tilapia-mark at any stage. No sexual dichromatism. Sexually mature fishes of both sexes with irregular black markings on lower jaw and lower limb of preoperculum.

Ecology

Food

The food (Green & Corbet *in* Trewavas *et al.*, 1972:80) consists mainly of epiphytic and epilithic filamentous algae, and the diatoms, rhizopods, rotifers and organic debris found among them. Since sponges covered much of the rock surface in shallow water, spicules from these also figured largely in the stomach contents. Feeding takes place in a characteristic manner, described by Green & Corbet thus: 'The adults opened their mouths very wide and applied them to the surface of the rock as though sucking material in'. They also fed from the stems of *Najas pectinata*. 'The fish turned on its side, so that the width of the mouth lay along the axis of the stem.'

This species was observed swimming in schools at the surface and there was evidence that they made use of the minute plant products that continually fall from the surrounding forest.

Juveniles were observed appearing to wrench something from the surface of rocks between closed jaws.

Breeding

In the field no mating or parental behaviour was observed, but green ovarian eggs, nearly ready to be shed, measured up to 4·5 mm in long diameter in a fish of 78 mm SL. This fish had 13 eggs in the right ovary, 27 in the left. A fish of 73·5 mm had 46 smaller (4·0–4·2 mm) eggs, 23 in each ovary, also green. Many ovaries contained yellow and rust-red bodies, probably atretic follicles, as well as creamy-yellow oocytes.

The fact that there is no sexual dichromatism suggests a biparental mouth-brooding function. This coincides with the opinion of Dr J. Hylton Pasqual, who kept this species in an aquarium in the nineteen-forties (memo. to Captain W. B. Dowson, then Fishery Officer, Lagos), and is confirmed by the recent work of Peters & Berns (1982*a*:42).

Habitat

This was the most abundant of the cichlids in shallow water of Barombi-Mbo, and the only one of the eleven cichlid species of the lake to be found outside it. The outlet of the lake is a clear shallow stream, the Kake, which falls over a sill into a gorge and proceeds by rapids to join the Kumba River, a tributary of the Mungo. In the Kumba River, shortly above the entry of the Kake and below the town of Kumba, two juvenile *S. lohbergeri* were caught in a pool, the water of which was enriched by waste from the town. They were assumed to be the offspring of individuals that had been washed into the Kake, and had made their way up the Kumba River to the pool.

Distribution

Lake Barombi-Mbo and the Kumba River, West Cameroon.

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
NHMW 13951 (holotype)	93	'Kamerun'	Haberer
1947.1.14.1–4	79–106	Cameroons (aquarium offspring of parents from Barombi-Mbo.)	coll. Pasqual; pres. Mackay, Edinburgh Zoo.
1961.10.18.15–17	48–96	Barombi-Mbo, Kumba	Eisentraut, 1955
1969.1.13.151–166	50–102	Barombi-Mbo	C. A. Wright
1973.5.14.874–948	48–102	Barombi-Mbo	J. Green, S. A. Corbet, J. Griffith & E. Trewavas
1973.5.14.951–956	46–87	Barombi-Mbo	J. Green, S. A. Corbet, J. Griffith & E. Trewavas
1973.5.14.949–950	25, 30	Pool in Kumba R., at Buea Rd Junction, Kumba	H. Disney

Sarotherodon steinbachi (Trewavas)

Tilapia steinbachi Trewavas, 1962*b*:178, figs 10, 11 (Barombi-Mbo, West Cameroon).
Tilapia (Sarotherodon?) steinbachi; Thys van den Audenaerde, 1968*b*:xxxix.
Sarotherodon steinbachi; Trewavas *et al.*, 1972:50, 80, figs 6, 7, 27.

TYPES. Holotype and paratype: 113 and 90 mm SL respectively, coll. M. Eisentraut and G. Steinbach in 1954. BMNH 1961.10.18.40–41.

Distinguishing characters

A *Sarotherodon* of small size (to about 115 mm SL), with rather deep body and decurved snout. Vertebrae 29–31. Mouth and teeth very small; lower jaw 26–31% length of head; teeth in 2–4, usually 3 series. Length of lower pharyngeal bone 45–49·5% length of head, its narrow, fragile anterior blade as long as the massive, nearly discoidal dentigerous area, which bears slender, crowded teeth. Gill-rakers 19–23 on lower part of first arch. Pectoral fin 36–40% SL. Eggs green, about 3·5×3·0 mm (or 4·5×3·5, Thys). No markings on body in life, a dark horizontal band in some preserved specimens. A tilapia-mark present up to 40 mm SL. No sexual dichromatism.

These characters distinguish it from *S. lohbergeri*, which is superficially similar. The large size of the pharyngeal bones is unique in the genus.

Description

Based on the holotype and paratype, and 22 specimens 52–96·5 mm in SL. Additional details from living and freshly caught fishes.

Proportions and meristic characters: see Table 18.

Teeth in jaws in 2–4, usually 3 series, 40–70 in outermost row of upper jaw; very small, movable, with slender shafts; outermost bicuspid, inner tricuspid.

Length of lower pharyngeal bone 45–49·5% length of head, width 34·5–38·0. Tooth-plate

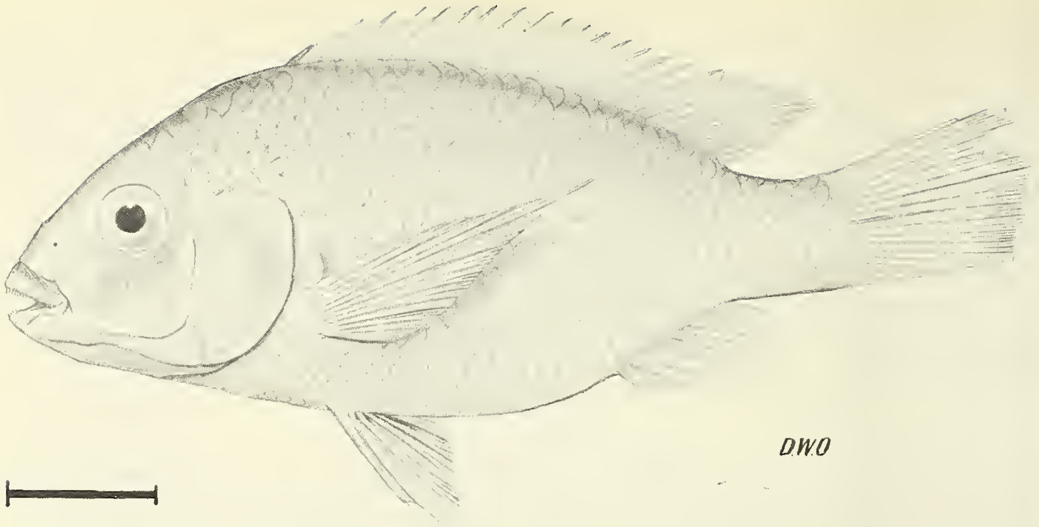


Fig. 28 *Sarotherodon steinbachi*, holotype. From Trewavas *et al.*, 1972: fig. 6. Scale = 20 mm.

Table 18. *Sarotherodon steinbachi*: proportions and meristic numbers.

N	22			
SL(mm)	52·0–96·5	Dorsal	XVI 10	1
As % SL			XVI 11	3
Depth	39·5–45·5		XVII 10	11
L. head	33·0–36·5		XVII 11	9
L. pect. fin	36·0–40·0		XVII 11(+1)	1
L. caud. ped.	12·5–16·0	Anal	III 8	4
Caudal ped. l/d	1·05–1·25		9	12
As % l. head			10	2
L. snout	31·0–39·0	Gill-rakers (lower)		
Eye	20·0–32·5		19	3
D. preorb.	20·0–26·0		20	3
Interorb.	30·0–35·0		21	11
Lower jaw	26·0–31·0		22	6
			23	1

massive, extending as far back as the apophyses. Posterior teeth with blunt major cusp and slight shoulder, in adults interspersed with teeth whose crowns have been worn down below the brown tip; anterior unicuspid, with backward-sloping, bilaterally bevelled crowns. Anterior upper pharyngeal teeth like the posterior lower. Pharyngeal muscles highly developed.

Gill-rakers short, (2–3) + (0–2) + (19–23) on the first arch (Table 18). Microbranchiospines on outer sides of arches 2, 3 and 4.

Vertebrae 29 (f. 7), 30 (f. 8) or 31 (f. 1). Ventral apophyses of third vertebra united below but without a spine, thickened and sloping back beneath the fourth, which appears to contribute to it. This modification enhancing its function of attachment for the unusually strong retractor muscles of the pharyngeal bones.

Scales of cheek in 2 series, rarely one or two of a third; in lateral line series 30–33, usually 31; between origin of dorsal and lateral line 3 or 3½; between bases of pectoral and pelvic fins 4; around caudal peduncle 16.

Dorsal and anal fins: see Table 18. Last dorsal spine 13–15%, third anal 12·5–15% SL.

Pectoral extending to above spinous anal. Pelvics colourless, not reaching vent. Caudal slightly emarginate, not scaly.

Genital papilla small in both sexes.

COLORATION. In life pearly yellow, countershaded to grey-blue above and white below. After preservation general colour dark grey on back with, in some, a darker band along middle of caudal and forwards along the horizontal myoseptum nearly to head. A tilapia-mark seen in only one specimen, 39·5 mm SL, dark grey, round and surrounded by a pale ring.

Ecology

Food

See Green & Corbet *in* Trewavas *et al.*, 1972. The intestine of a 75 mm fish measures 352 mm, 4·7 times the SL.

The main stomach contents in nearly all the 21 fishes examined consisted of organic debris. Benthic and epilithic diatoms, and sponge spicules were nearly always present, and many had inorganic particles in the stomach. Individuals were seen shovelling sand into the mouth, moving it about in the buccopharynx, then spitting out the sand and making swallowing movements. Hence the worn pharyngeal teeth. On the sponge-encrusted rocks it appeared to be raking the aufwuchs into the mouth by movements of the upper jaw (in contrast to the actions of *S. lohbergeri* on the same rock). *S. steinbachi* was also seen schooling at the surface; that it was feeding there was confirmed by the presence in some stomachs of plant hairs and parts of terrestrial insects.

Breeding

Ovarian eggs of 2·6–3·6 mm are oval and olive-green. Mating and parental behaviour were not observed; one male had a young cichlid of 12 mm SL in the mouth, but whether or not in a parental capacity could not be determined. Thys (1971:216) records two mouth-brooding females, one incubating eggs of 3·5×4·5 mm, the other young of 25 mm. Peters & Berns (1982*a*) recorded biparental mouth-brooding.

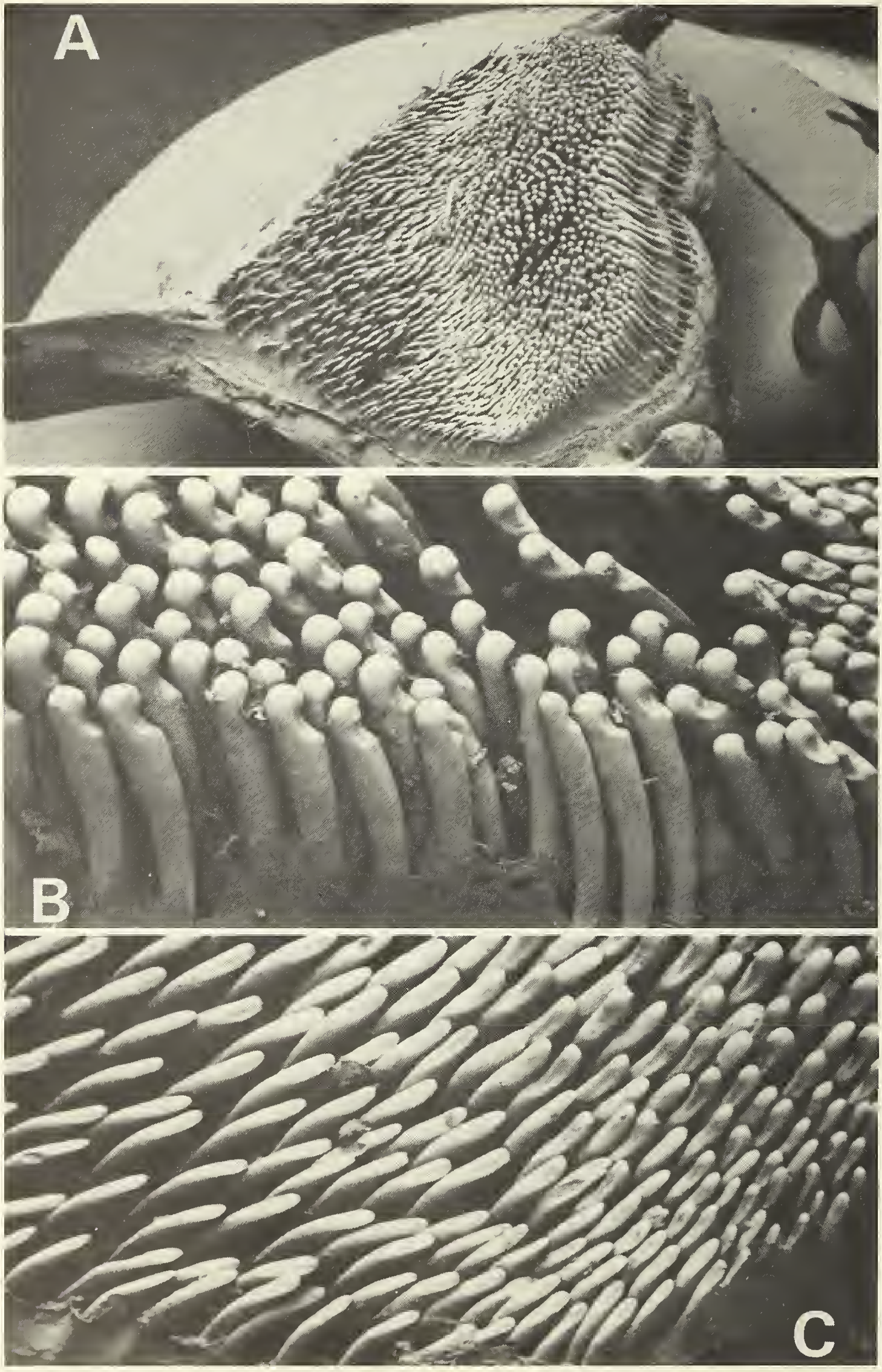
Distribution

Lake Barombi-Mbo, in shallow water near the shore.

Material examined

(all from Barombi-Mbo)

Museum & Reg. No.	SL(mm)	Collector
1961.10.18.40–41 (holotype & paratype)	113, 90	M. Eisentraut & G. Steinbach (1954)
1969.1.13.172–187	55·0–88·5	C. A. Wright
1973.5.14.957–973	39·0–96·5	J. Green, S. A. Corbet, J. Griffith & E. Trewavas


A
B
C

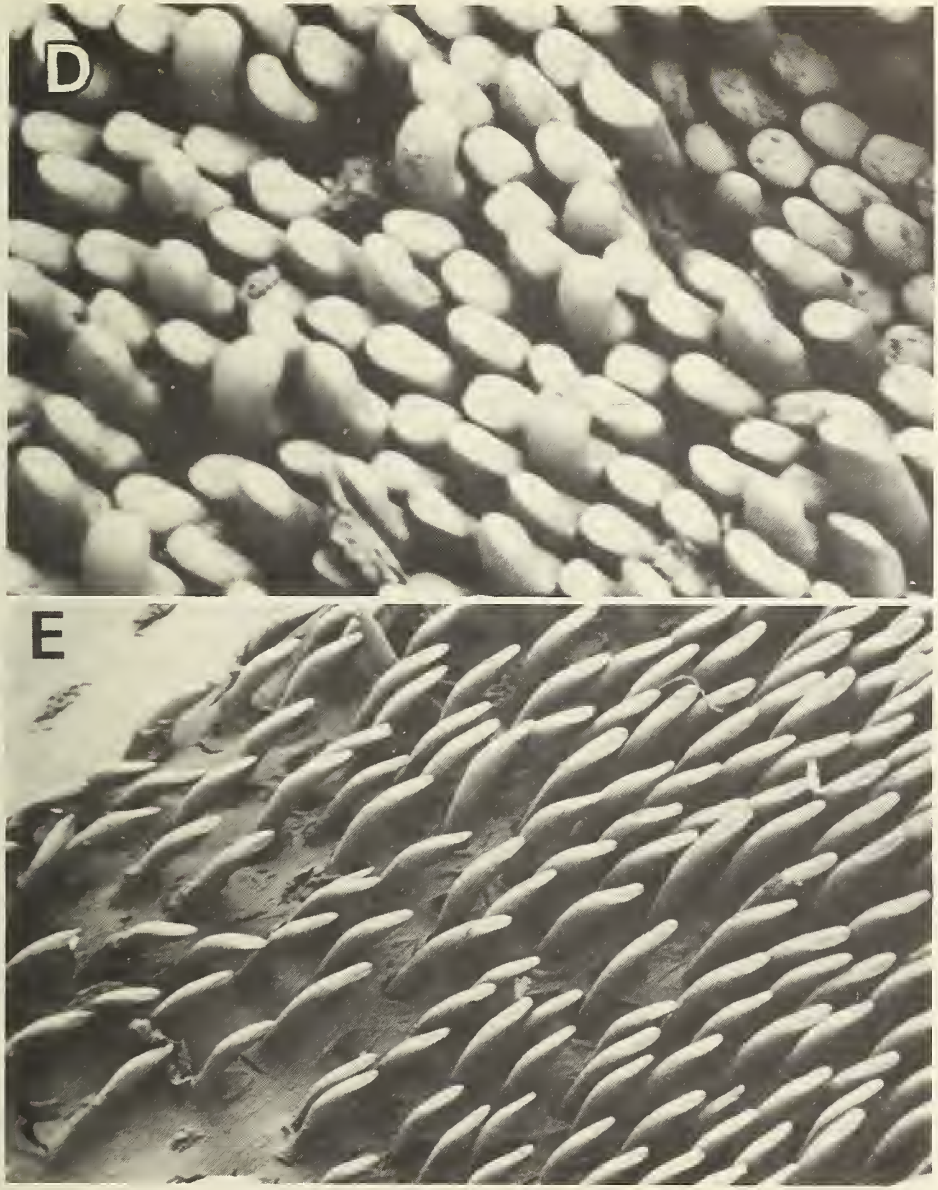


Fig. 29 *Sarotherodon steinbachi.* A, lower pharyngeal bone; B, anterior upper pharyngeal teeth; C, lower pharyngeal teeth at transition between posterior and anterior; D, some posterior lower pharyngeal teeth with worn crowns, interspersed with unworn replacement teeth; E, anterior teeth of lower bone. (Scanning electron micrograph, BMNH).

Sarotherodon linnellii (Lönnberg) & *Sarotherodon caroli* (Holly)

These are two sister-species confined to the small crater-lake Barombi-Mbo (see p. 75).

Common diagnosis

Sarotherodon species attaining a Standard Length of 150 or 185 mm. Vertebrae 29 (30). Head large, its length 40·5–48% SL in adults of 100 mm SL or more. Gill-rakers 15–20 on lower part of first arch. Lower pharyngeal with numerous, slender, posteriorly crowded teeth and a blade 2–3 times the length of the toothed area in adults. Length of intestine 2·3–2·5 times SL in adults. Eggs large, 5–5·5 mm in long diameter, brooded by female (and male ?).

Sarotherodon linnellii (Lönnberg)

Tilapia (Gephyrochromis) linnellii Lönnberg, 1903:42 (Elephant Lake = Barombi-Mbo).
Tilapia linnellii; Boulenger, 1915:159, fig. 104.
Tilapia linnellii (part); Trewavas, 1962*b*:174, figs 8, 9 (Barombi-Mbo).
Tilapia (Sarotherodon) linnellii; Thys van den Audenaerde, 1968*b*:xxxix.
Sarotherodon linnellii; Trewavas, Green & Corbet, 1972:52, 81, figs 8, 9, 27.

TYPES. Syntypes: Eight of TL 180–200 mm, of which I have examined two ♂♂ 156 + 36·5 and 163 + 41 mm. Swedish Mus. Nat. Hist., 9541 and one ♂ 147 + 35 mm, BMNH 1903.2.28.2, coll. G. Linnell, Elephant Lake, Cameroon (= Barombi-Mbo) in 1902. The 156 mm fish bears the label 'Type' and if a lectotype is needed should be selected.

Barombi names: *unga*, *kippé*.

Distinguishing characters

The common diagnosis above uses characters which differentiate *S. linnellii* from species other than *S. caroli*. The following are the features in which *S. linnellii* may be contrasted with *S. caroli* (see p. 90), although some are only statistical differences in overlapping ranges.

1. An intense black tilapia-mark present in the young from the stage when they are still in the maternal mouth until they reach *ca* 100 mm SL, after which it becomes vaguer in outline and fainter; it may be absent altogether above 120 mm SL or may still be recognisable at 150 mm SL.
2. Dorsal spines (XIV) XV or XVI, mode XV. Modal formula XV 12 (Table 20).
3. Gill-rakers on lower part of first arch 15–18, mode 17 (Table 20).
4. Diameter of eye in young of 60–90 mm SL 28–31% 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 those of *S. caroli* of the same size.
7. Breeding males green.

Description

Based on 42 specimens of 60–150 mm SL, including three syntypes, with details from others observed in the field and younger preserved specimens.

Proportions and meristic characters in Tables 19 and 20.

The shape of the body varies from the arched dorsum of a fish in good condition to one that tapers from the nape to the caudal peduncle as in Fig. 30. The latter is prevalent among breeding males, and is given the name 'kippé' by the fishermen.

Table 19. Proportions in *S. linnellii* and *S. caroli*, juvenile and adult.

		S. linnellii	*S. caroli*
		N=42	N=40
	SL (mm)	% of SL	% of SL
Depth	60–99	38·5–40·3	38·5–45·0
	100–150	37·0–42·0	39·0–44·0
L. head	60–99	37·5–40·5	39·5–45·0
	100–150	40·5–45·0	42·5–48·0
L. pect. fin		33·3–39·0	32·0–40·0
L. caud. ped.		11·5–15·5	11·5–14·0
Caudal ped. l/d		0·9–1·2	0·9–1·2
		% of head length	
L. snout	60–99	29·5–33·5	31·0–35·0
	100–150	34·0–42·0	34·5–41·0
Eye	60–99	28·0–31·0	21·5–27·5
	100–150	18·5–24·0	18·0–24·5
D. preorb.	60–99	17·5–21·0	19·0–23·5
	100–150	20·5–24·5	21·0–26·0
Interorb.	60–99	31·5–33·5	31·0–35·5
	100–150	33·5–38·0	33·0–38·5
Lower jaw ♂		32·0–37·5	32·0–36·0
♀		32·5–36·0	32·0–36·0
L. lower phar.	45	32·0	——
	64–95	35–40	38–40·5
	102–147	36·5–39	36·5–40·5
W. lower phar.	45	29·4	——
	64–95	27·5–30	25·5–28
	102–147	25–28	24–28
Lower pharyngeal		l. blade/l. toothed area	
	45–54	1·1–1·7 (N=4)	——
	64–95	0·8–1·8 (N=10)	2·1–3·0(N=8)
	102–147	2·0–2·5 (N=12)	2·3–2·8 (N=12)
	185	3·0(N=1)	——

The most striking feature in both this and *S. caroli* is the large head (or short trunk?) especially in adults. The young are distinguished from *S. caroli* by the larger eye, but there is no difference in this ratio in adults. In adults the deep preorbital bone is one of the features in which both species resemble *S. melanotheron* and related species.

The length of the lower jaw is 36% length of head or more in only three specimens and these are all males with enlarging testes; but three other males with similar gonads have a smaller mouth, and there is not enough evidence of a correlation between sex and size of mouth.

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

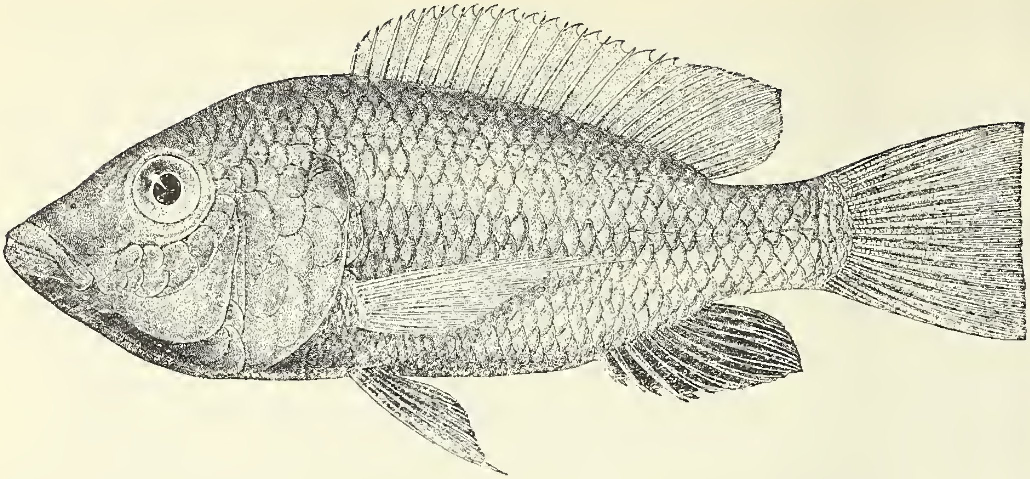


Fig. 30 *Sarotherodon linnellii*, a syntype, from Boulenger, 1915, fig. 104.

replacement teeth are usually fewer than the biscuspids of females of the same size, as the following figures will show.

Upper outer teeth in 10 females of 135–150 mm SL: 90–116
Upper outer teeth in 10 males of 139–163 mm SL: 70–86

(The unicuspid teeth of the three syntypes, all males, led Lönnberg to relate them to *Gephyrochromis*, an unrelated genus that had been defined on its simple teeth. The reservations expressed by Lönnberg were justified.)

The teeth are in 3 series in young of 50–100 mm SL, up to 6 in adults. 70–136 in outer row of upper jaw.

Pharyngeal teeth and bone, see Table 19 and Figs 31 & 33.

Gill-rakers (3–4) + (0–2) + (15–18), and see Table 20 and Fig. 35; a little longer than in *S. caroli.*

Scales in lateral line series 30–32; mode 31; 3 or 3½ between origin of dorsal and lateral line; 2 rows on the cheek, rarely one or two extra scales.

Dorsal fin see Table 20. Spines neither very long nor strong; length of last spine 12·5–15·5% SL; soft rays not prolonged beyond base of caudal. Third anal spine about as long as or a little shorter than last dorsal. Caudal truncate or very slightly emarginate.

Vertebrae 29 (14 + 15 or 15 + 14) in 15 specimens counted.

Size. Among all the collections available only one fish exceeded SL 160 mm. This was a male of SL 185 mm in good condition, with very small gonads and a small genital papilla. It had probably failed to breed at the usual size and so had been able to make better growth.

Coloration. The young are bright silver in general colour with an intensely black, horizontally elongate tilapia-mark surrounded by a clear zone. At 60–100 mm SL the dorsum and top of head are darker, the flanks silvery grey, and the tilapia-mark still conspicuous but no longer surrounded by a clear zone. As the gonads mature the lower parts of the head and the flanks become more metallic and green, and the whole fish may become predominantly green. Traces of the tilapia-mark often remain to maturity, but preserved fishes show various degrees of intensity or complete absence of this mark. Dr S. A. Corbet observed under water in Barombi-Mbo a green fish with a tilapia-mark courting a grey fish with none. As in other species it may at this stage be under emotional control. Most brooding females were silver-grey in general colour.

The fins are mainly of a neutral colour, but the pelvics in some are yellow.

Some adult fishes have areas of intense black on the lower parts of the head and body, but

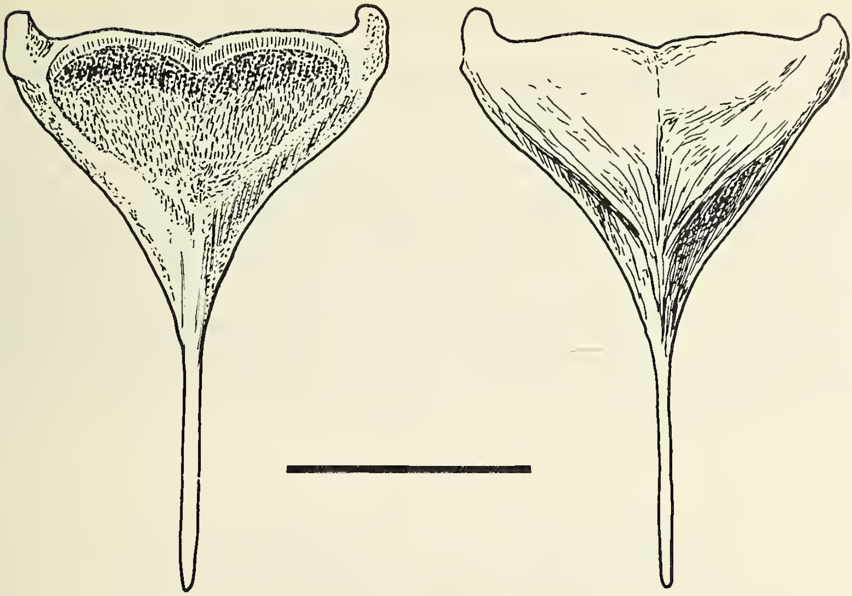


Fig. 31 *Sarotherodon linnellii*, lower pharyngeal bone. Scale = 10 mm.

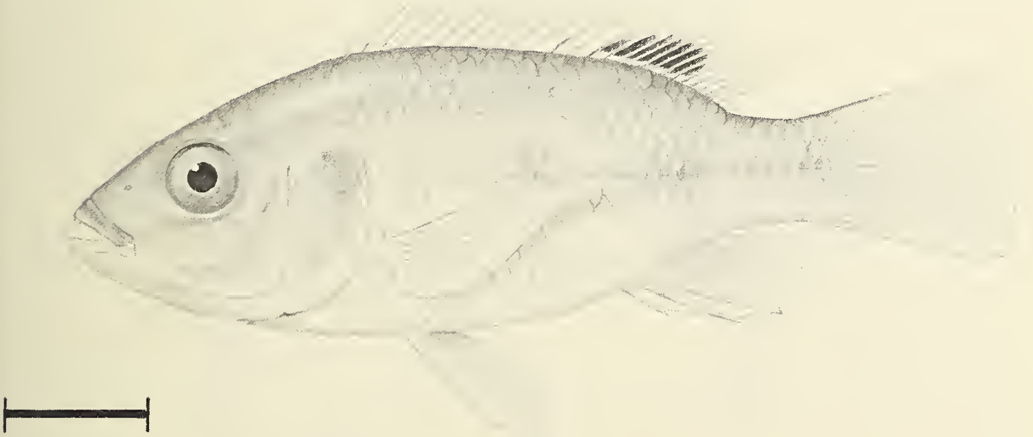


Fig. 32 *Sarotherodon linnellii*, young, showing the elongate tilapia-mark. Scale = 10 mm.

the presence or absence of such markings does not seem to be correlated with sex or stage of maturity. The green fishes all had gonads at some stage of activity, usually much fat among the viscera, and the body tapering rapidly.

Ecology

Food

See Green & Corbet in Trewavas *et al.*, 1972. Young of 20–70 mm SL had eaten mayfly (*Ephemeroptera*) larvae and various terrestrial insects among a diet in which animal items formed a high proportion. They were seen actively investigating potential food objects at the bottom and at the surface.

Adults feed predominantly on phytoplankton.

In a fish of 137 mm SL the intestine measures 330 mm, 2·47 times the SL.

Breeding

The smallest brooding female recorded is 118 mm SL, and several between this size and 160 mm had ripe ovarian eggs, or were brooding eggs or young in the mouth. The brooding fishes, eight in number, were all females (but Thys van den Audenaerde, in a letter, judged one brooding fish collected by him to be a male). Ripe eggs are 5–5·5 mm in long diameter, olive green with a white cap. The surface is beset with groups of microscopic filaments. The ovaries are paired, about equal in size. In a fish of 140 mm SL the right ovary contained 35 ripe eggs, in one of 150 mm 68, in one of 155·5 mm 62. Peters & Berns (1982*a*) record brooding by both sexes, predominantly by the female.

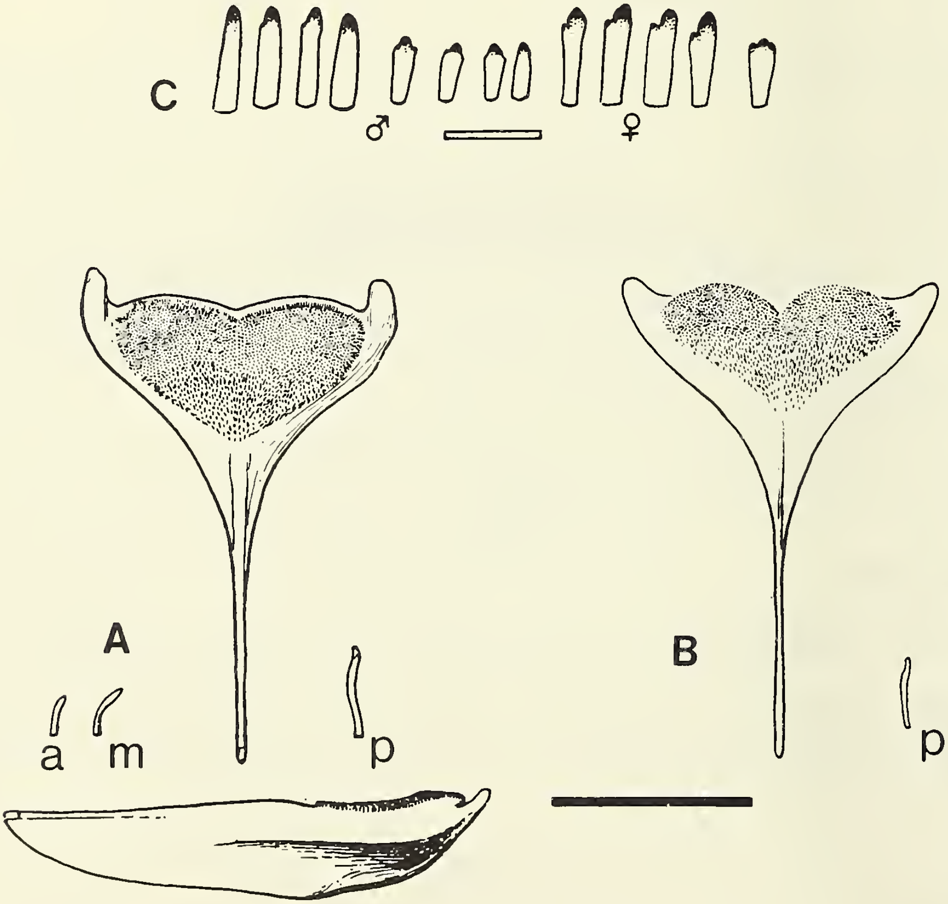


Fig. 33 A, *Sarotherodon linnellii*, lower pharyngeal bone with anterior (a), middle (m) and posterior (p) teeth. B, *S. caroli*, lower pharyngeal bone with an isolated posterior tooth. C, outer and inner jaw teeth of a male and female *S. linnellii*. Upper scale = 1 mm, lower = 10 mm.

Young with yolk sac absorbed in the mouths of three females measured 13·5–13·7 mm SL, 17 mm TL, and had large tilapia-marks.

Ovaries of brooding females contained oocytes of two sizes as well as rust-red and yellow bodies (atretic follicles ?), indicating that further breeding cycles were likely to follow the one then in its last phase.

The collections in which ripe females were found were made in the months of March and November. In March and April many *S. linnellii* were seen inshore around the rocks defending territory and courting.

Distribution

Barombi-Mbo, Cameroon.

Table 20. Frequencies of meristic numbers in *S. linnellii* and *S. caroli*. From Trewavas *et al.*, 1972.

	S. linnellii	*S. caroli*
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

Material examined

(all from Elephant Lake = Barombi-Mbo = Kumba Lake)

Museum & Reg. No.	SL(mm)	Collector
1903.2.28.2 (paratype)	147	Linnell
Bonn Mus.	45–148	Eisentraut
1961.10.18.18–19	140, 148	Eisentraut
1961.10.18.20–23	24–53	Eisentraut
1969.1.13.167–8	34, 52, & 24 juv. 15·0–17·5	C. A. Wright
1969.1.13.188–9	147, 150	C. A. Wright
1973.5.14.863–868	140–186	J. Green, S. A. Corbet, J. Griffith & E. Trewavas (1970)
1973.5.14.869–872	80–123	J. Green *et al.* (1970)
1973.5.14.873	19	J. Green *et al.* (1970)
1973.5.14.784–786 (brood from mouth of female)	86–96 13·0–14·5	J. Green *et al.* (1970)
1973.5.14.835–862	26–150	J. Green *et al.* (1970)
1973.7.18.177–201	18–24	J. Green & S. A. Corbet (1972)
1959.8.18.183–187	95–146	P. I. R. Maclaren
1979.7.18.456–458	84–88	H. M. Peters

***Sarotherodon caroli* (Holly)**

Tilapia caroli Holly, 1930:204, pl. 2, fig. 11 ('Kamerun').
Tilapia linnellii (part, *non* Lönnberg); Trewavas, 1962*b*:174 (Barombi-Mbo).
Sarotherodon caroli; Trewavas, Green & Corbet, 1972:54, 81, figs 9, 10, 11 (Barombi-Mbo).

TYPES. Holotype: 147·5+33 mm, NHMW; paratype, 142·5+33 mm, same data and reg. no. as holotype, both apparently males. Coll. Haberer, 'Kamerun'.

Barombi names: *fissi*, *unga*.

Distinguishing characters

The 'Common diagnosis' with *S. linnellii* on p. 84 gives the principal features distinguishing both species from other *Sarotherodon*. The following list is a guide to the distinction between this species and *S. linnellii* (see p. 84).

1. No tilapia-mark, at least at 62 mm SL or 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 20).
4. Diameter of eye in young of 62–99 mm SL 21·5–27·6% length of head.
5. Blade of lower pharyngeal bone always more than twice the median length of the dentigerous area, at least at 62 mm SL 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 grey smudges.

Description

Based on 40 specimens of 62·5–148·5 mm SL, including the holotype and paratype.

Proportions and meristic characters in Tables 19 & 20.

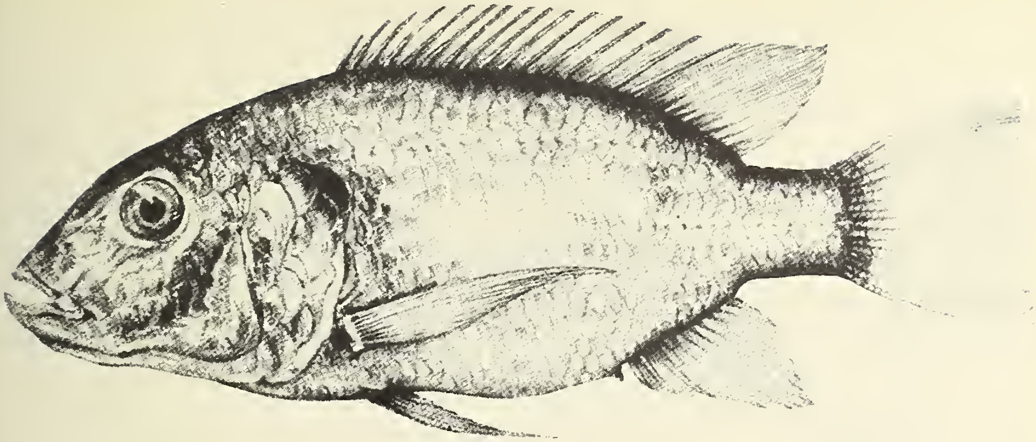


Fig. 34 *Sarotherodon caroli*, holotype. From Holly, 1930, pl. II, fig. 11.

Comments on the proportions: see *S. linnellii*, p. 000.

Teeth in the young are in 2 or 3 series, the outer bicuspid, inner tricuspid; from about 105 mm SL the tooth-band is four rows wide in at least part of its length, and from 136 mm the upper band is 4–5 rows wide, the lower 4–6. Females retain the bicuspid outer teeth and may even have a few tricuspids among them. In males the minor cusp is reduced to a shoulder or absent, but the inner teeth remain tricuspid. There are 64–118 teeth in the outer upper row in the males examined, up to 124 in the females, a difference that cannot be considered significant.

The toothed area of the lower pharyngeal is much reduced, and the blade is relatively long (Table 19 & Fig. 33).

Gill-rakers very short, (2–5) + (0–2) + (17–20), mode 19 on lower part (Table 20 & Fig. 35).

Scales in lateral line series 30–32, usually 30 or 31; $3\frac{1}{2}$ or 4 between origin of dorsal and lateral line; 2 rows on the cheek, rarely 3.

Dorsal fin see Table 20. Last spine 12·0–15·5% SL; soft rays not prolonged beyond base of caudal. Third anal spine 11·0–14·2% SL. Caudal truncate.

Vertebrae 29 (F.3) or 30 (F. 1); 14 + 15 or 14 + 16.

Size. The biggest female measured 145 mm SL, the biggest male 148·5 mm.

COLORATION. Young, at least from 60 mm SL upwards, have no tilapia-mark. The general colour is dull grey, but one male with small testes was metallic green like mature *S. linnellii*. Other mature males seen alive were bigger, and were dull grey in colour, usually with irregular dark grey or black smudges on the lower parts of head and body.

Ecology

Food

The intestine of a fish of 124 mm SL measured 293 mm, 2·36 times SL.

As in *S. linnellii*, the young are more omnivorous than the adults; the latter feed predominantly on phytoplankton (Green & Corbet *in* Trewavas *et al.*, 1972, fig. 27 & p. 81).

Breeding

The expedition of March/April 1970 (Trewavas *et al.*, 1972), which found *S. linnellii* in full breeding and brooding condition (see p. 88–9), saw no mature *S. caroli* until towards the end

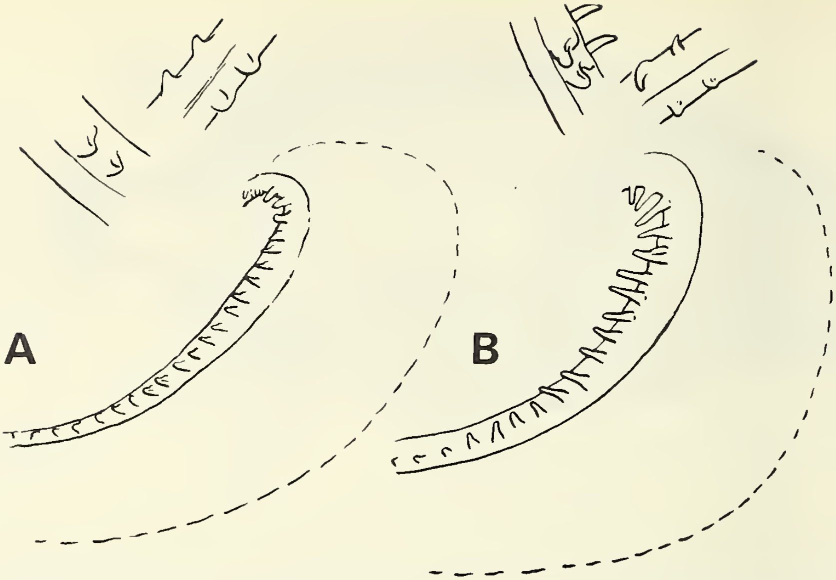


Fig. 35 First gill arch from: A, *Sarotherodon caroli*; B, *S. linnellii*, with portions of each to show the two series of rakers.

of March, and these were all males. They were not caught close inshore like the *S. linnellii* but in gill-nets set by the fishermen in deeper water. In spite of offered inducement no mature females were caught during the five weeks of the expedition, and the young found inshore were no smaller than 62 mm SL.

Three other collections (in addition to those containing the types), made in Barombi-Mbo, include specimens of *S. linnellii* or *S. caroli* or both. None of these contains ripe females of both species.

Maclaren's collection of September 1948 included a mature female *S. caroli* with ovarian eggs of 5·5–5·7 mm long diameter; there were three other *S. caroli* but no *S. linnellii.*

The Eisentraut collection of January 1955 included mature male and female *S. linnellii*, and young of 40–53 mm SL of the same species, but no *S. caroli.*

A collection made by Dr C. A. Wright in November 1963 included a ripe female *S. linnellii* with ovarian eggs measuring 5·2×4·2 mm, and a mature male of this species; a male and two females of *S. caroli* in the same collection were at an earlier stage of maturity, the biggest oocytes measuring 1·7 mm; and 26 young of 15·0–51·5 mm SL collected at the same time were all *S. linnellii.*

Although the collections including the types are too small to provide independent evidence, it may be noted that one contained *S. linnellii* but no *S. caroli*, the other *S. caroli* but no *S. linnellii.*

All this points to a non-synchronisation of the breeding cycles of the two species, and there is even a suggestion of separate breeding sites.

The males caught in March/April 1970 were dun-grey in colour with black or dark grey irregular patches on the lower parts of head and body. No histological examination was made of the testes, and it is not certain whether they were at an end of a breeding cycle or were about to begin one.

The large eggs must be mouth-brooded, but by which parent is unknown.

Distribution

Confined to Lake Barombi-Mbo, West Cameroon.

Material examined

(all from Barombi-Mbo, West Cameroon)

Museum & Reg. No.	SL(mm)	Collector
NHMW (types)	142·5, 147·5	Haberer
1959.8.18.183–187	95–147	P. I. R. Maclaren
1969.1.13.190–192	136·5–141·5	C. A. Wright
1973.5.14.745–778	62·5–147·0	J. Green, S. A. Corbet, J. Griffith & E. Trewavas

Genus *SAROTHERODON* – III

Sarotherodon galilaeus

Sarotherodon galilaeus (Linnaeus)

For synonymy and distribution see the subspecies

Distinguishing characters

A deep-bodied species (depth usually 43–56% SL, rarely as low as 38), usually pale in colour with fins uniform or inconspicuously marked except for the pink margin of the caudal. Melanin pattern of flanks either absent or forming vertical bars from dorsum to below middle of height, irregular in outline and sometimes represented by fragments. Occasional melanic individuals or populations. Caudal fin slightly emarginate, scaly only at base except in subspecies *boulengeri*.

Preorbital bone deep, in large fishes up to 28% length of head. Gill-rakers short, 19–26 (27) on lower part of first arch. Mouth small, lower jaw not exceeding 33% length of head, with very small teeth. Pharyngeal bone stout, with fine, crowded, unicuspid teeth, and long anterior blade, in adult twice as long as toothed area. Eggs about 3 mm long diameter, olive green, mouthbrooded by either or both parents.

Genital papilla of male small and simple.

Steinitz & Ben-Tuvia (1960) reported that in one of nine specimens examined, the third vertebra was not alone in contributing to the apophysis for attachment of the swimbladder. Which additional vertebra was involved was not recorded.

Subspecies

Sarotherodon g. galilaeus. Characters as the species, with melanic patches only in occasional individuals, not populations, and with the caudal naked except at the base. Depth of body usually more than 45% SL (but see p. 100). Vertebrae 28 to 30, rarely 27 or 31, mode 29 or 30 in different populations. Modal number of dorsal spines XVI. Widely distributed (see p. 95 & 110).

Sarotherodon g. multifasciatus. Characters as the nominate subspecies, but body more slender (depth 39·5–46·5% SL), and vertebrae 27–29, mode 28. Modal number of dorsal spines XV. Lake Bosumtwi, the rivers Tano (and Pra ?) in Ghana, and the rivers Bandama, Komoé and Nzi in Ivory Coast.

Sarotherodon g. borkuanus. Characters as the nominate subspecies, but all the populations dark in colour with melanic patches on lower parts of head and pectoral region. Lower pharyngeal bone less robust, with lateral lobes of toothed area narrow. Confined to the Saharan oases of Borku, Ennedi and Tibesti.

Sarotherodon g. sanagaensis. Characters as the nominate subspecies, from which it is doubtfully distinguishable by the general blue-grey to blue colour. Dorsal and caudal fins with round, clear spots on a blue-grey ground colour. Sanaga River system, Cameroon.

Sarotherodon g. boulengeri. Characters as the nominate subspecies, but caudal fin in adult covered in small scales. Lower part of the River Zaire (Congo), from Malewa Pool (Stanley Pool) to Matadi; lower Kasai; lower Ogowe (?). Fresh water.

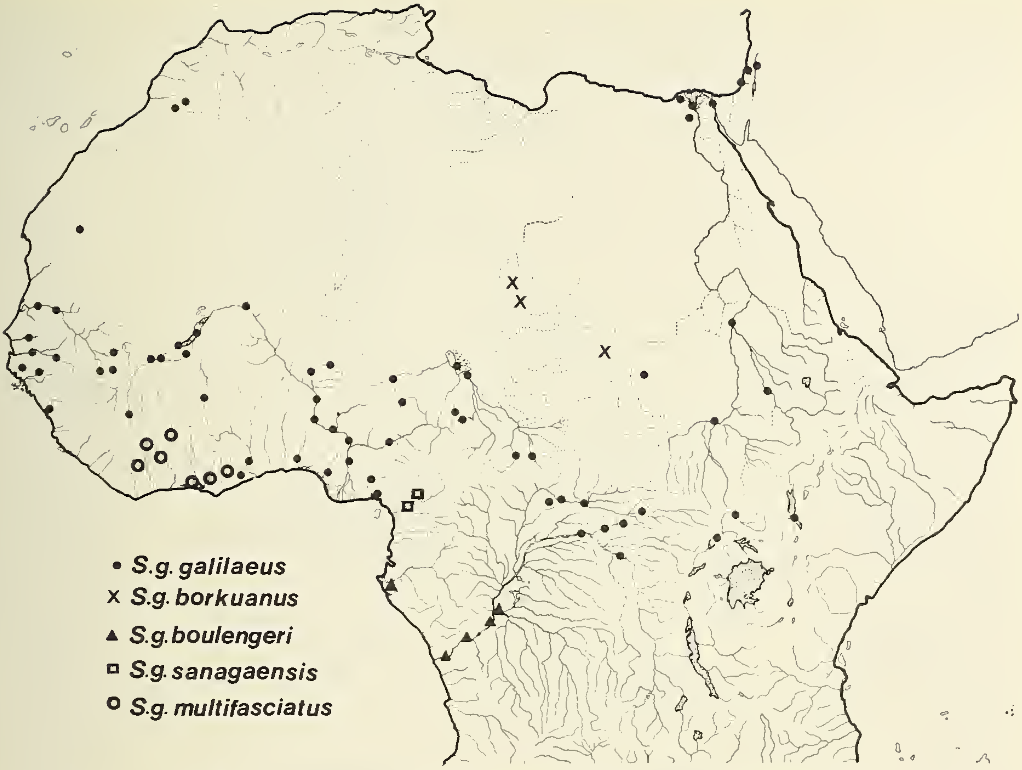


Fig. 36 Distribution of the subspecies of *Sarotherodon galilaeus.*

Sarotherodon galilaeus galilaeus (Linnaeus)

Sparus galilaeus Linnaeus, 1758:282 (*ex* Artedi and Hasselquist; Lake Genezareth = Tiberias; D XVII 14, A III 12).

Chromis galilaeus; Günther, 1862:273 (copied from Hasselquist).

Tilapia galilaea; Boulenger, 1899*a*:106, 114; *idem,* 1902*a*: 22; Pellegrin, 1903:80 (L. Menzaleh; ♀ incubates); *idem,* 1904:330; Boulenger, 1907*a*:534, pl. 95 (Nile); *idem,* 1915:169, fig. 109; Pellegrin, 1914:131, pl. 11, fig. 4 (L. Chad); *idem,* 1919*b*:206 (Gribingui); *idem,* 1922*a*:268 (Senegal); *idem,* 1923:280, fig. 60; *idem,* 1929:360 (Benue system, Cameroon); Pfaff, 1933:296 (Kabara, Middle Niger); Liebman, 1933: 886 (Tiberias, breeding); Svensson, 1933:91, pl. vii, fig. 3 (Gambia, juv); Trewavas, 1933:317, fig. 3c (Lake Rudolf); Bodenheimer, 1935:427, pl. 65, fig. 6 (Palestine); Hornell, 1935:84 (Palestine); Bodenheimer, 1937:262; Norman & Trewavas in Washbourn, 1938:56 (L. Huleh); Fowler, 1936:326, fig. 134; Monard, 1940:100 (Portuguese Guinea = Guinée Bissau); Trewavas, 1942:530 (Palestine); Irvine & Trewavas *in* Irvine, 1947:276 (Ghana); Girgis, 1948:124 (vernac. names); Pellegrin, 1949:138 (Middle Niger); Monod, 1949:41 (bionomics in West Africa); Gauthier-Lièvre, 1949:55 (food); Lépinay & Nemeth, 1949:229 (Draa, R., Morocco); Sandon, 1950:56 (Nile, colour); Monod, 1951:807 (Adrar, Mauretania); Estève, 1952 (Adrar); Steinitz, 1954:258–263 (history); Daget, 1954:337, fig. 130 (Middle Niger); Lowe-McConnell, 1955*b*:259 (Lake Albert); *idem,* 1955*c*:46, figs 1, 2, table I (fecundity); Yashouv, 1956, 1958 (bionomics in Israel); Jensen, 1957: (growth in Egypt); Greenwood, 1958:112, fig. 59 (Lake Albert); Lowe-McConnell, 1959:10; Wunder, 1960:13 (bionomics in Egypt); Ben-Tuvia, 1959 & 1960 (bionomics in L. Tiberias); Daget, 1960*a*:4 (West Africa); *idem,* 1960*c*:327 (Comoë, but see *S. g. multifasciatus,* & Upper Volta); *idem,* 1961*a*:511 (Middle Senegal R.); *idem,* 1961*c*:354 (Gambia R.); Elster *et al.,* 1960:70, 85, fig. 20; Elster & Vollenweider, 1961:286 (Lower Nile); El Bolok & Koura, 1961 (growth in Lake Tiberias); Chervinsky, 1961 (in fresh & brackish water); Daget, 1962*a*:160

Table 21. Frequencies of numbers of vertebrae and scales in the lateral line series in populations of *S. g. galilaeus* and related species. Numbers of vertebrae for *S. g. borkuanus* are from radiographs of the Ennedi collection reported on by Fowler (1949) kindly supplied by Dr and Mrs Böhlke of the Philadelphia Academy.

	Vertebrae					Scales lateral line						
	27	28	29	30	31	28	29	30	31	32	33	34
S. g. galilaeus												
Jordan Valley			15	22	1				22	4		
Na'aman, Kishon, Yarkon			5	13	1			2	13	5		
Lower Nile and Khartoum			8	6				3½	19	5½		
Lake Turkana (Rudolf)								1	4	1		
Lake Albert			6	1			1	7	5			
R. Ubanghi							2½	4½				
W. Africa (incl. data from Daget & Iltis)	1	17	152	16			1	44	20	1		
Lake Chad (Blache *et al*).						4%	36%	56%	4%			
S. g. sanagaensis (incl. Daget, 1960*a*)			10	2			6	8	2	1		
S. g. borkuanus		1	42	8				[30–31]				
S. g. multifasciatus												
Lake Bosumtwi	2	8	7			5	11	10	2			
Ivory Coast	2	62	5									
Tano R.		1					1					
S. g. boulengeri			6	2			1	3	2			
S. tournieri	1	2				1	3					
S. occidentalis			4	5					1½	1½		
S. caudomarginatus					3					4	3	1

(Corubal R. basin); *idem*, 1962*b* (growth of scales); Trewavas, 1962*b*:177 (Lake Barombi Kotto); Gosse, 1963:22. pl. 9, fig. 1 (Yangambi, Zaire); Daget & Stauch, 1963*b*: 103 (Benue R.); Peters, 1963*b* (number & wt. of eggs); Kraft & Peters, 1963 (egg structure & oogenesis); Fishelson & Heinrich, 1963:507 (breeding); Blache *et al.*, 1964: 237, fig. 131 (Chad); Thys van den Audenaerde, 1963: fig. 5; *idem*, 1964:112, pl. 10 (L. Albert & Zaire basin); Chervinsky, 1964 (failure to hybridize with *S. niloticus*); Daget & Iltis, 1965:266, fig. 168 (Ivory Coast); Chervinsky, 1965 (sex difference in length of fin-rays); Fishelson, 1966*a* & *b* (breeding & development); Apfelbach, 1966 (breeding); Greenwood, 1966:115 fig. 59 (L. Albert); Burchard, 1967:143, fig. 170 & pl. 10 (Nigeria); Fishelson, 1967:70 (colour, breeding); Heinrich, 1967*a* (reproductive behaviour); Destexhe-Gomez & Ruwet, 1967 (reactions of hatchlings); Thys van den Audenaerde, 1968*a*: synonyms; *idem*, 1968*b* (bibliography, subspecies & synonyms); Iles & Holden, 1969 (parental care); Petr, 1967*a* (food); Lawson *et al.*, 1969: fig. 18 (food), Loubens, 1969 (L. Chad); Daget, 1969 (Senegal R.); Fryer & Iles, 1972 (summary of bionomics; see index to that work); Lowe-McConnell, 1972:21, pl. 27 (key); Holden & reed, 1972:51 fig. 63: Goldstein, 1973:247 (photo); Lewis, 1974*a*:37, 91, fig. (Kainji); *idem*, 1974*b*:295.

Sarotherodon galilaeus; Trewavas, 1973*a*: 23; Corbet *et al.*, 1973:317, figs 5, 6 (food); Johnson, 1974; Sydenham, 1977:984 (Ogun R.); Ben-Tuvia, 1978:421, pl. 44); Kornfield *et al.*, 1980; Fishelson, 1980.

Sarotherodon galilaeus galilaeus; Trewavas, 1974:408.

Tilapia pleuromelas Duméril, 1859:253 (Senegal); Günther, 1862:271 (copied); Boulenger, 1899*a*:107, 118 (copied); Schultz, 1942:344.

Tilapia galilaea galilaea & *T. g. pleuromelas*; Thys van den Audenaerde, 1968*b*:xxxix; *idem*, 1971.

Tilapia lateralis Duméril, 1859:253 (Senegal); Günther, 1862:272 (copied).

Tilapia macrocentra Duméril, 1859:256 (Senegal); Boulenger, 1899*a*:117.

Table 22. Frequencies of dorsal and anal fin-ray numbers in populations of *S. galilaeus*. Figures from Daget are included for 'West Africa'; he gives spines and soft rays separately, but not totals or combinations. The figures for Lake Chad are from Blache *et al.*, expressed as percentages; they also do not give totals, but their dorsal soft rays are 11–14, mode 13, thus XVI 13 must be the commonest combination. Figures for the Sanaga River are from Daget (1960*a*), Thys (1966) and NHMW 13981–2.

	Dorsal spines				Total dorsal rays					Soft anal			
	XIV	XV	XVI	XVII	27	28	29	30	31	9	10	11	12
S. g. galilaeus													
Jordan Valley		1	26	4		11	20				16	14	
Medit. rivers			19	2		4	15	2			3	15	1
Lower Nile & Khartoum		1	27	5		5	26	2			8	10	2
Lake Turkana		3	4			4	2	1			2	4	1
Lake Albert		6	9		3	10	2			2	8	3	
Ubangui R.		1	7			6	2				5	2	
West Africa	1	42	120	2	3	30	41	1		3	56	107	2
Lake Chad		4%	96%										
S. g. sanagaensis		2	23	2	2	6	6			14	8	6	
S. g. borkuanus													
(Pellegrin)		[XV–XVI]								[9–10]			
(ANSP)		2	15	2		14	5			[9–11]			
S. g. multifasciatus													
Lake Bosumtwi	1	47	2		7	44	4	1		4	27	11	
Ivory Coast (Daget)		[XIV–XVI]											
Tano R.		1			1						1		
S. g. boulengeri			5	2		5	2			2	3	2	

Chromis niloticus (*non* Linn.); Günther, 1862:267 (part, specimens from Khartoum); *idem*, 1865:490 (part, Palestine); Steindachner, 1870 (part, Senegal); Tristram, 1884:164, pl. 18, fig. 1.

Chromis tiberiadis Lortet, 1883:135, pl. 6; Tristram, 1884:164; Barrois, 1894:252, 273, 300 (after Lortet); Vinciguerra, 1926:213.

Chromis microstomus Lortet, 1883:139, pl. 8, fig. 1 (Lakes Tiberias & Huleh); Barrois, 1894:(after Lortet); Tristram, 1884:167.

Tilapia aurea (*non* Steindachner); Trewavas, 1966*a*: fig. 2 only (from Tristram).

TYPES. Type of *S. galilaeus*: none.

Holotype of *T. pleuromelas*: 180+50 mm. MNHN A 9329, Senegal. Duméril's data corrected by Pellegrin, 1904, as D XV 14, A III 11, lower gill-rakers 24; see also Thys, 1968*a*.

Holotype of *T. lateralis*: 130+40 mm, MNHN A 9370, Senegal. Duméril's data corrected by Pellegrin, 1904, as D XVI 13, A III 11, lower gill-rakers 24; see also Thys, 1968*a*.

Holotype of *T. macrocentra*: 250+60 mm. MNHN A 9373, Senegal. Duméril's data corrected by Pellegrin, 1904, as D XV 13, A III 11, lower gill-rakers 23; see also Thys, 1968*a*.

Syntypes of *Chromis tiberiadis*: 3 fishes of 229, 239, and 265 mm SL respectively, from L. Huleh. Mus. Lyon 3084.

Syntypes of *Chromis microstomus*: 2 fishes of 92·0 and 106·5 mm SL respectively, from Lake Huleh. Mus. Lyon 3074; both with 21 lower gill-rakers.

Table 23. Frequencies of gill-raker numbers in samples of the subspecies of *S. galilaeus*. West African samples are divided into two groups, (1) from Chad, Niger, Benue and Volta basins, (2) from the Senegal, Gambia and Geba Rivers. Data for *S. g. sanagaensis* partly from Thys. The raker at the angle is omitted and specimens of less than 55 mm SL are usually omitted, although they probably contributed to the range quoted for *S. g. borkuanus*.

	Gill-rakers on lower part of first arch										
	18	19	20	21	22	23	24	25	26	27	28
S. g. galilaeus											
Jordan Valley			1	1	5	6	4				
Lower Nile			1	3	4	8	8	3			
Lake Turkana						1	6				
Lake Albert				1	2	6	2				
Ubangui R.			1	3	3	1					
W. Africa (1)			2	8	8	4	7		1		
W. Africa (2)				1	2	2	3	3	2	1	
S. g. sanagaensis		2	2	3	1	4	1	1			
S. g. multifasciatus			3	8	9	4		1			
Tano R.				1							
S. g. borkuanus		[19–21]									
S. g. boulengeri				1	2	1	3				

Distinguishing characters

See p. 94 and Tables 21 & 22.

Description

Topotypes

Based on 19 fishes of 62–223 mm SL from Lakes Huleh and Tiberias (Kinereth), and the River Jordan. Additional specimens from the same localities are included for meristic characters. Comments on other populations of the nominate subspecies follow on p. 99 ff.

Proportions are set out in Table 24 and meristic characters in Tables 21–23.

As the proportions indicate, this is a deep-bodied fish with a small mouth and wide interorbital space. The profile of the snout is straight and its measured length is increased by the width of the skull. The preorbital bone is deep, in adults contrasting with that of *O. niloticus* and *O. aureus*, found in the same waters.

Teeth very small with slender shafts, in 4–8 rows, 62–116 in outer row of upper jaw, outermost bicuspid, inner tricuspid.

Pharyngeal teeth very small and crowded, even the posterior having no minor cusp, their tips rounded or bilaterally bevelled; a broad band of dark-brown-tipped teeth posteriorly. Dentigerous area with rounded lateral lobes and short anterior apex. Lateral apophyses of bone scarcely or not extending behind the tooth-plate (Fig. 38). For proportions of bone see Table 24.

Gill-rakers on anterior arch (3–5)+1+(20–25) (Table 24). Microbranchiospines on outer sides of arches 2–4.

Vertebrae: see Table 21A. In one of those with 29 there are only 28 centra, one of them carrying two neural and haemal arches; in one with 30 two centra are abnormally short.

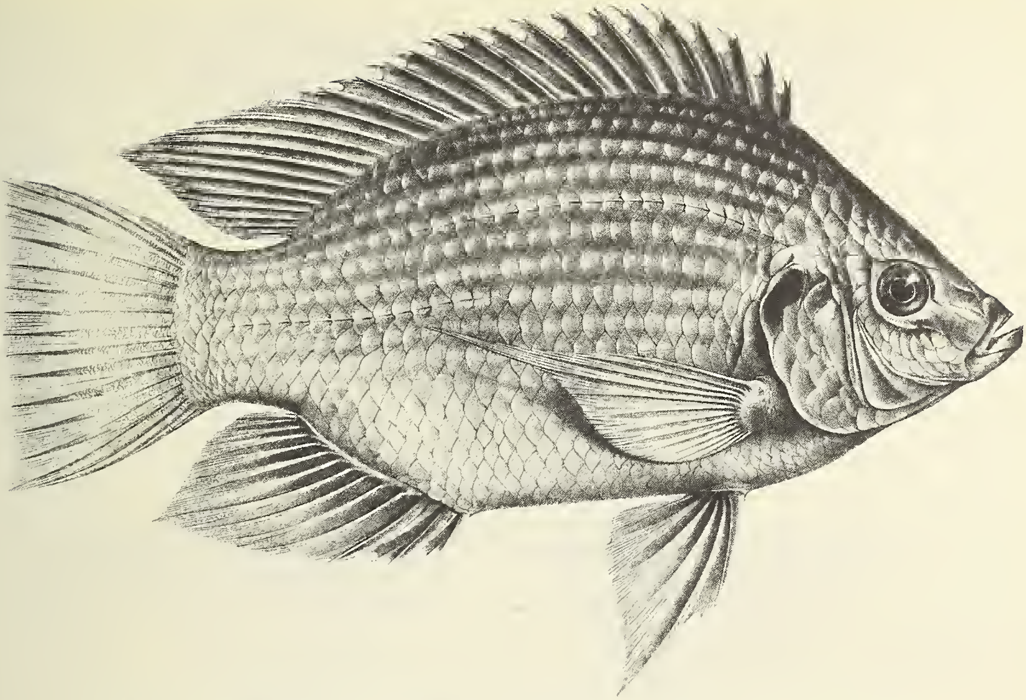


Fig. 37 *Sarotherodon g. galilaeus*, from Boulenger, 1907*a*, pl. 95. 340 mm SL.

Scales on cheek in two rows; in lateral line series see Table 21; $3\frac{1}{2}$–$4\frac{1}{2}$, usually 4 or $4\frac{1}{2}$, between origin of dorsal and lateral line.

Dorsal soft rays a little longer in mature males than in females (Chervinsky, 1965).

Caudal slightly emarginate, not densely scaled, but in large fishes small scales may extend on or between the rays for half the length of the fin.

Pectoral usually extending to above vent or spinous anal fin. Pelvic produced to a short white filament reaching the vent.

Genital papilla small in both sexes, subconical in male; a short, scalloped funnel in mature female.

COLORATION. The general impression is of a pale fish, silver-grey above to white below (cf. the Arab name *mousht abyad*, white mousht), in contrast to the darker colours of other cichlids in the same waters. In some emotional states it can show conspicuous markings. The details in Table 25 were provided by Dr Lev Fishelson and are based on three pairs sexually mature at 100–110 mm SL, living in an aquarium at Tel Aviv. Especially to be noticed are the black vertical bars on the body, which may be formed of a discontinuous array of spots or become continuous or entirely switched off in the same individual. In the preserved fishes available from the Jordan Valley they are present with more or less emphasis in smaller specimens, but absent in those of 130 mm SL upwards. In young of 30–90 mm SL 8 or 9 regular, facultative, juvenile bars are present on the body as in most young *Sarotherodon* and *Tilapia*.

The coloured dorsal margin, variously described as 'orange' or 'pinkish', is only occasionally mentioned in descriptions of other populations, but the broader, more intense pink or reddish margin of the caudal usually earns mention (see also p. 102).

Variation

The above description applies to this subspecies throughout its wide distribution, extending to

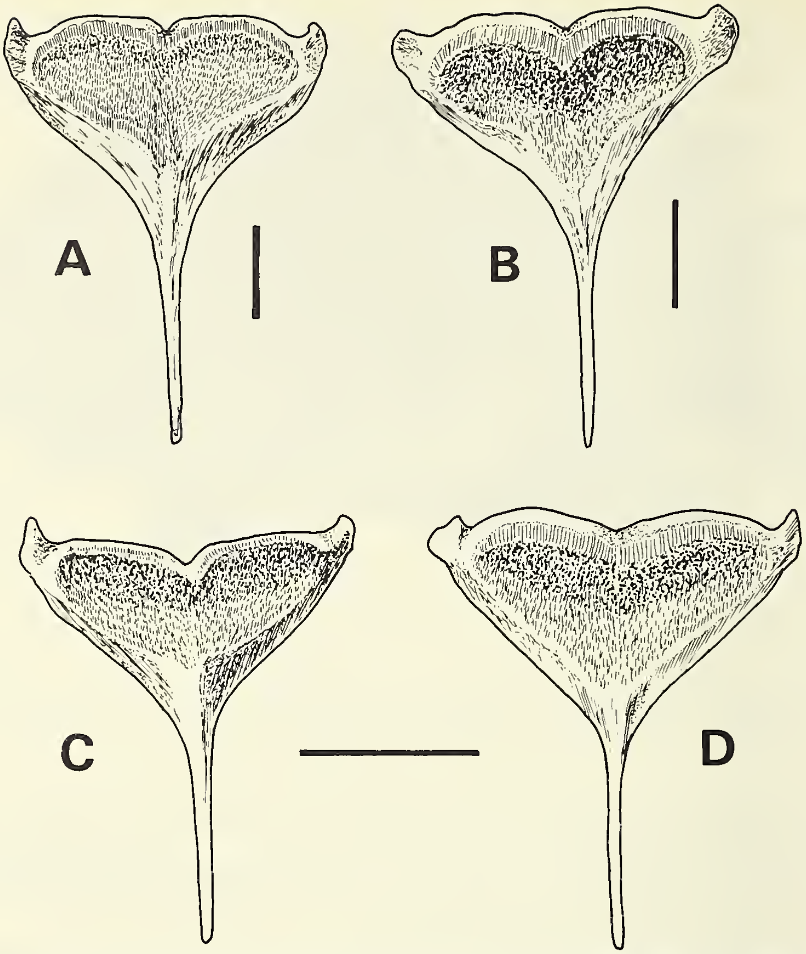


Fig. 38 *Sarotherodon galilaeus*, lower pharyngeal bones of: A, *S. g. galilaeus* from Lake Albert, 200 mm SL: B, *S. g. multifasciatus* from Lake Bosumtwi, 140 mm SL; C, *S. g. borkuanus* from Borku, 85 mm SL; D, *S. g. boulengeri* from Ogowe R., 88 mm SL. Scales = 5 mm.

the Nile, the Chad basin, West Africa, the Ubangui and West Cameroon, with the following qualifications.

In the Jordan Valley the only adult fish examined with a depth ratio of less than 45% SL is one of 208 mm SL preserved a century ago by Canon Tristram. Such a slender form is rare in other populations except Nungwa reservoir near Accra, and in Lakes Barombi Kotto and Mboandong in West Cameroon. From Nungwa five out of fourteen individuals gave a value of less than 45% and in one of them it was only 38%. In Lake Kotto the depth was 40·5–43·0% in three and the highest ratio was 46·5%. These samples account for most of the overlap with the characteristically more slender *S. g. multifasciatus*, but in meristic characters they agree with *S. g. galilaeus*. In contrast, eleven of 62 to 270 mm SL from the rivers Senegal and Gambia are all deep-bodied, the depth being 48–55% SL, thus in the higher part of the range of the topotypes.

The ratio length of head/SL does not seem to follow any allometric rule within the wide size-range used, nor to characterize a population. The highest values are in a Tiberias fish of SL 215 mm (39%), a Yarkon River specimen of 83 mm (38·6%), one from Lake Albert of SL 201 mm

Table 24. Proportions in specimens of *S. galilaeus galilaeus* from the Jordan Valley (topotypes) at SL 62–223 mm (N = 19). The last item is the length of the anterior blade of the lower pharyngeal bone divided by the median length of the dentigerous area.

As % SL	
Depth	43·0–56·5, usually more than 45.
L. head	32·5–39·0
L. pect. fin	(36) 37·5–50·0
L. last D spine	15·5–17·5
L. 3rd anal spine	14·0–16·5, always less than last dorsal.
L. caud. ped.	9·0–13·5
Caud. ped. l/d	0·6–0·9
As % l. head	
L. snout	29·0–41·0, positively allometric.
Eye	18·0–32·0, negatively allometric.
D. preorb.	19·5–28·5, positively allometric.
Interorb.	36·0–44·0, at SL over 110 mm not less than 38.
Lower jaw	28·0–32·5, with neither allometry nor sexual dimorphism.
W. pharyngeal	32·0–37·0
Med. l. phar.	35·5–41·5
Phar. blade/dent.	1·5–2·0 (1·25 in young).

Table 25. Colour in *S. g. galilaeus.* Observations by L. Fishelson.

	Non-reproductive	Reproductive	Brooding
Flanks	silvery	operculum brighter silver	same
Dorsum	light yellowish	greyish	greyish
Venter	white	silvery, dusky between pelvics	silvery, chin dusky
Black vertical bands on body	formed of distinct, rather irregularly placed spots	prominent, continuous	absent
Mid-lateral longitudinal band	formed of distinct black blots	?	absent
Fins: D general	transparent	blackish	transparent
soft part	6–8 yellow spots	—	yellow spots
margin	orange	pinkish	orange
C margin	orange	pinkish	reddish pink
V	blackish	blackish with pink margin	—
Iris	yellow	golden yellow with vertical black bar	?

(38·3%) and one of 270 mm from the Corubal River (about 38·5%). Small heads were found in two of 86 and 95 mm from the River Jordan (32·5 and 32·8%) and one of 201 mm from Khartoum (33·0%) (see also *S. g. sanagaensis,* p. 120).

The pectoral fin is rarely less than 40% SL, and probably when it is so it is a damaged and mended fin. It reaches 52% SL in one Lake Albert fish, but this is exceptional.

The preorbital bone reaches a depth of 29·4% length of head in a big fish (311 mm SL) from Birket Karun.

An interorbital width of more than 40% length of head is not reached by any of the fishes measured except some of those from the former Lake Huleh.

The mouth is small in all samples, but the lower jaw is as much as 33% length of head in two big fishes.

In meristic characters there are some regional differences. Table 21 shows that the modal number of vertebrae in the Jordan Valley and the Mediterranean rivers of Israel is 30, but in West Africa is 29. The scales in the lateral line series show the same difference of one in the mode, which is 31 in Asia and the Lower Nile, but 30 in West Africa and Lake Albert.

The modal number of dorsal fin spines is XVI throughout the subspecies, but the total number of dorsal fin-rays shows at least a shift in the mean on passing from East to West (Table 22). Again Lake Albert is aligned with the West.

Schultz (1942) and Thys (1968*b* & 1971) have used the name *pleuromelas*, Schultz for the whole species and for the wrong reason (believing *galilaeus* to be invalid) and Thys for the West African populations, without giving a reason. Daget & Iltis (1965) raised the question of a possible subspecific distinction between eastern and western populations, and suggested that vertebral numbers might prove decisive. The results given in Table 21 afford some support, but I think not enough to justify using the names. I am aware that this is a matter of opinion. I am influenced partly by the evidence of the Lake Albert sample, which in meristic characters falls with the western group, and also by the evidence from Jebel Marra that the distribution was continuous across the Sahara at a time geologically speaking not far distant. Moreover it is now known that wherever enough brooding parents have been examined this function is biparental in West Africa as well as in the Jordan Valley and that the species is ecologically as well as structurally uniform.

COLORATION. Many accounts have included descriptions of the colour in freshly caught fishes. From these a general account may be compiled.

The general colour is pale grey or greenish grey, head in mature fish brassy yellow, throat and belly white. Fins pale; dorsal without markings or with pale yellow spots (Trewavas, West Cameroon as well as Fishelson, Israel), or stripes (Blache *et al.*, Lake Chad) on a pale grey ground; the lappets colourless, pale grey, yellow with grey edge or pink, these variants having been observed in individuals of the same population (personal observation, Nungwa Reservoir, Ghana); caudal with definite mauve-pink margin grading to pale grey basally; pelvics colourless, pale grey or tinged pink or orange, with white leading edge and filament. Thys (pers. commn) observed red dorsal lappets in young, but not in adults, in the Senegal River.

In the Nile the colour is greenish grey with pink-edged caudal (Boulenger, 1907, from Loat). A specimen observed by me in Lake Albert had in addition to the pink margins of dorsal, anal and caudal fins, a few horizontal pink streaks on the scale-rows below the mid-lateral level. In some preserved Nile fishes, including that illustrated by Boulenger in 1907, dark streaks, one on each scale, give the effect of horizontal stripes.

Upon the general pale colour some adults, in most preserved samples, display the irregular vertical bars characteristic of this species and noted by Fishelson in his captive fishes, when they were not brooding young (see Fishelson, 1966*b*, fig. 8). In some populations the general silver-grey or buff colour is replaced by pale translucent yellow, and a large specimen from Lake Turkana was described as golden yellow all over (Welcomme, pers. commn).

Numerous captive individuals of about 200 mm SL, in a large tank at Baobab fish farm at Bamburi, near Mombasa, were very uniform in pigmentation, all exhibiting the dark irregular vertical bars on the upper three-fifths of the body and black pigment on the operculum and near the base of the pectoral fin. The basic colour was yellow-buff. This captive population originated from Lake Turkana. The tank, designed by Mr René Haller, was circular, about 15 m in

Fig. 39 *Sarotherodon g. galilaeus*, above, 120 mm SL from Benue River, BMNH 1971.9.28.177; below, young of 71·5 mm SL from Kioira, Falémé River, Lower Senegal, BMNH 1978.3.13.10.

diameter, irrigated, and contained also at least two species of *Oreochromis*. In these conditions none of the fishes exhibited territorial behaviour.

Exceptional colouring has been found in some samples or populations. Monod (1949) recorded from the Middle Niger a rare form with golden-yellow patches irregularly disposed and also a melanic form, in which the dark pigment may spread from the bases of the vertical fins to invade the whole body. In the BMNH, a sample of four from the Benue River includes two immature males of 120 mm SL with irregular black patches and smudges on the lower parts of the head, on the operculum and near the base of the pectoral, and some black spots on the posterior part of the dorsal (Fig. 39). Dr G. McG. Reid, who collected them, says that this colouring is typical of the Benue population (but there are some in BMNH without it). Similar intense black patches are present in a sample from Ras el Ain on the Yarkon River (which enters the Mediterranean near Jaffa), and are also characteristic of *S. g. borkuanus*.

Ecology

An admirable account of the ecology of *S. galilaeus* has been given by Johnson (1974), who used the same original sources as form the basis of the following summary. The reader is referred to Johnson for information more specifically related to fishery and fish-culture, and is advised to use Johnson's paper as well as the following account.

Most of our ecological knowledge is based on the nominate subspecies as understood here. The exception is S. A. Whyte's work (1975) on *S. g. multifasciatus*, which is discussed under that heading (p. 115).

Food

The intestine increases in relative length with the growth of the fish. Ben-Tuvia (1960) found the ratio length of intestine/total length to be 1·1 to 1·2 in young and 6·0 to 8·2 in adults, and Monod obtained a similar ratio (8·0) in a 30 cm West African example. Ben-Tuvia reported on the food in Lake Tiberias. In the stomachs of five very young specimens (TL 11–21 mm) he found mainly zooplankton, but older fishes fed mainly on phytoplankton, which was present in the gut according to the abundance of its component species in the lake.

In the Nile delta Wunder (1960) recorded rather different feeding habits. In fresh water the gut contained mainly epiphytic algae and bottom debris including disintegrating parts of higher plants and dead plankton. In winter and spring many stomachs of *S. galilaeus* from fresh water were filled with red chironomid larvae, and snails were also present. In water of high salinity in Lake Borollos this species was feeding on marine polychaets! This must be regarded as exceptional, but is a measure of the opportunism of *S. galilaeus*.

Gauthier-Lièvre (1949) analysed the gut-contents of several specimens of *S. galilaeus* and *O. niloticus* from the Niger and found a considerable spectrum of algal species present in both. The fishes were all captured within a few weeks, mostly within a few days in June, and what was present in the gut of one species was present also in the other in about the same quantities. Mme Gauthier-Lièvre deduced from the presence in all of some cells derived from Gramineae that the fishes browsed the young shoots and epiphytic growths, but in addition she found a notable proportion of planktonic algae, as well as some planktonic Crustacea, which were digested first.

Daget (1954) records that the diet in the Middle Niger consists of plankton and benthos, more of the latter. Petr (1967) and Lawson *et al.* (1969) also list adult *S. galilaeus* as feeding on phytoplankton and planktonic debris in Volta Lake, where *O. niloticus*, though with the same preference, is more omnivorous.

From Lake Barombi Kotto (West Cameroon) Corbet *et al.* (1973) examined six adult individuals, all of which had phytoplankton as the main stomach contents. In this lake the phytoplankton, dominated by *Microcystis*, is so dense that the water is opaque and green-brown in colour, and the two species of *Tilapia* resident in the lake also feed on phytoplankton, although one of them (*T. mariae*) elsewhere uses mainly epiphytic and epilithic algae, and the other (*T. kottae*) belongs to a section of the genus equipped for eating macrophytes.

In Lake Chad, Lauzanne & Iltis (1975) found that *S. galilaeus* fed mainly on the rich bottom film, filamentous blue-green algae being the most important component of the diet. They concluded that there was a degree of selection on the part of the fish, but were unable to point to a selecting mechanism.

Spataru (1976) also found evidence of selective feeding in Lake Kinneret (Tiberias), where among the species in the phytoplankton *Peridinium cinctum af westi* formed a high percentage of the food, not only in March–April, its blooming time, but also in Autumn, when it forms a lower percentage of the plankton. This species was efficiently digested.

Size and growth

Maximum sizes have been given as follows: Lake Tiberias 38 cm, 1100 g, but this limit may have been dictated by the mesh size of the nets used (Ben-Tuvia, 1959, 1960); Middle Niger 41 cm, 1694 g (Monod, 1949).

Growth studies have been made on the populations of Lake Tiberias (Ben-Tuvia, 1959, 1960; El-Bolok & Koura, 1961), of Noussa Hydrodrome in Lake Mareotis (Mariout), Nile delta (Jensen, 1958), Middle Niger (Daget, 1962), and Lake Chad (Blache *et al.*, 1964). In all these localities there are marked seasonal differences in temperature and in the Niger there is an annual regime of flood alternating with dry season. (The floods are the result, not of local rains, but of rains in the upland sources of the Niger.) Annual zones are produced on the scales and can be used to determine the age and to back-calculate the growth. Daget (1962*b*) made a thorough investigation of the relation between length of scale and standard length, and established the law governing this relation during the first two years and the different law governing it thereafter. The change was associated with the onset of sexual maturity, which slows the growth in both length and weight. The other investigators found the same change in growth-rate and Ben-Tuvia distinguished between its effect on male and female, finding it greater in the female. Most of his fishes over 33 cm TL were males.

A less extensive study by Banks & Holden (1965:24) found no significant difference between the sexes, but most of their specimens were believed to be under 2 years of age.

Table 26 reproduces figures given in two studies on Lake Tiberias, one for Noussa Hydrodrome and one for Lake Chad. El-Bolok & Koura used fishes caught in the northern part of Lake Tiberias near the outflow of a seasonal river whose estuary bed in the dry season was grazed and manured by cattle. Ben-Tuvia's samples came from a wider area in the lake. Jensen's population inhabited an area of 504 hectares in Lake Mariout enclosed by a concrete embankment, the water being not more than 3·5 metres deep at its highest level, with a pH of 8·12 to 8·50, and chlorinity fluctuating between 1·53 and 2·26 parts per thousand. Jensen (1958) and El-Bolok & Koura (1961) calculated their measurements for the end of the first, second, third etc. year of life. Ben-Tuvia's ages were I = 1+ years, II = 2+ etc. With this in mind, the table shows that the results of the two studies on Lake Tiberias are very close, but by comparison the growth of *S. galilaeus* in Noussa Hydrodrome falls off at the end of the third year, and thereafter growth is almost negligible. Of the environmental factors accounting for the difference it may be surmized that the shallowness of the Hydrodrome water, allowing the fishes no escape from the low winter temperatures of about 13°C, and the possible overcrowding (by other species) of this small area were the most important.

The figures for Lake Chad are converted, with the help of Ben-Tuvia's conversion diagram (1959, fig. 5), from the standard lengths given by Blache *et al.* (1964:239). They are the length of fishes with respectively 1 clear marginal zone on the scale, 1 marginal and 1 other, 1 marginal and 2 others etc., which roughly correspond to Ben-Tuvia's I, II, III etc. For the first two years growth appears to be a little faster than in Lake Tiberias, but after the third year the length is comparable to that attained by males in Ben-Tuvia's samples.

Table 26. *Sarotherodon galilaeus galilaeus.* Average total lengths (in cm) attained in successive years in Noussa Hydrodrome, Lake Mariout (Jensen, 1957), Lake Tiberias (El-Bolok & Koura, 1961; Ben-Tuvia, 1960), and Lake Chad (converted from Blache *et al.*, 1964). See text.

Year of life	1	2	3	4	5	6	7
Mariout, Jensen	8·3	21·6	25·3	27·7	28·1	29·8	
L. Tiberias, El-B and K	9·1	20·6	26·6	31·5	33·4	34·7	34·9
Year-group	I	II	III	IV	V	VI	VII
L. Tiberias,							
Ben-Tuvia ♂	13·8	22·7	27·4	31·5	32·5	34·1	35·3
♀	14·0	22·4	26·5	29·1	31·0	32·3	32·9
L. Chad, Blache *et al.*	14·7	24·8	28·0	31·2	32·5		

Table 27. *Sarotherodon galilaeus galilaeus.* Figures from El-Bolok & Koura (1961), Ben-Tuvia (1960), and Daget (1954) showing the weight (in grams) at corresponding total lengths (in cms). Ben-Tuvia's figures are read from his graph (fig. 4), Daget's are selected from a table (1954, p. 339).

Tiberias		Tiberias		Niger	
El-Bolok & Koura		Ben-Tuvia		Daget	
TL	W	TL	W	TL	W
20·6	193	20·5	175	20·5	199
26·6	427	26·0	420	26·5	415
31·5	722	31·0	700	31·0	652
33·4	865	33·5	880	33·0	828
34·7	974	35·0	1000	35·0	972
34·9	992				

Table 28. Comparison of length of head as % SL and depth of preorbital bone as % length of head in samples of *S. galilaeus* in the size-range 85–135·5 mm SL. Within this range there is no detectable allometry in the size of the head, but the ranges for depth of preorbital reflect a positive allometry in this measurement, and make the differences between ratios even less significant than the figures alone.

In the size of the head the small samples from Kotto and the Sanaga differ from each other, but each is included in the range of one of the bigger samples, that from Kotto in the Nigerian, that of the Sanaga in the Levantine.

	N	SL (mm)	Head % SL	Preorbital % head
Levant	11	85·0–131·5	32·5–35·0 $\bar{x}=34{\cdot}15\pm0{\cdot}25$	20·9–25·7 $\bar{x}=22{\cdot}8\pm0{\cdot}48$
Nile system	8	85·0–128·5	33·6–36·8 $\bar{x}=34{\cdot}65\pm0{\cdot}37$	19·8–24·3 $\bar{x}=21{\cdot}8\pm0{\cdot}53$
Nigeria	19	85·0–135·5	33·0–38·0 $\bar{x}=35{\cdot}23\pm0{\cdot}31$	19·7–26·1 $\bar{x}=23{\cdot}26\pm0{\cdot}35$
Kotto	4	120–131	35·0–35·2 $\bar{x}=35{\cdot}07\pm0{\cdot}05$	23·6–26·6 $\bar{x}=24{\cdot}8\pm0{\cdot}67$
Sanaga	4	88–131	32·0–34·6 $\bar{x}=33{\cdot}8\pm0{\cdot}61$	25·0–27·8 $\bar{x}=25{\cdot}8\pm0{\cdot}67$

Table 27 reproduces figures from three authors showing the relationship between weight and length. These are all averages from rather small numbers at a given length and the correspondence is remarkably close.

Salinity tolerance

The tolerances of this species have not been tested experimentally, but Wunder found that, together with *Tilapia zillii* and in contrast to *O. niloticus*, it was able to live in the more saline parts of the Nile delta lakes. Preliminary tests by Chervinski (1961) showed no adverse effect on the growth in ponds of 50% sea-water. Unlike *Tilapia zillii*, however, it failed to survive the very high salinity in Lake Qarun (El Zarka, 1961).

Jensen (1957) reported it in Lake Mariout at a chlorinity of up to 2·26 parts per thousand, and Fishelson (1980) found it more euryhaline than *O. niloticus* and described the microstructure of the gill-filaments in relation to adaptation to sea-water.

Temperature tolerance

Since *S. galilaeus* tolerates the winter temperatures of Egypt and the Mediterranean rivers of Israel it must be more cold-resistant than *O. mossambicus*, although probably confinement to shallow water in winter was partly responsible for retarding its growth in the conditions described by Jensen (1958). Heavy mortality was reported in the former Lake Huleh (Bodenheimer, 1935; Ricardo-Bertram, 1942) when the snow waters from Mount Hermon came down into the lake. The water temperature at that time reported by Ricardo-Bertram was 9°C. An attempt to introduce it to the hatchery at Jonkershoek, Cape Province, South Africa, came to an end when it failed to survive the winter there (Van Schoor, 1966; temperatures not given).

Breeding

The most profound studies of all aspects of reproduction in this species have been made on the population of Lake Tiberias, and on aquarium specimens derived from this population. Observations were made in the field by Bodenheimer (1927, 1935), Liebman (1933), and more systematically by Ben-Tuvia (1959; 1960); and in aquaria by Fishelson & Heinrich (1963), Fishelson (1966), Apfelbach (1966 & 1969*b*), and Heinrich (1967*a*). Peters (1963) and Kraft & Peters (1963) included the species in their studies of eggs and oogenesis in *Tilapia* (and *Sarotherodon*). See also Peters & Berns, 1982*a*.

The results of these studies will be summarized first, followed by what is known about breeding in African populations.

No sexual dichromatism has been observed, but after the second year males grow a little faster (Ben-Tuvia), and have longer soft dorsal and anal fin-rays (Chervinsky, 1965) than the female. Apfelbach (1969*b*), who had no fishes older than two years, considered them sexually monomorphic.

The breeding season in Lake Tiberias extends from the end of March or beginning of April to August. During this time a female produces two or more broods. A fish normally reaches sexual maturity at the end of its second year (or after its second winter), at a total length of 160–270 mm (average ♂ 227 mm, ♀ 224 mm).

Ripe eggs are green, oval, with a long diameter of 2·33–3·05 mm (averages of 2·1 to 2·9 in samples measured by Peters, 1963*b*, fig. 5) and a short diameter of 1·88–2·26 mm (Ben-Tuvia). The egg-sizes recorded by Monod (1949) and Daget (1954) in West Africa come within these ranges. The surfaces bear adhesive threads which are more sparse than in the substrate-brooders, but like theirs are evidently secreted by the follicular wall. This does not thicken, but shows by its basophil staining that it has a secretory function (Kraft & Peters).

The initiative throughout courting and mating is taken predominantly by the female. Male and female form a well bonded pair and remain together for several days or even as long as two weeks. Not only has this behaviour been repeatedly seen in the aquarium (Fishelson & Heinrich, 1963; Fishelson, 1966; Apfelbach, 1966; Heinrich, 1967), but it probably occurs in nature since Ben-Tuvia (1959, 1960), Fishelson and Peters (pers. commn) observed *S. galilaeus* swimming in twos near the shore in Lake Tiberias. The bond is firmer than in arena spawners, but less firm and durable than in substrate-spawners. It is comparable to that in *S. melanotheron.*

It is the female who is mainly responsible for excavating the nest, a depression made in the shallows near the shore, and she too is most active in defending the mating territory. Preliminary courting behaviour and pair-formation, though typical, are not essential. Heinrich found that when a ripe male and female were put together mating might occur without preliminaries (1967*a*:687).

The eggs are laid in batches of 20 to 40 and each batch is fertilized by the male as it is laid. They adhere in a mass in the pit and only after the whole clutch has been laid (and then after an interval of up to ten minutes) does one or the other parent, or do both take them into the mouth. This was the behaviour observed repeatedly by Heinrich, whose experimental animals were evidently under no stress, but in one case, where the parents were made anxious by the presence of potential egg-robbers, each batch was taken up as soon as it was fertilized. The latter behaviour was the rule among Apfelbach's pairs, which were in aquaria with other fishes, but when he isolated a pair they too waited until the whole clutch lay in the pit. In this matter the behaviour of *S. galilaeus* is evidently flexible.

The participation of both sexes in parental care first reported by Liebman (1933), has been amply confirmed by Ben-Tuvia and by the work on aquarium fishes, as well as in West Africa by Daget & Iltis (1965) and Iles & Holden (1968).

The pair bond is dissolved as soon as the eggs are safely in the parental mouth(s), and male and female then part. There is no indication of segregation of brooding fishes as in the arena-spawners, but Apfelbach (1969*b*) records that in an aquarium the brooding pair moves apart from the school. The developing larvae remain in the mouth until the yolk is absorbed and they have reached a length of 8–12 mm. If they swim out before the 14th day after fertilization they may be received again in the parental mouth at nightfall (Spieser, quoted by Wickler, 1965; Albrecht, quoted by Apfelbach, 1966), until the end of the 14-day period. After this there is no experimental evidence that the young either form a school together or have a contact reaction to the parents (Apfelbach, 1966; Destexhe-Gomez & Ruwet, 1967; Bauer, 1968), but Ben-Tuvia observed them swimming in a school in Lake Tiberias.

As in other species the number of eggs increases with the size of the female, giving a range of 770 to 5010 in fishes of 18 to 32 cm total length (Ben-Tuvia) and to 5700 in a fish of 700 g (Peters, 1963*b*). Ben-Tuvia found up to 1086 larvae in the parental mouth, but this number was thought to be reduced from a higher one by loss in the net. Brooding parents cease to feed.

West Africa. In the Middle Niger (Daget, 1962*b*), where there is a seasonal regime governed by the floods, periods of rapid growth alternate with periods of slow growth. A fish that was spawned early in the flood season may reach sexual maturity at the end of its first period of growth, before forming an annulus on the scales, if it has reached a minimum standard length of 97 mm for females, 120 mm for males. But the majority reach sexual maturity only during or at the end of their second period of growth, thus at about the same age as in Lake Tiberias.

In Lake Chad, Blache *et al.* (1964) also found that sexual maturity is attained during or at the end of the second year of life. Breeding starts in May and is at its height in June and July. A female with larvae in the mouth had mature ovaries. These authors saw the nests in shallow water on a sandy bottom and state that they are made by the males; but the sexes are difficult or impossible to distinguish in life and they do not recount how they came to this conclusion. Since they mention a brooding female one must assume that the only brooders in which the sex was verified were females.

Daget & Iltis (1965:267) however, reported mouth brooding by both sexes, more rarely by the male, in Ivory Coast and Holden (Iles & Holden, 1969) found eggs in the mouths of 5 females and 2 males, and fry in the mouths of 7 females and 5 males in the Niger and Sokoto Rivers, thus demonstrating that biparental brooding occurs in African as well as Asian populations.

The minimum sizes of these brooding fishes were TL 110 mm (♂) and 115 mm (♀) and a weight of 15 g in both. This is equivalent to about 90–94 mm SL and not very different from the size of the first year spawners recorded by Daget (1962*b*; and see above). The lengths of the brooding fishes listed by Iles & Holden form a gradual series from these minima to about 260 mm TL, but they were not necessarily collected at one time and place. Mr Holden informs me (in a letter of February 1978) that according to his records they were caught 'in the main-stream but where the river had flooded out over the grass', without more particular data for individuals. In this area, and that studied by Daget the same flooded and shrunken river regime submitted the fishes to varying and even precarious conditions, including the shrinking bodies of water which notoriously stimulate early breeding in *Sarotherodon* and *Oreochromis*. This is in contrast to the relatively stable conditions in Lake Albert (see below).

The greatest number of eggs found in one mouth by Holden was 958 in a female of 210 mm TL. The ovaries of all the brooding females examined by him were in the later stages of maturation (IV–VI), indicating that a further spawning cycle was in progress.

Lake Albert. Lowe (1955*c*) gives the maximum size of the eggs as 3×2·2 mm. Numbers of ovarian eggs vary from 538 in a fish of 16 cm TL to 1560 in one of 30 cm (Lowe, *loc. cit.*), a much lower number than found at this size in Lake Tiberias. Lowe lists this among the maternal mouth-brooding species, but does not give specific observations. She was probably quoting from Pellegrin and Boulenger.

Holden (pers. commn) examined females in samples from two localities in Lake Albert. At Mdaiga in May 1962 among a sample of 42 females the smallest classified as 'breeding' was 17 cm in TL (about 130 mm SL), one other was in the 19–20 cm class, and 11 were 21 cm or over. 'Breeding' was defined as his stage IV, with ovaries at least half the length of the body cavity, containing large, green eggs. At the second locality, Mtoroko, in February 1962, the minimum length of ripe females in a sample of 64 was 21 cm, 5 being in the 21–22 cm class and 12 of TL 23 cm or more. In both localities the smallest female caught measured 14 cm and was at stage II–III, an early stage of maturation. No seasonal markings were present on the scales in Lake Albert to enable the age to be estimated.

Lower Nile. The only brooding individuals from the Lower Nile observed by Pellegrin (1903) and Boulenger (1907*a*) were females. Pellegrin gave details of four females of 130–170 mm SL, one carrying in the mouth eggs of 2·4 mm, the others embryos of 5–9 mm. In the first, ovarian eggs were already 0·8–1·0 mm, in the others they measured 1·2–1·4 mm, so all would have been capable of a further spawning.

Habitat

In Lake Tiberias before the spawning season *S. galilaeus* is present in large schools throughout the lake. The schools disperse in March, when pairs come in to the shores in search of spawning places where the bottom is sand or gravel and plants are abundant (Ben-Tuvia, 1959, 1960). In the Middle Niger in the neighbourhood of Diafarabé and at the Kaïnji dam this species is found at the edge of sandbanks and over sandy bottoms, and does not accompany *O. niloticus* into the flooded swamps (Daget, 1954:339; Banks *et al.*, 1965:24). At the confluence of the Sokoto River with the Niger *S. galilaeus* was found both in the mainstream and in the flood-plain, but for most of the year the Middle Niger is almost stagnant. The same is true of the Ogun River (Sydenham, 1977) where *S. galilaeus* is the main commercial species. In general, *S. galilaeus* becomes more abundant in waters dammed to form a lake, and swims offshore feeding on the phytoplankton. This happened in Lake Kaïnji, Nigeria (Lewis, 1974:295), in Lake Nasser (R. Collinson, quoted by A. I. Payne, pers. commn), in Nungwa Reservoir, near Accra, and in quiet bays at the south end of Volta Lake (Petr, 1967). In Lake Barombi Kotto, West Cameroon, adult *S. galilaeus* were not caught in traps set near the shore, but by cast-nets in the open waters of this shallow lake. It is the most abundant species of the tilapias in Lake Chad (Loubens, 1969).

Distribution (Fig. 36)

Lake Huleh, Lake Tiberias (Kinereth), River Jordan; Mediterranean rivers of Israel; Nile, Blue Nile, Lake Albert, Aswa River; Lake Rudolf (Turkana); Jebel Marra; Lake Chad basin, Ubangui and Uelle Rivers; Draa River, Morocco; Adrar, Mauretania; West Africa from Senegal to Guinée, Volta and Niger basins and waters between these two; Cross River and Lake Barombi Kotto, Meme system.

In the southern rivers of Ivory Coast, the Tano and Pra (?) Rivers and Lake Bosumtwi in Ghana it is replaced by the subspecies *multifasciatus*. Absent from Sierra Leone and Liberia, where it is replaced by related species.

Among the fossil cichlids described by Sauvage (1907 & 1910) from the Miocene of Guelma, Algeria, there is one that is probably a tilapiine. The *Palaeochromis darestei* (1910, pl. IX) is deep-bodied with a caudal peduncle whose length is 0·6 of its depth and width produced dorsal and anal soft rays. No count can be made of the vertebrae and there are fourteen dorsal spines visible. It is possible that more spines may be present, some being hidden by the usual dovetailing.

The cichlids present today in Algeria are in the neighbourhood of Tuggurt, in the Oued Rihr system, and comprise *Tilapia zillii* (Gervais), *Astatoreochromis desfontainesii* Lacepède, and a species of *Hemichromis*. These are on the southern side of the mountains of Algeria, and Guelma is on the northern, but most of the uplift was subsequent to the period of fossilization.

Since the distribution of *S. galilaeus* is almost identical with that of *Tilapia zillii* and its close derivatives, its total absence from Algeria would be more surprising than its former presence there.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
Mus. Hist. nat. Lyon (Syntypes of *Chromis tiberiadis*)	229, 239, 265	L. Huleh	L. Lortet
Mus. Hist. nat. Lyon (Syntypes of *Chromis microstomus*)	92, 106	L. Huleh	L. Lortet
1864.8.23.34–37	131–215	Sea of Galilee = L. Tiberias	H. B. Tristram
1936.4.6.40–42	95–163	L. Huleh	R. Washbourn
1949.9.16.312–317	131–225	L. Huleh	C. K. Ricardo-Bertram
1935.3.28.6	75	L. Tiberias	J. Hornell
1938.11.1.14	113	L. Tiberias	A. Craig-Bennett
1942.4.7.1–2	90, 91	L. Tiberias	A. Craig-Bennett
1968.12.13.12–29	21·5–48·0	L. Tiberias	W. C. Beckman
1949.9.16.310–311	85, 96	Jordan system	C. K. Ricardo-Bertram
1949.9.16.332–6	103–108	Jordan system (Yarmuk)	C. K. Ricardo-Bertram
1949.9.16.353–354	62, 83	Na'amen, N. of Haifa	C. K. Ricardo-Bertram
1927.10.17.1–7	61–91	Ras-el-Ain (Yarkon R.), nr. Jaffa	F. W. Bewsher
1949.9.16.276–297	106–202	L. Tiberias	C. K. Ricardo-Bertram
1949.9.16.299–309	112–122	R. Jordan	C. K. Ricardo-Bertram
1949.9.16.322–331, 337	88–178	Na'amen, N. of Haifa	C. K. Ricardo-Bertram
1949.9.16.377	141·5	Kishon R.	C. K. Ricardo-Bertram
1907.12.2.3635	87·5	Freshwater pool at Ghet-el-Nassara, L. Menzaleh	Loat
1969.5.28.3	121	L. Menzaleh	N. Bishara
1907.12.2.3631–4	66–89	L. Mareotis, Nile delta	Loat
1907.12.2.3637–40	53–73	Canal, Zoological Gdns, Giza	Loat
1907.12.2.3636	90	Road to pyramid of Giza	Loat

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1960.3.14.2–3	90, 91	L. Edkou, Nile delta	A. Ezzat
1925.12.31.40	85	L. Timsah	Cambridge University Suez Canal Expedition (Munro-Fox)
1907.12.2.3647	191	Bahr Selah, Fayum	Loat
1907.12.2.3641–4	126–142, 311	Birket Karun, Fayum	Loat
1907.12.2.3645	80–104	Bahr-el-Tawilah, Fayum	Loat
1907.12.2.3648–57	100–129	Omdurman, Nile	Loat
1861.9.9.50	226	Khartoum	Petherick
1862.6.17.77	206	Khartoum	Petherick
1907.12.2.3659	225	Gondokoro	Loat
1907.12.2.3658	340	Rosaires, Blue Nile	Loat
1979.3.29.229–236	25–47	Lake Yirol, Bahr el Ghazal	Omer Cooper, Rhodes Univ. Exped. 1954
1965.7.27.108	174	Amballa, Sudan	Sir John Cass College Expedition
1961.12.1.330	96·5	Aswa R.	Uganda Game & Fisheries Dept.
1961.12.1.333–339	64–90	Aswa R.	Uganda Game & Fisheries Dept.
1936.3.12.15	158	Kaiso Lagoon, L. Albert	Pitman
1929.1.29.187–194 (11 fishes)	78–222	L. Albert	E. B. Worthington
1967.3.16.9–10	155, 167	Butiaba, L. Albert	R. H. Lowe, 1949
1933.2.23.43–45	95–148	L. Turkana (Rudolf)	E. B. Worthington
1979.9.17.1–3	133–151	L. Turkana (Rudolf)	R. Haller
1965.12.10.1	286	L. Turkana	R. Welcomme
1974.1.16.375–380	34–45	Katatoi Gorge, Turkwell R.	K. E. Banister
MRAC 58072–58137 (part, 7 fishes)	56·0–82·5	Yakoma, Ubanghi R. at confluence of Uele & Bomu	Rosy
1930.8.7.79	122	Kusseri, Lower Shari River	Glover
1953.4.28.247–8	107	Hadeija R.	E. Trewavas
1928.7.3.110–111	55–118	Kiyawa R., Katagum Nigeria 10°1′N 9°47′E	Ll. Lloyd
1959.8.18.181–2, 190	120–131	L. Barombi Kotto, Cameroon	P. I. R. Maclaren
1969.1.13.21	61	L. Barombi Kotto, Cameroon	C. A. Wright
Göteborg Museum	150	L. Barombi Kotto, Cameroon	Linnell
1973.5.14.779–782	122–145	L. Mboandong, Cameroon	E. Trewavas, J. Green, S. A. Corbet & J. Griffith

Museum & Reg. No.	SL (mm)	Locality	Cellector or donor
1973.5.14.783	69·5	L. Barombi Kotto, Cameroon	E. Trewavas, J. Green, S. A. Corbet & J. Griffith
1973.7.18.173–196	21–38	L. Barombi Kotto, Cameroon	J. Green, S. A. Corbet & E. Betney
1913.4.24.3–11 (25 specimens)	26–37	Cross R., probably at Obubra	W. A. C. Cockburn
1935.5.29.39	135	Shika R., Zaria, N. Nigeria	J. B. Welman
1957.11.27.1	100	Shika R., Zaria, N. Nigeria	W. S. Haynes
1904.1.20.63	165	Mureji, Niger R.	J. S. Budgett
1899.8.23.29–30,31	47–73	Jebba, Niger	Lugard
1908.10.21.8	59–123	Ogun R. at Aro, nr Abeokuta, Nigeria	G. E. Bruce
1908.12.9.65–69			
1909.3.3.29			
1916.11.7.24	83	Ibi, Benue	C. Francis
1959.8.18.147–149	83–90	Ibi, Benue R.	P. I. R. Maclaren
1907.5.3.34–35	90, 95	Ibi, Benue R.	H. L. N. Traill
1971.9.28.177–180	77–120	Benue R., between Ibi & Makurdi	G. McG. Reid
1953.4.28.247–248	108, 99	Hadeija R. and Lekki Lagoon	E. Trewavas
1953.4.28.274	101, 260	Lekki Lagoon, S. Nigeria	E. Trewavas
1959.8.18.146	135	Reservoir at Ibadan, Nigeria	P. I. R. Maclaren
1959.8.18.155	134	Oshun R., Nigeria	P. I. R. Maclaren
1949.10.21.7–10	69–103	Oshun R., Nigeria	P. I. R. Maclaren
1911.7.19.62–63	63, 64	Deert, mouth of Gurara R., trib. of Niger above Benue	J. J. Simpson
1902.11.10.239–240	48, 63	Abo, S. Nigeria	W. J. Ansorge
1902.11.10.241–248	57, 25·5–38·5	Agberi (=Agbede ?), S. Nigeria	W. J. Ansorge
Smithsonian Sorting Centre (9 fishes)	43–78	Accra	P. V. Loiselle
1949.10.20.101–102	124, 161	Volta R. at Asuchari	M. Noel Buxton
1960.1.4.28–29	109, 111	Nungwa reservoir, Ghana	J. D. Thomas
1935.9.2.177	152	'Gold Coast'	P. R. Lowe
1949.6.30.85–89	61–76	Kamba R., Black Volta, Ghana	K. S. Morris
1912.4.1.146	270	Geba R., Guinea Bissau	W. Ansorge
1885.1.31.11–12	94, 96	Gambia	Moloney
1900.6.28.197–201	67–205	Kaïdi, Senegal	Delhez
1900.6.28.202–203	44–51	St Louis, Senegal	Delhez
1978.3.13.10–11	40·5, 71·5	Kioira, Lower Senegal	D. Dorfman (XII, 1977)
1978.3.13.4–9	48·5–67·0	N'Dium, Lower Senegal	D. Dorfman (XII, 1977)

Museum & Reg. No.	SL (mm)	Locality	Cellector or donor
1978.3.13.12–15	36–38	Lac de Guiers, Senegal	D. Dorfman (XII, 1977)
1962.2.13.1–2	58·5, 118·5 & post larvae	Aquarium reference specimens	W. Wickler

Sarotherodon galilaeus multifasciatus (Günther)

Chromis multifasciatus Günther, 1902:333, pl. 31 (Lake Busum-chi—Bosumtwi, Ghana).
Tilapia multifasciata; Pellegrin, 1904:316 (from Günther); Boulenger, 1915:175, fig. 112; Pellegrin, 1923:283; Trewavas & Irvine *in* Irvine, 1947:17, 276; Lelek, 1968; Whyte, 1975.
Tilapia galilaea multifasciata (?); Daget & Iltis, 1965:266 (Guinean rivers of Ivory Coast).
Tilapia heudelotii (part, *non* Dumèril); Boulenger, 1915:175 (specimen 21 only, Lake Bosumtwi).

TYPES. Syntypes: 14 specimens, 43–112 mm SL from Lake Bosumtwi*, Ghana, collected by R. B. N. Walker. BMNH 1903.4.24.42–51.

Distinguishing characters

In accepting Daget's suggestion for the inclusion in this subspecies of the population of the southern rivers of Ivory Coast as well as that of Lake Bosumtwi, we distinguish *S. g. multifasciatus* by characters common to both areas.

The most important differences between this subspecies and *S. g. galilaeus* are meristic, as shown in Tables 21 and 22. Daget & Iltis (1965) point out that whereas the modal number of vertebrae in *S. galilaeus* from the Senegal, Gambia and Middle Niger Rivers is 29, that in the southern rivers of Ivory Coast is 28. This is also the number in our single River Tano fish and the mode in Lake Bosumtwi. The arithmetic mean in ivory Coast is 28·3, in Bosumtwi 28·29. The modal numbers of dorsal fin spines and of scales in the lateral line series are also low in *S. g. multifasciatus.* Daget & Iltis suggest further that there is a lower range of gill-raker numbers in *S. g. multifasciatus*, but the numbers available give dubious support to this (Table 23). It is possible, however, that Daget disposed of a greater number of *S. galilaeus* from the Senegal and Gambia basins than I have, and my highest ranges of gill-raker numbers come from these rivers.

Most of the proportions of 26 specimens of 90–137 mm SL from Lake Bosumtwi itself agree with those of topotypes of the nominate subspecies, *S. g. galilaeus*, with somewhat more restricted ranges explicable by the absence of bigger specimens. It seems likely that the smaller maximum size is characteristic of the lake population, but examples from the rivers show that the subspecies is capable of growing to at least 200 mm SL.

Proportions showing a possible significant difference from *S. g. galilaeus* are:

(i) Depth of body 39·5–46·5% SL, not only in the lake, but also in the Tano fish (42·5), and in the Ivory Coast specimens included by Daget, and Daget & Iltis (minimum 38·5). That this is not enough by itself is shown by two samples of rather slender fishes here included with *S. g. galilaeus* on meristic characters, one from Nungwa Reservoir, Ghana (depth of body 43·5–47·7% SL; dorsal spines XVI or XVII; scales in lateral line series 30 or 31), and one from Lake Barombi Kotto (depth 35·0–46·5% SL; dorsal spines XVI; scales 30 or 31).

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*Variously spelt Busum-chi, Bosumtwi, Busumtwi, Bosumtvi, Bosumtivi. My efforts to pronounce it failed to satisfy my Ashanti friend Mr S. A. Whyte.

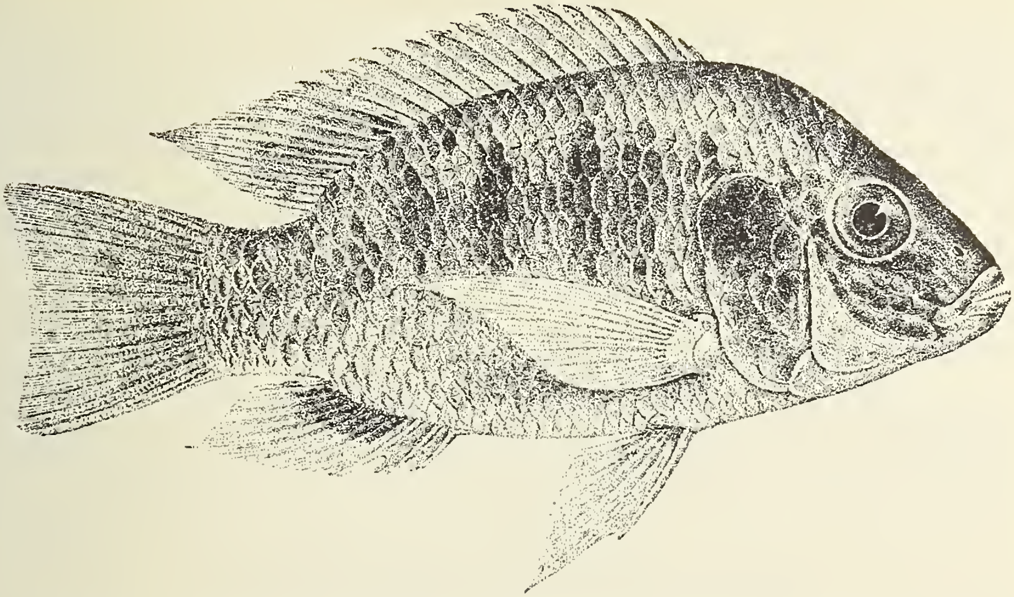

Fig. 40 *Sarotherodon g. multifasciatus*, from Boulenger, 1915, fig. 112, *ex* Günther, 1902.

(ii) Pectoral fin in the lake not exceeding 43% SL; but in the one R. Tano specimen available nearly 45%.

(iii) Interorbital width 32–38% length of head; but in the river fish nearly 40%.

The teeth in the lake fish are in only 3–4 rows, but in the bigger river fish in 5–6.

These data may be interpreted as indicating an historical divergence between the western Guinean forest population and the savannah population of *S. galilaeus*, expressing itself in meristic differences and a more slender form in the Guinean populations.

The fact that *Tilapia busumana* (Günther) is present in the Pra and Tano Rivers, as well as in Lake Bosumtwi, supports the parallel distribution postulated by Daget for *S. g. multifasciatus*. The presence of the subspecies in the Pra and Tano might have been predicted, and it was no doubt Dr Tyson Roberts' appreciation of this that led him to recognize the Tano fish here reported and to preserve it.

Records by Schultz (1942) and Fowler (1919) of *S. galilaeus* from Liberia have not been confirmed (see *S. occidentalis*, pp. 128, 131).

Ecology

Food

See Whyte, 1975: fig. 4 & Table III. As in other species, the juveniles of 2–4 cm TL are more carnivorous than adults, the greater proportion of their stomach contents consisting of insects from the water surface, mainly emergent chaoborids and chironomids, and the surface-dwelling Ranatridae, as well as land insects fallen on the water. About half of the 120 stomachs examined also contained small quantities of phytoplankton.

Adults (7 to 15 cm TL) fed almost exclusively on phytoplankton, the relative abundance of the components of which in the stomachs was a reflection of that in the littoral and limnetic plankton. Blue-green algae and desmids predominated. Tests on stomach and rectal contents showed that these were digested.

Contrary to the habits of *Oreochromis niloticus* in Lake George (Moriarty, 1973), both *S. g. multifasciatus* and *T. discolor* were found to feed at night, between 18.00 and 05.00 hours, a difference which may reflect the relative opacity of the two lakes and the need to keep out of sight of predatory birds. Whyte found that in open waters *S. g. multifasciatus* underwent a diel vertical migration, sinking to depths of up to 30 m by day and rising to the surface at night. In the littoral zone a similar migration had a horizontal component, bringing it by day to depths of about 15 m.

Breeding

See Whyte, 1975:44. Breeding fishes may be found throughout the year, but there is a peak from November to April, a period that includes both dry and rainy months, but when the air temperature is always high, 30–32°C in the afternoon. The subspecies (like *S. g. galilaeus*) breeds in the littoral zone at depths of 1 to 3 m. A shallow pit of 10–15 cm diameter and 4–6 cm deep is made by the male, in the one instance observed. The average dimensions of the eggs are $2{\cdot}3 \times 3{\cdot}2 \pm 0{\cdot}2$ mm, the colour 'olive to creamish olive', and they are brooded by (either or ?) both parents, generally in the littoral zone, but brooding individuals have been caught as far as 800 m offshore. Most of the mouth-held clutches that were counted were believed to be incomplete after losses in the net or on handling. The maximum number counted was 175 from the mouth of a male.

Habitat

Our knowledge of the ecology of this subspecies is derived from the work of Lelek (1968) and Whyte (1975), mainly the latter on the population of Lake Bosumtwi, the type locality.

Lake Bosumtwi lies in the forest zone of Ghana between the Pra River and its main tributary, the Ofin, at 6°30′N, 1°24′W, in a circular endorheic basin possibly of meteoric origin (Whyte, 1975; Smit, 1962; Schnetzler *et al.*, 1966). It is surrounded by a crater wall of varying degrees of steepness from which numerous streams enter the lake, five of them being permanent. Whyte explored the streams from source to mouth, as well as the littoral and open-water zones of the lake, and the following details are from his work.

The diameter of the lake is 8 km and its catchment area, bounded by the crater rim, is only 106 km^2. The maximum depth is 78 m. Evaporation from the surface results in a high concentration of sodium salts and a high pH and alkalinity, in sharp contrast to the streams.

Sarotherodon g. multifasciatus occupies the 'estuaries' of the streams, and the littoral and limnetic zones of the lake. It is the only fish species that may be found in the open waters throughout the year, although in the rainy season *Tilapia discolor* also spreads into the limnetic zone. Both species inhabit the littoral zone and the estuaries throughout the year, and *Tilapia busumana*, although more lotic than either, is common in the shallower littoral regions and in the rainy season moves as far as depths of 10 m. This zoning is probably related more to their respective feeding habits than to the direct effect of the water chemistry.

Distribution (Fig. 36)

Lake Bosumtwi, the Tano and (?) Pra Rivers, Ghana; and the Bandama, Komoe and Nzi Rivers, Ivory Coast. In fresh water.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1903.4.24.42–51 (14 syntypes)	43–112	L. Busum-chi (=Bosumtwi)	Walker
1899.10.26.3	108·5	L. Bosumtwi	Beddington
1917.4.20.24–25	70, 73	L. Bosumtwi	Spurrell
1922.9.29.4	104	L. Bosumtwi	Rattray
1942.12.30.11–13 (5 fishes)	97–137	Abonu, L. Bosumtwi	Junner
1942.12.30.14–17(5)	97–102	Isasi, L. Bosumtwi	Junner
1942.12.30.18–21 (8)	91–112	Isasi, L. Bosumtwi	Junner
1942.12.30.22–27 (7)	90–128	Isasi, L. Bosumtwi	Junner
1973.5.14.1195–1196	99·5, 104	L. Bosumtwi	Whyte & Trewavas
Tyson Roberts Colln	197·5	Tano R. at Samtetsi	Tyson Roberts

Sarotherodon galilaeus borkuanus (Pellegrin)

Tilapia borkuana Pellegrin, 1919*a*:150; *idem*, 1921*a*:177, fig. 84 (Ounianga Sérir, Borkou & Archei, Ennedi); Fowler, 1949:271, figs 80–87 (Fada, Ennedi); Estève, 1952:178 (Ounianga Kebir, Borkou); Daget, 1959:178, fig. 3 (Ennéri Maro, Tibesti); *idem*, 1968*a*:1584 (Ennedi).
Tilapia (Sarotherodon) galilaea borkuana; Thys van den Audenaerde, 1968*b*:xxxix; *idem*, 1971:216.

STATUS. As Pellegrin said in describing this form, it is evidently derived from *S. g. galilaeus* by segregation. One may add that its distinctive features seem to be related to its ecology and that its most striking character, the pigmentation, is not unknown as a variant elsewhere in the species (see p. 104).

TYPES. Syntypes: Eleven specimens of 57+14 to 130+35 mm, from Ounianga Sérir, Borku, collected during the mission of J. Tilho, 1912–1917. MNHN 1919.19–25, 27–29. No. 26 is 85 mm SL, BMNH 1919.8.15.2 presented by the Museum of Paris.

Distinguishing characters

See p. 94. Meristic characters are included in Tables 21–23. The vertebral and fin-ray numbers agree with those of other West African populations of *S. galilaeus.* The gill-rakers on the lower part of the first arch number 19–21, and so are restricted to the lower part of the range for the species. This may be because many of the examined specimens are very small; in the 85 mm fish examined by me they are 2+1+19 on the whole arch.

The depth of the body is 37·6–43·0% SL, length of head 33·3–37·6, pectoral fin as long as head (slightly longer in the 85 mm fish).

Pellegrin stated that the eye is bigger than in *S. g. galilaeus*, but in the 85 mm fish it compares with others of the same size. The pharyngeal bone is lighter than in *S. g. galilaeus* of the same size, and has a very long anterior blade (Fig. 38).

The notch in the edge of the suboperculum mentioned by Pellegrin, and plainly shown in his figure by Angel, is in a position where the edge is often slightly concave, but it seems more abrupt in *S. g. borkuanus*, perhaps because the skin has shrunk.

Size: mainly small. The biggest syntype is 130 mm SL and a fish of 90 mm was mouth-brooding young of 12 mm with resorbed yolk.

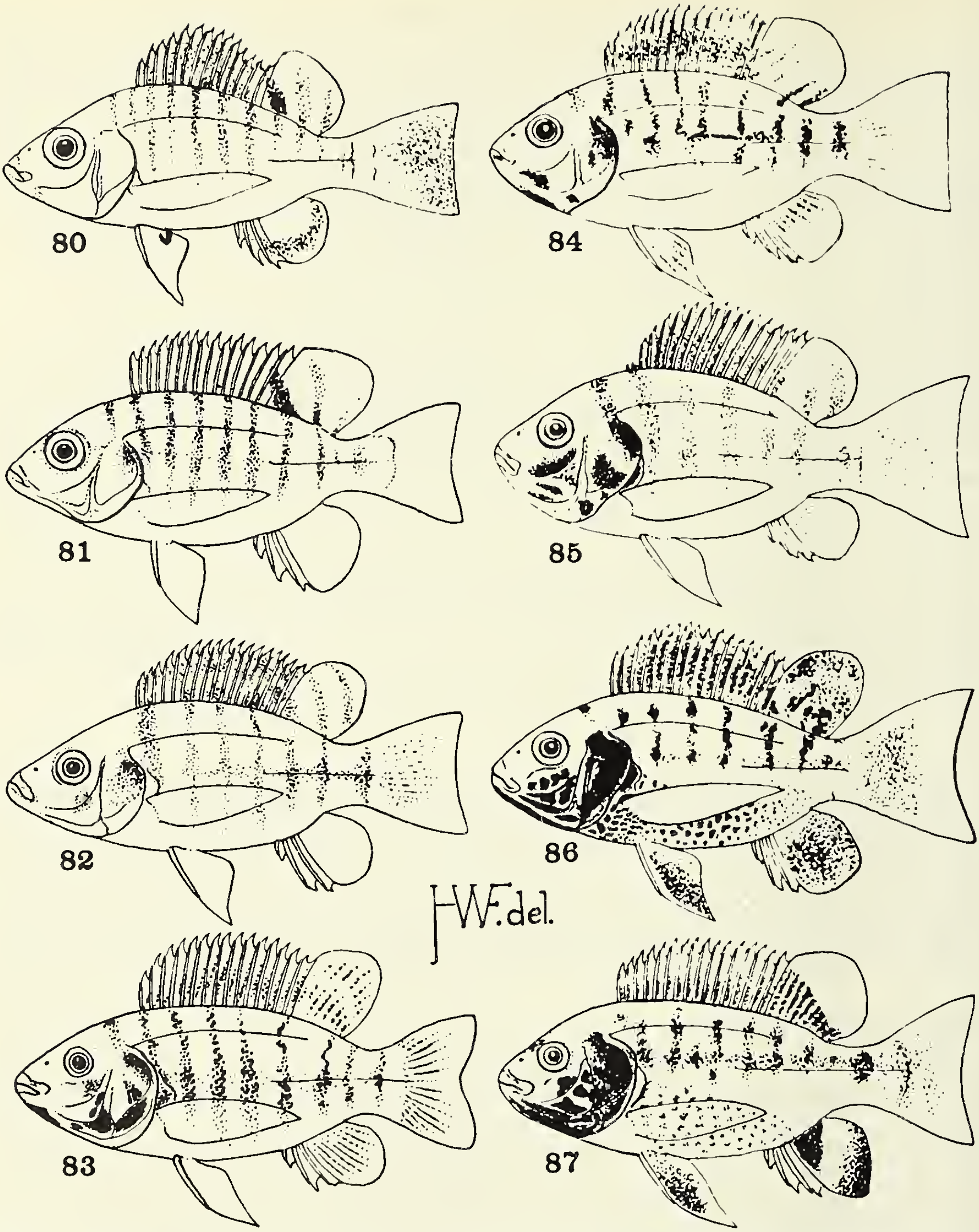

Fig. 41 *Sarotherodon galilaeus borkuanus.* Drawings from Fowler, 1949, figs 80–87, of specimens from Fada, Ennedi, to show variation in pigmentation. In order of their numbers the fishes are respectively 35, 49, 74, 95, 80, 96, 100 and 98 mm (SL or TL?).

Coloration. Pellegrin quoted the report of life-colours as black on the back, silvery with pearly sheen ventrally. His figure shows a black head and cleithral region, and a clouded spinous dorsal fin. Fowler's (1949) drawings (Fig. 41) of preserved fishes from the Ennedi were from eight individuals selected from fifty-two to show variation. If they are typical of their sizes they also show progressive development of the pigmentation. The 35 and 49 mm fry have the juvenile narrow vertical bars on the body and a tilapia-mark. Pigment then appears on the gill-cover, cheek, throat and vertical fins, and the shape and intensity of the vertical bars becomes more irregular, as in adult *S. g. galilaeus*. At 100 mm there is much melanin distributed in spots along the whole ventral and ventro-lateral surfaces, and the pelvics are dusky except their anterior edge. In life the head and back are dark purple (Thys, pers. commn), probably by an admixture of other chromatophores or iridocytes. As now preserved, according to information from Mrs E. Böhlke, the onset of head-pigmentation is less regular, the smallest in which it is found being 61 mm SL, but one fish of 94 mm SL has no such markings. By analogy with other populations and with *S. melanotheron* we have no reason to suppose it is confined to one sex, but its presence may signal the onset of sexual maturity.

Habits. In Borku these fishes spend the winters at the bottom of the lagoons and the summers among the reeds (Pellegrin, 1919*a*).

Distribution

Confined to the waters of Borkou, Tibesti and Ennedi, especially abundant in the small shallow lakes and 'gueltas'. These waters are within the periphery of the tectonic basin of Lake Chad (Fig. 42), described by Daget (1967). Daget summarized the evidence, including the presence

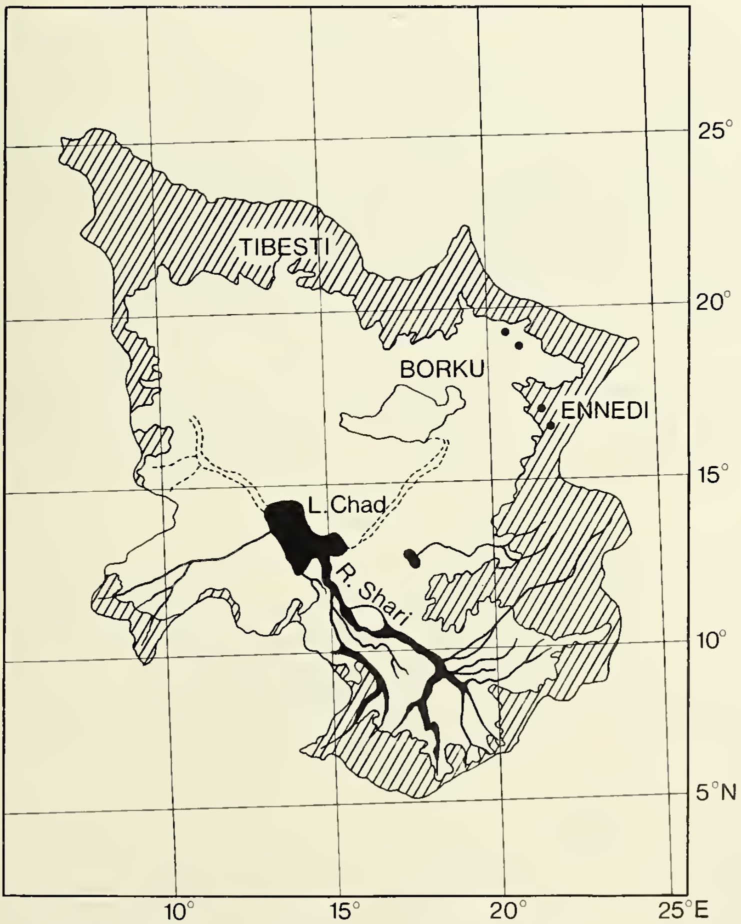

Fig. 42 The tectonic basin of Chad, based on the figure by Daget, 1967. Hatched areas over 500 m altitude.

of fossil fishes beneath the dunes, that the lake formerly filled this area during a period when the climate was of a humid, Mediterranean type. The present Lake Chad is confined to a relatively small area in the south-western corner. The deepest part of the area, 'les Pays Bas du Tchad', is lower than the present lake, which fails to overflow into it because not only is the evaporation rate high, but also the former overspill into the Bahr-el-Ghazal (not the part of the Nile with the same name) is blocked by the silt deposited at the mouth of the Shari-Logone, the chief feeder of Chad. The waters in which *S. g. borkuanus* is found have therefore been isolated from Chad by a distance of about 700 km for 7000–9000 years, according to Daget. They harbour a relict upland fish-fauna comprising about seven species in the Ennedi and nine at Tibesti (Daget, 1968*a*), among them also *Tilapia zillii*. Blache *et al.* (1964) record that a search in the peripheral pools and marshes of Lake Chad has shown that *S. galilaeus* is represented there by *S. g. galilaeus* and not by *S. g. borkuanus* (Blache *et al.*, 1964).

Ounianga Sérir (see Beadle, 1974, figs 11.3 & 11.5) is a shallow, slightly saline lake with muddy bottom and abundant aquatic vegetation (Pellegrin). Ounianga Kebir is a soda lake fed by fresh springs (Daget, 1959).

Material examined

The syntype mentioned above and radiographs of 51 specimens in ANSP.

Sarotherodon galilaeus sanagaensis (Thys van den Audenaerde)

Tilapia galilaea; Holly, 1927*a*:220 (Mbam R., Sanaga system); *idem*, 1927*b*:425 (Sanaga); Pellegrin, 1928:8 (Edéa, Sanaga basin); *idem*, 1929*b*:360 (Vouri basin ?); Holly, 1930:266 (part; Cameroon).
Tilapia heudelotii (*non* Dumeril); Pellegrin, 1929*b*:360 (Lake Ossa, Sanaga system, *teste* Thys).
Tilapia multifasciata (*non* Günther); Daget, 1960*a*:4 (Lom R., Sanaga system).
Tilapia schwebischi (part, *non* Sauvage); Thys, 1964:105 (*teste* Thys, 1966).
Tilapia sanagaensis Thys van den Audenaerde, 1966:14, pl. 1 & fig. 2 (Sanaga system); *idem*, 1968*b*:xxxix; *idem*, 1971:215.

TYPES. Holotype: male of 94·5 mm SL, purch'd at Edéa, probably caught in Lake Ossa, coll. Thys, 1964; MRAC 152635.

Paratypes: 7 specimens of TL 116·5–145·0 mm, all from Sanaga system, MRAC 20007 (coll. Monod) and 152636–641 (coll. Thys), and one of 119 mm TL from Mbam R., MNHW 7743, coll. Haberer.

Distinguishing characters

Thys compared this form with *S. mvogoi* of the rivers of southern Cameroon, from which it differs in the higher numbers of dorsal rays (totals 28 or 29, cf 24–27 in *S. mvogoi*), the shape of the snout profile and, at a given size, a less deep preorbital bone. From *S. galilaeus* he distinguished it only by colour, especially the presence of round clear spots on the dorsal and caudal fins, and the darker colour of the head and dorsum. The edge of the dorsal fin may be orange-coloured (Thys, 1971), though it was not so reported in the types.

Description and discussion

Meristic characters are detailed in Tables 21–23. These, and the proportions, fall within the ranges given for *S. g. galilaeus* (Tables 21–24), with the qualifications mentioned below.

Thys rightly states (1966) that there is no reason to identify the Sanaga population with *S. g. multifasciatus* as, at my suggestion, Dr Daget did in 1960, and I agree that the biogeographical picture is against this identification. I find it difficult, however, to define *S. sanagaensis* so as to exclude it from *S. galilaeus*, especially in view of the colour variation recognized in that species (p. 102). As I recorded in 1974 (p. 409), the specimen of 131 mm SL sent to the BMNH by Dr Daget has a very small head (or long trunk). The head ratio (32% SL), though not unknown is very rare in *S. g. galilaeus*, and is evidently close to that in the holotype of *S. sanagaensis* figured in pl. I of Thys (1966), and recorded in the text as 33·9%. But both among the paratypes and in three other Sanaga fishes examined by me the ratio is higher. According to Thys the range is 32·5–35·5% SL, in my specimens 32·0–34·6. This contrasts with 34–37% in seven of 120–150 mm SL from Barombi Kotto and very markedly with the Benue sample, one of which is figured (Fig. 39). This fish is 120 mm SL with a head-length of 45·5 mm, whereas the head of a 131 mm Sanaga fish measures only 42 mm. The depth of the preorbital bone is about the same in the two fishes, so that the ratio to the head length is greater in the Sanaga fish (Table 28). The difficulty of obtaining a repeatable measurement of the preorbital bone, and its notable allometric growth, are such that it would require a bigger sample to establish a difference. The Benue fish of Fig. 39 has 28 vertebrae, two others of the same sample have 29, as has the Sanaga fish of 131 mm, so the longer trunk is not to be explained by additional vertebrae. But these proportions are only the extremes in *S. galilaeus* and are not reflected in, e.g., the numbers of vertebrae (mode 29 in the Benue sample and other West African *S. galilaeus* and also in *S. sanagaensis*).

Thus proportions and meristic characters (Tables 21–23) support the inclusion of *S. sanagaensis* as a peripheral population of *S. galilaeus*, distinguished by the coloration. But *'Oreochromis' schwebischi* (p. 489) at sizes comparable to those at which specimens are available from the Sanaga might be described in the same terms. In *'O.' schwebischi*, however, the length of head is 34–38% SL, mean numbers of vertebrae, scales and dorsal spines are lower, and mature males are very different from *S. galilaeus*. It is necessary to compare mature fishes of the Sanaga population with mature *'O.' schwebischi*, and to have further details of the breeding behaviour of both before deciding the true position of *S. sanagaensis*.

The geographical location of *S. sanagaensis* is also equivocal. Thys (1966:89) has noted the proximity of the headwaters of the Sanaga River to both the Logone and the Benue systems and any student of the Sanaga population must take into account the introductions from the Chad basin to ponds in the Sanaga area (Thys, pers. commn). The record of *'T. galilaea'* from Yabassi, Vouri River, is said (Thys, 1966) to be doubtful. Neither *S. galilaeus* nor *'O.' schwebischi* has been reported from Cameroon south of the Sanaga River nor from Rio Muni (Roman, 1971), but *'O.' schwebischi* is present in the Ogowe and Chiloango.

Distribution

Known only in the Sanaga River system, Cameroon, and there distinguished from introduced *S. galilaeus* from the Chad basin by its colour (Thys, 1966:18).

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
NHMW 13981–2	104, 104	Kamerun (probably Mbam R.)	Haberer, 1907
BMNH 1972.1.27.4–5	88, 131	Lom, affluent of Sanaga R.	coll. Bard donor Daget

Sarotherodon galilaeus boulengeri (Pellegrin)

Tilapia boulengeri Pellegrin, 1903:121 (N'ganchou, Zaire R. below junction with Kasai R.); *idem*, 1904:318, pl. 5, fig. 3; Boulenger, 1915:182, fig. 117 (from Pellegrin); Poll, 1959:142 (Stanley Pool = Malebo Pool).
Tilapia galilaea (part); Thys van den Audenaerde, 1964:21, 112, fig. 19.
Tilapia galilaea boulengeri; Thys van den Audenaerde, 1968*b*:xxxix; *idem*, 1971:216
Tilapia andersonii (part, *non* Castelnau); Boulenger, 1915:171 (specimen no. 42 only); Poll, 1939*b*:43 (Stanley Pool = Malebo).

TYPES. Holotype: 160 + 43 mm from N'ganchou, coll. 'Mission a l'Ouest Africain', MNHN 1886–461.

Distinguishing characters

As *S. g. galilaeus*, but caudal fin in adult densely covered with scales and with its corners rounded, probably by wear. Already in a fish of 70 mm SL a dense scaly covering is present over three quarters of the fin, but the margin is truncate. At 88 mm the scaly coat is complete.

For distinctions from the geographically close *O. (Ny.) lepidurus* see below and Table 100, p. 407.

Description

The meristic numbers given in Tables 21–23 are based on eight specimens examined by me and fourteen reported on by Thys (1964). About five fishes were used by both observers. Differences in the numbers of soft dorsal and anal rays are due, as in other species, to different policies in counting the last ray, which, whether simple or forked, is counted by me as a whole ray if it is distinct from the penultimate to its base.

Proportions agree with those of *S. g. galilaeus* of the same size (Table 24). The body is deep (depth 44·5–50·0% SL) and the caudal peduncle short and deep, its length 0·6 to 0·7 of its depth. The depth of the preorbital bone is from 22·5% length of head at 70 mm SL to 28% in the holotype.

The lower pharyngeal bone and teeth are as in *S. g. galilaeus*, and the anterior blade is from 1·4 times the length of the toothed area at 88 mm SL to twice as long in the holotype (160 mm SL). The lateral apophyses project very slightly behind the dentigerous plate.

In numbers of vertebrae, scales and fin-rays *S. g. boulengeri* agrees with the nominate subspecies in Lake Albert and West Africa, and the gill-rakers are also typical for the species.

Young specimens may be preserved with 5 or 6 faint vertical bars on the body, sometimes emphasized mid-laterally, and a faint tilapia-mark. The caudal fin is without markings in preserved fishes. Life colours are undescribed.

Except for the scaly caudal fin, then, the *S. galilaeus* of the Lower Zaire resemble the nominate subspecies. In the same waters *Tilapia tholloni* and *Oreochromis lepidurus* also have densely scaled caudal fins, a fact which, as Thys suggests (1964), may indicate an environmental cause. Young *O. lepidurus* are at first sight easily confused with *S. g. boulengeri*, but there are several differences (Table 100). Adult males of *O. lepidurus* have a tasselled genital papilla, unlike *S. g. boulengeri*. In addition, the average depth of body and caudal peduncle are greater in *S. g. boulengeri*, and the maximum length of the pectoral fin is higher. The mouth of *S. g. boulengeri* is small, the lower jaw in the samples measured being less than 30% length of head v. 30–34% in *O. lepidurus*. Thys recorded that the distributions are complementary, *O. lepidurus* apparently being confined to the brackish water of the Zaire estuary, *S. g. boulengeri* to the marshy edges of the Central basin.

It must be considered also whether *S. boulengeri*, rather than being a scaly-tailed *S. galilaeus* may be scaly-tailed '*Oreochromis*' *schwebischi*. The difficulty of distinguishing between the two species in immature stages is discussed (see pp. 35–36), and known *S. boulengeri* are all smaller than the size at which males diverge in structure. The meristic characters in the seven specimens available agree better with *S. galilaeus* than with *'O.' schwebischi.*

Distribution

Lower part of the Zaire River from Stanley Pool (=Malebo) to Matadi; Lower Kasai; Lake Anengué, Lower Ogowe. Since there have been many introductions into the lagoons of the Lower Ogowe, it is possible that this species is not native there.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
MNHN 1886/461 (holotype)	160	N'ganchou, Zaire R.	Mission à l'Ouest Africain
MRAC 118068–70	102–116	Stanley (=Maleba) Pool, nr Bamu Is.	Mission Brien-Poll-Bouillon, 1957
MRAC 87663	91	Kalina, Kinshassa	Theunissen
1904.6.10.19	70	Kinshassa	Dutton, Christy & Todd
1972.8.11.1	88	L. Anengue, Lower Ogowe	Roux

Genus *SAROTHERODON* – IV
Species west of the rivers Niger and Volta

Sarotherodon tournieri
Sarotherodon occidentalis
Sarotherodon caudomarginatus

Nothing is known of the breeding biology of these species, except that a male of *S. occidentalis* has been recorded brooding young in the mouth (Thys, 1971). Their inclusion in genus *Sarotherodon* is based mainly on their geographical position, in which they appear to take the place of *S. galilaeus*, a species absent from this corner of West Africa, but otherwise widely distributed there (Fig. 43). The areas of *S. galilaeus* and *S. occidentalis* overlap in the Casamance and Corubal rivers. Preserved specimens of the two species are not easily distinguished.

The emarginate caudal fin, reaching an extreme in young *S. caudomarginatus*, is a character of other species of genus *Sarotherodon*, but is rare in the *Oreochromis*

Sarotherodon tournieri is an isolated species, but its deep body, small mouth and fine dentition suggest relationship to *S. galilaeus*, and its low metameric numbers to *S. melanotheron*.

Sarotherodon tournieri (Daget)

Tilapia tournieri Daget, 1964:594.
For synonymy see the subspecies.

Distinguishing characters

A deep-bodied *Sarotherodon* in which the depth in adults is 41·5 (juv.) to 56·4% SL, and the profile of the head curves evenly down to a very small mouth (lower jaw 29·5–32·0% length of head in adult). Teeth very small, depressible, slender, in 4 rows in adult. Scales 27–29 in the lateral line series; vertebrae 27 or 28; D XV 10–13; A III 8–12. Gill-rakers 16–20 on lower part of anterior arch. Pharyngeal with long blade and bristle-like, densely crowded teeth (Figs 45 & 48). Caudal slightly emarginate.

Two subspecies, *S. t. tournieri* (Daget) and *S. t. liberiensis* (Thys van den Audenaerde).

The type specimens of these came from adjacent rivers near the borderline between Liberia and Ivory Coast. *Sarotherodon t. liberiensis* was stated to be characterized by its colour, but life-colours of *S. t. tournieri* have not been described. The toothed area of the pharyngeal of *S. tournieri* is described by Thys (1971) as divided by a median toothless strip, and this appears to be so in two paratypes examined by me. But the appearance is due to the slope of the teeth of the two median series to right and left rather than to a gap between their bases (Fig. 45). In the paratype of *S. liberiensis* seen by me the teeth form a continuous, firm, velvet-like covering across the middle of the bone with no appearance of a division. Whether this difference is specific or related to the different sizes of the fishes examined must await further knowledge of the variation.

Thys (1971) bracketed *S. tournieri*, *S. liberiensis*, *S. occidentalis* and *S. caudomarginatus* as 'strongly interrelated and could be considered as only subspecies'. The two last-named, however, are well characterized species, and it remains to be seen whether the differences between the types of *S. tournieri* and *S. liberiensis* really characterize the populations from which they came.

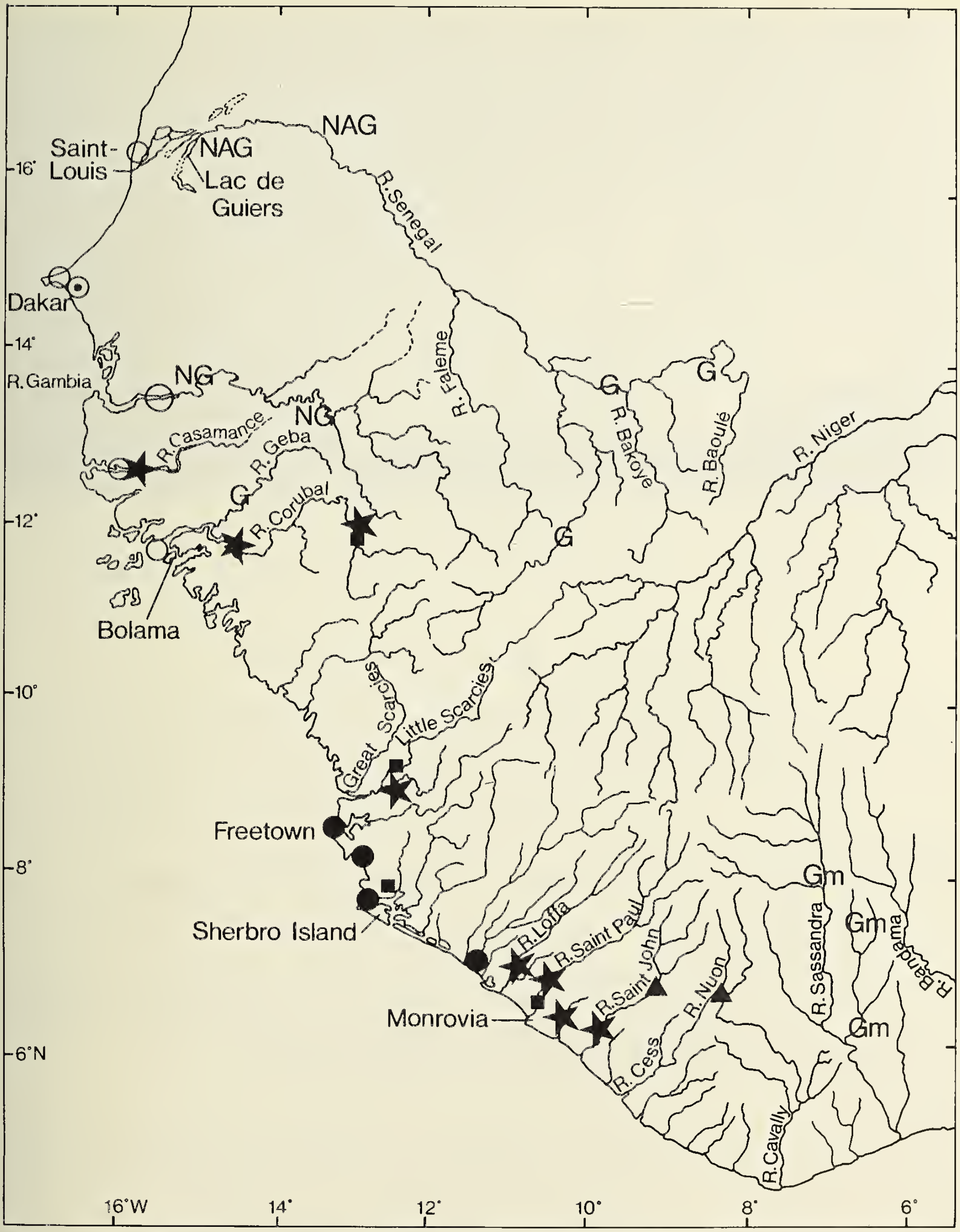

Fig. 43 Part of West Africa to show the largely complementary distribution of *Oreochromis niloticus, O. aureus* and *Sarotherodon galilaeus* on the one hand; and *Sarotherodon tournieri, S. occidentalis* and *S. caudomarginatus* on the other.

A = *Oreochromis aureus*
G = *Sarotherodon g. galilaeus*
Gm = *S. g. multifasciatus*
N = *Oreochromis n. niloticus*
O = *Sarotherodon melanotheron heudeloti*

⊙ = *S. m. paludinosus*
● = *S. m. leonensis*
★ = *S. occidentalis*
■ = *S. caudomarginatus*
▲ = *S. tournieri*

Fig. 44 *Sarotherodon tournieri* paratype of 82 mm SL, MNHN 1964–273. (Photograph, BMNH).

Sarotherodon tournieri tournieri (Daget)

Tilapia tournieri Daget, 1964:594; Daget & Iltis, 1965:265, fig. 167 (Cavally R., border of Ivory Coast & Liberia).

Tilapia (Sarotherodon) tournieri; Thys van den Audenaerde, 1968*b*:xxxix; *idem*, 1971:215 (on the types).

Types. Holotype: 112 mm SL from Cavally River at Toulepleu (6°35′N, 8°25′W). MNHN 1964/272.

Paratypes: 8 specimens, 35–89 mm SL, data as holotype. MNHN 1964/273.

Distinguishing characters

See above. Table 29 shows no difference between the subspecies that would not be expected given the different size-ranges, except possibly the numbers of scale-rows on the cheek. The fact that the numbers of soft dorsal and anal rays are outside the range given for *S. t. liberiensis* is explicable in terms of the different policies in counting the soft rays.

Description

See Table 29. The shape of the body is characteristic of the species, the deep trunk being followed by a short, deep caudal peduncle. In the paratypes examined there are only three rows of teeth in the jaws, the outer depressible, with narrow bases and obliquely truncate bicuspid crowns, the inner minute. The soft dorsal and anal fins are bluntly pointed. The toothed area of the lower pharyngeal has rounded lobes, and the blade is longer than the median length of the toothed part.

Coloration (see Fig. 44). Behind the dark nape there are 8–9 dark vertical bars on the body. Dorsal with grey lappets and with large, round, clear spots in a dark reticulum. Anal similarly marked. Caudal with small, dark rectangular spots, either irregularly arranged or in curved rows. Life colours not recorded.

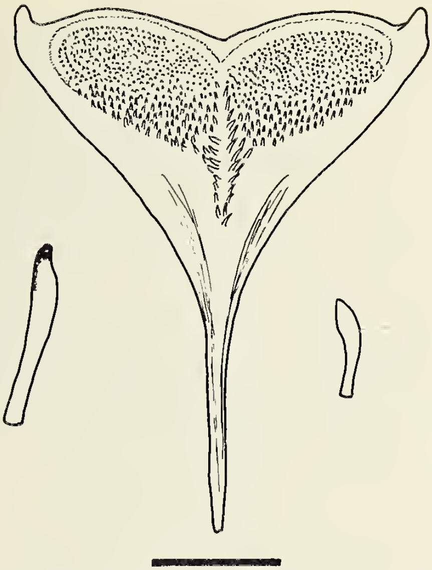

Fig. 45 *Sarotherodon tournieri.* Lower pharyngeal bone of a paratype. Scale = 3 mm.

Sarotherodon tournieri liberiensis (Thys)

Tilapia (Sarotherodon) liberiensis Thys van den Audenaerde, 1971:209, fig. (Toyebli, Cess or Nuon R., nr border of Ivory Coast & Liberia; & St John R., Liberia.)

TYPES. Holotype: ♀, 251 mm TL (179 mm SL), from Toyebli, Nuon R., 6°38′N 8°29′W, coll. Thys, 21.III.1969. MRAC 170.058.

Paratypes: 3, 35·3–63 mm TL, data as holotype, but coll.3.VIII.1968, MRAC 157.470–472; 3 ♂♂ 147–182 mm TL, from Toyebli, coll. Thys 20.III.1969. MRAC 170.059–061.

Distinguishing characters

See above and Table 29. The teeth in the specimen examined (which is much bigger than any *S. t. tournieri* seen) are in 4 rows in each jaw. The outer have a very small minor cusp and a broader, incurved major cusp, the inner are equally tricuspid. The pelvic fin ends in a filament extending to the first anal spine. The pointed tips of dorsal and anal fins end above the middle of the caudal fin, which is emarginate, the longest ray being 1·2 times the shortest. The scales become gradually smaller from the pectoral base to the chest, where they are regularly imbricating.

COLORATION. In the preserved 132 mm fish there is a small dark mark in the position of the tilapia-mark. Pale ovals form two rows on the posterior part of the spinous dorsal and are surrounded by a grey reticulum at the base of the soft dorsal and faintly in the middle of the caudal.

Life-colours are described by Thys (1971). Upper parts of head and back yellow-green, flanks silvery, each scale with a yellow spot or bar at base; soft dorsal, anal and caudal yellowish with rows of dark spots and with blackish margins; iris silvery, with yellow crescent near upper margin.

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector
MNHN 1964/273 paratypes of *T. tournieri*	34·6–83·2	Toulepleu, Cavally R.	J. Daget
MRAC 170.059 paratype of *T. liberiensis*	132	Toyebli, Cess or Nuon R.	D. F. E. Thys van den Audenaerde

Table 29. Proportions and meristic characters in *S. t. tournieri* (three paratypes) and *S. t. liberiensis* (one paratype examined by E. T. and data from the description by Thys van den Audenaerde, 1971). The 'lower jaw' measurement of Thys is evidently not the same as mine. The gill-raker numbers given by Thys include the one at the joint, but not those on the epibranchial.

	tournieri paratypes			*liberiensis* paratype (E. T.)	*liberiensis* all types Thys, 1971
SL(mm)	83	57·5	34·5	132	25–179
As % SL					
Depth	54·1	51·5	46·2	56·5	41·5(juv)–56·4
L. head	37·4	38·4	40·7	35·6	34·4–39·7
L. pect. fin	46·8	43·5	36·1	47·0	——
Longest D spine	19·9	19·1	——	19·3	17·4–19·6
L. caud. ped.	10·3	10·4	——	11·3	——
D. caud. ped.	18·0	19·6	——	18·5	——
As % l. head					
L. snout	35·7	37·1	35·5	39·0	——
Eye	27·6	30·3	31·9	23·0	19·1–23·7
D. preorb.	22·8	22·6	22·0	27·5	22·8–29·1
Interorb.	33·8	33·9	35·5	36·6	34·2–37·6
Upper jaw	24·4	27·6	28·4	28·0	——
Lower jaw	29·9	32·0	35·5	29·5	[23·3–26·2]
Caud. ped. l/d	0·6	0·5	——	0·6	——
Vertebrae	28	28	——	27	——
Scales lat. line	29	29	29	28	27–28
Scale rows cheek	3	3	3	2	2
Scales D-lat. line	3½	3½	3½	4	3½
Dorsal fin	XV 13	XV 13	XV 13	XV 12	XV 10–12
Anal fin: III	10	10	——	10	8–9
Gill-rakers	5+1+18	5+0+18	5+1+17	4+1+19	?+17–21

Sarotherodon occidentalis (Daget)

?*Chromis mossambicus* (*non* Peters); Steindachner, 1894:38 (St Paul R. & Soforeh Place, Liberia).
Tilapia galilaea (part, *non* Linn.); Boulenger, 1915:169 (specimen from Corubal R. only); ?Fowler, 1919:242 (Mt Coffee, St Paul R., Liberia).

Fig. 46 *Sarotherodon occidentalis*. Above, specimen of 81·5 mm SL from the type locality, Gaoual, Tomine River; below, adult of 142 mm SL from Corubal River at Tchitala.

Table 30. Proportions and meristic characters in adults of *S. occidentalis* from R. Corbal (142 mm), Sierra Leone (77·5, 110, 187 and 283 mm) and Liberia

SL(mm)	77·5	110	110·5	137·5	139·5	142·0	148·0	157·0	187·0	283
As % SL										
Depth	51	49·5	48·9	48·0	44·9	48·7	46·3	49·4	52·1	46·1
L. head	33·7	33·2	33·0	34·9	31·25	33·4	32·7	33·75	32·5	35·2
L. pect. fin	36·1	41·6	38·0	41·4	34·8	41·0	39·9	38·85	38·5	40·45
Last D spine	16·9	15·6	16·8	16·7	15·9	16·2	15·5	15·6	—	12·7
L. caud. ped.	12·9	14·0	12·2	10·9	9·7	13·0	11·5	11·5	10·4	11·1
D. caud. ped.	18·8	18·7	20·5	17·8	17·5	18·5	18·9	18·0	18·0	17·3
Caud. ped. l/d	0·7	0·75	0·65	0·6	0·55	0·7	0·6	0·6	0·58	0·65
As % l. head										
L. snout	32·6	36·9	39·7	44·4	42·0	40·1	42·3	45·3	42·6	44·7
Eye	32·6	28·2	26·3	24·2	25·2	22·2	23·1	22·6	22·1	19·1
D. preorb.	25·3	26·8	27·4	29·8	30·3	29·0	30·9	33·0	31·1	32·7
Interorb.	33·3	39·4	38·6	36·45	38·3	39·5	40·2	39·8	38·7	37·2
Upper jaw	26·8	25·9	26·3	22·9	28·2	26·0	24·7	26·4	29·0	27·1
Lower jaw	31·0	31·0	31·5	29·2	34·4	31·6	31·1	31·3	19·8	31·2
L. phar. bone	38·3	36·6	—	—	38·0	36·3	38·3	38·1	—	—
Upper/mid. caud. ray	1·2	—	1·3	1·25	1·2	1·35	1·25	1·4	1·3	—
Vertebrae	—	—	29	30	29	30	29	29	—	—
Scales lat. line	32	31	31	30	30	32	30	—	31	31
Scale-rows cheek	—	2(+1)	2	2	2	2(−3)	2	2	2	2(−3)
Scales D-lat-line	4	3½	3½	3½	4	3½	3½	—	3½	3½
Dorsal fin	XVII 13	XVIII 13	XVII 12	XVI 13	XVI 13	XVII 13	XVI 13	XVII 13	XVII 13	XVII 13
Anal fin III+	11	10	10	10	11	11	10	10	11	10
Gill-rakers	—	4+1+25	4+0+25	4+1+22	5+1+23	4+1+26	4+1+24	4+1+27	4+1+24	3+1+23

Tilapia pleuromelas (*non* Duméril); Schultz, 1942:344 (Harbel, Liberia).
Tilapia occidentalis Daget, 1962*a*:161, fig. 52, pl.13 (32) (Gaoual, Tominé R., upper Corubal system; Dubréka, coastal reagion of Guinée).
Tilapia (Sarotherodon) occidentalis; Thys van den Audemaerde, 1963:602 (list only); *idem*, 1968*b*:xxxix; *idem*, 1971:214 (Casamance R. to St John R., Liberia).

Synonymy

I am uncertain from Steindachner's brief description (1894) whether his *Chromis mossambicus* was this species, *S. caudomarginatus* or even *Tilapia guineensis*. He records 3–4 rows of scales on the cheek, which would favour the last named.

I have seen the three specimens from Harbel recorded by Schultz as *T. pleuromelas* (USNM 118818) as well as two others (USNM 191741) from the Moffa (Mafa) River catalogued as *T. galilaea* (Table 30). The latter locality is west of St Paul River; the label adds 'N. of C. Mount', i.e. probably Mount Coffee.

The three small specimens, 41·0–49·6 mm SL (TL 54–64 mm, a little shrunk from the time of Fowler's measurements), described by Fowler (1919) are also from St Paul River. They differ from *S. galilaeus* in the shape of the snout, which is gently decurved as in *S. occidentalis*, and the preorbital bone is bigger than in young *S. galilaeus* of this size (depth 25% length of head). The lateral lobes of the toothed area of the lower pharyngeal are also a little broader than in young *S. galilaeus* though it is less heart-shaped than in *S. caudomarginatus*. There are 20 gill-rakers on the lower part of the first arch and 2 or 3 rows of scales on the cheek. The body is deep (depth 49·6% SL in the 49·6 mm fish) and the caudal is slightly emarginate. Fowler described about seven dark vertical bands on the dorsal part of the body, but these have now faded, the only pigment remaining being the dark tips of the caudal, dorsal and anal fins. The pelvic filament extends to the second anal spine. There are 30 or 31 scales in the lateral line series. Dorsal XIV 13 or XV 12, Anal III 11 or 12. Vertebrae 29 (16+13), 30 (16+14), 30 (16+14).

Reference to Tables 30 and 31 shows that these have some of the characters of both *S. caudomarginatus* and *S. occidentalis*, but the shape of the snout is unlike *S. caudomarginatus* and the body is high for *S. occidentalis*. The number of scale rows on the cheek is equivocal, one specimen having three complete rows. The numbers of vertebrae, scales and anal fin-rays may be found in both species, and in *S. galilaeus*, but we have only one specimen of *S. caudomarginatus* and no *S. occidentalis* with a dorsal formula as low as in these. The formula XV 12 is common in West African *S. galilaeus*, XIV 13 less so. But the vertebral formula, 16+13 or 14, agrees with *S. occidentalis* rather than with *S. galilaeus*. I do not think these are *S. galilaeus*, but they provide the only record that shows that it is necessary to look again for this species in western Liberia.

TYPES. Syntypes: 4 specimens of 76–84 mm SL from Gaoual, Tominé R., MNHN 1959–110; and 2, 81 and 83 mm SL from near Dubréka, Guinée, MNHN 1960–491; all coll. J. Daget.

Distinguishing characters

A member of the group of species with small mouth and deep preorbital bone in adult. The eggs are large and brooded by the male (and female ?).

It has the highest numbers of gill-rakers of any species of the genus (range 22–27 on the lower part of the arch, mean of nine specimens, 24·4).

It differs from *S. galilaeus* in the more decurved snout profile, deeper preorbital bone at a given size (e.g. at 148 mm SL 30·9% l. of head, cf 24·5% in *S. galilaeus*; at 157 mm SL 33%, cf 25% in *S. galilaeus*), and in having 16 or 17 abdominal vertebrae instead of 15 although the total may be the same.

From *S. caudomarginatus* it differs in having only 2 complete rows of scales on the cheek and usually fewer in the lateral line series, and in the shape of the toothed area of the lower pharyngeal, which has concave sides and not the distinct heart-shape of *S. caudomarginatus* (Fig. 48). Dorsal spines XVI–XVIII.

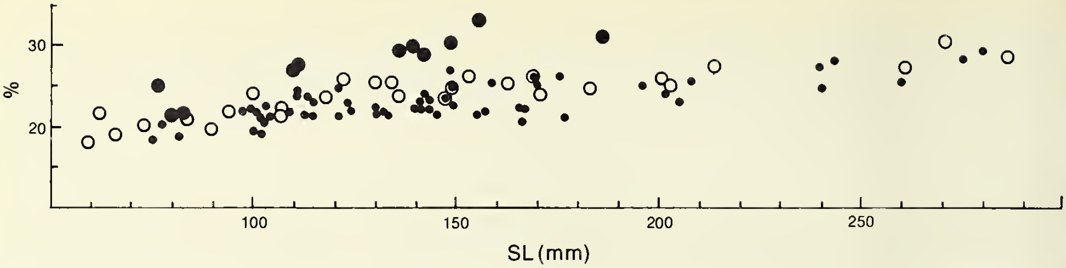

Fig. 47 Depth of preorbital bone as % length of head in *Sarotherodon galilaeus* (○); *S. occidentalis* (●); *Oreochromis urolepis* (●).

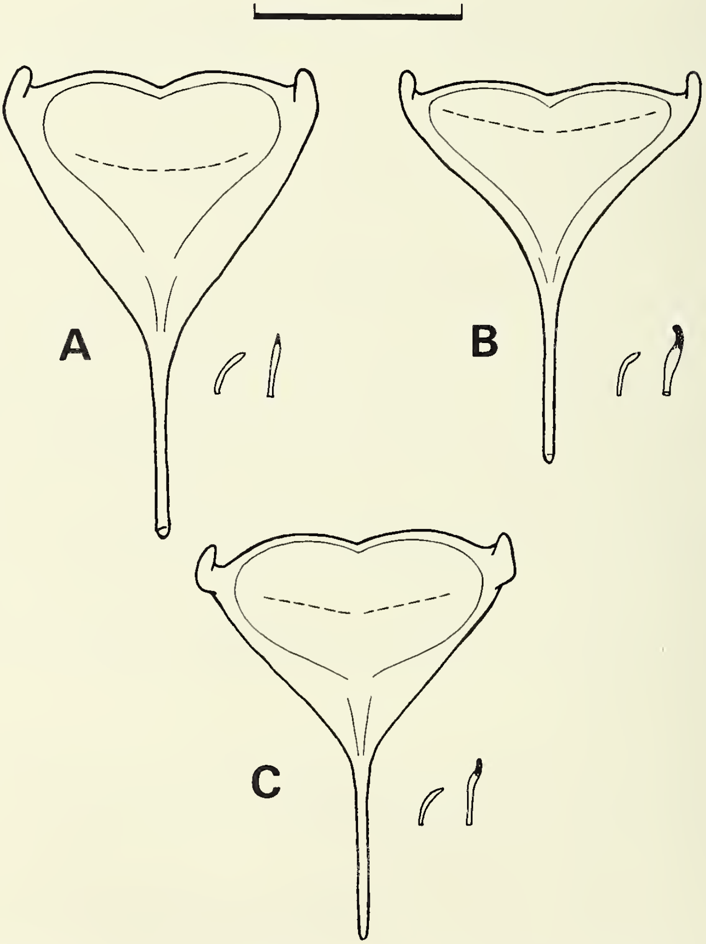

Fig. 48 Outline drawings of lower pharyngeals of: A, *Sarotherodon caudomarginatus*, MRAC 170371. 156 mm SL; B, *S. occidentalis*, Corubal River, BMNH 1910.11.28.13; 142 mm SL; C, *S. tournieri liberiensis*, paratype, MRAC 17059, 132 mm SL. Posterior and anterior teeth of each are drawn to a magnification 2·5 times as great. The broken lines show the limits of the bands of brown-tipped teeth. Scale = 10 mm.

Sarotherodon tournieri and *S. melanotheron* of adjacent waters have fewer vertebrae, scales and gill-rakers as well as differences in pigmentation.

Related species farther south (*S. mvogoi*, *S. linnellii* and *S. caroli*) also have fewer gill-rakers, vertebrae, dorsal rays and narrower toothed areas of the pharyngeal bone.

Description

Based on the specimens detailed in Tables 30 and 31 where the main proportions and meristic characters are given.

The head profile is evenly decurved in the young. In bigger fishes the convexity is most marked over the eye and the snout profile before this may be straighter, especially if the mouth is open.

The teeth in the jaws are very small, in three rows at 80 mm SL, to four in upper jaw and anterior part of lower in adults. In adults the lower band may broaden laterally to six rows. Teeth bicuspid in outermost row, tricuspid in inner rows, slender, movable, 48 to 100 in outer upper row.

The gill-rakers appear to be a little longer than in *S. galilaeus*, but no measurement is adequate to show the difference.

The shape of the lower pharyngeal bone and its toothed area are as in *S. galilaeus* (Fig. 48) and there is no 'parting' between the median rows of teeth as in the types of *S. tournieri*. The blade is a little shorter than the toothed area in the young, but 1·01 to 1·4 times as long in adults. The ratio is lowered by the extension of a few pairs of teeth forward on to the blade. The posterior teeth are slender, compressed, with a shoulder, the major cusp curved.

All the adults except the largest (283 mm SL) examined by me are males. The soft dorsal fin is moderately produced to a point, the longest ray 26·35% SL in the 148 mm fish. Third anal spine 9–13% SL in adults. The pelvic ends in a white filament extending to the genital papilla. The caudal fin is moderately emarginate, more so in adults (damaged in some).

The male genital papilla is conical or triangular, small, with a subterminal pore.

COLORATION. In the young, seven well-marked transverse bars on the body and a large, round tilapia-mark bordered fore and aft by a clear zone. These markings disappear in adults, but the tilapia-mark is still present in the 110 mm fish from Sierra Leone. One of the adults has a few vague dark markings on the flanks.

A colour photograph by Thys of a freshly caught specimen from the Casamance River (at Marsassoum) shows: snout and cheek purple; iris orange, darker above; nape and upper part of body soiled yellowish, grading to dead white on lower part of flanks and belly; lower lip, lower jaw, preoperculum and throat white; posterior dorsal lappets and upper edge of soft dorsal watery pink; a few vague dark spots on soft dorsal and centre of caudal; pelvic ending in a short white filament.

According to Thys (1971) the yellow colour is characteristic.

Ecology

Breeding

Thys (1971) reports an adult male with about seventy fry in the mouth, and a female with about 400 ovarian eggs of dimensions 3·4–4·0 × 5·0–5·7 mm. It is not known whether only the male or both sexes brood.

Distribution

West African fresh waters from the Casamance River to the St John River (Thys). Material to hand from the Corubal system, Sierra Leone and western Liberia. In Liberia the localities from which I have seen material are Harbel, on one of the shorter rivers between St Paul and St John, and Dia on the Moffa River. The latter is a spelling of Mafa, given in the Gazeteer (Washington, D.C.) as at 6°46′N, 11°22′W in the Loffa River system. Thys gives the St John as the eastern limit of the distribution.

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector
1910.11.28.13	142	Corubal R. at Tchitala	W. Ansorge
1959.8.12.6–7	80, 81·5	Gaoual, Tominé R., Upper Corubal system	J. Daget
1981,8,17.22, 52–3	77·5, 110	Old Quarry Pond, nr Port Loko, Sierra Leone	A. I. Payne
	187, 283	Taia R., Sierra Leone	B. McCarton
USNM			
118818 (3 fishes)	110·5–148·0	Harbel, western Liberia	W. Mann
191741 (2 fishes)	137·6–157·0	Dia, Moffa R., N. of C. Mount, Liberia	G. C. Miller
48505 (3 fishes)	41·0–49·6	Mount Coffee, St Paul R., Liberia	R. P. Currie

Sarotherodon caudomarginatus (Boulenger)

Tilapia caudomarginata Boulenger, 1916*a*:327, fig. 190 (North Sherbro District, Sierra Leone); Daget, 1962*a*:159, fig. 51, pl. xiii, fig. 31 (Gaoual, Tominé R., Corubal system).

Tilapia (Sarotherodon) caudomartginata; Thys van der Audenaerde, 1963:603 (list only); *idem*, 1968*b*:xxxix; *idem*, 1971:215 (western Guinée to St Paul R., Liberia).

Tilapia (Sarotherodon) sp. TOM; Thys van den Audenaerde, 1968*b*:xl (Tominé R., synonymy teste Thys, 1971).

TYPES. Syntypes: two of 54 + 11 and 62 + 14 mm to end of middle caudal rays, from Sierra Leone, North Sherbro District, coll. N.W. Thomas, BMNH 1915.5.19.17–18.

Distinguishing characters

A *Sarotherodon* with small mouth (lower jaw 27·0–31·5% l. of head in adults over 100 mm SL) and deep preorbital bone. Caudal fin deeply emarginate; each pelvic fin produced into a long filament extending to below some part of anterior half of base of anal fin. Three full rows of scales on cheek. Vertebrae 30 (f.1) or 31 (f.2). Dorsal spines XV or XVI. Toothed area of lower pharyngeal heart-shaped (Figs 48 & 50) with slender, bevelled teeth with no minor cusp. Fold of skin above upper lip bright yellow in life (Payne, pers. commn).

Description

Based on the specimens listed below (p. 138). Proportions, except for the smaller ones of Table 31, are taken only from fishes of over 60 mm SL. but meristic characters also from the young.

See Tables 31, 32 and 33.

Table 31. Proportions and meristic characters in young specimens of *S. caudomarginatus* and *S. occidentalis*. The 80 mm *S. occidentalis* has 31 scales on one side, 32 on the other. The 81·5 mm fish has 2 small scales at the anterior end of the lateral line series.

	Caudomarginatus				*occidentalis*	
SL(mm)	62	54	37	37	80	81·5
As % SL						
Depth	42·7	42·5	36·4	37·8	40·0	39·3
L. head	34·7	33·7	35·9	37·8	32·5	32·5
L. pect. fin	32·3	28·7	28·3	27·0	36·7	36·2
Longest D spine	13·2	15·0	13·5	14·8	11·1	12·5
L. caud. ped.	12·4	13·0	14·8	12·5	13·7	11·0
D. caud. ped.	16·9	16·6	16·5	15·1	17·5	17·3
As % length of head						
L. snout	37·3	38·5	39·2	39·3	34·7	35·5
Eye	25·6	27·5	27·1	25·7	29·0	28·3
D. preorb.	23·3	24·7	19·6	21·0	21·6	22·7
Interorb.	27·9	30·7	23·3	25·0	33·1	32·8
Lower jaw	30·2	33·0	34·6	32·2	27·7	30·2
Caud. ped. l/d	0·73	0·77	0·9	0·82	0·78	0·65
Upper/middle caud. ray	1·36	——	1·3	1·3	1·14	1·21
Vertebrae	31	31	31	31	30	30
Scales lat. line	32	33	33	32	31–2	31(+2)
Scale-rows cheek	3	3	3	3	2	2–3
Scales D-lat.-line	4½	4	4	4	3½	3
Dorsal fin	XVI 14	XVI 13	XVI 14	XVI 13	XVII 13	XVII 14
Anal fin: III+	13	13	13	12	12	12
Gill-rakers	6+1+24	7+1+24	5+1+22	6+1+21	7+1+24	6+0+24

Table 32. Frequencies of dorsal spines and soft rays in samples of *S. occidentalis* and *S. caudomarginatus*.

	XV	XVI	XVII	XVIII	12	13	14
S. occidentalis		3	6	1	1	8	1
S. caudomarginatus	4	16			1	9	7

Comparison of Tables 30 and 33 shows no significant differences in proportions between *S. occidentalis* and *S. caudomarginatus*. In Table 31 where younger fishes are compared, it appears that the snout in *S. caudomarginatus* forms a higher proportion of a longer head and the interorbital width is narrower. A relatively narrow interorbital also characterizes ten young from Little Scarcies River not included in Table 33. This is a size at which allometries are more evident than in older fishes. Nevertheless, this does express a difference in appearance between the young of the two species, *S. caudomarginatus* having a more acute snout, thrust forward rather than ventrally (cf. Fig 46 & 49). In older specimens the profile is convex over the eye and more ventrally directed in front.

Table 33. *Sarotherodon caudomarginatus.* Proportions and meristic numbers of five specimens from Little Scarcies River, Sierra Leone and one (156 mm) from St Paul River, Liberia. See also Table 31.

SL(mm)	62	114	116·5	116·5	134	156
As % SL						
Depth	46·4	47·4	48·9	48·1	48·1	49·0
L. head	34·7	34·2	36·9	34·8	33·5	35·25
L. pect. fin	34·1	39·9	38·6	39·5	42·8	42·3
Longest D spine	15·6	16·2	16·3	14·2	15·8	15·9
L. caud. ped.	13·1	12·3	11·6	12·2	12·7	13·1
D. caud. ped.	16·2	16·6	16·7	16·3	16·8	18·6
As % length of head						
L. snout	39·7	39·5	43·0	41·0	40·0	41·1
Eye	31·3	28·2	25·6	27·2	26·6	20·9
D. preorb.	26·6	29·0	26·9	28·6	26·8	26·4
Interorb.	30·8	32·3	31·8	33·6	35·5	33·1
Upper jaw	29·0	26·9	25·6	27·4	23·3	24·9
Lower jaw	33·6	29·0	27·2	28·4	31·5	28·7
Caud. ped. l/d	0·8	0·7	0·7	0·7	0·075	0·7
Upper/middle caud. ray	1·32	1·47	1·5	1·46	1·6	1·3
Vertebrae						30
Scales lat. line	32	33	32	34	32	31
Scales rows cheek	3	3	3	3	3	3
Scales D-lat.line	4	4	4	4	4	4
Dorsal fin	XVI 13	XVI 13	XVI 13+1	XVI 14	XVI 14	XV 12
Anal fin: III+	11	12	12	12	12	11+1
Gill-rakers	4+2+19	3+1+18	4+1+20	3+1+22	3+1+20	4+1+22

The difference in shape of the caudal fin is also more marked in the young, the corners of the fin (at least in males) becoming produced more in adult *S. occidentalis.* A measurement of the emargination is given in the tables by the ratio upper (longest) caudal ray over middle ray.

Both species have a pelvic filament, but this is longer in *S. caudomarginatus.*

The teeth are extremely small; the bicuspid outer form a fringe on a movable lip. In formalin-preserved fishes the inner are sunk in a mass of swollen papillae; they have three equal cusps and are in 1–3 series.

The gill-rakers, 18–24 on the lower part of the anterior arch, (16 in one juvenile), are in a lower but overlapping range than in *S. occidentalis.* There are no microbranchiospines in the types and Thys reports that they develop late and imperfectly.

The pharyngeal bone (Figs 48 & 50) is characteristic, resembling that of the unrelated *D. franchettii,* an inhabitant of warm alkaline waters (p. 507). In a fish of 117 mm SL the length of the bone is 38·8% l. of head, the width 28·1% and the blade is 1·4 times the median length of the toothed area.

Although the majority of samples of both *S. occidentalis* and *S. caudomarginatus* have a total of 29 or 30 dorsal rays, they are differently distributed between spinous and soft rays (see Table 32, in which ten young *S. caudomarginatus* not used in Table 33 are included). The formulae are D XV 12(f.1), XV 14 (f.3), XVI 13 (f.9), XVI 14 (f.7). A III 11 (f.3); III 12 (f.13); III 14 (f.3).

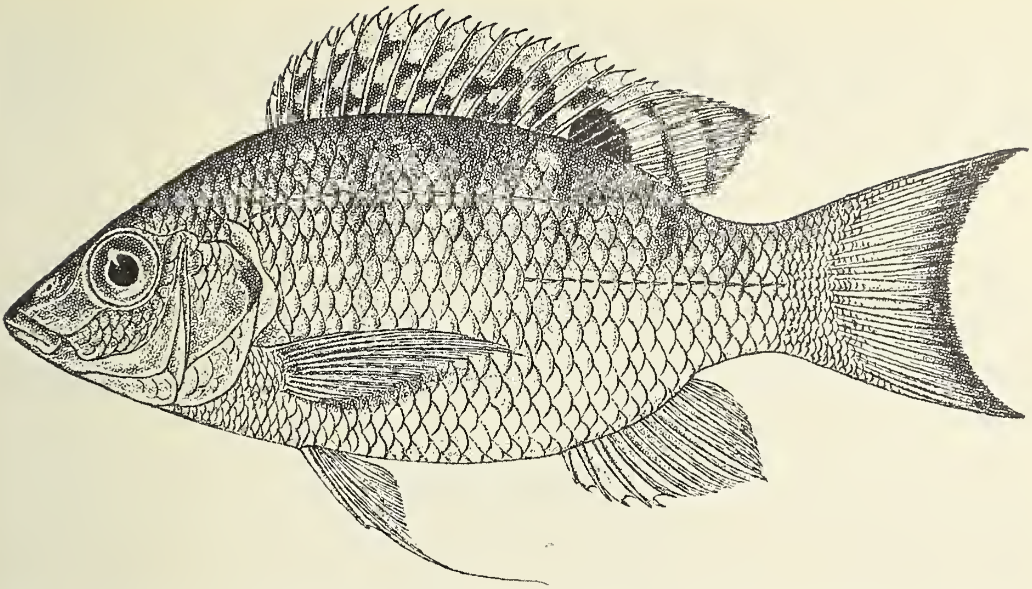

Fig. 49 *Sarotherodon caudomarginatus*, one of the syntypes, 62 mm SL. From Boulenger, 1915, fig. 190.

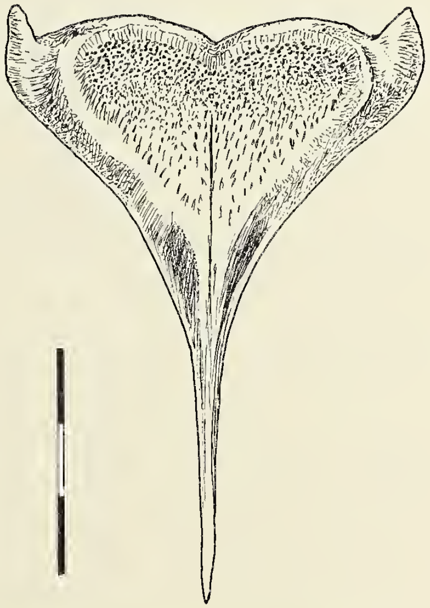

Fig. 50 *Sarotherodon caudomarginatus*, pharyngeal bone of a syntype. Scale = 3 mm.

Vertebrae 30 (f.1) or 31 (f.4).

Scales: see tables. There are 4–5 between bases of pectoral and pelvic fins, smaller, but imbricating on the chest.

Genital papilla of male small and conical or with a shallow notch.

Coloration. The margins of dorsal, anal and caudal fins are black. A tilapia-mark is present on the dorsal fin in the young, but is smaller and of a less regular shape than in *S. occidentalis*. At SL 116 mm it is no more than a slightly darker grey part of an oblique band or series of spots on the dorsal fin. In life the flanks are silvery-whitish with an orange-yellow spot on each scale (Thys, 1971). The lower parts of head and trunk are white and the fold of skin above the uppoer lip is bright yellow (A. I. Payne, pers. commn).

Ecology

Nothing is reported on the ecology of this species.

Distribution

West African rivers from the Corubal River system to the St Paul River, western Liberia. Fresh water.

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1915.5.19.17–18 (syntypes)	54, 62	North Sherbro District, Sierra Leone	N. W. Thomas
1959.8.12.8–9	37, 37	Gaoual, Tominé R., Corubal system	J. Daget
1981.6.19.168–175		Little Scarcies R., Sierra Leone	A. I. Payne
(13 fishes)	45–62		
(4 fishes)	114–135		
MRAC 170371	156	Mount Coffee, barrage lake on St Paul R.	D. F. E. Thys van den Audenaerde

Genus *OREOCHROMIS*
Subgenus *OREOCHROMIS* - I

Oreochromis niloticus
Oreochromis aureus

The type species of subgenus *Oreochromis*, *O. hunteri*, is a small population of a special environment; but through the species of the Pangani system (pp 357–374) it is linked with the series in the lower reaches of the eastern rivers, from *O. mossambicus* in the south, to *O. spilurus* in Kenya and Somalia.

The two species described in this section are isolated geographically from these eastern species. The nearest relative of *O. niloticus* seems to be *O. esculentus* of Lake Victoria, which resembles it in the low degree of sexual dichromatism, the edge of the dorsal fin being grey or black in contrast to the bright red margin of mature males of the eastern species; and both have a relatively narrow preorbital bone and rather high meristic numbers. *Oreochromis aureus*, however, has in the male the bright red margin of dorsal and caudal fins common in the eastern species. Although it too has a rather narrow preorbital bone, it may well be historically closer to the eastern species than to *O. niloticus.*

Oreochromis niloticus and *O. aureus* are brought together in this section because of the need to distinguish them where they live together in the Nile delta and the coastal rivers of Israel, the Chad basin, the Middle Niger, and the Senegal River. The distribution of *O. aureus* also includes the Jordan Valley, but it has not been recorded in the Nile above the delta, nor in the tropical lakes in which the subspecies of *O. niloticus* dominate the fauna (Albert, Edward/George, Kivu, Turkana, Baringo & the Ethiopian lakes). The ecology of the two species appears to be very similar, although in the Nile delta their preferences differ slightly. In its coloration, especially male breeding colours, and in its metameric numbers *O. aureus* is nearer to the eastern species of subgenus *Oreochromis* than is *O. niloticus.* It is now separated from them by the Horn of Africa and the Red Sea. But the Red Sea area was not always an environment hostile to cichlids and the invasion by Indian Ocean water is dated Upper Pliocene (Gregory, 1921:343). It may have been that invasion that separated what is now *O. aureus* from the *Oreochromis* of Somalia and Kenya. *O. aureus* remained in the Jordan Valley and the Nile delta, from which the Tethys Sea had by then retreated. In the delta it met with *O. niloticus*, which we must suppose descended from the Upper Nile as Tethys withdrew. The extension westwards of both species was probably in Pleistocene times and subsequent to their meeting.

This speculative history is put forward as an attempted explanation of the partial sympatry of the two species, the curious restriction of the nilotic population of *O. aureus* to the delta and the absence of *O. niloticus* from Lake Tiberias and the River Jordan. The fossil teeth described by Avnimelech & Steinitz (1952) in continental Upper Pliocene beds near the Lower Jordan (see p. 199) fit into this story, but as a specialized population comparable to *O. s. percivali* within the superspecies *O. spilurus.*

The alternative hypothesis, that they are sympatric sister-species, is supported by the two shared characters in which both differ from the eastern species, namely the narrow preorbital bone and the non-enlargement of the jaws in mature fishes.

The sympatric existence of the two species is possible only because they do not interbreed unless they are given no choice. The genetic bar to interbreeding is demonstrated by the results of placing males of one species with females of the other, giving no opportunity to either to mate with its own species. When *O. niloticus* is the female parent the F_1 is 100% male. The reciprocal cross produces 75% males.

The results of experimental interbreeding of *O. niloticus* with eastern species are doubtfully indicative of degree of relationship. On the one hand, the cross *O. niloticus* × *O. urolepis hornorum* gives an all-male F_1, but produces very few offspring (Lovshin *in* Pullin & Lowe-McConnell, 1982:303). On the other hand, *O. niloticus* is said to cross with *O. mossambicus* with a normal, 1:1 sex-ratio (Mires, 1977, citing Pruginin).

Oreochromis niloticus (Linnaeus)

For synonyms and bibliographies see the subspecies.

The ecology of the superspecies is reported after the descriptions, on p. 183.

Distinguishing characters

Gill-rakers (18, 19) 20–26 (27, 28) on lower part of the first arch.

Scales in lateral line series 30–34, usually 31–33. Modal number of dorsal spines XVII, except in some subspecies (Tables 35 & 36).

Depth of preorbital bone not exceeding 22% length of head. Lower jaw without any allometry in either sex above 50 mm SL, its length 29–35 (37·5)% length of head (exception see p. 180). Length of lower pharyngeal 28–34% length of head; means in samples from the subspecies 29·8–32·1 (Table 37).

Genital papilla of male short and conical or bluntly bifid at tip.

Caudal fin covered with narrow vertical stripes (exception pp. 164, 180). Upper margin of dorsal fin black or grey, the melanin sometimes slightly mixed with red, not orange or vermilion even in breeding males. Head and trunk of breeding male suffused with red; in some localities lower jaw, chest, pelvics and anterior part of anal fin black.

Of these the most diagnostic are the regular and definite striping of the caudal fin (in most subspecies), not vague or variable as in the partially sympatric *O. aureus*; the red flush of the breeding male and the dark margin of the dorsal fin. At least in the nominate subspecies the high number of dorsal spines is almost equally diagnostic, contrasting with *O. aureus* in which XVII is a very rare number (Table 48). The relatively short pharyngeal bone is a character shared with *O. aureus*.

In Lakes Albert and Edward/George there is no *O. aureus*, and the average scale and fin-ray counts are lower (an example of character displacement?). *O. niloticus* is there easily distinguished from *O. leucostictus* (see p. 221) by colour, dentition and numbers of scales and vertebrae.

In Lake Victoria, to which *O. niloticus* has now been introduced, the red and black breeding colours are matched rather closely in *O. esculentus*, and field workers have had the impression that this species is the endemic representative of *O. niloticus* (Lowe, 1958). *O. esculentus* (p. 209) lacks the caudal stripes, has a longer caudal peduncle and fewer gill-rakers, and the pharyngeal bone is longer, with finer and more densely crowded teeth.

In Ethiopia, Lake Turkana (Rudolf) and Lake Baringo there is no species that could be confused with it. *O. spilurus*, which is found on the eastern side of the Ethiopian-Somali watershed, has a red dorsal margin in the breeding male, a more vaguely marked caudal fin, lower meristic numbers and breeding males have enlarged jaws.

Distribution

NATURAL DISTRIBUTION. The Yarkon River, nr. Tel Aviv; the Nile, Jebel Marra, Lake Chad basin; Niger system; Volta River; Gambia River; Senegal River; Lakes Albert, Edward, Kivu and the shallower parts of Lake Tanganyika; Lake Tana (Tsana) and the other Ethiopian lakes, Ergino

River (Omo system), Lake Turkana (Rudolf), Suguta River, Lake Baringo. Absent from Sierra Leone and Liberia, and from Ivory Coast except the upper tributaries of Niger and Volta. Absent from Cameroon, except from the Cameroonian parts of the Chad basin, and the Benue system. Absent from the western rivers of Gabon, Rio Muni, the Zaire and southwards and from all the eastward-flowing rivers of Africa. Absent from Lakes Victoria and Kioga until introduced about 1951–53.

Further details under the subspecies.

DISPERSAL BY MAN. Already in 1924 the species had been introduced into Lake Bunyoni, Uganda, allegedly from Lake Edward. Because of slight differences from the Lake Edward population the Bunyoni population was given a specific name (*T. inducta* Trewavas), but this cannot be maintained (see below, p. 158). There have been subsequent plantings in Lake Bunyoni and, from either Lake Edward or Lake Albert, directly or via ponds into many small lakes and dams in Uganda and Rwanda. In about 1951, probably unintentionally with *Tilapia zillii*, it was introduced into Lake Victoria, where it has flourished (Welcomme, 1976*b*). Okedi *et al.* (1976) recorded it among the species that had ascended the River Kagera and were breeding in a shallow lagoon in the upper reaches. Batches from Lake Turkana were taken by Pruginin to ponds at Kajansi, Uganda and bred there. Both this subspecies (*O. n. vulcani*) and stocks originally from the Ugandan lakes have been used in pond culture in Israel.

The stock used in pond-culture at Bouake, Ivory Coast, is from the tributaries of the Niger and Volta in the northern part of that territory, and that in the ponds of Cameroon from the Cameroonian part of the Chad basin (Bard, 1962*a-c*). We have specimens that were caught feral in the Lower Congo near Kinshassa. Thys (1964:29–30) reports introductions into ponds and small lakes of Ruanda-Urundi from Kivu or Tanganyika, and into the upper Uele and Ituri from Lake Albert.

Before the recognition of the distinctness in Lake Tiberias (Kinneret) of *O. aureus*, the latter was distributed from Israel to the Americas under the name of *T. nilotica*, and most of the supposed '*niloticus*' in American ponds have proved to be the 'blue' tilapia. None has been verified as true *niloticus*. It is known that more recent exports have been from ponds where *O. niloticus* have been encouraged to hybridize with *O. aureus* so that a high percentage of fry would be males (Mires, 1977). It was introduced into Thailand as a gift from the Emperor of Japan (Thiemmedh, 1966).

Subspecies

Although several names have been given to the species as here understood, the only considered division into subspecies (Thys, 1964) dealt only with the section of the distribution from Lake Tanganyika to the Nile. The wide area covered provides a number of different types of habitat and includes areas now isolated by land-barriers or other obstructions. It is only necessary to go back to the Upper Pleistocene to find the links between these areas and the isolation of some is historically temporary. Among the latter are the crater-lakes on the Central Island of Lake Turkana. Although the population of one of them has characteristics that could provide a structural definition of a subspecies, consideration of its probably not distant past continuity with the main lake population, and its possible near future renewal of that continuity have led me to extend the use of the name, that I gave it in 1933, to cover the whole of the Lake Rudolf population as a subspecies of *O. niloticus*.

Other equally small populations are so placed that their isolation in a restricted, peculiar environment seems likely to be of long duration. Such are the inhabitants of hot alkaline springs near Addis Ababa (*O. n. filoa*), and those of similar waters in the Suguta system (*O. n. sugutae*). It is convenient to provide them with names, if only to preserve their identity for any future experimenter or fish manager.

Fig. 51 Natural distribution of the subspecies of *Oreochromis niloticus.*

The population of Lake Albert, although having some peculiarities, is here included in *O. n. eduardianus.* It is now geographically linked with the nominate subspecies through the Albert Nile and the swampy part of the Upper Nile.

Seven subspecies are recognized.

Oreochromis n. niloticus (Linn).
The Yarkon River, entering the Mediterranean near Jaffa; the Nile from below the Albert Nile to the delta; Jebel Marra between Lake Chad and the Nile; Lake Chad basin, and the rivers Niger, Benue, Volta, Gambia and Senegal. Doubtfully native in the Jordan Valley (see p. 148), but now stocked there artificially.

Scales in lateral line series 31–34, mode 32 or 33 in different populations. Vertebrae 30–32, mode 31.

Dorsal spines (XV) XVI–XVIII, mode XVII. Of 90 specimens, 1 had XV, 11·1% XVI, 76·7% XVII and 11·1% XVIII. Total dorsal rays 29–31, mode 30. Modal formula XVII 13 (Tables 35, 36).

Teeth in jaws with rather stout shafts, in 3–4 series up to 200 mm SL, 4–6 series above this size, a seventh at 330 mm; outermost bicuspid (Fig. 54).

Lower pharyngeal (Fig. 55 & Table 37) with firm teeth in an approximately triangular dentigerous area, whose median length is from a little less than that of the blade to 1·5 times as long; width of bone equal to or greater than its length. In a fish of about 300 mm SL a few anterior upper pharyngeal teeth are tricuspid, the main cusp being sharply hooked, the third a brown-tipped shoulder.

Table 34. Frequencies of vertebral numbers in samples of populations of *O. niloticus*, with means and standard deviations of the samples.

Vertebrae	26	27	28	29	30	31	32	Mean
O. n. niloticus								
Israel (coastal)					7	27	1	30·8±0·447
Lower Nile						11	3	31·2±0·426
Niger						9	1	31·1±0·316
O. n. eduardianus								
L. George				2	2			29·7±0·488
L. Edward					3			
L. Albert				1	8	4		30·3±0·599
L. Albert (Buhuku)				3	17			29·85±0·366
O. n. cancellatus								
Ergino R.						5	1	30·9±0·323
L. Ganjule					1	8		
L. Tana					1	2		
O. n. filoa	1		3	7	6			29·0±0·061
O. n. vulcani								
Crater A					1	7	1	31·14±0·525
Crater C and main lake						10	5	
Loiengalani					1	3		
O. n. baringoensis				(1)	4	6		30·6±0·516
O. n. sugutae				3	6	1		29·8±0·632

Pectoral fin 33·0–43·5% SL. Length of caudal peduncle 10–12% SL, 0·5–0·9 of its depth.

Vertical stripes on caudal fin distinct, very little or no anastomosis. Breeding males with red flush on lower parts of head and body and on dorsal and caudal fins. No extensive black areas on lower parts of head and body, although pelvics may be tinged black.

Females mated with male *O. aureus* (in Israel; Fishelson, 1962) or with male *O. macrochir* (in Ivory Coast; Jalabert *et al.*, 1971) produce an all-male F_1.

Oreochromis n. eduardianus (Boulenger)

Lakes Edward and George, and the small lakes and streams of their basins; Lake Kivu; Ruzizi River and Lake Tanganyika; Lake Albert.

Scales in lateral line series 30–32 (33), usually 31 or 32. Vertebrae 29–31, mode 30.

Dorsal spines (XV) XVI or XVII. Of 102* specimens 1 had XV, 24·5% XVI and 74·5% XVII; total rays 27–30, mode 28 or 29, modal formula XVII 12 (Tables 34–36).

Teeth in jaws with shafts as in *O. n. niloticus* or a little more slender, in 3 or 4 series up to SL about 160 mm, 4–6 above this size; outermost all bicuspid, rarely one or two with a third cusp. Except in Lake Albert, but also in some of its lagoons, lower pharyngeal teeth finer and more numerous than in *O. n. niloticus*, and on a smaller dentigerous area with concave sides, its median length always less than that of the blade, sometimes less than three quarters; width of bone equal to or a little greater than its length, 29·0–33·4% length of head (Fig. 55).

With some exceptions the vertical stripes on the caudal fin are distinct, with anastomoses only basally. Breeding males with throat, chest, pelvic, dorsal and anal fins black, head and flanks flushed red.

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*Numbers recorded by Poll (1939*a*) and Thys (1964) are included. Lake Albert is excluded.

Table 35. *Oreochromis niloticus.* Meristic characters in the subspecies (read across p. 145).

	Scales lat. line					Dorsal spines				
	30	31	32	33	34	XIV	XV	XVI	XVII	XVIII
O. n. niloticus										
West Africa		1	11	5			(1)	2	16	5
R. Yarkon		1	9	4				6	22	1
Nile		1	12	13	2			2	33	6
O. n. eduardianus										
L. Albert (excl. Buhuku)	3	4	4					9	13	
Thys, 1964		12	8				1	9	10	
Buhuku	2	2						16	5	
L. Edward/George		13	8					7	16	
L. Kivu	1	8	4					8	6	
L. Tanganyika		6	9	1			1	6	10	
O. n. cancellatus			5	29	4			28	65	6
O. n. filoa	2	9	3	1		9	19	5		
O. n. vulcani										
L. Rudolf basin			3	17	2		1	18	9	
Crater C			1	3	2		1	7		
Crater A			6	5	1		2	23		
Stream at Loiengalani			2	8	1		1	17	3	
O. n. baringoensis			12	6				28	1	
O. n. sugutae		7	5	2		1	13	18		

The population of Lake Albert and the Albert Nile is included here, but differs from that of Lakes Edward/George and Kivu, not only in having somewhat coarser teeth, but also in its longer and stronger dorsal and anal fin-spines (see Table 42 & p. 159).

It is probably this subspecies, which when mated with male *O. variabilis*, gives an F_1 of 100% males, but with *O. leucostictus* only 94% (Pruginin, 1965). Mires (1977) reports also that with *O. aureus* males it gives 90% males in the F_1, but there is some doubt of the purity of the stock (see p. 205).

Oreochromis n. cancellatus (Nichols)
Ethiopia: Lake Tsana, Lakes Zwai to Gandjule (= Abeia) and Stefani, the Ergino River (Omo system), and the Awash River.

Scales in lateral line series 32–34, mode 33.

Dorsal spines XVI–XVIII, mode XVII; modal formula XVII 12. Total rays 28–30, mode 29. Vertebrae 30–32, mode 31 (Tables 34 & 35).

Teeth in jaws with stout shafts in the rivers, usually more slender in the lakes; in 4–5 series at 100–200 mm SL. (4)5–7 above this size; outer bicuspid.

Pharyngeal teeth variable, but frequently finer than in *O. n. niloticus*, and usually in the lakes covering a shorter dentigerous area. Width of bone from a little less to a little more than its length.

Table 35 *continued*

Dorsal totals							Modal	Lower gill-rakers		
26	27	28	29	30	31	32	Formula	N	Range	Mode
								65	19–26	21 = 22
			3	19	4		XVII 13			
			2	17	10		XVII 13			
			4	22	14	1	XVII 13			
								57	20–26	21 = 22
			11	8	3		XVII 12			
	1	1	11	7			XVI 13			
		5	15	1			XVI 13			
		11	11	1			XVII 11 = XVII 12			
	1	7	4				XVII 11			
	1	7	7	2			XVII 12			
		15	74	10			XVII 12	34	19–25	22
8	19	5	1				XV 12	10	18–23	20 = 22
								34	20–28	21
		1	8	19			XVI 14			
		1	3	4			XVI 14			
			8	14	3		XVI 14			
		1	9	9	1		XVI 13			
		17	11	1			XVI 12	16	20–23	21
1	3	17	10	1			XVI 13 = XV 13 = XVI 12	15	18–23	20

Length of caudal peduncle usually 12·0–14·5% SL (less than 12 in only 7 of 45 measured), 0·8–1·0 of its depth. Length of pectoral fin usually over 37% SL.

Stripes of caudal fin often anastomosing in adult to form a reticulum in centre of fin. Breeding male colours not described except in Lake Langano where the whole fish becomes blue-black.

Oreochromis n. filoa subsp. n.

Hot alkaline springs in the Awash system.

Scales in lateral line series 31–33. Dorsal spines XIV–XVI, mode XV; total dorsal rays 26–29, mode 27; modal formula XV 12. Vertebrae 26–30, mode 29 (Tables 34 & 35).

Pharyngeal teeth fine and rather crowded; lower dentigerous area with more rounded lobes than in other subspecies (one examined). Length of pectoral fin less than 37% SL.

Other characters as in *O. n. cancellatus* of the same size. Life colours unknown.

Oreochromis n. vulcani (Trewavas)

Lake Turkana and the crater lakes on its Central Island; also the stream entering the lake at Loiengalani.

Scales in lateral line series 32–34, mode 33.

Dorsal spines XV-XVII, mode XVI (in 80% of specimens); Total dorsal rays 28–31, mode 30, modal formula XVI 14 (XVI 13 at Loiengalani). Vertebrae 30–32, mode 31 (Tables 34 & 35).

Teeth in jaws with slender to very slender shafts and curved crowns with rounded edges; in 4–7 series from 100 mm SL upwards; outer bicuspid, interspersed in adult with tricuspids (Fig.

Table 36. *Oreochromis niloticus*. Percentage frequencies of numbers of dorsal spines in the subspecies and populations. If the two entries for Lake Albert are combined the result is 58·5% with XVI, 41·5% with XVII. The respective percentages given by Thys (1964:28) are very close to this, namely 60 and 40.

	N	XIV	XV	XVI	XVII	XVIII
O. n. niloticus						
Yarkon, Nile, W. Africa	94	—	1·06	10·63	75·53	12·76
O. n. eduardianus						
L. Albert (excl. Buhuku)	22	—	—	40·9	59·1	—
L. Albert (Buhuku)	21	—	—	76·2	23·8	—
Ls Edward, George, Kivu & Tanganyika	54	—	1·8	38·8	59·26	—
O. n. cancellatus	89	—	—	28·28	65·65	6·06
O. n. filoa	33	27·27	57·57	15·15	—	—
O. n. vulcani						
Main Lake Turkana	28	—	3·57	64·3	32·1	—
Crater C	8	—	12·5	87·5	—	—
Crater A	25	—	8·0	92·0	—	—
Loiengalani	21	—	4·76	80·95	14·28	—
O. n. baringoensis	29	—	—	96·55	3·45	—
O. n. sugutae	32	3·12	40·6	56·25	—	—

54). Width of lower pharyngeal bone equal to, or less than, its length, 28–32% length of head or even less in Crater-lake A. Length of caudal peduncle 10·4–13·8% SL, but in Crater-lake A 11·4–14·6; ratio length/depth 0·65–0·9, but in crater A 0·73–0·98.

Caudal marked with wavy vertical stripes in young, these becoming more irregular in large specimens. General body colour of mature male dark green with blue iridescence or (in Crater A) dark blue-black; or (Chervinski, 1967) with ventral surface turning black at peak breeding phase.

Females mated with male *O. aureus* give an F_1 of 80–90% males (Chervinski, 1967; Pruginin *et al.*, 1975; Mires, 1977).

Oreochromis n. baringoensis subsp.n.
Lake Baringo, Kenya.

Scales in lateral line series 32 or 33. Vertebrae 30 or 31.

Dorsal spines XVI or XVII, XVII in only one of 29 examined; total rays 28–30, mode 28, nearly approached by 29 (Tables 34, 35 & 36).

Teeth in the jaws with stout shafts; in 4 or 5 series; outer bicuspid in young, becoming gradually replaced by tricuspids from *ca* 160 mm SL, until at 220 mm SL all are tricuspid.

Pharyngeal teeth as in *O. n. vulcani* or a little coarser.

Length of caudal peduncle 10·0–13·5% SL, 0·65–0·9 of its depth. Pectoral fin 38·0–43·2% SL in 18 of 23 fishes measured; of the 5 with lower values 4 are less than 50 mm SL.

Caudal fin with vertical stripes distally, but proximal markings more irregular in adult.

Oreochromis n. sugutae subsp.n.
Suguta River (between Lake Baringo and Lake Turkana but having no surface connection with either) and its tributary, Kapedo River and its warm alkaline springs.

Scales in lateral line series 31–33, usually 31 or 32.

Dorsal spines XIV–XVI, mode XVI; total rays (26) 27–30, usually 28 or 29.

Teeth in the jaws with moderately slender shafts, the outer bicuspid at up to 170 mm SL, except in males that breed in the hot springs at a small size (about 130–145 mm), in which some of the teeth have stouter shafts and tricuspid crowns.

Lower jaw in some mature males up to 39% length of head.

Blade of lower pharyngeal bone equal to or a little shorter than median length of dentigerous area.

Pectoral fin relatively short, 28–36% SL.

Markings of caudal fin variable, from none through vague series of spots to a coverage of wavy stripes that run into a reticulum over a smaller or larger area. In mature male posterior part of caudal red.

Oreochromis niloticus niloticus (Linn.)

Labrus niloticus Linnaeus [1757:346]; 1758:286; *idem.* 1766:477; Gmelin, 1786:1290 (Egypt); Sonnini, 1799:395, pl. xxvii fig. 1 (Egypt).

Chromis niloticus: Cuvier, 1817:266 (*ex* Linn.); *idem*, 1829:263 (Nile); Günther, 1869:216 (Nile).

Chromis nilotica; Cuvier *in* Guerin-Meneville, 1844, pl. xliv, fig. 1; Sauvage, 1880:211 (L. Mareotis); ?Lortet, 1883:pl. vii (probably a composite of *O. aureus* and *O. niloticus*); Mitchell, 1895:12, pl. ii (L. Menzaleh).

Chromis niloticus (part); Günther, 1862:267 (Nile, all except synonym *Labrus melanogaster*); ?Steindachner, 1864 (Sea of Genezareth); *idem*, 1870 (synonyms for Nile & West Africa only); Peters, 1868:23 (refs. to Hasselquist, Linnaeus and Cuvier only); Pfeffer, 1893:21, pl. iii, figs 1–4 (Nile specimens only); *idem*, 1896:10, fig. 7 (refs to Nile only).

Tilapia nilotica (part); Boulenger, 1899:112 (excl. syn. *spilurus* and all localities except Nile & West Africa); Pellegrin, 1904:309; Boulenger, 1907*a*:523, pls xciii, xciv; *idem*, 1915:162, fig. 106 (Nile, excl. specimens of *O. aureus*; Senegal, excl. specimens of *O. aureus*; Niger; Chad basin); Monod, 1949 (West Africa, excl. specimens of *O. aureus*).

Tilapia nilotica; C. L. Boulenger, 1908 (Lake Qurun = Karun); Pellegrin, 1914*a*:130, pl. 11, fig. 3 (L. Chad, description composite); *idem*, 1923:279 (West Africa); Daget, 1948:45 (Middle Niger); Sandon, 1950:57, pl. 9, fig. 1 (Nile); Daget, 1954:341, fig. 131 (Middle Niger); *idem*, 1957:163 (Upper Volta); *idem*, 1960*c*:330 (Upper Volta); *idem*, 1961*c*:354 (Badi & pool at Simenti, Upper Gambia system); Jensen, 1957 (Nile delta); Peters 1959 (eggs); *idem*, 1961*a* (interorbital width); Elster & Vollenweider, 1961:286 (Nile delta); Peters & Brestowsky, 1961 (analysis of genetic components of behaviour by hybridization); Fishelson, 1962 (Israel); Dambach, 1963 (comparative behaviour); Kraft & Peters, 1963 (eggs); Daget & Stauch, 1963*b*:103 (upper Benoué); Banks, Holden & Lowe-McConnell, 1965 (Niger); Peters, 1965*a* (inborn behaviour patterns); *idem*, 1965*b*:293 ff. figs 5, 7 & 12; Fishelson, 1966*a* (development); *idem*, 1966*b*:70 figs 7, 12, 13; Trewavas, 1966*a*: figs 1c & d, 4 (definition; Israel, Nile, West Africa); Burchard, 1967:142, fig. 167 & pl. 10 (Northern Nigeria); Heinrich, 1967 (comparative behaviour & relationships); Bailey, 1968:200 (key); Bauer, 1968 (behaviour); Lessent, 1968 (hybrids); Botros, 1970 (condition); Jalabert *et al.*, 1971 (hybrids); Holden & Reid, 1972:51 fig. 64; Lowe-McConnell, 1972:121, pl. 27; Lewis, 1974:37, 91, fig; Peters & Berns, 1978*a* (rudiments of adhesive organs).

Tilapia nilotica nilotica (excl. the L. Albert specimens); Thys van den Audenaerde, 1964:84; *idem*, 1968*b*:xxxviii.

Sarotherodon niloticus; Trewavas, 1978; 1982*b*; several authors in Pullin & Lowe-McConnell, 1982.

Oreochromis niloticus; Trewavas, 1981*a*; 1982*a* & *b*, addendum; Schoenen, 1982: 164.

?Chromis guentheri Steindachner, 1864:228, pl. 8, figs 3 & 4 ('West Africa').

Tilapia calciati Gianferrari, 1924 (Setit R., trib. of the Atbara, approx. 14°30′N, 36–37°E).

TYPES. Type of *Labrus niloticus*: none preserved
Type of *Chromis guentheri*: NHMW 32598. SL 87 mm.
Type of *Tilapia calciati* in Milan (?).

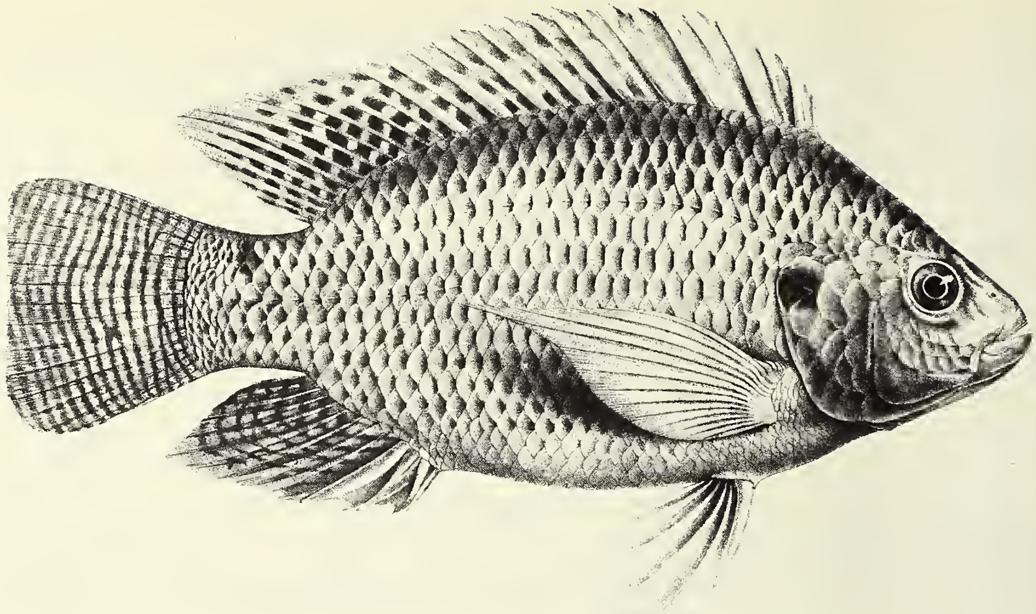

Fig. 52 *Oreochromis n. niloticus.* From Boulenger, 1907*a*, pl. 93.

Distinguishing characters and distribution

See pp. 142–6, and Tables 34 to 38 & 48. Most reports of the presence of *O. niloticus* in the Jordan Valley were based on specimens of *O. aureus* (see p. 206 & Trewavas, 1966*a*). The presence of definite vertical stripes on the caudal fin is associated in the Nile and West Africa almost constantly with XVII (or XVIII) dorsal spines, a combination characteristic of *O. niloticus.* But two preserved specimens from the Jordan Valley have a striped caudal and XVI dorsal spines. One of these is from Tristram's collection with the locality 'Galilee', the other was purchased in Damascus in 1959 by Dr Beckman and said to have been caught in Lake Tiberias. With it was a fish with horizontal inter-radial caudal stripes. The meristic numbers of both were identical, but the pharyngeal teeth were coarser in the fish with a vertically striped caudal. It is these specimens that prevent a categorical denial of a natural population of *O. n. niloticus* in Lake Tiberias. Ben Tuvia (1981) considers it not native to the lake.

Descriptions

Based on 41 specimens from the Nile (Sobat, Blue Nile) and from the Yarkon River near Jaffa.

For proportions and frequencies of numbers of dorsal rays see Tables 35, 36 & 38.

The deepest-bodied fishes are a few young of about 90 mm SL in which the ventral outline is rounded and the gut gorged with food. All of a depth less than 40% SL had been in aquaria for some time at Tel Aviv and had probably not fed normally. If these extremes are excluded the range is 40–47 at all sizes, usually over 42 (mean of 9 from the Yarkon River 43·6, of 17 from the Nile 44·13% SL). The length of head is variable, showing only a rough negative allometry. The length of the anal spine is also variable, but except in four fishes from the Baro River, a tributary of the Sobat, is not more than 17% except in young of 100 mm SL or less.

Diameter of eye and depth of preorbital show the usual complementary trends, being approximately equal at SL about 200 mm. There is neither allometry nor sexual differentiation in the size of the jaws.

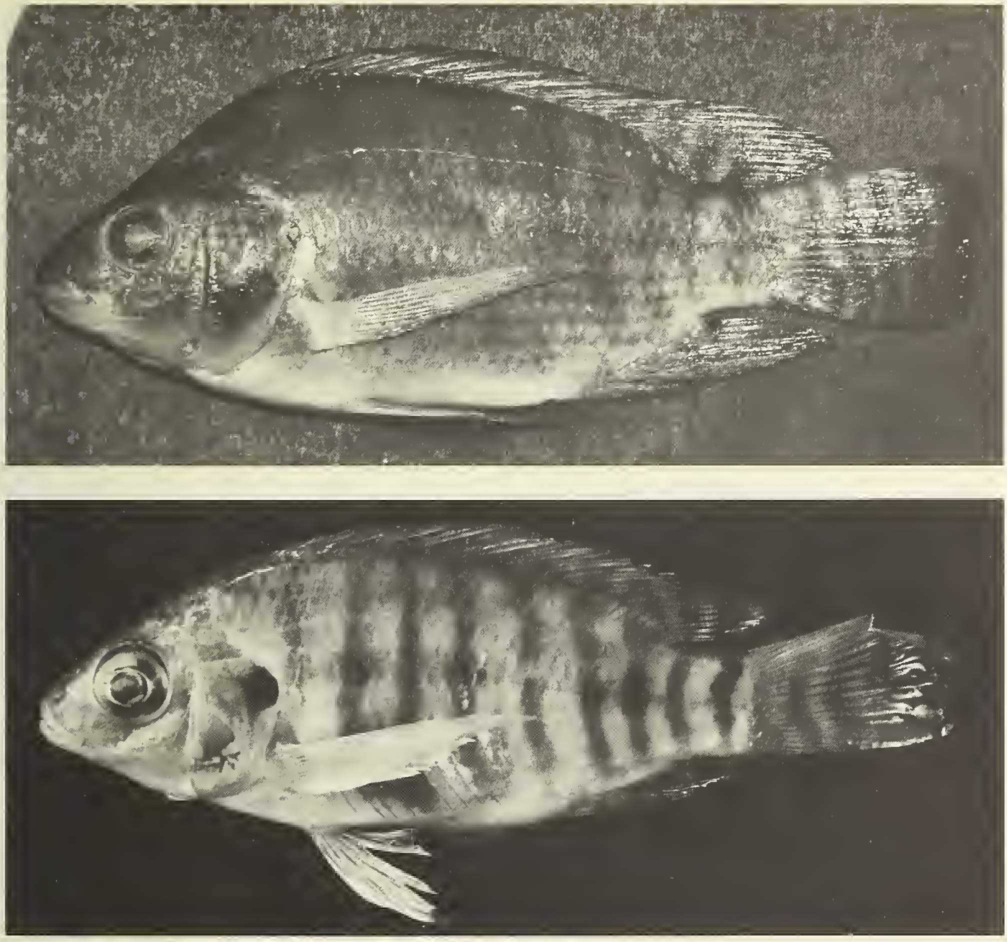

Fig. 53 Young *Oreochromis n. niloticus* from: above, Gambia River at Georgetown, 85 mm SL; below, Senegal River at Kioira, 52·5 mm SL.

Teeth in the jaws in 3 or 4 series below 200 mm SL, 3–5, rarely 6 above this length; outer bicuspid, in adults with stout shafts and obliquely truncate major cusps (unless worn) (Fig. 54); inner tricuspid; 58–90 teeth in outermost row of upper jaw in fishes over 100 mm SL.

Width of lower pharyngeal bone 33·0–35·5% length of head (eight specimens from the Nile and near Jaffa), but in three that died in captivity at Tel Aviv only 29·2–31·7%. Median length of bone 27·8–33·4. Blade ± the median length of toothed area, which is triangular or with very slightly concave sides. Teeth firm and regular (Fig 55 & Table 37).

Gill-rakers 19–25(26) on lower part of first arch.

Scales usually in 2, rarely 3 rows on the cheek; in lateral line series (31) 32 or 33 (34), 4–5 between origin of dorsal and lateral line, 5–9 between bases of pectoral and pelvic fins. See Table 35.

Dorsal fin, see Tables 35 & 36. In the Nile the two specimens (in a total of 40) with XVI spines show their exceptional character in that one has the compensatingly high number of 15 soft rays, and in the other a radiograph reveals two 'predorsal' bones instead of the usual one. In both populations the modal combination is XVII 13.

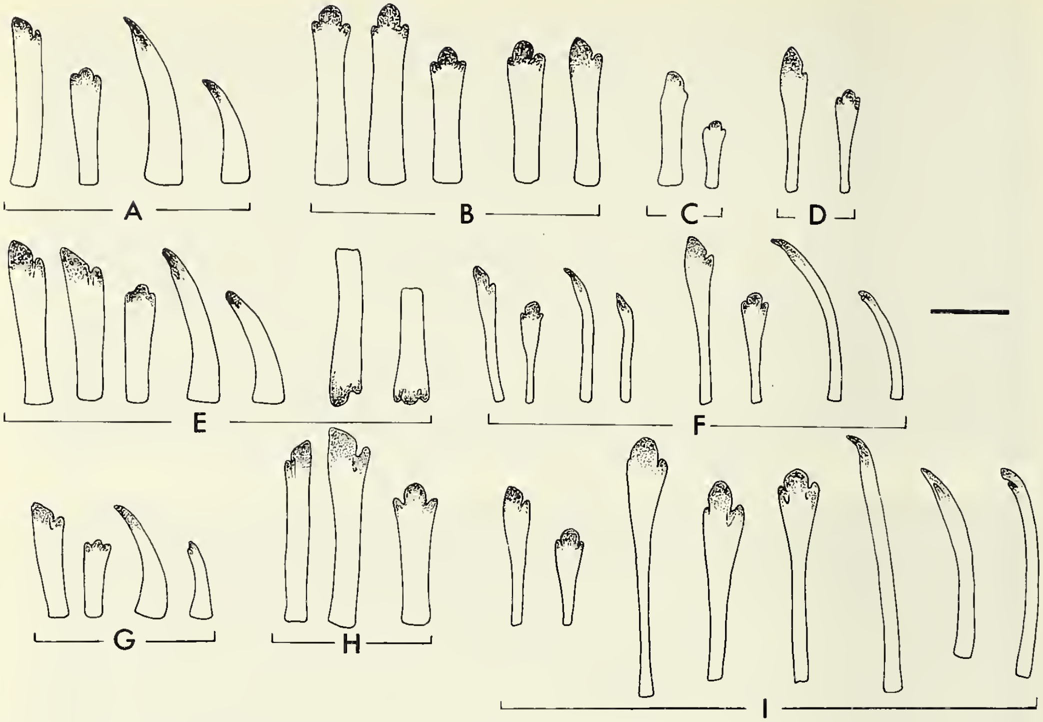

Fig. 54 Teeth from the jaws of subspecies of *Oreochromis niloticus*: A, *O. n. cancellatus* from Lake Abaia, one outer and one inner in frontal and lateral views from a specimen 195 mm SL; B, *O. n. baringoensis*, two outer and one inner from a fish 225 mm SL (left) and two outer from a fish 155 mm SL; C, *O. n. filoa*, outer and inner from a fish 115 mm SL; D, *O. n. cancellatus* from Lake Ganjule, outer and inner from a fish 152 mm SL. E, *O. n. niloticus* from Lake Menzaleh, (left) two outer and one inner from lower jaw of a 240 mm SL fish, (right) the same from the upper jaw; F, *O. n. vulcani* from Lake Turkana, an outer and an inner from each of two fishes of (left) 137 mm and (right) 250 mm SL; G, *O. n. niloticus* from Baro River, Sobat system, outer and inner (140 mm SL); H, *O. n. cancellatus* from Lake Tana, two outer and one inner (217 mm SL); I, *O. n. vulcani* from the type locality, crater-lake A on Central island, Lake Turkana; left to right, an outer and an inner from a 120 mm SL fish, two outer and an inner from a 255 mm SL fish, in frontal and lateral views. Scale = 1 mm.

Anal III 9–11. Caudal truncate, unless the corners are worn away; not densely scaled, although small scales may extend for some distance on the rays in large specimens.

Genital papilla of male conical.

Coloration. The basic pattern of dark vertical bars and two horizontal dark bands, often represented by two or three mid-lateral dark blotches, and a blotch on the top of the caudal peduncle, is variously manifest in preserved fishes. Regular dark vertical stripes on the caudal fin are characteristic of the species.

The colour of breeding males has been described by C. L. Boulenger (1908) for the lower Nile, and by Fishelson (1962) and Trewavas (1966*a*) for aquarium specimens at Tel Aviv derived from the Yarkon River, Israel. These agree in attributing a rose-red colour to the head and lower parts of the body; a red flush also covers the dorsal and caudal fins, causing the stripes of the melanin pattern to appear purple. Except in some on the pelvic fins, there is no mention of jet-black lower surface and fins (such as is described for breeding males in Lakes Albert and Edward) either by these authors or in the more recent studies by El Zarka *et al.* (1970), and Payne (pers.

Table 37. *Oreochromis niloticus.* Dimensions of lower pharyngeal bone in the subspecies: median length as % length of head and in relation to width; length of blade as times median length of dentigerous area.

Subspecies	N	SL(mm)	L. phar. as % l. head Range	Mean	rel. to w.	blade/dent.
niloticus	26	55–280	28·0–33·4	30·64	= or <	0·6–1·2 (1·3)
eduardianus	25	75–253	29·0–33·3	30·5	= or <	0·6–1·3
Buhuku Lagoon	3	89–140	31·1–32·5	—	= or >	1·1–1·36
cancellatus	24	97·5–235	29·4–33·2	31·3	= or < rarely >	0·8–1·38
vulcani (type locality)	7	81–245	30·8–33·4	32·1	>	1·0–1·55
L. Turkana & Crater C	13	56–238	28·5–33·4	31·35	> rarely <	0·75–1·16
sugutae	7	67–169	27·8–32·7	29·9	approx. =	0·56–1·07
baringoensis	4	145–246	29·0–31·1	29·8	< to >	0·7–1·48
filoa	2	65, 116	34, 29	—	> or <	0·9, 1·07

Table 38. *Oreochromis n. niloticus.* Proportions in samples from the Nile and Yarkon rivers.

	SL 200–305 n = 99	100–190 n = 17	50–99 mm n=13
Proportions as % SL			
Depth	34·0–45·5	37·5–47·0	40–56
L. head	31·5–37·0	32·0–38·0	33·0–40·5
L. pect. fin	36·5–41·7	33·8–43·5	33·0–41·2
L. 3rd anal spine	13·2–15·5	13·7–18·9	13·0–19·2
L. caud. ped.	10·2–12·0	8·5–12·0	9·4–12·1
Caudal peduncle l/d	0·6–0·9	0·5–0·9	0·55–0·8
Proportions as % length of head			
L. snout	33·3–38·0	28·8–36·0	(23·5) 27·0–33·3
Eye	15·0–18·5	18·6–23·6	22·0–30·5
D. preorb.	17·8–22·0	16·0–19·0	15·0–19·0
Interorb.	(34·6) 37·0–41·0	33·0–40·0	31·4–38·8
L. lower jaw	30·8–35·6	29·6–33·8	29·2–35·2

commn). Both these latter studies state that there is little difference in appearance between the sexes at breeding time, in contrast to the marked sexual dichromatism of *O. aureus*, and Heinrich (1967*a*:747) says the same of his aquarium stock.

Lortet, in describing the Lake Tiberias '*niloticus*', but perhaps having in mind the Egyptian, writes (1883:138), '*Ce poisson est noirâtre sur le dos; le plus souvent même il est presque entièrement noir, sauf sur le ventre qui présent des reflets plus clairs. Les nageoires sont d'un gris verdâtre.*' Lortet's pl. vii, however, which purports to illustrate a Tiberias specimen, may have been based on his colour-sketch of an Egyptian fish and shows the usual colour-pattern, with no black areas.

Sauvage (1880:211) also states that the body is olive-green with some ill-defined black patches, the anal and caudal fins blackish. Neither of these descriptions resembles exactly those of *O. n. eduardianus*, but a study of the colour-phases of the Egyptian population would be instructive.

At present most of the *O. niloticus* cultivated in ponds in Israel are not from native stock. Some were introduced from Lake Albert and some from Lake Turkana, both after a period in ponds at Kajansi, Uganda. Later, stock was imported from Ghana. The fish culturists have now come to regard the black lower parts of the mature fishes as normal, and Mires (1977) records that a 'new strain' has appeared with red pigment and hardly any black. This is the 'goldfish' mutation. The Turkana (Rudolf) strain, known in Israel as *T. vulcani*, was kept separate in Kajansi ponds by Mr Pruginin, and also in Israel, but the others may be more mixed (see p. 205).

Discussion

Notes on populations from various localities

Oreochromis n. niloticus *in West Africa*

In West Africa the distribution is Soudanian. In the Senegal River it coexists with *O. aureus* as in the Lower Nile and Middle Niger, but in the Gambia River it has been recorded only twice. The first record (Daget, 1961*c*) was at Badi and Sementi in the upper part of the river. These were young specimens, and although they had a typical dorsal formula of XVII 12 and a well-banded caudal fin one of them had the exceptionally low vertebral count of 29. The second (S. O. Kullander, unpublished) was from Georgetown, McCarthy Island, where Budgett, Svensson and Johnels all made large collections without finding it. A photograph of one of these (Fig. 53), a young fish of about 85 mm SL, shows the banded caudal fin. Radiographs of two revealed the following counts: vertebrae 16 + 14, 16 + 15, D XVII 11, XVII 13, A III 9, III 9.

Between the Gambia and the Volta this species and *O. aureus* are replaced by the Guinean forms of genus *Sarotherodon.*

Daget found in the Middle Niger no specimens with as few as XVI dorsal spines, and the same is true of most samples in the BMNH from Senegal, Sokoto and the Kiyawa River. In Lake Chad, however, the samples examined by Blache *et al.* (1964), and the few in BMNH include some with XVI. Of the six specimens from the Lower Benue two have XVI; of three from Abo and two from Asaba, Niger Delta, one has XV, three XVI and one XVII.

With these exceptions the West African samples agree with the nilotic and the same description covers both. Daget (1954) records that in the Niger the pelvics are blackish, but says nothing of a jet-black ventral surface as recorded for breeding males of *O. n. eduardianus* (p. 155).

The maximum size reported is from the Shari Delta, 395 mm SL, TL 47 cm, weight 3650 g (Blache *et al.*, 1964:240).

Oreochromis n. niloticus *in Jebel Marra*

A single specimen from Amballa agrees in most characters with samples from the Nile and West Africa. It is 240 + 57 mm long. The toothed area of the lower pharyngeal is rather small, with finer teeth than usually in this subspecies, though less fine than in Lake Edward. The Caudal fin is covered with small scales.

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
Asia			
1927.10.17.8–14	51–103	Ras-el-Ain, nr Jaffa	Bewsher
Tel-Aviv Univ. (3 fishes)	180–280	Probably Yarkon R.	Fishelson

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
Tel-Aviv Univ. P 628, 927	130, 171	Probably Yarkon R.	Fishelson
Nile			
1861.9.9.8–9	289–305	Lower Nile	Petherick
1896.10.24.1–2	100, 113	Lake Menzaleh (Manzalla)	Mitchell
1898.5.30.6	315	Nile, nr Cairo	Mitchell
1962.8.29.1–8 (from the duplicates)	68–132	Lower Nile	Loat
1907.12.2.3347–3349	93–101	Lake Mareotis (Maryut)	Loat
1907.12.2.3354–3357	91–164	Lake Edkou	Loat
1907.12.2.3373	82	Ghet-el-Nassarah, Nile delta	Loat
1907.12.2.3383	71	Bahr-el-Tawilah Lake Menzaleh	Loat
1907.12.2.3484–3493	189, 247 & 16* fishes, 24–59	Nile, nr Samannud	Loat
1907.12.2.3499	245	Nile, nr Cairo	Loat
1907.12.2.3500–3501	86, 116	Nile, nr Cairo	Loat
1907.12.2.3506–3507	65, 72	Pool between Cairo & Giza	Loat
1907.12.2.3509	330	Zoological Gardens, Giza	Loat
1907.12.2.3510–3519	69–278	Beni Souef	Loat
1907.12.2.3520	201	Bahr Selah, Fayum	Loat
1907.12.2.3521–3530	131–250	Birket Karun, Fayum	Loat
1907.12.2.3531	225	Assiout to Abu Tig	Loat
1907.12.2.3532	213	Luxor	Loat
1907.12.2.3533–3540	53–99	Luxor to Assuan	Loat
1907.12.2.3541–3546	69–272	Assuan	Loat
1907.12.2.3547–3548	116, 117	Ibrim	Loat
1907.12.2.3549	193	Abu Simnel	Loat
1907.12.2.3550–3554	76–163	Kosheh, Nubia	Loat
1907.12.2.3556	160	Hannek	Loat
1907.12.2.3557	245	Abu Zugoli, Blue Nile	Loat
1905.10.26.36–37	69, 71	Rosaires, Blue Nile	Flower
1905.10.26.38	44·5	Wad Medani, Blue Nile	Flower
1907.12.2.3558	113	Kaka, White Nile	Loat
1907.12.2.3559–3572	34–162	Gharb-el-Aish	Loat
1907.12.2.3573–3579	95–136	Fashoda	Loat
1907.12.2.3580	296	Lake No	Loat
1907.12.2.3581–3586, 3338–3342	17–51	Lake No	Loat
1907.12.2.3587–3590	107–272	Gondokoro (S of lat. 5°N)	Loat
1907.12.2.3591–3630	juv.	Gondokoro (S of lat. 5°N)	Loat
1900.9.22.31	192	Gabt-el-Megahid, White Nile	Flower
1905.10.16.90–91	76, 97	Between Khartoum and Sobat	Zaphiro (coll.) Macmillan (pres.)
1905.10.16.44–46	112–138	Polkom, Baro R.	Zaphiro (coll.) Macmillan (pres.)

* A mixture of *O. niloticus* and *O. aureus*. D XVII in 8, XVI in 4, XV in 4

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1950.5.31.10–12	10–14	Juba, Sudan	Lewis
1965.7.27.107	240	Amballa, Jebel Marra	Sir John Cass College Exped.
West Africa			
1900.6.28.186–193	43–192	Kaidi, Senegal	Delhez
1978.3.13.37–41	51–72	Matam, Lower Senegal	Dorfman
1978.3.13.46	72	N'Dium, Lower Senegal	Dorfman
1978.3.13.47	50·5	Bakel, Lower Senegal	Dorfman
1978.3.13.45	52·5	Kioira, Faleme R. Lower Senegal	Dorfman
1946.3.8.13	116	Kamba R., Black Volta system	K. S. Morris
1948.6.30.90–91	58, 80	Kamba R., Black Volta system	K. S. Morris
1944.2.9.34	55	Estuary of Volta R.	Irvine
1884.6.9.30–31	112, 194	Niger R.	Forbes
1904.1.20.62	213	Mureji, Northern Nigeria	Budgett
1910.10.19.5	76·5	Jebba, Niger R.	Firmin
1911.7.19.60–61	65, 68	Deert, mouth of Gurara R., Niger	Simpson
1902.11.10.236–238	45–68	Abo, Lower Niger	Ansorge
1902.11.10.203	34·5	Agberi, S. Nigeria	Ansorge
1959.8.18.156	145	Asaba, Lower Niger	Maclaren
1969.3.26.66–67	85, 85·5	Pools at Asaba, Lower Niger	R. A. Whitehead
1928.7.3.108, 109	134, 198	Permanent forest pool, Sherifan, Nigeria	Lloyd
1930.3.22.252–253	142, 143	Kiyawa R, nr Katagum, northern Nigeria	Lloyd
1956.6.21.51	50	Hadeija R., nr Wudil	Roloff
1953.4.28.246	91	Hadeija R.	Trewavas
1969.3.25.6–7	125, 137	Sokoto R. at Birnin Kebbi	Holden (May, 1957)
1956.6.21.44–50	30–42	Hadeija R., nr Chalowa	Roloff
1971.9.28.181–186	103–140	Benue R., between Ibi and Makurdi	Reid
1909.7.27.48–50	37·5–55	Komadugu R., Chad basin	MNHN (coll. Tilho & Gaillard)
1905.5.15.28	188	Lake Chad	Gosling
1928.7.4.84–85	163, 127	Shari R., below junction with Logone R.	Markham
Introductions			
1978.1.10.16–21	83–115	Kuilo R. at crossing of old Matadi Road	Clark

Oreochromis niloticus eduardianus (Boulenger)

Tilapia nilotica; Boulenger, 1901:157 (Kivu, record only); *idem*, 1906*b*:571 (Lofu, Tanganyika); *idem*, 1910*a*:240 (Ruwenzori, record only); *idem*, 1914:253 (Ls Edward & Albert); Greenwood & Lund, eds, 1973 (L. George); Moriarty & Moriarty, 1973; Moriarty, D. J. W., 1973; Moriarty, C. M., 1973; Moriarty *et al.*, 1973 (feeding in Lake George).

Tilapia nilotica (part); Boulenger, 1915:162; Worthington, 1932*c*:28, 78, tables 8 & 9 (Ls Edward & Kikorongo); Trewavas, 1933:314, fig. 3A (Ls Edward & George); Poll, 1939*a*:35, fig. 13 (L. Edward);

Poll & Damas, 1939:30 (L. Edward); Poll, 1946:255 (L. Tanganyika); *idem*, 1956:28 (L. Tanganyika); Fish, 1955:88 (food); Lowe-McConnell, 1958:139, tables I–III, figs 2, 3, 4b, 5.

Tilapia nilotica nilotica (part); Thys van den Audenaerde, 1964:82, 84, pl. viii (L. Albert).

Tilapia eduardiana Boulenger, 1912*c*:138 (Ruwenzori); *idem*, 1915:166, fig. 107; Regan, 1921:633; Worthington, 1932*c*;32, 78; Trewavas, 1933:317 (all referring to the syntypes only).

Tilapia nilotica eduardiana; Thys van den Audenaerde, 1968*e*:xxxviii (Ls Edward, Kivu, Tanganyika & Ruzizi R.).

Tilapia regani Poll, 1932:32 (L. Kivu); David & Poll, 1937:259.

Tilapia nilotica var. *regani*; Pellegrin, 1933*b*:174; *idem*, 1935*a*:385.

Tilapia nilotica regani; Poll, 1939*a*:48, 73 (Kivu & Ruzizi R.); Poll & Damas, 1939:62 (Kivu); Thys van den Audenaerde, 1964:82, 86, pl. vii, tables IV & V (Ls Edward, Kivu, Tanganyika).

Tilapia inducta Trewavas, 1933:317, fig. 2 (L. Bunyoni, introduced).

TYPES. Syntypes: six specimens in alcohol, 113–142 mm SL, and one skeleton, BMNH 1907.4.20.21–26, collected from a crater lake at 'Ruwenzori, S. E. 3,200 ft' on the Ruwenzori Expedition 1905–6 led by R. B. Woosnam. This is Lake Kikorongo, in the flood-plain of Lake George (see pp. 156–7).

Holotype of *T. regani*, 245 mm TL MRAC 20811, coll. Schouteden at Kissenyi, Lake Kivu; paratypes, 245–247 mm TL, MRAC 20812, 20813, data as holotype, and 228–247 mm, MRAC 21053–21055, coll. Schouteden at Ngoma, Kivu.

Holotype of *T. inducta*, a female of 250 mm SL, BMNH 1933. 2.23.121, coll. Worthington in Lake Bunyoni

Distinguishing characters and distribution (see p. 143)

Discussion

Notes on populations from various localities

Lake Edward/George

This population is isolated from that of Lake Albert by the rapids in the Semliki Gorge, which prevent upward movement of cichlids. It has, therefore, no opportunity of being influenced by the Lake Albert population, and unlike the latter cannot have mixed with Lower Nile or Soudanian fishes for a long period, dating back to Mesolithic times, 8000–10 000 years ago (Beadle, 1974:180, quoting Greenwood, 1959, and de Heinzelin, 1957).

In contrast to the Nile population from Bahr el Ghazal to the delta, the Edward/George samples have lower modes and means of the meristic numbers (Tables 34–36); and in contrast also to Lake Albert finer and more crowded pharyngeal teeth, occupying a smaller area on the lower pharyngeal bone (Fig. 55).

The teeth in the jaws have slightly more slender shafts than in Lake Albert and the Nile; in sizes from 70 to 125 mm SL they are in 4 series, from 225 to 260 mm in 4–5.

The caudal fin is marked with the typical vertical stripes. As in Lake Albert, breeding males become jet-black on the ventral surface, lower fins and dorsal fin. Thys van den Audenaerde (pers. commn) says that in some small Ruanda lakes *O. n. eduardianus* is black all over.

Proportional differences between this and *O. n. niloticus* are not significant. The length of head shows wide variation, but no allometric trend, being 34–37% SL. A specimen of 79 mm SL and two of 253 and 259 mm all have it approximately 37% and two of 124 and 225 mm both give a value of 34%. The third anal spine measures 12–16% SL in all specimens over 70 mm SL except two in which it is 17·2% (see Table 42). The lower jaw is 29·6–34·6% length of head except in a female of 259 mm SL in which it is 37·5, the highest value found in this species, being approached only by one in the peculiar population of Crater Lake A on Central Island, Lake Turkana, and by the problematical *O. n. sugutae* (p. 180).

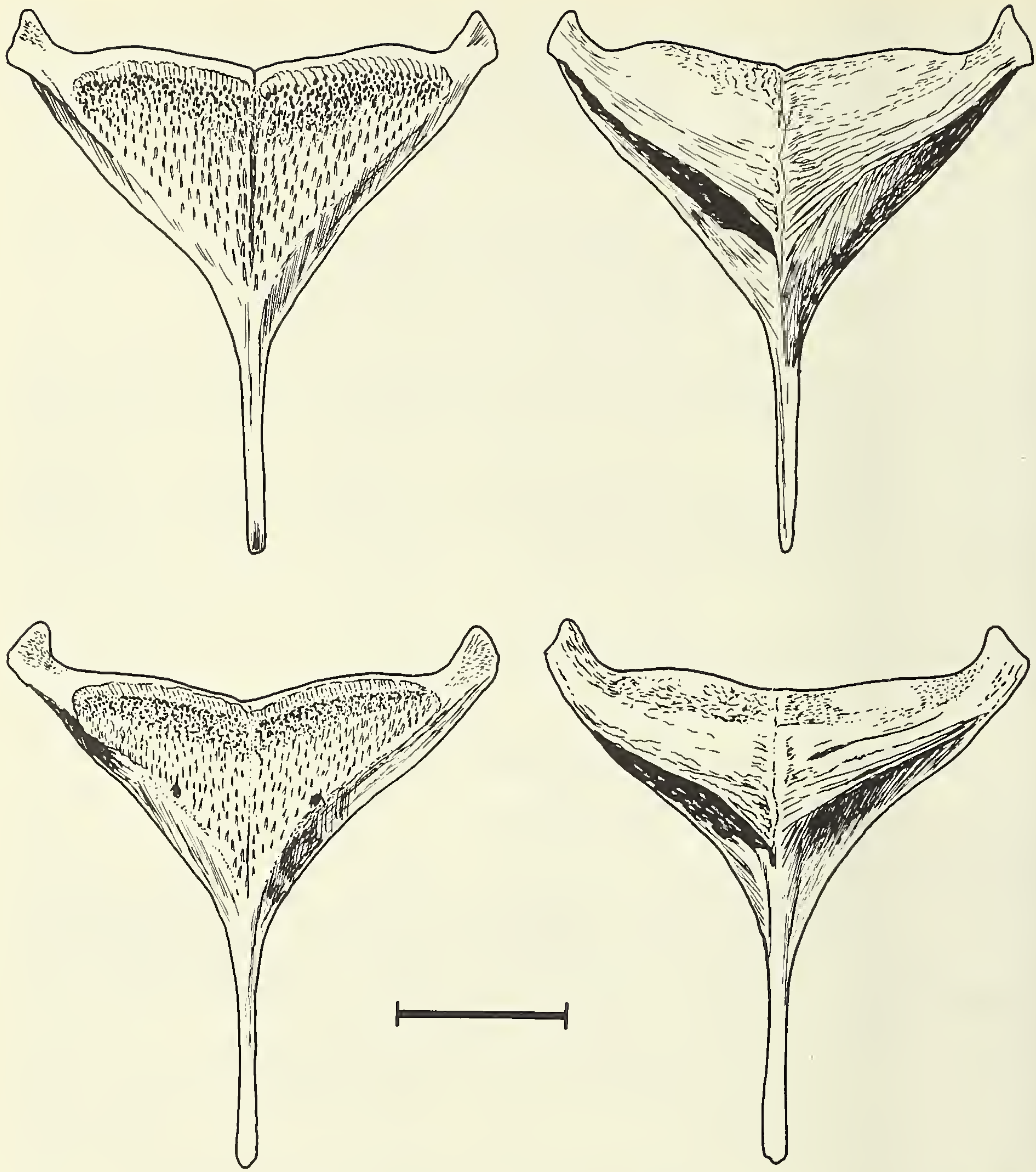

Fig. 55 Lower pharyngeal bones, dorsal and ventral views of: above, *Oreochromis n. niloticus* from the Nile, 300 mm SL; below, *O. n. eduardianus* from Lake Edward, 260 mm SL. Scale = 10 mm.

Lowe-McConnell (1958) recorded that in Lake Edward this species is most abundant near the shores, captures in the open water being few and from the surface layers. Verbeke (1959) says that it occurs over rocky bottoms and in sandy, exposed localities as well as with *O. leucostictus* in more sheltered places with muddy bottom.

THE TYPES OF *Tilapia eduardiana*. In years of very heavy rains Lake George is known to overflow into Lake Kikorongo, near Mohokiya and the north-west corner of Lake George. Worthington (1932*c*:78) gives Mr Dent's account of a visit to this lake in 1905, when he found in it large numbers of tilapias, of which most were blind, and many being washed up on shore in a dead

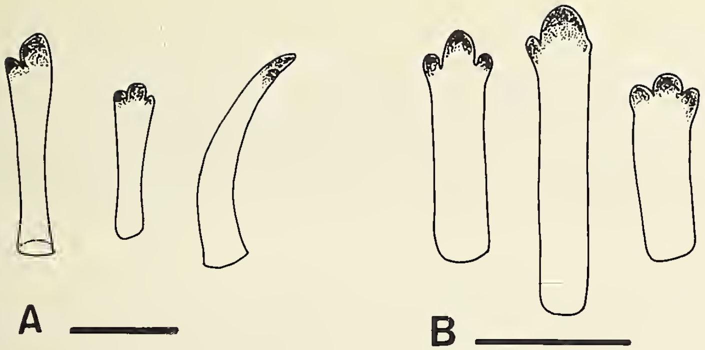

Fig. 56 A, *Oreochromis niloticus eduardianus*: two views of an outer tooth and one of an inner tooth from a fish 235 mm SL. B, *O. n. sugutae*: an inner and two outer teeth from a fish of 145 mm SL, cf. Fig. 54. Scales = 1 mm.

or dying condition. Mr Dent was a member of the Ruwenzori expedition led by R. B. Woosnam in 1905–6, and his visit was no doubt the occasion of the collection of the seven specimens of distressed tilapias that were later made the types of *T. eduardiana* Boulenger. These were said to be distinguished by their long fin-spines, and although the spines are less stout than in the Lake Albert *O. niloticus*, they are comparable in length, namely (13·5) 17·6–20·4% SL. The high measurement is partly due to the shrunken condition of the tissues around the base of the spine, which in healthy fishes reduce the measured, exposed part of the spine. The fish with the low value of 13·5% seems to be the only one that was not blind, having a normal-seeming lens and cornea. The others have no lens and there are opaque patches on the cornea.

Lake Kikorongo is the one of the Katwe crater lakes nearest to Lake George and is mapped in fig. 13.1 of Beadle (1974). Beadle, who visited it in 1931, described it in 1932 (p. 201) as being fed by under-water springs, which, although alkaline, were less so than the lake itself. The chemistry of the lake fluctuates very widely as it is influenced alternately by flooding and evaporation, and the tilapias (and *Clarias*) which survive the early stages of evaporation eventually succumb to the increasing alkalinity, either directly or by the extinction of their favourable food-organisms. Beadle found the plankton to consist of *Arthrospira*. The parallel with Buhuku Lagoon, Lake Albert, at Lowe's visit in 1950 is obvious (p. 159) and there is a less exact parallel with the population of a crater of Central Island, Lake Rudolf (p. 176).

The types of *T. eduardiana* are 'hunger-forms', with large heads (length 36·6–39·8% SL), and the lower pharyngeal dentition is reduced, in one consisting of only four rows of teeth at the posterior edge of the bone. Other characters place them with *O. niloticus* and not *O. leucostictus*, namely size and shape of jaws and pharyngeal, number of scales (31–32 in lat. line series), D XVI 12–13 or XVII 11–12. They differ from typical *O. niloticus* in the absence of vertical stripes on the caudal fin, which is dusky or with a few vague spots; and in two the tilapia-mark persists at 113 and 125 mm SL.

Two other specimens from this region lack the stripes on the caudal fin. They were collected by Captain Pitman in 1948 in a crater lake south of the Kazinga Channel, and may be part of the sample from Lake Nkugute suspected by Lowe-McConnell (1958:135) to be hybrids with introduced *O. esculentus* because of the less well defined caudal stripes and minor meristic differences. But, in Lake Kikorongo at least, there is no reason to suspect interference by man before 1905, so it is equally possible that the Nkugute fishes were exceptional *O. niloticus*.

Finally, the types of *O. n. eduardianus* represent a temporary and subsequently exterminated section of the *O. niloticus* of Lake George and have no separate taxonomic status. They are, however, the bearers of the first name distinguishing his subspecies.

Lake Bunyoni

The name *Tilapia inducta* was rashly given to a specimen from Lake Bunyoni, believed to represent an introduced and modified population. The pharyngeal dentition is coarser than in Lake Edward samples, but can be matched in Lake Albert, and the subsequent history of stocking Lake Bunyoni reduces interest in this lake to that of a fishpond. Further trials have been made with *O. niloticus* and also with *O. spilurus niger* and *O. esculentus*, but according to Lowe-McConnell (1958:134) the influence of the two latter species, at first evident, had vanished by 1952 and the survivors resembled *O. niloticus.*

Lake in Maramazambo Forest

Four immature specimens, 62–68 mm in SL, were collected in this small crater-lake on the escarpment east of Lake Edward and south of Lake George. They agree with *O. n. eduardianus* in the low numbers of dorsal rays, XV 12, XVI 13, XVII 11 and XVII 11 respectively (see Table 35). Faint vertical bars are already present on the caudal fin.

Lake Kivu

Whereas in Lakes Albert and Edward *O. niloticus* prefers the shallower waters, in Lake Kivu, whose volcanic shores slope steeply into the lake, the species has no choice but to live in water of about 10 m depth over a rocky bottom. Capart (1955, 1956; see also Verbeke, 1957*a*: 125, 127) has located the schools by echo sounder in the day time (at night they disperse), and Lowe-McConnell (1958:139) has examined catches from two such schools. They included fishes of both sexes, breeding and non-breeding, and some of the females were brooding young. It seems that the tilapias have adjusted their breeding habits to the limiting topography of the lake and their feeding habits to its special chemistry. They are reported to feed on the planktonic bacterium, *Spirillum*, for much of the year (Capart, quoted by Fish, 1955; and Lowe-McConnell, 1958:140); Verbeke (1957*b*) gives a more varied diet, with emphasis on plankton, but states that they also feed on sediments rich in bacteria.

In spite of these differences, preserved specimens resemble samples from Lake Edward in the pharyngeal dentition, meristic characters and the rather large average size of the head (Thys, 1964). The geological history of the lake, which originated as a barrage lake formed by the blocking of a former affluent river of Lake Edward by the eruption of the Virunga volcanoes (Cahen, 1954; Beadle, 1974), was justifiably used by Thys to support the union of these now separated populations as one subspecies.

Lake Tanganyika

The River Ruzizi was formed as an overflow of Lake Kivu and now unites it with Lake Tanganyika. Thys (1964:87–89) lists specimens of *O. niloticus* from the Ruzizi and its tributaries, as well as from the fluviatile zone of Lake Tanganyika. He believes that it is to this relatively recent connection that Tanganyika owes its population of *O. niloticus.* Meristic and dental characters are in sufficient agreement to support this view, and the inclusion of the Tanganyika population with those of Kivu and Edward/George in one subspecies. Tanganyika specimens in the BMNH were collected in Burton Gulf, at Usumbura, near the outlet to the Lukuga River and at Lofu. Christy's diary makes it clear that the first three were all shallow water areas, and he describes the locality at Biera at the head of Burton Gulf as 'almost like a large lake, shut off from the Gulf by a long out-jutting sandspit. Still, shallow water, hard mud bottom, many patches of rushes and water plants . . . One or two streams entering it.' Recently, however, Bailey & Stewart (1977) record the capture of *O. niloticus* in more open waters of the lake.

Lake Albert

In distinguishing the populations of Lakes Edward/George, Kivu and Tanganyika from the

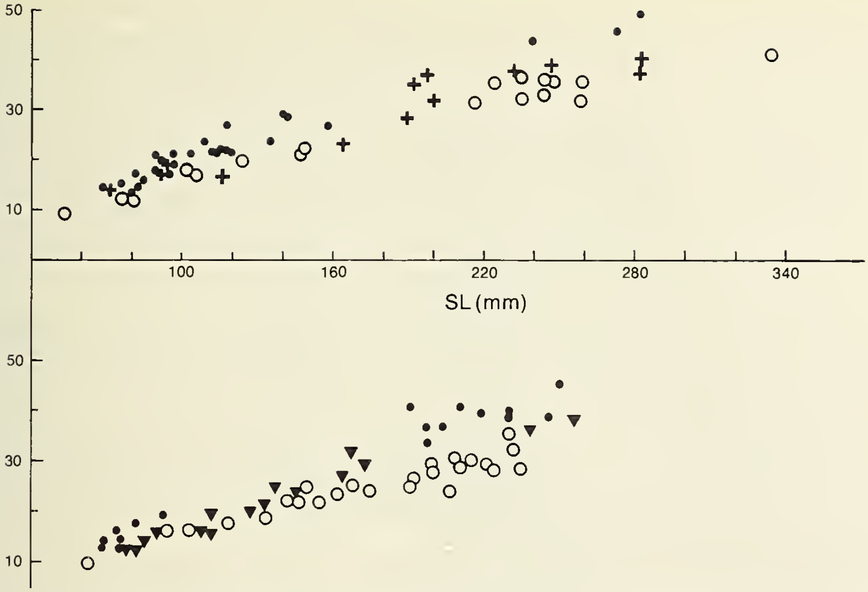

Fig. 57 Length of anal spine in samples from populations of *Oreochromis niloticus.* Above: Lakes Edward, Kivu and Tanganyika (○); Lake Albert and Wadelai (●); Lower Nile (+). Below: Ergino River and Ethiopian lakes (excluding Lake Zwai) (○); Lake Turkana and Crater-lake C (▼); Crater-lake A (●).

nominate subspecies, Thys 1(1964) included the Lake Albert population in *T. n. nilotica*, and indeed based his characterization of *T. n. nilotica* on Lake Albert samples, having only two specimens from the Lower Nile at his disposal. The only structural character on which he relied was the length of the fin-spines, which is greater in Lake Albert than in the southern lakes. Table 42, however, shows that this contrast is less marked between the southern lakes and the Lower Nile, the *O. niloticus* of Lake Albert being outstanding in the length of the spines. With them agree two specimens from the Victoria Nile below the Murchison Falls, one from the Albert Nile at Wadelai, and four from Gondokoro on the Nile just south of 5°N. Adults of the West African samples measured by me fall into a range for length of anal spine similar to that of the Lower Nile (Table 42 & Fig. 57). Spines as long as in Lake Albert are found elsewhere in *O. n. vulcani* (Lake Turkana).

Worthington (1929*a* & *b*) described the lagoons of Lake Albert, some of which communicated with the main lake by wider or narrower openings while others were closed. One of the latter was Buhuku Lagoon (Worthington, 1929*b*, fig. 16A), from which a sample was brought to the BMNH. These fishes were mature at a small size (about 90 mm SL), and they had lower numbers of dorsal rays than samples from other parts of the lake. Table 36 shows the contrast in frequencies, 76% of the Buhuku sample (N = 21) having XVI dorsal spines as against 41% (N = 22) from elsewhere in the lake; mean total numbers of rays are respectively 28·8 and 29·6.

Of three Buhuku specimens examined the pharyngeal blade is 1·3 times as long as the dentigerous area in two, equal to it in the third. Among eight specimens from elsewhere in the lake, seven have the blade equal to or a little less than the dentigerous area and only one has it longer (1·36 times).

In Lake Albert *O. niloticus* is mainly an inshore species (Capart, 1956; Lowe-McConnell, 1958), and some of the specimens that we have contrasted with the Buhuku sample probably came from lagoons only narrowly communicating with the lake, so that they would have spent their larval and postlarval weeks in conditions resembling those of Buhuku in density of population, and alkalinity and warmth of water. Lowe-McConnell (1958) described such a colony in Tonya Lagoon, from which at times a mass exodus to the lake took place. No samples from Tonya are available, nor any meristic data from them, but like the Buhuku fishes they were mature at a small size. With the evidence from Buhuku that such lagoon conditions produce a lowering of the mean number of dorsal fin-rays, one may postulate that the contribution of lagoon-bred subpopulations to the general population of the lake might account, at least in part, for the lower range and mean of metameric numbers in Lake Albert as compared with the Nile.

The topography and relations of the Lake Albert lagoons are not stable. Lowe reported the shrunken condition of Buhuku when she visited it twenty-two years after Worthington. The *O. niloticus* in it were dead or moribund, many evidently blind, with the cornea opaque (cf the syntypes of *T. eduardiana*, p. 157. The topography of the lagoons at Butiaba was different when I visited them in 1965 from that mapped by Worthington.

In contrast to the stunted fishes of the lagoons, Lowe-McConnell reported specimens up to 45 cm TL from Ndiga Bay, and well-grown specimens are fished in the shallow waters of the delta of the affluent Semliki River.

The meristic characters of the Lake Albert samples are compared with those from other localities in Tables 34–36. In seven specimens from Gondokoro, the Albert Nile and the Victoria Nile below the Murchison Falls the dorsal fin-formula is XVI 12 (f.1), XVI 13 (f.1) or XVII 12 (f.5), thus conforming to the frequency pattern of Lake Albert rather than the Lower Nile, and they have strong anal spines.

Lowe-McConnell (1958) records that in Lake Albert, as in Lake Edward/George, the breeding male, in addition to intensification of the red colour on flanks and head, develops black pigmentation on the ventral surface and pelvic fins; the lower jaw, dorsal fin and anterior part of the anal may also become black. The same is noted by Greenwood (1958 & 1966) and by Thys (1964:82) but it is not recorded for *O. n. niloticus*, either in the Lower Nile or in West Africa.

Except in the fin-spines, proportions in Lake Albert are not significantly different from elsewhere.

The Lake Albert population, therefore, shows affinity to *O. n. eduardianus* in meristic characters and male breeding pigmentation, to *O. n. niloticus* in the dentition of jaws and pharynx, but differs from both in the average length of its fin-spines.

There are two possible interpretations of the affinities of the population of Lake Albert and the Albert Nile.

(*a*) Giving weight to the male pigmentation and the incidence of XVI dorsal spines, to include it in *O. n. eduardianus*, postulating its derivation from the Lake Edward population or from an older fauna common to both lakes. Beadle (1974:177 and fig. 13.3) has emphasized the effectiveness of the Semliki Rapids as a barrier to fish migration between the two lakes. Although upstream migration would clearly be impossible for cichlids, the fry might be swept down and could probably survive and breed en route in the streams and pools of the forest, as *O. leucostictus* evidently does (p. 226). The dentition of jaws and pharynx may be influenced by feeding habits. Except in lagoons, Lake Albert is poor in phytoplankton and *O. niloticus* is said to feed there on epiphytic diatoms (Lowe-McConnell, 1958), whereas in Lake George a diet of pure phytoplankton, mainly blue-green algae, is used by adults.

This interpretation assumes an environmentally induced diversity in a genetically homogeneous population.

(*b*) Giving more weight to the pharyngeal dentition, to regard the Lake Albert population as composite, consisting of *O. n. eduardianus* and an element derived from the Nile after the union of the Albert Nile with the White Nile, an Upper Pleistocene event according to Berry & Whiteman (1968). Evidence for this would require that the analysis of breeding populations should show segregation of an *O. n. niloticus*-like group and an *O. n. eduardianus*-like group, in the same way that the members of the Lake Malawi species-flock have established and maintained their integrity.

Meanwhile I adopt a nomenclatorial grouping in accordance with interpretation (*a*).

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1907.4.20.21–26 (syntypes of *T. eduardiana*)	113–142	'Ruwenzori, SE, 2,300 ft' (probably L. Kikorongo)	Woosnam Ruwenzori Expedn. 1905–6
1895.4.17.44–45	71, 80	'Foot of Ruwenzori, 5–6,000 ft'	Scott Elliot
1906.9.7.45	253	L. Edward	Moore
1914.4.8.3	124	L. Edward	Schubotz
1933.2.23.1–7	102–259	L. Edward	Worthington
1967.9.13.4–5	126, 134	Crater-lake c. 19 km S. of Kazinga Channel	Pitman (1948)
1933.2.23.8–11	53·5–105	L. George	Worthington
1938.12.6.11	38	L. George	Worthington
1925.8.7.5	71	An Ankole lake	Barbour
1972.6.5.26–29	62–68	Crater-lake on escarpment in Marumazambo Forest, E. of Ls Edward & George	Greenwood
1906.9.6.123	245	South end of L. Kivu	Moore
1906.9.8.221	245	Lofu, L. Tanganyika	Cunnington
1935.6.14.2436–2441	148–335	L. Tanganyika, Burton Gulf	Christy
1933.2.23.121 (holotype of *T. inducta*)	250	L. Bunyoni (intro.)	Worthington
1904.1.19.23	240	Wadelai, Albert Nile	Budgett
1936.3.12.2–3	118, 135	Buligi, Victoria Nile below Murchison Falls	Pitman
1909.7.27.47.	142	Butiaba, L. Albert	MNHN
1914.4.8.1.	114	L. Albert	Schubotz
1929.1.24.195	282	L. Albert (St. 94)	Worthington
1929.1.24.198–9	55, 89	Kaiso, L. Albert	Worthington
1929.1.24.196–7	67·5	Mahagi	Worthington
	109	Stomach of a darter, L. Albert	
1929.1.24.200–205 (17 fishes)	39–100	Buhuku Lagoon, L. Albert	Worthington
1929.1.24.206–216	72–122, 282	Buhuku Lagoon (St. 91) Butiaba (St. 176)	Worthington
1967.3.16.1–2	158	Butiaba, L. Albert	Lowe-McConnell
	193	Ntoroko Lagoon, L. Albert	
Introduced and reference specimens			
1966.12.9.11	152	L. Victoria (Intro.)	Apfelbach
1968.7.30.1–8	87–174		Ref. specimens for research by Apfelbach

Oreochromis niloticus cancellatus (Nichols)

Tilapia nilotica (part); Vinciguerra, 1896:25 (Lake Abbaia); *idem*, 1898:244 (Ganana Dulei R., trib. of Sagan, affl. of L. Stefani); Boulenger, 1904:333 (L. Ganjule, Suksuki R.); *idem*, 1906*d*: 559 (Ergino R., trib. of Omo, L. Ganjule, Lakes Zwai & Suksuki, record only); *idem*, 1907*a*:523 Lake Tsana); *idem*, 1915:162 (specimens from Ethiopian lakes & rivers); Fowler, 1931:80 (Lake Stefani); Pellegrin, 1935*c*:137 (Omo R.).

Tilapia cancellata Nichols, 1923:2, fig. 2 (Abano R., Awash system; Tortonese, 1940:207.

Tilapia nilotica cancellata; Thys van den Audenaerde, 1968*b*:xxxviii (Hawash R.).

TYPES. Holotype: AMNH 8187, 50 mm SL. Paratypes, two of 50 and 145 mm SL from the same locality, 'the waterhole of a hippopotamus in the Abano River, about 6 kilometers west of Addagalla, Abyssinia'.

Distinguishing characters

See p. 144, and Tables 34–36 & 39

The range of depth of body is as in *O. n. niloticus*, but the mean is less. The most slender fishes are from Lakes Tana and Langano. If these are omitted the range is 38–44 (47)% SL, less than 40·5 in only three, mean for 31 specimens 41·74. In the ten from Lake Langano the depth is 36·1–40·5% SL, mean 38·46. In the Tana sample (n = 9) it is 37·6–40·0%, mean 39·34. The single specimen with 47% was from Lake Abaia.

The caudal peduncle is relatively long and slender, the length/depth ratio being less than 0·8 in only three measured and in several being 1·0 or over.

The modal dorsal formula in these populations, XVII 12, is lower than in *O. n. niloticus* and equal to that of some sections of *O. n. eduardianus* (Tables 35 & 39). About 28% of the 99 specimens examined have XVI dorsal spines and only nine have more than the modal 29 total rays.

The length of the pectoral fin is 35–45% SL, usually 38–41 (in 85% of those measured), thus resembling *O. n. niloticus* but differing from *O. n. filoa* (see below).

The pigment on the body usually forms a reticulum or spots based on the scales, but mature males may be uniformly dark. The pattern of vertical wavy lines on the caudal fin is less regular than in *O. n. niloticus* and frequently forms a reticulum in the middle of the fin (Fig. 59).

Distribution

NATURAL DISTRIBUTION. Lake Tana; the lakes of the Ethiopian Rift Valley excluding Lake Turkana; Awash system, excluding the pools fed by hot springs; the Omo River and its tributary the Ergino. Shortridge (1940) states that Lakes Zwai, Abbyata and Chamo are fresh, the other lakes of the chain are brackish or saline.

The mountain range south of the Awash, in which its southern tributaries arise, forms the barrier between the distribution of *O. niloticus* and *O. spilurus*, and the mountains east of Lake Stefani also separate the two species.

Oreochromis niloticus is the only cichlid in these waters. Although *Tilapia zillii* and *Sarotherodon galilaeus* both inhabit Lake Turkana, neither has been found in the waters from which *O. n. cancellatus* is here recognized.

TRANSPORTATION BY MAN. Although carp and rainbow trout have been introduced to Ethiopian waters, I know no record of the introduction of non-native tilapias. Bazzi (1955) recorded the stocking of lakes of volcanic origin near Bishoftu with *O. niloticus* obtained from Lake Matahara. A lake formed by a hydroelectric dam on the Akaki River was stocked with native tilapias (see p. 166). Fry from Lake Harobi were successfully stocked in Lake Aramaio (between Dire Dawa and Harar). None of these operations modifies the general pattern of geographical distribution of the subspecies.

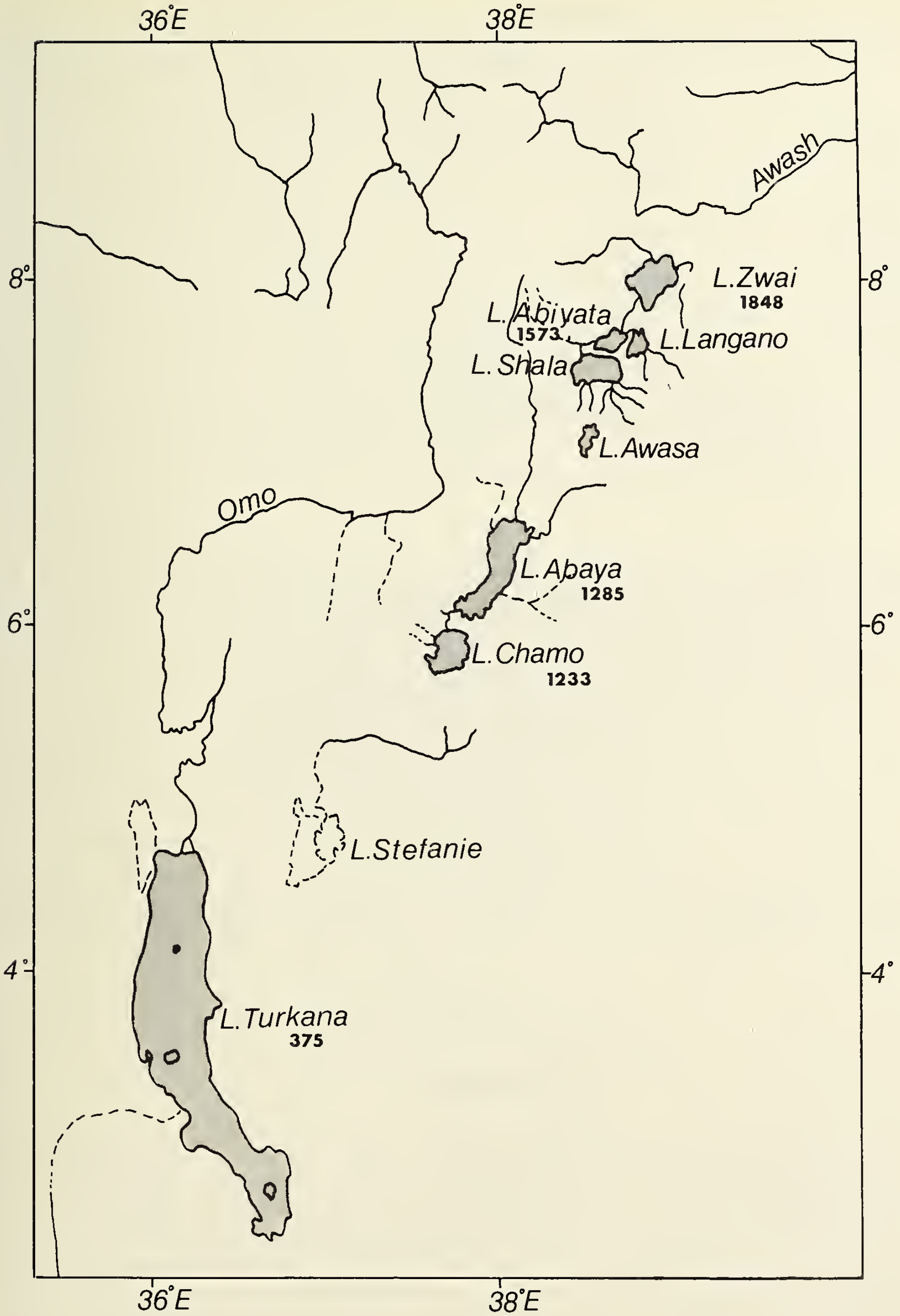

Fig. 58 The lakes of Ethiopia. The numbers are the surface levels in metres above sea level.

Table 39. Dorsal fin-rays in *O. n. cancellatus.*

	XVI 12	XVII 11	XVI 13	XVII 12	XVII 13	XVIII 12
L. Tana		1		9		
Zwai & Suksuki	1	1	3	15	2	1
Langano	3	3		4		
Chamo	3		7	6	1	
Abaia basin			1	11		1
Stefani basin	3		2	3		
Awash			4	3	1	
L. Koka			1	3		
Eringo R.				2		4
Totals	10	5	18	56	4	6

Total dorsal rays: 28 (f. 15), 29 (f. 74), 30 (f. 10)

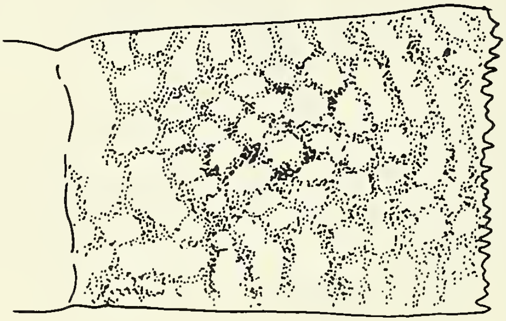

Fig. 59 Pigment pattern of caudal fin in *Oreochromis n. cancellatus,* a fish from Lake Zwai. Natural size.

Discussion

Notes on populations from various localities

Lake Tana (Tsana)

This lake is the source of the Blue Nile. Nevertheless, its *O. niloticus* resembles that of the other Ethiopian lakes more than of the Blue Nile at Abu Zugoli, Rosaires and Wad Medani. The river leaves the lake as the Great Abbai, which after about 30 km falls 13 m into a narrow gorge as the Tissisat Falls. Bini (1940) described the lake as shallow and oligotrophic, poor in plankton and in bottom fauna, and this no doubt accounts for the slender body and caudal peduncle of its tilapias.

Besides *O. niloticus* the only fish species recorded from the lake are three species of *Clarias, Varicorhinus beso* Rüppell, *Garra quadrimaculata* (Rüppell), *Barbus intermedius* (with which Banister in 1973 synonymized all the other names given to the *Barbus* of Lake Tana), and *Noemachilus abyssinicus* Boulenger. Only the *Clarias* are nilotic species and they belong to a widespread species-complex. *V. beso* is recorded from a tributary of the Blue Nile as well as other Ethiopian rivers, but not from the Nile itself; *G. quadrimaculata* is an Ethiopian species, and *B. intermedius* extends beyond Ethiopia into Lake Baringo and the eastern rivers of Kenya. The relationship of the *O. niloticus* of Lake Tana to Ethiopian populations rather than to *O. n. niloticus* is thus in line with that of the other elements of the fish fauna.

The pharyngeal dentition is as in *O. n. niloticus*, but the teeth of the jaws have more slender shafts and, except in the smallest, are arranged in 5–7 rows, 62–80 in the upper outer row. In the 98 mm fish there are 4–5 rows.

The pattern of stripes on the caudal fin is fairly regular, though faint, but leaves the posteroventral field unmarked, as preserved.

Colour. Boulenger describes a colour-sketch made by Degen thus: 'Pale grey with small olive-brown and blue spots, the preoperculum and gill-cover with a dull red border, the bases of the dorsal spines bright yellow, the iris grey with a bright yellow circle round the pupil.' Males collected in Lake Tana by the Sandhurst Ethiopian expedition of 1964 are described as having the back slaty black, belly grey or whitish, horizontal dark stripes (the spots on the series of scales?); in some a purple area around the pectoral fin, which has red rays; pelvic and anal fins black; caudal with black or reddish vertical stripes.

The Ethiopian Rift Valley

This valley contains a chain of lakes (Fig. 58) from Lake Zwai in the north to Lake Turkana and on to Lake Baringo. An eastern branch contains the Awash River (Hawash, Auasc), which flows towards the Red Sea but does not enter it. The type locality of *T. cancellata* Nichols is the Abano River, a seasonal river in the basin of Lake Abbe, an expanse of water in the lowland, swampy part of the Awash system. With 32–34 scales in the lateral line series, 20–25 lower gill-rakers, four approximately vertical stripes on the caudal fin, D XVII 12 or XVI 13, the types have the essential characters of *O. niloticus.* A larger specimen (which I have not seen) caught with the types had a rather densely scaled caudal fin (Nichols, 1923).

Two specimens of 116 and 207 mm SL from Quola* on the Awash resemble in all respects the samples from the Ergino River and the Ethiopian Rift lakes, especially in the anastomosis of the caudal stripes to form a reticulum. Teeth of jaws and pharynx are as in *O. n. niloticus.*

Lake Zwai (Zuai) communicates by the short river Suksuki with the lake of that name, also known as Hora Abgiata. A short channel unites this with Lake Langano. We have no tilapia from Lake Awasa (Auàsa). A considerable distance separates this from Lake Abaya (Abeia, Pagade or Marguerita), whose surface is 1285 m above sea level. It is continuous by a channel with Lake Ganjule (= Shamo, Ciamo or Ruspoli). Lake Stefani, lying within the Rift Valley to the north-east of Lake Turkana, is shallow and surrounded by swampy land. A sample of young *O. niloticus* was collected in 1896 in Ganana Dulei, a tributary of the Sagan River, an affluent of Lake Stefani, by the expedition on which Bottego met his death. The eight examined, 31–53 mm in SL, show by their scale-counts (32–34) and fin-ray numbers (Table 39; A III 9–11), their purtenance to *O. n. cancellatus*, and their pharyngeal teeth are also coarser than those of fishes of the same size from beyond the eastern escarpment, assigned to *O. spilurus.*

The teeth in the jaws of all the samples are variable some being shaped as in *O. n. niloticus*, others more slender, but none having the contrast between the long, slender shaft and the broad curved crown characteristic of the population of Lake Turkana. The pharyngeal teeth, too, are firm, the width of the bone from slightly less than its length to slightly more and the blade from a little shorter than the median length of the toothed area to a little longer.

Several of the sample from Lake Suksuki were mature males and had the jaw teeth worn, probably by digging. The dark marks on the scales are emphasized in these and the throat and lower fins are dark. Males from Lake Langano were reported to be dark blue-black all over.

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*I have not been able to find this on a map. It may be Zuquole, due south of Addis Ababa.

A sample from Lake Akaki

Five specimens from Lake Akaki, described as a cool, shallow, muddy lake 20 km SE of Addis Ababa, have dorsal fin-formulae more resembling those of *O. n. filoa* than *O. n. cancellatus*, namely XIV 13 (f.1), XVI 11 (f.1), XVI 12 (f.2) and XVI 13 (f.1), but in size and proportions they agree with *O. n. cancellatus* (head 32·4–36·5% SL, pectoral fin 39·4–41·3%). If this is the man-made lake mentioned on p. 162 they may have been stocked, and the possibility arises that they may have been taken from the hot-spring waters as fry after the meristic numbers had been determined but with the potentiality for more normal growth and proportions. If this is so it would be evidence of the impermanence of the characters on which *O. n. filoa* is defined. Examination of later generations of this population for meristic numbers and size at sexual maturity would provide a test.

Their fin-ray numbers are not included in Tables 35–37 & 39.

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
AMNH 8187 (Holotype of *T. cancellata*)	50	Abano R., eastern part of Hawash basin	B. Brown
AMNH 8201 (one of the paratypes)	50	Abano R., eastern part of Hawash basin	B. Brown
4 other specimens	27–37	Abano R., eastern part of Hawash basin	B. Brown
1902.12.13.452–3	166, 207	Quola*, Hawash R.	Degen
1969.5.2.17–25	183–247	L. Koka, Awash system 95 km SE of Addis Ababa	Fischtal
	and 111–159	L. Akaki, Awash system 20 km SE of Addis Ababa	Fischtal
Mus. Genoa, C, E. 15126	31–53	Ganana Dulei, tributary of Sagan R., affl. of L. Stefani	Bottego, 10.7.1896
1908.1.20.205–6	115, 173	Ergino R., trib. of Omo	coll. Zaphiro pres. McMillan
1937.4.20.106–8 (4 specimens)	95–145	Ergino R., trib. of Omo	coll. Zaphiro pres. McMillan
1905.7.25.78	127	L. Ganjule (Chamo)	Neumann
1908.1.20.208–210	132–149	L. Ganjule	coll. Zaphiro pres. McMillan
1937.4.20.109–113 (8 specimens)	97–141	L. Ganjule	coll. Zaphiro pres. McMillan
1968.9.11.25–41	171, 72–104, 16–47	L. Ganjule	Sandhurst Ethiopian Expedition 1966
1968.9.11.13–22	66·5–141·0	L. Langano	Sandhurst Ethiopian Expedition 1966
1968.9.11.23–24	99, 136.5	Slow-flowing pool in Darse R., L. Abaya	Sandhurst Ethiopian Expedition 1966
1895.12.31.62	200	L. Abeia (Abaya)	Donaldson-Smith
1905.7.25.100–101	42, 52	Suksuk R., L. Zwai	Neumann and Erlanger

Museums & Reg. No.	SL (mm)	Locality	Collector or donor
1908.1.20.215–18	118–206	L. Suksuki (= Hora Abgiata)	coll. Zaphiro pres. McMillan
1937.4.20.100–101 (3 specimens)	132–208	L. Suksuki (= Hora Abgiata)	coll. Zaphiro pres. McMillan
1968.9.11.13–22	67–141	L. Langano	Sandhurst Ethiopian Expedition 1966
1908.1.20.211–214	174–235	L. Zwai	coll. Zaphiro pres. McMillan
1937.4.20.102–5	41–232	L. Zwai	coll. Zaphiro pres. McMillan
1902.12.13.446–451	98–230	Zegi and Bahardar, L. Tana	Degen
1968.9.11.9–12	171–187	Offshore Island, rocky bottom, c. 3·2 m, L. Tana	Sandhurst Ethiopian Expedition 1964

*Perhaps Zuquole, S. of Addis Ababa.

Oreochromis niloticus filoa subsp.n.

Tilapia nilotica (part); Boulenger, 1904:333 (hot springs of Hawash River 'near Filoa', Ethiopia; record only); *idem*, 1915:162 (specimens 256 & 257 only).

Types. Holotype: ♂, 115·5 mm SL, collected in 1900 by Neumann and Erlanger in hot springs of the Awash system; BMNH 1905. 7.25.98 Paratypes: ♀, 77·5 mm SL, same data as holotype, BMNH 1905.7.25.99; and 2 ♂♂ and 4 ♀♀ of 55–96 mm SL collected in the same hot-spring waters in 1968 by the Sandhurst Ethiopian expedition, BMNH 1968.11.11.1–5.

Distinguishing characters and distribution (see pp. 142–145)

Description

For meristic characters see Tables 34–37, for proportions Table 40.

Of 15 specimens, 7 have only 4 lateral-line openings in the preorbital bone on one or both sides.

Table 40. Proportions in *Oreochromis niloticus filoa.*

SL (mm)	115·5 (holotype)	70–96 N = 3	48·5–64·5 N = 4
As % SL			
Depth	43	38–45	37–38
L. head	36·3	36–39	37·5–39
L. pect. fin	35·5	32·5–36·0	34·5–35·5
L. caudal ped.	14	13·5–14·5	12–13
As % length head			
Eye	22·7	22·6–25·3	27–29
D. preorb.	19	18–19	—
Interorb.	34	28–34	28–29
Lower jaw	33·5	33·0–34·5	34–35
Caud. ped. length/depth	0·75	0·85–0·9	0·8–0·9

Teeth in 3–4 series, part of a fifth in the holotype; with rather slender shafts, but not as in *O. n. vulcani*.

Gill-rakers on first arch (2–3) + 1 + (20–23). Microbranchiospines present on outer sides of second to fourth arches.

Pharyngeal teeth as in small specimens of other subspecies, the lateral lobes of the toothed area a little more rounded than in a Cairo fish of the same size.

Scales in 2–3 rows on the cheek, 4 or 4½ between origin of dorsal and lateral line (and see Table 35).

Dorsal XIV 12–13, XV 11–13 or XVI 12–13 (see Table 35). Anal III 8–10, usually III 9; third spine in fishes of 70–116 mm SL 12·0–15·6% SL, 33·3–42·8% length of head.

Genital papilla of male conical or with a terminal notch.

COLORATION. Recently preserved specimens are dark in colour, the dark spots on the scales becoming smaller towards the ventral surface. In a ripe male of 96 mm SL the lower part of the cheek and operculum are very pale grey (reminiscent of *O. mossambicus*), but may have been red in life. Vertical series of dark spots on the caudal are present but less regular than in *O. n. niloticus*. In mature males, the anal fin is black between the rays, dorsal grey with series of black spots on the soft part and posterior part of spinous; lappets with black edge. In females and young the melanin is more diffuse.

Ecology

Dr P. Morris records that these fishes congregate in large schools at night at the edges of the clear, alkaline pools into which the hot-springs erupt, where the water is then cooler (38·5°C). During the day they are not to be seen and have presumably withdrawn to deeper water.

Breeding

Three of the types are ripe males of 92·0–115·5 mm SL, and a female of 64·5 mm contains loose ovarian eggs of 2·6–2·7 mm long diameter; so breeding occurs at a small size. The collectors of 1968 recorded that several fishes carried eggs in the mouth. When the samples reached the Museum the only extra-ovarian eggs were a few among the gill-filaments of the two ripe males, but there were none in the pharyngeal cavity of either sex. They may have got under the gill-covers of the males accidentally during capture.

Discussion

During their journey of 1900, Neumann and Erlanger collected two *Oreochromis*, a male of 115·5 mm and a female of 77 mm, in 'Hot springs of the Hawash River near Filoa'. 'Filoa' or 'Filhoa', I understand, is the Amharic word meaning 'hot spring', and of these there are several in the neighbourhood of Addis Ababa.

In 1967 I examined and returned to Professor R. M. Baxter of Addis Ababa University, who collected them, eight small specimens, also from a 'hot stream in Awash National Park' at 1000 m altitude; the Sandhurst Ethiopian Expedition of 1968 added fifteen from 'Filhua, in warm springs', and a further sample was brought by the Royal Holloway College expedition of 1970. They are all evidently from the same general locality as that of the sample of 1900. They show by their colour-markings, dentition and numbers of scales, and gill-rakers their purtenance to *O. niloticus*, but they all differ from the Ethiopian subspecies, *O. n. cancellatus*, as well as from others in the low numbers of vertebrae and dorsal fin-rays (Tables 34 & 35); the scale numbers are also low. In the small fish with only 26 vertebrae there are only 25 centra, two of the neural spines corresponding to a deformed centrum.

That low meristic numbers are often associated with high temperature is well known. If such characters are to be recognized as entitling to subspecific rank, they should have acquired some genetic basis in the population. This only experiment can discover. Direct influence of temperature can only act before the number of segments has been determined, thus while the embryo is still being brooded in the parental mouth. This excludes the possibility that the population is directly recruited from individuals that have been spawned and brooded in cooler waters, and have made their way as free-swimming young into the warm pools, although the parents of at least some of each generation may have entered in this way. Some of the available samples are mature fishes found breeding and brooding in the pools at a very small size. Dr P. Morris informs me that the pools discharge into streams that at first run away from the Awash and only later join it, as the Kassam River, after a devious course, so that these populations are isolated to a considerable degree. That their physiology has become adapted to the high temperature he judges from the fact that they die on transfer to cooler water much sooner than the fishes from other Ethiopian waters. This is a common phenomenon in the absence of acclimatization.

Probably, therefore, the hot-spring population is mainly self-perpetuating, but whether its characteristics are irreversible is unknown.

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1905.7.25.98–99 (holotype & paratype)	77, 115·5	Hot springs of Hawash R., 'nr. Filoa'	Neumann & Erlanger
1968.11.11.1–14 (including paratypes)	23–96	Hot springs of Hawash (Filhua)	Sandhurst Ethiopian Expedition, 1968
1971.4.1.25–32	17·5–65·0	Pools around hot springs in Awash National Park, Shoa (water 38·5°C)	Royal Holloway College Expedition 1970 (P. Morris)

Oreochromis niloticus vulcani (Trewavas)

Chromis niloticus; Günther, 1896:218; *idem*, 1897 (*in* A. Donaldson Smith, 1897:378) (L. Rudolf = Turkana).

Chromis tristrami (part); Günther, 1896:218 & 1897:378 (L. Turkana, the damaged specimen with D XV 13, teste Fowler, 1931).

Tilapia nilotica (part); Boulenger, 1915:163 (specimen 275 only); Trewavas, 1932:314 (L. Turkana & Crater-lake C, Central Island); Pellegrin, 1935*c*:137; *idem*, 1935*d*:415; Worthington & Ricardo, 1936:368; Lowe-McConnell, 1958:291; Mann, 1964:54, 59, 60 (L. Turkana); Chervinski, 1967 (description, hybrids in Israel); Hopson, 1976:87; Harbott, 1976:27 (food).

Tilapia vulcani Trewavas, 1932:315, fig. 1 (Crater Lake A, Central Island, L. Turkana); Worthington & Ricardo, 1936:380; Pruginin, 1965; *idem*, 1969 (hybrids); Pruginin *et al.*, 1975 (hybrids); Avtalion *et al.*, 1965 (hybrids); Avtalion *et al.*, 1976 (serum proteins).

Tilapia crassispina Arambourg, 1947:472, figs 1, 5, 56, 83 & 84, pls 38 and 39 (Lower Pleistocene beds above N. end of L. Turkana).

TYPES. Syntypes: seven specimens of 120–245 mm SL from Crater Lake A, Central Island, L. Turkana (see map 1, Worthington, 1932*b*, pl. iv and Hopson, 1976); BMNH 1933.2.23.71–76.

Holotype of *T. crassispina* a nearly complete skeleton of a fish of 240 mm SL; MNHN 858; paratype MNHN 859.

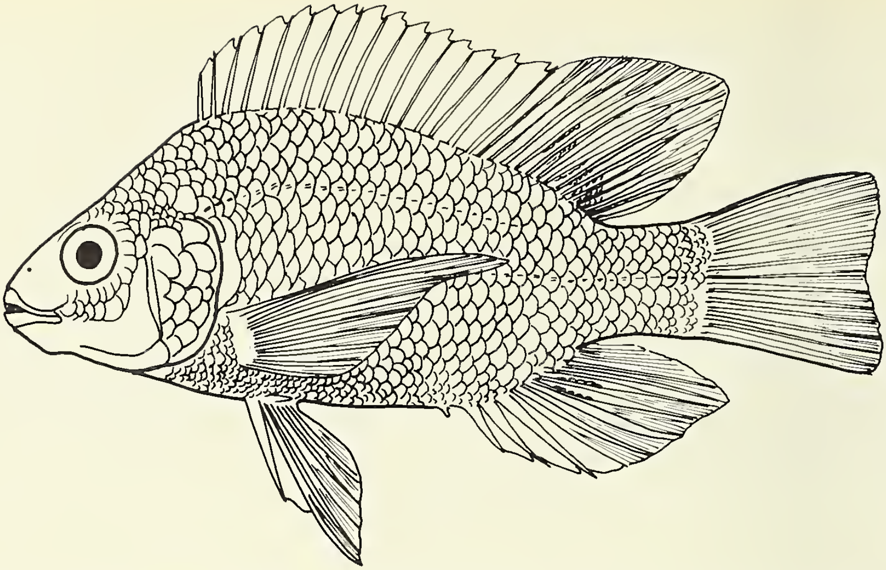

Fig. 60 *Oreochromis niloticus vulcani.* Outline drawing of a syntype from Crater-lake A, Central Island, Lake Turkana. Re-drawn from Trewavas, 1933.

Distinguishing characters

See also p. 145 & Tables 34–37. The main distinctions between this and *O. n. cancellatus* are the lower mean numbers of dorsal spines, the higher numbers of soft rays and the usually more numerous, more slender-shafted teeth (Fig. 54), the number of rows being rarely as many as six in the Ergino River, but 4–7 in Lake Turkana fishes of the same size.

Proportions in samples of subpopulations are set out in Table 41. Comparison with the corresponding proportions in *O. n. niloticus* (Table 39) shows no significant contrasts, except that, as in *O. n. cancellatus*, the caudal peduncle is a little longer, especially in Crater A. The range of relative depth of body is the same, the leanest fishes being those of Crater A, which resemble the captive aquarium specimens of *O. n. niloticus* and aquarium reared *O. n. vulcani* described by Chervinski (1967). Even the big heads of the Crater A fishes (types of *O. n. vulcani*) give a ratio within the range of *O. n. niloticus.*

Chervinski (1967) described a sample bred from the offspring of a single female and brought to Israel by Pruginin in 1965. These were reared at Dor, part in a heated aquarium and part in ponds. Some of the measurements are obviously not comparable with mine, but the meristic numbers in his samples agree in the high percentage of individuals with XVI dorsal spines, especially in the pond-bred moiety.

Lowe-McConnell (1958) states that in East African *O. niloticus* the distribution of black pigment in breeding males is on the lower fins, lower parts of the body and the dorsal fin, although she does not describe the males of Lake Turkana separately. In at least some localities the male becomes dark all over, except the transparent red-rayed pectoral fins and the white genital papilla. This general colour is described as dark green with blue iridescence (Mr R. Haller, pers. commn) and as dark blue-black from Crater-lake A (the Worthington collection and Dr R. Welcomme) and a preserved male of 93 mm from Loiengalani is black. Mr Haller states that the caudal margin is red. Numerous well-grown males, offspring of Lake Turkana *O. niloticus,* in a tank at Mr Haller's fish-farm near Mombasa had the top of the head bright sky-blue and very conspicuous from above. Chervinski (1967), describing some precociously

Table 41. Proportions in samples from different subpopulations of *O. niloticus vulcani*. 'Other' includes the main Lake Turkana and Crater C of Central Island. 'Loy.' = Loyengalani, the stream entering the lake at this locality.

SL	198·5–370·0		103·0–196·5			68·0–99·0 mm		
	Crater A	Other	Crater A	Other	Loy.	Crater A	Other	Loy.
N	9	3	2	11	3	7	4	6
Proportions as % SL								
Depth	37·1–42·8	45·7–46·7	41·0, 43·1	40·7–50·0	36·5–43·1	38·6–41·5	42·0–42·8	38·4–40·8
L. head	33·8–37·5	31·6–32·8	37·1, 37·7	32·6–36·0	33·5–34·0	36·0–39·0	33·3–36·0	35·2–38·4
L. pect. fin	36·4–41·7	34·4–39·3	40·0, 40·8	35·4–45·5	39·0–41·3	38·0–43·2	34·8–40·0	33·8–39·7
L. caud. ped.	11·4–14·6	10·5–13·2	12·1, 12·5	10·2–13·8	12·3–12·9	12·5–14·4	12·6–13·8	11·7–13·5
L. 3rd A spine	15·6–18·2	14·6–15·1	18·8, 21·6	15·5–18·4	16·6–18·5	17·9–23·6	15·1–17·5	14·0–15·0
Caud. ped. l/d	0·73–0·98	0·65–0·83	0·76, 0·85	0·65–0·87	0·83–0·85	0·84–0·97	0·8–0·9	0·75–0·9
Proportions as % length of head								
Snout	33·2–35·0	34·6	31·9, 33·8	29·2–34·9	28·2–33·9	27·2–31·4	29·5–31·5	30·0–35·0
Eye	20·7–27·4	18·4–20·0	22·4, 27·4	20·6–26·3	22·0–25·5	30·8–36·0	25·7–26·6	26·7–31·3
D. preorb.	18·6–21·3	19·2–20·2	19·0, 19·1	16·1–19·7	17·8–19·1	13·6–17·0	13·8–18·9	14·3–19·0
Intorb. w.	38·0–45·5	38·5–42·8	38·6, 39·8	32·4–38·0	34·5–38·7	28·7–31·8	33·0–35·0	25·4–31·4
Lower jaw	32·2–36·8	29·9–33·2	33·6, 35·2	31·6– 35·2	31·7–35·8	30·1–34·0	31·5–33·3	32·4–35·6

breeding males in aquaria at Dor, states that the ventral surface becomes red, changing to black at the peak breeding phase. Unfortunately he does not compare them with the *O. niloticus* native to Israel*.

Dark males are known also in the *O. n. cancellatus* of Lake Langano, but it is not known how widespread such coloration may be in this subspecies.

Avtalion *et al.* (1975, 1976) and Herzberg (1978) found that the proteins of the serum and mucus gave electropherograms distinct from those of other strains of *O. niloticus* examined by them. But Avtalion (1982) gives some importance to transferrins and an esterase common to *O. n. vulcani* and all other strains of *O. niloticus* in Israel, whether native or imported from Uganda or Ghana. They are absent from *O. aureus.*

Hybridization with *O. aureus* as so far reported (Pruginin *et al.*, 1975) does not give 100% males in the F_1, although the proportion is very high when the male parent is *O. aureus* (see pp. 192, 205).

Distribution

Lake Turkana (Rudolf) and its affluent streams (except the Omo River?); crater-lakes on Central Island.

Although the name was originally intended to distinguish the population of Crater-Lake A from the population of the main lake and the rest of the superspecies, it now seems that the basic characters of the crater fishes are shared by the whole population of Lake Turkana and distinguish it from others. Moreover, the crater population cannot be assumed to be permanently isolated from that of the main lake, and its peculiarities are probably dependent on its environment. The name '*vulcani*' is therefore now extended to cover the whole Lake Turkana population as a subspecies of *O. niloticus.* It has already been used in this sense by Pruginin (1965), Pruginin *et al.* (1975) and others, because of apparent chemical and genetic peculiarities.

Lake Turkana occupies the floor of a deep part of the Rift Valley, its surface being now 375 m above sea level, and its depth reaching 90 m in the north basin and 150 m in the south (Hopson, 1976). Its only considerable affluent river is the Omo, which collects water from a wide area in the Ethiopian Highlands and brings it into the north end of the lake by a swampy delta. Other rivers, the largest of which are the Kibish in the north, the Kaliokwell and Turkwell in the west, and the Kerio at the south end, flow into the lake only during the very short rainy seasons if at all, but probably feed it under the dry river beds. Springs from the base of the escarpment also feed the lake. A small river at Loiengalani may enter the lake seasonally at the south-east shore. It supports a population of early breeding *O. n. vulcani.*

Raised beaches well above the present level (Worthington & Ricardo, 1936; Beadle, 1932; Fuchs, 1939) show that the basin formerly contained much more water, even allowing for the relative lowering of the floor by faulting. A recent estimate (Butzer & Thurber, 1969; Butzer *et al.*, 1972; Beadle, 1974:142) puts the highest level, 9500 years ago, at about 80 m above the present surface. The molluscan remains in the raised beaches show that the alkalinity of the lake was then much lower (Fuchs). Evaporation has left Lake Turkana with a high alkalinity and salt content, but Beadle (1932 & 1974) believes that this would be higher unless there were some underground seepage. There is no surface outlet.

The fish fauna is nilotic (Worthington & Ricardo, 1936) and Fuchs (1939) estimated that the lake overflowed to the northwest in the early Middle Pleistocene, establishing (or re-establishing) a connection with the Nile which lasted from 10 000–7000 years bp and gave its present nilotic fauna to Lake Turkana (see also Harvey & Grove, 1982).

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*In his Table 7 Chervinski (1967) includes total numbers of dorsal rays in *O. niloticus* of Lake Kinnereth, attributing them to me. They must have been from my paper of 1942, and were later (Trewavas, 1966*a*) recognized as referring to *O. aureus.*

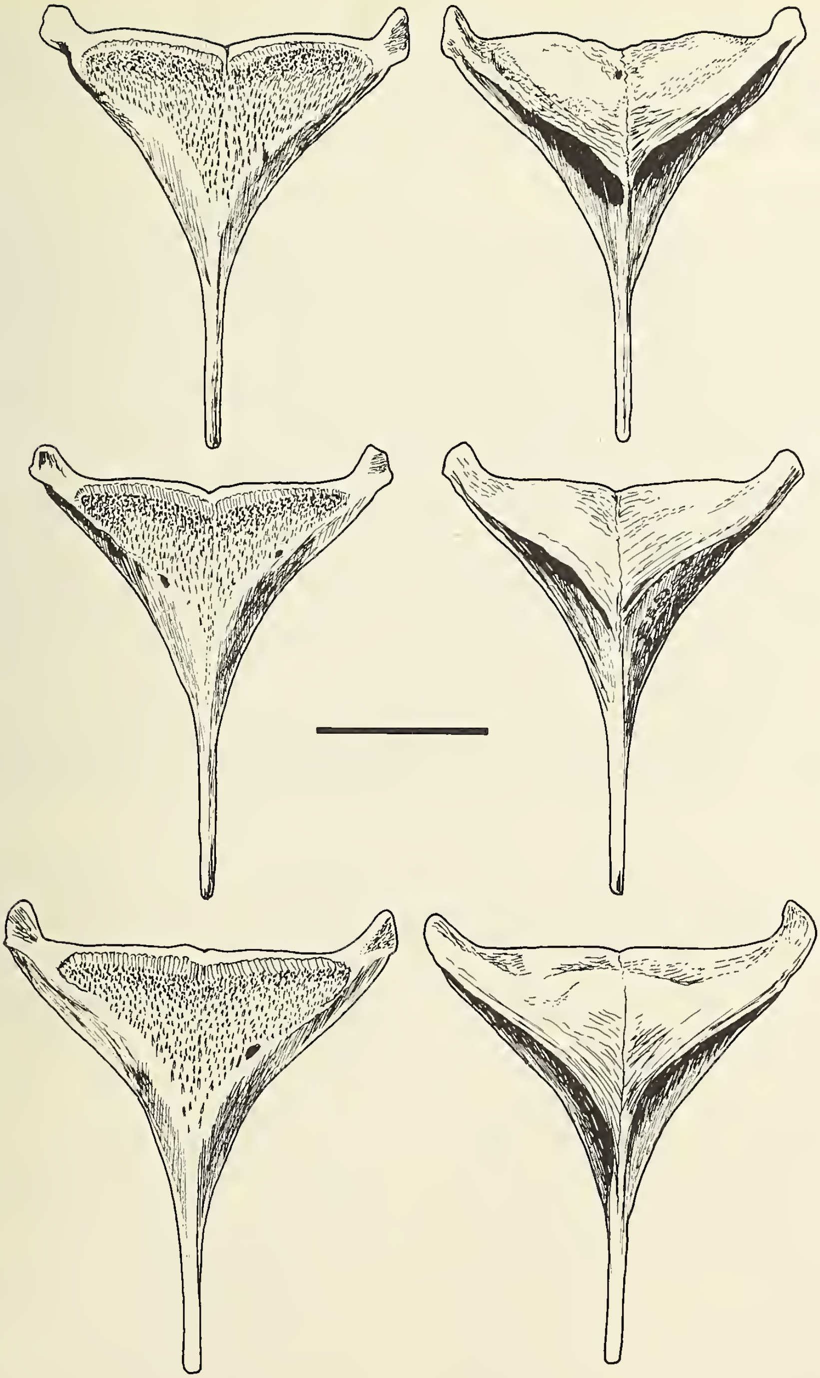

Fig. 61 Lower pharyngeal bones of *Oreochromis niloticus*, dorsal and ventral views. Above, *O. n. vulcani* of 240 mm SL from Lake Turkana; middle, *O. n. vulcani* of 230 mm SL from Crater-lake A, Central Island, Lake Turkana; below, *O. n. baringoensis* of 210 mm SL. Scale = 10 mm.

Butzer & Thurber (1969) have described the geology of the Lower Omo basin, which is an extension of the Lake Turkana Rift. How early was the connection between this and the higher part of the Omo, where it is joined by the River Ergino, has not been established and our present samples from the latter river are too small to allow more than tentative assignment of them to *O. n. cancellatus* rather than to *O. n. vulcani.*

Fossil remains

Arambourg (1947) described fossils from beds on the west shore of the now dry Sanderson's Gulf, considering them to be contemporary with the Kaiso Beds of Lake Albert (Lower Pleistocene), and to represent a fauna that preceded the present one. Like the Kaiso Beds, they included one genus (*Clarotes*) not found in the present faunas of either Lake Albert or Lake Turkana, as well as some caudal spines of a freshwater ray, assigned to *Potamotrygon*, not known in either lake or even in the Nile (but cf. *P. garouensis* Stauch & Blanc of the Benue River). The remains of well grown specimens of *Oreochromis* were described under the new name *Tilapia crassispina* and compared with *O. niloticus.* The number of vertebrae, 16+14, is higher than in *Tilapia zillii* and the shapes of the teeth of jaws and pharynx exclude both *T. zillii* and *S. galilaeus.* Differences cited from *O. niloticus* were the more posterior position of the anal fin relative to the dorsal, the very robust anal fin-spines and the shape of some of the teeth. All the teeth, except possibly one sharply hooked isolated pharyngeal tooth, might be included within the range of variation in *O. niloticus*; the photograph of the holotype shows that the position of the anal fin is due to distortion of the fossil; and the anal spines, though strong, may be matched within *O. niloticus*, particularly the present populations of Lakes Albert and Turkana. Their length is compared with that in other populations in Table 42; see also Fig 57.

Although *T. crassispina* was a member of the old and probably replaced fauna, it cannot on the evidence be excluded from the present *O. niloticus*, and its XVI dorsal spines are the modal number for *O. n. vulcani.* It is even possible that this species, given the well-known ability of tilapias to maintain a breeding population in very small pools, was one of few survivors of the early fauna.

Table 42. Length of third anal spine in samples from the subspecies of *Oreochromis niloticus* compared with that of the fossil *Tilapia crassispina.* The samples are divided into size-groups to expose any allometry, but variation almost completely masks any allometric trend.

N	SL(mm)	Anal spine % SL Range	Anal spine % head Range	Mean
Nile				
7	65–99	14·7–19·2	41·6–56·1	47·5
11	106·5–192·5	13·7–19·1	41·3–50·35	45·8
12	201·0–304·5	13·1–17·0	37·2–48·3	43·9
West Africa				
6	63·5–97·0	14·5–17·8	39·7–47·5	44·6
10	107–191·5	14·6–18·1	41·5–51·5	46·6
L. Albert (excl. Buhuku)				
4	72–95	16·9–20·0	45·4–51·8	48·0
8	114–193	16·5–22·6	45·3–58·7	52·2
1	282	17·4	47·7	
Wadelai, Albert Nile				
1	239	20·1	55·5	

Table 42 *continued*

N	SL(mm)	Anal spine % SL Range	Anal spine % head Range	Mean
Buhuku, L. Albert				
8	68–104	18·8–21·3	47·1–55·4	51·2
L. Edward/George				
4	76–105	14·7–17·3	41·4–49·6	44·2
8	124–259	12·2–17·2	34·8–46·5	42·1
Ls. Kivu & Tanganyika				
6	148–245	13·1–15·4	37·7–45·8	40·8
1	335	12·1	34·4	
L. Tana				
1	98	13·5	36·7	
8	171–230	14·0–15·3	39·2–43·8	41·5
L. Zwai				
12	141·5–235	11·9–15·7	32·9–45·8	38·8
L. Suksuki				
7	118–208	11·6–14·8	33·3–43·8	40·0
L. Langana				
2	66·5, 90·5	15·8, 15·5	42·8, 41·1	41·95
6	108–140·5	12·0–17·0	37·5–46·6	42·6
L. Abeia				
2	125·5, 200	14·1, 16·7	42·9, 41·2	42·05
Ergino R.				
4	94·5–145	15·2–17·0	44·4–47·8	46·45
L. Turkana (Rudolf) (excl. Crater A)				
6	81–109	15·1–16·9	45·3–49·3	47·3
10	111·5–173	15·5–18·5	46·4–55·2	49·4
1	256	14·8	46·8	
1	370	14·6	45·2	
L. Turkana (Crater A)				
7	68–92	17·9–22·6	49·0–55·2	53·04
11	190–250	15·6–21·6	44·6–58·2	49·8
Tilapia crassispina (holotype)				
1	240	20	52·7	

Samples from subpopulations

In Lake Turkana *O. n. vulcani* is most abundant in shallow water (0–5 m). Near the western shore it was caught in the sheltered water of Ferguson Gulf, but otherwise it is commonest near the calmer eastern shore (Hopson, 1976). It grows to a size unequalled elsewhere in this species (except possibly in the introduced population of Lake Victoria), specimens of 63 and 64 cm

TL, weighing over 4·3 kg being common (Worthington, 1932; Worthington & Ricardo, 1936; Lowe-McConnell, 1958). Such large fishes attain a length of 39 cm before reaching sexual maturity, but Mr Peter Bayley informs me that even in some locations of the main lake maturity may be attained at a smaller size. Mann (1964*b*) has suggested that low fishing intensity may account for the abundance of large fishes, but no growth studies other than length/weight ratios have been made (see p. 186).

The crater lakes on Central Island were sampled by the expedition of 1930–31 (see Worthington & Worthington, 1933, fig. 2 & pl. 10). Crater lake C was then about 1·3 km in diameter and separated from the main lake by a wall only about 1·5 m above the surface. It has since been reconnected with the lake (Beadle, 1974, quoting Hopson). This sample comprised eight small fishes, one of them, of 103 mm SL, having enlarging testes. The dorsal spines number XVI in seven, XV in the eighth. The alkalinity of the water was high (0·113 N), sufficiently so for the blue-green alga *Arthrospira* to flourish and to be the only alga present (Beadle, 1932 and 1974). The low numbers of spines and the small size at maturity are reminiscent of the *O. niloticus* of Buhuku Lagoon, Lake Albert (p. 156 & Table 36).

Crater lake A lies in two interconnected craters and is about twice as large as the former size of Crater lake C. In 1930 it was separated from the main lake by a wall 6·5 m high, but Beadle found evidence that not long before the expedition of 1930 the level of the lake must have overtopped the barrier. Although more alkaline than the main lake it was less so than Crater lake C, and its pH at 9·5 was equal to that of the main lake. Its planktonic flora consisted of sparse diatoms and the zooplankton was also meagre. As well as the samples of 1930–31 we have some of 1965 that have maintained the characteristics of the earlier population. Already at 68–92 mm the teeth are in 5–7 series and at all stages their shafts are long and slender (Fig. 54). In adults some of the outer teeth are tricuspid. The lower pharyngeal bone is narrow with a small dentigerous area and a long blade (Fig. 61). Apparent differences in proportions are mainly due to the lean condition, but dorsal and anal spines measure longer than in the main lake. Our samples include no specimens with XVII dorsal spines (Tables 35 & 36). The blue-black colour of mature males has been mentioned.

Four samples of *O. niloticus* from Loiengalani, at the south-east shore of the lake, have been received at the BMNH. One comprised three fishes of 163–173 mm SL that were probably caught in the lake. The others were collected at different times in a stream (or streams?) rising from Mount Kulal near the 'safari-camp'. The latter were all small fishes not exceeding 93 mm SL. Among those observed by Dr Foersch were brooding females, who spat eggs from the mouth, and his collection included two females with ovarian eggs a little less than 1 mm in diameter, and one of 61 mm in which they measured 1·2 mm. Mr Hopson's collection included a black male with enlarged testes, two females with ovarian eggs of 1·8 mm and one of 65 mm in which there were 33 eggs of 2·5 mm, thus nearly ripe, in the right ovary.

Dr Foersch describes the locality from which his samples came. The stream issued from a small swamp fed by hot springs and dried up about 100 m from the source. No fishes were present at the source, where the water temperature, taken in the afternoon, was 37°C, but the fishes were living in water of 35°C. Later analysis of a water sample (by Dr Lüling of Bonn) showed that it was much less alkaline than the lake water. The following comparison of the main features of both waters was selected by Professor L. Beadle (pers. commn).

	Stream at Loiengalani	Lake Turkana
Chloride (meq./L)	0.62	10–15
Sulphate (meq./L)	0.46	1–15
Alkalinity (meq./L)	5	20–25
pH	7.2	9.5–9.7
conductivity (μmho at 20°C)	602	2000–3000

Among the factors possibly influencing small size and early maturity are these chemical differences, the high temperature and the confined space of the waters. Since the alkalinity is very near that of Lake Tanganyika the chemistry is unlikely to be the causal factor. The high temperature and confined space are often present together in the environment of 'stunted' populations, and the spatial factor is rarely absent (but cf. Lake Sibaya, p. 300).

The vertebral numbers (15+15 or 15+16) are typical of *O. niloticus*, and the fin-ray counts of *O. n. vulcani* (see Tables 34–36). Probably this stream is at some seasons in communication with the lake and its population may be recruited from the lake as fry.

Material Examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1933.2.23.71–76 (syntypes of *T. vulcani*)	199–230	Crater-Lake A, Central Island, L. Turkana	Worthington
1933.2.23.78–85	54–92	Crater Lake A, Central Island, L. Turkana	Worthington
1965.12.10.6–15	70–250	Crater Lake A, Central Island, L. Turkana	Pruginin & Welcomme
1933.2.23.63–69	78–112	Crater Lake C, Central Island, L. Turkana	Worthington
1933.2.23.32–45	81–256	Ferguson Bay, L. Turkana	Worthington
1933.2.23.53–62	26–49 (8 fishes) and several 11–23 mm	L. Turkana (Ferguson B.), Turkwell mouth, Central Island and east shore	Worthington
1938.12.6.6–7	33, 43	Ferguson Spit, L. Turkana	Worthington
1908.1.20.207	370	NE of L. Turkana	Zaphiro
1965.12.10.2–5	163–173	Loyengalani, L. Turkana	Pruginin & Welcomme
	44–54	Loyengalani, fresh water from Mount Kulal	Coe
1981.2.17.339–348	32–93	Stream at Loyengalani	Hopson
	61–68	Stream at Loyengalani	Foersch
1966.12.17.1–2	99, 146	Pond at Dor, Israel (introduced)	Chervinski

Oreochromis niloticus baringoensis subsp.n.

Tilapia nilotica (part); Trewavas, 1932:314; Worthington & Ricardo, 1936:387; Ssentongo & Mann, 1971:25; Ssentongo, 1974:99.

TYPES. Holotype: ♀, 246 mm SL, paratypes 2 ♂♂, 4 ♀♀ of 154–242 mm and 3 juveniles of 43–114 mm SL, collected by E. B. Worthington on the Cambridge Expedition to the East African Lakes, 1930–31; BMNH 1933.2.23.12–31.

Distinguishing characters

See p. 146 and Tables 34–37 & 44. The geographical situation of *O. n. baringoensis* requires its comparison with *O. spilurus*. Features placing it with *O. niloticus* are: (i) 30 or 31 vertebrae in ten of the specimens radiographed; in the eleventh there are 29 centra, one of which has two neural and haemal spines; (ii) 32 or 33 scales in the lateral line series (usually 30 or 31 in *O. spilurus*); (iii) 20–24 gill-rakers on the lower part of the first arch (usually 15–19 in *O. spilurus*); (iv) the absence of hypertrophy in the jaws of adults; the lower jaw is 30·0–35·5% length of head at all sizes; (v) the black or dark grey lappets and upper edge of the dorsal fin (cf orange or red in *O. spilurus*). The depth of the preorbital bone in adults is as in *O. niloticus* (17·9–20·1% length of head in fishes of 110–246 mm SL), and less than in the eastern species, including *O. spilurus* Fig. 81 & Table 57.

Characteristic of the subspecies are the tricuspid outer teeth of adults (Fig. 54), the relatively low mean number of vertebrae and the modal dorsal formula of XVI 12. The lower pharyngeal bone (Fig. 61) is slender, its width 29·0–32·4% length of head, from a little less to a little more than its length; the toothed area is rather small, its median length contained 1·1 to 1·5 times in the length of the blade, its teeth less coarse than in *O. n. niloticus*, resembling those of many *O. n. vulcani*. The nature of the dentition is probably related to the nature of the available food, but although the jaw-teeth become tricuspid they remain relatively stout in contrast to the slender-shafted teeth of *O. n. vulcani*.

The length of the pectoral fin is 38·8–43·2% SL in adults of 110–246 mm SL, 35·0–41·5% in juveniles (Table 44).

The colour of *O. n. baringoensis* is very pale compared with other populations and this may well be an environmental effect in this shallow lake with little shade. Field notes by Mann and Ssentongo (pers. commn) give the following details: the red flush characteristic of the males of other populations is usually absent (but Mr R. Haller (*in litt.*) records its presence). Pelvic and anal fins of breeding males are tipped with dark grey, but the black pigment of throat, chest and belly seen in ripe males of *O. n. eduardianus* (with which these observers were familiar) is replaced by dusky grey. In females and immature fishes the body is pale slate-grey; chest, belly and pelvics are white. In mature males the slate-grey or slate-green is a little darker, especially on the back. The vertical stripes of the caudal are dark brown on a light grey ground. As in other subspecies, the pectoral rays are red to light brown and seven or eight vertical bars may appear on the flanks.

The maximum size reported is 36·0 cm TL (Worthington & Ricardo, 1936). Mature individuals are reported from 18 cm TL. Ssentongo & Mann (1971) and Ssentongo (1974) speculate on the reasons for the low maximum size and low size at maturity in this population, but no growth studies have been made.

Distribution

Lake Baringo

Description of the locality. Lake Baringo is a shallow lake, nowhere more than 7·5 m deep (Beadle), situated in the eastern Rift at about 1°N, 35°30′ E, south of Lake Turkana and nearly 610 m higher. It is believed to have an underground outlet to the north, emerging as the Suguta River, and is fed by rivers Tigger and Ol Aribel, so that it is less alkaline than Lake Turkana, although the salt content varies with the season (Beadle, 1932; Jenkin, 1936).

The Pleistocene history of the region has been examined and discussed by Fuchs (1950). Lake Baringo is considered to be the modern representative of the much larger Middle to Upper Pleistocene Lake Kamasia, whose shores extended to include the Kapthurin River to the west, the Bogoria River to its headwaters south of Lake Harrington, as far as Baringo Post to the east and to Kapedo in the north. The nilotic fauna of Baringo, which as formerly in Lake Turkana once included the characteristically nilotic mollusc *Melanoides tuberculata* (Müller), reached this region with the same Middle Pleistocene influx as supplied Lake Rudolf. Fuchs describes the probable late Middle and Upper Pleistocene changes in the extent and nature of the waters in the Kamasian basin. According to him, Lake Baringo may have overflowed to flood the area near Kapedo in the late Upper Pleistocene. If this was so, the tilapias of Lake Baringo and the Kapedo area have been isolated from each other only since this time, but both have been isolated from Lake Turkana since the formation of the volcanic barrier to the south of that lake in Middle and Upper Pleistocene times (see pl. 32 of Fuchs, 1939).

Of the non-cichlid fishes of the Baringo basin, the *Barbus* has been named as a distinct subspecies of the mainly Ethiopian *B. intermedius* Rüppell (Banister, 1973), a species extending beyond the lakes and rivers of Ethiopia across the 'Awash-Shebeli and Lake Stefani-Juba watersheds into the eastern rivers of Kenya. The *Labeo* was identified as *L. cylindricus* Peters and the *Clarias* as *C. mossambicus* Peters, both eastern units of a species-complex having also nilotic members, so that without more taxonomic analysis than they have received they give no evidence as to the origin of the Baringo fauna. The small *Barbus*, *B. lineomaculatus* Boulenger is also East African and the relationships of the *Aplocheilichthys* are uncertain.

O. niloticus was the only cichlid species collected in Lake Baringo in 1931 and the only one recently (June 1969) found there by Ssentongo & Mann (1971). A suggestion in the Report on Kenya Fisheries for 1964 that another species may have found its way there from stocked dams to the East has not be substantiated. Ssentongo & Mann suggest that it may have been based on a mature *O. niloticus*, which darkens rapidly upon death and desiccation.

In January 1931 the water was green with the blue-green algae *Microcystis* and *Aphanocapsa*, with smaller quantities of diatoms and a varied zooplankton.

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1933.2.23.12–22 (holotype and paratypes)	93–246	L. Baringo	Worthington
1933.2.23.23–31	51–83	L. Baringo	Worthington
1969.7.17.84–93	170–195	L. Baringo	Mann
1980.4.18.84	110	L. Baringo	Darlington

Oreochromis niloticus sugutae subsp.n.

TYPES. Holotype: a mature male, 145 + 39 mm, from 'R. Karpeddo', collected by Sir Vivian Fuchs in 1938 (see Fuchs, 1950).

Allotype: a ripening female, 99·5 + 26·0 mm, collected by Dr M. J. Coe in 1970 at the foot of the gorge south of Kapedo township.

Paratypes: 8 of 67·0–141·5 mm SL, collected by Fuchs with the holotype; 1 of 83·5 mm SL collected by H. Money-Coutts; 16 of 62–171 mm SL collected by Coe with the allotype and the Kinyang River above its confluence with the hot springs.

Turkana name. *Kwo-ki-ni* (Coe, 1971)

Distinguishing characters

See p. 146 and Tables 34–37. The short pectoral fin (30–36% SL in adults) characterizes this population (Table 44 & Fig. 62). How unique the colour-pattern is can only be known when more comparative knowledge of neighbouring populations is available. *O. n. sugutae* shares with *O. n. vulcani* and *O. n. baringoensis* a low number of dorsal spines, and with *O. n. baringoensis* also a low average number of total dorsal rays (Table 35). Both these subspecies also have a tendency, like *O. n. sugutae* to replace the bicuspid outer teeth of mature fishes with tricuspids. The large mouth of sexually mature individuals is unique in the *niloticus* series, and would have been judged of more than subspecific importance but for the geographical and structural affinity of this population with those of Lakes Baringo and Turkana.

Description

Based on the holotype, allotype and paratypes, with some meristic characters also from a few smaller fishes. See also Tables 34–37.

Proportions as % SL. Depth of body 37·5–43·0, length of head 32·0–37·7, length of pectoral fin 28–36, of caudal peduncle 10·6–14·0; depth of caudal peduncle 14·5–15·9; length of third anal spine 13·0–16·0.

Proportions as % length of head. Length of snout 30·5–39·7, positively allometric; diameter of eye 18·5–24·0, negatively allometric; depth of preorbital bone 16·5–20·0, a little less than eye up to SL about 160 mm, when the two are approximately equal; interorbital width 31–39; length of lower jaw (28·5) 30·0–34·5 in sexually immature fishes of all sizes, but 35 and 35·7 in two nearly ripe females and 37–39 in three mature males from Kapedo Springs.

Width of lower pharyngeal 29–33, approximately equal to its length at all sizes, the blade from 0·6 to as long as the median length of the toothed area.

Caudal peduncle length/depth 0·68 to 0·9.

Teeth of jaws in 4–6 rows, 40–68 in outer row of upper jaw; outermost bicuspid, with moderately slender shafts except in two males from Kapedo in which the teeth have stouter shafts and some of them are tricuspid (like the Baringo adults), others worn or broken (Fig. 56).

Gill-rakers 18–24 on lower part of first arch. Microbranchiospines present in the usual places.

Scales on the cheek usually in 2 series, rarely 3; in lateral line series 31–33, usually 32; 4, 4½ or 5 from origin of dorsal to lateral line.

Table 43. Dorsal rays in *Oreochomis n. sugutae.*

Dorsal	XIV 12	XV 12	XV 13	XVI 12	XV 14	XVI 13	XVI 14
Frequency	1	3	9	8	1	9	1

Anal III 9–10 (III 11).

Caudal slightly emarginate or truncate; in one specimen lower rays rather densely scaled.

Genital papilla of male conical, with a subterminal pore.

Coloration. In alcohol many specimens have 9 or 10 dark vertical bars on the sides well marked, and smaller ones show also one or two blotches along the mid-line. Small Kapedo specimens may be uniformly pale. In some, the melanin forms a spot on each scale or a reticulate pattern around the scales. Soft dorsal and often anal spotted. Caudal uniformly pale, or part pale and part with faint series of spots, or with vertical stripes tending to run into a reticulum on a smaller or greater part of the fin.

In the more sexually advanced males both soft and spinous parts of dorsal with round, pearl-white spots in addition to the dark spots; lappets edged with black and notches between posterior lappets reduced. Pigment uneven on throat and chest. Pelvics and anal dark, but not pitch-black.

Life colours (from Coe, 1971): general colour of flanks and top of head greenish, darkening to red-green or brown-green in mature fishes and to brownish on the back. A well-marked opercular spot. Caudal stripes brown. In mature males operculum pink, iris with a bright red border, branchiostegal membrane yellow, chest and belly off-white, pelvics and pectorals pale yellow, anal orange-yellow with silvery spots and reddish edge; caudal with posterior two-thirds red; vertical stripes on caudal brown and green-blue; dorsal dark brown with silver-white spots on membranes.

Mature females with cheeks and operculum iridescent green; iris with dull red border, lips pinkish, throat, chest and belly white, spotted black; pectoral pale yellow, suffused pink; stripes of caudal brown on a pale ground suffused pink; pelvics pale with greenish inner border; anal brown with pale translucent patches; dorsal with fawn patches; lappets narrowly edged with brown.

Ecology

Breeding

The five specimens from the Suguta River have small, quiet gonads and have probably not bred.

Of those from Kapedo Springs, two females of 72·5 and 100 mm SL respectively, have swollen ovaries with eggs 2 mm in diameter, and three males of 130–145 mm have prominent genital papillae and in two the testes are enlarged and have the appearance of spent and partly spent gonads.

These mature specimens have enlarged jaws, more so in the males than the females, a feature that has not been noted in any other population of *O. niloticus*.

Distribution

The Suguta River and its tributary the Kinyang or Kapedo in the neighbourhood of the hot springs that feed it (Kapedo is also spelt Karpeddo). The locality has been described by Fuchs (1950) and Coe (1971), from whom the following details are taken.

Description of the locality. The Suguta River formerly belonged to the Rudolf (Turkana) basin, but its connection with the lake was cut off by Middle and Upper Pleistocene volcanic activity (Fuchs, 1950). One of its sources is believed to be fed by an underground outflow from

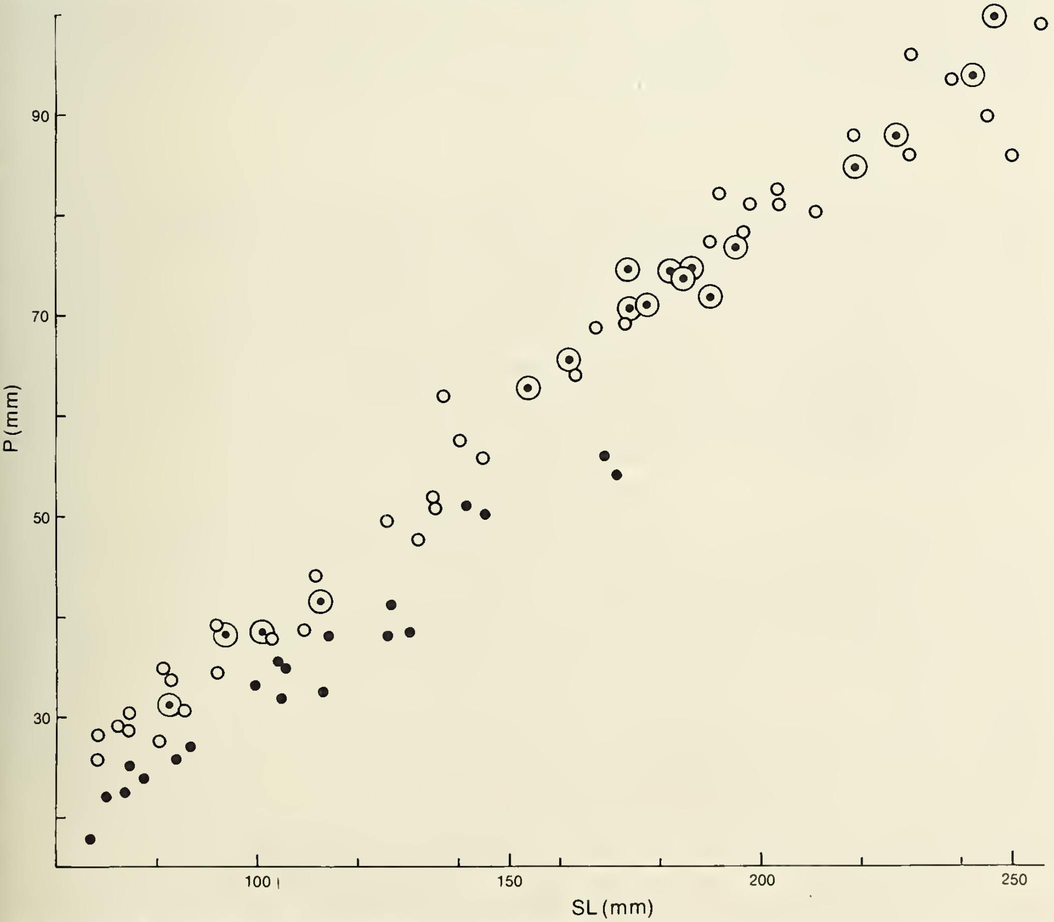

Fig. 62 Length of pectoral fin in *Oreochromis n. vulcani* (○); *O. N. baringoensis* (⊙); and *O. n. sugutae* (●). Ordinate, length of pectoral in mm. Abscissa, SL in mm. The vertical scale is twice the horizontal.

Table 44. Length of pectoral fin in *O. n. baringoensis* and *O. n. sugutae*.

	N	SL(mm)	Pectoral % SL
O. n. baringoensis	10	51–93	35·0–41·5
	13	110–246	38·8–43·2
O. n. sugutae	7	43–100	27·0–34·0
	12	104–145	30·0–36·0

Lake Baringo (Gregory, 1921:107; Beadle, 1932:179), and at Kapedo, about 32 miles (51 km) north of Lake Baringo, it receives water from hot soda springs. Within a comparatively small area this provides a diverse group of environments for fishes. At their emergence the springs are too hot for fish life. Above its confluence with the spring water the river is cooler and silt-laden; below the confluence it is warmer and more alkaline. Where Coe's collections were made it was possible for the fishes to move through waters varying in temperature and alkalinity, but 41°C was lethal and they mostly kept to water of 38°C or less.

The part of the Fuchs collection containing the holotype and other large-mouthed males was taken from water with a temperature of over 90°F (32°C), and some smaller fishes in spring water of 100°F (38°C). The allotype was from 'fresh water' (i.e. drinkable by domestic animals). Other specimens of the Coe collection were taken with the allotype or in the Kinyang River above its confluence with the hot springs.

Discussion

The large mouth of breeding fishes and the variability of the caudal markings suggest comparison with *O. spilurus*, its eastern neighbour. But, as with *O. n. baringoensis*, the higher numbers of gill-rakers and scales are characteristic of *O. niloticus*, and *O. spilurus* has fewer dorsal soft rays.

In the low numbers of dorsal spines this population contrasts more with *O. n. niloticus* than with the populations of Lakes Turkana and Baringo, and this feature is no doubt partly attributable to the historic relationship with these, especially the latter. The influence of the warm, alkaline springs in which the majority of our samples were caught cannot be overlooked; the meristic parallelism with *O. n. filoa* is obvious from Table 35.

The short pectoral fin is characteristic of this population (Table 44), and the breeding colours are different from any reported for the superspecies.

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1967.6.14.1–13 (holotype, allotype and paratypes)	31–145	Soda springs at Karpeddo, Suguta system	Fuchs and MacInnes 29–30.1.1938
1967.11.16.1–2	34, 83·5	Karpeddo	Money-Coutts, 1948 (pres. H. Copley)
1971.3.1.9–14	23·0–126·5	Karpeddo, alkaline springs	Coe (East African Rift Valley Exped'n. 1970)
1971.3.1.15–19	22–78	Karpeddo, alkaline springs that flow into NgMyang R., nr confluence with Suguta R.	Coe
1971.3.1.1–8	87–171	Suguta R. (Kinyang)	Coe

The Ecology of *Oreochromis niloticus*

The area occupied by this superspecies extends from 8°S to 32°N and from 6000 ft (1830 m) to sea level. The temperature, seasonal range of temperatures, and the chemistry of the waters cover wide ranges (see details under the subspecies and also Beadle, 1974, where further references may be found).

Food

Naguib (1954) examined contents of stomach and intestine of *O. niloticus* living in a stagnant pond near Cairo, taking samples in different months during a year. He found that in most months there was a great preponderance of plant food—blue-green algae, diatoms and parts of macrophytes—and even in one month when chironomid larvae were taken in large quantities these amounted to less than 50%. The average proportion of plant food, even including this unusual month, was 82·9%. The classic study of food and digestion in any tilapia is now that of the Moriartys and their associates (1973) on *O. niloticus eduardianus* in Lake George, Uganda. This has been summarized also by Lowe-McConnell (1975:167).

The young 'fry' are omnivorous, actively pursuing copepods, hydracarines and various insects, both aquatic larvae and terrestrial insects that fall on the water. They also ingest aufwuchs and detritus, pecking at these. Gradually they take more phytoplankton until on their reaching 6 cm TL this forms almost the entire diet, taken by gulping and selected to some degree by size in the mucus-trap mechanism and pharyngeal jaws. The phytoplankton of Lake George is dominated by the blue-green alga *Microcystis.* This and *Lyngbya* and *Melosira* were relatively more abundant in the gut contents than in the water, but the smaller *Synedra* and *Anabaenopsis* were less so.

The membranes of diatoms may be lysed in a medium of lower acidity than is required for blue-green algae, and Moriarty (1973) has demonstrated clearly that at the beginning of a feeding period, when the stomach is contracted, the food passes almost directly from the oesophagus to the pyloric end of the stomach and is exposed to secretions of pH no lower than 2, and at this level for a short period only. This is sufficient to break down the membranes of diatoms, but blue-greens and the green alga *Chlorella* taken at this period pass through the intestine undigested. When the stomach has expanded and the food can spend some time in the fundus of the stomach, which at that time offers a medium of pH 1·4, the membranes of the blue-green algae are also destroyed and the intestinal enzymes are able to make efficient use of the bulk of the phytoplankton. Moriarty & Moriarty (1973) calculated that the average proportion of carbon assimilated from Lake George phytoplankton by *O. niloticus* (in the laboratory) during a 24-hour day was about 43% of the total ingested.

Feeding in Lake George is a day-time activity, beginning a little before dawn and ending at sunset, and digestion is usually completed about two hours after midnight. The earlier reports (Fish, 1955) that *Microcystis* was not digested were due to the fact that the diel rhythm was not appreciated. Also there is a resemblance between the bottom deposits in Lake George and the digested matter in the lower intestine, which deceived earlier observers into the belief that the bottom deposits were the source of the food.

Harbott (1975) used the methods of the Moriartys to study the feeding of *O. niloticus* in Lake Turkana (Rudolf). Earlier studies by Fish (1955), and Lowe-McConnell (1958), had found the *O. niloticus* in this lake able to digest blue-green algae, which there formed the bulk of the phytoplankton. Harbott found that the pH of the stomach secretions in *O. n. vulcani* did not fall below 2·5, and he assumed that some cells stay long enough in the stomach for lysis to occur at this level. Nevertheless some of the blue-green algal cells reached the rectal region of the gut unharmed, whereas diatoms, protozoa and invertebrates were digested. Harbott reported a diel feeding rhythm, which was shorter than in Lake George; for fishes of the size comparable with the Lake George samples feeding took place from 08.00 to 14.15 hrs; for larger fishes it was longer, starting at 05.00 hrs and continuing until between 16.00 and 18.00. Since the weight per unit length was as high as in Lake George*, Harbott concluded that assimilation efficiency must be greater in the Lake Turkana population.

The food resources of the many and diverse waters inhabited by *O. niloticus* are varied. Nowhere is the plankton more dense than in Lake George, and we have seen that the population of this lake and Lake Edward is characterized by a finer pharyngeal dentition. It cannot therefore be assumed that the different reports of the food of other populations are wholly due to the less detailed nature of the studies.

Lowe-McConnell (1958, Table 1) listed the food in several East African waters in which the species either occurs naturally or is introduced. Epiphytic diatoms were the main food in Lake Albert, phytoplankton in Lake Edward, but this author (in 1958) followed Fish (1955) in his mistaken opinion that the main food in Lake George came from the flocculent bottom deposits. In the small lakes and dams to which it had been introduced, where the water was opaque with planktonic algae, the plankton was the source of food; where the water was clear *O. niloticus* turned to epiphytic growths and benthic algae. In Lake Kivu nanoplankton and the planktonic bacterium *Spirillum* formed its food for the greater part of the year.

In the shrinking alkaline lagoon at Buhuku, Lake Albert, where the plankton in 1950 was almost entirely composed of *Microcystis*, *O. niloticus* was stated to be feeding on the bottom mud, but was thin and sickly (Lowe-McConnell, 1958, figs 1 & 3).

In the delta lakes of the Nile, Wunder reported (1960:13) that it feeds on epiphytic algae as well as coarse plant material in process of natural disintegration. Occasionally isolated chironomids were present in the gut. In the Nile *O. niloticus* is rare in the deep parts and favours weedy canals. Wunder noticed that it approached *T. zillii* in both diet and dentition, which is coarser than in *O. aureus* and *S. galilaeus*.

In the middle Niger Daget (1954) found that it utilizes phytoplankton as well as getting nourishment from the bottom mud, and he also listed it among species destructive to young rice plants.

The formation of barrage lakes in the Niger at Kainji, and in the Volta has resulted in an increased abundance of tilapias, especially *O. niloticus*, which Petr (1967; see also Lawson *et al.*, 1969) says prefers phytoplankton and planktonic detritus, although it will also feed on higher plants and periphyton. It is the dominant fish species in places where trees and shrubs have been submerged, and it flourishes in pools and oxbow lakes left by the retreating rivers in the dry season, in which the algal biomass is very high (Banks *et al.* 1965). At Kainji this species is also found in the swampy, flooded grasslands in the wet season, in contrast to *S. galilaeus*.

Worthington & Ricardo (1936) examined nine stomachs of *O. n. baringoensis* and found them all to contain phytoplankton, mostly *Microcystis* and *Botryococcus*, with rotifers and parts of Cladocera.

In conclusion, *O. niloticus* is capable of using a wide range of food materials, but from a total length of about 5 cm is almost entirely herbivorous. Although macrophytes are not its typical food, these form part of its diet in certain waters. Where, however, phytoplankton is abundant this forms the bulk of its diet, as in Lakes George and Turkana. The extreme of microphagy is encountered in Lake Kivu, where the bacterium *Spirillum* is reported to be its staple food. The different emphasis on possible food items is reflected in the relative coarseness or fineness of the pharyngeal dentition and to some extent also of the teeth of the jaws.

Growth and condition

Growth studies have been made on the populations of the Nile delta lakes (Jensen, 1958; Elster & Vollenweider, 1961; El-Zarka *et al.*, 1970), in the Sudan (Mahdi *et al.*, 1973), at Kainji, Niger

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*Harbott (1975:36) says 'higher', but the regression line of his fig. 2 is very close to that of fig. 3 of Lowe-McConnell for the species in Lake George.

Table 45. Total length in mm at end of each year of life in samples of populations of *O. niloticus* from the Nile. Numbers in brackets are the numbers of specimens used. Figures taken from Jensen (1958), El-Zarka *et al.* (1970) and Mahdi *et al.* (1973; the catches used by Mahdi *et al.* included no fishes of age-group I). and from Payne & Collinson (1983). The lengths recorded for Lake Mariut are calculated averages.

	L1	L2	L3	L4	L5
Noussa Hydrodrome (Jensen)	92·0 (238)	205 (207)	257 (200)	288 (191)	307 (131)
Mariut (El-Zarka *et al.*)	83·7	211·9 (141)	291·9 (73)	326·9 (14)	375·9 (2)
Sudan (Mahdi *et al.*)		255–275	285–325	345–415	425–525
L. Nasser (Payne & Collinson)	79	222	261	357	418

Table 46. *Oreochromis niloticus.* Comparison of weight/length relationship in different waters. Selected figures from Lowe-McConnell (1958, table II) and, for the Niger, from Daget (1954:343). Numbers in brackets give the number of specimens on which the average was based.

			Weight (g)		
TL (cm)	L. Turkana	L. George	L. Edward	L. Albert	Niger
28	500(1)	471(16)	—	414(3)	—
30	—	578(16)	612(5)	517(2)	—
30·5	—	—	—	—	535(1)
31	600(1)	649(31)	636(20)	—	—
35	—	930(40)	902(8)	836(1)	845(5)
37	1100(2)	1086(18)	—	944(2)	1065(4)
40	—	1474(3)	—	1247(1)	1190(1)
40·5	—	—	—	—	1340(1)
42	1700(1)	—	—	1568(3)	—
42·5	—	—	—	—	1630(1)
56	4725(2)	—	—	—	—
61	5100(1)	—	—	—	—

River (Banks *et al.*, 1965), in Lake George (Lowe-McConnell, 1958:151; Gwahaba, 1973, 1978), and on the introduced population in Lake Victoria (Rinne, 1975). Some of these results are summarized in Table 45.

In Lakes Mariout and Menzaleh of the Nile delta, at about 32°N latitude, and in the Sudan at about 22°N the seasons are well enough marked to register annual growth changes on the scales. At Kainji, about 10°N, and the Sokoto River, rings were laid down in the scales, but not all individuals laid down a single ring each year, and Banks *et al.* concluded that this is probably the lowest latitude at which an annual growth rhythm is registered on the scales of fishes, at least in West Africa.

At the Equator other methods than scale-reading have been used. A marking experiment enabled Lowe-McConnell (1958) to estimate that in Lake George an individual of 23 cm TL would add 9–10 cm in a year, and on this basis the average length of sexual maturity (28 cm) would be reached at 2 years of age. Although in Lake George there is no well-defined breeding season, cohorts of young are produced in peaks of breeding activity, and these enabled Gwahaba (1978) to use length frequency analysis to estimate growth rate. The growth in length was faster in the young and diminished from TL 10 cm, leading to a TL of about 25 cm in 2 years.

For Lake Victoria, Rinne (1975) extrapolated from the growth per month added by tagged and recaptured fishes during a few months of freedom. He found *O. niloticus* capable of growing to 16 cm in the first year of its life, 24 cm by the end of the second year and 30 cm at the end of the third. These lengths are close to those obtained by Mahdi *et al.* in the Sudan.

Growth rates and sizes in stocked lakelets, dams and ponds vary as in other species. In a pond at Kajansi, Uganda, the species reached 17 cm (98 g) in 7–8 months and was then sexually mature (Lowe-McConnell, 1958).

In this species Lowe-McConnell (1958, fig. 4) reported no evidence of differential growth in the sexes in the Great Lakes, but at Kainji, River Niger, Banks *et al.* (1965, fig. 11) found both growth rate and maximum size to be higher in males, males reaching a maximum of 42·0 cm and females 32·8. Also Lowe-McConnell found that males grew larger than females in two populations where the fishes were in poor condition and breeding at a small size, namely in Buhuku Lagoon (Lake Albert) and a pond at Kajansi. Bard (1962*b*) reported the same in ponds in Cameroon.

The maximum size of 64 cm TL is that recorded by Worthington & Ricardo (1936) and Lowe-McConnell (1958) for the Lake Turkana population (*O. n. vulcani*), but the weight for length (condition) of this population is the same as that for Lake George (Lowe-McConnell, 1958, fig. 3; Harbott, 1975, fig. 2). Nevertheless, subpopulations of *O. n. vulcani* show that growth (or maximum size) is dependent as elsewhere on external conditions. Examples are the dwarf populations recorded by Worthington & Ricardo in a lagoon on Ferguson Spit and in Crater Lake C on Central Island, and the population of a stream fed by hot springs and entering Lake Turkana at Loiengalani on its eastern shore (see p. 176).

In comparison with the values for Lake George, Lowe-McConnell's figures for a smaller sample from Lake Albert are a little lower and about equal to weights given by Daget (1954:343) for the species in the Middle Niger.

The introduced population in Lakes Victoria and Kyoga evidently grows well. Okedi (1971) recorded weights of 4–7 kg in Lake Kyoga.

In Lake Mariout (El-Zarka *et al.*, 1970) only small fishes were found in abundance, but at 28–35 cm TL their weights were about the same as those in Lake Albert and the Niger. Botros (1979) also recorded the condition factor in Lake Mariout, finding it to diminish between TL 18 and 30 cm. He attributed this to the fact that sexual maturity is attained in this population towards the end of the first year of life.

Maximum sizes and sizes of sexual maturity vary and are related, as shown by Table 1 of Lowe-McConnell (1958) and the selected figures of Table 47 herewith. Figure 63, taken from Lowe-McConnell, shows a correlation between the size of sexual maturity and the condition of the fish as indicated by its weight at TL 20 cm. Whether the relationship is a causal one, or whether both a poor condition and early maturity are the result of a third factor (e.g. stress), requires further investigation.

The population of Lake Baringo (*O. n. baringoensis*) has a low maximum size of TL 36 cm and maturity is attained at 18 cm (Ssentongo & Mann, 1971).

Salinity tolerance

Fishelson (1980) states that mortality of *O. niloticus* in hypertonic water was much higher than in *S. galilaeus*, *O. aureus* and *Tilapia zillii*, although hybrids with *S. aureus* were able to live in very saline ponds.

Temperature tolerance

Experiments on the resistance of *O. niloticus* to high temperatures were conducted by Bishai

Table 47. Examples of maximum recorded length and length at maturity in samples of populations of *O. niloticus*, taken from Lowe-McConnell (1958, table I), Wanjala & Marten (Lake Victoria), Ssentongo & Mann (1971; Lake Baringo) and (Loyengalani) from specimens in the BMNH.

	Max. TL	TL at maturity
L. George	40	28
L. Albert (open water)	42	28
Buhuku Lagoon, L. Albert	♂ 26	14
	♀ 23	12
L. Edward	36	25
L. Victoria (introduced)	——	24
L. Turkana (Rudolf)	63	39
Stream at Loyengalani (L. Turkana basin)	♂ 12	12
	♀ 9·5	8
L. Baringo	36	18

(1965). The upper lethal temperature was determined by increases of 1°C per day and, although varying according to age and acclimatization procedure, permitted no increase above 39–40°C. The resistance of both post-larvae (13–32 mm) and adults (over 90 mm TL) was less than that of juveniles between these sizes, and the median resistance time of the post-larvae was less than that of adults. The resistance time of the juveniles was also affected by the increase of acclimatization time up to 35°C, whereas that of the post-larvae was not. When however, acclimatization temperature was raised above 35°C both post-larvae and juveniles had their median resistance time increased.

Some doubt must hang over the identity of the species used at this date, and the '*Tilapia nilotica*' of McBay's experiments (1961) was certainly *O. aureus*.

The springs in which *O. n. sugutae* was collected registered temperatures of 90–100°F (33–38°C) (Coe, pers. commn, 1970), see p. 181.

Breeding

In *O. n. niloticus* of the Nile delta El-Zarka *et al.* (1970:195) state that there is no marked external difference between males and females, both sexes at breeding time having a prevailing red flush on the belly and lower flanks, although this is brighter in the male. Payne (pers. commn) confirms this. In Israel the contrast is unmistakable and C. L. Boulenger (1908) also observed the red flush of the male. In full breeding condition this also covers the back and dorsal and caudal fins, where it blends with the characteristic black markings to give them a dark purple colour. Pelvics may be tinged with black. Never are the margins of dorsal and caudal fins bright red as in many other species, including the sympatric *O. aureus*. A red or pink caudal margin has been recorded for *O. n. sugutae* and for some *O. n. vulcani* (p. 170), but not for other populations.

In *O. n. eduardianus* of Lakes Edward/George and Albert, as well as the red flush, the lower parts of head and body and the dorsal pelvic and anal fins become black in breeding males (Lowe-McConnell, 1958; Greenwood, 1958 & 1966). In some Ruanda lakes where it has been introduced the whole fish may become black (Thys, pers. commn).

In *O. n. cancellatus* males may become black on the throat and lower fins, and in Lake Langano they may be uniformly dark. The latter is also true of males in Lake Turkana, especially in Crater-lake A of Central Island, where body and fins are intensely blue-black.

Because of differential movements of the sexes, the *sex ratio* can be reliably judged only from a whole population. Lowe-McConnell (1958) had such an opportunity when a pond was drained at Kajansi, revealing twice as many males as females. This may, however, indicate differential survival.

Breeding season. With its wide distribution, *O. niloticus* well illustrates the dependence of breeding cycle on latitude.

In Israel near Tel Aviv *O. n. niloticus*, in common with other cichlids breeds in April–May. At this time, the winter with its rains is over and the temperature is rising. No data on the histology of the gonad cycle have so far been recorded from this region, the northern limit of distribution of the species. (Ben Tuvia's observations on the '*T. nilotica*' of Lake Tiberias were made before it was realised that all or most of the supposed *nilotica* in this lake were *O. aureus.*)

In the Nile delta spawning occurs from April to August, with the peak in May, when ripe fishes constitute 33·5% 'of the catch', and June, when they are 21·9% (El-Zarka *et al.*, 1970:195). In April spawning starts when the air temperature rises to 19°C. In May the temperature averages 21·6°, in June 23·8°. During July and August it rises still higher, but spawning decreases. From September to March these authors observed no spawning in Lake Mariut except a few isolated cases in January.

In Lake Nasser (lat. 22–24°N) the breeding season is more extended and the gonadosomatic index showed two peaks, for females in April and September, for males March and September (Latif & Rashid, 1972). The testes are adapted to a wide breeding season, having a reserve of spermatogonia ready for the following cycle or a later stage of the same cycle (Latif & Saady, 1973*a*). Viable spermatozoa were found in February, in advance of the breeding season. In the female, oogonia are dividing in September. Only in January and July were no fishes found with eggs of diameter more than 2 mm, in February, June and August only 6–9% of females over 30 cm, in other months 17–60% (60% in September, 36% in May, 33% in April).

Holden (quoted by Lowe-McConnell, 1958:153) recorded that in Northern Nigeria (about 12°N) breeding takes place in the flood season, here June-July, and Banks *et al.* (1965) give the same season, but probably a more extended period, at Kainji (about 10°N). Farther south in Nigeria breeding is not restricted to one season (Holden, unpubl., quoted by Lowe-McConnell and by Banks *et al.*).

In *O. n. eduardianus*, living in equatorial waters, breeding individuals are found all the year round, but in Lake Victoria catches of the species are smaller in the dry months of June and July. From this fact, by analogy with *O. esculentus*, Lowe-McConnell's (1958) tentative conclusion was that the species forms denser inshore aggregations, probably for spawning and brooding, in rainy periods. Gwahaba (1978) found breeding intensified in the wetter months in Lake George.

Some data on *age and size of sexual maturity* are given in the section on growth (p. 186) Table 47 & Fig. 63), where it is noted that the size of maturity is related to the maximum size attained in a given population and also apparently to the condition of the fishes. There are other examples where condition does not seem to be involved. Fig 64, taken from Gwahaba (1973), shows that in Lake George in 1960 (as also recorded earlier by Lowe-McConnell) it was not until the females reached TL 28 cm that 100% of them were mature, whereas in 1971–2 there were no immature females above TL 24 cm. Gwahaba was inclined to explain this as the result of increased fishing intensity between the two surveys and suggested that the removal of the bigger fishes before they had bred had resulted in selection for early breeding and dwarfing. This is the only suggestion to my knowledge that a genetic factor might be involved in the age and size of maturity, and is against evidence from other populations of *O. niloticus* and other species of *Oreochromis*.

The subpopulation of Buhuku Lagoon in Lake Albert was in 1929 and 1950 an example of early breeding linked with poor condition (Table 47), females being mature at 12 cm, males at 14 cm. But the dwarf breeding fishes of the thermal waters at Loiengalani, Filoa and Suguta did not appear to be in poor condition.

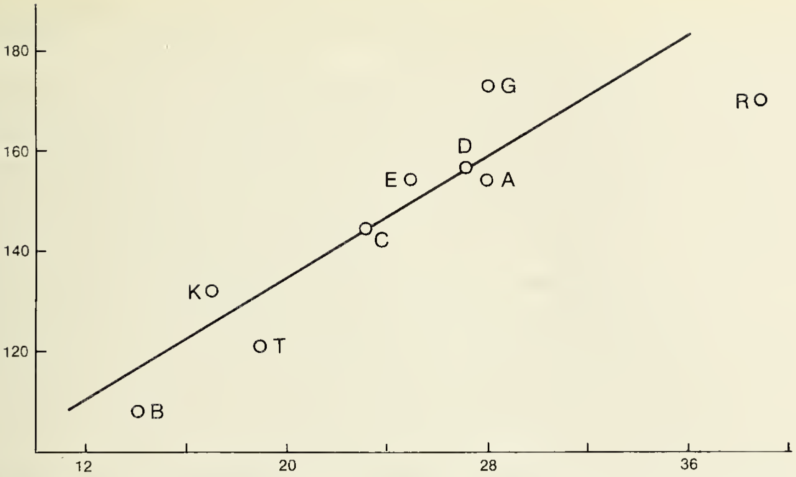

Fig. 63 *Oreochromis niloticus.* Relation between length at sexual maturity and condition as indicated by weight at 20 cm TL. From Lowe-McConnell, 1958, fig. 5. Samples from Buhuku Lagoon (B), Chanagwora (C), Lake Katinda (D), Lake Edward (E), Lake George (G), Lake Kijanebalola (K), Lake Turkana = Rudolf (R), Tonya Lagoon (S), Lake Albert (T). Ordinate: mean weight in grams of fish at 20 cm TL, abscissa: maturation size (cm).

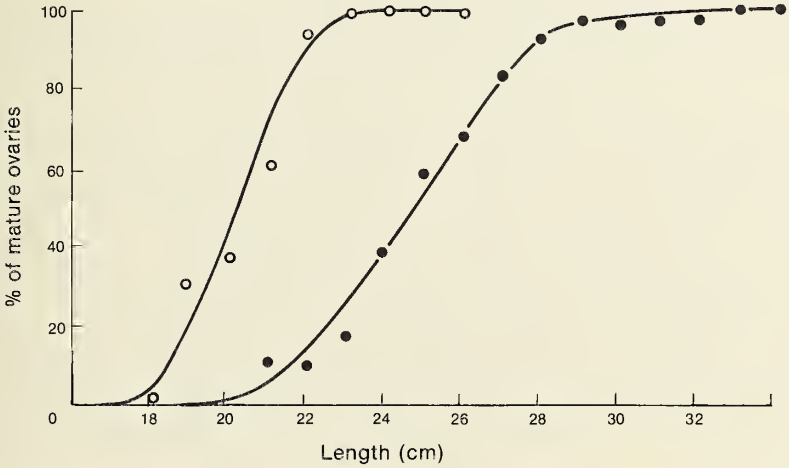

Fig. 64 *Oreochromis niloticus.* Length at sexual maturity in Lake George in 1960 (●) and 1971–72 (○). From Gwahaba, 1973, fig. 3.

Experimental control of reproduction by hormones has been tried by Babiker & Ibrahim (1979).

Nest and spawning locality. The nest is a circular depression up to 1 m in diameter and half a meter deep (C. L. Boulenger, 1908; Pruginin, pers. commn), or of diameter about twice the length of the male making it (Lowe-McConnell, 1958). It is made in firm sand in water from 0·6 to 2 m deep, a situation also preferred in Lake Baringo (Worthington & Ricardo, 1936) and Lake Victoria (Welcomme, 1967*b*), although Welcomme found ripe individuals also in muddy fringing lagoons.

In Lake Kivu such localities are rare, and ripe males and brooding females have been caught in one school off a steep lava shore (Lowe-McConnell). Elsewhere females carrying young or eggs in the mouth seem to frequent swampy shores. In Lake George's shallow, opaque waters there is said to be little segregation of the sexes.

The gross *appearance of ovaries and testes* at different stages has been described by Babikar & Ibrahim (1979*a*), and their microscopic appearance, oogenesis and spermatogenesis by Latif & Rashid (1972) and Latif & Saady (1973*a* & *b*).

The ripe egg is yellow and pear-shaped. Lowe-McConnell (1955*c*) reported the maximum size of ripe eggs observed by her to be 4·3×3·7 mm (from a fish of TL 29 cm), the minimum 2·8×2·5 mm (from a 57 mm fish). This says nothing about the average size in the respective fishes. Peters (1963*b*) found that in other species this increases with the size of the fish, and among five *O. niloticus* examined by him the only egg-weight less than 5 mg was obtained from females weighing less than 50 g. Bauer (1968:48) gave a range of 2·1–3·1 mm, not of the long diameter, but of half the sum of long and short diameters. Daget (1954) gave dimensions of 2·3×1·9 mm. Personal observations of eggs in the mouths of museum specimens are: from five of 232–282 mm SL from the White Nile, Blue Nile and Lakes Edward and Albert 3·0–3·4×2·2–2·5 mm; from a female of 89 mm SL from Buhuku Lagoon, Lake Albert, eggs of long diameter 3·4 mm. Two females from Lake Baringo contain loose ovarian eggs of 3·4×2·2–2·5 mm.

The largest ovarian egg observed by Latif & Rashid in *O. niloticus* of Lake Nasser measured 2·95 mm (average of long and short diameters). Babiker & Ibrahim (1979*a*) found that the size of ripe eggs varied individually, but that this bore no relation to the weight of the whole ovary, a result not inconsistent with the finding of Peters (1959, 1963*b*) that the number of eggs is inversely related to the average egg-weight in the ovary.

In February and August, the months preceding the peak gonadosomatic indices in Lake Nasser, Latif & Rashid found up to seven sizes of eggs or oocytes in an ovary. Although eggs, even of whole batches, may be resorbed, this indicates the possibility of several spawnings in a season.

Lowe-McConnell (1955*c*) counted ripe ovarian eggs in several fishes and obtained numbers ranging from 340 in a fish of 17 cm TL to 3706 in one of 57 cm. Monod's (1949) figure of 3260 in a 35 cm West African fish accords with this range. A maturing female of 75 mm SL from a stream in the Lake Turkana basin contained about 106 ovarian eggs of 2·5 mm.

Worthington (Worthington & Ricardo, 1936:379) observed in Lake Turkana circular schools of diameter about 3–4 m in which several hundred fishes swam round and round in the same direction. The spawning behaviour in an aquarium has been described by Lowe-McConnell (1958:155), Fishelson (1962) and Heinrich (1967*a*:712). Fishelson and Heinrich described the gathering in a school of (or including) ripe females at the surface above the mating territories of the males, and related that from time to time a female would come down to spawn with a male. It was probably this phase that was observed by Worthington (cf. also *O. lidole*, p. 478 and *O. squamipinnis*, p. 476–7). No lasting pair-bond is formed. When the female is accepted by a male both partners engage in throwing out sand and cleaning the nest, and both reciprocally perform the 'T-stand', a position that appears more functional when the female combines it with snapping at the sperm-laden water. Even by the female, however, the two activities are not necessarily combined. The eggs are laid in about 20 batches, during a period of 45 minutes to 2 hours, but about half of them are laid in the first four batches. They are picked up by the female as they are laid, before, during or after fertilization.

The feeding instinct of the male is inhibited immediately before and during the spawning act, but is quickly resumed afterwards. This appears to present a problem if a male is immediately visited by a second ripe female, and Heinrich observed in three such cases that a T-stand on the part of the male resulted in his taking the eggs into his mouth as they were laid. They were then either swallowed or, in one case, retained in the mouth. This male retained the eggs for eight days although examination showed that they were unfertilized. This observation suggests that such a mismatching of the phases of the partners may account for some of the rare instances of finding eggs in the mouth of a male of a maternal mouth-brooder in nature. El Zarka *et al.* (1970) record that in Lake Mariut both sexes mouth-brood but more often the female.

DEVELOPMENT. Nussbaum & Chervinsky (1968) succeeded in rearing eggs after removing them from the maternal mouth at the stage of the closure of the blastophore. The females used were pond-bred descendants of Lake Turkana stock. At 'stage 16' the retinal pigment was already developed. Pectoral fin-buds appeared at stage 21 when the head was about 1 mm long; the mouth opened at stage 24 (head 2 mm); the yolk-sac was fully absorbed at stage 28. When development took place at 37°C, this stage was reached on the 8th day after removal from the mouth, but at 27°C the larva had not got beyond stage 26 at this time, with the yolk-sac small but still evident.

O. niloticus was one of the species in which Peters (1965) and Peters & Berns (1978) demonstrated that rudimentary, non-functional adhesive glands, corresponding to the functional glands of *Tilapia* and other substrate-brooders, made a brief appearance on the 3rd and 4th days of development and then regressed. Fishelson (1966) also investigated developmental stages of *O. niloticus*, comparing them with the same stages in *Tilapia tholloni* and *S. melanotheron* ('*macrocephala*'). The caudal network of blood vessels, which in *Tilapia* is the main larval respiratory organ, is less developed and of shorter duration in both mouth-brooders and the network of vessels on the surface of the yolk functions for oxygenation of the blood as well as for supplying food from the yolk for development. The water surrounding the yolk is kept in motion by fanning movements of the pectoral fins when these develop; this corresponds functionally to the caudal movements of substrate-brooded larvae.

The bigger egg (compared with *Tilapia*) results in a longer period of dependence on the yolk for food and a postponement of independent life. This relationship also obtains between mouth-brooders with different sizes of eggs, *O. niloticus* holding a position intermediate between *Tilapia* and *S. melanotheron* corresponding to the intermediate size of its egg. Fishelson (1966) has demonstrated this in almost every detail of development, summing it graphically in his fig. 66.

Dambach (1963) and Bauer (1968) investigated the development of behaviour in the young of this species for comparison with *Tilapia* and *S. melanotheron.* Dambach demonstrated a schooling reaction among the postlarvae which is independent of the parent-offspring reaction, although reinforced by it. Bauer studied the contact behaviour of extra-orally reared young to the parent or to surrogate parents in the form of dark or transparent spheres. He found that in *O. niloticus* this was at its maximum just before or at the time at which release from the mouth would have been due. At 27°C this was at about the 11th day after spawning.

The maximum size of young found by Lowe-McConnell (1955*c*) in the maternal mouth was 13·5 mm TL; the yolk was then absorbed. According to Fishelson (1966) this length is reached only on the 21st day after hatching in young reared extra-orally at 27°C, but it is possible that the young observed by Lowe-McConnell may have returned temporarily to the mouth. Bauer records that in extra-orally reared young at 27°C the contact reaction to the surrogate mother is retained, though weakened, for 38 days or more after hatching.

Hybrids

Hybrids have been obtained for two purposes: by Peters and his associates, Bauer and Heinrich (see Bauer, 1968:27–31), in order to identify genetically based components of behaviour patterns; and by Israeli fish-culturists (for a summary see Mires, 1977), in order to obtain all-male broods and so to avoid precocious breeding in ponds with its unfavourable effect on growth.

The former group used the method of artificial fertilization. Successful crosses, extending to the second filial generation were obtained between *O. niloticus* and *S. melanotheron*, but back-crossings between F_1 individuals and the parent species seldom survived to hatching and then only for a short time. The reciprocal cross produced a successful F_1, but no F_2. The same experimenters even succeeded in growing hybrids of *O. niloticus* ♂ and *Tilapia tholloni* ♀, but the F_1 consisted entirely of females. The reciprocal cross resulted in high mortality of embryos.

Considering the distant relationship of the species involved, the positive results were surprising and a tribute to the technique of the Tübingen laboratory. The results support the degrees of relationship estimated from structural and behavioural data.

In Bauer's experiments the duration of contact behaviour of young hybrid *O. niloticus* ♂ ~ *S. melanotheron* ♀ towards surrogate parents was partly intermediate between that of the parent species, partly resembled one parent or the other. It was therefore not entirely dependent on the size of the egg, and Bauer concluded that a genetically controlled factor was at work, Heinrich (1967, fig. 51) also found that in the same cross, the sum of the fertilizing movements was intermediate between that of the parent species, although the number of spawning movements made by the females more closely resembled that in *S. melanotheron.*

Fishelson (1962) put *O. niloticus* ♀ and *O. aureus* ♂ together in one tank and obtained an all-male brood. Following this, experimental and commercial hybridization has been continued. A summary of the results to that date was given by Mires (1977). Experimenters with *O. niloticus* and *O. aureus* determined that the normal sex-ratio in broods of each species separately was approximately 1:1.

Pruginin (1965 & 1969) made the following crosses involving *O. niloticus* at Kajansi, Uganda.

♂	♀	% ♂s in F_1	No. of fishes
O. leucostictus	*O. niloticus*	94	160
O. hornorum	*O. niloticus*	100	?
O. niloticus	*O. hornorum*	75	200
O. aureus	*O. niloticus*	100	400
O. s. niger	*O. niloticus*	85	206
O. hornorum	*O. n. vulcani*	98·2	219

Mires (1977) adds that Pruginin obtained an approximately 1:1 ratio in crosses (both ways) between *O. mossambicus* from South Africa and *O. niloticus.* In these experiments the stock of *O. niloticus* was from Lake Albert.

Later in Israel, Pruginin *et al.* (1975) reported further experiments with male *O. aureus* and females of *O. niloticus* stock originally from Lake George (*O. n. eduardianus*) and Lake Turkana (*O. n. vulcani*). The Lake George stock gave in various single-pair matings with *O. aureus* broods of 96–100% ♂s; the *O. n. vulcani* 90–98% from several trials, but not a single brood of 100%.

Multiple spawnings in ponds were then tried with both stocks. From the *O. n. eduardianus* the experimenters chose for this purpose the offspring only of mothers that in the single pair matings had given all-male broods. These mothers were remated with unselected ♂ O. niloticus and their female offspring continued to give all-male broods when mated with male *O. aureus.*

The *O. n. vulcani*, however, gave in ponds such discrepant results (52–63% ♂) that infiltration of cross-bred fishes was suspected. Chervinski (1967) had earlier made the same cross at Dor and obtained 82% males.

These results must be considered in the light of electrophoretic analyses of proteins reported by two members of the same team in collaboration with Avtalion (Avtalion *et al.*, 1976), who came to the conclusion that the amount of polymorphism revealed in the electropherograms of their stock of '*Tilapia niloticus*' indicated that it was not pure. Contamination by cross-breeding with *O. aureus* was implied. They were satisfied with the purity of part of their stock of *O. n. vulcani*, but another part was suspect.

Lessent (1968) crossed *O. niloticus* from the Upper Volta with *O. (Ny.) macrochir* stock originating from Shaba, Zaire. When the female was *O. niloticus* there was an all-male F_1. The reciprocal cross gave 75% males. See also p. 451.

Altogether males of four species mated with female *O. niloticus* have given F_1 of 100% males. These are *O. aureus*, *O. u. hornorum*, *O. variabilis* and *O. macrochir.* In at least three of these the reciprocal cross produced 75% males. This is a result similar to that produced in Malacca with *O. u. hornorum* and *O. mossambicus* (Hickling, 1960), and analyzed with a theoretical explanation (based on the conclusions of Haldane, 1922) by Chen (1969) and Chen & Tsuyuki (1970). This postulates that in *O. u. hornorum* the male is the homogametic sex, in *O. mossambicus* the female, and further that the male-determining genes of *O. u. hornorum* are 'stronger' than the female-determining genes of *O. mossambicus*. The results of some of their back-crosses were, however, not explained by this theory. Jalabert *et al.* (1971) found similar difficulties in explaining the back-crosses from the *O. niloticus* ~ *O. macrochir* hybrids of Lessent (1968) at Bouake, and they suggested that there might be some autosomal influence.

Avtalion & Hammerman (1978) and Hammerman & Avtalion (1979) elaborated a theory on these lines that would explain all the known results of Chen & Tsuyuki (1970), Lessent (1968) and Pruginin *et al.* (1975) and they proposed further genetical experiments to test it.

The experiments reported by Lessent (1968) and by Jalabert *et al.* (1970) were prompted by observations on introduced populations in Lake Itasy, Madagascar, and confirmed the interpretation by Moreau of the changes in this population as the result of hybridization between *O. macrochir* and *O. niloticus*. See pages 451–452 of the present volume, and the reports of Moreau (1979) and Daget & Moreau (1981).

From the taxonomic point of view, the small difference between the mating performance of *O. n. eduardianus* and *O. n. vulcani*, if it can be confirmed, reinforces the subspecific status given to these on structural grounds.

Oreochromis aureus (Steindachner)

Chromis aureus Steindachner, 1864:229, pl. 8, fig. 5 (West Africa).

Tilapia aurea; Trewavas, 1966*a*:259, figs 1a & b, 3–5 (not fig. 2) (Israel, Lower Nile, West Africa); *idem*, 1966*d*; Chervinsky, 1965:703 (sexual dimorphism); Fishelson, 1967:figs 2–6, 14 (breeding in Israel); Chervinski, 1968:157 ff. (population characteristics); Fishelson & Popper, 1968:244 (hybrids, salinity tolerance); Loya & Fishelson, 1969 (same); Yashouv, 1969 (culture, hybrids); Chervinsky, 1971 (sexual dimorphism); Mires, 1969 (culture); Hines *et al.*, 1971; Holden & Reid, 1972:51, fig. 65; Goldstein, 1973: fig. on p. 229; Avtalion *et al.*, 1976 (electrophoretic specific marker); Avtalion & Mires, 1976 (electrophoretic detection of pseudohermaphroditism); Bayne *et al.*, 1976 (feeding in ponds); Boyd, 1976 (culture); Stanley & Jones, 1976 (*Spirulina* as pond food); Mires, 1977 (culture and hybrids); Herzberg, 1978 (chemistry of surface mucus).

Sarotherodon aureus (or *aureum*); Trewavas, 1973:23; Mayland 1978:30; Ben-Tuvia, 1978:422, pl. 47.

Oreochromis aureus; Trewavas, 1981*a* & *b*; 1982*a* & *b*, addendum; Schoenen, 1982.

Chromis niloticus (or *nilotica*) (non. Linn.); Günther, 1865:490 (Ain Fashka; L. Tiberias); Steindachner, 1870:964 (part West Africa); Sauvage, 1880:211 (L. Mareotis, excl. two of 75 mm); Lortet, 1883:137 (L. Tiberias; the fig. of pl. 7 is probably composite of *O. aureus* & *O. niloticus*); Tristram, 1884:164.

Tilapia nilotica (part); Boulenger, 1889:112; *idem*, 1907:523 (Nile delta, specimens with 15 or 16 dorsal spines only, referred to on p. 527); *idem*, 1915:162; Pellegrin, 1904:309; Trewavas, 1942:528 (Jordan Valley, not the Jaffa specimens).

Tilapia nilotica (non Linn.); Trewavas in Washbourn & Jones, 1938:556 (L. Hula); Tortonese, 1938:43 (R. Jordan, record only), Ben Tuvia, 1960:169, fig. 10 (L. Tiberias, L. Hula, bionomics); Chimitz, 1957:19 (Asraq); McBay, 1961 (bionomics in Alabama).

Tilapia nilotica var. x, El Zarka *et al.*, 1970:161, 162, 166 (Nile delta).

Tilapia affinis (part, synonym *C. aureus* only); Boulenger, 1889:127.

Tilapia melanopleura (part, synonym *C. aureus* only); Pellegrin, 1904:329; Boulenger, 1915:190.

Tilapia nilotica exul Steinitz, 1951*a*:531; *idem*, 1951*b*:514 (Ein Fashka).

Tilapia aurea exul; Trewavas, 1966*a*:271.

Tilapia monodi Daget, 1954:344, fig. 132 (Middle Niger & Senegal); Blache *et al.*, 1964:241, fig. 133 (L. Chad). Daget & Stauch, 1963:103 (Upper Benue).

Tilapia lemassoni Blache & Miton, 1960:217 (Lower Logone & Lower Shari); Blache *et al.*, 1964:242, fig. 134.

Tilapia kacherbi (nomen nudum) Wunder, 1960:13 (Egypt)

Tilapia kashabi (nomen nudum) Elster & Vollenweider, 1961:286 (Egypt).
Tilapia sp. ('blue'), Fishelson, 1962:2, figs 1 & 3, photo. 2 (Israel).

Notes on the synonymy

Trewavas (1966*a*) redescribed the lectotype (holotype?) of *Chromis aureus* Steindachner, showing that it agreed essentially with the species now bearing that name. She restricted its type-locality ('West Afrika') to Senegal. This seems to be the only name given separately to this species before *T. n. exul* Steinitz, 1951.

The status of *T. n. exul* was discussed by Trewavas (*op. cit.*), who provisionally retained the name *exul* as a subspecies of *O. aureus* confined to the waters of Ain Fashkha. Ain Fashkha, on the NW shore of the Dead Sea, is a swampy area of about 1 km² that includes (or included) an open basin of about 150–200 m². The area is fed by numerous springs of diverse and seasonally varying temperature and salinity, ensuring that the water is both warm (27°C) and alkaline during the whole year. Drainage is into the Dead Sea, which isolates it from other waters capable of supporting fish-life; the fresh waters of the River Jordan are 10 km distant.

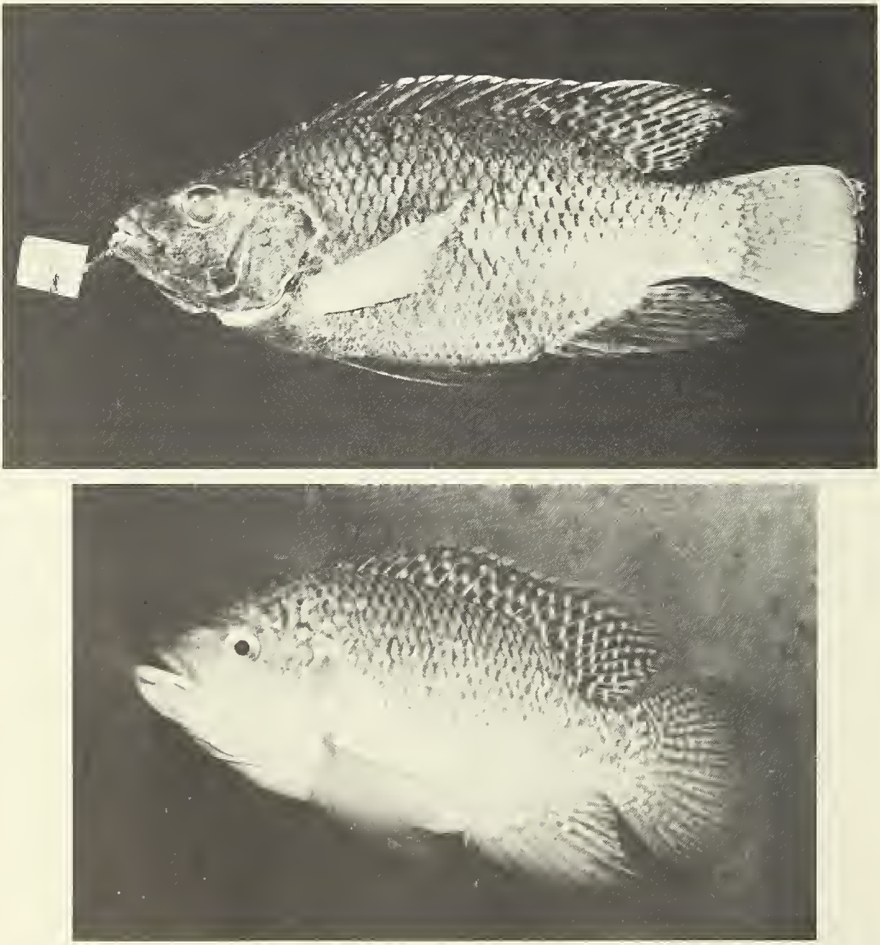

Fig. 65 *Oreochromis aureus*, preserved and living specimens. The preserved fish is a male, showing the white (red in life) margin of the dorsal fin and the irregular pigment pattern of the caudal. The broad, plain margin of the caudal is red in life. (Photograph, L. Fishelson)

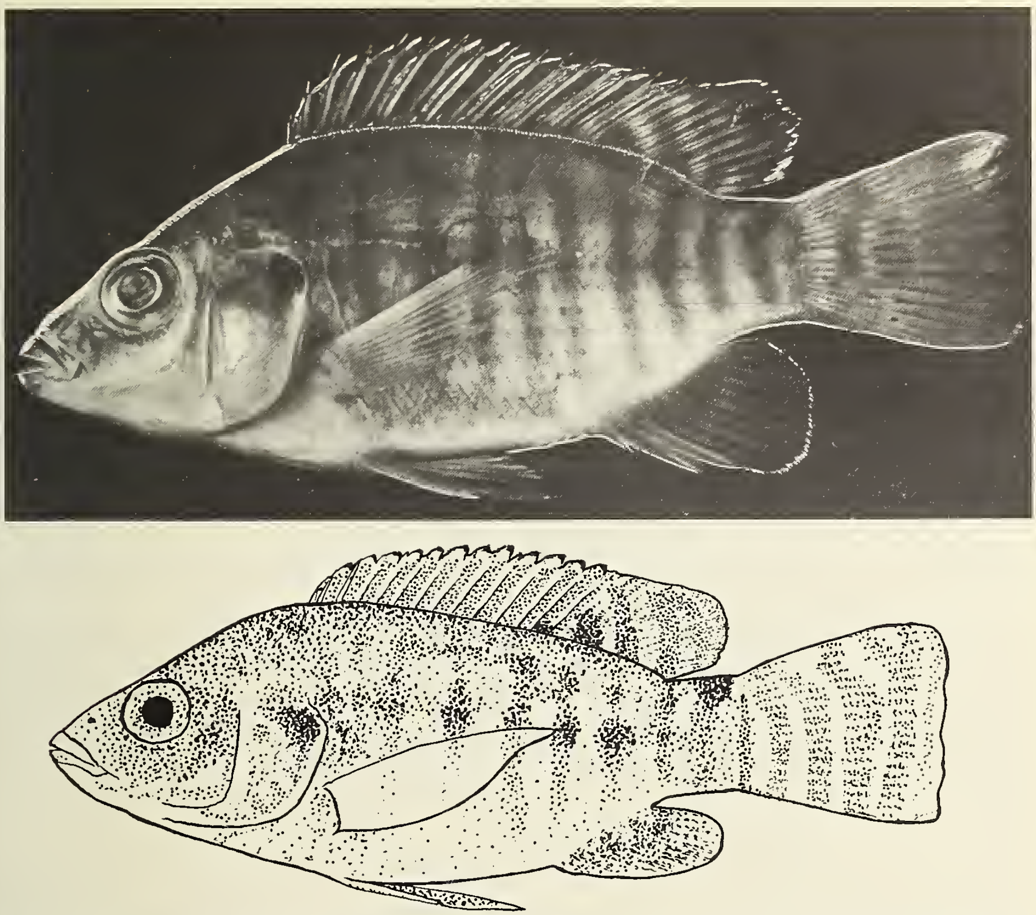

Fig. 66 *Oreochromis aureus* young, from the Lower Senegal River, 46 mm SL (Photograph BMNH); and from Ain Feshkha, 53 mm SL (drawing). The caudal in these individuals bears vertical stripes, at this stage indistinguishable from those of *O. niloticus*. Identification is based on the numbers of dorsal fin rays.

The meristic differences between this and other populations of *O. aureus* may be seen from Tables 49 & 50. In addition the head is on average relatively longer (or the trunk relatively shorter). The surmise that an original report (Steinitz, 1951*b*) of a red colour on the chest was based on living specimens of *Tilapia zillii* is confirmed by Fishelson (unpublished), who visited Ain Fashkha several times in 1967, observed and collected fishes of both species, and kept them in aquaria in Tel Aviv for nine months. He found that '*T. a. exul* has a colour-pattern and behaviour typical of the *T. aurea* populations found in other parts of Israel'.

Chervinski (1968) also compared samples from Ain Fashkha with *O. aureus* of Dor, near Haifa, with the same results, and found parallel differences (fewer dorsal rays, longer head, bigger eye) in the Ain Fashkha *Tilapia zillii* when compared with those of Dor. This strongly supports the conclusion that the characteristics of the Ain Fashkha populations of both species are due to environmental influence. The conditions postulated by Trewavas (1966*a*) for not recognizing '*T. n. exul*' as a separate taxon have therefore been fulfilled, except the testing of the offspring of transferred fishes for the differentiating meristic and proportional characters.

Furthermore, there is evidence that the waters of Ain Fashkha have since been stocked from elsewhere and that an exotic species, probably *O. mossambicus*, has hybridized there with *O. aureus*.

The figures of the types of *T. monodi* and *T. lemassoni* are impressions misleading in some respects. Daget's (1954) figure 132 of *T. monodi* shows the caudal fin rounded and completely covered by a dark reticulum, whereas Daget describes it as marked with a network and with a clear pink margin ('franchement rose'). The figure of '*T. monodi*' in Blache *et al.* (1964, fig. 133), if accurate, could not be conspecific. Blache & Miton (1960) do not compare *T. lemassoni* with *T. monodi*. Blache *et al.* (1964) differentiate the two by the pigment patterns of the caudal fin, but both patterns are found in the population of the Jordan Valley. Examination of the types of both names fails to reveal any specific difference between them, and between either and the eastern populations of *O. aureus*. Daget & Stauch (1963) record *T. monodi* from the upper tributaries of the Benue River, and these authors and Blache *et al.* (1964) point out that the head waters of one of these tributaries, the Mayo Kebbi, rise in a marshy area that also drains into the basin of the Logone River, whose delta is the type locality of *T. lemassoni*. Indeed, the fact that *T. monodi* has not been recorded from the Lower Benue nor the Lower Niger suggests that the source of the Upper Benue population is probably the Chad basin.

The local name (*kacherbi*, *kashabi*) adopted (but not 'clothed') by Wunder (1960) and then by Elster & Vollenweider (1961) illustrates the fact that field-workers have never confused *O. aureus* with *O. niloticus*. El Zarka *et al.* (1970: 161, 162, 166) also distinguished it as '*T. nilotica* variety X, x, or ⋆'†. Boulenger (1907) noticed the lower mean dorsal fin-ray numbers in his '*T. nilotica*' from the Lower Nile, but misinterpreted this as a more variable population than the others. Trewavas (1942) similarly misinterpreted the low meristic numbers in the Jordan Valley as ecophenotypical. Steinitz (1951) and Daget (1954) combined field and taxonomic skills to put names to their observations. Finally Fishelson demonstrated to me at Tel Aviv the segregation for breeding and the different coloration of the two species in one aquarium, prompting me to review the collections and literature of the whole species-complex (Trewavas, 1966*a*).

Types. Lectotype: NHMW 32874, 106 + 27·5 mm, from 'Westafrika'. It is catalogued as type of *Chromis aureus* and bears the accession date 1855.VI.4, which compares well with that (1855.VI.) of the presumed type of *Chromis dumerilii* described at the same time. Its total length (133·5 mm my measurement, 138 mm Dr Kähsbauer's) agrees sufficiently well, allowing for shrinkage during a century in alcohol, with the lowest of Steindachner's numbers (140–155‴), and its appearance with that of Steindachner's pl. 8 fig. 5. Steindachner did not say how many types he had. The caudal still bore (in 1956) the vague markings shown in the figure and the dorsal formula is XV 12. Dr Kähsbauer informed me that in the old catalogue these specimens of 1855 were listed as presented by Mr Parreyss, of whom nothing else is recorded in the museum.

Type locality, designated by Trewavas (1966*a*) as Senegal.

Holotype of *T. exul*: Hebrew University, Jerusalem, Cichl. 1209, Ein Fashkha, 11.XII.1943, coll. H. Mendelsohn and H. Steinitz. Total length 165 mm. Paratypes Cichl. 1210–1212, 99–132 mm TL, same data as holotype.

Syntypes of *T. monodi*: Six specimens of 85–95 mm SL, MNHN 1960–490. Type locality Diafarabé, Mali. Daget did not select a holotype; all the specimens listed by him in the original description were collected by himself in 1950 and 1951. Only eleven syntypes were preserved in Laboratoire d'Hydrobiologie, Diafarabé (accession number H-51-245). Six of these were transferred to Paris in 1960. A specimen of 205 mm SL (MNHN 1954–6) brought by Blanc and d'Aubenton was later erroneously designated as holotype by Blanc (1962:224). It was not part of the original series of types. (Information from Dr Daget.)

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†I must take the blame for this, having identified a small specimen sent to me as *T. nilotica* before I had seen living specimens.

Syntypes of *T. lemassoni*: MNHN 1959–222, two males of 94·5 and 102 mm SL from Mares de Mbele, a swampy area of the Lower Logone subject to flooding. Coll. personnel of Centre d'Étude des Pêches at Fort Lamy, Chad, where also some paratypes were deposited.

Distinguishing characters

The features placing this species in subgenus *Oreochromis* are:

1. Mouth-brooding by the female, who leaves the male's territory with the brood.
2. Establishment of breeding territories by males, probably in spawning arenas (see p. 204).
3. Male genital papilla simple, or at most with a narrow flange.
4. Gill-rakers on lower part of arch 18–26; microbranchiospines present.

O. aureus resembles *O. niloticus* and differs from most species of the subgenus in the narrow preorbital bone (depth not exceeding 21·5% length of head in fishes up to 213 mm SL), the short blade of the lower pharyngeal, and in the absence of enlargement of the jaws in mature fishes (lower jaw not exceeding 36·8% length of head, usually less).

It differs from *O. n. niloticus* in the following characters:

1. The caudal fin never bears the regular dark vertical stripes characteristic of *O. niloticus*, but has a broad pink to bright red distal margin.

Table 48. Meristic differences between *O. n. niloticus* and *O. aureus*. Figures for the Niger are taken from Daget (1954). The coastal river of Israel yielding *O. niloticus* is the Yarkon River, near Tel Aviv, that yielding *O. aureus* is the Na'aman River (now reported to be unfit for fish life), between Haifa and Ako (= Acre). The numbers in brackets of the dorsal spines of *O. aureus* indicate very rare numbers of spines (see text). The Jordan Valley samples do not include any from Ain Fashkha.

	O. n. niloticus	*O. aureus*
Vertebrae:		
range	30–32	28–31
mode	31	30
mean: Jordan Valley	——	29·35 (n = 51)
Israel coastal	30·8 (n = 35)	29·9 (n = 15)
Nile	31·2 (n = 14)	30·2 (n = 9)
Niger	31·1 (n = 10)	29·9 (n = 11)
Dorsal spines:		
range	16–18	(14) 15–16 (17)
mode	17	16
Total Dorsal rays:		
range	29–31	27–30
mode: Jordan Valley	——	28
Israel coastal	30	29
Nile	31	29
mean: Jordan Valley	——	28·27 (n=48)
Israel coastal	30·24 (n = 29)	29·00 (n=11)
Nile	30·59 (n = 42)	29·24 (n=33)
Niger	29·92 (n = 51)	28·85 (n=55)

2. The breeding male assumes an intense bright metallic blue on the head, sometimes extending as a paler blue on the body, a vermilion edge to the dorsal fin and a more intense pink on the caudal margin; chin and chest may be blue-black. In the breeding female the edges of dorsal and caudal fins are a paler, more orange colour.
3. There are lower but overlapping ranges of numbers of vertebrae, scales and dorsal fin-rays. The modal number of dorsal spines is XVI (Tables 48 & 50).
4. Results of interbreeding experiments indicate that the male is the homogametic sex, in contrast to *O. niloticus*, in at least some subspecies of which it is the female (Pruginin *et al.*, 1975; Mires, 1977).
5. The electrophoretic haemoglobin pattern distinguishes it from at least *O. n. vulcani* (Hines *et al.*, 1971) and that of the hybrid is distinct from both parents. Serum proteins are also distinct (Avtalion *et al.*, 1976).

O. n. eduardianus is less contrasted in meristic numbers, but retains the distinction in colour, notably the vertically striped caudal fin and the grey edge to the dorsal.

O. leucostictus, which is sympatric with *O. n. eduardianus*, is not otherwise the representative of *O. aureus* in Lakes Edward/George and Albert, but differs from it in many ways, including the coloration, lower mean numbers of vertebrae and scales and finer teeth, especially on the pharyngeal bone.

O. aureus is one of the species of subgenus *Oreochromis* with only three anal spines.

Description

Based on the type of '*C. aureus*', the lectotype of *T. monodi* and the syntypes of *T. lemassoni*, and on 61 specimens preserved in the BMNH from the whole range of the species, as well as 6 preserved and a few living fishes seen in Tel Aviv University. Data from Daget (1954) are also included.

Proportions as % SL. Depth of body 35–49, usually over 40; in types of *T. monodi* up to 52. Length of head 33·0–37·2 at SL 58–110 mm, 33·0–35·8 at 110–225 mm SL. Length of pectoral fin 29·0–40·5 (the lower measurements probably of fins with damaged tips). Length of caudal peduncle 9–14, usually 11–13.

Caudal peduncle length/depth ratio usually about 0·7, rarely 0·5 (some West African specimens) or 1·0 (one from Israel).

Proportions as % length of head. Snout 25·5–31·0 below 100 mm SL, 28·5–40·0 above this size. Diameter of eye 23–30 at 58–103 mm SL, 18–23 above this length to 240 mm, 16·7 at 255 mm. Depth of preorbital bone 16·0–19·5 at SL below 100 mm, 17·5–23·0 above this size; approximately equal to eye at 140–180 mm, when both are usually 19–21 (Fig. 13). Interorbital width 28·5–38·5, with little indication of allometry, but values of 36 or over are all at 120 mm SL or more and values below 31 are very rare. Length of lower jaw 29·5–36·8, usually 31–35.

Teeth. In 3–5 rows in the jaws, bicuspid in the outermost (except a few posterior unicuspid in large fishes), tricuspid in the others, shaped as in *O. niloticus*, but sometimes, especially in the Jordan Valley, with main cusp a little broader and more curved than is typical for *O. n. niloticus* (Fig. 67); 52–76 in outer row of upper jaw.

Gill-rakers (4–7)+1+(18–22) on the anterior arch in Israel and Egypt, (5–8)+(21–26) in the Niger River (Daget) and Senegal. Microbranchiospines present on outer sides of 2nd to 4th arches.

The width of the *pharyngeal bone*, 10–13% SL (mean of 34 specimens 11·21) and 30·5–33·5% length of head, is about the same as in *O. n. niloticus*, but the median length is less, 24–31% of the head and always less than the width (width/length 1·1–1·28, cf. 28–33% and 1·0–1·18 in *O. n. niloticus*). The difference is better seen in the narrower lobes and more concave sides of the toothed area in *O. aureus* (Fig. 68; see also Daget, 1954, figs 131 & 132). The blade is approximately equal to the median length of the toothed area (ratio 0·7–1·3). In Israel the pharyngeal teeth are finer and a little more crowded than in *O. niloticus*, but I do not find this difference in fishes from the Nile.

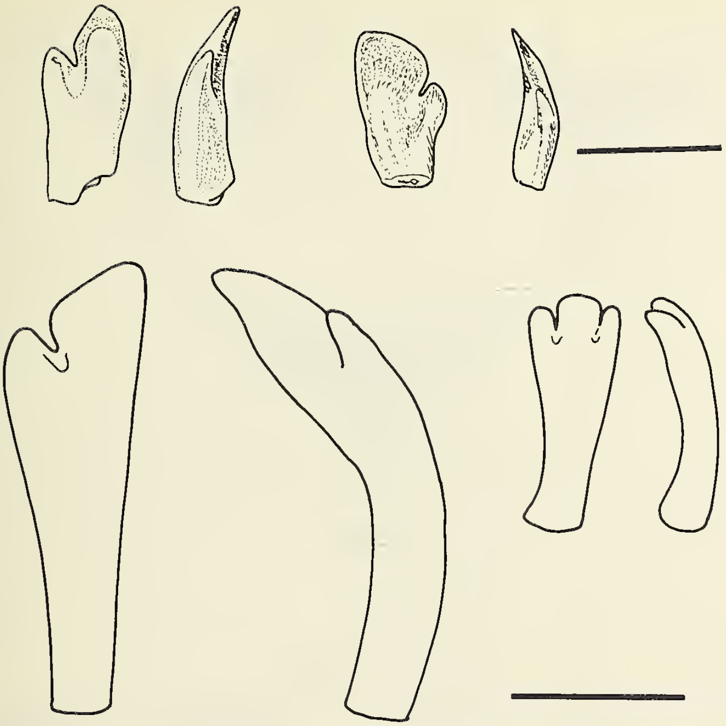

Fig. 67 *Oreochromis aureus*: two teeth, an outer and an inner, from a fish of 117·5 mm SL and (top row) teeth from Pliocene deposits (after Avnimelech & Steinitz, 1952). Scales = 0·5 mm.

Scales. Cheek with 2 or 3 horizontal series. Lateral line series 30–33, mode 32; 4–5 between origin of dorsal and lateral line, 5–7 between bases of pectoral and pelvic fins.

Dorsal (XIV) XV-XVI (XVII) 12–15; XVII recorded once in West Africa by Daget, found also in one fish from Lake Huleh and two from the Lower Nile; XIV once in West Africa. For totals and frequencies see Table 50. Last spine 13·3–17·4% SL.

Anal III 9–11; third spine 11·0–16·4% SL, a little shorter than last dorsal, but stronger.

Pelvics not greatly produced; pale, dark or dusky.

Caudal truncate, often with rounded corners, usually scaly only at the base and between rays on upper and lower parts of the fins.

Vertebrae: see Tables 48 & 49.

Genital papilla of mature male conical (pers. obs.) or with narrow bifid flange (Fishelson, 1962).

Size. In the flood-plains of the Middle Niger it may reach 370 mm SL and a weight of 2300 g (Daget).

A small (SL 58 mm), dark specimen from the Nile delta received a special note and colour-sketch by its collector, A. Loat. It was described as a black variety of 'shabar' and was evidently a melanistic *O. aureus*.

COLORATION. The young (Fig. 66) have the usual facultative grey vertical bars on the body and a tilapia-mark which has disappeared when the SL reaches 100 mm. At this stage the caudal may bear vague vertical markings similar to those of young *O. niloticus*.

In adults general body colour grey-blue, darker above, white on belly. Dark vertical bars appear on the body in some emotional states, and specimens may be preserved with a dark lateral

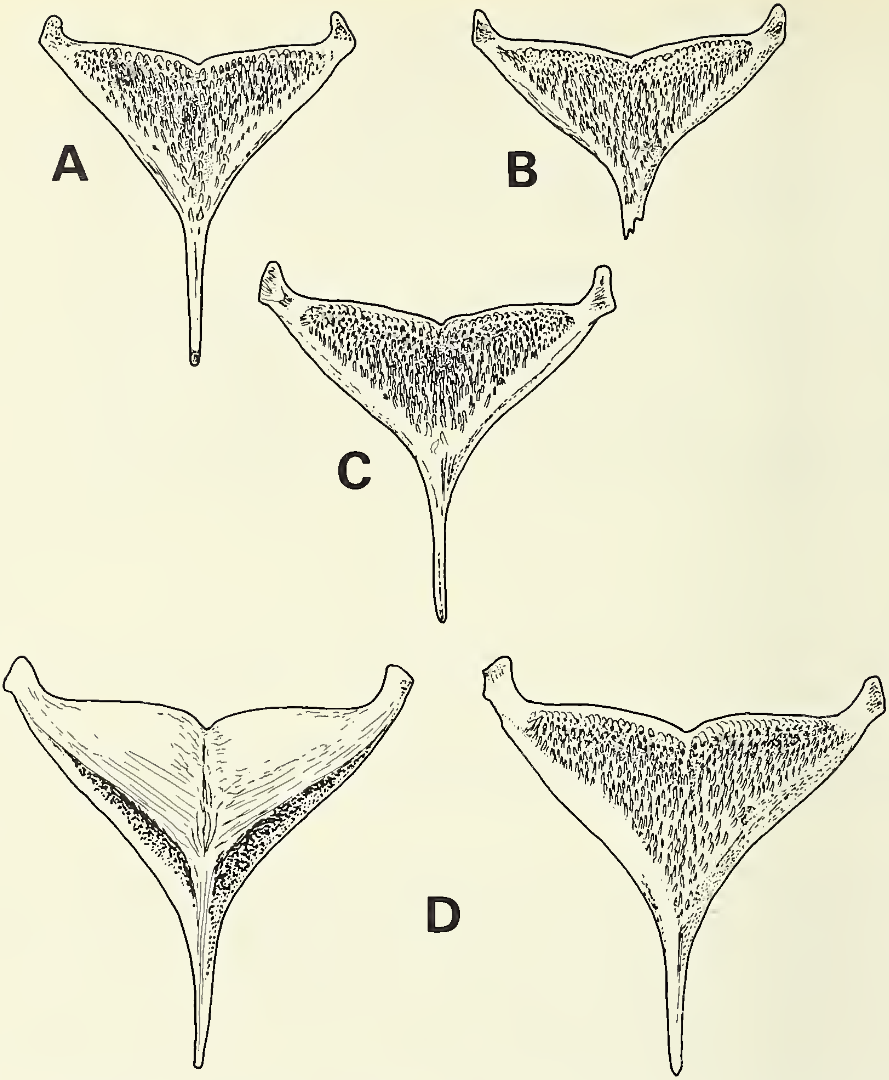

Fig. 68 Lower pharyngeal bones of: A, *Oreochromis n. niloticus* of 102 mm SL from Ras el Ain near Jaffa; B, *O. aureus* of 92 mm SL from Ain Feshkha, shore of Dead Sea; C, *O. aureus* of 110 mm SL from Asraq; D, *O. aureus* of 140 mm SL from Middle Niger, dorsal and ventral views.

band, or with 2 + 1 mid-lateral blotches on the vertical bars and a blotch on the top of the caudal peduncle. In darker individuals each scale may carry a dark spot except ventrally (preserved fishes), or the flanks may bear a reticulate pattern based on the scales. Dorsal fin with dark and light spots alternating on posterior half, pearly white spots on this and proximal half of caudal and posterior part of anal. Upper margin of dorsal vermilion or orange (white when preserved). Caudal with a broad pink to red margin; rest of fin either without markings or with irregular spots or a dark reticulum with light interstices over part or nearly the whole of the fin; rarely the grey spots may be arranged in wavy vertical rows and young and one or two adult specimens have faint vertical stripes. Anal pale, clouded or with a few spots. Eye with red iris crossed by a black bar. In West Africa, types of both *T. monodi* and *T. lemassoni* were described as having

Table 49. Frequencies of total numbers of vertebrae, obtained from radiographs, in samples of populations of *O. aureus*. To the counts reported by Steinitz for the sample including the types of *T. exul* have been added that of the specimen shot at Ain Fashkha by Tristram's companion in 1864 (the modal 29) and those from Villwock's collection of 1964. The counts for aquarium specimens at Tel Aviv, originally from Hula, have been obtained by adding one to those on which Fishelson based his report; he omitted the last, ural centrum, which I count as one. The low modal number of these is probably due to the fact that they were descended from one or a few wild pairs. Dor numbers are from Chervinski (1968).

	'*T. exul*' Ain Fashkha	Lower Jordan	Lake Tiberias	Lake Hula		Na'aman	Dor	Egypt	Niger '*monodi*'	Chad '*lemassoni*'
				BM	Tel Aviv					
27	1									
28	6	2	3				2			
29	26	1	6	5	41	2	16		2	2
30	5	1	10	9	4	11	48	7	8	7
31			1			1	6	2	1	1
N	38	4	20	14	45	14	72	9	11	10
Mode	29	—	30	30	29	30	30	30	30	30
Mean	28·79	—	29·45	29·64	29·09	29·93	29·81	30·2	29·9	29·9

Table 50. Total numbers of dorsal fin-rays in samples of populations of *O. aureus*. The lower means for West African samples may be due to different bias in the counting of the last ray on the part of Daget and Blache & Miton, whose figures are used, but cf a parallel difference between eastern and western populations of *S. galilaeus* (p. 97). The difference between the Jordan Valley on the one hand, and the Na'aman River and Egypt on the other, is real and is paralleled in the vertebral numbers. The same is true of the very low numbers at Ain Fashkha, from Steinitz (1951), Trewavas (1966*a*) and Chervinski (1968). The numbers from the Fish Culture Research Station at Dor, near Haifa, are those of Chervinski (1968).

	'*T. exul*' Ain Fashkha		Lower Jordan	Lake Tiberias	Lake Hula	Na'aman	Dor	Egypt	'*monodi*' Niger	'*lemassoni*' Chad
	St. & T.	Ch.								
25	1	1								
26	4	11					1			
27	33	27		1	2		28		Totals not given	
28	4	7	1	11	15	2	46	3		
29	1		3	8	10	7	20	21		
30					2	2	12			
N	43	46	4	20	29	11	95	55	55	31
Mode	27	27	—	28	28	29	28	29	—	—
Mean	27·00	26·9	—	28·35	28·41	29·00	27·9	29·24	28·85	28·48

the melanin pattern of the body well-marked. '*T. monodi*' had a pink or orange dorsal margin and a pink caudal margin, with the rest of the caudal covered with a reticulum, the chest and belly pale greyish or tinged with yellow (Daget, 1954). Life colours are not given for the types of *T. lemassoni*, which were said to be differentiated by the caudal pattern of inter-radial stripes (Blache *et al.*, 1964), but this is also one of the variants in the Jordan Valley population.

The name used in the Nile delta, *Kashabi*, is said to mean 'stone' (Wunder, 1960), in reference to the colour, the paleness of which has led some (Elster & Vollenweider, 1961) to consider it related to *S. galilaeus.*

Ecology

Food

Ben Tuvia (1959, 1960) measured the gut of adults of 23–25 cm TL and found it to be 8·0–9·4 times the length of body (SL). The food in Lake Tiberias was mainly phytoplankton and small quantities of zooplankton. Wunder (1960) recorded the food of '*T. kacherbi*' in the fresh waters of the Nile delta as minute epiphytic algae of which only the diatoms appeared to be digested. He contrasted this with the coarse plant material eaten there by *O. niloticus*. McBay (1961), who like Ben Tuvia, studied this species under the name *T. nilotica*, before the two species had been recognized as distinct in Israel, recorded the food in ponds in Alabama. Adults of 15–22 cm TL, in addition to the pellet food with which they were supplied, fed almost exclusively on phytoplankton and this was the most important item at all sizes. Much smaller quantities of other items were taken apparently opportunistically. As in other species, the young were found to have a more varied diet, including large quantities of copepods and Cladocera. In one pond these Entomostraca equalled the phytoplankton in volume in the 5 and 7·5 cm size-groups and exceeded it in the 2·5 cm young.

Growth (Table 51)

Ben-Tuvia (1959, 1960) estimated the total lengths of the year-classes in 67 males and 53 females in Lake Tiberias (under the name *T. nilotica*) by reading the otoliths. Workers on the Nile delta populations have used annual rings on the scales (see Table 51).

El Zarka *et al.* (1970, tables 4, 6) found *O. aureus* (as '*T. nilotica* var. x') to make slower growth than *O. niloticus* in Lake Mariut, and Payne & Collinson (1981) found the same after the first year. Growths reported by Ben-Tuvia for Lake Tiberias show better results at year-class III. Not only is it probable that conditions are more favourable in Lake Tiberias than in the shallow Lake Mariut, but year-class III of Ben-Tuvia is probably older than L3 of workers on

Table 51. *Oreochromis aureus*: total length in cm attained in successive years. The columns are staggered to indicate the probable different significance of the year-classes used by the different authors.

Year-classes			I		II		III	
Ben-Tuvia (Tiberias)	♂		8–16		16–27		22–31	
	♀		8–14		15–25		21–28	
Payne & Collinson								
		L1		L2		L3		L4
Mariut		11·1		16·8		17·9		
Menzaleh		8·8		16·3		19·3		21·5

the Egyptian populations, for whom this means 'at the end of the third year of life'. Payne & Collinson found no significant difference between growth-rates in Lake Mariut and Lake Menzaleh.

Chervinsky (1965) claimed that in ponds at Dor growth is better than in Lake Tiberias, and (*idem*, 1966) he found no significant difference between the growth-rates of this species in fresh and saline ponds.

Efforts to avoid the checks on growth resulting from precocious breeding have involved several methods.

The selection of males by examination of the genital papilla in the young in order to obtain all-male populations has proved too fallible, at least in fishes of less than 80 g weight (Yashouv & Halevy, 1967).

Ekstein & Spira (1965) brought about destruction of the ovaries by adding oestrogens to the aquarium water of young individuals at the time of differentiation of the gonads. Androgens had only a variable effect.

Pagán-Font (1975) reared batches of young in cages of two mesh-sizes, experimenting with different densities and having controls swimming freely in the ponds in which the cages were suspended. Fry were produced by the controls and in the cages of 3 mm mesh, but where the mesh was 6 mm no offspring were found although the females had spent gonads. The bigger mesh had evidently allowed the eggs to escape, preventing mouth-brooding. The growth of the deprived parents was not recorded.

Hybridization to produce all-male broods was successful when *O. aureus* was the male parent and *O. niloticus* the female (Fishelson, 1962; Pruginin *et al.*, 1975), but only under the most rigorous experimental conditions (see p. 205).

Salinity tolerance

In the Nile delta *O. aureus* is found in both fresh and brackish water (A. I. Payne, pers. commn), although Wunder (1960) observed it only in fresh water. It is native in the Jordan Valley, where the salinity varies from place to place and from year to year. Chervinsky (1966) compared its growth in ponds with Cl at 300 mg/l and others where it was 6000 or 10 000 mg/l, and found no significant difference. Fishelson & Popper (1968) and Loya & Fishelson (1969) observed hybrid *O. aureus* and *O. niloticus* behave normally in ponds of very high salinity (2000–8000 mg/l Cl), but this says nothing about the ability of either species to reproduce in such conditions.

The waters near the mouth of the Senegal River include the brackish estuary and lagoons with *S. melanotheron* and *Tilapia guineensis*, and fresh waters with *S. galilaeus*, *O. niloticus*, *O. aureus* and *Tilapia zillii*.

Temperature tolerance

McBay (1961) found that the young fishes (up to 10 cm) were less tolerant of low temperatures than bigger ones, a temperature of 48°F (9°C) being lethal in certain circumstances. Lower temperatures might be tolerated by bigger fishes for short periods, so that a warm day might compensate for a cold night, but in general temperatures below about 5°C prolonged for a few days produced signs of distress.

Israel is the most northerly part of the range of *O. aureus*, and of the genera *Sarotherodon* and *Oreochromis*. The Jordan Valley probably provides a suitable environment the year round. Nevertheless, breeding is there seasonal and a temperature of 20°C is the minimum for a breeding population (McBay, 1961; Fishelson, 1967). Ponds in Israel are found to require sufficient depth to enable *O. aureus* to retire to the stable temperature of the bottom during winter.

Breeding

Reproduction has been studied in *O. aureus* under the name of *T. nilotica* by Ben-Tuvia (1959,

1960) in Lake Tiberias, and by McBay (1961) on imported stock in ponds and aquaria in Alabama; and as 'the Blue *Tilapia*' (1962) and *T. aurea* (1967) by Fishelson in aquaria in Tel-Aviv. Further observations were made by Chervinsky (1965) in ponds at Dor, near Haifa, and (1968) at Ain Fashkha. Liebman's record (1932) of two brooding females in Lake Tiberias must also refer to this species.

Sexual dimorphism. The colours of breeding males are described on p. 198. As in most species, the soft rays of the dorsal and anal fins are longer in mature males (Chervinsky, 1965). Some males in breeding condition at Tel-Aviv had the vermilion margin of the dorsal fin thickened and entire. In the collection of the BMNH the most advanced male is from Lake Menzaleh; in it the dorsal margin is thickened and the notches are reduced but not closed. Dr Payne (pers. commn) did not find any fin with entire margin among many examined in the breeding season of 1979 in Egypt. Chervinsky (1971) found differences in proportions between the sexes in ponds at Dor, where growth is fast. Males had a mean body depth and a length of the pectoral fin significantly greater than females, and females had a longer lower jaw. In Lake Tiberias no such differences were found. Although Chervinsky had reasonable samples, thirty-six of each sex from each locality, the characters chosen are among the most variable, and his 'lower jaw' measurement is evidently not the same as mine. Nevertheless, the different results associated with different growth-rates are worthy of attention. Similar results were obtained by Chervinsky (1967*a*) with *Tilapia zillii*, and it is of interest that Lowe-McConnell (1958) found a difference in size between the sexes of early maturing, pond-reared *O. niloticus*, but not in well-grown lake fishes of the same species.

Breeding season. In Israel breeding occurs from the end of March or the beginning of April to the end of May. A temperature of 20–22°C is the minimum for breeding, as McBay (1961) also found in Alabama. In the Nile delta the season extends into November, with a peak in early summer (Payne & Collinson, 1983).

Age and size of maturity. Chervinsky stated that reproduction occurs in the second year of life at Dor and this must also have been the age of ripe females of 22–25 cm whose eggs Ben-Tuvia examined. But in the brood-ponds of Alabama the ovaries of some individuals started to mature when they were about 50 days old and 10 cm in length. At Ain Feshkha, Chervinsky (1968) found females of 58 and 60 mm SL with well developed ovaries containing few eggs.

Behaviour. Fishelson (1967) states that mature males establish a territory of 0·7–1·0 m and defend it by aggressive behaviour, including lateral display, lateral biting and mouth to mouth combat. The territory established, the male digs a spawning pit, using mouth and fins. McBay's account differs in that his males first dug and defended a spawning pit, and then defended the surrounding territory by frontal display. As the season advanced the territories of dominant males increased in size to an area of 2–3 m radius and less successful males were excluded. In the Alabama ponds the nests were dug in water of about 60 cm depth in a sandy substrate. Both Fishelson and McBay state that the male swims out to passing schools of mixed sexes and leads a female to the nest. Courting behaviour in the nest consists of lateral display by both sexes with nipping and tail-flapping. McBay describes an attitude that resembles a T-stand, the male nudging the lower abdomen of the female and causing circling movements by both.

Both observers describe laying of eggs in batches, the male gliding over each batch as it is laid and fertilizing, and the female then immediately taking them into her mouth. She then moves away, in the ponds seeking the deeper water, and the male renews spawning activities with another female.

Mature eggs measure approximately 2 × 3 mm (McBay), and Fishelson records that one female may hold as many as 2000 in the mouth. The fecundity was measured for the population of Lake Menzaleh by Payne & Collinson (1982), who provided a curve based on their counts of ripe ovarian eggs. These ranged from 350 at SL 105 mm to 1600 at SL 153 mm. Payne & Collinson (1981) extracted formulae for the relationship between the number of eggs and SL or TL, valid for both *O. aureus* and *O. niloticus* in the Lower Nile.

Hatching occurs about three days after oviposition and the eggshells are swallowed by the mother (Fishelson). Incubation time varies with the temperature. Both McBay and Fishelson give 13–14 days at 25–27°C. The young then remain in a concentrated school near the parent's head for a few days (3 days, McBay), reentering the mouth at any sign of danger, or at a gesture by the parent. After five days this parent-offspring relationship comes to an end.

When the young cease to return to the mouth the female enters a new reproductive cycle if the temperature is suitable.

Fishelson found that removing the eggs or early embryos from the mouth resulted in immediate initiation of a new cycle, and that in this way the number of spawnings from a single female, in the controlled conditions of an aquarium might be increased to as many as eleven in one year, with the production of ten times as many eggs as normally.

In Alabama, the young mature females of 10–18 cm spawned at intervals of 33 to 59 days, producing an average of 462 eggs during the spawning season at temperatures of 25°C or higher (McBay, 1961).

Hybrids

Fishelson (1962, 1967) kept several *O. niloticus* from the Yarkon River, and *O. aureus* from Hula together in a large aquarium at Tel Aviv University, and found that the species segregated for mating. When a mature male *O. aureus* and a mature female *O. niloticus* were put together in a separate aquarium, where neither had the opportunity of mating with its own species, they readily mated together and produced a brood of 700 young, all of which proved to be males. An attempt at the reverse cross failed. The male hybrids were capable of fertile mating with females of either parent species.

This indicates a degree of reproductive isolation that would effectively keep the two species pure in natural conditions, and in the Nile delta, where the two species occur together, Payne & Collinson (1983) examined 'several hundred' *O. aureus* and *O. niloticus* checking meristic and colour characters, without finding any evidence of hybridization except possibly two specimens from a pond on a fish farm. The production of an F_1 generation of males has been utilized in pond culture. Whether because of less rigorous conditions or because the restriction to males is not invariably 100%, the hybrid populations in ponds are described as 'almost monosexual' (Loya & Fishelson, 1969; see also Pruginin *et al.*, 1975 and Mires, 1977). The desirability of an all-male population in fish culture rests on the faster growth of males and the avoidance of dwarfing and over-population resulting from early mating.

Yashouv (1969), however, considered that the growth of the hybrid male was not as good as that of *O. aureus*, and that for piscicultural purposes the effort (not always successful) to produce an all-male population was not worth while. Pruginin *et al.* (1975) also found no evidence of heterosis (hybrid vigour), but they have become commercially successful.

It was probably this species, and not *O. niloticus* as they thought, that Avault & Shell (1968) hybridized with *O. mossambicus* in ponds and aquaria in Alabama. They found its resistance to lowered temperature greater than that of *O. mossambicus* and that the hybrids were intermediate in this respect. In the F_1 generation they found 70% males and in the F_2 90%. Growth of the hybrids was faster than that of either parent.

Mires (1977) quotes an otherwise unpublished result of experiments by Pruginin & Hulata. Hybrids between *O. mossambicus* from South Africa and *O. aureus* showed a normal, approximately 1:1 sex-ratio, thus differing from the report of Avault & Shell. The same divergence from Avault & Shell would obtain if the fishes used by these two authors were the true *O. niloticus* since Pruginin obtained the same result with the latter species and *O. mossambicus*.

For further results of hybridization experiments between *O. aureus* and the subspecies of *O. niloticus* see under the latter species (p. 192).

HORMONE TREATMENT. Jensen & Shelton (1979) used estrogens to turn genotypic males into phenotypic females, then mated the latter with untreated males, so producing all-male offspring. Guerrero (1975) and Eckstein & Spira (1975) used hormones on the young to influence gonadal differentiation, but Mires (1977) considered these methods to be unsuitable for large scale commercial fish culture.

Distribution

Natural distribution. River Senegal; Middle Niger as far south as Busa; upper tributaries of the Benue River; Lake Chad and the Lower Shari and Logone Rivers; Lower Nile from near Cairo to the delta lakes; Na'amen River (between Haifa and Akko = Acre (this population perhaps now exterminated by pollution); Yarkon River, near Tel Aviv: Lake Huleh; Lake Tiberias = Kinereth; River Jordan and its tributaries; the oasis of Ain Fashkha, on the shore of the Dead Sea.

Not recorded from the Volta River or rivers west of this in Ghana, nor from Ivory Coast, Liberia and Sierra Leone; Daget's surveys of the fish-faunas of Guinée including the upper parts of the Corubal River system, and of the upper and middle Gambia, as well as other surveys of the Gambia, have failed to find it.

There is no record of its occurrence in the Nile above Cairo. Dr A. I. Payne (pers. commn), who recently studied the tilapias in Egypt, did not find it at Beni Souef, and his partner on this mission (R. Collinson) examined catches at Lake Nasser without finding it. Neither the Loat collection, which was the basis of Boulenger's publication of 1907, nor earlier collections in the BMNH included specimens from above the delta that could be assigned to this species.

O. aureus is accompanied throughout its range, except probably in the Jordan Valley, by the structurally similar *O. niloticus*. Most, or all, of the older records of '*T. nilotica*' from the Jordan Valley were based on *O. aureus*. Lortet (1883) and Vinciguerra (1926) attributed the colour-markings of *O. niloticus* to their specimens from Lake Tiberias, but Lortet's Tiberias specimens are no longer preserved in the Museum at Lyon and his figure may have been based partly on an Egyptian specimen; Dr Tortonese informs me (in a letter of February 1972) that Vinciguerra's are *O. aureus*. Ricardo-Bertram (1944) also described a striped caudal fin, but all her preserved specimens from Lake Tiberias (about 40) prove to be *O. aureus*. The present population of Lake Tiberias includes *O. niloticus* by artificial stocking.

In West Africa *O. aureus* appears to be outnumbered by *O. niloticus*, but from the Nile delta the large collection made by Loat in 1899 included 70 *O. aureus* and 41 *O. niloticus*.

Possible pliocene occurrence. Teeth of a tilapia in an Upper Pliocene bed west of the River Jordan below Lake Tiberias were reported by Avnimelech & Steinitz (1952). Those of their figs 4 and 5 may have been of this species, or *O. niloticus*. Such a shape may, however characterize a special population (cf. *O. spilurus percivali*, Fig. 85).

Dispersal by man. With *Tilapia zillii*, *O. aureus* was introduced into the oasis of Asraq, east of Amman, about 1930 and survives there. The species is used in experimental and commercial fish culture in Israel, and was transferred for experimental breeding to Kajansi, Uganda in 1964–6. It was sent from Israel to Jonkershoek, Cape Province, South Africa, for cultivation in ponds, where its limited success was reported by Van Schoor (1966) under the name *T. nilotica*. His description of the colours, as well as some samples later sent to the BMNH confirm that these were *O. aureus*.

At least some of the accounts of '*T. nilotica*' cultivated in ponds in USA refer to *O. aureus* imported, probably from Israel, before the two species were recognized as distinct. Such is McBay's account (1961) of its ecology in ponds in Alabama, as shown by a photograph kindly sent to me by Mr McBay together with his remembered description of the life-colour. The species is feral in Florida (Goldstein, 1973).

Dr Fishelson informs me that large numbers of hybrids between *O. aureus* and *O. niloticus*, all (or nearly all!) males, are exported annually. The same is recorded by Mires (1977).

In Israel itself much stocking of ponds, rivers and Lake Tiberias has taken place, using this species, *O. niloticus* of various strains, native and imported, and hybrids between them. See Mires (1977).

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
NHMW 32874 (lectotype)	135	'Westafrika'	Parreyss
1900.6.28.194–5	80, 96	Ka'idi, Senegal	Delhez
1978.3.13.1	47	Lac de Guiers, Senegal	Dorfman
1978.3.13.2	59	Maram, Lower Senegal	Dorfman
1978.3.13.3	72	N'Dium, Senegal	Dorfman
	140	Diafarabé	Daget
MNHN 1952–6	208·5	Diafarabé	Blanc & D'Aubenton
1957.11.15.1	25	near Kano	Hannay
1956.6.21.53	81	Hadeija R., nr. Wudil	Roloff
1909.7.27.50	38	Komadugu R., Chad system	coll. Tilho & Gaillard pres. MNHN
MNHN 1959–222 (syntypes of *T. lemassoni*)	94·5, 102	Mares de Mbele, Lower Logone	Centre d'Études des des Pêches a Fort Lamy
BMNH			
1907.12.2.3508	140	Pond near Bedreshen, S. of Cairo	Loat
1907.12.2.3504–5	164, 171	Pool by road from Cairo to Giza	Loat
1907.12.2.3362–6	171–225	Fresh water canal entering L. Borollos	Loat
	67–111	L. Borollos	Loat
1907.12.2.3379	58	Ghet el Nassara	Loat
1907.12.2.3380–82	104–126	Bahr el Tawilah	Loat
1907.12.2.3367–72	102–238	L. Menzaleh	Loat
1960.3.14.1	93	L. Menzaleh	Ezzat
1969.5.28.4	115	L. Menzaleh	Bishara
1907.12.2.3358–61	121–177	L. Edkou	Loat
1861.9.9.10–12	144, 233	'Nile'	Petherick
1979.7.23.9–10	94, 95·5	?	?
1864.8.23.109	92	Dead Sea	Tristram
ZMH (27 fishes)	48–74	Ein Feshkha	Villwock
1971.4.28.4–5	109, 117	Tel Aviv ex Ein Feshkha	Fishelson
1864.8.23.37a	177–195	Galilee	Tristram
1949.9.16.298	175	L. Tiberias	Ricardo-Bertram
1949.9.16.371–384	77–147	L. Tiberias	Ricardo-Bertram
1942.4.7.3–6	92–104	Galilee	Craig-Bennett
1967.5.19.1	124	Damascus market ex L. Tiberias	Beckman
1949.9.16.385–389	118–142	Lower Jordan	Ricardo-Bertram
1935.2.28.7	123	L. Huleh	Hornell
1936.4.6.49–52	103–158	L. Huleh	Washbourn
1949.9.16.318–320	135–161	L. Huleh	Ricardo-Bertram
1949.9.16.356–370	131–164	L. Huleh	Ricardo-Bertram
Tel Aviv Univ. P. 926, P. 1716–17, P. 1719–20	129–213	Hula	—

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1956.2.24.32	110	Sheshan Springs, Asraq (intro.)	Chimitz
1956.2.24.33–34	108, 112	Druze Springs Asraq (intro.)	Chimitz
1965.11.24.10	85	Asraq (intro.)	Trewavas
1949.9.16.338–347	111–177	Naamen R.	Ricardo-Bertram
1949.9.16.348–352	58–109	Naamen R.	Ricardo-Bertram
1970.3.19.15	180	Florida (intro.)	Buntz

Subgenus *OREOCHROMIS* – II

Oreochromis esculentus
Oreochromis leucostictus

These two species are brought together for convenience only. *O. esculentus* inhabits Lake Victoria, *O. leucostictus* Lakes Edward/George and Albert, and the Semliki catchment between them. They show no close resemblance to each other and none to their respective companions, to which they hold the role of 'complementary species' (see p. 515). It is suggested, but without strong evidence, that *O. esculentus* and *O. niloticus* may be vicariating species in Lakes Victoria and Edward/George respectively. No suggestion can be offered for a close relative of *O. leucostictus*, which, although well characterized, has no striking peculiarities. The rich phytoplankton of Lake George offers the same feeding ecology to both its *Oreochromis*, and makes the lake water too opaque for observations of breeding ecology. Evidence from Lake Victoria, where both *O. niloticus* and *O. leucostictus* have now been introduced, suggests that they may occupy different breeding zones, but no full comparative ecological studies have been made of the two species in that lake.

The natural complementary species of *O. esculentus* in Lake Victoria was *O. variabilis*, but among the differences between this and *O. leucostictus* is the presence in male *O. variabilis* of a genital tassel, of which there is no sign in *O. leucostictus*.

Oreochromis esculentus (Graham)

Tilapia galilaea (part, *non* Linn.); Pellegrin, 1905*b*:183 (Kavirondo Gulf).
Tilapia variabilis (part) Boulenger, 1906*c*:447; 1911*b*:76; 1915:167.
Tilapia eudardiana (part); Boulenger, 1915:167 (Lake Gangu, juv.).
Tilapia sp. Dobbs, 1927:107, fig. 4 on pl. opp. p. 107 (Lake Victoria).
Tilapia esculenta Graham, 1928:210, pl. 9, fig. 1, pl. 10 Fig. A, pl. 11; *idem*, 1929:111–145, figs 1, 58–62 (bionomics & fishery); Worthington, 1929*b*:109, tables 19, 20 (in Lake Kioga); *idem*, 1932*c*:66 (in Lake Nabugabo); Gould, 1951 (introduction to Korogwe); Fish, 1951; *idem*, 1954; *idem*, 1955 (food); *idem*, 1956 (respiration); Greenwood, 1953*a* (feeding mechanism); *idem*, 1966:114, fig. 58; Kelsall, 1954 (breeding place and season); Holden, 1955 (rings on scales); Lowe, 1955*a*:364 pl. 17B (in ponds; nests); *idem*, 1955*b* (distinguishing features); *idem*, 1955*c* (fecundity); Lowe-McConnell, 1956*b* (bionomics); *idem*, 1957:370 (distinguishing features); Garrod & Newell, 1958 (rings on scales); Garrod, 1959 (growth); *idem*, 1960*a* (fishery); *idem*, 1963*a* (mortality); Cridland, 1960 (food); *idem*, 1961 (reproduction); Welcomme, 1964*a*: table 1; *idem*, 1964*d*:18 (habitat of young); *idem*, 1964*e*:131, fig. 3 (young); *idem*, 1966*a*, *b* & *c* (ecology); Trewavas & Fryer, 1965 (hybrids with *S. amphimelas* in Ls Kitangiri & Singida); Bailey, 1966 (distribution in dams); Payne, 1971 (growth in ponds); Bailey *et al.*, 1978:109 ff. (ecology in Nyumba ya Mungu reservoir); Denny, Bowker & Bailey, 1978:139 ff. (food in Nyumba ya Mungu); Bailey & Denny, 1978:151–157 (status in Nyumba ya Mungu).

Notes on the synonymy

The only record of IV anal spines in this species is based on the determination, as *esculentus*, of some of the fishes recorded from the Kavirondo Gulf by Pellegrin (1905) as *T. galilaea*. Among his specimens Pellegrin had some from brackish water in the Maji Chumvi River (Mombasa), but there do not seem to be any from this locality now catalogued in the Paris Museum (MNHN). I have examined four specimens of Alluaud's collection of this time. Of these 1904/172 and 173 are *O. variabilis* (q.v.) and I determine now 1904/178 and 179 as *O. esculentus*. Their standard lengths are respectively 90 and 86 mm, and the 86 mm one is the fish with IV

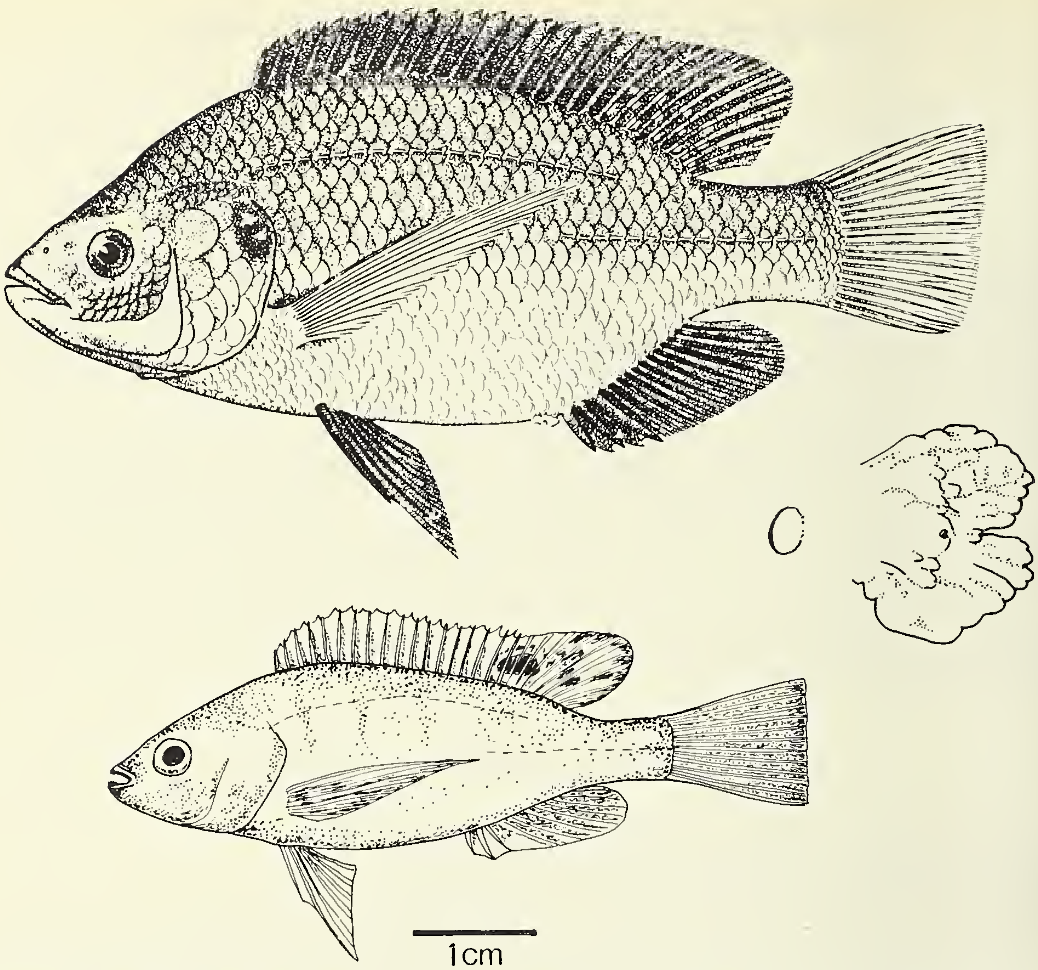

Fig. 69 *Oreochromis esculentus*: above, holotype, 231 mm SL, from Graham, 1928, pl. IX; below, juvenile, after Welcomme, 1964e, fig. 3; right, genital papilla of the holotype (×3·5).

anal spines. The locality name on the label is 'L. Victoria', but I have considered whether this may be a mistake. If they were from the Maji Chumvi River they could only be *O. spilurus*, but they each have a conspicuous tilapia-mark. This is characteristic of *O. esculentus* at that size, but in *O. spilurus* it can hardly be detected above 75 mm SL, and between 50 and 75 mm it is merely a blacker part of the striped or reticulate pattern of the fin. In addition, both have XVII dorsal spines and 32 scales in the lateral line series, 8 or 9 over the top of the caudal peduncle, rare numbers in *O. spilurus* but common in *O. esculentus*.

This species was known to fishermen from time immemorial under the name *ngege*, as distinct from *O. variabilis* (*mbiru*), and this fact was fortunately brought to the attention of Michael Graham in 1927, at the outset of his fishery survey of the lake, by Mr C. M. Dobbs. Dobbs (1927) mentioned them briefly in a note on fishing in the Kavirondo Gulf, calling attention to the difference in the margin of the dorsal fin, which is red in *O. variabilis*, but not (usually) in the ngege. The description and naming of the species were left to Graham.

TYPES. Holotype, a male of 231 + 52 mm, from Lake Victoria, coll. M. Graham; BMNH 1928.5.24.99.

Paratypes: 38 specimens of 109–294 mm SL from Lake Victoria, coll. M. Graham (see p. 220). Local name: *Ngege*.

Distinguishing characters

The appearance of the living fish suggested to an experienced field-worker (Lowe-McConnell, 1956) relationship to *O. niloticus*. With *O. esculentus* this has in common:

1. Male breeding coloration a general reddish colour with black ventral parts and dorsal fin; lappets of dorsal fin not bright red or orange.
2. No enlargement of the jaws in mature male.
3. A rather shallow preorbital bone, its depth not exceeding 21% length of head (to 22% in *O. niloticus*).
4. Numbers of scales in the lateral line series and the high modal number of dorsal spines (XVII). But these are not unique to the two species.

Numbers 2 and 3 are shared also with *O. aureus*.

O. esculentus differs from *O. niloticus* as follows:

1. No vertical stripes on the caudal fin.
2. Lower numbers of soft dorsal rays and therefore of total dorsal rays (cf. Tables 35 & 52).
3. Lower modal number of lower gill-rakers (mode 18, v. 21 or 22 in *O. niloticus*; see table 35).
4. Finer teeth in jaws and pharynx.
5. A longer lower pharyngeal bone, 33·0–35·5% length of head (see Table 120).
6. Caudal peduncle as long as or, usually, longer than deep (depth greater than length in *O. niloticus*).
7. *O. niloticus*, in common with many other species, is often preserved with three or four mid-lateral spots and another on the top of the caudal peduncle. This pattern is not found in our samples of *O. esculentus*.
8. Male genital papilla opening between a pair of often spongy lobes (papilla conical or with a slight distal notch in *O. niloticus*).

The differences from *O. niloticus* are much greater than those between the subspecies of the latter. From *O. leucostictus* there are still greater differences (p. 221). The distinctions between *O. esculentus* and the sympatric *O. (Nyasalapia) variabilis*, beginning with the subgeneric character of the tasselled genital papilla in the latter, are listed in Table 52 and on p. 414.

The possibility that *O. esculentus* is related to the peculiar species *O. amphimelas*, with which it has hybridized in Lakes Kitangiri and Singida, is mentioned on p. 403. With this it has in common rather high numbers of vertebrae and a long caudal peduncle. The preorbital of *O. amphimelas* is narrower than that of any other species of *Oreochromis* and its other peculiarities are not foreshadowed in *O. esculentus*. Among many of the latter a single specimen from Lake Kyoga has been found with two small scales on the postero-ventral corner of the preorbital bone. In this bone there are always five lateral line openings in *O. esculentus*.

Description

Based on the holotype and 24 other specimens of 109–248 mm SL, from Lakes Victoria, Kioga and Nabugabo; and on 5 juveniles, 51–63 mm SL from Lake Kwania, part of the Kioga complex.

Proportions as % SL. Depth of body (37·8) 40·5–45·4, juv. 39·8–42·7. Length of head 33·0–37·5, over 34·0 in three quarters of specimens over 100 mm SL, 35·0 or over in 11 of these and in the five juveniles. Length of pectoral fin 39·0–44·0, juv. 34·7–39·8. Length of caudal peduncle 12·0–15·8,

Caudal peduncle length/depth (0·84) 0·9–1·15.

Proportions as % length of head. Snout (28·6) 31·0–38·2, juv. 27·2–30·0. Diameter of eye

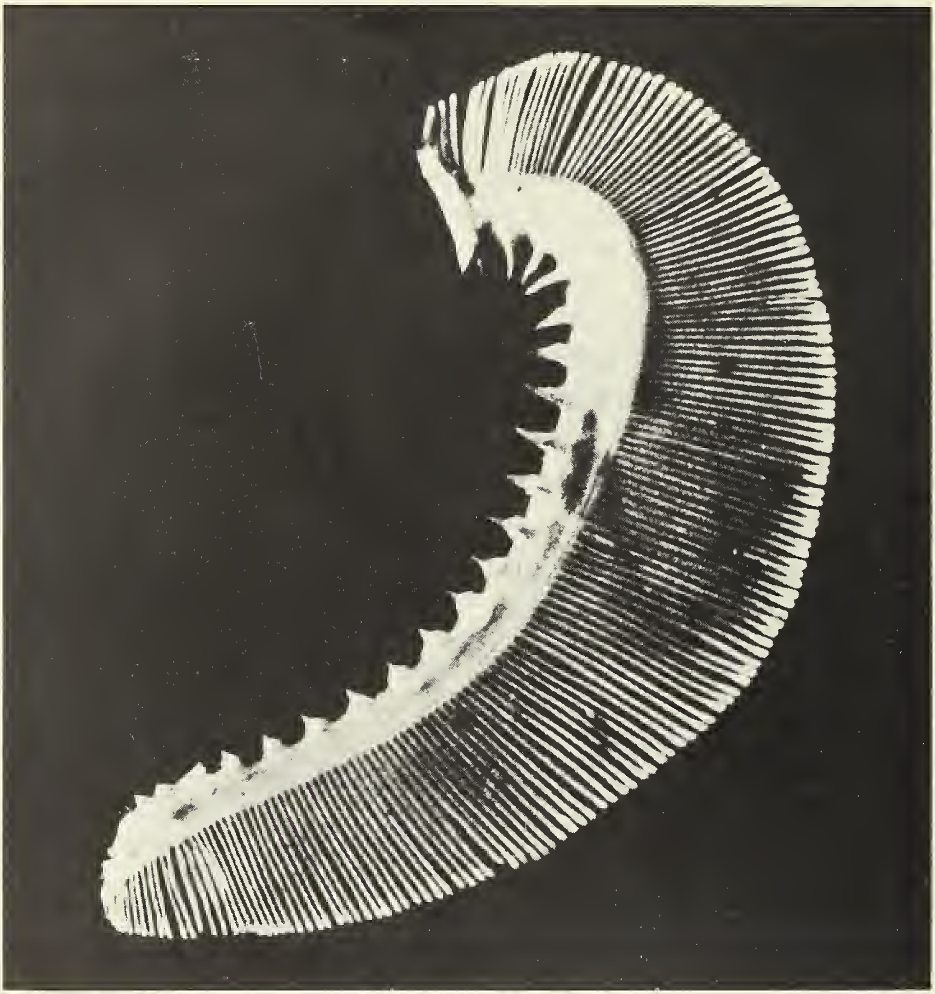

Fig. 70 *Oreochromis esculentus*, first gill-arch. From Graham, 1928, pl. X.

26–29 in the juveniles, 19·0–24·8 at SL 109–185 mm, 16·0–18·8 at 190–248 mm (see Fig. 130). Depth of preorbital 14·0–16·4 in juveniles, 16–18 at 109–140 mm, 17·0–19·9 (20·8) above this length; approximately equal to diameter of eye at 180–200 mm SL, when both are about 18–20%. Interorbital width (38·2) 41·0–47·5, juv. 36·0–41·0. Length of lower jaw 31·0–35·0 in all except a large male of 243 mm SL in which it is 36·6, although 30·8–35·0 in six males of about the same size; there seems to be no allometry.

Teeth in 2–3 series in juveniles, 3 at 100–150 mm SL and 4–5 above 240 mm; outer bicuspid, with an occasional tricuspid in some adults; inner tricuspid; 60–92 in outer series of upper jaw.

Gill-rakers (15) 16–19 (20, 21) on lower part of anterior arch, in one 19+3 very small rakers. Total number on the arch (18) 20–24 (27 in the exceptional fish), mode 22. Microbranchiospines on outer sides of 2nd, 3rd and 4th arches.

Lower pharyngeal bone in adult longer than wide: length 33·0–35·5%, width 29·0–32·5% length of head; teeth fine and crowded; blade 1·3 to twice median length of dentigerous area (10 specimens measured).

Scales on cheek usually in 3 rows, occasionally 2; between origin of dorsal and lateral line

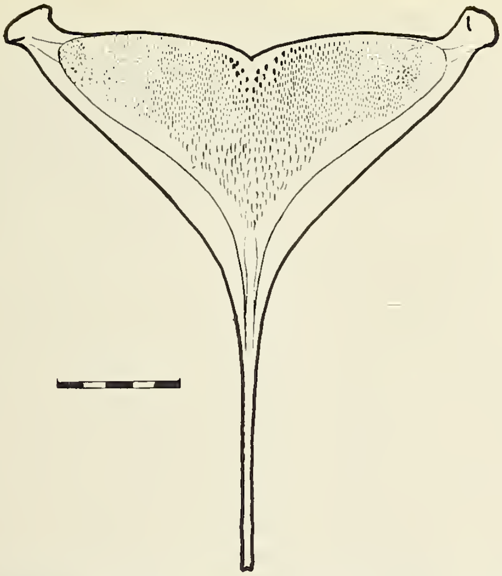

Fig. 71 *Oreochromis esculentus*, lower pharyngeal bone of a fish *ca* 200 mm SL. Scale in mm.

4–5½, usually 4½ or 5; over top of caudal peduncle above lateral line 8 or 9. For lateral line series see Table 52.

Dorsal	XVI 11	XVII 10	XVII 11	XVIII 10	Anal III	10	11	12
Frequencies	2	4	11	7		12	10	1

See also Table 52. For a doubtful record of IV anal spines see p. 209.

Caudal truncate, often rounded by wear in adult, not densely scaled, but in large specimens small scales may extend on the rays nearly to the margin and are rather dense on the upper and lower rays.

Vertebrae 30 (f.2) or 31 (f.2).

Genital papilla of male not prolonged, but may be bluntly bifid and (e.g., in the holotype, Fig. 69), have a number of short lobes of a spongy texture.

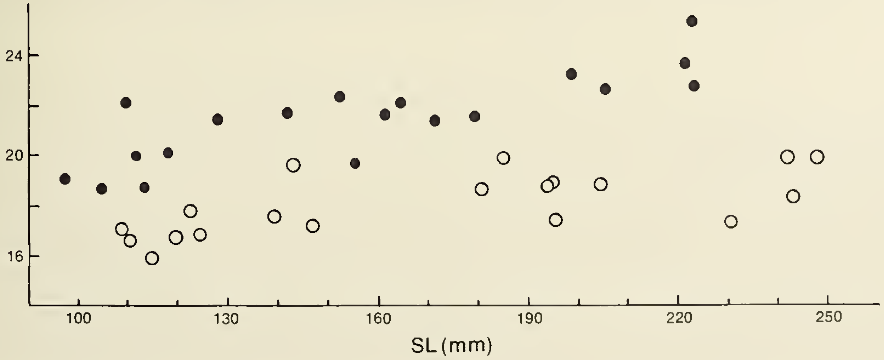

Fig. 72 Depth of preorbital bone as % length of head in *Oreochromis variablis* (●) and *O. esculentus* (○).

Table 52. Meristic characters in *O. esculentus* and *O. variabilis*. Frequencies given by Lowe (1957) are shown separately. Her gill-raker numbers are a little higher because she included the raker at the joint with the lower series. Graham (1928) recorded as few as 29 scales in the lateral line series of *O. variabilis* and XV dorsal spines in two of the forty-three specimens of the same species.

		O. esculentus		*O. variabilis*	
		E.T.	Lowe	E.T.	Lowe
Vertebrae	29			1	
	30	2		4	
	31	2		1	
Scales lat. line	31	2		11	22
	32	13	10	5	11
	33	7	12	1	1
	34	2	1		
	35		1		
D spines	XVI	2		11	11
	XVII	20	10	24	16
	XVIII	8	4	1	
D totals	27	6		4	
	28	18		26	
	29			7	
Gill-rakers on lower part	15	1			
	16	2			
	17	9		2	
	18	10	4	7	
	19	6	13	7	2
	20	1	5	6	11
	21	1	2	6	14
	22				9
	23				1

Size. Total lengths of 40 to 50 cm were quoted by Lowe-McConnell (1956:52) from the report of the Lake Victoria Fisheries Service for 1952, but fishes of more than 36 cm were rare. One of 43 cm weighed 5½ lbs (about 2·5 kg).

Coloration. General colour of female and non-breeding male olive-brown to watery green, grading to cream or silvery white below. Soft vertical fins usually with round white spots. Young with a clear-ringed, conspicuous tilapia-mark, which may still be detected up to 170 mm SL, although then not ringed.

Breeding male colours predominantly black and red, the black involving the whole ventral surface from mouth to anus, the pelvics and the anterior part of the anal fin, as well as the dorsal fin. In contrast to *O. variabilis* the dorsal fin typically has no bright red or orange border, although in a few specimens the posterior lappets and the upper edge of the soft dorsal are white as preserved and Lowe (1955*b*; Lowe-McConnell, 1956*b*:6) mentions dark crimson lappets on this fin. The white or greenish white spots on dorsal and caudal may be intensified in the male. The sides of head and body above the black area are crimson and elsewhere the scales are grey with pinkish-fawn edge (Lowe-McConnell, *loc. cit.*).

Ecology

Food

The length of the intestine was measured by Welcomme (1967*b*) in several fishes from 70 to 290 mm SL. The intestine increases in length with the length of the fish and up to 170 mm also increases in relative length. Welcomme obtained values of from 6·7 times SL at 70–110 mm to 9·1 times at 150–170 mm. Thereafter values obtained were a little lower than 9.

This is the species on which Greenwood's clarification of the feeding mechanism in *Oreochromis* was based (1953). It was the earlier, over-simplified view of the filtering function of the gill-rakers that led Graham (1929) to suppose that the planktonic organisms in the stomach must have been ingested in aggregates from the bottom film. Later evidence of the overwhelmingly planktonic nature of the food (Fish, 1951, 1955: Lowe-McConnell, 1956*b*, Welcomme, 1967*b*; Bailey *et al.*, 1978), and of the association of concentrations of *O. esculentus* with blooms of the diatom *Melosira*, established the species as a plankton-feeder using the mucus-trap mechanism combined with the combing action of the pharyngeal teeth. The fish is non-selective, in the sense that all organisms of a size capable of being retained by these means are passed into the stomach. But it is selective in that the schools follow the concentrations of diatoms in the lake (Gee & Gilbert, 1967). Payne (1971) found rotifers and flagellates also common in the gut of pond-reared individuals. He noted that its strong preference for plankton was a factor limiting its growth in ponds where plankton was scarce. Only when plankton supplies were at their lowest would it make use of supplementary foods. Bailey, Churchfield, Petr & Pimm (1978, fig. 2) also found zooplankton as an occasional, and very minor, constituent of the stomach contents in an otherwise purely phytoplankton diet in Nyumba ya Mungo reservoir. See also Denny & Bailey (Eds), 1978:149.

Lowe-McConnell (1956*b*) demonstrated that in peak breeding condition ('running ripe') the feeding of males was reduced, a high percentage having empty or only partially filled stomachs. None of the brooding females examined by her had a full stomach and in most of them it was completely empty. Welcomme (1967*b*) attempted to quantify similar observations, but the data do not lend themselves to more precise expression than Lowe-McConnell's arbitrary categories of 'stomach empty, approximately empty' etc. to 'full'. In the artificial conditions of an aquarium Cridland (1961) recorded that the small brooding females continued to feed and did not lose condition. Loss of weight in these corresponded to the weight of eggs spawned and was soon made good.

O. esculentus, like many other, perhaps all, species of tilapias, lays down a store of fat in the form of a ribbon among the intestines. Lowe-McConnell (1956*b*) recorded that this is not found in young fishes, but is macroscopically visible in those from a total length of 20–23 cms upwards. There was considerable variation in the amount of fat present in ripe males. In spent females, at the end of a spawning phase, there was generally no fat, and in several cases such females had greatly enlarged gall-bladders.

Growth

As with other species, there is evidence that the size at which breeding occurs, and probably also the rate of growth and maximum size are related to the size of the inhabited body of water. Lowe's observation (1955*a*) of a pond population at Korogwe, individuals of which had grown to 16–19 cm TL in under seven months, was not followed beyond the period of her visit. Whitehead (1959*b*) referred to 'a smaller and perhaps stunted form of *T. esculenta*' in Lake Sare, a lagoon in the swamp at the mouth of R. Yala, Kenya.

Garrod (1959) attempted to estimate the average growth-rate of sections of the Lake Victoria population. He based his calculations on the presence in the scales of rings of irregular or broken circuli, which Holden (1955) and Garrod & Newell (1958) showed to be related to the use of calcium reserves during the period of starvation accompanying sexual activity in the male and

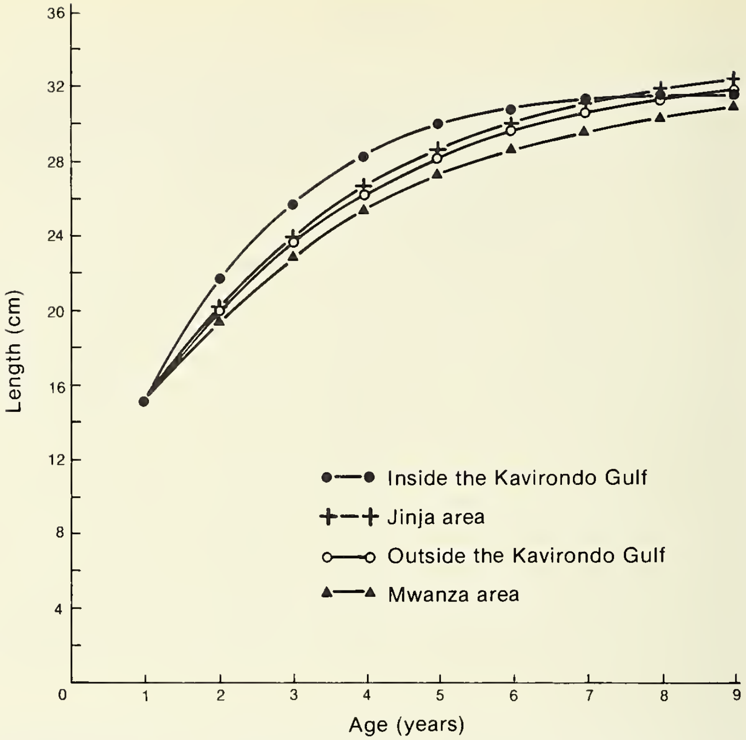

Fig. 73 Growth in length of *Oreochromis esculentus* in Lake Victoria. From Garrod, 1959.

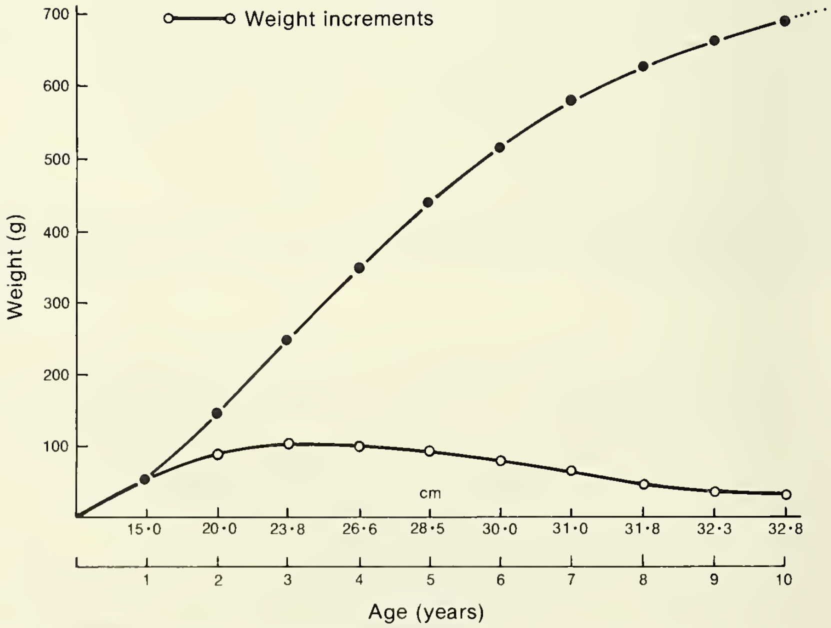

Fig. 74 Growth in weight of *Oreochromis esculentus* in Lake Victoria. From Garrod, 1959.

brooding in the female, as observed by Lowe-McConnell (1956*b*). Combining the evidence of peak breeding activity during rainy seasons with that of increased weight of fishes of a particular length-range between these seasons, Garrod (1960*b*) assumed that in the northern part of the lake an individual fish was likely to underego two breeding periods each year and in the south only one period. On this basis he used the scale-rings to calculate the tentative growth-curves reproduced in Figs 73 & 74. According to this *O. esculentus* reaches a length of about 30 cm in 9 years, and the growth-rate is the same at three of the four areas sampled. Although it is initially more rapid within the Kavirondo Gulf it declines more rapidly, so that the maximum size (or asymptotic length) is about the same as elsewhere. Throughout the lake the species appears to breed at an age of between 2 and 3 years and is full-grown at about 10 years. Both Graham (1928) and Garrod (1959) noted that, especially in the Emin Pasha Gulf, large (up to 50 cm) individuals were found of unusual shape and heavy fin-spines (Graham, 1928, pl. xi). Both authors considered that these fishes had survived there because the fishery is less exploited there than elsewhere. In one of them the number of rings on the scale (15) was the highest found and was considered to indicate an age of about ten years, thus not older than many 30 cm fishes. Garrod suggested that they were a late maturing group that had been able to maintain a higher growth-rate than the average.

In 1960, when the yield from the fishery showed a decline, there was evidence that the maximum size was slightly higher (Garrod, 1960*b*). Garrod interpreted this as the result of bigger available food supplies resulting from the reduction of the tilapia population by increased fishing intensity. This interpretation should be taken with reserve, as annual fluctuations in breeding stock and activity (also recorded by Garrod) must be taken into account.

Breeding

In a given environment the sexes grow at the same rate and mature at the same size (Lowe, 1955*a*; 1956*b*; Garrod, 1959). Cridland (1961) stated that over a period of twenty-three months the average growth of males of ten aquarium bred pairs was faster than that of females, but this is not apparent from his figures.

As with other species the size of initial breeding is determined by the environment. Garrod reports that in aquaria this may occur at 10 cm and an age of 5 months. In a pond at Korogwe, to which the species had been introduced, Lowe (1955*a*) found that both sexes had bred when they were under seven months old and had reached a length of 16–19 cm TL. In Lake Victoria the minimum breeding size was 20–21 cm, in some localities 19 cm.

Both Lowe-McConnell (1956*b*) and Garrod (1959) tested samples from known spawning areas for the percentage of 'mature' fishes at different lengths that were breeding or had bred. Lowe-McConnell obtained a lower figure for the size at which 50% were breeding in the Kavirondo Gulf than in the more open bays in the Jinja area, respectively 22 and 25–26 cm TL and a corresponding difference in the size at which 100% were ripe (resp. 26 and 28 cm) for the year 1952. A similar difference was found between the breeding populations in the relatively enclosed Smith Sound in the south of the lake and a more open southern beach at Majita. Samples taken in a later year and analysed by Garrod (1959) produced somewhat discrepant results. The length, calculated from scale-checks (see Growth, p. 215), at which 50% bred for the first time was respectively 22·5, 23·0 and 23·8 cm in the Jinja area, the Kavirondo Gulf and the southern (Mwanza) area, thus not lower in the Kavirondo Gulf. But according to Garrod's calculations the Kavirondo fishes would reach this size at an earlier age. As Garrod wrote, the discrepancy between these and Lowe's results, the latter based on observation, may reflect a real difference or may be due to sampling bias. Both authors took into account the behaviour of *Oreochromis* males (by analogy with other species), who migrate to a spawning area and defend territory there, the smaller males often being prevented by the bigger ones from holding territory and therefore also from coming into breeding condition. However that may be, it seems that the majority of individuals, when they reach 26 cm TL are breeding or have bred, and on the spawning grounds 100% of fishes of this length are in full breeding condition.

Nests were not definitely identified in Lake Victoria's turbid waters. At Korogwe pond (Lowe, 1955*a*) the nests were circular, basin-shaped pits about 30 cm in diameter, corresponding to the small size of the breeders. They were close together and more numerous than the surviving breeders. It is not known whether some of them were made by non-survivors, or whether one male may make several pits as in *O. mossambicus.* (*O. a. grahami* did this in a territorially overcrowded aquarium. See p. 385 and Coe, 1966). In aquaria each male made a single pit (Lowe-McConnell, 1956*b*:5) which he defended for a week or more in full breeding colours, during which time he would spawn with visiting females. He would then leave the nest for a few days with diminished intensity of colouring, then return and resume activities.

Spawning sites were identified in Lake Victoria as the places where ripe males congregated and predominated in numbers over the females.

Interpreting catch statistics on the basis of these known behavioural traits, Lowe-McConnell reached the following conclusions:

> Breeding fishes are found throughout the year. Data from certain areas showed that these were spawning grounds, namely Hannington Bay and Pilkington Bay (but not Ekumu Bay) in the Jinja area; Kavirondo Gulf in the east; Smith Sound and a beach at Majita in the south. In the north peak numbers of breeding fishes were found on the spawning grounds in April and October, the two rainiest months of the year. In the south most breeding activity occurred in October to May in Smith Sound, but at Majita Bay no marked diminution of spawning was noted at any time in the year of investigation.

The Smith Sound spawners were probably drawn from a relatively local and homogeneous population, whereas Majita possibly attracted all the ripe males from a wider area.

The ovaries show that a female may have a succession of three or more broods in a spawning period, and it was surmized that this would be followed by a period of rest. Males remain sexually active for a long period. Cridland (1961) recorded seven broods from one pair in twenty-one months.

Ripe ovarian eggs are pear-shaped, with a long diameter of about 4·5 mm (Lowe, 1955*c*). Lowe found some evidence that fewer eggs were produced in the last brood of a series than the first (but this was not confirmed in Cridland's aquarium experiments), and also that the maximum number produced increased with the size of the female, ranging from 324 in a fish of 17 cm TL to 1672 in one of 36 cm (See also Lowe-McConnell, 1975:219).

Females brooding eggs in the mouth were sometimes caught with ripe males, but more often they had moved off to the shelter of weed beds or swampy places. The young become independent at a length of about 15 mm.

The young were found by Lowe in 1952 in channels in papyrus swamp. Newly released young were most abundant in such nurseries in the Jinja area in November, and by tracing this abundant age-group through subsequent months Lowe estimated the minimum growth at about 1 cm per month. The fishes were estimated to be about one year old at 12 cm.

With the rise in lake level in the early nineteen-sixties lagoons were formed in the flooded land behind the papyrus swamps. In contrast to *O. variabilis*, some *O. esculentus* entered these pools, and ripe males and brooding females were found among them. The flooded grassy margins of the pools were occupied by the early stages (Welcomme, 1964*e*).

Movements

Like other species of *Oreochromis*, fishes of this species move to different zones or biotopes during their life-history. At about 12 cm total length they move from the nurseries into open water and there is evidence that at this stage they school together. Inshore and offshore movements affecting a wide range of size groups have been observed to occur at widely separated parts of the lake at the same time, but by what environmental event they are initiated is unknown.

Among the results of experimental trawling in the open lake Gee & Gilbert (1967) record that *O. esculentus* was the only tilapia caught over muddy bottoms. Its preference for muddy bays is illustrated in the map of fig. 304 in Fryer & Iles (1972).

Marking experiments show that individual fishes may travel considerable distances, but one fish recaptured after fourteen months 150 miles from the point of release was exceptional. Others have been recaptured after 229 to 700 days close to the place where they had been marked. The records suggest that the fishes show some conservatism in their location, but move about enough to ensure a long-term homogeneity of the lake population.

As Graham (1929) already found, this species does not ascend affluent rivers as *O. variabilis* does. Whitehead (1959*b*) also noted the absence of the species from the eastern affluent rivers, although a few *O. esculentus* fry might occasionally be found among the schools of *O. variabilis* entering river mouths.

Hybrids

Hybridization with *O. amphimelas* in Lakes Kitangiri and Singida is described on p. 398 and Table 99, and there will be found the evidence for identifying one parent as *O. esculentus* and for believing it to be introduced. Mann's report (1965) on Lake Kitangiri was written before the analysis of this earlier collection was published (Trewavas & Fryer, 1965), and he referred to the tilapias as *Tilapia* A, B and C. I have examined ten of Mann's specimens at the laboratory at Jinja and found among them only one *O. amphimelas.* Five others labelled *Tilapia* B and two labelled *Tilapia* A are *O. esculentus.* Two other '*Tilapia* B' are probably also *O. esculentus,* the only details suggesting a possible contribution from *O. amphimelas* being the low number of dorsal spines (XV) in one, 16 gill-rakers on the lower part of the arch in both (but 18 on one side in one), numbers not unknown though rare in *O. esculentus* and too high for pure *O. amphimelas,* and the slightly concave dorsal profile of the head. If this collection was representative of the population it may be that by 1964 conditions in Kitangiri had enabled the two species to keep apart. It seems that *O. esculentus* had maintained its position in the lake.

In Lake Singida only one fish in a collection including eight *O. esculentus* and four *O. amphimelas* appeared to be a possible hybrid (Table 99 on p. 399). It has the numbers of fin-rays and gill-rakers characteristic of *O. esculentus,* but a short pectoral fin and reduced series of microbranchiospines suggest an admixture *O. amphimelas.*

Distribution

NATURAL DISTRIBUTION. Lake Victoria, Lake Nabugabo, Lakes Kioga and Kwania, and the Victoria Nile above the Murchison Falls; the Malawa River, Uganda and 'Lake Gangu, west of Lake Victoria' (exact location not discovered). When Okedi *et al.* (1976) explored the Kagera River in 1974 they found *O. esculentus* only at the mouth, although other species penetrated to the Upper Kagera. Whitehead too (1959*b*) in the eastern tributaries of Lake Victoria found young *O. esculentus* only in pools in the swamp that blocks the mouth of the Yala River, whereas dense schools of young *O. variabilis* migrated upstream.

Reports on the recent status of the population in Lake Victoria vary. After 1954, when *Tilapia zillii* was introduced into the lake, *O. niloticus* and *O. leucostictus* also appeared there, probably introduced incidentally with the *Tilapia* (Lowe-McConnell, 1956*b*:2). It was later supposed that *O. niloticus,* which became very successful, had displaced *O. esculentus.* Wanjala & Marten (1976) wrote that the latter had 'virtually disappeared' from Kenyan waters, but the trawling survey of 1969–1971 by Kudhongania & Cordone (1974) found that in the waters explored the biomass of *O. esculentus,* estimated as 11 829 metric tonnes, was greater than that of any other *Oreochromis.* One may question the reliability of the identification.

DISPERSAL BY MAN. This species was taken to the ponds at Korogwe, Tanzania, in 1950 (Gould, 1951; Lowe, 1955*a*) and thence was distributed to some dams in Tanzania, but without exact records. Bailey (1966, table III) recorded the locations of dams in which he found it in 1963–4, and these ranged from the coastal zone and the foot of the Usambara and Pare ranges, through the eastern Rift area and the Central Plateau, to Iringa and Njombe in the Southern Highlands. To some other localities it may have been taken from ponds at Kajansi and Mwanza. It was identified in Lake Kitangiri where it was interbreeding with *O. amphimelas* (Trewavas & Fryer, 1965, and see pp. 219 & 398). It was believed to have entered this lake from dams in the Williamson Diamond Mines district via the River Manonga, that flows from the mining area to enter Lake Kitangiri at its northern end.

Lake Singida was stocked from Korogwe with species probably including *O. esculentus* (see p. 399); and Lake Babati, a small lake 16–19 km long and 3–6 km wide situated about 168 km south of Arusha, has been reported to contain this species as its most abundant tilapia (Nhwani, 1975), probably also the result of stocking, directly or indirectly, from Korogwe. The man-made lake Nyumba ya Mungu in the upper Pangani now contains a significant biomass of *O. esculentus*, believed to owe its presence in the Pangani system to earlier stocking from Korogwe (Bailey *et al.*, 1978).

In Lake Singida, as in Kitangiri, there is some evidence that hybridization has occurred between *O. esculentus* and *O. amphimelas* (see p. 399), but in the Nyumba ya Mungu Reservoir *O. esculentus* and the native Pangani species seem to have kept apart. A verbal report from Dr A. I. Payne records that in 1980 *O. esculentus* in Nyumba ya Mungo was the most abundant species in the catches but remained small in size.

O. esculentus has been tried in several small dams in Uganda (Lowe, 1955*a*), and Payne (1971, 1974) made a study of it in ponds and dams in Tanzania, near Lake Victoria, but unless waters are rich in plankton it does not make good growth.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1928.5.24.99 (holotype)	231	L. Victoria	M. Graham
1928.5.24.58–67 (paratypes)	146–294	L. Victoria	M. Graham
1928.5.24.68–77 (paratypes)	109–260	L. Victoria	M. Graham
1928.5.30.1–6 (paratypes)	219–270	L. Victoria	M. Graham
1928.5.30.7–12 (paratypes)	163–246	L. Victoria	M. Graham
1906.5.30.455	256	nr. Entebbe, L. Victoria	Degen
1906.5.30.457	255	Buganga, L. Victoria	Degen
1911.3.3.164	240	Ripon Falls, L. Victoria	E. Bayon
1911.3.27.22	169	Victoria Nile, between L. Kyoga & Murchison Falls	F. H. Melland
1929.1.24.226–239	182–191	L. Kyoga	E. B. Worthington
1933.2.23.120	203	L. Nabugabo	E. B. Worthington
1935.8.33.16–26	199–225	L. Nabugabo	C. R. S. Pitman
1967.3.18.4–5	185, 195	Sesse Is. L. Victoria	R. H. Lowe (1950)
EAFFRO (not preserved)	204	Masesse fish-market	E. Trewavas
1962.2.6.69–71	84–152	Malawa R., Uganda	M. P. Cunningham

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1912.1.25.22–28	36–49	L. Gangu*, W. of L. Victoria	G. M. Woodhouse
1965.7.8.1–3	119–269	L. Kitangiri, Tanzania	J. G. Lockley & G. Fryer
1966.7.14.153–159	103–175	L. Singida, Tanzania	R. G. Bailey
1975.10.7.103–107	110–149	Nyumba ya Mungu, Pangani system	R. G. Bailey
1981.7.7.58	112, 136	Nyumba ya Mungu	A. I. Payne
Hybrids with *O. amphimelas*			
1965.7.8.9–12	150–235	L. Kitangiri	J. G. Lockley & G. Fryer

*In spite of efforts, no one has since located this lakelet. These specimens were assigned by Boulenger to *T. eduardiana.*

Oreochromis leucostictus (Trewavas)

Tilapia nilotica (part) Boulenger, 1914:253; (Lake Albert); *idem*, 1915:162 (specimens 239, 240 & 242, Lakes Albert & Edward); Worthington, 1932:28 (Lakes Edward & George).

Tilapia leucosticta Trewavas, 1933:318, fig. 3B (Lake Edward/George); David & Poll, 1937:256 (Lake Edward); Poll, 1939:36, fig. 14 (Lake Edward & Rutschuru R.); Poll & Damas, 1939:35, figs 13, 37; Rep. EAFRO, 1953 (1954):18, 20, 36, 38 (bionomics); Lowe, 1955*b*; *idem*, 1955*c*:46–52, fig. 2 (egg), tables I and II; *idem*, 1957; Elder & Garrod, 1961 (hybrid with *O. s. niger*); Garrod, 1963 (growth increments); Greenwood, 1963:68 (in Aswa R.); Thys van den Audenaerde, 1964:108, fig. 18 pl. x (taxonomy); Welcomme, 1964*a–d* (ecology); *idem*, 1964*e*:133 fig. 5 (juv.); *idem*, 1966*a–c*; *idem*, 1967*a* & *b* (bionomics in Lake Victoria); Gewalt, 1966 (hot-spring biotope, Ruwenzori); Elder, 1966 (in Lake Naivasha); Hyder, 1969 (histology of testis); Jochen, 1969:231, 1 fig. (behaviour in aquarium); Elder, Garrod & Whitehead, 1971 (hybridizing with *O. s. niger* in Lake Naivasha); Goldstein, 1973: fig. on p. 240 (?); Loiselle, 1975 (photos); *idem*, 1977*b* (behaviour in aquarium); Siddiqui, 1977 (bionomics in Lake Naivasha).

Sarotherodon leucostictum; Mayland, 1978:305, fig.; Staek, 1975, fig. 263.

Tilapia trewavasae Poll, 1939*a*:37, figs 15 & 17 (Rutshuru R., southern affluent of Lake Edward).

TYPES. Syntypes: Two females of 209 and 216 mm SL and an immature fish of 163 mm, from Lake George and Kazinga Channel, coll. E. B. Worthington 1930–31, BMNH 1933.2.23.122–124.

Types of *T. trewavasae*: holotype, 185 mm SL from Rutschuru R. at May ya Moto; paratypes, 75–105 mm from Rutshuru R. and its tributary Molindi R., coll. G. F. de Witte; MRAC R.G.64789–64794.

Distinguishing characters

An *Oreochromis* in which the lower jaw is not longer than 34% of the head, the preorbital depth not more than 23·2%; the teeth of jaws and pharynx are very small, those of the lower pharyngeal restricted to the posterior part of the pad; the dorsal fin is usually without a red marginal band (but see Staek, 1975, fig. 263). The general colour of adults is dark olive-green with pearly white spots on the body, especially in an area above the anal fin, and in a dark reticulum on caudal fin; the genital papilla is intensely white in both sexes. Vertebrae 27–29, mode 28; scales in the lateral line series 28–30 (31, 32).

Description

Based on the three syntypes, and two males of 183 and 232 mm SL respectively from Lake Edward, with meristic data and separate proportions for six young of 57–98 mm SL from Lake Edward; and on ten of 124–208 mm SL from Lake Albert.

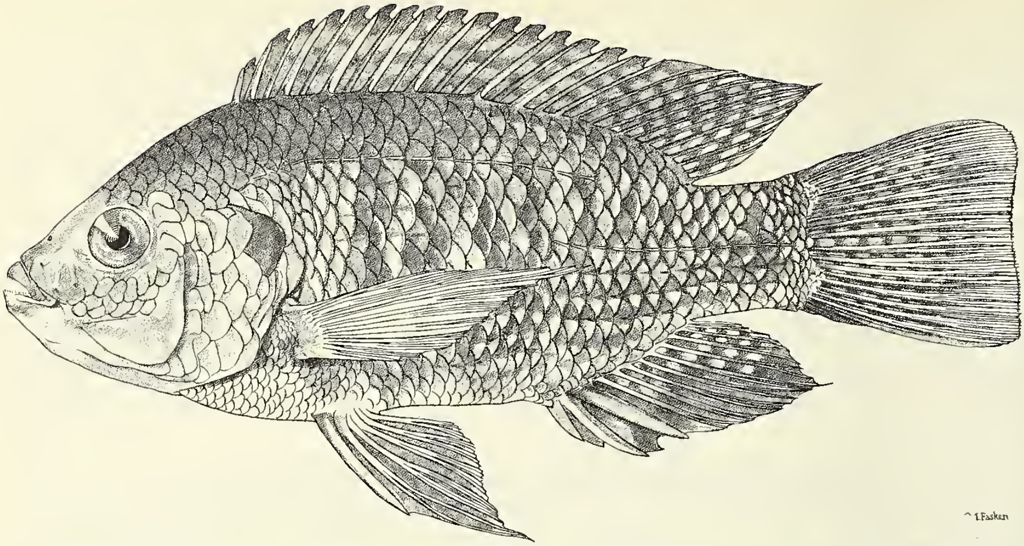

Fig. 75 *Oreochromis leucostictus*, Syntype, female of 216 mm SL. Drawn by M. Fasken.

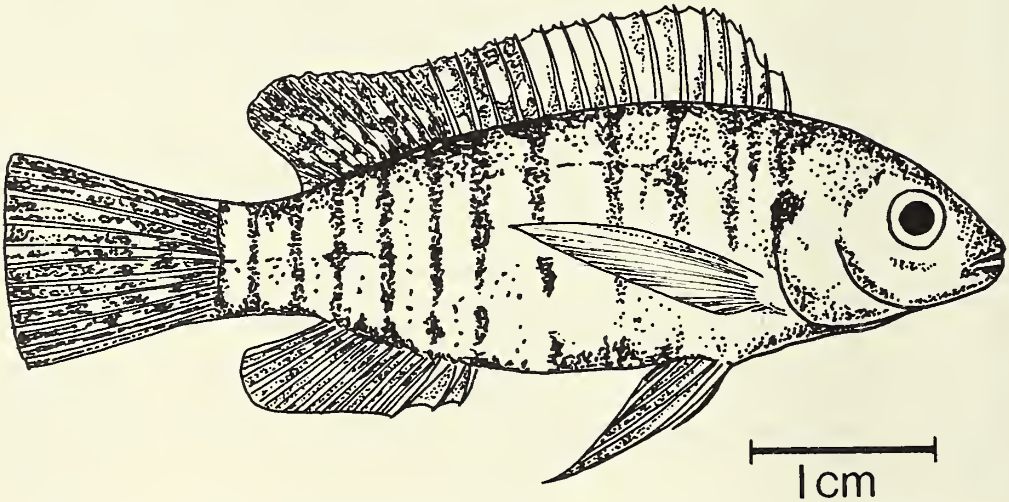

Fig. 76 *Oreochromis leucostictus*, juvenile of 44 mm SL. After Welcomme,. 1964*e*, fig. 5.

Proportions are set out in Table 53.

There is no firm evidence of difference in proportions between the populations of Lakes Edward/George and Albert, although the samples are too small and do not provide enough of corresponding sizes for satisfactory assessment. From 57 to 86 mm SL we have specimens only from Lake Edward, from 123 to 195 mm SL one from Lake George and eleven from Lake Albert, from 208 to 232 mm SL four from Lake Edward and only one from Lake Albert.

Lowe-McConnell (1957) states that the fin spines are longer and stronger in Lake Albert than Lake Edward, but where I can compare specimens of equal size I find:

at 125·0 mm in Lake Albert 3rd anal spine 15·7% SL
at 123·5 mm in Lake George 3rd anal spine 14·5% SL
at 208·0 mm in Lake Albert 3rd anal spine 15·9% SL
at 209·0 mm in Lake George 3rd anal spine 15·3% SL

Table 53. *Oreochromis leucostictus.* Proportions in samples from Lakes Edward/George and Albert and in six young from Lake Edward.

SL (mm)	123·5–232	57–98
Proportions as % SL		
Depth	38·8–47·0	38·7–44·0
L. head	33·0–37·0	35·3–37·4
L. pect. fin	35·0–43·0	34·8–40·8
L. 3rd anal spine	12·3–15·3 (Ed./G'ge)	14·8–17·0
	14·8–18·1 (Albert)	
L. caud. ped.	10·0–12·3 (Ed./G'ge)	10·8–14·0
	8·2–11·8 (Albert)	
Caud. ped. l/d	0·65–0·75 (Ed./G'ge)	0·65–0·9
	0·5–0·72 (Albert)	
Proportions as % l. head		
L. snout	31·3–38·8	28·5–33·4
Eye	18·5–24·0 (Ed./G'ge)	28·0–30·6
	20·4–23·3 (Albert)	
Depth preorb.	18·0–21·5 (Ed./G'ge)	16·4–17·5
	18·7–23·2 (Albert)	
Interorb.	37·8–44·3 (Ed./G'ge)	33·8–38·8
	36·8–43·5 (Albert)	
Lower jaw	29·6–34·0	27·7–30·0
W. lower phar.	30·0–33·5	30·5–32·4
L. lower phar.	29·0–35·5	30·0–36·5

These differences cannot be considered significant, but they are in the same sense as in the bigger samples of Lowe (see also Table 52).

Eye and preorbital are aproximately equal at 140–208 mm SL in Lake Albert. In Lake Edward of the three specimens of 183–216 mm SL only in that of 216 mm does the preorbital reach equality with the eye.

Teeth very small, in 4–6 series (up to 8 in larger specimens according to Lowe, 1957); with slender shafts in young and medium-sized specimens, stouter in large; outermost bicuspid, inner tricuspid.

Gill-rakers (3–5) + 1 + (19–23) on the first arch. Microbranchiospines on outer surfaces of 2nd, 3rd and 4th arches.

Lower pharyngeal bone (Fig. 77) slender, its width usually less than, occasionally equal to, its median length. Teeth very fine and crowded, restricted to the posterior part of the pad in adult; blade 1·3–2·9 times the median length of the tooth-bearing area. The flanges on either side of the apex of the triangular area are unusually broad.

Scales on cheek in 2 series, rarely one or two scales of a third; in lateral line series 28–30 in Lake Albert, 29–31 in Lake Edward/George; between origin of dorsal and lateral line 3–4½; over top of caudal peduncle above lateral line 7.

Dorsal fin: see Table 54. Lowe-McConnell, using a larger sample, also found (1957) that the modal number of spines is XVI in Lake Albert and XVII in Lake Edward. The modal total number of rays in our samples is the same in both lakes, but the mean is slightly higher for this small sample in Lake Edward/George. The 'Ruwenzori' sample of Table 54 will be mentioned below.

Anal III (IV) 9–10 in Lake Edward/George, III 9–11 in Lake Albert. Four spines have been found in only one specimen, a syntype, although Lowe checked numerous specimens for this character.

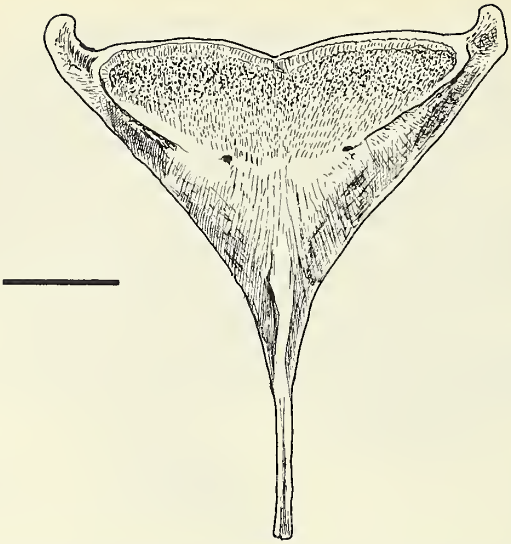

Fig. 77 *Oreochromis leucostictus.* Pharyngeal bone of a fish 210 mm SL. Scale = 10 mm.

Table 54. Dorsal rays in populations of *O. leucostictus.*

Dorsal	XV 12	XVI 11	XV 13	XVI 12	XVII 11	XVI 13	XVII 12	XVIII 11
Edw/George				2	4		5	
Ruwenzori	1	1	1	7	3	2		1
Albert	1	1		7	1	1		1

Total dorsal rays	27	28	29
Edw/George		6	5
Ruwenzori	2	11	3
Albert	2	8	2

Soft dorsal rays extend from a little beyond the base of the caudal (♀) to the middle of the fin (♂) in the lake specimens, farther in large specimens stocked in the Teso dams (Lowe, 1957).

Vertebrae in Lake Edward/George 28 (f.2) or 29 (f.3), in Lake Albert 27 (f.2) or 28 (f.5), in the streams or pools near Bundibugwo, Semliki catchment, 27 (f.2), 28 (f.7) or 29 (f.2).

Genital papilla small, but white and conspicuous throughout life, crenellated in mature fishes of both sexes.

Coloration. Life colours have been described by Damas (in Poll & Damas, 1939), Lowe-McConnell (1957:356), Welcomme (1964*d*, *e*, young), Jochem (1969), and I add my personal observations.

Usually dark olive green with whitish spots on the flanks formed by the paler centre of each scale. In an aquarium these spots were described by Loiselle (1975) as silvery green. If a pattern is present on the caudal fin it consists of bluish white spots in a dark reticulum, but this may be restricted to the base or middle of the fin or masked by melanin. Colouring in general rather rich with a plentiful admixture of melanin that becomes concentrated in the lower parts in the breeding male and the pelvics of the breeding female. The iridescence of the opercular blotch and the preorbital bone produces a dark violet effect.

The whole body of the breeding male may become very dark blackish to blue-green, but intense white spots stand out on the body above the anal fin. The iris becomes bright yellow and in life is crossed by an oblique dark bar. The dorsal margin may then have some red colour

(Staek, 1975, fig. 263), but this is mixed with melanin, is not the opaque bright red of e.g. *O. aureus* and disappears as the fish dies, leaving the lappets black. The lower lip may be bluish green or greenish white in the living male, but becomes dark in preserved fish. The branchiostegal membrane may have yellow patches in non-breeding fishes and ripe females, but is black in brooding females.

The genital papilla is intense Chinese white in both sexes throughout life.

The young have 8–12 dark vertical bars on the body and the tilapia-mark is an indistinct marbling on a yellowish background, no longer distinguishable at 65–70 mm SL.

The colour-photograph by Hilmar Hansen reproduced in Goldstein (1973) is not typical. The bigger mouth and general appearance suggest a young *O. aureus*.

Ecology

Food

Poll & Damas (1939), followed by Thys (1964) record that in Lake Edward the food consists of phytoplankton. Other reports stress the importance of bottom deposits in Lake George, Lake Albert, in ponds and dams in which the species is stocked and in the lagoons fringing Lake Victoria (Fish, 1955; Lowe-McConnell, 1957; Welcomme, 1970) and also in the more inshore zone of Lake George (Moriarty, in Pullin & Lowe-McConnell, 1982). Welcomme found that whereas rhizopods and diatoms were digested, green and blue-green algae reached the end of the gut unchanged. Moriarty *et al.* (1973:311) record briefly that in the open waters of Lake George *O. leucostictus*, like *O. niloticus*, feeds on the dense phytoplankton of that lake, in which the blue-green alga *Microcystis* preponderates. They imply that, as in the case of Lake George *O. niloticus*, the impression that planktonic algae were not digested (Fish, 1955) was due to the failure to appreciate the diel rhythm of feeding and digestion, as a result of which the food intake at certain periods would pass directly to the pyloric end of the stomach from the oesophagus, failing to spend time in the fundus of the stomach, where alone the acidity is sufficient to lyse the membranes of most green and blue-green algae. If therefore, the intestinal contents are examined in the morning, the food in the lower end of the intestine is what has been ingested before the stomach has filled and expanded, and the impression is gained that these tougher organisms are not assimilated.

Lake George is, however, exceptional in maintaining a dense standing crop of plankton throughout the year, and in other localities bottom deposits may be a more important source of food, as Lowe and Welcomme report. But Welcomme's observation that apart from diatoms, green and blue-green algae are not digested may point rather to a different rate and period of digestion of these items, with wastage of the tougher organisms at the beginning of the feeding period.

Siddiqui (1979) also noted a preference for detritus in the introduced population in Lake Naivasha, but there he reported chironomid larvae to be the main food item.

Size and growth

Lowe-McConnell (1957) quotes a growth in ponds to 9 cm and 20 g in about three months. Welcomme estimated, by the method of progression of modes, a mean growth-rate of about 6 mm in SL per month for the first six months in the lagoons of Lake Victoria.

Garrod (1963) calculated growth increments per unit time for fishes between 16 and 28 cm from tagging data in Lake Victoria. His results fell into two groups with asymptotic lengths respectively of 30 cm and 28 cm, consistent with observed maximum sizes of male and female of this species. This method did not permit conclusions on growth rate of younger fish so that we have no estimate of the growth throughout life and age reached in open waters.

Together with a smaller length at sexual maturity, Welcomme found a lower condition factor in the most isolated of the lagoons investigated by him.

Further studies of the growth of the introduced population in Lake Naivasha were made by Siddiqui in 1974–5 (Siddiqui, 1977). At this time the lake level was evidently higher than at the time of the studies of Elder & Garrod (compare fig. 3 of Elder, Garrod & Whitehead, 1971, with fig. 1 of Siddiqui, 1977). This would favour the increase of *O. leucostictus*, and in fact Siddiqui stated that neither within the papyrus belt nor outside it did his catches include *O. s. niger* nor hybrids of this species with *O. leucostictus*, but only pure *leucostictus*. Siddiqui's figures for growth therefore referred only to the latter. He did not give separate figures for growth in a lagoon and in the open lake, but mixed the catches from three fishing stations, two of which were respectively 30 and 25 m beyond the papyrus belt, the third a lagoon within the papyrus zone. In agreement with other studies, he found that the maximum sizes attained were greater in males than in females, males reaching a total length of 310 mm, females rarely more than 280 mm, thus close to the maximum sizes in open waters of Lake Victoria.

Environmental requirements

Lowe-McConnell (1957) suggested that in Lakes Edward and Albert *O. leucostictus* was ecologically complementary to *O. niloticus* in the same way that in Lake victoria *O. variabilis* is related to *O. esculentus*. But the behaviour of *O. leucostictus* in Lake Victoria since its introduction there shows that the correspondence is not exact. Although the food of *O. variabilis* and *O. leucostictus* is similar, neither their feeding grounds nor their breeding and brooding areas strictly coincide.

Welcomme's reports (1964–1967) on the success with which this species colonized the shallow lagoons forming round Lake Victoria when the water level rose, show that it is more tolerant of the fluctuating conditions in such biotopes, especially of low oxygen concentrations, than either of the endemic species of Lake Victoria or other introduced species. It is also tolerant of high temperatures, up to 38°C (Welcomme, 1964*d*:20). Even in its native lakes Lowe showed that it is essentially a species of lagoons, especially closed or nearly closed lagoons, and it is only in such parts of Lakes Albert and Edward/George that it outnumbers *O. niloticus*. Damas (*in* Poll & Damas, 1939), who fished in more open waters near the western shores of Lake Edward, found that there *O. niloticus* was the more abundant, as it is also in Lake George.

In Lake Naivasha, Elder *et al.* recorded its preference for lagoons within the papyrus belt in contrast to *O. s. niger*, which preferred the open lake within about 46 m of the papyrus fringe (see Elder *et al.*, 1971: tables 14–16 and fig. 9). At reduced lake levels, with reduced flooding of the papyrus, *O. leucostictus* had been forced to use the same breeding grounds as *O. s. niger*, with the consequent production of hybrids, which were abundant at the time of the visits of Elder and Garrod in 1961–2 (recorded in Elder *et al.*, 1971). Although this was a time of severe floods, it followed a period of very low lake level when the papyrus mat had settled on the bottom. In 1974–5 Siddiqui (1977 & 1979) found that the lake level had risen and the hybrids were rare and more nearly resembled *O. leucostictus*. *Oreochromis s. niger* had disappeared. Any future studies of *O. leucostictus*, in Lake Naivasha should take account of the possibility that its genome may retain traces of its brief encounter with *O. s. niger*. Phenotypic evidence (in breeding colour) of such admixture was found, in 1962 by Elder and Garrod (Elder *et al.*, 1971:129), in individuals which otherwise, in appearance and habitat, resembled *O. leucostictus*.

Gewalt (1966) described a pool in the Mongello stream, where cool water from the Ruwenzori forest mixes with that of numerous hot-springs. Here he found numerous small *O. leucostictus*, up to 85 mm TL. The temperature in the pool ranged from 27°C to 82°C, the pH from 7·0 to 9·0, according to the proximity of the hot springs, and the fishes were most abundant near the point of entry of the cool stream. When they fled from the net they did not hesitate to swim through water up to 70°C, although in the highest temperatures they did not linger.

The specimens listed below from Bwamba and near Bundibugyo evidently came from the same system of streams and swamps fed by hot-springs. Mr Ridley (pers. commn) gives an account of the 'Mongiro River' (probably another spelling of Mongello); at the point where he collected, '*Haplochromis*' sp. was more abundant than *O. leucostictus*.

The specimens taken alive to Berlin by Gewalt soon grew in aquaria to a total length of 13 cm, so the small size of the collected individuals was evidently not genetically based.

Oreochromis leucostictus is less lake-bound than some species, as witness Poll's record of it in R. Rutschuru (1939*a*) and Welcomme's (1967*b*) of its occurrence in affluent rivers of Lake Victoria after its introduction there, although at opportunity it colonized areas of lateral flooding.

Breeding

Sex ratio. Both Lowe-McConnell (1957) and Welcomme (1970) noted that differential movements of the sexes made it difficult to determine a sex-ratio. Elder *et al.* (1971) pointed out that mesh size of the nets acting on differential size of the sexes added a complicating factor, and they claim no biological significance for their figures. Siddiqui (1977), however, based an estimate on his figures and arrived at a factor of 1·0 : 0·5 in favour of males. His tables 1 and II show his data classified respectively on month of capture and on size-classes. The monthly ratios ranged from 1·0 : 0·2 to 1·0 : 0·7 (1·0 : 0·0 at the highest size. The difference between the two ratios suggests that this estimate too may be affected by differential movements of the sexes, but in only one month (Nov. 1974) were females in excess of males. This was a month in which catches included a rather high percentage of brooding females, though not the highest (Siddiqui, 1977, fig. 3). A high percentage was caught in April 1975, when the sex ratio in the catches was 1·0 : 0·49. The fact that Siddiqui mixed the catches from his three fishing stations, not necessarily in equal numbers, introduces an unknown factor. Some support for his conclusion derives from the ratios in the size classes below the minimum breeding size, which are near the average.

Even if we could rely on this ratio, the history of hybridization in Lake Naivasha means that it may not be normal for the species.

Breeding season. The habitats of *O. leucostictus,* both original and resulting from the activities of man, are so near the Equator that changes in length of day are negligible and temperature is relatively constant. Hyder (1970) and Siddiqui (1977) carried out studies throughout a year or more, both on the introduced population of Lake Naivasha. Hyder used catches made fortnightly in one area for sixteen months, Jan. 1968 to end of April 1969, an area chosen because it was a brooding site. Siddiqui fished fortnightly in three places over a period of twelve months in 1974–5. Both authors found ripe males and females in every month of the year, and Siddiqui found no evidence of a restricted season or a peak reproductive period. Hyder, however, found a peak in gonadal activity in February–March of both years, and that in the months July to September the gonads of the majority were in a quiescent state. By correlating these fluctuations in reproductive activity with temperature, sunshine and rainfall, Hyder came to the conclusion that gonadal development was favoured by periods of high temperatures and clear skies with sunshine, and that the actual spawning was probably triggered by the onset of rains following such periods. Persistent rainy periods were accompanied by a check on breeding activity. Hyder's results point rather to responsiveness to environmental conditions than to an established rhythm and are consistent with Welcomme's (1967:266–7) failure to find any such rhythm in Lake Victoria.

Size at maturity. Table 55 shows that in Lake Albert, in Butiaba Lagoon, and in populations of ponds and dams stocked ultimately from Lake Albert, the maximum sizes attained and the minimum size at sexual maturity are both higher in males than in females. The same sex differences were found by Siddiqui (1977) in Lake Naivasha, the males becoming ripe from 18 cm TL, the females from 16 cm. His biggest brooding female measured 28 cm TL, but he recorded the fecundity (number of ripe ovarian eggs) of an exceptionally big female of 32 cm, a size usually only attained by males. In Lake Edward/George, however, Lowe found no sex differences in either the maximum size or the size of maturity in her samples.

In the lagoons of Lake Albert and Lake Victoria fishes were found breeding at a smaller size than in either main lake. In Lake Victoria differences were found between the more isolated lagoons and those with freer communication with the lake (Welcomme, 1966*b*, 1967*b*), the mini-

Table 55. Maximum lengths observed and minimum sizes at sexual maturity in *Oreochromis leucostictus* in different environmental conditions. From Table III of Lowe-McConnell (1957:373) with additions from later authors. Welcomme's SL has been converted to TL with the aid of his formula.

Type of water	Place	Maximum TL (cm) recorded ♂	♀	Minimum size (TL) of maturity observed ♂	♀	Author
Lake	Edward	23	24	22	21	Lowe (1957
	George	27	30	26	26	Lowe (1957)
	Albert	28	20	15	14	Lowe (1957)
	Victoria	30·5	28·0	—	—	Garrod (1963*b*)
				20·7	17·3	Welcomme (1967*b* & 1970)
	Naivasha	—	—	15	15	Hyder (1970)
	Naivasha	—	—	18	16	Siddiqui (1977)
Lagoon	Butiaba (L. Albert)	20	17	14	10	Lowe (1957)
	Ntoroko (L. Albert)	19	—	17	—	Lowe (1957)
	L. Victoria					
	most isolated	24		13·4	8·9	Welcomme (1970)
	intermediate	28		15·8	10·7	Welcomme (1970)
	least isolated	36		17·0	11·6	Welcomme (1970)
Dam	Opuyo (Teso)	32	26	30	22	Lowe (1957)
	Kidetok (Teso)	29	21	24	20	Lowe (1957)
Pond	Kajansi (Uganda)	17	16	14	12	Lowe (!957)
	Kisumu (Kenya)	16	14	8	7	Lowe (1957)

mum size of breeding being lower in the former. Welcomme attributed this to the entry of larger males from the main lake into the less isolated lagoons and their ousting of the smaller males from the breeding sites. If this hypothesis were correct we should expect higher percentage increases in the steps of the series for males than for females. In fact the reverse is true and other explanations come to mind such as higher temperatures resulting from the shallowness of more isolated lagoons, as well as lower oxyen concentrations.

Four of the specimens collected in the hot-spring-fed pool at the foot of Mt Ruwenzori (see p. 226) were ripening females of 79–98 mm SL, thus comparable in size to breeding females in the open lagoons of Lake Victoria.

Welcomme (1967*b*) noted that the length at which fishes of this species become mature in Lake Victoria is the same as in Lake Albert and lower than in Lake Edward/George. Since the Lake Victoria stock was derived from Lake Albert the possibility of a genetic difference presents itself, but remains a question until the several influencing factors can be analysed.

The minimum age of breeding is known only for Kajansi Pond populations, where it is three months at a total length of about 9 cm (Rep. Uganda Game & Fisheries for 1954–5).

Hyder (1970) has given an account of the histology of the testis and a gross classification of stages of testicular development based on his results. Siddiqui (1977) described the naked-eye appearance of these stages in both ovaries and testes, so that from the work of both Siddiqui and Hyder the gross appearance may be equated with the histology. Hyder interpreted his evidence as indicating that the activity of the interstitial tissue in the testes influences the produciton of nuptial coloration, as well as the spermatogenetic and spermatokinetic activity of the testicular lobules.

Spawning behaviour has been observed in aquaria by Lowe-McConnell (1957), and by

Greenwood, quoted by Lowe-McConnell, and by Jochem (1969). The male, having assumed breeding colours, established territory and made one nest, occasionally more, a simple depression with diameter about equal to the length of the fish. It was made by mouth-digging. In an aquarium with mixed species swimming in a group near the surface he then approached females of his own species and stimulated one of them by nipping and tail-slapping to follow him down to the nest. The relative sizes of male and female seemed to be unimportant. Spawning and fertilization were not described, but the female was observed to brood the eggs, and to have a black throat during this activity. The male retained his breeding colours and behaviour for at least two months.

In the lagoons of Lake Victoria Welcomme records that the nests are made in shallow water 15–60 cm deep, are 16–20 cm in diameter and 1–4 m apart. There they were dug in the coarse leaf-debris or on shallow muddy bottoms.

The eggs are described as yellow (Lowe-McConnell, 1957; Siddiqui, 1977) or dark olive-green (Elder *et al.*, 1971). The discrepancy may possibly be explained by comparison with my observations on *Tilapia guineensis*, in which ovarian eggs are bright yellow until just before they are ready to be shed, when they become olive-green. Their size is given as about 3 mm (personal observation), 3 × 2 mm (Lowe-McConnell), 3·2 × 2·4 mm (Welcomme) or 3·3 mm (Siddiqui). The number of ovarian eggs ready for one spawning varies from 100 in a fish of 7 cm TL to about 950 in one of 26 cm (Lowe, 1957) and an estimated 1328 in a very large fish of 32 cm in Lake Naivasha (Siddiqui). Welcomme obtained corresponding figures for a larger number of lagoon specimens, his maximum being 642 for a female of about 24 cm TL. For each size-group he obtained lower numbers at the end of a rainy season (December) than at the beginning (October) (1967, Table IV), and this he interpreted as evidence that the rains stimulated the ripening of the ova and spawning, that more batches of eggs than one were laid in succession by each female, and that her later batches were smaller in numbers than her earlier, an interpretation parallel with that of Lowe (1955) for *O. esculentus.* Gwahaba (1978) also found breeding activity to be intensified in the rainy season in Lake George.

Brooding females from the lagoons of Lake Victoria were found in pools adjacent to the lagoons, and fry spent their early days in shallow grassy swamps.

Development. In aquaria the eggs hatched about six days after fertilization, and the young fishes swam actively and emerged from the mouth five days later. For about two weeks they were brooded in the mouth at night and when danger threatened by day, then at night only for a further week (Greenwood, quoted by Lowe-McConnell, 1957).

Welcomme recorded that the fry had absorbed the yolk and swam freely at a total length of about 8 mm, 11–15 days after fertilization, the time depending on temperature; but the final release occurred at 9·0–11·5 mm and an exceptional batch of fry of 12·2 mm was taken from the mouth of a female of 15 cm. Females are retentive of brooded larvae even when caught in a seine net, and Welcomme made an estimate of the number of young surviving to the size of release by counting brooded fry in females of his seine hauls. He concluded that losses of immobile young were very low, and that whereas the numbers of eggs produced increased roughly as the square of the SL of the mother, the number of eggs or larvae brooded increased in direct proportion to the length; that is, the brooding efficiency does not keep pace with the rate of egg production as the parent fish grows.

An account by Jochem (1969) of mating, spawning and brooding by a pair in aquarium contains enough similarities to the above observations to give confidence that the same species was involved—superior size of male, colour, including presence of white spots above the anal fin, early release of the brood, and return of the young to the mouth at night for about eight days after release. But the author noted that the female took a more active part in nest making, and he thought the pair were possibly behaving abnormally because milt was shed and snapped at by the female before the eggs were laid, and the eggs were white. The genital papilla of the spawning male became thickened distally.

Loiselle (1975) recorded the carrying of eggs and fry for 14 days in an aquarium and the release of young at 10–12 mm TL at a temperature of 85°F (c. 30°C).

Hybrids

Hybrids with ♂ *O. niloticus*, originally from Lake Albert, and also with *O. s. niger* were obtained by Pruginin (1965) in ponds in Uganda, in both cases with an F_1 of 90% males. With *O. niloticus* the hybrids exhibited the vertical stripes on the caudal fin characteristic of *O. niloticus*, but the shape and breeding coloration of *O. leucostictus*. No morphological analysis was made.

For a fuller account of hybridization with *O. s. niger* see p. 256, and the account by Elder, Garrod & Whitehead (1971) and Elder & Garrod (1961).

Distribution

Natural distribution. Lakes Edward/George and Albert; affluent rivers and streams of these lakes and of the Semliki River; tributaries of the Aswa River, where it is not certain whether it occurs naturally or has been introduced (Greenwood, 1963).

Dispersal by man. From Lake Albert this species has been stocked in many ponds and dams in East Africa, and also in Lakes Victoria and Kioga, where it has flourished. It was taken to Lake Naivasha, and to a dam at Tebere in Kenya unintentionally with *Tilapia zillii*. In both these places it interbred with another introduced species, *O. spilurus niger*, eventually (1974–5) supplanting this species in Lake Naivasha (Siddiqui, 1979).

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1895.4.17.46	86	L. Edward	Scott-Elliot
1904.1.19.21–22	136, 138	Butiaba, L. Albert	J. S. Budgett
1906.9.7.46	232·5	L. Edward	J. S. Moore
1933.2.23.44–45	93, 110	L. Albert (?)	E. B. Worthington
1933.2.23.122–124 syntypes	123·5, 209, 216	L. George & Kazinga Channel	E. B. Worthington
1933.2.23.125–129	57–76	L. Edward	E. B. Worthington
1914.4.8.2	124	L. Albert	H. Schubotz
1952.2.26.41–49	127–208	L. Albert	R. H. Lowe
1961.12.1.328–330	94–197	Tributaries of Aswa R.	Uganda Game & Fisheries Department
1967.9.13.1–3	89–103	Ntotoro R. at main road 18·5 km from Bundibugwo, Bwamba	Lord Richard Percy and M. Ridley
1969.3.6.22	95	Bwamba	Lord Richard Percy
1967.9.13.6	135	L. Isunga, Toro, Uganda	C. R. S. Pitman
1967.9.13.7–16	79–98 (4) 38·0–57·5(6)	Hot springs (50–60°C) 25·7 km ENE of Bundibugwo, Uganda	British Ruwenzori Expedition, 1951–2
1967.3.16.6–8	152·5	Kidetok dam, Teso, intro. from L. Albert	R. H. Lowe-McConnell
	178·0	Opuyo dam, Teso, intro. from L. Albert	R. H. Lowe-McConnell
	183·0	L. Edward, Kigezi shore	R. H. Lowe-McConnell
1967.	116·5	Malacca (sent inadvertently from Kisumu ponds with a consignment of *T. zillii*)	C. F. Hickling
1968.8.15.1–3	36–43	Mongello stream, Ntoro, Semliki, Uganda	W. Gewalt (Feb. 1966) (see Gewalt, 1966)

Subgenus *OREOCHROMIS* – III

Oreochromis spilurus

Oreochromis spilurus is the most northerly of a series of five species of the subgenus *Oreochromis* inhabiting the lower parts of the eastward-flowing rivers, from the Webi Shebeli and Juba in Somalia, to Algoa Bay in South Africa. They differ from *O. niloticus* and *O. esculentus* in the enlargement of the jaws in mature fishes and in having a bright red margin to the dorsal fin in mature males. Some of them have IV anal spines in all or a proportion of individuals. The colour feature, but not the enlargement of the jaws, is shared with *O. aureus*, which, as suggested (p. 139), may be more closely related to these than to *O. niloticus*, which shares much of its area of distribution.

Fig. 78 shows the distribution of the eastern species, from north to south *O. spilurus*, *O. korogwe*, *O. urolepis* (and *O. u. hornorum*), *O. placidus* (and *O. p. ruvumae*) and *O. mossambicus*. Most of these species have an upstream related form. *Oreochromis s. spilurus* and the upstream *O. s. niger* area treated as subspecies. The small group of ecologically differentiated species of the Upper Pangani are specifically distinct from *O. korogwe* of the lower reaches. *Oreochromis urolepis*, with its subspecies *O. u. hornorum*, is apparently the only species of *Oreochromis* native to the rivers which it inhabits (with the possible exception of the Great Ruaha; see p. 429). *Oreochromis placidus ruvumae* is believed to be the only tilapia native to the Ruvuma River, but in the Zambezi *O. p. placidus* is replaced in the Upper Shire, and Lakes Malawi and Chilwa by *O. shiranus*. *Oreochromis mossambicus*, which is present with *O. placidus* in the Lower Zambezi, is replaced in the Middle Zambezi by *O. mortimeri*, which differs from it in male coloration. Structurally *O. andersonii* seems to continue the *mossambicus–mortimeri* series in the Upper Zambezi, and extends also to the Ngami region and the Cunene in Angola.

Of the species of the lower reaches of the eastern rivers the resemblance in meristic and morphometric characters between *O. s. spilurus*, the northernmost, and *O. mossambicus*, the southernmost, is very close (see Table 76), the main difference being in the male breeding colours; but *O. urolepis* stands out in the series by its higher meristic numbers. Its distinctness is emphasized by the results of hybridization with *O. mossambicus*, the F_1 being all male when *O. u. hornorum* provides the male parent.

The records of *O. p. placidus* and *O. u. urolepis* suggest that these do not normally extend to brackish water, but the other forms seem to be euryhaline, and *O. s. spilurus* and *O. mossambicus* can live and breed in sea water.

The distinctness of the fish fauna of the eastern rivers of Kenya from those of both Lake Victoria and the Nile has been discussed by Whitehead (1962*b*), who has also summarized the evidence that the watershed between the eastern drainage of this part of Africa, and the drainage westward to the Congo (Zaire) system may, in Pliocene times, have been west of the present eastern shore of Lake Victoria. The presence of *O. spilurus* in the southern Uaso Nyiro, and in the Lower or Middle Pleistocene of the present Kavirondo Gulf area, contributes to this evidence.

Oreochromis spilurus (Günther)

Chromis spilurus (Günther, 1894*c*:89, pl. 10 (Mwangudo River, Voi system, Kenya).
For synonyms and further bibliography see the subspecies.

This species is here understood to include, as well as *O. s. spilurus*, *O. s. niger* (Günther) of the upper Athi system and *O. s. percivali* (Boulenger) of a pool near the Northern Oaso Ngiro, and to go back in time to include a Middle or late Lower Pleistocene population of Rawe and

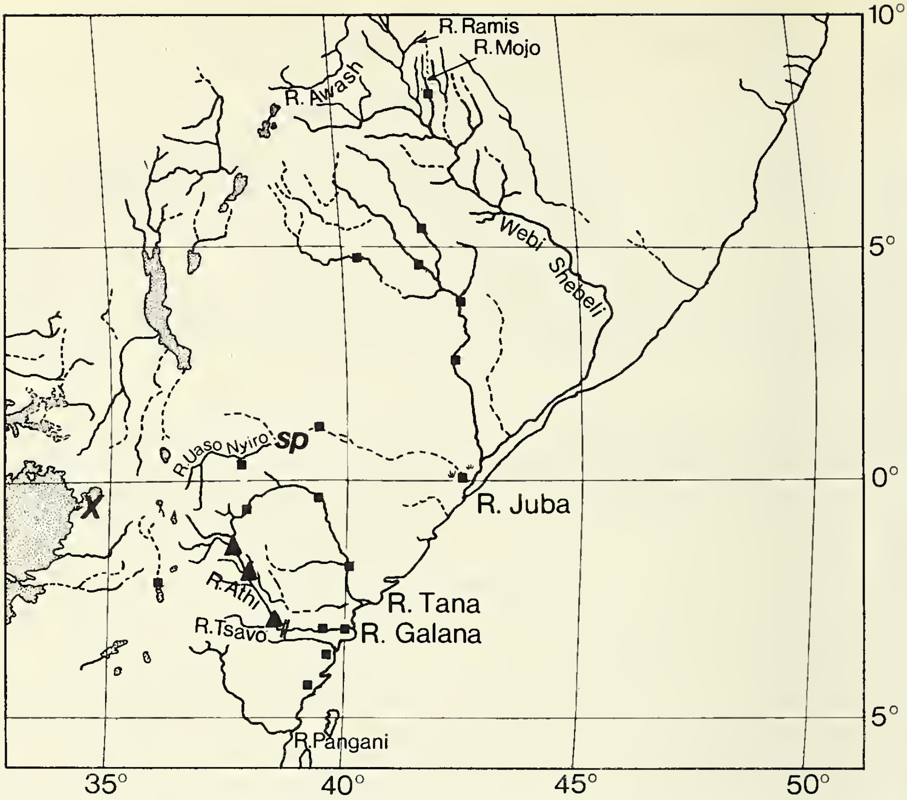

Fig. 78 Maps of East Africa to show the distribution of some of the species of the subgenus *Oreochromis*: **g, j, p,** *O. pangani girigan*, *O. jipe* & *O. p. pangani*; □, *O. u. urolepis*; **h,** *O. u. hornorum*; **k,** *O. korogwe*; ○, *O. mossambicus*; •, *O. mortimeri*; △, *O. p. placidus*; **r,** *O. p. ruvumae*; ■, *O. s. spilurus*; ▲, *O. spilurus niger*; **sp,** *O. s. percivali*; ●, *O. shiranus shiranus*; **c,** *O. shiranus chilwae*; **X,** location of fossil *O. spilurus*.

Falls and rapids constituting barriers to upstream migration of cichlids are shown by a double line crossing a river. These are: Lugard's Falls on the Athi River; the Kabora Bassa and Victoria Falls on the Zambezi; the rapids of the Kafue Gorge and the Murchison Rapids on the Shiré River.

Kanam in the Kavirondo Gulf region. The fossils were formerly (Trewavas, 1937) assigned to '*Tilapia nigra*', because all the ten specimens in which the spinous anal is preserved have IV anal spines, but it is now know that IV anal spines may occur in *O. spilurus*, in some populations as an exception, but in others as a rule (see p. 247–8 on the Juba and Shebeli populations). The fossils are here renamed *O. spilurus sensu lato*.

In the Athi River, including its lower part, the Sabaki, a special situation obtains, which is discussed below.

Distinguishing characters

Gill-rakers (13, 14) 15–19 on lower part of first arch. Modal number of vertebrae 28, 29 or 30 (in different populations). Anal spines III, III–IV, IV or IV–VI (in different populations). Mature males and larger mature females with jaws enlarged, so that the lower is 38–48% length of head. Mature male never black, its colours including red or orange margins to dorsal and caudal fins, bright sky-blue areas or spots on dorsal, anal and pelvics, yellow or yellow-green on lower flanks. This may not be the high territorial colour of males, for in *O. s. spilurus* males are known with the whole body brilliant electric blue and the vertical fins black, and an exceptional *O. s. percivali* had throat and belly electric blue.

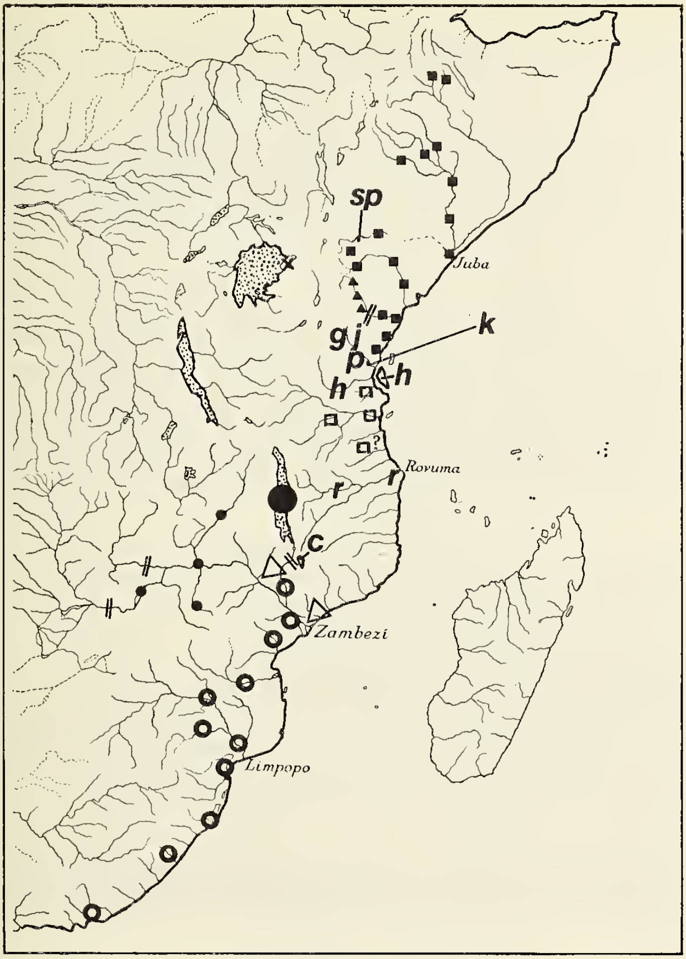

Fig. 78 (caption opposite)

Distribution (Figs 78 & 142)

Eastward-flowing rivers of Africa from the Webi Shebeli to the River Mwena in southern Kenya and probably Lake Momella in northern Tanzania; Northern Uaso Nyiro and Southern Uaso Nyiro. In Lower or early Middle Pleistocene the species apparently extended to the present Kavirondo Gulf area, which may then have drained eastwards.

A note on the localities

1. The type locality was named Mwangaden River by Günther, but the collector, J. W. Gregory (1896:208) spelt it Mwangudo. The name, which I do not find on modern maps, must belong to the lower Voi system or to a short river near the lower Voi. Gregory mentioned it as being in the course of his itinerary between Mangea Mountain and Mwaiba after passing Sokoki. Mt Mangea is about 16 km south of the lower Athi, Sokoke is a district SE of this, and the Voi mouth is between Sokoke and Mwaeba. Kilifi, Takaunga and the Rare River are all associated with the system of creeks that includes the mouth of the Voi River.

2. Tanganiko does not appear on modern maps. Other collections received from A. B. Percival at about this time included some from the neighbourhood of Mombasa. Taita and Rabai are near Mombasa and the Maji Chumvi, a short river issuing at Mombasa.

3. Lugard's Falls are a series of rapids in the Athi River about 100 miles (161 km) from its mouth, and below the 500 m contour line. They include a 12 ft fall which Whitehead (1969:524) states is a barrier to upstream migration for cichlids, although possibly not for *Barbus*.

4. Kibwezi, type locality of *O. s. niger*, is a tributary that joins the Athi about 60 miles (96 km) above Lugard's Falls; part of its course is underground. The Makindo and Simba Rivers join the Athi about 20 miles (32 km) above this. Both junctions are between the 500 and 1000 m contours.

5. The Tsavo River, an important tributary, rises mainly on the slopes of Kilimanjaro, but receives some streams from the Teita Hills. It joins the Athi about 24 km above Lugard's Falls.

6. Wild fish from the Upper Athi came from the river not far from its source at the foot of Doinyo Sabuk. The river is here on the plateau and about 1500 m above sea-level.

7. The locality in the Webi Shebeli system at which A. Donaldson Smith collected *O. spilurus* was a water hole near Sheikh Husein (7°43´32´´N, 40°44´30´´E). Günther distinguished between these and the *O. niloticus* brought by the same collector from the other side of the watershed.

8. The ponds at Sagana, north of Nairobi, at about 1220 m altitude, were originally stocked with fish from dams, and these had been stocked with *O. s. niger* since 1922. Later *O. s. niger* and *O. s. spilurus* were taken to Sagana from different parts of the Athi River for the experiments of Van Someren and Whitehead. These experiments are described below, but the fishes concerned do not form part of the study material here used.

9. Lake Naivasha is an alkaline lake on the upwarped plateau in Kenya, at about 1830 m above sea level, in an enclosed drainage system. Talling & Talling (1965) summarized its physical and chemical characteristics. The conductivity is high, 318–335 μmho as taken at different times in 1960–1 by the Tallings, who also report a value of 400 μmho recorded by Fish in 1952. The pH is 8·8–9·0, the sodium concentration 41–45 mg/l, the potassium 19·0–22·6 mg/l, and there was also a moderately high concentration of silica (SiO_2 30–32·5 mg/l). The lake contained an abundance of a spirilliform organism, possibly the myxophycean *Spirulina* (Talling, 1962). The only native fish is the small cyprinodont *Aplocheilichthys antinorii* Vinciguerra. The lake was

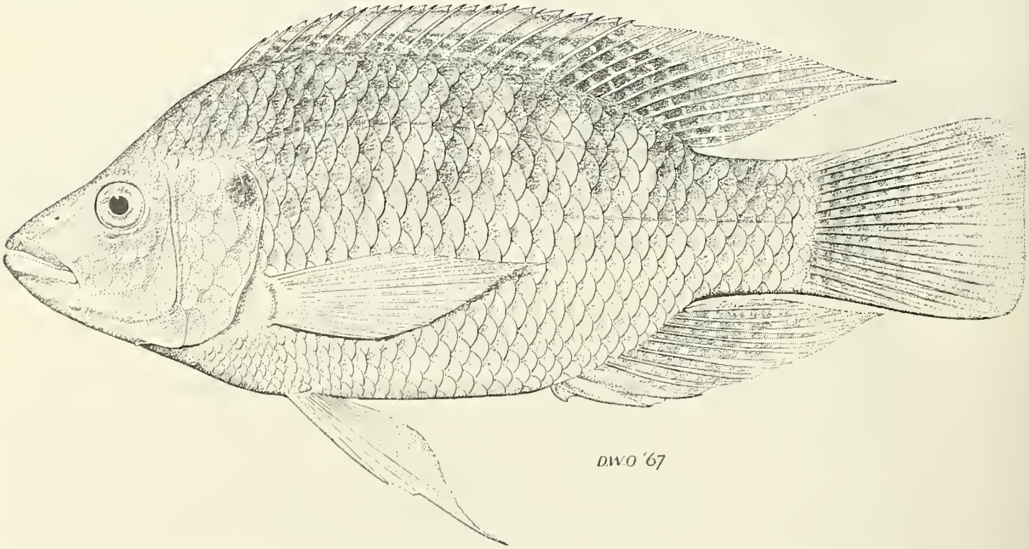

Fig. 79 *Oreochromis s. spilurus*, male of 176 mm SL from Garissa, Tana River.

originally stocked with *O. s. niger* and the American black bass, *Micropterus salmoides*, both probably from stocked dams in Kenya. An outline of the history of the stockings and fishery has been given by Elder *et al.* (1971), but no precise records were kept, and their statement that tilapias were scarce in the early 1930s hardly accords with the experience of the Cambridge Expedition of 1930–31, which brought back a good collection of *O. s. niger* from the lake. In 1956 black bass and *Tilapia zillii* were introduced from ponds at Kisumu and this consignment, evidently unintentionally, included some *O. leucostictus* (see below, p. 256–7).

10. The Northern Uaso Nyiro (or Ngiro) is an isolated river that rises in the Mount Kenya massif not far from the source of the Tana. It flows roughly west to east and ends a short way east of the Lorian Swamp. It is continued as a dry water-course to the river Juba, but has no surface links with it at present. The Uaso Nyiro contains a fish population known to science only from preserved specimens, which were named *Tilapia nyirica* by Lönnberg (1911). I have been unable to characterize them as distinct from *O. s. spilurus*. At varying distances from its south bank are several hot springs, which spread into pools and flow eventually into the river. Their history, ecology and fish populations have been the subject of a study by K. L. I. Campbell (1981). One of the springs is the type locality of *O. s. percivali* (Boulenger), a peculiar population with a long history of isolation from the river and other springs, for which I have retained the name at subspecific rank.

Subspecies

Three subspecies are recognized (see also Trewavas, 1966*c*), distinguished by the modes of their meristic characters (Table 56). These are associated with their respective habitats.

Oreochromis s. niger inhabits the plateau of Kenya at altitudes above sea-level of about 500 m and more, and has higher mean numbers of vertebrae and dorsal and anal fin-rays than *O. s. spilurus*. The latter inhabits the lower reaches of rivers from the Kenya–Tanzania border to the

Table 56. Distinguishing characters of the subspecies of *O. spilurus*. A = *O. s. spilurus* from coastal rivers south of the Athi, lagoons near the Athi mouth and the Tana River up to Garissa. B = lower 48 km of the Athi and pools and lakes in its flood-plain. N = number of specimens. Details in Tables 58, 59, 60, 62, 65, 67, 68.

	O. s. spilurus		*O. s. niger*	Fossils	*O. s. percivali*
	A	B			
Vertebrae: N	30	10	33	1	14
range	28–30	29–30	29–31	30	28–29
mode	29	29	30		28
Anal spines	III(–IV)	III–IV	IV–V(VI)	IV	III(–IV)
Dorsal spines: N	100	322	124	1	25
range	XV–XVII	XIV–XVII(XVIII)	(XIV)XVI–XVIII(XIX)	XVII	XIV–XV
mode	XVI	XVI	XVIII		XV
Scales lat. line: N	48	11	54	—	
range	29–31	30–31	30–32	—	29–31
mode	30	30	31	—	30
Caudal peduncle					
length % SL		10·0–14·5	6·7–11·8	—	12–16
length/depth		0·7–0·9 (1·0)	0·4–0·8	—	0·8–1·0

Juba and Webi Shebeli. Not enough is known about the populations of these two rivers to be sure that they have not their counterparts of *O. s. niger*, but for the present they have been included in the nominate subspecies.

The third subspecies, *O. s. percivali*, is a small population of a pool fed by hot springs. It parallels hot spring populations of other species in having lower mean numbers of vertebrae and fin-rays, and a small size and presumably low age of sexual maturity; its head is larger and its jaws broader and stronger than those of members of the nominate subspecies at the same size (Fig. 87 & Table 70).

There is already some evidence that these characters are unstable and related to the environment, and that hybridization between *O. s. spilurus* and *O. s. niger* occurs naturally in the Lower Athi (= Sabaki or Galana) River, (see pp. 258–259), but because the names at present have some meaning in nature they are retained here.

The Lower or Middle Pleistocene fossils of Rawi and Kanam near the shore of the Kavirondo Gulf are here (as by Trewavas, 1966*c*) referred to by a binomen only, although they may be part of the ancestral *O. s. niger*.

Oreochromis spilurus spilurus (Günther)

Chromis spilurus Günther, 1894*c*:89, pl. x (R. Mwangaden = Mwangudo, Voi system, S. of Mombasa); *idem*, 1896*b*:218 (Shebeli R.).

Tilapia spilurus spilurus; Trewavas, 1966*d*:400 (eastward flowing rivers of Kenya and Somalia, except upper Athi).

Tilapia nigra spilurus; Thys van den Audenaerde, 1968*b*:xxxvi.

Sarotherodon niger spilurum; Mayland, 1978:309, fig. (Lake Momella in northern Tanzania).

'*Chromis niloticus* Hasselq. var. *mossambicus* Pets.' (*non* Peters); Fischer, 1884:27 (part) (Nguruman).

Chromis niloticus (part, *non* Linn.); Vinciguerra, 1895:28 (Juba R.); *idem*, 1897:344 (Ueb R., trib. of Juba).

Tilapia nilotica (part, *non* Linn.): Boulenger, 1899*a*:112; Pellegrin, 1904:273 (syn. *T. spilurus* only); Boulenger, 1904:303 (Modjo R., Shebeli system); *idem*, 1912*d*:675 (Uaso Nyiro); *idem*, 1915:166 (specimens 278–303, 307–316); Vinciguerra, 1912:302 (Juba system); *idem*, 1927:257 (Juba); Senna, 1915:181 (Juba); D'Ancona, 1939:166 (Daua Parma, trib. of Juba).

Tilapia galilaea (*non* Linn., part); Pellegrin, 1905*b*:183 (brackish lagoons of Maji Chumvi R., Kenya).

Tilapia nyirica Lönnberg, 1911:41 (Northern Uaso Nyiro).

Tilapia natalensis (part, *non* Weber); Boulenger, 1915:158 (specimens 1–11).

Tilapia browni Nichols, 1923:1, fig. 1 (Ramis R., trib. of Webi Shebeli).

Tilapia mossambica (part, *non* Peters); Trewavas, 1937:383 (Kenya); Copley, 1958:128, fig. 75 (Lower Athi & Tana); Whitehead, 1962:605 ff. (Lower Athi & Tana).

Oreochromis d'anconai Caporiacco, 1947:197 (Daua Parma, trib. of Juba).

'*Tilapia shirana* (?)' (*non* Boulenger); Haller, 1974:20, pl. opposite p. 19 (cultured in ponds near Mombasa).

TYPES. Syntypes: eleven specimens of 43·5–90 mm SL, coll. J. W. Gregory in the Mwangudo River, south of the Lower Athi. BMNH 1893.12.2.3–12.

Syntypes of *Tilapia nyirica* in the Swedish National Museum, and two of 40 and 43 mm SL in BMNH, 1911.11.20.3–4.

Holotype of *Tilapia brownii*: 105 mm SL, AMNH 8186.

Holotype (105 mm SL) and paratypes of *Oreochromis danconai* in the Zoological Museum, Florence, Italy.

Distinguishing characters: see Table 56.

Description

Based on: A, 34 specimens of 70–192 mm SL (including three of the syntypes) from the rivers of Kenya south of the Athi system, lagoons near the coast north of the Athi mouth and from the Tana River; B, 15 of 77–168 mm SL from the lower Athi (Sabaki) and ponds and lakes in its flood-plain.

For meristic characters additional smaller specimens from the same localities are used.

Proportions are given in Table 57 and Fig. 81.

The diameter of eye and depth of preorbital, showing a rough allometry in opposite senses, are approximately equal between 145 and 170 mm SL.

Teeth in 3 or 4 (5) series; outermost bicuspid in young and sexually inactive fishes and, except for a few lateral, in females of whatever gonad condition up to SL 163 mm (the largest available), unicuspid in sexually mature males from SL 130 mm upwards, inner tricuspid in all except a spent male of 131 mm in which some are unicuspid, others tricuspid; 42–70 in outer series of upper jaw.

Gill-rakers 16–19 on lower part of anterior arch. Microbranchiospines on outer sides of 2nd, 3rd and 4th arches.

Lower pharyngeal bone about as long as wide, blade a little shorter (young) to a little longer than median length of dentigerous area, which has concave sides and nearly straight posterior edge (Fig. 80).

Scales on cheek in 2 or 3 series. Lateral line series 29–31; 4 or 4½ from origin of dorsal to lateral line, 5 or 6 between bases of pectoral and pelvic fins. Scales becoming gradually and moderately smaller towards the ventral surface.

Dorsal XIV–XVII 10–13. Analysis of these formulae is given in Tables 59 & 60, and Fig. 82. The species shows an unusually wide range of totals and of combinations of spines and soft rays.

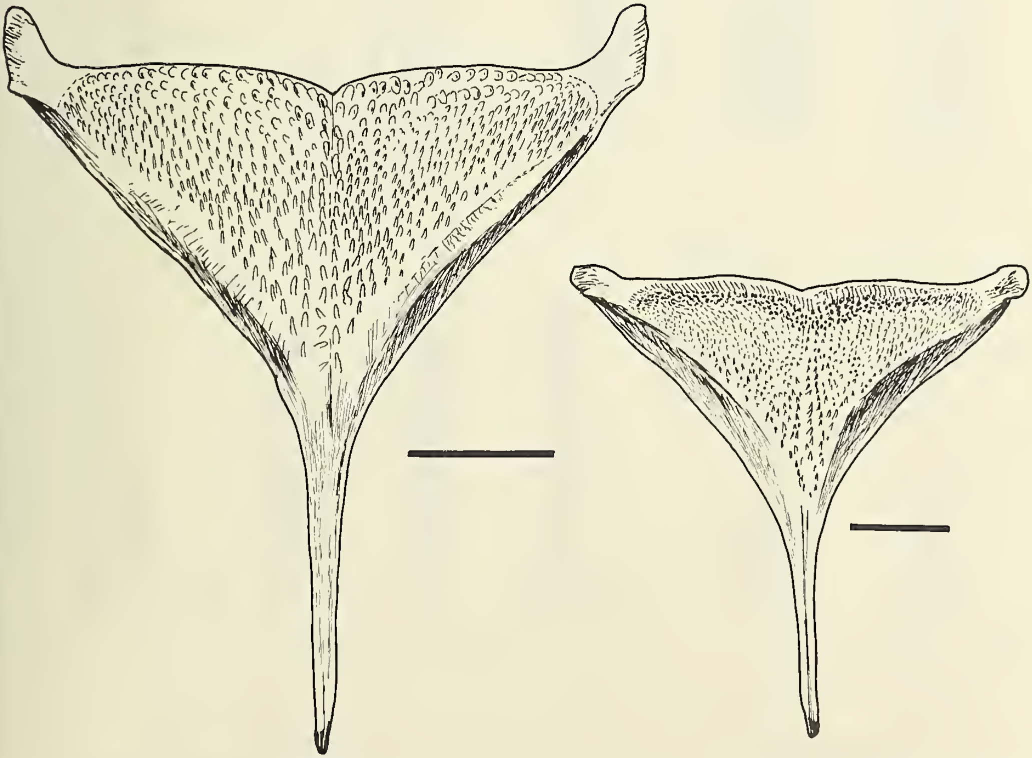

Fig. 80 *Oreochromis spilurus spilurus*, left, lower pharyngeal bone of a fish 166 mm SL from Lake Marikano in the flood-plain of the lower Athi (=Galana or Sabaki); *O. s. niger*, right, lower pharyngeal bone of a fish of 210 mm SL from Lake Naivasha, BMNH 1928.11.10:21. Scales = 5 mm.

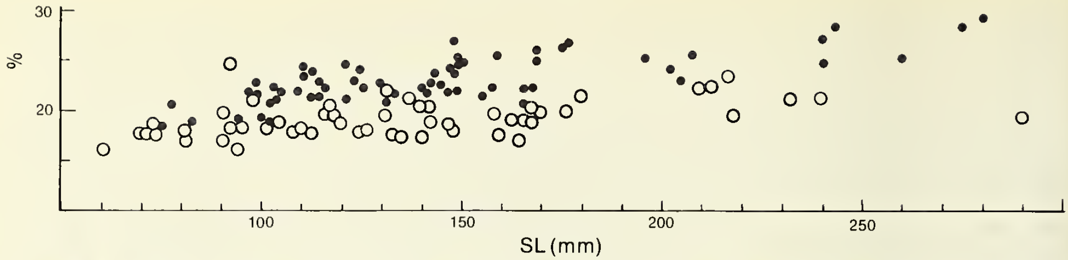

Fig. 81 Depth of preorbital bone as % length of head in *Oreochromis spilurus* (○) and *O. urolepis* (●).

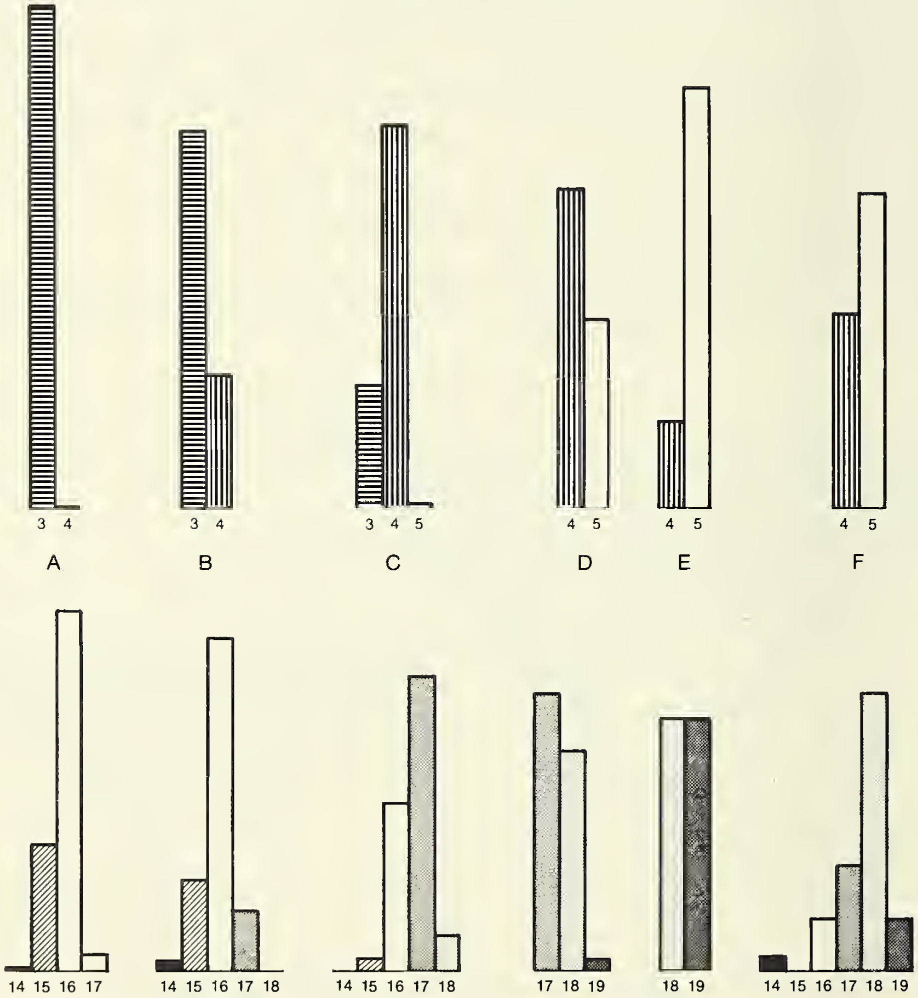

Fig. 82 Percentage frequencies of anal (3–6) and dorsal spines in samples of *Oreochromis spilurus* (see also Table 59).

A, all localities except the Athi River from its source to the Indian Ocean. Anal fin, N = 523; dorsal, N = 117

B, lower 48 km of Athi River (= Sabaki or Galana). Anal fin, N = 393; dorsal, N = 325.

C, Athi River at Parker's Camp, 64 km below Lugard's Falls. Anal fin, N = 666; dorsal, N = 197.

D, *O. s. niger*, from Kibwezi, Makindo and Tsavo Rivers. N = 46.

E, *O. s. niger*, from Doinyo Sabuk, near source of Athi River. N = 6.

F, *O. s. niger*, from Lake Naivasha, 1930–1931, introduced. N = 29.

In both groups the modal total is 27, with 28 also well represented. In both groups the modal combination is XVI 11 with XVI 12 not far behind. XV 12 is also a common combination in group A, but not in group B and XVII spines occur in only three of group A, the larger sample, but in thirteen of group B.

In spite of these differences in distribution of spines and soft rays the mean totals for the two groups are very close, respectively 27·36 and 27·22.

Six of the seven specimens of group A with 25 or 26 rays are from the highly saline pool at Ngomeni, but no unusual water chemistry is reported for the similar specimens of group B.

Anal III–IV 9–10; IV spines very rare in group A, present in 34% of B (Table 59 & Fig. 82). Since Tables 56 and 59 were compiled these data have been confirmed by collections of young fishes from three short rivers south of Mombasa and two tributaries of Kilifi Creek north of Mombasa. Of 73 fishes the only ones with IV anal spines were two of sixteen collected below a dam in the Shimba Hills.

Caudal fin truncate, not thickly scaled except at base.

Genital papilla of male conical or club-shaped, with a subterminal pore. In a precociously ripe male of 98 mm SL the papilla is bluntly bifurcate beyond the pore.

Table 57. Proportions in *O. s. spilurus*. The four largest in group A (see text & Table 56) are all males. No specimens of this size are available in group B.

	A		B
SL (mm)	70–161	170–192	77–168
Proportions as % SL			
Depth	37·0–46·4	37·0–46·0	38·4–47·5
L. head	33·4–38·0	34·2–35·2	34·5–35·2
L. pect. fin	(34·2) 36·0–41·0	38·0	37·2–44·0
L. lower jaw ♂	11·9–15·0	13·1–15·2	(10)11·7–15·1
♀	11·7–14·5	—	11·9–13·7
L. caud. ped.	10·0–14·5	12·3–13·5	11·0–14·2
Caud. ped. l/d	0·7–0·95(1·0)	0·7–0·95	0·7–0·9
Proportions as % l. head			
L. snout	(28) 30·0–35·8(37)	36·7	30·0–37·1
Eye	20·0–26·0	20·0	(18)19·0–26·7
D. preorb.	17·0–20·0(21·2)	20·0–22·0	15·8–19·8
Interorb.	28·4–36·7	35·8–37·1	32·7–38·6
Lower jaw ♂	33·3–40·8	38·4–43·3	32·3–41·3
♀	33·0–39·4	—	31·6–38·0
W. lower phar.	30–33		

Table 58. Frequencies of numbers of vertebrae in samples of *O. s. spilurus*

Vertebrae	28	29	30
L. Chem Chem	4	13	
Garissa (Tana R.)	1	10	2
Marikano (Mouth of Sabaki, = Lower Athi)		9	1

Table 59. Frequencies of numbers of anal and dorsal spines in *O. spilurus* from eastern rivers of Kenya. In some cases larger samples have been used for one fin than the other. Data from Whitehead, 1962*a* are included.

		Anal			Dorsal					
		III	IV	V	XIV	XV	XVI	XVII	XVIII	XIX
	O. s. spilurus									
A	Tanganiko, Rabai, Taita	19				3	14	2		
	Kilifi, Rare, Mwangudo	23				4	16			
	coastal region nr. Athi, L. Chem Chem, Ngomeni	59			1	11	27			
	L. Chem Chem (Whitehead)	373	1		(not separately recorded)					
	Tana R. from Garsen to Saka	47	1			9	29	1		
B	Lower 30 miles of Athi (Sabaki) and lakes within its flood-plain: BMNH	59	22		2	11	49	18	1	
	Whitehead	234	78		4	47	171	22		
C	Athi R., 40 miles below Lugard's Falls (Whitehead)	160	501	5	1	4	65	115	12	
	O. s. niger									
D	Kibwezi, Makindu, Tsavo		29	17				25	20	1
E	Doinyo Sabuk		1	5					3	3
	Naivasha 1930, 1931		11	18	1	0	3	6	16	3

Table 60. *Oreochromis s. spilurus.* Frequencies of dorsal formulae, total dorsal rays and numbers of dorsal soft rays in two groups of samples (see Table 59).

Dorsal	A	B	Total D rays	A	B
XIV 10	0	1	24	0	1
XV10	1	1	25	1	1
XIV 12	1	0	26	6	4
XV 11	4	4	27	58	30
XVI 10	1	0	28	33	20
XV 12	20	4	29	6	1
XVI 11	38	20			
XVII 10	0	6	Soft D rays	A	B
XV 13	1	0	10	2	8
XVI 12	30	14	11	44	30
XVII 11	2	6	12	52	19
XVI 13	5	0	13	6	0
XVII 12	1	1			

Size. Copley (1958:128) says that this subspecies grows to 23 cm (TL); the largest specimen used by Whitehead for his measurements (1962, table 7, figs 6 & 7) is under 160 mm SL. In the BMNH the largest female is 163 mm SL, male 192 mm (24 cm TL). Haller (1974) has shown, however, that the species (wrongly identified at that time by him as *Tilapia shirana*) is capable of growth to a total length of 40 cm and a weight of 1200 g in twelve months and in two years to over 2 kg. This was, however, in special conditions of tank culture with running water and nutritious food, and the fishes used were all males.

COLORATION. Females and immature males have a yellow-buff background colour with a mid-lateral series of blotches and a more dorsal parallel series. Pelvic and anal fins are predominantly sky-blue. Preserved specimens usually have a dorsal blotch on the caudal peduncle (the origin of the name *spilurus*). Mature males are brighter, with golden-yellow colouring, especially on the posterior part of the flanks, and conspicuous bright blue areas on dorsal, anal and pelvic fins and with orange or red dorsal lappets. A male of about 12 cm TL (with III anal spines), freshly caught at Lake Jilore, had the whole body metallic royal blue and the vertical fins and pelvics black, and this colouring was also seen in a bigger fish, reliably identified as *O. s. spilurus*, in an aquarium at Mbwapa. It is clear that there is more to be learnt about colour-changes in this species, but in most phases of the males the yellow colour on the flanks and the light blue areas on the fins appear to be characteristic. Such colouring was described by Whitehead (1962*a*) in this subspecies and *O. s. niger*, and was seen personally in the tanks at Bamburi and in a pond at a farm near the Kedong River (affluent of Lake Magadi) that contained a stocked mixture

Table 61. *Oreochromis s. spilurus.* Changes in the jaws and teeth. A and B are groups as in Table 56; A′ is from a pond near Mombasa. Gonad conditions are: inactive (qt), starting (stg), ripening (rpg), ripe (rp) and spent (sp). The length of lower jaw (l.j.) is expressed as % length of head and % SL.

	SL (mm)	Sex	Gonad	l.j. % head	l.j. % SL	Outer teeth if not bicuspid	Inner teeth if not tricuspid
A	72	♀	rpg	36·7	13·9		
A	74	♂	stg	34·6	12·1		
A	81	♂	qt	33·3	12·3		
A	81	♂	rpg	38·7	14·0		
A	84	♂	rpg	40·6	15·0		
A	90	♀	rpg	35·4	13·8		
B	97	♂	qt	33·3	12·4		
A′	98	♂	rp	41·9	16·3		
A	102	♀	rp	39·4	14·5		
A	105	♂	stg	32·8	11·9		
A	118	♀	stg	34·0	11·9		
A	131	♂	sp	38·4	13·3	unicuspid	one row unicuspid
A	136	♂	rpg	40·4	14·6	unicuspid	a few unicuspid
A	140	♀	rpg	37·6	13·0		
A	142	♀	rpg	37·8	14·0		
A	146	♀	rpg	38·0	13·7	a few lateral unicuspid	
B	158	♂	rpg	40·7	14·5	some unicuspid	
A	162·5	♀	stg	35·1	12·6		
A	163	♀	stg	36·6	13·6		
A	164	♂	rpg	40·8	14·9	minor cusp reduced	
B	166	♂	sp?	40·1	15·1	some with minor cusp reduced	some worn
B	168	♂	rpg	41·3	14·3	some unicuspid	
A	176	♂	sp	38·4	13·1	few unicuspid	
A	187	♂	stg or sp?	41·0	14·0	unicuspid	
A	192	♂	stg or sp?	42·2	15·0	unicuspid	

of *O. s. spilurus* and *O. s. niger*. Well-coloured males in this pond also had bright yellow caudal fins.

Whitehead reports that the colouring is the same in *O. s. niger*, but that in *O. s. spilurus* the blue and yellow areas are brighter, and that marks on the scales are red in contrast to grey. He states that these differences persist when the two are kept together at Sagana ponds, or in an aquarium, and that they appeared in the offspring of the captive fishes.

CHANGES IN THE JAWS AND TEETH (Table 61). The largest specimen available is 192 mm SL (thus smaller than any *O. s. niger* in which the extreme change to all unicuspid teeth has been found). Up to this length *O. s. spilurus* shows the same relation between length of jaws and gonad condition as does *O. s. niger* in the same size range. Elongate jaws are found in ripe, ripening or spent individuals of both sexes. In a mouth-brooding female of 102 mm the jaw is even a little longer than in a spent male of 131 mm (but these came from different rivers); and immature males have an equally small relative jaw size whether at 81, 97 or 150 mm SL. It is interesting to compare the 'quiet' and ripening males of 81 mm in Table 61, both of which come from the same sample (they are syntypes). The 84 mm male from Lake Jilore has only moderately enlarged testes, but has other signs of a breeding fish—white and thick-skinned lower lip and thick, dark lower fins, produced soft dorsal and anal rays, and prominent genital papilla.

The ripe male of 98 mm SL (123 mm TL) of Table 61 came from a pond near Mombasa, and has a relatively longer snout and jaws than any other. Its proportions and meristic numbers are common to *O. spilurus* and *O. mossambicus*, but there is no evidence that *O. mossambicus* has been introduced in Kenya, and the colouring is not that of a typical male *O. mossambicus*. The scales of the lower half of the body are well supplied with iridocytes as well as scattered melanophores, and each has a black curve parallel to and near the posterior edge. This is evidently a precociously ripe male *O. s. spilurus*.

With the exception of these two small fishes a jaw-length of 15% SL is reached or exceeded only in males of 164 mm SL or over among those available, but we have no females of more than 163 mm SL.

The indications are that the jaws enlarge when the gonads swell in both sexes; that between standard lengths of 72 and 163 mm the degree of enlargement is dependent on gonad condition, and not on size or sex; that at about 130 mm SL and above sexual ripeness in the male is accompanied by simplification of the outer and some of the inner teeth, but in females, even when ripe, the majority of outer teeth remain bicuspid and all the inner tricuspid, up to the largest available (163 mm SL). On the analogy of *O. s. niger*, it might be expected that if females grow longer than 200 mm they might replace their notched teeth by unicuspids.

Distribution (Fig. 78)

Coastal rivers of Kenya from the Mwena River near the Tanzania border to the Lower Athi (=Sabaki or Galana) below Lugard's Falls, pools and lakes in the Athi flood-plain and coastal lagoons near its mouth, including the warm and saline Lake Chem Chem; Lower and Middle Tana, Northern Uaso Nyiro, Juba system and Webi Shebeli; Nguruman (Southern Uaso Nyiro). Probably also in Lake Momello, south of the Kenya–Tanzania border (see Mayland, 1978:309, photo by H. Hansen).

Discussion

A population of *O. s. spilurus* in the Southern Uaso Nyiro?

In 1884 Fischer recorded, from the collections of the Hamburg Museum, four specimens from the Nguruman region of the Eastern Rift Valley as '*Chromis niloticus* var. *mossambicus*'. Three of them, not longer than 8 cm and with D XII–XIII 10–12, are evidently the species later described as *O. alcalicus* (Hildendorf). The fourth was from a stream running into the Southern Uaso Nyiro (see Fig. 78), measured 22 cm and had fin-formulae D XVI 12, A III 11, thus outside the range of *O. alcalicus,* but agreeing with *O. spilurus* (and some other species).

Five young fishes of 25–42 mm SL sent to the BMNH as from 'Lake Natron' by the late Mr Hugh Copley in 1946 are not *O. alcalicus.* The fin formulae in three of them are D XVI 11–12, A III 9–10, in a fourth D XVII 11, A IV 9; there are 15–18 lower gill-rakers and microbranchiospines are present even at 42 mm SL; the vertebrae number 14 + 15 in two, 14 + 16 in three. They compare very closely with young *O. spilurus* in proportions and I cannot find any reason to exclude them from it. As in young *O. spilurus* the tilapia-mark is scarcely distinguishable, in contrast, for instance, to *O. esculentus* at this size.

Oreochromis spilurus has not been found in Lake Natron by other collectors (Albrecht, 1967*b* & 1968*a*; Coe, 1969). It is possible that Mr Copley's specimens had a wrong locality label, especially as the colour-notes sent with them apply better to *O. alcalicus* than to *O. spilurus.* But it is also possible that they came from the Uaso Nyiro above the swamp by which that river enters the lake, and together with Fischer's record they point to the distinct possibility that *O. spilurus* is present in the Nguruman valley. If subsequent collecting confirms the existence of *O. spilurus* in the Rift Valley, it will form an interesting link with the Lower Middle Pleistocene fossils of Kanam, identified by me in 1937 as *T. nigra*, and now listed as *O. spilurus sensu lato* (p. 268 & Fig. 142). Mr I. S. C. Parker, who has fished often in this river, informs me that he has never caught a tilapia here.

***Oreochromis s. spilurus* north of the Tana River** (Table 62)

Populations of *Oreochromis* north of the Tana River have been described from the Northern Uaso Nyiro, springs that drain into it from the south, the Juba River and its tributaries, and upper tributaries of the Webi Shebeli. To some of them specific names have been given, but of these only *O. percivali* has here been retained, as a subspecies of *O. spilurus* (p. 260). What is known of the others is not enough to support separation from *O. s. spilurus.*

Tables 62 and 67 record the meristic numbers of the samples available.

Uaso Nyiro system

1. The Uaso Nyiro (Fig. 83) whose name means 'muddy river' (Campbell, 1981), is the type locality of *Tilapia nyirica.* As well as the syntypes, 14 specimens in BMNH have III anal spines and only one has IV. The modal dorsal formula is XVI 11 as in *O. s. spilurus* of the more southern rivers, and the fish with IV anal spines has only 8 anal soft rays. The vertebrae number 29 and 30 in the two radiographed. There are 2 or 3 rows of scales on the cheek.

All except one (in the BMNH) are small, 40–89 mm in SL; the adult, 186 mm in SL, is a male with a white lower lip, a concave upper profile of the snout and a long lower jaw (39·2% length of head, 12·6% SL). Its outer teeth are unicuspid or with reduced minor cusps, but some of them have the brown tips worn off; the inner teeth are tricuspid.

2. The hot springs near the south bank of Uaso Nyiro (Fig. 83).

The fishes of the pools formed by these springs have been studied by K. L. I. Campbell (1981) along a 40 mile stretch of the river. The geological history of the area, which he takes from Jennings (1967) and Williams (1966) (see map, Fig. 83), reveals the former existence of lakes on the site of the present river and springs, with two chains of high land forming dams in a north–south direction and preventing the fusion of the lakes, so that for instance Spring D of Campbell's map was part of one lake and Spring E (near Chanler's Falls) of another, quite separate lake.

All the springs have outlets to the river, but Campbell considers that cichlids could not at present swim up these streams to the pools. The populations of the springs and that of the river must, however, all have been ultimately derived from a single population.

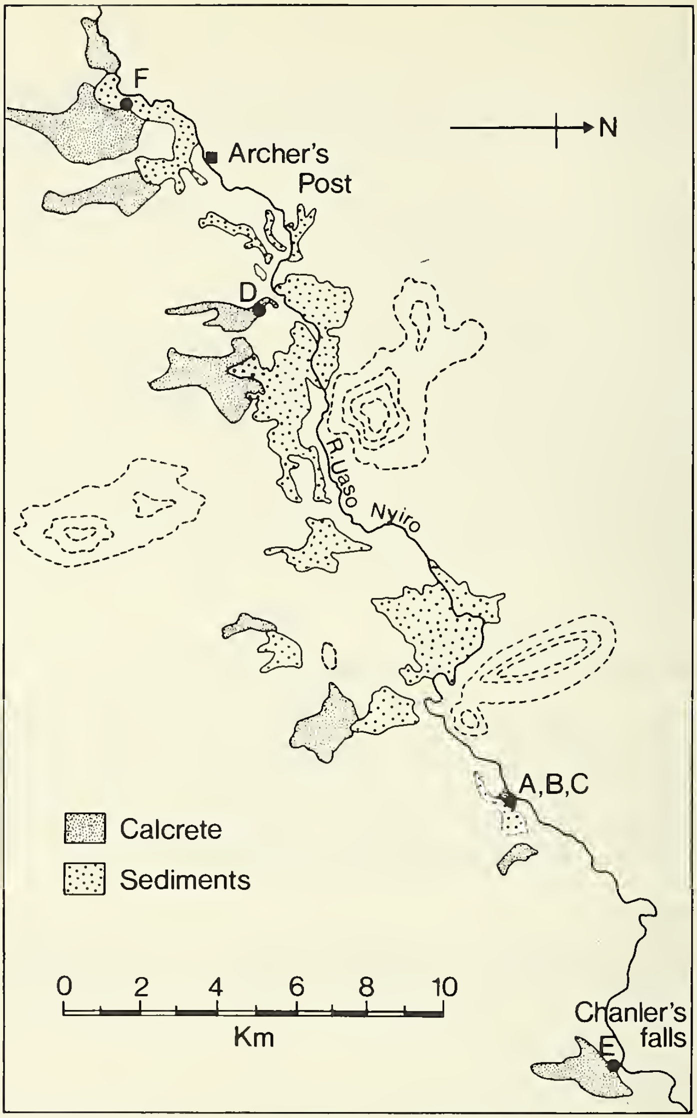

Fig. 83 Part of the Northern Uaso Nyiro (= Oaso Ngiro) showing the locations of the pools from which cichlids have been described. From K. Campbell (1981), by permission.

More effective than their physical isolation is probably the different quality of their waters in contrast to the river, and to a less extent to each other. The temperature is high and Campbell states that it is constant in all the pools at 30–31°C. Blaney Percival in 1912 gave the temperature of the spring near Chanler's Falls (Spring E of Campbell and the type locality of *O. s. percivali*) as 100°F (=38°C). The water in all the pools is clear and alkaline.

Buffalo Springs. The BMNH has three samples of small fishes from Buffalo Springs, collected in 1960–61, and Whitehead (1962) has reported on a collection made by himself. This is the same body of water as Spring F of Campbell's study, but Campbell's fishes were in a stream, Whitehead's in a pool.

As can be seen in Tables 62 and 67, the meristic numbers are those of *O. s. spilurus*, but the high percentage with IV anal spines in Whitehead's sample is notable. A single specimen collected by M. Coe in 1961 (and included in Table 62) also has IV anal spines, but may have been preserved for that reason. Buffalo Springs have been stocked (I.S.C. Parker, pers. commn).

The sizes of the fishes comprising our samples seem to be typical of the population. Whitehead states that individuals were breeding at a small size, and he records the male breeding colour as 'dusty blue-grey on the flanks and the blue of the fins less bright' than in *O. s. niger*. In the BMNH a male of 68·5 mm SL has testes starting to enlarge; the dorsal lappets are white as preserved, but there are no changes in the jaws and teeth. Two females, respectively 55·5 and 61·0 mm, have loose eggs of 2·1 mm diameter in the enlarged ovaries. In the smaller the outer anterior teeth are simple and slender, probably by wear, but the jaws are not enlarged.

Campbell found no mature fishes at this locality on his visit in 1975. The stomach and intestines in the fry were full of 'unicellular organisms ... measuring 8 by 12 µm' and there were no inorganic particles as in some fishes of the other springs. He concluded that they were not bottom-feeders.

Microbranchiospines were present in Campbell's samples on the outer sides of arches 2, 3 and 4 and in one specimen also on the inner sides of arches 2 and 3.

Other springs in the Uaso Nyiro basin. Four springs between Buffalo Springs and the one that is the type locality of *O. s. percivali* were explored by Campbell (1981), who named them Springs A, B, C and D (see map, Fig. 83). From his collections he presented some to the BMNH (see list, p. 250).

The numbers of dorsal and anal spines in samples from these springs in Table 62 are taken from Campbell's report, but the formulae in Table 67 are from my own counts, because it seems that Campbell and I do not always agree in the counts of soft rays (see p. 39). Vertebral numbers are from specimens in the BMNH.

Meristic numbers are in agreement with those of more southern populations of *O. s. spilurus*. So also are most of the proportions, but special attention has been paid to certain proportions for comparison with *O. s. percivali* (Table 70, p. 267). These are the size of the head, width of mouth and length of pectoral fin. Specimens of equal size from a number of samples of *O. s. spilurus* have been compared with *O. s. percivali*.

The length of head in the fishes of Spring D, as well as of *O. s. percivali* seems at first to be greater than in *O. s. spilurus*, but this is probably because of the early maturity of the spring fishes. The head is also rather big in the sample of *O. s. spilurus* from Lake Chem Chem, a warm lake in which maturity may also occur at a small size. But the mean head-length is low in the Chem Chem sample, in contrast to that in both Spring D and *O. s. percivali*.

The pectoral fin is as long in Spring D as in *O. s. spilurus*, in contrast to the short fin of *O. s. percivali*.

But a wide mouth and thick lips characterize the fishes of Spring D (perhaps also of A, B and C) no less than *O. s. percivali*.

Campbell (1981) found that the diet varied in the different springs, probably corresponding to opportunity. In Spring D the fishes appeared to be detritus feeders, the gut containing, along with fine mud and sand particles, numerous diatoms and fragments of higher plants. Fishes from this spring had a much longer intestine than those from elsewhere, the gut in 8 specimens measuring 5·9 to 7·8 times the SL, a range that was not approached by fishes of similar size from Springs A, B and C, nor by *O. s. percivali*, in all of which the ratio was between 2·4 and 4·4. One of eight specimens from Buffalo Springs, however, showed a ratio of about 6·8*.

The strangest feeding habits were described for the population of Spring A, which, as well as taking filamentous and unicellular algae (green or blue-green?) often ate 'large numbers of snails (*Melania tuberculata*)' and small 'clam shrimps' (*Ostracoda*). Some of the snail shells in the intestines were unbroken, sometimes with their inhabitants unharmed, others were broken and the snails digested. But the most surprising habit observed by Campbell was the removal

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*cf. A similar difference in length of intestine, associated with different diets, between populations of *Tilapia rendalli* introduced into Madagascar (Moreau, 1971). The size of the fish should also be taken into account.

Table 62. Frequencies of vertebral, and dorsal and anal spine numbers in samples of *O. s. spilurus* from rivers north of the Tana River in Kenya and Somalia.

Author or Museum No.	Locality	Anal spines III	IV	Dorsal spines XV	XVI	XVII	Vertebrae 29	30
Northern Uaso Nyiro & its springs								
Lönnberg, 1911 (*T. nyirica*)	Below falls	all			all		—	
BMNH 1912.3.22.125–134	Below falls	9	1	2	5	3	1	1
BMNH 1912.2.22.135–8	Above falls	5	0	0	4	1	—	
Whitehead 1962	Buffalo Springs	58	32	—	—	—	—	
BMNH 1961.11.14.16–26	Buffalo Springs	10	2	1	9	2	8	3
BMNH 1967.11.16.9–14	Buffalo Springs	6	0	0	6	0	—	
Campbell 1975	Buffalo Springs	7	2	1	8	0	—	
Campbell 1975	Spring A	106	0	6	5	0	1	
Campbell 1975	Spring B	11	0	1	10	0	6	
Campbell 1975	Spring C	28	7	4	2	0	—	
Campbell 1975	Spring D	54	0	1	11	0	5	
The Juba River system								
Genoa 15131	Bardera, 1908	2	0	0	1	1	—	
Senna, 1915	Bardera, 1913	4	8		(mode XVII)		—	
Genoa 15124	Lugh, 1895	12	1	1	6	3	—	
Genoa 15124	R. Ueb, 1896	0	3	0	0	2	—	
Genoa 15130	Ganale Doria		1	0	0	1	—	
D'Ancona, 1939 & Caporiacco, 1947 (*O. danconai*)	Daua Parma	0	52	(XVIII in one, the type of *O. danconae*)			—	
BMNH 1975.1.20.20–30	nr. Baidoa, between Juba & Webi Shebeli	0	10	2	5	1	—	
Webi Shebeli system								
BMNH 1895.12.31.64	an upper tributary	1	0	0	1	0	—	
BMNH 1905.7.25.96–97	Modjo R.	2	0	0	0	2	—	
Nichols, '*T. browni*'	R. Ramis	0	1	0	0	1	—	

of larger snails from the shell before swallowing the soft parts. Campbell observed fishes in the pool 'getting a hold on the head and by movements of the jaws slowly pulling it out of its shell'.

This is an astonishing habit for an *Oreochromis*, only paralleled among the lake species of the haplochromine group by species in which the jaw teeth are specially adapted for the purpose (see Greenwood, 1974:37 for Lake Victoria; and Bertram, Borley & Trewavas, 1942:60 for Lake Malawi). But these latter are believed to crush and discard the shell before swallowing the mollusc. The operation described by Campbell seems to require more skill, and is achieved with a dentition specialized for quite a different diet. No wonder the teeth are often broken.

Campbell (1981) states that the diet in Springs B and C was as in Spring A, presumably also *Escargots aux algues vertes* on occasion.

Colour. The breeding coloration of males is described by Campbell (1981), who states that it is similar to that of *O. s. niger* as described by Whitehead (1962*a*:623), but there are differences. Like *O. s. spilurus* and *O. s. niger*, these fishes have a golden yellow appearance, the yellow being purer at the margins of the scales of the lower half of the flanks; the iris is silvery white; the pectoral fin is clear with red rays; the dorsal lappets and caudal margin are red. The soft dorsal and caudal fins are described as golden-brown with blue-green spots in Spring A, but with red-brown spots between yellowish rays in Spring D. A difference from *O. s. niger* is in the colour of throat and belly, which are said to become dark blue-black during courtship, but at other times are dusty blue. Given the difficulty of describing these changeable colours, which look different as the lighting changes, the similarities to the other populations are enough to indicate relationship. The prevalence of golden yellow on the flanks seems characteristic.

The genital papilla is white and prominent in mature fishes of both sexes.

Breeding. Campbell (1981) observed the construction of mating depressions by males both in Spring A and in the aquarium. In Spring A this was preceded by unorganized digging, but eventually a depression 18 to 22 cm in diameter and 5 cm deep was made. In the aquarium, fishes from Spring D mated in such a pit after courtship activities that involved digging by both partners, lateral display by the male with fins erect and circling by both within the depression, culminating in egg-laying, the immediate picking up of the eggs by the female, followed by fertilization taking place in the mouth. Campbell states that eight similar 'runs' took place, presumably with eggs being laid and fertilized each time. The female then left, but visited another displaying male. Because his pit was behind a rock the observer could not see whether she again spawned, but her visit was short, about 1½ minutes.

As far as aquarium conditions allow, this would seem to have the necessary elements of the formation of a mating arena by males with accompanying polyandry and possibly polygyny, such as has been described for other species of the subgenus *Oreochromis*. At the end of these activities the female with her eggs joined a group of females and immature males.

The Juba River (Giuba or Ganana)

The tributaries of this river rise on the eastern side of the watershed east of the chain of Rift Valley lakes from Lake Zwai to Lake Turkana. Collections have been made by Italian travellers and have been described by Vinciguerra (1895, 1896, 1897, 1912, 1927), Senna (1915), D'Ancona (1939) and Caporiacco (1947), usually under the name *Chromis niloticus* or *Tilapia nilotica*.

Di Caporiacco's specimen was one of the 52 described by D'Ancona, all of which had IV anal spines. On this account Caporiacco referred them to *Oreochromis* Günther and renamed them *O. d'anconai*. This sample came from Malca Guba, high up on the tributary river Daua. One of two specimens from another tributary, Ganale Doria, has IV anal spines (Vinciguerra, 1912). Three very small ones from the Ueb River, also a tributary, all have IV. From the main river one of thirteen from Lugh has IV, the rest III (recorded by d'Ancona, 1939, from Senna, 1915), two from Bardera have III (Mus. Genoa C.E.15131), but one of a further sample of twelve from the same locality has IV (Vinciguerra, 1896). Two from Giumbo, near the mouth of the Juba, are recorded without comment (Vinciguerra, 1927), so probably have III. In Somalia, between the Juba and Webi Shebeli, nine small specimens in the BMNH all have III anal spines.

So we have in the Juba system a pattern similar to that noted by Whitehead in the Athi and Tana, a higher proportion of IV-spined individuals in the upper reaches of the river, to 100% (apparently) at Malca Guba.

I have seen several of these samples, those in the Genoa Museum thanks to the kindness of Dr Tortonese and Dr Delfa Guilia. The gill raker numbers (15–18 on the lower part of the arch) agree with those of *O. s. spilurus* and *O. s. niger.* As in *O. spilurus* there is some correlation between the numbers of dorsal and anal spines. Counts of dorsal spines were not given for the Malca Guba sample by d'Ancona, but in the one specimen made the type of *O. d'anconai* by Caporiacco there are XVIII, a number common in *O. s. niger* but not in *O. s. spilurus.*

It is interesting that one expedition, the last and fatal one of Bottego, crossed the watershed into the Rift Valley and brought back a sample of *Oreochromis* from an affluent of Lake Stefanie (Vinciguerra, 1898). They are preserved in Genoa (C.E.15126), and agree with *O. niloticus* of the same region in the number of gill-rakers (3–5 + 1 + 18–20), scales (32–34 in the lat. line series) and total numbers of dorsal rays (28 or 29), and all have III anal spines. I have examined eight of them, 31–53 mm SL; there are five still smaller. This marks the watershed as the boundary between *O. niloticus* and *O. spilurus.*

Webi Shebeli (Fig. 78)

From the upper tributaries of this river Donaldson Smith brought a collection of fishes, among them a single *Oreochromis* recorded by Günther as *Chromis spilurus.* It has a gill-raker count of 15, a dorsal formula of XVI 11 and a rather large mouth (lower jaw 38% of head) and agrees well with *O. s. spilurus.* The two '*T. nilotica*' from Neumann and Erlanger's expedition, taken in a tributary of the Shebeli variously spelt Modjo or Mojo, are also *O. spilurus*; and *T. browni* Nichols, from the neighbouring tributary Ramis, is evidently conspecific with these. Only *T. browni* has IV anal spines, the rest III. In the absence of knowledge of the populations or of the living fish I cannot find any reason for separating them from *O. s. spilurus.*

The tributaries of the Webi Shebeli rise on the southern side of a range of mountains which on the north is the source of the Awash. Neumann and Erlanger brought *O. niloticus* from this river system and Barnum Brown brought a fish, the type of *T. cancellata* Nichols (1923) from a river NE of these mountains, running towards, but probably not reaching, the sea. It has the number of gill-rakers, dorsal rays and scales which characterize *O. niloticus.* These few specimens point to the Shebeli–Awash watershed as a dividing line between the areas of distribution of *O. niloticus* and *O. spilurus.*

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1893.12.2.3–12 (syntypes)	43·5–90	Mwangudo R., Giriama territory, (basin of Voi R.)	J. W. Gregory
1890.3.27.10–11	78, 84	Taita, inland of Mombasa	Wray
1902.1.16.37–43	47–63·5	Tanganiko, coast region of Kenya	A. Blaney Percival

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1909.6.5.7–16	32–110	Rabai, 12 miles from Mombasa	S. L. Hinde
1953.8.6.80 now at MRAC	165	L. Marikano, in Lower Athi flood-plain	W. E. Frost
1953.8.6.321–330	77–114	L. Marikano, in Lower Athi flood-plain	W. E. Frost
1953.8.6.112–136	104–135	L. Jilore, Lower Athi	W. E. Frost
1953.8.6.137–169	34–84	L. Jilore, Lower Athi	W. E. Frost
1953.8.6.83–97	105–166	Ponds in flood-plain of Lower Athi	W. E. Frost
1953.8.6.98–111	78–111	Wengi in flood-plain of Tana R., near Garsen	W. E. Frost
1953.8.6.81–82 no. 82 now at MRAC	162·5, 143	Garsen, Lower Tana	W. E. Frost
1953.8.6.319, 320	136·5	Powell's Camp, Tana R.	W. E. Frost
1953.8.6.295–318	44–176	Garissa, in pool nr Tana R.	W. E. Frost
1946.12.28.10–12	105–192	Garissa	H. Copley
1967.11.16.21–24	18·0–46·5	Garissa	P. J. P. Whitehead
1968.9.3.1	136	Garissa	J. Adamson (coll.) H. Copley (pres.)
1969.3.6.67–70	33–55	Saka, Tana R.	Lord Richard Percy
1966.9.13.7–11	75–133	Sagana ponds	E. Trewavas
1979.9.4.34	140	Tana R.	M. Hyder
1955.1.18.95–101	35·5–108·0	Rare R. at Takaunga	H. Copley
1955.1.18.83–88	19–65	Nosovuni R., Kilifi Kenya	H. Copley
1955.1.18.43–82	28–90	Ngomeni, coastal region, N. of mouth of Athi. Salinity 41‰	H. Copley
1955.1.18.40–42	150–161	'Kongoni', Lower Athi	H. Copley
1957.11.28.11–27	54–87	L. Chem Chem, 27 miles from Malindi	H. Copley
1946.12.28.13–17	25–42	'Lake Natron' (?)	H. Copley
1911.11.20.3–4 (two of the syntypes of *Tilapia nyirica*)	40, 43	N. Uaso Nyiro, below Chanler's Falls	E. Lönnberg
1912.3.22.125–134	29·5–87·0 186	N. Uaso Nyiro, below Chanler's Falls	A. Blaney Percival

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1912.3.22.135–138	63–89	N. Uaso Nyiro, above Chanler's Falls	A. Blaney Percival
1961.11.14.16–26	36–61	Buffalo Springs, nr N. Uaso Nyiro	Cunningham Van Someren
1967.11.16.9–14	47·0–68·5	Buffalo Springs	J. D. L. Fleetwood
1967.11.16.8	66·5	Buffalo Springs	M. Coe
1979.7.18.425	52	'Spring A', N. Uaso Nyiro (Fig 83)	K. L. I. Campbell (1975)
1979.7.18.435–440	31–52	'Spring B', N. Uaso Nyiro	K. L. I. Campbell (1975)
1979.7.18.430–434	52–59	'Spring D', N. Uaso Nyiro	K. L. I. Campbell (1975)
1979.7.18.426–429	39–57	Stream Boji, N. Uaso Nyiro system	K. L. I. Campbell (1975)
1976.7.13.1–5	92·6, 107	Bamburi Cement Co., nr Mombasa, ex Aruba dam,	R. D. Haller
	96·5, 107	Bamburi Cement Co., ex Tana R., east of Garsen	R. D. Haller
	126·5	Bamburi Cement Co., 4th generation ex Sagana	R. D. Haller
1967.7.31.1	96	Pond near Mombasa	M. Hyder
1971.11.15.69	23·5	near Mombasa	Vane Burton
Genoa Mus.		Juba system	
C.E.15131	2 fishes, 71·5, 72	Bardera (R. Ganana)	U. Ferrandi, 1908
C.E.15124	5 fishes 68·0–108·5	Lugh	Bottego, 1895
C.E.15124	9 fishes 39–61	Lugh	Bottego, 1895
C.E.15124	4 fishes 20–35	R. Ueb	Bottego, 1896
C.E.15130	1 fish 95·5	Ganale Doria	Citerni
BMNH		Webi Shebeli system	
1895.12.31.64	74·6	Water holes near Sheik Husein, nr Wabi R.	Donaldson-Smith
1905.7.25.96–97	69·2, 93·2	Modjo R., Webi Shebeli	Neumann & Erlanger
		Between rivers Juba & Webi Shebeli	
1975.1.20.20–24	61·0–74·5	Baidoa, Somalia	Kouchazov
1975.1.20.25–27	19·5–30·0	Rivo Cement reservoir	Kovchazov
1975.1.20.28	27·0	Manas, Somalia	Kouchazov
1975.1.20.29–30	20, 27·5	Burhakaba, Somalia	Kouchazov

Oreochromis spilurus niger (Günther)

Oreochromis niger Günther, 1894*c*:89, pl. ix (Kibwezi R.); Pellegrin, 1904:355.

Tilapia nigra; Boulenger, 1899*a*:110; *idem*, 1915:152, fig. 99; Trewavas, 1937 (part, not the fossils); Copley, 1952*a*:234, fig. 160 (introductions, food, habits); *idem*, 1952*b* (spawning); *idem*, 1953 (spawning, culture); *idem*, 1956 (genital papilla); *idem*, 1958:116, fig. 69 (natural history); Brown & Van Someren, 1953 (pond culture); Lowe-McConnell, 1958:134 (introduction into L. Bunyoni); Van Someren & Whitehead, 1959*a* & *b*, 1960*a* & *b*, 1961*a* & *b* (sex ratio, growth, etc. in ponds); P. J. P. Whitehead, 1962*a* (taxonomic relationship to '*T. mossambica* in Kenya' i.e. *O. s. spilurus*, hybrids, colour etc.); Van Someren, 1962*a* & *b* (population control in ponds).

Tilapia spilurus nigra; Trewavas, 1966*c*:401 (classification); Elder, Garrod & Whitehead, 1971:103 ff. (hybrids with *O. leucostictus*).

Tilapia nigra nigra; Thys van den Audenaerde, 1968*b*:xxxvi.

Tilapia nilotica athiensis Boulenger, 1916*b*:345 (Makindu & Tsavo rivers).

Tilapia athiensis; Hubbs, 1918:16 (Athi R.).

Oreochromis athiensis; Pellegrin, 1926:388 (nr. Nairobi).

Tilapia browni (*non* Nichols); Fowler, 1936:324, figs 141–146 (Athi, R., variation in melanin-pattern in young).

TYPES. Syntypes: ♂ and ♀, respectively 212+58 and 169+44 mm, collected by J. W. Gregory in pools of the Kibwezi River. BMNH 1893.12.2.1–2.

Syntypes of *T. nilotica* var. *athiensis*: 39 specimens, one of 160 mm SL, the rest 33–87 mm, from Makindu and Tsavo Rivers, Athi system. BMNH 1915.12.2.88–102.

Distinguishing characters

Vertebrae 29–31, mode 30; dorsal spines XVI–XVIII, exceptionally XIV or XIX, mode (in samples in BMNH) XVIII; scales in lateral line series 30–32, mode 31. Length of caudal peduncle 6·7–11·7% SL, 0·4–0·8 of its own depth.

Table 63. Proportions for two size-groups of *O. s. niger*.

	SL 76–162 mm	SL 169–290 mm
Proportions as % SL		
Depth	38·2–46·3	44·0–54·0
L. head	32·6–35·4	33·7–36·8
L. pect. fin	37·0–42·0	34·3–42·5
L. lower jaw	10·25–12·7	♂13·9–16·5 ♀13·5–16·2
L. caud. ped.	8·5–11·5	6·7–11·8
Caud. ped. l/d	0·5–0·8	0·4–0·7
Proportions as % length of head		
L. snout	30·0–37·8	34·2–41·6
Eye	25·0–19·3	19·5–16·0
Interorb.	30·2–38·4	32·6–37·7 (40 in a ♂ of 212 mm)
D. preorb.	16·7–20·8	19·3–23·4
L. lower jaw	33·0–38·5	♂37·4–44·8 ♀40·0–44·8
W. lower phar.	30·0–34·5	

Description

Based on 24 specimens, comprising the syntypes of *O. niger*, three of the syntypes of *T. nilotica* var. *athiensis*, eight other wild fishes, and eleven from introduced stock in Lake Naivasha (collected 1930–31) and Lake Bunyoni (not later than 1935).

Proportions (Table 63) are given for two size-groups, the smaller of which can be directly compared with both geographical groups of *O. s. spilurus* (Table 57). The biggest male is 232 mm SL, the biggest female 290 mm.

The diameter of the eye and depth of preorbital bone are allometric in opposite senses and are approximately equal at *ca* 160 mm SL. Upper profile of snout straight or slightly convex in young, becoming concave in mature fishes with the elongation of the jaws.

Teeth in 3 or 4 series up to 120 mm SL, 4 or 5 above this length; outer bicuspid, inner tricuspid except in large mature fishes, in which many or all are replaced by unicuspid teeth or teeth with very small minor cusps, in both sexes; 57–74 in outer row of upper jaw (Table 64).

Gill-rakers short, 15–19, usually 16–18 on lower part of anterior arch. Microbranchiospines on outer sides of 2nd, 3rd and 4th arches.

Lower pharyngeal teeth slender, not densely crowded; dentigerous area with concave sides, nearly straight posterior edge and moderately narrow lobes (Fig. 80). Blade from 2/3 to $1\frac{1}{2}$ times median length of dentigerous area.

Scales in 2 or 3 series on cheek; 30–32 in lateral line series, 4 or 5 from origin of dorsal to lateral line, 5–7 between bases of pectoral and pelvic fins; not becoming abruptly smaller on lower flanks.

Dorsal XVII–XIX 9–11 (12); exceptionally (Lake Naivasha, 3 specimens) XVI 9–11 and in one (also Lake Naivasha) XIV 11. Totals in wild fish (26) 27–29, mode 28, in Lake Naivasha 25–30, mode 29. Modal number of spines about equally XVII and XVIII in the Kibwezi, Simba and Tsavo Rivers, XVIII in the Naivasha samples (Tables 59 & 65 and Fig. 82).

Anal IV–V (VI) (8) 9–10 (see Tables 59 & 65).

Vertebrae 29–31, mode 30.

Caudal truncate, not heavily scaled.

Genital papilla of male short, club-shaped or with a shallow distal notch.

Size. Maximum sizes in wild populations have not been recorded. Whitehead (1962*a*) records a male of 305 mm SL at the Sagana ponds and a female from the introduced population of Lake Naivasha measures 290 mm SL as preserved. Weight varies widely. Van Someren & Whitehead (1960) record that in a breeding pond a male of total length 32·0 cm weighed about 1 lb (454 g), but in a 'monosex' pond a male already reached this weight at 29·5 cm. The deep bodies of the fishes from the Lake Naivasha collection of 1930–31 show that the weight/length ratio must have been very high in the then unsaturated environment of the recently stocked lake.

COLORATION. In spite of its name *O. s. niger* is not black and in its brilliant male breeding colours is distinguished from its congeners *O. hornorum* and *O. mossambicus*, in which the male is black. On death, however, the general body colour becomes dark and the bright colours of the fins give place to black.

The young are silvery with dark vertical bars on the body (as in most *Tilapia*, *Sarotherodon* and *Oreochromis*), more distinct in dying or preserved fishes. On one bar a mid-lateral spot may be faintly emphasized. The caudal fin is usually marked with more or less regular bars. The tilapia-mark is small and not sharply delimited, no longer distinguishable above 90 mm SL. Cridland (1962) states that in aquarium-reared young the tilapia-mark disappears 60 days after hatching, i.e. at an average length of 30·5 mm.

In a female of 127·5 mm SL (observed by me at Sagana) the preorbital was brassy-green, the nape brassy and the snout darker, the lower lip white. The flanks were yellowish silver with faint vertical bars and no lateral spots; throat and isthmus were yellow; the caudal was marked with a grey reticulum with yellowish intersterstices; the lappets of the dorsal fin were narrowly tipped with red.

The breeding male has been described by Whitehead (1962*a*:622, repeated in Elder *et al.*, 1971) and I have seen specimens at Sagana substantially agreeing with his account and with a cast in the National Museum in Nairobi faithfully painted by Mr Mitten. I quote Whitehead for males over 200 mm in SL.

> Flanks silver-grey, with yellow on the outer edges of the scales, especially on the lower half of the flank; seven to nine dark vertical bars extending from the base of the dorsal to midway down the flank, the bars not always visible and quickly lost on removal from the water; lower part of head and belly white or yellow. Head, dorsal surface and operculum variable, from grey-brown to olive-brown; a dark grey spot at posterior angle of operculum . . . Upper lip dark grey, lower lip yellow, becoming white at the corners; a dark grey bar immediately below the lower lip, but rest of throat variable, from yellow or white to dusty green. Dorsal fin: lower portion of spinous part and whole of soft part grey, with yellow spots on the soft portion and on the posterior third of the spinous; lappets bright red. Anal fin bright blue on spinous part, grey with yellow spots on soft portion. Caudal fin grey with yellow spots, the margin bright red. Pelvic fins deep blue. Pectoral rays vermilion, membrane colourless.

Cridland (1962:29) records that the most striking feature in the colour of his, probably rather small, breeding males was the 'silver-coloured iris . . . on a dark blackish-brown colouration of the anterior part of the fish'. Elder *et al.* (1971:119) also record that *O. s. niger* normally has white eyes.

The male (probably high territorial) coloration of electric blue body and black fins has not been reported for *O. s. niger*, but remained unrecorded for *O. s. percivali* and *O. s. spilurus* until this study. Efforts to find a fully grown population of pure *O. s. niger* in 1981 were unsuccessful.

CHANGES IN THE JAWS AND TEETH (Table 64). As in *O. s. spilurus*, both the enlargement of the jaws and the replacement of notched teeth by unicuspids are related to size and maturity. Both changes take place in females as well as males. The smallest male *O. s. niger* available with

Table 64. Changes in the jaws and teeth of *O. s. niger*.

SL (mm)	Gonad	L.j. % head	L.j. % SL	Outer teeth if not bicuspid	Inner teeth if not tricuspid
100·5	♀ rp	37·0	13·0		
107	♂ stg	35·0	12·1		
119	♂ qt	35·2	12·2		
120	♂ rpg	34·1	12·1		
180	♀ rpg	41·0	14·6	few posterior unicuspid	
209	♂ stg	44·8	16·5	unicuspid	most unicuspid
212	♂ ?	41·0	13·9	most unicuspid	most unicuspid
216	♀ rpg	40·5	14·1	unicuspid posteriorly and anteriorly	
216	♀ rp	43·7	16·0	unicuspid	
217	♂ rpg	37·4	13·8	posterior unicuspid	
232	♂ stg or sp	41·5	14·3	most unicuspid	inmost row & many others unicuspid
240	♀ rp	44·8	16·2	most unicuspid	few unicuspid
290	♀ rp	44·0	15·5	unicuspid	unicuspid

Table 65. Inverse correlations between numbers of spines and soft rays in the anal fin in a sample of *O. s. spilurus* from Lake Jilore in the Lower Athi flood-plain, and *O. s. niger* in the Makindu and Tsavo tributaries of the Athi River. Note the difference between the two populations in the numbers of soft rays in IV-spined members.

	Spines \ Soft	8	9	10	11
O. s. spilurus: L. Jilore	III	1	6	15	
	IV	4	7		
O. s. niger (types of '*T. n. athiensis*')	IV	0	7	20	2
	V	3	12	2	0

unicuspid outer teeth measures 209 mm in SL and most of its inner teeth are unicuspid also; its lower jaw is 16·5% SL. A ripe female of 216 mm SL has unicuspid outer teeth and a lower jaw length of 16% SL. All the specimens in the BMNH over 217 mm in SL are from Worthington's Lake Naivasha collections of 1930–31 and they are, as far as I can discover, bigger than any used by Whitehead (1962*a*) or by Elder *et al.* (1971). They include females as well as males and indeed the two biggest are females (Table 64), measuring 240 and 290 mm in SL. Their lower jaws are respectively 16·2 and 15·5% SL; both have unicuspid outermost teeth and one has a few, the other all the inner teeth also unicuspid. These fishes are also bigger than any *O. s. spilurus* available and suggest that in both subspecies if females grow big enough they, as well as the males, will exhibit the long jaws, concave profile and unicuspid teeth characteristic of mature fishes in this group of the subgenus *Oreochromis*.

The small ripe female of 100·5 mm SL at the head of Table 64 is from stock introduced into Lake Nakuru two years before her capture. Although her profile remains convex and the teeth are bi- and tri-cuspid, the jaws are relatively longer than those of males of approximately the same size with less developed gonads.

We have no evidence to suggest that the jaws can regress and the teeth be replaced again by bicuspids between breeding periods.

Ecology

Food

Brown & Van Someren (1953*a*) stated that *O. s. niger* is not a plankton feeder, but grazes on the algal film of underwater surfaces. By increasing the surfaces with papyrus screens and hurdles they obtained better growth in ponds. Van Someren & Whitehead (1959*b*) explain the better growth in shallow ponds as a result of good algal growth on the bottom mud, brought about by good illumination. The main food consists of diatoms (Whitehead, 1959). Copley records that at a large size *O. s. niger* will eat insect larvae and, at least in a confined space, even small fishes.

Growth

Growth of *O. s. niger* in ponds at Sagana, Kenya, has been studied experimentally by Brown & Van Someren (1953), Van Someren & Whitehead (1959*a* & *b*, 1960*a* & *b*, 1961*a*, *b* & *c*), and Van Someren (1962). As in other fishes the growth in length follows an asymptotic curve under uniform conditions, and is very sensitive to adverse or improved conditions. Van Someren & Whitehead concluded that growth is not necessarily halted or slowed down by the attainment of sexual maturity or even directly by breeding. They attributed the limited growth of a breeding pond population to increased population density consequent on the addition of offspring. Their evidence for this was the resumption of a healthy growth-rate by males removed on attaining sexual maturity from a pond of breeding fishes to a lightly stocked pond of males only ('monosex culture').

Independently of population density the same experimenters found that growth was affected by the depth and turbidity of pond water. The turbidity of their ponds was caused, not by plankton, but by colloidal particles, differences in turbidity being related to differences in the nature of the soil. At equal stocking rates fish grew better in clear and shallow (30 cm deep) ponds, and this Van Someren & Whitehead attributed to greater light penetration having a beneficial effect on the algal growth at the mud surface. As Hickling (1962) has noted, shallow ponds have not been found favourable for other cultured fish, carp for example, but carp feeding habits are different and depth has another significance where annual temperature fluctuations are considerable.

Van Someren & Whitehead found that the growth of their male *O. s. niger* (in 'monosex' ponds) showed two mild annual peaks, and this was also attributed to the alternation of clear and cloudy skies as well as to the effects of wind and rain. They suggested that the direct effects of temperature on metabolism and the effect of light intensity and temperature on algal growth probably acted together to produce the fluctuations in the growth of the fish.

The same authors suggest that the amount of available food may exert its effect on the fish in a way that may be modified by the schooling behaviour of the species. They found, for example, that as many as three size-groups could coexist in a pond without interfering with each others' growth-rate and in this way a pond could support a larger biomass than if all the fish were stocked at the same size.

As with other fishes (*cf.* M. E. Brown, 1957:372, on *Salmo*), differential growth-rates have been demonstrated as between members of a single brood (see *Report on Kenya Fisheries* for 1961 (1962)), and this must depend on behavioural and social factors.

The results of Haller (1974) with *O. s. spilurus* grown in flowing water would also be relevant to *O. s. niger.* Haller attributes the improved growth to the failure to establish mating territories in such conditions.

Some preliminary experiments on the effect of living-space were recorded in *Rep. Kenya Fisheries,* 1961 (1962), but no evidence was found of the influence of the volume of water as distinct from the amount of bottom grazing per fish.

When Lake Naivasha was stocked with fry in 1926, growth was there so rapid that seventeen months later *O. s. niger* of 1½ lbs (680 g) were caught (Copley, quoted by Beauchamp, 1954:24). To achieve this the fish must have had an abundance of food of good quality, and the lake then provided an unsaturated environment.

Differential growth of the sexes was observed by Brown & Van Someren (1953*a*) and was the basis of early experiments in 'monosex culture', the larger (male) individuals being selected on size from a pond of fingerlings only 10–12 cm in total length, and sexually immature. An experiment recorded in *Report on Kenya Fisheries* 1956 (1957) on growth of males and females in separate ponds at Sagana stocked at the same densities gave the following results (lbs converted to grams).

Average growth in 8 months:

Males from	7·3 cm to 21·4 cm and from	8·16 g to 172·5 g
Females from	8·4 cm to 14·7 cm and from	11·9 g to 54·5 g

Further results were recorded by Van Someren & Whitehead (1960*a*).

Cridland's aquarium-hatched young at the age of 90 days also showed differential growth. His figures are (1962:32):

34 males, average length	58·2 mm
13 females, average length	53·8 mm

He notes that mortality was considerable.

It still remains to be shown whether, given time, the female is capable of attaining the same maximum size as the male in the same environment, as our samples would suggest.

Breeding

The sex-ratio in adults is given as 55–60% males (Brown & Van Someren, 1953; Van Someren & Whitehead, 1959*a*) in ponds at Sagana.

No conclusive figures are given for the age at first maturity, but in ponds it is a matter of months rather than years, 6 months and 8 months being the ages found in different batches.

The size of first spawning depends on population density. Thus, in an experiment reported by Brown & Van Someren (1953), the average size of first spawning in a quarter-acre pond stocked with 300 fish was 12·5 cm (♂) and 10·5 cm (♀); in a pond of the same size stocked with 600 fish, 10·5 cm (♂) and 9·0 cm (♀); but the offspring of these spawned at an average length of 8·8 cm. At both stocking rates spawning occurred at approximately four-weekly intervals, but the experiments were not suited to show whether the same individuals were concerned.

The number of eggs laid depends on the size of the female. Cridland (1962*a*), working on aquarium fishes, found that a female of 7·5 cm, the smallest of his spawners, laid 44 eggs, whereas one of 17·0 cm produced 692 in her first recorded brood and more in successive broods (contrast Lowe, 1956*b*, on *O. esculentus*). Cridland found that the shape of the eggs differed slightly as between small and large clutches, the average dimensions in five small clutches being 2·41 × 1·84 mm, in five large clutches 2·39 × 1·98 mm, but we may doubt if this difference is significant.

In the BMNH collection a small sample from a dam includes a female of 78·5 mm (TL about 9·5 cm) with pear-shaped ovarian eggs of 2·5–3·0 mm long diameter. She retains, as preserved, the vertical stripes of the juvenile and the jaws are not hypertrophied. Arnoult (1954) records yellow eggs of 2 mm diameter from the mouth of a brooding female of an introduced population in Madagascar.

The breeding of a small pair (♂ about 15 cm, ♀ 10 cm) was observed in a pond by Copley (1952*b*). The mating pit was the shape and size of a saucer. In this the female laid the eggs in batches, the male following closely and apparently fertilizing. The female picked up the newly spawned eggs as they were laid. From this description it seems that the eggs were fertilized before being taken into the mouth, but Mr Copley was not then alerted to the other possibility. Cridland (1962*a*) found that both methods might be used; either the male might fertilize the eggs as they were laid, or the female might pick up the eggs first and then suck the milt into her mouth.

Copley later (1958) gave the size of the spawning pit for the species as up to 45 cm in diameter and 25 cm deep. Presumably the size depends on the size of the male excavating it. The pits were made in very shallow water with shelving bottom. Elder *et al.* (1971:117) add that the pit frequently has subsidiary small pockets at the periphery, and in the spawning act as observed by them they conclude that the eggs are fertilized in the female's mouth. The eggs are bright yellow.

Sexual dichromatism is marked at breeding time (see under 'Coloration' above) and males grow faster than females (see under 'Growth' above), but maximum sizes recorded for the sexes are close. Elongation of the jaws and simplification of the teeth occur in both sexes; for details see p. 253.

Hybrids

Elder, Garrod & Whitehead (1971), following and compiling the work of Whitehead (1960), Elder & Garrod (1961), and Elder (1966), describe the results of hybridization between *O. s. niger* and *O. leucostictus* in Lake Naivasha, a body of water to which neither species is native. *O. s. niger* had been introduced deliberately and *O. leucostictus* accidentally with *Tilapia zillii*.

The recognized hybrids were intermediate between the parent species in numbers of scales, fin spines and gill-rakers, in length of pectoral fins, size of mouth and shape of pharyngeal tooth pad as well as in colour pattern and even the colour of the iris. The authors point out that although these data amply support the hypothesis of hybridization they do not necessarily give a picture of an F_1 generation, but point to back-crossing between the hybrids and the parent species (introgression), with some evidence that *O. s. niger* is the species most frequently involved. As Welcomme (1967*b*) showed for Lake Victoria, *O. leucostictus* both lives and breeds in 'lagoons' within the fringing papyrus swamp, and Elder *et al.* (1971) found that *O. s. niger* remained in the lake beyond the edge of the papyrus. From time to time when the lake level fell the papyrus lagoons closed or became inaccessible to the fishes, and presumably at these times *O. leucostictus* would be forced to occupy the same breeding zone as *O. s. niger.*

Proof that the cross can occur was obtained in experimental tanks, when both ♂ *O. s. niger* with ♀ *O. leucostictus* and the reciprocal cross were successful (Elder *et al.*, 1971, pl. II). The breeding behaviour of the two species, which without the interference of man would never have met, was observed to be very similar, and this 'more than offset the marked differences in breeding coloration' (Elder *et al.*, 1971:135).

Confirmation was also obtained that the hybrids were fertile by keeping some in ponds and finding that they bred, producing viable offspring.

When in 1974–5 Siddiqui visited Lake Naivasha, the water level was higher and he recorded (1977 & 1979) that *leucostictus* was virtually the only *Oreochromis* in the lake, no trace being detected of *O. s. niger*, and the few surviving hybrids being much closer structurally to *O. leucostictus* than were those of 1961–62. This illustrates how quickly a change in ecological balance combined with introgressive hybridization can favour one of two related species (see also pp. 451–452).

A similar accidental conjunction of these two species in ponds at Tebere, Kenya, had produced hybrids.

The same cross was made in experimental ponds by Pruginin (1965), who obtained 21 F_1 hybrids, only one of which was a female. The male parent was *O. leucostictus.* The reciprocal cross was not tried.

Pruginin (pers. commn) has also mated ♀ *O. s. niger* with ♂ *O. u. hornorum*, originally from Zanzibar, obtaining an F_1 generation of 100% males, as seems to be general when the male parent is *O. u. hornorum.*

A further cross was made with *O. niloticus* (Pruginin, 1965). When the male parent was *O. s. niger* 85% of the F_1 were male and all the offspring had IV anal spines. In the reciprocal cross the sex ratio was nearer normal, namely 43% ♂, 57% ♀, and about half of each sex had IV anal spines, the rest III.

The intersubspecific cross has been made without difficulty at Sagana ponds when only males of *O. s. spilurus* and females of *O. s. niger* were present (Whitehead, 1962*a*). The offspring showed a high percentage of individuals with IV anal spines and 84% of them were males. Whitehead's interpretation of the subpopulation of *O. s. spilurus* in the 80 km of the Athi below Lugard's Falls as the result of hybridization between the subspecies seems well based. About 64 km from the Falls a sample revealed 75·3% of individuals with IV anal spines, 24% with III and only 0·7% with V. Just below the Falls a much higher proportion of V-spined individuals was present. In the lowest 40–50 km of the Athi (Sabaki or Galana) about 25% have IV anal spines, and this is here interpreted as representing the lower end of a hybrid chain, where the influence of *O. s. spilurus* predominates.

Whitehead's original interpretation of the hybrids in Lake Naivasha as involving *Tilapia zillii* (1960) proved to be mistaken. No natural or accidental crossing of a species of *Sarotherodon* or *Oreochromis* with one of *Tilapia* is known, their breeding habits being far too dissimilar, but Bauer (1968) has succeeded in rearing offspring from artificial fertilization between ♂ *O. niloticus* and ♀ *T. tholloni.* They were all females.

Distribution

Natural distribution. The Athi River and its tributaries above Lugard's Falls; upper tributaries of the Tana River (Thuchi River, *teste* Whitehead, 1962*a*).

Dispersal by man. Stocked in farm dams in Kenya since 1922; in Lake Naivasha in 1926 and subsequently; in Lake Nakuru (which later dried up) and also in Lake Bunyoni in Uganda, where it seems to have been unsuccessful (Lowe-McConnell, 1958). The subspecies has been transported to Madagascar, where although it at first succumbed to the winter temperatures of a pond at high altitude, it was later reported to be surviving and multiplying on the high plateau (Arnoult, 1953). Le Touzey reported in 1952 (*teste* Chimitz, 1955, title 65) that from Lubumbashi (=Elizabethville) it had been sent to the then French Equatorial Africa for pond culture, but there is no record of its subsequent success in either locality.

Stocking in Kenya is now so widespread that it is difficult to find there any waters where a pure population of *O. s. niger* exists without admixture of *O. s. spilurus* or of other species.

Discussion

The evidence for the taxonomic status of *O. s. spilurus* and *O. s. niger*

Most of the evidence on which to base the taxonomic rank of the two forms is provided by the work of P. J. P. Whitehead (1962*a*). Whitehead's material was almost entirely from the Athi River, including the lower 160 km which also are known as the Galana or Sabaki. The boundary between the two parts is at Lugard's Falls, above which there is no record of native *Oreochromis* with only III anal spines.

Whitehead's investigation was begun with the possibility in mind that the two so-called species might represent a cline exemplifying the phenomenon of increased metameric numbers with decreasing temperature. Although he found few differences beside the meristic, his geographical and experimental evidence led him to conclude that the meristic differences had a genetical basis and that the two forms were 'incipient species'. Trewavas (1966*d*:402) treated them as subspecies.

1. The length of the caudal peduncle, which is greater in *O. s. spilurus* although the ranges overlap (Table 56). Samples from beyond the Athi agree with *O. s. spilurus* in this feature, where known.

2. More intense colouring in the mature male in the Lower Athi than in *O. s. niger*. Observations in 1981 found two male specimens of *O. s. spilurus* with a coloration that has not so far been recorded in *O. s. niger*. One of these was in an aquarium and was reliably identified as *O. s. spilurus*. The other was a freshly caught fish of about 12 cm TL with III anal spines from Lake Jilore. Both had the whole body electric blue and the vertical fins and the pelvics black. Efforts at this time to find a population of pure *O. s. niger* in Kenya failed, most waters having been stocked from mixed sources.

3. Meristic differences. Whitehead's concentration on the Athi River produced a picture that needs to be somewhat modified by the inclusion of samples from other coastal rivers of Kenya, including the Tana (Tables 59, 60 & 62). Whitehead established that in the Athi River the boundary between the two forms is at Lugard's Falls, where a waterfall of 3–4 m prevents the movement upstream of *O. s. spilurus*, but allows the 'contamination' of the downstream population by *O. s. niger*. Whitehead considered the 80 km below the falls to be 'a zone of overlap', in which the number of anal spines was III–V, with progressively higher proportions of III and lower of V as distance below the Falls increased. The lowest 48–50 km of the river Whitehead con-

sidered to be inhabited by pure *O. s. spilurus*, in which about 25% had IV anal spines. He recognized, however, that the population of Lake Chem Chem comprised almost 100% III-spined individuals. Lake Chem Chem is a lagoon, probably a relict of the former course of the lower Athi (Whitehead, pers. commn).

Table 59 and Fig. 82 show that the Chem Chem population is typical in this respect of samples from coastal rivers from Mombasa to the Voi, of coastal lagoons near the Athi mouth and of the Tana River up to Saka, near the 200 m contour. These samples, which include the syntypes of *Chromis spilurus*, must be considered as typical of this subspecies, while it is the lower Athi (Sabaki) which is exceptional in the high proportion of IV-spined fishes. It seems possible that not only the 80 km immediately below Lugard's Falls, where even V-spined individuals are common, but also the whole of the Lower Athi (Sabaki) and its flood-plain are 'contaminated' by *O. s. niger*.

The alternative explanations of the differences in meristic numbers, namely the effect of temperature or a genetic difference, are not necessarily mutually exclusive.

(i) In the known population samples a higher number of anal spines is correlated with a higher mean number of dorsal spines. This is shown in Whitehead's tables 3 & 4, and fig. 3, and in Table 59 of the present study. A particular example is provided by the 39 syntypes of '*T. nilotica* var. *athiensis*', among which those with IV anal spines have a modal XVII dorsals, those with V a modal XVIII. But the mean number of dorsal spines is higher in IV-spined *O. s. niger* than in IV-spined *O. s. spilurus* of the lower Athi (Table 65 & Whitehead, 1962*a*).

(ii) Evidence from small samples in which vertebrae or lateral line scales were counted, supports the view that broadly the form with the higher range of dorsal and anal spines has also higher modal numbers of vertebrae, scales and total dorsal rays, that is, that the higher numbers of spines are indicators of higher segmental numbers.

But this is true only as between populations, and within populations there is some indication of an inverse correlation between spines and soft rays. See Whitehead, 1962*a*:612, and Table 65 of the present study.

(iii) That populations are not immediately labile in this respect is shown by the fact that Lower Athi fishes bred at Sagana ponds (about 1220 m altitude) did not develop numbers characteristic of *O. s. niger*.

(iv) That a genetical factor is involved was shown by the fact that IV-anal-spined *O. s. spilurus* from the Lower Athi, when mated together at Sagana, produced both III- and IV-spined offspring. Phenetically similar IV-spined *O. s. niger* have no III-spined offspring.

(v) The same conclusion was drawn from the fact that, although the two forms readily interbred when only one sex of each was present, the sex ratio was disturbed, 84% of the offspring being males. In this experiment the male parent was *O. s. spilurus* from a Lower Athi population.

If the present interpretation of the Lower Athi population is correct, Whitehead's results should apply *a fortiori* to populations 'uncontaminated' by *O. s. niger*. The present conception of *O. spilurus* is of a superspecies, in which populations at higher altitudes have a higher percentage of individuals with IV (or more) anal spines and correspondingly higher mean metameric numbers. Among these populations a Lower Pleistocene one of Rare, Kavirondo Gulf area, and a modern one at the Daua River, Juba system, have uniformly IV anal spines, as far as is known; that of the Upper Athi has IV–VI anal spines, never III, and is here distinguished subspecifically as *O. s. niger*. It probably developed its higher segmental numbers, and a shorter caudal peduncle, in isolation from the rest of the superspecies and only secondarily penetrated to the Lower Athi in a one-way movement over the 3·5 m barrier of Lugard's Falls, finding there the lowland subspecies, with which it hybridized, introducing to that population the higher meristic numbers, which by that time had become genetically based.

Not enough is yet known of the Juba populations to judge whether they can be similarly divided.

The inclusion of *O. s. percivali* in the same superspecies is based on rather different arguments.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1893.12.2.1–2 syntypes of *O. niger*	♂ 212, ♀ 169	Pools in bed of Kibwezi R., trib. of Athi R.	J. W. Gregory
1915.12.2.88–102 syntypes of *T. n.* var. *athiensis*	38 specimens, 33–37 and 160	Makindu and Tsavo Rs, Athi system system	S. L. Hinde
1909.11.15.41–42	61, 63	Simba R.	A. B. Percival
1914.9.21.6–7	45, 48	Tsavo R.*	S. L. Hinde
1928.11.10.22	110	Tsavo R.	Dent
1937.6.4.61–63	93–120	Doinyo Sabuk, on trib. of Athi	H. Copley
1953.8.6.331–333	95–140	Athi R. at Kayata, about 25 miles from Thika	W. E. Frost
Introduced or captive fishes			
1928.11.10.19–21	216–233	L. Naivasha	Dent
1933.2.23.87–112	66–290	L. Naivasha	E. B. Worthington
1935.8.23.14–15	120, 217	L. Bunyoni	C. R. S. Pitman
1937.12.11.19–24	26–115	'Bradley's dam', Nairobi	H. Copley
1938.12.7.1–8	66–120	Lake Nakuru	Dent
1966.9.13.3	121	Kajansi ponds, Uganda	E. Trewavas
1966.9.13.4–6	60·0–170·5	Sagana ponds, Kenya	E. Trewavas

*Hinde's specimens were registered as from the Isavo River, but this must be the Tsavo of the Athi system and not the Isavo or Itsavo of the Kavirondo Gulf drainage.

Oreochromis spilurus percivali (Boulenger)

Tilapia percivali Boulenger, 1912*d*:676, pl. xxxix, fig. 3 (hot spring near Chanler's Falls, Northern Uaso Nyiro); *idem*, 1915*b*:210, fig. 135; Copley, 1958:124 (type-locality); Trewavas, 1966*d*:407.

TYPES. Syntypes: 5 ♂♂ and 2 ♀♀ of 36–62·5 mm SL and one skeleton from the locality mentioned above. BMNH 1912.3.22.139–147.

Distinguishing characters

Meristic characters: see Tables 56 & 67–69. Pectoral fin short, 27·4–34·3% SL (mean 30·8). Mouth wide, with thick lips; jaws and pharyngeal bones stout, swollen and spongy in some specimens (see Table 70 & Figs 85–87). Microbranchiospines absent or reduced in the type-locality.

Description

Based on the seven whole syntypes and fifteen other specimens listed on p. 268. Proportions are given separately for 9 females and 13 males in Table 66, and some also in Table 70.

The profile of the snout descends in a straight line to the thick lips and broad mouth.

The teeth are relatively large, 30–56 in the outer row of the upper jaw, fewer in the 33 and 27 mm fishes. In the two smallest (♀♀) there are 3 series in each jaw, in all the others 4 or (at

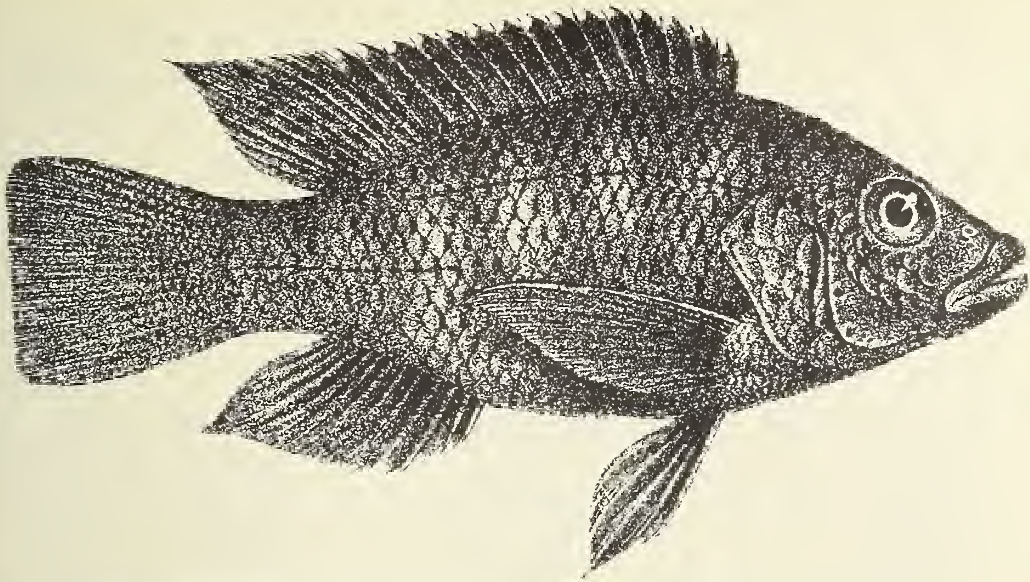

Fig. 84 *Oreochromis spilurus percivali,* holotype. From Boulenger, 1912*d*, pl. 79, fig. 3.

62·5 mm SL) 5. In all, whether ♂ or ♀, with large or small gonads, some to most of the teeth have the brown crowns worn off. Intact crowns, including any newly erupted, have a broad major cusp (Fig. 85), but the major cusp may be lanceolate and both shapes may be present in one jaw, the lanceolate then evidently the result of wear on a broad crown. The notch of a bicuspid tooth is always set obliquely to the long axis of the tooth. Each tooth has a considerable curvature. The outermost row may contain tricuspid as well as bicuspid teeth and there may be bicuspids among the inner teeth.

Gill-rakers (1–3)+1+(13–16) in outer series of first arch, short. No microbranchiospines in most specimens, but in a few incomplete series were present on one or two arches and three had series on the outer sides of the usual three arches (Campbell, pers. commn).

Lower pharyngeal bone with blade equal to median length of toothed area, which is triangular, covered with slender, but not crowded teeth, the posterior bicuspid. Dentigerous parts of both lower and upper bones swollen and spongy (like the premaxillary) in the two examined.

Scales in 2, occasionally 3 rows on the cheek; 29–31 usually 30, in the lateral line series, 3–4 between origin of dorsal and lateral line, about 4 between bases of pectoral and pelvic fins; small, but mostly imbricating on chest and belly.

For dorsal and anal fin-ray numbers see Tables 67 & 68.

Caudal truncate, scaly only on basal half or less, less on middle rays than on upper and lower.

Vertebrae 28 or 29 (Table 68). One specimen with 28 vertebrae has one of the caudal centra elongate, with a flange behind both neural and haemal spines, suggesting an incomplete division into two vertebrae.

Genital papilla white, in mature males 1·5–2·0 mm, prominent, conical or club-shaped with a subterminal pore; in females very close to first anal spine.

Intestine in 11 specimens 2·6–3·7 times the standard length (Campbell, 1981).

COLORATION. The life colours were described by Copley (1958:124). Females green, darker on back, white on belly. Mature males rich brown to black, lighter on belly; lips enlarged, prominent and white; tail orange-coloured, with spots and narrow vertical bars of crimson.

Campbell (1981) also describes the male breeding colours. The colour is a more uniform golden than in fishes from the other springs (which have the yellow of the flanks confined to the margins

Table 66. Proportions in *O. s. percivali.*

	9 ♀♀, 33–48 mm SL	13 ♂♂, 42·6–62·5 mm SL
Proportions as % SL		
Depth	36·4–41·4	36·3–43·2
L. head	38·8–43·0	37·6–41·5
L. pect. fin	27·7–33·2	28·3–34·3
L. last D spine	11·6–14·0	13·0–16·0
L. last A spine	12·0–14·0	11·0–14·0
L. lower jaw	(12·7)14·3–15·5	13·2–16·0
W. mouth	13·0–17·0	13·0–18·0
L. caudal ped.	12–16	
Proportions as % length of head		
L. snout	31·3–33·3	31·0–37·0
Eye	22·6–30·5	22·0–25·0
D. preorb.	14·7–15·7	14·4–17·4
Interorb.	23·0–26·8	24·3–28·0
L. lower jaw	35·0–35·9	34·0–40·0
W. mouth	33·0–42·0	34·0–44·0
W. lower phar. (3 specimens)	—	28·5–30·9

Table 67. *Oreochromis s. spilurus* and *O. s. percivali.* Dorsal and anal fin-rays of populations in the Uaso Nyiro (=Oaso Ngiro) system.

Dorsal formulae	River	Buffalo Springs	Spring D	*percivali*
XIV 11	—	—	—	9
XV 10	—	—	—	5
XIV 12	—	—	—	2
XV 11	1	1	—	5
XVI 10	2	2	1	—
XVII 9	—	1	—	—
XV 12	1	—	—	1
XVI 11	9	13	4	—
XVII 10	1	1	—	—
XVII 11	2	—	—	—
XVIII 10	—	1	—	—
XVII 12	1	—	—	—
Dorsal totals				
25	—	—	—	14
26	3	4	1	7
27	11	14	4	1
28	2	1	—	—
29	1	—	—	—
Anal formulae				
III 8	—	1	—	—
III 9	9	9	5	4
IV 8	1	1	—	—
III 10	7	6	—	16
IV 9	—	2	—	1

Table 68. *Oreochromis s. percivali.* Frequencies of numbers of dorsal and anal spines, and vertebrae.

	Anal spines		D. spines		Vertebrae	
	III	IV	XIV	XV	28	29
BMNH 1912.3.22.139–147 and 1967.11.16.15–20	12	1	4	9	5	1
Campbell, 1976	56	0	5	7	3	5
Totals	68	1	9	16	8	6

Table 69. Frequencies of lower gill-raker numbers in samples from populations of *O. spilurus.*

Gill-raker numbers	13	14	15	16	17	18	19	20
O. s. spilurus in								
coastal river systems			3	21	27	10	3	1
Northern Oaso Nyiro			8	4	3			
Buffalo Springs		5	4	2	2			
Spring D		1	4					
O. s. percivali	1	6	4					

of the scales). The anal fin has grey spines and yellow soft rays. Throat and belly white becoming light blue during courtship. Caudal and pectoral fins containing more orange than in the populations of the other springs.

Preserved females and immature fishes are lighter brown with faint vertical bars, in some emphasized in the middle of the flank. In the mature males the melanophores are mixed with abundant guanophores, indicating a rich iridescence in life. An ill-defined tilapia-mark is present in most.

Ecology

Food

Campbell (1981) found the gut to contain filamentous green algae, which were digested, and also unicellular and four-celled algae. The latter were apparently not digested (photosynthesis was obtained from rectal contents). They were probably blue-green algae and the same species were found to form a carpet on the floor of the spring. Parts of insect cuticle were present in the gut and the fishes were seen to consume dead insects thrown on the water. No snails or amphipods were eaten by *O. s. percivali,* in contrast to the fishes of some of the other springs. (Campbell does not state whether these animals were present in the Chanler's Falls springs.)

Breeding

The five male syntypes have enlarged testes and prominent genital papillae, and are evidently ripe or nearly so. Two other males of 51·5 and 56·5 mm SL are also near breeding condition.

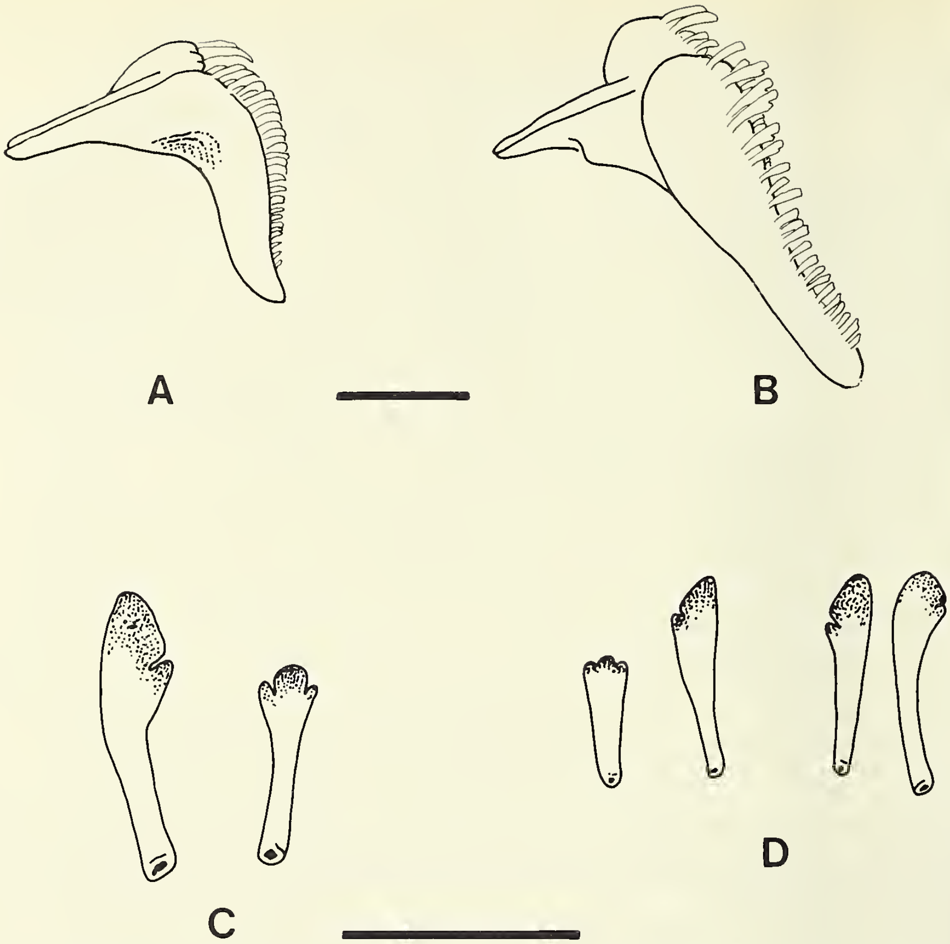

Fig. 85 Premaxillary of: A, *Oreochromis s. spilurus* of 56 mm SL; B, *O. s. percivali* of 54 mm SL (the crowns of most of the teeth are broken). Scale = 3 mm; C, teeth from the jaws of *O. s. percivali* of 62 mm SL; D, teeth from the jaws of *O. s. spilurus*, 2 specimens, left, from Ngomeni, Kenya coast 61 mm SL, and right, from Uaso Nyiro above the Falls 64 mm SL. Scale = 1 mm.

Ovarian eggs measure 1 mm in the syntype of 36 mm SL, 1·7 mm in that of 42 mm. The skin of the lips and jaws of mature males is thick and spongy. No observations have been made on breeding behaviour in the wild, but Campbell (1981) observed that young fishes of this population transferred to an aquarium began to show some of the morphological and behavioural features of mature males from 2 cm TL.

A captive pair of *O. s. percivali*

In 1975 Mr J. Nice of Harlow, Essex, brought back from Mr Haller's ponds at Bamburi, near Mombasa, a pair of tilapias that had originally been collected from the spring at Chanler's Falls. Unfortunately the male was dead, but Mr Nice described its colours when alive as very dark above, but brilliant electric blue on throat and belly. The lips were thick and spongy and the width of the mouth was 40·2% length of head, 13·7% SL. This fish was 126·5 + 30 mm long, thus twice as big as any known from the type-locality. The growth had been put on in the favourable environment of Mr Haller's ponds. The female was a little smaller. Her head, upper part of the body and caudal fin were a metallic bronze. On the lower half of the body every scale

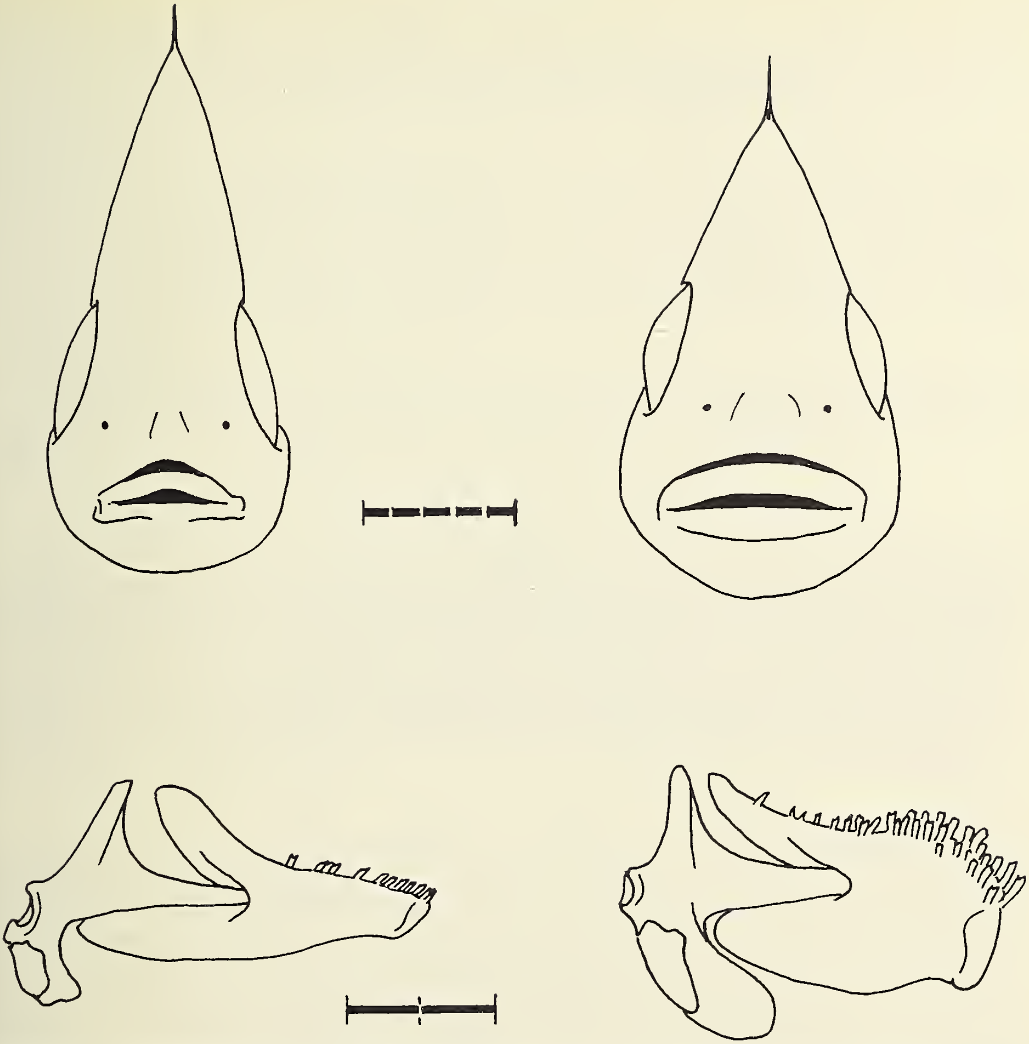

Fig. 86 Frontal view of head and medial aspect of lower jaw: left, *Oreochromis s. spilurus* of 47 mm SL from the lower Tana; right, *O. s. percivali* of 46 mm SL from a pool near Chanler's Falls, Northern Uaso Nyiro. Scales in mm.

was pale iridescent blue with a darker edge. The lower half of the head was tinged with iridescent blue, the lower lip was blue and from it a blue streak extended backwards. Though deprived of her mate, she spawned successfully with a male *O. spilurus* in Mr Nice's aquarium.

The preserved male has a short pectoral fin (29·2% SL); the length of the caudal peduncle is equal to its depth, 15% SL. Other proportions (except the width of mouth) show differences from the spring fishes in agreement with expected allometric trends (e.g. head 34% SL), but the eye is smaller than in *O. s. spilurus* of the same size. The dorsal fin-formula (XV 12) and the anal (III 10) are characteristic of *O. s. percivali*. But the fish has a full complement of microbranchiospines on the outer sides of gill-arches 2, 3 and 4.

Distribution

The type-locality and possibly other springs in the area. The temperature of the spring was given

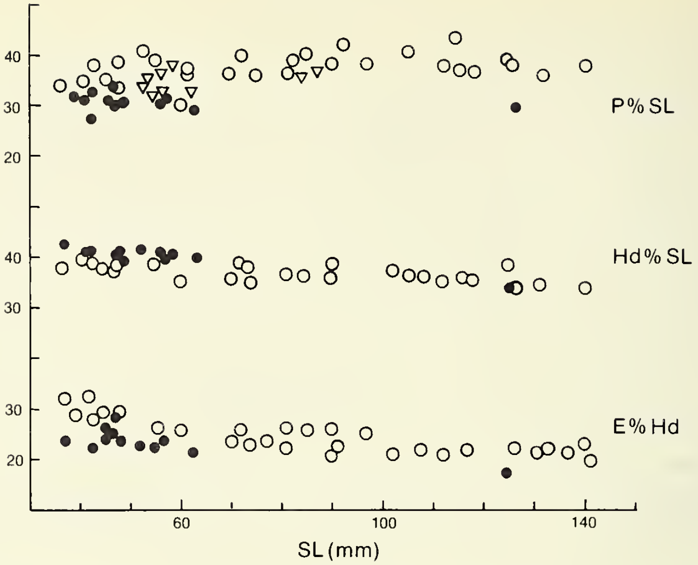

Fig. 87 Proportions in *Oreochromis s. spilurus* (○) compared with those of *O. s. percivali* (●) of comparable sizes. P = length of pectoral fin as % SL; Hd = length of head as % SL; E = diameter of eye as % length of head. The 125 mm SL *O. s. percivali* is a male reared in an aquarium of Mr R. Haller (p. 264). It is seen that *O. s. percivali* has a shorter pectoral fin than *O. s. spilurus*, and the small wild specimens have a longer head. The eye of the wild *O. s. percivali* is a smaller proportion of its bigger head, and the aquarium-reared fish also has a smaller eye although its head is no longer than that of *O. s. spilurus*. The length of the pectoral fin in fishes from 'Spring D' (▽) is not significantly different from that of *O. s. spilurus*.

by the collector of the syntypes in 1912 as 100°F (38°C), but the temperature of one of the pools now fed by these springs was 30–31°C in 1975 (Campbell, pers. commn). Mr Campbell informs me that the stream issuing from the main spring near Chanler's Falls was dammed in World War I for watering cattle; the stream issuing from the pool so formed enters the river Uaso Ngiro about 45 m away. A subsidiary spring nearby forms only a small pool before passing to the river. It is separated by damp grass from the bigger pool and the water from it passes to the river as a narrow stream. It was in the subsidiary spring that Mr Campbell collected his samples. See Fig. 83.

Discussion

Relationship and status

The present conception of *O. spilurus* as comprising all the *Oreochromis* populations of the defined area (p. 233), including that of the Uaso Nyiro, is a *prima facie* reason for regarding *percivali*, and the populations of the other springs of the Uaso Nyiro, as parts of that superspecies.

Two questions arise from the study of *O. s. percivali*:

1. Which of its peculiarities are functions of the environment and which, if any, are genetically established.
2. What is its status vis-à-vis the populations of the other springs?

The slender evidence of the pair reared at Bamburi points to the broad mouth and thick lips of the male, the short pectoral, small eye and certain features of the coloration as being characteristic. The meristic numbers were doubtless established in the pool before capture. The presence of microbranchiospines is not unknown in the parent population, but could also be a growth phenomenon. The ease with which the female spawned with *O. s. spilurus* is no evidence in the context of *Oreochromis* species. These details appear to support the retention of the name, but at subspecific level.

Relationship to the *Oreochromis* of the other springs is difficult to assess. The broad mouth and thick lips also characterize mature males from Spring D of Campbell (Fig. 83). These D fishes have their own peculiarities, notably the very long intestine (5·9 to 7·8 times the SL in fishes of the same size as those of *O. s. percivali* that have a ratio of 2·6 to 3·7), which is probably related to a diet mainly of diatoms (Campbell). The Spring D fishes have not the low numbers of vertebrae and dorsal fin-spines nor the short pectoral fin that characterize *O. s. percivali* (Tables 62 & 69).

These considerations persuade me to retain the name *O. s. percivali* for the population of the springs near Chanler's Falls only, at least until experimental evidence is forthcoming that the meristic characters, the thick lips and the coloration are labile divergences from typical *O. s. spilurus.*

Table 70. Some proportions in samples from populations of *O. spilurus*. The first five samples are from the Lower Athi and Tana and neighbouring waters (for details of the localities see p. 233 and Fig. 83). They are selected for their small size for comparison with the next three samples, from the springs of the northern Uaso Nyiro system. Some samples include individuals not suitable, as preserved, for some of the measurements and the reduced numbers used are indicated in these cases below the ranges.

Locality	N	SL (mm)	Head % SL	Pectoral % SL	W. mouth % head	% SL
Mwangudo R.	5	43·6–66·0				
		Range	34·4–38·3	34·3–36·0	28·2–29·8	9·85–11·0
		Mean	35·9	35·57	29·4	10·6
L. Jilore	7	34·2–75·5				
		Range	35·7–41·5		26·0–30·2	10·2–11·8
		Mean	38·1		28·35	10·8
Chem Chem	6	47·5–61·0				
		Range	37·7–40·2	30·7–41·1	28·9–34·0	11·6–13·2
		Mean	38·7	37·4	32·1	12·4
Saka	3	44·7–55·0				
		Range	37·4–38·5	30·9–38·2	33·3–34·9	12·6–13·4
		Mean	37·9	35·1	34·4	13·0
Ngomeni	10	48·0–90·5				
		Range	36·6–39·6	34·3–39·6	29·5–38·0	11·3–13·5
		Mean	37·8	37·5	33·5	12·6
Buffalo Springs	15	38·5–68·7				
		Range	35·6–40·0	33·2–37·2	29·0–39·1	10·5–14·5
			(N=15)	(N=10)	(N=11)	(N=11)
		Mean	37·8	34·95	33·9	12·8
Spring D	5	52·5–59·0				
		Range	39·3–41·1	33·0–38·0	37·2–39·1	14·8–16·0
			(N=4)	(N=5)	(N=4)	(N=4)
		Mean	40·3	35·6	37·9	15·3
percivali	22	34·1–62·5				
		Range	37·6–43·0	27·4–34·3	32·7–44·0	13·0–18·2
		Mean	40·4	30·8	38·9	15·25

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1912.3.22.139–147 (syntypes)	36·5–62·5	Hot spring near Chanler's Falls, Northern Uaso Nyiro, Kenya	Blaney Percival
1967.11.16.15–20	27·5–46·0	The same	Fleetwood
1979.7.18.416–424	39·0–48·5	The same	Campbell
1979.5.22.5	126·5	The same, via Bamburi Cement Co. near Mombasa	Nice

Fossil *Oreochromis spilurus* of Kanam and Rawi, Kenya

Tilapia nigra Trewavas, 1937:381, fig. 1 (6)–(9).

The list below (taken from Trewavas, 1937) is of a collection of fossils made by Dr L. S. B. Leakey in 1934–5. Some of them bore a locality label, but after the paper of 1937 was published Dr Leakey informed me that all were originally labelled, and gave me further information about the sites. The correct localities and age are, in Dr Leakey's words:

> Lake muds of Middle Pleistocene (or possibly Lower) age at Fish Cliff, Kanam, and at Rawi in the south Kavirondo district of Nyanza Province, about a mile to the south of the Kavirondo Gulf, near Homa Mountain.

One specimen, however (P.20181), was labelled 'Kanam West'. The exposure at this locality, according to Dr Leakey, was Lower Pleistocene.

This puts the probable age of most of the fossils, judged by Dr Leakey from associated mammalian bones, a little later than in my original paper, but this does not alter their significance.

They were assigned to *O. s. niger* in the first place because in all the ten specimens in which the spinous anal fin is complete there are four spines. On the present interpretation of the *Oreochromis* of Kenya, not all the populations that include individuals with more than three anal spines are assigned to *O. s. niger*. The Kanam and Rawi fossils are therefore now conceived as representing a population of *O. spilurus* possibly, but not certainly, ancestral to *O. s. niger*.

The fossils are the remains of fifteen fishes, most of which were about 100–200 mm in SL. No gill-rakers or pharyngeal teeth were distinguishable. The dentition of the jaws, the number of vertebrae (30 in the one complete vertebral column), and the interorbital width (observable in one specimen) are in agreement with *Oreochromis*. In the jaws of the 200 mm fish the outer teeth have a reduced minor cusp as in mature individuals of *O. spilurus* and other species of the eastern rivers of Africa. One specimen has a complete spinous dorsal fin with XVII spines.

Dr Leakey, in his letter of 11.V.1937, wrote that the presence of this eatern-type tilapia in the Kavirondo area gave important support to his opinion that up to the end of the Middle Pleistocene Lake Victoria was linked to some of the eastern rivers, and that the vertical uplift of the land between Lake Victoria and the coast at that time altered the drainage systems. Kent (1942) also adopted this view, according to which the Kanam and Rawi fossils are no exception to the rule that the only *Oreochromis* species with IV anal spines belong to the eastern drainage systems.

The Athi, the Tana and the Northern Uaso Nyiro all rise at present on the eastern side of the eastern Rift Valley, and with one of these the lagoon in which the Kanam and Rawi fishes died must have been linked. At the time of fossilization the fishes must have been isolated from

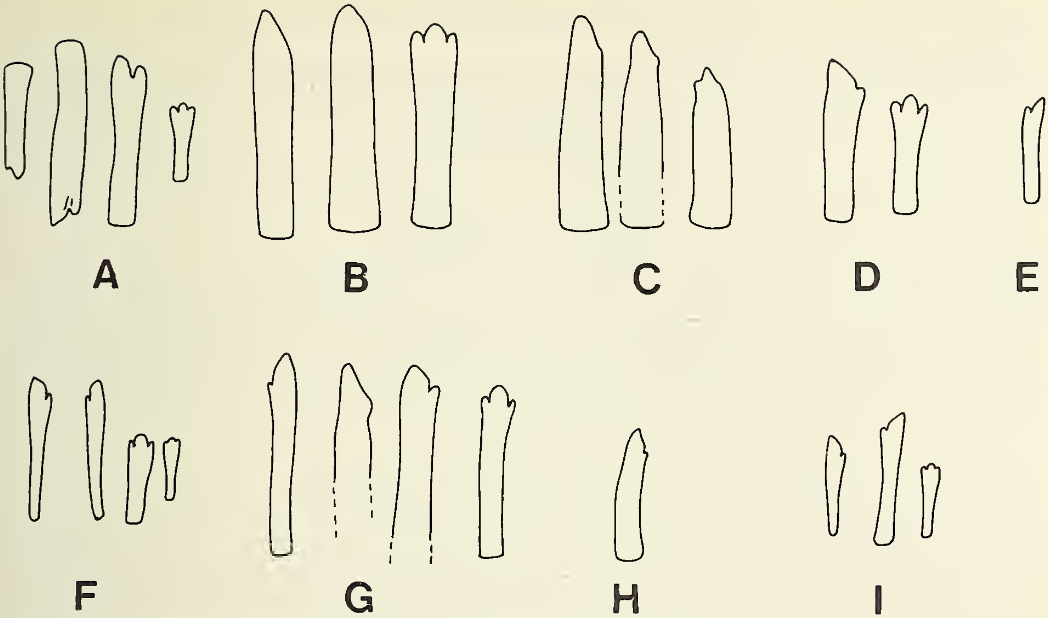

Fig. 88 Teeth from the jaws of: A–E, *Oreochromis s. niger*; F–I, fossil *O. spilurus*. A, 162 mm SL, Athi system; B, 210 mm SL Athi; C, 205 mm SL, Naivasha; D, 170 mm SL Athi; E, 127 mm SL, Naivasha; F, 140 mm SL, P.20175; G, *ca* 200 mm SL, P.20174; H, 100 mm SL, P.20190; I, *ca* 125 mm SL, P.20180. The tricuspid teeth are from an inner series. Re-drawn from Trewavas, 1937, fig. 1.

the lake or river at a period of desiccation, as tilapias often are at present. Finally their lagoon also dried up, leaving their remains to inform us of long past events and topography.

As pointed out above (p. 242–3), the probable existence at present of an isolated population of *O. s. spilurus* in the Nguruman Valley (Southern Uaso Nyiro system) is another indication of the same change in drainage systems.

Annotated list of fossil *O. spilurus* registered in the Department of Palaeontology

P.20173. Nearly complete specimen, 154 mm in SL. Vertebrae 15+15 or 14+16; one of the caudal centra with two neural and two haemal arches. Seventeen dorsal and four anal spines. 16 principal caudal rays.

P.20174. Fish Cliff, Bed 5. Head and trunk of a fish of about 200 mm. Precaudal vertebrae 14. Four anal spines. Outer teeth with major cusp well developed and minor very small or absent (fig. 88(G)).

P.20175. SL 140 mm. Four anal spines. Outer teeth with rather slender shafts and unequally biscuspid crowns (fig. 88(F)).

P.20176. Parts of five fishes, 100 to 150 mm in SL. In one, percaudal vertebrae 12+?, caudal 16. In another, anal with IV 10 rays.

P.20177. Caudal region of small specimen. Impressions of about 16 vertebrae, perhaps all caudal. Anal with four spines and probably 9 soft rays. Dorsal incomplete.

P.20178. Vertebrae and fins of a fish of about 180 mm (excluding caudal). Vertebral column incomplete anteriorly. Precaudal vertebrae?, caudal 16. Dorsal ?+XIV 9 or 10. Anal with four spines.

P.20179. Fairly complete fish. Precaudal vertebrae ?+12, caudal 15. Dorsal with 11 soft rays. Anal IV 10. 16 principal caudal rays.

P.20180. Fish Cliff, Bed 7. Head and a few anterior ribs and dorsal fin-spines of a fish of about 125 mm SL. Interorbital width as in a spirit-specimen of *S. s. niger* of the same length. Outer teeth bicuspid, inner tricuspid (fig. 88(I)).

P.20181. Kanam West. Very imperfect fish. Four anal spines and base of a fifth ray which may have been spinous or flexible.

P.20184. Incomplete fish. Four anal spines.

P.20190. Imperfect head, with part of dorsal fin. Some teeth (fig. 88(H)).

Subgenus *OREOCHROMIS* – IV
Species of lower parts of the eastern rivers of Tanzania

Oreochromis korogwe
Oreochromis urolepis

The two species (one comprising two subspecies) described here resemble others of the eastern rivers of Africa in the enlargement of the jaws in mature fishes, especially males. *Oreochromis korogwe* further resembles both *O. spilurus* and *O. placidus* in the frequent possession of four anal spines, and the numbers of vertebrae and gill-rakers are similar to those of *O. spilurus*, *O. placidus* and *O. mossambicus*. *Oreochromis urolepis* intervenes between *O. korogwe* and *O. placidus* and is distinguished from both by the higher mean numbers of vertebrae, dorsal rays and gill-rakers (Table 76), and the somewhat coarser pharyngeal dentition. In the latter feature it is approached by *O. placidus*, whose subspecies *O. p. ruvumae* is geographically close. The latter has, however, usually IV anal spines, whereas no variation from III has been found in either subspecies of *O. urolepis*. The distinction from *O. mossambicus* is supported by what is known of the male breeding liveries and especially by the results of hybridization (p. 288). There is also evidence that *O. u. urolepis* is less euryhaline than *O. mossambicus*.

Oreochromis korogwe (Lowe)

Chromis niloticus (part); Pfeffer, 1893:21 (a specimen from Korogwe, D XVIII 9, A IV 9); *idem*, 1896:10, fig. 7.

?*Tilapia heudeloti* (*non* Duméril); Seitz, 1949:204–221, figs 1, 3, 5–8 (aquarium specimens of unknown origin).

Tilapia mossambica korogwe Lowe, 1955*a*:352, 356, pl. 16 D(Korogwe, Pangani R.).

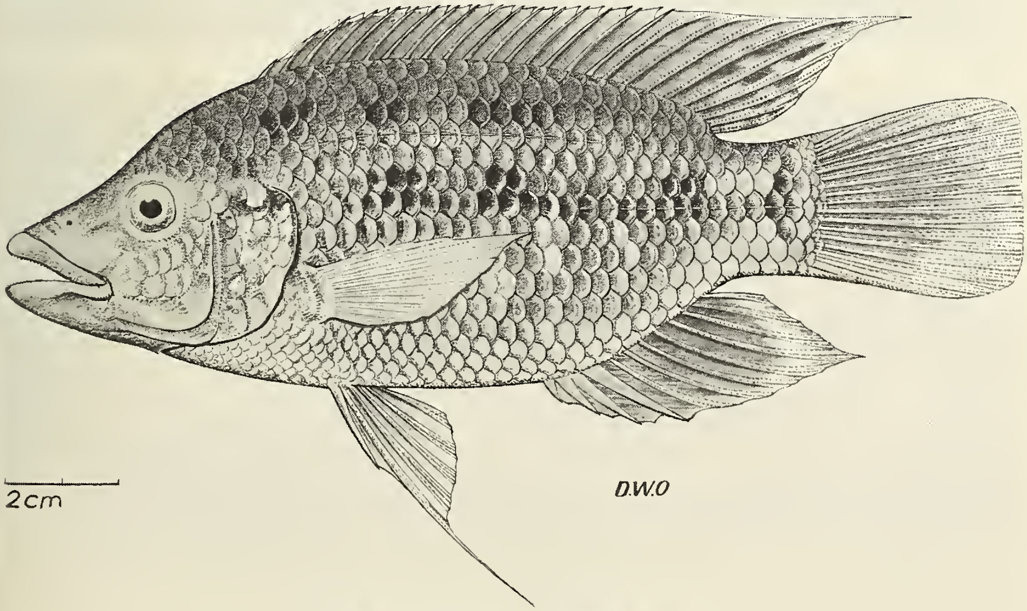

Fig. 89 *Oreochromis korogwe*, holotype.

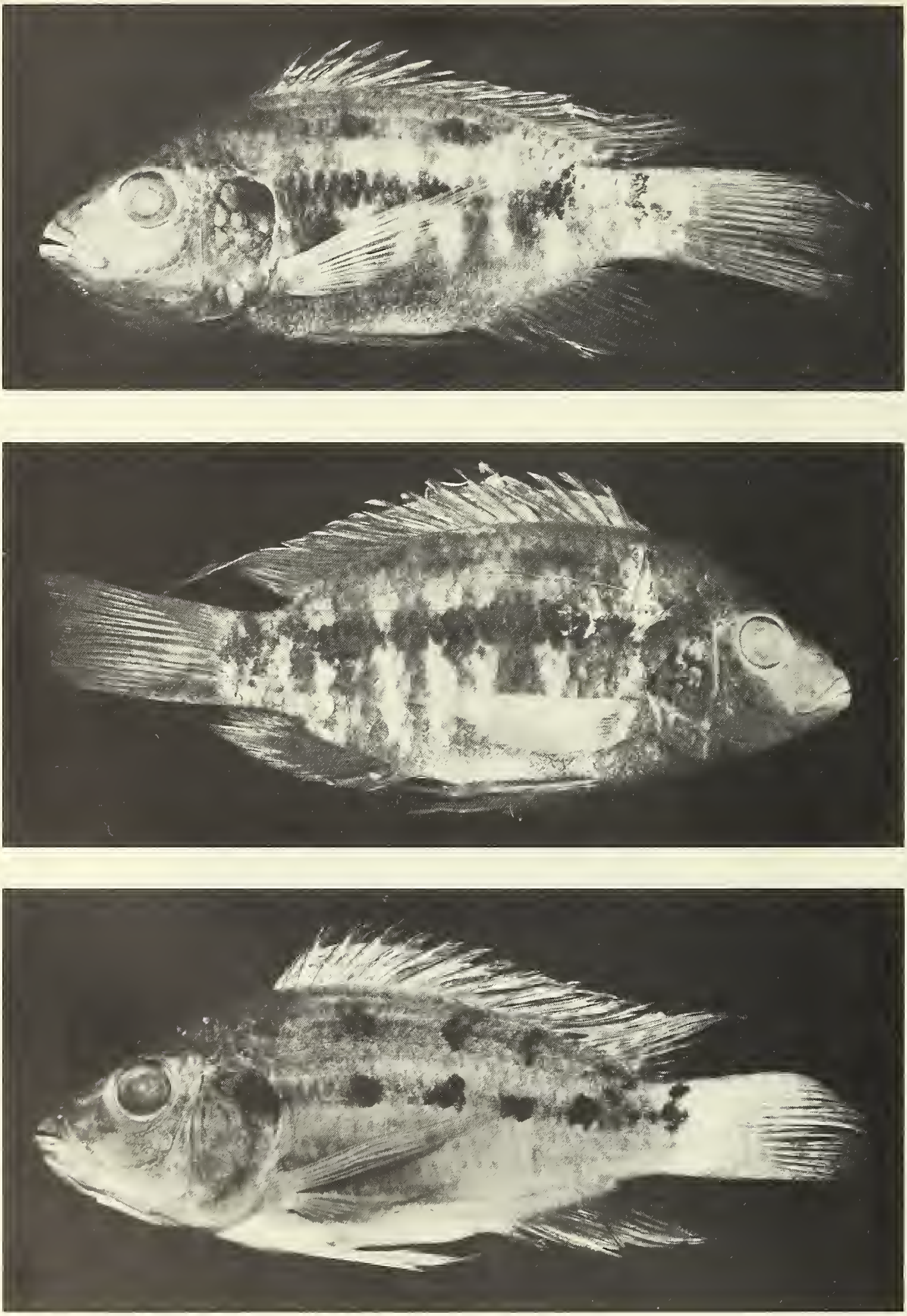

Fig. 90 *Oreochromis korogwe.* Two males (upper *c.* 95 mm SL and middle *c.* 120 mm SL) and a female *c.* 100 mm SL from Mlingano Dam, near Tanga. (Photograph, BMNH).

?*Tilapia mossambica k.*; Kraft & Peters, 1963; Peters, 1963*a* (aquarium specimens of unknown origin); Bauer, 1968:30
Tilapia korogwe; Trewavas, 1966*c*:407

TYPES. Holotype: male 140+43 mm, from Korogwe ponds, 1951, coll. R. E. Gould. BMNH 1952.2.26.37.

Allotype: female, 91+29 mm, Korogwe ponds, coll. R. H. Lowe. BMNH 1952.2.26.5.

Distinguishing characters

An *Oreochromis* in which about 50% of individuals have IV anal spines, the modal numbers of vertebrae (29), dorsal rays (27) and gill-rakers (15) are low, and the jaws of breeding males are enlarged. In females and non-breeding males the horizontal and vertical elements of the melanin pattern are conspicuous, especially at their junctions, where blotches are often drawn out vertically. In breeding males the throat and chest are black and broad dark vertical bars are conspicuous on the lower half of the body (Fig. 90).

Description

Based on the types and 10 other specimens described by Lowe from Korogwe Ponds; also on one male from the Zigi River, north of Tanga, two (unsexed, gonads destroyed, probably female) from the Pangani River, and seven from a dam at the Sisal Research Centre between Korogwe and Tanga; in all 22 specimens, 85–161 mm in SL. In addition, 10 young from the dam are included for meristic characters.

Proportions as % SL. Depth of body 37·0–45·6. Length of head 33·0–39·6, not more than 37·5 above 100 mm SL. Length of pectoral fin 31–40, usually 33·0–38·5. Length of caudal peduncle 9·7–12·4, 0·6–0·9 times its depth, which is 13·1–15·8% SL.

Proportions as % length of head. Length of snout 33·7–42·5. Diameter of eye 22–27 at 85–100 mm SL, 19·5–23 at 100–121·5 mm, 19–20 at 125–160 mm SL. Depth of preorbital bone (18·4) 19·5–22·5 (24·3). Interorbital width 32·0–37·6 (41·5), with no detectable allometry. Length of lower jaw 43·2 and 36·7 in the two known females; 34·8–44·8 in the known males, rarely less than 36.

Lips rather thick; maxillary extending nearly to below eye in some males.

Teeth in 3–5 series; outer bicuspid, or with minor cusp reduced or absent in breeding or recently spent males, 46–66 in outer row of upper jaw; inner tricuspid.

Gill-rakers on lower part of anterior arch 14–16, rarely 17, mode 15, mean 15·2 (38 specimens; see Table 76).

Lower pharyngeal bone with blade as long as or a little longer than toothed area, which has concave sides and fine teeth (Fig. 91).

Vertebrae (in 18 dam fishes): 29 (f.15) or 30 (f.3), Table 76.

Scales on cheek usually in 2 rows, occasionally 3, in lateral line series 29–31, between origin of dorsal and lateral line 3½ or 4, between bases of pectoral and pelvic fins 4–6; small on chest.

Dorsal XVI 9 in one, XVII–XVIII 9–10 in the rest; modal combination XVII 10. (For frequencies see Table 76). Anal III–IV 9–11; there are III in 18, IV in 20 and the remaining specimen has the fourth ray thick like a spine in its basal two-thirds, but is flexible, though simple distally. Caudal truncate. Pelvic drawn out into a long filament in mature males.

COLORATION. In alcohol, females and sexually inactive males have the basic melanin pattern very strongly marked, the horizontal and vertical bands usually represented by intense black blotches, which may be contiguous. A blotch on the top of the caudal peduncle is usually well-marked. The caudal fin may be immaculate (as in Lowe's specimens) or may have part of its area crossed by vertical bars or series of spots.

In some males, including the holotype, the vertical bars are stronger on the lower half of the flanks and the spaces between them on the abdomen, as well as an uneven and variable area on the operculum, may be whitish silver or aluminium-coloured. The branchiostegal membrane is black in males, pale in females. The genital papilla is white in both sexes and in males is conspicuous against the dark background (Fig. 90).

In life, Lowe writes of breeding males that they 'did not have a marked breeding dress' (1955*a*:364) and describes the corner of the caudal fin as white. One sexually inactive male seen by me in the Zigi River had a general dark iridescent blackish green colour, more green and iridescent on the snout, and a narrow red margin along the length of the dorsal fin. Lowe's observations rule out the brilliant breeding colours of *O. spilurus* or the white throat of *O. mossambicus.*

For further information on colour see notes on possible aquarium strains (p. 275).

Size. Up to 20·8 cm (161+47 mm). This fish, from the Pangani River, is damaged, but was probably a female. All mature males so far examined have been from ponds and may have been breeding precociously. The conclusion that the species attains no great size would therefore be premature.

Ecology

Nothing is known of this species except in ponds, where Lowe reports the presence of insect remains and algal filaments in the stomachs. Before the isolated specimens of Pangani tilapias had been recognized as representing distinct species, Major Gould found that some ('*T. mossambica*') would tolerate transference to salt water while others would not (Lowe, 1955*a*:356). It seems probable that *O. korogwe* is the euryhaline species.

Breeding

Nothing is known (but see p. 275). The dentition and enlarged mouth of mature males speak for digging and a degree of sexual dimorphism. The genital papilla in both sexes is small and flanged. Of the 20 preserved specimens whose sex can be determined, only 2 are females. Whether this indicates the normal sex-ratio is not known.

Distribution

Natural distribution. Lower part of the Pangani system and the neighbouring Zigi River.

Dispersal by man. Mlingano dam, south of the Pangani River and probably other dams in Tanzania.

Discussion

Relationship

Relationship to the other species of *Oreochromis* in the Pangani system is not close. Although *O. jipe* has four anal spines, its speckled colour pattern and high meristic numbers relate it to *O. pangani* and not to *O. korogwe.*

The resemblance in structure and behaviour to *O. mossambicus* that led Lowe and Peters to regard it as a subspecies of the latter is probably based on a true relationship between the three coastal species, *O. mossambicus, O. korogwe* and *O. spilurus,* but the different colours of the breeding males support the view of their specific distinctness.

In spite of the high incidence of four anal spines in both *O. korogwe* and *O. placidus,* the shape of body and fins in mature *O. placidus* and its coarser pharyngeal teeth are against regarding it as the southern representative of *O. korogwe. Oreochromis mossambicus* seems better suited to this role. If this is so, and if *O. p. ruvumae* is rightly placed as a subspecies of *O. placidus,* then the Ruvuma fish would also be less close to *O. korogwe* than is *O. mossambicus.* But further

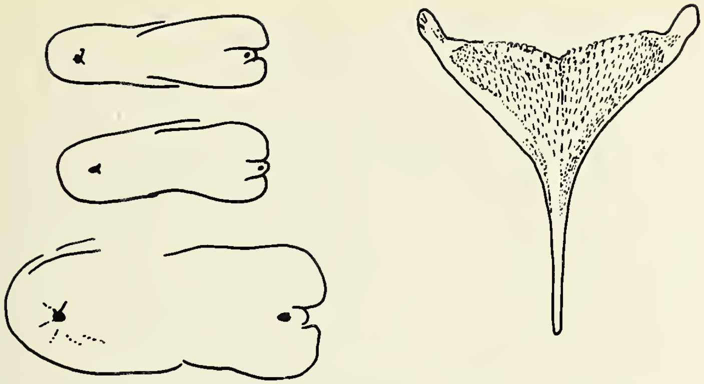

Fig. 91 *Oreochromis korogwe.* Left, male genital papilla: above, two aquarium specimens; below, the holotype. Right, lower pharyngeal bone of a fish 155 mm SL.

knowledge is required concerning *O. p. ruvumae* before this can be stated with confidence. *Oreochromis u. urolepis* and *O. u. hornorum*, with their higher meristic numbers and coarser pharyngeal teeth, although geographically intermediate at the present day and doubtless belonging to the same subgenus, seem structurally a little farther removed.

Two aquarium strains, probably of *Oreochromis korogwe*

1. The species whose aggressive behaviour was described by Seitz (1949) under the name of *Tilapia heudeloti* (= *Sarotherodon melanotheron*) is clearly not that species. Seitz himself noted the difference in body form between his fish and Boulenger's figure of the much larger specimen of '*T. heudeloti*', and noted also the colour-differences between his own specimens and Meinken's description of *T. heudeloti.* Seitz was perhaps reassured by the black throat and chest in some *S. melanotheron* (= *T. heudeloti* of authors) and in his displaying male, but these are not comparable, the black patches in *S. melanotheron* being variable in size and position, sometimes absent. In *S. melanotheron* the basic pattern of bars is not or only feebly expressed in adults, whereas in Seitz's fish, as in *O. korogwe*, it is strongly and characteristically emphasized. The body is deeper in *S. melanotheron*, the mouth smaller and the caudal fin slightly emarginate.

Seitz obtained his experimental animals from the Berlin aquarium; their origin was unknown. He gave no structural diagnostic characters, but the melanin pattern and the shape of head, snout and body and caudal fin are consistent with their identification as *O. korogwe.* The supply of aquarium fishes to Germany from Tanga near the mouth of the Pangani was and is very probable.

If this is so the following details from Seitz will supplement the foregoing account. Females and inactive males have a narrow red edge to the dorsal fin. As well as a general iridescence, the black opercular spot may be gold-rimmed. In breeding males the brick-red dorsal margin is more conspicuous, red colour may extend from the caudal margin over about two thirds of the fin area and the pectoral rays are red. The lower parts of head and chest below a horizontal line from angle of mouth along the lower rim of eye to below opercular spot are dark and in the roused fish become intense black. The brachiostegal membrane, which is exposed when the throat is sunk in lateral display, shares this black hue, which is under nervous control. Along the flanks the vertical elements of the melanin pattern become intensified and, especially below the mid-lateral line, are separated by brilliant white areas, giving the black-white contrast pattern of Seitz (cf. Fig. 90). The lower lip is flesh-coloured or light blue. The iris becomes black, with a narrow gold rim around the pupil and blue-grey spots breaking its outer circumference.

Both sexes become sexually mature in the aquarium at a total length of 7 cm.

2. Professor H. Peters of Tübingen deposited as reference specimens in the BMNH six small

fishes of 40–55 mm SL and twelve fry of 20–28 mm. These were determined by me in 1957 as possibly *T. m. korogwe* Lowe, and the batch from which they came was used for studies on eggs and oogenesis by Kraft & Peters (1963) and Peters (1963*a*) under the name of '*T. mossambica k*'.

They have D XVI–XVII 10–12 and a gill-raker count of 14–16. All have III anal spines except one with IV, and the latter has an abnormally low dorsal formula of XIII 10. The males are sexually mature, with elongate snouts and jaws (lower jaw 39–43% length of head) and a white genital papilla of the same shape as in the holotype of *O. korogwe* (Fig. 91). The colour pattern agrees very well with that described by Seitz for his '*T. heudeloti*'. The lower pharyngeal bone has a long blade and very fine teeth, agreeing quite well with *O. korogwe.*

Professor Peters' specimens are probably closely inbred, which might explain the high proportion with three anal spines, and I can find no better match for them than *O. korogwe.*

A ripe female of 47·5 mm SL has loose ovarian eggs of 2·3×1·6 mm. Kraft & Peters give the presumably long diameter as varying between 1·9 and 2·9 mm. The surface of the egg, as in most mouth-brooders, is not provided with adhesive threads.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1952.2.26.37 (holotype)	140	Korogwe pond	R. E. Gould
1952.2.26.5 (allotype)	91	Korogwe pond	R. H. Lowe
1952.2.26.28–36, 38	85–141	Korogwe pond	R. H. Lowe
1949.7.20.1–2	128, 161	Pangani R.	R. E. Gould
1966.7.14.86–102	48·0–121·5	Mlingano Dam, Sisal Research Centre, between Korogwe & Tanga	R. G. Bailey
Doubtful specimens			
1957.11.6..26–43	20–54	Aquarium stock	H. M. Peters

Oreochromis urolepis (Norman)

For bibliography and synonymy see the subspecies, of which there are two, *O. u. urolepis* and *O. u. hornorum.*

Distinguishing characters of the species

1. Genital papilla of male simple or with a scalloped edge.
2. Jaws of sexually mature males becoming enlarged, often resulting in a concave upper profile.
3. Females and non-breeding males silvery or steel-grey with 2–4 mid-lateral blotches and a more dorsal series usually evident. Caudal with narrow vertical stripes in upper half. General colour of breeding males dark olive to black, with margin of dorsal fin and margin or upper half of caudal bright red, pink or orange.
4. Vertebrae 29 or 30 (14+15, 15+14 or 15+15).
5. Dorsal spines (XV) XVI–XVIII, mode XVII; total dorsal rays 27–30, mode 29.
6. Anal spines III.
7. Lower gill-rakers 19–27, mode 22.

8. Pharyngeal teeth slender, but firm, not crowded; blade of lower bone 0·9–1·25 times length of dentigerous area.
9. Depth of caudal peduncle greater than its length.

Character 1 is shared with all species of the subgenus *Oreochromis.* Number 2 characterizes all the species of *Oreochromis* in the eastward-flowing rivers of Africa, but differentiates them from *O. niloticus, O. aureus, O. leucostictus* and *O. esculentus.* The diagnostic value of the meristic characters can be seen from Table 76, in which it is clear that the mode of XVII dorsal spines differentiates *O. urolepis* from *O. s. spilurus* to the North and *O. mossambicus* to the South, and that these both have usually lower gill-raker numbers. *Oreochromis korogwe* of the Lower Pangani, although it also has a high number of dorsal spines, has a lower modal total of rays as well as a lower range of gill-rakers, frequently IV anal spines and different pigment-pattern. *Oreochromis placidus* has usually IV anal spines.

The species of the Upper Pangani (p. 357) and Lake Jipe have a different colour-pattern and higher meristic numbers, notably 31–34 vertebrae.

Status of the subspecies

The populations of *O. urolepis* have been described under two subspecific names because the incidence and significance of the scaly caudal are not fully known, and data on the male breeding colours are incomplete. The results of interbreeding with other species are established only for the population known as *hornorum* and this is a practical reason for retaining the name.

Oreochromis urolepis urolepis (Norman)

Tilapia adolfi Steindachner, 1916:182 (part *et non* Steindachner, 1909) (specimens from Ulangi R., trib. of Rufigi R.).

Tilapia urolepis Norman, 1922:688 (Rufigi R., near Mpanganye); Trewavas, 1966*c*:411, table 1 (Rufigi, Mbemkuru & Kingani basins, Tanzania); Thys van den Audenaerde, 1968*b*:xxxvii.

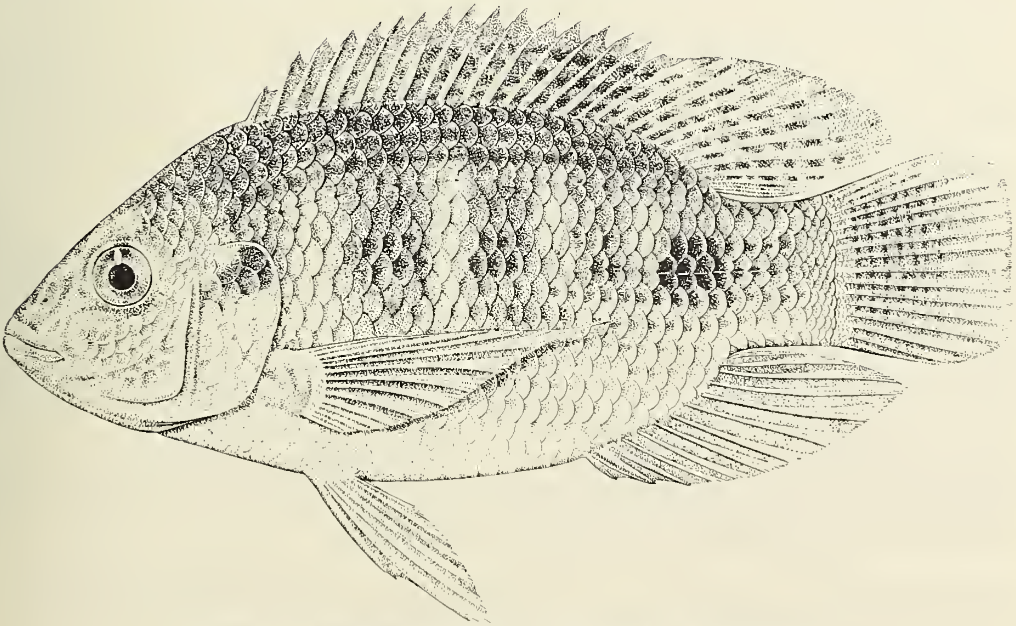

Fig. 92 *Oreochromis urolepis urolepis*, female, of 200 mm SL.

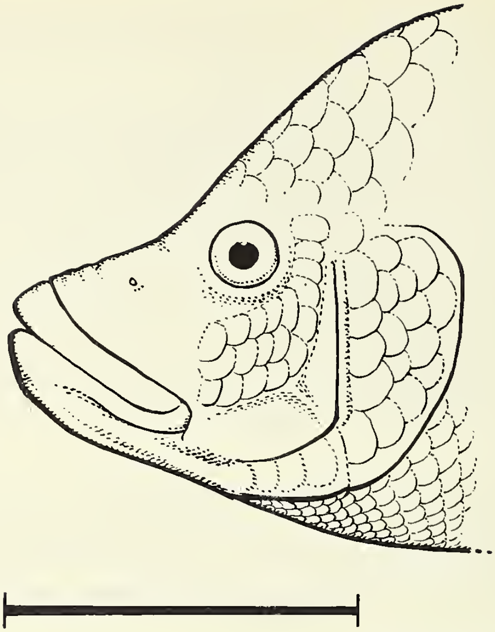

Fig. 93 *Oreochromis u. urolepis.* Head of a male 355 mm SL from the Kilombero River at Ifakara. Scale = 10 cm.

TYPES. Holotype: ♂ 150 + 40 mm, found preserved at Mpanganye, a former German post, by A. Loveridge. BMNH 1922.4.18.21.

Distinguished from *O. u. hornorum* by the development on the caudal fin of adults of a dense scaly covering (at least in the Rufigi basin).

Distribution

The Rufigi River and its tributaries the Kilombero and Great Ruaha, but not in the delta; the Kingani and Mbemkuru rivers, all in Tanzania.

Oreochromis urolepis hornorum (Trewavas)

Tilapia adolfi Steindachner, 1916 (part *et non* Steindachner, 1909) (specimens from Mukondokwa R., Wami system, near Kilosa, Tanzania).

Tilapia mossambica (*non* Peters); Lohberger, 1930:94 (Wami R.).

Tilapia nilotica (*non* Linn.); Lohberger, 1930:94 (Wami R.).

Tilapia sp. Talbot & Newell, 1957:118 (Zanzibar); Hickling, 1959:27, pl.; *idem*, 1960:1*; *idem*, 1963:152.

Tilapia mossambica Zanzibar strain; Prowse, 1964; *idem*, 1965:14; Pruginin, 1965; Chen, 1966*a*:36; Chen & Prowse, 1964:13 (cultured in Malacca).

'*Tilapia hornorum* subsp. *zanbibarica* Trewavas' (sic), *nomen nudum*† Chen, 1966*a*:37.

Tilapia hornorum Trewavas, 1966*c*:409, table 1; *idem*, 1968:246; Chen, 1967:43–47; *idem*, 1969:719, fig. 1 (hybridization, nest); *idem*, 1970; Chen & Tsuyuki, 1970 (protein chemistry); Mires, 1977; Avtalion & Hammerman, 1978; Hammerman & Avtalion, 1979 (genetics).

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*'An unnamed species of the mossambica group', 'the *Tilapia* from Zanzibar' or 'the African *Tilapia*', in contradistinction to 'the Malayan Tilapias', i.e. '*Tilapia mossambica* acclimatized since about 1942 in Malaya'.

†This name was misprinted from the unpublished programme of the FAO/UN Fish. Rep. **44**.

TYPES. Holotype of *T. hornorum* and lectotype of *T. adolfi* Steindachner, 1916: the specimen figured by Steindachner (1916, pl. v), 167+45 mm, NHMW 24782 (Fig. 95); paratype of *T. hornorum* NHMW 24783, 166+45 mm, both from the Mukondokwa River, Wami system, collected by the brothers Adolf and Albin Horn.

Distinguished from *O. u. urolepis* apparently by the failure to develop a dense scaly covering on the caudal fin, and possibly by the pigmentation of the breeding male. The name is retained at subspecific level until more detailed comparisons can be made between the populations of the four river systems concerned.

Distribution

NATURAL DISTRIBUTION. The Wami River system; Zanzibar (possibly introduced).

DISPERSAL BY MAN. There is evidence that this species was introduced from the Wami to Zanzibar in 1918 by Dr W. M. Aders and we have no evidence of its previous existence there (see Trewavas, 1966*c*). Cichlids collected by Sir John Kirk and recorded by Boulenger under the headings *Tilapia mossambica* and *T. natalensis* are in fact *O. mossambicus* and were collected not in the island of Zanzibar, but in Mozambique (see p. 315). The species is now well established in Zanzibar and thence was transported to Malacca at the former tropical Culture Research Station for experimental purposes. It was also sent to the fish ponds at Sagana, Kenya and at Kajansi, Uganda. It is well known as *Tilapia hornorum* for the experiments of Chen and Pruginin on its hybridization with *O. mossambicus* and others (see p. 288).

Description of both subspecies

Based on the holotype of *T. urolepis* and twenty-one specimens of 142–355 mm SL from the Rufigi River and its tributaries the Kilombero and Great Ruaha (lower reaches); and on the holotype and paratype of *T. hornorum* and twenty-four other specimens from the Wami system, ranging from 100 to 240 mm SL.

For meristic characters several smaller specimens are included and separate notes are added on samples from the Mbemkuru River, south of the Rufigi; the Kingani River, north of the Rufigi; and from Zanzibar.

Proportions are set out in Table 71 and meristic characters in Tables 72 and 76. Special attention is given to the length of the lower jaw in Tables 73–75.

The increased length of both jaws is responsible for the longer snout and therefore head in sexually mature males. For example, a female and male from the Great Ruaha measure respectively 110 and 113 mm in SL, but the body behind the head is 73 mm long in both, the additional length in the male being accounted for by the enlarged jaws. In these small specimens the profile is straight in the male, decurved in the female, but in larger males it becomes concave (Fig. 93).

The species is notable for the deep preorbital bone, its ratio equalling that of *Sarotherodon galilaeus* (see Fig. 47) and exceeding that in *O. spilurus* (Fig. 83) and *O. mossambicus*. There is no evidence that the bone shares in the hypertrophy of the parts of the snout in males, and it is indeed this fact that accounts for the change in shape of the snout in large males.

The teeth are in 4–7 rows in the upper jaw, 4–6 in the lower, 50–110 in the upper outermost row. The outermost are bicuspid, the inner tricuspid, but the outer may become unicuspid in mature males, at least partly by wear. In two males of *O. u. hornorum*, of 148·5 and 240 mm respectively in SL the teeth of both outermost and inmost rows are unicuspid.

Gill-rakers: see Table 76.

Lower pharyngeal bone (26 specimens), width about equal to the median length or a little greater: length 28–33% length of head, usually 30–32; width 28–35%, usually 29·0–32·5. Blade

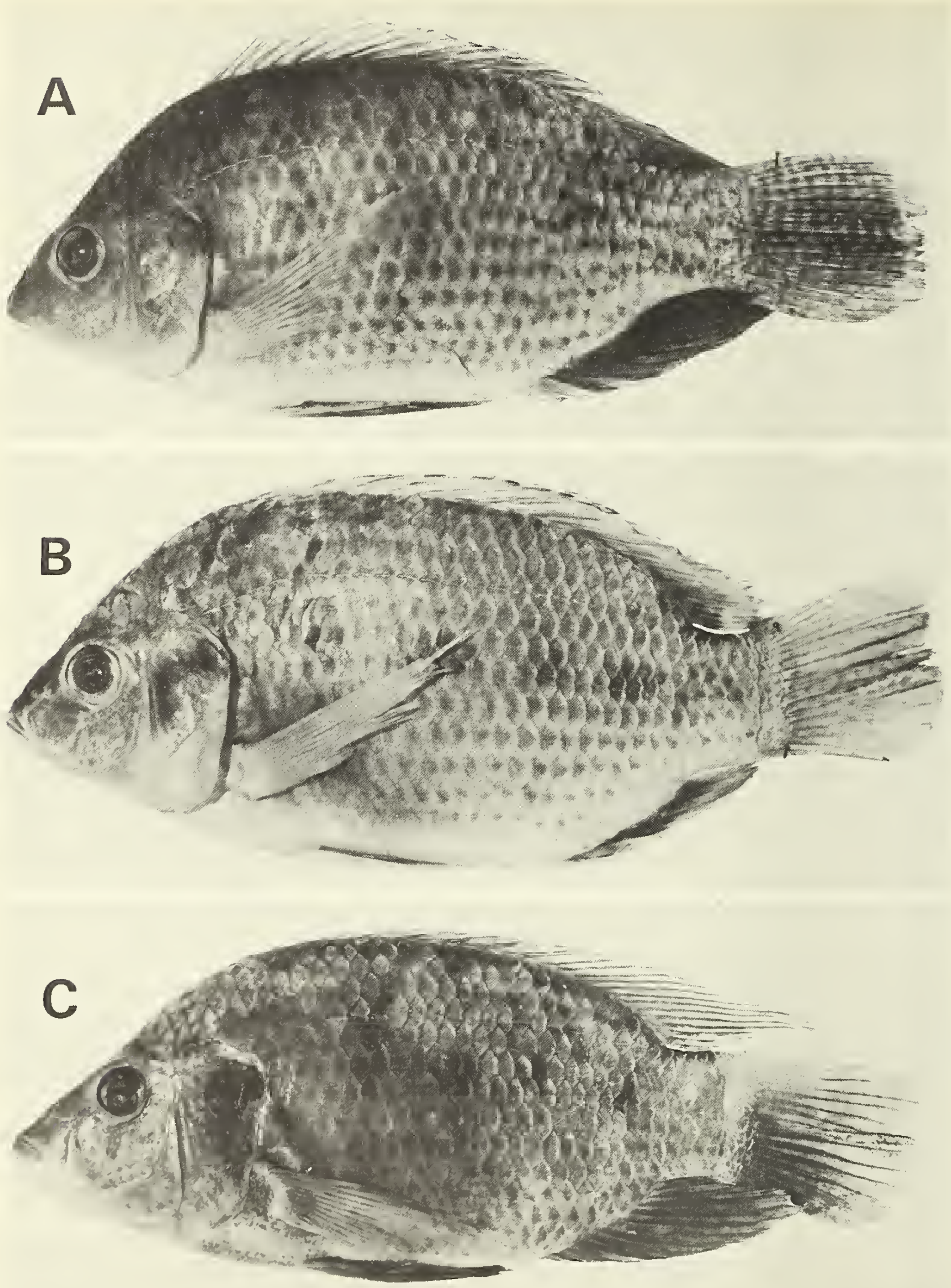

Fig. 94 *Oreochromis u. urolepis*: A, of 125 mm SL from the Kingani River; B, female of 145 mm SL from Rufiji River at Utete; C, male of 203 mm SL from the Kingani River. The pigment pattern of the caudal fin is more pronounced in the smallest fish, in which its scaly covering is less dense. (Photograph, BMNH).

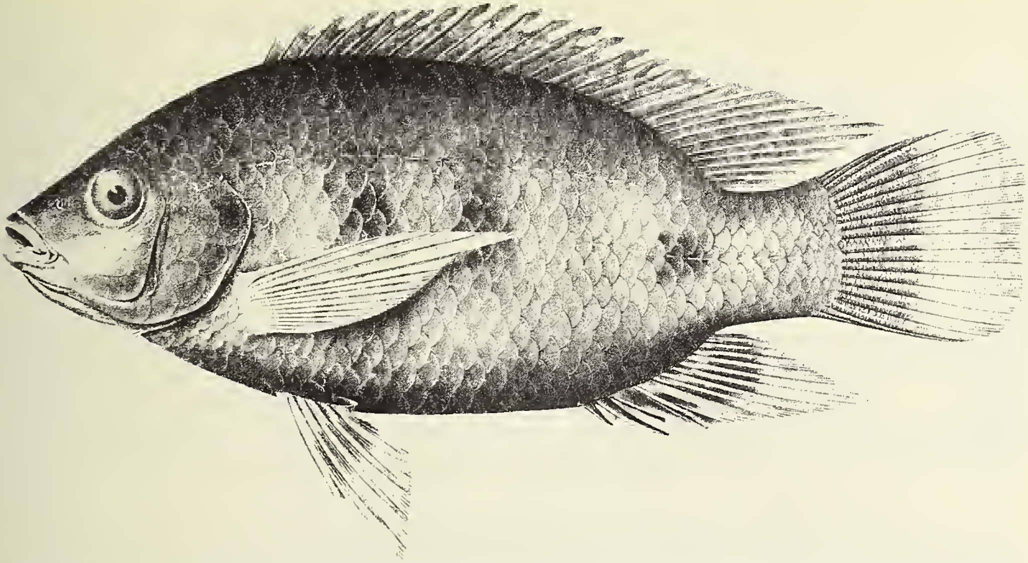

Fig. 95 *Oreochromis urolepis hornorum*, holotype (the lectotype of *Tilapia adolfi* Stdr, 1916) from the Wami River system, 167 mm SL. From Steindachner, 1916.

Table 71. Proportions in *O. u. urolepis* and *O. u. hornorum*. There are no specimens available from the Wami River above SL 240 mm, nor have any from the Rufigi and Kingani been used below 124 mm. Some differences are therefore due to allometry.

	O. u. urolepis		*O. u. hornorum*
N	27		26
SL (mm)	124–355		100–240
Proportions as % SL			
Depth	41·5–52·0		38·0–45·5
L. head	32·0–37·5		30·5–37·7
L. pect. fin	32·4–44·0		29·5–37·8
L. caud. ped.	8·4–11·6		9·5–12·8
Caud. ped. l/d	0·5–0·7		0·6–0·8
Proportions as % l. head.			
L. snout	♀, 37·0–42·5		♀, 32·8–38·0
	♂, 37·0–47·0		♂, 39·4–45·0
Eye			
at SL 124–203	20·0–23·0	at SL 100–202	19·0–25·7
at SL 207–310	16·0–20·5	at SL 220–227	18·2
at SL 355	15·0	at SL 240	16·2
D. preorb.			
at SL 124–203	22·0–27·0	at SL 100–202	18·4–24·2
at SL 207–240	25·0–27·2	at SL 220–240	23·0–25·0
at SL 252–355	28·0–28·6		
Interorb.	34·5–42·5		32·8–41·0
Lower jaw			
♀ SL 143–310	31·6–38·6	♀ SL 100–220	32·8–36·7
♂ SL 126–276	33·6–46·7	♂ SL 124–240	36·5–49·7

Table 72. Frequencies of dorsal formulae in *O. u. urolepis* and *O. u. hornorum.*

	Rufigi	'Dar es Salaam'	Kingani/ Ruvu	Mbemkuru	*urolepis* totals	Wami system	Zanzibar	*hornorum* totals
XVI 11	2				**2**			
XVI 12	1		5		**6**	5	1	**6**
XV 13	1				**1**			
XVII 11	4	1	4		**9**	4		**4**
XVI 13	1	4	2	1	**8**	2	3	**5**
XVI 14	1				**1**			
XVII 12	13	10	5	3	**31**	11	11	**22**
XVIII 11	3				**3**	3		**3**
XVI 14		2		1	**3**		1	**1**
XVII 13	7	6	2	1	**16**	3	2	**5**
XVIII 12	1				**1**			

0·8–1·35 times the length of the dentigerous area, usually approximately equal to it. Pharyngeal teeth slender, but firm, not crowded, on an approximately triangular area (Figs 97 and 98).

Scales 30–32 in the lateral line series, 3½–4½, usually 4, from origin of dorsal to lateral line, 3–7 between bases of pectoral and pelvic fins; 2–3, usually 3 rows on the cheek. A gradual transition in size between the flank scales and the smaller scales of the belly.

Vertebrae 29 or 30 (14+15, 15+14 or 15+15). See Table 76.

Dorsal fin, see Tables 72 and 76. Anal III 9–12, usually 10 or 11. Soft dorsal and anal fins prolonged in mature males, the dorsal nearly to end of caudal. In large fishes minute scales may cover the distal parts of the soft rays in the Rufigi population.

Caudal truncate in young, but in large fishes the rays and membrane become covered with a dense layer of small scales. In the Rufigi River this feature is much more evident than has been observed in other populations. The size at which the scaly covering develops varies. In the type of *O. urolepis* (150 mm SL) it is well developed and the fin is rigid, with two rounded lobes; but some others between 150 and 200 mm SL have more flexible fins. In other populations the covering is less dense and the fin remains flexible. No intact specimens from the Wami system over 200 mm SL have been examined for this feature. One of 205 mm SL from the Mbemkuru has no dense caudal squamation.

COLORATION. General colour in females and non-breeding males grey or silvery, with (in the Rufigi population) a pink or mauve tinge on lower parts of head and in some on chest and belly and on edges of some of the flank scales; two to four mid-lateral blotches usually evident; in the young these are on the intersections of more or less vague longitudinal and transverse bars. Upper half or two-thirds of caudal with narrow grey vertical stripes or reticulations on a paler ground. Upper edge of dorsal fin red in males, not or more narrowly in females.

In a ripening male the snout and lower parts of the head become iridescent, the red margin of the dorsal more pronounced; in the Rufigi population a pink flush covers the upper half of the caudal. In the most highly coloured males of the Rufigi population the general colour was dark olive grey, the upper lip pinkish, rays of the upper part of the pectoral red, the red margin of the dorsal broader and brighter, and the soft dorsal suffused with red; the rose-red of the upper half of the caudal was more intense and the colour extended along the whole margin of the fin. In such a fish the vertical stripes of the caudal had usually disappeared. Payne & Collinson (1982) reported black territorial males in the Rufigi. In *O. u. hornorum* the mature male is almost entirely black, the lips pale or black and throat and branchiostegal membrane variable.

Young with the usual vertical bars on the body. Tilapia-mark present up to about 85 mm SL, but less intense than in some other species.

A sample from R. Kingani

Four specimens of 126–207 mm SL from the Kigongoni Ferry near Bagamoyo agree with the described Rufigi sample, but the caudal rays are densely scaled only in the biggest. A ripening female of 189·5 mm SL extends the range in some of the more variable proportions, having a slightly longer head (38·5% SL) and lower jaw (38·4% length of head) than any female in the Rufigi sample. Vertebrae in 8 specimens radiographed are 29 in 7, 30 in 1, thus with a lower mode than in the Rufigi sample, but the samples are too small for the difference to be deemed significant.

Specimens of uncertain locality

Specimens in the Vienna Museum from 'Dar es Salaam' and 'Mtoni Nyanza' probably came from the Kingani system. Locally 'Mtoni' is river or stream and 'Nyanza' a lake or pond. They are too small to have developed a scaly caudal, but resemble *O. urolepis* in essential features, except that one of them is one of only two specimens of this species found to have XV dorsal spines. In a male of 73 mm SL the gonads were ripening, suggesting that they came from a small body of water.

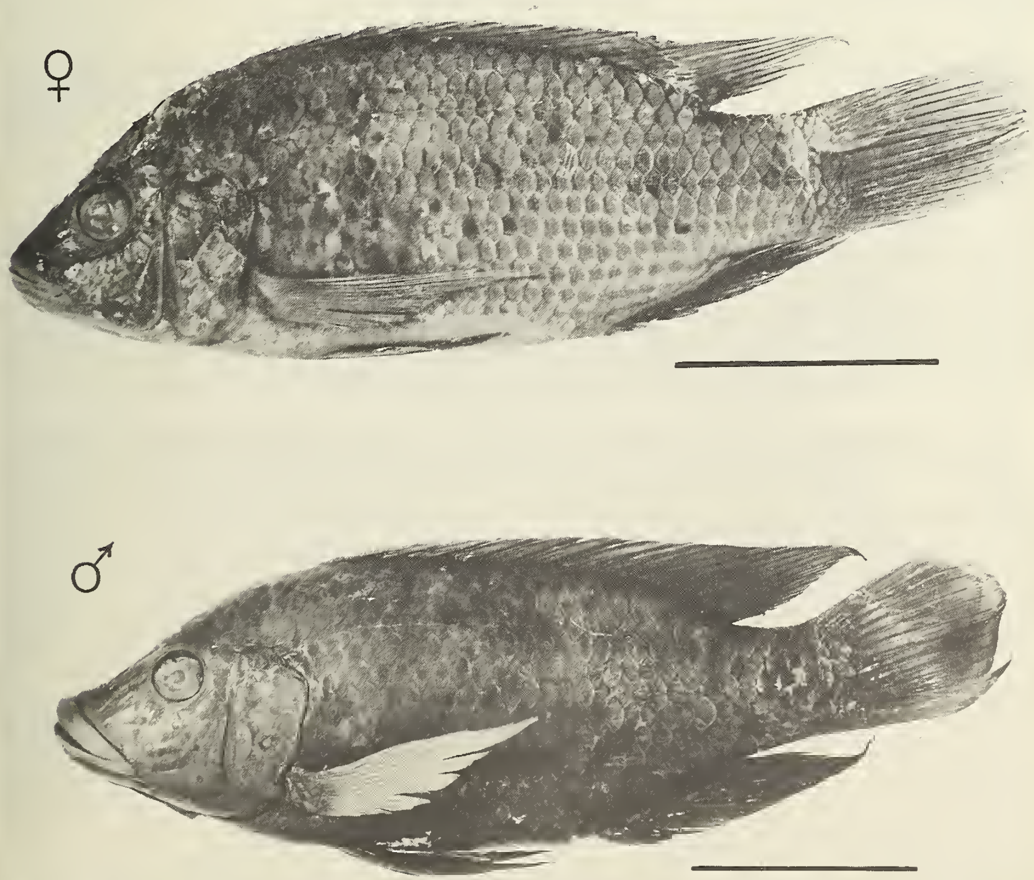

Fig. 96 *Oreochromis u. hornorum.* Female and male from Zanzibar. Scales = 5 cm. (Photograph, BMNH)

Specimens from the Mbemkuru River

The five fishes of 52–205 mm SL from this river, which flows to the Indian Ocean south of the Rufigi, agree with the Rufigi population in all details except the scaly coat of the caudal, which as in most species is limited to the proximal quarter and a short distance along the upper and lower rays, even in a fish of 205 mm. The lower gill-rakers number 19–22, the fish with 19 on the left side having 21 on the right. The dorsal formula is XVI 13 (f.1), XVII 12 (f.2), XVI 14 (f.1) or XVII 13 (f.1). The pharyngeal dentition matches that of the Rufigi population. Three to five mid-lateral blotches are present; the caudal is immaculate or with narrow vertical bars or series of spots on the upper part. A tilapia-mark is evident in three of 52–97 mm SL.

The 205 mm fish is a ripe female with an egg of long diameter c. 2·8 mm lodged in the oviducal opening. In this and another female of 123 mm the lower jaw measures 38·0–38·5% length of head.

The Zanzibar samples

These agree in proportions with the mainland samples, the longest snout being that of a male

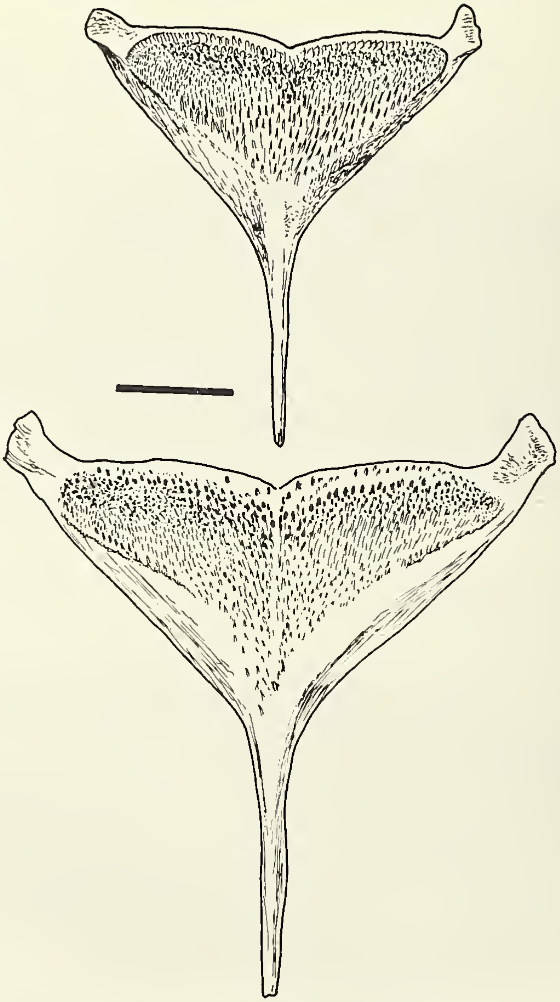

Fig. 97 *Oreochromis u. urolepis.* Lower pharyngeal bones of the holotype and a fish 201 mm SL from the Kingani. Scale = 5 mm.

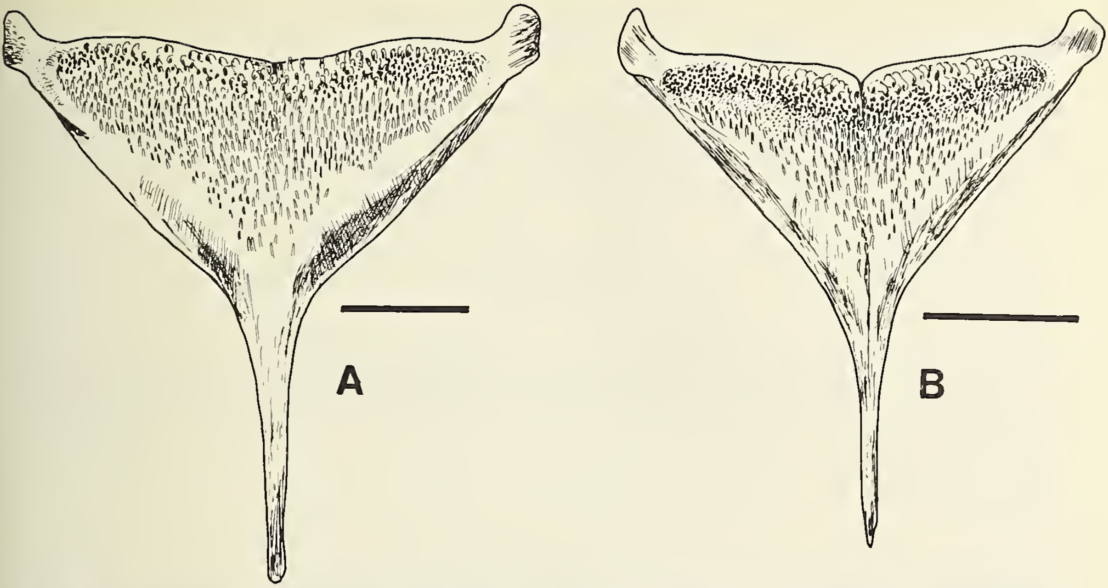

Fig. 98 *Oreochromis u. hornorum.* Pharyngeal bones of specimens of: A, 210 mm SL from Kilosa; B, 158 mm SL from Zanzibar. Scales = 5 mm.

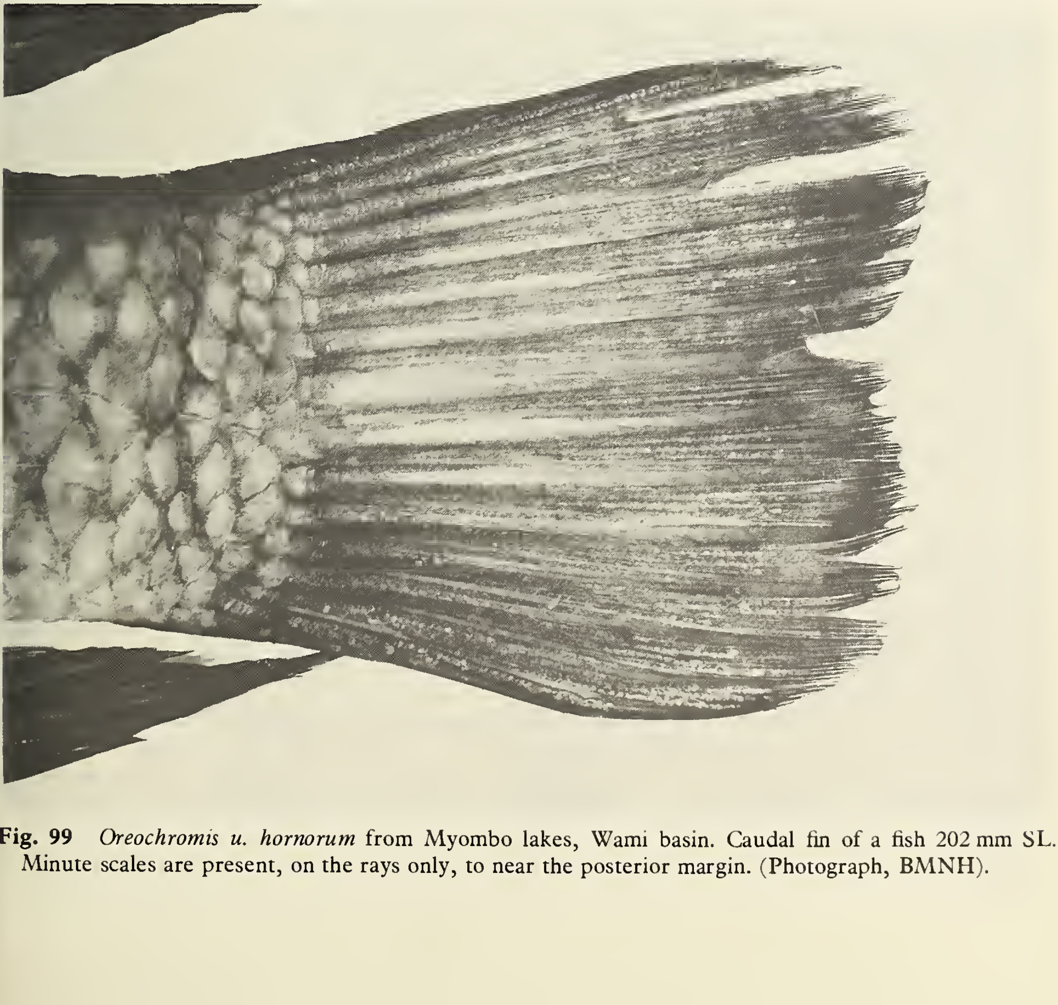

Fig. 99 *Oreochromis u. hornorum* from Myombo lakes, Wami basin. Caudal fin of a fish 202 mm SL. Minute scales are present, on the rays only, to near the posterior margin. (Photograph, BMNH).

of 169 mm SL, in which it is 44% head-length, and which has enlarged jaws. This fish also has a deep preorbital (26·3% length of head) and some of its outermost teeth and those of the inmost row are unicuspid.

Many of the other Zanzibar specimens, including four precocious breeders, are smaller than those used for the description and have juvenile proportions (relatively narrower preorbital and interorbital, shorter jaws, larger eye). For meristic data see Table 76.

Ecology

Food

A preliminary study by Talbot & Newell (1957) showed that in the saline ponds of Zanzibar *O. u. hornorum* was feeding on unicellular algae and detritus, including decayed fragments of macrophytes. Although filamentous algae and small invertebrates were present in the ponds they were not ingested.

Growth

In fertilized freshwater ponds at Malacca the growth of six marked males and six females of Zanzibar stock was measured over a period of 44 days. In contrast to *O. mossambicus* reared in the same conditions, the increase in length of females was the same as that of males, and the increase in weight of females was greater by nearly half (0·44) (Hickling, 1959, Table III).

Salinity and temperature tolerance

In the Rufigi River *O. u. urolepis* was not found in the brackish water of the lower delta in spite of diligent search (A. I. Payne, pers. commn). From the head of the delta upwards into the main tributaries, Kilombero and Great Ruaha, it is abundant. It inhabits the small lake Chemchem near Utete, where the pH in July 1965 was 8·4 and the temperature 26·5°C. This lake is fed by a hot soda spring of the same pH and a temperature at emergence of 52°C. Where it debouches into the lake the temperature of the stream was 36–38°C, and at this place young *O. urolepis* of 9–31 mm were abundant.

Reports on *O. u. hornorum* suggest that it is more tolerant of brackish water. Talbot & Newell (1957) made a gradual transfer of young from a stream in Zanzibar to ponds at Chukwani more saline than the sea (35·1 ppm). There they not only grew but bred. This transfer involved also a change of about 10–12°C in temperature, from a range of 26·2–28·1°C in the stream to 37–38°C in the pond.

Gould (1951) also records that specimens collected from lakes near Kilosa survived transference to marine ponds at Tanga.

Breeding

Freshly caught fishes, from a backwater at the head of the Rufigi delta at Utete, were examined for breeding condition on 1 August 1965. The dry season was well advanced and the retreating waters had exposed circular spawning pits of about 75 cm diameter and 15 cm deep in the middle, of a simple basin-shape without raised rim. These could only have been made by *O. u. urolepis* and fishermen confirmed this belief.

At this time few fishes were breeding. The males examined included one with large, brown testes (recently spent ?); its genital papilla was large, conical, without appendages and white, the rim of the pore being red with full capillaries. Some females contained ovarian eggs up to 2·1 mm diameter, thus probably not fully ripe (see note on Mbemkuru fishes above).

Fishing near the junction of the Great Ruaha with the Rufigi in December, 1979, Payne & Collinson (pers. commn) found the catch in some backwaters to consist almost entirely of black (territorial) males. The same results were obtained repeatedly from the same places. This is evidence of arena spawning. A month later the fishes had dispersed and fry were found in the shallows.

Fry were also found by these authors in September, and Bailey and Trewavas found them abundant in August in the lagoons of the Lower Rufigi and in the flood-plain of the Kilombero. This indicates that some spawning occurs also in the dry season. Possibly there are several breeding cycles throughout the year, with synchronized peaks at any one locality.

The largest female obtained (by R.G.B. & E.T.) in the Lower Rufigi was 232 mm in SL, from the Kilombero 310 mm; the largest males were respectively 252 and 355 mm. The largest individual taken from the Kingani was also a male. Sexual differentiation in size of jaws and in colour is described above. All the fishes used for Table 73 had bicuspid outer teeth except a ripening male of 110·5 mm, in which some of them were unicuspid, and an apparently spent male of 252 mm, in which many had reduced minor cusps. Mating was not observed.

The sex-ratio of *O. u. hornorum* was tested by Pruginin at Kajansi ponds in Uganda in a sample of 360 fishes and found to be 1 : 1.

Sexual dimorphism in the size of the lower jaw is detailed in Table 74 and summarized in Table 75. Changes in the teeth of males have been noted on p. 279, and the breeding colours are described under 'Coloration'.

Table 73. Relation between length of lower jaw and size, sex and gonadal phase in *O. u. urolepis*. The phases recognized are: quiet (qt), starting (stg), ripening (rpg), ripe (rp) and spent (sp). Especially in bigger fishes a 'quiet' gonad may be recovering from a previous spawning.

N	SL (mm)	Sex	Gonad	Lower jaw % head	Lower jaw % SL
4	142–171	♀	qt or stg	31·6–33·1	10·7–11·7
6	213–310	♀	qt or stg	34·9–37·0	11·5–13·5
4	110–210	♀	rpg or rp	34·3–38·6	13·2–14·8
11	113–207	♂	qt or stg	33·6–37·5	11·5–13·3
5	225–276	♂	qt or stg	35·3–41·1	12·1–14·9
1	110·5	♂	rpg	43·0	15·0
2	207, 252	♂	sp	41·7, 45·2	15·0, 16·9
1	355	♂	qt (recovered sp?)	46·7	17·3

Table 74. Correlations of length of lower jaw with size, gonadal phase and sex in *O. u. hornorum*. Abbreviations as in Table 73.

					Lower jaw	
	N	SL (mm)	Sex	Gonad	% head	% SL
Wami	4	99·5–155	♀	stg or qt	32·8–36·7	11·0–12·9
	3	132–220	♀	rpg, rp or sp	34·0–36·4	10·7–13·5
Kajansi	1	97	♀	rp	36·0	12·9
Zanzibar	4	81·0–157·0	♀	rpg or rp	31·0–36·0	10·7–12·6
Wami	2	140–227	♂	qt or stg	37·0, 42·0	12·5, 15·8
	6	124·5–146	♂	?	36·6–43·6	11·8–16·5
	3	146–202	♂	rp or sp	38·9–49·7	14·2–17·7
Kajansi	1	148·5	♂	sp	48·0	16·3
Zanzibar	5	78–169	♂	stg or rpg	31·0–40·5	11·1–14·2
	2	169, 175·5	♂	rp	45·6, 41·8	15·4, 15·5

Table 75. *Oreochromis urolepis.* Summary of relation between length of lower jaw and sex, based on data used for Tables 73 and 74. The Zanzibar specimens smaller than 100 mm SL are excluded, but all samples include some fishes that are sexually immature.

Locality	Sex	N	SL (mm)	Lower jaw % head Range	Lower jaw % head Mean	Lower jaw % SL Range	Lower jaw % SL Mean
Rufigi, Kingani	♂	16	110–355	33·6–46·7	38·2	10·5–17·3	13·6
& Mbemkuru	♀	15	123–310	31·6–38·6	35·6	10·7–14·8	12·6
Wami system	♂	12	124–240	36·6–49·7	41·9	11·8–17·7	15·2
	♀	7	99–220	32·8–36·7	35·1	11·0–13·5	12·03
Zanzibar	♂	5	132–175	36·5–45·6	40·5	12·6–15·5	14·3
	♀	2	148–157	36·0, 32·2	34·1	12·6, 11·3	11·95

The size and age at sexual maturity are, as in other species, dependent on the environment. Talbot & Newell (1957) found that their sample, bred in a saline pond in Zanzibar, was mature at a smaller size than the parent population of a freshwater stream, but no measurements of the size at first maturity in either environment were given, and several factors were involved in the change.

Mating pits of *O. u. hornorum* transported to Malacca were described as simple basin-shaped depressions without raised rim (Hickling, 1960).

Three large females were caught in August 1965, in Lake Kiharaka on the Myomba sisal estate near Kilosa. They weighed 380–425 g. One of the ovaries of the largest contained about 490 buff-yellow eggs of long diameter 2·5 mm; in addition there were about 120 smaller yellow oocytes measuring 1·05–1·2 mm and a number of still smaller (0·5–0·85 mm). In another the largest eggs were 2·8–3·0 mm in long diameter. This indicates that these females were prepared for three successive spawnings and that eggs reach about 3·0 mm. In a 97 mm female of Zanzibar stock introduced into Kajansi ponds, Uganda, the eggs measured 3·1 mm.

Hybrids

Oreochromis u. hornorum has been crossed with several other species. Males of *O. u. hornorum* mated with *O. mossambicus* (Hickling, 1959, 1960, 1962), *O. niloticus* from Lake Albert (Pruginin, 1969, 1967) or *O. s. niger* (Pruginin, 1967) give 100% males in the F_1. The reciprocal crosses have been effected with *O. mossambicus* and *O. niloticus* as the male parents and *O. u. hornorum* as the female. The sex-ratios in the F_1 were respectively 70–80% and 75% male.

When *O. u. hornorum* males were mated with *O. niloticus vulcani* of Lake Turkana, males constituted 98·2% of the F_1, and with *O. aureus* 90%. These ratios were obtained by Pruginin from samples of over 200 F_1 fishes.

A genetic explanation for the results of the crossings between *O. u. hornorum* and *O. mossambicus* was proposed by Chen (1967 & 1969) and recorded by Fryer & Iles (1972:170). This assumed that in *O. u. hornorum* the male is the homogametic sex, and that the male-determining genes of this species are dominant over the female-determining genes in *O. mossambicus.* It is further postulated, that in *O. mossambicus* it is the female that is homogametic, and that the male-determining gene in *O. mossambicus* is dominant over the female-determining gene in *O. u. hornorum.* This would account for the 75% of males in the reciprocal cross as well as for the all-male F_1 when *O. u. hornorum* is the father. But a different theory is required to explain the 90–98% male F_1 when *O. u. hornorum* is mated with *O. n. vulcani* or *O. aureus.* Geneticists continue to modify the theory (see p. 309; Avtalion & Hammerman, 1978; Hammerman & Avtalion, 1979).

All these results indicate that there is a difference between *O. u. hornorum* and its experimental partners in the sex-determining mechanism either in substance or in degree.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
O. u. urolepis			
1922.4.18.21 (holotype)	150	Mpanganye, Lower Rufigi	A. Loveridge
1969.2.11.51–62	142·5–252·0	Backwater of Rufigi R. and L. Logongwe, Utete	R. G. Bailey & E. Trewavas
1969.2.11.89–90	48·5, 58·0	Pool on Utete–Mohoro road, Rufigi delta	R. G. Bailey & E. Trewavas
1969.2.11.91–130	9·0–49·5	Chem-Chem, nr Utete	R. G. Bailey & E. Trewavas
1969.2.11.75–88	37–310 and head of 355	Kilombero R., Rufigi system and pool in Kilombero flood-plain	R. G. Bailey & E. Trewavas
1969.2.11.63–74	32·0–207·5	Kigongoni Ferry, Kingani (=Ruvu) R., nr Bagamoyo; and pool of Ruvu R., c.50 miles from Dar es Salaam	R. G. Bailey & E. Trewavas
1919.11.12.6–26	27–79	'Dar es Salaam'	J. Pomeroy
1926.1.25.5–10	38–49	'Dar es Salaam'	R. R. Scott
1930.3.8.60–66	43·0–110·5	'Dar es Salaam'	A. Loveridge
1928.1.18.2–4	52–123	Mbemkuru R. at Tendaguru	Kershaw (Migeod Expedition)
1929.9.23.7–8	97, 205	Mbemkuru R.	British Museum East African Expedition
1981.1.14.80–122	80–198	Great Ruaha	A. I. Payne
1981.1.14.123–126	92–149	Mkalinzo Sands, Rufigi R., nr junction with Gt. Ruaha	A. I. Payne
MRAC	♂ 243 & ♀ 208	Kilombero R.	R. G. Bailey & E. Trewavas
NHMW 24775–6 (two of the syntypes of *T. adolfi* Steindachner, 1916)	♀♀ 260, 280	Ulanga R., nr Ifakara	Adolf & Albin Horn
NHMW 32383–9	78·5–109·5	'Mtoni Nyansa' inland of Dar es Salaam	F. H. Meyer, 1898
NHMW 32379–80	126·5, 141	'Mtoni Nyansa' inland of Dar es Salaam	F. H. Meyer, 1898
O. u. hornorum			
Wami system			
NHMW 24782 (Lectotype of *T. adolfi* and holotype of *T. hornorum*)	167	Mukondokwa R., Wami system, nr Kilosa	A. & A. Horn
NHMW 24783 (Paratype of *T. hornorum*)	166	Mukondokwa R., Wami system, nr Kilosa	A. & A. Horn
NHMW 18869–71	130–144	Wami R.	A. & A. Horn

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1966.7.14.118–127	68–202	Myombo lakes, nr Kilosa, Wami system	R. G. Bailey, 1962
1966.7.14.128–135	121–146	Pond at Ilonga Research Centre, nr Kilosa, stocked from Mkata R., Wami system	R. G. Bailey & E. Trewavas
1969.2.11.24–25	200, 227	L. Kiharaka, Myombo Estate, nr Kilosa	R. G. Bailey & E. Trewavas
1969.2.11.26–34	71–105	Myombo lakes, nr Kilosa, Wami system	R. G. Bailey & E. Trewavas
1968.2.16.1	240	Korogwe, ex Myombo lakes	R. E. Gould
1968.	55·5–124·0	Mazizi dam, Msaka, Bagamoyo Distr., stocked from Wami R.	R. G. Bailey, 1963
Examined but not preserved, or preserved in Tanzanian Fisheries collection			
4 fishes	117–169	Dam at Ilonga Research Centre, nr Kilosa	R. G. Bailey
5 fishes	66–76	Pond at Ilonga	R. G. Bailey
4 fishes	62–84	Stream, tributary of Mkata R., Wami system	R. G. Bailey
6 fishes	64–141	Pond at Ilonga	R. G. Bailey & E. Trewavas
Zanzibar			
1918.1.31.2–5	39–73	Zanzibar	W. M. Aders
1946.12.21.1	169	Zanzibar	J. D. Robertson
1950.11.6.1–4	78–91	Zanzibar	P. King
1955.12.8.7–9	33–52	Zwige Zwige stream in upper estuarine reaches, Zanzibar	F. H. Talbot
1957.11.28.1–10	4 ♂, 132–175, 2 ♀, 148·5, 157, 4 juv., 78–82·5	Mzinga Mzinga R., Mkotomi, Zanzibar	F. H. Talbot (EAMFRO)
1966.9.13.1–2	97 (♀), 144 (♂)	Kajansi ponds, Uganda, via Sagana, Kenya, ex Zanzibar	Y. Pruginin
Specimens of doubtful identity			
1966.7.14.136–142	75–115	Pond near Morogoro	R. G. Bailey, 1964

Table 76. Frequencies of meristic numbers in the species of the eastward-flowing rivers. For *O. placidus* numbers for the two subspecies, *O. p. placidus* and *O. p. ruvumae* are recorded separately; similarly for *O. urolepis*, the populations of *O. u. hornorum* from the Wami system (W) and Zanzibar (Z), and the vertebrae of samples of *O. u. urolepis* from the Rufigi (R) and Kingani (K). For fuller accounts of the numbers in *O. s. spilurus* see pp. 235 ff, Tables 56, 58, 60, 62 & 67. Dorsal spine numbers for *O. s. spilurus* include records from Whitehead (1962*a*). *Oreochromis andersonii* is added for comparison with *O. urolepis* although the waters that it inhabits are only secondarily part of the eastward-flowing system.

			urolepis				*placidus*			
	s. spilurus	*korogwe*	*hornorum*		*urolepis*		*placidus*	*ruvumae*	*mossambicus*	*andersonii*
			W	Z	R	K				
Vertebrae										
28	5								3	
29	32	15	3	3	1	7	12	2	2	
30	3	3	5	13	8	1	11	2	17	1
31							1	1	1	16
32										2
D spines										
XIV	4									
XV	47								14	
XVI	158	1	7	5	5		21		45	34
XVII	10	17	26	13	34		22	14	1	29
XVIII		4	3		5		6	2		2
XIX								2		
D totals										
25		1								
26	2							1	4	
27	36	24			2		2	4	18	
28	32	14	9	1	4		21	18	36	4
29	6		23	14	17		29	1	2	29
30			4	3	9		1	1		32
x̄	27·79	27·31	28·86	29·10	29·03		28·55	27·83	27·5	29·56
Anal spines										
III	See Tab. 59	18	54		32		(1)	2	60	80
IV		20					51	29		
V							1			
Gill-rakers										
14		8							1	
15	1	16							1	
16	23	12					5	5	9	
17	23	2					5	10	19	
18	10						10	3	20	
19	5		2	1			5		10	
20			6	9	3		2		2	1
21			12	4	3					6
22			13	4	13					8
23			1	2	6					14
24			1		5					8
25					2					2
26			1							
27					1					1

Subgenus *OREOCHROMIS* –V

Oreochromis mossambicus

Oreochromis mossambicus (Peters)

Chromis niloticus (*non* Linn., part); Müller & Peters, 1844:32 (Mozambique); Günther, 1862:510 (Natal); Peters, 1868:23, pl. 4, figs 1–4 (Mozambique); Martens, 1869:142 (from Peters); Weber, 1897:148 (Natal & Transvaal).

Chromis (Tilapia) mossambicus Peters, 1852:681 (Mozambique).

Chromis niloticus var. *mossambicus*; Peters, 1855:267; Weber, 1897:148 (Illova R., Natal).

Chromis mossambicus; Günther, 1862:268; Steindachner, 1870:967 (excl. all synonyms & pl. 4, fig. 3).

Tilapia mossambica; Boulenger, 1899*a*:111; Pellegrin, 1904:309; Boulenger, 1915:154, fig. 101 (Mozambique to Natal, excl. specimen from Upper Shiré); *idem*, 1916*a*:327 (Natal); Gilchrist & Thompson, 1917:483, fig. 120; Roloff, 1937:80, fig.; Trewavas, 1937:383 (part); Jubb, 1961:131, pl. 78 (not pls XV & XVI); *idem*, 1967:161 (part), pl. 35? (not fig. 190 or pl. 36); Jubb & Gaigher, 1971:19; Jubb, 1974: figs 3, 5A, 8.

Sarotherodon mossambicus; Bell-Cross, 1976:219, fig.; Voss, 1977: pl. 16 (colours of expression); Hodgkiss & Man, 1977 (Hong Kong); Man & Hodgkiss, 1977*a* & *b* (bionomics in a Hong Kong reservoir); Bruton, 1979 (many refs & figs 3 B–D); Pullin & Lowe-McConnell, 1982.

Oreochromis mossambicus; Trewavas, 1981*a* & *b*; 1982*a* & *b*: 12; Schoenen, 1982.

?*Chromis dumerilii* Steindachner, 1864:225, pl. 7, fig. 1 (but locality given 'West Afrika').

Chromis vorax Pfeffer, 1893:151, pl. 2, figs 9–11 (Quellimane); *idem*, 1896:12, fig. 8.

Tilapia vorax; Boulenger, 1899*a*:125; Pellegrin 1904:322; Boulenger, 1915:156, fig. 102 (all after Pfeffer); Gilchrist & Thompson, 1917:485, fig. 1 (Transvaal) (all figs under this name are from Pfeffer).

Chromis natalensis Weber, 1897:147 (Illova R., Natal).

Tilapia natalensis; Boulenger, 1899*a*:113; 1901*b*:457 (excl. Congo basin); Pellegrin, 1904:311; Boulenger, 1915:157 fig. 103 (Mozambique to Cape Province; excl. specimens 1–11 & 18–22); Gilchrist & Thompson, 1917:486, fig. 122 (Transvaal, Natal, Cape Province); Fowler, 1934: Seitz, 1949:221, figs 9–19 (behaviour in aquarium); Baerends & Baerends van Roon, 1950 (behaviour in aquarium); Elliot, 1955 (photo of male, popular account); Le Danois *et al.*, 1957: opp. p. 108 (col. photo. of male).

Notes on the synonyms

Müller & Peters (1844) gave the first brief account of the material later named *T. mossambica*, with fin-formulae for four specimens, namely D XIV 12, A III 10; D XV 12, A III 10; D XVI 12, A IV 10; D XVII 13, A IV 11. The two with IV anal spines were probably *O. placidus*. Further evidence that *O. placidus* formed part of the original material derives from the geographical range given by Peters (1868), which extends farther north than the known range of *O. mossambicus*, to 11°S, that is to the Ruvuma River.

Chromis dumerilii Steindachner. Steindachner later included this among the synonyms of *T. nilotica*, and Boulenger, who had seen the type, put it in *T. mossambica* in spite of the locality given by Steindachner as 'West Africa'. If the locality label is indeed wrong, the specimen now marked 'Typus?' of this species (NHMW No. 3290), which I also have seen, might be *O. mossambicus*. It now measures 86 + 24 = 110 mm (Steindachner 113 mm) and has a relatively longer lower jaw than the West African species (36·9% length of head, 14% SL). Its meristic characters agree with those of *O. mossambicus* or *O. spilurus* except that the dorsal formula, XV 10, is a combination not recorded for either. It remains a *species dubia*.

Types. Lectotype: selected from the material of W. C. H. Peters' collection in the Zoologisches Museum der Humboldt Universität Berlin at my request by Dr H. J. Paepke, with the following information. ZMB 2806, probably ♂, SL 105 mm, length of head 44 mm, of lower jaw 18 mm

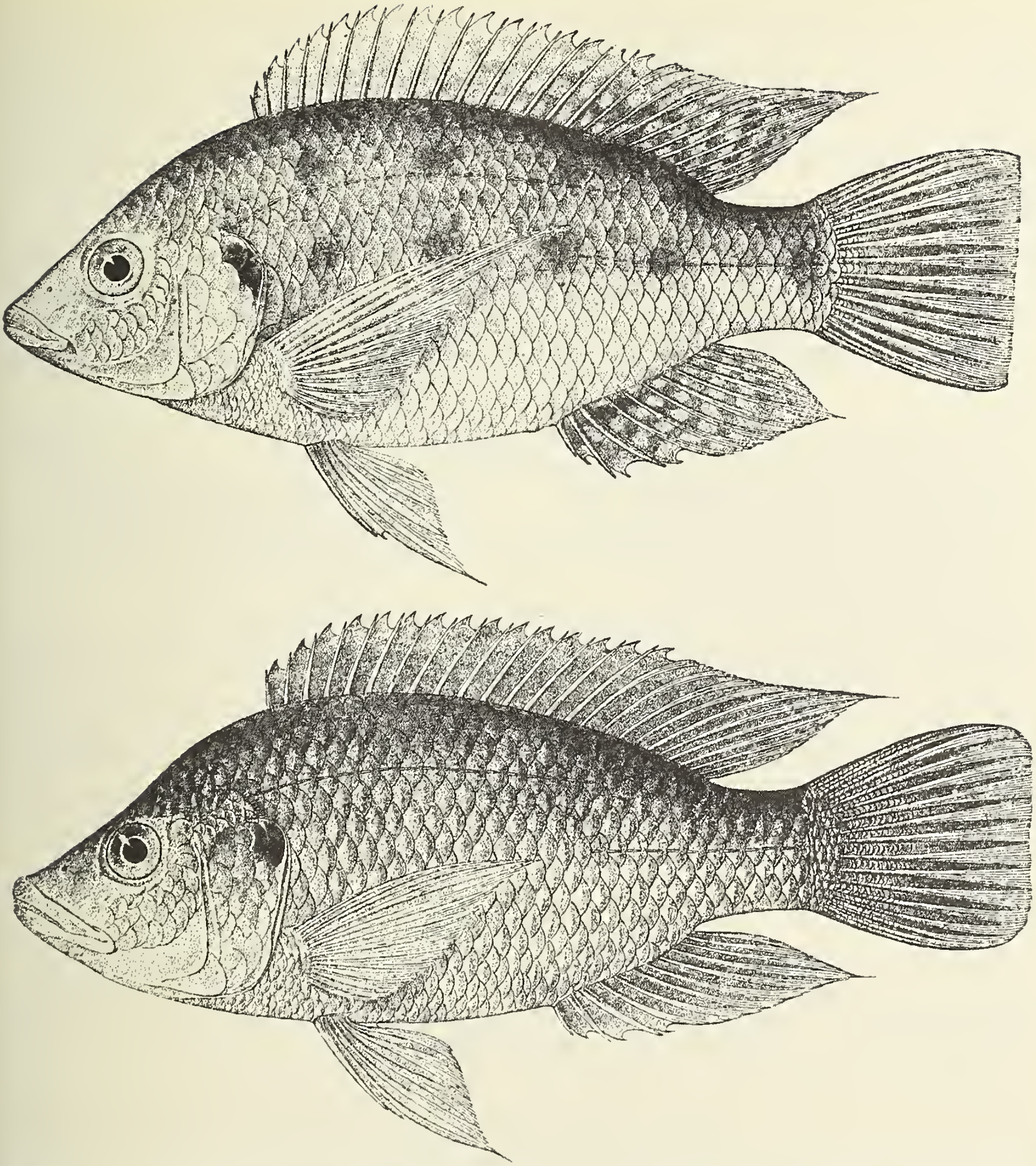

Fig. 100 Upper: *Oreochromis mossambicus* of 120 mm SL from Durban. From Boulenger, 1915, fig. 103. Lower: *O. mossambicus*, male of 120 mm SL, Mozambique, from Boulenger, 1915, fig. 101.

(40·9% l. of head); D XV 11, A III 8; Mozambique. The jar containing it bore the name *Chromis mossambicus* and an asterisk signifying 'Type'. It was catalogued according to Peters' later (1868) synonymy as *Chromis niloticus*.

Paralectotypes: one specimen of 88 mm SL in the same jar as the holotype (ZMB 2806) and three of 74–115 mm SL (ZMB 16035) also of Peters' collection, from Mozambique; two males of 101 and 120 mm SL, two females of 96 and 108 mm and three of uncertain sex, 77–105 mm, collected by W. C. H. Peters in the Lower Zambezi and presented to the British Museum from the Berlin Museum, BMNH 1861.5.2.58–64.

'Official' English name in southern Africa: *Mozambique tilapia* (Jackson, 1975).

Recently, this species has received much attention in the literature, most of the contributions being not, or not primarily, taxonomic. Those containing at least some first-hand zoological information are referred to in appropriate places in the following text. Early articles on dispersal and culture are listed in the works of Atz (1954, 1957), Chimitz (1955, 1957) and Riedel (1965), and the bibliography of Thys van den Audenaerde (1968*b*). These are included in a comprehensive bibliography of the tilapias by Balarin (ms.) and the selective one of Schoenen (1982).

Distinguishing characters

1. Genital papilla of male simple or with a shallow distal notch.
2. Jaws of sexually mature males enlarged, often causing the upper profile to become concave.
3. Female and non-breeding male silvery with 2–5 mid-lateral blotches and some of a more dorsal series. Breeding male black with white lower parts of head and red margins to dorsal and caudal fins.
4. Vertebrae 28–31, mode 30.
5. Dorsal spines XV–XVII, mode XVI; Total dorsal rays 26–29, mode 28.
6. Anal spines III.
7. Lower gill-rakers 14–20, modes 17 or 18.
8. Pharyngeal teeth very fine, the dentigerous area with narrow lobes, the blade in adults longer than dentigerous area.
9. Caudal fin not densely scaled.

Character 2 is shared with the other species of the eastward flowing rivers, and both 1 and 2 distinguish them all from the subgenus *Nyasalapia*. The meristic characters are shared with *O. mortimeri*, and both species are close to *O. s. spilurus* in numbers of vertebrae, dorsal rays and gill-rakers (Table 76). *Oreochromis placidus* usually has IV anal spines and a higher number of dorsal spines (Table 76). *O. urolepis*, as Table 76 shows, has higher numbers of gill-rakers and higher mean numbers of dorsal rays, its pharyngeal teeth are somewhat coarser and adults may have a densely scaled caudal. Hybridization shows that its sex-determining mechanism is different. The striking contrast of the white lower parts of the head with the black general colour in territorial males is characteristic of *O. mossambicus*.

Description

Based on the paralectotypes in BMNH and on three specimens collected by Sir John Kirk in Mozambique in 1867, nineteen from the Lower Shiré and five from Inharrime, Mozambique; in all 34 specimens (18 males, 7 females and 9 of uncertain sex), 77–213 mm in SL. Some qualitative characters and the colours are taken also from other specimens.

Proportions as % SL. Depth of body 36·0–49·5, usually over 40. Length of head 32·3–37·0 in females, 34–39 in males. Length of lower jaw 11·0–16·5 in females, 11·7–17·4 in males (see p. 297), over 13 in 4 of the 15 females measured, but in 17 of the 21 males. Length of pectoral fin 30·0–44·5 (below 35 only in the old specimens collected by Peters and Kirk). Length of caudal peduncle 10·0–13·7 (0·7–1·0 times its depth).

Proportions as % length of head. Length of snout 32–37 in females, 33–43 in males. Diameter of eye 20–25 up to SL about 150 mm, 17·5–19·0 above this length. Depth of preorbital bone 20·0–22·7 in females and most males, but 24·5 in a male of 101·0 mm SL. Interorbital width 30·3–38·7 at 77–128 mm SL, 36·0–43·8 above this length. Length of lower jaw 32·0–45·5 (see pp. 296–297).

Maxillary ending between nostril and eye in females and immature males, but below anterior edge of eye in breeding males. The lengthening of the jaws in the latter often produces a characteristic concave upper profile.

Teeth in 3–5 series; in the young bicuspid in the outermost, except sometimes a few posterior small upper teeth which may be simple, tricuspid in all inner rows. As the fish increases in size some of the outer teeth are replaced by unicuspids until in very large individuals all outer teeth are simple, and in very large males some of the inner teeth too. The change seems to take place earlier in males than in females (see p. 297). In both sexes, but especially in males, the brown crowns may be broken off or worn down, probably as a result of nest-digging, and in ripe males the tooth-bands may be broadened by separation of the rows by the thickened gums, causing the outer teeth to appear on the outside when the mouth is closed.

Gill-rakers on lower part of anterior arch (14, 15) 16–19 (20); see Table 76.

Lower pharyngeal bone. Width usually less than its length (of 21 specimens measured, less in 14, equal in 5, slightly more in 2), 10–11·8% SL (mean of 22 specimens 10·45) and 26–32 (33·8)% length of head. Blade as long as or longer than median length of toothed area. Pharyngeal teeth very fine, pointed, those of posterior two rows stronger than those in front, dark-brown-tipped, with a low minor cusp. Toothed area with concave sides and rather narrow lobes, the anterior teeth sparse (Fig. 101 & 103).

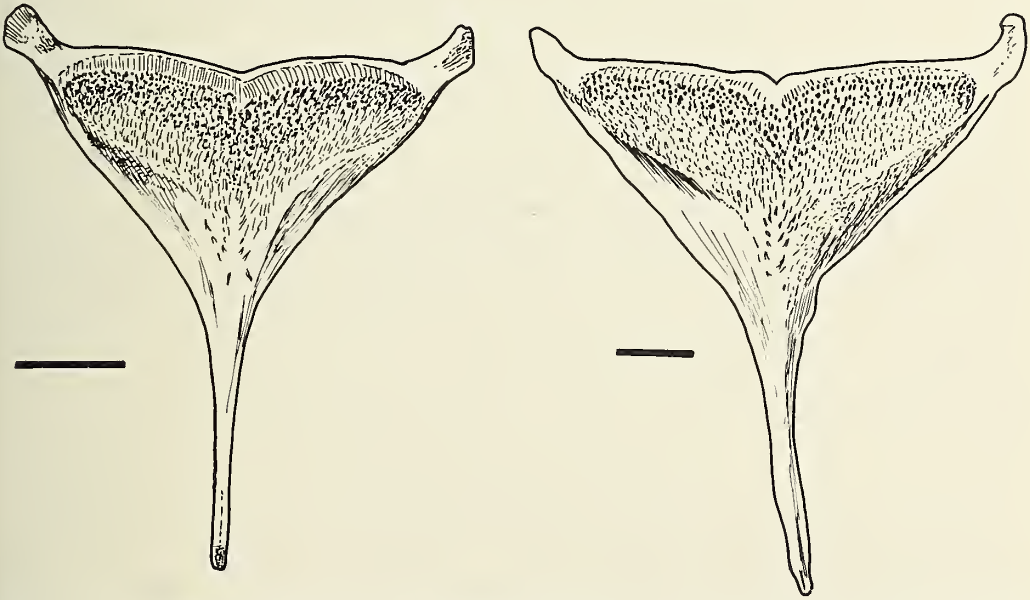

Fig. 101 *Oreochromis mossambicus.* Lower pharyngeal bones of: left, a fish 220 mm SL from Middle Letaba River, Transvaal; right, one of 280 mm SL from 'Kosi Bay', Kwazulu. Scales = 5 mm.

Vertebrae 28–31, mode 30 (23 specimens; Table 2).

Scales. Three, occasionally two, rows on the cheek. 30–32 in the lateral line series, mode 31; $3\frac{1}{2}$–$4\frac{1}{2}$ between origin of dorsal fin and lateral line, 4–6 between pectoral and pelvic fin-bases.

Dorsal XV–XVI (XVII) 10–13, modal combination XVI 12, total number of rays 26–29, mode 28 (see Table 76).

Anal III 9–12, usually 10 or 11.

Longest soft dorsal ray extending to above proximal part of caudal in females and immature males, but in breeding males to half or three quarters length of caudal. In the latter case anal also produced, but not so far.

Caudal truncate, often with rounded corners.

Size. Maximum sizes have been reported, variously by weight or length as follows: 6 lb 4 oz (2830 g) in Umfuli River, Zimbabwe [Rhodesia] (Jubb, 1967:239); 5 lb 9 oz (2580 g) in Transvaal (Lombard, 1959); 38 cm and 1206 g in Java (Vaas & Hofstede, 1952); 4–5 lb (1814–2268 g) 'monosex' in Jamaica (Rep. Jamaican Min. Agric. Lands, 1959). See also 'Growth', p. 300.

Coloration. The basic melanin pattern of two horizontal and six or seven vertical bars is never fully realized in this species. Baerends & Baerends van Roon (1950, fig. 22 a & b) illustrate the greatest expression respectively of horizontal and vertical bands, associating them with different emotional states. These are the 'striped' and 'barred' phases of Neil (1964, pl. 20). More commonly, at least in preserved specimens, females and sexually inactive males have no bands, but may have the intersection points of the facultative bands represented by three or four upper and two to five mid-lateral blotches, or some or all of these may be absent. The syntypes of *T. natalensis* were described as having no markings on the body (the 'neutral' phase of Neil, 1964, pl. 2 A). They may come and go in the living fish and may become more intense as the fish dies. Neil's 'hatched' phase is this with the blotches united by very faintly indicated stripes and bars.

The ground colour may be pale watery olive (a pond specimen), or a bright silver-grey (at Kanjedza, Lower Shiré). Baerends & Baerends van Roon state that the female becomes silvery as she reaches reproductive condition, but younger wild fishes may also be silvery. In the Malacca ponds Hickling states (1960:2) that there is much yellow about the chin and throat. I did not see this in Lower Shiré specimens, but a sexually inactive male living in a Zambian pond (imported from Natal) had the throat, branchiostegal membrane and the outer pelvic rays bright yellow.

In fry up to about 60 mm SL vertical bars are present with or without the mid-lateral blotches, but with no horizontal stripes. A clear-ringed tilapia-mark is present up to about 80 mm SL, above which size it may be detected as the intensified lower end of a grey oblique bar.

The breeding male, when territorial, courting, mating and for some time subsequently, becomes deep blue-black to black all over except for a white area on the lower part of the operculum, preoperculum, cheek and branchiostegal membrane, with scarlet margins on dorsal and caudal fins, and red pectoral rays. The throat and cheek are described as white by most observers (Seitz, 1949; Baerends & Baerends von Roon, 1950; Vaas & Hofstede, 1952; Bruton, pers. commn; Voss, 1977; my personal observation on aquarium and wild fishes), but as 'livid yellow' by Hickling (1960).

A mottled phase in the active male has been described, some of the spots uniting to form longitudinal zig-zags. Seitz (1949, figs 11–13), who describes the normal breeding male as black, even velvety black, attributes the assumption of the mottled pattern portrayed in his figure to the bright lighting used in photography. Other photographs, for example that by P. Jochem in Tangerding, 1977, and those on pages 55 and 71 of Goldstein, 1923, show the same pattern, although Tangerding describes the typical black body of the breeding male. Heinrich (1963) and Neil (1964) found the mottled pattern only in the pre-courting, aggressive phase. The males seen by me in the Lower Shiré area, which were probably in this phase, were black in the upper 2/3 or 3/5 of the body, but mostly mottled in the lower parts, many of the ventral scales having black centres and white edges; the white cheeks and scarlet margins of dorsal and caudal fins were conspicuous.

Albinism. In Taiwan, where this species is cultivated in ponds, a strain has appeared in which the skin is almost devoid of pigment. Two of these sent to the BMNH by Dr W. S. Ling, FAO Regional Officer for Asia and the Far East, had black pigment only in sparsely scattered pin-point spots and in one or two asymmetrical black blotches. Dzwill notes (1962) that such colour variants in domesticated fishes are generally due to a single recessive gene. The strain is encouraged in Taiwan because it is reputed to have a better flavour than normally coloured fishes, cf. the 'maradadi' colour variety of *O. variabilis.*

Strains with melanin reduced or absent are now used by fish-culturists elsewhere.

Changes in the jaws and teeth. The wide range of variation in the relative length of the jaws prompts an enquiry into its possible correlation with size, growth rate, sex or gonadal condition. The lower jaw was measured in 38 specimens at standard lengths of 57–282 mm. The ratios are plotted in Fig. 102, from which the following facts emerge.

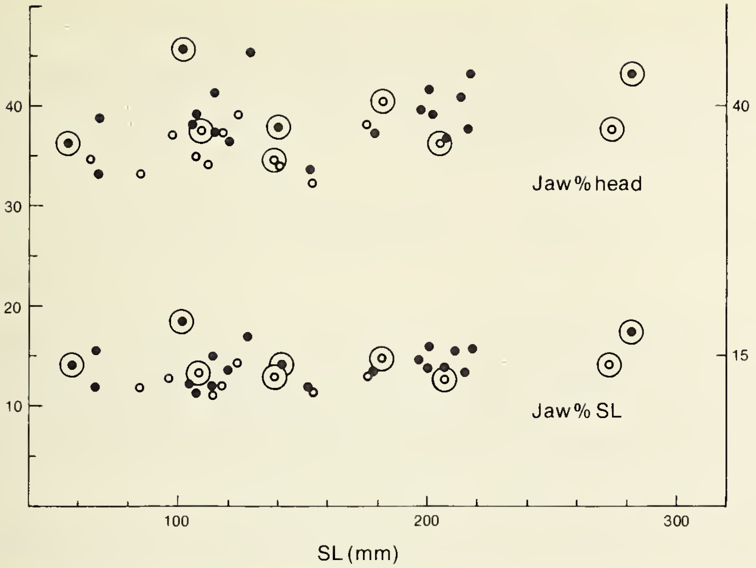

Fig. 102 *Oreochromis mossambicus.* Length of lower jaw expressed as % length of head and % standard length. ● = ♂, ○ = ♀. Sexually ripe individuals indicated by a large circle surrounding the symbol. In the case of the 101 mm fish this is a guess, because the viscera have been removed. The 181 mm female has the ovaries almost completely discharged.

The lower jaw in 22 males is 11·7–17·4% SL, 33·0–45·5% length of head; in 16 females it is 11·0–14·8% SL, 33·0–40·5% length of head. The jaw is over 15% SL and over 40% length of head in eight males. The female with the biggest jaw is 181 mm in SL with ovary partly discharged.

There appears to be a basic allometry affecting both sexes, so that no fish of more than 160·0 mm SL has a jaw less than 12·5% SL or 35·0% length of head. Enlargement of the jaws affects both sexes but is earlier in the male. The two largest fishes plotted are the breeding male and female from 'Koso Bay', probably the large brackish lagoon there (3·5‰ salinity according to Allanson & van Wyk, 1969). In them the enlargement in the female is less than that in the male.

The specimens available were taken at various times spread over a century and at various places, including a swamp in the Zambezi delta, a lagoon in the flood-plain of the Shiré, a coastal lagoon in Kwazulu, a warm stream in California, where the species has become feral, aquarium stock in Canada, as well as localities no more accurately specified than the name of the nearest town—Beira, Durban, etc. No order in the allometry of the jaws can be expected from data on samples for which the factors affecting growth-rate and maturity are so diverse. Moreover Seitz (1949), concluded that the degree of enlargement of jaws and lips in males was individual in his aquarium stock.

The crowns of the teeth are often broken off in breeding fishes of all sizes, the result probably of digging, but true unicuspid teeth with brown crowns have not been found in females under 210 mm in SL, except 1–3 teeth in two 'ripening' females of 107 and 117 mm. (Very few females over 120 mm SL are available.) Of the males, the smallest with a few unicuspid teeth is the 101 mm fish with very long jaws. From 120 mm upwards, out of 13 males examined only two, both with small gonads, have all the outer teeth bicuspid. From 200 mm SL most of the outer teeth are unicuspid and those with two cusps have the minor cusp reduced. The largest male, 283 mm in SL, has unicuspid teeth also in the two inmost rows. No females between 206 and

273 mm are available. The female of 273 mm has all the outer teeth unicuspid or with reduced minor cusp.

We may conclude that the change to unicuspid teeth is a function of size and occurs earlier in males than in females. Possibly in most populations of this species females rarely reach a size at which their teeth would become unicuspid.

Ecology

Food

Studies of food and digestion in *O. mossambicus* have been made on several stocked or aquarium populations, and on the natural populations of Lake Sibaya and St Lucia Lagoon.

The gut was described by Kamal Pasha (1964), who found the intestine of a 13 cm fish to measure 103 cm. Gastric glands are present and the intestine has columnar and goblet cells throughout. Nagase (1964) determined the digestive enzymes. No special equipment was found for digesting cellulose.

Fish (1960) found that *O. mossambicus* digested carbohydrates more easily than the carnivore (*Perca*) with which he compared it, producing a greater quantity of amylase, in accordance with its bias towards plant food.

Vaas & Hofstede (1952) studied the food in fresh and brackish ponds in Java. They found that the young feed mainly on diatoms from the plankton and periphyton as well as other unicellular green algae and small crustacea. The stomachs of their older fishes contained decaying vascular plants and filamentous algae in fresh water, *Enteromorpha* and *Chaetomorpha* in brackish. They reported that blue-green algae with a mucous envelope passed undigested through the gut; and that cultures could be made from the tough-walled cells of *Scenedesmus* and *Pediastrum* taken from the rectum. Of the dinoflagellates, *Peridinium* passed undigested through the gut, but the more fragile *Ceratium* was often digested.

In Ranu Lamongan, a crater-lake in eastern Java, Green *et al.* (1976) found *O. mossambicus* (still named *ikan mujair*, after the fishery officer who introduced it) as a member of the fauna. Fry of 8–18 mm were feeding on zooplankton, with cyclopoid copepods, rotifers and ostracods almost equal in importance. Some of the stomachs were packed with rotifers and the authors judged that these fry were feeding selectively. The adults (65–215 mm) fed mainly on phytoplankton, in which *Nitzschia* and *Synedra* predominated, but some of them also contained 'brown debris', presumably organic detritus.

In freshwater ponds in Transvaal, Le Roux (1956) reported that zooplankton, mainly Entomostraca, constituted the most important part by volume in individuals of less than 5 cm TL and continues to be important up to 7·5 cm. Above 5 cm, however, phytoplankton was the main food item when it was abundant in the pond, otherwise vascular plant material, but whether fresh or decaying Le Roux did not state. (It is possible that the species, imported from Zambia, in Le Roux's ponds was *O. mortimeri*, which had not then been distinguished from *O. mossambicus*).

Opportunism in feeding is illustrated by the report by Neil (1966) that in Hawaiian ponds *O. mossambicus* of no great size will eat *Gambusia* of 3–4 cm and in aquaria will eat young of its own species. Schuster (1952:95) stated that in the brackish *tambaks* of Java 'when plants are lacking it will feed on whatever small animals it can find'. Like several other species it will take the angler's bait, but the teeth of jaws and pharynx are not adapted for feeding on metazoa or living vascular plants. Its reported usefulness in Java in malaria control (Hofstede & Botke, 1950) depends on its ability to clear a pond or ditch of floating filamentous algae that are the breeding places of *Anopheles ludlowi*. A beneficial effect of *O. mossambicus* on the balance of organisms in Plover Cove Reservoir, Hong Kong, acting through the food-chain, was reported by Man & Hodgkiss (1977*b*).

The general consensus based on studies of wild or stocked populations is that juveniles are omnivorous and adults feed mainly on detritus. Detritus feeding was reported by Kelly (1956), Dendy *et al.* (1967), Man & Hodgkiss, 1977*b* and by the following special studies.

Bruton & Boltt (1975) studied the natural population in Lake Sibaya, Kwazulu. The fry, up to about 8 cm TL, are omnivorous, but their main source of food consists of the diatoms (especially Nitzschioid) in the mulm of decaying vegetable matter in the littoral pools in which they live. Juveniles above this size also rely on benthic and epiphytic diatoms, and adults are evidently opportunistic, although the bottom deposits and periphyton provide them with the bulk of their food. Terrestrial insects fallen on the water were present in 28 of 164 stomachs examined, but phytoplankton was present in only a few, a fact associated with the paucity of this food source in Lake Sibaya.

Bowen (1976*a* & *b*; 1979) followed the observations of Bruton & Boltt with more detailed studies on the same population. He measured the intestine in twenty-one preserved fishes and found a mean of 3·93 times SL. The range was not given, nor was the ratio related to the size of fish. The lower mean ratio compared to that of Kamal Pasha may be the difference between preserved and fresh specimens, but the findings of Campbell (1981) on *O. spilurus* (see p. 245) show that the possibility of a diet-related difference need not be ruled out.

Like *O. niloticus* in Lake George, *O. mossambicus* in both Lake Sibaya and the Hong Kong reservoir (Man & Hodgkiss, 1977*b*) feed by day. In Lake Sibaya the juveniles feed in the shallow waters where the detrital floc is richest in diatoms, the bigger fishes farther out from shore, where the density of the diatoms in the bottom deposits is lower. This was demonstrated not only by direct observation of the fishes, but also by studying the distribution of their feeding marks, conical pits made by the snouts of the fishes as they bite into the detritus. The size of these marks was found to be related to the size of the fishes making them.

The pH of the stomach is lowered only as the stomach fills. A moderately low pH was sufficient to lyse the cell-membranes of the diatoms, but the bacteria abounding in the detritus were much more efficiently digested when the pH was below 2·0. Bowen (1976*a* & *b*) found the stomachs of actively feeding fishes to have a pH below 2·5, with the most common values at 1·5 and 1·25, and occasionally as low as 1·0. In such an acid medium no protease activity could take place, nor was any detected. Further digestion proceeded in the intestine, in a medium of pH 8·0–8·8.

Bowen found that the most common diatom in the stomachs of juveniles was the naviculoid *Mastogloia elliptica* (Agardh) Cleve, and all the most important diatoms were at least partly benthic. Further evidence of bottom-feeding was the presence of sand grains in all stomachs. Observations showed the juveniles almost constantly feeding on the bottom, with only an occasional nibble at epiphytic growths.

Adults, in the cool season, were feeding in somewhat deeper water, but they were not found at the bottom in depths of more than 12 m. In water of these depths, as Bruton & Boltt found (1975, fig. 4 & pl. I), they kept to the upper part of the water column. In one sample from a part of the lake where the bottom sloped gradually from the shore, Bowen found evidence in the intestine of an alternation between bottom-feeding and suspension-feeding, segments of the intestine containing alternately brownish material with sand grains and green material consisting of planktonic algae and no sand grains. Bowen also demonstrated experimentally that *O. mossambicus* from this population are capable of ingesting and digesting suspended particles (in this case of a blue-green alga).

Although the algae and bacteria are important constituents of the food, Bowen estimated that they were not enough to account for all the energetic requirements of the fish, and he concluded that the fragments of decaying vascular plants that make the bulk of the detritus floc (i.e. detritus in the narrower sense) must also contribute some nourishment. In a later study, Bowen (1980) found that the quality of the detritus of lakes varies, and that the growth and condition of *O. mossambicus* is correlated with the amount of non-protein amino-acids present.

The regime in Sibaya, though favourable for juveniles, results in adults that are lean, with low condition factor and limited growth in length. Elsewhere, as is well shown in a contrasting photograph by Bowen (1979) they may have a much greater weight : length ratio. A study of the food of this species in plankton-rich waters would be interesting.

Whitfield & Blaber (1978) studied the food in the brackish lagoon St Lucia in Zululand, finding that the percentage occurrence of animal matter fell from 70% in young up to 5 cm TL to 40% at 5–8 cm and thereafter was very low, giving place to filamentous algae (*Enteromorpha* and *Rhizoclonium*) and diatoms epiphytic on these, with very little evidence of bottom-feeding in the form of inorganic particles.

With regard to the more omnivorous habits in most situations of young below 8 cm TL, it may be relevant that Mathavan *et al.* (1976) found that in 'fingerlings' an admixture of animal food with a diet of *Spirogyra* increased the efficiency of digestion and absorption of the alga, a result not obtained with *Lepomis.*

Finally, the evidence points to a mainly detritivorus diet for *O. mossambicus* although it is able to take advantage of particulate food in plankton and periphyton when this is available. See further in Bowen (1981 & 1982).

Oreochromis mossambicus has been used as an experimental fish in an investigation into the manganese requirements in the food and water (Ishai & Dollar, 1968), but as yet no general conclusions are drawn from the results.

Growth

Growth has been studied in the natural population of Lake Sibaya, South Africa, by Bruton & Allanson (1974). Lake Sibaya is a freshwater dendritic lake near the coast in 32°40′E, 27°25′S. It is thus subject to seasonal changes in temperature and rainfall that are reflected in the growth rate, and in the seasonal nature of feeding and reproductive activities. The lake is not rich in nutrients and the maximum size of individual *O. mossambicus* is low, about 24 cm SL, 26 cm TL, rarely 30 cm.

In the scales, bands of regular circuli are separated by rings formed of widely spaced bent or fragmented circuli. The rings are formed during the pre- and post-breeding feeding migrations, respectively in September–October and in January, and Bruton & Allanson believe that the spacing of the circuli is due to increased growth of the basal layers of the scale at these times. In support of this they cite their finding that in this lake the length of scale radius and length of fish increase isometrically. Scale readings were supported by counts of rings on otoliths and zones on opercula, which, however, were often not as clearly defined as those of the scales. On the well-supported assumption that two rings were formed in a scale each year, these authors found that both sexes grew in the first year to an average SL of about 8·4 cm. The females then spawned, but the males usually did not mature until their second year and the male growth-curve was henceforward steeper than that of the female, until at the end of the fifth year males averaged about 18·5 cm SL and females 15·0 cm. The corresponding average weights were about 205 and 125 g respectively.

This is therefore a slow-growing, early maturing population.

Where the temperature is favourable *O. mossambicus* lives and breeds without difficulty in ponds and dams, and its growth rate and condition will respond to fertilization of the ponds and supplementary feeding, as well as to stocking densities.

In such environments also the growth of the male is more rapid than that of the female. The difference is slight if the sexes are separated, but much more marked when they are together. This was demonstrated by Vaas & Hofstede (1950) in experiments conducted in five ponds of equal size, receiving water independently from the same source and stocked at the same density with fry of 50–60 mm (TL?), 24 to each pond. Their results are summarized in Table 77, abstracted from their Table XV (1952:49).

Growth was slower in both sexes in the ponds where breeding takes place, but in both ponds numbers 14 and 15 the male growth was not reduced even to the level of that of the segregated

Table 77. Growth of ♂ and ♀ *O. mossambicus*, segregated (24 individuals of one sex) or together (12 of each sex) in ponds in Java. From Vaas & Hofstede, 1952. See text.

Pond no.	Sex	No. of fishes	Size reached in 10 weeks Length (mm)	Weight (g)
11	♂	24	158·5±3·31	74·97±4·48
10	♂	24	152·5±4·74	58·40±3·47
13	♀	24	143·4±2·41	49·72±2·63
14	♂	12	147·9±2·95	52·44±3·39
	♀	12	109·2±1·22	20·92±0·95
15	♂	12	145·5±3·57	52·84±4·13
	♀	12	116·3±0·97	23·01±0·60

Table 78. From Hickling, 1959:28.

Pond no.	Sex	No. of fishes	Av. size at start Length (cm)	Weight (g)	Av. size after 44 days Length (cm)	Weight (g)
H 24	♂	15	8·6	12·5	15·9	72·8
H 29	♀	14	9·3	14·8	13·6	41·4

females in pond 13. The retardation in the female must therefore be put down either to an inborn sex-linked difference or to greater expense in egg production than in sperm production, possibly reinforced, as in Lake Sibaya, by earlier maturity, and not, as Van Someren & Whitehead believed for *Oreochromis spilurus niger*, directly to the increased population density resulting from breeding.

Table 78 gives figures from Hickling (1959:28) showing a similar result. This experiment, which was designed, not to give an absolute growth rate for one species in known conditions, but to compare it with that of *Oreochromis urolepis hornorum* living in the same ponds, does nevertheless give a difference between segregated males and females of the same order as that obtained by Vaas & Hofstede.

A few examples of growth in a known period may be given.

1. Males grew to a total length of 35 cm in 8 months from hatching in brackish water in Malaya (Hickling, 1950:290; LeMare, pers. commn, illustrated by a specimen of 248 mm SL, BMNH 1948.12.20.1). The sexes were not segregated, but the largest fishes were males.
2. In a brackish pond in Java the species may reach a weight of 1 lb (454 g) in 8 months (Schuster, 1952).
3. Marked females of 6–10 cm TL, set at liberty in lightly stocked, fertilized ponds at Malacca, reached 23–25 cm and 200–250 g in 200 days (Hickling, 1959).
4. In freshwater ponds in Madras *O. mossambicus* attains 22 cm and 4–5 oz (113–142 g) in 8 months; growth then proceeds slowly to 30 cm and 8 oz (ca 227 g) in 16 months. These fishes have matured and bred at 9–10 cm at an age of 3 months (Devados & Chako, 1953; Chako & Krishnamurti, 1954).
5. In Transvaal, in fertilized ponds with 'normal stocking rate' it reaches an average weight of 1 lb (454 g) (range 3/4–1½ lbs) in three years (Lombard, 1959). This is much less than the maximum size recorded by the same author (5 lbs 9 oz = 2545 g) for a wild fish of unknown age

in a naturally stocked dam, or by Jubb (1967:239) 6 lbs 4 oz (=2837 g) for a wild fish of unknown age in Umfuli River, Zimbabwe.

In ponds in Transvaal, where breeding is halted and growth slowed by cool winters, optimum stocking rates have been determined for rearing ponds in the first year (2800 fish per half-acre), second year (1400 fish per half acre), and for 'production ponds' of the third year (700 fish per half acre) ($\frac{1}{2}$ acre $= c.$ 2023 m^2). There the fishes are considered marketable at a weight of about 450 g (Lombard, 1959).

In tropical ponds efforts have been directed to preventing the stunting that results from early and repeated breeding. The methods used have been controlled cropping (Chimits, 1957, for details and references) or segregation of the sexes ('monosex culture'). In this species, advantage has been taken of the faster growth of males to segregate them by repeated selection of the larger individuals before they have bred, a method which is not infallible. Selection by examining the genital papilla is risky too since it must be done on immature fishes, in which the papilla is still small. In Guyana, population control by means of predatory species has been practised with some success in brackish ponds (Allsopp, 1960).

At the Malacca Institute all these methods were abandoned in favour of hybridization with *O. urolepis hornorum*, producing an F$_1$ generation of 100% males which made better growth than the males of either parent species (see p. 309).

Temperature tolerance

When cultivated in Egyptian ponds this species was unable to survive the winter, succumbing when the temperature had been below 14°C for several days (Koura & El Bolok, 1958). Attempts to keep it in ponds at Jonkershook, Cape Province, South Africa, succeeded through mild winters, but failed in the severe winter of 1963 (van Schoor, 1966; temperature not given). Du Plessis & Groenewald (1953) and Lombard (1959) state that the lower lethal temperature is about 10°C, and the species will not survive in Highveld waters of South Africa nor in dams that are fed by cold Highveld waters. Even in the Lowveld, where occasional frosts occur, it will survive in dams only if there is a place, at least 6 ft deep, where the fish can avoid surface fluctuations.

T. P. Chen (1954; *teste* Chimits, 1957) found 10°C to be the lower lethal temperature in Taiwan, but the species failed as in Egypt, to survive a sustained temperature of 14°C.

Maruyama (1958) noted temperature-correlated diel movements in ponds in Japan; by day the tilapias occupied surface layers and were active, gulping air at the surface when the water became very warm, but at night they lay at or near the bottom in groups, and remained inactive and relatively unresponsive. 16°C was found to be the lower critical temperature.

Bruton & Boltt (1975) attributed the movement of the adult *O. mossambicus* of Lake Sibaya away from the shallows in the cooler months and also at night in the breeding season to the more constant temperature in the deeper water, and Bruton (1976) added that several factors influenced these movements, including vulnerability to predators, especially *Clarias gariepinus* by night and birds by day, which make the terraces unattractive to *O. mossambicus* once the necessities of the breeding season are past.

Kelly (1956), experimenting in ponds in Alabama, U.S.A., found similar lower temperature limits. Feeding ceased at 15·5°C, deaths occurred at 11–14° and at 9° there was 100% mortality.

Allanson & Noble (1964) found that the species could be acclimatized quite rapidly to gradual changes of temperature from 23°C to 30°C, but more slowly to a lowering from 23°C to 15°C. They established that for their stocks the upper lethal temperature lay between 38°20 and 38°25 C, thus lower than the 41°C at which *O. alcalicus grahami* usually succumbs (Coe, 1966). The upper 'lethal temperature' given by Spaas (1959*b*), for *O. macrochir* and *Tilapia rendalli* of the Centrtal Plateau in Katanga (=Shaba), is the mean temperature at which 50% of his experimental fishes succumbed and so it is not strictly comparable (see p. 446).

Fujita *et al.* (1966) tested stock of *O. mossambicus* that had been acclimatized to 20°C for 20 days and found that they survived over 12 hours at temperatures between 10°C and 35°C, but quickly collapsed at 5° and 40°. Peak activity occurred at 32°C.

Discrepancies in these reports of upper and lower critical temperatures are probably due to the different degrees of acclimatization and conditioning of the stocks. There is also a salinity-dependent difference in temperature-tolerance. Allanson, Bok & van Wyk (1971) showed that exposure to 11°C, in fresh water, produced in *O. mossambicus* a secondary chill coma associated with decreases in plasma osmolarity, and sodium and chloride ion concentration. The same temperature in sea water diluted to 5‰ NaCl produced none of these symptoms.

Bruton & Taylor (1979) contrasted a mass mortality of this species in a freshwater lake connected with Lake St Lucia, Natal, when the temperature fell to and was sustained at 13°C, with its tolerance of equally low temperatures in brackish water. They noted that the mortality did not involve the young.

The toleration by *O. mossambicus* of wide ranges of temperature and salinity is associated by Perez & Maclean (1976) with the presence in adults of two types of haemoglobin, one of which, developing at the age of 47 days, is less adversely affected in its affinity for oxygen by high temperatures and salinity than the other, which is present throughout life. These authors suggest that 'the presence of a second haemoglobin allows the adult to exploit environments which are both warmer and more saline than can be tolerated by the larvae'. *Oreochromis mossambicus*, however, not only survives as an adult in such conditions, but can also breed in them, and young *Oreochromis* of 2–5 cm commonly live in warmer water than adults. The experiments of Bishai (1965) may be relevant to these considerations (see p. 186).

Salinity tolerance

The coastwise distribution of the species and its presence in the lower reaches only of the southern rivers argue for a high salinity tolerance. One report, that in Bushman's River near Algoa Bay, the southern limit, the species is not found more than a mile from the ebb and flow (Lt Col L. Basil Gardiner, quoted by Harrison, 1947), suggests that it may be only its tolerance of salt water that permits its migration to a lower temperature area than any of its congeners has reached. This opinion is expressed also by Allanson, Bok & van Wyk (1971), as a result of their experiments on its reactions to low temperatures in fresh and salt water (see above).

Fowler (1934) reported the species from Durban Bay in water of high salinity. Farther north, in the lagoons of Kosi Lake and Inharrime, when the tilapia and marine fishes are found together it is rather in brackish or even fresh water than in salt (Tinley, 1964; Day, Millard & Broekhuysen, 1954).

Evidence for the tolerance of water of the concentration of the sea comes from the transported fish. Already in 1949 Myers recorded that this species had been kept in sea water in New York aquarium for seven years. In the London Zoo they so easily settled and bred in water of 35‰ NaCl that they were reared in the marine tanks as forage fish (*The Times*, 12.III.1958). *Oreochromis mossambicus* has been cultivated in brackish water in Java (Schuster, 1949, 1952), Malacca (Hickling, 1950), Taiwan (T. P. Chen, 1953 & 1954), Hawaii (Brock, 1954), Jamaica (Rep. Jamaican etc., 1960), and other West Indian Islands and in Guyana (Allsopp, 1960). It was introduced into the very saline Salton Sea in California, and from there colonized a river fed by a warm mineral spring (St. Amant, 1966). It has been used as live bait for tuna (Brock & Takata, 1955; Shomura, 1964; Jones, 1964).

Brock (1954) reported an experiment in which he reared two halves of a single brood in fresh and salt water respectively. The difference in growth rate was not significant and both batches spawned successfully. Canagartnam (1968) performed a similar experiment in Ceylon (Sri Lanka), obtaining successful spawning in 100% sea-water, with even better growth than in fresh. Hodgkiss & Man (1977) also noted that the slowing of growth of this species in a reservoir in Hong Kong during the course of their study was associated with a decrease in salinity of the water.

The physiological basis of adaptation to fresh and salt water was investigated by Potts *et al.* (1967). They experimented with young of an inbred stock taken from the maternal mouth and reared for five or ten weeks to a weight of 0·5 to 3·0 g. The drinking rate was higher in salt water, but not enough to account for the greater part of the sodium influx, which the authors believed must take place through the gills. In fresh water the permeability of the tissues to water was relatively high, to salts relatively low; in sea water or concentrations higher than sea-water the relative permeabilities were reversed. In terms of adaptation, the high permeability to water in fresh water and the high permeability to salts in strong solutions was unexplained, and the authors' concluded: 'On the other hand there is no doubt that *Tilapia mossambica* is a most successful and prolific fish in a wide variety of external media'.

Experimental studies on chloride regulation were also carried out by Vasantha (1964) on freshwater adapted and salt-water adapted fishes. The salt-water batch swallowed water, but the fresh-water did not. In the salt-water adapted fishes both blood and muscles showed a slight increase in chloride content, but this was negligible compared with the contrast in the medium. An attempt was made to judge the production of urine, and although the quantity was very small it was only in the hypotonic medium that urine was excreted.

Ramamurthi (1965) briefly reports similar results.

Experiments on hypophysectomy (Handlin *et al.*, 1964) seemed to show some connection between the activity of the hypophysis and osmotic control.

Fukusho (1969) compared the salinity tolerance of *O. mossambicus* with that of *O. niloticus* and *Tilapia sparrmanii.* Only *O. mossambicus* had a good survival rate in 100% sea water. He examined the kidney and found it to be typical of freshwater fishes, and contrasting with that of the marine fish *Abudefduf vaigiensis,* in which the nephron has a convoluted distal segment for the resorption of water. He therefore concluded that probably the gills and not the kidneys mediated the adjustment to changed salinity.

Krishnamurthy & Bern (1973) examined the kidney of *O. mossambicus* transferred from fresh to salt water and found changes in the juxtaglomerular cells during the period of adjustment, followed by a period of stabilization.

Drought tolerance

Not only is *O. mossambicus* able to survive extreme reduction of the body of water in which it finds itself during the dry season by precocious breeding (below), but Donnelly (1978) has collated several reports of the survival of this species in a layer of moist sand covered by up to 3 m of sand, the upper 2 m of which was quite dry.

Breeding

In tropical latitudes the only records of breeding periods are for introduced populations in Java, Malacca, Madras and Sri Lanka, where breeding occurs throughout the year.

In the Highveld of the Transvaal, (22°44′ to 25°44′S), breeding starts in the Spring (October) after a winter of inactivity, when the temperature of the water reaches 18°C, and continues until March (du Plessis & Groenewald, 1953). During these months an individual female may produce three broods (du Plessis & Le Roux, 1960).

In the freshwater Lake Sibaya in the coastal plain at 27°25′S, the season is September to February, with peak activity in October to December (Bruton & Allanson, 1974), and there too a female may have more than one brood in a season, as judged from the presence of ripening ova in mouth-brooding fishes and from tagging experiments. Jubb (1967) and Crass (1964) also report a succession of broods in southern Africa.

The size and age of maturity, as in other species, depend on environmental conditions. In shallow ponds in Java, and Malacca and Madras spawning may occur at an age of 2–3 months and a total length of 6–10 cm in the female, 7–13 cm in the male. In brackish water ponds in

Hawaii, spawning occurs at the age of 3½ months and then at intervals of 1½ months (Elliott, 1955). Riedel (1965) reported that in an introduced population in Lake Moyua, a shallow lake in Nicaragua, *O. mossambicus* were mature at an age of 5–6 months and a length of 12–14 cm. In a man-made lake in Sri Lanka 100% of females were mature at 28 cm TL, of males at 30 cm (Da Silva & Chandrasoma, 1980).

In Lake Sibaya the natural population is relatively slowgrowing and the female may spawn at the end of her first year, the male at two years (Bruton & Allanson, 1974). In 1971 and 1972 the smallest female observed with ripe gonads measured 68 mm SL and the smallest found actively breeding 84 mm SL. The corresponding figures for males were 104 and 120 mm SL respectively. The lengths of the breeding population in this lake in 1971–2 ranged, for males from 120 to 210 mm SL, mode 170 mm, for females 80 to 150 mm, rarely up to 180 mm, mode 110 (1971) or 120 (1972). In 1975, however, the summer level of the lake was 1·5 m higher, providing a greater area of a depth suitable for nest-making, and smaller males were able to establish territories. Males of 110 mm SL then comprised about 8% of the breeding population and there was a gradual rise to a mode of 160 mm (Bruton, 1979).

The following sporadic observations from the field and museum collections hint at a variety of population dynamics.

A natural population in Kanjedza Lagoon, a shallow body of water of about 36–38 hectares at about 16°S in the flood plain of the Lower Shiré, was sampled in October 1965. It then included ripe females of 154 mm SL and males in territorial colours (but with small testes) of 178–213 mm. The temperature was not recorded, but in the Lower Shiré it is very high throughout the year. Age and growth-rate are not known in this population.

Among the preserved specimens examined are:

a ripe male from 'Durban' of 57·5 mm SL;

one of C. H. Peters' original specimens of 101 mm SL with the external characters of a breeding male (gonads removed);

another of C. H. Peters' specimens, with ripening ovarian eggs, at 96 mm SL and a third of 108 mm SL with loose ovarian eggs of full size;

the holotype of *Chromis vorax* Pfeffer, a male of 114 mm SL in which the testes have the flabby, tough-walled appearance suggestive of recently spent condition on capture. It was caught in a swamp at Quelimane, Mozambique; and

a mature male and female from Kosi Bay, Zululand, respectively 282 and 273 mm in SL. From the head backwards their lengths are identical, the extra 8·5 mm of the male being accounted for by the produced jaws and snout. It is of course possible that this equality was dictated by the dimensions of the container used by the collector.

Some of these records and observations support the generalization that males grow faster than females, and possibly attain a greater maximum size (see also p. 300).

The differential breeding colours of the sexes have been described on p. 296. The black livery of the male is assumed at the onset of territorial behaviour that begins the breeding cycle. Bruton & Boltt (1975) describe the first sign of breeding activity to be a gathering together in schools composed mainly of males at the surface offshore, and Bruton says (pers. commn) that at this time the black pigmentation is assumed, with the white lower parts of the head and the red fin-margins. The males then swim inshore to the shallow waters of the terraces that characterize the floor of the littoral region of Lake Sibaya. There they establish and defend their territories. Each male excavates a basin-shaped pit. Neil (1966) observed that in ponds in Hawaii a male might sometimes make more than one pit, taking one eventually as his headquarters, and the same was reported by Seitz (1949) in an aquarium study.

Loiselle (1971*b*:4) stressed the essential relation of the black colour pattern with territoriality rather than with breeding. Neil (1964), who recorded this as the livery of ripe males, stated that once assumed it is not readily discarded; but this perhaps applies only to males in possession of territories, because the Baerends (1950:144) stated that males not having a territory 'become black now and then', and a male intruding on the territory of another and accepting defeat quickly loses his dark colour (see also Fryer & Iles, 1972: fig. 225). Moreover, in nature territories appear to be guarded only in daytime. In Lake Sibaya some of the males leave their pits at night for deeper water and 'sleep' in pale colours (Bruton, pers. commn). The males is full livery caught in my presence in Kanjedza Lagoon, Lower Shiré, retained their colours in the net. The body was either totally black or had the lower parts mottled black and white. None of them, however, was fully ripe and several had very narrow white testes. They may therefore be assumed to have been in the early territorial phase. None of them had the broken or worn teeth suggestive of recent engagement in digging or fighting, and in none were the jaws greatly enlarged, although they were longer than in the accompanying females.

The white lower parts of the head have an important function in stimulating the female and synchronizing the spawning activities. They are used by the male in both aggressive and sexual displays (Seitz, 1949; Baerends & Baerends van Roon, 1950). The black, red and white of this striking pattern are said to be the most conspicuous colours to the human eye under water (Dr J. Lythgoe and Dr M. Bruton, pers. commn).

The size of the mating pit is related to the size of the fish. The males observed by Vaas & Hofstede (1952), breeding from a length of 7–13 cm, rarely a little longer, were evidently overcrowded; a photograph shows pits close together, 35 cm in diameter and 6 cm deep in the middle. Lombard (1959) gives the average diameter as 1 ft (30 cm), but does not give the size of his breeding fish. In Lake Sibaya the nests varied from 15 to 140 cm. In 1971–2 all those smaller than 65 cm were in water less than 1·5 m deep and all except three above 70 cm were on the slope between the terrace and the profundal zone, in water from 2·0 to 6·3 m (Bruton & Boltt, 1975, fig. 10). Most of these nests were well separated from each other, those in the macrophyte fringe averaging 1·1 m apart, those on barren substrates 2·1 m. Only three pairs of nests were in contact with each other.

In 1975, with higher lake level, bigger nests were built in areas previously too shallow, and in one such area the biggest nest was 184 cm in diameter, the biggest so far recorded for a cichlid. Bruton estimated that the amount of sand excavated in the two or three days of digging was 0·45 m^3 (Bruton, 1979).

Da Silva & Chandrasoma (1980) also found the average size of nests to increase up to a water depth of 55 cm and to level out in size in deeper water.

The Baerends (1950) used a laboratory tank of about 125 × 35 × 50 cm and found that at first this was only sufficient for the territory of one male, who commanded the whole of the bottom for some time, until at last a second male managed to make a pit in the opposite corner of the tank and hold territory there. The authors realized that in nature other males from the shoal might also be able to establish themselves.

Hickling described and photographed nests with a raised rim pitted with 'finger-marks'. Lombard's photograph (1959, fig. 16) and those of Jubb (1967, fig. 191 A; 1974, fig. 8) of part of a drained dam floor show nests with raised rims, but the irregularities of the inner slopes of the rims do not resemble Hickling's 'finger-marks'. Bruton (pers. commn) also saw no 'finger-marks', although he says that such depressions are often made by feeding activities of fishes in ground occupied by abandoned nests.

A photograph by Schapitz (1958) of a male with open mouth shovelling coarse gravel over the rim of his nest is accompanied by an account of the process which describes him as working horizontally from the centre to the periphery like a bull-dozer, in contrast to the substrate-spawners (*Tilapia* spp.), who stand nearly vertically, head down, for their digging operations. The 'finger-marks' of Hickling look like the results of nose-digging in a pit already made by bull-dozing, and nose-digging is one of the activities described for both male and female during courting (Baerends & Baerends van Roon, 1950). Whether or not such marks are durable may depend on the nature of the soil. In any case they cannot be considered diagnostic of *O. mossambicus*.

When an adult conspecific enters the territory, the male in possession spreads his fins and branchiostegal membrane in lateral display. Subsequent proceedings depend on the intruder's reaction. If it flees it is chased, if it returns the display it is attacked, but if it remains and swims or rests normally the display passes into invitation and leading towards the centre of the nest at the focus of the territory. Sometimes preliminary displays are omitted (Baerends & Baerends van Roon, 1950; Neil, 1966) and the visitor showing the right colour-pattern and behaviour is immediately led to the pit and spawning begins.

Rodman (1966) and Lanzing (1974) report sound production during mating, presumably by grinding the pharyngeal teeth, the swimbladder providing resonance.

The female then lays a batch of eggs in the pit and immediately turns to pick them up. The male swims over the same ground, emitting sperm, and the female snaps at the place where the milt must be, thus effecting fertilization in her mouth. Seitz (1949), the Baerends (1950), Bohrer (1953) and Peters & Heinrich (1967) all independently observed this method of fertilization, and Bohrer saw that the female sometimes sucked sperm directly from the male, afterwards making chewing movements so that all the eggs were bathed in the seminal fluid.

The Baerends (1950) reported that often the male will pick up some of the eggs, but he will swallow them; in only one case did a male retain the eggs for about a day. Vaas & Hofstede (1952) found that males may exceptionally brood eggs. Bruton & Bolt (1975:436) found one male with eggs in the mouth and another carrying young fry, but these were the only exceptions among a large number of brooding fishes. Axelrod & Burgess (1976 and 1977) published a photograph by G. Marcuse of a male accepting young into its mouth, but describe it as exceptional. The fish has the lower parts of the head white, as in breeding males, but the body-markings include two rows of blotches joined by faint grey bars.

Further batches of eggs are laid with the same or another male until all the ripe eggs are shed. Vaas & Hofstede, however, state that the female discharges all the eggs at one spawning and that mature females spawn at intervals of 30 to 40 days. Bohrer gives a similar interval, 4 to 5 weeks, between spawnings in an aquarium. Crass gives 6 or 7 weeks as the length of a spawning cycle, Bruton & Boltt 36 days in Lake Sibaya. The Baerends (p. 142) report that the male seems able to fertilize almost continuously for many consecutive months in aquaria, presumably in constant conditions.

Dadzie (1968) described the structure of the egg and its follicle, and (1969) the testis and spermatogenesis.

The number of eggs produced at a spawning varies with the size of the fish. Figures in Table 79, given by different observers, suggest that if the size of the fish is standardized the fecundity could be expressed in a formula similar to that devised by Payne & Collinson (1983) for *O. aureus* and *O. niloticus*.

Table 79. Numbers of ripe ovarian eggs or numbers produced at a single spawning recorded for *O. mossambicus* of different sizes.

Size of fish	No. of eggs	Locality	Author
80 mm TL	80	Java, ponds	Vaas & Hofstede, 1952
110 mm TL	300	Java, ponds	Vaas & Hofstede, 1952
A range of sizes	50–1000	Transvaal, ponds & dams	Lombard, 1962
365 g	910	Nicaragua, a lake	Riedel, 1965, 1976
120 mm (TL?)	120	Aquarium (laid in 4 batches)	Bohrer, 1953
?	400	Madras	Chako & Krishnamurti, 1954
150 mm SL	650	Hong Kong, reservoir	Hodgkiss & Man, 1978
200 mm SL	1200	Hong Kong, reservoir	Hodgkiss & Man, 1978
250 mm SL	1754	Hong Kong, reservoir	Hodgkiss & Man, 1978
20–31·9 cm TL	360–1775	Sri Lanka, reservoir	Da Silva & Chandrasoma (1980)

Figures for incubated eggs or embryos given by Riedel (1965, 1976) are low, but were taken from gill-netted fishes. Chako & Krishnamurti found one carrying 350 fertilized eggs. Bruton & Boltt (1975) found 11 to 579 eggs in the mouths of four females of 125 to 158 mm SL, and 74 to 226 young carried by seven of 106 to 166 mm SL. The fish with 579 eggs also had 12 young of about 6 mm, a reminder that the fry have an inborn instinct to enter a convenient mouth.

The eggs are pear-shaped, bright yellow or yellowish brown in fresh water, paler in salt water. They have neither filaments nor adhesive layer (Kraft & Peters, 1963; Dadzie, 1968). The long diameter, as given by several authors, ranges from 1·9 to 3·0 mm, almost the whole range being included in the observations of Peters (1963*b*) (1·9–2·9). Other ranges are: 2·0–2·2 (Vaas & Hofstede, 1952), 3 mm (Chako & Krishnamurti, 1954), 1·9–2·6 (Fishelson, 1966), 3 mm (Aravindan & Padmanabhan, 1972), 2·7–3·0 mm (personal observations from loose ovarian eggs in four fishes of 108–273 mm SL).

In three ripe females some of the gill-rakers of the first arch are expanded distally as if for better retention of the eggs (see also Fig. 135).

The eggs hatch after 3 to 5 days (Vaas & Hofstede, 1952; Lombard, 1962) and the fry are released from the maternal mouth at the 10th to 14th day after spawning (Vaas & Hofstede, 1952; Bohrer, 1953; Russock & Schein, 1977). After this they remain near the mother fish until about the 22nd day, entering the mouth for rest or safety.

The reaction of the young to an acceptable model, presented for the first time, begins to dwindle at the 16th day, according to the experiments of Russock & Schein (1977). These periods were a little longer in the experiments of Destexhe & Ruwet (1967), who found that there was an immediate following response to a parental model, if presented for the first time, 22 to 23 days after spawning. The difference is partly due to the fact that Russock & Schein took hatching time as their base-line. These latter authors demonstrated, by artificially rearing the eggs taken from the maternal mouth immediately after fertilization, that the response of the fry is according to an inborn 'schema', both in its nature and its timing, and does not depend on 'imprinting' by the activities of the mother. The interest of the mother and her young in each other comes to an end synchronously.

In the natural population of Lake Sibaya, Bruton & Boltt (1975) confined a number of brooding females in a plastic-lined pool and observed the whole brooding period to last for 20–22 days. Lombard (1959) gives a similar period of 2 to 3 weeks.

Aravindan & Padmanabhan (1972), working on specimens of an introduced population in Kerala, showed that a few eggs of a ripe batch might remain undischarged and become atretic. They were absorbed by the cells of their follicle, which became hypertrophied and increased in number. These authors found that there were oogonia and oocytes at various stages in the germinal endothelium, and considered that these would provide material for at least six successive spawnings.

Figures of developmental stages are given by Vaas & Hofstede (1952) and Chako & Krishnamurti (1954).

Fishelson (1966) included *O. mossambicus* as one of the three mouth-brooding tilapias whose development he compared with that of the substrate-brooder *Tilapia tholloni.* He found that the yolk was absorbed into the abdomen on the 8th to 10th day, according to the size of the egg, in contrast to the 6th day in *T. tholloni*, and in contrast also to *S. melanotheron* in which the corresponding time was 13–15 days for the much larger eggs of that species. The capillaries of the tail and ventral fin-fold are less developed than in the substrate brooders and dwindle at an earlier age, but the vitelline network is more important. This network is ventilated by rapid movements of the pectoral fins from the 5th or 6th day.

Lanzing (1976*a*) also described the respiratory network in the tail.

Hulata & Rothbard (1978) reported 'Siamese twinning' by their ventral surfaces of two pairs of embryos of *O. mossambicus* introduced into ponds at Dor, Israel. They survived for 8 days.

The only field observations on the behaviour of the brooding fish are those of Bruton & Boltt (1975) on Lake Sibaya. Having taken the eggs into their mouths the females retire in a school to well-vegetated slopes and bays at a depth of about 1·5 to 5 m. After 7–8 days the young occasionally leave the parent's mouth, but swim rapidly back again when danger threatens. The female attracts the fry by flapping her pectoral fins, opening her mouth and facing the school. Towards the end of the three weeks brooding period the parent swims to shallow water to release the fry, often in eulittoral pools, where they spend their early life exposed to predation by several species of birds, although relatively safe from piscivorous fishes. No doubt the habit of bringing the young to the shallows has been favoured in the course of evolution because of the latter advantage.

SEX DETERMINATION. Clemens & Inslee (1968) succeeded in changing the sex of presumptive females to functional males by adding methyl testosterone to the food. The treated males mated with normal females. Seven of these males sired broods consisting of females only, and the authors interpreted this as the result of genetic sex-determination with the female the homogametic sex. This is in agreement with postulated genetic explanations of the results of hybridization of *O. mossambicus* with *O. u. hornorum* (see below). Nakamura & Takahashi (1973) investigated gonadal differentiation with a view to determining the time of effective hormone treatment.

Hybrids

1. *Oreochromis mossambicus* has been hybridized with *O. u. hornorum*, first at the former Fish Culture Research Station at Malacca, where *O. u. hornorum* then went under the name of 'the Tilapia from Zanzibar' or 'the African Tilapia' (Hickling, 1959, 1960, 1962; Chen, 1966*a*). When the male parent was *O. u. hornorum* the F_1 generation was 100% male, when the male parent was *O. mossambicus* both sexes were present in the F_1 in the proportion 75% ♂, 25% ♀. The F_1 individuals of both crosses were fertile and bred freely with the opposite sex of both parent species with a 1 : 1 sex ratio.

The offspring of the cross in which *O. mossambicus* was the male parent were few and this cross evidently has limited viability, but the all-male broods comprised normal numbers, so differential survival was excluded as an explanation and a genetical explanation was sought.

Experimental crosses were made by Chen (1967; see also Fryer & Iles, 1972:170), who postulated that in *O. u. hornorum* the homogametic sex is the male, in *O. mossambicus* the female, and that the male-determining genes of *O. u. hornorum* are dominant over the female-determining ones of *O. mossambicus*. Chen's theory required four different sex chromosomes, which he named X and Y in *O. mossambicus*, W and Z in *O. u. hornorum*.

An alternative theory put forward by Avtalion & Hammerman (1979) agreed with Chen's in identifying the respective homogametic sexes, but showed that there might be only three kinds of sex-chromosomes, the Z of Chen's theory being no different from the Y. A decisive influence, according to this theory, would be wielded by a pair of autosomes, AA for *O. mossambicus* and aa for *O. u. hornorum*. The authors showed that this would account for the sex-ratios in all the crosses obtained by Chen.

These and other all-male hybrids are valuable to fish culturists because of their better growth, and the possibility of segregating the all-male broods and so avoiding the checks to growth consequent on breeding.

Six F_1 hybrids of each cross are preserved in the BMNH. These are all males, 132–152 mm SL, and like both parent species the darkest specimens have largest testes, have the jaws hypertrophied and some of the outer teeth unicuspid. In the paler specimens the lower jaw measures 32·6–39·6% length of head, in the darker ones 42–45·5%. The lower pharyngeal bone has a dentigerous area with broader lobes than in the Lower Shiré *O. mossambicus*, but matches fairly well those from Inharrime in Mozambique or specimens of *O. urolepis hornorum* of comparable size. Some had had the dorsal fin cut when alive for purposes of identification, so fin-ray counts are reliable only for nine. Meristic comparisons are as follows

	O. mossambicus (wild)	Hybrids	*O. urolepis hornorum*
Total dorsal rays			
No. of specimens	60	9	54
Range	26–29	28–29	28–30
Mode	28	28=29	29
Gill-rakers			
No. of specimens	62	12	20
Range	14–20	18–21	19–23
Mode	17=18	19	20

The overlap of ranges is more here than in the findings reported by Chen (1966*a*), but in both cases the hybrids are intermediate between the two parent species, and intermediacy is also reported for the male coloration (Hickling, 1959).

2. Iversen (1968) reported hybridization of *O. mossambicus* with *O. niloticus*. The morphology of the hybrids was not described, but their temperature tolerance was said to be intermediate between those of the parent species; growth-rate and survival rate were said to be better, and food conversion more efficient than in the parent samples.

3. In the school of H. M. Peters at the University of Tübingen crosses were obtained by artificial fertilization between *O. mossambicus* (origin unknown) and three other species, namely *Sarotherodon melanotheron* (aquarium stock from Aronson), *Tilapia zillii* (from Israel) and *T. tholloni* (origin unknown). Eggs of *O. mossambicus* with sperm of *S. melanotheron* gave no results, but the reverse cross produced females only (Bauer, 1968). Hybrids of *O. mossambicus* ♀ *and T. tholloni* ♂ showed high mortality among the embryos; in the reverse cross only females were obtained by Bauer, but a few males also by Heinrich (1967). Eggs of *T. zillii* fertilized by *O. mossambicus* sperm gave good results (the reverse cross was not tried), (Bauer, 1968), and some of the offspring obtained were sent to Dr Whitehead at the BMNH. I examined two of these when they died at standard lengths of 105 and 109 mm respectively. There was sufficient intermediacy to support the supposition that male chromatin was involved. Both had D XVI 11. The numbers of gill-rakers, 3+2+11 and 4+1+10 were intermediate. The blade of the lower pharyngeal bone was intermediate in length; in one the dentigerous area was almost devoid of teeth except those of the two posterior rows, which were slender and bicuspid, with brown crowns. In this fish the teeth of the jaws were very poorly developed and buried in the gums, and the fish was probably suffering from a dietary deficiency. In the other, the pharyngeal was well toothed, teeth of the posterior row being tricuspid as in *T. zilli*. One had a female urinogenital papilla and a flabby gonad, the other a very small papilla and undeveloped gonads.

Hybrids between the two genera have never been obtained in nature, nor in aquaria except by artificial fertilization.* The object of the Tübingen experimenters was to test the heritability of the behaviour patterns of the young.

General physiology, structure and behaviour

The ease with which this species can be kept in captivity has resulted in its being used for general physiological studies. The effects of hypophysectomy have been examined by Handlin *et al.* (1964); protein chemistry by Nandi & Bern (1963); the neurosecretory system by Nayar & Menon (1960) and Takasugi & Bern (1962); and Nagase (1964) has studied the location and activity of the digestive enzymes. Sivadas (1964) has described the islets of Langerhans.

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*Ibrahim (1976:136) claims that hybrids have been obtained between *T. zillii* and *O. andersonii* with an F_1 of 100% males, but the evidence for this, then said to be 'in the press' has not yet (to my knowledge) been published. The reference given was 'Ibrahim & Lema, 1974. *E. Afr. J. trop. Hydrobiol. Fish.*' but the latest number of this journal to appear (vol. 4 no. 1) does not contain it.

Lanzing & Higginbotham have given electron scanning microscopic pictures of the scales (1974) and teeth (1976); Lanzing & Wright described the ultrastructure of skin (1974) and scales (1976); and Lanzing (1976*b*) the fine structure of the fins.

Cheney (1968) found that the volume of red cells in the blood was negatively allometric with the weight of the fish.

Russock & Schein (1978) demonstrated that recognition of conspecifics was independent of experience.

Predators and parasites

Allsopp (1960) has touched on this aspect of the ecology of *O. mossambicus* in brackish ponds in Guyana. Here it was preyed upon by marine and brackish species of *Centropomus*, *Cynoscion*, *Promicrops* and *Tarpon*, to the benefit of the growth of the survivors. In the months when salinity was highest it was heavily attacked by argulids, but these parasites disappeared when the salinity was reduced to 12 parts per thousand. in Lake Moyua, Nicaragua, Riedel (1965) reported that the fry are subject to heavy predation by two birds, *Podiceps dominicus* and *Podilymbus podiceps*, and regarded it as a useful check on population density in this shallow lake.

Bruton & Boltt (1975) have examined the extent to which *O. mossambicus* is preyed upon in Lake Sibaya by *Clarias gariepinus*, and a number of species of birds. It is particularly vulnerable when the adults move into the shallows for breeding purposes and when the fry are using the nursery grounds. Fry are not safe from avian predators even when in the maternal mouth, for these authors report (p. 437) that some species, including *Larus cirrocephalus* Vieillot, will remove the opercula and consume the brood.

The same authors found that *Clarias gariepinus* fed heavily on the three cichlid species of Lake Sibaya, mainly on juveniles, but also on adult *O. mossambicus* up to 150 mm SL. They considered that the movement of *O. mossambicus* away from the terraces at night may have been, at least in part, a response to the reverse movement of the *Clarias*.

Distribution

NATURAL DISTRIBUTION AND HABITAT. The type localities are given (Peters, 1852) as 'Tette, Sena, Quellimane, Lumbo, Inhambane, Querimba', thus embracing the Lower Zambezi up to Tete and the coastal parts of Mozambique from Quelimane, just north of the Zambezi delta, southwards nearly to the Limpopo. Of the Zambezi tributaries it is known in the Lower Shiré and the Mazoe. In 1868 Peters gave an extended range of all standing waters and rivers from 11 to 26°S, thus from the Rovuma to the Limpopo, near the coast and as far as 220 km inland. But Peters had some specimens with IV anal spines and XVII dorsal (Peters & Müller, 1844; Peters, 1868), which were no doubt *O. placidus*, and there is no firm record of *O. mossambicus* as a native fish north of Quelimane.

Gaigher (1973), who surveyed the fishes of the Limpopo system, placed *O. mossambicus* in his Group C, 'Pool-loving species confined to the warmer Middle- and Low-Veld streams'.

Jubb (1967) and Whitfield & Blaber (1976) give the Pongola River (about 27°S 31°E) as the southern limit of the distribution in fresh water, but its wide salinity tolerance allows it to extend in estuaries farther south (see p. 303), as is confirmed by many records and examples. This kind of distribution extends as far south as Bushman's (Boesmans) River, just north of Algoa Bay (Harrison, 1947). Mr W. W. Roberts reports (pers. commn) that from the Umtavina River, on the Natal–Cape Province border, southward to Algoa Bay the species is present in the lower reaches of the rivers, but not above the first formidable obstacle. Liversidge (*in* Farquarson, 1962) states that 'during floods in the eastern Cape, fresh water from the Sundays River flowed along the coast to well beyond Bushmans River mouth'. It is thus conceivable that fish might get from one to the other with only a small degree of salt tolerance. We know that the tolerance of *O. mossambicus* is ample for these conditions (see p. 303).

Whitfield & Blaber (1979) find that it is only in closed estuaries and coastal lakes that this southern distribution is represented. Several factors affect it. The fish avoid strong currents and in such conditions will remain in vegetation near the banks. Suitable breeding sites and marginal vegetation for the shelter of the young are required, and although considerable salinity is tolerated, rapid changes are not. In such favourable coastal waters if marine piscivorous fishes are absent *O. mossambicus* may be common.

In the fresh waters of the rivers Pongola and Mkuzi in Zululand well grown specimens are caught in flowing water (Bruton, pers. commn), so it seems that rivers may provide a very favourable environment if breeding sites and sheltered nursery grounds are at hand.

In the Lower Shiré, and as far south as the Save and Sodwana, *O. mossambicus* coexists with *O. placidus* (Jubb, 1967; samples provided by Dr M. Bruton), and as far south as the northern part of Natal with *Tilapia rendalli.* Crass (1959) reports that, as might be expected, the balance between this species and *T. rendalli* depends on the nature of the biotope. In clear water with coarse vegetation *T. rendalli* prevails, but where the microflora makes the water turbid and marginal vegetation is less, *O. mossambicus* is the more abundant.

Records from the Middle Zambezi and its tributaries, notably the Luangwa River, refer usually to *O. mortimeri,* but these have been greatly complicated by stocking from areas where *O. mossambicus* is native, or from ponds and dams originally stocked with *O. mossambicus.* Many of these movements have been traced and recorded by Jubb (1974).

Records from Tanzania and Kenya refer to other species. The specimens listed by Boulenger (1915, nos 1 & 2, & fig. 101) as from 'Zanzibar Coast' were from Mozambique, whither Sir John Kirk journeyed to make collections (see *Proc. zool. Soc. Lond.* 1867:953). Those listed from 'Lakeside, Cape Peninsula' by Gilchrist & Thompson (1917:487) were not from Cape Province (Jubb, *in litt.*). 'Lakeside' was the name of the residence of the donor.

DISPERSAL BY MAN. It is probable that *O. mossambicus* first reached Java as an aquarium fish. In 1939 Pak Mudjair, a member of the fisheries staff in that island, recognized its value as a pond fish and it soon became established in freshwater and brackish ponds in Java (Schuster, 1949). Vaas & Hofstede, research officers in the Freshwater Fisheries Department of Java, published in 1952 the first study of the bionomics of the species. During the war of 1939–1945 it was transported by the Japanese to other Indonesian islands and to the Malay Peninsula, Celebes (Suluwesi) and Taiwan. From the Fish Culture Research Institute in Malacca it was later distributed directly or indirectly to almost all tropical and subtropical countries of the world. The story of its subsequent spread has been summarized by Atz (1954, 1957), Chimitz (1956, 1957), Hickling (1963) and Hubbs (1968). The dangers and advantages of introduction have been discussed by Capon (1963) and Prowse (1963*a* & *b*). It has now become feral in California (St Amant, 1966) and Texas (W. H. Brown, 1961). The BMNH recently received specimens from the Gilbert and Ellice Islands (Kiribati) and others that had been caught swimming with reef fishes in Fanning Atoll, Sandwich Islands (see Lobel, 1980). It has been used in fresh and brackish ponds in Guyana, thriving better in the latter (Allsopp, 1960). Berra *et al.* (1975) and Glucksman (1976) give an account of its introduction (in 1954) and spread in Papua New Guinea and on Bougainville Island. To judge from the few data on gill-raker numbers there may have been an admixture of *O. u. hornorum* in the original consignment to New Guinea from Malacca. Differences in the intensity of male coloration were found between the populations of two bodies of water of different qualities.

Jubb & Petrick (1970) described a sample (from a captive population) sent to them from Australia by W. J. B. Lanzing. Although its import to Australia is now forbidden (Lanzing, pers. commn and letter of June, 1980 from Dr Burke Hill of the Queensland Fisheries Service to R. S. V. Pullin), it is present there in more than one pond or dam.

Specimens examined by me from Java, Malaya, Singapore, California, and the Gilbert and Ellice Islands (Kiribati) agree well with those from its natural habitat in proportions and meristic characters. Samples from the Botanic Gardens, Singapore received in 1960 and 1966, however, show a subtle difference in the pharyngeal dentition. The teeth lack the brown colour of the

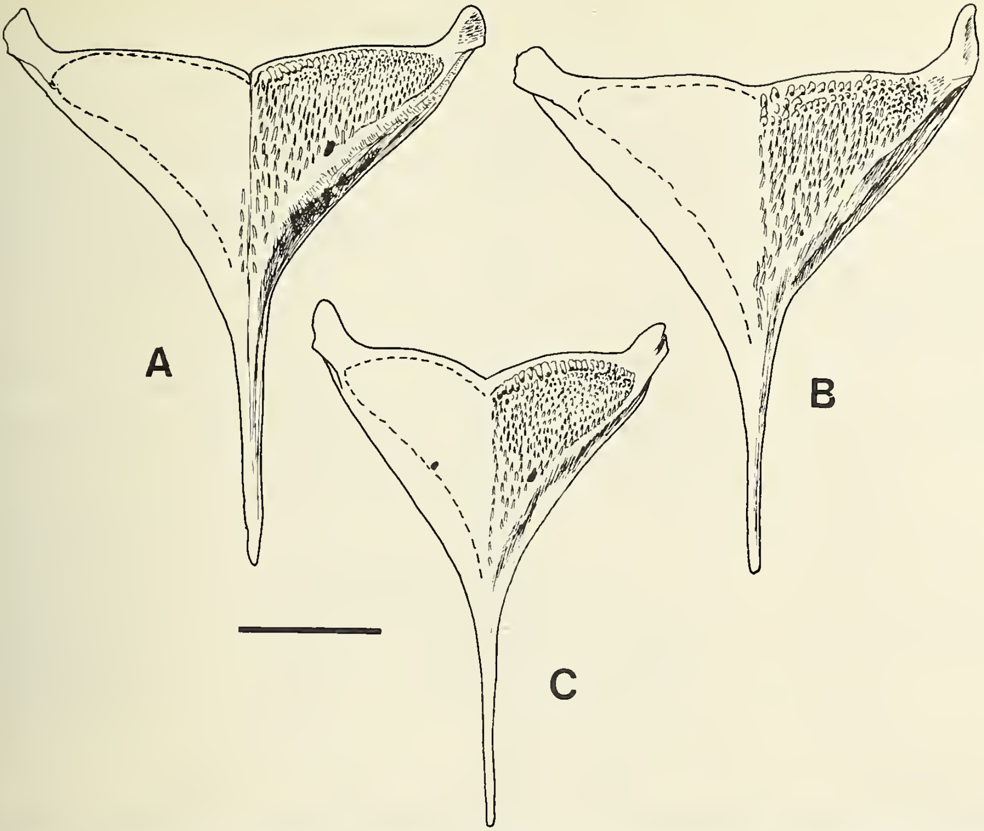

Fig. 103 Variation in the pharyngeal dentition of *Oreochromis mossambicus*. Lower pharyngeal of fishes: A, 174 mm SL from Port Herald, Lower Shiré; B, 155 mm SL from Inharrime, Mozambique; C, 128 mm SL from an introduced strain in the Botanic Gardens, Singapore. Scale = 5 mm.

crowns, which suggests that the water may be poor in available iron, but there is also a difference in the shape of the dentigerous area, its lateral lobes being broader and the sides less concave than in other populations (Fig. 103). In African populations the pharyngeal is rather uniform, with the exception of the coarser-toothed bones of samples from Inharrime (Fig. 103).

Mironova (1965–1976) has published a series of studies on the growth and energy conversion of *O. mossambicus* in ponds and aquaria in U.S.S.R. Population studies have been made on a stocked lake in Nicaragua (Riedel, 1965, 1976), and a reservoir in Hong Kong (Man & Hodgkiss, 1977*a* & *b*; Hodgkiss & Man, 1977, 1978), and behavioural studies in ponds in Hawaii (Neil, 1966).

O. mossambicus has been moved from its native waters also within Africa. Such movements in South Africa and Zimbabwe (formerly Rhodesia) (see Jubb, 1974) have brought it into the drainage systems occupied naturally by *O. mortimeri*, increasing the difficulty of distinguishing between these two very similar species.

Some specimens sent by Dr de Barres Machado were the first indication that *O. mossambicus* was being used in fishponds in Angola. Dr Machado informs me that it has been officially introduced from Mozambique to Malanje and Cela in Angola. In Mozambique, where it is native, it is cultivated in fish ponds with *Tilapia rendalli* (Costa, 1960).

O. mossambicus is used as a laboratory animal for experiments in physiology and behaviour, and Arrignon (1969) has given an account of its rearing and maintenance for such purposes.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1861.5.2.58–59	101 & 120 syntypes	Zambezi	W. C. H. Peters (Berlin Museum)
1861.5.2.60–64	77–106	Zambezi	W. C. H. Peters (Berlin Museum)
1868.2.29.14–16	113–128	'Mozambique'[1]	Kirk
ZMH 399 holotype of *C. vorax*	114	Swamp nr Quelimane. Mozambique	Stuhlmann
ZMH 400	74·5 (as *T. vorax*)	Quelimane, Mozambique	Stuhlmann
1966.7.28.16–20	142–192	Port Herald, Lower Shiré	R. H. Lowe, 131.ix.46
1966.7.26.1–14	107–213	Kanjedza Lagoon, Lower Shiré, ca 3 miles ESE of Chikwawa at 16°2½'S, 34°50½'E, ca 300 ft a.m.s.l.	Malawi Fisheries Res. Unit (D. Eccles & R. Kirk) & E. Trewavas 1.xi.65
1966.7.26.15–16	66, 70	Kanjedza Lagoon, Lower Shiré, ca 3 miles ESE of Chikwawa at 16°2½'S, 34°50½'E, ca 300 ft a.m.s.l.	Malawi Fisheries Res. Unit (D. Eccles & R. Kirk) & E. Trewavas 1.xi.65
1966.7.26.63–68	41·5–47·5	Pool in bed of Lower Shiré at Chikwawa[2]	Malawi Fisheries Res. Unit (D. Eccles & R. Kirk) & E. Trewavas 1.xi.65
AMNH 14110	181	Beira	—
1907.4.29.143	87	Beira ('lake in swamp')	Grant
1966.6.8.1–5	108–171	Inharrime, ca 300 km N of Lourenco Marques at neck of Lagosa Poelala[3]	Cape Town University Biol. Expedition to Portuguese E. Africa, Jan.–July, 1954
1907.3.15.42	97	Inkomati R., nr Komati Poort, Transvaal	Bruce
1906.11.19.89–90	280, 275	Koso Bay, Zululand	Warren
1906.11.19.9	47	Indukuduku, Zululand	Warren
1905.3.7.195–197	80, 207, 217	Umfulosi Station, Zululand	Grant
1906.11.19.91	47	Inkusi R., Natal	Warren
1911.3.6.1	175	Crocodile R., Transvaal	Methuen
1911.3.6.2	217	Middle Letaba R., Transvaal	Methuen
1907.4.9.81	92	Klein Letaba R., Transvaal	Grant
1907.5.30.1	126	Dewaars R., Transvaal	Gilchrist
1904.6.28.35	85	nr. Durban	Queckett
1894.7.10.15–24	36–86[4]	nr. Durban	Bowker
1862.8.28.23–24	127–127	nr. Durban (Port Natal)	Ayres
(unreg.; 3 fishes)	95–102	nr. Durban (Port Natal)	Ayres
1863.12.15.40–41	80, 87	nr. Durban (Port Natal)	Ayres
1863.12.19.6	210	nr. Durban (Port Natal)	Ayres
NHMW 32599	56·5 (paratype of *C. natalensis*)	R. Illova, Natal (1904)	Max Weber
1915.6.28.20	175	Winkel Spruit, Natal	Durban Museum
1904.8.17.13–18	47–140	nr. Durban	Abraham
1906.6.2.3–11	60–119	nr. Durban	Abraham
1900.11.6.56–57	31, 68	Buffalo R., nr East London, S. Africa	Gilchrist

Museum & Reg No.	SL (mm)	Locality	Collector or donor
1907.5.30.2	178	Kanoogha R., nr East London, S. Africa	Gilchrist
1977.6.27.1451–1596	26–76	Pongola R., Natal	H. Kok, Natal University
1951.8.27.30–32	88–130	Tanganda R., trib. of Sabi R.	R. Jubb
Introduced and aquarium specimens examined			
1947.4.11.1–6	39–40, 140, 169	Singapore	Tweedie
1948.12.20.1–2	248[5]	Malaya	Le Mare (Chief Fisheries Officer)
1969.7.17.39–83	40–127	Botanic Gdns, Singapore	National Museum, Singapore
1949.5.23.1–7	87–144	Java	Hardenberg
1956.4.6.7–8	107, 117	Chilanga ponds, Zambia (introduced)	Hickling
1956.4.6.5–18	104–136	Mazoe dam (introduced?)	Hickling
1966.9.7.1–4	27–140	East shore of Salton Sea, California, at a hot mineral-water spa	St Amant[6] 15.i.1964
1966.7.14.84–5	114, 117[7]	Taiwan	S. W. Ling
1968.10.10.1–4	16–33[8]	Bonin Is. 27°N 144°E, Yatsusegawa R.	K. Fujita
1966.10.12.1–2	65, 75	Aquarium specimens (ref.)[9]	Rixner, Univ. Mainz
1966.6.7.1–2	66, 68	Aquarium specimens (ref.)	Setterington (Toronto)
1969.3.6.62–3	59, 90	Aquarium specimens (ref.)	New
1968.4.18.1	87·5	Aquarium specimens (ref.)	Cichocki
1973.11.13.33–6	90–136	Aquarium specimens (ref.)	Whiting
1968.12.2.1–3[10]	47·5–78·5	Ugab R., Namibia 13°30′E 12°10′S (intro.?)	coll. Dixon pres. Jubb
1968.12.2.4[10]	84·5	Kuiseb R., Namibia (intro.?): no. 1025	coll. Dixon pres. Jubb

[1] Formerly attributed to Zanzibar, but the fishes Kirk sent at this time were from Mozambique. See *Proc. zool. Soc. Lond.* 1867, pp. 952–3.

[2] Caught with *O. placidus* of same size.

[3] Caught with *T. rendalli.*

[4] One of SL 57·5 mm is ♂ rp., 85 mm is ♀ rpg., rest immature.

[5] Mature male, 8 months old.

[6] see *Calif. Fish Game* **52:** 54–55 (1966).

[7] Colour variety.

[8] Intro. probably by U.S. Navy.

[9] ref. = reference specimens for aquarium studies by donors.

[10] Identity doubtful.

Subgenus *OREOCHROMIS* – VI

Oreochromis mortimeri
Oreochromis andersonii

Oreochromis mortimeri (Trewavas)

Tilapia mossambica (part, *non* Peters); Trewavas, 1937:383 (Luangwa specimens); Jubb, 1953:697 (part); Mortimer, 1962*a*:185–195 (Luangwa R.); Jubb, 1961:131, pl. 78 (Middle Zambezi system only); Jackson, 1961*a*:26; 1961*b*:100 (Luangwa & Middle Zambezi); Munro, 1967:407 (Lake McIlwaine, Hunyani system); Donnelly, 1969:195 ff. (Lake Kariba); Jubb, 1967:162, fig. 190 & pl. 36 (teste letter of 15.ix.1973) (Ngezi dam, Umniati R.).

Tilapia mossambica, *T. natalensis* and the Lower Luangwa specimens identified as *T. kafuensis*; Pitman, 1934 (Luangwa R.).

Tilapia mortimeri Trewavas 1966*c*:413; Matthes, 1969:47 (food); Jubb, 1974:3, figs 1, 2 (Ngezi dam, Umniati R.).

Sarotherodon mortimeri; Bell-Cross, 1976:217, fig. on p. 218.

Sarotherodon mossambicus mortimeri; Balon, 1974*a*:43–45, figs; Balon & Coche, 1974:573 and elsewhere in this work; Krupka, 1974:343 (population dynamics).

TYPES. Holotype: BMNH 1932.12.16.878, a male of SL 212 mm, from Chiwande, Luangwa Valley, about 412 m above sea level, collected by C. R. S. Pitman.

Paratypes: BMNH 1932.12.16.866–877 and 879–888, twenty-two specimens of SL 70–200 mm, with the same data as the holotype.

Distinguishing characters

Resembling *O. mossambicus* in proportions and meristic characters, except that the caudal peduncle is relatively shorter. The colours of the breeding male are predominantly iridescent blue-green to bronze, with iridescent spots on dorsal and caudal fins, in contrast to the deep black body with contrasting white throat of male *O. massambicus*. In both species the margins of dorsal and caudal fins are red.

As in *O. mossambicus* the jaws are greatly produced in mature males. (See Balon, 1974*a*, figs on pp 43 & 44).

Description

Based on 24 specimens of 103–273 mm SL, including the holotype; 14 other fishes collected by Pitman in the Luangwa Valley; 5 collected in the Luangwa Valley by Colin Tait and myself; and 4 in the Zambian Fisheries collection collected by M. A. E. Mortimer, of which 2 are from Feira at the Luangwa-Zambezi confluence and 2 from Kariba reach of the Zambezi before the building of the dam. Meristic data are taken also from additional specimens of the same collections.

Proportions as % SL. Depth of body 39–46 (51·5 in one ♂ of 235·0 mm SL). Length of head 34–39, with no apparent allometric trend at these sizes. Length of pectoral fin 35·4–42·6. Length of caudal peduncle 8·8–12·4, 0·5–0·8 times its own depth.

Proportions as % length of head. Length of snout 33–43; below SL 130 mm none more than 36·8 (mean of 11 = 34·6), above 130 mm none less than 36·8 (mean of 13 = 39·1). Upper profile concave in large breeding individuals. Diameter of eye negatively allometric, depth of preorbital positively, the two approximately equal at 117–125 mm SL.

At 103–112 mm eye 24·2–22·0, preorbital 18·9–21·6

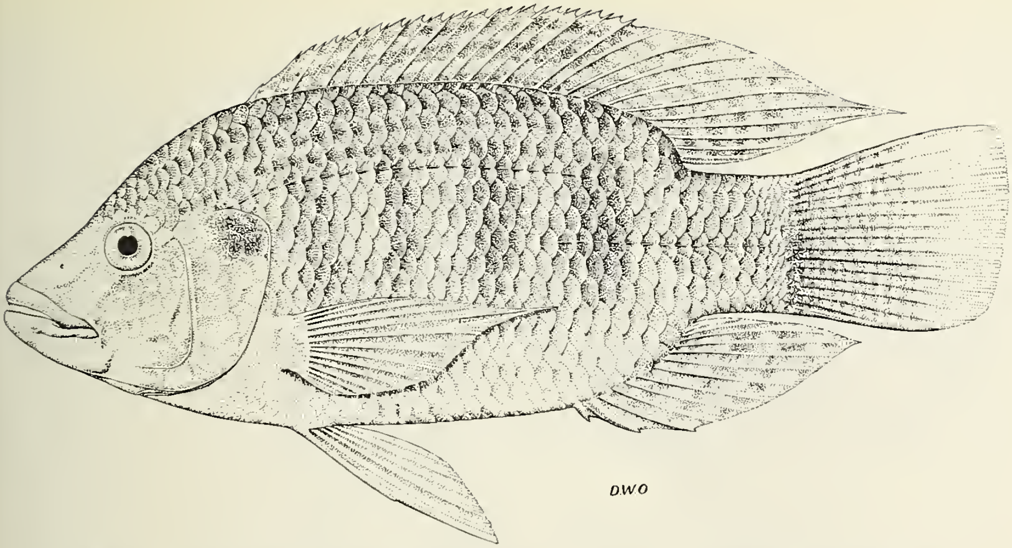

Fig. 104 *Oreochromis mortimeri* holotype, male, 212 mm SL, Chiwande, Luangwa River.

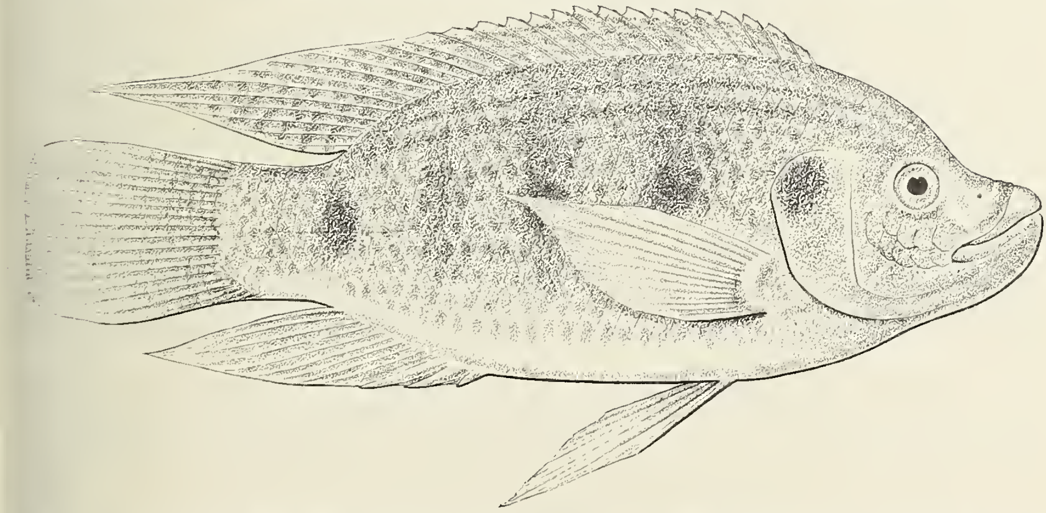

Fig. 105 *Oreochromis mortimeri,* male, 172 mm SL, from a pool near Mfuwe Lagoon, Luangwa River.

At 117–200 mm eye 21·6–18·0, preorbital 20·4–23·2 (25·4)
At 210–273 mm eye 19·1–15·8, preorbital 23·1–23·9

Interorbital width 32·0–39·0; all values over 36·6 are in fishes of 200 mm SL or over. Length of lower jaw in ♀ 32·8–38·5, in ♂ 39·0–44·0 (46) at 124 mm SL or over, 31·8–41·5 below this length.

Maxillary ending between nostril and eye.

Teeth in 3–5 series; in most specimens outer bicuspid (except a few small posterior in upper jaw) and inner tricuspid, but in ripening to spent males over 135 mm SL some outer are simple and some have a reduced minor cusp.

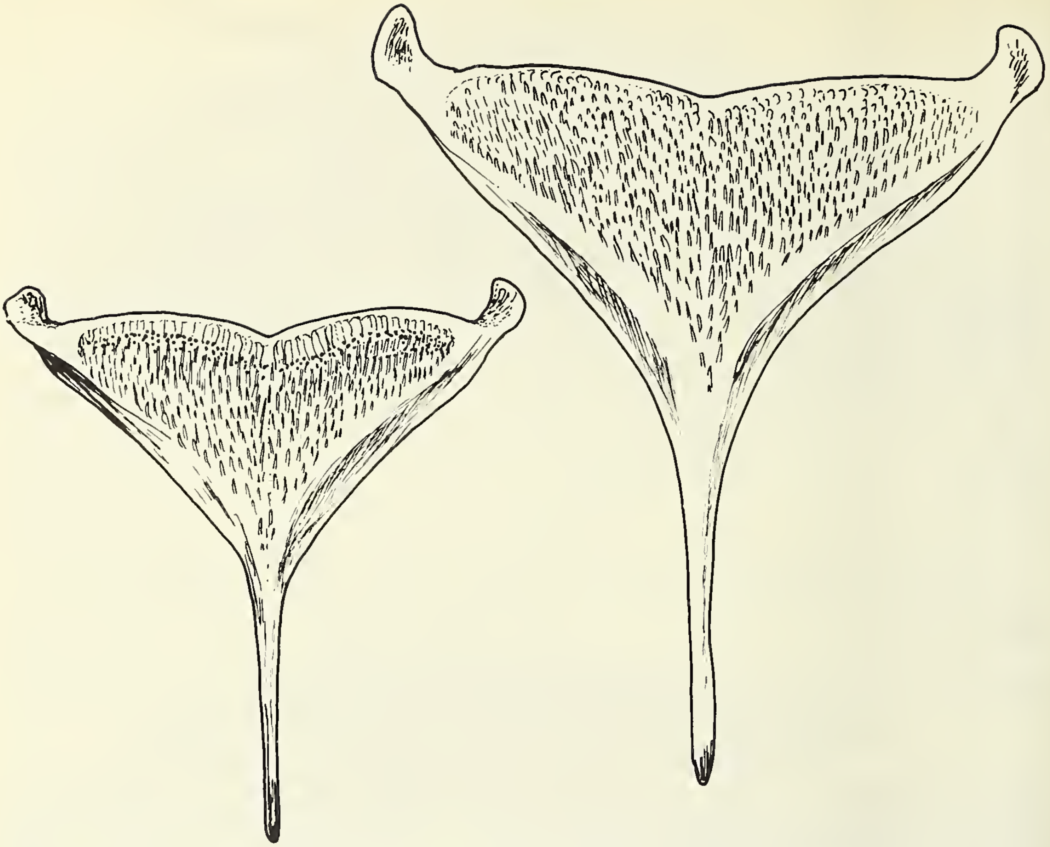

Fig. 106 Pharyngeal bone from *O. mortimeri*: left, a fish of 110 mm SL; right, one of 200 mm SL.

Gill-rakers on lower part of anterior arch 16–20, mode 18, mean (of 51 specimens) 18·2. (The specimens seen by me have no bridge between upper and lower rakers as described by Jubb (1974).)

Lower pharyngeal bone narrow, its width 30–31% length of head (5 measured); teeth fine; sides of dentigerous area concave, its lobes a little rounder than in most *O. mossambicus* or *O. andersonii*; blade in adult 1·0–1·5 times the median length of the dentigerous area (Fig. 106).

Scales in 2–3 rows on cheek; 30–32 in lateral line series, mode 31; 3½–4 from origin of dorsal to lateral line, 4–6 between bases of pectoral and pelvic fins.

Dorsal formulae	XVII 10	XVI 12	XVII 11	XVI 13	XVII 12	XVII 13
Frequencies	1	19	12	11	21	6

Total dorsal rays	27	28	29	30	
Frequencies	1	31	32	6	Mean (of 70) 28·61).

Anal III 10–12, mode III 11.

Caudal truncate, occasionally with lower or both corners rounded; not heavily scaled.

Vertebrae 29 (f. 5) or 30 (f. 14).

Size. Jubb (1967:239) gives a maximum recorded weight for '*T. m. mossambica*' of Lake McIlwaine of 6lb 2½ oz (about 2·7 kg); this may have been *O. mortimeri*. Bell-Cross (1976:218) gives 3·2 kg for Lake Kariba. The largest fish recorded by Krupka (1974:345) was 390 mm SL and 2·9 kg; this fish was estimated to be 8 years old, an age rarely attained. See also Balon, 1974*a*.

Coloration. In life greenish grey or grey-blue with a darker spot on each scale, usually white on ventral surface; lower part of cheek and operculum bluish. Females and sexually immature males often with one to three dark mid-lateral blotches, which may appear only as the fish dies. Dorsal with orange-red upper edge, broader in male than in female. Caudal with crimson margin and usually with a grey reticulum on proximal two-thirds with pale or iridescent interstices. Well-coloured fishes with rows of green iridescent spots on dorsal fin and sometimes with a group of shining white spots on posterior rays of dorsal and anal. A small specimen in aquarium at the Kariba research station had a gold spot above and below the black opercular spot

Breeding males have a predominantly light blue colour, darker above and on the head, with much iridescence. Mr B. G. Donnelly found that some of the large males in Lake Kariba became black, but in these the gular region and lower gill-cover became dark green or blackish, not white as in *O. mossambicus* (Donnelly, quoted by Jubb, 1974:3). Bell-Cross (1976) also records occasional black specimens with a black throat. Munro (pers. commn about 1970) who had just finished his study of the fishes of Lake McIlwaine, said that the '*T. mossambica*' there had no black males and were the indigenous species. But the possibility of subsequent stocking in the Hunyani basin from the Mazoe (Jubb, 1974) cannot be ruled out and both species, or hybrids between them, may be present in Lake Kariba.

A sample from Kariba. Details of 20 specimens collected in the Kariba gorge in 1959, before the building of the dam, were recorded by Mr M. A. E. Mortimer (unpublished).

They extend the range of the dorsal fin-ray numbers by including three with only XV spines; and they include none with a total of 30 rays. The totals are: 26 (f. 1), 27 (f. 4), 28 (f. 8), 29 (f. 7), mean 28·05. This mean is about midway between that of the (mainly) Luangwa sample described above and that of those on which the description of *O. mossambicus* (p. 291) is based. The gill-raker count is 18–20, and the caudal peduncle is short and deep as in *O. mortimeri*, its length 10–12% SL and 0·53–0·72 of its own depth. Mr Mortimer saw no black males in this subpopulation and there seems no doubt that *O. mortimeri* and not *O. mossambicus* inhabited the Middle Zambezi before the dam was built and is still the dominant *Oreochromis* of Lake kariba.

Pond specimens. Both *O. mortimeri* (ex Kariba) and *O. mossambicus* (ex Natal) were living in ponds at Chilanga (Zambia) in 1965, when I examined some. They maintained the difference in the caudal peduncle, that of *O. mossambicus* being as long as deep or a little longer, of *O. mortimeri* having its length 0·6–0·7 of its depth. None of these was in breeding colour.

Ecology

Food

Munro (1967) has described the food of this species (under the name *Tilapia mossambica*, see above under 'Coloration') in the man-made lake McIlwaine, on the Hunyani River, a southern tributary of Lake Kariba.

In the stomachs of juveniles diatoms predominated. In adults plant food accounted for 83% by volume, of which 52% consisted of filamentous algae and diatoms and 31% of fragments of higher plants, including *Lagerosiphon major*. Dipterous larvae, mainly chronomids, made up 5·2% and Cladocera and copepods 11·7%. Most of this food could be obtained by scraping the algal film of under-water surfaces, especially of vascular plants, but the Cladocera and copepods speak for some plankton-feeding.

The collections were made from September to November and no data are available for the rest of the year.

Matthes analysed the stomach contents of fry, juveniles and adults in Lake Kariba, and also found that adults feed mainly on algae gathered from a substrate. Any fragments of higher plants were such as might be incidently ingested. Below a length of 7 cm the young were more omnivorous, their stomachs including small invertebrates, even insect larvae, as well as algae. Phytoplankton was the main component only in very young fry released from the maternal mouth in relatively deep water and making their way in small shoals to the littoral zone.

Breeding

Mortimer (1962*a*) reports that this species breeds several times in a season, even when transplanted to the plateau, where the indigenous species, *O. andersonii*, breeds once or rarely twice.

Field observations giving information on breeding are meagre. They were made during a few days' collecting near Mfuwe Camp, in the South Luangwa Game Reserve, by Colin Tait and myself in the dry season at mid-September, 1965. The Luangwa River there runs in a low rift valley below the 2000 ft (610 m) contour in mopani forest. At this season it meanders, brown and narrow, between sand-banks and its bed is bounded by abrupt sandy cliffs. Its smaller tributaries are represented by dry beds of coarse gravel, and the pools and lagoons in its flood-plain have shrunk, and are surrounded by zones of dried mud pitted by the feet of hippopotamus and buffalo. Breeding *O. mortimeri* were caught in four localities.

1. Mfuwe Lagoon, about 2·5 km long and 27–36 m wide, fringed by beds of *Ceratophyllum*, *Pistia* and *Vossia* in which are abundant *Pseudocrenilabrus philander*, *Alestes imberi* and small species of *Barbus*. In gill-nets of assorted mesh-size were caught numerous *O. mortimeri* and *Hydrocynus vittatus* and fewer *Labeo altivelis*, *L. congoro* and *Distichodus schenga*. One hour after being set the nets were already well-supplied, indicating a dense population.

The *Oreochromis* measured, females 22·0–28·5 cm TL and males 29·5–32·5 cm (SL respectively 180–225 and 234–265 mm). The testes of one male of 32 cm were nearly ripe. A female of 28·5 cm carried yolked embryos in her mouth, the long diameter of the yolks being 3 mm. None of the other individuals was fully ripe, but some had swelling gonads.

2. A shrinking, weedy pool about 18 m long in a depression a few metres from Mfuwe Lagoon; it was nowhere more than about 60 cm deep, with a bottom of black mud. *Ps. philander*, in brilliant colour, was the most abundant fish species and there were a few small *Barbus*. One male *O. mortimeri* of 22 cm TL (172 mm SL) with testes moderately enlarged was caught and preserved (Fig. 105). Dorsal and anal soft fins are much produced, the snout profile is concave and the lower jaw 46·1% length of head; outer teeth are simple or with a reduced minor cusp. The colour was intense bronze to blue-green with much iridescence and the red edges of dorsal and caudal fins were conspicuous. The head was dark, iridescent, greenish, a little paler below, but without a white area. Chest, belly and lower surface of caudal peduncle were white and there were bluish white spots in a buff area at the posterior edges of dorsal and anal fins.

3. A smaller pool, about 9 m long and very narrow, of the same nature as no. 2, in a depression near the Luangwa bank, with *Ceratophyllum*, *Nymphaea* and *Pistia*. Our catch from it comprised three small species of *Barbus*, young *Clarias* c.f. *gariepinus*, numerous *Ps. philander*, a young *Tilapia rendalli* and a male *O. mortimeri* of 78·5 mm SL with large, white testes, prominent genital papilla and produced snout, although the lower jaw measured only 37% length of head.

4. At the edge of the dry bed of a seasonal tributary (Ikatete R.) of the Luangwa a spring issued as a short, clear stream which disappeared after a few metres into the gravel. In it were caught three small species of *Barbus*, a young *Labeo* and a female *O. mortimeri* of 68·8 mm SL, carrying in her mouth 137 oval, orange-coloured eggs measuring 2·5×1·7 mm. This fish was also brilliantly iridescent. The general colour was bronzy, the scales above the lateral line having their posterior halves turquoise blue, those below it having a brown central spot. The top of the head had a metallic gleam, the preorbital bone was iridescent; there was a short turquoise-blue iridescent streak below the lower jaw*, and the lower part of the operculum showed the same colour. Dorsal and caudal fins were red-edged. Two of the four dark vertical bars on the body were emphasized as mid-lateral blotches.

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*Such a streak is found in many cichlid fishes, including *Tilapia sparrmanii* and *Pseudocrenilabrus philander*.

Oreochromis mortimeri therefore may breed at 68·8 mm SL (♀) or 78·5 mm (♂). Such small breeders were found only in very small bodies of water, whereas in a water the size of Mfuwe Lagoon the only breeding fishes caught were of *ca* 250 mm (♂) and 220 mm (♀) SLs. Since these waters are all interconnected in time of flood the tilapias must be considered as members of one population. They illustrate the phenomenon well-known in the tilapias, that the size and age at which these fishes breed is related to the size of the body of water in which they find themselves (see p. 33).

Mortimer (unpublished) records a female of 192 mm SL brooding eggs in the mouth and one of 185 mm carrying yolked embryos, both from the Luangwa Valley. Details of the environment are not available.

In Lake Kariba, Matthes (1969) records that the young are released from the maternal mouth in relatively deep water at a length of about 1 cm, and then swim in small shoals to their littoral feeding grounds. It is probably this species whose habits Donnelly (1969) described under the name *Tilapia mossambica*. In Lake Kariba it may be found breeding throughout the year, with a peak from October to December. The nests are said by fishermen to be made in water of about 4 m depth. Young up to 10 cm TL prefer water of 30 cm depth or less on a gently sloping shore. Between 11 and 19 cm TL they are found in depths of 30–60 cm and then leave the nurseries. They are believed to breed at an age of 2 years.

Hybrids

Oreochromis mortimeri, ex Middle Zambezi (under the name *Tilapia mossambica*), and *O. andersonii* (Castelnau), ex Kafue River, were crossed at Chilanga and Mwekera, Zambia, both places being in the Kafue basin at altitudes of over 4000 ft (1312 m) (Mortimer, 1962*a*). At Chilanga, where wild stock of *O. mortimeri* was used, only where the male parent was *O. mortimeri* were offspring produced. At Mwekera, where inbred pond stock of both species was used, the reciprocal cross was also successful. The F_1 included both sexes, but the sex ratio could not be recorded because of mortality. Among the survivors males were more numerous than females.

Thirteen of the hybrids were deposited at the BMNH and showed intermediacy in several numerical characters (Table 80). The hybrids were fertile and, like the parent *O. mortimeri*, but unlike *O. andersonii*, bred several times in a season.

Distribution

Middle Zambezi and its tributaries, including the Luangwa River (except probably the upper reaches of its tributaries Lunsemfwa and Mulungwishi above the escarpment), the Hunyani River and Lake Kariba. Since *O. mossambicus* has been stocked in some dams in the Hunyani basin, the possibility of confusion with this species both in that system and in Lake Kariba into which the Hunyani flows must be taken into account (see Jubb, 1974).

Discussion

Relationships

The distinction between *O. mortimeri* and *O. mossambicus* is very narrow, depending mainly on the coloration of mature males. Jubb, who was familiar with the latter species, had seen living specimens of *O. mortimeri* only before he was alerted to this difference, and some of the differences he describes (1974) between preserved specimens of both (as in the shape of the gill-rakers) cannot be confirmed in my material. The references to Jubb's figures of 1967 in the synonymy above are included on his own evidence (*in litt.* 15.IX.1973) after he had consulted his field notes and Hilda Jubb's colour notes. The prolonged soft rays of dorsal and anal fins

Table 80. Meristic characters in *O. mortimeri* and *O. andersonii* (from three populations), and hybrids between *O. mortimeri* from the Middle Zambezi and *O. andersonii* from the Kafue.

					O. andersonii	
		O. mortimeri	Hybrids	Kafue	Okovango	Angola
Gill-rakers	16	3				
	17	9				
	18	21	2			
	19	15	9			
	20	6	1			1
	21		1	5	1	
	22			5	1	2
	23			3	9	2
	24			1	7	
	25			1	1	
	26					
	27			1		
Scales 1.1.	30	6				
	31	21			1	
	32	14	8	4	5	2
	33		4	7	9	3
	34			3		
	35			2		
D Spines	XVI	26	8	4	25	5
	XVII	37	5	10	10	9
	XVIII			2		
D soft rays	10	1				
	11	12		1	1	1
	12	40		9	12	5
	13	17	6	6	20	9
	14		7		2	
A soft rays	10	19				
	11	26		11	1	5
	12	6	13	4	37	10
	13			1	13	2

may not be a specific distinction. My own action in proposing specific rank for *O. mortimeri* was based on field experience of both species within the space of a couple of weeks. See discussion on p. 519.

Dr Jubb believes that Lake McIlwaine was stocked with *O. mossambicus*, but I have accepted Munro's statement that the species studied by him in that lake did not have the characteristic male coloration of *O. mossambicus*. The present situation in Lake McIlwaine may be different. Two observers who are familiar with both species, Mr Donnelly (teste Jubb, *in litt.*) and Mr F. Junor (pers. commn) are as impressed with the difference as I was, and the specific name stands as an hypothesis until its implications are refuted—or perhaps until hybridization makes it irrelevant except historically.

Balon (1974*a* & *b*) prefers to consider *O. mortimeri* a subspecies of *O. mossambicus*. The great similarity of the two taxa and the fact that they occupy adjacent geographical areas is consistent with this view. I keep the specific rank because the major difference is in the breeding coloration and so might be expected to mediate a degree of reproductive isolation.

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1932.12.16.804–841	52–113	Luangwa Valley	C. R. S. Pitman
1932.12.16.842–861	60·0–77·5	Luangwa Valley (Mpika Distr.)	C. R. S. Pitman
1932.12.16.862–865	82–112	Luangwa Valley (Mpika Distr.)	C. R. S. Pitman
1932.12.16.866–877 (paratypes)	111–198	Luangwa Valley, at Chiwanda	C. R. S. Pitman
1932.12.16.878 (holotype)	211	Luangwa Valley at Chiwanda	C. R. S. Pitman
1932.12.16.879–888 (paratypes)	72–200	Kapamba R., Luangwa Valley	C. R. S. Pitman
1969.9.25.313–318	15–26	Stream nr Fort Jameson	C. Tait & E. Trewavas
1969.9.25.319–361	13·0–54·5	Spring in bed of Mwombosa R., trib. of Luangwa R.	C. Tait & E. Trewavas
1969.9.25.362	78·5	Pool, 8 km from Mfuwe, Luangwa Valley	C. Tait & E. Trewavas
1969.9.25.363–402	10·0–54·5	Shallow pool with sandy bed and no macrophytes in Luangwa flood-plain	C. Tait & E. Trewavas
1969.9.25.403	68·8	Spring in dry stream-bed (Ikatete R.), Luangwa South, about 13 km from Mfuwe	C. Tait & E. Trewavas
1969.9.25.404–410	135–240	Mfuwe Lagoon, Luangwa South Game Park	C. Tait & E. Trewavas
1969.9.25.411–413	14–19	Pool with muddy bed and *Pistia*, *Ceratophyllum*, *Nymphaea* in Luangwa flood-plain	C. Tait & E. Trewavas
1969.9.25.414–415	36, 38	Mfuwe Lagoon	C. Tait & E. Trewavas
Zambian Fisheries Collection			
	2,	Feira, at Zambezi-Luangwa confluence	M. A. E. Mortimer
	2, 119, 128	Kariba reach of Middle Zambezi, before building of dam	M. A. E. Mortimer

Oreochromis andersonii (Castelnau)

Chromys andersonii Castelnau, 1861:14 (Ngami Region).

Tilapia andersonii; Boulenger, 1911*c*:415; *idem*, (part), 1915:171 (specimens 1–3, 10–21, 25; not fig. 110; Okovango & Mossamedes); Gilchrist & Thompson, 1917:493 (not fig. 125); Regan, 1922:251; Pitman, 1934:323; Fowler, 1935*a*:280 (list only); Barnard, 1948*a*:448 (key); Sklower, 1951:288; Williams, 1960:86 (Kafue); Mortimer, 1960:42 ff., pl. I (natural history; growth in ponds); Jackson, 1961:101; Jubb, 1961:131, pls 77 & XVII; Mortimer, 1962*a* (hybrids); *idem*, 1962*b* (salinity tolerance); Thys, 1963:603 (list only); Jubb, 1963:31 (excl. syn. *intermedia*); Mortimer, 1964 (in dams); Pike & Carey, 1965:82 (Kafue); Bell-Cross, 1965:31, fig. 34 (nest & its location); Carey & B. Bell-Cross, 1967:17 (ova); Jubb, 1967:161, fig. 189 & pl. 34; Mortimer, 1967:63; Kelley, 1969 (Upper Zambezi); Duerre, 1969 (Upper Zambezi); Jubb & Gaigher, 1971:13, 19 (Botswana); Chapman *et al.*, 1971 (bionomics in Kafue basin); Lagler *et al.*, 1971 (Kafue fishery); Bell-Cross & Kaoma, 1971:240 (Kariba); Bell-Cross, 1972:10; Dudley, 1974 (growth); Balon, 1974*a*:55, 56.

Tilapia (Sarotherodon) andersonii; Trewavas, 1966*c*:414 (neotype designated).

Tilapia (Sarotherodon, Oreochromis) andersonii; Thys van den Audenaerde, 1968*b*:xxxvii & 384.

Sarotherodon andersonii; Kapetsky, 1974:501 ff. figs 77, 78 (population dynamics in Kafue); Bell-Cross, 1976:213, pls 21 & 57; Dudley, 1979:205 ff.

Tilapia kafuensis Boulenger, 1912:138; *idem*, 1915:153, fig. 100 (R. Kafue); Gilchrist & Thompson, 1917:481, fig. 119 (locality corrected to Upper Zambezi by Jubb, 1960); Fowler, 1932:239 (Okovango region); *idem*, 1935*a*:280 (faulty synonymy); Pitman, 1934:323 (part; Kafue R., Mpika & Serenje portions of Luangwa system); Barnard, 1948:448 (key).

Tilapia natalensis (part, *non* Weber); Boulenger, 1916:327 (Kafue).

Types. Holotype: lost.

Neotype: male, 242 mm SL from the Okovango River, coll. Woosnam, BMNH 1910.5.31.72 (designated by Trewavas, 1966*c*).

Holotype of *T. kafuensis*: 286 mm SL, from the Kafue River, coll. Codrington. BMNH 1908.11.6.47.

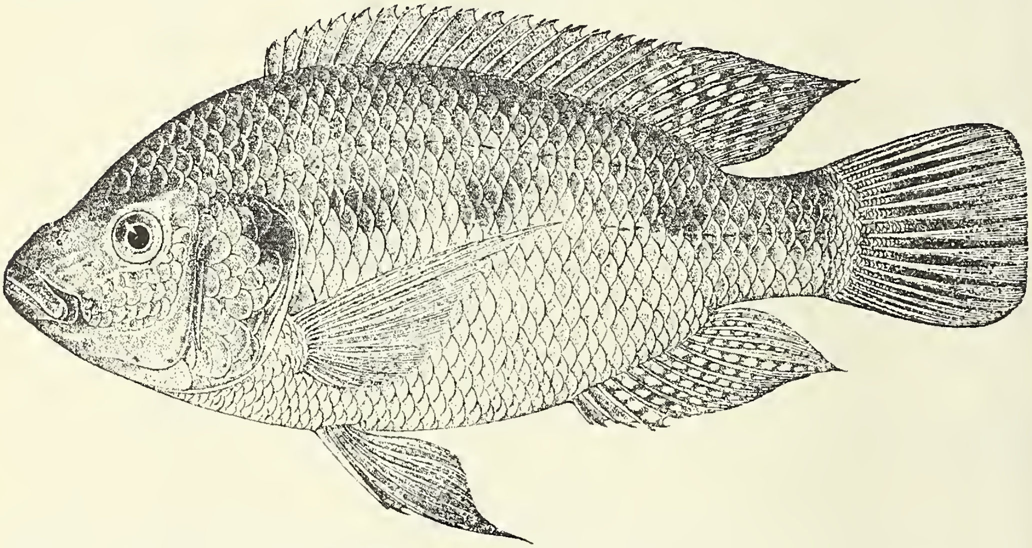

Fig. 107 *Oreochromis andersonii.* Holotype of *Tilapia kafuensis* 286 mm SL. From Boulenger, 1915, fig. 100.

Distinguishing characters

1. Male genital papilla bluntly conical with a narrow flange slightly notched in the middle. Jaws enlarged in breeding males, which in this species are normally not less than 30 cm in TL.
2. Scales in lateral line series 31–35, usually 32 or 33. Scales of cheek in 3 full rows.
3. Vertebrae 30–32, mode 31.
4. Total dorsal rays 28–31, mode 29 or 30 in different populations, usually with fewer spines and more soft rays in the Okovango population than in the Kafue or Angola (as far as the samples available show, Table 82).
5. Pectoral fin in adults 34–43% SL.
6. Depth of body 40·5–50·5% SL, generally more slender than *O. macrochir* in the same waters.
7. Colour-pattern of non-breeding fish and female always including three or four conspicuous mid-lateral blotches and a red margin on dorsal and caudal fins. Breeding male with red margins broader and brighter and general dark, iridescent purplish-brown colour of head, back and flanks, masking the lateral blotches.
8. Nest a simple circular depression.

Some of these features distinguish it from the sympatric *O. macrochir*, others from the more nearly related *O. mortimeri*.

Oreochromis andersonii resembles *O. urolepis* in the expression of the mid-lateral series of spots and in having rather high meristic numbers. There are, however, differences in the meristic characters. Table 76 shows that the ranges of vertebral numbers barely overlap in our samples, and that although ranges of dorsal spines, total dorsal rays and lower gill-rakers are alike, modes and means are higher in *O. andersonii*. In *O. andersonii* the similar dorsal totals are composed of lower average numbers of spines and higher numbers of soft rays, and the numbers of anal soft rays are usually higher (*O. andersonii* 11–13, *O. urolepis* 9–11). Other differences are the presence of vertical series of spots on the caudal fin of *O. urolepis* but not of *O. andersonii*, and the much more marked enlargement of the jaws in males of *O. urolepis* (Tables 73, 74 & 81). In assessing the importance of this last character it must be remembered that it is variable and is linked to the size and age of maturity, which vary with the environment.

It is also difficult to define *O. andersonii* vis-à-vis *O. niloticus*. The two species agree in meristic numbers. *O. andersonii* lacks the vertical stripes on the caudal characteristic of *O. niloticus* and unlike *O. niloticus* has a red dorsal margin that is broader and brighter in the mature male. *O. andersonii* has three rows of scales on the cheek, *O. niloticus* usually two. The pharyngeal teeth are finer than in the nominal subspecies of *O. niloticus*, but are matched in some of the other subspecies. Finally, even such meagre evidence as we have of the enlargement of the jaws in mature males of *O. andersonii* is lacking for *O. niloticus*.

Description

Based on 36 fishes of 108–344 mm SL, including the neotype, from the Okovango River, and the holotype of *T. kafuensis*. Meristic characters of smaller fishes are also included.

For proportions and meristic characters see Tables 76, 81 & 82. Numbers of gill-rakers are recorded in Table 80 p. 322, for comparison with *O. mortimeri* and hybrids between the two species.

Oreochromis andersonii is a less deep fish than *O. macrochir*, the depth rarely exceeding 45% SL and that not in the biggest specimens to hand; those in which it is 49–51% SL are eleven of 108–148 mm SL caught in the Ngami region by Lundin in about 1950. The profile is usually straight, in contrast to the steeply decurved snout of *O. macrochir*, and the caudal peduncle is often longer and more slender.

The ratio depth of preorbital/length of head is nearly constant, at sizes between 108 and 286 mm SL being 20–24% length of head, the big male of 344 mm SL giving a ratio of only 24·8%. This is in agreement with *O. mortimeri* but contrasts with *O. macrochir*, in which it reaches 27% in fishes of about 250 mm SL and over. Eye and preorbital reach equality at approximately 125–130 mm SL, as in *O. mortimeri*.

Jaws. I have examined only four fishes over 30 cm in TL (the size at which 50% are found in breeding condition). One of them is the holotype of *T. kafuensis*, 36 cm in TL, probably a female and in any case not in spawning livery. The lower jaw is 36·3% length of head. The other three are males, respectively *ca* 30, 35 and 40 cm in TL, with the lower jaw respectively 36·0, 33·4 and 42·0% length of head. The last is the only one with no trace of lateral blotches and is the only one available that shows the characteristic enlargement of the mouth in breeding males. It suggests that this feature is the same as in *O. mortimeri*, *O. mossambicus* and related species, but in agreement with the late onset of breeding is normally confined to bigger fishes.

Teeth in 3–4 series in juveniles, 3–5 up to SL 150 mm, 4–6 from this size to 277 mm, 7–8 in one of 286 mm; 48–54 in outer row of upper jaw in juveniles, 60–114 in adults; outer bicuspid, inner tricuspid. In large males the notch in the outer teeth may be insignificant, apparently because of wearing down of the cusps.

Width of *lower pharyngeal* bone about equal to its length, 28·0–33·4% length of head; blade 1·0–1·3 times the median length of the toothed area, which has relatively acute lateral lobes.

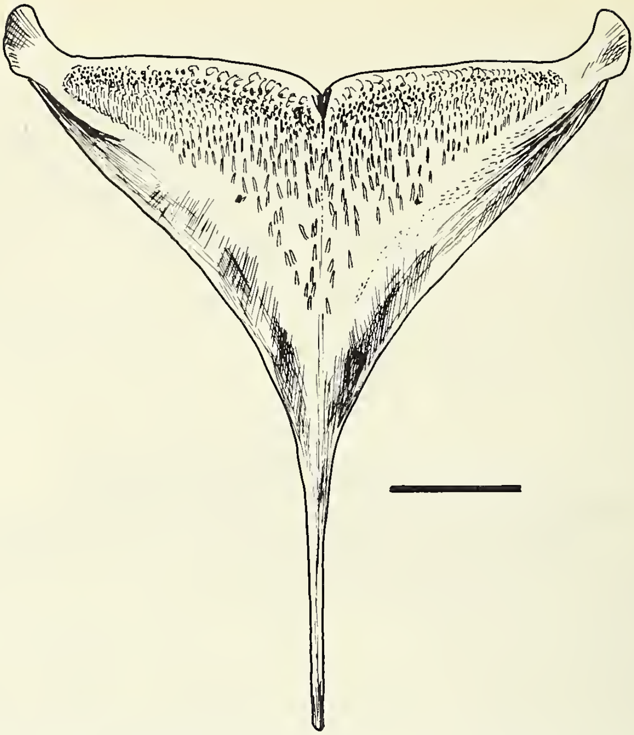

Fig. 108 *Oreochromis andersonii*, pharyngeal bone of the neotype, a fish of 242 mm SL from the Ngami district. Scale = 5 mm.

Teeth slender, not densely crowded, the posterior with a marked second cusp or shoulder.

Gill-rakers (4–7) + 1 + (21–27) on anterior arch (see Table 80). Microbranchiospines present on the outer sides of arches 2–4.

Scales on cheek in 2–4 rows, usually 3 full rows; in lateral line series (31) 32–34 (35), mode 33 in both populations; 4–5 between origin of dorsal and lateral line, 5–8 between bases of pectoral and pelvic fins.

For fin-ray numbers see Table 82. The single upper Zambezi specimen examined has D XVI 14, thus agreeing with the Okovango samples.

Caudal truncate, scaly only at the base.

Size. Mortimer recorded the greatest authenticated weight of a wild fish as 1814 g, but Jubb (1967:239) quoted records of 5lb (2268 g) for the Kafue and 7lb (3174 g) for the Upper Zambezi. Kelley (1969:60) gave 50 cm and 3050 g as the maximum found in his survey of the Upper Zambezi floodplains. Chapman *et al.* (1971) gave a maximum total length for males in the Kafue basin of 45 cm, females rarely more than 36 cm; at 45 cm the weight would be about 1790 g (Lagler *et al.*, 1971:123).

Coloration. Silvery blue-grey, darker on top of head and back, with typically 2–4 mid-lateral black spots as in Fig. 107. Both sexes with edges of vertical fins pink to red, the red flush extending in some individuals over greater part of caudal and anal. Soft dorsal and anal variously marked, some with numerous white oval spots; others with fewer white spots on anal and dark spots or bars on dorsal and; some (in alcohol) with no spots but with more or less extensive dark clouding. Caudal sometimes spotted basally, but usually without spots.

Breeding males with generally darker colour, masking the mid-lateral spots and with brighter red dorsal margin.

Table 81. *Oreochromis andersonii*. Proportions in samples from different populations. A = Cunene system, Angola; O = Okavango & Lake Ngami region; K = Kafue.

	A	O	O	K	K	K
N	5	20	3	7	3	6
SL(mm)	58–83	108–148	189–241	162–220	277–344	60–72
Proportions as % SL						
Depth	44–47	44·5–50·5	39–43	41·5–45	40·4–45·3	41·5–44·0
L. head	33–37	34·3–36·7	34–35	33–35	32·0–35·6	33·5–36·5
L. pect. fin	36–40	37·5–43·5	34·5–41·5	36·0–39·5	34·0–37·5	33·0–37·5
L. caud. ped.	12·4–13·4	9·5–13·0	12·4–13·4	10·7–13·6	11·0–13·5	11·5–13·0
D. caud. ped.	13·7–15·0	14·2–17·5	14·5–15·4	14·5–16·4	13·7–15·1	13·1–13·9
Caudal ped. l/d	0·8–0·9	0·65–0·76	0·8–0·9	0·7–0·9	0·7–1·0	0·8–1·0
Proportions as % length of head						
L. snout	30·4–33·3	33·7–37·8	34·0	35·0–40·0	40·0	32·0–35·8
Eye	24·3–27·0	21·0–25·0	18·2–21·2	18·0–21·4	15·4–17·5	25·0–31·5
D. preorb.	18·0–22·0	20·4–24·0	21·0–22·7	20·8–23·8	23·6–24·8	17·5–20·4
Interorb.	30·0–37·0	35·0–41·0	36·0–36·8	36·0–39·6	39·5–40·0	33·0–36·5
Lower jaw	31·0–35·0	31·0–35·0	32·5–36·0	30·2–34·0	33·4, 36·3, 42·0	29·0–33·0

Table 82. *Oreochromis andersonii*: frequencies of numbers of fin-rays in samples from different populations. A = Cunene system, Angola; O = Okovango, Ngami & Etosha basins; K = Kafue.

D fin	A	O	K	D spines	A	O	K	D totals	A	O	K
XVI 12		2	1	XVI	5	26	4	28	1	2	1
XVII 11	1			XVII	10	12	12	29	10	7	12
XVI 13	5	5	3	XVIII			2	30	4	23	5
XVII 12	5	2	8					31		6	
XVIII 11			1	D soft rays totals							
XVI 14		16		11	1		1				
XVII 13	4	7	4	12	5	4	10	Anal soft rays			
XVIII 12			1	13	9	12	7	11	5	1	11
XVI 15		3		14		19		12	10	31	9
XVII 14		3		15		3		13	2	10	1

Six to ten faint vertical bars appearing in dead fish. Young with a tilapia-mark, which disappears or becomes part of the barred pattern of the fin at *ca* 70 mm SL. Up to *ca* 110 mm SL vertical bars on the body may predominate and the mid-lateral spots may be faint or absent.

Ecology

Food

Mortimer's investigations (1960) showed that in ponds *O. andersonii* is predominantly a bottom feeder, taking mainly algae from the mud surface. The stomachs were found to contain detritus and inorganic particles. Diatoms and blue-green algae were the organisms most constantly present. These results were confirmed by Chapman *et al.* (1971) who also found filamentous algae in some larger fishes. In the Upper Zambezi region both Kelley (1969) and Duerre (1969) found periphyton to be overwhelmingly the most important food source for adults, plant detritus taking a secondary place. This was usually true too of the young of the year, but in one sample of 5 individuals fish made up 44% of the stomach contents by volume. Chapman *et al.* (1971) report that in the stomachs of young of 2–3 cm diatoms predominate, but 'animal matter' is more abundant than in adults.

Observations by Mortimer (1960) in aquaria showed contrasting behaviour in *O. andersonii* and *O. macrochir*, the latter taking food at the surface and in mid-water, the former waiting until it reached the bottom.

Le Roux's rather different results (1956) were on fishes wrongly identified as *T. andersonii* (see Mortimer, 1960).

Growth

The relation between age and growth in length in the Kafue floodplain is shown in Fig. 109, after Kapetsky (1974), in which growth is seen to be more rapid than that of *O. macrochir*. The differential growth of the sexes is also plain for both species.

Mortimer (1960) tested the growth in weight for pond dwellers during the first sixteen months

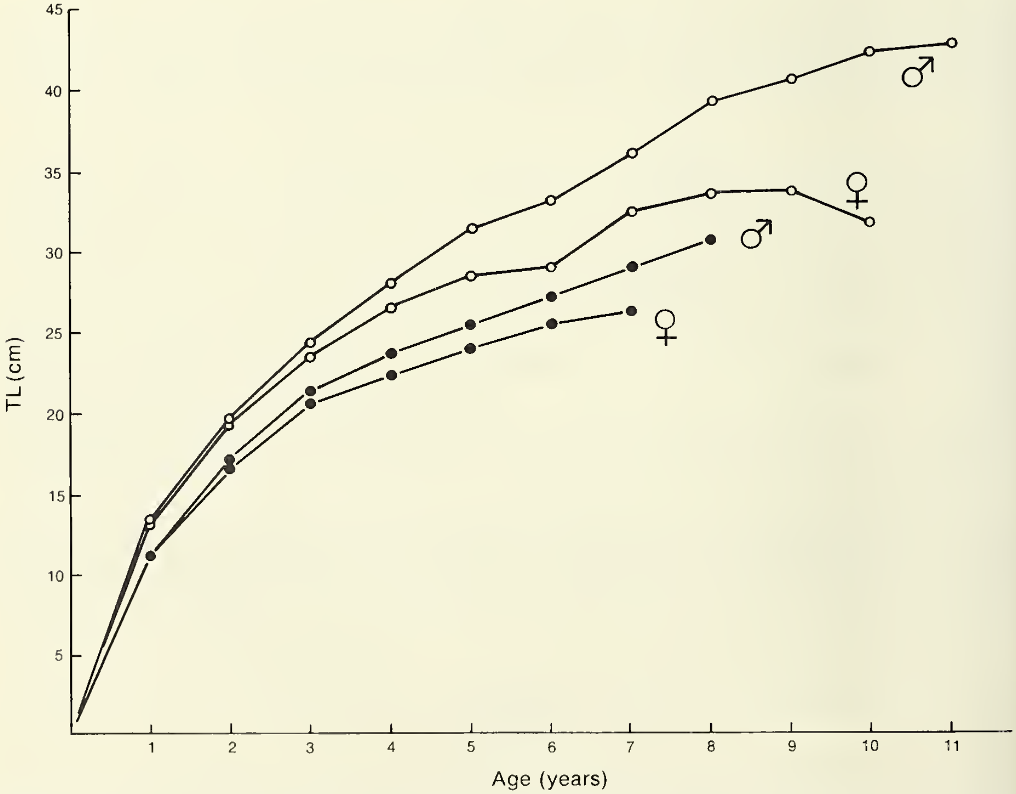

Fig. 109 Growth in length of males and females of *Oreochromis andersonii* (○) and *O. macrochir* (●) in Kafue River. Redrawn from Kapetsky, 1974, fig. 77.

of independent life under various conditions of food supply, density of stocking and the presence or absence of *O. macrochir* and *Tilapia rendalli*. The ponds were at Mwekera and Chilanga in the Kafue catchment area on the Zambia plateau.

Nearly all growth took place in the warm months of September to April, when the mean monthly temperature was over 20°C.

The presence of the other two species in the pond did not adversely affect the growth of *O. andersonii*, a result that Mortimer attributed to their complementary feeding habits.

Growth in *O. andersonii* was more rapid than in *O. macrochir* or *T. rendalli* in the same ponds and stocked at the same density. Mortimer attributed this, at least in part, to greater breeding activity on the part of *O. macrochir* and *T. rendalli*.

Mortimer (1960) admitted that the value of his growth experiments at different densities of stocking was affected by heavy predation by birds and otters, especially in the smaller ponds, but the comparative rates for *O. andersonii* and *O. macrochir* are confirmed by the results of Chapman *et al.* (1971), Dudley (1974, 1979) and Kapetsky (1974) on a wild population.

Dudley (1974) predicted that the closure of the Kafue Gorge dam might affect the growth of the tilapias but his post-impoundment study (1979) failed to confirm this, although it indicated a possible influence on the reproductive potential of the population (see below).

Salinity tolerance

Preliminary experiments by Mortimer (1962*b*) gave evidence of a wide tolerance, comparable with that of *O. mortimeri* (then included in *O. mossambicus*). Both these species survived the gradual addition of NaCl to a tank of fresh water up to 26‰. Deaths occurred only at 35·5‰. They also survived transference from 30‰ NaCl to fresh water, although taking one or two hours to recover from the shock*. This was in contrast to *O. macrochir*, which succumbed to such treatment.

Breeding

Sexual dimorphism. The male breeding coloration is described on p. 324 and the difference between the sexes is growth rate on p. 328. In only one individual, a male of 344 mm SL, have I observed enlarged jaws. In comparison with *O. mortimeri* and *O. mossambicus* this is a low incidence of jaw hypertrophy, but *O. andersonii* normally breeds at a greater age and size than these species, and I have not seen breeding males from precociously breeding populations of *O. andersonii*.

Size and age of maturity. In the Kafue River *O. andersonii* was reported (Rep. N. Rhodesia Game & Tsetse Dept., 1955) to breed at about 8 oz (226 g), i.e. about 24 cm TL or 190 mm SL, but the sexes were not recorded separately. Chapman *et al.* (1971) found in 1969–70 no ripe individuals in the Kafue floodplain less than 26 cm TL, at 26–29 cm only one of 32 males and 2 of 10 females were ripe, and it was only among those of 30 cm and over that as many as 50% were ripe (cf. also Table 83). The same authors found that the species rarely spawns before it is 3 years old, and is usually not less than 4 years at its first spawning.

Dudley (1979) found evidence in the fluctuating abundance of year-classes that the reproductive performance on the Kafue floodplain is higher in relatively dry years than in wet. Correlated with this result, perhaps causally, he found among his samples that females came into spawning condition at smaller sizes in dry years than in wet (Table 83). For this he offered the explanation that lower floods resulted in the fishes entering a stressed phase earlier than otherwise, giving a shift towards the precocious breeding characteristic of tilapias in small and shrinking bodies of water.

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*These ratios were recorded as percentages in 1962*b*, but were corrected in a subsequent report (1964) to thousandths.

Such precocious breeding must account for Mortimer's results in ponds at Mwekera and Chilanga in the Kafue catchment area, where females of known age spawned at 11–15 months, the average size of the females being 15·5–21·6 cm TL (Mortimer, 1960, tables 8 & 9) though not all the females in the ponds were necessarily responsible for the broods. In some of the ponds no breeding had occurred during this period, an indication that the ages and sizes recorded were indeed minimal. The smallest found brooding eggs in the mouth was 17·6 cm and 89 g, and some even smaller had mature ovaries. The species was introduced in ponds near Mwanza, Tanzania, in the hope that it would not reproduce precociously, but its behaviour in this respect was no different from that of other species (Lema *et al.*, 1976).

Table 83. Percentage of females in spawning condition in samples taken in the Kafue floodplain in the 'dry years' of 1964–5, 1965–6, 1966–7, and in the 'wet years' of 1969–70, 1975–6. All samples were taken in the months October to January. From Dudley, 1979. Figures in brackets are the numbers of fishes in the samples.

	Dry years	Wet years
Length group (TL in cm)	% (n)	% (n)
18–22·9	2 (44)	0 (77)
23–25·9	18 (16)	0 (57)
26–29·9	18 (11)	9 (31)
over 30	38 (16)	46 (136)

Spawning season and localities. Breeding did not occur in the ponds at temperatures below 21°C, which on the Zambian plateau excludes the months May to September. From October to April spawning activities have been observed, but the main breeding months are November and December (Mortimer, 1960). October to December are also the months in which Kelley (1969) and Duerre (1969) found ripe gonads in the Upper Zambezi, and Chapman *et al.* (1971) in the Kafue.

The nest is made in water slightly deeper than is normally occupied by those of *O. macrochir*, and is a simple bowl-shaped depression without a raised rim (Mortimer, 1960, fig. 1a opp. p. 52; Bell-Cross, 1965, fig.). The diameter varies, probably in relation to the size of the fish, the largest seen (by me) in a drained pond at Chilanga being about 75 cm in diameter and nearly 30 cm deep. Mortimer (1960) described the construction of the nest by the male, who used both mouth and fins. In a pond filled with vegetation the fish bit off or uprooted the plants in the space required. Mating behaviour has not been reported.

Ovaries of brooding females in ponds showed no evidence of a second batch of ripening eggs, and in only two instances did a female produce a second brood in the same season (Mortimer), one in November, the other in December. Similar data are not available for fishes breeding at the 'normal' age of 3 or 4 years, but *O. macrochir* in the same ponds produced three or four broods in a season.

The number of ripe ovarian eggs per fish in six pond fishes of 17 to 26 cm is given by Mortimer (1960) as 356–567, the number of eggs found being brooded in a mouth 529 to 730 in two females, the number of brooded embryos 168±10 to 561 in three fishes of 23–27 cm. These numbers are lower than those recorded for *O. macrochir* in the same waters (p. 450). The size of the eggs is not recorded. Thus the fecundity of *O. andersonii* is relatively low, but from the fishery point of view this is compensated by the good growth rate in open waters (Fig. 115).

Distribution

Natural distribution. Mossamedes and the Cunene River in Angola; Okovango River, Ngami region and Etosha Pan; Upper Zambezi; Kalomo River; Kafue River. It is reported from a tributary (Mwomboshi or Mwambashi) of the Lunsemfwa River, itself a plateau tributary of the Luangwa, but possibly it was inadvertently stocked there. There is also a single report from Lake Kariba (Bell-Cross & Kaoma, 1971:240) where it was first seen in 1969, and Jackson found a single specimen in the Kabora Bassa region during a preimpoundment survey. Both these Middle Zambezi records are believed to have resulted from accidental entry from the Upper Zambezi, but they may have been due to inadvertent stocking together with *O. macrochir*. Otherwise *O. andersonii* is absent from the Middle Zambezi and the Luangwa River, as well as from the Bangweulu region.

This species and *Clarias gariepinus* contribute the greatest share by weight to the Kafue floodplain fishery (Everett, 1974).

Dispersal by man. The stocking of this species in many dams in Zambia was well documented by Mortimer (1964), who saw that they were confined to dams in the upper tributaries of rivers in which the species was native. Reports of stocking of *O. andersonii* in Shaba and South Africa are due to confusion with *O. macrochir macrochir* (Mortimer, 1960), but it is said to have been put into farm dams in Mashonaland (Jackson, 1961*b*).

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1907.6.29.163	68·5	Mucopa R., Mossamedes	Ansorge
1907.6.29.164–5	82, 83·5	Tala Kilau, Dongwenna, Mossamedes	Ansorge
1907.6.29.166–175	32·0–54·5	Dongwenna Swamp, Mossamedes	Ansorge
1910.5.31.71 (neotype)	242	Okovango R.	Woosnam
Swedish National Museum (49 fishes)	108–149	Ngami Region at Runter Kapako and Sambi	Lundin
1968.12.2.5–7	76·5–103·5	Ekuma R., basin of Etosha Pan	Jubb & Gaigher (coll. Tinley)
1908.11.6.47 (holotype of *T. kafuensis*)	286	Kafue R.	Codrington
1932.2.4.55–56	183, 196	Kafue R. at Mumbwa	Pitman
1969.9.25.38	71·5	Chiansi Lagoon, Kafue R.	Carey & Trewavas
1956.4.6.4–6	71·5–162·0	Chilanga ponds ex Kafue	C. F. Hickling
1974.2.7.8	174	Kafue R.	Sklower 21.10.1950
1937.4.22.89	67	Balovale, Upper Zambezi	Vaughan-Jones
Museum of Zambian Fisheries Research Sta., Chilanga			
3 fishes	39–68	Chiansi Lagoon, Kafue R.	All Zambian fisheries personnel
U.V. 508	344	Kafue R. at Luwato	(Sept. 1955)
U.V. 509	175·5	Kafue R. at Luwato	(Dec. 1954)
CB 528–9 (3 fishes)	191–277	Ceres, in Kafue floodplain	

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
DB 36	171·5	Chibondo dam, Kafue system	(Nov. 1961)
DB 293	220·5	Bolanda dam, Kafue system	(Oct. 1960)
DB 180	194	Momboshi R., Lunsemfwa system, on the plateau	(Feb. 1960)

Subgenus *OREOCHROMIS* – VII

Oreochromis placidus
Oreochromis shiranus

Oreochromis placidus (Trewavas)

For synonymy and bibliography see the subspecies.

Distinguishing characters

An *Oreochromis* with usually IV anal spines, with enlarged jaws and unicuspid teeth in large males. Lower pharyngeal with rather coarse teeth, well covering the triangular toothed area, whose median length usually exceeds or equals that of the anterior blade.

Distribution

NATURAL DISTRIBUTION. Lower parts of the eastward flowing rivers from the Sodwana area at 27°32´S to the Lukuledi River which enters the Indian Ocean near Lindi, Tanzania, at about 10°S. It may be that it owes its presence in the Lukuledi and in Lake Rutamba, in the neighbouring Lupululu system, to introductions in the nineteen-fifties.

In the Sodwana area it is found in Mgobezeleni Lake, a freshwater lake connected by a stream with the estuary (see Bruton & Appleton, 1975; Bruton, 1975). In the Sabi (=Save) system it is said to occur naturally only below the Chirabira Falls on the Sabi River and the Selawandoma Falls on the Lundi (Jubb, 1958; 1961; 1967). The type came from the Idunda River, tributary of the Buzi, which enters the ocean south of Beira. The species has been collected in the Pungwe River (Jubb, 1961), which enters the sea near Beira from the northwest. It is present in the Lower Zambezi and Lower Shiré below the Kapachira Falls (Tweddle & Willoughby, 1979), and probably also in the Mazoë (Jubb, 1974:5).

Between the Zambezi and the Ruvuma there are no detailed records, but its presence, if a little modified, in the Ruvuma and farther north suggests that it will be found in the many rivers of the Mozambique coastal plain. It is probably the *'Tilapia nigra'* of Cardozo (1954), and the species mentioned by Costa (1960:26) as possibly *'T. nigra* or *T. shirana'*, no doubt because it had more than III anal spines. Costa believed it had been imported from Rhodesia for fishponds in Milange, Zambézia, but it may well have been native.

In the Zambezi and southwards it is usually caught with *O. mossambicus*, and both species inhabit the Lower Shiré as far as the Kapachira Falls, which constitute an insurmountable barrier (Tweddle *et al.*, 1979). The Mpatamanga Gorge, situated farther upstream in the course of the Murchison Rapids, is therefore inaccessible to *O. placidus*, and the suggestion (Trewavas, 1966*b*:55) that the precociously breeding fishes found by Jubb (1940*a*) in a pool in the gorge were this species is therefore untenable (see p. 348).

Oreochromis placidus ruvumae is said to be the only tilapia in the Ruvuma. In the Lupululu River *Tilapia rendalli* is also present, but was almost certainly introduced (Dr Bernascek, *in litt.*).

DISPERSAL BY MAN. *Oreochromis placidus* from the Lower Lundi has been introduced in Lake Kyle, a reservoir in the Upper Lundi system (Jubb, 1967, 1974; Bell-Cross, 1976).

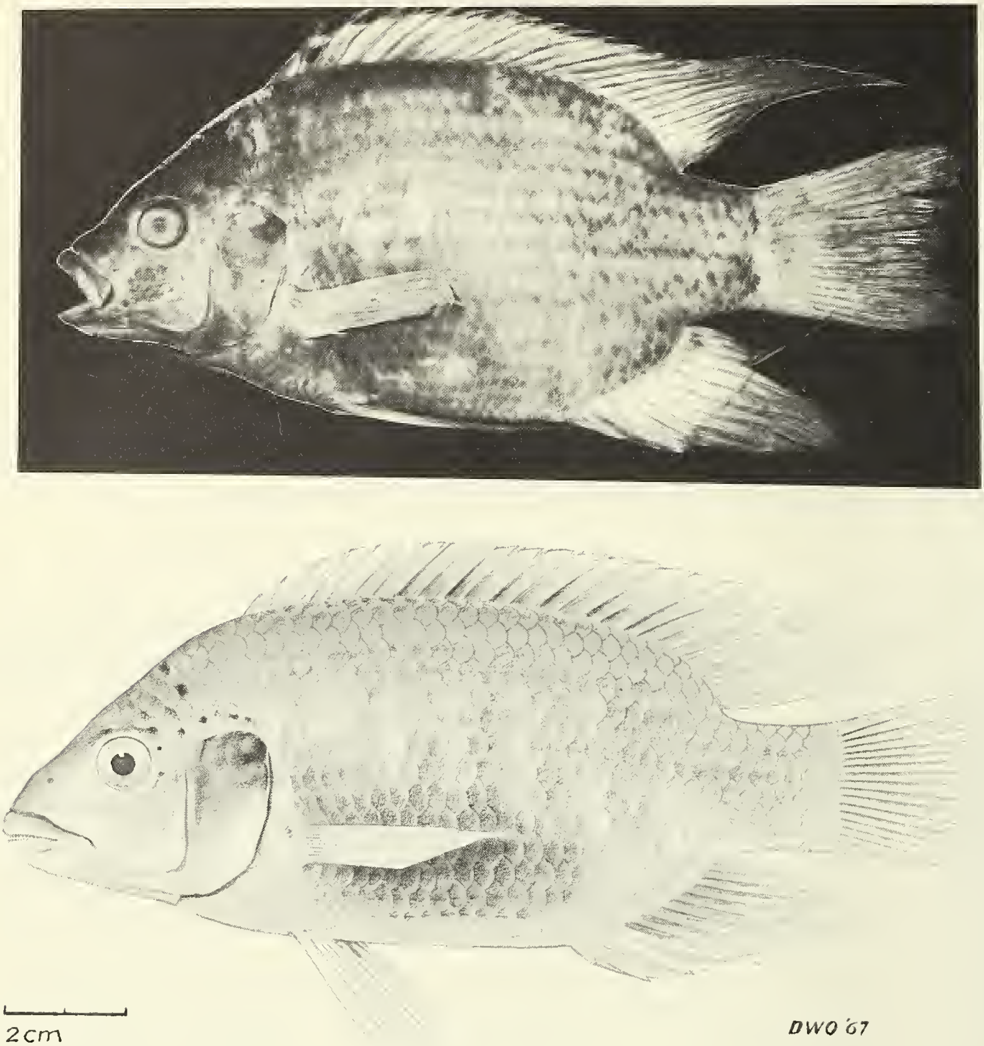


Fig. 110 Above, *Oreochromis placidus placidus*, male *ca* 120 mm SL from Mgobezeleni, Sodwana; specimen in Albany Museum, Grahamstown, coll. M. Bruton. Photograph BMNH. Below, *Oreochromnis p. ruvumae*, holotype.

Subspecies

Oreochromis p. placidus. Dorsal XV–XVIII 11–13; totals 27–29 (30). Known to a length of 35·5 cm TL. Large adults with soft dorsal rays reaching vertical through distal quarter of caudal length. Lower Zambezi and southwards.

Oreochromis p. ruvumae. Dorsal XVI–XIX 9–11; totals 26–28 (29, 30). Not known to reach lengths over 21 cm TL. Soft dorsal and anal rays less elongate (allometry?). The rivers Ruvuma and Lupululu.

Details of meristic characters of the two subspecies are given in Table 76 and compared with those of *O. mossambicus*. *Oreochromis p. ruvumae* has a higher mean number of dorsal spines and lower numbers of soft rays than *O. p. placidus*, but there are also statistical differences between populations of *O. p. placidus*. The subspecific division is maintained here pending the acquisition of more knowledge of both subspecies, especially *O. p. ruvumae*.

Oreochromis placidus placidus (Trewavas)

Chromis niloticus (*non* Linn., part) Müller & Peters, 1844:33 (Mozambique).

Tilapia shirana; Boulenger, 1915:152 (part, specimen no 8 only) (Buzi system).

Tilapia placida Trewavas, 1941:306 (Idunda R., Lower Buzi, Mozambique); Jubb, 1958:186 (Lower Sabi R.); *idem*, 1961:129, fig. 75, pl. 13 (Lower Sabi-Lundi system); *idem*, 1963:30; *idem*, 1967:159, fig. 187, pl. 32; Trewavas, 1966*c*:54 (Lower Zambezi, Lower Shiré, Pungwe, Lower Buzi & Sabi-Lundi systems); *idem*, 1966*d*:419; Bell-Cross, 1973:14 (Buzi R.); Jubb, 1974:11, fig. 4B.

Sarotherodon placidus; Jubb & Skelton, 1974:1, figs 1–3 (Lower Lundi); Bell-Cross, 1976:221, fig.; Tweddle *et al.*, 1979 (Lower Shiré).

?*Tilapia nigra* (*non* Günther); Cardozo, 1954; Gonçalves Sanches, 1959:169 (District of Moçambique); Costa, 1960:26.

TYPES. Holotype: sex unknown, 151 mm SL, the Idunda River, tributary of the Lower Buzi, Mozambique. Coll. C. F. M. Swynnerton. BMNH 1907.7.2.19.

Common English name. *The black tilapia.*

Distinguishing characters

See above and Tables 76 & 84. The breeding colours of the male, which include black throat and chest, are so far unknown in *O. p. ruvumae*.

Description

Based on the holotype, five specimens from the Lower Sabi-Lundi system, five from Sodwana and seven from the Lower Shiré system, in all eighteen fishes of 100–273 mm SL. Meristic characters are taken also from smaller fishes.

Proportions as % SL. Depth of body 37·0–53·5, usually 41–47. Length of head 32·4–34·7 in females, 32·2–36·8 in males. Length of pectoral fin (31) 33–44, not correlated with locality or size. Length of caudal peduncle 9·35–12·9 (0·5–0·88 times its own depth, less than 0·8 in specimens over 110 mm SL).

Proportions as % length of head. Length of snout 33·7–42·0 in females, 35·5–42·3 in males. Diameter of eye 21·0–26·5 at 105–160 mm SL, 16–21 above this length. Depth of preorbital bone 19·5–25·0, positively allometric without apparent sexual differentiation; equal to diameter of eye at ca. 150 mm SL, when both are about 21%. Interorbital width 36–42, showing no correlation with sex or size at this range (but relatively narrower in smaller fishes). Length of lower jaw 30·5–38·5 in females, 33·5–42·0 in males (possibly longer in a male of 273 mm so preserved that measurement is difficult).

Maxillary not reaching vertical from anterior edge of eye.

Teeth in 3–6 series; inner tricuspid; outer bicuspid in young and females (except a few simple upper posterior), but in large males all or most unicuspid; 54–80 in outer row of upper jaw (42–54 in young).

Gill-rakers short, 16–20 on lower part of anterior arch, mode 18 (see Table 76).

Lower pharyngeal bone (Fig. 111), measured in seventeen specimens: length 30–35% length of head, width 29·6–36·0; width greater than median length in 12, equal in 1, less in 4; blade shorter than length of toothed area in 13, slightly longer (1·1–1·2) in 4. Pharyngeal teeth slender,

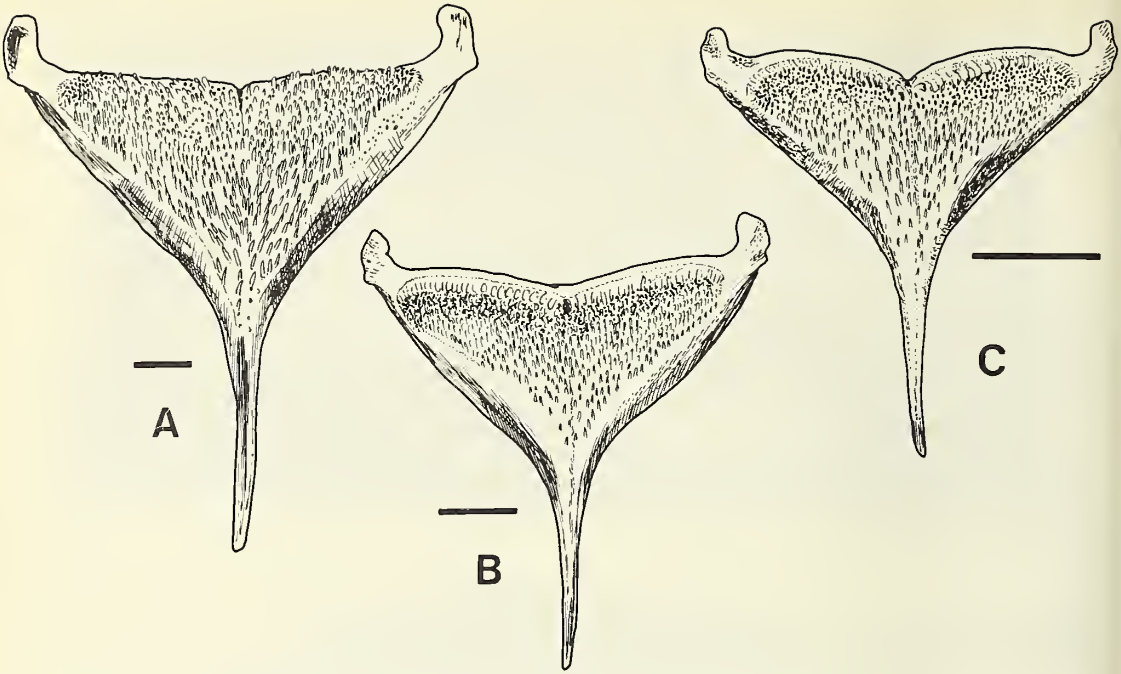


Fig. 111 *Oreochromis p. placidus.* Pharyngeal bones of: A, a fish 250 mm SL from Lundi River; B, one of 159 mm SL from Port Herald, Lower Shiré; C, one of 92 mm SL from Kanjedza, near Chikwawa, Lower Shiré.

pointed, somewhat coarser and less crowded than in *O. mossambicus*, those of two or three posterior rows stronger than the rest. Dentigerous area nearly triangular, well covered with teeth in adult.

Vertebrae 29–31 (Table 76).

Scales in 2 or 3 series on cheek; 30–32 in lateral line series, $3\frac{1}{2}$–$4\frac{1}{2}$ between origin of dorsal and lateral line, 4–6 between pectoral and pelvic fins; usually 18 or 19 around caudal peduncle, but on one large fish 22, those on the lower edge of the peduncle being very small.

Dorsal (XV) XVI–XVIII 10–13(14) (see Table 84); modal formula XVII 12. Anal (III) IV (V) 8–11 (see Table 84); in one fish with three spines the third is bifurcated at the tip; the one with five spines is from a tributary of the Lower Shiré.

Some fishes, especially males, have very long dorsal and anal soft rays, the longest dorsal ray of a male of 170 mm SL measuring 39·7% SL and extending to a vertical at $\frac{3}{4}$ the length of the caudal. In the same fish the longest anal ray is 33% SL. Testes and genital papilla in this fish are both small. Another male of 208 mm SL has a dorsal ray of 31% SL and an anal of 29%. These are the longest in the material at hand, but Bell-Cross (1976) reports that in breeding males they may extend to the end of the caudal fin or beyond.

Pelvic fin extending to vent or first anal spine in females, to first to third anal spine in males.

Caudal truncate or, in young, very slightly emarginate, not densely scaled, but in large specimens minute scales may extend on the rays to near their distal ends.

Genital papilla of (sexually inactive) males a simple cone with terminal pore.

Size. The largest recorded is 35·5 cm TL, taken in the Lower Lundi River (Bell-Cross, 1976).

Coloration. In young, up to 150 mm SL, according to Bell-Cross and personal observation, silvery to steel-grey, whitish below, with three lateral spots and faint vertical bars appearing under some conditions or on preservation. In sub-adults and non-breeding adults the scales may be outlined in black (Bell-Cross), or dark upper and lower fields of the scales may together form longitudinal stripes on the body. Breeding males (Bell-Cross) are 'very dark grey on head and body with throat and all fins black' with a red or orange margin on the dorsal and grey/black marblings on the gill-cover. The all-black or very dark colour of males is also reported for the population of the Lower Shire River by D. Tweddle (pers. commn).

Ecology

Habitat

Bell-Cross (1973, 1976) found that *O. p. placidus* prefers quiet pools with marginal vegetation. It has been reported only from fresh water and low altitudes and latitudes, so that its salinity and temperature tolerances are probably narrower than those of *O. mossambicus*.

Nothing is known concerning breeding or food preferences of this subspecies.

Discussion

Relationships

The hypothesis implicit in the (1941) description of the holotype as representing a distinct species has since been supported by field workers, especially Jubb (1958, 1961, 1967), Jubb & Skelton (1974) and Bell-Cross (1973, 1976). It is now evident that mature males are easily distinguished from the syntopic *O. mossambicus* by the colour, as well as by the deep body and prolonged fins, but with sub-adults and juveniles it is not so easy.

Since the most obvious feature distinguishing the two species is the number of anal spines, and Jubb & Skelton (1974) and Bruton (1975) believe that an occasional *O. placidus* may have III, I have searched for other features that may help to determine individual preserved fishes. Tables 84 & 85 represent results of this search. In them all III-spined fishes seen by me are named *O. mossambicus* and all IV-spined *O. placidus*. The V-spined fish from the Lower Shiré system and the one with a bifurcate third spine are included with the latter.

Shape of body (Table 85). The type of *O. placidus* and several of the fishes from Sodwana and the Lower Lundi have very deep bodies and caudal peduncles (Fig. 110), but others from the Lundi and all the Shiré samples collected in 1947 are no deeper than *O. mossambicus*. The Port Herald (Shiré) fishes appear to be in much poorer condition than the *O. mossambicus* caught at the same time; two *O. placidus* of 145 and 160 mm SL having a body depth of 40·7 and 41·7% SL, and a caudal peduncle depth of about 14%; whereas three *O. mossambicus* of 142–162 mm SL have a body depth of 45·6–49·2% and a caudal peduncle depth of about 15·7%. These *O. placidus*, however, are recognizable as such by their coarser pharyngeal dentition and traces of dark stripes along the scale-rows of the *placidus* type. Mr D. Tweddle, who has studied both species in the Lower Shiré, informs me that the deeper body is characteristic of *O. placidus*.

From Sodwana, one female with four anal spines has *mossambicus*-like pigmentation and body shape. Its pharyngeal dentition is rather coarse for *mossambicus* (but less so than the Inharrime specimens mentioned on p. 313 & Fig. 103). It is possible that this fish may be a hybrid, such as might have resulted if a change in water level or salinity had caused the breeding sites of the two species to overlap (cf. the history of *O. spilurus niger* and *O. leucostictus* in Lake Naivasha, p. 256–7). A sample of 28 young *O. mossambicus*, from 30 to 65 mm in TL, caught at Sodwana at the same time had uniformly III anal spines, suggesting that this character is relatively stable, at least in the *O. mossambicus* of this locality (but see p. 338).

Meristic numbers (Table 84). Numbers of soft anal rays show a slight tendency to vary inversely with the number of anal spines, but it is only the means that show this trend.

Table 84. Frequencies of fin-ray numbers in populations of *O. mossambicus* and *O. placidus*.
The sample of 33 *O. mossambicus* from the coastal rivers is from Sodwana where *O. placidus* was also caught. It includes many young fishes, in some of which the last ray of the soft dorsal fin may not yet have been formed and this may have lowered the mean. It was not included in the samples of Table 89. The sample of 36 is from various other localities from the Zambezi delta southwards and includes only fishes of 100 mm SL and over. Two specimens from Lake Rutamba, Lupululu River system are included with *O. p. ruvumae.*

Anal soft rays			8	9	10	11	12	M
Coastal rivers	*O. mossambicus*	N=29		3	13	12	1	10·38
	O. p. placidus	N=16		3	9	4		10·06
Lower Shiré	*O. mossambicus*	N=20			3	17		10·85
	O. p. placidus	N=32	1	3	23	4	1	10·03
Ruvuma etc.	*O. p. ruvumae*	N=20	1	6	13			9·60
Dorsal spines			XV	XVI	XVII	XVIII	XIX	M
Coastal rivers	*O. mossambicus*	N=33	2	29	2			16·00
		N=36	9	26	1			15·70
	O. p. placidus	N=17	1	12	4			16·18
Lower Shiré	*O. mossambicus*	N=27	6	20	1			15·81
	O. p. placidus	N=33		9	18	6		16·91
Ruvuma etc.	*O. p. ruvumae*	N=20		1	14	3	1	17·65
Soft Dorsal rays			9	10	11	12	13	M
Coastal rivers	*O. mossambicus*	N=33		7	26			10·79
		N=36			16	16	4	11·60
	O. p. placidus	N=17			1	8	8	12·41
Lower Shiré	*O. mossambicus*	N=27			3	16	8	12·18
	O. p. placidus	N=33			13	20		11·61
Ruvuma etc.	*O. p. ruvumae*	N=20	1	9	10			10·45
Dorsal totals			26	27	28	29	30	
Coastal rivers	*O. mossambicus*	N=33	8	24	1			26·60
		N=36	3	14	19			27·40
	O. p. placidus	N=17		1	6	10		28·53
Lower Shiré	*O. mossambicus*	N=27		3	21	3		28·00
	O. p. placidus	N=33		1	15	16	1	28·51
Ruvuma etc.	*O. p. ruvumae*	N=20	2	4	12	1	1	27·75

The mean total number of dorsal rays is higher in *O. placidus* both in the coastal rivers and in the Lower Shiré. The greater difference in the coastal samples is due to the lower totals here for *O. mossambicus* rather than to a higher mean for *O. placidus.* In the coastal rivers the high totals of *O. placidus* have been achieved through increased numbers of soft rays, but in the Lower Shiré (as in *O. p. ruvumae*) by increased numbers of spines. Table 76 shows that this difference is not reflected in the numbers of vertebrae.

These data show that the only reliable criteria for determination of juvenile and sub-adult members of *O. placidus* and *O. mossambicus* are the numbers of anal spines and the pharyngeal dentition.

In individuals smaller than 100 mm TL the difference between the pharyngeal dentitions can hardly be detected. Further, Jubb & Skelton (1974) quote a report from Mr F. Junor that suggests that the fourth anal spine may develop rather late in ontogeny. Mr Junor's evidence came from a large number ('several hundred') of young *Oreochromis* between 5 and 7 cm TL taken from the Lower Lundi for stocking Lake Kyle. Three-spined and four-spined young were placed in separate ponds, but later it was found that 60% of the supposed three-spined had a

Table 85. Body proportions in *O. mossambicus* and *O. p. placidus*. It is clear that the sample of *O. placidus* from Port Herald, Lower Shiré, was exceptionally slender. That this is unusual is confirmed by Mr D. Tweddle who says (pers. commn) that in the Lower Shiré *O. placidus* is usually more deep-bodied than *O. mossambicus*.

		O. mossambicus	*O. placidus*
Depth of caudal peduncle: % SL			
Coastal rivers:	SL < 100 mm	N = 9	N = 6
		13·45–15·6	15·6–18·5
	SL > 100 mm	N = 23	N = 9
		13·4–16·3	(15·4)16·0–19·0
Lower Shiré:	SL < 100 mm	N = 2	N = 11
		13·6–14·0	14·9–17·0
	SL > 100 mm	N = 19	N = 8
		14·3–16·2	13·9–16·7
Depth of body: % SL			
Coastal rivers:	SL < 100 mm	N = 9	N = 6
		38·0–44·0	43·8–49·0
	SL > 100 mm	N = 23	N = 9
		36·0–45·5	42·0–53·5
Lower Shiré:	SL < 100 mm	N = 2	N = 11
		41·7–43·1	43·4–47·0
	SL > 100 mm	N = 19	N = 8
		38·8–49·2	37·0–42·8

fourth spine. When the difficulty of counting spines in hundreds of young living fishes is taken into account it is plain that this experiment should be repeated, but the report adds to the uncertainty in separating young fishes into the two species.

Jubb & Skelton also found three adult three-spined fishes that on other characters they would place in *O. placidus*.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1907.7.2.19 (holotype)	151	Idunda R., trib. of Lower Busi (Mozambique)	C. F. M. Swynnerton
Malawi Fisheries collection	280	Lower Lundi R.	F. Junor
Malawi Fisheries collection (4 fishes)	240–273	Lower Lundi R.	Bernard Carp Expedition
Malawi Fisheries collection (6 fishes)	62·0–80·5	Lower Lundi R.	Bernard Carp Expedition
1952.2.20.145–149	105–109	Port Herald, Lower Shiré	R. H. Lowe

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1966.7.26.43–56	72–111	Kanjedza Lagoon, Lower Shiré	Malawi Fisheries Research Organization & E. Trewavas
1966.7.26.57–62	24.5–47.0	Kanjedza Lagoon, Lower Shiré	Malawi Fisheries Research Organization & E. Trewavas
1976.6.18.4	160	Mgobezeleni, Sodwana	M. Bruton
Albany Museum, Grahamstown AM/P 2155 (5 fishes)	106–208	Mgobezeleni, Sodwana	M. Bruton
1977.11.9.1	127	Nkuzi R., trib. of Lower Shiré	D. Tweddle
1978.8.3.2060	113	Chikwawa, Lower Shiré	Tweddle & Willoughby
1978.8.3.2092	148	Makhanga, Lower Shiré	Tweddle & Willoughby

Oreochromis placidus ruvumae (Trewavas)

Tilapia ruvumae Trewavas, 1966*b*:52

TYPE. Holotype: ♂, 134+40 mm from the Upper Ruvuma, formerly in the Tanzanian Fisheries Collection, now BMNH 1966.8.22.1 (Fig. 110). Allotype: BMNH 1966.8.22.2, from the same collection.

Description

Based on the holotype, the allotype, three other specimens in the Tanzanian Fisheries Collection, all from the Upper Ruvuma; and thirteen specimens collected at Kionga near the Ruvuma mouth by F. H. Meyer in 1898, and deposited in the Vienna Museum (NHMW 32468–32475 and 32507–32511). Two of these are now in the BMNH. A note is added on the Lake Rutamba specimens.

The Ruvuma fishes comprise 10 females, 82·5–161·5 mm SL and 8 males, 83–134 mm SL.

Proportions as % SL. Depth of body 37·5–45·0 with no apparent allometry. Length of head 34·2–36·2 in females, 33·4–37·8 in males. Length of pectoral fin 34–41. Length of caudal peduncle 9·5–11·8, 0·6–0·8 times its own depth from 100 mm SL upwards, 0·7–1·0 below this size.

Proportions as % length of head. Length of snout 31–40 in females, 30–43 in males, with a rough positive allometry in both sexes. Diameter of eye 19·5–23·6 from 100 mm SL upwards, 20–24 below this size. Depth of preorbital bone less than diameter of eye at SL up to 108 mm (♀) or 101 mm (♂), up to 23% length of head above these sizes. Interorbital width 35–39, with no apparent correlation with size of fish. Length of lower jaw 31·8–36·4 in females, 30–37 in males, 41·5 in one male with a very concave upper snout profile.

Maxillary ending in front of eye in most, but in some males extending to below anterior edge of eye.

Teeth coarser than in *O. mossambicus,* in 4–6 series in upper jaw, 4–7 in lower, 42–64 in outer row of upper jaw; outer bicuspid, inner tricuspid. In one male some outer with crowns broken off, probably by digging.

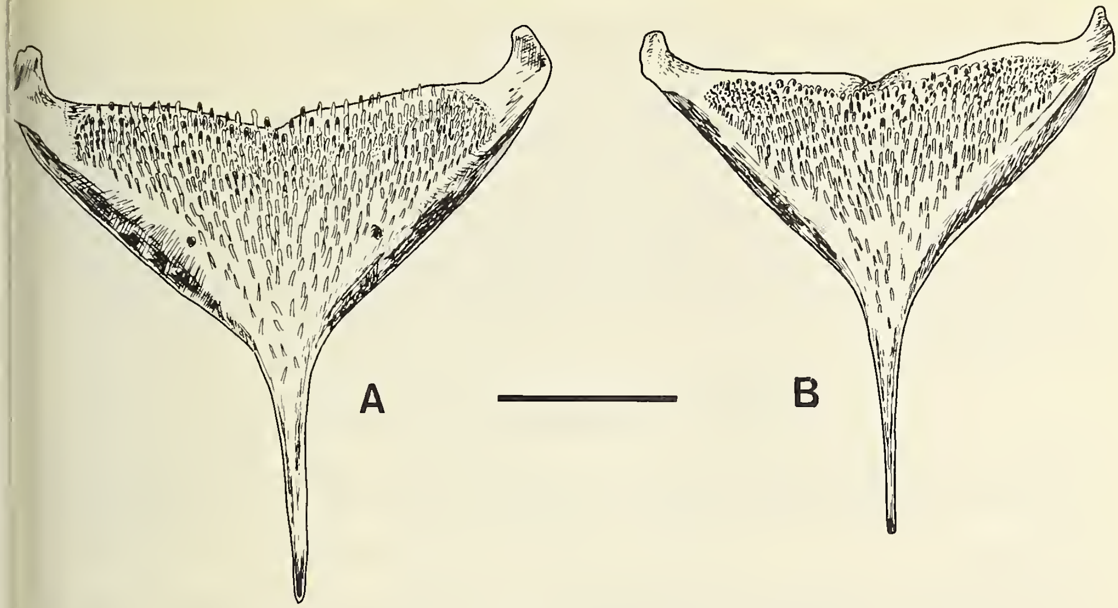


Fig. 112 Lower pharyngeal bones of *Oreochromis p. ruvumae*: A, a fish 134 mm SL; B, one of 116 mm SL.

Gill-rakers 16–18 on lower part of anterior arch, mode 17, mean (of 18 specimens) 16·9.

Lower pharyngeal bone rather large for this group of species, its width 33–36% length of head, its blade a little shorter than the median length of the toothed area, which is well covered with slender, pointed, but relatively coarse teeth.

Vertebrae 29 or 30.

Scales on cheek in 2, 3 or 2–3 rows; 30–32 in the lateral line series, 3–4 between lateral line and origin of dorsal fin, 16 or 18 around caudal peduncle.

Dorsal XVII–XIX 9–11; modal combination XVII 11 (see Table 84).

Anal III 10 in one, IV 8–10 in all the others; modal number of soft rays 10.

Size. A collector's note with the Tanzanian fisheries collection states that this species occurs throughout the Ruvuma River and does not grow much larger than these specimens.

COLORATION. Preserved Ruvuma specimens now pale, females with 1–3 small blotches mid-laterally; male darker with traces of vertical bars emphasized in a diamond shape mid-laterally; snout and throat dark; dark flecks on postorbital and occipital lateral line openings; a few spots on soft dorsal; margin of dorsal white (as preserved); caudal immaculate.

A SAMPLE FROM LAKE RUTAMBA, NEAR LINDI, TANZANIA. Two brooding females of 83 and 84·5 mm SL were collected in 1979 in the small Lake Rutamba in the Lupululu system, west of Lindi, and also about 170 young of 13–27·5 mm SL. The two adults resemble *O. p. ruvumae* rather than *O. korogwe* in the number of gill-rakers (2 + 1 + 16 in both). In proportions they agree with the above description of *O. p. ruvumae* except that the head is longer in one (38% SL), and in the same fish the pectoral is 42% SL and the eye 29·5% length of head, the lower jaw 37·5%. This brings the jaw-length up to the level in males except the one Ruvuma male whose shape shows it to be at peak sexual maturity. In one the dorsal formula is XVI 10, and the anal III 10, in the other XVIII 10 and IV 9.

The black pigment is better preserved than in the Ruvuma specimens. Narrow black vertical bars are present on the body, and there are four mid-lateral black blotches and one on the top of the caudal peduncle. The tilapia-mark is still present and in one there are two other black blotches on the base of the soft dorsal. The caudal has a few dark spots in one and irregular faint wavy vertical stripes in the other.

The 83 mm fish carried, in the mouth, several yellow eggs of long diameter 2 mm or a little more. One similar egg is under the operculum of the other.

The young have the narrow vertical bars of the body well marked and a broadly ringed black tilapia-mark. Other black blotches on the base of the dorsal fin are the basal ends of oblique bars whose distal parts are fainter. Eight young of 20–27·5 mm SL have four anal spines, the others have three. The biggest with three is 24 mm in SL. This may well indicate that the fourth ray, if it becomes a spine, only does so late in ontogeny (cf. Whitehead's observation on *O. spilurus niger*, 1962*a*).

Ecology

Nothing is known of breeding in the Ruvuma population except that the breeding male may have enlarged jaws and its genital papilla is conical with a pair of small flanges near the tip.

Distribution

The Ruvuma River on the Tanzanian–Mozambique border, from the 'Upper Ruvuma' to Kionga at the mouth; Lake Rutamba, Lupululu system, and the Lupuledi west of Lindi.

Discussion

Relationship

These populations are linked with *O. placidus* because of the prevalence of four anal spines and the relatively coarse pharyngeal dentition. The numbers of gill-rakers and geographical range also favour its relationship to *O. placidus* rather than to *O. korogwe*, which it also resembles.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1966.8.22.1–2 (holotype & allotype)	106, 134	Upper Ruvuma	Tanzanian Fisheries personnel
Tanzanian Fisheries Collection Illonga (3 specimens)	108·0–161·5	Upper Ruvuma	As above
1957.12.3.10–11	99, 102	Kionga, Ruvuma	F. H. Meyer (NHMW, exchange)
NHMW 32470–32475 & 32507–32511	82·5–101·0	Kionga, Ruvuma	F. H. Meyer
1982.1.12.1–2	83, 84·5	Lake Rutamba, Lupululu system, Tanzania	G. Bernascek
1982.1.12.7–31	13·0–27·5	Lake Rutamba	G. Bernascek

Oreochromis shiranus (Boulenger)

For bibliography and synonymy see the subspecies, of which there are two.

Distinguishing characters of the superspecies

Usually IV anal spines, rarely III or V.

Vertebrae 29 or 30; scales in lateral line series 31 or 32, rarely 33.

Lower gill-rakers 16–21, usually 17–19.

Jaws enlarged in big mature males, but outer teeth mostly remaining bicuspid.

Genital papilla of male simple.

Length of pharyngeal bone from a little less to a little more than its width; blade 0·8–1·26 length of toothed area (Table 88). Teeth slender and firm (Figs 114, 116 & 117).

Caudal fin scaly, but less densely than in the *O. squamipinnis* group.

Coloration: see the subspecies. Breeding male becoming very dark to black, but not with white lower parts of head.

Distribution

Lake Malawi basin and Upper Shiré; Lakes Chilwa and Chiuta.

Subspecies

Oreochromis shiranus shiranus (Boulenger): The Shire above the Murchison Rapids, and its tributaries; Lake Malawi and its tributary rivers, streams and lagoons; Upper Shire. The few caught at Chikwawa were mostly damaged (Tweddle & Willoughby, 1979).

Oreochromis shiranus chilwae (Trewavas): Lake Chilwa and its basin; Lake Chiuta? The subspecies are distinguished by the following characters.

(*a*) Coloration. *Oreochromis s. shiranus* is predominantly dark olive green with bright yellow or white ventral surface; margins of dorsal and caudal fins in mature males are bright orange-coloured. *Oreochromis s. chilwae* in Lake Chilwa is more silvery in general colour, with red instead of orange-coloured margins to dorsal and caudal fins. Coloration in the Chiuta population is similar to that of *O. s. shiranus.*

(*b*) Size. *Oreochromis s. shiranus* is commonly found up to TL 36 or 37 cm, but *O. s. chilwae* rarely exceeds 25 cm, although occasional individuals have been reported at 32 and even 39 cm (Furse, 1979).

(*c*) The size of the eggs, reported (Kirk, 1967*b*:304; *idem*, *in* Furse *et al.* 1979:191) as $3{\cdot}5 \times 2{\cdot}7$ mm in *O. s. shiranus*, and $2{\cdot}5 \times 2{\cdot}0$ mm in *O. s. chilwae.*

(*d*) Proportions. Tables 86 & 87 show little difference except in the maximum ratios of depth of body and the minimum interorbital width. Fig. 117 shows that although the fishes with deepest bodies and narrowest interorbital spaces are from Lake Chilwa the zone of overlap is wide, and the Lake Chiuta examples do not conform to this division.

(*e*) The mean numbers of spines and soft rays in the dorsal fin. Table 89 shows that the samples from Lakes Chilwa and Chiuta have more spines and fewer soft rays than *O. s. shiranus.*

On the status of these populations see 'Discussion' on pp. 353–5.

Oreochromis shiranus shiranus Boulenger

Oreochromis shiranus Boulenger, 1896:916, fig. (Shiré R.).
Tilapia shirana; Boulenger, 1898:4; *idem*, 1899:111; *idem*, 1915:151, fig. 98 (excl. no. 8 in list on p. 152);

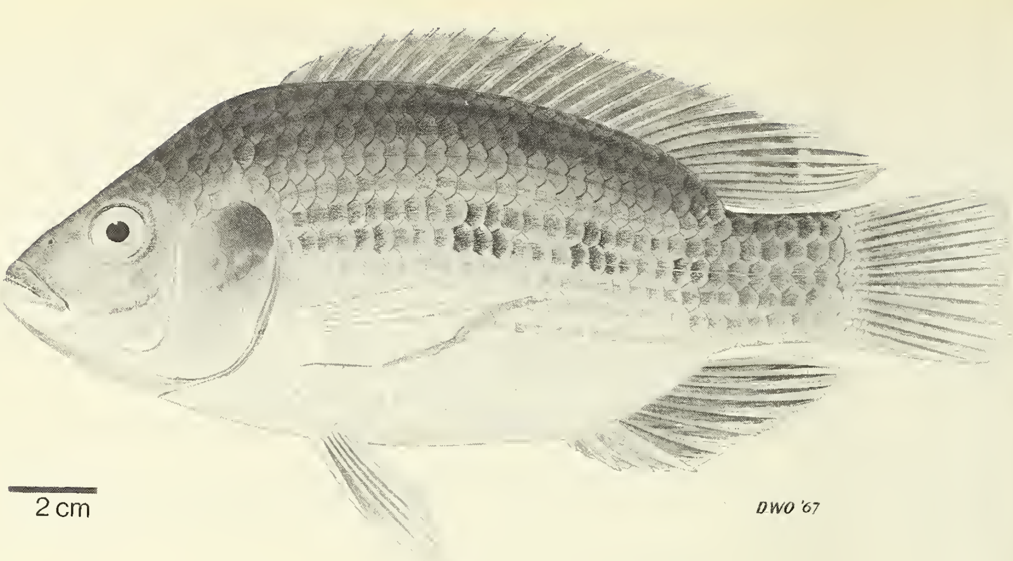


Fig. 113 *Oreochromis shiranus shiranus*, female from Liwonde, Upper Shiré.

Regan, 1922*a*:677; Trewavas, 1941:295; Bertram *et al.*, 1942:37–39, 89–112; Lowe, 1952:3, 10, 24–26, 31–36, 57, 110, 112, pls 1B, 2B (nest), 3C; *idem*, 1953:1035–1041; Fryer, 1956:5; Jackson, 1961*c*:557; Jackson *et al.*, 1963:68 (key); Jubb, 1940*a*:10 (Shiré R.); Kirk, 1967*a* & *b*; Goldstein, 1973:249 (photo).

Tilapia (Sarotherodon) shirana shirana; Trewavas, 1966*b*:52; *idem*, 1966*c*:418–9.

Sarotherodon shiranus shiranus; Furse *in* Furse *et al.*, 1979:191, fig. 11.3; Kirk, *in* Furse *et al.*, 1979:202 (comparison with *S. s. chilwae*).

Sarotherodon shiranus; Tweddle *et al.*, 1979:7–9; Tweddle & Willoughby, 1979:19, 21 (Murchison Rapids).

Tilapia placida (part, *non* Trewavas, 1941); Trewavas, 1961*b*:55 (Mpatamanga Gorge, Shiré R.).

Types. Syntypes: Six specimens of 92–225 mm SL from Upper Shiré River, coll. P. Rendall, BMNH.

Description

Based on 30 fishes of 85–245 mm SL from Lake Malawi and the Upper Shiré.

Proportions and meristic numbers: see Tables 86, 88 and 89.

Of seventeen fishes over 140 mm SL only six have the lower jaw measuring 38% length of head or more. Of these the smallest (143 mm) could not be sexed because it was gutted and the genital papilla damaged. All the others were males and the only one recorded as 'ripe' was a 230 mm dark fish from the Upper Shiré at Liwonde, with lower jaw 44·6% length of head. In a dark fish of 193 mm it was 44·8%.

Gill-rakers (2–4) + 1 + (17–21), mode 19 on the lower part of the arch.

Teeth of jaws in 5–7 rows in fishes of 150 mm SL and over, 4–5 in smaller; outer bicuspid, inner tricuspid.

Vertebrae 30 (seven specimens: 15 + 15 in five, 16 + 14, 14 + 16).

Scales 31 or 32 (33) in lateral line series, $3\frac{1}{2}$ or 4 between origin of dorsal and lateral line, 4–7 between bases of pectoral and pelvic fins; in 2–3 rows on the cheek.

Anal IV 9–11, rarely with III spines, exceptionally with V. Caudal fin truncate with rounded corners, usually shorter than in Lakes Chilwa and Chiuta; scaly only on the rays and between their bases. This contrasts with the densely scaled caudal of the Malawi species of the subgenus

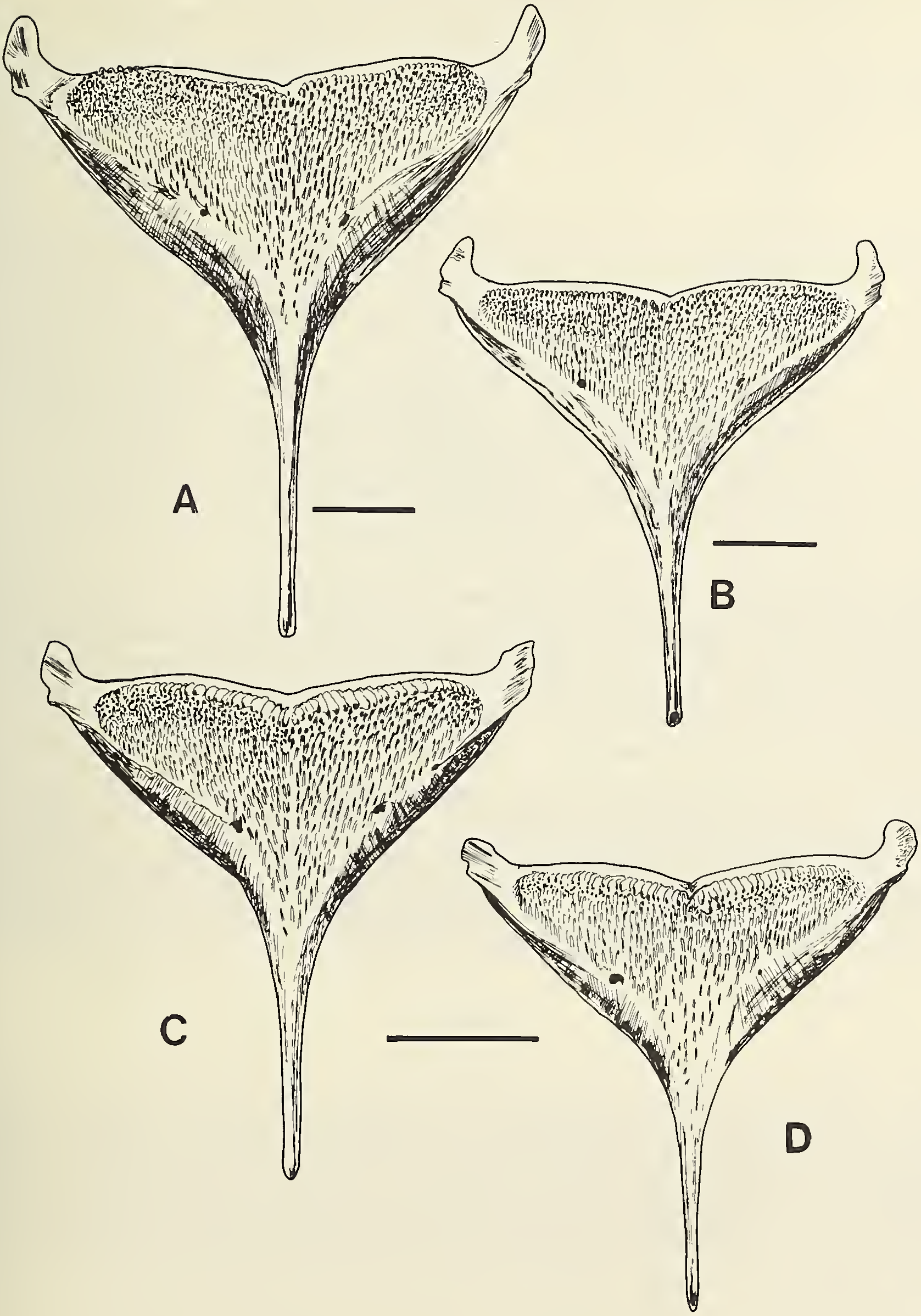


Fig. 114 Lower pharyngeal bones of *Oreochromis s. shiranus*: A, a fish of 255 mm SL; B, one of 183·5 mm SL; C, one of 147·5 mm SL; D, one of 140 mm SL. Scales = 5 mm.

Table 86. *Oreochromis shiranus shiranus.* Proportions in three size-groups.

SL (mm)	80–122	132–166	182–245
N	9	9	12
Proportions as % SL			
Depth	38–45	40–44	36·5–45·0
L. head	32·5–34·5	32·0–35·5	33·0–34·0
L. pect. fin	33·3–39·3	31·5–38·0	33·0–38·5
L. caud. ped.	11·8–14·3	11·0–14·5	11·0–13·0
D. caud. ped.	13·7–15·5	13·7–15·5	13·7–14·5
Caud. ped. l/d.	0·81–0·97	0·75–1·0	0·75–0·9
Proportions as % l. head			
L. snout	29·5–33·3	33·0–39·0	33·0–42·0
Eye	20·7–25·6	20·5–24·8	17·5–21·5
D. preorb.	20·1–21·0	20·8–23·5	22·5–27·3
Interorb.	36·4–44·0	39·0–43·0	39·5–44·5
Lower jaw	29·0–37·0	33·0–40·4	34·0–44·6

Nyasalapia (see p. 460), but that *O. shiranus* in Lake Malawi may not be immune to attacks of the scale-eating *Corematodus* is suggested by the fact that the fin is usually shorter in Lake Malawi specimens than in those of Lakes Chilwa and Chiuta, where this marauder is not present (Fig. 115).

Genital papilla of male not tasselled, but in some with a thick, scalloped narrow flange.

Size. Maximum recorded 37 cm TL.

Coloration. See p. 343. A dark mid-lateral band may be present, entire or broken, and a series of spots near the upper lateral line. In breeding males these are masked by the general dark green to black colour. The orange colour of the dorsal and caudal fin-margins is characteristic. Aquarium specimens seen by me lacked the rich olive and yellow colouring of wild fishes and had a basic buff shade. The photo by M. Oliver in Goldstein (1973:249), shows a basic golden-yellow colour with green vertical fins; this was a young fish.

Ecology

Food

The stomachs examined contained microscopic algae usually mixed with a high proportion of vascular plant fragments. *Oreochromis s. shiranus* feeds on the epiphytic growths of the submerged parts of aquatic plants at the edges of reed-beds and sudd, and is reported by owners of rice-fields to eat the young rice shoots. When phytoplankton is abundant, as at times when the lake surface is clouded with the teeming vegetative phase of *Anabaena*, a diet of pure plankton may be taken.

Growth

Lowe (1952: fig. 8 & table 2) estimated the growth-rate by means of zones on the opercular bones and the progression of length-frequency modes. She concluded that the average lengths attained in the first four years were respectively 10·0, 18·0, 22·0 and 25·5 cm, and weights 16, 110, 210 and 342 g. There was some evidence that males grew faster than females. Faster growth was made by the first generation of this species in a newly stocked dam, where they reached 16–22 cm (mode 19 cm) in 11–12 months, but as Lowe pointed out (1952:20) this was newly flooded land where growth may be expected to be above average.

The maximum length observed by Lowe in the lake, the estuaries and the Shiré was 29 cm, but the Christy collection includes some of 30 cm and other reports, including some from Chia Lagoon, increase the range to 37 cm.

Breeding

Information is obtained from Ricardo-Bertram *et al.* (1942), Lowe (1952), and Fryer (1956).

In the southern part of Lake Malawi the main breeding season is from September to March, possibly with two peaks. Farther north the season extends into April.

In the main lake females breed from 17 cm TL (c. 135 mm SL) and males from 22 cm (180 mm SL), and these were believed to be in their second and third years respectively (Lowe, 1952). In Lake Kingiri a male of 14·5 cm (115 mm SL) was found to have enlarging testes about 3·5 mm wide, showing that precocious breeding occurs in this population (see also *O. lidole* from this lake, p. 479). In a pool in the Mpatamanga Gorge (Shiré River in the course of the Murchison Rapids), ripening male and female respectively of 100 and 81·5 mm SL were found by Jubb.

Basin-shaped nests have been found in places where circumstantial evidence pointed to their purtenance to this species (Lowe, 1952:34, pl. 2B). They are made in shallow water from 15 cm to 1·5 m deep, in sand or sand-banks overlaid with light mud in the neighbourhood of reeds or other rooted plants near the lake shore or in creeks or estuaries. When a stocked dam was drained, nests were found about 4 m below the surface. The diameter is from 50 to 90 cm, probably according to the size of the fish, the depth of the basin 15 cm below the substrate level and the rim raised about 7–8 cm. The nests observed were a metre or so apart (Lowe). Territorial males are not necessarily in nuptial coloration. Lowe records seeing males in pale colours defending nests. Although there may be some wear on the crowns of the teeth there is no sign of replacement of bicuspid by unicuspid teeth.

Ripe eggs are yellow, pear-shaped, of long diameter 3–4 mm (Lowe), or measuring 3·5 × 2·7 mm (Kirk). Lowe counted 520–618 ripe ovarian eggs per fish in three of TL 20–21 cm.

Females brood eggs and young in the mouth until the young reach a length of about 10 mm. Brooding females have not been caught over the nests but only in basket traps set in the reeds, and it is evident that it is to such localities that they retire after spawning.

Young up to about 10 cm TL are common among fringing vegetation or in sudd channels.

Habitat

This is one of the commonest fishes in the Lake Malawi basin and is especially abundant in reedy lagoons and estuaries, where it is caught in traps and scoop-nets. It is also an almost constant constituent of seine hauls on sandy beaches. Lowe reported that the largest specimens seen by her were in Chia Lagoon, an extremely eutrophic expansion of a short river entering Lake Malawi south of Kota Kota and Sani. It is characteristic of zones III and IV of Jackson *et al.* (1963). It adapts well to dams and ponds and has been found (probably introduced) in Lake Kingiri, a crater lake a few kilometers north of Lake Malawi.

In the Upper Shiré, Lake Malombe and the reedy shores of the slow-flowing river provide a favourable habitat, as does the barrage lake at Liwonde. Tweddle *et al.* (1979) found it at many sites in the course of the Murchison Rapids and even below the Kapachira Falls. But it was restricted to sheltered places such as among the roots of fringing vegetation, which it was induced to leave only by electro-fishing. At the lower sites most individuals were in poor condition and damaged, a result, as their captors remarked, either of their rough passage or of failure to compete with the Lower Shiré fauna.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1896.10.5.1 (syntype)	225	Upper Shiré R.	coll. Rendall, pres. Johnston
1896.10.5.12–16 (syntypes)	92–176	Upper Shiré R.	coll. Rendall, pres. Johnston
1906.9.7.27–28 (29, skel.)	174–218	'L. Nyasa'	Moore
1921.9.6.72–74	132–208	'L. Nyasa'	Wood
1935.6.14.87–96	102–220	Shiré Bar, L. Malawi	Christy, 1925
1935.6.14.97–98	225, 235	Vua, L. Malawi	Christy, 1925
1935.6.14.99–104	88–150	Mwaya, L. Malawi	Christy, 1925
1935.6.14.105–110	145–212	Deep Bay, L. Malawi	Christy, 1925
1935.6.14.111–116	120–245	Shiré Bar, L. Malawi	Christy, 1925
1935.6.14.117	223	SW arm of L. Malawi	Christy, 1925
1935.6.14.118–122	79–242	Karonga, L. Malawi	Christy, 1925
1935.6.14.123–126	90–152	Nyungwe, L. Malawi	Christy, 1925
1935.6.14.2428–2435	75–250	Karonga (no. 1763) and SE arm of L. Malawi	Christy, 1925
1943.9.9.4	110	SW arm of L. Malawi	Christy, 1925
1952.2.20.143–144	153, 174	Lilongwe, Malawi	Lowe (1946–7)
1960.2.26.5–11	25–100	Mapatamanga Gorge, Shiré R.	Jubb
1966.7.25.3–9	120–230	Liwonde, Upper Shiré	Malawi Fisheries Research Unit and E. Trewavas
1966.12.9.14–15	115, 147	L. Kingiri, N. of L. Malawi	Albrecht
1972.8.25.40–45	80–193	Kagodze R., trib. of Shiré R.	Tweddle
1977.8.25.46–55	122–166	L. Chiuta	coll. Tarbit, pres. Tweddle
1966.7.20.1–10	40–146	L. Chiuta	Maclean Chirwa & R. G. Kirk
1967.3.3.15, 16	82, 89	L. Chiuta	Maclean Chirwa & R. G. Kirk
1978.8.3.2062–7	30·0–60·5	L. Chiuta	Pyart, Snucins, Tweddle & Willoughby

Oreochromis shiranus chilwae (Trewavas)

Tilapia sp., near *mossambicus*; Lowe, 1952:87 (L. Chilwa)
Tilapia (Sarotherodon) shiranus chilwae Trewavas, 1966*b*:52; *idem*, 1966*d*:419; Kirk, 1967*a*; *idem*, 1967*b*; Kalk, 1970; Morgan, 1971; Furse *et al.*, 1979:191 ff., fig. 11.3 (general biology); Loiselle, 1979: fig. (colour photo, aquarium).

TYPES. Holotype: male, 145 + 43 mm; allotype; female, 133·5 + 40·0 mm, coll. Mr Robert Kirk in Lake Chilwa, BMNH 1966.7.19.1–2. Paratypes: 18 adults and 10 young collected at the same time and place as the holotype.

Description

Based on 27 specimens of 109–168 mm SL from Lake Chilwa, collected in 1946 and 1965.

Proportions. See Table 87 and Fig. 118. Fig. 118 shows the tendency to a rather deep body and narrow interorbital space. Of 15 fishes over 130 mm in SL 10 were males, and in 9 of them the lower jaw measured 38% length of head or more; the 5 females had the jaw 33·0–37·5%, and in the tenth male (164 mm SL) the measurement was 35·2%. The measurements of eye and preorbital bone were about equal at 124–134 mm SL, when both were 19·5–21·5% length of head.

Teeth in 4–6 series, outer bicuspid, inner tricuspid, 42–68 in outer row of upper jaw. In a male of 168 mm SL some outer teeth had the minor cusp reduced; in one of 146 mm the outer row included a few unicuspids.

Pharyngeal teeth, see Figs 116 & 117 and Table 88.

Vertebrae 29 (f.3) or 30 (f.17).

Scales in 2 or (usually) 3 rows on cheek, 31–32 (33) in lateral line series, 4–4½ from origin of dorsal to lateral line, 5–7 between bases of pectoral and pelvic fins.

Dorsal rays see Table 89. Anal usually IV 9–11, III 9 in one, V 10 in one. The specimens with III and V spines were both in the sample collected by Lowe in 1946. Messrs Eccles and Kirk have examined 2000 specimens without finding a single variant from IV. Caudal truncate or very slightly emarginate, scaly only at the base.

Coloration. The tilapia-mark may be visible up to 8 cm TL, but not above this size. Adults yellowish silvery, greenish on back, with a dark mid-lateral band or series of spots and also a more dorsal series. A broad red caudal margin and in bigger fishes a bright orange-red margin to the dorsal fin. Breeding males darker and iridescent, with black lower parts of head, throat and belly and dusky lower fins (Furse *et al.*, 1979, fig. 11.3; Loiselle, 1979) but with no yellow colouring. Ripe females also becoming more dusky, with the red of the caudal fin intensified. Genital papilla white in both sexes.

A sample from Lake Chiuta. From Table 89 it appears that the Chiuta sample shares with *O. s. chilwae* the high average number of dorsal spines, but Fig. 118 shows that the narrow differences in proportions that distinguish *O. s. chilwae* from *O. s. shiranus* do not characterize the Chiuta samples. Mr D. Tweddle says (pers. commn) that he cannot distinguish the Chiuta fishes in the field from *O. s. shiranus* of the Lake Malawi basin. Even the yellow ventral colouring is present in Lake Chiuta.

Ecology

Growth

Furse *et al.* (1979) record that as the lake recovered young *O. s. chilwae* of 2–3 cm were found in January and February. By November of the same year the modal length had risen to 10 cm.

Salinity tolerance

The resistance of the subspecies to increased alkalinity was tested (Furse *et al.*) in comparison with that of *Tilapia rendalli*. It was found to be higher but not as high as that of *O. alcalicus*. It is therefore well adjusted to its peculiar environment.

Breeding

Mature males are distinguished by the coloration and the enlarged jaws (see above). The breeding season is September to May, with a peak in November–January. In aquaria, ponds and streams

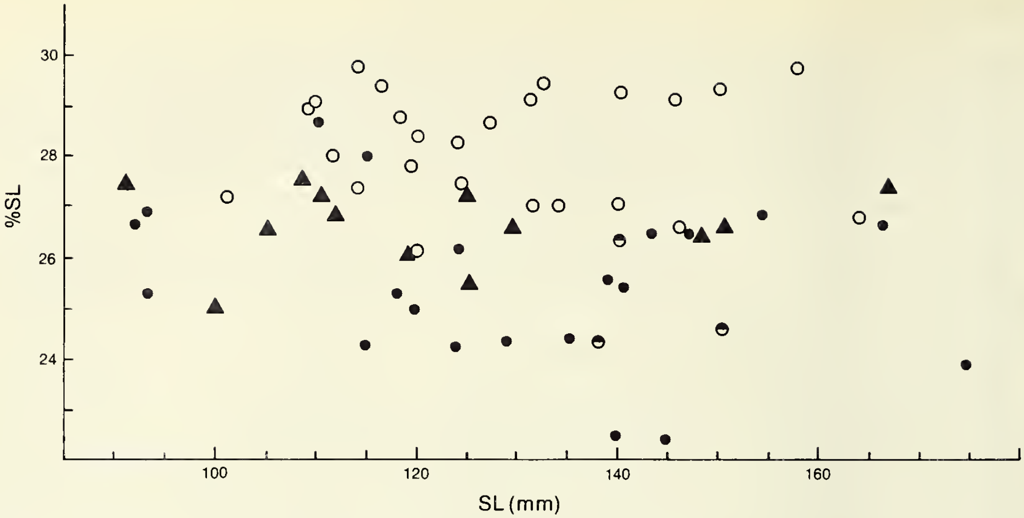


Fig. 115 Length of caudal fin in *Oreochromis shiranus*. ●, Lake Malawi; ◓, River Koyodzi; ○, Lake Chilwa; ▲, Lake Chiuta.

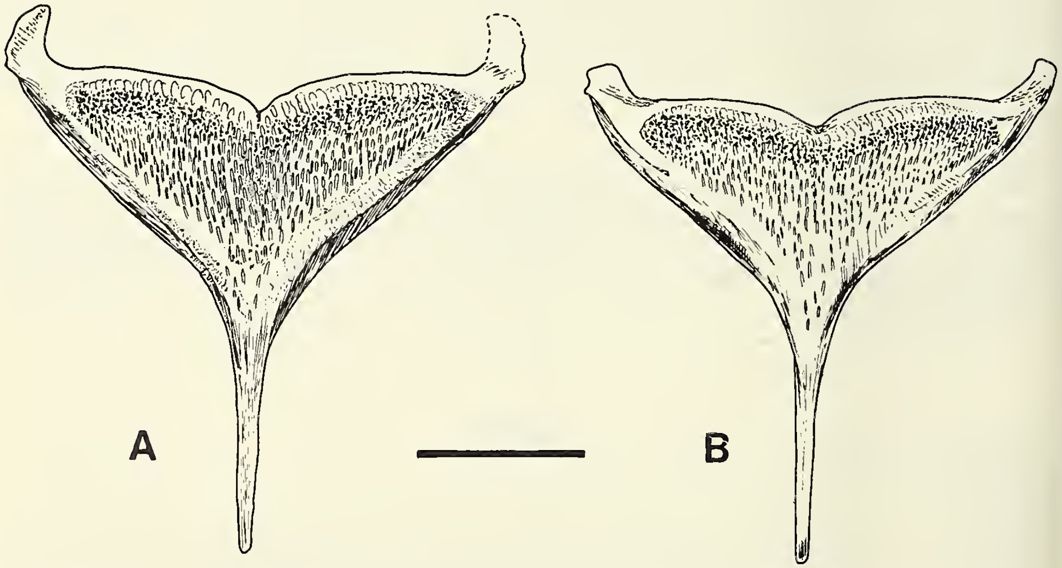


Fig. 116 *Oreochromis shiranus* from Lake Chiuta. Lower pharyngeal bones of: A, a fish of 135 mm SL; B, one of 123 mm SL. Scale = 5 mm.

the fish breeds at a length of 100 mm, but in Lake Chilwa breeding begins early in the second year of life at 125 mm (female) or 150 mm (male). The nest is a simple saucer shape and the long diameter of the eggs is 2·6–2·7 mm. A female of 150 mm SL carried orange-yolked embryos in her mouth, the yolks measuring 2·6 mm.

Furse (*in* Furse *et al.*, 1979) records that the embryos remain in the maternal mouth for 14 days, after which they leave the mouth for temporary forays for a further week. They are then

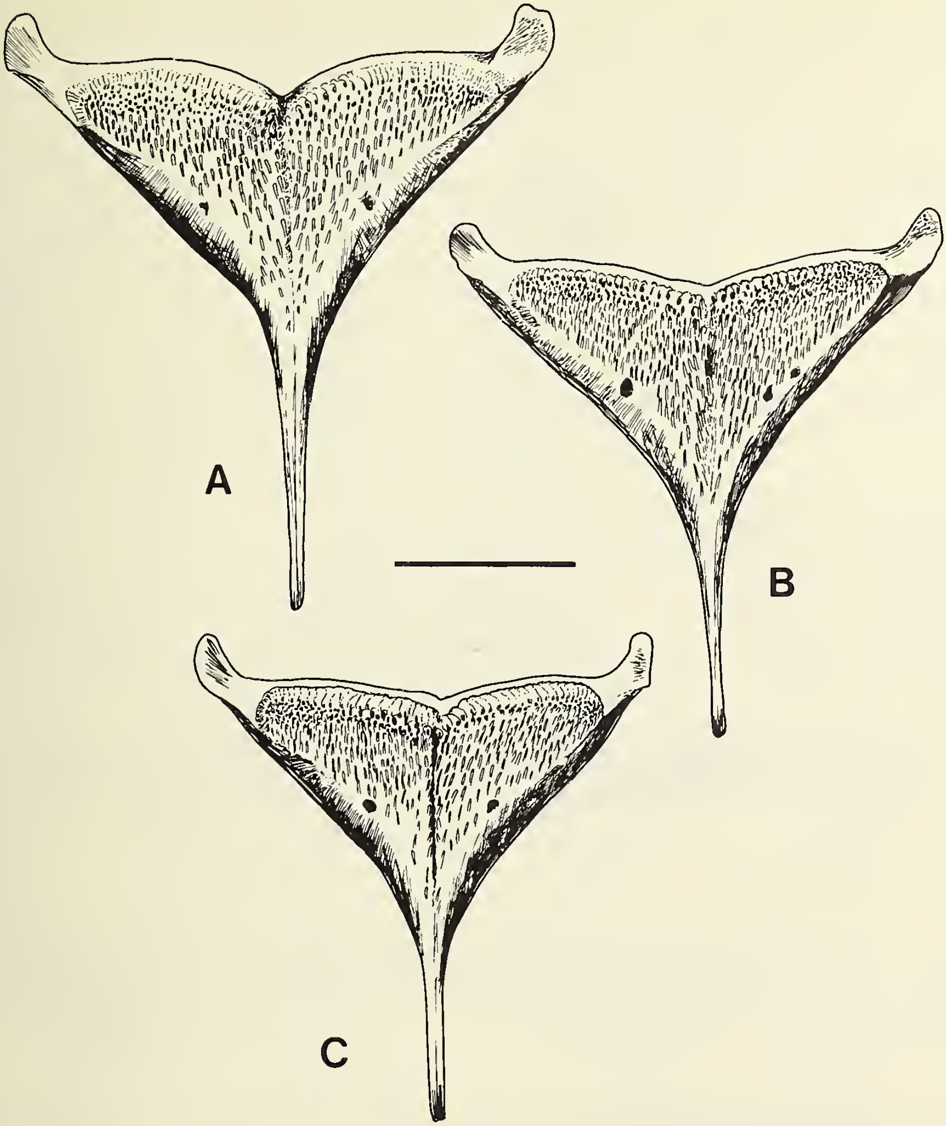


Fig. 117 *Oreochromis shiranus chilwae* from Lake Chilwa. Pharyngeal bones of: A, a fish of 133 mm SL; B, one of 123 mm SL; C, one of 115 mm SL. Scale = 5 mm.

10 mm long and become independent, but the yolk is not fully absorbed until they are 14 mm long, 32 days after being spawned.

In 90 days the young have reached 40–50 mm (temperature not given).

Habitat

Lake Chilwa (= Shirwa) as an ecological system has been well studied and documented, especially with regard to its fishery, by Kirk (1967*a* & *b*; 1970), Kalk (1970, 1971). A. Morgan

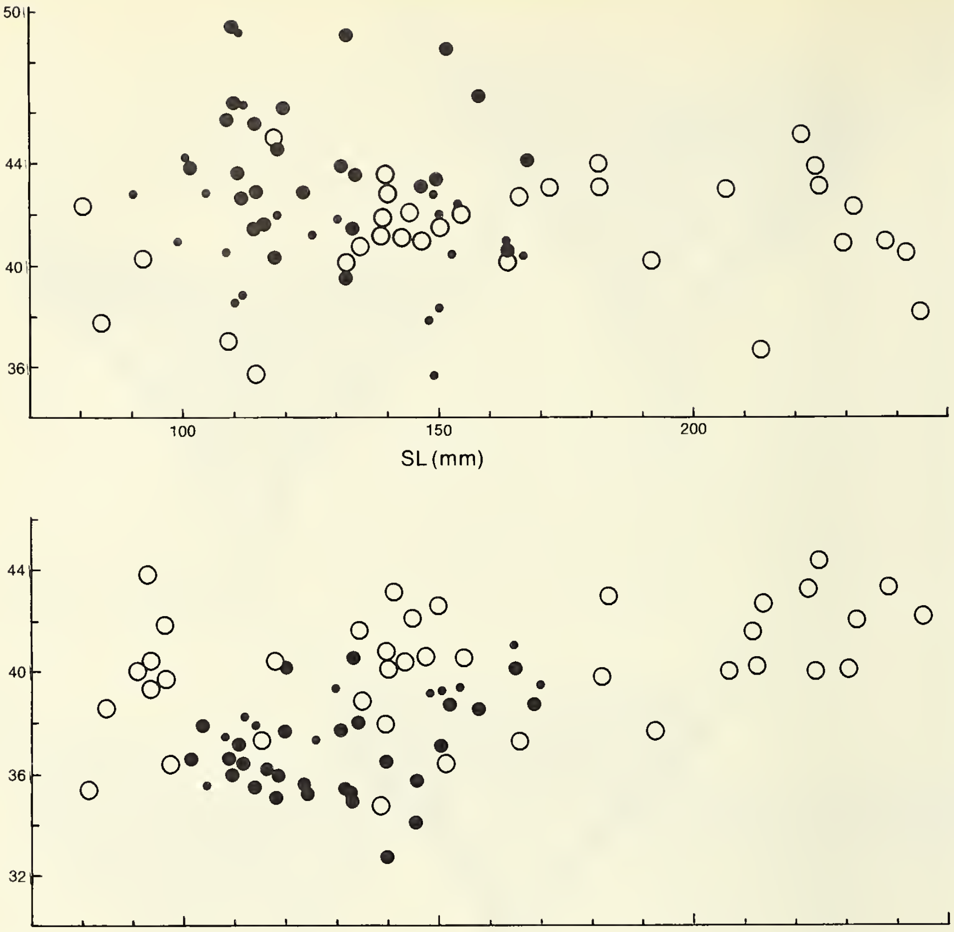


Fig. 118 *Oreochromis shiranus.* Above: depth of body as % of SL. Below: interorbital width as % length of head. ○, *O. s. shiranus*, Lake Malawi basin; ●, *O. s. chilwae* from Lake Chilwa; •, a sample from Lake Chiuta.

& Kalk (1970), P. R. Morgan (1971) and Mzumara (1967). This knowledge has been brought together by the same authors and others in the book edited by Kalk *et al.* (1979). See also Beadle, 1974: 277 ff., figs 19. 5–8, and Fig. 119 herewith.

The lake is a closed basin, when full with about 700 km² of open water, and a volcanic island, Chisi, within it. The depth does not exceed 3 m and the water is saline, evaporation being the only means of loss. Periodically it shrinks and dries up—the last 'death' was in 1967. During the course of its shrinkage mass mortalities of *O. s. chilwae* occurred by asphyxiation as the strong SE winds stirred the deoxygenated bottom mud into the shallow water. As shrinkage continued the alkalinity increased to an extent that resulted in the death of the algae *Oscillatoria* and *Anabaena*, and their replacement by a bloom of *Arthrospira* and *Spirulina*; both events causing depletion of oxygen and further mortality. The survivors took refuge in the surrounding springs, pools and lagoons, and bred there (Furse *et al.*, 1979). When the lake recovered they returned and Furse *et al.* record that it took three years for the population to yield its previous proportion of the fishery.

Table 87. *Oreochromis shiranus chilwae*, and a sample from Lake Chiuta. Proportions in two size-groups of each. The numbers in brackets are from the 57·5 mm fish.

	Lake Chilwa		Lake Chiuta	
SL (mm)	101–120	124–164	57·5–119	126–167
N	13	18	9	8
Proportions as % SL				
Depth	40·3–49·5	39·5–49·0	38·4–43·0	35·7–42·8
L. head	31·2–35·6	31·4–35·4	32·3–35·2	33·5–35·3
L. pect. fin.	31·0–37·4	33·0–36·5	34·0–38·6	32·0–38·6
L. caud. ped.	11·5–13·6	10·0–13·3	(15·7)10·8–12·8	10·7–12·7
D. caud. ped.	13·5–15·2	13·5–15·2	12·0–14·8	13·4–14·6
Caud. ped. l/d	0·7–1·0	0·7–0·97	0·8–0·95	0·76–0·9
Proportions as % l. head				
L. snout	33·0–36·8	34·0–40·5	30·3–35·1	36·7–38·3
Eye	20·0–25·5	17·7–21·6	(28·2)23·3–25·0	21·1–24·2
D. preorb.	18·8–22·0	19·8–24·0	18·0–21·1	19·0–23·4
Interorb.	35·0–39·5	32·7–40·7	33·3–38·3	35·0–39·5
Lower jaw	29·0–37·3	33·2–41·2	30·3–35·6	35·0–40·7

Table 88. *Oreochromis shiranus*: dimensions of lower pharyngeal bone in different populations. The last item is the ratio of length of blade to median length of dentigerous area.

	O. s. shiranus	Lake Chilwa	Lake Chiuta
N	13	14	9
SL (mm)	92–230	112–168	91–167
Pharyngeal			
Length % head	29·6–31·7	(24·3)27·6–32·9	30·4–33·8
Width % head	29·8–32·5	29·2–33·7	32·1–34·8
Length/width	0·9–1·06	0·8–1·0	0·9–0·98
blade/dent.	0·8–1·26	0·9–1·2	0·8–1·04

Discussion

Different opinions have been held concerning the geological history of Lake Chilwa, but Lancaster (1979) states that there is no evidence to support the suggestions of Dixie (1926), and of Garson & Walshaw (1969) that the Proto-Chilwa was linked to Lake Malawi and that the Malawi-Chilwa system drained independently to the Indian Ocean near Quelimane. Neither Chilwa nor Chiuta harbours any of the endemic species of Lake Malawi other than *O. shiranus*. *Astatotilapia callipterus* (Günther), which is common to the two basins, is a member of the marginal fauna of Lake Malawi and is found in streams and lagoons in its basin. It is possibly synonymous with and certainly closely related to, *Astatotilapia swynnertoni* of R. Busi and some other

Table 89. *Oreochromis shiranus.* Meristic characters in subspecies and populations.

	O. s. shiranus		*O. s. chilwae*	
	L. Malawi	R. Koyodzi	Chilwa	Chiuta
XV 12	1			
XVI 11	6	1		
XVII 10	1	1	3	3
XV 13	1			
XVI 12	8		1	
XVII 11	8	1	7	3
XVIII 10			2	7
XVII 12	9	1	12	
XVIII 11	1		13	10
XVII 13	1	1		
XVIII 12		1	1	1
XIX 11			1	
Dorsal totals				
27	8	2	3	3
28	17	1	10	10
29	10	1	25	10
30	1	2	2	1
Dorsal spines				
XV	2			
XVI	14	1	1	
XVII	19	4	22	6
XVIII	1	1	16	18
XIX			1	
Gill-rakers (lower)				
16		2	3	2
17	1		7	8
18	8	2	13	4
19	10	2	4	5
20	5			
21	2			

eastward rivers of Mozambique (Bell-Cross, 1976:201; Greenwood, 1979:284). The fish fauna, therefore, gives no reason to postulate a connection with Lake Malawi–Upper Shiré waters since the northern and southern parts have united to form the present Lake Malawi, a Pleistocene event (Dixie, 1926).

Lake Chiuta is today separated from Lake Chilwa by swampy land across which a sandy ridge divides the two basins even when Chilwa is full. But at least one of the former shore-lines traced by Lancaster (1979, fig. 2; & Fig. 118, based on Lancaster) is continuous between the two lakes.

Lancaster recalls that at the close of the Cretaceous (65–70 million years ago), the region now occupied by the Upper Shiré and the Shiré Highlands was a broad up-arched area. Drainage from it flowed north and east to an ancestral Phalombe–Lugenda River. It was later, in the Tertiary, that rifting lowered the Upper Shiré Valley and eventually the drainage from the Shiré Highlands was separated into the westward to the Upper Shiré and the eastward to the Chilwa–Chiuta depression.

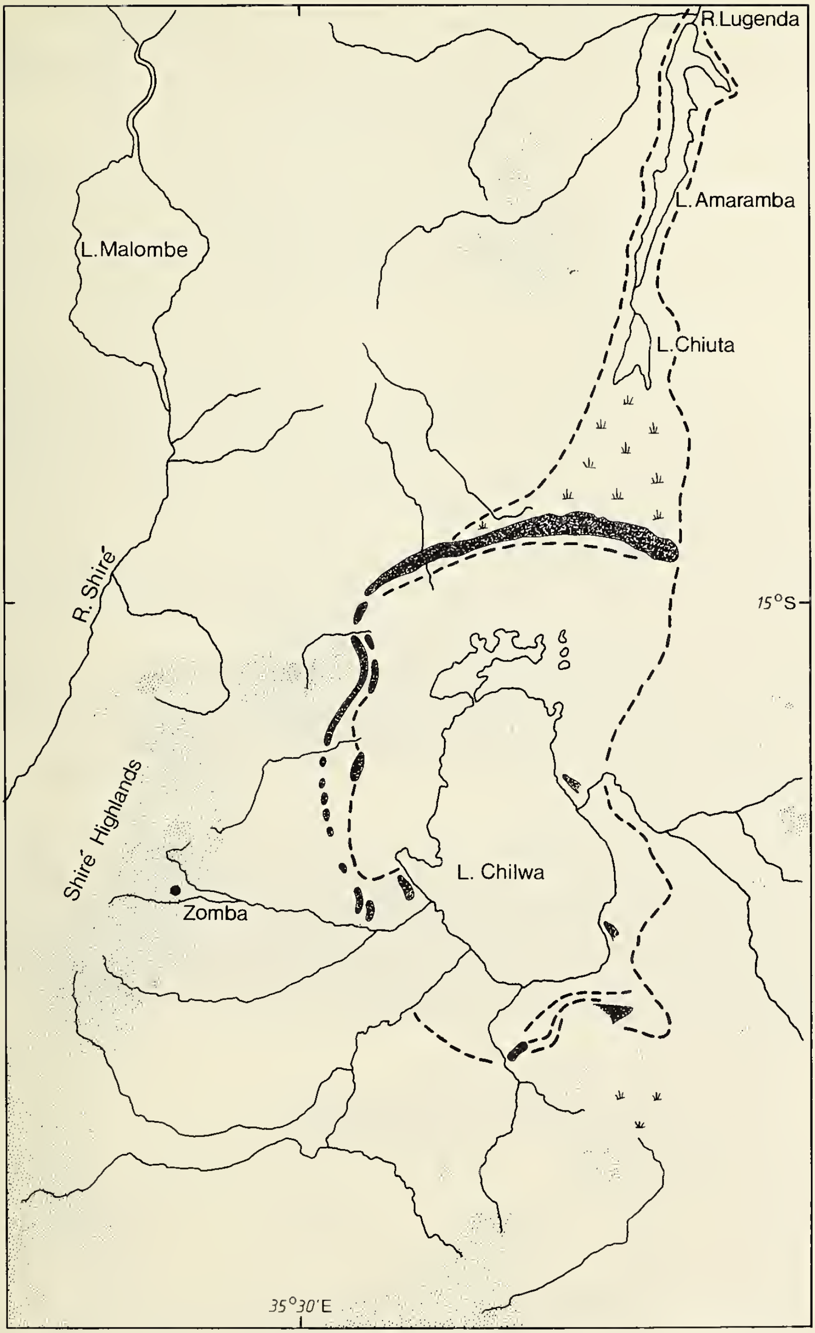


Fig. 119 Lake Chilwa and its surroundings, based on the map of Lancaster, 1979, fig. 2.6. Light shading, land over 1000 m above sea level; dark shading, the sand bar.

We have no direct evidence of the nature of the Tertiary fish fauna of the region, but it seems possible that *O. shiranus* already existed there as the highland representative of *O. placidus*, and that whatever there is in common between the Upper Shiré and the Chilwa–Chiuta system was already so before the complete separation of the two drainage systems, and well before the extension southwards of Lake Malawi and its characteristic endemic fish fauna.

Lakes Chilwa and Chiuta were both originally open lakes and would provide normal habitats for *O. shiranus.* Lake Chilwa much later became closed by the formation of the sand-ridge and its inbred population of *O. shiranus* would become modified in response to the increasing salinity of the waters. Until then, connection with the Chiuta population, and the older separation of both from the Shiré population, left their mark in the higher mean number of dorsal spines in both Chilwa and Chiuta as compared with the Shiré population; but otherwise, closer resemblance between the Chiuta and Shiré fishes reflects the similarity of the habitats.

Whether or not the special features of the Chilwa *O. shiranus* have become genetically fixed is a question still unanswered. The colour-difference—red instead of orange for the fin margins—loses value in the light of the existence of the same difference in colour between the fin markings of *Astatotilapia callipterus* (Günther) of Lake Malawi basin and Lake Chilwa (pointed out to me by D. Eccles in 1965). How constant may be the presence or absence of the black pigmentation of the belly in breeding males, illustrated in Dr Digby Lewis's drawing in Furse *et al.* (1979, fig. 11.3), is not recorded.

Tarbit (1972) found slight differences in serum esterases between the two subspecies and Kirk (*in* Kalk *et al.*, 1979:205), who has seen the full script of which only the abstract is published, states also that the chemical resemblances found by Tarbit support their nearer relationship to each other than to any other species investigated by Tarbit.

I therefore retain the subspecific names as a record of the present state of our understanding of these related populations, but note that there is less reason for recognizing the Lake Chiuta population than that of Lake Chilwa as distinct from the nominate subspecies.

Affinities of *O. shiranus*

The enlargement of the jaws in mature males, the simple genital papilla and the presence of IV anal spines indicate relationship with *O. mossambicus* and *O. placidus* of the Lower Shiré, Lower Zambezi and the eastern coastal rivers. Although *O. mossambicus* has only three anal spines, it belongs to the group of species in which an increased number of anal spines may be a fixed or variable character. The relationship supports the theory that *O. shiranus*, unlike the tasselled species, entered Lake Malawi from the south.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
O. shiranus chilwae			
1966.7.19.1–2 (holotype and allotype)	146, 133	L. Chilwa	R. G. Kirk
1966.7.19.3–30 (paratypes)	43–146	L. Chilwa	R. G. Kirk
1966.7.28.1–15	109–168	L. Chilwa	R. H. Lowe (1946–7)
1966.7.19.45	150	L. Chilwa	Trewavas & Malawi Fishery Research Unit

Subgenus *OREOCHROMIS*–VIII Species of the south-eastern drainage of Kilimanjaro

Oreochromis pangani pangani
Oreochromis pangani girigan
Oreochromis jipe
Oreochromis hunteri

Fig. 120 Lake Jipe. From a sketch by Sir Harry Johnston in his book *The Kilima-Njaro Expedition* (1886).

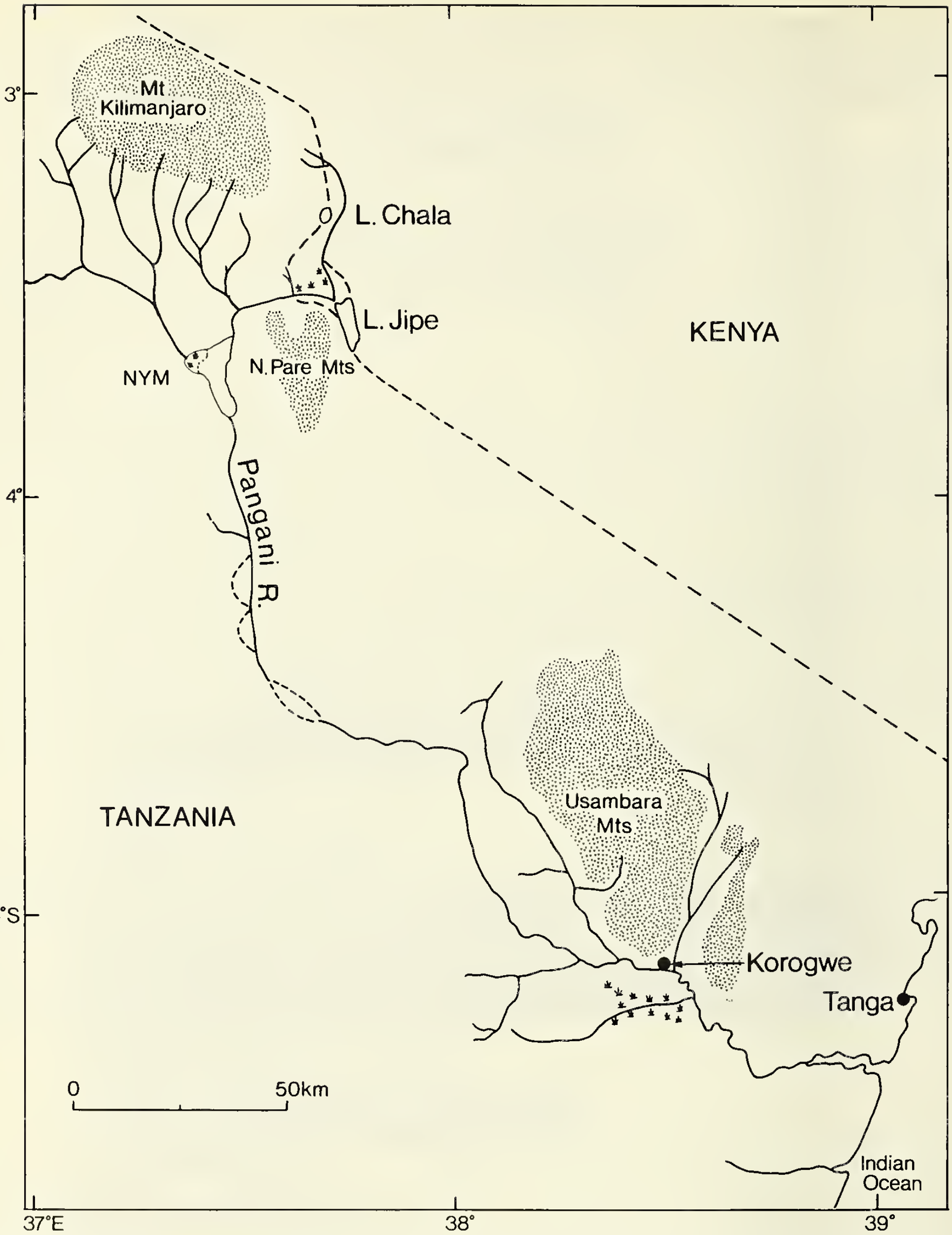


Fig. 121 Map of the Pangani River, based on those of Lowe (1955*a*) and Denny & Bailey (1976). NYM = Nyumba ya Mungu.

Group characterization

The group is characterized by high numbers of vertebrae (31–34), scales (33–38 in the lateral line series), and dorsal fin-rays (totals 28–31; see Table 91). Except in some *O. hunteri* there is a characteristic pattern of dark spots on head and body, one spot to each scale; the spots on the head are of diverse sizes and shapes and some scales are unmarked.

Microbranchiospines are present.

The nest, where known, consists of two or more series of pits surrounding a larger central pit (Lowe, 1955*a*).

Distribution

Natural distribution. Pangani River system; Lake Jipe, a shallow lake communicating in the wet periods with the Pangani River; and Lake Chala, an isolated lake in a crater (or caldera ?) about 12 miles (19 km) from Lake Jipe. *Oreochromis p. pangani* is confined to the river, *O. hunteri* to Lake Chala. *O. jipe* and *O. p. girigan* were originally found in Lake Jipe, and *O. p. girigan* has not been critically identified elsewhere. *Oreochromis jipe* is well established in the river and in the reservoir Nyumba ya Mungu formed by damming its course, but whether naturally or as a result of stocking from Korogwe is unknown.

Dispersal by man. *Oreochromis jipe* and *Oreochromis girigan* were taken from Lake Jipe to ponds at Tavetta, near the lake.

From 1950 both these and *Oreochromis pangani* were cultivated in ponds at Korogwe, fed from the Pangani. Thence they were distributed to several ponds and dams in Tanzania. Bailey (1966) reported *O. jipe* from dams near Tanga and Korogwe, and in the Usambara Mountains, and *Oreochromis p. girigan* doubtfully from the same. *Oreochromis p. pangani* has been stocked in the same waters and also at Arusha (Kilimanjaro Province), and in the following dams in the Eastern Rift Province: Mbula, Iramba, Singida, Manyoni, Kondoa, Dodoma, Mpwapwa, as well as Lake Singida. *Oreochromis jipe* is now well established in the Pangani system.

Oreochromis pangani pangani (Lowe)

Tilapia nilotica (*non* Linn.); Günther, 1866:111 (Pangani R.).
Tilapia nilotica (part, *non* Linn.); Boulenger, 1915:166 (specimen no. 306 only, Pangani R.).
Tilapia pangani Lowe, 1955*a*:352, 356, pl. 15 & 16c (Pangani R. & Korogwe ponds).
Tilapia (Sarotherodon) pangani; Trewavas, 1966*c*:408
Tilapia (Oreochromis) pangani; Thys van den Audenaerde, 1968*b*:xxxvii.
Sarotherodon pangani; Denny *et al.*, 1978:145 (food); Bailey *et al.*, 1978 (ecology); Bailey & Denny, 1978 (in Nyumba ya Mungu).

Type. Holotype: male, 236 + 74 mm, coll. Major R. E. Gould in the Pangani River, near Korogwe, 1949. Allotype: female, 189 + 46 mm, coll. R. H. Lowe in 1951 in a pond at Korogwe stocked from the Pangani River. BMNH 1952.2.26.39,40.

Distinguishing Characters

Teeth of jaws of moderate strength (Fig. 123). Pharyngeal teeth slender, but not crowded, the dentigerous area having pointed lobes and a narrow apex, its median length approximately equal to that of the blade (blade 0·9–1·1 times dentigerous area). Pectoral fin usually not more than 36% SL. Three anal spines. See also p. 358.

Description

Proportions and main meristic characters are set out in Tables 90 & 91 and other details above.

Dorsal fin

XVI 13	XVII 12	XVII 13	XVIII 12	XVII 14	XVIII 13	XIX 12
f.1	4	6	8	3	3	2

Anal III 11 or 12, rarely 10.

Distribution of vertebrae between abdominal and caudal: 16 + 16 (f.1) or 16 + 17 (f.2). In one of the latter two caudal vertebrae are very short antero-posteriorly, but complete.

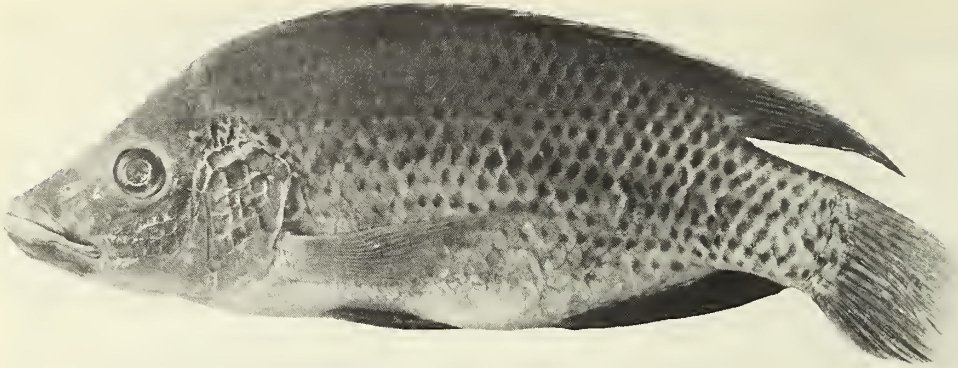


Fig. 122 *Oreochromis p. pangani* of 216 mm SL from Korogwe fish-ponds, 1951.

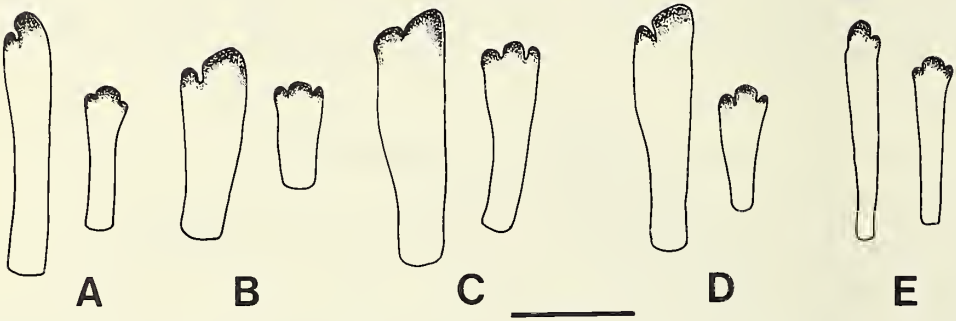


Fig. 123 Teeth from the outermost and an inner row of: A, *Oreochromis jipe* 195 mm SL; *O. p. girigan*, 171 mm SL; C, *O. p. girigan*, 204 mm SL; D, *O. p. pangani*, 190 mm SL; E, *O. hunteri*, 198 mm SL. Scale = 1 mm.

In older individuals the profile from tip of snout to interorbital region may be concave, more so in males than in females. No sex-related difference has been found in the length of the jaws, the two longest lower jaws being those of a male of 246 mm SL (41% length of head) and a female of 230 mm SL (42·5%).

The teeth of the outermost row are bicuspid, the minor cusp showing some diminution by wear only in a ripening male of 246 mm SL of those available. Inner teeth are tricuspid (Fig. 123D).

There are three rows of scales on the cheek or two rows with one or two additional scales.

The genital papilla of ripening males is prominent and in the 246 mm fish has a scalloped edge around the subterminal pore.

Coloration. Young with 9–11 dark vertical bars on the body. A tilapia-mark in specimens less than 90 mm in SL.

In adults vertical markings are faint or absent. The basic body colour is olive-brown or grey dorsally, grading to pale on the belly; or the belly may be blackish. Irregularly shaped spots on the scales are variable, from completely covering the body to few and faint. Adults (males?) develop a golden sheen on the cheek, operculum and flanks and the lower lip may become green.

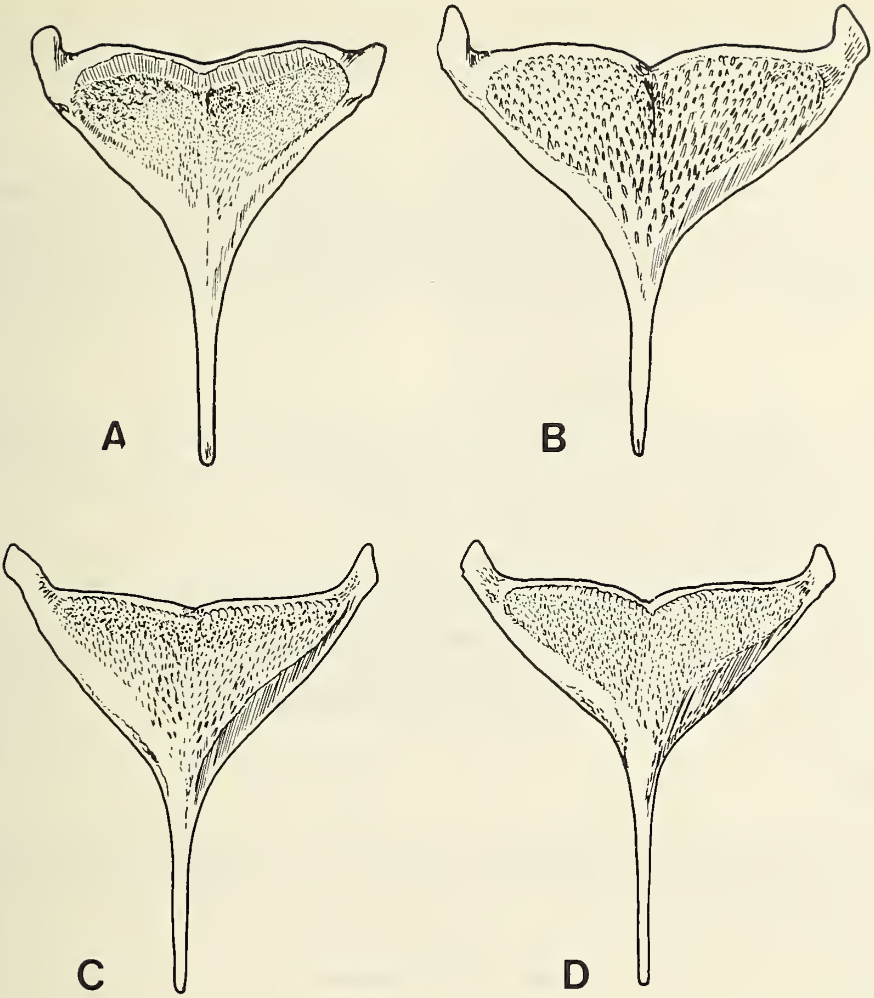


Fig. 124 Pharyngeal bones of: A, *Oreochromis jipe*, 175 mm SL; B, *O. p. girigan*, 175 mm SL; C, *O. p. pangani*, 178 mm SL; D, *O. mossambicus*, 160 mm SL. After Lowe, 1955*a*, pl. 16.

The caudal may have spots centrally, but these are not aligned as stripes and in breeding males the fin may become black except for a red dorsal margin. There may be spots on the spinous dorsal and oblique dark bars on the soft; in breeding males the upper edge of both parts is orange-red (Lowe, 1955*a*; Bailey, 1978) and the pelvics may be blackish.

Ecology

Food

In the upper Pangani (Ruvu) in a preimpoundment study Bailey (1975) reported the food as diatoms, filamentous algae and fragments of macrophyte tissues. When Nyumba ya Mungu reservoir was enclosed the studies by Bailey *et al.* (1978:131, figs 2, 5), and Denny *et al.* (1978:145) showed that the periphyton is the most important source of food for both this and *O. jipe*, such planktonic algae as were included being species also found among the periphyton and not necessarily indicating a planktonic feeding habit of the fish as was assumed by Petr (1975).

Size and growth

Growth rate has not been estimated. In Nyumba ya Mungu Bailey *et al.* (1978) found females up to TL 31·5 cm and males to 47 cm, these large males considered by them to be late breeders. The longest fish weighed 1·7 kg. Fishes of a given weight were significantly longer than those of *O. esculentus* in the same waters, a difference that reflects the longer body with more vertebrae in *O. pangani*.

Breeding

In Nyumba ya Mungu, Bailey *et al.* (1978:126) found that females of *O. pangani* and *O. jipe* mature at a minimum TL of 20·0 cm and a modal length of 22·5–25·0 cm, although Okorie (1974, quoted by Bailey *et al*) had reported a somewhat lower figure for both (resp. 17·0 and 21·0–23·0 cm), perhaps in a different month or year.

There is no evidence for a peak spawning period; mature fishes may be found throughout the year. Breeding pits were described by Lowe (1955) in a pond at Korogwe; each male constructs a central pit surrounded by two or three series of smaller pits.

Ovarian eggs in gonads deemed of maximum size were counted by Bailey *et al.* in two fishes of 20 and 26 cm TL and numbered respectively 446 and 990. They were over 1·4 mm in diameter, but no extruded eggs were measured for comparison.

Distribution

The Pangani River, so far reported only above the Power Station Falls. Stocked in ponds and dams (see p. 359), and also in Lake Singida. This species was among those taken from Korogwe in 1964 to a pond at Ilonga, near Kilosa, but probably no longer survives there.

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1865.9.21.11	142	Pangani R.	Playfair
1949.7.20.3–4	178–196	Pangani R.	R. E. Gould
1952.2.26.39 (holotype)	236	Korogwe pond ex Pangani R.	R. E. Gould
1952.2.26.40 (allotype)	189	Korogwe pond ex Pangani R.	R. H. Lowe
1952.2.26.50–52	184–206	Korogwe pond ex Pangani R.	R. H. Lowe
1952.2.26.86	182	Korogwe pond ex Pangani R.	R. H. Lowe
1969.2.11.35–36	171, 211	Pangani R., between control dam and falls	E. Trewavas, 1965
1969.2.11.37	246	Mkomazi market, ex pond, Pangani basin	E. Trewavas, 1965
1969.2.11.38–40	42–59	Pangani R., between dam and falls	E. Trewavas, 1965

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
MRAC	190	Korogwe pond	E. Trewavas
1960.2.25.1	230	Aquarium specimen doubtful origin	W. Wickler
1968.7.30.30–31	122, 131	Aquarium specimen doubtful origin	R. Apfelbach
1972.12.20.17	113	Nyumba ya Mungu, Pangani system	T. Petr
1975.10.7.145–152	42–177	Nyumba ya Mungu, Pangani system	R. G. Bailey
1975.10.7.155–160	96·5–266	Nyumba ya Mungu, Pangani system	R. G. Bailey
Unregistered (skin)	223	(Mainland opposite) Zanzibar	Playfair

Oreochromis pangani girigan (Lowe)

Tilapia girigan Lowe, 1955*a*:352 & 355, pls 14 & 16b (Lake Jipe & Taveta ponds).
Tilapia (Sarotherodon) girigan; Trewavas, 1966*c*:408.
?*Tilapia girigan*; Bailey, 1966 (dams in the Pangani system, stocked).

TYPES. Holotype: male, 210+49 mm, allotype female, 177+45 mm, both from Lake Jipe, coll. R. H. Lowe, 1951. BMNH 1952.2.26.3–4.

Distinguishing characters

Teeth of jaws with stout shafts. Pharyngeal teeth coarse, not crowded, the lower covering a triangular area whose median length is longer than that of the blade. Pectoral fin (30) 32·0–37·6% SL, below 36% in 16 of 19 adults examined. Three anal spines. Colour as in *O. p. pangani.*

Description

Proportions and meristic characters are set out in Tables 90 and 91, and other details above and on p. 358–9.

The upper profile of the head is straight or, in a large ripe male, concave. The only specimen with a lower jaw longer than 36% length of head is the ripe male of 250 mm SL, in which it is 40%. The teeth are in 5–7 series, the outer bicuspid except in the one large ripe male, in which the cusps have become worn; the inner teeth are tricuspid.

Vertebrae 16+16, 16+17 or 17+16.

Two, occasionally three rows of scales on the cheek.

Genital papilla of ripe male prominent and blunt, not elaborate.

COLORATION. The pattern of spots covers the whole body except the narrow grey belly and the spots are usually emphasized along the mid-lateral line. The caudal may have irregular spots or be uniformly pale or dark, in large specimens nearly black except a red edge. In mature males the lappets of the dorsal fin and the upper edge of the soft fin are white as preserved, probably red in life.

Table 90. Proportions in specimens of approximately the same size-range of species of the Pangani system. Of *O. hunteri* two specimens have been excluded from some proportions; one is represented by a head alone, the other is a dry skin (the holotype). Noticeable are the more slender body and longer caudal peduncle of *O. hunteri* and the longer pectoral find of *O. jipe.* A sample of smaller *O. hunteri* is added.

	jipe	*p. pangani*	*p. girigan*	*hunteri*	*hunteri*
N	11	14	20	5+2	16+2
SL(mm)	134–214	128–250	142–246	125–253	52–99
Proportions as % SL					
Depth	34·4–40·7	(33)35·7–42·0	37·0–43·6	30·4–35·9	30·5–34·4
L. head	32·0–36·5	30·8–35·0	31·8–36·0	33·0–37·4	34·6–38·0
Mean	33·9	35·5	33·6	36·1	36·6
L. pect. fin	34·3–41·2	29·4–37·3	(30)32·0–37·6	(29·6)33·5–37·0	(31·5)33·5–37·2
<36% (f.)	2	12	16	4	17
36% or more (f.)	9	1	3	1	1
L. caud. ped.	10·8–13·8	11·0–14·8	10·4–13·4	14·0–16·8	13·7–17·5
Caud. ped. l/d	0·8–1·1	0·7–1·0	0·8–1·0	1·2–1·4	1·1–1·46
Proportions % l. head					
L. snout	35·0–39·7	32·5–42·5	33·2–40·5	35·2–37·6	33·4–37·0
Eye	18·7–23·2	17·0–20·0	16·7–22·7	18·8–23·4	22·6–27·0
D. preorb.	19·3–21·8	20·4–24·9	18·5–22·9	20·5–22·1	16·0–21·6
Interorb.	32·2–37·8	34·2–41·1	34·0–38·6	32·7–37·0	27·5–32·3
Lower jaw	28·6–33·4	30·1–41·0	30·0–36·0(40)	31·5–36·0	31·0–36·0

Table 91. Meristic characters in the species of the Kilimanjaro region. Frequencies are given except for the scale-counts (which, especially in *O. hunteri*, may be different on the two sides of the body owing to slight irregularities), gill-rakers and teeth.

		O. p. pangani	*O. p. girigan*	*O. jipe*	*O. hunteri*
Vertebrae	31				2
	32	1	1	1	3
	33	2	6	2	15
	34	2			1
D spines	XVI	1			8
	XVII	13	5	4	22
	XVIII	11	14	9	
	XIX	2	1	2	
Total D rays	28				5
	29	5		3	10
	30	14	12	10	15
	31	8	8	2	
Anal spines	III	27	20	2	8
	IV			13	26
Scales					
lat. line		33–36	33–36	33–36	34–38
mode		34	34	34	34=35
D-lat. line		4–4½	4–4½	4–5	4–7
cheek rows		2–3	(2)–3	2	(2)–3
Gill-rakers					
(lower limb)		16–21	17–20	18–22	18–21
usually		18–20	18–20	18–20	19 or 20
Teeth: no. of rows					
upper		4–6	5–8	6–7	3–6
lower		4–6	5–7	5–7	3–6
no. in outer row					
upper jaw		46–68	52–66	60–82	48–88

Ecology

Food

Lowe (1955*a*) observed that stomachs of specimens from Lake Jipe contained fragmented macrophytes (*Najas* sp.), as well as epiphytic diatoms and other algae. In ponds at Taveta, where higher plants were not available both this and *O. jipe* were feeding from the bottom, but the particles in *O. p. girigan* were coarser than in *O. jipe*, testifying to the role of the pharyngeal teeth in the preparation of food.

Breeding

Lowe was uncertain whether the nests she described at Taveta ponds were made by this species or *O. jipe* (q.v., p. 368). Up to 60 eggs of long diameter 3·3 mm have been found in the mouth of the female.

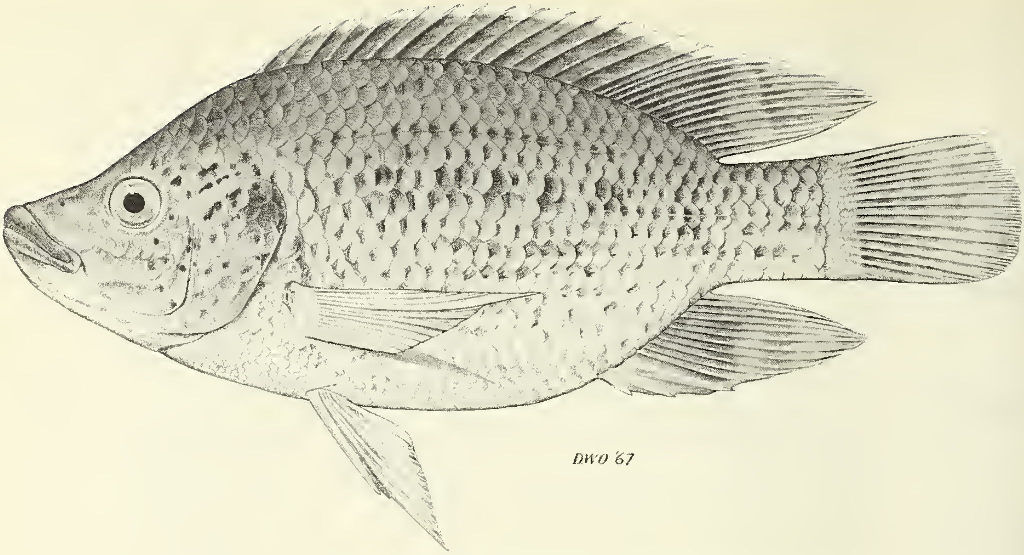


Fig. 125 *Oreochromis pangani girigan* male of 210 mm SL. Holotype.

Distribution

Known only from Lake Jipe, whence it was taken to ponds at Taveta, near Lake Jipe and at Korogwe. Possibly distributed from Korogwe to dams in the Pangani system, but not certainly identified there since.

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector, donor
1952.2.26.3 (holotype)	210	L. Jipe	R. H. Lowe
1952.2.26.4 (allotype)	177	L. Jipe	R. H. Lowe
1952.2.26.6–22 (no. 22 now at MRAC)	129–250	Ponds at Taveta, ex L. Jipe	R. H. Lowe
1975.10.7.108	190	L. Jipe	R. G. Bailey

Oreochromis jipe (Lowe)

Tilapia jipe Lowe, 1955*a*:352, 354, pls 13 & 16A (Lake Jipe).
Tilapia (Sarotherodon) jipe; Trewavas, 1966*c*:408
Tilapia (Oreochromis) jipe; Thys van den Audenaerde, 1968*b*:xxxvii.
Sarotherodon jipe; Bailey *et al.*, 1978:114 ff.; Denny *et al.*, 1978:141 ff,; Bailey & Denny, 1978:155 (in Nyumba ya Mungu).

TYPES. Holotype: male, 162+45 mm; allotype: female, 140+35 mm; both from Lake Jipe, coll. R. H. Lowe, 1951. BMNH 1952.2.26.1–2.

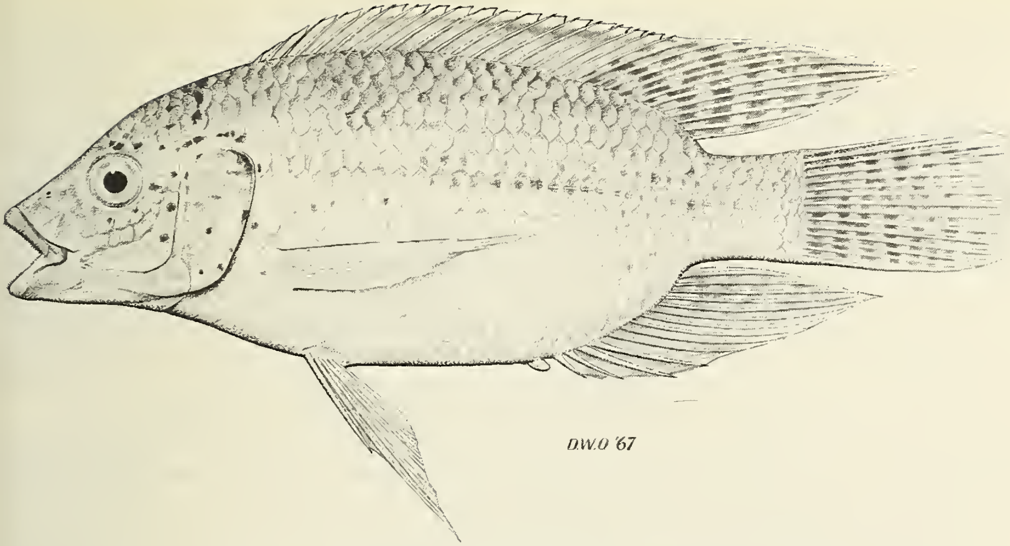


Fig. 126 *Oreochromis jipe* male of 162 mm SL. Holotype.

Distinguishing characters

Teeth of jaws with slender shafts in young, uniformly slender in adults. Pharyngeal teeth very fine and crowded; dentigerous area with rounded lobes and short apex, its median length nearly always less than that of the blade. Pectoral fin 34·3–41·2 % SL, below 36% in only two of nine adults.

Anal spines IV in 75% of a sample of 70, III with a partly ossified fourth in 7%, III in 17% and V in one (Lowe, *loc. cit.*).

Description

Proportions and meristic characters are listed in Tables 90 and 91, and other characters above and on p. 358–9.

The upper profile of the head is steep and approximately straight. The mouth is small and the jaws are not enlarged in fishes of the size-range of Table 90. The teeth of the jaws are in 5–7 series in adults, very slender, up to half the posterior outer of the upper jaw becoming unicuspid in bigger fishes, inner tricuspid except the inmost row in one male of 203 mm SL, which includes several unicuspids. In two specimens the outermost row includes a few tricuspids.

A large male (345+40 cm) has a slightly concave profile and in the following proportions exceeds the ranges of the sample of Table 90.

Depth 44·2% SL, length of head 30·1. Length of snout 42·3% length of head, diameter of eye 17·9, depth of preorbital bone 24·0, interorbital width 43·4, length of lower jaw 35·0.

Most of these differences are expected from the usual allometry. The lower jaw is relatively shorter than the maxima in even smaller specimens of the other Pangani species.

The outer teeth are unicuspid in this fish, with the brown crowns reduced or completely eroded.

Two rows of scales on the cheek. Commonest number of scales in the lateral line series 34. Scales on chest very small; on the belly the median row and three on each side of it noticeably smaller than the flank scales.

Dorsal fin

XVII 12	XVIII 11	XVII 13	XVIII 12	XIX 11	XVIII 13	XIX 12
f.2	1	1	7	1	1	1

Anal soft rays	10	11	12
Anal spines III(f.)		1	1
Anal spines IV(f.)	3	7	2

Vertebrae 16 + 16 (f.2) or 16 + 17 (f.1).

Coloration. Non-breeding fishes light grey or grey-green with numerous dark brown or black spots, each on one scale, but of irregular sizes and shapes, and some scales unmarked. Seven to nine vertical bars on the body and a mid-lateral longitudinal band generally formed by emphasis of the spots. Scales of belly pale with dark edges. Spots extending on top and sides of head to varying degrees, often strong at the temporal lateral line pores. Dorsal fin with dark spots or reticulum on the spinous part, oblique bars on the soft. Anal barred posteriorly. Caudal with vertical dark bars proximally, sometimes becoming irregular or fading out distally.

Mature male with green and purple sheen on the body, cheeks and opercula; dorsal margin bright orange, caudal margin crimson; pelvics and often also edge of anal bluish green (Lowe, 1955*a*). K. L. I. Campbell (pers. commn) adds that he observed yellow spots on the dorsal and anal, and that the caudal margin was yellow to orange. The dark mottlings on the flanks become more intense during aggressive or courting behaviour. Bailey *et al.* (1978) describe the colour of the dorsal and caudal edges as ‘orange-red’. At all stages they emphasize the value for field diagnosis of the vertical stripes on the caudal fin. In life the dark spots are accompanied by golden-yellow spots.

As in related species, the young have 9–12 dark vertical bars on the body.

Ecology

Food

The studies of Denny *et al.* (1978), and Bailey *et al.* (1978) established the overwhelming importance of microscopic algae as food for *O. jipe* and this was mainly periphyton, although the presence of inorganic particles and organic debris showed that food was also taken from the bottom. In ponds containing no macrophytes Lowe (1955*a*) observed both this and *O. p. girigan* feeding from the bottom, but the particles in the stomachs of *O. jipe* were finer than those in *O. p. girigan*, as would be expected from the contrast in the pharyngeal dentition.

Breeding

In the samples described by Lowe (1955*a*) from the Lake Jipe and the ponds at Taveta the maximum size of males and females was the same, 32 cm. In Nyumba ya Mungu, however, although females grew only to about 30 cm males were found at nearly 50 cm TL (Bailey *et al.*, 1978, fig. 3). These large males had non-active gonads and were believed to owe their large size and presumably more rapid growth to a postponement of breeding activities. Lowe made a similar assumption for the faster growing males in the Taveta ponds, linking it with the high sex-ratio in favour of males that she found there. This would assume the exclusion of some males from forming mating territories, which might happen in the restricted space of a pond, but is less likely in a larger water such as Nyumba ya Mungu (cf the large males with small gonads found in populations of *O. squamipinnis* and *Sarotherodon linnellii*).

Breeding individuals were found in Nyumba ya Mungu in every month in which samples were taken and no peak season was detected. Lowe (1955*a*) described breeding pits in Taveta ponds but could not be sure whether they were of this species or *O. p. girigan*. They were similar to those of *O. p. pangani*, consisting of a central pit surrounded by two or three series of smaller pits (Lowe, 1955*a*, pl.17A).

Ovarian eggs, counted by Lowe in fishes of 15–21 cm TL, numbered 200 to 250. Up to 167 eggs were found in the mouths of brooding females. In the ovaries of three bigger, ripe females of 23·5–24·5 cm from Nyumba ya Mungu Bailey *et al.* counted 437–570. At an earlier stage of gonadal development and a TL of 18·0–27·5 cm they found 1100–1984 smaller eggs or oocytes.

Distribution

Lake Jipe. The Pangani River ? (see page 373).

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
1952.2.26.2 (holotype)	162	L. Jipe	R. H. Lowe
1952.2.26.1 (allotype)	140	L. Jipe	R. H. Lowe
1952.2.26.23–27 (7 fishes, one now in MRAC)	175–214	Ponds at Taveta ex L. Jipe	R. H. Lowe
1968.2.16.2–3	157, 161	Ponds at Korogwe, ex L. Jipe	R. E. Gould
1972.12.20.18–19	71–84	Nyumba ya Mungu, a reservoir in the Upper Pangani	T. Petr (pres. Bailey)
1974.1.16.435–437	43–108	Nyumba ya Mungu	T. Petr (pres. Bailey)
1975.10.7.111–113	170–212	Nyumba ya Mungu	R. G. Bailey
1975.10.7.114–127	40–158	Lambeni R., a stream entering Pangani R. below Nyumba ya Mungu	R. G. Bailey
1975.10.7.128–134	51–218	Lambeni R.	R. G. Bailey
1975.10.7.135–144	49–156	Nyumba ya Mungu	R. G. Bailey
1975.10.7.161–163	244–345	Nyumba ya Mungu	R. G. Bailey
1979.5.22.4.	149	L. Jipe, 1.5.76, kept in tank at Bamburi, near Mombasa, until 14.9.77	R. Haller

Oreochromis hunteri Günther

Oreochromis hunteri Günther, 1889:70 (Lake Chala, Kilimanjaro); Pellegrin, 1904:354.
Tilapia hunteri; Boulenger, 1899*a*:110; *idem*, 1915:149, fig. 97; Lowe, 1955*a*:364 (young, L. Chala)
Tilapia (Oreochromis) hunteri; Thys van den Audenaerde, 1968*b*:xxxvii.

TYPES. Holotype: a skin 253 mm in SL; coll. H. C. V. Hunter in Lake Chala (Chyala), Kilimanjaro. BMNH 1893.3.22.12.

Fig. 127 *Oreochromis hunteri* of 165 mm SL: above, whole fish; below, head of same specimen to show ventral scales.

Distinguishing characters

Teeth very small, in narrow bands. Pharyngeal bone narrow, its width about 26% length of head, with fine teeth, crowded posteriorly, the blade equal to the median length of the toothed area in young, about 1½ times as long in adult. Pectoral fin usually less than 36% SL (Table 90).

Anal spines IV in 26(76·5%), III in 8 (23·5%) of 34 counted. Scales of chest and belly very small, in some individuals showing an abrupt transition from the flank scales for a short distance behind the pectoral-pelvic interspace. In some the dorsal scales may also be small. Caudal peduncle longer than deep.

Colour darker than the Upper Pangani species.

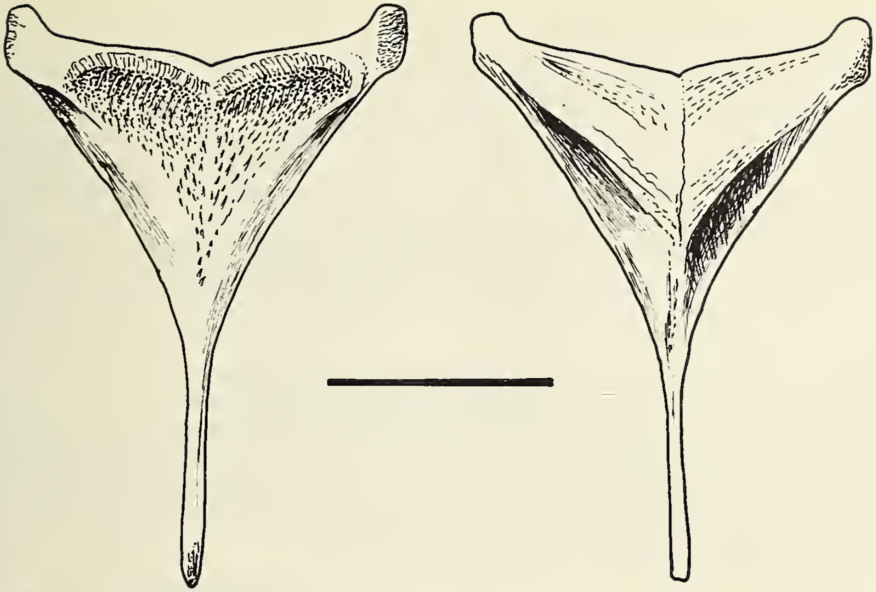


Fig. 128 *Oreochromis hunteri.* Pharyngeal bone of a fish 200 mm SL. Scale = 10 mm.

Description

Based on the holotype, five specimens of 125–198 mm SL and a head of 53 mm (probably from a fish of about 150 mm SL) and on 18 fishes of 52·5–99·0 mm SL, with further meristic characters from a few smaller fishes.

Proportions and meristic characters are detailed in Tables 90 and 91 and see the 'Distinguishing characters'.

The upper profile of the head is approximately straight, the mouth terminal with the jaws meeting evenly. The lower jaw is more than 34·6% length of head in only one of the adults (the severed head), but the sample is too small to give evidence that the jaws do not become enlarged.

The teeth are smaller and more slender than even in *O. jipe* (Fig. 123E). In the largest specimens a few of the outer teeth are tricuspid and some of the posterior may be unicuspid, but most are bicuspid. In adults many teeth are worn or broken, probably the result of browsing on the rocks. The inner series are irregular and the tooth-bands are narrower than in *O. jipe* and *O. pangani.* In the biggest fish (holotype) teeth of the inmost row are unicuspid.

The pharyngeal teeth are small and slender, restricted to a small area (Fig. 128).

The number of scales in the lateral line series shows equal modes at 34 and 35, higher numbers being often due to interpolation of smaller scales, in some cases on one side only.

The dorsal formulae are distributed as follows:

XVI 12	XVII 11	XVI 13	XVII 12	XVII 12+1	XVII 13
f.4	1	4	8	6	9

The total anal rays are 14–16 with a strong mode at 15. The frequencies of combinations of spines and soft rays are as follows:

Anal soft rays	10	11	12	13
Spines III		1	6	1
Spines IV	5	19	1	

Division of vertebrae into abdominal and caudal as follows:
Total 31: – 14 + 17 in 1, 16 + 15 in 1
Total 32: – 15 + 17 in 3
Total 33: – 15 + 18 in 13, 16 + 17 in 2
Total 34: – 17 + 17 in 1

COLORATION. Noted from living fishes by Col. D. F. Smith, then Assistant Fish Warden, Kenya, who collected some of the specimens used for this account.

Adult metallic blue-black on upper parts of head and body, shading to iridescent dark greenish blue on lower parts of gill-cover and jaws and to blackish bronze on the flanks; breast speckled dark green and white, belly grey on white. Some individuals (males?) with edge of dorsal fin dark orange.

Young bronze on flanks, greenish bronze on back, cream on belly; head as adult but not so dark; caudal and dorsal fins dark green, lower fins paler iridescent green.

A checkered effect in both young and adult produced by the darker anterior part of each scale.

In alcohol young fishes (less than 100 mm SL) have a well-marked dark mid-lateral longitudinal band, continuous or emphasized on 11–13 narrow dark vertical bars, which also bear a series of 5–7 blotches above the upper lateral line. The tilapia-mark, present though variably emphasized at these sizes, is horizontally elongate.

Ecology

Food

Lowe (1955*a*) observed the young feeding on algae and debris from the bottom between the rocks near the shore of Lake Chala. They were accompanied by numerous crabs. There is no information on the food of adults.

Breeding

No information.

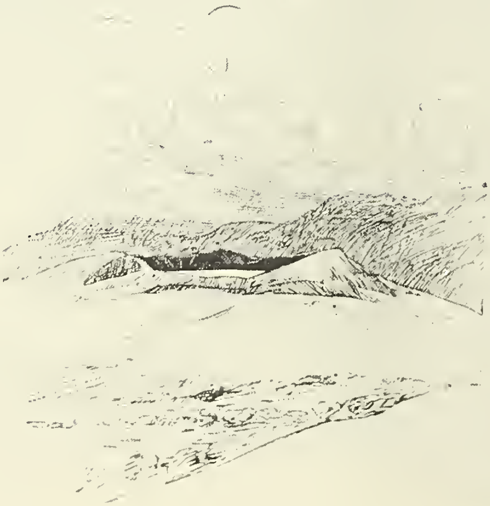


Fig. 129 Lake Chala, Kilimanjaro. From a sketch by Sir H. H. Johnston in his book *The Kilima-Njaro Expedition* (1886).

Distribution

Natural distribution. Confined to Lake Chala (see Figs 121 & 129), a deep, clear lake in a high-walled volcanic basin, with surface area about 10·5×2·0 km. It lies between the 500 and 1000 m. contours in the foothills of Kilimanjaro. Although within the area of the Pangani drainage it has neither inflow nor outlet at present, but in the past may have communicated with Lake Jipe according to the opinion, based on the topography of the area, of the late Mr Hugh Copley (letter of 21.X.1946).

Dispersal by man. *Oreochromis hunteri* has been transported to the fishponds at Bamburi, north of Mombasa (pers. commn, Mr R. Haller).

Material examined

All Lake Chala, Kilimanjaro

Museum & Reg. No.	SL(mm)	Collector or donor
1889.3.22.12 (holotype, skin)	253	H. C. V. Hunter
1902.11.8.27 (head)	—	Blayney Percival
1946.12.28.18–22 (five) (five)	125–198 72·5–98·0	coll. D. F. Smith pres. H. Copley
1952.2.26.53–73 (no. 73 now MRAC)	55–99	R. H. Lowe
1980.9.25.90–91	85, 90	R. Haller

The inter-relationships and possible history of the Upper Pangani species

An attempted reconstruction of the evolutionary history of the four taxa of the Upper Pangani, including Lakes Jipe and Chala, is hampered by the fact that when the fishes were first described *O. jipe* had already been taken from the lake, and *O. pangani* from the river to stock the ponds at Korogwe. At that time *O. jipe* and *O. p. girigan* were known only in Lake Jipe, and *O. p. pangani* only in the Pangani River. Then extensive stocking of lakelets and dams was carried out from Korogwe. *O. jipe* is now abundant in the Pangani and has naturally colonized the reservoir Nyumba ya Mungu together with *O. p. pangani* and *O. esculentus*. The presence of the latter is almost certainly due to stocking in the nineteen-fifties, but it is conceivable that *O. jipe* was already present in the river and was either not found or not recognized by Gould when he collected for his ponds. *O. p. girigan*, however, has never been captured since, except in Lake Jipe, where Bailey found it again in 1974. It was not among the species identified by Bailey in the Upper Pangani either before or after impoundment of Nyumba ya Mungu.

Other stockings, e.g. of *Tilapia rendalli*, have been 'successful' in the area (deplorably so from the zoogeographical point of view). In 1965, Berthold Mwaya of the Tanzanian fisheries staff, and I witnessed the capture of large specimens of *T. randalli* in the Zigi river, a stream north of Tanga. The fishermen who caught them believed them to be native, but the men had been in the area only seven years and the stocking operations were earlier.

Possibility 1.

If *O. jipe* and *O. p. girigan* were endemic to Lake Jipe and *O. p. pangani* to the river, as seemed to be the case when Dr Lowe-McConnell collected them, their history may have been as follows. Previously there was one *Oreochromis* species in the Upper Pangani system. Isolation of Lake Jipe for a long period resulted in the population there becoming more specialized in its structure for periphyton feeding (short jaws, movable teeth in wide bands, finer pharyngeal teeth), and it increased the numbers of fin-spines. At some time during such a period it intitiated a colony in Lake Chala (birds? high winds?), producing a population that eventually differentiated in this new environment into *O. hunteri*. A wet period later united Lake Jipe with the river and allowed the still generalized *O. pangani* to enter the lake. There it found the periphyton-feeding niche occupied by *O. jipe* and specialized in coarser detritus. In time its dentition coarsened to match this diet and another period of isolation allowed the differentiation of *O. p. girigan*.

Another possible factor mediating the intralacustrine differentiation of the two migrations would be environmentally induced differential shift in the breeding cycles during the period of isolation.

Lowe's (1955*a*) examination of the gut-contents of these species found a corresponding difference in the food of *O. jipe* and *O. p. girigan* (pp. 365 & 368). Bailey's researches twenty years later in Nyumba ya Mungu (Bailey *et al.*, 1978, fig. 2 on p. 117) found *O. p. pangani* and *O. jipe* both abundant in the man-made lake and both feeding on periphyton. 'Microscopic algae' were the principal food item in both species, but filamentous algae and higher plant tissues were more frequently present in the stomachs of *O. p. pangani* than in *O. jipe*. This suggests that *O. p. pangani* grazed the periphytom more closely than *O. jipe*, and that the comb-like teeth of *O. jipe* enable it to extract microorganisms from among the filaments.

Possibility 2.

A reconstruction based on the supposition that *O. p. pangani* and *O. jipe* differentiated in the river would still require the aid of dry periods, during which parts of the originally uniform population would be isolated in pools and swamps. When a wet period later gave both species access to Lake Jipe, their differences would there be exaggerated and *O. p. girigan* would develop its present characteristics.

The former history would most easily explain the increase in fin-spine numbers in *O. jipe* and the origin of *O. hunteri*.

Both reconstructions assume an initial change in habits, resulting in the selection of heritable changes in structure and accompanied by an environmentally induced differential shift in breeding cycles.

O. hunteri, the type species of *Oreochromis*, is one of the least known. Its clear resemblances to *O. jipe*, as well as the geographical propinquity, establish its relationship to the Upper Pangani forms. Together they comprise a well-defined group, distinguished by the high meristic numbers and coloration. The electrophoretic analysis by McAndrew & Majumdar (1983; see p. 21) found that in its protein chemistry *O. jipe* diverged more from the other six species of *Oreochromis* than did *Sarotherodon galilaeus* or *Tilapia zillii*. The significance of this cannot be judged until a similar analysis is made of *O. pangani* and *O. hunteri* and compared with one of *O. korogwe* as well as with the *Oreochromis* already analysed by these authors. Their species included *O. spilurus* and *O. mossambicus*, northern and southern members of the series, including *O. korogwe*, inhabiting the lower reaches of the rivers entering the Indian Ocean (see p. 231 & Fig. 78). If the Upper Pangani species prove to be grouped on their basic chemistry as they are on their meristic and colour features this would be significant for the internal classification of the species of *Oreochromis* as here understood.

Subgenera *ALCOLAPIA* and *VALLICOLA*

Oreochromis alcalicus
Oreochromis amphimelas

These two species were brought together by Thys (1968*b*) as one subgenus, but some of their resemblances are believed to be responses to similar environmental conditions (pp. 32–5) and are counterbalanced by striking differences. Each is here treated as the type and only species of its own subgenus. For definitions of the subgenera see pp. 27, 29.

Oreochromis (Alcolapia) alcalicus and *Oreochromis (Vallicola) amphimelas* have in common the following characters, in which both differ from other subgenera of *Oreochromis*:

1. Low numbers of gill-rakers, respectively 9–14 and 12–16 on the lower part of the first arch.

   A few species of *Oreochromis* may exceptionally have fewer than 16 gill-rakers, but 16 is the maximum only in our samples of the small fishes constituting a population of *O. spilurus* (*O. s. percivali*) in a thermal spring.

2. Absence of microbranchiospines, a condition found elsewhere only in some individuals of *O. s. percivali.*

3. Scales of nape, chest and belly very small.

   Very small dorsal and ventral scales are found also in *O. hunteri* and, ventral only and less extreme, in *O. pangani*, *O. jipe* and *O. (Neotilapia) tanganicae.*

4. Low numbers of dorsal spines, respectively IX–XIII and XII–XIV.

   XIV, the maximum number in the two species, is an uncommonly low number in *Oreochromis*. It is found, as a minimum, in two individuals in the crater lake Chungruru (p. 471), in four of thirteen individuals of *O. s. percivali*, in nine of thirty-three. *O. niloticus filoa* and in one of thirty-two *O. n. sugutae*. These are all populations of special environments, the three last-named from warm, alkaline waters.

5. A short pectoral fin, respectively 18·5–27·8 and 21·5–32·3% SL, c.f. maxima of 36–44·9 in other *Oreochromis* and minima rarely less than 33.

   Among other species of *Oreochromis* the lowest ranges of pectoral fin length (% SL) are:

   O. niloticus sugutae 30–36 at SL 104–145 mm; 27–34 at 43–100 mm.
   O. spilurus percivali 27·7–34·3 below SL 62·5 mm and also at 126 mm.
   O. salinicola 27–32 below SL 80 mm.
   O. hunteri (29·6) 33·5–37 at SL 125–253 mm.
   O. pangani 29·4–37·6 at SL 128–246 mm.
   O. urolepis 29·5–44 at SL 100–345 mm.
   O. shiranus 31–39 at SL 80–245 mm.

   Other species have maxima of over 40% except *O. korogwe* (38·5) and *O. lepidurus* (39).

6. Eye small (Fig. 130).

7. Only four lateral line openings in the preorbital bone. Sections of the bone in *O. alcalicus* reveal the presence of only three neuromast organs.

   The shape of the bony canals differs as between the two species. In *O. (A) alcalicus* the branch canals are narrow tubes; in *O. (V.) amphimelas* the bony canals have wider openings, but they are spanned by skin and the external pore of each is minute. See page 403.

   In the hybrids between *O. amphimelas* and *O. esculentus* (p. 398) there are five openings.

8. No tilapia-mark, but in some *O. alcalicus* an inconspicuous, unringed mark may be present in the same place on the dorsal fin.

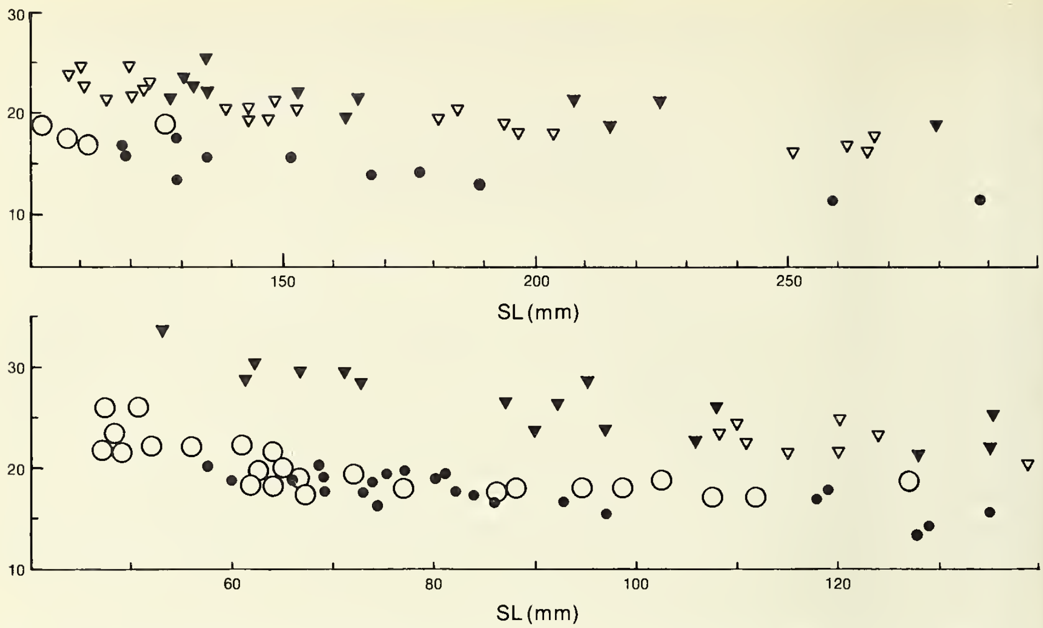


Fig. 130 Diameter of eye as % of head in *O. alcalicus* (○); *O. amphimelas* (●). For comparison some *O. esculentus* (▽); *S. galilaeus* (▼). The scale of SL in the upper diagram, for the bigger fishes, is half that in the lower.

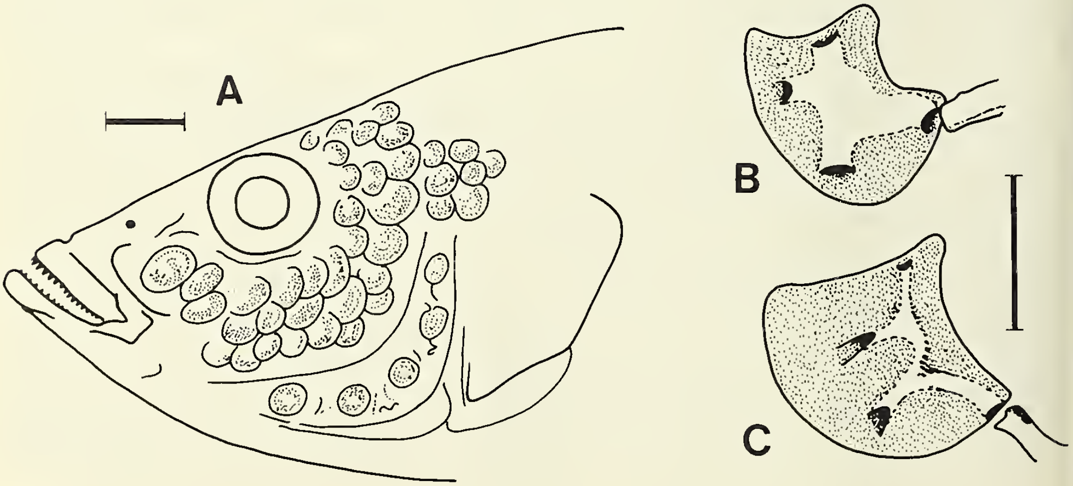


Fig. 131 A, head of *Oreochromis amphimelas* of 59 mm SL showing rugose scales of preorbital and cheek: stripped preorbital bones of B, *O. amphimelas*; C, *O. alcalicus*. Scales = 3 mm.

Oreochromis (Alcolapia) alcalicus and *Oreochromis (Vallicola) amphimelas* differ as follows:

	O. alcalicus	*O. amphimelas*
Vertebrae	27–30 (mode 28)	30–32 (mode 31)
Scales lateral line	27–30 (mode 27 or 28)	30–34 (usually 31–33)
Dorsal spines	slender, flexible in some males	stout
Postorbital part of head as % length of head (Tables 96 & 97)	usually < 50%	usually > 50%
Preorbital bone (Fig. 132)	deep	exceptionally shallow
Preorbital bone (Fig. 131)	naked	scaly

Oreochromis (Alcolapia) alcalicus (Hilgendorf)

For synonmy and bibliography see the subspecies.

Distinguishing characters

See above and for the subgenus (p. 27 & p. 29).

Subspecies

Two subspecies, *O. a. alcalicus* and *O. a. grahami*, distinguished mainly by the colour of breeding males, in which the throat and belly become yellow in *O. a. alcalicus*, white in *O. a. grahami*; and the posterior part of the caudal fin becomes red in *O. a. alcalicus*, 'orange-red' in *O. a. grahami*. A black oblique bar across the eye in *O. a. grahami* males has not been recorded in *O. a. alcalicus*. Certain differences in behaviour and diel rhythm have also been recorded, but their value cannot be assessed until the range of variation is known.

Structurally these two forms are so similar that on the basis of preserved specimens they would be treated as one taxon.

Oreochromis (Alcolapia) alcalicus alcalicus (Hilgendorf)

Tilapia alcalica Hilgendorf, 1905:407 (volcanic cavity at Ndadaleni, near Nguruman salt lake = Lake Natron); Boulenger, 1915:188, fig. 122; Albrecht, 1967*b*:375 ff, 1 fig.; Coe, 1969:1–14, figs 1, 2 (structure and behaviour in aquaria and in nature).
Tilapia (Alcolapia) alcalica; Thys van den Audenaerde, 1968*b*:xxxiii, xxxv; *idem*, 1971:205.
Sarotherodon alcalicum alcalicum; Mayland, 1978:299.

TYPES. Syntypes: some (six?), including the biggest specimen of 50 mm TL, in ZMB, and three of 27·5–35 mm SL and a juvenile in BMNH, registered 1905.7.25.29–31, from the type locality, coll. O. Neumann, Dec. 18, 1893.

Distribution

Lake Natron, and creeks and pools around its shore.

Oreochromis (Alcolapia) alcalicus grahami (Boulenger)

Tilapia mossambica; Woodhouse, 1912:95 (Boulenger's preliminary determination; Lake Magadi).
Tilapia grahami Boulenger, 1912*b*:519; *idem*, 1915:211, fig. 136; Copley, 1958 (colours); Whitehead, 1959*a*:1510 (no microbranchiospines); Coe, 1966 (habitat, bionomics in natural and experimental conditions); Albrecht, 1967*a*:31*b*:316–324, illus. (habitat, behaviour); *idem*, 1968*a* & *b* (behaviour); Albrecht, Apfelbach & Wickler, 1968 (breeding behaviour); Vareschi, 1979 (in Lake Nakuru).
Sarotherodon alcalicus grahami; Trewavas, 1973:23; Mayland, 1978:299, fig. on p. 300; Vareschi, 1979.

TYPES. Syntypes: five specimens of 30–49 mm SL from springs on the eastern shore of Lake Magadi, coll. J. W. Graham. BMNH 1911.1.26.6–10.

Distribution

NATURAL DISTRIBUTION. Lake Magadi.

DISPERSAL BY MAN. Lake Nakuru

Description of both subspecies

Proportions and meristic data are summarized in Tables 92 and 93. The following notes supplement the tables and the list of distinguishing characters (p. 375–6).

The head may be relatively bigger in smaller fishes, e.g. in a female of 30 mm SL of *O. a. grahami* the head-length is 43% SL.

The general appearance of the head changes in the bigger fishes of the Nakuru introductions, when the snout appears more conical, although the proportion of the snout relative to the length of head does not increase. The eye is small, its diameter exceeded by the depth of the preorbital bone in the bigger size-group of the Nakuru population, although the preorbital itself is not very deep. The interorbital width remains less than in more typical *Oreochromis* of the same size (cf. Table 38 of *O. niloticus*). The pectoral fin is short at all sizes, comparing with that of *O. amphimelas*, but contrasting with most other species.

The gill-rakers of some brooding females are expanded, especially in the large females of the Nakuru sample (Fig. 135). Even where they remain conical their integument is thicker than in males. Microbranchiospines are absent from the arches of the Nakuru transplants as well as in both subspecies in their native lakes.

In Lakes Natron and Magadi the numbers of scales in the lateral line series are variable, the lateral line tubules are reduced in size and several scales of the series are unpierced. The canals of the head are also reduced in size. In the sample from Nakuru the numbers of scales are restricted to the modal 28 or 29 and the tubules are slightly bigger, though still small, and lacking in some scales of the series.

All samples of both subspecies, however, show the abruptly smaller scales on chest and belly, usually non-imbricating and often interrupted by naked patches, especially near the bases of pectoral and pelvic fins. The exposed surfaces of the bigger scales have a granular ornamentation along the circuli, the outermost granules having minute points, giving a very finely ctenoid edge.

The presence of only two rows of scales on the cheek in most specimens from Lake Nakuru is perhaps related to the greater regularity of the scales in general in this population.

The range in numbers of both spines and soft rays in the dorsal fin is unusually wide (Table 92). The spines in some breeding males of *O. a. alcalicus* have a slender, slightly flexible distal section with a blunt tip. This is responsible for the extended height of the fin noticed by Coe (1969) in displaying males of this subspecies. In *O. a. grahami* I have not found such prolongations, the spines ending in a sharp point as in other species. In some males of both subspecies the notches between the dorsal lappets are reduced and in one from Lake Magadi they are obliterated and the edge of the fin is thickened.

Table 92. *Oreochromis* (*Alcolapia*) *alcalicus.* Proportions and meristic characters in samples of *O. a. alcalicus* from Lake Natron and *O. a. grahami* from Lake Magadi and an introduced population in Lake Nakuru (two size-groups).

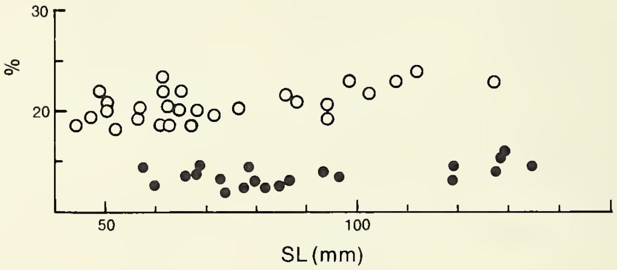
	O. a. alcalicus		*O. a. grahami*	
	L. Natron	L. Magadi	L. Nakuru	L. Nakuru
N	15	14	5	8
SL (mm)	34·0–68·6	38·0–67·7	47·0–66·5	94·5–127·0
Proportions as % SL				
Depth	30·0–38·5	28·0–34·2	34·0–36·8	33·0–38·8
L. head	34·4–38·2	35·0–38·0	34·0–36·0	32·4–37·1
L. pectoral fin	22·2–26·6	18·5–23·0	24·0–27·8	24·4–27·8
L. last D spine	12·1–22·2	16·2, 22·4	25·5–26·8	21·1–24·8
L. caud.	22·3–26·5	20·1–25·6	24·5–26·5	21·0–25·0
L. caud. ped.	13·0–15·8	13·4–16·2	14·7–17·0	10·6–14·1
Caudal ped. l/d.	0·8–1·2	0·85–1·1	0·9–1·2	0·85–1·1
Proportion as % l. head				
L. snout	(25)29·0–39·5	29·0–42·0	32·9–37·7	33·0–38·3
Eye	17·5–24·3	20·7–24·8	19·9–26·2	17·3–18·0
D. preorb.	(16·9)18·0–20·0	17·3–23·2	19·9–21·8	19·3–23·7
Inter orb.	24·3–29·6	21·4–25·5(28·0)	26·4–31·5	27·6–31·9
Lower jaw	30·0–36·4	31·0–36·5	34·6–37·9	30·8–36·7
Scales lat. line	25–30 (mode 27)	26–29 (mode 27=28)	29	28–29
Scales cheek (rows)	3–4	3(–4)	2	2
Lower gill-rakers	11–14	9–13	11–13	11–14
Dorsal	IX–XIII 11–15	X–XIII 11–14	XII–XIII 12–13	XI–XIII 12–13
D totals 22	2	2	—	—
23	1	4	—	1
24	13	6	1	1
25	8	2	1	5
26	4	—	2	1
Vertebrae 27	21	1	—	—
28	17	16	9	
29	1	2	—	
30	1	—	—	

In two specimens of our samples of each subspecies there are only two (II) anal spines, in all the rest III and 9–11 soft rays.

Diversity in vertebral numbers, and in their distribution between abdominal and caudal is marked in both subspecies. Temperature at a critical period, operating through rate of development, is known to affect metameric numbers (see especially Garside, 1966, and references therein), and it is to be expected that the locations to which females take the broods will vary considerably in this parameter. In *O. a. alcalicus* four syntypes include two with 29 and 30

Table 93. Frequencies of dorsal formulae in samples of *O. alcalicus*

		alcalicus	*grahami*	
Total rays	Formulae		Magadi	Nakuru
22	XI 11		2	1
23	X 13	1		
	XI 12		3	1
	XII 11		1	
24	X 14	1	1	
	IX 15	1		
	XI 13	1		
	XII 12	10	4	2
	XIII 11		1	
25	XIII 12	2	2	6
	XII 13	5		
	XIV II	1		
26	XIII 13	3		2
	XII 14	1		1



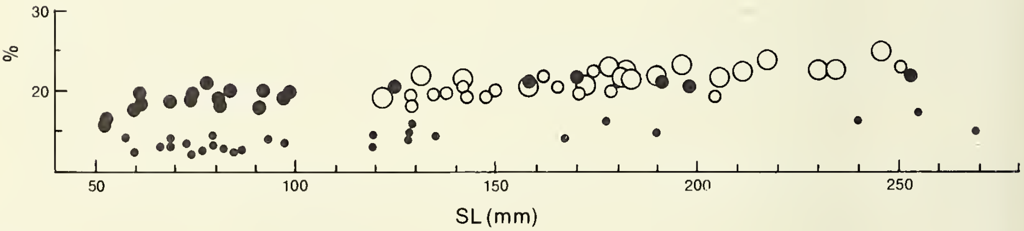


Fig. 132 Above, depth of preorbital bone as % length of head in *Oreochromis alcalicus* (○); *O. amphimelas* (●). Below, depth of preorbital bone as % length of head in *O. p. pangani* (○); *O. p. girigan* (∘); *O. hunteri* (●); *O. amphimelas* (•).

vertebrae respectively, higher numbers than found in any of the 36 fishes of another sample. It may be relevant that the types were caught in a volcanic cavity near the lake, not in the lake itself. The temperature of this pool was not given; it was stated to be weakly alkaline and very sulphurous. *O. a. grahami* has a marked mode at 28, and the 9 radiographed examples from the transplanted population all have 28. Not all the radiographs of this subspecies permitted recognition of the division between abdominal and caudal vertebrae, but in 7 from Magadi in which this was possible the division was 13 + 15. This was also the modal division in the Nakuru sample, but in one it was 12 + 16 and in two 14 + 14, the only equal division observed in either subspecies. The distribution in the sample of *O. a. alcalicus* collected by Dr Coe is:

12+15 in 16
12+16 in 13
11+16 in 3
13+15 in 2
13+14 in 2

In two specimens of *O. a. grahami* and one of *O. a. alcalicus* the spondylophyseal apophysis is on the third vertebra. In one of these there is no left apophysis. The spine is short and thick.

The teeth have a characteristic shape, in which the major cusp is bluntly truncated and the minor cusp much shorter. They are arranged in three or four rows, those of the outer row bicuspid, except 2 or 3 small simple upper teeth posteriorly. The inner are tricuspid, but the inmost row may consist of unicuspid teeth. Teeth may be damaged by wear and especially in bigger fishes the minor cusp may be in this way reduced or worn entirely away and the major sharpened to a point. In older fishes (the bigger ones from Nakuru) many teeth may be lost and irregularities such as a few tricuspids in the outermost row or bicuspids in the inner rows may occur.

The median length of the lower pharyngeal bone is greater than its width even in fishes as small as 40 mm SL and the blade is always longer than the dentigerous area (1·3–2·1 times). The posterior teeth have a well-marked shoulder.

The genital papilla is conical, prominent and white (*O. a. grahami*) or yellow (*O. a. alcalicus*) in the mature male, less prominent, but swollen in the mature female.

Coloration. Non-breeding females have a generally olive to mauve colouring of head and flanks, darker on the back with grey edges and spots on the vertical fins. The lower parts of the flanks and belly are free of melanophores and the black peritoneal lining may show through the thin body wall. Mature females have an overall golden hue. In the male the flanks are pale blue.

The colours listed in Table 94 are mainly those of breeding males. (See Fig. 133; and, in colour, the figure on p. 300 of Mayland, 1978). In comparison with breeding females the black becomes more intense, notably in the opercular blotch, the anterior part and edge of the dorsal fin and the outer edges of pelvic and anal fins. In addition a variable amount of melanin appears along the middle of the belly and in a zone surrounding the anus and genital papilla, often intensified near the papilla and near the bases of the pelvic fins (Fig. 133). An oblique bar across the eye is intensely black with a brilliant white upper edge in the breeding male of *O. a. grahami*, duller in the female. The swollen and brilliant white lateral parts of the lower lip of the mature male are characteristic of both subspecies, but the striking eye-bar has not been recorded in *O. a. alcalicus*. In full colour the blue spots on the scales become iridescent.

In both sexes the posterior half of the dorsal fin has typically a row of conspicuous white spots on a black ground along its base and the white (or blue?) spots on the scales are bigger on the caudal peduncle (Figs 133 & 134).

In some of the large females from Lake Nakuru the lateral parts of the lower lip are swollen and white as in males, and in one a zone of sparse melanophores surrounds the vent, but these features have not been seen in smaller mature females.

These changes accompanying sexual activity in males evidently involve an increase in the amount of melanin, the expansion of melanophores and an increase in guanophores. Table 94 shows also that parts coloured red in the male *O. a. alcalicus* are orange in *O. a. grahami*, parts yellow in *O. a. alcalicus* are white or transparent in *O. a. grahami*. This is probably a quantitative rather than a substantive difference. (A similar difference was brought to my attention by Mr D. Eccles between the *Haplochromis callipterus* of Lake Chilwa, which has red ocelli on the anal fin, and the same species in Lake Malawi, in which the ocelli are orange).

Fig. 133 see p. 383.

Ecology of the subspecies

Food

The gut is long and coiled as in other species of *Sarotherodon* and *Oreochromis*.

The rocks and chert gravel of the lagoons inhabited by *O. alcalicus* are encrusted with blue-green algae and on this the fishes have been observed to spend much time browsing. The algae have been found to make up 90% of the stomach contents, the rest consisting mainly of copepods and dipterous larvae (Coe, 1966). Food is taken also from the mud and the surface film. Albrecht (1967*a*) reports that feeding is accompanied by sucking noises and continues even in brooding females (Coe and Albrecht). The time of most active feeding for *O. a. grahami* is the evening, for *O. a. alcalicus* the early morning (Albrecht). Young *O. a. grahami* eat eggs as they are shed by the female (Woodhouse, 1912; Albrecht, 1967*a* & 1968*a*), and much of the time and energy of the territorial males is occupied in driving them off. They also hunt invertebrates at the surface. Young *O. a. alcalicus* were not observed to eat eggs.

Fig. 133 *Oreochromis alcalicus grahami*, two views of a male preparing a nest. Characteristics are the white lip, the black bar through the eye and the white genital papilla surrounded by a black area. (Photograph, Professor W. Wickler; reproduced also in Albrecht *et al.*, 1968; fig. 1).

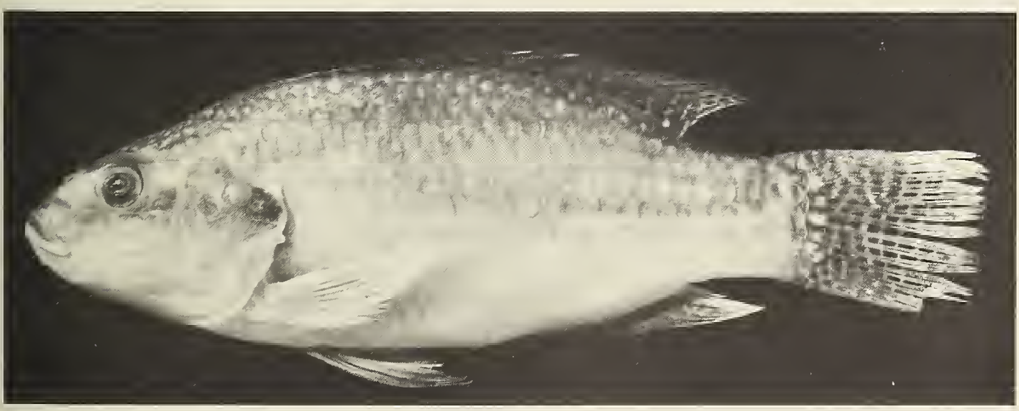


Fig. 134 *Oreochromis alcalicus grahami*, 124 mm SL. A female from Lake Nakuru, where the species has been introduced.

The introduction of *O. a. grahami* to Lake Nakuru was said to be for the purpose of mosquito control; but since Crustacea and dipterous larvae constitute such a small percentage of the food in Lake Magadi, it is not surprising that in Lake Nakuru too the abundant alga *Spirulina platensis* should be the almost exclusive food (Vareschi, 1979). Probably, as in other species of *Oreochromis*, it is only at small sizes that these fishes are significantly carnivorous.

Size and growth

The preserved specimens of both subspecies from their native lakes are all less than 80 mm in SL (10 cm TL). In Lake Magadi the maximum TL was reported as 10 cm (Coe) or 12 cm (Albrecht). Albrecht records that fishes that had passed through a pump filter at less than 3½ cm had grown, in the concrete tank into which the water was piped, in about four weeks to a length of about 12 cm (Albrecht, 1967*a*:324). In freshwater aquaria Albrecht *et al.* succeeded in rearing *O. a. grahami* to 10 cm TL, but no more. In Lake Nakuru, however, *O. a. grahami* has reached a total length of 15–20 cm (Vareschi, 1979). Although the water there may be as alkaline as in Lake Magadi, the temperatures are lower and there are wider spaces, allowing freer movement and less overcrowding. Vareschi (1979) concluded that by 1973 the population had not yet reached its maximum density.

Copley's claim (1958) that *O. a. grahami* will grow to a large size in fresh water has not been confirmed and taken with his assertion that it became indistinguishable from *O. niloticus* must give rise to the suspicion that he was handling a different species (see p. 243). It may be worth noting that he had transferred his fishes to ponds, whereas Albrecht *et al.* (1968), who aimed to test his assertion, used aquaria.

Fossils from the High Magadi Beds include remains of a tilapia estimated to have measured up to 130 mm TL, *ca* 105 mm SL, (Whitehead, unpublished). As these beds are about 12 m above the present lake level the lake must have been, at least temporarily, both bigger and more dilute than at present. It is probable, though not certain, that these fishes were also *O. a. grahami.*

Temperature tolerance

Coe (1966) records that both in nature and in the laboratory *O. a. grahami* is extremely active at temperatures between 32 and 39°C. At lower temperatures it was less active, and at 20–30°C became sluggish and lost the courting colours. In view of later experimental work and the success of the introduction to Lake Nakuru, where the temperature is from 19 to 25°C, this reaction is probably due to lack of acclimatization. In Lake Magadi these fishes browse on the blue-green algae of the hot springs, approaching the hot sources where the algae are thickest until, at about 40°C, they are obliged to turn back. The lethal temperature is between 41 and 42°C.

Tests by Reite *et al.* (1974) also found 40°C the upper limit of tolerance. An abrupt change from 22–23° to 35–36°C was lethal. At the lower end, 10–12°C resulted in death after 1–2 hours, but at 16°C the fishes survived beyond 24 hours.

After sunset the shallow waters of the lagoons where *O. a. grahami* feed rapidly become cooler, falling to 26°C, and the fishes then leave for the deeper places where fluctuations are less extreme. (cf. the diel movements recorded by Maruyama (1958) and Bruton (1979) for *O. mossambicus*, and by Welcomme for the young of the Lake Victoria species). Similar diel movements are recorded for *O. a. grahami* in Lake Nakuru (Vareschi, 1979).

Chemical tolerances

The waters of the natural habitats of *O. alcalicus* are extremely alkaline and rich in salts, especially of sodium (see p. 389). Individuals of *O. a. grahami* have been transferred in the laboratory to fresh tap-water and, after a period of adjustment, resumed their vigour and their colours, provided that the temperature was kept high. Although Coe's (1966) captives did not breed in such conditions, Albrecht *et al.* (1968) obtained all normal activities, including breeding and development, in fresh water.

Lykkeboe *et al.* (1975) have investigated the blood of *O. a. grahami*, and found a high and variable pH of the blood and a high plasma osmolarity. The haemoglobin has a low pH sensitivity, which assures the stability of its function relative to pH change. Reite *et al.* (1974) found the pH tolerance of *O. a. grahami* to extend from 5 to 11, lower (pH 3–4) or higher (12) values proving lethal in 2–6 hours.

The blood of both subspecies was also tested by Leatherland *et al.* (1974) for the sodium and potassium content of the plasma relative to environmental concentrations. The adaptability to a change to fresh water appeared from these experiments to be of a different nature in the two subspecies, *O. a. alcalicus* tolerating a considerable loss of plasma Na^+, *O. a. grahami* having the ability to maintain plasma Na^+ levels. These results must be regarded as preliminary in view of the fact that there was considerable mortality among the experimental animals, but further experiments confirm the special nature of the adaptability of *O. a. grahami*, when compared with other euryhaline fishes (Eddy *et al.*, 1981, where further references may be found).

Breeding

The gonads are paired.

Because of differential movements of the sexes estimates of sex-ratios have a limited significance. Woodhouse records a preponderance of males in *O. a. grahami* and among the Magadi specimens used for the present description the ratio is 3:1. Males have been reported to grow larger than females, but in the collection from Lake Nakuru the four largest are females and Dr Vareschi, who collected them, says (pers. commn) that all the biggest specimens collected by him were female.

Studies of breeding behaviour in field and aquarium have been made by Coe (1965 & 1969), Albrecht (1967*a* & *b*, 1968*a* & *b*), and Albrecht *et al.* (1968).

Oreochromis a. grahami. In nature Coe (1966) found breeding taking place whenever he visited Lake Magadi, in seven months spaced round the year. In the laboratory, individuals continued to breed for a period of two years from the time they became mature with only brief rests.

Whenever he is engaged in breeding activities the male's colours are as described on p. 381 and in Table 94, and these are retained even during his feeding intervals. Small females, as preserved, retain the transverse bars of juveniles, but larger females become golden-yellow in life. Adverse conditions, especially reduction of temperature, cause cessation of breeding with loss of breeding colours (Coe, 1966).

Coe's (1966) description of the breeding pit may be summarized thus: The male makes a circular pit about 6 in (15 cm) in diameter and 3 in (7 cm) deep. If the substrate is firm this will have a raised rim. It is dug for preference against a bank or some solid substance serving as a wall (Woodhouse, 1912, and Albrecht, 1968*a* & *b* noticed this too). The male first makes a depression with his belly (Coe), then fashions the pit by digging vertically, nose down. Each male has normally one pit and they are separated by 30–60 cm according to the space available.

An analysis of the pit-digging was made by Albrecht (1968*a*) by providing different kinds of substratum. In nature, in mud or fine sand the pit resembles an amphitheatre of 7–9 cm diameter with a series of three to five terraces. In rocky places it may be a simple depression. In an aquarium floored with very fine sand a male of 6 or 7 cm TL dug with his mouth a circular pit of 2 or 3 cm diam. surrounded by a few much smaller subsidiary pits (about 0·5 cm diam.). This was the simplest kind of pit. More complicated was a structure consisting of the usual pit with subsidiary pits upon a mound surrounded by something resembling a ditch and vallum, with some subsidiary pits on the edge of the vallum, the whole about 20 cm in diam. Three males made and occupied such structures. They were not complete rounds, but one side was formed by part of the wall of the tank.

Table 94. Colour in *O. a. alcalicus* and *O. a. grahami*, mainly from Coe (1965 and 1969). The colours listed are mainly those of the breeding male.

	O. a. alcalicus	*O. a. grahami*
Snout		grey-mauve
Top of head	pale olive-green	grey-mauve
Flanks	8–10 dark vertical bars	dark vertical bars
	in ♂ disappearing at height of breeding	
	ground-colour becoming reddish during sexual activity	
Scales	pale blue centres	peacock-blue centres
Operculum	pale yellow with green iridescence; opercular blotch faint	pale iridescent blue; opercular blotch black
Iris	black; pupillar rim red	an oblique black bar across eye bordered above and below with white; pupillar rim orange
Lower lip, ♂	left and right thirds or whole lip brilliant white	
Throat and belly	brilliant lemon-yellow	white
Dorsal fin	basal part pale yellowish with grey spots; margin black	transparent with grey to black spots; margin black
Caudal fin	spotted proximally with yellow-blue, margin or broader distal area with crimson wash in male	transparent with grey to black spots, margin black, but in breeding male distal part orange

Albrecht *et al* observed that as building proceeded the subsidiary pits in the simpler structures would merge to form a terrace, and several such, placed concentrically, would produce the amphitheatre-like nest observed in field by Coe (1966) and Albrecht (1968*a*).

In Lake Magadi the males leave their territories in the evening at about 1700 hours and return to them about a quarter of an hour before dawn-twilight at new moon, or half an hour earlier at full moon.

They are then ready for the visiting females and breeding activities are more actively pursued by both sexes in the mornings than after noon.

Neighbouring territory holders seldom interfere with each other, but each male has constantly to defend his territory against wandering males and the numerous invading young fishes. He performs frontal display with exhibition of the opercular spot, and raising and lowering of the black dorsal fin. The white lower lip of another male (or a simplified model featuring such a white area) evokes strong aggressive behaviour, in which frontal display is followed by lateral display, blows by the caudal fin and mutual circling, after which the intruder usually leaves.

When the visitor is a gravid female, a brief and simple courtship follows her entry. In aquaria the male leads the female to the central pit, but in nature leading is omitted or minimal and

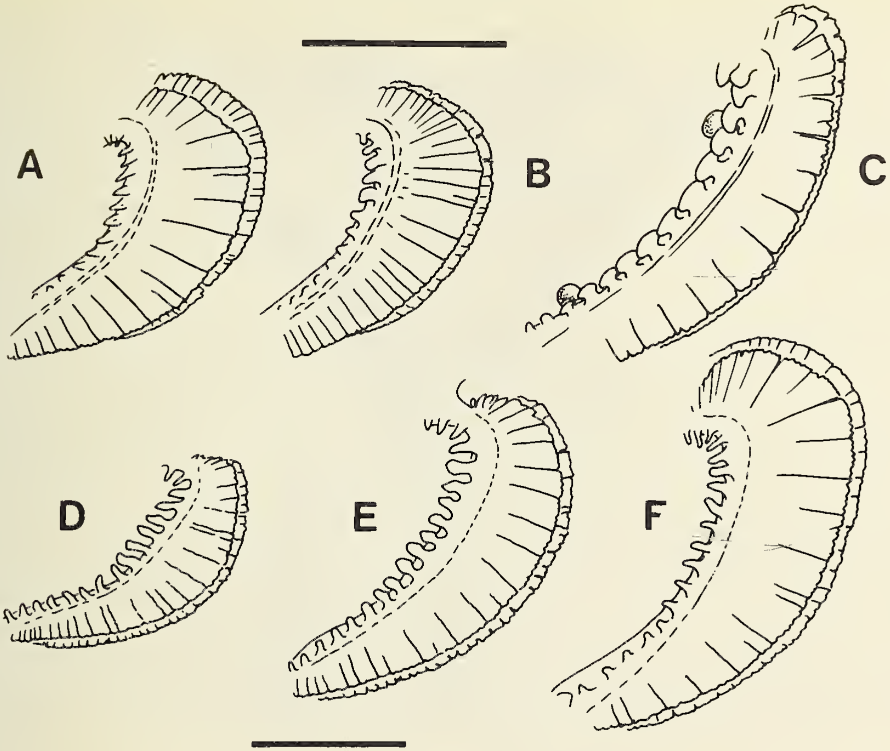


Fig. 135 First gill-arch in lateral view of : A, *Oreochromis a. alcalicus* ♂, 72 mm SL; B, *O. a alcalicus* ♀, nearly ripe, 77 mm SL; C, *O. a. grahami*, brooding ♀, 122 mm SL, Lake Nakuru; D, *O. amphimelas* ♀, 97 mm SL (syntype of *Tilapia manyarae*); E, *O. amphimelas*, brooding ♀, 128 mm SL, Lake Eyasi; F, *O. amphimelas* ♀, 128 mm SL, Lake Eyasi. The gonadal condition of F is unknown, but the firm condition of the muscles suggests a non-breeding fish, perhaps immature; the shape of the gill-rakers is as in males. Gill-filaments diagrammatic.

the female moves spontaneously to the centre. After varying periods the eggs are laid, 3 to 10 at a time; they are yellowish and seem to stick together. The female picks them up instantly and the male swims with his genital papilla near her mouth, probably emitting sperm. Albrecht (1968*a*:383) did not see any snapping at the white papilla by the female, but he suggests that it may act as an 'egg-dummy' in the same way as the complex papilla of *O. variabilis*.

Only seldom does a female spawn twice or thrice with the same male, so that the 50 eggs found by Coe (1966) in a mouth may have been fertilized by several males.

Often preliminaries lead only to a false spawning, the male being distracted by intruders including would-be egg robbers, and Albrecht (1968*a*) estimates that in crowded pools a male spawns only with every thirtieth female who visits him, and about 3 or 4 times a week.

The diameter of the eggs is reported as 1·8 to nearly 2·0 mm, its shape as spherical and the colour pale yellow (Coe, 1966). The Woodhouse collection includes ovaries containing eggs of this size but also some loose eggs of 2·5×2·0 mm. Two females of 122 mm SL from Lake Nakuru contain ovarian eggs of 2·7×1·8 mm and there were a few of the same size in the mouth of one of them. The brooding female moves off to an area which she shares with feeding fishes of both sexes and herself continues to feed while brooding. There is no evidence that she swallows any of her brood, but her non-brooding companions do so, 'dashing to her mouth to

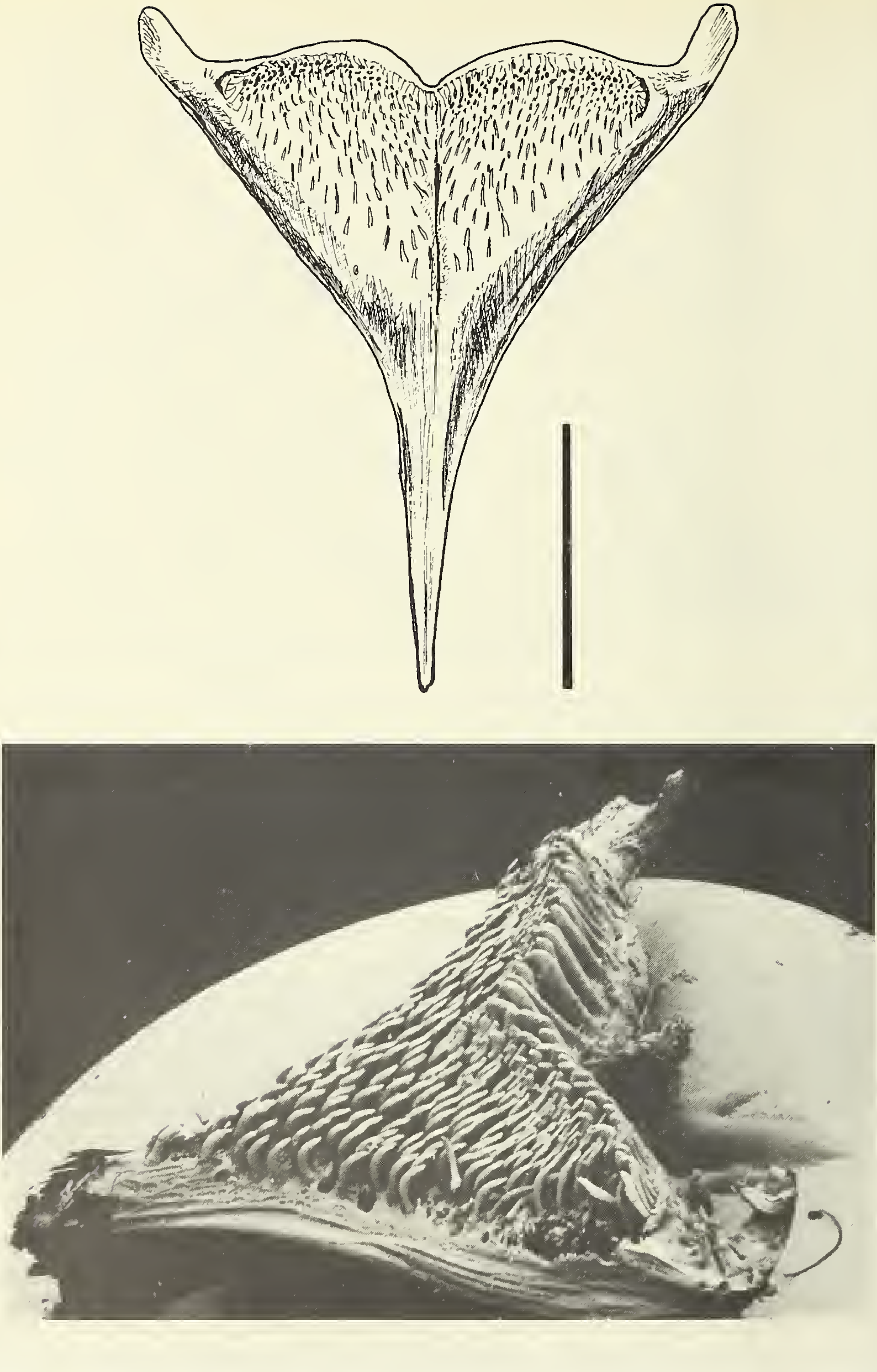


Fig. 136 *Oreochromis alcalicus grahami*, lower pharyngeal bone of a specimen 85 mm SL. Scale = 3 mm; and scanning electron micrograph of a tooth-plate from a specimen 95 mm SL.

snatch protruding eggs or fry' (Coe, 1966). Those that survive to the size of release number only 5 to 20. Coe gives the size of release as 8–10 mm. A female of 107·5 mm SL from Lake Nakuru held young of 11 mm TL in the mouth.

The brooding period is reported as 12–16 days (Coe, 1966) or 11–13 days (Albrecht *et al.*). Developmental stages have been figured by Coe (1966:170) and by Albrecht *et al.* (1968, fig. 4), and nurslings of various stages were preserved by Woodhouse (1912) and by Vareschi (1979) from Lake Nakuru. Pigmentation of the body starts early and even before the yolk is completely absorbed the top of the head is dark and transverse bands appear on the body.

The young are released in the shallows of Lake Magadi at about 37°C. Here they remain with no further maternal care until they attain a total length of 15 mm, when they join the non-breeding shoals.

The smallest brooding female found by Coe was only 25 mm in SL, the smallest ripe male 35 mm. These are the smallest breeding sizes known for wild tilapias (a very small *Sarotherodon melanotheron* was recorded by Aronson in an aquarium population (see p. 54).

In an aquarium Albrecht *et al.* (1968) observed a young fish on the 38th day after release from the maternal mouth and at a length of 25 mm begin to assume male breeding colours; by the 44th day he built his first mating pit, and on the 46th day had mated with a small female.

***Oreochromis a. alcalicus*.** In addition to the replacement of yellow and orange by orange and crimson in the breeding male, Albrecht (1967*b*) reports the following differences from *O. a. grahami* in diel rhythm. Early in the morning, before taking possession of their pits, the males feed on the slimy algal growths—noisily, as *O. a. grahami* does at night. Sexual activity is greater after noon than before, the reverse of *O. a. grahami's* rhythm.

Behaviour of young male fishes towards breeding adults was different too. They stole no eggs, but tried to take part in fertilizing. If a male left his pit it was entered by young for courting. A young male may make a small pit on the edge of that of a large male and mate there with a small female.

Albrecht saw too that fighting between larger and smaller males seemed better balanced than in *O. a. grahami*, so that the large male was not so unduly preoccupied with this activity.

A female of 78 mm SL had 23 nearly ripe eggs in each ovary, each egg measuring approximately 2·0×1·6 mm.

Description of the habitats

LAKE NATRON lies in the eastern Rift between 2°12′S and 2°40′S at about 36°E at an altitude of 610 m a.s.l. Its length is 56 km, its width about 22 km and it is fed by the Southern Uaso Nyiro which rises about 100 km to the north in the Mau Massif. Two smaller rivers, Peninj and Moinik, enter it from the west and hot springs rise near the shore.

It is the most alkaline of the African lakes known to have a natural population of fishes, having an average carbonate alkalinity of 2,600 meq./L (quoted by Talling & Talling, 1965, from Guest & Stevens, 1951). Its appearance from the air has been described by Albrecht (1967*b*:374–5). White streaks of crystalline trona form the greater part of the surface and the water appears pink to blood-red (Myxophyceae or bacteria). Coe (1966) collected *O. alcalicus* in creeks draining the swamp by which the Southern Uaso Nyiro enters the lake, and recorded there an afternoon water temperature of 32·8° near the shore and 30·6° at a depth of 2 ft, a pH of 10 and specific gravity of the water 1·2. Albrecht observed the species in pools fed by hot springs.

LAKE MAGADI lies in the same Rift about 30 km farther north, between 1°43′ and 2°00′ at an altitude of 606 m and covers an area of 107 km². The geology and physiography were described by Baker (1958) and summarized by Coe (1966), who collected and observed *O. a. grahami* there in 1962. He gives a vivid account with photographs of the habitat. Illustrated accounts are also given by Albrecht (1967*a*) and Mayland (1978). The lake basin is occupied by a thick layer of trona, composed of sodium salts, of which 80·9% is Na_2CO_3 and $NaHCO_3$.

The trona is flooded only after heavy rain. Lagoons around the edge of the lake are fed by alkaline hot springs and it is in these restricted waters that the fishes live. In them sodium was recorded at 38 000 mg/L, chlorine at 22 600 mg/L and the carbonate alkalinity was 1180 meq./L. Water from some springs is piped into a large concrete tank before it is used for evaporation. The numerous *O. a. grahami* living in this tank grow bigger than those in the shallow springs entering the lake directly.

The separate pools and lagoons are brought into communication with each other during heavy rains and there is evidence that some of the otherwise separate colonies of *O. a. grahami* can then intermingle. Others are so far isolated that contact can occur only in exceptionally rainy years. The temperature of the water varies widely in the different springs and there is a gradient from the source of each spring outwards in the pool that is fed by it. Except in the hottest springs blue-green algae (*Spirulina* (or *Arthrospira*?) *platensis*) encrust the rock and gravel and are browsed by the tilapias, which live there in daytime temperatures of 28–40°C.

About 12 m above the present lake level fossil remains of a larger, unidentified tilapia (probably *O. a. grahami*) show a former higher level of the lake, estimated by ^{14}C dating of the fossils to have been reached 9,120±170 years ago, possibly during a rapid flood (Butzer *et al.*, 1972; White, 1953). There are also fossiliferous beds at about the same level above Lake Natron and Coe (1969) considers that the two lakes were probably joined in a strip of old lake beds between the eastern Rift escarpment and Mount Shomboli. The close similarity of their tilapias supports this conclusion.

LAKE NAKURU lies at 0°20′S, 36°5′E at an altitude of 1 760 m. Its maximum depth in 1929 (Jenkin, 1936) was 2·8 m (and about the same in 1972–3) and it covered an area of about 50 km². It is bracketed by the Tallings (1965) with Lakes Magadi, Natron and Eyasi as among the most alkaline lakes of Africa. Its chemical, physical and biological properties have been investigated by Beadle (1932), Jenkin (1936), the Tallings (1965), LaBarbera & Kilham (1974), Melak & Kilham (1974) and Vareschi (1978 & 1979). *O. a. grahami* was introduced into Lake Nakuru in 1953 and 1959, and again in 1962 after the lake had dried up and reformed.

Lake Nakuru is fed by alkaline hot springs and by streams from the Mau escarpment, but its chemistry and area are greatly influenced by rainfall and evaporation. The temperature fluctuates widely, but is lower than in Lakes Magadi and Natron. At 9.30 am on April 22nd, 1929, its temperature at the surface was 24·1°C, at a depth of 1·75 m 20·5°. Three weeks later after heavy rain the temperature at 0·25 m was 19·7°C, at a depth of 1·5 m 21·8° (Jenkin, 1936). In June 1969 Melak & Kilham (1974) found the temperature rather evenly distributed from the surface to a depth of 2·5 m, ranging from 21 to 22°C through 24 hrs on one June day, but on the previous day rising in the afternoon to 23–25° at the surface. The dominant alga is *Spirulina* (or *Arthrospira*) *platensis*, accompanied, as it usually is, by the copepod *Paradiaptomus africanus* (see La Barbera & Kilham, 1974). There are numerous predatory birds; flamingos and hippopotamuses enrich the water with nitrogen from their excreta.

The main contrasts with Lake Magadi are therefore the lower temperature (related to the higher altitude) and the wider space available to the fishes.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
O. a. alcalicus			
1905.7.25.29–31	27·5–35·0	Volcanic hole near lake Natron	Neumann
1966.7.14.45–83	40–77	L. Natron, eastern side at north end of El Doinyo Gelai	Coe
1966.12.9.44–86	19–68	L. Natron	Albrecht
1967.9.13.22	44·5	Northern creeks of L. Natron	Coe

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1967.9.13.23–29	39–61	Northern creeks of L. Natron	Coe
1968.7.30.72–105	21–71	Eastern shore, L. Natron	Apfelbach
1979.7.18.365–379	33–55	L. Natron, Sept. 1975	Campbell
1979.7.18.380–408	22–33	Spring, north shore, L. Natron	Campbell
O. a. grahami			
1911.1.21.6–10 (syntypes)	30–49	L. Magadi	J. W. Graham
1912.4.26.1–30	11·6–36·0 & embryos	L. Magadi	Woodhouse
1915.12.2.103–182	19–38	L. Magadi	Hinde
1928.3.28.1–4	35–46	L. Magadi	Cust
1966.7.14.1–44	16–68	Southern lagoons of L. Magadi	Coe
1966.12.9.16–43	16–47	L. Magadi	Albrecht
1967.9.13.40–45	32–46	Large hot springs, west of High Magadi Beds	Coe
1967.9.13.30–39	19–45	Hot springs between High Magadi Beds	Coe
1967.11.16.7	63	?	Coe
1967.11.16.39–140	14–47	L. Magadi	Whitehead, 1959
1968.3.1.1–3 (dry)	57–68	Little Magadi	Coe
1979.3.5.150–216	36–66		'Aquarium Nurseries'
1968.7.30.42–51	18–70	L. Magadi	Apfelbach
1968.9.6.136	95	L. Nakuru (introduced)	Dunn
1979.3.5.366–400	31·5–127·0	L. Nakuru (introduced)	Vareschi

Oreochromis (Vallicola) amphimelas (Hilgendorf)

Tilapia amphimelas Hilgendorf, 1905:405 (Lake Manyara); Boulenger, 1915:188; Trewavas & Fryer, 1965:110–115, 117, figs 2, 4*a–b*, 5*a–c* (Lakes Kitangiri, Eyasi & Singida; hybrids); Makerere Exped. Rep. 1961 (L. Manyara); Beadle, 1974:269.
Tilapia manyarae Hilgendorf, 1905:406 (L. Manyara, ♀ & young); Boulenger, 1915:187, fig. 121.
Tilapia (Alcolapia) amphimelas; Thys van den Audenaerde, 1968*b*:xxxv.

TYPES. Syntypes: two males of TL 136 and 93 mm and a fish (sex ?) of 70 mm, in ZMB, coll. O. Neumann.

Syntypes of *T. manyarae*: two females of TL 85 and 140 mm in ZMB and one of 93 + 21·5 mm in BMNH as well as eleven smaller specimens of TL 47–65 mm, of which four of SL 38·5 to 53·5 mm are in BMNH, the rest in ZMB, all coll. O. Neumann, November 1893, in the Manyara basin. The BMNH specimens are registered 1905.7.25.24–28.

No other species of *Oreochromis* has been collected in the Manyara basin and the descriptions of Hilgendorf are so exact that there is no need to select a lectotype. The recognition, supported by new collections and the field notes of the Makerere Expedition of 1961, that the two nominal species represent respectively male, and female and young of one species confirms Hilgendorf's own suggestion.

Distinguishing characters

As for the subgenus (p. 27, 29). The narrow preorbital bone and its scaly covering are diagnostic. In addition, the general appearance is distinctive, especially in well-grown fishes. The upper

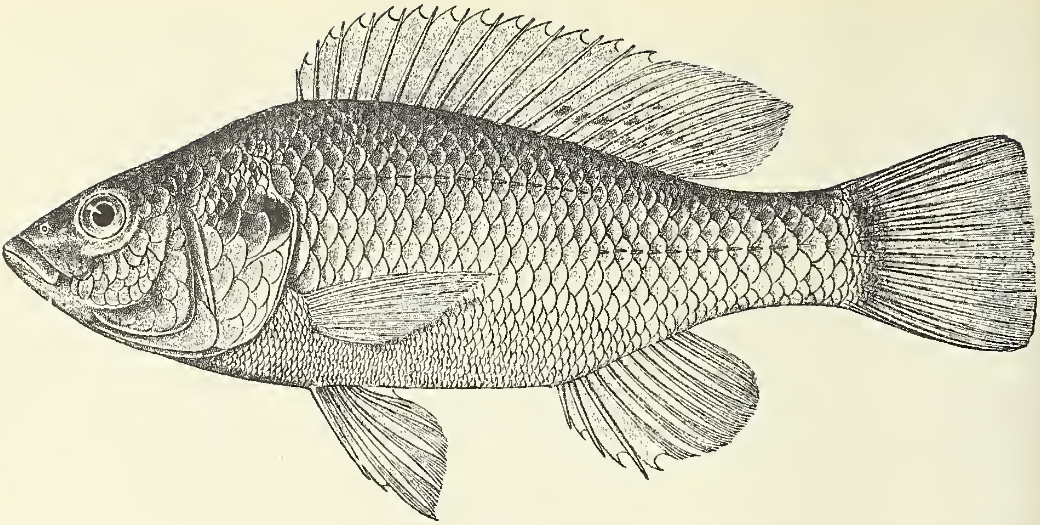


Fig. 137 *Oreochromis amphimelas*, one of the types of *Tilapia manyarae* 38 mm SL. From Boulenger, 1915, fig. 121.

profile of the head is nearly horizontal and in specimens of 130 mm SL and over there is a steep rise from the occiput to the dorsal fin (Fig. 138). The caudal peduncle is long and dorsal and anal fins do not reach its posterior end when adpressed.

Description

Tables 95 and 98 give the proportions and some meristic characters of samples, listed below, from the four lakes.

Comments on the proportions. The range of head-length is wide in the alkaline lakes and in both Manyara and Eyasi the fishes with the biggest heads are breeding females of 58·0–86·5 mm SL (Manyara) or 97 mm (Eyasi).

The proportions of the head are characteristic. The eye is very small, the preorbital bone very narrow, the interorbital space relatively narrow, and the jaws and snout are not enlarged in breeding fishes. In small specimens the nearly horizontal upper profile of the head grades smoothly into the dorsal profile of the trunk (Fig 137), but in the larger fishes of Lakes Kitangiri and Singida it rises steeply at the occiput to the origin of the dorsal fin (Fig. 138).

The postorbital part of the head occupies a greater percentage of the total head-length than in most species and is usually more than 50%, the only exception found being a small male from Lake Manyara in which it is 47·4% (Table 96). (The postorbital measurement was obtained by adding together the length of snout and diameter of eye, and subtracting the result from the total head-length. Since the snout measurement is oblique it is slightly more than a sagittal measurement would be and gives a conservative figure for the excess of postorbital length). The biggest specimens, from Lake Kitangiri, have the highest ratio, namely 54·5 and 60·3. The small size of the eye contributes to this unusual balance and the snout is also rather short. A comparison with *O. alcalicus*, in which the eye is also small but the snout is longer, points the contrast (Table 97). In *O. alcalicus*, from three localities, the postorbital length is 38·3–56·8% length of head, 50 or more in only 4 of 35 specimens measured; the bigger females from Lake Nakuru (SL 107·5–127·0 mm) have ratios of 43·5–46·9%. In 10 specimens of *O. esculentus* from Lakes Kitangiri and Singida the postorbital region is 45·7–49·8% in seven, 50·0–50·8 in three. This

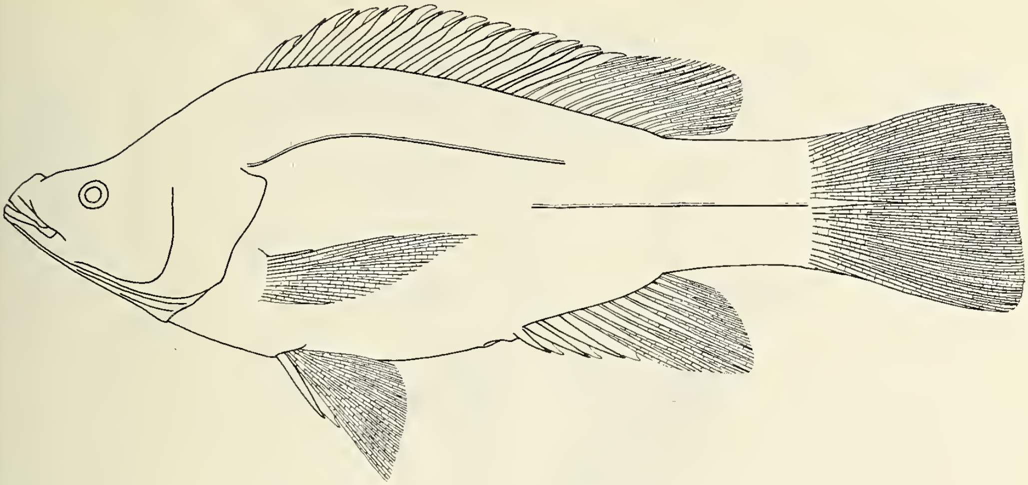


Fig. 138 *Oreochromis amphimelas*, female, from Lake Kitangiri, 265 mm SL.

species has a bigger eye and the proportions of the head are typical of species and specimens in which the snout and jaws are not prolonged.

The teeth are in narow bands. In Lake Manyara there is only one row in fishes less than 50 mm in SL, two or three in other specimens from this lake, up to four series in the big specimens from Lake Kitangiri. In all, the teeth are very small and specimens with all teeth intact are very rare. Many teeth are worn, so that the minor cusp is blunt or absent. Some of the teeth in males appear to be true unicuspids, with a single, sharp, brown point. The teeth of Fig. 139 are chosen from females and appear to retain the original shape. In females teeth of the inner rows are bluntly tricuspid, but in males those of the inmost row are usually unicuspid and the intermediate rows contain bi- and tri-cuspids.

The gill-rakers of the first arch number (2–4) + 1 + (12–15), 16 or 17 lower rakers in one specimen from Lake Eyasi. They are short and bluntly triangular in males, often expanded to square or spade-shaped in females (Fig. 135).

No microbranchiospines.

The pharyngeal teeth are very fine and numerous, the toothed area in adults covering less than half the median length of the bone, in the very young about half (Fig. 140*b*). A marked division between the teeth of right and left sides as in Fig. 140*a* is not universal.

Scales in 2 or 3, usually 3, rows on the cheek and usually extending on to the preorbital bone; 30–34, usually 31–33 scales in the lateral line series, 5–8 between origin of dorsal and lateral line, 6–10 between bases of pectoral and pelvic fins. An abrupt transition between the normal scales of the flanks and the much smaller scales of chest and belly. Scales of dorsal row smaller than those below them, but no naked area at base of dorsal.

Fins. Dorsal, see Table 98. Anal III 8–10, mode III 9, in Lake Manyara; III 10–11, mode III 10 in other lakes. Soft fins blunt, not reaching vertical from base of caudal, at least in females.

Vertebrae. Totals are shown in Tables 2 and 98. The distribution between abdominal and caudal is, in Lake Manyara 13 + 17 (f.2), 14 + 16 (f.6), 14 + 17 (f.12) or 15 + 16 (f.1); in Lake Eyasi 14 + 17 (f.2) or 14 + 18 (f.2); in Lake Kitangiri 14 + 17 (f.5) or 13 + 17 (f.1).

Thus the modes or means of the metameric numbers are lower in Lake Manyara than elsewhere. Although we have not sufficient data on temperature the low level of the surface of Lake Manyara and of the valley in which it lies as compared with the other lakes must be accompanied by higher temperatures, and this probably, as elsewhere, results in a faster rate of growth and a tendency to lower numbers of vertebrae and in this case also of dorsal and anal fin-rays.

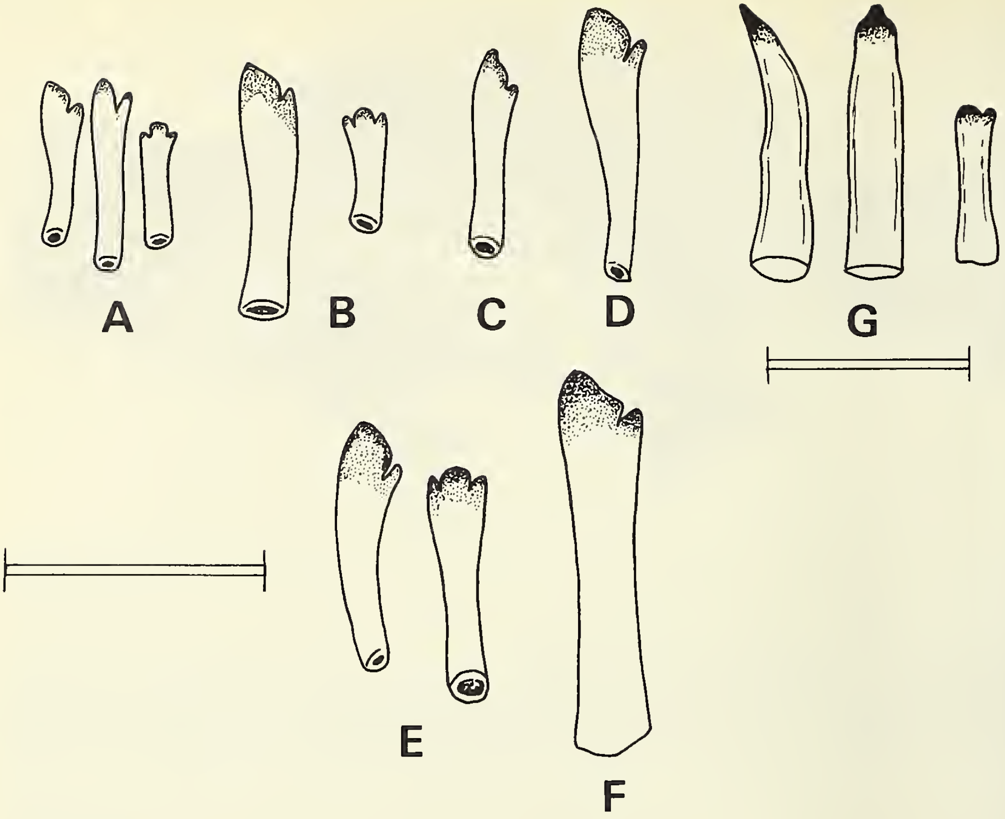


Fig. 139 Teeth from the jaws of *Oreochromis amphimelas*, *O. esculentus* and a probable hybrid. Especially in *O. amphimelas*, the shape of the crown is usually simplified by wear and the teeth figured have been chosen for their relative completeness.

A, *O. amphimelas* 87·5 mm SL, Lake Manyara. Two outer teeth, one inner.
B, *O. amphimelas* 128 mm SL, Lake Eyasi. One outer tooth, one inner.
C, *O. amphimelas* 177 mm SL, Lake Singida. One outer tooth.
D, Hybrid, 169 mm SL, Lake Singida. One outer tooth.
E, *O. esculentus*, 164 mm SL, Lake Victoria. One outer tooth, one inner.
F, *O. esculentus*, 181 mm SL, Lake Kioga. One outer tooth.
G, *O. amphimelas* ♀, *ca.* 250 mm SL, Lake Kitangiri. Two views of an outer tooth and one of an inner.
Scales = 1 mm.

The open proximal ends of the teeth show that they are curved in a plane at right angles to the plane of the page. G is from Trewavas & Fryer, 1965, and the scale is smaller than for A–F.

Genital papilla of male approximately spherical or bluntly conical, pigmented.

Size. None bigger than the 140 mm (TL) syntype of *T. manyarae* has been collected in Lake Manyara. From this basin all were taken in the dry season from restricted waters. The ability of the species to grow much bigger is demonstrated especially by the Kitangiri specimens, the biggest of which is a female of 269 + 64 mm.

The four specimens from Lake Eyasi were collected by Mr Kambona from one fisherman's catch. Among them one mature female of 97 mm SL has a body-depth of only 28% SL in contrast to 35·4–36·6% in the other three, and a long head measuring 40·5% SL in contrast to 34–36%

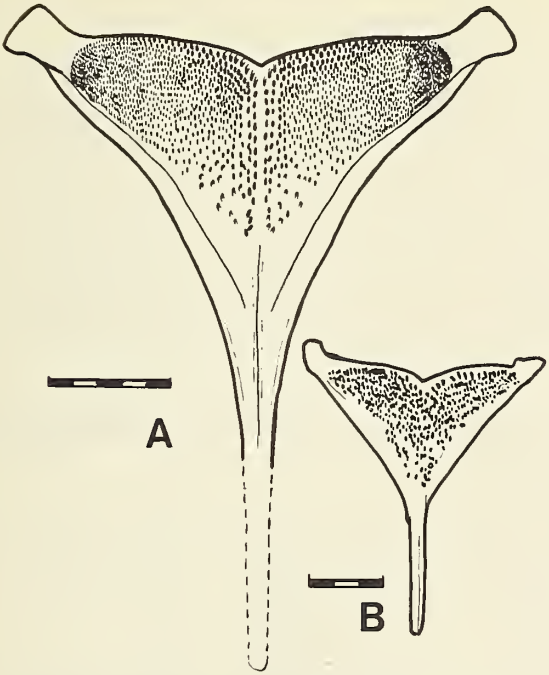


Fig. 140 *Oreochromis amphimelas*, pharyngeal bone of: A, ♀ 240 mm SL from Lake Kitangiri; B, ♀ 93 mm SL from Lake Manyara. Scale bars in mm.

in the others. Her emaciated condition may be due to a brooding fast, but, combined as it is with the long head (or short trunk), it suggests that her growth has been influenced by more rigorous conditions than had been experienced by the other three fishes, one of which was also a female, but in what sexual phase is unknown.

Coloration. Life-colours were described from memory by O. Neumann (*in* Hilgendorf, 1905) as including light blue and pink markings. Field notes by Mr Biribonwoha, member of the Makerere Expedition of 1961 to Lake Manyara, describe the general body colour of females as orange-silver, light grey dorsally, with seven or more dark grey vertical bands from the dorsum to below the lateral line; caudal and pelvic fins light orange; iridescent patches on the gill-covers and a blue streak on the cheek; throat yellowish orange. Males have darker head and body and the vertical fins (except caudal?) are black, the soft dorsal and anal with white oblique lines.

One sample from a very saline pool was darker than the rest, but invidivuals from this pool kept in aquaria became even paler than the river samples.

Preserved specimens from the Makerere Expedition in the BMNH comprise three lots. One from the Makuyuni River includes 9 males and 16 females. Both sexes have plain cream-coloured caudal fins (small, sparse melanophores can be seen with the microscope) and in females the anal and pelvics are, like the caudal and dorsal, only faintly dusky. In males the dorsal, anal and pelvics are grey to black, especially at the edges, and there are series of white dots on the soft dorsal. Another sample of three males and one female agrees with the first. A third sample, whose label had disintegrated, is probably from the very saline pool mentioned above; the body is darker, the caudal is lightly peppered and the pelvics are dusky even in females; in males they are only a little blacker.

There is no tilapia-mark even in the smallest specimen available (26 mm SL).

Table 95. *Oreochromis (Vallicola) amphimelas*, proportions and scale counts.

Locality	L. Manyara	L. Eyasi	L. Kitangiri				L. Singida
N	29	4	1	1	1	2	4
SL (mm)	57–97	82–128·5	119	135	190	240, 269	119–177
Proportions as % SL							
Depth	29–34 (♀) 29–43 (♂)	28·0–36·6	37·8	34·5	40·1	41·6, 37·5	31·8–35·6
L. head	32·0–40·8	35·9–40·5 (♀) 34·1, 34·4 (♂)	37·8	34·0	35·0	31·7, 33·3	32·8–34·5
L. pect. fin	(21·4)23·7–28·0	27·5–32·3	26·7	27·0	30·5	31·7, 29·4	22·0–26·4
L. last D spine	13·7–17·3	14·2, 14·4 (♀) 15·2, 15·5 (♂)					11·4–15·0
L. caud. ped.	14·6–19·0	17·1–18·4	17·5	18·0	15·6	16·9, 16·7	16·8–19·5
Caudal ped. l/d	1·1–1·66	1·3–1·7	1·2	1·4	1·04	1·1, 1·2	1·25–1·35
Proportions as % l. head							
L. snout	(25) 26·6–30·0	27·1–29·6	29·3	29·0	—	28·6, 28·2	28·8–32·0
Eye	16·5–22·4	13·5–17·8	15·6	15·5	12·8	11·9, 11·5	13·8–15·9
D. preorb.	12·0–15·5	12·5–15·1	13·3	14·4	15·2	17·0, 15·0	14·1–16·6
Interorb.	24·2–28·0 (30·8)	27·0–29·3	31·2	29·0	30·5	35·0, 33·0	28·8–34·8
Lower jaw	33·0–37·0	30·9–33·2	36·0	33·5	33·3	32·7, 32·8	32·4–37·0
Scales lateral line	30–32	32	32	31	—	33, 32	32–34
Scales cheek (rows)	(2) 3	2–3		2–3		3–4	2–3

Table 96. Ratio of postorbital part of head to total head-length in samples of *O. amphimelas*

Locality	N	Sex	SL	Postorb. as % l. head
Manyara	13	♀	58–97	50·5–54·9 (X̄ 53·35)
	9	♂	57–81	(47·4) 50·4–56·5 (X̄ 52·64)
Eyasi	2	♀	97, 128	55·1, 59·1
	2	♂	82, 128·5	55·1, 57·8
Kitangiri	2	♀	110, 135	55·1, 55·4
	2	♂	240, 269	59·5, 60·3
Singida	4	♀	119–177	52·1–56·2

Table 97. Ratio of postorbital part of head to total head-length in samples of *O. alcalicus*. For comparison with Table 96.

Locality	N	Sex	SL	Postorb. as % l. head
Natron	4	♀	58–77	47·2–56·8 (X̄ 50·8)
	4	♂	52–72	40·8–51·3 (X̄ 46·53)
Magadi	2	♀	38·1, 40·6	43·2, 43·4
	5	♂	50–68	39·3–45·6 (X̄ 41·96)
Nakuru	7	♀	48·6–127·0	40·7–46·9 (X̄ 44·59)
	6	♂	50·5–94·5	38·3–48·7 (X̄ 44·12)

Table 98. Frequencies of numbers of dorsal fin-rays and vertebrae in samples of *O. amphimelas*.

Dorsal formula	XII 11	XIII 10	XII 12	XIII 11	XIV 10	XIII 12	XIV 11	XIV 12
Manyara	2	2	3	10	5	2		
Eyasi			1			1	2	
Kitangiri					1	1	1	2
Singida				1		2	1	

Dorsal totals	23	24	25	26	Vertebrae	30	31	32
Manyara	4	18	2			8	13	
Eyasi		1	3				2	2
Kitangiri		1	2	2		1	5	
Singida		1	3					

Ecology

Breeding

Most of the Manyara specimens available have gonads enlarging or ripe and some have young in the mouth. Since the species can grow to a total length of 30 cm the subpopulations sampled at Manyara must be regarded as precociously breeding. Males from 74 mm SL had enlarged, white testes and a female of 79 mm and one of 81·5 mm had ovarian eggs of long diameter 2·2 and 2·4 mm respectively; in the mouth of one of them was an egg of the same size. The mature female of 97 mm from Lake Eyasi suggests that the minimum breeding size there may not be very different.

Members of the Makerere expedition reported that the species is a mouth-brooder. Their notes appear to take the sex of the brooding parent for granted, and since they report the condition of the ovaries of some of them it may be accepted that it is the female. However, in the mouths of a male and a female, sent to the BMNH, both an egg of 2·2–2·5 mm long diameter and advanced cichlid larvae were present, and the stomachs of both fishes contained embryos and young of assorted sizes. The ovaries of the female were full of eggs of about 2·2 mm, and the young in the stomachs were alsmost certainly offspring of their own species, possibly swallowed during or after capture.

Records made on several days from 29 April to 23 June 1961 in one locality are consistent with a postulated breeding cycle of about 7 weeks, during which the majority of members of a subpopulation are in phase. At the beginning many had fry in the mouth, but few had completely discharged ovaries. Towards the end many ovaries were empty and brooding parents were becoming rare; some ovaries contained ripening oocytes, evidently starting a new cycle.

Hybrids

In Lake Kitangiri, in addition to *O. amphimelas*, specimens that agreed with *O. esculentus* (see p. 219) were found, in both the collection of 1958 reported on by Trewavas & Fryer (1965), and that of the survey of 1964 by Mann (1965). These or their ancestors probably escaped as fry from a dam in a tributary of the Manonga River, an affluent of Lake Kitangiri. The dam was stocked from ponds where fishes from Lake Victoria were bred (as well as *Tilapia rendalli*, which also gained access to Lake Kitangiri). Four fishes from the earlier collection and two of ten examined by me from Mr Mann's collection have characters intermediate between *O. amphimelas* and *O. esculentus* as shown in Table 99, fourth column. They have the general appearance of *O. amphimelas*, the bigger fishes having the concave profile and steep rise from the occiput to the dorsal fin. The ventral scales are small, but the transition between them and the flank scales is less abrupt. There are more dorsal spines than in *O. amphimelas* (XV or XVI); the gill-rakers are in the upper part of the *amphimelas* range and are not expanded in the female. Microbranchiospines are absent in one, but present though with shortened series in two, and a fourth has them on the second arch only (others not examined for this feature). The vertical fins lack the white spots usual in *O. esculentus*; the pectoral fin may be short or approach the proportions characteristic of *O. esculentus* and the pelvics have a short filament reaching the vent or origin of the anal fin. These fishes were interpreted by Trewavas & Fryer as hybrids between the two species present in the lake and at such a short time after the supposed invasion by *O. esculentus* may have been F_1. A female of 184·5 mm SL contained ovarian eggs of long diam. 2·5 mm, suggesting that the hybrids are fertile.

A small collection from Lake Singida contains specimens of *O. amphiumelas*, *O. esculentus* and *O. pangani*. The two latter were probably stocked from Korogwe in the nineteen-fifties, but *O. amphimelas* is probably native. There are four specimens agreeing with *O. amphimelas* (Table 99, third column) and eight with *O. esculentus*, but one fish is intermediate between these two (Table 99, fifth column). In this fish the concave profile, short pectoral and pelvic fins and small eye suggest *O. amphimelas*, but the numbers of dorsal rays and gill-rakers are as in *O. esculentus* and there are no scales on the preorbital bone. There are white spots on dorsal and anal fins, a faint reticulum on the caudal and a small tilapia-mark. Microbranchiospines are present, but on the 3rd and 4th arches the series are very short. It indicates that in Lake Singida too there is some hybridization between the two species.

Distribution

Lake Manyara, in the eastern fork of the Eastern Rift Valley in Tanzania; and Lakes Eyasi, Kitangiri and Singida in the western fork and its continuation. In spite of the fact that its presence

Table 99. Comparison of fishes from Lakes Kitangiri and Singida determined as *O. amphimelas* and as intermediate between *O. amphimelas* and *O. esculentus*, with *O. esculentus* from both these lakes and Lake Victoria.

	O. amphimelas			Intermediate		*O. esculentus*	
		L. Kitangiri	L. Singida	Kitangiri	Singida	Singida	Kitangiri & Victoria
No. of specimens	1	4	4	6	1	8	30
Profile resembling	*amphimelas*		*amphimelas*	*amphimelas*	*amphimelas*	*esculentus*	*esculentus*
SL(mm)	135	190–269	119–177	150–235	151·5	103–175	110–242
Depth as % SL	34·5	37·0–41·6	33·6–35·6	39·5–44·5	38·2	37·8–46·5	41·5–47·5
L. pect. fin % SL	26·0–31·7		23·3–26·4	28·0–36·5	29·0	33·4–39·6	38·0–44·0
L. caud. ped. % SL	15·6–18·0		16·8–19·5	12·5–15·5	16·1	11·9–17·7	12·0–15·8
Caud. ped. l/d	1·4	1·04–1·2	1·25–1·35	0·9–1·1	1·1	0·8–1·16	0·8–1·15
Eye % head	15·5	11·5–12·8	13·8–15·9	15·3–16·7	15·5	16·3–20·9	16·5–24·0
Interorb. % head	29·0	33·0–35·0	28·8–30·5	34·5–39·0	34·8	37·1–43·0	41·0–47·5
D. preorb. % head	14·4		14·1–16·6			15·2–18·3	
Scales on preorb. bone	abs.	pres.	pres. (3) abs. (1)	pres. or abs.	abs.	abs.	abs.
Scales D-lat. line	7	6–8	6–8	5–6	6	4, 4½, 5	4½–5½
Scales lower flank and belly		Very small, transition abrupt		transition less abrupt		transition gradual	
Microbranchiospines		abs.	abs.	pres. or abs.	pres., but reduced	pres.	pres.
Lower gill-rakers		12–15	14–16	15–16(18)	19	17–20	(15,16) 17–21
Dorsal fin	XV 12	XIII 12 or XIV 11–12	XIII 11–12 XIV 11	XV–XVI 11–12	XVI 11	XV 10, XVI 10, XVI 11, XVII 10	XVI–XVIII 10–11

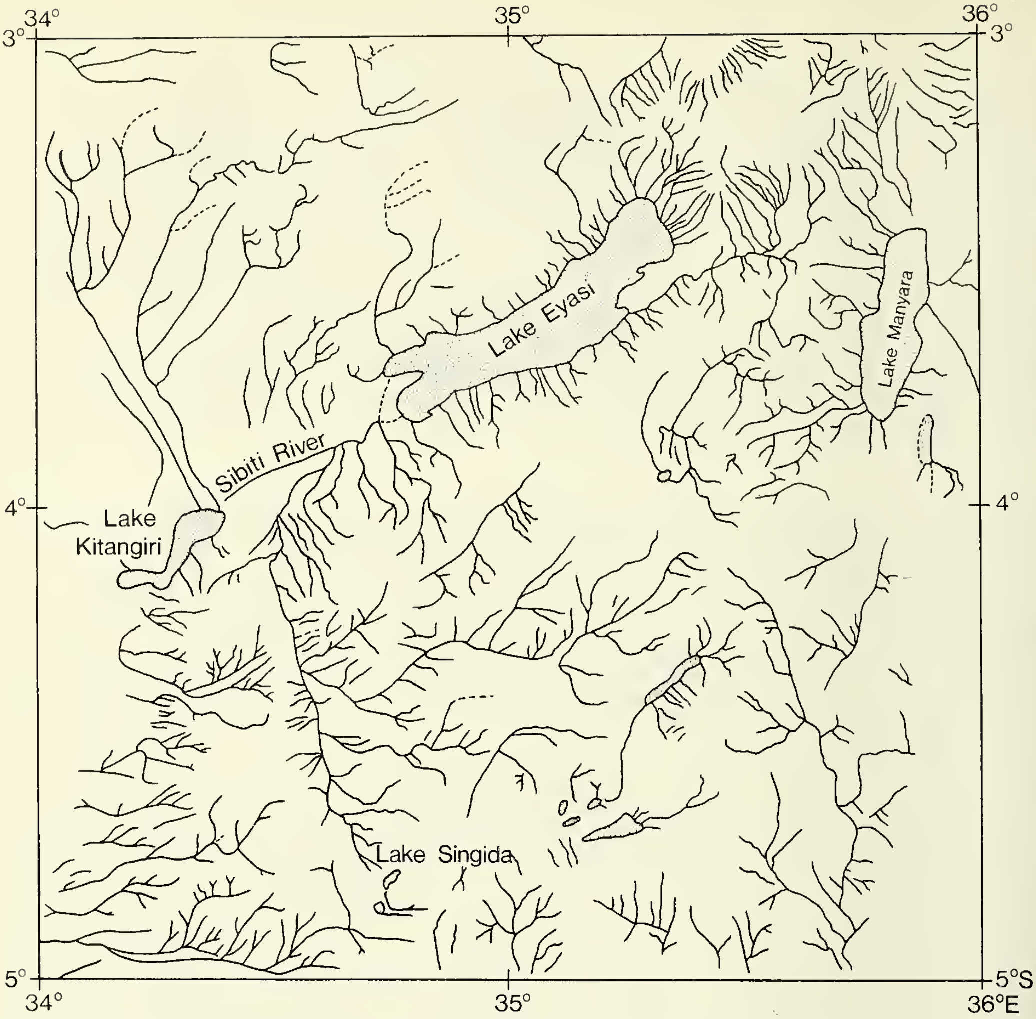


Fig. 141 Parts of northern Tanzania, showing distribution of *Oreochromis amphimelas* named localities.

in the western fork was discovered after considerable stocking operations had taken place in the country, it is probable that *O. amphimelas* is native to all these lakes. It seems unlikely that the stunted population of Lake Manyara would be used as a source of fry for commercial stocking, although this is not impossible in view of the fact that we have one specimen that had been taken from Lake Manyara and grown in a pond. The geographical relationships of the lakes make the identity of their fish populations credible (Figs 141 & 142).

Notes on the habitats

Lake manyara is situated between 3°22′S and 3°50′S and at about 35°45′E, is bounded on the west by an escarpment, but on the east by gently sloping land. Gregory (1921) thought that the eastern shore represented an older worn-down cliff, since the rocks composing are faulted and farther south the depression is continued as a rift valley between east and west scarps. The surface is 960 m above sea level. In the dry season evaporation leaves most of the lake's area as a salt flat with a few streams flowing on to it (Beadle, 1962). The sodium is present mostly

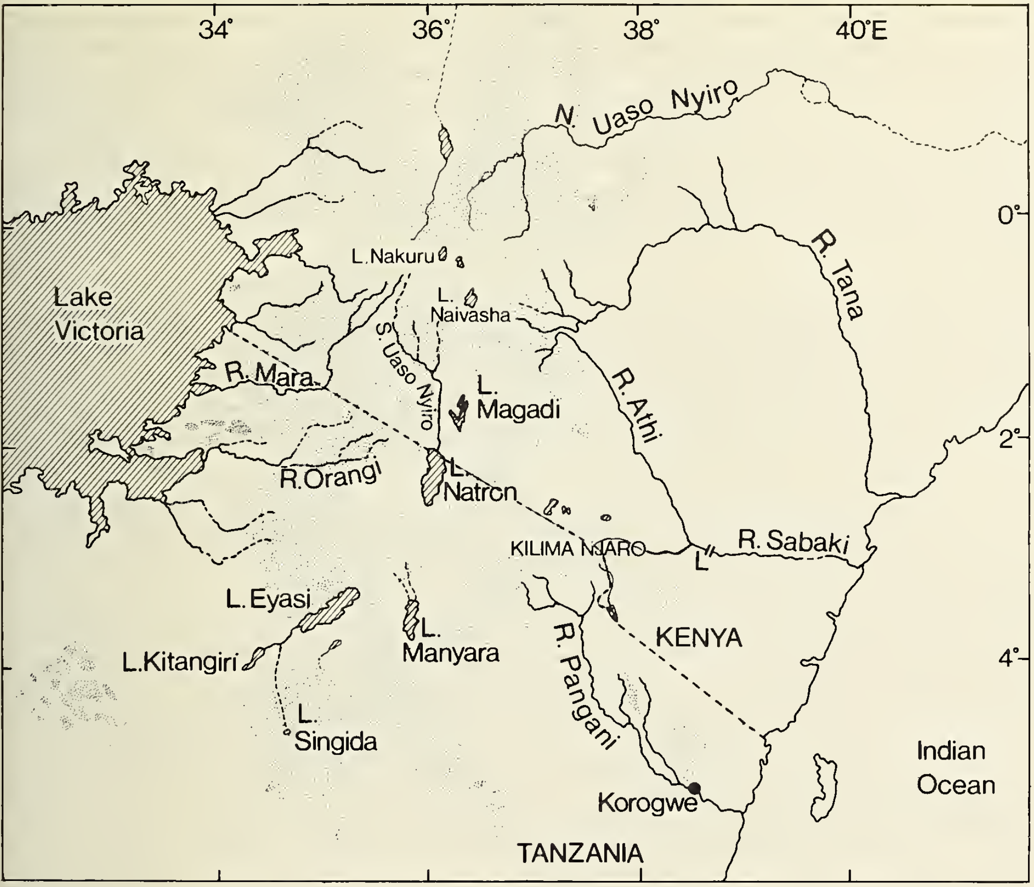


Fig. 142 Parts of Kenya and Tanzania, showing the areas of distribution of: (i) *Oreochromis spilurus*, the rivers Tana and Athi (L = Lugard's Falls), Northern and Southern Uaso Nyiro (= Oaso Ngiro); (ii) *O. alcalicus*, in Lakes Magadi and Natron; (iii) *O. amphimelas*, in Lakes Manyara, Eyasi, Kitangiri and Singida; (iv) part of the area of *O. variabilis*—Lake Victoria and the Orangi River in the Serengeti Plain; (v) the Pangani group (p. 357). Areas over 1000 m a.s.l. shaded.

as bicarbonate. Collections have naturally been made in the dry season, when travelling is possible, and *O. amphimelas* was taken in the affluent river, Makuyuni, in a highly saline, alkaline pool in the estuary of this river (which subsequently dried up), a similar pool on the western shore, and in relatively fresh streams in swamps at southern and northern ends of the basin.

In the fresher streams other fish species were also taken, including a *Clarias*, some widespread small species of *Barbus*, and a haplochromine of the *Astatotilapia bloyeti* complex. The last-named is of some interest, since although it is widespread in Tanzania, neither this nor any other haplochromine is found in the eastward flowing rivers of Kenya.

Lake eyasi is the largest of the lakes in which *O. amphimelas* has been found. It lies in a western fork of the Eastern Rift, at the same latitude as Manyara but some 48 km west of it, between 34°43′ and 35°20′E. The volcanic mountains to the north now separate both this and Manyara from the Kenya part of the Rift containing Lakes Natron and Magadi. Eyasi's surface is about 1045 m above sea level. Gregory (1921) recorded that the surface was formerly much higher but has been reduced by evaporation, resulting in concentration of the salts. An analysis of a sample of water from the north end of the lake, published by Lenk in Baumann's *Durch*

Massailand (1894:293) revealed high proportions of sodium chloride and sodium bicarbonate. The concentration of sodium as quoted from Jaeger (1911) by Talling & Talling (1965) is 4480 mg/L. that of chlorine 4366 mg/L. La Barbera & Kilham (1974) give the conductivity as 23 500 µmhos/cm^{-1} and state that this was the water of highest conductivity found by them to support copepods.

There is no information on the distribution of *O. amphimelas* within the basin. A deposit associated with Stone Age man in Mumba Cave in this basin includes vertebrae of a tilapia and clariid bones (Greenwood, 1957). The tilapias were estimated to have been up to 30 cm in SL, much larger than any in the small sample described here, but they may have been brought from a distance.

Lake kitangiri, lying SW of Lake Eyasi in a continuation of the same Rift, drains by the River Sibiti in the wet season towards Lake Eyasi, but the river reaches this lake only in exceptionally wet years. Mann surveyed the fishing in 1964 and a preliminary report on it was published in 1965. The depth does not normally exceed 5 metres (Mann, 1965). Around the edge of the lake are salt springs that feed it and in the middle are believed to be fresh springs, so that the alkalinity varies very much from place to place (Mann, unpubl.). In 1969 the conductivity was found by La Barbera & Kilham (1974) to be 696 µhmos/cm^{-1}. The carbonate alkalinity was measured in 1960–1 by Talling & Talling (1965) as 6·65 meq./L and the sodium content, mainly as sodium bicarbonate, as 155 mg/L. pH values measured by Mr Hammond at Tulia, a lake-shore locality, varied from 9·0 in September 1958 to 7·5 in May 1961.

Affluent rivers are the Wembere from the south and the Manyonga from the north-west. The Manyonga River rises in a swamp that is also the source of streams flowing into Lake Victoria at Smith Sound. A tributary of the Manyonga, the Nhumbu, includes two dams near Shinyanga, and these dams were stocked years ago with fish, including *Oreochromis (Oreochromis) esculentus* and *Tilapia rendalli*. Both these species have now been found in Lake Kitangiri. It is likely that *O. esculentus* escaped from the dams as fry; *T. rendalli* was first noticed in Kitangiri in January 1962, a month after one of the dams had broken. Neither species is likely to have reached Kitangiri from the swamp watershed, but this may account for the presence of some of the other species recorded from the lake, e.g. *Protopterus* sp., *Labeo victorianus*, *Schilbe mystus*, *Pseudocrenilabrus multicolor*. Other species have a wide distribution including Tanzania and Lake Victoria, and they may be native to Lake Kitangiri (some of them are still only tentatively determined). *O. amphimelas* too may well be a native species.

Lake singida, to the south of Lake Kitangiri and Eyasi, could credibly have had a connection with Lake Kitangiri via the Wembere Sunklands or with Lake Eyasi via the Sibiti River. It is at the southern end of a depression tentatively continuing the Eyasi Rift (Gregory, 1921, quoting Obst, 1912). Although its fish fauna was unknown before it was stocked from Korogwe it is possible that its *O. amphimelas* is native. It is less saline than Lake Manyara; the conductivity found in 1969 by La Barbera & Kilham (1974) was 5740 µmhos/cm^{-1}.

Discussion

Relationships

Evidence for and against a special relationship between *O. alcalicus* and *O. amphimelas* appears on pp. 375–7 in the form of similarities and differences. Of the characters held in common, 1 (low numbers of gill-rakers) characterizes also *O. s. percivali* and, in comparison with its putative relations, *O. salinicola* (p. 455) within the genus *Oreochromis*. Number 2 (absence of microbranchiospines) is rare, but is found in some individuals of *O. s. percivali* and also in genus *Danakilia* of a similar habitat. *Danakilia* also has very small scales on chest and belly and a short pectoral fin, yet other features speak against a close relationship between this and either of the two species under consideration. These characters may therefore be ecotypical parallelisms, although the presence of small ventral scales in species of more normal habitats shows that this is not necessarily associated with shallow flowing water.

The expanded gill-rakers of the first arch in some brooding females is a feature not unique to these two species. They have been observed in *Oreochromis mossambicus* (p. 308) and also in a species of *Serranochromis* (Trewavas, 1964, fig. 5) and in *Pseudocrenilabrus multicolor* (see Reinboth, 1956, fig. 7). This phenomenon may be transient and more common than the records show.

The shared character of only four lateral line openings in the preorbital bone is more impressive. Other inhabitants of thermal waters (*O. s. percivali*, *O. salinicola*, *Danakilia franchettii*) have the more usual number of five; but among fifteen specimens of *O. niloticus filoa*, a hot spring population, seven have only four openings on one or both sides. If a rapid rate of development is responsible (see p. 33) we have to assume that the persistance of the character in the probably later-maturing *O. amphimelas* of Lake Kitangiri indicates that it has been genetically fixed in that species.

The geographical propinquity of populations of Lake Natron and Lake Manyara is also impressive. In the eastern Rift Valley they are separated only by volcanoes which may be younger than the fish populations. But other relationships are geographically credible (Fig. 142).

Albrecht, after studying both *O. alcalicus* and *O. variabilis* in the field, was struck by the similarity of nest construction and breeding behaviour in the two species. His population of *O. variabilis* was in the Orangi River, a tributary of Lake Victoria in the Serengeti Plain, not far distant from the Rift in which Lakes Magadi and Natron lie. An important difference between *O. variabilis* and *O. alcalicus* is the subgeneric character of a tasselled male genital papilla in *O. variabilis*, but the shape of the snout is similar in the two species.

The alternative geographical relationship of *O. amphimelas* is with the species of the south-eastern slope of Kilimanjaro, *O. hunteri*, *O. jipe* and *O. pangani*. Morphologically the chief shared apomorphy with these is the high number of vertebrae and relatively long caudal peduncle. There is also the shared feature of very small ventral scales, but if we regard this as ecologically mediated its value as an indicator of relationship is weakened. However, in common with the reduced number of lateral-line units of the preorbital, it persists in the ecologically different environment of Lake Kitangiri, the history of whose population we can only surmise.

The ease with which *O. amphimelas* has interbred with *O. esculentus* does not necessarily indicate a near relationship of these two species (but a small specimen of the latter from Lake Kioga has two small scales on the posterior corner of the preorbital bone). It supports the inclusion of *Vallicola* in *Oreochromis* as a subgenus. The spontaneous interbreeding of well-defined species (*O. s. niger* and *O. leucostictus*) and even subgenerically distinct species (*O. macrochir* and *O. niloticus*) is well documented (see pp. 256 & 451).

The existence of a group of striking peculiarities in each species (Table 99) and especially in *O. amphimelas* while enabling us to define them as subgenera does not necessarily imply a profound historical division between them and the more 'normal' species of *Oreochromis.*

Post (1965) gave a haploid number of '24?' chromosomes for *O. alcalicus grahami*, admitting it to be unreliable. If verified, it would be among the characters of this species capable of an alternative interpretation as plesiomorphic (primitive), the others being low numbers of vertebrae, scales, fin-rays and gill-rakers and only four lateral line openings in the preorbital bone. It is a feature less easily attributable to environmental influence. All other known tilapiine haploid numbers are 22 (p. 12), a reduction from a basic 24.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1905.7.25.24–28 (syntypes of *T. manyarae*	38·5–93	L. Manyara	O. Neumann
1965.12.21.1	86	L. Manyara	P. J. P. Whitehead
1965.7.8.8	118	Pond, ex L. Manyara	M. Hammond
1966.5.2.1–25	57–97	Makuyuni R. affluent of L. Manyara	Makerere University Expedition, 1961
1969.1.15.35–37	76·0–88·5	Makuyuni R.	Makerere University Expedition, 1961
1969.1.15.38–47	26–73	L. Manyara basin	Makerere University Expedition, 1961
1966.7.14.148–151	82·0–128·5	L. Eyasi	J. Kambona (coll.) R. G. Bailey (pres.)
1965.7.8.4–7	135–269	L. Kitangiri	A. W. White and M. Hammond (coll.) J. G. Lockley, per EAFFRO (pres.)
1966.7.14.143–147	119–177	L. Singida	R. G. Bailey (then Fisheries Research Officer Tanzania)
EAFFRO	190	L. Kitangiri	M. J. Mann

Hybrids with *O. esculentus* are listed under that species, p. 221.

Subgenus *NYASALAPIA*–I

Oreochromis angolensis
Oreochromis lepidurus

The subgenus *Nyasalapia* (pp. 28–30) comprises fourteen species in which mature males have a tasselled genital papilla and no enlargement of the jaws. The fifteenth is *O. salinicola* (p. 454).

With the exception of the genital tassell I have found nothing in common to distinguish them from subgenus *Oreochromis*, which they resemble in breeding habits. Their vertebral numbers range from 28 to 33, the outermost teeth of the jaws in adults from bicuspid in females, unicuspid in males of *O. angolensis*, through mixed bi- and tricuspid to all tricuspid with slender shafts in *O. karomo*. In *O. squamipinnis* the nest (in aquarium) is a simple saucer-shaped depression, but in five species there is a central mating platform (in the others it is not described).

The subgeneric value of the tassel is therefore open to question in its roles both of uniting the species possessing it and of excluding some without it (see discussions of relationships of *O. leucostictus*, *O. alcalicus* and *O. tanganicae*).

The eleven (or twelve) Central African tasselled species seem, however, to be a natural group (see p. 31), but the two described in this chapter are more isolated, both geographically, being confined to the lower parts of Rivers Zaire, Bengo and Quanza (see Fig. 155), and, in the case of *O. angolensis* in its dental characters and coloration.

The natural distribution of the subgenus does not include any of the rivers flowing to the Indian Ocean except the Upper Zambezi and the Kafue and Kalomo, tributaries of the Middle Zambezi, waters that were only secondarily united with the Middle and Lower Zambezi.

Oreochromis (Nyasalapia) angolensis (Trewavas)

Tilapia flavomarginata (part, *non* Boulenger, 1899*b*); Boulenger, 1910*b*:560 (Quanza & Bengo Rivers).
Tilapia andersonii (part, *non* Castelnau); Boulenger, 1911*c*:415 (part of syn. *flavomarginata* only); *idem*, 1915:171 (nos 26–38 only); Fowler, 1919:248 (Quanza R. at Cunga); *idem*, 1932:81 (Quanza R. at Cambambe).
'*Tilapia (Loruwiala) angolensis* Trewavas' Thys van den Audenaerde, 1968*b*:xxxvi (*nomen nudum*).
Sarotherodon (Nyasalapia) angolensis Trewavas, 1973*b*:27, pl. I (Lower Quanza & Bengo).

TYPES. Holotype: male of 196 mm SL, from Quanza R. at Cambambe, coll. W. J. Ansorge. BMNH 1911.6.1.140.

Paratypes: 27 specimens comprising 12 males, 6 females and 9 juveniles, of 43–204 mm SL from the Lower Quanza at Cambambe and Cunga, collected by W. J. Ansorge in 1910 and W. H. Brown in 1889. They are in the collections of the BMNH, the Vienna Museum and the Philadelphia Academy of Natural Sciences (all coll. Dr Ansorge), and in the U.S. National Museum (coll. W. H. Brown). See list on p. 409.

Local name. *Cacusso*.

Distinguishing characters

Genital papilla in both sexes complex, in the male elongate, bifid and tasselled.

Gill-rakers 21–26 on lower part of arch.

Outer teeth of jaws in females and young males bicuspid except a few lateral unicuspids, but in mature males many replaced by unicuspids, until at about 200 mm SL nearly all outer teeth are unicuspid and the posterior are enlarged.

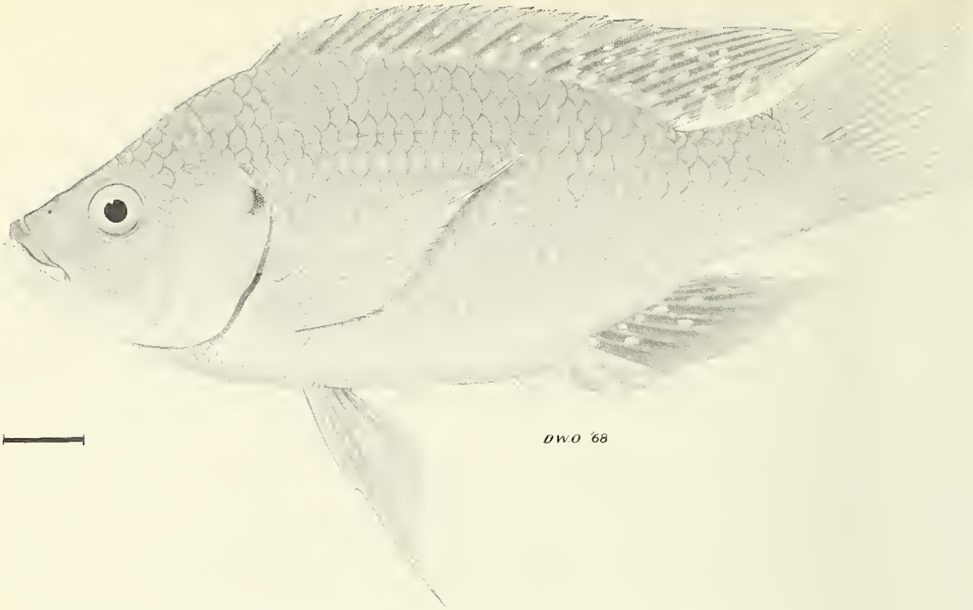


Fig. 143 *Oreochromis angolensis*, holotype. Scale = 20 mm.

Pharyngeal teeth fine and dense; blade of lower bone longer than toothed area.

Vertebrae 29.

Dorsal spines XV or XVI, rarely XVII; total dorsal rays 27 (f.28) or 28 (f.9).

Caudal fin not scaly.

White spots on pelvic fins of mature males and on dorsal, anal and base of caudal in both sexes.

The dentition and coloration of mature males are diagnostic.

Description

Based on the holotype and paratypes and several specimens from the Bengo system, altogether 37 specimens of 43–204 mm SL.

Proportions and meristic characters, see Table 100 and the 'Distinguishing characters'.

Upper profile of head straight.

Last dorsal spine 16·0–20·0% SL, third anal 13·0–17·5.

Preorbital bone showing very little allometry and about equalling diameter of eye at 140–204 mm SL. Length of jaws showing no correlation with size of fish or sex.

Gill-rakers of first arch (2–1)+1+(21–26). Microbranchiospines present on outer sides of 2nd, 3rd and 4th arches.

Teeth of jaws in 4–6 rows at above 140 mm SL, 3–4(5) at smaller sizes, 60–92 in outer row of upper jaw at 100 mm SL or more. Teeth of inner rows tricuspid, but the middle cusp may be worn down in mature males. The lateral unicuspid teeth of mature males (see 'Distinguishing characters') are evidently replacement teeth, the single cusp being pointed, but in large males anterior teeth may also become unicuspid by wear. Unworn bi- and tricuspids have spoon-shaped, curved major cusps.

Length of lower pharyngeal bone (in five fishes of 140–190 mm SL) 37–40% length of head, width 28·5–31·0. Toothed area with rounded lobes and weak posterior notch. Blade 1·1–1·9 times median length of toothed area.

Table 100. Proportions and meristic characters in *O. lepidurus*, *O. angolensis* and also in *S. galilaeus boulengeri*, a form geographically close to *O. lepidurus*, which it resembles in having a scaly caudal fin. *S. g. boulengeri* does not develop a tasselled genital papilla, and may also be distinguished by its deeper body, deeper and shorter caudal peduncle and deeper preorbital bone. In addition the mean numbers of dorsal rays and, probably, of vertebrae are higher.

Ranges given by Thys (1964) for *O. lepidurus* are shown below and a little to the right of those obtained by me, but Thys's data for preorbital bone and lower jaw are omitted because they are evidently measured in a different way. The sizes of samples (N) used by Thys are shown by two numbers, the first in which the meristic numbers are counted, the second, in brackets, in which measurements also were taken.

	S. g. boulengeri	*O. lepidurus*	*O. angolensis*
N	7	6 Thys 19(10)	30
SL (mm)	70–160	58·5–136 47–145*	90–204
Proportions as % SL			
Depth	44·5–48·2	38·5–44·5 42·0–47·8	38·0–44·0
L. head	33·8–35·7	34·3–36·0 33·5–36·3	33·3–36·0
L. pect. fin	36·5–39·0	34·4–37·4 33·8–39·1	33·0–39·1
L. caud. ped.	10·4–12·75	12·0–14·3	12·5–15·3
D. caud. ped.	16·5–18·6	15·2–16·9	14·1–15·6
Caud. ped. l/d	0·6–0·7	0·8–0·9 0·52–0·66	0·8–1·0
Proportions as % length of head			
L. snout	31·6–35·6	32·0–35·5(44·8) 35·2–41·9	31·0–35·5
Eye	21·0–28·6	24·5–32·0 25·1–29·4	20·0–26·0
D. preorb.	22·5–28·0	20·5–24·5	18·0–22·0
Interorb.	38·0–41·3	35·5–41·2 36·9–40·5	37·0–40·5
Lower jaw	28·6–31·1	30·0–34·0	29·3–34·0
Lower gill-rakers	21–24	20–24 19–24	21–26
Vertebrae	29, 30 (N=2)	28 (N=3)	29 (N=3)
Total dorsal rays	27–29 (mode 28)	25–27 (mode 27) 24–27 (mode 26=27)	27 or 28 (mode 27)
Anal soft rays	9–11	9 8–9	8–10

*Calculated from the range of TL given by Thys (1964:107). This does not agree with the range given in the table in the same paper.

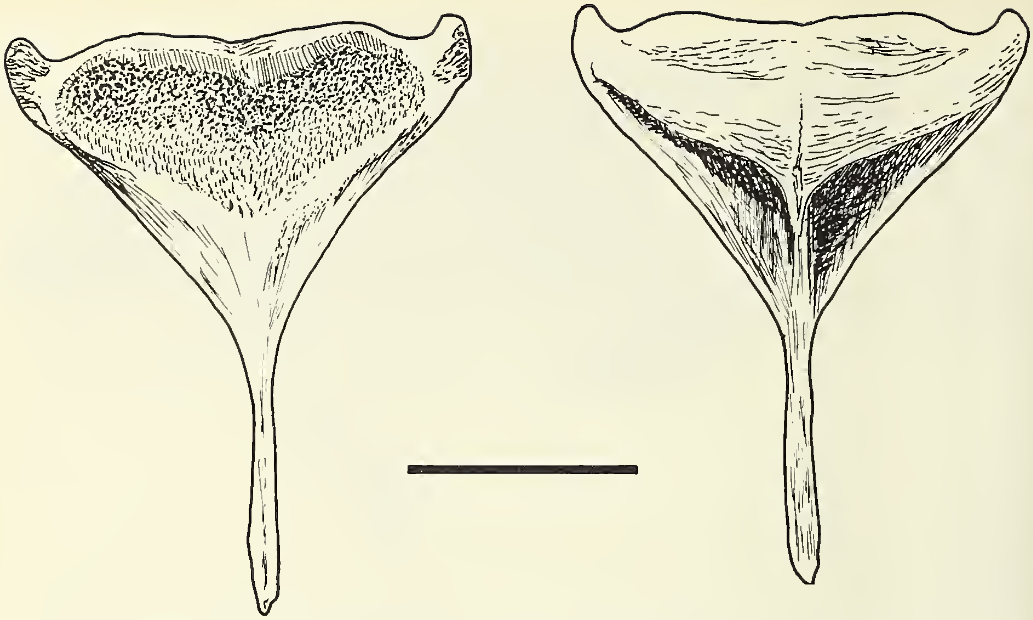


Fig. 144 *Oreochromis angolensis,* lower pharyngeal bone of a fish 220 mm SL, dorsal and ventral views. Scale = 10 mm.

Scales on cheek in 2–3 rows, in lateral line series 29 (f.1½), 30 (f.20), 31 (f.9½) or 32 (f.1); 4 or 4½ from origin of dorsal to lateral line, 4 or 5 between bases of pectoral and pelvic fins.

Dorsal XV 12 (f.17), XVI 11 (f.11), XVI 12 (f.8) or XVII 11 (f.1). Anal III 8 (f.1), 9 (f.15) or 10 (f.16). Soft dorsal in mature males reaching vertical at about half length of caudal.

Pelvic fin produced into a filament reaching vent or origin of anal.

Genital papilla of male in preserved fishes to hand up to 12 mm long, bifid, with tubercles and filaments. Papilla of female with uneven edge and shorter filaments. Loose ovarian eggs 3 mm in long diameter.

Coloration. Counter-shaded, the head and dorsum darker in mature males. Conspicuous white spots on dorsal and anal fins and usually on base of caudal. Similar spots on pelvic fins of males of 145–204 mm SL, a few in a female of 151 mm and a fish of uncertain sex of 198 mm, none on pelvics of smaller fishes of either sex and none in a female of 150 mm SL. Mature male reddish with a silvery-white spot on each scale of 8–11 rows below upper lateral line (Dr Machado, pers. commn), and with posterior dorsal lappets and upper edge of soft dorsal fin red (white when preserved).

Ecology

No data. Other species with tasselled genital papilla are maternal mouth-brooders.

Distribution

North-western Angola in the Bengo River, and the lakes and lagoons in its basin; and in lower reaches of the Quanza (Cuanza) River as far up as the cataracts at Cambambe, 10–13 km above Dondo.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
NHMW 24679–83 (paratypes)	87·5–204·0	Quanza R. at Cambambe	Ansorge
1911.6.1.140–142 (holotype & paratypes)	196, 138, 198	Quanza R. at Cambambe	Ansorge
1911.6.1.143–147 (paratypes)	43–177	Quanza R. at Cunga	Ansorge
USNM 42323/327	148	Quanza R. at Cunga	W. H. Brown
42324/328–9	141, 157·5	Quanza R. at Cunga	U.S. Eclipse Exped. 1889
42325/330–335 (paratypes)	125·5–150·5	Quanza R. at Cunga	
ANSP 37976–81 (paratypes)	46·5–155·0	Quanza R. at Cambambe	Ansorge
1911.6.1.138–9	191, 195	Bengo R. at Cabiri	Ansorge
1911.6.1.148–150	90–130	L. Panguila, Bengo R.	Ansorge
Ang.6936 (Lisbon)	146, 154	L. Bamba, Cacuaco, basin of Bengo	
Ang.6938	159, 165	L. Bamba, Cacuaco, basin of Bengo	
Ang.6944	151, 154	L. Bamba, Cacuaco, basin of Bengo	

Oreochromis (Nyasalapia) lepidurus (Boulenger)

Tilapia lepidura Boulenger, 1899*a*:116 (Lower Congo and Angola); *idem*, 1901:459; Pellegrin, 1904:317; Boulenger, 1915:181, fig. 116 (excl. specimens from Bolobo); Nichols & Griscom, 1917:726 (Maleba & Zambi, estuary of Zaire R.); Thys van den Audenaerde, 1963:579; *idem*, 1964:20, fig. 17 and pl. IX.

TYPES. Lectotype, male, 136+28 mm from 'Angola'; BMNH 1873.7.28.8, pres. Monteiro. Paralectotype: 114+25 mm (sex unknown) from 'lower Congo'; BMNH 1887.1.13.5, coll. F. Hens (not well preserved).

Distinguishing characters

An *Oreochromis* (subgenus *Nyasalapia*) in which the mature male has a tuberculate genital papilla, some of the tubercles prolonged into filaments. Caudal fin of adults densely scaled, usually with a reticulate pattern of melanin. Vertebrae 28, total dorsal rays 24–27, lower gill-rakers 19–24. In adults snout long, preorbital bone deep and blade of lower pharyngeal 2–2·3 times the median length of the toothed area. Outer teeth of jaws bicuspid unless by wearing down of minor cusp. A maternal mouth-brooder.

Distinctions from the geographically close *S. galilaeus boulengeri*, in addition to the tasselled genital papilla, may be seen from Table 100 and its legend. From *O. angolensis* it is distinguished by the scaly tail-fin and in adults the long snout and deeper preorbital bone.

Its breeding habits, which are undescribed, probably also distinguish it from *S. galilaeus boulengeri*.

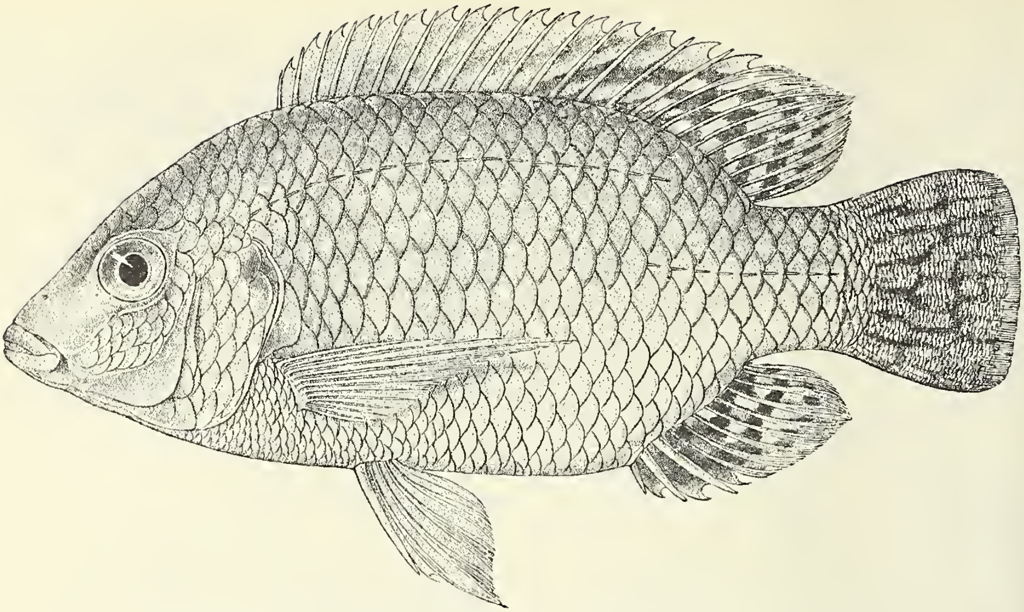


Fig. 145 *Oreochromis lepidurus,* lectotype. From Boulenger, 1915, fig. 116.

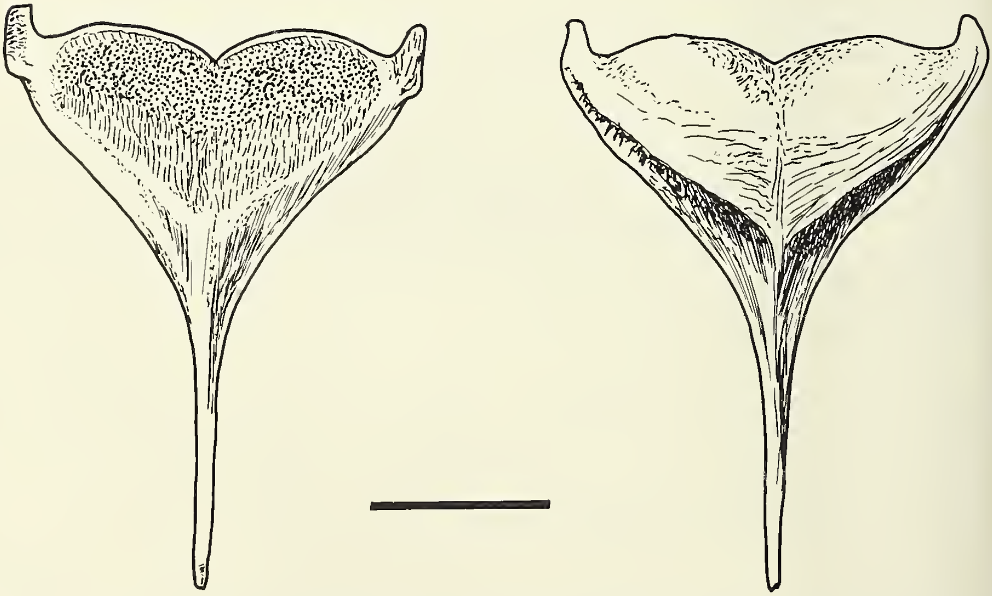


Fig. 146 *Oreochromis lepidurus,* pharyngeal bone of a fish 110 mm SL, dorsal and ventral views. Scale = 5 mm.

Description

Based on the specimens listed below. For proportions and meristic characters see Table 100. See also 'Distinguishing characters', above.

The mouth in the lectotype is very wide, but since this measurement depends on the position of the jaws it does not seem capable of use for comparative purposes.

Teeth with slender shafts, the outer spoon-shaped with a small minor cusp that may be worn down; inner tricuspid with the cusps subequal. Tooth bands of four rows, widening to five at the sides of the lower jaw; 86 teeth in outer upper row of the lectotype.

Lower pharyngeal bone (Fig. 146) length 34·3% length of head in the lectotype, width 30·6; lateral apophyses extending behind the toothed area, which is heart-shaped, including a broad area of dark-brown-tipped very slender teeth.

Scales on cheek in 2 or, usually, 3 rows; in lateral line series 29 or 30, 4 from origin of dorsal to lateral line, 5 between bases of pectoral and pelvic fins.

Dorsal XVII 10 (lectotype), XVI 9–11 (f.5) or XV 12 (f.1). Thys gives also XV 9–11.

Size. Thys (1964) records total lengths up to 182 mm (SL about 145 mm).

Coloration. In preserved fishes buff with faint traces of about eight vertical bars on dorsal half of body and a vaguely outlined tilapia-mark. Caudal covered with a grey reticulum.

I do not feel certain that the fishes figured and described by Sterba (1959:544, fig. 940; 1962:743, figs 939, 940 & 1119) are really of this species. One, a female, has conspicuous black blotches along the sides, which do not appear in the preserved material and look more like *Tilapia tholloni.* It is possibly from Sterba that Thys describes the colour, including red spots, one on each scale, on the lower parts of the flanks and the belly becoming red at breeding time.

Ecology

Thys (1964) reports that it is microphagous, using plankton.

He records a female of TL 165 mm carrying yolked embryos in the mouth.

Distribution

Lower Zaire River, probably only in brackish water. No precise locality is given for the lectotype, but since collections from the Bengo and Quanza Rivers did not include this species (pace Thys, 1963, fig. 4), it probably came from the Angolan side of the Lower Zaire, or from one of the coastal rivers between this and the Bengo.

Material examined

Museum & reg. no.	SL (mm)	Locality	Collector or donor
1873.7.28.8 (lectotype)	136	'Angola'	J. J. Bianconi, pres. Monteiro
1887.1.13.5 (paralectotype)	114	'Lower Congo'	F. Hens
1902.4.14.12	58·5	'Lower Congo'	pres. Brussels Museum
1912.2.2.13	70	Boma, Lower Congo	J. Arnold
1899.11.27.78–79	59, 65·5	Boma, Lower Congo	Delhez
MRAC 47546	82·5	Lower Zaire	Schwetz

Subgenus *NYASALAPIA* – II

Oreochromis variabilis, Oreochromis upembae
Oreochromis malagarasi, Oreochromis rukwaensis

Oreochromis (Nyasalapia) variabilis (Boulenger)

Chromis niloticus (*non* Linn.); Hilgendorf, 1888:76 (record of a piebald specimen).
Tilapia galilaea (*non* Linn., part); Pellegrin, 1905*b*:183 (Kavirondo Gulf).
Tilapia variabilis (part) Boulenger, 1906*b*:447; 1907*a*:529, fig. 37; *idem*, 1915:167, fig. 108.
Tilapia variabilis; Dobbs, 1927:107; Graham, 1928:208 ff, pl. 9, figs 2, 3 pl. 10B (distinguished from *O. esculentus*); *idem*, 1929:24, 145, 146, 184, figs 3, 8 (bionomics, fishery); Gould, 1951 (introduction into ponds); Lowe, 1955*a*:365 (in ponds at Korogwe); *idem*, 1955*b*:260 (introductions, distinguishing features); *idem*, 1955*e*: (fecundity); *idem*, 1956*a*:151, fig. 3c & d, pl. 9, fig. 2 (breeding); *idem*, 1956*b*:53 ff (bionomics); *idem*, 1957:370 (distinguishing features); *idem*, 1959; Whitehead, 1959*b* (presence in rivers); Fryer, 1960, 1961 (bionomics); Thys, 1963:602; Welcomme, 1964*a* (habitat of young); *idem*, 1964*c* (natural hybrids); *idem*, 1964*e* & *f* (young); *idem*, 1966*a* & *b* (ecology); Albrecht, 1968*a*:386 (breeding in Orangi R., Serengeti); Fryer & Iles, 1972 (see fig. 168 & index to that work); Okedi *et al.*, 1976 (in a lagoon in Upper Kagera R.); Wanjala & Marten, 1976 (maturity).
Sarotherodon variabilis; Schoenen, 1979:54, figs.

Notes on the synonymy

The specimens determined by Pellegrin in 1905 were collected by Alluaud in 1904 and I have examined four of them. They all bear the locality label 'Lake Victoria' although Alluaud collected tilapias also in the Maji Chumvi River, a small stream flowing to the sea. I determined two of them as *O. esculentus* (q.v.), and nos. 04/172 and 173 as *O. variabilis*. These were respectively 203 and 162 mm in SL, and for their determination I relied on the following characters: depth of preorbital bone more than 1/5 length of head, 2 series of scales on the cheek, teeth in 5–6 series, a few of the upper outer row tricuspid in the 203 mm fish, scales in lateral line series 32, 31, over top of caudal peduncle 7; D XVII 11, XVI 12; gill-rakers on lower part of arch 20, 18.

Hilgendorf, 1888: one of the specimens collected by A. G. Fischer in Lake Victoria and recorded by Hilgendorf as *Chromis niloticus* was, as Boulenger recognized, *O. variabilis*, for it was described as a piebald (hellscheckigen Spielart). This was the first collection brought to a European museum from Lake Victoria.

Dobbs (1927) was the first to record, from the fishermen's names and his own observations, that there were two species of tilapias in the lake, and Graham (1928) followed Dobbs' information with a name and description of the second (*O. esculentus*).

Types. Lectotype: female, 189 mm in SL from Lake Victoria, near Entebbe; coll. E. Degen. BMNH 1906.5.30.456.

Paralectotypes: seven fishes of 113–229 mm SL from Entebbe and Bunjako, Lake Victoria, coll. E. Degen. BMNH 1906.5.30.429, 431, 458–462.

Local name: *Mbiru.*

Distinguishing characters

Graham (1928) and Lowe-McConnell (1957) have both tabulated the diagnostic characters of *O. variabilis* and *O. esculentus*, which originally were the only tilapiine species to be found in Lake Victoria. Lowe-McConnell included also in her table the characters of *O. niloticus* and *O. leucostictus*, both of which have now been introduced into Lake Victoria.

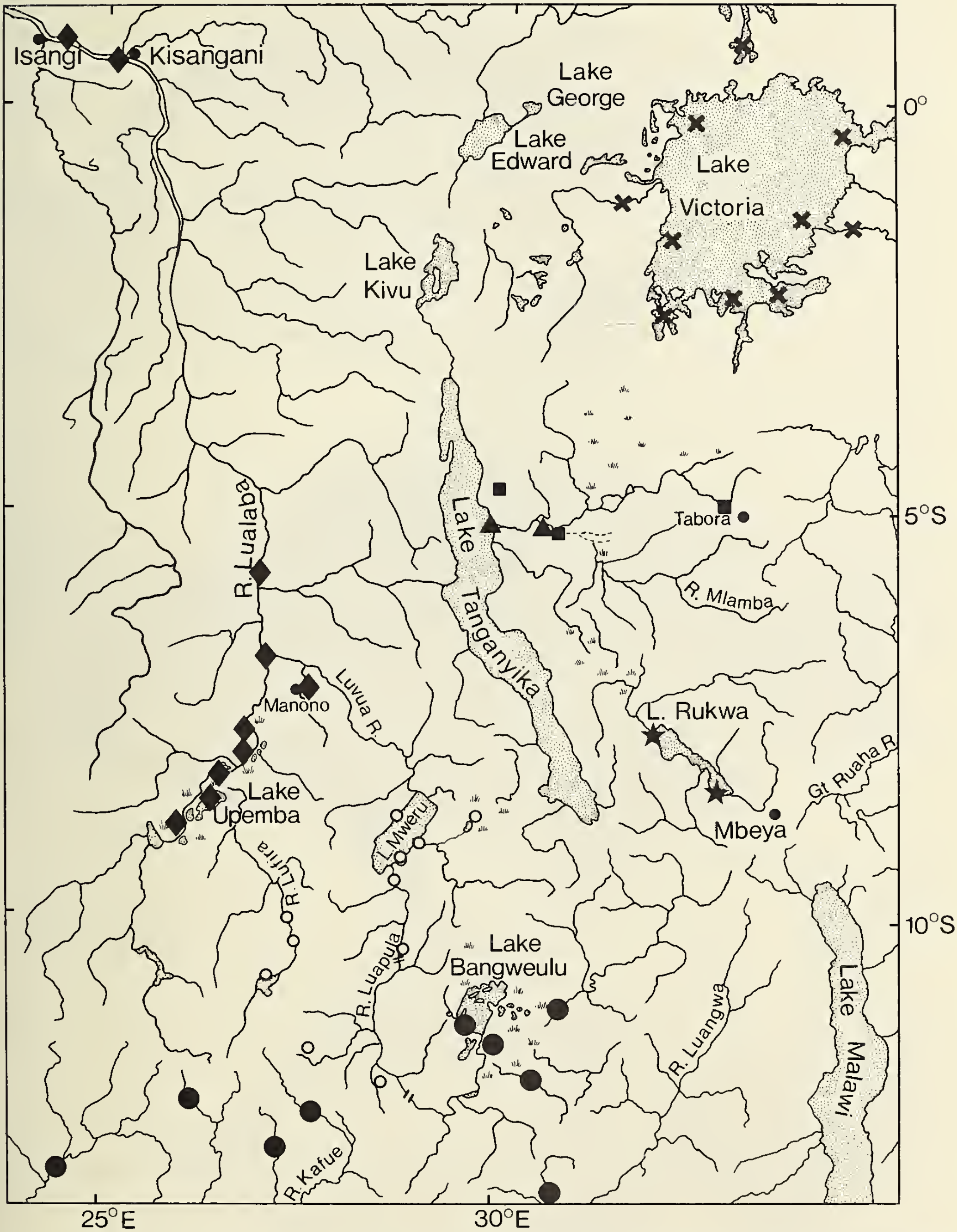


Fig. 147 Part of Central Africa to show distribution of: *Oreochromis upembae* (◆); *O. malagarasi* (■); *O. karomo* (▲); *O. rukwaensis* (★); *O. macrochir mweruensis* (○); and parts of the areas of *O. variabilis* (×), and *O. m. macrochir* (●). Smaller black discs are towns.

1. The breeding male of *O. variabilis* is distinguished from *O. niloticus* and *O. esculentus* b the intense orange to scarlet colour of the margin of the dorsal fin and the long, tasselle genital papilla, as well as by the general body colour. The orange dorsal margin is presen also in grown females and non-breeding males, though narrower and less brilliant.
2. The tilapia-mark is absent in young longer than 15 mm SL (Welcomme) whereas in *O. esculentus* it is conspicuous and with a clear ring up to about 70 mm SL and may still be detecte up to 170 mm.
3. The profile usually has a convexity immediately before the eye.
4. There are usually two rows of scales on the cheek in contrast to usually three in *O. esculentus*
5. In half-grown and full-grown fishes there are 4–7 series of teeth in the jaws, 3–5 i *O. esculentus.*
6. There are differences in the ranges and/or modes of numbers of scales, fin-rays and gill-raker (see Table 52).
7. Graham found the ratio depth of preorbital to length of head to be more than 1:5 in O *variabilis,* 1:5 or less in *O. esculentus.* My measurements give broadly the same result i specimens of 110 mm SL and above Fig. 72.
8. The gill-rakers are longer (Fig. 149; cf. Fig. 71).
9. Whereas *O. esculentus* does not mount beyond the estuaries, *O. variabilis* enters rivers fro the lake.

Oreochromis variabilis differs from both *O. malagarasi* and *O. upembae,* its nearest relative in the suppression in most phases of blotches on the flanks (but see p. 417), in the body colou of mature males, which is blue-grey to blue-black, cf. yellowish in *O. upembae,* in the shap of the profile, which in *O. malagarasi* and *O. upembae* lacks the 'bump' before the eye, a lowe modal number of soft dorsal and anal rays, and a higher modal number of vertebrae (Table 52 & 103). *Oreochromis upembae* also differs from *O. variabilis* in having usually narrow vertic stripes on the caudal fin.

Table 101. Proportions in *O. variabilis.*

N	26	12
SL	85·5–246 mm	50–78 mm
Proportions as % SL		
Depth	39–47, usually 40–46	42–48·5
L. head	31·8–38·6 (no allometry)	33·6–37·3 (38)
L. pect. fin	39–45 (less in 3 fishes in which probably incomplete)	36·6–43·5
L. caudal ped.	11·7–14·5	10·5–14·7
Caudal peduncle l/d	0·8–1·0	0·8–1·0
Proportions as % l. head		
L. snout	30·0–42·5	25–30
Eye at 85·5–142 mm	23·8–27·4	26·5–31·0
at 150–246 mm	16·2–22·3	
D. preorb. at 85·5–142	18·5–21·8	17·0–19·5
at 150–180	19·8–22·2	
at 198–246	22·8–25·8	
Interorb. at 85·5–128	37·3–41·5	34·0–39·6
at 142–246	41·0–48·0	
but in 3 from Orangi R. 152–157 mm SL	36·0–37·8	
Lower jaw	27·0–34·7	29·6–31·5

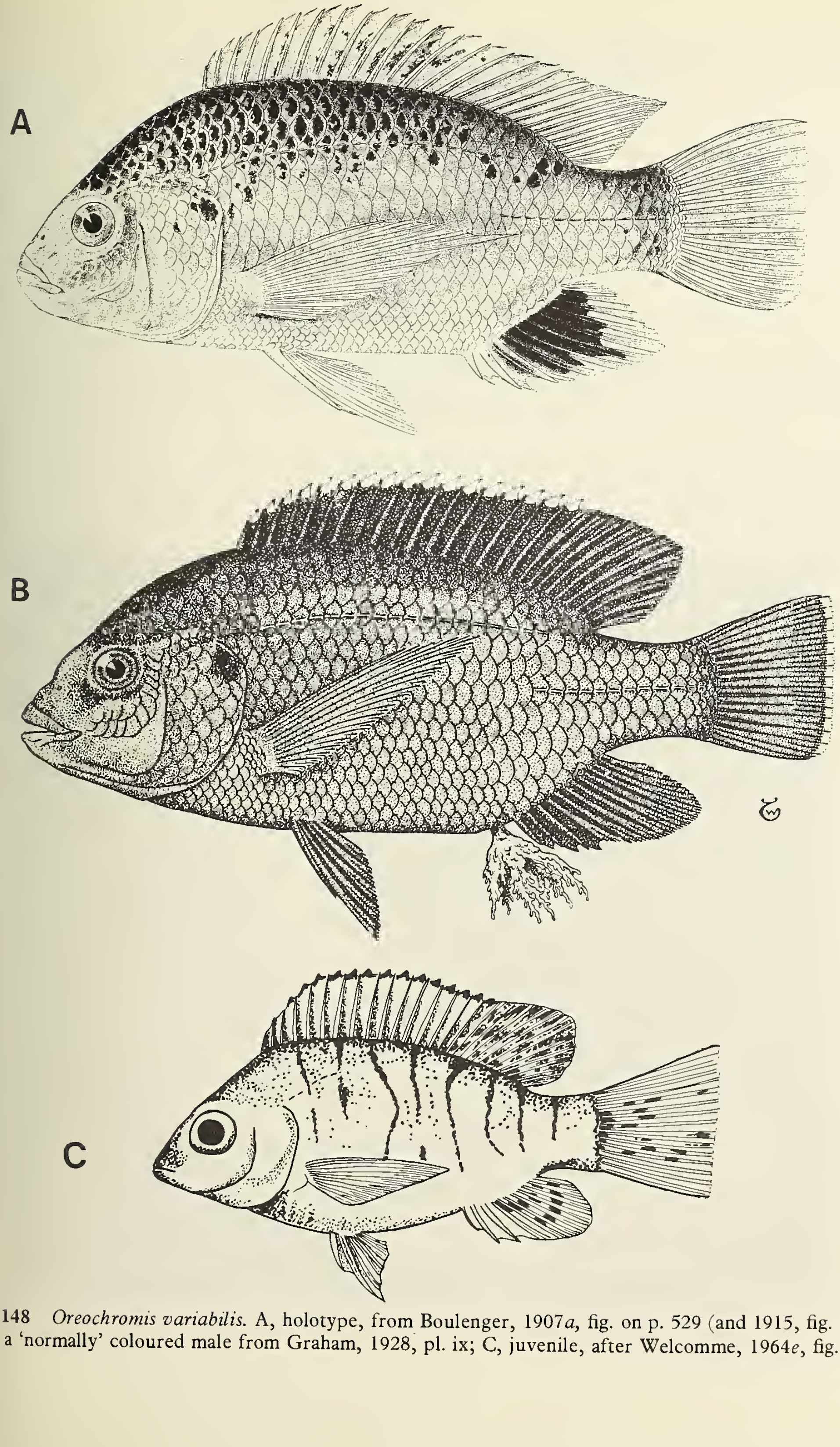


Fig. 148 *Oreochromis variabilis.* A, holotype, from Boulenger, 1907*a*, fig. on p. 529 (and 1915, fig. 108); B, a 'normally' coloured male from Graham, 1928, pl. ix; C, juvenile, after Welcomme, 1964*e*, fig. 6.

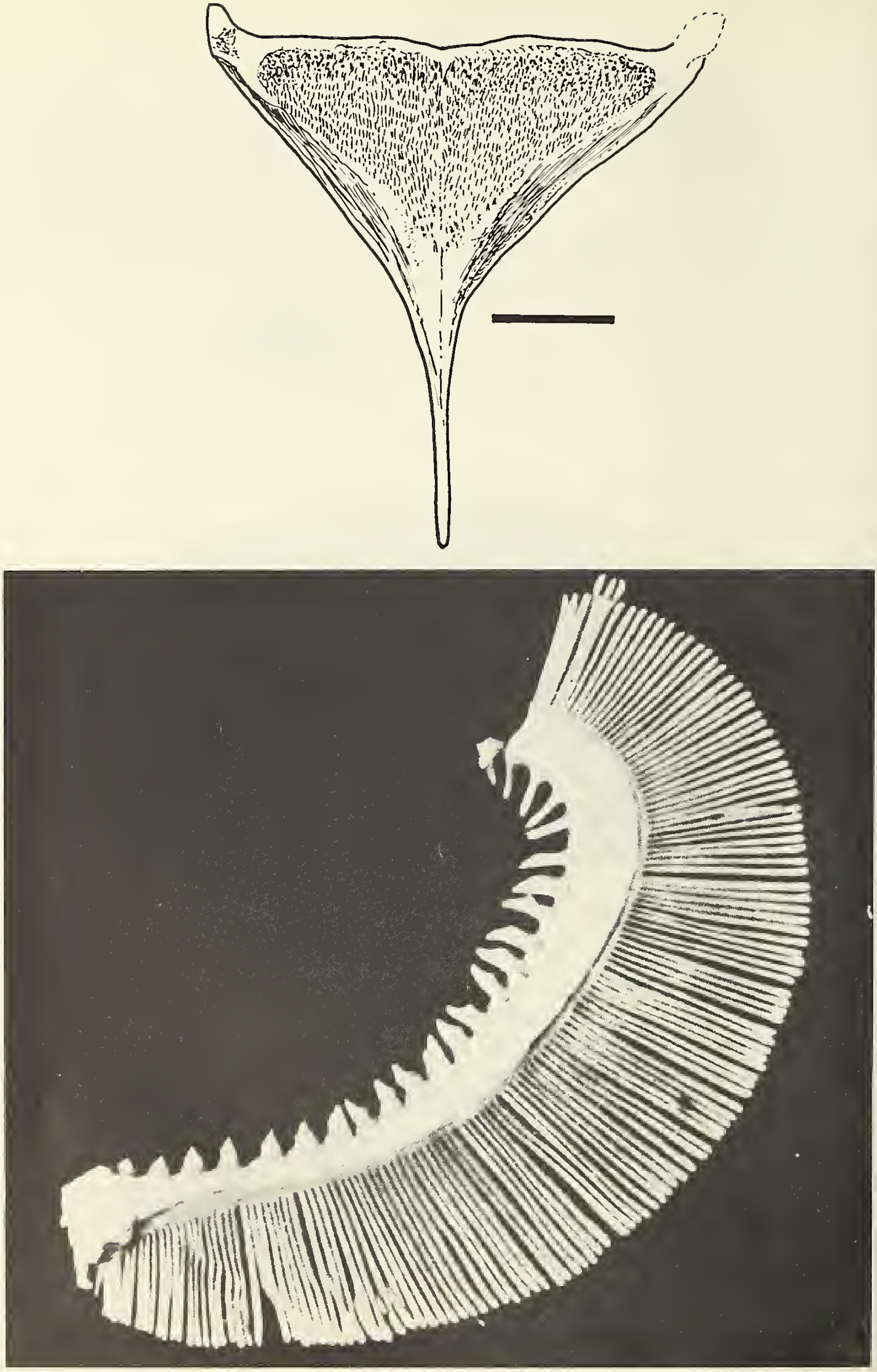


Fig. 149 *Oreochromis variabilis*, pharyngeal bone from a fish 200 mm SL (scale = 5 mm) and first gill-arc from Graham, 1928, pl x B.

Description

Based on 26 specimens 85·5–246·0 mm in SL from Lakes Victoria, Kioga, Salisbury and Ikimba, and the Orangi River (Serengeti), all localities in the general drainage basin of Lake Victoria and the Victoria Nile. Also, separately for proportions, of 12 young, 50–78 mm in SL.

Proportions: see Tables 101 and 104.

Above 140 mm SL there is no fish with a lower jaw ratio of less than 28% length of head, below this length none more than 31·5. There is no difference in the length of the lower jaw correlated with sex; the highest values, 34·2–34·7, are obtained from the two largest males and the two largest females measured.

The diameter of eye and the depth of preorbital are approximately equal between 152 and 178 mm SL, when both are 19·4–22·3% length of head.

It is noticeable that the young are as deep-bodied as the adults (in contrast to *O. esculentus*) and that the length of head shows individual variation at all sizes.

Teeth in 3 series at 50·0–57·5 mm SL, 4–5 series up to 150 mm SL, (4) 5–6 (7) series above this length; with slender shafts. Outer bicuspid, but in ripe males with the minor cusp reduced or absent, in some mixed with a few tricuspids; inner tricuspid. Outer series of upper jaw 56–92, 40–60 in the young.

Gill-rakers on the first arch (2–5) + (0–1) + (17–21), mode 19 on the lower part; totals 21–27, mode 24 = 25 in adults. The respective modes are a little lower in the young, suggesting that the full complement is attained at about 60 mm. Microbranchiospines present from *ca* 70 mm SL.

Width of lower pharyngeal bone less than its median length, 34·6% length of head at 105 mm SL, 31·6–33·4 at 150–120 mm SL, 29 at 224 mm SL; blade 1–1·5 times median length of dentigerous area.

Scales on cheek in 2 series, rarely one or two scales of a third row. Lateral line series 31–32 (33) (see Tables 52 & 103); 3½–4½ from origin of dorsal to lateral line, 4–6 between bases of pectoral and pelvic fins, 7 over top of caudal peduncle above lateral line.

Dorsal XVI–XVIII 10–12; modal formula XVII 11; totals 27–29, mode 28. Anal III 9–11, mode 10 (Table 103).

Caudal truncate, not heavily scaled, but minute scales may extend a considerable distance along the rays, especially upper and lower. In large fishes all the rays are scaly to near the posterior margin.

Vertebrae 29 (f.1), 30 (f.4) or 31 (f.1).

Genital papilla bifid in males in which the gonad is beginning to develop, growing to a long tassel in ripe males.

Coloration. In the young, transverse bars on the body are very narrow and may be curved and the tilapia-mark is present only up to 15 mm SL (Welcomme, 1964f).

'Normal' colour. The general colour of females and non-breeding males is neutral, variously described as green-brown (Lowe-McConnell, 1956*b*), pale green on sandy bottoms, pale blue-grey in rivers and dark blue-grey in muddy habitats (Graham, 1928). Such fishes have a narrow orange edge to the dorsal fin, but not to the caudal. Preserved often show two or three vague dark mid-lateral blotches and one on the top of the caudal peduncle.

Breeding males are blue-grey with a porcelain-like surface (Graham) or, e.g. in Lake Salisbury (Lowe-McConnell), blue-black with a blue-green sheen on the head, bright orange margins to dorsal and caudal fins, greyish belly, black pelvics and bright orange or creamy genital tassel. Graham described the dorsal and caudal margins as scarlet, Albrecht (1968*a*) as orange-red; it is an intense, opaque colour. Albrecht noted that the iris was black, with a bar extending from it on to the cheek (preorbital?), whereas in females it is red with a dark bar.

'Maradadi' individuals. Some fishes have a pattern of segregated chromatophores, expressively known to the fishermen as 'maradadi' (= brightly coloured). The figure by Boulenger (1907 & 1915) showing this pattern is reproduced here as Fig. 148, and it was described by Hilgendorf (1888), Graham (1928), Lowe-McConnell (1956*b*) and Fryer (1961). The most frequent form of this consists of black dorsal blotches on a pale orange background; there is a rarer piebald pattern and occasional individuals are white. Maradadi fishes are more frequent among females, but also occur among males. They are otherwise quite normal and apparently breed indifferently with 'normal' or maradadi partners. The heredity and histology of the pattern have not been analysed.

Ecology

Food

This has been investigated by Fryer (1961), Fish (1955), and Lowe-McConnell (1956*b*). The very young, while they are still returning to shelter in the parental mouth, feed on planktonic algae, especially *Melosira*, and may ingest also small copepods. They soon concentrate on the algal growth on the shelving rocks in the shallow places that constitute the nursery ground in the Jinja area of Lake Victoria, and presumably in similar places in the rivers. The adults also feed predominantly on bottom algae, some of the planktonic organisms that are found in their stomachs being probably such as have settled on the bottom or been washed shorewards from open waters but they also feed directly on plankton (Lowe-McConnell).

In the shallow rock-based nursery grounds near Jinja, Fryer showed that young *O. esculentus* do not compete with young *O. variabilis* for food, but the young of the introduced *Tilapia zillii* do so, and, being more aggressive were thought possibly to be a threat to the survival of *O. variabilis*. In other biotopes the topographic range of young *O. esculentus* may overlap that of this species (Lowe-McConnell, 1956*b*).

Growth

Fryer (1961) has attempted to estimate the average growth rate of this species in Lake Victoria. He established by marking experiments that growth is very slow after sexual maturity. One female caught, marked and liberated at 23·3 cm TL was the same length when captured 805 days later. By constructing six sections of a growth-curve from marking data and connecting the sections, Fryer estimated that it grows to 12 cm in its first year, and that the majority of females do not breed until they are four years old. A fish of 28 cm was estimated to be 11–13 years old. In contrast to this is Lowe's (1955*a*) record of pond-reared broods, which reached 13–19 cm in six and three-quarters months and were then breeding.

Estimates by Rinne (1975), who used fishes in ponds, in cages in the lake and tagged fishes free in the lake, differ from those of Fryer. Two groups of this species reared in cages at different densities gave contrasting results. Those not crowded grew 7 times as much in length, over 17 times as much in weight as those in the crowded cage. Few tagged and recaptured specimens were available for Rinne's studies, but on the basis of these and the results from the uncrowded cage he estimated a much faster growth for *O. variabilis* in the lake, his theoretical curve giving as much as 17 cm in the first year of life and up to 24 cm by the end of year 2.

Fryer's tentative growth-curve shows a contrast in growth-rate, not only for the pond fishes (for this there are parallels), but also with that of *O. esculentus* in Lake Victoria as postulated by Garrod (1959). The difference gains credence from the lower maximum length and weight recorded for *O. variabilis*, and also from the results of aquarium experiments (Cridland, 1960:158) in which, under identical conditions and with the same food, *O. variabilis* was greatly outstripped by *O. esculentus* (weight at 9 months 7·7 g in *O. variabilis*, 23·7 g in *O. esculentus*). In interpreting these results it has to be remembered that *O. esculentus* is probably more tolerant of aquarium conditions than *O. variabilis*.

Breeding

We owe our information on breeding in this species to Graham (1928), Lowe (1955*a* & *c*, 1956*a*

& *b*), Fryer (1961), Albrecht (1968*a*) and Apfelbach (1969*b*). See also Fryer & Iles (1972, fig. 168).

In confined waters *O. variabilis* may breed at 16 cm TL (125 mm SL); in Lake Salisbury males were breeding at 18–23 cm, females at 17–22 cm; in Kavirondo Gulf mature individuals of 17 cm are recorded (Wanjala & Marten, 1976); and two brooding females of 18·5 and 18·7 cm were recorded in Lake Victoria (Fryer, 1961). Otherwise the minimum size of mature fishes in open waters in Lake Victoria is 20 cm, and in both Kenya waters and the Jinja area of the lake about 50% are mature at 22 cm. A curve of the length frequency of brooding females in a catch by non-selective gear shows that the majority of these were between 23·0 and 25·4 cm (Fryer, 1961, fig. 4). Catches in gill-nets not set at the brooding grounds contain a progressively higher proportion of males with increasing size of mesh. This shows that males attain a higher maximum size and possibly grow faster (Fryer), although Lowe found no difference in size attained by the sexes after six and three-quarters months in ponds.

In breeding males both halves of the bifid genital papilla become much branched so that the whole forms a tassel 3 to 4·5 cm long, conspicuously coloured bright orange or creamy white, and the body and fins assume breeding colours (see p. 417).

Nests. In Lake Victoria males make nests on sandy bottoms in shallow water, often on exposed shores. In Lake Salisbury Lowe (1956*a*) observed nests in a water-lily swamp where the water was 15 cm to 1 m deep and the sandy bottom was covered with a thin layer of mud and detritus. Lowe also saw them in flowing water in the Victoria Nile, and Albrecht and Wickler observed them in the shrunken, dry season Orangi River near the bank.

Each nest consists of a central shallow saucer 13–25 cm in diameter, with a raised rim about 2 cm high, around which is a circle of small pits (6 or 7, Lowe; 11 or 12 in a photograph by Mr Y. Pruginin) made by nose-digging. This structure is the centre of a larger pit, 30–90 cm in diameter, surrounded by a higher vallum. The raised nest within a pit has been described and figured by Albrecht (1968*a*), it appears in Pruginin's photograph of a pond in Kajansi, Uganda, and in Lowe-McConnell's photograph (1956*a*, pl. 9, fig. 2) from Lake Salisbury and agrees with her description of the Victoria Nile nests. The early breeders in a pond at Korogwe made simple circular depressions.

Where there is no overcrowding a male may make several such nests and defend them all by patrolling the whole territory. If another male digs a pit between them, even encroaching on one or more of them, he is not challenged and there is mutual respect for territory.

Courting. The outer vallum is the territorial limit defended until a ripe female visits the nest, when courtship, with tail-slapping and leading to the centre occurs and the male's digging activities are concentrated on the central structure.

In the absence of females the male's territorial behaviour dwindles and he may join a passing school, becoming paler, with the opercular spot more conspicuous.

Sex-play. Once a female remains in the nest showing readiness to spawn the mutual sex-play known as 'false spawning' may occur, with the pair making the T-stand. As the male glides forward displaying his now yellow anal fin and genital tassel, the female snaps at the tassel. During this play the male's colour changes; back and belly become quite black and on the paler sides cross-bars appear; the operculum becomes almost white, the head yellow-brown above and the pelvics yellow. The ground colour of the female appears translucent and it is now that there appears the familiar pattern of two interrupted longitudinal bands, a series of spots on the base of the dorsal fin and the blotch on the top of the caudal peduncle. Her eye becomes dark.

Spawning. After such mutual stimulation Albrecht observed a female spawn on the nest. In 1½ minutes she laid, in three batches, about 200 yellowish eggs which she picked up smartly, then ensured fertilization by sucking at the male's genital tassel.

After spawning, the pair remained 75 minutes in the pit and continued mutual play. Finally the male relaxed his spread fins, especially the pelvics and the female immediately left the pit. The male followed and soon resumed the normal territorial colours.

Such is Albrecht's (1968*a*) account of the spawning, probably the only complete one, since it is not clear that the behaviour described by Lowe-McConnell (1956*a*) culminated in egg-laying and fertilization.

Eggs measure 2·5–4·5 mm in long diameter and are yellow and pear-shaped (Lowe-McConnell). Ripe ovarian eggs numbered 323 to 547 per fish in six of 20–26 cm TL (Lowe-McConnell). In the mouth of a 25 cm female Fryer counted 513 eggs, but a parent of 25·5 cm was found with the mouth well-packed with 228 advanced young, giving an indication of the loss of young during incubation, although some may have become successfully independent. In Lake Salisbury females with eggs or young in the mouth were caught in traps among the water lillies (Lowe-McConnell), but in the Jinja area of Lake Victoria special brooding areas were used, off rocky shores in depths of one metre or more (Fryer).

The young become independent at a length of 14–17 mm, the majority at 15 mm. They then go to very shallow water over rocky ledges and feed on the epilithic growths; or they may be found in swamp-channels (Lowe, 1956*b*), where presumably epiphytic algae are their food.

Oreochromis variabilis is not one of the species for which the pools and lagoons formed by the flooding of the papyrus areas and forest have provided additional nursery grounds. It apparently requires better oxygenated waters. Whitehead (1959*b*) reported that the fry are abundant in the flood pools left by the eastern affluent rivers of Lake Victoria. Here, of course, survival is precarious.

Number of broods. Ripening eggs have been found in the ovaries of brooding females. Fryer has shown (1961) that a marked brooding female has produced another brood after 130 days, but he pointed out that this was not necessarily the only brood that she had produced since marking. It showed that at least three broods might be produced in a year by one female. Lowe (1955*c*) includes *O. variabilis* among the species in which the ovaries may contain oocytes of three or more size groups, indicating that an individual fish may produce three or four broods in succession.

Movements. Fryer (1961) has described the movements characteristic of different phases of the life history in the north-west part of Lake Victoria. When they become independent, at about 15 mm, they move into the shallow nursery area over shelving rocks (as stated above). Whitehead (1959*b*) observed them at this stage moving in schools from the lake shore up the eastern affluent streams. In the lake, as they grow they move to slightly deeper water over similar or different bottoms. Between 8 and 17 cm they move about in schools, mostly near rather exposed shores. Garrod (1960*b*) described such schools off Buvuma Island as 'almost entirely monosexual with quiescent gonads'. After 17 cm, schooling is less marked, and the habitats are more varied until spawning and brooding requirements lead the fishes to suitable places.

Marking experiments (Fryer, 1961; Rinne, 1975) have shown no fixed pattern of movements, but among them were enough examples of recapture at or near the locality of marking after a long interval (45 to 805 days) to suggest a degree of preference for one locality. In some cases this was a brooding locality to which females had returned with the brood, and the phenomenon could be classed as 'homing' (Fryer, 1961:9) in the restricted sense of using the same area twice, although there is of course no evidence that a fish returns to brood at the site of its own hatching.

Hybrids

Welcomme (1964*c* & 1966*a*) reported that since the introduction of *O. niloticus* into Lake Victoria it is common to find young fishes that can only be interpreted as hybrids between this and *O. variabilis.* At that time no adult hybrids had been found, probably because it was yet too early since the introduction for a generation of hybrids to mature.

For comparison Welcomme arranged for the two putative parent species to be crossed at Kajansi ponds, and I have examined ten of these crosses, which are also immature fishes of 65–73 mm SL.

Table 102. Frequencies of numbers of gill-rakers on the lower part of the anterior arch in samples of *O. variabilis* from Lake Victoria basin, *O. niloticus* from Lake Albert, putative hybrids of these species from Lake Victoria described by Welcomme ('wild') and pond hybrids from a pond at Kajansi, Uganda. Frequencies of total numbers of dorsal rays from the same samples, omitting the wild hybrids, for which Welcomme did not give this count.

		O. variabilis		Hybrids		*O. niloticus*
		Welcomme	BMNH	Wild	pond	Lake ALbert (BMNH)
Gill-rakers	17		2			
	18		7			
	19	6	8	1		
	20	14	7	9	1	
	21	4	6	13	5	6
	22	2		1	4	4
	23			1		5
	24					7
	25					2
Dorsal totals	27		4			
	28		25			
	29		7		10	5
	30					7
	31					3

1. At this size *O. variabilis* has no tilapia-mark, and *O. niloticus* and the pond hybrids have only a vestige or none.
2. The caudal fin, usually immaculate in *O. variabilis*, and with vertical dark stripes in *O. niloticus*, is 'intermediate' in the wild hybrids, and in the pond hybrids has series of spots forming less regular bands than in *O. niloticus*.
3. The colour of the lappets of the dorsal fin is orange in *O. variabilis*, black or grey in *O. niloticus*, orange in 43% of the wild hybrids, yellow in the pond hybrids (or some of them?) (pers. commn from Dr M. Gee and Dr P. H. Greenwood, who saw them alive).
4. The length/depth ratio of the caudal peduncle is 0·71–0·9 (Welcomme) or 0·85–1·04 (my measurements) in *O. variabilis*, 0·66–0·8 in *O. niloticus*; 0·66–0·85 in the wild hybrids, 0·7–0·9 in the pond hybrids.
5. Meristic characters are listed in Table 102.
6. I have examined the lower pharyngeal bone in three of the pond hybrids. It is indistinguishable from that of *O. niloticus*, but perhaps at this size it would be difficult to see any difference.

From the information available Welcomme's interpretation of the intermediate individuals from Lake Victoria as hybrids between these two species seems acceptable. Whether this will have any effect on the fertility of the stock is unknown (cf. p. 452).

Distribution

NATURAL DISTRIBUTION. Lake Victoria and its affluent rivers; the Victoria Nile above the Murchison Falls; Lakes Kioga, Kwania and Salisbury.

DISPERSAL BY MAN. This species has been transported to ponds and dams, especially in Uganda. In June 1950 it was taken to the ponds at Korogwe, Tanzania (Lowe, 1955*a* & *b*), but Bailey's survey of the stocked dams in Tanzania (1966) recorded it from only one place outside the Lake Victoria basin, namely Maswa on the Central Plateau. The presence of *O. variabilis* in the Aswa

River, an important tributary of the Bahr el Jebel, is probably the result of stocking (Greenwood, 1963). Those in the Orangi River, Serengeti, may be there naturally, since this river drains into Lake Victoria.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1906.5.30.456 (Lectotype)	189	Entebbe	E. Degen
1906.5.30.458,459 (paralectotypes)	113,217	Bunkajo	E. Degen
1906.5.30.429,431 (paralectotypes)	197, 229	Entebbe	E. Degen
1906.5.30.460–462 (Paralectotypes)	31·00–35·2	Bunkajo	E. Degen
1906.5.30.432–441	50–78	Entebbe	E. Degen
1911.10.28.13,14	170–210	Entebbe	C. C. Gowdry
1928.1.25.20,21	103, 132	Jinja, Ripon Falls	C. R. S. Pitman
1928.5.24.78–87	97–265	L. Victoria	M. Graham
1928.5.24.88–97	101–267	L. Victoria	M. Graham
1928.5.24.98	238	L. Victoria	M. Graham
1928.5.30.13–18	147–215	L. Victoria	M. Graham
1967.3.16.3	199	Sesse Is., L. Victoria	R. H. Lowe
1958.12.4.1–7	80–120	Entebbe	C. R. S. Pitman
1929.1.24.221–224	110–188	L. Kioga	E. B. Worthington
1929.1.24.219–220	175–198	L. Kioga	E. B. Worthington
1958.12.5.195	57·5	L. Salisbury	C. R. S. Pitman
1962.2.6.67,68	86·5–125·0	Malawa R., Uganda	M. P. Cunningham
1967.3.16.22.23	161, 178	L. Ikimba, Bukoba District, Uganda	G. J. Lockley
1966.12.9.87–95	114–163	Orangi R., Serengeti	H. Albrecht
1961.12.1.340	122	Trib. of Aswa R. (introduced?)	Uganda Game & Fisheries Department
EAFFRO (not preserved)	172, 222	Masesse Market, nr. Jinja	E. Trewavas
Hybrids with *O. niloticus*			
1967.7.31.2–11	65–73	Kajansi ponds, Uganda	EAFFRO (R. L. Welcomme

Oreochromis (Nyasalapia) upembae (Thys)

Fig. 150

Tilapia nilotica (part *non* Linn.); Boulenger, 1920*a*:8, 37 (Stanley Falls = Boyoma Falls); Poll, 1933*b*:13 (Luvua & Lualaba Rs., & Lake Upemba); *idem*, 1938:406 (Lualaba system); *idem*, 1948:6 (Lualaba R.) Gosse, 1963:221, pl. ix, fig. 2 (Yangambi).

Tilapia christyi (part) Boulenger, 1920*a*:8, 37 (Stanley Falls, one syntype, teste Thys, 1964).

Tilapia nilotica upembae Thys van den Audenaerde, 1964:83, 92, pl. vii, fig. 3 & text-fig. 14 (Upemba regio Luvua R., Lualaba to Yangambi); Poll, 1976:107.

Tilapia (Loruwiala) upembae; Thys van den Audenaerde, 1968*b*:xxxvi.
Sarotherodon upembae; Banister & Bailey, 1979:255 (Upemba region & Lualaba R.).

Types. Holotype: a female of 187 + 50 mm from Nyonga, Upemba region, coll. G. F. de Witte, May, 1925. MRAC 21002.

Paratypes: 21 specimens in MRAC and IRSN, coll. G. F. de Witte at Nyonga; M. Poll at Mayumba; Mission Piscicole Katanga at Lake Kabamba, Mulongo and Lake Lukushi, Manono; and by M. H. Bredo at Maka. All these localities are in the Upemba, Lualaba and Lower Luvua basins of the Upper Zaire system*.

Fig. 150 Above, *Oreochromis malagarasi*, holotype; below, *O. upembae*, 196 mm SL from Lualaba-Lukuga confluence.

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*There are slight discrepancies in the register numbers of paratypes given by Thys (1964) on p. 92 and the lists on pp. 93 and 94. Fewer specimens have been used for the counts in his table IV and more for his table V. Thys based his account on an ample material from the Lualaba and the Zaire down to Isanga and Yangambi.

Distinguishing characters

1. Mature fishes with a bifid and tuberculate genital papilla, prolonged into a cream-coloured tassel in breeding males, in which the edges of the dorsal and caudal fins are orange-coloured or red.
2. Two to four dark blotches mid-laterally from operculum to caudal peduncle and a blotch or top of caudal peduncle. This, though part of the basic pigment pattern of tilapias, is distinctive in that the blotches are rather large and vaguely outlined and persist in adults (except some breeding males). It is identical with that of *O. malagarasi*, *O. karomo* and some phases o *O. variabilis*. Caudal fin with dark, narrow, vertical stripes or series of spots, only a littl less regular than in *O. niloticus*.
3. Caudal rays rather densely scaled to near edge.
4. Caudal peduncle deep (Table 104).
5. Vertebrae 29 in eight (15+14 or 14+15), 30 in one.
6. Scales in lateral line series 28–31, mode 30 (Table 103).
7. Dorsal spines XIV–XVI, mode XVI; soft rays 11–13 (Table 103).
8. Outer teeth bicuspid, in some fishes becoming unicuspid by wear. Lower pharyngeal teet fine, the tooth area with rounded lateral lobes, the blade 1·15–1·5 times the medial lengt of the toothed area.
9. Lower gill-rakers 20–25.
10. Interorbital width 38·8–43·3% length of head.

Among the tasselled tilapias (subgenus *Nyasalapia*) this most resembles *O. malagarasi*, whic differs in having a less scaly caudal fin, the scales usually confined to the basal parts of the rays and in lacking the regular dark stripes or series of spots on the caudal. In *O. malagarasi* th modal number of dorsal spines is the same but the range is higher (XVI–XVII). The two tax should perhaps be considered only subspecifically distinct and are among those indicating th ancient continuity of the Malagarasi and the Lualaba, and for which Lake Tanganyika prove to be a barrier.

Samples of *O. rukwaensis* from Lake Rukwa itself differ from these in lacking the mid-later blotches (but see p. 433), and although the meristic characters are very close *O. rukwaensis* h a somewhat narrower head, expressed in a slightly narrower interorbital region.

Oreochromis variabilis, which belongs to the same group, has higher numbers of vertebr and scales and dorsal fin-spines (Table 103), and a more slender caudal peduncle (Table 104 In it the pattern of mid-lateral blotches is also occasionally expressed.

From *O. macrochir*, the geographically nearest species and also one of the tasselled grou *O. upembae* is distinguished primarily by its melanin pattern. No lateral blotches are prese in adult *O. macrochir* and spots on the caudal are absent or fewer and more irregular. Th numbers of vertebrae (30–32) and scales (lateral line series 31 or 32, usually 32) in the Mwe and Lufira samples of *O. macrochir* are usually higher and the pectoral fin is often longer (Fi 152).

The original confusion of *O. upembae* with *O. niloticus* was probably influenced by the vert cally striped caudal fin; but it is one of the peculiarities of *O. niloticus* not to have the opaq red edge to the dorsal fin, but instead a grey or black edge that may become flushed to purp in the breeding male. The presence of a genital tassel is the most important difference fro *O. niloticus*.

Description

Based on eleven fishes of 118–210 mm SL, including the holotype and two paratypes, and seve- teen young 55–106 mm SL from the Upemba region and the ponds at Manono, Luvua Riv (see p. 413).

Proportions and meristic characters are set out in Tables 103 & 104. See also the 'Distinguis- ing characters' above.

COLORATION. Banister & Bailey (1979:256) describe the colours of a freshly caught adult male thus: 'Dark grey-green above becoming yellowish on the flanks and suffused with black on the throat, chest and abdomen. The operculum was yellowish purple with a distinct opercular spot and there were three large black mid-lateral blotches on the flanks. The proximal parts of the dorsal, caudal, anal and pelvic fins were grey-black. The margin of the dorsal fin was crimson, becoming underlined with white posteriorly. The caudal fin was characterized by a series of wavy, purple-red, vertical stripes and a red distal margin. A short, bifid, cream-coloured genital tassel was present.'

This male was possibly not in peak breeding condition. In one figured by Gosse (1963, pl. ix, fig. 2) the lateral blotches are masked by the dark breeding colour. In this photograph the white (red in life?) dorsal lappets are plainly visible, the dorsum, belly and upper parts of the head are very dark, but the lower limb of the preoperculum and the posterior part of the branchiostegal membrane are pale.

The young have eight narrow vertical bars on the body, with mid-lateral blotches on the 2nd, 3rd and 6th. A tilapia-mark is present with a clear ring up to about 68 mm SL and is detectable, but weaker, up to 84 mm SL.

Ecology

Food

Nothing is reported.

Breeding

Gosse (1963) recorded that the female broods the young and eggs in the mouth in the shelter of sandbanks in the Zaire at Yangambi. Ovarian eggs in a fish of 140 mm SL measure 3 mm in long diameter, but are probably not fully grown. A male of 175 mm from a pond at Manono had a prolonged genital tassel, though not fully developed; its testes were enlarging.

Distribution

Upemba region and the Lualaba River to Yangambe and Isange on the Upper Zaire. A fish of swamps and shallow lakes.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1976.10.12.232	203	Lualaba R. at Lukuga confluence	K. E. Banister, Zaire River Expedition, 1974–75
1976.10.12.256	54·5	Lualaba R. at Malemba Kulu, 8°02′S 26°48′E	K. E. Banister, Zaire River Expedition, 1974–75.
1976.10.12.257–259	28, 73, 76	Lualaba R., 20 km S of Nyangwe	K. E. Banister, Zaire River Expedition, 1974–75
1976.10.12.265–267	61–84	Mulemba on L. Zimbambo, 8°04′S 26°50′E	K. E. Banister, Zaire River Expedition, 1974–75

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1976.10.12.238–239	59·5, 60	Luvua R. at Ankoro	K. E. Banister, Zaire River Expedition, 1974–75
1976.10.12.251	144	L. Mulenda, papyrus 8°45′S 26°01′E	K. E. Banister, Zaire River Expedition 1974–75
1976.10.12.275–282	100–150	L. Kabamba at Mulongo, 7°51′S 27°00′E	K. E. Banister, Zaire River Expedition, 1974–75
1967.8.21.1–2 formerly MRAC 84413	175	Mares de Manono	Mission Piscicole à Katanga, 1947
MRAC 21002 (holotype)	187	Nyonga, Upemba region	G. F. de Witte
MRAC 21003 (paratype)	175	Nyonga, Upemba region	C. F. de Witte
MRAC 84109 (paratype)	210	Manono, L. Lukushi	Mission Piscicole à Katanga, 1947
MRAC 84414	140	Mares de Manono	Mission Piscicole à Katanga, 1947
MRAC 84511–84517	80–111	Mares de Manono	Mission Piscicole à Katanga, 1947
AMNH 6324	54	Stanleyville (=Kasenyi)	American Museum Congo Expedition, 1909–1915

Oreochromis* (*Nyasalapia*) *malagarasi sp. n.

Fig. 150

'*Tilapia nilotica* subsp. ?'; Lowe-McConnell, 1956*a*:142 (Malagarasi swamps at Katare); *idem*, 1958:135, 141 (description, food); Hickling, 1961:224.
Tilapia aff. *nilotica*; Thys van den Audenaerde, 1964:27 (Malagarasi delta).
Tilapia upembae (part); Thys van den Audenaerde, 1968:xxxvi; Bailey, 1968:195, 201.

TYPES. Holotype: female, 165+40 mm, from the Malagarasi swamps at Katare; coll. R. H. Lowe-McConnell. BMNH 1967.3.16.16.

Distinguishing characters

A tasselled species, resembling *O. upembae* from which it differs in the following features:

1. Mid-lateral blotches present as in *O. upembae*. Caudal fin either without spots or with a few irregularly arranged or in quincunx.
2. Caudal rays variously scaly but the inter-radial membranes usually free of scales.
3. Vertebrae 29 in three (16+13), 30 in six (16+14 or 15+15).
4. Scales in lateral line series 30–32, mode 31 (Table 103).
5. Dorsal spines XVI or XVII; soft rays 12 or 13 (Table 103).
6. Outer teeth mainly bicuspid, but often including a few tricuspids.

This population is so similar to *O. upembae* that it is probable that they had a common ancestor when the Malagarasi was part of the Zaire system. It forms the same kind of link between *O. upembae* and *O. variabilis* as does *Serranochromis janus* between the other species of *Serranochromis* and the piscivorous species of *Harpagochromis* Greenwood, 1980, in Lake Victoria (see Trewavas, 1964:48).

Table 103 Meristic numbers in samples of four populations of tasselled tilapias in central Africa. For fin-rays frequencies, for all gill-rakers and scales ranges and means. ZRE=Zaire River Expedition, 1976, as well as four specimens in MRAC seen by both Thys and myself and therefore recorded twice. A specimen of *O. variabilis* with D XVII 10 is recorded only in the totals.

Dorsal fin	XV 11	XIV 13	XV 12	XVI 11	XV 13	XVI 12	XVII 11	XVI 13	XVII 12	XVIII 11	XVII 13
rukwaensis				1		9		7	1		1
malagarasi						2		7	2		1
upembae (Thys)	1		5	10	1	28		7			
upembae (ZRE)	2	1	2	6	2	14		1			
variabilis				3		8	17		6	1	

Dorsal totals	26	27	28	29	30
rukwaensis		1	9	8	
malagarasi			2	9	1
upembae (Thys)	1	15	29	7	
upembae (ZRE)	2	9	16	1	
variabilis		4	25	7	

Anal fin	III 9	10	11	12
rukwaensis		13	6	
malagarasi		2	9	1
upembae (Thys)	2	21	26	3
upembae (ZRE)	1	16	11	
variabilis	6	14	2	

Vertebrae	29	30	31
rukwaensis	6		
malagarasi	3	6	
upembae (Thys)	—	—	—
upembae (ZRE)	8	1	
variabilis	1	4	1

	Lower gill-rakers		Scales lat. line	
rukwaensis	range 20–22	mean (N=17) 20·94	range 30–32	mean (N=14) 31·71
malagarasi	range 20–24	mean (N=12) 21·08	range 30–32	mean (N=9) 30·90
upembae (Thys)	range 20–24	mean (N=10) 22·7	range 28–31	mean (N=72) 29·9
upembae (ZRE)	range 20–25	mean (N=9) 22·3	range 30	mean (N=9) 30
variabilis	range 17–21	mean (N=28) 19·25	range 31–33	mean (N=19) 31·42

Table 104. Proportions in specimens of approximately the same size-range of four populations of centra Africa, *O. variabilis*, *O. upembae*, *O. malagarasi* and *O. rukwaensis*.

	rukwaensis	*malagarasi*	*upembae*	*variabilis*
N	11	12	10	15
SL (mm)	105–247·5	125·5–197	118–187	105–224
Proportions as % SL				
Depth	43·8–50·85	41·0–48·7	43·1–45·0	39–46
L. head	32·0–36·2	32·6–35·2	34·2–35·8	32·1–36·7(38·
L. pect. fin	35·2–42·7	38·2–42·9	38·5–41·3	40·0–44·5
D. caud. ped.	15·2–16·9	14·6–16·6	15·8–18·5	14·0–15·5
L. caud. ped.	10·4–13·3(14·3)	9·7–13·1	10·0–14·0	11·7–14·5
Caud. ped. l/d	0·6–0·8	0·6–0·87	0·6–0·8	0·8–0·98
Proportions as % l. head				
L. snout	33·4–42·0	28·2–37·0	32·8–36·0	30·4–38·8
Eye	18·6–23·5	20·3–25·8	19·2–25·0	17·3–27·4
D. preorb.	20·3–25·9	20·2–23·6	19·2–24·0	18·7–25·4
Interorb.	34·6–40·1	(36·8)40·0–43·5	37·9–43·0	38·0–48·0
Lower jaw	30·2–38·4	28·4–33·8	29·0–34·3	27·0–34·7

Description

Based on the twelve specimens listed on p. 430, 125–197 mm SL.

Proportions and meristic characters are set out in Tables 103 and 104, and other details are listed above ('Distinguishing characters'). These indicate a relatively shallow-bodied fish, but Thys (1964:27) has linked with this species a specimen from the Malagarasi delta with a depth of 53·8% SL and a correspondingly deep caudal peduncle.

The eye and preorbital measurements are about equal from 165 mm SL and even at 195 mm there is very little difference.

Gill-rakers (3–4)+1+(20–24) on first arch.

The length of the lower pharyngeal bone is greater than its width and 33–38% length of head; the blade is as long as the median length of the toothed part in a fish of 125·5 mm SL, to 1·4 times as long in a 172 mm fish from Lake Lugoya, Kasulu District. The pharyngeal teeth are slender, those of four posterior rows brown-tipped and bicuspid, the anterior are more crowded.

The mouth is small and there is no difference correlated with age or sex. The teeth are in 4–6 rows in each jaw, with slender shafts. Several specimens have a few tricuspids among the bicuspid outer teeth; inner tricuspid.

Scales on cheek in 2 rows; 4–6½ between origin of dorsal and lateral line.

The genital papilla is bifid in females and males. In one male of 183 mm SL there is a short double tassel, but no fish of this collection is in peak breeding condition.

Ecology

Food

Lowe-McConnell (1958) records that in the Malagarasi swamps both this species and *O. karomo* were feeding on the soft, flocculent bottom deposits, which consisted of finely divided plant material and many protozoa and bacteria. The plant material had mostly passed through the guts of *Alestes* and *Distichodus*, which were feeding on water-lily leaves. The young were feeding on fish offal near the canoe-landings.

Breeding

In the month of August, when the sympatric *O. karomo* was observed breeding, there was no breeding activity among the *O. malagarasi*, and the specimens caught were either immature or had been gutted when received, allowing of no observations on gonads. Of the preserved fishes, six of 180–197 mm were males. There were four females of 125–169 mm, one younger male and one unsexed.

It seems possible that the breeding fishes in ponds at Mbeya observed by Albrecht (1968) and believed to be *O. rukwaensis* were really *O. malagarasi* (see p. 433).

Distribution

NATURAL DISTRIBUTION. The Malagarasi River from its delta to the swamps of its upper reaches.

DISPERSAL BY MAN. The dams in which this species is known to have been stocked are within its natural area, the Malagarasi basin. Igombe dam near Tabora is one of these. But there is some evidence that it was stocked more widely before it was recognized as a distinct species (see p. 433).

Discussion

Problematical specimens

1. A fish of 129mm SL from Usambara, Lake Tanganyika, is preserved at Tervuren (MRAC). It is a female with the gential papilla prolonged into two unequal lobes of irregular outline. The interorbital measurement is rather low, 31·5% length of head. Meristic numbers are common to several species and within the ranges of *O. malagarasi*. It may be this species and if so is the only specimen recorded from the lake.

2. Petr (unpubl.) in a preimpoundment survey in 1972 of the Great Ruaha, recorded *O. urolepis* from that river and sent five so named to the BMNH. Two juveniles from an upper tributary are too small for determination. From the lower part of the river one of 73 mm may be *O. urolepis*, but a male of 173 mm has a bifid genital papilla about 4 mm long and a dentition of jaws and pharynx resembling that of a tasselled species, especially in having an admixture of tricuspids among the bicuspid teeth of the outer series of the jaws. A smaller male has a simple genital papilla, but the dentition is also more like that of *O. malagarasi* than *O. urolepis*. Mid-lateral dark blotches are common to these two species. They are present in the 73 mm Ruaha fish and in the 173 mm male, but the 118 mm fish is almost uniformly dark. The chief difference from the known *O. malagarasi* is the presence of XVIII dorsal spines in two of these.

The Great Ruaha is believed to have formerly flowed from East to West (Haldemann, 1962; Banister & Clarke, 1980) and may well have an *Oreochromis* different from that of the Rufigi. But it is also possible that *O. malagarasi* was stocked in some farm dam in the Ruaha basin. The fact that Petr also found in the Great Ruaha A *Tilapia*, either *T. zillii* or *T. rendalli*, would support the latter theory, since no *Tilapia* is known to be native to Tanzania east of Lake Tanganyika, and *T. rendalli* is known to have been imported to Korogwe for stocking purposes (Gould, 1951).

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1967.3.16.16–17 (holotype, 165 mm, and paratype)	152, 165	Malagarasi swamps at Katare	R. H. Lowe-McConnell (1952)
1967.3.16.18–21	183–197	Malagarasi swamps at Katare	G. J. Lockley (1949)
1971.6.23.89	172	L. Lugoya, Kasulu Distr.	G. J. Lockley
1966.7.14.113–117	125–180	Igombe Dam, nr. Tabora	R. G. Bailey
?1974.1.16.438–9	73, 118	Great Ruaha	T. Petr
?1975.10.8.42	173	Great Ruaha	T. Petr

Oreochromis (Nyasalapia) rukwaensis (Hilgendorf & Pappenheim)

Fig. 151

Tilapia nilotica rukwaensis Hilgendorf & Pappenheim, 1903:212 (Lake Rukwa).
Tilapia rukwaensis; Ricardo, 1939*a*:652; *idem*, 1939*b*:26–29; Lowe, 1955*b*:262; Lowe-McConnell, 1959: (mention only); Hickling, 1960:200–204 (recent history of Lake Rukwa); Wickler, 1962*a*:153, fig. 15 Mann, 1964*a* (fishery); ? Albrecht, 1968*a*:391 (breeding); Bailey, 1968:202 (key).
Tilapia (Loruwiala) rukwaensis; Thys van den Audenaerde, 1968*b*:xxxvi.
Sarotherodon rukwaensis; Schoenen, 1979:53.

Types. Types (syntypes) in ZMB.

Fig. 151 *Oreochromis rukwaensis*, 247 mm SL, BMNH 1942.12.31.146.

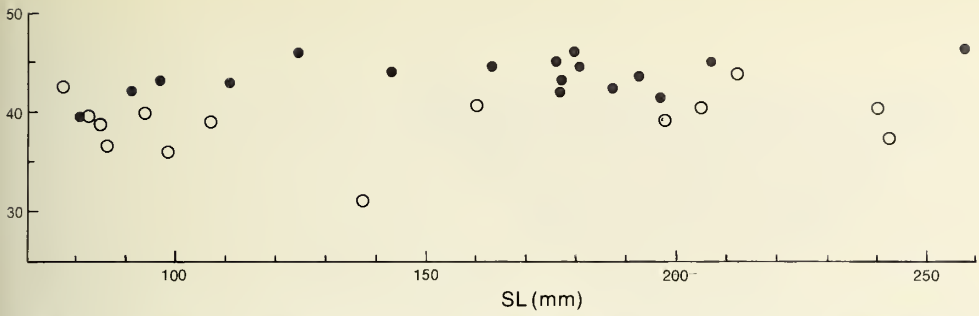

Fig. 152 Length of pectoral fin as % SL in *Oreochromis macrochir* (●); and *O. rukwaensis* (○).

Distinguishing characters

An *Oreochromis (Nyasalapia)* with a bifid and tuberculate genital papilla in both male and female, in breeding male produced into a double tassel up to 5 cm long.

1. Preserved adults from Lake Rukwa without markings on body; young also unmarked or with 6–8 grey vertical bands. (Mature fishes believed by Albrecht to be this species in ponds at Mbeya have mid-lateral blotches like those of *O. upembae* and *O. malagarasi.*) Breeding male black or dark blue-green with margins of dorsal and caudal fins orange and genital tassel orange-yellow. Caudal fin without markings or with a few vague spots or dark between the rays.
2. Caudal fin free of scales except basally.
3. Vertebrae 30 (15+15; N=6).
4. Scales in lateral line series (30) 31 or 32, mode 32 (Table 103).
5. Dorsal spines (XV) XVI or XVII, mode XVI; soft rays usually 12 or 13 (Table 103).
6. Outer teeth bicuspid, in mature fishes occasionally with a few tricuspids.
7. Lower gill-rakers 20–22.
8. Interorbital region in adults 34·5–40% length of head.

It differs from *O. variabilis* in the shape of the profile, the deeper caudal peduncle, the shape of the pharyngeal bone and in having no 'maradadi' forms reported.

From *O. upembae* and *O. malagarasi* the Lake Rukwa samples differ in lacking the characteristic mid-lateral blotches of these species, in the slightly narrower head as measured by the interorbital width and the higher average number of vertebrae and of scales in the lateral line series.

Oreochromis macrochir is very difficult to distinguish from *O. rukwaensis* on technical features. The steep profile figured for *O. macrochir* by Boulenger and Thys (1964, pl. VIII) is found in well-grown specimens but not in smaller fishes and has not been observed in the Lake Mweru population. A characteristic feature of *O. macrochir* is the presence of black spots in the temporal region and on the gill-cover, distinguishing it from *O. rukwaensis.* The lower pharyngeal dentition in the Zambezi and Bangweulu populations of *O. macrochir* is also distinctive, the teeth being finer and more crowded than in *O. rukwaensis.* The pectoral fin, which gave its name to *O. macrochir,* is usually, but not always, longer than in *O. rukwaensis* (Fig. 152).

Description

Based on eighteen specimens (listed on p. 434), comprising seven males of 105–243 mm SL and three females of 93–198 mm and eight of 43–107 mm of uncertain sex, all in BMNH.

Proportions and meristic numbers are set out in Tables 103 and 104. See also 'Distinguishing characters', above.

The teeth are in 4–6 series in specimens over 100 mm in SL, 3–4 below this size; with slender shafts and broader, curved crowns; those of outermost row bicuspid except that three mature fishes have a few tricuspids among them; inner rows tricuspid.

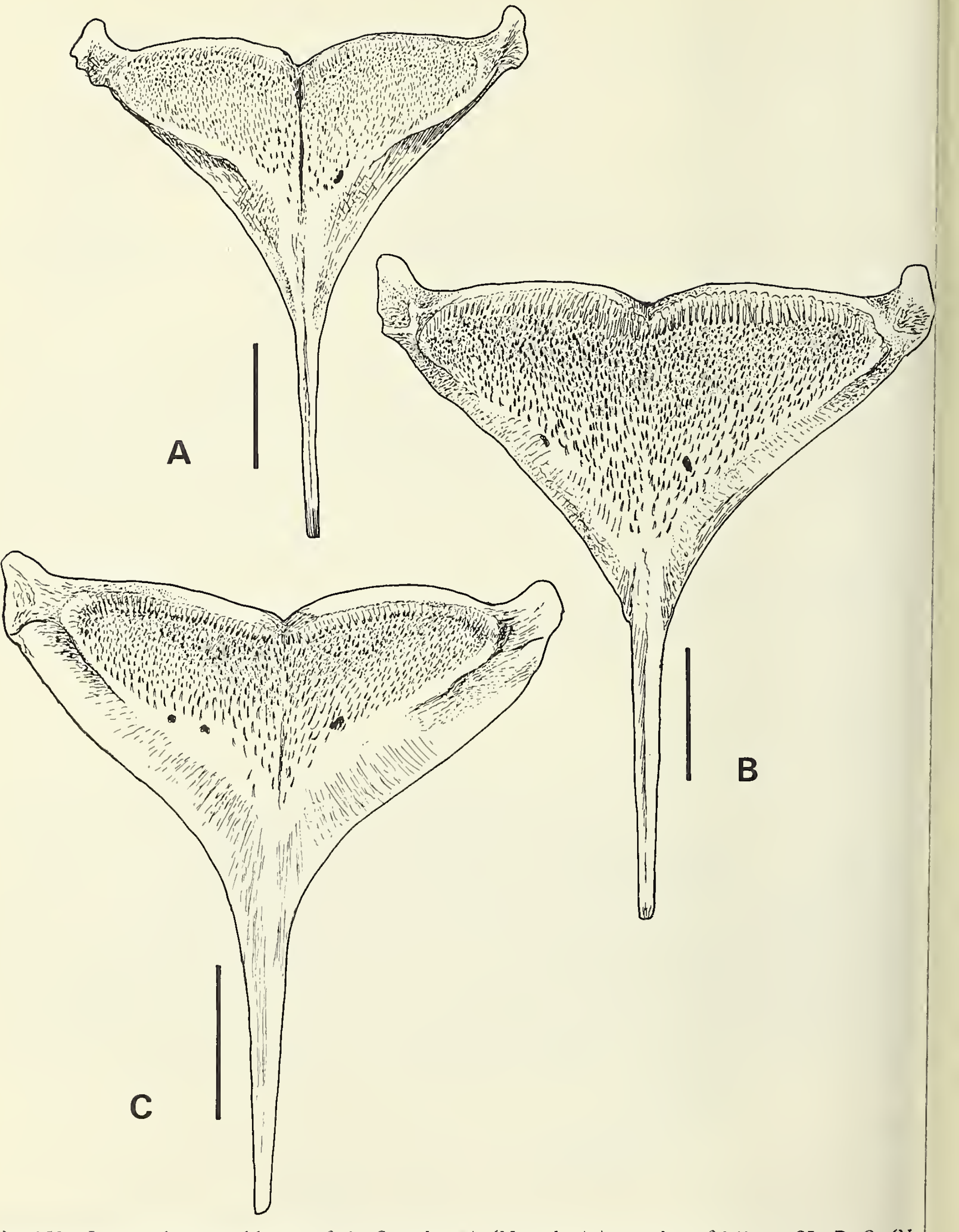

Fig. 153 Lower pharyngeal bones of: A, *Oreochromis (Nyasalapia) upembae* of 150 mm SL; B, *O. (Ny. rukwaensis* of 195 mm SL; C, *O. (Ny.) malagarasi* of 172 mm SL. Scale = 5 mm.

Scales on cheek in 2 rows, rarely 2 or 3 scales of a third row present; 4 or 4½ between origin of dorsal and lateral line.

Caudal fin very slightly emarginate in young, truncate in adults.

Size. The biggest available is about 31 cm in TL, a male with genital papilla 5 cm long and elaborately branched. Two of the small fishes reported by Ricardo from the river at Zimba are preserved in the BMNH. They have been gutted so that the state of the gonads cannot be described, but the male of 105 mm SL (13·5 cm TL) has a bifid genital papilla of 7 mm. Its two branches are scroll-like, not branched, but the size of the papilla shows that it was mature. This and a female of TL 12 cm preserved with it are no doubt the two sexually mature fishes reported from this locality by Ricardo (1939*a*:654).

COLORATION. Preserved adults are uniformly pale, without markings on the body. The vertical fins and the pelvics are either likewise pale or may be dusky between the rays. The young (22–84 mm) are also pale, but some show 6–8 grey vertical bands on the flanks and the soft dorsal may be marked with dark oblique bands or with clear ovals on a grey ground; in this pattern the tilapia-mark may be indicated by a darker grey, but most are without even this vestige of a tilapia-mark. This description applies to specimens in the BMNH and is in agreement with that of Hilgendorf & Pappenheim (1903).

Living fishes in a pond near Mbeya, in the Southern Highlands of Tanzania, believed to be *O. rukwaensis,* were described by Albrecht (1968*a*). Their pigmentation, however, included four mid-lateral dark blotches behind the opercular spot, and these have never been described in *O. rukwaensis* from the lake. It seems possible, therefore, that they were *O. malagarasi*, although there is no record of stocking any species but *O. rukwaensis* in these ponds (Bailey, 1966). It may be recalled that in 1950, a time of extensive stocking in Tanzania (Gould, 1951), *O. malagarasi* was not a recognized species.

Schooling fishes in these ponds were yellow-brown with a pale eye and dark opercular spot and the above-mentioned four lateral blotches, the first two often united. Spawning females were similar, but with a dark eye and pale opercular spot; dorsal and caudal margins may be orange.

Breeding males were mainly black with orange margins to dorsal and caudal fins. The pelvics were black or yellowish and the long genital tassels orange-yellow. There were iridescent marblings on gill-cover and snout.

Ecology

Breeding

Breeding of the pond-fishes understood to be *O. rukwaensis* was observed by Albrecht (1968*a*). Territories were constructed by males in shallow water. Where there was ample space they were similar in structure and grouping to those of *O. variabilis*, each territory consisting of a central raised mating platform in the middle of a large circular depression.

Males were already occupying these territories at sunrise, when the water temperature was 12°C and they left for deeper water in the late afternoon when the temperature rose to 25°C.

On his territory the male was coloured as described above, with the genital tassel up to 2·5 cm long. When he left the territory and joined the school he paled (though retaining the orange fin-margins) and resembled the schooling fishes, resuming his breeding colours on returning to the territory. Photos by Albrecht, published by Schoenen (1979) show a male dragging his tassel on a gravel substrate.

Courting behaviour and leading of the females to the mating platform were observed to be as in *O. variabilis.* Where the pits were smaller and closer together there was less ceremony and females entered the pits voluntarily and were briefly led to the centre. Pseudo-spawning and then true spawning followed.

In the ponds females brooding eggs and young rejoined the schools, and the eye became pale again and the opercular spot dark as in other members of the school.

Precocious breeding was reported by Ricardo (1939*a*) in the river at Zimba in the Rukwa basin. Males with elaborate genital papillae from the lake measure 26–30 cm in TL, females about 25 cm.

Distribution

The closed basin of Lake Rukwa.

This basin has been described by Ricardo (1939) and Hickling (1960), and its history is discussed by Banister & Clarke (1980), who give further references. The map of Fig. 147 is taken partly from Ricardo, who showed the courses of the rivers as though they were permanent, but the levels of both rivers and lake fluctuate widely as they are subject to long periods of drought alternating with periods in which the annual rains are sufficient to maintain a large but shallow lake. Lake Rukwa lies in a deep rift trough at an altitude of 820 metres, between 8° and 9°S. In 1936 it was about 144 km long, the maximum dimensions of the deeper south-eastern basin being about 48 and 24 km, and the greatest width of the northern basin about 40 km. The lake is shallow, its greatest depth estimated at 5 or 6 metres. The water is alkaline and turbid, but appears to be a favourable environment for fishes, being fertilized by hippos and crocodiles, and many species of birds.

The shallow northern basin has completely dried up during periods of several years of drought, and the southern basin and rivers were greatly reduced at these times. Nevertheless, *O. rukwaensis* survived in sufficient numbers to restore the population to its former level in a year or two.

The rivers entering Lake Rukwa have common watersheds with the Malagarasi in the north, the Great Ruaha and the Rufigi to the south and east, small rivers entering Lake Tanganyika to the north-west. To the south and south-west the sources of the Momba River are not far from those of the Chambezi, which merges with the Bangweulu swamps, and the source of the Songwe (Tributary of the Sita) is not far from that of the river of the same name which flows from the other side of a volcanic mountain mass into Lake Malawi.

Material examined

All collected by C. K. Ricardo and J. Owen, 1936.

Reg. No. BMNH	SL (mm)	Locality
1942.12.31.146	247·5	L. Rukwa
1942.12.31.147–150	137–240	L. Rukwa
1942.12.31.151–153	77–205	L. Rukwa
1942.12.31.154 (2 fishes)	198, 143	L. Rukwa
1942.12.31.155–164 (22 fishes)	32–90	L. Rukwa
1942.12.31.165–166 (11 fishes)	15–22	River entering SE end of L. Rukwa
1942.12.31.167–171 (11 fishes)	22·5–98·0	L. Rukwa
1942.12.31.172–173	93, 105	River near Zimba, L. Rukwa
1942.12.31.174–176	14–55	Luika R., L. Rukwa
1942.12.31.177–186 (numerous young)	10–31	Reeds near shore and tow net at edge of L. Rukwa

Subgenus *NYASALAPIA* – III

Oreochromis macrochir & *Oreochromis salinicola*

Oreochromis (Nyasalapia) macrochir (Boulenger)

[?*Chromys Sparmanni* Castelnau, 1861:12 (Ngami Region)].
[?*Chromys Chapmannii* Castelnau, 1861:15 (Ngami Region)].
Tilapia natalensis (part, *non* Weber); Boulenger, 1901:457 (Mweru, Lufira); *idem*, 1915:158 (two specimens from Lofoi only); Poll, 1933*b*:139 (Lofoi & Mweru); *idem* 1937:140 (Sandoa, Kasai); *idem*, 1938:418 (Bangweulu).
Tilapia macrochir Boulenger, 1912*c*:139 (Upper Zambezi & Bangweulu); *idem*, 1915:160, fig. 105 (Zambezi, Kafue, Bangweulu, Mweru); *idem*, 1920*b*:30 (Mweru, Lower Luapula); Gilchrist & Thompson, 1917:488, fig. 123; Fowler, 1932:237 (Upper Zambezi); Poll, 1933*b*:139 (Mweru, Luombwa R., trib. of upper Luapula); Fowler, 1935*a*:280 (Chobe R.); Ricardo, 1939*b*:63 (Bangweulu); Ricardo-Bertram, 1943:211 (Bangweulu & Chambezi R.); Barnard, 1948*a*:451 (Okovango); De Bont, 1950*a*:495, fig. 8; *idem* 1950*b*: figs 70 (nest of *S. m. macrochir*) & 71 (nest of *S. m. mueruensis*); De Bont & De Bont-Hers, 1950 (growth); De Bont, Deceuninck & Detaille, 1950: (food); Arnaud, 1953; *idem*, 1959 (introduced into Madagascar); Huet, 1953 & later editions to 1973:193 ff., figs. 278, 282; De Bont, 1954:167, 171; Chimitz, 1955:13, fig. (summary of culture; nest); Jubb, 1958 (Chobe R.); Mortimer, 1960*a* (Kafue R., bionomics); Bard, 1960*a* & *b* (growth, hybridization); Jackson, 1961*b*:98; Jubb, 1961:130, pls XIV & 76; Ruwet, 1961 (Lufira R.); Jackson, 1962*a*:31 (Mweru); Mortimer, 1962*b* (salinity tolerance); Ruwet, 1962:244; *idem*, 1963*a*:171; *idem*, *1963b*:242 (breeding in Lufira R.); Thys van den Audenaerde, 1963:579, fig. 4 (distribution); Thys, 1964:22, 95, fig. 15, pl. VIII; Mortimer, 1964:78; Bowmaker, 1964:19 (Bangweulu); Carey, 1964:20 ff.; *idem*, 1965:11–15 (Mweru); Bell-Cross in Mortimer, 1965, fig. 25; Wickler, 1965 (behaviour); *idem*, 1966*a*, *b* & *c* (behaviour); Trewavas, 1966*c*:415; Voss & Ruwet, 1966:173 (behaviour); Ruwet & Voss, 1966:786, fig. 2 (behaviour); Jubb, 1967:161, fig. 188 & pl. 33; Poll, 1967:293, fig. 141 (Angolan part of Upper Zambezi); Ruwet, 1968:977 (behaviour); Kelley, 1968 (Upper Zambezi); Duerre, 1969 (Upper Zambezi); Penrith, 1970:166, pl. 1 (mouth of Cunene R.); Chardon & Vanderwalle, 1971 (structure of head); Chapman *et al.*, 1971 (Kafue); Jalabert *et al.*, 1971 hybrids); Lagler *et al.*, 1971:94; 122, 124 (Kafue); Bell-Cross, 1972 (Upper Zambezi); Fryer & Iles, 1972 (see index to that book).
Tilapia (Loruwiala) macrochir; Thys van den Audenaerde, 1968*b*:xxxvi.
Sarotherodon macrochir; Balon, 1974:463, 468, 495; Kapetsky, 1974:501 ff., figs 77, 78 (growth); Poll, 1976:18; Bell-Cross, 1976:215, fig. on p. 216; Dudley, 1979 (growth in Kafue flood-plain); Voss, 1977: pl. 16 & pp. 65–69 (colour-patterns of expression); Mayland, 1978:306, 372 (figs); Schoenen, 1979; Avtalion & Hammerman, 1978 (hybrids); Hammerman & Avtalion, 1979: (genetics); Daget & Moreau, 1981 (hybrids); Lowe-McConnell, 1982:86, 93 ff., figs 4–5.
Tilapia andersonii (part, *non* Castelnau); Boulenger, 1911*b*:415 (Ngami region); *idem*, 1915:171 (specimens 4–9, from Okavango & three from Dongwenna Swamp); De Bont, 1950*b*:fig. 70 on p. 309 (nest of Zambezi type).
Tilapia intermedia Gilchrist & Thompson, 1917:482 ('Sawmills, Bulawayo', stated by Jubb, 1960*b* to be error for Upper Zambezi).
Tilapia sheshekensis Gilchrist & Thompson, 1917:489 (Sheshekе, Upper Zambezi, c. 125 km above Victoria Falls); Fowler, 1935*a*:280 (Chobe R.).
Tilapia galilaea (*non* Linn.); Gilchrist & Thompson, 1917:490 (Victoria Falls); Pellegrin, 1936*c*: (Cubango R.).
Tilapia squamipinnis (*non* Günther); Gilchrist & Thompson, 1917:4 (Kafue R.).
Tilapia alleni Fowler, 1932:238, fig. 1 (Thamalakane R. at Maun, Botswana); *idem*, 1935*a*:280.
Tilapia kafuensis (*non* Boulenger); De Bont, 1950*a*: fig. (nest).

Types. The types of Castelnau's species from Lake Ngami are lost and there is nothing in the descriptions of *C. Chapmanii* and *C. Sparmanni* to favour the use of the names for one species of *Oreochromis* rather than another. The names have not been used since their publication and

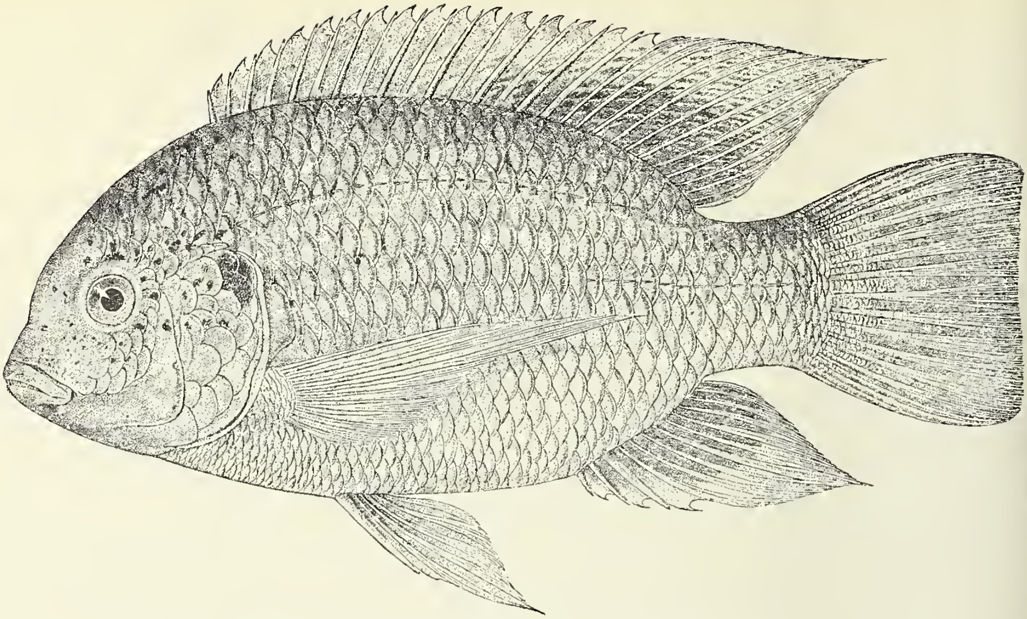

Fig. 154 *Oreochromis macrochir*, lectotype. From Boulenger, 1915, fig. 105.

I here follow the usual practice and adopt *O. macrochir* as the earliest valid name.

Lectotype of *Tilapia macrochir*, here designated, 271 mm SL, from the Upper Zambezi BMNH 1908.11.6.35.

Paralectotypes of *T. macrochir*, ten specimens, 130–271 mm SL, from the Upper Zambezi and the Maramba River, 2 miles above Victoria Falls, BMNH 1908.11.6.36–46; three specimens 100–258 mm SL from Bangweulu region, 1907.11.30.15–17, and four, 143–195 mm SL also from the Bangweulu region, 1911.1.27.30–33.

Syntypes of *T. intermedia*, two of 58 and 74 mm SL from the Upper Zambezi (teste Jubb in South African Museum, Cape Town.

Holotype of *T. sheshekensis*, 62 mm SL, from Upper Zambezi, in South African Museum.

Holotype of *T. alleni*, 176 mm SL, a male with complex genital papilla 5·8 mm long, from Thamalakani River at Maun; ASP 53193.

Holotype of *O. macrochir mweruensis* subsp.n., male 207 + 60 mm from Mobanga, Mweru coll. Mission Piscicole Katanga 1947, BMNH 1967.8.23.1, formerly MRAC 85070.

Distinguishing characters of the superspecies

1. Genital papilla large and tuberculate or scalloped in mature fishes of both sexes, in breeding males prolonged into a double tassel which reaches a length of 25 mm or more. Mouth no enlarged in breeding male.
2. Body in adults with no conspicuous mid-lateral blotches, but these may be weakly indicated in young. Vertical bands sometimes present in young, in adult only as an expression of submission. General colour lighter or darker olive-green. Black or dark brown flecks in the temporal region, below the eye and on the gill-cover, mostly associated with the openings of the lateral line system. Caudal irregularly spotted centrally in young but unpatterned in adult Head, body and vertical fins of breeding male iridescent dark green to blue-black with red edge to dorsal and caudal fins.
3. Caudal scales variable, not on the inter-radial membranes except at the base; never stiffening the fin.

4. Caudal peduncle deep (Tables 105 & 106).
5. Vertebrae 30 or 31 (32) (see p. 442).
6. Scales in lateral line series usually 31 or 32, on cheek in two or three rows.
7. Modal dorsal formulae XVI 12 and XVI 13. Soft rays of anal fin usually 10 or 11 (Tables 107 & 108).
8. Teeth of jaws in 4–7 series, with slender shafts; outer bicuspid, in large females with some tricuspids among them, in large males some worn to unicuspids.
9. Lower gill-rakers in fishes of 90 mm SL or more 20–26, usually 22–24.
10. Pectoral fin long, when complete 40–50% SL, its tip vertically above some part of anal fin base.

The required comparisons are with *O. upembae* and *O. rukwaensis* in the north, and with *O. (Oreochromis) andersonii* in the Zambezi basin.

Oreochromis rukwaensis lacks the dark flecks in the temporal region and gill-cover and its pharyngeal teeth are less fine and crowded. It has usually a straighter profile, but it closely resembles *O. macrochir* and has the same male breeding coloration.

Oreochromis upembae and *O. andersonii* both lack the dark temporal spots and both have conspicuous lateral blotches. *O. upembae* usually has fewer scales in the lateral line series and a somewhat coarser pharyngeal dentition.

Oreochromis andersonii has a higher range of lateral line scales. It is a more elongate fish and does not develop a genital tassel. At a given size its preorbital bone is shallower and there are three complete rows of scales on the cheek. The nest is a simple saucer-shaped depression.

The tasselled species of Lake Malawi differ in having a definite pattern of characteristic vertical bars on the body in females and non-breeding males, in the densely scaled caudal fin and the longer, more slender caudal peduncle. Each of these species has its characteristic lower pharyngeal bone and dentition, all of which are different from that of *O. macrochir* (Figs 156–159; cf. Fig. 168). Three of these species and *O. chungruruensis* have the same male breeding livery as *O. macrochir.*

Since *O. macrochir* has been introduced in Gabon its distinction from *Sarotherodon mvogoi* must also be emphasized. The latter has a deeper preorbital bone at a given size and fewer vertebrae (28) and scales (27–30 in the lateral line series). See Table 15.

Subspecies and natural distribution

Oreochromis macrochir macrochir (Boulenger)

Toothed area of lower pharyngeal with broadly rounded lobes (Fig. 157). Mating territory having a central volcano-shaped mound with a flat or slightly concave top, surrounded by a ditch and vallum (groove and boundary ridge).

Upper Zambezi, Okovango and Ngami region, Cunene basin, Kafue River, Chambezi River and Bangweulu region. Absent from the Middle Zambezi and Luangwa River, but Mortimer (1964) records of two tributaries of the Luangwa that it is native in the plateau reaches of the Mulungushi, but not in the upper Lunsemfwa, although it has now been stocked in the latter.

Both nest and pharyngeal bone are known in the Bangweulu region, the Kafue and Upper Zambezi. The pharyngeal in the Okovango and Cunene basins agrees with these in the shape of the toothed area. There is also a Zambezi-type pharyngeal in the few specimens I have seen from the Luembe River, an Angolan tributary of the Kasai. Dr Machado suggests (pers. commn) that *O. macrochir* owes its presence there to river capture from the Upper Zambezi (see also Bell-Cross, 1972:9) although it is not present in the neighbouring tributaries, Luashimo and Chiumbe. In view of the pharyngeal structure this seems a more probable explanation than a possible escape from ponds at Chikapa (Tshikapa) on the Kasai, where De Bont and Thys record that it has been introduced for pond culture from the ponds near Lubumbashi.

Fig. 155 Distribution of *Oreochromis macrochir* (■), see also Fig. 147; *O. angolensis* (●) and *O. lepidurus* (▲).

Oreochromis macrochir mweruensis subsp. n.
Toothed area of lower pharyngeal with more acute lobes (Fig. 158). Mating territory largely occupied by a low mound with a number 6–12) of grooves or crests radiating from the small central concave area ('star-shaped nest').

Mweru and lower Luapula; the Lufira River. There is also a population in Mweru-wa-Ntipa, a region of swamps and shallow saline lakes east of Lake Mweru, to which is connected at times of heavy rain by the Kalungwishi River. The pharyngeal in specimens from Mweru-wa-Ntipa has a bigger toothed area than in Mweru (Fig. 159), but the nests have not been described there. Absent from the Lualaba River except one locality marked by Thys (1964, fig. 15) near its source. One record in the Luvua River, an eastern tributary of the Kasai.

The division into subspecies follows suggestions from Jackson (1961:99), Thys (1964:23), Fryer & Iles (1972:112), and personal suggestions from Mortimer and Carey in 1965. Mr Carey had the impression that the Mweru form did not develop the steep profile of the Zambezi form,

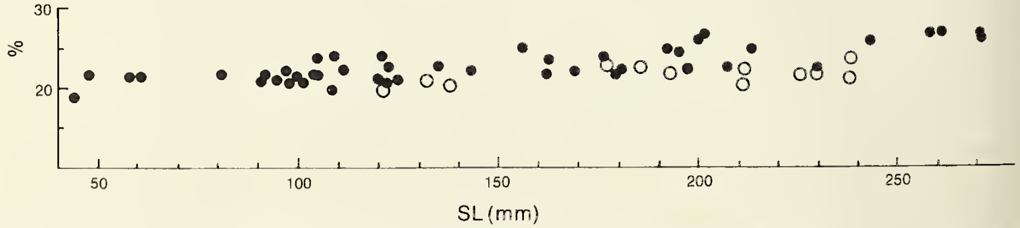

Fig. 156 Depth of preorbital bone as % length of head in *Oreochromis m. macrochir* (●) and *O. m. mweruensis* (○).

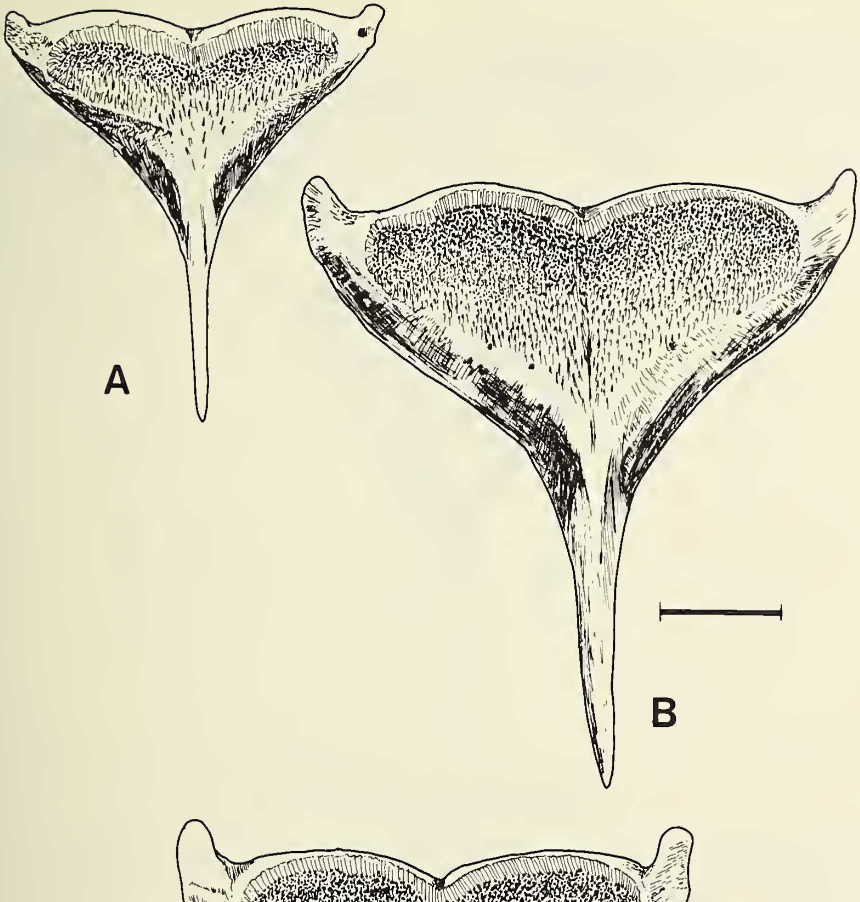

Fig. 157 *Oreochromis m. macrochir.* Pharyngeal bones from: A, a fish of 126 mm SL from the Kafue River; B, one of 197 mm SL from the Kafue; C, one of 210 mm SL from Lake Ngami Region. Scale = 5 mm.

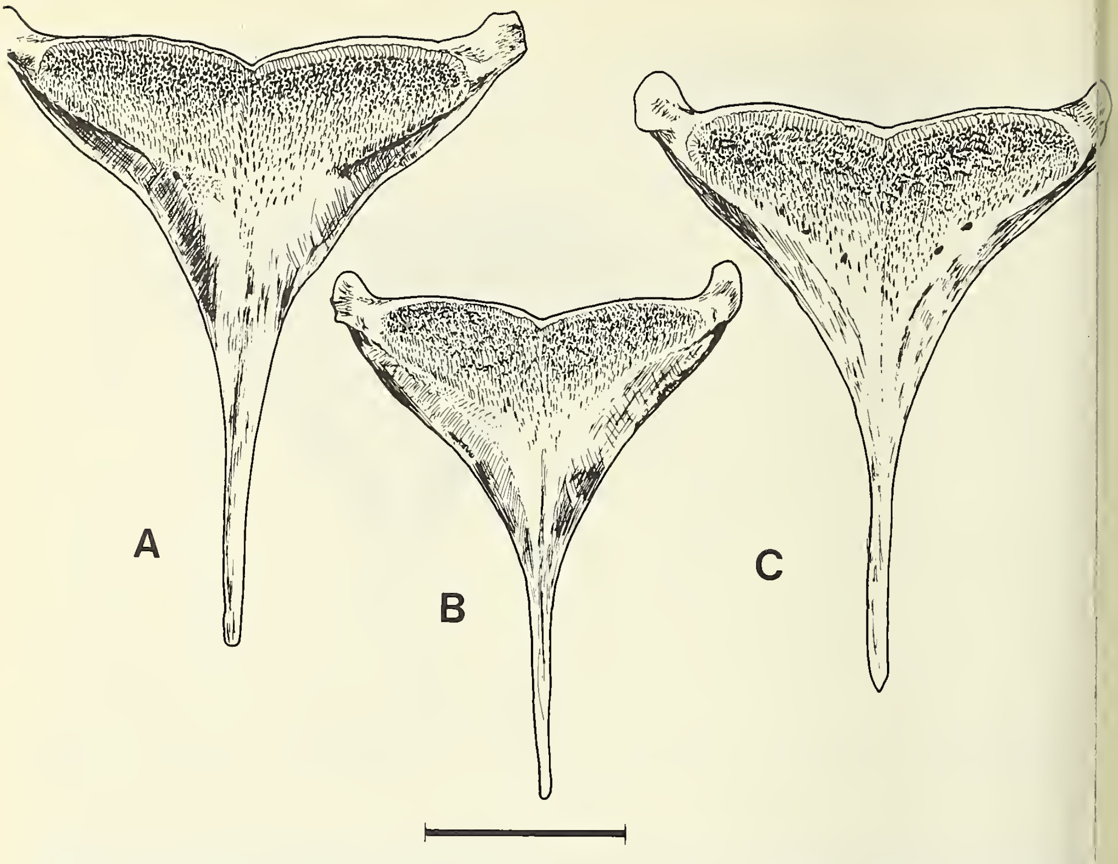

Fig. 158 *Oreochromis macrochir mweruensis.* Pharyngeal bones of: A, a male of 238 mm SL: B and C, fishes of 185 and 226 mm SL from Lake Mweru. Scale = 10 mm.

but I could not confirm this difference at the sizes observed. The pharyngeal dentition was the only morphological feature in which I was able to find a distinction. For an assessment of the nest structures see pp. 448–9.

DISPERSAL BY MAN. This species has been used extensively for stocking dams and ponds, including many in Zambia (Mortimer, 1964) and Zimbabwe. Large quantities of fry were put into Lake Kariba from the ponds at Chilanga (near Lusaka), but the species was slow to establish itself (Bowmaker, Jackson & Jubb, 1978:1212), perhaps by unsuccessful competition with the native *O. mortimeri* (Van der Lingen, 1973). It was believed to have hybridized there with *O. mortimeri* (Jubb, in a letter 13.9.1967), but no evidence was given. It was successfully stocked in the man-made lakes Kyle and McIlwaine (Jubb, 1967; Marshall, 1979) respectively in the Lundi and Hunyani river systems.

Bell-Cross (1973 and 1976) records the presence of *O. macrochir* in the Revue River, Middle Buzi system, Mozambique. He writes that this might be explained as an escape from dams in the Upper Buzi, but he does not rule out the possibility of its natural occurrence there, unlikely as this seems in view of the discontinuity between the Buzi River and the rest of its distribution.

Oreochromis macrochir has been cultivated in ponds in Zaire, not only near Lubumbashi (= Elizabethville) where it is native, but also at Manono near the Luvua-Lualaba confluence, at Yangambi, at Chipaka on the Kasai, in the Central basin of the Zaire, at Kinshassa, Djoumona, the Uele and in Kivu (De Bont, 1950*a* & *b*; De Bont & De Bont-Hers, 1950; De Bont,

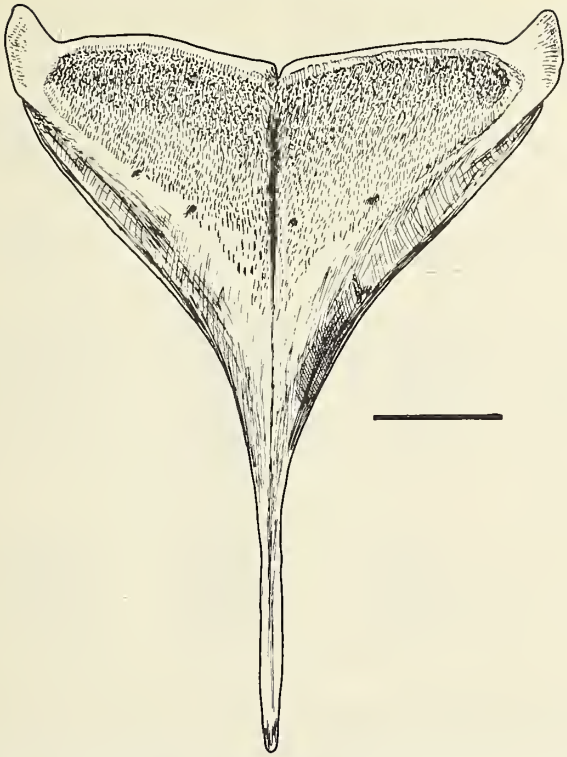

Fig. 159 *Oreochromis macrochir*. Pharyngeal bone from a fish of 236 mm SL from Lake Mweru-wa-Ntipa, Zambia. (Collection of Zambia Fisheries Museum, no., CB 490). Scale = 5 mm.

Deceuninck & Detaille, 1950; Charpy, 1955; Thys, 1964 and 1966). From Zaire it has been transported farther afield, to the Ogowe system (Thys, 1966; Bard, 1962*b*; Meschkat, 1967); to Cameroon (Bard, 1960; Thys, 1966:82); to Bouake, Ivory Coast (Lessent, 1968; Jalabert *et al.*, 1971); and to Madagascar (Arnoult, 1953 & 1959; Kiener, 1963; Meschkat, 1967; Daget & Moreau, 1981; and see pp. 451–2 below).

This was among the species taken to Korogwe on the Pangani River for distribution to Tanzanian dams, but does not seem to have been used extensively for this purpose. Payne (1974) reported small numbers in dams in the north-western region.

From Bouake *O. macrochir* was sent to France, where it lived and bred in captivity for some years and was used for electrophoretic studies by Baron (1975). The stock studied in aquaria by Wickler (1965*b*, 1966*a*) in Germany came directly from the Lufira.

Description

Based on the specimens listed on pp. 452–3, the proportions mainly on those of 91–171 mm SL, the meristic characters also on smaller fishes (Tables 105–108). See also the 'Distinguishing characters'.

Oreochromis macrochir is a notably deep-bodied fish with a blunt snout and a deep caudal peduncle. The long pectoral fin (see Fig. 152), which gave it its name, reaches to a vertical above some part of the anal fin-base; but several other species have as long a fin, notably the tasselled species of Lake Malawi. The caudal fin is truncate in adults, slightly emarginate in the young.

The preorbital bone is deep in adults, although at a given size it is shallower than in such western species as *S. mvogoi* and *S. melanotheron* (Fig. 10). The jaws are not greatly enlarged

Table 105. Proportions in samples from populations of *O. macrochir*. Mweru-wa-Ntipa, 'The Lake of Mud', is a swampy region east of Lake Mweru.

	Mweru	Mweru-wa-Ntipa	Bangweulu Region	Kafue
N	13	3	11	7
SL (mm)	121–238	153–224	100–258	125–207
Proportions as % SL				
Depth	44–51	42·5–45·5	43–51	45–53
L. head	32·8–35·5	35·4–38·4	31·25–36·36	33·6–35·2
L. pect. fin	41·5–46·0	40·3–44·6	42·2–46·7	41·6–46·4
L. caud. ped.	9·8–12·3	9·8–11·7	10·8–12·7	12·5–13·6
D. caud. ped.	14·6–17·4	14·8–15·6	16·6–17·2	14·8–16·76
Caud. ped. l/d	0·6–0·75	0·66–0·8	0·6–0·75	0·64–0·84
Proportions as % l. head				
Snout	31·6–38·3	35·6–36·9	35·2–37·5	33·0–37·0
Eye	17·7–23·2	17·5–19·6	20·0–26·6	19·5–23·1
D. preorb.	20·0–25·4	20·2–21·6	20·0–27·3	21·4–22·9
Interorb.	40·0–47·9	36·4–40·1	35·1–46·6	40·3–42·5
Lower jaw	28·1–33·8	28·6–32·4	31·3–35·7	28·1–33·3

in breeding males, but the three specimens in which the lower jaw exceeds 35% length of head (35·4–35·8%) are males of 230–271 mm SL with fringed genital tassels.

The teeth of the jaws have slender shafts and moderately expanded crowns. Many adults include a few tricuspid teeth among the bicuspids of the outer series, and in one large female (243 mm SL) the posterior half of the outer upper series on each side comprises tricuspids only. In large males, on the other hand, the shafts become relatively stouter and the minor cusp may be worn away (males of 260 and 271 mm SL).

The pharyngeal teeth are very fine and the toothed area of the lower bone has a short apex, giving a high ratio of blade to toothed area (up to 1·6 in adults). The posterior teeth have a well marked shoulder. The more rounded shape of the lateral lobes of the toothed area in the nominate subspecies has already been referred to (Figs 156–159).

The vertebrae have been counted in 17 *O. m. macrochir* and 7 *O. m. mweruensis* from the following localities: Cunene River mouth; Dongwenna swamps; Ngami region; Balovale, Upper Zambezi; Chambezi River; Lower Luapula; Lake Mweru; Lufira River at Lofoi. The results are:

No. of vertebrae	29	30	31	32
O. m. macrochir	1	15	1	
O. m. mweruensis		3	3	1

This suggests a higher mean number in *O. m. mweruensis*. The single count of 29 was in one of four from Balovale, Upper Zambezi; the other three had 30. Only two specimens from the Lufira River were examined and they had respectively 31 and 32. These, which are not recorded in Table 108, also had high numbers of scales (32, 33) and dorsal fin-rays (XVII 12, XVII 13).

Size. In the Upper Zambezi Kelley (1969) recorded a maximum length of 43 cm and weight 1786 g; but it is capable of greater growth, at least in dams, and Bell-Cross gives an angling record of 2527 g in Pembi Dam, Umvukwes. Jackson (1961) records a weight of 5 lbs (2270 g) in Mweru. In the Kafue River the size appears to be lower, males reaching a maximum of 33 cm TL and females 30 cm (Chapman *et al.*, 1971).

Table 106. Proportions in samples of populations of *O. macrochir*. The Luembe River is a tributary of the Kasai system and its head waters are very near to those of the Upper Zambezi. Five of the syntypes from the Upper Zambezi are bigger than any other samples available.

	Upper Zambezi		Luembe R.	Ngami Region	
N	7	5	4	11	4
SL (mm)	130–201	243–271	99–194	100–135	169–230
Proportions as % SL					
Depth	47·5–53·7	50·2–55·7	42·8–46·5	49·0–53·0	43·3–47·6
L. head	32·4–34·5	33·6–38·3	31·2–35·4	34·0–35·3	32·0–34·6
Pect.	40·6–45·3	43·1–49·0	40·0–43·0	41·5–49·5	38·5–44·7
L. caud. ped.	12·2–13·8	10·6–13·0	11·6–16·6	10·8–13·3	11·3–11·7
D. caud. ped.	16·5–18·4	17·5–18·5	15·6–17·2	15·45–16·7	14·8–16·6
C. ped. l/d	0·6–0·8	0·5–0·7	0·7–0·9	0·5–0·8	0·7–0·76
Proportions as % l. head					
Snout	33·0–39·4	37·1–41·9	36·0–41·2	31·4–39·0	34·4–41·6
Eye	19·7–24·1	15·9–18·9	21·6–27·2	23·0–28·4	20·1–21·8
D. preorb.	23·1–26·6	26·3–27·0	22·9–26·3	20·3–24·0	23·0–25·3
Interorb.	38·8–41·5	38·8–42·7	34·5–39·7	36·6–41·0	37·7–40·3
Lower jaw	30·1–33·6	30·5–35·8	30·0–34·3	27·3–34·0	31·9–35·4

Biochemistry. Fryer & Iles (1972:333–4) report that Malecha (1968) found polymorphism in the transferrins in this species, probably *O. m. mweruensis*.

COLORATION. Young silvery with 8–10 narrow, dark, facultative vertical bars on the body. Tilapia-mark, if present in preserved fish, merely a darker part of whatever pattern (barred or reticulate) decorates the dorsal fin. Caudal with a few dark spots centrally or immaculate.

Adult females and non-breeding males watery green, in some with dark centres to the scales giving the effect of longitudinal stripes. Head darker green, snout blue-green, iridescent. No mid-lateral blotches. Colour of lower jaw and branchiostegal membrane variable, unpigmented or with melanin variously and irregularly present, in some (including a syntype) in transverse stripes under the chin as in the type of the synonymous *T. alleni* Fowler. Adults with dark flecks in the temporal region, on the gill-cover and below the eye, mostly associated with openings of the lateral line system. Caudal with a few spots, or dark between the rays. Margin of dorsal fin dusky or partly pale reddish.

Breeding males with body and vertical fins very dark green, nearly black, iridescent with a bright red margin to spinous and soft dorsal fins and to caudal. Genital papilla white.

According to Ruwet & Voss (1966) and Voss (1977, pl. 16) dark vertical bars like those of juveniles appear in adults assuming an attitude of inferiority in a combat situation and in brooding females. The size and age of these fishes is not recorded.

A SAMPLE FROM THE KALOMO RIVER. Balon (1974:459) recorded a survey of the Kalomo River, a tributary of the Middle Zambezi entering it from the north some 60 km as the crow flies below the Victoria Falls. Like the Kafue, the greater part of its course is on the plateau, and it falls rapidly to its lower course in a gorge by which today it enters the Zambezi (see also Bell-Cross, 1972). Historically, like the Kafue, its upper part was part of the Upper Zambezi–Okovango complex. As in the latter and the Kafue, *O. andersonii* and *O. macrochir* were both present on the plateau, but the *O. macrochir* were recorded from one locality only, Luese stream, and were determined as an introduced hybrid of *O. andersonii* and *O. macrochir* (Balon, *loc. cit.*, 461, 463). I have examined the two adults (168 and 104 mm SL) and numerous juveniles (40–76 mm

Table 107. Frequencies of dorsal formulae in samples from populations of *O. macrochir*. The two commonest formulae are the same for the populations with the volcano-shaped mating pits and those with the star-shaped pits.

	XV 12	XVI 11	XV 13	XVI 12	XVII 11	XV 14	XVI 13	XVII 12	XVI 14	XVII 13
Cunene system		3		1						
Ngami region			3	3	1	4	11			
Upper Zambezi						2	7		2	1
Luembe R.				3	1					
Kalomo system		2		11	1		2	6		2
Kafue	1	2		10						
Bangweulu and Upper Luapula				4		2	7		1	
Totals	1	7	3	32	3	8	27	6	3	3
Mweru and Lower Luapula	1		1	5			8			
Mweru-wa-Ntipa				3						

SL) of Dr Balon's collection of the supposed hybrid, and cannot find any evidence of *O. andersonii* ancestry. The adults are rather slender for *O. macrochir* (depth 41 and 43·8% SL) with a rather slender caudal peduncle (Length/depth 0·97 and 0·83), and Table 107 shows that although the modal dorsal formula is one of the two modes of *O. macrochir*, nine specimens of 24 counted have XVII dorsal spines, a number commoner in *O. andersonii* and also in *O. mortimeri* than in *O. macrochir.* The pharyngeal, examined in one adult, is unlike that of *O. andersonii* and cannot be distinguished from that of *O. macrochir* (cf. Figs 108 & 157).

The history of the introduction is not given. An attempt was made to introduce *O. macrochir* into Lake Kariba, but it was not successful (Van der Lingen, 1973) and it is rumoured (without supporting data) that it may have hybridized with *O. mortimeri*. Since *O. macrochir* and *O. andersonii* are sympatric throughout much of their distribution, and since *O. macrochir* has been introduced into Lake McIlwaine, where *O. mortimeri* is native, apparently without hybridizing (Jubb, in litt. 13.9.1967) there would seem little likelihood of *O. macrochir* forming stable hybrids with either (unless they were forced by the topography to use the same breeding place). From the geographical position and history of the Kalomo River the presence of both *O. andersonii* and *O. macrochir* would be expected and, in the absence of further evidence I determine the Luese River specimens as *O. macrochir.*

Table 108. Meristic numbers in samples of populations of *O. macrochir.*

	Dorsal spines			Dorsal totals					Soft anal rays			
	XV	XVI	XVII	26	27	28	29	30	9	10	11	12
Cunene system		4			3	1			4			
Ngami region	7	14	1			7	15			11	8	1
Upper Zambezi	2	9	1				9	3		4	8	
Luembe R.		3	1			4			3		1	
Kafue	1	12			3	10				7		
Bangweula & Upper Luapula	2	12				4	9	1		10	4	
Totals	12	54	3		6	26	33	4	7	32	21	1
Mweru & Lower Luapula	2	13			1	6	8			5	9	
Mweru-wa-Ntipa		3				3					3	

Ecology

Food

Carey (1965*a* & *b*) observed young *O. m. mweruensis* up to 5 cm TL feeding on epiphytic filamentous algae in the swampy areas of the flooded banks of the Lower Luapula. Most fingerlings of 5–20 cm had mud and detritus in the stomach and only a few had plankton. These young were found in swampy areas at the south end of the lake and on the banks of the Luapula. Adults caught at the southern end of the lake during the summer (September to April) also were mostly feeding on bottom deposits, but those that migrated to the deeper northern end during May to August 'fed almost exclusively on plankton'.

De Bont *et al.* (1950) studied the stomach contents of *O. macrochir* reared in ponds fertilized with waste from flour-mills. The fishes were considered in four size-groups. In all of them algae were present, diatoms being the most universal. Protozoa were commonly present in the smaller size groups; Cladocera, Copepoda and Ostracoda especially characterized the food of the smallest size-class (2·2–3 cm) and were rarely found in fishes over 7·5 cm. Although the epiphytic growths were used the macrophytes themselves were not eaten by this species.

Mortimer (1960:53) observed the feeding behaviour of examples (probably from the Kafue River) in aquaria. They normally fed near the surface and caught offered food in mid-water, in contrast to *O. andersonii* in the same aquarium, which waited for the food to reach the bottom.

In the flood plains and river channels of the Upper Zambezi, where plankton is negligible, Kelley (1969), Duerre (1969) and Bell-Cross (1972) report that food is almost entirely periphyton, supplemented by a little organic debris.

In the flood-plain of the Kafue Chapman *et al.* (1971) found both diatoms and detritus in the stomachs of adults, but fewer inorganic particles than in *O. andersonii*, indicating less dependence on bottom feeding. Some larger adults use filamentous algae (epiphytic?). Young of 2–3 cm also contained diatoms, but more animal matter than adults. (In this report the young of *O. macrochir* and *O. andersonii* were lumped together.)

The dentition of *O. macrochir* suggests adaptation to grazing on epiphytic growths, but with the usual opportunism the species is evidently able to use both detritus and phytoplankton. Like other microphagous species, it may be tempted by the angler's worm.

Temperature requirements

Spaas (1969*a* & *b*) tested stock from Mweru for upper and lower lethal temperatures. He defined 'lethal temperature' as that at which 50% of his experimental animals were dead after 24 hours. The mean lower lethal temperature was 11°C. The upper mean lethal temperature for young of up to 50 g was about 38·7°C, for bigger fishes, up to 300 g, about 37·5°C. This is in line with the observations of Carey (1965*a* & *b*) that the young, but not the adults, were tolerant of very warm water in the swamps of the southern shore of Mweru and the banks of the lower Luapula, where the oxygen concentration and the pH were both low. Both lethal temperatures, however, are well outside the extremes encountered in the natural environment.

Spaas found the optimum for growth 23–24°C. For breeding a minimum of 21–23°C is required (De Bont, quoted by Mortimer, 1960). During the main part of the breeding season at the south end of Lake Mweru water temperatures were 25·3–27·8°C (Carey, 1965*a*).

Salinity tolerance

Preliminary experiments by Mortimer (1962) found *O. macrochir* (and *Tilapia rendalli*) less resistant to an increase in salinity than *O. mortimeri* or *O. andersonii.**

Growth

De Bont & De Bont-Hers (1950) and De Bont (1954) plotted the growth in length in ponds of *O. m. mweruensis* during the first year, and Mortimer (1960, figs 8–14) did the same for growth in weight in ponds on the Zambian plateau of *O. m. macrochir* for comparison with *O. andersonii.* Mortimer's experiments were designed to show the influence on growth of temperature, added food and different stocking densities. In every case the growth of *O. macrochir* was slower than that of *O. andersonii*. Growth was faster in the warmer months than the cooler.

The pre- and post-impoundment studies of Dudley (1974, 1979) and Kapetsky (1974) on the *Oreochromis* of the Kafue floodplain also depended on an annual growth-rhythm that was registered on the scales by an annulus beginning to be formed in October–January, the warm season and also the breeding season. Growth was back-calculated with the use of an empirically deter-

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*See p. 329. The concentrations were given as percentages, but corrected to thousandths in the Report for the following year.

mined relation between TL, SL and scale radius. The results in terms of total length are seen in Fig. 109, taken from fig. 77 of Kapetsky (1974). This shows, not only the inferior growth in length of *O. m. macrochir* as compared with *O. andersonii*, but also the difference in both species between the growth-rates and maximum sizes of males and females.

Breeding

Sexual dimorphism. The male breeding colours are described on p. 443. Males grow faster and reach a greater maximum size than females. This was suggested by De Bont & De Bont-Hers (1950) from their measurements of a single brood of *O. m. mweruensis*. Kelley (1969) found that the biggest individuals of *O. m. macrochir* in the Upper Zambezi were males and Chapman *et al.* (1971) found the same in the Kafue. Marshall (1979) measured adults in Lake McIlwaine and reported that 90% in the 30–32 cm range were male. Very few exceeded 32 cm. The growth studies of Dudley (1974, 1979) and Kapetsky (1974) also demonstrate the differential growth of the sexes (see Fig. 109). Charpy (quoted by Chimitz, 1957) stated that in the warm ponds at Djoumouna, Congo, males reached a weight of 100 g in a year, 1·4 times that of females, a ratio possibly increased by the early breeding in these waters.

Size and age at maturity. The smallest breeding fish in Mweru was 18 cm in TL, but most individuals do not spawn until they reach 20–22 cm, and it was not until 27–28 cm that Carey found 50% mature (1965*a* & *b*, fig. II B 5). In the ponds at Lubumbashi fishes of 20–22 cm are 10 or 11 months old (De Bont & De Bont-Hers). In the Kafue, Chapman *et al.* (1971) record spawning usually at the end of the second year, but 'possibly earlier'. But Mortimer (1960) quotes Charpy as stating that in the warmer ponds in Djoumouna, Congo, breeding occurs at 14 cm and 8 months. Marshall (1979) observed the breeding of *O. m. macrochir* of Kafue stock in Lake McIlwaine. The size at which 50% have mature gonads is 17 cm (♀) or 18 cm (♂) SL. These lengths correspond to 21·5 and 22·5 cm TL and so are lower than those given by Carey for the same percentage in Mweru.

Spawning season and localities. Oreochromis macrochir requires for breeding a temperature not lower than 21–23°C (De Bont, 1950*a* & *b*; Huet, 1973). On the Central African plateau, in the basins of the Kafue, Upper Zambezi, Mweru, Luapula and Lufira, these temperatures are reached and exceeded in the summer season, from September to March. In former French Equatorial Africa, where *O. macrochir* has been introduced, there is no 'cold' season and the species breeds throughout the year (Charpy, quoted by Mortimer, 1960).

Shallow water is required, and this is found in the flood-plains of the rivers and at the southern end of Lake Mweru. Carey (1964, 1965*a* & *b*) demonstrated an annual breeding migration from the northern end of Lake Mweru, where the water is up to 10 m deep, to the southern shores and the islands of Kilwa and Isokwe and along the banks of the lower Luapula, where there is abundant swamp vegetation. There is also a spawning ground in the delta of the Kalungwishi River on the eastern shore. The migration begins in July and by September–October is almost complete. By November the fishermen's catches at the south end are at a peak and those at the northern end are minimal. Spawning was observed in 5–10 ft (1·5–3·0 m) of water. The star-shaped nests were made on a sandy substrate by the males, who cleared spaces in the vegetation where necessary.

De Bont (1950*b*) states that in ponds the nests are made at a depth of 30 to 150 cm.

Separated by high land from the Mweru basin, the Lufira River and the man-made lake in its course also support a population of *O. m. mweruensis*. Observations made in December 1959 and January–February 1960 were recorded by Ruwet (1962, 1963*b*), who found a favourable observation post on the barrage wall at Mwadingusha. On the slightly sloping bottom made of the material piled against the barrage by the current was a spawning ground comprising 200 territories almost in contact with one another. A few pairs of *Tilapia rendalli* and about 100 of *T. sparrmanii* were also spawning in this area. *Oreochromis macrochir* of the Lufira population finds also favourable spawning grounds along the banks of the lake and the meandering river and on the alluvial banks that mark the former course of the river across the barrage lake, at an average depth of 120–130 cm.

Ruwet (1962) noticed that the choice of a site was more influenced by the depth of water than the nature of the bottom. A depth of 1–1·3 m resulted in active nest building, but when the water sank to 15 cm spawning decreased, and at 12 or 10 cm the fishes left for deeper water. When the level rose again they returned. In water more than 150 cm deep no nests were made.

Mortimer (1965, fig. 34; & pers. commn) states that the nests of *O. m. macrochir* are always

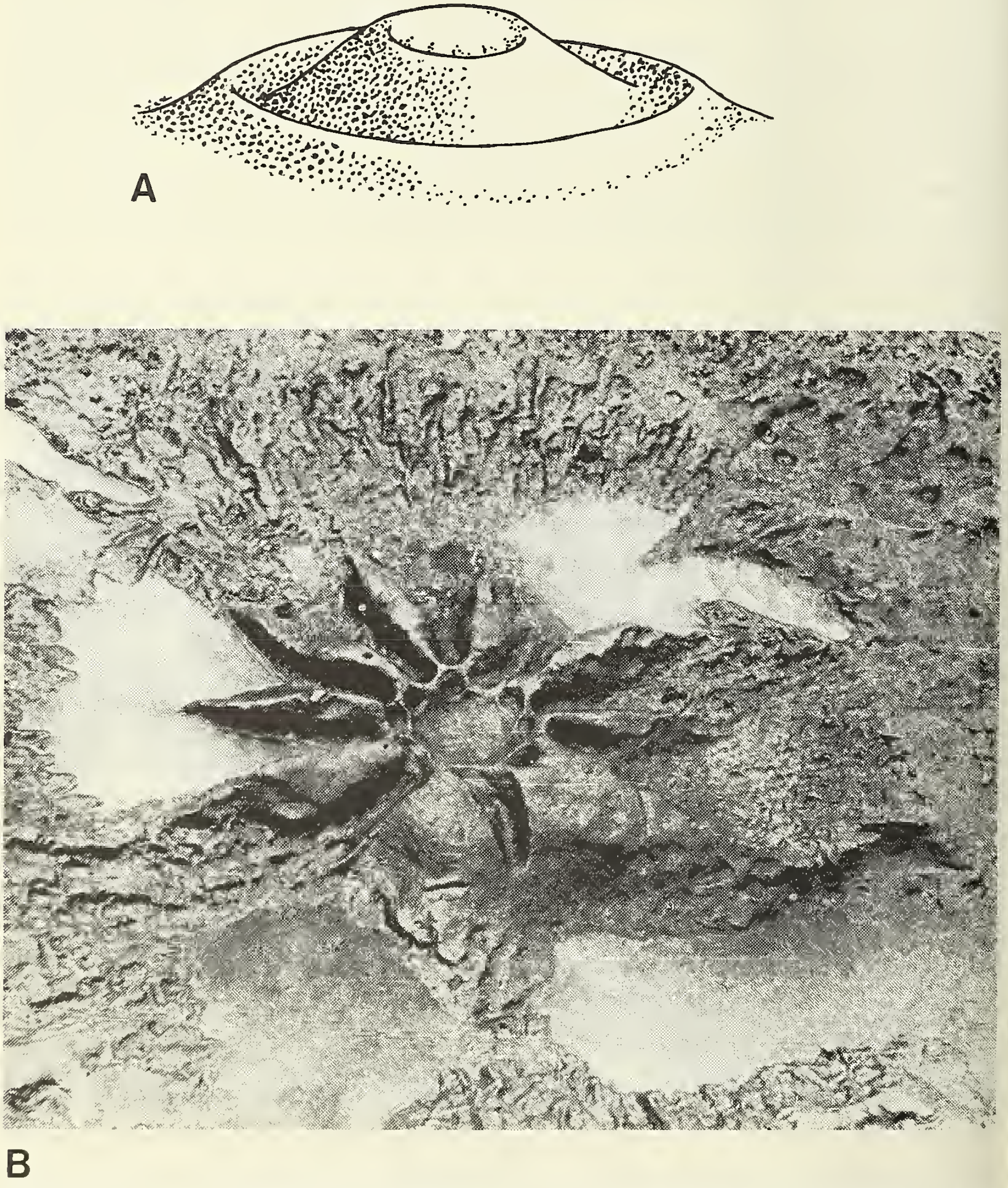

Fig. 160 Nests of: A, *Oreochromis m. macrochir*; B, *O. m. mweruensis*. A, is from a sketch of a nest i a pond at Chilanga, Zambia; B, is from a photograph in Huet, 1973, fig. 182, by kind permission.

nearer the shore than those of *O. andersonii*, which is sympatric with it in the Zambezi basin. Dudley (1979) studied the population dynamics of the *Oreochromis* of the Kafue floodplain and found a correlation between poor year-classes and years of high water-levels in the dry months at the beginning of the breeding season. He suggested that in a dry year the fishes would enter a stressed phase earlier and would be induced to breed at smaller sizes, so increasing the breeding population. One may also suggest that if the water is high during the first months of the breeding season the areas in which it is shallow enough for nest-building would be reduced and some males would be unable to establish territories. If both these influences were operative the contrast between the breeding potential of the *Oreochromis* in high and low floods would be marked. Dudley (1979) even sugested the possibility of controlling the reproductive success of the floodplain populations by means of the Kafue Gorge dam. A similar suggestion was made by Ruwet (1962) for the Lufira population.

The movements of expression throughout the reproductive phases, including the aggressive territorial behaviour, have been analysed by Voss & Ruwet (1966) and Ruwet & Voss 1966). Balthazart (1972) used their data to test a statistical method proposed by Burton (1970) for analysing the behaviour of *O. mossambicus*. The method was designed to make quantitatively clear the parts played by the motivations of flight, attack and sexual competition resulting in fights between males, but Balthazart concluded that the data in their present form were less precise than the method required.

The mating territories or nests of the two subspecies, providing the chief recognisable distinction between them, deserve special attention.

The nest of *O. m. macrochir*, described as 'volcano-shaped', is a truncated cone surrounded by a circular ditch and vallum (groove and boundary wall). The cone is higher than the boundary wall of the territory, its sides being at an angle of about 35–45° with the ground. The top is slightly concave and is the mating-platform. The whole is constructed by the male and defended as his territory. Fig. 160A is a nest of the Kafue *O. m. macrochir* observed being guarded by a male among vegetation in a pond at Chilanga, Zambia. The cone is less steep and the boundary closer to it than in Mortimer's drawing (1960; copied by Fryer & Iles, 1972, figs 50 & 152). It agrees better with De Bont's photographs (1950*a*, fig. 11; 1950*b*, fig. 70) of Zambezi-type nests*. As in *O. mossambicus* (p. 306) the territory is probably smaller among vegetation than in open waters.

The nest of *O. m. mweruensis* is often described as 'star-shaped'. De Bont (1950*a* & *b*) described it as a squat, truncated cone occupying the central part of a circular depression with a diameter of 50–300 cm according to the size of the male. At the top of the cone is a shallow concavity and the sides carry a number (7–12) of radiating crests. De Bont's two photographs (1950*a*, fig. 11; 1950*b*, fig. 71) and that of Fig. 160B (from Huet, 1973, fig. 282) show variation in the number of crests and in the width of the territory outside them. They also show small secondary holes around the edge of the concave central platform, similar to those described for *O. variabilis* by Lowe-McConnell (1956*a*, pl. ix, fig. 2). These small holes were stated by Ruwet (1962, 1963*b*) for the Lufira nests, to be at the points of contact of the central platform with the radiating grooves which score the sides of the low cone†. Ruet (1962) and Fryer and Iles (1972) describe the radii as grooves, De Bont (1950) and Thys (1964) as crests. Fig. 160B shows that if the grooves are close together the material between them is thrown into crests, whereas if they are more widely separated the intervals are flatter and the grooves are the conspicuous structures. Ruwet referred only to grooves and described their construction by the male, who propels himself violently, snout down, mouth open, from centre to periphery with tail-lashings.

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*De Bont misidentified these respectively as of *T. kafuensis* (1950*a*) and *T. andersonii* (1950*b*) under the former of which names fry of *O. macrochir* had been imported into Katanga (Shaba) from Kafue stock in 1948.

†This is not, therefore, an additional cone inside the grooved part as shown in the reconstruction by Fryer & Iles (1972, fig. 50) of the Lufira nest. Ruwet's description is not accompanied by a drawing of a complete nest.

The presence of both types of nests in the ponds at Lubumbashi may be due to the introduction of Kafue stock in 1948, but there is an alternative possibility. The ponds were stocked from 'Moeru-Luapula', probably from the dense spawning grounds of southern Mweru and the Lower Luapula. The division between the Bangweulu *O. m. macrochir*, which builds a Zambezi type nest (Fryer & Iles, 1972; D. Harding, pers. commn, 1965), and *O. m. mweruensis* must be somewhere in the course of the Luapula, which flows between the two lakes. The long stretch of this river, which forms the boundary between Zambia and Shaba, is not zoogeographically uniform. Jackson (1961:xiii) and Bell-Cross (1969*a*) pointed out that the Johnston and Mumbatuta Falls together form a barrier dividing the Mweru fauna from that of the Bangweulu region. But, as shown by the map of De Bont (1950*a*, p. 476), the ponds are supplied with water from the Lubumbashi and other tributaries of the Kafubo River, which flows into the Upper Luapula, and through these channels may well have received an admixture of the Zambezi-type *O. macrochir*.

Ruwet (1962) considered the Lufira nests to be intermediate between the star-shaped and the volcano-shaped, and he also says that nests vary according to the coarseness of the particles composing the bottom, the grooves being deeper in finer, more malleable mud. In coarse gravel he says the nests are simpler.

Even allowing for these variations, there still seems to be a gap between the two structures, which are reported to be seen within the same pond at Lubumbashi. Carey (pers. commn), who worked on both Mweru and Kafue populations, found them quite distinct.

De Bont (1954:1171) crossed the two subspecies, placing in one pond two males of *O. m. macrochir* and two females of *O. m. mweruensis*, and in another pond two pairs in which the males were *O. m. mweruensis*. In each pond the nests were of the type characteristic of the subspecies of the male. The offspring were reared to reproductive size and their nests 'n'étaient pas indentiques'. Thys (1964:23), however, records that the nests were intermediate in three filial generations. This points to a genetically based difference.

Nevertheless, both nests have the essentials of those of some other tasselled species (*O. variabilis*, *O. rukwaensis*, *O. karomo*), namely a central mating platform more or less raised from the bottom of a bigger breeding territory.

Mating has been observed by Ruwet (1962, 1963*b*) in the Lufira and by Wickler (1965, 1966*a* & *b*) in aquarium fishes originating from the Lufira. When a ripe female enters a territory of a male he goes through a courtship display and if this is successful the female places herself over the central platform. After mutual stimulation she emits a batch of eggs (Ruwet estimated about fifty, Wickler about ten) and the male takes her place on the platform. The female touches his genital tassel with her mouth and according to Huet he then emits sperm, some of which is taken into the female's mouth and some presumably fertilizes the eggs lying on the platform. These are then taken one by one into the female's mouth, so having a double chance of fertilization. Wickler, seeing a long filament being mouthed by the female, speculated that this might be a kind of spermatophore, but there is no proof of such a special nature of this thread*. No doubt the whole tassel is bathed in sperm when this is emitted, and the female mouths several branches of it (Wickler, 1965, 1966*a* & *b*; Fryer & Iles, 1972, pl. 6a; Mayland, 1978:306, 372).

Further batches of eggs are laid by the female, either with the same or with other males. Likewise, if his first mate leaves him a male may receive other females successively in his territory and mate with them. Consequently both polyandry and polygyny characterize the behaviour of *O. macrochir* and the overall genetic homogeneity of the colony is assured.

The *number of eggs* produced in one spawning varies with the size of the female. De Bont (1950) counted 1369 ripe ovarian eggs (size of fish not given), and 973 held in the mouth of

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*'Ich habe keinen Zweifel, dass dieser spermatophoren-artige Faden die Spermen birgt: was sie zusammenhalt muss noch untersucht werden.' Wickler, 1966*a*. In preserved fishes one thread of the tassel may be longer and thinner than the rest and in one of Wickler's photos (1966*a*, fig. 4) such a thread is clearly a branch of the papilla. Wickler had the impression that sperm was emitted before the first batch of eggs was laid.

one. Carey (1964) gave 1100–1300 for Lake Mweru. Bowmaker (1964) gave for two fishes of 23·9 and 25 cm TL only 516–519 eggs in each. Carey & B. Bell-Cross (1967) counted 469 eggs in one Kafue ovary, which, if the gonads were equal in size would give a total near that obtained for the Mweru fishes. Marshall (1979), for *O. m. macrochir* introduced into Lake McIlwaine, gave 1000–1500 according to size, and found up to 800 brooded in the mouth.

Ripe eggs are about 3 mm in long diameter and greenish brown (Wickler, 1966). Carey & B. Bell-Cross (1967) found an average long diameter of 3·57 mm in one Kafue female.

The *number of broods* produced in one season depends on the temperature. Pond fishes on the Zambian plateau (at Mwekere and Chilanga) produce about four broods in a season (Mortimer) and in Shaba four to six (De Bont), with an interval of five weeks between broods. Carey (1964) observed recovering gonads in brooding females at the south end of Mweru and in the Luapula. Reports from Charpy (quoted by Mortimer, 1960; and Chimitz, 1957) of introduced pond fishes in Djoumouna, Congo, where the temperature is high throughout the year, state that a female may have up to eight spawnings in a year at intervals of 6–7 weeks.

Brooding females carry their eggs to vegetated localities. According to De Bont (1950*b*) the alevins swim out of the mouth before the yolk is absorbed, but remain in a swarm ('cloud') near the parent, returning to the mouth in case of danger. Finally, after about 21 days, at a length of 13–15 mm, they become independent, but still in a shoal among the grasses and other marginal and swamp plants. In such nurseries they will tolerate the high temperatures and low oxygen concentrations of the swamp water until they reach a TL of 18–20 cm (Carey), whereas the adults move away from the southern end of Mweru, which has become invaded by swamp water, and migrate back to the deeper northern end.

Ruwet (1962:265–9) points out the adaptive value of the mobility of the brooding females in waters where the level is changed drastically by artificial means, and Carey testifies to the advantage to the young of shelter from predacious fishes in the shallow, weedy swamps.

Hybrids

An account of hybridization between *O. macrochir* and *O. niloticus* in Lake Itasy, Madagascar, where both were introduced, is given by Daget & Moreau (1981).

Lake Itasy, with an area of 35 km², is situated on the high plateau of Madagascar at 1,221 m altitude. Before the introduction of *O. macrochir* in 1958 the lake had had a long history of introductions. Its native cichlid, *Ptychochromis betsileanus* had practically disappeared, as had the introduced Madagascan cichlid, *Paratilapia polleni*. *Tilapia rendalli* had been introduced with initial success in the peripheral zone of the lake.

The introduction of *O. macrochir* had an immediate explosive success, but then, in 1961, *Tilapia zillii*, *Oreochromis niloticus* and *O. mossambicus* were added. *Oreochromis mossambicus* did not become acclimatized, but *O. niloticus* did.

In 1965 and 1966 a new fish was recognized and dubbed 'tilapia troisquarts'. This fish partook of the characters of both *O. macrochir* and *O. niloticus* and was believed to be a cross between them.

Experimental crossings of these two species were carried out at Bouake, Ivory Coast, and reported by Bard (1962*c*), Lessent (1968) and Jalabert *et al.* (1970). When *O. niloticus* was the female parent the F_1 was 100% male. The reverse cross produced 75% males. Back-crossing with the parent species was possible and produced fertile offspring. These hybrids proved to resemble 'tilapia trois-quarts' and confirmed the hybrid nature of the latter.

Morphological and meristic characters gave further support to this belief. The figured pharyngeal bone (Daget & Moreau, 1981, from Vincke, 1971) resembles that of *O. niloticus*, the meristic numbers are nearer to those of *O. macrochir*, a male photographed in Plate 1 of Daget & Moreau has the vertically striped caudal fin characteristic of *O. niloticus*, but the female of the same plate has an unmarked caudal. No mention is made of a genital tassel.

The population was monitored by Moreau from 1963 to 1975. Table 1 of Daget & Moreau shows a diminution of *O. macrochir* from 85% by weight of the catch in 1963 to 1% in 1969 and its total disappearance by 1971, while the hybrid increased from 5% in 1965 to 74% in 1969, then diminished to 38·8% by 1975, after which analysis could not be continued. Meanwhile the catch of *O. niloticus* increased steadily to 55·5% of the total in 1975.

The elimination of *O. macrochir* was attributed partly to competition for breeding sites, partly to greater vulnerability to fishing methods. The hybrid became mature at a smaller size than *O. macrochir* in Lake Itasy. The nets with smaller mesh caught *O. macrochir* before it had spawned, whereas the hybrid caught in the same nets had already left offspring.

The causes of decline of the hybrid population were a decrease in fecundity of the females (Daget & Moreau, fig. 3) and a deterioration in their physiological condition. Moreover, they became sexually mature at a smaller size between 1969 and 1975 and this would affect their growth and the proportion by weight that they contributed to the catch.

The population of phenetic *O. niloticus* that finally dominated the catch was not, as Daget & Moreau point out, genetically the same as the original introduced stock. Moreover, on analysing its growth-rate by back-calculation from the scales (valid in this seasonal climate), they found it to consist of two subpopulations with different growth-rates for both males and females, and concluded that it was genetically heterogeneous.

The authors note a parallel with the history of stocking Lake Naivasha (see p. 257, above) and point out the unpredictability of the results of placing species in a new ecological environment, both physical and biotic, however successful it may seem at first.

Distribution

See pp. 437–438.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1908.11.6.35–36 (Syntypes; lectotype 271 mm)	201, 271	Zambezi, above Victoria Falls	Codrington
1908.11.6.37–46 (Syntypes, paralectotypes)	130–271	Maramba R., 2 miles above Victoria Falls	Codrington
1937.4.22.89	46·0–60·5	Balovale, Upper Zambezi, 1031 m	Vaughan-Jones
State Mus., Windhoek or S. Afr. Mus., Cape Town	186	Mouth of Cunene R.	M-L. Penrith
1937.5.3.1–3	45–72	Dongwenna Swamp, Mossamedes	Ansorge
1973.8.3.21 (formerly ANG 6940 in Lisbon)	194	Luembe R., trib. of Kasai R.	A. de B. Machado
Lisbon ANG 6937, 6941, 6943	99·0–153·5	Luembe R.	A. de B. Machado
1910.5.31.75–78	169–230	Ngami Region	Woosnam
1979.5.22.6	135	Thamalakani R, Ngami Region	Banister
1979.5.22.7–9	100–121	Sharobe Lagoon, Okovango	Banister

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
R. M. Stockholm (17 fishes)	44–122	Okovango system, Botswana	Lundin
ROM 29850	104, 168 and (22 fishes) 40–76	Luese Stream, trib. of Kalomo R.	Balon
1908.8.18.13	48	Hot spring, near Kafue R.	Mowbray
1932.2.4.47–53	125–207	Kafue R. at Mumbwa	Pitman
1969.9.25.411–413	34–173	Chiansi Lagoon, Kafue R.	Carey & Trewavas
Fisheries Museum, Chilanga, Zambia (5 fishes)	34–39	Chiansi Lagoon, Kafue R.	Zambia Fisheries Research personnel
1974.2.7.9	160	Kafue R.	Sklower
1907.11.30.15–17 (Syntypes; paralectotypes)	100–258	Bangweula Region	Melland and Foulon
1911.1.27.30–33 (Syntypes; paralectotypes)	143–195	Bangweulu Region	Melland
1932.12.16.679	148	Lukulu R., Mpika Distr., Bangweulu Region	Pitman
1932.12.16.771	162	Chambezi-Namipundu confluence	Pitman
1943.5.27.7–10	81–187	Bangweulu Region	Ricardo
1899.11.27.100	62	Mweru	Exped. Lemaire
1920.5.26.124	59	Lukonzolwa, Mweru	Stappers
1920.5.26.121–2	46–68	Luapula at Kasenge	Stappers
1967.8.23.1 (holotype of *O. m. mueruensis*; formerly MRAC 85070)	206·5	Mobanga, Mweru	Mission Piscicole Katanga
1967.8.23.2	222·5	Aquarium fish, offspring of Luapula parent	Huet
Univ. Michigan	177	Mweru	Balon
Examined fresh, not preserved (7 fishes)	185–238	Mweru at Nchelenge	Bell-Cross & Trewavas
1900.12.13.17–18	56, 68	Lofoi, Lufira R.	Exped. Lemaire
1968.7.30.21	171	Aquarium fish, offspring of Lufira parent(?)	Apfelbach
Zambian Fisheries Research Mus., Chilanga (3 fishes)	153–224	L. Chisi, Mweru-wa-Ntipa	Zambian Fisheries personnel
1969.2.11.42–45	116–129	Korogwe ponds, Tanzania (introduced from Shaba)	R. G. Bailey

Oreochromis (Nyasalapia) salinicola (Poll)

Tilapia natalensis (part, *non* Weber); Boulenger, 1901*a*:457; *idem*, 1915:157 (Moa-Chia = Mwashia).
Tilapia salinicola Poll, 1948*a*:15, figs 4, 5 (Mwashia); Thys van den Audenaerde, 1963:579, fig 4; *idem*, 1964:30, 100, table VI bis. pl. VIII.
Tilapia (Loruwiala) salinicola; Thys, 1968*b*:xxxvi.

Types. Holotype: TL 96 mm, in Inst. R. Sci. nat. Belg. reg. no. 81.

Paratypes: 279 specimens of TL 30–88 mm in Inst R. Sci. nat. Belg., nos 82–85; 10 specimens of TL 45–73 mm in MRAC, nos 78091–100; all collected by H. Bredo in 1938–9 in the saline springs at Mwashia, Shaba.

Distinguishing characters

A population of *Oreochromis* not known to exceed 96 mm in TL, distinguished from neighbouring species by the low numbers of gill-rakers, 15–18 lower on first arch (cf. 20–26 in *O. macrochir* and *O. upembae*). This and the length of the pharyngeal bone exclude it from genus *Tilapia*. The form is more slender than in *O. macrochir* of the same size (depth not more than 38·5% SL; in juvenile *O. macrochir* 42·5–45·5), the interorbital region is narrower and the lower jaw a little longer. The presence of three dark blotches along each flank also distinguishes it from *O. macrochir*, in which the juveniles have usually only dark vertical bands, but not from *O. upembae*. A genital tassel has not been found, but the species is not known to attain the size at which this would develop.

Proportions and meristic characters would not exclude it from *O. (Oreochromis) mossambicus*, with which (as *T. natalensis*) Boulenger identified some very small specimens, but its geographical position supports the action of Thys (1968*b*) in placing it in the same subgenus as *O. macrochir* and *O. upembae*.

Description

Based on the description by Thys (1964), who used 10 fishes of 48–77 mm TL (approx. 34–53 mm SL). In brackets are data from two specimens in BMNH of 59 + 15 and 44 + 13 mm if they are outside the ranges given by Thys.

Proportions as % SL. Depth of body 33·3–38·3; length of head 31·9–35·8 (36, 36·4); length of pectoral fin 27·8–32·1; length of caudal fin 25·5–30·8; length of caudal peduncle (14·5–14·8), depth (13·6, 12·0).

Caudal peduncle l/d 0·88–1·14.

Proportions as % length of head. Snout 17·6–35·5 (31·1, 37·5); diameter of eye 26·3–33·3; depth of preorbital bone (21·2, 22·5); interorbital width 24·1–31·3; length of lower jaw 29·6–35·5 (35·8, 38·5).

Teeth in 3–4 tows, 32–40 in outer row of upper jaw; outermost bicuspid.

Lower gill-rakers 15–18, modes 16 and 17. Microbranchiospines present on outer sides of 2nd to 4th arches.

Pharyngeal teeth very fine; toothed area with rounded lateral lobes, its length about equal to that of the blade. Width of bone slightly greater than its length, which is 35·8% length of head in a fish of SL 59 mm.

Vertebrae 30 (2 specimens).

Scales in lateral line series 29–32, mode 31; from origin of dorsal to lateral line $4\frac{1}{2}$–$5\frac{1}{2}$; on cheek in 2 rows, in some with an extra scale or two; around caudal peduncle 16–19, mode 18.

Dorsal fin XVI 11 (f.2), XVII 11 (f.6), XVII 12 (f.1) or XVII 13 (f.1); in the 59 mm fish in BMNH XV 11. Anal III 8–9, mode 9.

Coloration. 8–10 dark vertical bars on upper half of body; three mid-lateral blotches on the 2nd to 4th (2nd and 3rd) and the 8th (6th) and, in some, one at the end of the caudal peduncle. A few spots on soft dorsal and caudal fins. Outer edge of pelvic fin dark.

Ecology

Bionomics

No information.

Breeding

The 59 mm fish contains ovarian eggs of 1·5 mm diam., so that sexual maturity must be within the sizes known.

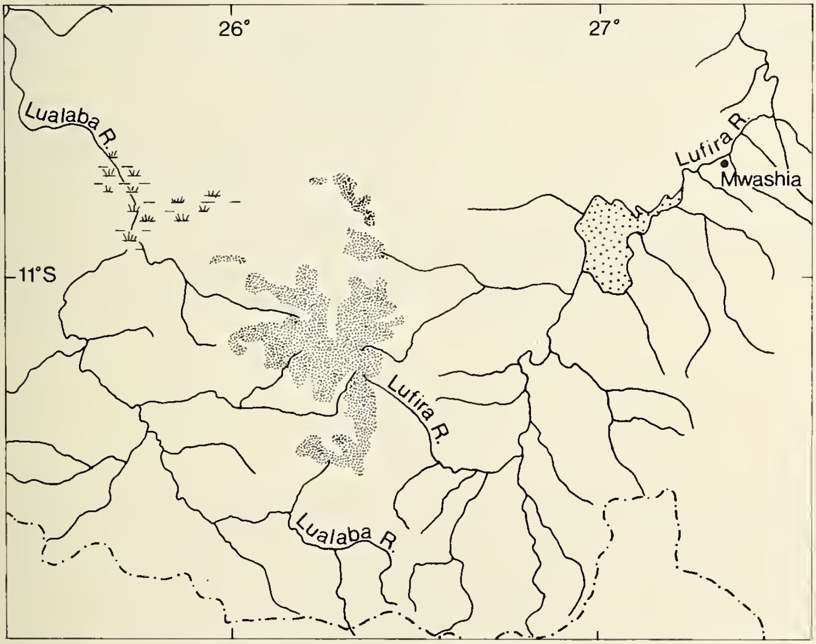

Fig. 161 Part of Shaba, to show the location of *Oreochromis salinicola* and the headwaters of the rivers Lualaba and Lufira. · — · — · — Border between Zambia and Shaba (Zaire). This is also the watershed of the Zambezi to the south and the rivers Lualaba and Lufira to the north. Shading denotes land above 1524 m altitude. Barrage lake on the Lufira dotted. Based on the 1 : 1,500,000 map of Zambia published during the period of the Federation of Rhodesia and Nyasaland, and a map of Zaire ('Congo Belge'), Brussels, 1953.

Distribution (Fig. 161)

Known only from Mwashia (also spelt Moa Chia, Mwashya), a region of saline springs near the Lufira River below the barrage lake at Mwadingusha. The waters are reported to contain 2·5–3·5% NaCl (Thys, 1964:136) and to be at a slightly higher temperature than the Lufira. The salt is locally exploited.

Discussion

Relationships

The only other species of *Oreochromis* in the Lufira basin is *O. macrochir*, but the head-waters of the Lufira and the Lualaba are very close together (Fig. 161), with possibilities of river-capture. The peculiarities of *O. salinicola,* namely small size, early maturity and low numbers of gill-rakers, also characterize other species of warm saline waters (see pp. 32–35). Geographically its most probable origin is as a specialized population of *O. (Ny.) macrochir* although the pigment pattern is more suggestive of *O. (Ny.) upembae.*

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector
1900.12.13.19–21	29	Moa-Chia, Katanga (=Mwashia, Shaba)	Lemaire, 1899–1900
1967.8.23.3–4	59, 44	Mwashia, Shaba	Depasse, 1951 (exch. from MRAC)

Subgenus *NYASALAPIA*—IV
The Lake Malawi species—flock

Oreochromis karongae, Oreochromis saka
Oreochromis squamipinnis, Oreochromis lidole, Oreochromis chungruruensis

In addition to *O. shiranus* (p. 343), a Lake Malawi species with eastern affinities (subgenus *Oreochromis*), Lake Malawi harbours four* closely related endemic species of *Oreochromis*, which were united by Thys (1968*b*) as subgenus *Nyasalapia* (type-species *C. squamipinnis* Günther).

These are: *Oreochromis karongae* (Trewavas)
Oreochromis saka (Lowe)
Oreochromis squamipinnis (Günther)
Oreochromis lidole (Trewavas)

Related to the group and probably derived from it is a fifth species, *O. chungruruensis* (Ahl), inhabiting a crater-lake in the Rungwe Mountains, north of Lake Malawi.

For synonymies see the separate species (pp. 461–465).

The habitat
Fig. 162

Lake Malawi is the southernmost lake in the Great Rift Valley, lying between 9°29′S and 14°25′S. It is 603 km long, and from 28 to 87 km wide. Its surface is nearly 500 m above sea level and its greatest depth, at about one third of its length from the north end, is 758 m. An illustrated account of the lake is given by Mayland (1982).

The climatic conditions, considered as environment for fishes, were described by Lowe (1952:21, 103), and the lake was described by Beadle (1974)† who gave some account of its recent history, drawing on the work of Pike & Rimmington (1965). The annual cycle is controlled by the south-east trade wind (*mwera*), which prevails from March to September, at times reducing the surface temperature by 4–6°C between 21·5° and 29·0°C and mixing the waters to below the thermocline. In the northern part of the lake there is a deep, permanently anoxic zone, but the southern end is shallower and provides a good environment for tilapias. In the north they are confined to the shore zone (zones IV–V of Jackson, 1961*c*).

In addition to annual fluctuations in level there are longer cycles, during the last of which the level sank from about 474 m above sea level in 1870 to 469 m in 1915, rising again to 472–474 m in recent years (1935–1965) (Beadle, 1974, fig. 17.1). These fluctuations may well have been instrumental in causing the division into species of the tasselled tilapias, which are reproductively isolated by their breeding seasons, and the locations and depth of their spawning arenas (as well as by male breeding colours).

The outlet of Lake Malawi is the River Shiré, at the extreme southern end. The river soon expands into the shallow Lake Malombe and then proceeds to join the Lower Zambezi at Port Herald. About 100 km below its origin from Lake Malawi the gentle flow of the Shiré is interrupted by a series of cataracts, the Murchison Rapids, impassable to cichlids and several other species of fishes, and this forms the southern boundary of the endemic fauna (see Tweddle *et*

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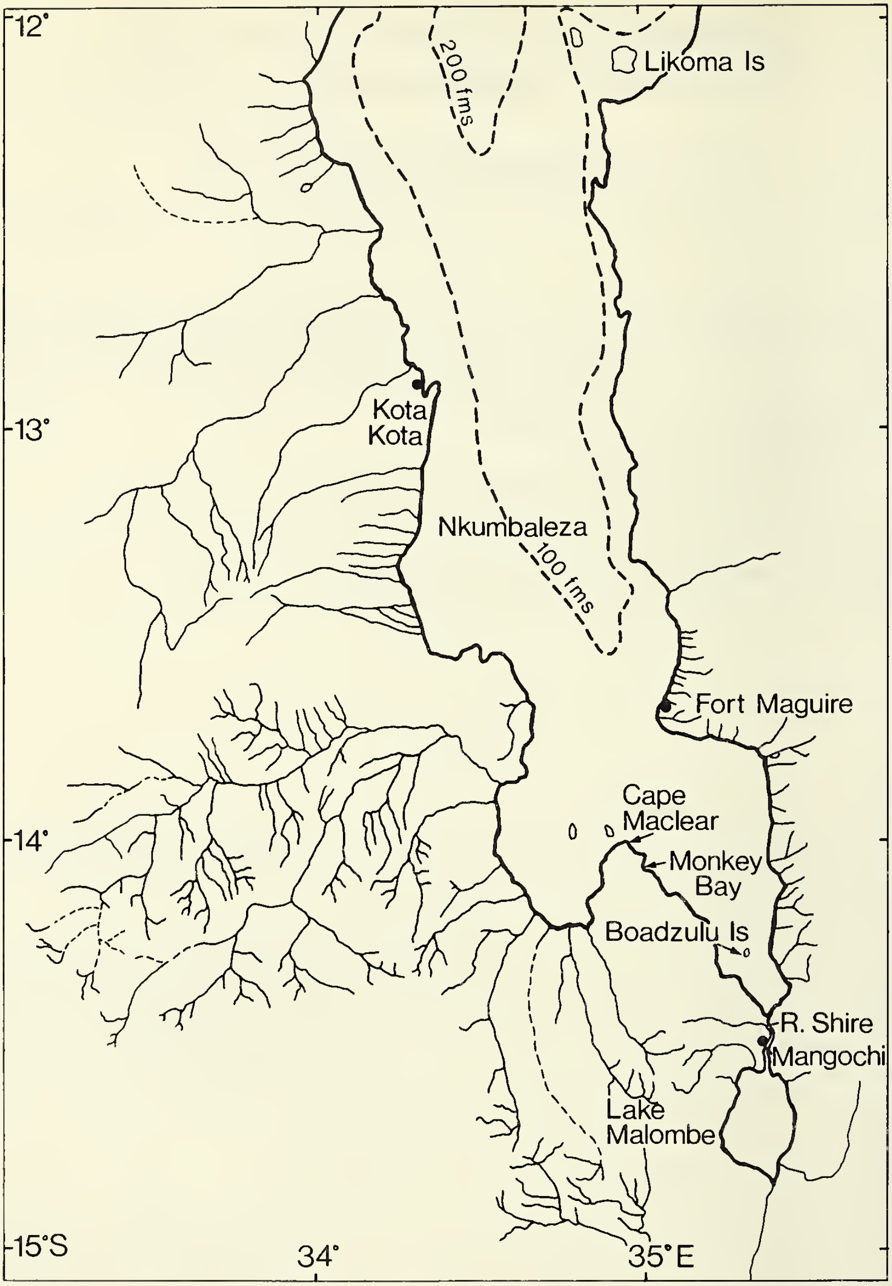
*See p. 476 footnote. †2nd edition 1983.



al., 1979). Below the rapids *Oreochromis* is represented by *O. (Oreochromis) mossambicus* and *O. (O.) placidus.*

North of Lake Malawi, in Tanzania, are the volcanoes of the Rungwe Mountains, in several of whose extinct cones are crater-lakes, described by Kerr-Cross (1895:114) and Fuelleborn (1906:280). From one of these, the Kiunguvuvu of Kerr-Cross and Tschungruru of Fuelleborn, Fuelleborn brought samples of cichlid fishes, described by Ahl (1924) as *Tilapia chungruruensis.* Kerr-Cross described the lake water as 'sweet and good', and inhabited by fishes and tadpoles. Apart from springs feeding the lake there was neither inflow nor outlet on the surface, though

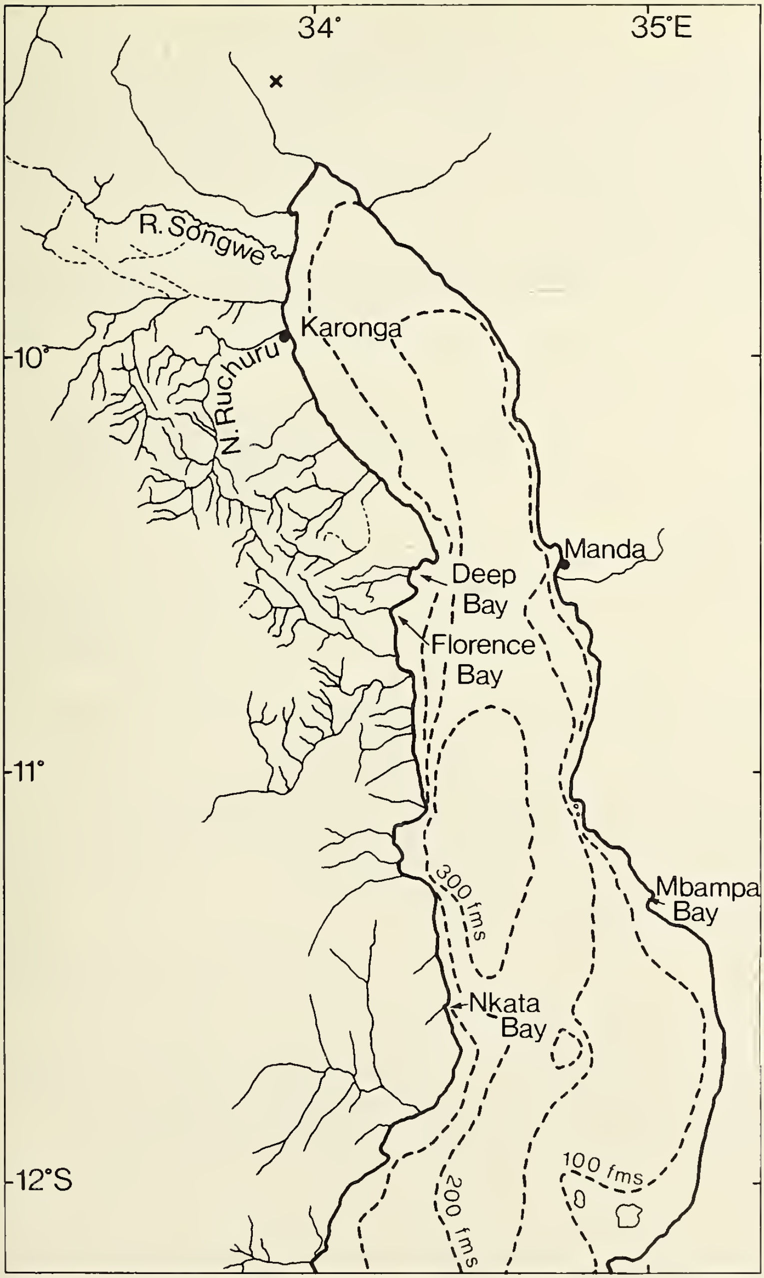


Fig. 162 Left (p. 458), Lake Malawi, southern half; right (above), Lake Malawi, northern half with approximate location of Lake Tschungruru (Chungruru) ×.

both observers suggested that there might be subterranean drainage. The distance from Lake Malawi measured on the sketch-map of Kerr-Cross is about 48 km, but about 25 km on map F3 of 'Deutsch Ost-Afrika', and as Fuelleborn suggests, the lake was probably stocked from Malawi. The holotype and ten paratypes ('cotypes') of *Tilapia chungruruensis* prove to belong to two species (Trewavas, 1976).

Group characters

Collectively the five species are characterized as follows:

1. Genital papilla prominent and bifid in breeding fishes, in the mature male each branch bearing tubercles and filaments (Fig. 171).
2. Adult melanin pattern emphasized in the vertical bars, which extend from the dorsum for varying distances downwards. In the breeding male these disappear, but may reappear in the dying and preserved fish.
3. Interorbital width in adults of 145–285 mm SL: (44) 45–55·5% length of head (Fig. 163).

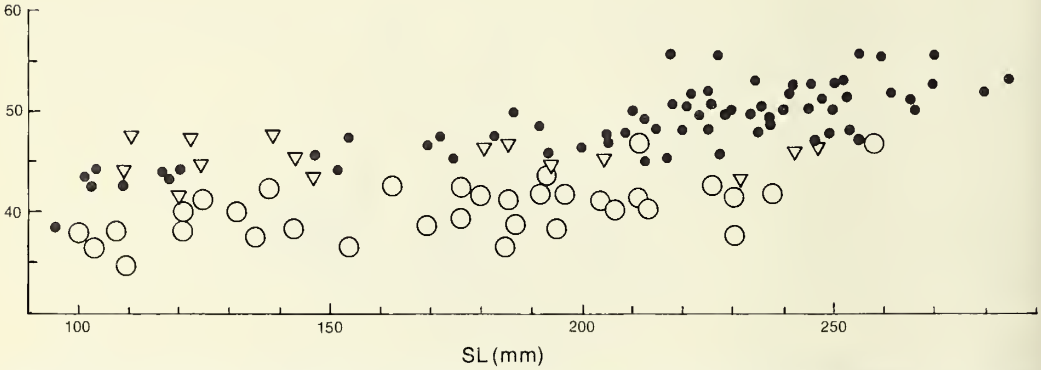


Fig. 163 Interorbital width as % length of head in the four tasselled species of Lake Malawi (●), compared with that in *Oreochromis macrochir* (○) and *O. esculentus* (▽).

4. Caudal peduncle as long as or longer than deep (Tables 109 & 110).
5. Caudal fin scaly, emarginate; in adults both upper and lower lobes rounded.
6. Scales in lateral-line series 32–35, mode 34.
7. Vertebrae 30–32, usually 31 or 32 (Tables 2 & 112).
8. Lower gill-rakers 17–22 (usually 19 or 20).
9. Outer teeth of jaws bicuspid in young up to about 200 mm SL. Above this size many individuals with a varying admixture of tricuspid outer teeth, or in males of unicuspids, the latter mostly by wear. In Lake Chungruru the change occurs at about 100 mm SL.
10. Testes broad, white and sinuous when fully ripe.
11. There is evidence (D. Eccles, pers. commn) that the nest, in nature, consists of a central mating platform surrounded by a circular, basin-shaped territory.
12. Essentially lacustrine fishes feeding partly or mainly on phytoplankton.

Not only is this combination of characters diagnostic of the Malawi group, but the long, relatively slender caudal peduncle is unique in *Nyasalapia*, and these species have the widest interorbital space in the genus. No other tasselled species has such a high number of vertebrae or lateral line scales. The only other tasselled species with a densely scaled caudal fin is *O. lepidurus* of the lower Zaire (pp. 409–411), otherwise a very different fish. In both cases the same waters harbour scaly-tailed species of other genera. In Lake Malawi cichlids of the genus *Corematodus* have the habit of rasping the surface from the tail-fins of other species, especially, in the case of *C. shiranus*, those of *Oreochromis*. The scaly covering becomes more dense in the adult, the fin becomes relatively shorter and both upper and lower halves acquire rounded margins, no doubt eroded between the file-like jaws of *Corematodus*. It may not be too far-fetched to suggest that in Lake Malawi the development of a scaly covering for the caudal fin is a response to the attacks of *Corematodus*. The bigger of the two known species, *C. shiranus*, in turn exhibits the same pigment pattern as *Oreochromis* of this group, among the schools of which it is known to swim. This is a co-evolutionary phenomenon and an example of mimicry of obvious advantage to the *Corematodus* (Trewavas, 1947*b*; Fryer & Iles, 1972:210).

In addition to the genital tassel, these species resemble others of the Central African group in having an admixture of tricuspid teeth in the outer rows of both jaws, and in faourable conditions, a 'nest' with a central mating platform.

Oreochromis (Nyasalapia) karongae (Trewavas)

Tilapia squamipinnis (part); Boulenger, 1894:4; *idem*, 1915:183 (specimen no. 7); Regan, 1922*a*:676; Trewavas, 1935:72.

Tilapia karongae Trewavas, 1941:295–6, fig.; Bertram *et al.*, 1942:23, 25, figs 5C, D, 6A; Lowe, 1952:3, 8, 10–12, 31, 41, 105, fig. 1, pl. IA; *idem*, 1953:1040; Lowe-McConnell, 1955*c*:51, 52; idem, 1959:19; Jackson, 1961*c*:558; Jackson *et al.*, 1963:69; Fryer & Iles, 1972:548.

Tilapia (Nyasalapia) karongae; Thys, 1968*b*:xxxv.

Sarotherodon karongae; Trewavas, 1976:153.

Types. Holotype and paratype by original designation: male, 250 + 40 mm and female, 218 + 38 mm, from Karonga, near the northern end of Lake Malawi; coll. Christy, October 1925. BMNH 1935.6.14.40–41.

Malawian names. *Manindi* (black ♂); otherwise as *O. saka*.

Oreochromis (Nyasalapia) saka (Lowe)

Tilapia squamipinnis (part); Boulenger, 1915:183; Regan, 1922*a*:676; Trewavas, 1935:72; *idem*, 1941:229, 300 ('dark specimens'); Bertram *et al.*, 1942:33 ('dark males'), fig. 5B.

Tilapia saka Lowe, 1952:3–41, 45, 57, 95–105, 112, 117, figs 1–7, 9–13, pls IA, IB, IIIC; *idem*, 1953:1035 ff.; Lowe-McConnell, 1955*c*:51, 52; *idem*, 1959:18 ff.; Jackson, 1961*c*:559; Jackson *et al.*, 1963:69; Fryer & Iles, 1972 (see index to that work).

Tilapia (Nyasalapia) sake (sic); Thys, 1968*b*:xxxv.

Types. Syntypes, by subsequent designation Lowe, 1953: male, 244 + 56 mm and female, 218 + 46 mm, from the southeast arm of Lake Malawi, coll. Lowe. BMNH 1952.2.20.2–3.

Malawian names. *Chambo* (general), *kayawa* (adult ♀ and non-breeding ♂), *chambo langazime* (adult ♀ and non-breeding male); *saka*, *biriwiri* (breeding ♂); *kasawala* (young to about 20 cm TL).

Oreochromis (Nyasalapia) squamipinnis (Günther)

Chromis squamipinnis Günther, 1864:311; *idem*, 1894*a*:621 (pl. liii?).

Tilapia squamipinnis (part); Boulenger, 1898:4; *idem*, 1899:177; Pellegrin, 1904:282; Boulenger, 1915:183 (fig. 118?); Regan, 1922*a*:676; Trewavas, 1935:72; Trewavas, 1941:298, fig.

Tilapia squamipinnis; Bertram *et al.*, 1942:25–31, 126–130, figs 4A,B, 6B; Lowe, 1952:3, 5–65, 95–102, 104, 105, 110–112, figs 1–3, 5–7, 9–13; *idem*, 1953:1036 ff.; Lowe-McConnell, 1955*c*:51, 52; *idem*, 1959:12, 18 ff.; Jackson, 1961*c*:559; Jackson *et al.*, 1963:68; Fryer & Iles, 1972 (see index to that work); Berns *et al.*, 1978.

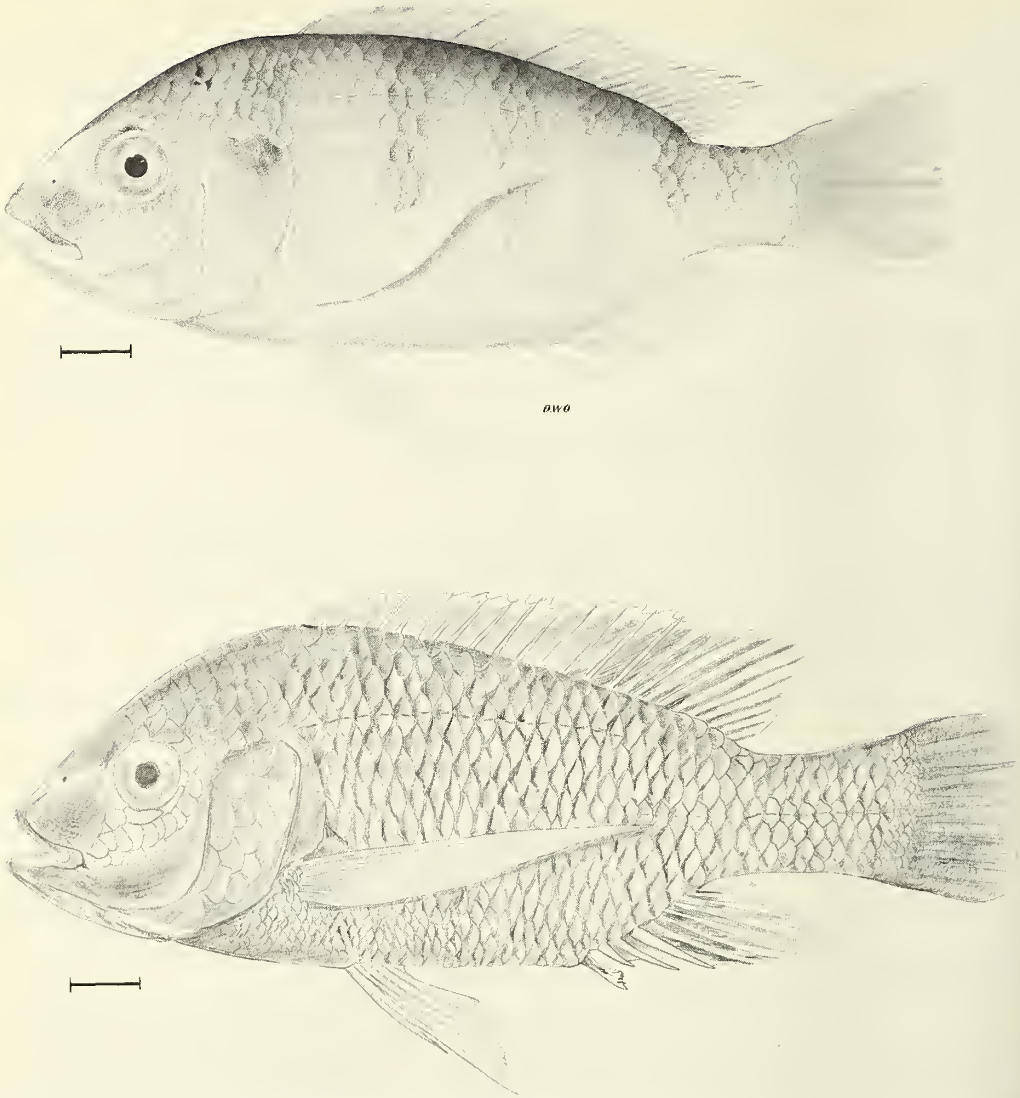


Fig. 164 Above, *Oreochromis (Nyasalapia) squamipinnis*, male BMNH 1936.6.14.76; below, *Oreochromis (Ny.) saka*, male, holotype BMNH 1952.2.20.2. Scales = 20 mm.

Tilapia (Nyasalapia) squamipinnis; Thys, 1968*b*:xxxv.
Sarotherodon squamipinnis; Trewavas, 1976:149.

Types. Syntypes: half-skins, 150–250 mm in SL, coll. J. Kirk in 1861 in the southern part of Lake Malawi; see page 479. From these a lectotype of SL 155 mm was designated by Trewavas, 1941. To fix the specific indentity more surely Lowe (1953) selected as 'hypotypes' a male of 250 + 50 mm and a female of 175 + 40 mm from the southeast arm of Lake Malawi, respectively BMNH 1935.6.14.76 (coll. Christy) and 1952.2.20.1 (coll. Lowe).

Malawian names. *Chambo* (general), *ching'anga* (♂), *ngwalu* (♂), *nchesichesi* (♂), *kayawa* (♀ and non-breeding ♂), *zeya* (immature), *kasawala* (young up to about 20 cm TL).

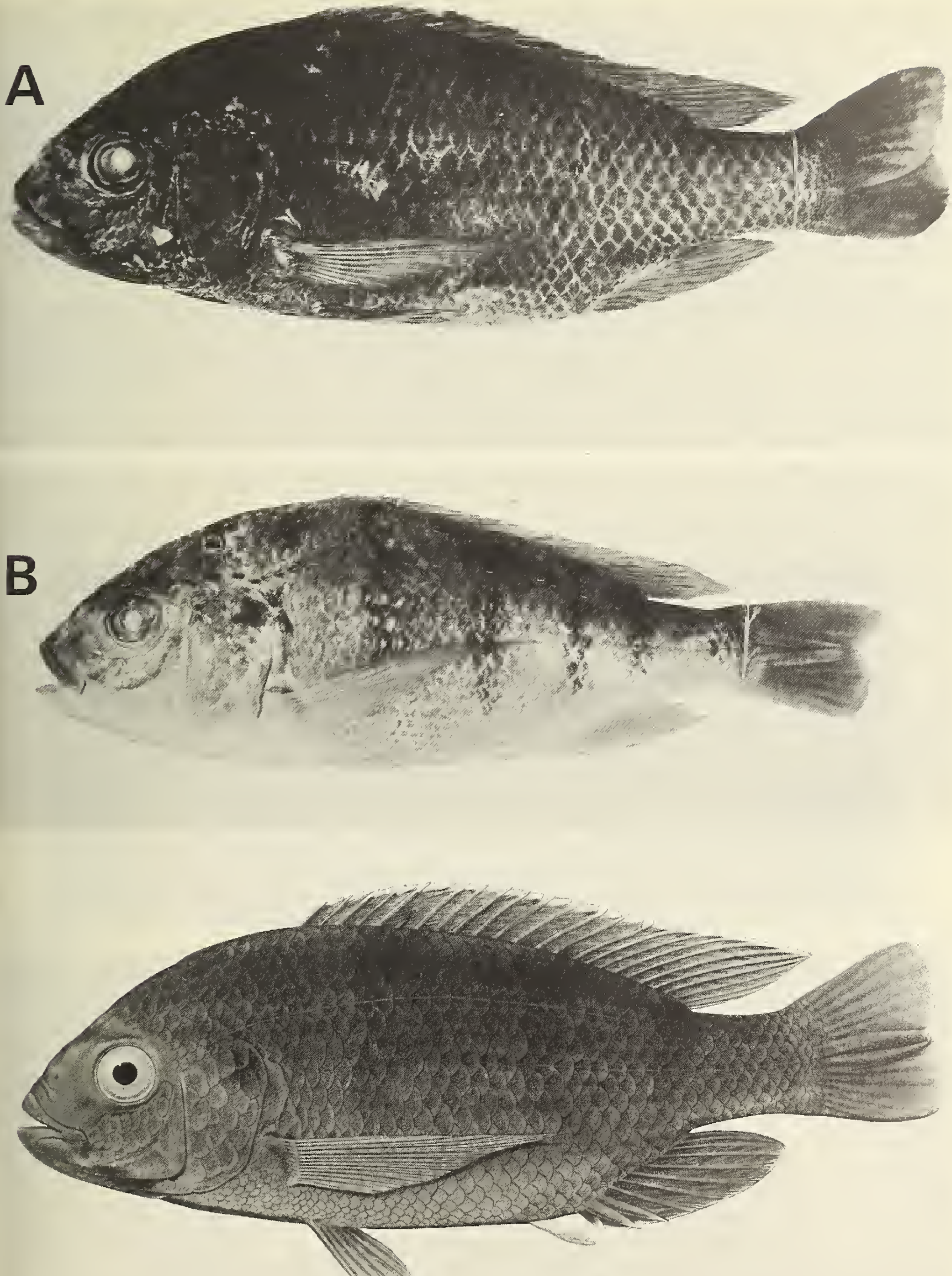


Fig. 165 *Oreochromis (Nyasalapia) karongae*. Photographs of: A, male (type), 250 mm SL; B, female, 225 mm SL; below, drawing of the holotype.

Fig. 166 *Oreochromis (Nyasalapia) lidole*, female, a syntype, 260 mm SL. BMNH 1940.6.28.1–3. Drawn by D. W. Ovenden.

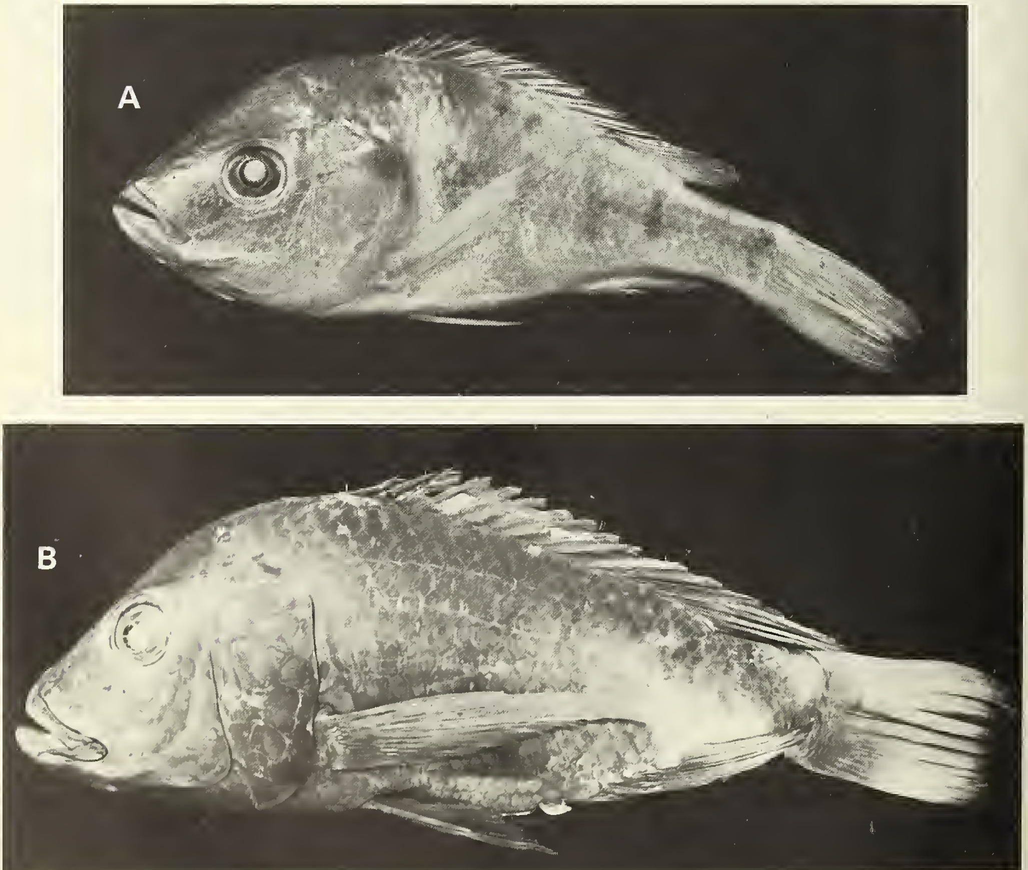


Fig. 167 A, *Oreochromis (Ny.) lidole* from Lake Chungruru, 125 mm SL: B, *Oreochromis (Ny.) chungruruensis*, male, holotype, 153 mm SL.

Oreochromis (Nyasalapia) lidole (Trewavas)

Tilapia squamipinnis (part); Boulenger, 1915:183 (specimens 8, 9); Regan, 1922*a*:676; Trewavas, 1935:72.
Tilapia chungruruensis (part) Ahl, 1924:86 (crater-like Tschungruru).
Tilapia lidole Trewavas, 1941:296–7, 301, fig.; Bertram *et al.*, 1942:34–36, 132–3, fig. 4C, D & fig. 6C.; Lowe 1952:3, 7–28, 31–34, many refs to pp. 65, 98, 101, 104, 106–108, 112, figs 1–4, 8, 9, 14, 16, 18, 20, pl. IA; *idem*, 1943:1036 ff.; Trewavas, 1949; Lowe-McConnell, 1955*c*:51, 52; *idem*, 1959:18 ff.; Jackson, 1961*c*:558, Jackson *et al.*, 1963:69; Fryer & Iles, 1972 (see index to that work).
Tilapia (Nyasalapia) lidole; Thys, 1968*b*:xxxv.
Sarotherodon lidole; Trewavas, 1976:151, pls 1, 2 and 3B.

TYPES. Holotype, by original designation; female 285+55 mm, from the Shiré bar, collected during the fishery survey of 1939. BMNH 1940.5.28.1.

Malawian names. *Dole (lidole, madole), galamula, lolo (malolo).*

Oreochromis (Nyasalapia) chungruruensis (Ahl)

Tilapia chungruruensis (part) Ahl, 1924:86 (Lake Tschungruru, a crater-lake in the Rungwe Mountains, north of Lake Malawi).
Sarotherodon chungruruensis; Trewavas, 1976: pls 1, 2 and 3A.

TYPES. Holotype: male, 153+40 mm, coll. Fuelleborn, about 1923. ZMB 208.

Lectoparatypes: two specimens, 51 and 69 mm in SL, same data as holotype. The holotype was designated 'type' by Ahl and 29 others were 'cotypes'. The type and ten of the 'cotypes' were examined by Trewavas (1976), who identified eight of them as *O. lidole*. The other nineteen 'cotypes' have not been re-examined and their identity is doubtful.

Distinguishing characters of the species

The species are distinguished among themselves as follows (data for two samples of *O. lidole* from crater-lakes are given separately). See also Tables 109–111, Fig. 168; and Fryer & Iles (1972, fig. 266).

Oreochromis karongae

1. Breeding male black
2. Length of head 30·8–36·0% SL, mean of 28 (147–289 mm SL) 35·79.
3. Lower pharyngeal with large toothed area with straight or slightly convex sides; median length of bone 1·14–1·32 times its width and 38·2–42·2% length of head; blade 1·0–1·7 times median length of toothed area.
4. Length of lower jaw 28·4–34·5% length of head, mean (of 27) 30·39.
5. Teeth of jaws in 4–5 (6) rows.
6. Limits of breeding season and locality unknown.

Oreochromis saka

1. Breeding males black, in some with white or yellowish dorsal lappets.
2. Length of head 34·7–39·8% SL, mean of 17 (182–261 mm SL) 36·55.

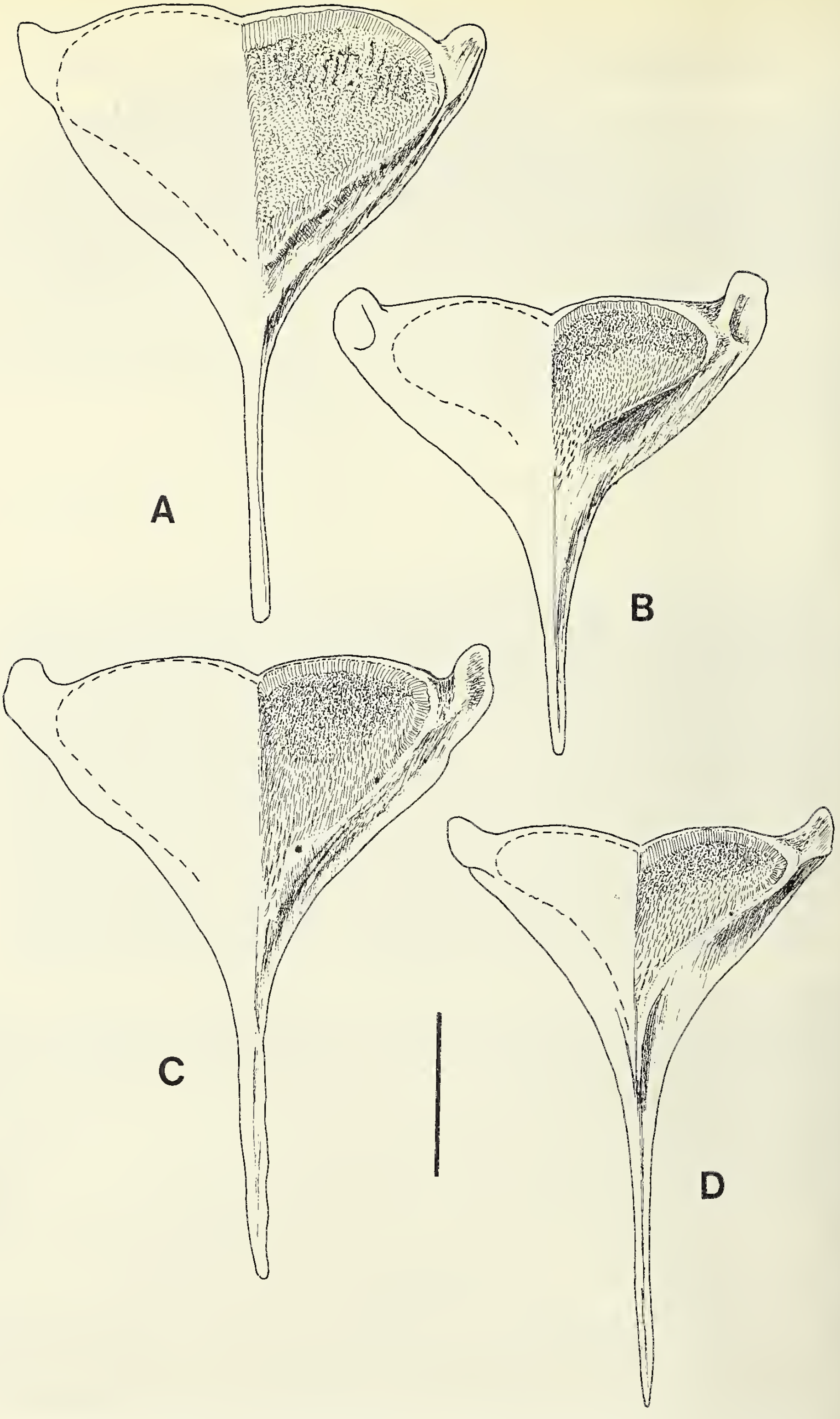


Fig. 168 Pharyngeal bones of four Malawi species of subgenus *Nyasalapia*. A, *O. karongae* 29 cm TL; B, *O. squamipinnis* 27 cm TL; C, *O. saka* 30 cm TL; D, *O. lidole* 29 cm TL. Scale = 10 mm.

Table 109. Proportions in the four tasselled species endemic in the Lake Malawi basin.

	karongae	*saka*	*squamipinnis*	*lidole*	
N	20	16	11	12	3
SL (mm)	209–266	182–261	174–269	153–265	282–285
Proportions % SL					
Depth	35·3–42·8	36·4–44·3	36·5–43·7	35·7–43·1	36·3–38·2
L. head	30·8–36·0	34·7–39·8	35·6–38·6	35·5–39·0	37·1–40·5
L. pect. fin	37·3–44·4	37·0–42·1	37·2–43·5	35·5–41·8	39·3–40·7
L. caud. ped.	12·8–17·6	12·8–17·6	13·1–15·7	14·1–17·1	17·2–17·4
D. caud. ped.	11·5–13·0	12·0–13·1	11·7–13·4	11·3–13·7	11·5–11·8
Caud. ped. l/d	1·0– 1·4	1·0– 1·4	1·05–1·3	1·14–1·36	1·48–1·5
Proportions % l. head					
L. snout	36·5–41·5	36·6–43·1	34·2–42·4	37·2–44·5	40·6–42·8
Eye	19·1–25·7	19·5–24·8	19·1–25·2	17·9–23·9	18·6–17·3
D. preorb.	22·5–25·9	22·7–26·6	22·8–26·4	21·2–25·9	25·0–25·5
Interorb.	44·6–55·5	45·0–53·1	45·3–55·0	46·5–52·0	49·3–49·4
Lower jaw	30·0–33·7	31·4–35·0	31·4–34·9	31·3–36·9	36·8–39·5
Mean l. head % SL	33·79	36·55	37·15	36·50	
Mean l. lower jaw % head	30·39	33·29	33·42	36·70	

3. Lower pharyngeal toothed area with concave sides; median length of bone 1·2–1·3 times its width and 35·5–39·2% length of head; blade 1·3–2·1 times median length of toothed area.
4. Length of lower jaw 31·4–34·6% length of head, mean (of 16) 33·29.
5. Teeth of jaws in 4–5 rows.
6. Main breeding season August to November. Breeding localities in about 4 m depth, near vegetated shores.

Oreochromis squamipinnis

1. Breeding male silvery blue with white and pale blue top of head and dorsum and white dorsal margin.
2. Length of head 35·7–38·0% SL, mean of 11 (174–279 mm SL) 37·15.
3. Lower pharyngeal toothed area with concave sides; median length of bone 1·26–1·36 times its width and 37·6–40·6% length of head; blade 1·6–2·4 times the median length of the toothed area.
4. Length of lower jaw 31·4–34·0% length of head, mean (of 11) 33·42.
5. Teeth of jaws in 3–5 rows.
6. Main breeding season December to February. Breeding localities in about 16 m depth, usually off sandy shores.

Oreochromis lidole in Lake Malawi

1. Breeding male black.
2. Length of head 34·4–38·5% SL, mean of 14 (191–265 mm SL) 36·5, of 9 bigger fishes (270–289 mm SL) 37·0.
3. Lower pharyngeal with small toothed area with concave sides; median length of bone 1·3–1·5 times its width and 33–40·6% length of head; blade 2·1–3·2 times median length of toothed area.

Table 110. Comparison of the proportions of the holotype and paratypes of *O. chungruruensis* with *O. lidole* from Lake Tschungruru and with young specimens from Lake Malawi. The latter are too young to be determined specifically, but are either *O. saka*, *O. squamipinnis* or *O. lidole* or a mixture of these. Only two of the examined paratypes of *O. chungruruensis* have the rank of lectoparatypes, the remaining eight are identified as *O. lidole*.

	Seventeen young of uncertain specific identity		*lidole* from L. Tschungruru		*chungruruensis* paratypes	*chungruruensis* holotype
N	10	7	4	4	2	1
SL (mm)	54–82	101–123	65–123	125–143	51, 69	154
Proportions % SL						
Depth	39·7–42·6	39·8–43·1	34·8–40·0	38·5–39·4	37·6, 38·4	38·5
L. head	32·1–36·5	33·5–34·6	39·4–42·0	39·6–42·4	37·3, 37·7	40·5
L. pect. fin	34·7–38·3	40·8–43·1	38·0–39·6	40·4–43·3	38·3, 35·0	42·0
L. caud. ped.	13·3–16·0	14·6–16·6	15·3–16·0	14·9–16·8	15·7, 13·8	16·0
D. caud. ped.	11·9–13·3	12·6–14·0	11·2–12·0	10·8–11·8	11·7, 12·0	12·2
Caud. ped. l/d	1·0– 1·35	1·1– 1·2	1·3– 1·36	1·3– 1·57	1·3, 1·15	1·57
Proportions % l. head						
L. snout	28·6–32·7	31·8–34·7	33·8–37·4	35·0–39·0	29·0, 30·8	38·0
Eye	28·6–34·4	24·5–29·8	22·2–24·4	21·3–22·3	29·0, 27·0	20·5
D. preorb.	15·4–18·4	19·5–22·1	18·7–22·7	22·1–23·8	16·8, 17·7	24·2
Interorb.	36·0–41·9	42·5–44·3	34·0–44·5	39·8–44·2	32·8, 31·6	39·7
L. lower jaw	29·0–31·6	28·9–32·0	27·8–34·0	34·2–39·6	32·8, 32·0	39·0
Pharyngeal						
L. % head	34·0–39·5	36·5–39·5	36·3–37·5	34·0–40·7	31·6, 34·6	35·5
w. % head	32·5–34·2	29·6–31·8	26·0–27·8	25·6–28·6	31·6, 32·7	28·6
l/w	1·05– 1·16	1·2– 1·3	1·3– 1·4	1·3– 1·5	1·0, 1·06	1·24
blade/dent.	1·14– 1·8	1·2– 1·4	1·8– 3·4	2·7– 3·9	2·3, 2·2	1·4

Table 111. Proportions of pharyngeal bone in species of *Oreochromis (Nyasalapia)* in Lake Malawi and Lake Tschungruru.

Species	N	L. phar. % head Range	L. phar. % head mean	blade/l. dent. area	l/w
saka	11	35·5–39·15	37·44	1·2–2·2	1·2–1·3
saka or *squamipinnis**	6	37·6–39·5	38·0	1·2–1·4	1·2–1·3
squamipinnis	4	37·6–40·6	38·7	1·6–2·45	1·2–1·4
karongae	14	34·6–44·0	40·42	1·0–1·55	1·1–1·3
lidole (Malawi)	19	31·8–45·1	38·16	2·1–3·2	1·3–1·6
lidole (Lake Tschungruru)	8	34·0–40·7	37·4	1·7–3·9	1·4–1·5
chungruruensis	3	31·6–35·5	—	1·2–1·4	1·0–1·2

*Juveniles, 101–123 mm SL.

4. Length of lower jaw 31·3–40% length of head; mean (of 14 of 191–265 mm SL) 36·7, mean (of 8 of 270–289 mm SL) 38·33.
5. Teeth of jaws in 3 or 4 rows, rarely expanding to 5.
6. Main breeding months October and November. Breeding localities in deeper water than *O. saka*, off sandy or rocky shores.

Oreochromis lidole in Lake Kingiri (2 fishes of 139 and 162 mm SL)

1. Breeding male black (?).
2. Length of head 38·5% SL.
3. Lower pharyngeal toothed area small; median length of bone 1·38, 1·37 times its width and 37·6, 36·0% length of head; blade 1·9, 2·2 times median length of toothed area.
4. Length of lower jaw 31·8, 32·3% length of head.
5. Teeth of jaws in 3 series.

Oreochromis lidole in Lake Chungruru (N = 5; 123–143 mm SL)

1. Breeding male black, with white dorsal fin-margin.
2. Length of head 39·4–42·4% SL.
3. Lower pharyngeal bone with restricted toothed area; median length of bone 37·5–40·7% length of head and 1·32–1·47 times its own width; blade 2·7–3·9 times median length of toothed area.
4. Length of lower jaw 34·0–39·6% length of head.
5. Teeth of jaws in 3 (–4) rows.
6. Breeding habits unknown.

Oreochromis chungruruensis (N = 3, SL 51, 69, 154 mm)

1. Breeding male black.
2. Length of head 37·7, 37·6, 40·5% SL.
3. Toothed area of lower pharyngeal with concave sides; median length of bone 1·0–1·24 times its width and 31·6, 34·6, 35·5% length of head; blade 1·2–1·4 times median length of toothed area.

4. Length of lower jaw 32·8, 32·0, 39·0% length of head.
5. Teeth of jaws in 4 or 5 rows.
6. Breeding habits unknown.

Comments on the distinguishing characters

The species are most easily distinguished in the respective breeding season by the colour of the territorial males and by the sexually active females associated with them. It is from such fishes that the morphological distinctions have been obtained. Even so, although *O. lidole* and *O. karongae* can be distinguished at immature sizes (for *O. lidole* not below 16 cm TL), *O. saka* and *O. squamipinnis* are very difficult to distinguish morphologically from each other.

As Lowe showed (1952, 1953), the *Oreochromis* in Lake Malawi form a series according to their breeding locations and their preferred habitats, *O. shiranus* adding to the ecological series at the inshore end, with *O. lidole* the most open water species and the most dependent on phytoplankton. In association with this ecology a reduced pharyngeal dentition and small jaw-teeth in narrow bands characterize *O. lidole. Oreochromis karongae* has a distinctive pharyngeal bone, with a very broad tooth-plate extending to or behind a line joining the tips of the lateral apophyses. Its lower jaw is shorter and its tooth-band often wider than in the other species. Young individuals have been observed feeding on epiphytic algal growths, and these possibly form a proportion of the adult diet.

Although a similar comparison distinguishes the intermediate species *O. squamipinnis* and *O saka*, these are much more alike in the dentition and the overlap makes definition difficult. Lowe devised a 'character-index' in which the number of tooth-rows and the length of the lower jaw reinforce each other, with the following result: length of lower jaw in mm divided by the numbe

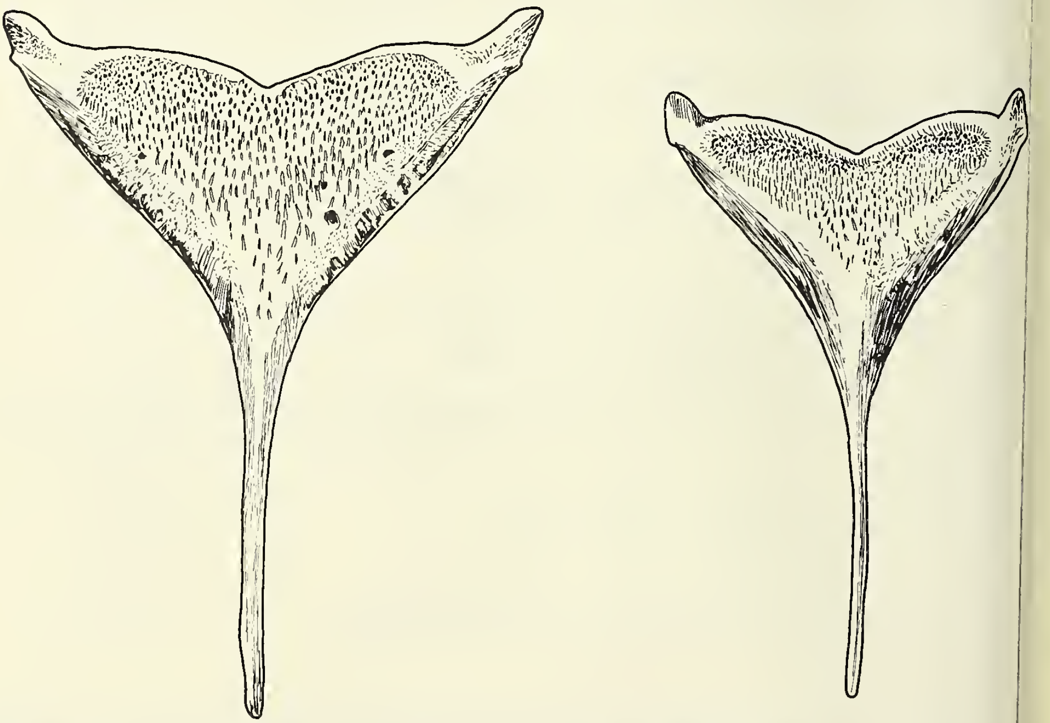


Fig. 169 Pharyngeal bones of: left, the holotype of *Oreochromis chungruruensis*; right, an *O. lidole* 125 mm SL from the same lake. After Trewavas, 1976, pl. 3.

of tooth-rows usually more than 6 in *O. squamipinnis* and usually less than 6 in *O. saka*. In less quantitative terms, *O. saka* tends to have a shorter jaw and wider bands of teeth than *O. squamipinnis*.

In Lake Tschungruru the contrast is marked between *O. lidole*, with three rows of small teeth and *O. chungruruensis* with four to five.

PROPORTIONS (Tables 109–111). Most of the proportions are very uniform in the four species within Lake Malawi. Although the fishermen claim to distinguish *O. lidole* by its bigger head, this is registered in the ratio length of head to SL only in bigger fishes. These are the ones that come inshore in large numbers in the breeding and brooding seasons. They also have the broadest interorbital space. From this massive head the body tapers away to the narrow caudal peduncle, whereas in *O. saka* and *O. squamipinnis* the highest part of the body is usually behind the origin of the dorsal fin. This contrast in shape also holds between *O. lidole* and *O. chungruruensis* (Figs 167 & 169).

In the samples from Lake Tschungruru the head is very big at all sizes in *O. lidole* and the male holotype of *O. chungruruensis* also has a big head, although the young of that species are more normal in proportions.

The specific differences in the pharyngeal bone and dentition are summarized in Tables 110

Table 112. Meristic characters in the tasselled species of Lake Malawi and crater-lakes Kingiri and Tschungruru. Abbreviations: KAR = *O. karongae*, SQUA = *O. squamipinnis*, LID.K. = *O. lidole* from L. Kingiri, LID.TSCH. = *O. lidole* from Lake Tschungruru, CHU = *O. chungruruensis*.

	KAR	SAKA	SQUA	Young	LIDOLE	LID.K	LID.TSCH.	CHU
Dorsal fin								
XIV 11							1	1
XV 10	1				1		1	
XV 11	1	2			1		6	1
XVI 10	5	5	2	4	10			
XV 12	1							1
XVI 11	16	5	4	9	14	1		
XVII 10	5	2	2	1	3	1		
XVI 12	1							
XVII 11	1							
Dorsal totals								
25	1				1		2	1
26	6	7	2	4	11		6	1
27	22	7	6	10	17	2		1
28	2				1			
Anal fin								
III 8	3	1	1		2	1	1	
9	24	15	9	10	7		4	1
10	4	2	1	1	3	1	3	1
11								1
Scales lat. line series								
32				1	1		1	2
33	13	5	1	2	4	1	2	
34	15	6	5	5	17	1	4	
35	1	1	1		3			
36	1							

& 111, and Figs 168 & 169. The small size and reduced dentition of the bone in *O. lidole* ar even more extreme in Lake Tschungruru.

Meristic characters (Table 112). These are uniform in all four species in Lake Malawi an the two specimens from Lake Kingiri, but the eleven fishes from Lake Tschungruru have onl XIV or XV dorsal spines, numbers rare or absent in Lake Malawi.

The gill-rakers number (2–4)+(1–2)+(17–22) in all five species, but the extreme number 17 and 22 are rare and among 85 in which they are counted the lower rakers are 19 or 20 i 52. The three specimens of *O. chungruruensis*, however, all have 2+1+17.

Size. The maximum size among the known specimens of *O. karongae* is 31 cm TL (266+43 mm) The 1410 mature males of *O. squamipinnis* handled by the survey of 1939 (Bertram *et al.* 1942:126) measured 19–36 cm TL and weighed 250–820 g, whereas the same report (p. 132 records of *O. lidole* 132 spent females of 29–39 cm TL and 450–1100 g, and 22 males of 33–38 c and 740–980 g. Lowe's growth-studies (1952:101) likewise included *O. squamipinnis* and *O. sak* only up to 36 cm and 857 g, but *S. lidole* up to 38 cm and 1090 g. These maximum sizes ar paralleled by the respective sizes at maturity (see pp. 473–6, 478).

Exceptionally big fishes of *O. squamipinnis* and *O. lidole* are recognized by special names Ngong'o (Chiyao) and Makumba (Chinyanja), and even those of *O. squamipinnis* may reac 39 cm and 1100 g. They are in non-breeding colours, and when examined prove to have quiescen gonads and much fat among the viscera (cf. also *Sorotherodon linnellii*, p. 86).

Coloration. Breeding colours are described above and on pp. 474–6, 479. Non-breeding fishe of the four species in Lake Malawi are silver-grey, darker on the dorsum, with black vertica bars of unequal length from the dorsum to mid-flanks. The ground-colour is often more fawn-grey in *O. saka* and *O. lidole* and the black bars may be dimmed. This pattern contrasts wit that of *O. shiranus* and most of the Malawi fishes of the *Haplochromis* group, in which the tw horizontal bands prevail or an oblique band characteristic of many Malawian cichlids; this fac makes the vertical bars of the mimic, *Corematodus shiranus*, the more remarkable, especiall since the smaller species, *C. fasciatus*, wears the commoner livery of the lake.

In Lake Tschungruru the females and young have a mid-lateral series of 4 or 5 spots verticall drawn out and a fainter dorsal series, a more usual pattern in *Tilapia* and *Oreochromis*.

Ecology

Food

All three of the species that were studied in the field were found to be feeding mainly on phytoplankton, any fragments of vascular plants included being such as might have been stirred u from bottom deposits near the shore. Both the survey of 1939 and Lowe in 1946 witnessed bloom of *Anabaena*, during which *O. squamipinnis*, *O. saka* and *O. lidole* (and also *O. shiranus*) wer exploiting this organism, swimming in small schools with mouths open at the surface. Stomach examined then contained almost pure *Anabaena* with a little *Nitzchia* and *Peridinium*.

From her extensive studies Lowe (1952:37) concluded that the preferred food of the thre species is phytoplankton. When this is less plentiful *O. lidole* swims farther afield in search o more and *O. saka* and *O. squamipinnis* turn to detritus.

Young up to 20 cm TL swim in schools inshore and include epiphytic growths in their diet Very young, even before the yolk is fully absorbed, were found to be ingesting dinoflagellate and *Melosira* and *Navicula*.

Although microphagy is the rule, these, like other species may be caught on a moving bait The occasional presence of fry of their own species in the mouths of males has been interprete as accident in the flurry of a seine haul.

The diet of *O. karongae* has not been studied. During 1978–80 the lake level was high an near Karonga a large area of shore was flooded and turned into wetlands ('dambo'). Fishermen cut passages between the lake and one of the large pools so formed, and set traps in them for tilapias. As *O. karongae* is the most abundant species of *Oreochromis (Nyasalapia)* in this region, it is probably this species that provided most of the catch, revealing a preference for marshy areas and probably for periphyton as food (D. Tweddle, pers. commn, 1981). At present this remains hypothesis, influenced by the nature of the dentition.

Movements and schooling

Much information on these activities was gathered and interpreted by Lowe (1952:37–39). Little is known about *O. karongae*, but the other three Malawi species were studied in the south-east arm of the lake, the River Shiré and Lake Malombe. Breeding movements are described separately.

All three species school actively. The extent to which they do so was illustrated by Lowe from observations on a large seine haul. As the seine was drawn *O. squamipinnis* formed a school inside the net-wall, and although smaller fishes were able to escape through the meshes many of them turned and re-entered the net to join the school. Such schools may be formed of both sexes and usually of fishes of approximately the same size. They are seen near the surface when the water is calm (see observations on feeding, above), but when winds disturb the water and in colder weather there is evidence that the fishes skulk near the bottom.

The schools of *O. lidole* keep to more open water and range farther than the other two species. In 1946–7 the only *O. lidole* found south of Boadzulu Island, and in the Shiré between Lakes Malawi and Malombe were brooding females. In the early part of 1939 the only *O. lidole* caught off Kota Kota were spent and brooding females. Males came nearer to this and other open beaches in October, the breeding season.

Young, newly released from the maternal mouth, form close family schools, and when this phase is past long banks of young, up to 12 cm TL, remain close to shore in warm, calm weather. As they exceed this length they move farther from shore in small schools.

The aquarium observations of Berns *et al.* (1978) produced further evidence that the schooling tendency in *O. squamipinnis* is stronger than that in e.g. *O. niloticus* and *O. mossambicus*, and intraspecific aggression is correspondingly less.

Breeding

Oreochromis (Ny.) karongae

The genital papilla is large and tuberculate in breeding fishes of both sexes and in males its branches and filaments increase its length to 21 mm or more. Males become black with broad white margins to dorsal, caudal and in some also anal fin. In females and non-breeding males the black vertical bars of unequal lengths are conspicuous against the silvery flanks.

The collections include dark males with well-developed genital tassels from 212 to 266 mm SL (TL 24–31 cm) and only six adult females, four of which, of 218 to 227 mm SL are mature. The suggestion that females mature at a smaller size and reach a lower maximum length needs to be tested on greater numbers. The female of 227 mm carried ripe ovarian eggs, and was caught with one of 222 mm brooding young of 20 mm in the mouth.

No year-round monitoring of gonad state has been recorded. Christy collected, in 1925 at Karonga in August and at Vua and Deep Bay in October, dark males with genital tassels in each place. Lowe found ripe, spent and brooding females at Karonga in March 1946, indicating breeding activity in February and March. Either there is a long breeding season or there are two peaks.

Breeding sites have not been surely ascribed to this species.

A brooding female of March, 1946, held 324 young of 15 mm in her mouth. The length of the brooding period and maximum size of mouth-held young have not been recorded.

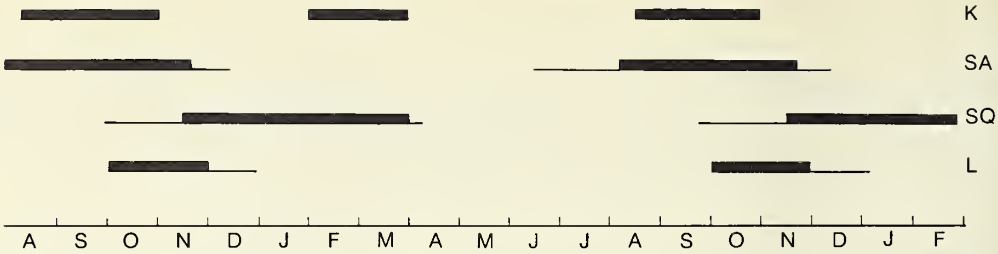


Fig. 170 Breeding seasons; *Oreochromis karongae* (K); *O. saka* (SA); *O. squamipinnis* (SQ); *O. lidole* (L) in Lake Malawi. Based on Lowe, 1952, fig. 13, and other data in the same Report. The thick lines indicate the main breeding seasons, the thin extensions periods when a few breeding individuals have been found.

Oreochromis (Ny.) saka

No difference has been demonstrated between the sexes in size. Breeding males are black, often with white or yellowish edges to dorsal and caudal fins. The breeding female may also be black, but without the contrasting fin-margins, or she may be brownish or retain the brownish-grey colour with vague vertical dark bars of sexually inactive fishes.

The minimum breeding size found by Lowe (1952:24–25) was 25 cm TL, at three years of age, but the modal breeding size for both sexes was 29 cm.

The main breeding season was established from the collections of Borley in 1941 and by Lowe in 1946 as September to November, but individual males may come into breeding condition as early as July and an exceptional ripe male was caught as late as 9th January (Fig. 170). These dates were gathered at the south end of the lake, and the season is the same as far north as Kota Kota. At Karonga in March, 1946, Lowe (1952:105) recorded a few spent females of this species, which suggests a longer breeding season in the north, but she found no sexually active males there.

Oreochromis saka forms breeding colonies in water of 2–4 m depth off reedy shores, where the males excavate and defend large saucer-shaped nests. Evidence for this was gleaned by Lowe in several places from Lake Malombe and the Shiré to Karonga. Eccles (pers. commn, 1965), however, describes a nest of this species made among growths of *Valisneria*, in which a central platform is surrounded by a narrow ditch and a steep overhanging rim (Fig. 173). Nests are probably smaller in shallow water among vegetation (see p. 478).

Lowe counted ripe ovarian eggs in six fishes believed to be *O. saka*, finding 176–300 per fish. In common with *O. squamipinnis* and *O. lidole*, the long diameter of these was 4–5 mm (Lowe-McConnell, 1955*c*). Berns *et al.* (1978) record *O. saka* of 515 g body-weight caught in August 1968, of which the average weight of ovulated eggs was 50·1 mg.

Young up to 24 mm TL were found being brooded in the maternal mouth. In the laboratory eggs (of this or *O. squamipinnis*) taken from the mouth developed to the stage of involution of the yolk-sac in 5½ days and the yolk was absorbed in another week (Lowe, 1952:30). The probable brooding period was estimated as three or four weeks.

Oreochromis (Ny.) squamipinnis

Field observations recorded by Bertram *et al.* (1942) and Lowe (1952) have been supplemented by aquarium studies by Berns, Chave & Peters (1978).

No size difference between the sexes has been demonstrated. The characteristic part of the male territorial coloration is the iridescent bluish-white top of the head and antero-dorsal part of the body, while the dorsal fin has a broad white margin. Caudal and anal fins may also have white margins. The flanks are pale silvery blue, the belly white. Berns *et al.* record that the body of the male below the white upper parts was often black, although this might fade to light blue, but the members of the 1939 and 1946–7 surveys did not observe black-bodied males of

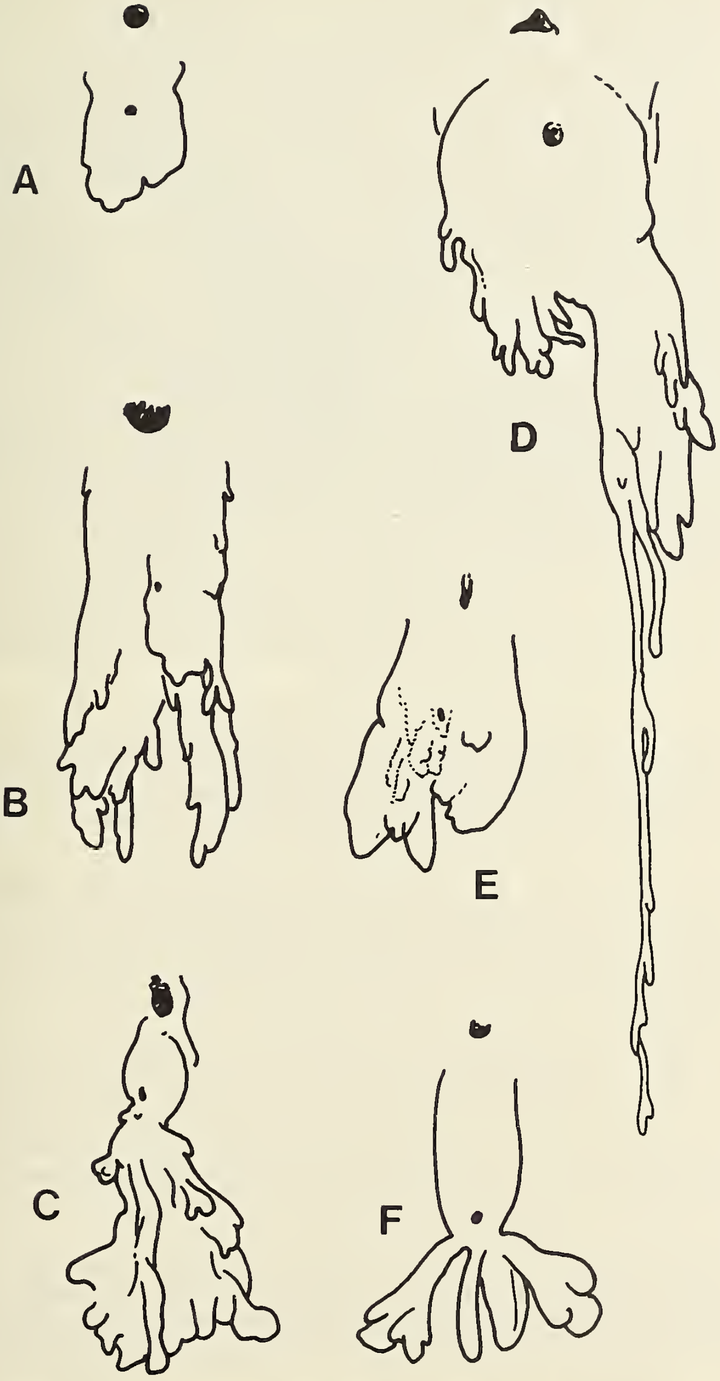


Fig. 171 Male genital papilla in preserved specimens of: *Oreochromis squamipinnis* 200 mm SL; B, *O. squamipinnis*, 242 mm SL; C, *O. saka*, 187 mm SL: D, *O. lidole*, 289 mm SL: E, *O. karongae*, 209 mm SL: F, *O. chungruruensis*, lectoparatype of 144 mm SL. The anus and urogenital opening are shown.

this species. The actual spawning, however was not observed in the field and possibly the black coloration may be assumed fleetingly at times of intense sexual activity (cf. figs 3 & 6 of Berns *et al.*)*. The iris and pelvic fins become black.

Females keep the silver-grey colour of non-breeding fishes, the dark bars or parts of them coming and going with emotional changes.

The main breeding season is the rainy one, December to April, although a few males have been seen in breeding dress as early as the end of September. Fully ripe males are recorded from 15 November to 3 April by Lowe at the south end of the lake and in March, the month of her visit, at the north (Fig. 170). Between 29 January and 8 February, 1939, several seine hauls were observed on open beaches near Kota Kota. They included numerous male *O. squamipinnis* in light blue breeding dress and accompanying females. At sizes of 29–33 mm TL the latter were all spent and some retained young in the mouth. At the same time traps set among reeds and papyrus caught of this species only spent females, some retaining young of 15 mm. On 13 February the same observers recorded in the Shiré, between Mangoche and Lake Malombe, catches of mature males and spent females. On 3 March at Florence Bay, in the northern half of Lake Malawi, traps set at the mouth of a stream and also gill-nets were catching spent females of 27–29 cm TL: but fishermen reported that females with young in the mouth and pale blue males were caught in January and February, and that they expected fishes with eggs inside in May and June. This suggests that at least in the northern part of the lake there may be a second breeding season for this or *O. saka*.

The spawning areas are in deeper water than those of *O. saka*, the evidence pointing to depths of 16 to 20 m. Lowe (1952:30) recorded a ring-net catch in about 20 m which comprised twenty-seven running-ripe males of *O. squamipinnis*, all with empty stomachs and in full light-blue breeding dress. They came to the surface with distended swim-bladders, and had evidently been on their mating territories in this rather deep water.

Lowe (1952:23–24) gives the minimum and modal sizes of first maturity as respectivley 23 and 27 cm TL at an estimated age of three years. This agrees, as far as size is concerned, with the results of Bertram *et al.* (1942: 31 & 126), but these authors observed at Kota Kota a few fishes of 17–19 cm TL with 'ripe' or 'spent' gonads and one of 18 cm with young in the mouth. In an aquarium, Berns *et al.* (1978:239) had breeding fishes of 17 months old and 9·7–11·2 cm in SL.

Ripe ovarian eggs numbered 370–549 in fishes of 25 to 27 cm TL (Lowe, 1952; Lowe-McConnell, 1955*c*). Berns *et al.* record counts from six females of 26·7 to 34·9 cm, which, judging by the season at which they were caught, were either *O. squamipinnis* or *O. lidole.* They ranged from 186 (at 26·6 cm) to 1461 (at 34·9 cm). In smaller, aquarium-bred fishes the same authors counted newly-laid eggs in the mouths, obtaining from 49 in a fish of body-weight 20 g to 232 in one of 100 g.

These authors gave the size of the egg as half the sum of long and short diameters, finding a range of 2·2–4·3 mm, usually between 3·0 and 4·2; averages of four spawnings ranged from 3·3–4·1 mm. Lowe-McConnell (1955*c*) gave the long diameter in this species, *O. saka* and *O. lidole* as 4–5 mm. Berns *et al.* record an average egg-weight of 35·3 mg from a lake fish of 474 g body-weight. This fish had ovulated, but in another of body-weight 500 g ovarian eggs still not ovulated weighed 46 mg. Berns *et al.* also found considerable variation in size of the eggs in a single clutch, as Peters (1963*b*) had in other species.

In the smaller, laboratory-reared fishes the weights of the eggs were lower. Fig. 8 of Berns *et al.* gives a maximum average egg-weight of 28 mg (in a fish of body-weight 150 g).

Mating behaviour has been observed in the aquarium by Berns *et al.* The male digs a simple circular pit and defends it. He makes forays towards a group of schooling females swimming

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*This male coloration has since been observed in the field by D. Tweddle (pers. commn, 1981), who thinks it may characterize a fifth species.

Fig. 172 Breeding pair of *Oreochromis squamipinnis*. The pair are in the T-position, with the male forming the horizontal part of the T. Note the white dorsal parts of head and nape and the white margin of the dorsal fin of the male and the black marks in the temporal region of the female. From Berns *et al.*, 1978, fig. 6, by kind permission.

at the surface, but the female who comes down to the nest usually appears to do so on her own initiative. She engages in some sand-digging at the centre of the territory and the mating behaviour then includes the T-stand, with the nose of one fish at the genital papilla of the other, both partners alternately forming the horizontal part of the T. The eggs are laid in batches and immediately picked up by the female as the male glides over them to fertilize. The branches of his genital papilla may pass through her mouth and the water is then doubtless full of sperm, so that the eggs are fertilized in the mouth as well as on the ground.

In the laboratory at 27°C the eggs hatch in 4½ to 5 days. The secretion of gas into the swimbladder starts on the 9th or 10th day and the embryos are then able to swim about in spite of their large yolks. Lowe observed that if the brood was spat out in the disturbance of a net haul the young composing it remained swimming together in a tight ball of about 15 cm diameter. The young of a swarm were all at the same stage of development, from yolk-laden embryos to young with fully absorbed yolk. The younger they were the tighter the swarm (cf. Bauer, 1968, on other species).

Both Lowe and Berns *et al.* estimated the brooding period at 3 to 4 weeks, followed by a further two weeks when the young remain near the parent and can return to the mouth for shelter.

Berns *et al.* observed the diminution of the male's elaborate genital papilla during his spawning period, apparently both by wear and by shrinkage or resorption. The same was observed in males that held territory but did not spawn. One such 17 cm in SL, had a pair of tassels 9 cm long, which had diminished to 6 and 7 cm when he left his territory after 28 days. In a spawning male the shrinkage is greater, amounting to 2 cm for each of successive spawnings.

Oreochromis (Ny.) lidole

Information has been published by Trewavas (1941), Bertram *et al.* (1942:34–36), and Lowe (1952:31–34, fig. 14 & table 25).

No difference in size has been found between the sexes, the biggest male in the collections being only 4 mm longer than the biggest female. Breeding males become black with white margins to dorsal and often also caudal and anal fins. The female retains the colour of the non-breeding fish, but with the dark bars less well marked.

Breeding starts at about 28 cm TL and an age of three years (Lowe, 1952:23–24).

Ripe males were caught in seines on open beaches at Kota Kota and Mkumbaleza in October 1941, but in January–February 1939 only spent females were caught in seines near Kota Kota. Lowe recorded the breeding in the southern parts of Lake Malawi as October–November. A few males were coming into breeding dress as early as July, but none was found with full testes until October. By January most females have released their young, but some of those caught in Jan/Feb at Kota Kota, and in February in the Shiré River, still had young of 40–42 mm in the mouth. An exceptional brooding female was found as late as May, to the surprise of the native fishermen (Lowe, 1952:33).

Eccles (pers. commn, 1965) observed large basin-shaped nests of this species with a central raised platform (Fig. 173).

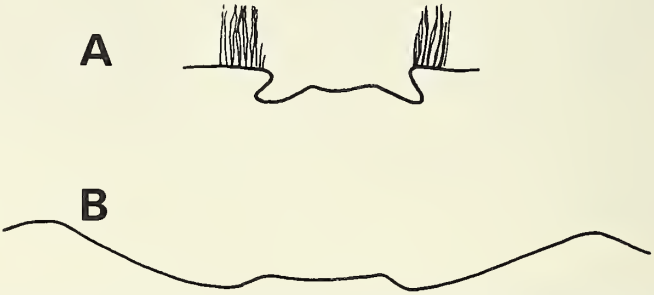

Fig. 173 Sections of 'nests': A, *Oreochromis saka* in a space cleared among *Valisneria*; B, probably *O. lidole*. From sketches made by D. Eccles from memory in 1965. For the small size of the mating territory in a vegetated area compare *O. mossambicus* in Lake Sibaya (p. 306).

The spawning arenas are in deeper water than those of *O. saka*, and off clean sandy or rocky shores. One breeding ground was known to be in about 8 m depth, and evidence of others was found in water too deep for observation from a boat. No spawning grounds or breeding males were found at the extreme southern end of the lake, where the water is shallow and the shores reedy, but brooding females went there with their young and spent males moved there to feed.

Lowe (1952) recorded an incident that indicates that the females congregate over the mating territories occupied by the males. In November 1945 she passed in a motor launch over a shoal of females (recognized as *lidole* by herself and the experienced fishermen of the company). The fishes were circling in an area about 5 m in diameter over a known *lidole* spawning-ground and continued this movement undisturbed by the boat, behaviour contrasting with that of feeding shoals, which would flee when the boat approached. This female behaviour corresponds to that described by Berns *et al.* for *O. squamipinnis* in an aquarium, and also to that of *O. niloticus vulcani* in Lake Turkana (Rudolf) (Worthington & Ricardo, 1936:379).

Ripening yellow ovarian eggs in five *O. lidole* numbered 364–542 (Lowe, 1952). Mating has not been observed, but there is evidence that the eggs are picked up quickly by the female, who then swims away to shallower water. Lowe had evidence that while the young are still subsisting on yolk the mother fishes do not come into the reed beds as the other species do, but stay in open water, probably in schools separate from the feeding schools of younger fishes and spent males. The brooding period is long, and together with the time when the young are received again in the mouth at night or for shelter is estimated to last several weeks. Young of up to 52 mm in length and an exceptional one of 58 mm were taken from the mouths of *lidole* mothers.

At this size fewer young can find room in the mouth and many must fall prey to piscivorous fishes, crabs and birds, though some may join the schools of young tilapias that find shelter among the grasses and reeds.

Until the yolk is absorbed the brooding fishes feed very little; their stomachs are generally empty and their condition is poor. The males too are in poor condition after spawning and move into shallower, richer water to recover.

From the crater-lake Tschungruru (=Chungruru) two male *O. lidole* of SL 141 and 143 mm SL are mature. They are dark brown, probably faded from black, (though one is now bleached on one side), with white-margined dorsal fins; the anal and caudal have narrow white margins in one, in the other they are wholly dark. The genital papilla is large and speckled with melanin; in one it has a single short filament, in the other it is distally bifid, each division having 4–6 short branches. The testes are at an advanced stage. A male of 126 mm SL has a papilla of 8 mm, bluntly bifid at the tip and although the basic body-colour is rather dark, a darker pattern of mid-lateral blotches is conspicuous. It is therefore at about 140 mm SL (17·5 cm TL) that males of this population become mature. A female of 123 mm SL (15 cm TL) contains one ovarian egg of long diameter 3 mm as well as some smaller and is therefore also mature.

From the two specimens from Lake Kingiri the gonads have been removed. A male of 162 mm SL (20·5 cm TL) had a genital papilla with a short tuberculate appendage. It had a white-margined dorsal fin and the body had a dark spot at the base of each scale. It would appear to be nearing maturity at a smaller size than *O. lidole* of Lake Malawi.

Oreochromis (Ny.) chungruruensis

The holotype is a uniformly dark male of 154 mm SL (19·5 cm TL) with a genital papilla bearing two bunches of short branches (Fig. 169F). The size of maturity cannot therefore be very different from that of *O. lidole* in the same lake.

Material examined

BMNH Reg. No.	SL (mm)	Locality	Collector or donor
O. (Nyasalapia) squamipinnis			
1864.6.28.19 (skin) (fig'd syntype)	250	'Nyassa'	J. Kirk
1864.2.10.6 (skin, syntype)	170+	'Nyassa'	J. Kirk
1864.1.9.57–58 (syntypes) (one lectotype)	155, 232	'Nyassa'	J. Kirk
1864.1.9.69 (skin, syntype)	78	'Nyassa'	J. Kirk
1863.12.21.2–3 (skin, syntype)	172, 210	'Nyassa'	J. Kirk
1896.10.5.7–8	145, 205	Upper Shire R.	Rendall (coll.) Johnston (pres.)
1935.6.14.62–63	250 and three doubtful 253–290	Shiré bar	Christy
1935.6.14.47–51	96–245	Shiré bar	Christy
1935.6.14.76–79 (including one 'hypotype')	230–270	Bar to Nkudzi	Christy

BMNH Reg. No.	SL (mm)	Locality	Collector or donor
1935.6.14.42–45 & 57	135–280	Monkey Bay	Christy
1935.6.14.64–71	82–250	Southwest arm of L. Malawi	Christy
1940.5.28.7–12	101–124	Bar to Fort Maguire	Christy
1935.6.14.41a	255	Karonga	Christy
1940.5.28.4–6	185–280	SE arm of lake	Christy
1943.2.17.4–6	238–255	Kota Kota	Borley
1952.2.20.1 (hypotype)	174	SE arm of lake	Lowe
1952.2.20.41–43	171–189	Salima	Lowe
?1952.2.20.40	202	Nkudzi	Lowe
O. (Nyasalapia) saka			
1952.2.20.2–3 (syntypes)	218, 244	Mbolera, SE arm of Lake Malawi	Lowe
1952.2.20.4–6	210–252	Mbolera, SE arm of Lake Malawi	Lowe
1943.2.17.7–8	187, 261	Kota Kota	Borley
1943.2.17.10–11	205–241	Kota Kota	Borley
1952.5.14.2	202	Fort Johnston (=Mangoche)	Borley
(unreg.)	251	?	Rhoades
1908.10.27.73–75	212–228	'Nyassa'	Rhoades
1935.6.14.82–85	238·5–252·0	Shiré Bar (Oct.)	Christy
1921.9.6.70–71	170, 230	'Nyassa'	Wood
1935.6.14.28–32 (3 juv. doubtful)	98–204	Mwaya	Christy
1935.6.14.46	265	Shiré bar	Christy
1935.6.14.58–61	171–281	Shiré bar	Christy
?1952.2.20.40	202	Nkudzi	Lowe
Young *saka* or *squamipinnis*:	specific identity uncertain		
1893.11.15.16–22	57–82	L. Malawi & Upper Shiré	Johnston
1893.11.15.23	22	'Zomba'	Johnston
1897.6.9.258–267	34–63	Kondowe to Karonga	Johnston
1921.9.6.223	64	'Nyassa'	Wood
1940.5.28.7–12	101–123	Shiré bar to Fort Maguire	Christy
O. (Nyasalapia) lidole			
1940.5.28.1–3 (holotype and paratypes)	245–285	SE arm	Fishery Survey, 1939
1908.10.27.71–72	255, 265	'Nyassa'	Rhoades
1935.6.14.38–39	250, 265	Karonga	Christy
1935.6.14.80–81 (6 fishes)	260–285	Bar to Nkudzi	Christy
1943.2.17.1–3, 7–18 7–18	225–289	Mkumbaleza, Kota Kota and Sani	Borley
1952.2.20.67–69 (13 fishes)	153–228	SE arm of L. Malawi	Lowe

BMNH Reg. No.	SL (mm)	Locality	Collector or donor
1966.12.9.12–13	139, 162	L. Kingiri, crater-lake 8 km N of L. Malawi	Albrecht
ZMB 208 (part) (8 fishes)	65·5–143·0	L. Chungruru	Stuhlmann
O. (Nyasalapia) karongae			
1906.9.7.30	245	'Nyassa'	Moore
1935.6.14.40, 41	250 (holotype) 217 (paratype)	Karonga	Christy
1935.6.14.33–37 (7 fishes)	64·5–253·0	Vua (Aug.)	Christy
1935.6.14.72–75	215–235	Vua (Aug.)	Christy
1935.6.14.52–56	225–240	Deep Bay	Christy
1940.54.28.13–16	92–169	Vua (Sept.)	Christy
1952.2.20.61–66	210–233	Karonga (March)	Lowe
O. (Nyasalapia) chungruruensis			
ZMB 208 (part) (holotype)	153	L. Chungruru (Tschungruru)	Stuhlmann
ZMB 208 (part) (lectoparatypes)	51, 79	L. Chungruru (Tschungruru)	Stuhlmann

Subgenus *NYASALAPIA*—V

Oreochromis karomo

Oreochromis (Nyasalapia) karomo (Poll)

Tilapia karomo Poll, 1948*b*: 5, figs 1–4 (delta of Malagarazi R.); *idem*, 1956: 46 figs 6–8; Lowe-McConnell, 1955*c*: 50, table II, figs 1, 2; *idem*, 1956*a*, 141, figs 1–3, pls VII, VIII and pl. IX fig. 1 (breeding); *idem*, 1959: 20; Peters, 1961, table 1 (interorbital width); Wickler, 1962*a*:153; Thys van den Audenaerde, 1963: 588, 594; *idem*, 1964: 22, 126, table VI, figs 4, 5, 22 and pl. XI; Bailey, 1968:195, 201, fig. 4; Fryer & Iles, 1972 (see index to that work).
Tilapia (Neotilapia) karomo; Thys van den Audenaerde, 1968*b*: xxxv; *idem*, 1971: 240.

Types. Holotype: TL 275 mm (230 mm SL), delta of Malagarazi R., coll. M. Poll, 1947; MRAC 105777. Paratypes: TL 230–296 mm, MRAC 105778–780, with same data as holotype; four fishes of TL 93–249 mm, IRSNB 273, same data as holotype. One of these paratypes is now in BMNH, 1960.9.30.394.

Etymology. *karomo* is the local name for this species.

Distinguishing characters

A tasselled species. Adults with all the teeth of the jaws tricuspid, with long, slender shafts, arranged in broad bands. Jaws much enlarged, projecting forwards to form a long snout, with the tooth-bands meeting in the horizontal plane. Maxilla with a flange resting on the premaxilla at the curve between its two arms (Figs. 175–176).

Description

Based on a male paratype of 187 mm SL from the delta and 11 specimens of 124–220 mm SL, 10 of which are males, from the Malagarazi swamps at Katare; incorporating also meristic characters from two smaller fishes and some data from Poll (1948*b*) and Thys (1964).

Proportions as % SL. Depth of body (39·6) 41·4–46·5; length of head 35·8–38·3; length of pectoral fin 36·0–42·5, of last dorsal spine 15·3–19·4, of longest dorsal ray 25·0–28·6, of third anal spine 12·2–16·1. Length of caudal peduncle 10·5–13·0, depth 14·5–16·0.

Poll and Thys record a lower but overlapping range for the length of head (34·3–327·8). In two fishes of 76 and 78 mm SL I find a ratio of 39–40.

Caudal peduncle length/depth 0·7–0·9.

Proportions as % length of head. Snout (35·7) 38·9–44·8; diameter of eye 15·4 at 210·0 mm SL to 25·5 at 124·0 mm SL (and 29·0 at 78·0 mm SL); depth of preorbital bone 20·6–24·2, equal to diameter of eye at 142 mm SL when both are about 21%; interorbital width 37·4–41·3; length of upper jaw 31·1–36·3, of lower jaw 33·0–37·8. Length of lower pharyngeal bone 38·3, its width 32·6 in a fish of 189 mm SL; in this the blade is nearly twice as long as the median length of the toothed area.

Fig. 175, comparing the jaws of *O. malagarasi* and *O. karomo* of almost equal length, shows that the contrast is greater than the ratios reveal, because the longer jaws of *O. karomo* also add to the length of head. As well as their greater length, the jaw bones are more massive. The premaxillary pedicels (ascending processes) are reinforced posteriorly and, asymmetrically, on their lateral faces.

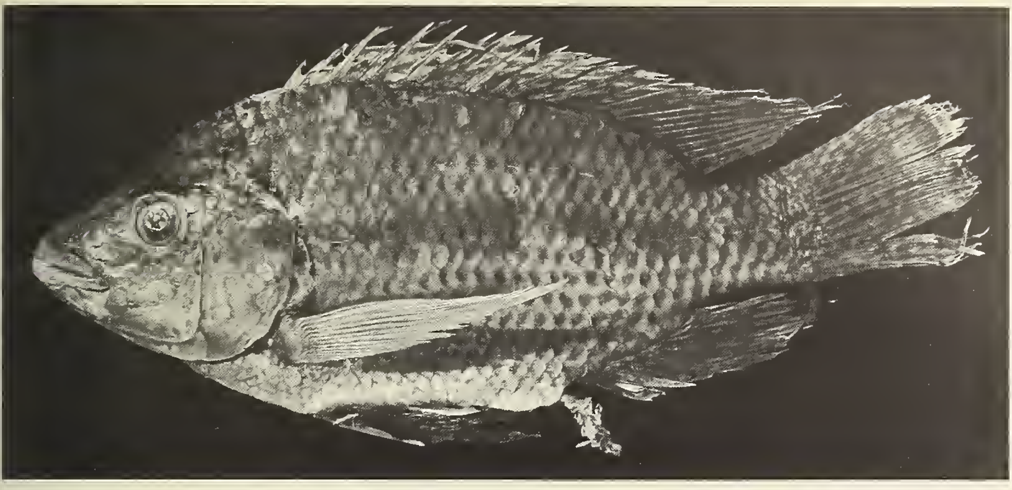

Fig. 174 *Oreochromis (Nyasalapia) karomo* of 220 mm SL.

The marked depression on the maxilla for the processus maxillaris of the palatine in *O. karomo* indicates a more controlled relation between the two bones in this species.

The broad part of the maxilla that receives the palatine process may be called the palatine shelf of the maxilla. Its ventro-lateral edge is slightly concave in *O. malagarasi* and all other species in which it has been examined, except *O. karomo*. Along this edge the skin is firmly attached to both maxilla and premaxilla, in contrast to the fold of skin that intervenes between the distal parts of the two bones, allowing them to move more independently of each other. The same edge provides attachment for the maxillo-palatine and maxillo-nasal ligaments. In *O. karomo* an additional flange (*f*) extends from this edge (which now becomes a mere ridge) to overlie the premaxilla at the angle between its dentigerous and ascending arms.

This flange and the shape and forward extension of the jaws are unique in the genus, the premaxillary pedicels measuring (from between the two front teeth to their tips) 23·8–29·0% length of head (cf. 20–23·5% in *O. malagarasi* of comparable sizes).

Teeth movable, with long slender shafts and broad, curved crowns. The major cusp of the outermost teeth is much broader than the minor ones, especially the third cusp, on the mediad side of the tooth. In the young of 76 and 78 mm SL all the outer teeth are bicuspid. At 122 and 143 mm SL most teeth of the outermost series are still bicuspid, only two or three near the symphysis having a small third cusp. From 170 mm upwards all are tricuspid (Fig. 176).

Pharyngeal teeth slender, crowded and movable, the posterior lower and anterior upper with a hooked cusp and a shoulder (Fig. 177).

Gill-rakers $2-3+1-2+18-20$ on the first arch.

Vertebrae 29 $(15+14)$ in 8 specimens.

Scales in 2 or 3 rows on the cheek, 29–31, usually 30 or 31, in lateral line series (28–30, usually 29, Thys), 4 or 4½ from origin of dorsal fin to lateral line, 4–5 between bases of pectoral and pelvic fins, 16 around caudal peduncle.

Dorsal XV 12 (f.1), XV 13 (f.4), XVI 12 (f.5) or XVI 13 (f.4). The same variants are recorded by Thys (1964) with a mode at XV 13.

Anal III 10–11. Pelvic fin extending to vent or genital papilla.

Genital papilla enlarged, bifid and dentritic in mature fishes of both sexes, but in mature females the length is only about 5 mm, whereas in breeding males it may be 10–15 cm, with semi-transparent filaments and blobs of bright orange tissue.

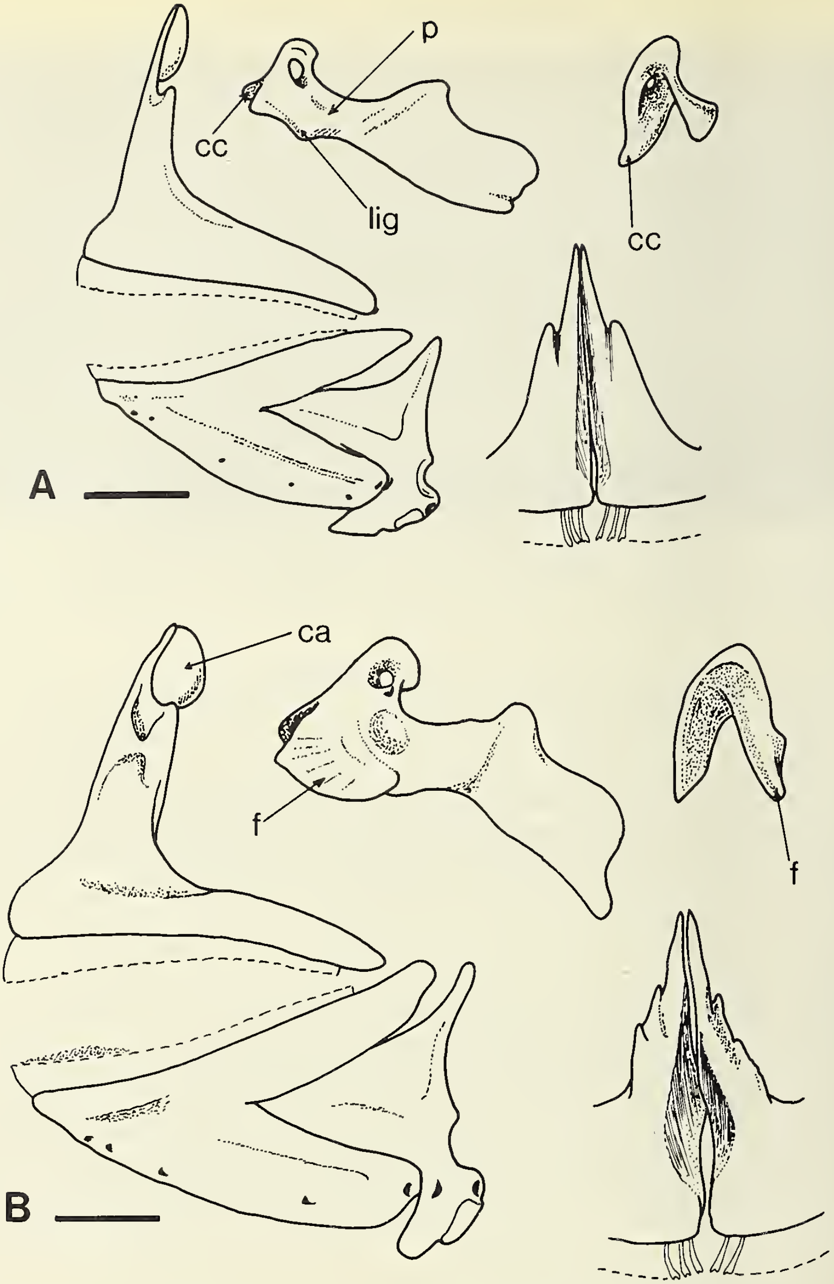

Fig. 175 Left upper and lower jaws of: A, *Oreochromis malagarasi*; B, *O. karomo*. The length of head, length from posterior edge of operculum to base of caudal fin and standard length of the two fishes are respectively: *O. malagarasi*: 56 + 132 = 188 mm; *O. karomo*: 60·5 + 113·5 = 174 mm.

The jaws are in lateral view (left), with the maxillae (above) and the premaxillae (below) in anterior views. ca = rostral cartilage; cc = cranial condyle of the maxilla; f = flange of maxilla in *O. karomo*; lig = place of attachment of maxillo-palatine and maxillo-nasal ligaments; p = knob of maxilla in front of surface for maxillary process of palatine in *O. malagarasi*, depression for the same process in *O. karomo*; ra = retroarticular. The shaded groove at the meeting of left and right premaxillae is filled with cartilage, but only the bony part is shown. A few anterior teeth are indicated in the front view of the premaxillae; in the lateral view the edge of the outermost row is shown by a broken line.

Fig. 176 *Oreochromis karomo*. Above, dentition of upper and lower jaws; below scanning electron micrographs of some of the teeth. (Both photographs, BMNH).

Coloration. Ground colour of non-breeding fishes olive, darker on the upper part of the body by reason of black centre to each scale. Three or four large, dark mid-lateral blotches, in preserved fishes often united by a vague band. Black spots associated with the openings of the lateralis system of the temporal region, the infraorbital canal and the vertical limb of the preopercular. Series of spots or stripes on the dorsal fin. Caudal covered with dark spots, in one preserved specimen in vertical rows, in the others more irregular or in quincunx and often mixed with pale spots.

Breeding males in life brilliantly coloured, giving a general impression of bright blue and orange, the orange colouring the margins of dorsal and caudal fins and the long genital papilla.

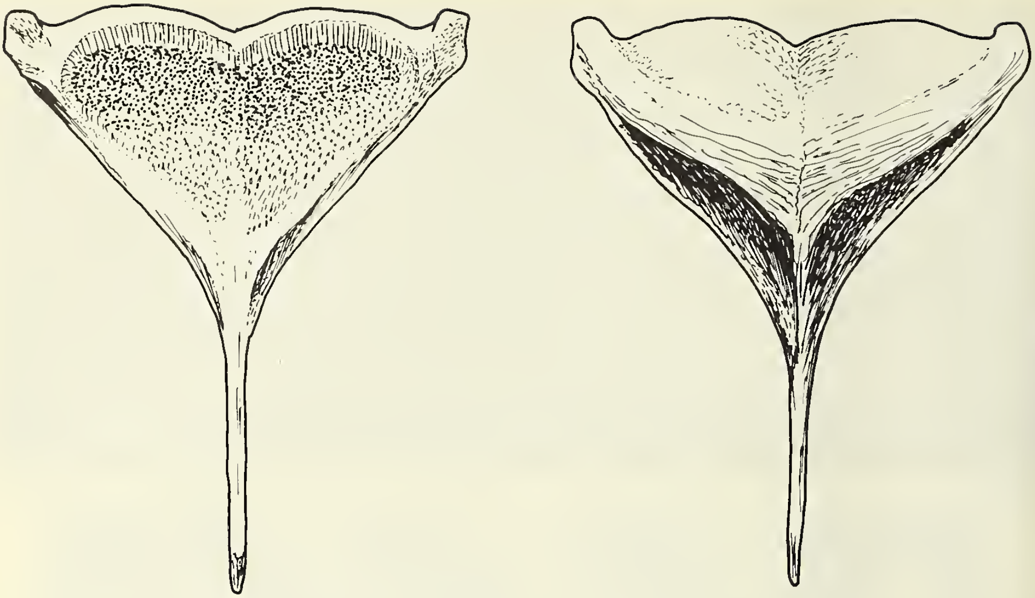

Fig. 177 *Oreochromis karomo.* Lower pharyngeal of a fish 125 mm SL.

General body colour blue-grey with purplish sheen, head blue-green with peacock-blue lips; the broad bands of teeth appearing pink. Pectorals grey, pelvics with blue markings and black leading edge; caudal and soft dorsal with light blue spots and streaks.

Mature females less brightly coloured, without the orange of the caudal margin, but with orange dorsal margin and below it oblique rows of whitish spots. Lips peacock-blue as in male; opercular spot violet (Lowe-McConnell, 1956*a*).

Poll (1948) describes the dorsal margin as carmine.

Ecology

Food

The breeding individuals observed spent little time feeding, but males were seen scooping up algal debris from the bottom, and occasionally they moved to the adjacent weed beds and rasped epiphytic algae. The latter method is one to which the dentition is well adapted.

Breeding

Breeding in the natural environment was described by Lowe-McConnell (1956*a*). A breeding colony was observed in August 1952 in the Malagarazi swamps at Katare, about 160 km upstream from the delta.

The genital papilla and nuptial coloration of males are described above. The breeding males observed were from 25 to 30 cm TL, the females all smaller, 18–25 cm.

A spawning arena occupied by about seventeen males in a space clear of vegetation, but surrounded by beds of water-lilies (*Nymphaea*), *Chara*, *Utricularia* and *Ceratophyllum*, was kept under observation. The water was clear and ½ to 1½ m deep and the nests (mating platforms), already complete when observations started, were here 3–4 m apart, except at the edges of weed beds, where two nests separated by a stand of plants might be as little as 2 m apart (cf. *O. mossambicus* in Lake Sibaya, p. 306).

Each mating platform was a circular area of fine sand surrounded by a low ridge on the top of a mound about 10 cm high. This was constructed and kept clean by the male. Around one platform a few small pits were seen, similar to those of *O. variabilis* and *O. macrochir*. Thys (1964:129) stated that the platform may be 10–15 cm in diameter and the mound 30 cm high with a base of 1 m. A well defined territorial area, such as is known in *O. macrochir* and *O. variabilis* was not observed by Lowe-McConnell, but its limits may have been inconspicuous because boundary fighting had almost ceased when observations began. Each male spent most of his time near the mating platform, quiescent at night, but starting at daybreak to clean and guard the nest, and from 1100 hrs onwards swimming out to any passing female and leading her to the platform. Individual males remained each by his own nest during the nine days of observation. If a male left his nest to seek shelter from a disturbance he would return to the same nest again, swimming near the surface with depressed dorsal fin as he passed rapidly over the territories of other males.

As in other species, females frequently swam in schools above the territories of males, and one would occasionally leave the shoal to swim down, when she would be led to the platform. Other females approached singly, swimming near the bottom.

On arriving at the centre the female mouths the nest, the male facing her and wagging nose and tail. The male then passes over the nest dragging his tassel. Probably the sperm is then emitted, but it is invisible in the water. The performance may be repeated before the female eventually lays a batch of eggs on the platform, in one case about 50 at a time. She immediately turns and picks them up in her mouth, while the male continues to drag his tassel over the nest, presumably fertilizing. Two, three or more batches of eggs may be laid by the same female before she leaves the nest, each batch being accompanied by the same sequence of movements. Such a normal spawning occupies no more than 5 minutes.

In another observed spawning the female went directly to one nest and laid almost immediately, the whole process occupying no more than two minutes. Lowe-McConnell (1956*a*) suggested that this might have been a return to a known nest.

At the other extreme, a visiting female was seen evidently not in a complete state of readiness, and although both partners went through the same motions repeatedly no eggs were laid. The male was in a high state of arousal and the process occupied a much longer time than usual.

The females with their mouths full of eggs retire to the shelter of the water-lilies to brood. The eggs are large, $5{\cdot}2 \times 4{\cdot}5$ mm in a 21 cm female, and larvae of 11 mm were found in the maternal mouth, still with large yolks. The length of the brooding period is unknown.

Numbers of 90–240 ripe ovarian eggs were found, depending on the size of the fish, and there were 3 or 4 sizes of eggs or oocytes in an ovary.

Young of 2–6 cm remain in schools in the shallows and schools of 6–15 cm juveniles were seen feeding among the nests.

Sex ratio. As in other species sex ratio is difficult to determine because of differential movements of the sexes. Lowe-McConnell records that catches taken at some distance from the spawning grounds included a great preponderance of males with quiescent gonads, whereas the few females found with them had ripe or ripening ovaries. This suggests schooling by size. At this size females, but not males, would be ripening and leaving the school for the spawning grounds.

Distribution

The delta and basin of the Malagarazi River, Tanzania. In the delta it was caught near the mud banks deposited by the river.

Bell-Cross & Kaoma (1971) recorded it from the Zambian waters at the southern end of Lake Tanganyika, but the Belgian expedition of 1946–7 did not find it outside the Malagarazi and the record needs confirmation.

The Malagarazi swamps and the important fishery there for this species, and *O. malagarasi* have been described by Macquarie (1940) and Hickling (1961:224).

Discussion

Relationships

The genital papilla and the type of nest relate this species to the tasselled group, including *O. macrochir* and *O. variabilis*. Its nearest relatives are probably *O. upembae* and the sympatric *O. malagarasi*, which also resemble it in the large lateral blotches. All these species differ from *O. karomo* in having a mouth and dentition conforming to the majority of *Oreochromis* species, but it is noteworthy that they have a tendency to replace some of the outer teeth with tricuspids.

Thys (1968*b*:xxxv) placed *O. karomo* in *Neotilapia* with *O. (Ne.) tanganicae*, but the only resemblances between them are the tricuspid, movable teeth and the geographcial propinquity. The differences between them are formidable, namely:

	O. karomo	***O. tanganicae***
Jaws	prolonged forwards	short and broad
Lower jaw % l. head	33·0–37·8	31·0–35·5 (38)
Length head % SL	35·8–38·3	31·7–36·0
Occipital crest	moderate	high
Vertebrae	29	31 (or 30)
Dorsal rays	mode 28	usually 29 or 30
Lower gill-rakers	18–20	22–26
Genital papilla	complex, tasselled in male	simple
Scales of belly	approx. same size as those of flank	very small, with abrupt change of size
Caudal fin	truncate	emarginate
Melanin pattern	large, black, midlateral blotches	facultative vertical stripes

In all these features except the large head and prolonged jaws *O. karomo* resembles *O. malagarasi*, which is sympatric with it, and it is clear that the similarity of its jaw teeth to those of *O. tanganicae* is an example of convergence. Similar teeth are present in other genera, notably *Petrochromis* and *Petrotilapia*.

Material examined

Museum & Reg. No.	SL(mm)	Locality	Collector or donor
BMNH			
1960.9.30.394 (paratype)	187	Delta of Malagarazi R.	Poll. Exped. Hydrobol. Tanganyika, V. 1947
1960.9.30.395–6	76, 78	Delta of Malagarazi R.	Poll. Exped. Hydrobol. Tanganyika, V. 1947
1967.3.16.14–15	187, 220	Malagarazi swamps at Katare	Lowe, 28. VIII. 1952
1971.6.23.80–88	124–195	Malagarazi swamps at Katare	Lockley

Oreochromis schwebischi (Sauvage)

Melanogenes microcephalus (*non* Günther and Bleeker); Sauvage, 1884:196, fig. (Franceville, Ogowe).

Hemichromis schwebischi Sauvage, 1884:198, pl.v, fig. 2 (Franceville, Ogowe).

Paratilapia schwebischi; Boulenger, 1898*b*:144 (on the type); Pellegrin, 1904:268 (type & another large specimen from Franceville); Boulenger, 1915*b*:365 (on the type).

Tilapia schwebischi; Trewavas, 1962*b*:178 (synonymy); Thys van den Audenaerde, 1964:102, pl. 2 & fig. 16 (Chiloango & Ogowe systems); *idem*, 1966:25, pl. 3 & fig. 2 (Ogowe); Daget & Stauch, 1968:42 (Kouilou & L. Cayo, Loémé); Trewavas, 1969:273 (Ivindo R., Ogowe system).

Tilapia (Loruwiala) schwebischi; Thys van den Audenaerde, 1968*b*:xxxvi.

Tilapia lata (part, *non* Günther); Boulenger, 1899*a*:125 (syn. *M. microcephalus* of Sauvage only).

Tilapia flavomarginata Boulenger, 1899*b*:123, pl. xlvi (Kalombo Lagoon, Mayombe, Chiloango system); *idem*, 1901:458 (same); Pellegrin, 1904:313 (Franceville, Ogowe); *idem*, 1906:469; *idem*, 1907*a*:37, fig. 4; *idem*, 1907*b*:557 (Ngomo, Ogowe); *idem*, 1908*a*:348 (Ngomo); *idem*, 1915:503 (Ogowe); Daget, 1960*a*:5 (lakes of Lower Ogowe); *idem*, 1961*d*:585 (Niari Kouilou); Loubens, 1965 (Lower Ogowe).

Tilapia heudeloti (*non* Deméril); Pellegrin, 1908*a*:348 (Ngomo); *idem*, 1930:202 (Passa, Ogowe) (lists only; det. Thys, probably on localities).

Tilapia andersonii (*non* Castelnau); Boulenger, 1912*a*:25 (Chiloango system); *idem* (part), 1915:171, fig. 110; David & Poll, 1937 (part):240 (Lubuzi-Lukula confluence).

Note on the synonymy

Pellegrin (1904:314) noticed the close resemblance between his '*T. flavomarginata*' of the Ogowe River and '*Hemichromis schwebischi*', but deferred provisionally to the definition of the genera based on the dentition and did not synonymize them. Parallel changes in the dentition of other species and specimens in an intermediate phase, supported by the field observations of Loubens (1964), enable us to recognize the synonymy.

The possibility that '*T. sanagaensis*' and '*T. boulengeri*' are related rather to '*O*'. *schwebischi* than to *Sarotherodon galilaeus* is discussed on pp. 121–122. For reasons given there and on pp. 493–4 they are not included in this synonymy.

TYPES. Holotype: ♂, 260+65 mm from Franceville, Upper Ogowe, coll. Schwebisch; MNHN 1884–492.

Holotype of *T. flavomarginata*: sex?, 223+61 mm, from Kalombo Lagoon, Mayombe, Chiloango system, coll. Cabra; MRAC 276; paratype ♂, 208+52 mm, data as holotype; BMNH 1899.11.27.95.

Distinguishing characters

Vertebrae 27–29, mode 28; scales in the lateral line series 28 or 29 (30). Lower gill-rakers 20–25. Caudal fin emarginate. Pharyngeal with fine and crowded teeth on a broad dentigerous area, with a long blade.

Mouth small in immature fishes, but in mature males preorbital bone and jaws enlarged and upper profile of head often concave. Outermost teeth bicuspid, and inner tricuspid in immature fishes and females; all teeth becoming unicuspid in mature males. Male genital papilla spade-shaped, not bifid. Margins of dorsal and caudal fins red in mature males.

The peculiarity of this species is that, except that the modal numbers of vertebrae and lateral line scales are lower, the characters listed in the first paragraph, as well as the general

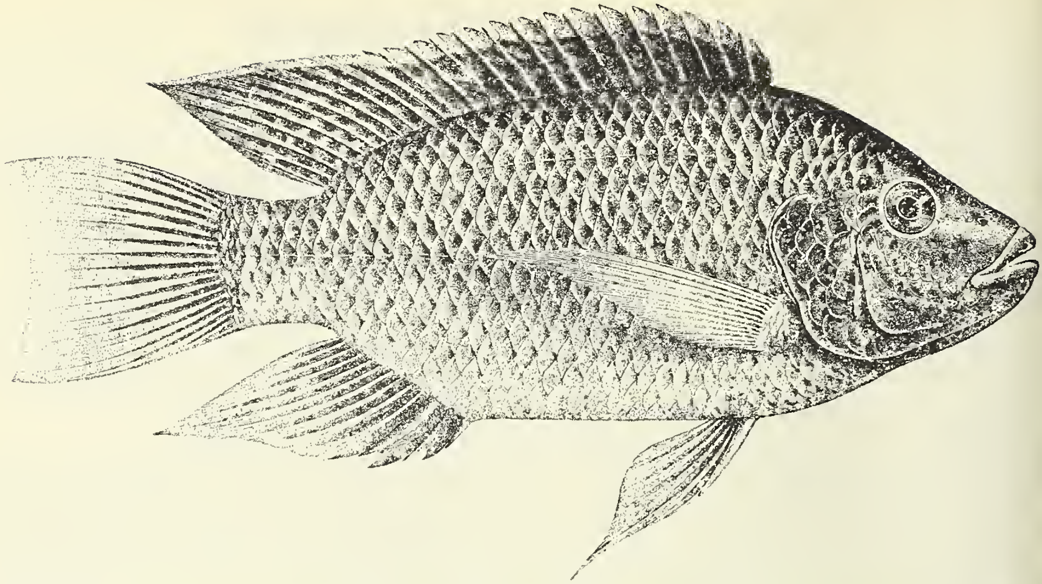

Fig. 178 '*Oreochromis*' *schwebischi*, holotype of *Tilapia flavomarginata.* From Boulenger, 1915, fig. 110.

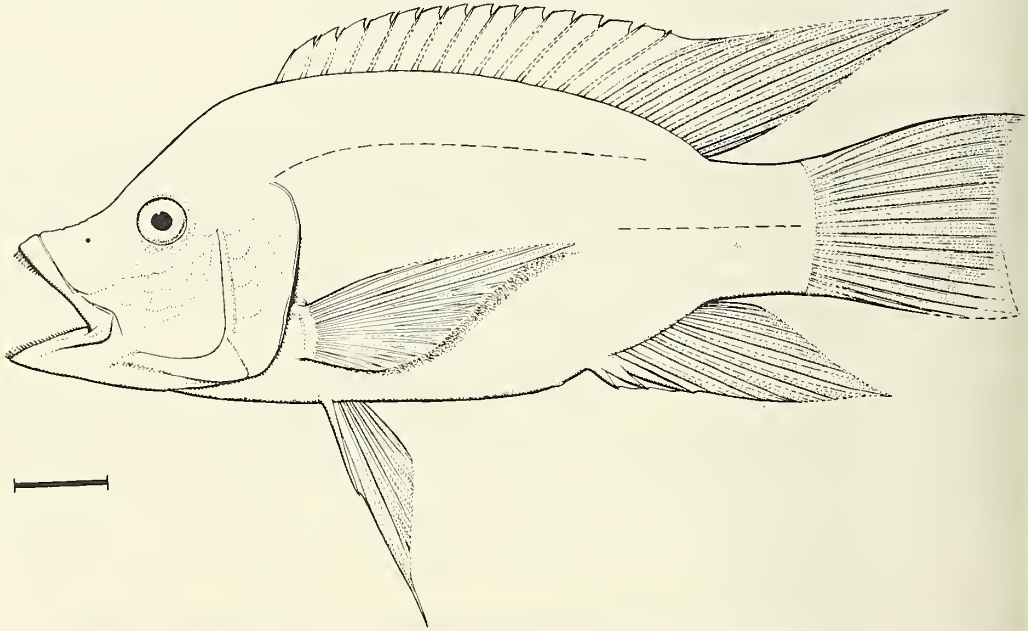

Fig. 179 '*Oreochromis*' *schwebischi* male, outline drawing from the holotype. Scale = 20 mm.

appearance, are those of *Sarotherodon galilaeus*, whereas the structures and coloration of the mature male and what is known of the breeding habits are characteristic of *Oreochromis*. Hence the uncertainty of the generic assignment.

The changes in the head of the mature male and its coloration also distinguish it from *Sarotherodon mvogoi*, which is present in the Ogowe system. *Oreochromis macrochir*, which has been introduced into ponds in Gabon and Congo, differs in having a bifid, tasselled male genital papilla as well as higher numbers of vertebrae and scales and a shallower preorbital bone. *Oreochromis andersonii* has more vertebrae (30–32) and scales in the lateral line series (31–35).

Description

Based on the types of both synonyms and on 14 other specimens of 95–196 mm SL from the Ogowe and Chiloango basins. Some details are added from Thys (1964 and 1966) and from Loubens (1965).

Proportions as % SL. Depth of body 42·5–49·5; length of head 34·0–38·0; length of pectoral fin 37·5–44·5; length of caudal peduncle 9·0–12·5, depth 15·4–16·8.

Caudal peduncle length/depth 0·6–0·85.

Proportions as % length of head. Length of snout 31·0–37·5 at SL up to 183 mm 41·0–45·5 in the four of 196–260 mm (probably all males); diameter of eye 17·5–27·0, negatively allometric; depth of preorbital bone 20·3–29·5, positively allometric, approximately equal to diameter of eye between 105 and 130 mm SL; interorbital width 33o40; length of lower jaw 28·5–32 in ♀♀ and young up to 156 mm SL and in the two ♂♂ of 180 and 182·5 mm SL, 34·5–38·5 in the four of 196–260 mm SL.

Upper profile of head straight in young, becoming slightly concave over the eyes at *ca.* 140 mm SL and markedly concave in large males.

Teeth in 3–4 series up to 150 mm SL, 4–6 above this size, 64–100 in outer row of upper jaw; outer bicuspid, with slender shafts and spoon-shaped crowns with a lateral notch, in specimens up to 183 mm SL; in the ♂♂ of 196 and 208 mm some upper are unicuspid, some evidently by wear, others by replacement. In the ♂ of 223 mm SL nearly all the teeth are unicuspid, many with unworn crowns. In the 260 mm holotype, probably a ♂, all teeth are simple and the mouth is greatly enlarged.

Gill-rakers on first arch (3–5) + (0–1) + (21–25) (20 in one of ten specimens examined by Thys, 1964; and in one of 32 examined by Loubens, 1965); most frequent number on the lower part 23 in the present samples and those of Loubens.

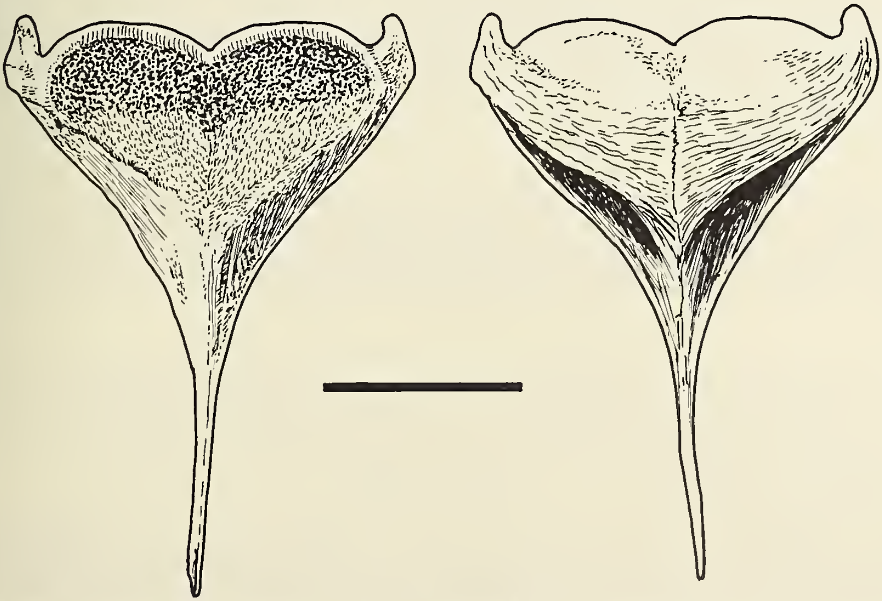

Fig. 180 *'Oreochromis' schwebischi*, lower pharyngeal bone of a fish 200 mm SL. Scale = 10 mm.

Lower pharyngeal bone longer than wide, its median length 35·5–40·0% length of head, width 29–34%; blade 1·2–1·85 times the length of the toothed area, which has broad lateral lobes and a short apex; teeth very slender, the posterior dark-tipped forming a definite transverse zone.

Vertebrae 27 (f.1) or 28 (f.7) (Loubens); specimens in BMNH 28 (f.6), 29 (f.1).

Scales of cheek in 2 or, more usually, 3 horizontal rows; in lateral line series 28–30, usually 29; between origin of dorsal and lateral line 3½–4; between bases of pectoral and pelvic fins 4 or 5; not much smaller on belly than on flanks.

Dorsal XIV 12 (f.1), XV 12 (f.4), XV 13 (f.11) or XVI 12 (f.1), thus modal total 28 (Thys, 26 or 27, mode 27, owing to different bias in counting soft rays).

Anal III 9–11, usually 10.

Pelvic fin reaching vent when laid back. Caudal slightly emarginate, not heavily scaled although the upper and lower rays are generally well covered with minute scales.

Genital papilla of male embedded in a pair of fleshy lobes, but not elongate or fringed in the specimens available; that of female short and slightly crenulate.

Size. Maximum standard lengths recorded are, ♂ 300 mm, ♀ 245 mm (see section on growth).

COLORATION. In life (Thys, 1966:28) generally pale with greyish back and olive snout (but lips paler); in mature male each scale of flank with a purple spot ('rouge-bleu', Thys; 'violacé', Loubens) at its centre; many black spots distributed on occiput and gill-cover, some of them at the apertures of the sensory canals of this region. Dorsal fin of male with a marginal band of yellowish colour, darkening to red at the edge—probably confined to this sex, to judge from a preserved female in which the margin is dusky as the rest of the fin. Caudal with red margin; anal dusky, sometimes tinted red at the lower margin. Spinous dorsal with narrow, pale oblique markings between the spines; soft dorsal with series of dark and pale spots; similar spots often on posterior part of anal. Caudal with some clear spots between the rays.

Younger fishes with 6–8 dark vertical bars on the body. A tilapia-mark is present still at 95 mm SL, present but fainter at 108 mm, absent above this size.

Ecology

The following summary of the ecology of this species is taken from Loubens (1965). M. Loubens was a member of the Brigade d'Hydrobiologie stationed at Lambarene, and this report was the result of observations made in 1960–62 in the lakes and river of the Lower Ogowe and recorded under the name of *Tilapia flavomarginata* before the synonymy of this name with *schwebischi* had been established.

Food

The intestine is very long, 10·8–14·8 (mean 12·5) times the SL in 29 specimens of 90–260 mm SL. There is no regular allometric trend, ratios of about 11·5 being found at 100, 195 and 260 mm. No detailed analysis of the food has been made. Stomachs contained algae, mainly unicellular or in short filaments. Brooding females usually fast.

Growth

There is no seasonal arrest of growth, the surface temperatures of the waters in this region remaining at 24–32°C throughout the year. Consequently, no annual zones are formed on the scales or bones by which growth-rate might be calculated. Even the brooding fast of the female leaves no mark on the scale.

The newly freed young at first add 6–9 mm to the length in 15 days, then (between 23 and 32 mm SL) continue at the rate of 6 mm in 15 days. Continued growth at this rate would give a SL of 145 mm in one year, a figure close to the average length of one-year-old females obtained by other means. Males grow more rapidly than females and from weak modes appearing in the dry season Loubens came to the following tentative conclusions:

Males at 1 year old are *ca.* 185 mm SL, at 2 years 245 mm.
Females at 1 year old are *ca.* 150 mm SL, at 2 years 185 mm.
Males of more than 270 mm and females more than 222 mm are rare. Maximum sizes observed were: ♂ 1,130 g and SL 300 mm; ♀ 630 g and SL 245 mm.

Breeding

Season. Breeding occurs mainly in the long dry season from June to September and in the short dry period in February. In the flood plain of the lower Ogowe the floods cover suitable nursery grounds with too great a depth of water and the shallower flooded grass-lands have no suitable substratum.

Nests are made on sandy or loamy bottoms in water 40–80 cms deep, or more sparsely in depths of a metre or more. They are circular basins of diameter 115–185 cm, about 20 cm deep in the middle with a rim raised 7–8 cm above the surrounding level. They are aggregated in suitable places and may be contiguous or even cut into one another. A smaller, cleaner area in the middle is probably the spawning place.

Diel movements. During the day the fishes take refuge in deeper places from the high temperatures and intense illumination of the nesting sites, and spawning occurs at night, as has been demonstrated by night fishing methods. The behaviour has not been observed.

Size of maturity. The minimum lengths at which 50% of individuals are ripe or spent are: ♀ 140 mm SL, ♂ 200 mm. The smallest ripe individuals caught in these localities were ♀ 125 mm SL, ♂ 175 mm.

Gonads. Ripe testes are white, 'Some millimetres' wide, and sinuous. Ripe ovaries are about 4% of the body weight. Eggs have a long diameter of 3 mm and are light chestnut in colour. The number of ripe ovarian eggs varies from 220 at 130 mm SL to 575 in one fish of 180 mm SL. The latter number was exceptionally high for a fish of this size and was not exceeded even by one of 205 mm, which had 540.

Oral incubation is practised by the female.

As in other species, ripening ovaries are found in brooding females. Allowing for this overlap, there is time in one season for a female to have up to three broods.

Pellegrin early recorded (1907*a* & *b*) buccal incubation by the female in this species in the lower Ogowe. From the observations of the collector (Haug), he recorded a breeding season from August to the beginning of October. Some of his dimensions diverge a little from those of Loubens: eggs 3·5–4 × 2·5–3 mm; nests 30–100 cm in diameter, 10–30 cm deep, excavated on a bottom of sand or clay at a depth of 20–60 cm. A female of 230 mm TL carried about 100 yellow eggs in the mouth; her ovaries were flaccid and contained oocytes of various dimensions not exceeding 1 mm.

Young. Two young of respectively 22 and 30 mm SL from Boué, Ogowe, probably belong to this species. The 30 mm specimen has 29 scales in the lat. line series, D XV 13 and 19 lower gill-rakers, perhaps not yet the full complement. Both are silvery with 5 or 6 short grey vertical bars on the back and a strong tilapia-mark. They were caught in a small pool near the river.

Distribution

Upper and lower Ogowe and its tributary the Ivindo; Chiloango system; Niari Kouilou.

Discussion

Relationships

Before sexual maturity preserved specimens are indistinguishable from *Sarotherodon galilaeus.* Fig. 181 shows that at this stage there is no significant difference in the proportions of interorbital

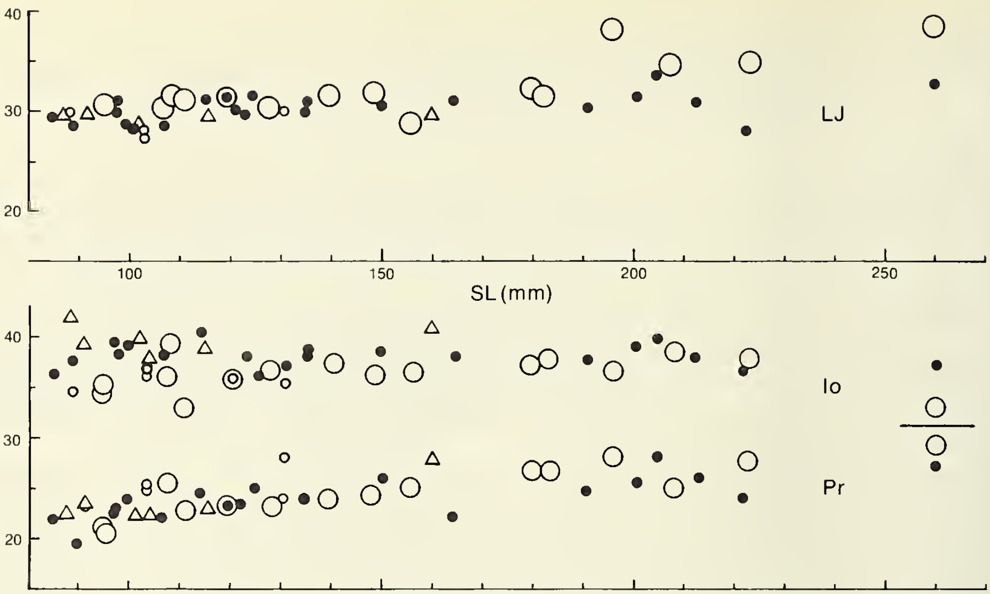

Fig. 181 Proportions as % length of head in *Sarotherodon g. galilaeus* (●), *'Oreochromis' schwebischi* (○) and *S. g. boulengeri* (△). Four Sanaga fishes of 88, 104, 104 and 131 mm SL are indicated by small circles (○). The graph shows that in depth of preorbital (Pr) and interorbital width (Io) there is no significant difference between *S. g. galilaeus* and *'O' schwebischi*. These are also alike in length of lower jaw (LJ) up to SL 156 mm, but males of *'O' schwebischi* above this size have longer jaws than *S. g. galilaeus*. The specimens of *S. g. boulengeri* of 88–160 mm SL agree with both species, but their interorbital ratios are among the greatest, partly because of the short head (see Table 100).

width, depth of preorbital bone and length of jaws. The dentition of jaws and pharynx is also identical in the two species. The detailed likeness in shape of both the lower pharyngeal bone and its teeth is especially striking. In life there is probably a distinction in colour, and modal numbers of vertebrae, scales and dorsal spines are lower (but the samples are small).

At sexual maturity the males diverge markedly. Figs. 179 & 181 show the enlargement of the jaws in males above 156 mm SL, and in these the teeth become firm and unicuspid, a condition never encountered in *S. galilaeus*. These changes, with the orange margin of the dorsal fin and the large testes, are features characteristic of *O. (Oreochromis)*. Only maternal mouth-brooding is recorded, but whether the behaviour of the sexes at the mating pits is *Oreochromis*-like is unknown.

The resemblance to *S. galilaeus* and the geographical location are against the inclusion of *schwebischi* in *O. (Oreochromis)*, and the absence of a genital tassel is against its inclusion in *O. (Nyasalapia)*. The species is perhaps best regarded as a *Sarotherodon* that has developed reproductive features largely paralleling those of *Oreochromis*.

On page 121 the question is posed: is *S. sanagaensis* a peripheral population of *S. galilaeus* or a northern extension of the range of *O. schwebischi*? The answer depends on details so far unknown of the structure and habits of sexually mature *S. sanagaensis*.

The same doubt surrounds the status of *S. boulengeri*.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
MNHN 1884–92 Holotype	260	Franceville, Ogowe	Schwebisch
MRAC 276 Holotype of *T. flavomarginata*	223	Kalombo Lagoon, Mayombe, Chiloango system	Cabra
1899.11.27.95 Paratype of *T. flavomarginata*	208	Kalombo Lagoon, Mayombe, Chiloango system	Cabra
1912.4.1.546	183	Luali R. at Buco Zau	Ansorge
1912.4.1.547	180	Lebuzi R. at Lala Muno	Ansorge
1912.4.1.548	96	Luculla R., Chiloango system	Ansorge
1912.4.1.549	120	Lebuzi R. at Boma Vonde	Ansorge
1909.7.27.56	196	Ngomo, Ogowe	Haug
1961.12.4.8	108	L. Ezanga, lower Ogowe	Daget
1967.10.12.41–42	22, 30	Boué, Ogowe	Cambridge West African Expedition
1969.4.15.2–3	108	Makokou,Ivindo R.	Géry
ANSP 38549	107·5	Lebuzi R. at Kaka Muno	Ansorge
MRAC 1742–3	128, 149	Lebuzi R. at Kaka Muno	Ansorge
MRAC 41767–9	95–140	Confluence of the Lubuzi & Luali Rs	Dartevelle
MRAC 52979	156	Luali R., Chiloango system	Dartevelle

Subgenus *NEOTILAPIA*

Oreochromis tanganicae

Oreochromis (Neotilapia) tanganicae (Günther)

Chromis tanganicae Günther, 1894*b*:630, fig.
Tilapia tanganicae; Boulenger, 1898*a*:5; *idem*, 1899*a*:113; Trewavas, 1946:241; Poll, 1946:350; *idem* 1956:36, figs 5, 7, 8, pl. II figs 1–3, pl. X, fig. 1; Thys van den Audenaerde, 1964:121, fig.21, pl. XI.
Neotilapia tanganicae; Regan, 1920:38; David, 1936:155; David & Poll, 1937:268; Poll, 1946:276, 350, pl I, fig. 13.
Tilapia (Neotilapia) tanganicae; Thys van den Audenaerde, 1968*b*:xxxv.
Petrochromis tanganicae; Boulenger, 1901*a*:480; *idem*, 1901*c*:158; Pellegrin, 1904:351; Boulenger 1915:268, fig. 182; *idem*, 1920*b*:47; Borodin, 1936:27.
Sarotherodon tanganicae; Brichard, 1978:272.
Petrochromis andersonii Boulenger, 1901*b*:13; Pellegrin, 1904:351; Boulenger 1907*a*:535, pl. XCVI; *idem* 1915:269,. fig. 183; Borodin, 1936:27.
Neotilapia andersonii; Regan, 1920:38.
Haplochromis fasciatus (*non* Perugia) Borodin, 1931:49; *idem*, 1936:18, pl. I, fig. 6.
Tilapia nilotica (part, *non* Linn.); David, 1936:155.

TYPES. Syntypes: two young, 70+18 and 75+20 mm, 'Lake Tanganyika'; coll. Coode-Hore, BMNH 1889.1.30.7–8.

Holotype of *Petrochromis andersonii*: male, 350+82 mm erroneously attributed to Lake Albert, coll. J. E. S. Moore, BMNH 1906.9.7.48.

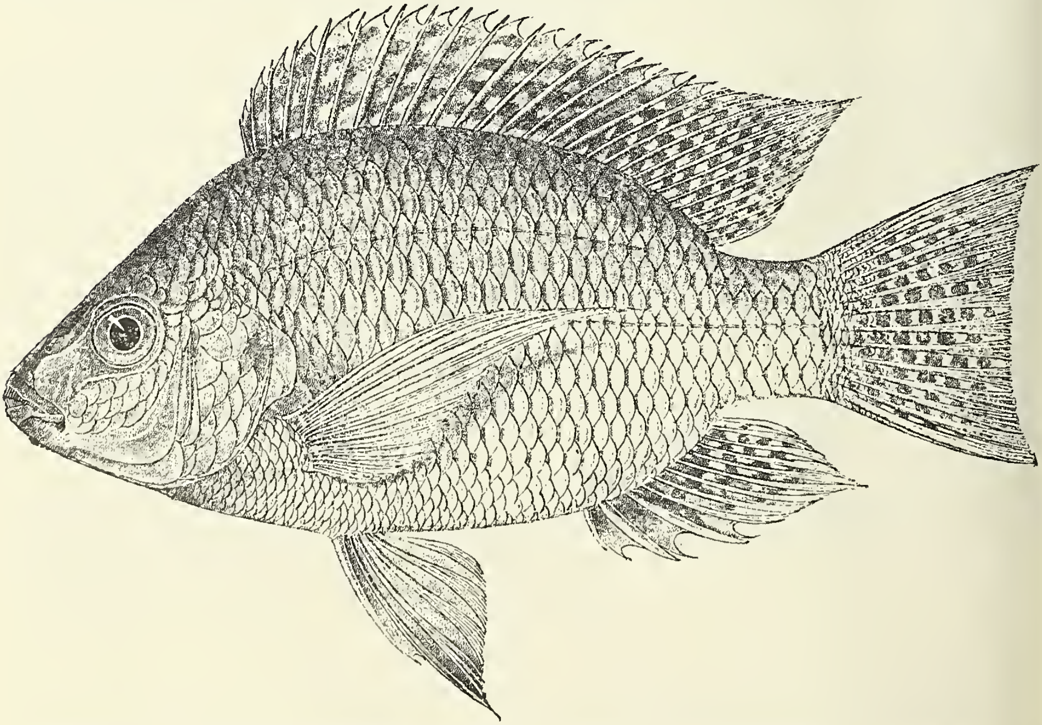

Fig. 182 *Oreochromis (Neotilapia) tanganicae*, 176 mm SL. From Boulenger, 1915, fig. 182.

Syntypes of *Haplochromis fasciatus*: two young, 42+10 and 49+11 mm, Ujiji, Lake Tanganyika, coll. Loveridge. MCZ 32622.

Distinguishing characters

Teeth in up to ten irregular rows with slender shafts and broad curved crowns, all tricuspid at sizes above 70–120 mm SL; below 70 mm outermost row bicuspid.

Jaws not prolonged, the lower short and broad, 31·0–35·5% length of head (38 in a large male), the premaxillary pedicels 22·8–25·0%.

Preorbital bone deep, 24–29% length of head in fishes of 100–310 mm SL, to 30·3% in one of 350 mm.

Body deep, depth 43·5–51·0% SL.

Scales of chest and belly very small but imbricating.

Melanin pattern of body in facultative vertical bands of constant width, not extending to the ventral surface, usually invisible in large preserved fishes. Vertical fins spotted.

Lower gill-rakers 22–26.

Vertebrae 31 (f.10) or 30 (f.1), 16+15 or 15+15.

Description

For proportions and main meristic numbers see Tables 113 & 114, and Fig. 182.

The teeth, with their long slender shafts (5 mm in the 350 mm fish) are similar to those of *O. karomo*, but are arranged parallel to the edge of the jaw in irregular, close-set rows. In the young the outermost row in both jaws consists of bicuspid teeth. These gradually become replaced by tricuspids, beginning with the lower jaw, then the mediad teeth of the upper and finally all the outer teeth. The first tricuspid replacement teeth are asymmetrical, the mediad cusp being smaller than the laterad. In older fishes there are two or three rows on the outer side of the lower lip; they appear to have been pushed on to the outer side of the jaw by the expansion of the tooth-band. They are shorter than those of the third or fourth row, which now take their place on the edge of the jaw. Some fishes are preserved with the mouth wide open as it would be when pressed against a flat surface to mow the algal growths.

The pharyngeal teeth are small and crowded, but the posterior are compressed and have a distinct shoulder. They are less slender and reduced than those of *S. galilaeus*. The toothed area is heart-shaped (Fig. 183). In a fish of 120 mm SL the median length of the lower pharyngeal is 35% length of head, 1·2 times the width and the blade is 1·3 times the median length of the toothed area. The corresponding ratios in one of 218 mm SL are 40·4, 1·9 and 1·65.

Gill-rakers (3–4)+(1–2)+(22–26). Microbranchiospines on the outer sides of arches 2–4.

Scales in the lateral line series almost constantly 33, 32 in only two of twenty-one counted*; 4½ between origin of dorsal and lateral line; 16–18 around caudal peduncle. Transition between the small scales of chest and belly and the bigger flank scales rather abrupt.

Dorsal fin rather high, the last spine measuring 15·5–17·0% SL in fishes of 100–230 mm SL, about 14% in those over 300 mm, the third anal 11·5–15·8% in the same group. Longest soft dorsal rays prolonged in mature male to a vertical about half way along the caudal. Caudal emarginate.

The maximum size reported by Poll (1856:38) is 38 cm and 1050 g. This is exceeded by the type of *P. andersonii*, of which the TL is 43 cm, SL 350 mm.

Coloration. The general colour is greenish, white on the belly, and there are both dark and pale spots on the vertical fins. Each scale carries a brownish or pink spot (Poll, 1956), and has an iridescent margin (Thys, 1964). The photo on p. 272 of Brichard (1978) shows a young fish with pink, black-tipped dorsal lappets.

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*In a bigger sample Poll (1956) also found two with 31 and eight with 34. The mode was 33.

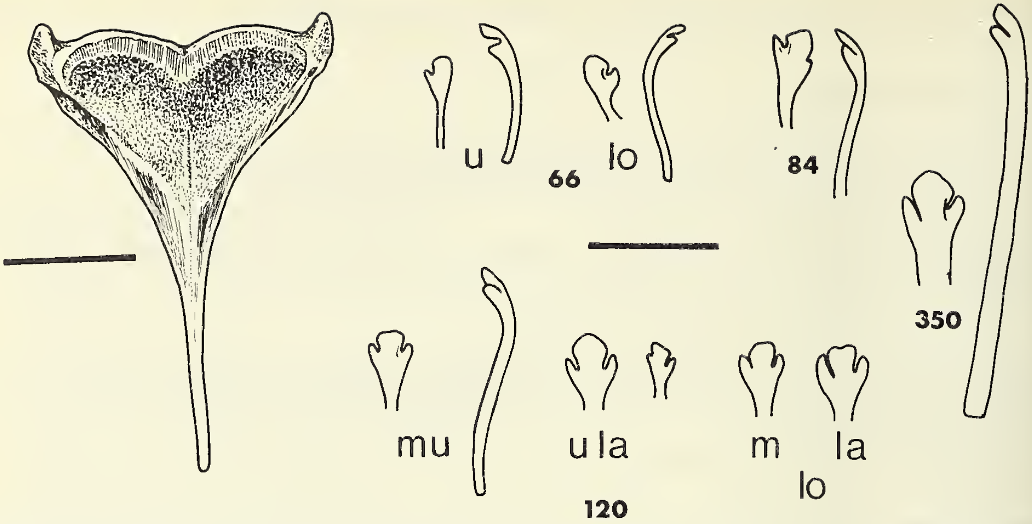

Fig. 183 *Oreochromis (Neotilapia) tanganicae*, lower pharyngeal of a fish 260 mm SL (scale = 10 mm); and teeth from the outermost row of the jaws to show replacement of bicuspids by tricuspids. The numbers give SL in mm of the respective fishes. u = upper jaw; lo = lower; m = middle part of jaw; la = lateral. Of some teeth only the crowns are figured. Scale = 1 mm.

Fig. 184 *Oreochromis (Neotilapia) tanganicae*, depth of preorbital bone as % length of head.

Table 113. Proportions in samples of *O. tanganicae.*

SL	90–110	117–230	310	350
N	5	11	1	1
Proportions as % SL				
Depth	43·4–46·0	43·5–51·1	43·8	44·0
L. head	34·3–36·0	31·7–34·5	35·4	33·4
L. pect. fin	38·0–42·0	39·8–44·3	43·4	43·2
L. caud. ped.	13·2–14·6	11·5–14·6	12·7	14·4
D. caud. ped.	13·5–15·7	13·8–16·4	15·2	15·6
Caud. ped. l/d	0·9– 1·0	0·7– 1·0	0·8	0·9
Proportions as % l. head				
L. snout	36·6–42·5	38·0–46·4	42·0	44·5
Eye	22·7–27·3	21·0–26·2	19·6	18·8
D. preorb.	23·6–24·9	24·5–29·0	28·5	30·3
Interorb.	39·0–41·0	39·8–46·3	41·5	42·3
L. lower jaw	31·4–35·5	31·0–34·5	31·0	38·0
L. premax. ped.	23·7	23·8–25·2	22·8	—

Table 114. Dorsal rays in *O. tanganicae* (frequencies).

		BMNH	Poll, 1956		BMNH	Poll, 1956
XVI	12	3		Total D. rays		
XVII	11		1	28	3	1
XVI	13	10	36	29	10	37
XVII	12		1	30	18	18
XVI	14	11	10	31	3	
XVII	13	6	8			
XV	15	1				
XVI	15	3				

Ecology

Food

Poll (1956) reports seeing this species on two occasions browsing the surface film of sheltered waters. Stomachs contained large quantities of the diatoms *Pinnularia* and *Navicula* with some sand-grains. The dentition, however, seems suited to rasping filamentous blue-green algae from submerged surfaces.

Breeding

Poll (1956) records that catches off sandy beaches included brooding females of TL 23–35 cm (i.e. 180–290 mm SL). Alevins of 12–20 mm were found in the mouths, and at 14 mm the yolk sac was resorbed. Young of 13 mm were found swimming freely, so possibly the bigger ones were at the stage of temporary return. Broods of up to 307 alevins were counted, but were believed to be incomplete. Poll had no information on nests or male coloration. Thys (1964) writes that the nest is a shallow pit.

Adults in the BMNH have had the viscera removed, but those in which the genital papilla is not destroyed, including the large male of 42 cm TL (350 mm SL) have a small genital papilla. In one of 38 cm the 4·5 mm long papilla has a small distal notch, in others it is simple. There is therefore no evidence of a tassel or even an enlarged papilla. Although Poll found brooding areas in water of less than 10 m depth, spawning sites have not been located.

Distribution

Lake Tanganyika, in the coastal areas and river mouths.

Discussion

Relationships

Reasons are given on page 488 for rejecting the claim of Thys (1963, 1964, 1968*b*), based on the dentition and geographical propinquity, that the species bears a special relationship to *O. (Ny.) karomo*. Although in both species the jaw teeth are tricuspid in adults, the jaws in *O. (Ny.) tanganicae*, instead of being longer than in other tilapias, as in the case in *O. karomo*, are short and more transverse. Nor is there any reason to place it in subgenus *Nyasalapia*, no elaboration of the genital papilla having been observed.

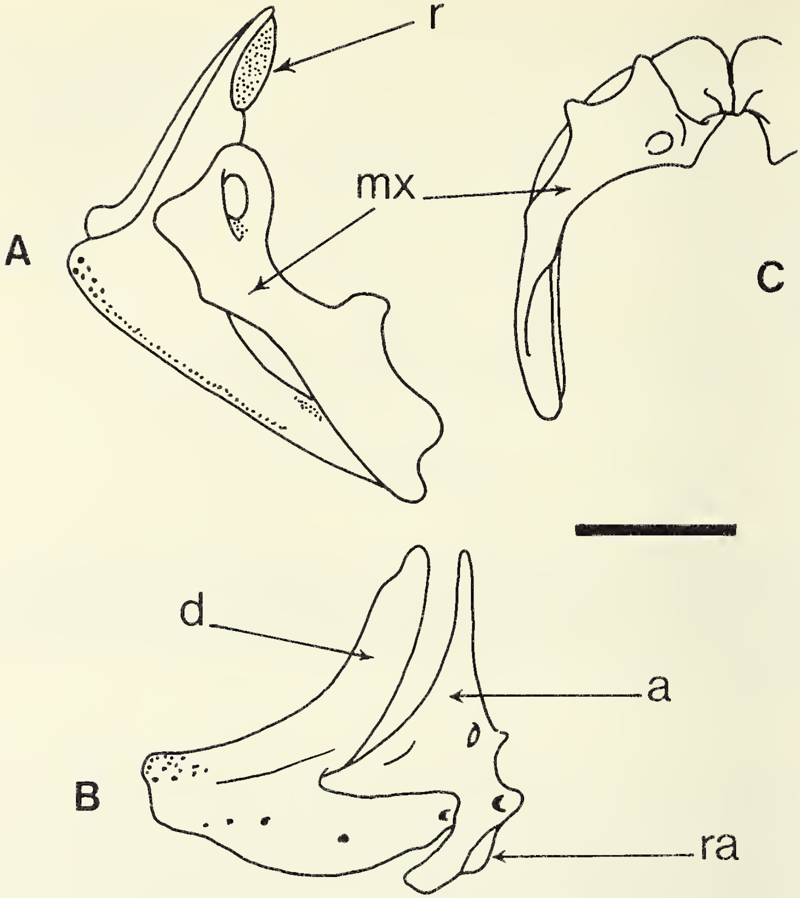

Fig. 185 *Oreochromis (Neotilapia) tanganicae.* Lateral views of A, left upper and B, lower jaws of a fish 140 mm SL; C, dorsal view of left upper jaw and part of right. The areas of implantation of the teeth are indicated. Scale = 5 mm.

Boulenger (1901*a*) placed this species in *Petrochromis,* a Tanganyikan genus of rock fishes whose four species do not exceed a TL of 20 cm. Boulenger's action was based on the tricuspid teeth of *Petrochromis,* and the presence of both in Lake Tanganyika. Regan (1920), giving only brief detailed reasons, realized the general resemblance of *O. tanganicae* to the tilapias and placed it with this group with a new generic name.

Petrochromis has in common with the tilapias (and several other genera) two features believed to be plesiomorph within the Cichlidae, namely:

1. A pharyngeal apophysis of the base of the skull with facets formed from the parasphenoid alone.
2. The ventral vertebral spine for the attachment of the anterior end of the swimbladder and the posterior attachment of the pharyngeal retractor muscles is based on the third vertebra. I have verified this in only two specimens, one *P. fasciolatus* and one *P. polyodon.* In both there is also a slender buttress from the fourth vertebra on one side only, a condition that is also found as an exception in *Sarotherodon* (Fig. 5).

The specialized characters shared by *Petrochromis* and *Neotilpaia* are:

1. All jaw teeth tricuspid, in broad bands.

2. Jaws, including the premaxillary pedicels (ascending processes) short and wide, capable of wide opening bringing both upper and lower into the same vertical plane so that they can be pressed against a flat surface of rock or plant.
3. Fine, crowded pharyngeal teeth on a broad dentigerous area.
4. Very small scales on chest and belly.

Even these specializations have, on inspection, weakened claims as indicators of relationship.

1. The outer teeth become tricuspid in *O. (Ne.) tanganicae* only from 70 mm SL, in *Petrochromis* they are tricuspid from the beginning, at least from 45 mm SL. Also the cusps are more nearly equal than in *O. (Ne.) tanganicae.* Bands of tricuspid teeth are found also in *Petrotilapia* of Lake Malawi and in *O. (Nyasalapia) karomo*, in both of which there are reasons for regarding their development as examples of convergence.
2. This method of using the jaws characterizes also *Petrotilapia*, and is within the repertoire of many species with bicuspid outer teeth, e.g. *Pseudotropheus* spp., *Sarotherodon lohbergeri, Oreochromis niloticus, O. (Ny.) karongae.* Moreover, the shape of the jaws differs in detail, notably, in *Petrochromis* the maxilla is so much twisted that its palatine shelf is nearly horizontal, whereas the slope in *O. (Ne.) tanganicae* and other tilapias is about 45°.
3. There are many independent examples of this type of pharyngeal dentition, e.g. *Sarotherodon galilaeus, O. (Nyasalapia) saka, O. (Oreochromis) jipe* and species of *Pseudotropheus.*
4. The small size of the scales of chest and belly is a character found in several lineages. It is especially characteristic of rock-fishes and dwellers in rapids, although it is not confined to them. In the present study it has not been given a rigid significance. On page 35 its association with a habitat of shallow, warm, alkaline waters is considered to detract from its value as an indicator of relationships. But in the *Oreochromis* of Kilimanjaro and the Pangani (pp. 357 ff) its linkage with other similarities (high meristic numbers, coloration, geographical association) as well as with adaptive differences, allows it to be used as one of the characters defining the group. (It has even been used by Greenwood, 1979:294, as the sole apomorphy defining a genus of geographically scattered species of haplochromines, an action of desperation in a difficult group.) However, there are at least some cases in which it is a matter of convergence and, as between *Petrochromis* and *Neotilapia*, I would consider it to have no value at all as an indicator of relationship, in face of the many differences.

The peculiarity of squamation in *Petrochromis* extends to the cheek, on which the scales are mostly non-imbricating and usually fail to cover the cheek. In *O. (Ne.) tanganicae* the cheek is well covered with three rows of scales as in other tilapias.

In addition to the flaws in the superficial resemblances, further examination of the anatomy of *Petrochromis* and *Neotilapia* shows many differences, in which *Neotilapia* is a typical tilapiine and *Petrochromis* diverges. Among them may be mentioned the supraoccipital crest, which in the tilapias is high, with a near vertical posterior edge, in *Petrochromis* low with the posterior edge sloping upwards and forwards; the parietal crests, which in *Petrochromis* end over the middle of the orbits, in tilapias extend more anteriorly; the ethmoid region, strongly decurved in *Petrochromis,* gradually sloping in the tilapias; the nasal bone, almost rectangular in *Petrochromis,* with a marked lateral wing in the tilapias (the last also noted by Regan).

Petrochromis also has only 10–15 lower gill-rakers, and only one gonad develops.

In sum, Regan's dissent from Boulenger's view of the relationship of *O. (Ne.) tanganicae* and his grouping of the species with the tilapias is amply justified.

With regard to its relationship within the tilapiines we are still in the dark. No species of *Sarotherodon* or of subgenus *Nyasalapia* has very small ventral scales. Slender, crowded pharyngeal teeth on a broad bone are found in *Sarotherodon* and also in subgenera *Oreochromis* and *Nyasalapia.* The high gill-raker numbers and the deep preorbital bone can be matched in *Sarotherodon* and in subgenus *Oreochromis.* The important reproductive and parental habits are still unknown. The retention of a distinct subgenus for this species only is justified in the present state of our knowledge.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
BMNH			
1889.1.30.7–8 (syntypes)	70, 75	'Lake Tanganyika'	Coode-Hore
1906.9.6.155	238	Kilambo	Moore
1906.9.7.48 (holotype of *Petrochromis andersonii*)	350	'Lake Albert' (error)	Moore
1906.9.8.256	173	Nyamkolo	Cunnington
1906.9.8.257	150	Kituta	Cunnington
1919.1.16.126			
1919.2.25.34–36	81–102	Albertville	Dhont De Bie
1920.5.25.97–103	20–33	Uvira, L. Tanganyika	Stappers
1920.5.25.128–130	29–35	Mth of Lobozi R.	Stappers
1920.5.25.133	265	Kilewa Bay	Stappers
1960.9.30.173–369	16–233	L. Tanganyika (various localities)	Explor. Hydrobiol. Lac Tanganyika (1946–7) Exchange from MRAC
1967.3.16.13	163	Kigoma	Lowe-McConnell
1980.9.25.1–63	18–51	Usumbura	Christy, 1927
1980.9.25.64	50	Kala	Christy, 1927
1980.9.25.65–69	34–55	Mpulungo Nyamkolo	Christy, 1927
1980.9.25.70–72	49–56	Kirando	Christy, 1927
1981.1.16.55–56	45, 48	Burton Gulf	Christy, 1927
1981.1.16.1–54	25–164	L. Tanganyika	Christy, 1927
1981.1.16.57–79	84–310	L. Tanganyika	Christy, 1927
1981.1.16.100–108	125–310	L. Tanganyika	Christy, 1927
MCZ 32622 (syntype of *H.* fasciatus Borodin)	42, 49	Ujiji, L. Tanganyika	Loveridge

Genus *DANAKILIA*

Danakilia franchettii

DANAKILIA Thys

Tilapia (Danakilia) Thys van den Audenaerde, 1968*b*:xxxv. Type by original designation *Tilapia franchettii* Vinciguerra, 1931:105.

The generic characters are listed on p. 32 for comparison with those of *Sarotherodon* and the subgenera of *Oreochromis*. They are also those of the one included species, and are listed here in a different order.

1. Outer as well as inner teeth of the jaws tricuspid, but not with long slender shafts.
2. Preorbital (lacrimal) bone deep, its depth 20·5–26·3% length of head at 38–74 mm SL. Snout correspondingly long.
3. Lower pharyngeal bone short, its median length 27–32% length of head at 45–74 mm SL; blade shorter than dentigerous area. Pharyngeal teeth fine in young, but in adult including a group of enlarged, flattened teeth.
4. Lower gill-rakers 10–12; on whole arch 13–16, mode 15.
5. Vertebrae 27 (N=5). Spondylophyseal apophyses involving the second and fourth as well as the third (one specimen).
6. Scales in lateral line series 27–28 (25 in one).
7. Dorsal spines XIII–XV, total dorsal rays 23–25, mode 24.
8. Scales of chest and belly very small, non-imbricating but contiguous.
9. No microbranchiospines.
10. Mouth-brooders, with few and large eggs reaching a long diameter of 3·5 mm.

D. franchettii inhabits Lake Afrera (Giulietti) and the adjoining swamp in the Danakil depression near the shore of the Red Sea, at 13°28′ N and approx 40°40′ E (see Fig. 12).

The only other fish reported from these waters is *Aphanius dispar* (Rüppell).

Relationships

Roberts (1975:314) cited me as considering *D. franchettii* to be related to *Sarotherodon galilaeus*, but the discovery of *Iranocichla hormuzensis* Coad, 1982, in southwestern Iran has thrown new light on the significance of the characters listed above. Although at present separated by the arid Arabian peninsula, the mutual relationship of the two species is geographically the most likely (see Coad, 1982:35). With insufficient knowledge of *D. franchettii* Coad suggested a relationship between *I. hormuzensis* and *Tristramella*, a genus of the Jordan Valley and the waters of Damascus. This is a suggestion worth investigation for both *I. hormuzensis* and *D. franchettii*, but the most obvious relationship of these is with each other.

The characters pointing to this relationship are numbers 2, 3 and 4 of the list (above). The long snout, involving a deep preorbital bone, is common to both species and is unusual in such small fishes. Important features of the lower pharyngeal are: the stout dentigerous part of the bone and the short blade; the shape of the pharyngeal teeth, those immediately in front of the posterior row being bevelled in the young, but in the adult either including a central group of enlarged flattened teeth (*D. franchettii*) or being wholly replaced by large flattened teeth forming a pavement (*I. hormuzensis*). In *Tristramella* the two characters appear in different species, the long snout in *T. sacra*, a group of enlarged pharyngeal teeth in *T. magdalenae* and *T. simonis intermedia*.

Character 5 may be compared with Table 3 of Coad (1982), which shows variation among ten specimens of *I. hormuzensis* in the involvement of vertebrae 3 to 5 in the spondylophyseal apophyses. The single specimen of *D. franchettii* dissected by me at least shows that this apophysis is not confined to the third vertebra. Steinitz & Ben-Tuvia (1960) described the variation in this feature in *Tristramella*. Seeing that there is also some variation in *Sarotherodon* (p. 10 above) this character has only a supporting role, unless indeed it points to *Sarotherodon* as a near relative of *Tristramella*.

If the relationship of *D. franchettii* and *I. hormuzensis* be accepted, the meristic numbers (characters 4–7) can be interpreted in its light. The numbers of vertebrae, lateral line scales, dorsal spines and totals are all lower than those of *I. hormuzensis*, which has respectively 28–30 vertebrae, mode 29; XIV–XVI dorsal spines; 14–19, mean 16·2, gill-rakers on the whole first arch. The number of scales in the 'lateral series' given by Coad is not strictly comparable with my count, but is in any case higher than in *D. franchettii*. These are differences of the same kind as those characterizing populations of thermal and alkaline waters in comparison with their putative related forms (pp. 33–4). The waters inhabited by *I. hormuzensis* are mostly saline and the air temperature is high throughout the year, but, as described below, *D. franchettii* occupies the narrow zone where both temperature and salinity are close to the limits of tolerance, and this is sufficient to explain the low meristic numbers.

Character 9, absence of microbranchiospines, also seems to be ecologically conditioned (p. 34). An age (or size) factor may operate, but microbranchiospines are present in equally small *I. hormuzensis*.

Character 8, the squamation of chest and belly (and nape), is more variable in *I. hormuzensis* than in *D. franchettii* and the cheek in *I. hormuzensis* is never completely scaled. In this feature, as in the pharyngeal dentition, *I. hormuzensis* is more specialized than *D. franchettii*, but the trend in both is the same. (See p. 35 for ecological correlations with this feature).

Both species are mouth-brooders, but no data are available as to whether they are arena spawners like *Oreochromis*, or form a pair-bond like *Sarotherodon* and probably *Tristramella*.

Finally, the outermost jaw-teeth of *I. hormuzensis* are bicuspid and the tricuspid shape of the teeth of *D. franchettii* (character 1) remains unique. By anology with the tricuspid teeth in species of *Oreochromis*, this should be regarded as a specific character, leaving no reason to consider *Iranocichla* and *Danakilia* as separate genera.

The morphological evidence of relationship is supported by the zoogeography of the region. *Aphanius dispar* is a euryhaline cyprinodont inhabiting waters of varying salinity near the coasts of the Red Sea, along the southern part of the Arabian peninsula, around the Gulf of Oman and the Persian Gulf. Related, isolated populations have been recorded from localities near the western shore of the Dead Sea (Steinitz, 1951*c* & 1953). It is one of the species associated with *Iranocichla hormuzensis* in southwestern Iran. The other fishes found by Coad in these streams are: the euryhaline marine species *Boleophthalmus boddarti* and *Chanos chanos*, and the freshwater cyprinids *Garra* cf. *persica* and *Cyprinion watsoni*. Species of *Garra* occur all around the Arabian Peninsula and in Africa and the Levant. *Cyprinion* has been recorded from near Jedda on the eastern coast of the Red Sea. A Miocene–Oligocene fossil '*Tilapia*' (no details)* has been recorded from the Jisan basin by G. F. Brown (1970:83). The survival of two related cichlids on the opposite sides of the once habitable desert is evidence of the more widespread occurrence of their ancestor(s) in Arabia in the Late Pliocene/early Pleistocene, which is considered to be the last long humid period in what is now the Arabian desert (Hötl, 1978; see also the discussion in Banister, 1973:132). Coad also suggested that the Euphrates–Tigris system may once have been more favourable to cichlid life, and pointed out the proximity of the head waters of the

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*Dr K. E. Banister has examined this on my behalf and reports that the fragmentary remains cannot be identified even at family level.

Euphrates to Syrian waters and so to the waters harbouring *Tristramella*, but the link (if any) between *Tristramella* and *Danakilia* may have been via the Red Sea basin and the Jordan Rift. See also p. 139.

The possibility of relationship with *O. (Alcolapia) alcalicus* is not easily dismissed. It too has a deep preorbital bone (Fig. 188) and a small eye, 9–14 lower gill-rakers, and low numbers of vertebrae (mode 28) and dorsal spines (IX–XIII). The snout, though giving a similar measurement, is more decurved and in the three specimens dissected the spondylophyseal apophyses are on the third vertebra alone. The most striking difference is in the pharyngeal bone, which has a restricted dentigerous area with fine, compressed teeth, and an anterior blade that is always longer than the dentigerous area. The breeding pattern is of the *Oreochromis* type, but we have no data from *Danakilia* to compare with this. The absence of microbranchiospines, and the reduced squamation of chest and belly are almost certainly ecologically induced parallelisms.

Danakilia franchettii (Vinciguerra)

Tilapia franchettii Vinciguerra, 1931:105; Tortonese, 1940:207; *idem*, 1963:337.
Tilapia (Danakilia) franchettii; Thys van den Audenaerde, 1968*e*:xxxv.

TYPES. Holotype: 84 mm SL in the Genoa Museum; C.E.31294.

Paratypes: sixty-one, up to 55 mm SL in the Genoa Museum and seven, 20–74 mm in SL in BMNH (1931.4.15.1–4). All these were collected in Lake Giulietti (=Lake Afrera) in Dancalia on the expedition led by Baron Raimondo Franchetti in 1929.

The holotype is the specimen whose proportions and meristic characters were given by Vinciguerra. The paratypes, including those sent by Vinciguerra to the BMNH, were used by him for description of colour pattern and certain measurements were taken from two of them. Tortonese (1963) lists them all as syntypes under the register number C.E.31294.

Distinguishing characters

As for the genus, see pages 32 & 503.

Description

Based on the paratypes in the BMNH and several specimens collected by Monsieur J. Varet in 1968, kindly lent by Professor Th. Monod. Twelve of the specimens of 1968 are now in the BMNH, the rest in MNHN (Paris). All details are taken from 20 specimens, 38–74 mm in SL, and the meristic numbers and colour-notes from several more, including three of 33·5–50·0 mm collected by M. Bolton in 1972.

Table 115. *Danakilia franchettii.* Frequencies of fin-ray numbers in samples from Lake Afrera and the neighbouring swamps.

	Dorsal formulae						Totals		
	XIII 10	XIV 9	XIV 10	XV 9	XV 10	XIV 11	23	24	25
Lake edge	1		10		1	4	1	10	5
Swamp		1	3	6	6	1	1	9	7

Anal fin				
III	7	8	9	10
Lake edge	1	12		
Swamp	1	6	9	1

Proportions as % SL. Depth of body 36–45; length of head 37·5–43·5, rarely less than 39·0; length of pectoral fin 34·0–38·0 in the swamps, 26·0–33·0 in the lake; length of caudal peduncle 12·5–16·5; length of lower jaw 13–16.

Proportions as % length of head. Length of snout 35·5–42·0; diameter of eye 24·5–27·0 at 38–57 mm SL, 22 at 69 mm, 21 at 74 mm; depth of preorbital 20·5–26·3, less than eye at SL up to 50 mm, greater above this length; interorbital width 28·5–34·0; length of lower jaw 32–37.

Striking features of the proportions are the relatively large head (or short trunk), the long, conical snout, the deep preorbital bone and small eye. The shorter pectoral fins of the lake fishes seem complete, but may have been mended after earlier damage. In contrast to the swamp fishes, the postero-ventral corner of the caudal fin is worn away in the lake fishes (Fig. 186).

Teeth all tricuspid,* except where the brown crowns are obviously worn off, in 3–4 series, 2 in the very young; 32–52 in the outer series of upper jaw.

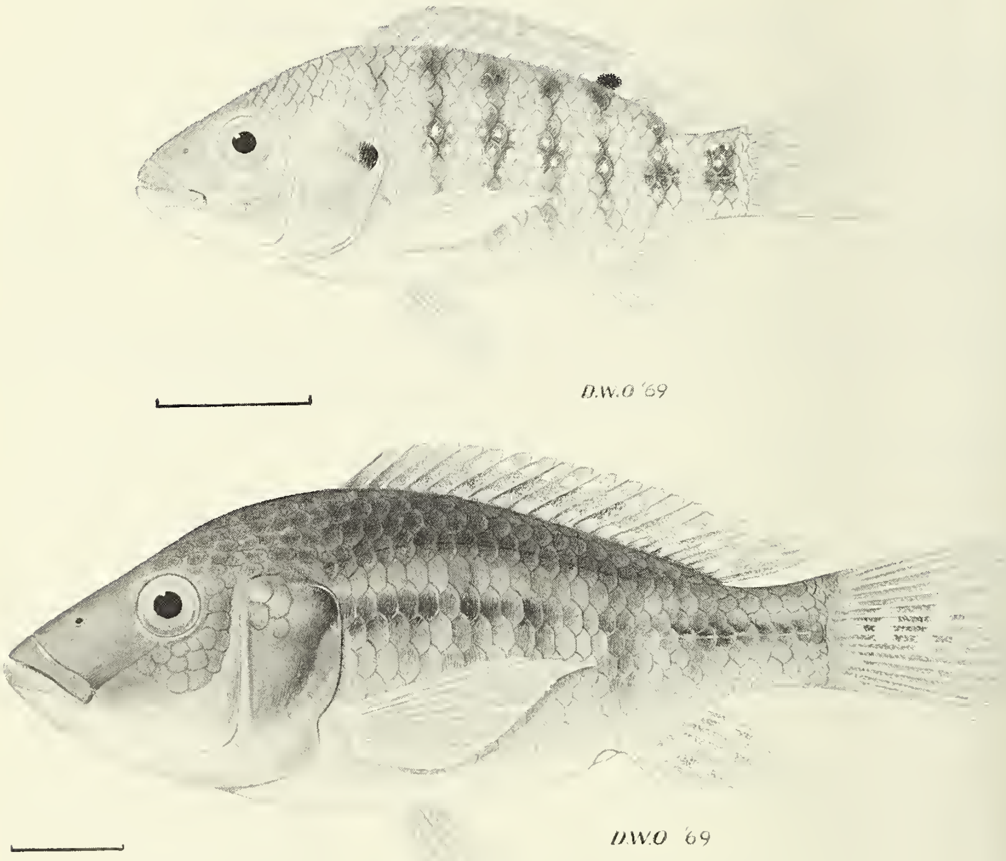

Fig. 186 *Danakilia franchettii.* Above, 40 mm SL from Lake Afrera (=Giulietti); below, 69 mm SL from the swamp. Scale = 10 mm.

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*Vinciguerra described them as unicuspid, but they are tricuspid in the paratype in the BMNH and Dr Tortonese informed me, in a letter dated 2.VII.1966, that this is so too in all the types in the Genoa Museum. This correction was also made by Thys (1968*b*).

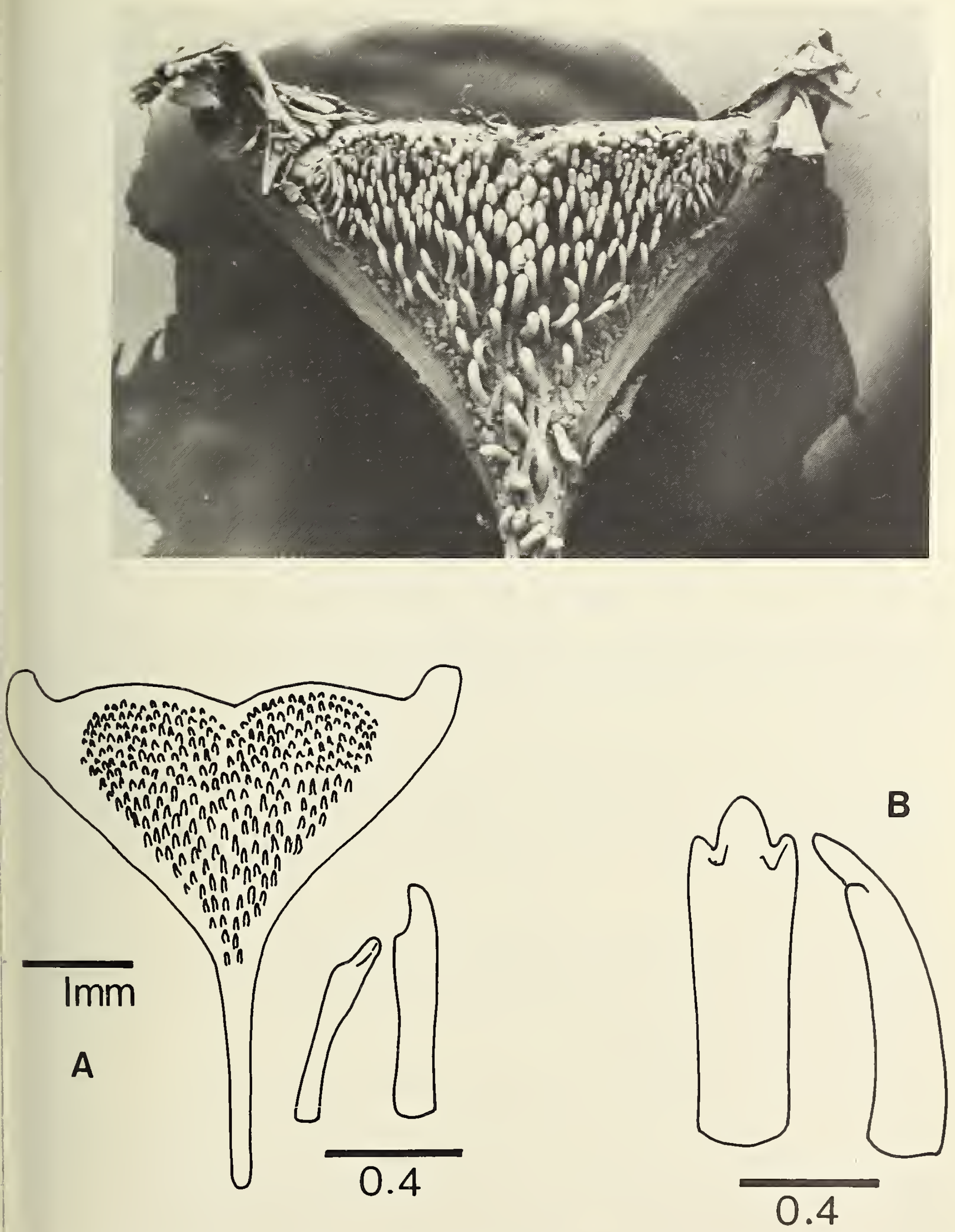

Fig. 187 *Danakilia franchettii.* Above, scanning electron micrograph of lower pharyngeal bone from a fish of 74 mm SL; below, A, drawing of the same from a fish of 39 mm SL, with two teeth, an anterior and a posterior; B, two views of a tooth from the outermost row of the upper jaw of a fish 74 mm SL.

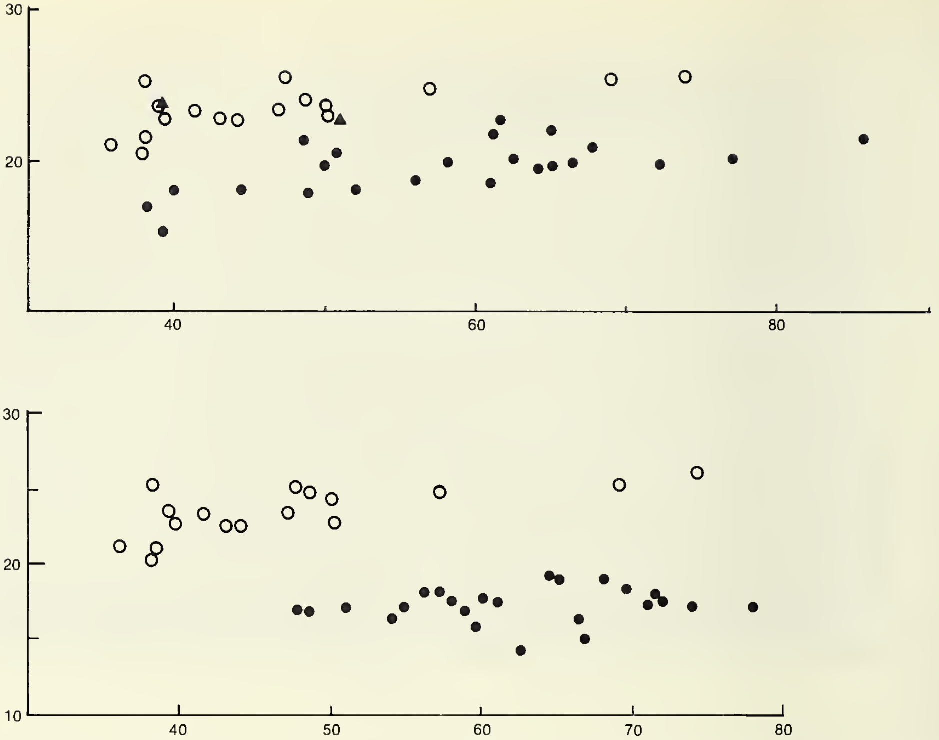

Fig. 188 *Danakilia franchettii.* Above, depth of preorbital bone (○) as % length of head, compared with that of *Oreochromis alcalicus* (●) and of two paratypes of *Iranocichla hormuzensis* (▲); below, the same, compared with that of *O. niloticus* and *O. aureus* of the same size (●).

Lower pharyngeal bone with heart-shaped dentigerous area extending forwards on the blade, so that the toothless part of the blade is only about half to three quarters of the median length of the toothed area. Teeth fine, those of the posterior row compressed, bicuspid with rounded tips turned forwards, those of four or more rows in front of these bevelled in the young, in larger specimens including a group of enlarged and flattened teeth; anterior teeth unicuspid.

Gill-rakers on first arch (2–3)+1+(10–12). No microbranchiospines.

Scales 27–28 (25 in one) in the lateral line series, 3 or $3\frac{1}{2}$ between lateral line and origin of dorsal, 4–5 between pectoral and pelvic fin-bases; small, non-imbricating but usually contiguous on chest and belly; in 2 or 3 series on the cheek. Scales of flank with rugose circuli in the exposed part, but not very heavy.

Dorsal and anal fins, see Table 115.

Caudal very slightly emarginate.

Genital papilla small, conical in male, with scalloped edge in mature female.

Coloration. Lake samples of M. Varet's collection are pale grey above to white on chest and belly, and have a silvery spot in the centre of each scale below the level of the upper lateral line and on some above its posterior part. Six or seven dark vertical bars on the body are crossed by two nearly horizontal bars, which may be broken into 3–6 mid-lateral blotches on some of the vertical bars and 3–5 blotches of a more dorsal series. The dorsal fin has numerous clear oval or round spots (devoid of melanophores), which form two series on the spinous part and more on the soft. A few similar spots may be present on the otherwise very faintly peppered caudal fin and one or two on the anal (Fig. 186).

The swamp samples and Mr Bolton's lake fishes (all probably fixed in formalin) are without silvery spots and generally much darker (Fig. 186, lower).

SKELETON. An alizarin preparation shows the tilapiine character of a pharyngeal apophysis formed from the parasphenoid alone. The anterior edge of the supraethmoid bone is rounded and does not meet the vomer. The ventral apophysis on the third vertebra is triangular in lateral view, with the base of the triangle extended forwards to the posterior end of the second centrum and backwards to the anterior end of the fourth. Whether there is bony fusion between the apophysis and the second and fourth vertebrae cannot be seen. There is one predorsal bone between the first and second neural spines (a general cichlid character).

Ecology

Food

Stomach contents of one of the swamp fishes included numerous green algae, of which *Scenedesmus* and a *Coelastrum-like* form were the most common. A comparison with the diet of the lake fish would have been interesting, but these had evidently been lured to the collector's net with ground bait and their stomachs were full of starch grains.

Among the coils of the intestine in the ripe and near-ripe females were abundant fat-ribbons. There was much less fat in the immature.

Breeding

A female of 44 mm SL has the ovary swollen with pear-shaped eggs of 3·5×2·3 mm; ten eggs fill the right ovary and about the same number the left. No smaller oocytes are present. One of 39 mm SL is less advanced, each ovary containing 9 eggs of 2·3×1·6 mm, already pear-shaped. A still less advanced lake female of 43·5 mm SL has in the right ovary 13 or 14 oval eggs of 0·6–0·7 mm long diameter and a few smaller oocytes. To judge from the ripe ovaries, some of these would have degenerated as yolk accumulated in the others. A swamp female of 69 mm SL, whose wide genital opening shows that she has spawned, has a few 1 mm oocytes in the rather thick-walled, flaccid ovaries and was probably preparing to spawn again.

No individuals were found with eggs in the mouth, but such large eggs are doubtless incubated in this way.

No structural dimorphism of the sexes was detected nor, as preserved, any dichromatism.

Distribution

Lake Giulietti (Afrera) in Dancalia and the swamps in its neighbourhood. The lake, about 25 km long and 8 km wide with a surface area of about 70 km², is a closed (endorheic) basin near the southern end of the arid depression between the Dancalian Mountains and the Ethiopian highlands. It is surrounded by volcanoes and fed by numerous hot springs near its SE and SW shores.

According to Franchetti (1930) this was part of an ancient arm of the sea, but Vinessa de Regny (1924), who described the geology of the area, considered that the Quaternary sea only reached the northern part of the depression (where the salt lake El Bad is a relic of it), and that Lake Afrera owes its existence to the hot alkaline springs from the basaltic rocks in its neighbourhood.

Martini (1969)* came to the same conclusion as to the origin of the lake as a result of the study of the chemistry of the waters. He noted that, although the ancient arm of the sea must have extended to the site of the present lake, the deepest part of the depression is to the north and to it is restricted the relic of the sea (Lake El Bad). The southern part is a huge evaporation

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*I am indebted to Prof. Th. Monod for this reference.

formation and the chemistry of Lake Afrera (Guilietti) is the result of solution in the hot springs from the upper layers of this formation. The supply of water from the springs keeps pace with evaporation from the lake, so that the size of the lake remains constant while its salinity increases.

The springs have a temperature of 43–50°C and a pH of 6·8–7·9, their sodium content is 0·5–1·0 g/l, chlorine 0·9–3·9 g/l. At the edge of the lake the sodium concentration has risen to 16·9 g/l, chlorine to 37·3. Within the lake the salinity is much higher, Na up to 44 g/l, Cl to 94, so that the fishes (*Aphanius dispar* as well as the cichlid) occupy restricted areas between the high temperature of the springs and the high salinity of the lake, at the point of entry of the streams to the lake, as noted by Martini, and by both collectors, M. Varet and Mr Bolton.

Material examined

Museum & Reg. No.	SL (mm)	Locality	Collector or donor
1931.4.15.1–4 (7 of the paratypes)	20–74	Lake Giulietti (Afrera), Dancalia, Ethiopia. 13°28′N 41°E	coll. Franchetti pres. Vinciguerra
1969.7.8.2–7	38–50	Lake Giulietti (Afrera), Dancalia, Ethiopia	coll. J. Varet pres. Th. Monod
MNHN (6 fishes)		Lake Giulietti (Afrera), Dancalia, Ethiopia	coll. J. Varet
1969.7.8.8–13	38–69	A swamp at foot of Mt Afdera south of Lake Giulietti	coll. J. Varet
1969.7.8.14	36	A swamp at foot of Mt Afdera, south of Lake Giulietti	coll. J. Varet
1973.10.16.31–35	33·5–48·5	Outflow of hot spring at its entrance to Lake Giulietti	coll. M. Bolton

General considerations

Speciation in *Sarotherodon* and *Oreochromis*

Students of the large and diverse cichlid species flocks of Lake Victoria and the Great Lakes of the African Rift Valleys have been struck by the fact that the tilapias either do not share in this explosive speciation or do so only to a very small degree. Lowe-McConnell (1959) called attention to the contrast, and Fryer & Iles (1969) attempted to explain it.

Fryer & Iles gave as a possible reason for conservatism the alleged generalized condition of the tilapias, which allows them to adapt to new conditions without diversification.

As an explanation this is open to objections. First, it is usual to believe that a generalized organism retains more potential for adaptive change than a specialized one. More importantly, it is necessary to define a generalized fish. Reproductively the mouth-brooding tilapias are highly specialized, especially *Oreochromis*, which in its breeding habits is closely convergent with the *Haplochromis* group. Trophically a generalized fish would surely be one feeding mainly on small invertebrates as most riverine cichlids (and other fishes) do (Lowe-McConnell, 1975 : 208; Matthes, 1964*b*) and indeed many haplochromines of the Great Lakes too. But although very young *Tilapia*, *Sarotherodon* and *Oreochromis* are usually omnivorous, including copepods, rotifers etc in their diet as well as diatoms, adults of all three genera become specialized for vegetarian diets, having notched teeth and long intestines; *Tilapia* for feeding on macrophytes or periphyton, *Sarotherodon* and *Oreochromis* on epiphytic, epilithic or planktonic algae, species of all three genera frequently using detritus.

These feeding habits and structural adaptations are uncommon among fishes, although a few 'Haplochromis' have evolved in the same direction (e.g. *'H'. similis* in Lake Malawi, *Neochromis nigripinnis* in Lake George, a few in Lake Victoria, as shown in fig. 7 of Greenwood, 1974).

Fryer & Iles were probably impressed by the adaptability of *O. mossambicus* to a range of salinity and temperature, and its ability to use a variety of food if phytoplankton is not abundant. This species has nevertheless the long intestine and the dental equipment suited to microphagy. It is far from obvious, moreover, why adaptability to a wide range of physical conditions should have inhibited speciation in lakes. The reason seems more likely to lie in the specialized trophic habits and structures.

The tilapias are sometimes referred to as riverine fishes, but they are not typically inhabitants of flowing waters. A seine drawn across a major river catches few cichlids and fewer *Sarotherodon* or *Oreochromis*. These fishes can be caught in backwaters, lagoons and flood-plains (cf. Gaigher, 1973) and in the pools and swamps left in the flood-plains in the dry season. The quieter, rich waters of the relatively shallow Lake Victoria and the shallower parts of the Rift Valley lakes provided the environments to which most of the tilapias are adapted. A few, the more specialized planktonophages, prefer large expanses of open water and quickly become more abundant when the waters in which they live are dammed to form lakes. Thus *Sarotherodon galilaeus* became the dominant tilapia in the quieter parts of Volta Lake and in Nungwa reservoir in Ghana, in Lake Kainji in Nigeria and in Lake Nasser in the Nile (Latif, 1976 & see p. 110); and the introduced *Oreochromis esculentus* soon outnumbered the native *O. pangani* and *O. jipe* in Nyumba ya Mungo reservoir in River Pangani (Payne, pers. commn).

Whatever the reason may be, the tilapias on the whole exhibit allopatric speciation, with one species of a genus or subgenus in any one river-system or groups of systems. Before illustrating this (pp 516–18) we must examine some examples of sympatric speciation.

Sympatric speciation

Sarotherodon and *Oreochromis* are not without examples of sympatric speciation*. These are:

1. *Oreochromis (Nyasalapia)* in Lake Malawi (see pp. 457–481). The four (or five) species

of this subgenus in Lake Malawi have so much in common (synapomorphies) that it is certain that they had a common ancestor. This would probably have been similar to *O. (Ny.) saka*, the most inshore-swelling and the most trophically flexible of the three species living in the southern half of the lake (Lowe, 1952 and 1953). From this the structurally very similar *O. squamipinnis* has diverged in breeding coloration, breeding season and mating site, possibly aided by changing lake levels. *Oreochromis (Ny.) lidole* is the species that has become most dependent on phytoplankton with dentition of both jaws and pharynx reduced. *Oreochromis (Ny.) karongae*, which is confined to the northern half of the lake, has developed dentally in a different direction. The tooth-bands of the jaws are wider, the teeth have long slender shafts and most of the outermost become tricuspid; the dentigerous area of the pharyngeal bone is greatly enlarged. So far its feeding habits have not been reported, but from the nature of the dentition an emphasis on periphyton is to be expected (Liem, 1980, fig. 6, iv).

Not only is it unlikely that fishes with these dental specializations would revert to insectivory or aspire to mollusc-eating (but see p. 245), but the shore zone of Lake Malawi is crowded with species of the *Haplochromis* group that have preempted these niches.

2. The endemic species of Barombi-Mbo, Cameroon. The species of *Sarotherodon* described on pages 75–93 are four of eleven endemic cichlid species in this small and young lake. Among these four and the extra-limital *Myaka myaka* the pattern of speciation largely parallels that of *Oreochromis (Nyasalapia)* in Lake Malawi (see also p. 35). For these and for five of the other endemics one or two ancestral species of *Sarotherodon (S. galilaeus* and/or *S. melanotheron)* were suggested (Trewavas *et al.*, 1972), and for the eleventh (*Pungu*) an ancestral *Tilapia*. The six putative descendants of *Sarotherodon*, for which three new generic names were proposed, had diversified in a manner reminiscent of the haplochromines of the eastern lakes, and it was suggested that they were enabled to do so because of the absence of preempting *Haplochromis*. There may have been multiple invasions of the same riverine species, but the differentiation must have proceeded in the lake itself.

3. In Lake Jipe, in the Pangani system, two related species exist together. On page 374 suggestions are made as to what past history might have led to their differentiation, enhanced by separate invasions by one riverine source species, *Oreochromis pangani pangani*.

4. In the Malagarazi swamps, Tanzania, two species of *Oreochromis (Nyasalapia)* exist together, *O. malagarasi* and *O. karomo* (pp. 426 & 482). They differ strongly in the dentition of jaws and pharynx, and in the shape of the jaws, although they have both been seen feeding on detritus. *Oreochromis (Ny.) karomo*, however, has also been seen using periphyton, and its broad bands of tricuspid teeth are of a type elsewhere associated with rasping the algal growths from surfaces of plants or rocks (see Liem, 1980). There is evidence that their breeding cycles do not coincide (Lowe-McConnell, 1956*a*).

Oreochromis malagarasi has also its allopatric, more similar sister-species, *O. upembae*, in the Lualaba and the Upemba region, from which it is now separated by Lake Tanganyika.

Possible courses of sympatric speciation

If we ask how changing lake-levels can, in Lake Malawi, aid reproductive isolation we can only put forward hypotheses or 'models'. Let us imagine a population, say of *O. saka*, with a mating arena in a particular locality at a depth of 4 m, that returns to this arena in subsequent mating seasons and subsequent generations. Let us now suppose that the lake-level rises so that this arena is covered by 8 m of water. The mating population may either: (1) continue to spawn in the same location and so become accustomed to a deeper arena or; (2) seek another location at the old depth. Part of the population may make choice (1) while another part makes choice (2). We then have two subpopulations breeding at different depths and if these habits are perpetuated through overlapping breeding generations we have a basis for segregation and differentiation. The initial choices have produced a situation in which allotopic but sympatric differentiation may proceed.

The spatial difference following a change in lake-level differs according to the slope of the shore zone. Some reedy places may be eliminated in a steeply shelving area, but only diminished in a more gradually shelving place.

Evidence for the possibility of such a change is at present a mere hint. Mr Rodney Wood, an early collector of Malawi fishes, verbally informed Dr Lowe-McConnell (then Miss R. H. Lowe) that he had observed the same breeding ground being used by chambo (*O. saka* or *O. squamipinnis*) in years respectively of low and high lake-levels. There is evidence of specific depth preferences among the Lake Malawi species (pp. 474–478) and also in other species, e.g. *O. macrochir* both in Zambia and in the Lufira (pp. 448–9).

How narrow may be the spatial and morphological differences between populations of cichlids, and how inexplicably rigid such assortative mating may become is dramatically illustrated by the observations of Marsh, Ribbink & Marsh (1981) on the superspecies *Petrotilapia tridentiger* in Lake Malawi. This may represent an early stage in segregation and differentiation.

The question of which species, external to Lake Malawi, is most nearly related to the hypothetical source species of the *squamipinnis* flock leads to consideration of the tasselled species described on pages 412 to 453. Comparison of the tables in these sections and Tables 109–112 (pp. 467–469) shows that in contrast to the Malawi flock these all have a deeper body, shorter and deeper caudal peduncle with length/depth ratio always less than 1, lower modal numbers of vertebrae and lateral line scales, higher modal numbers of gill-rakers and a narrower interorbital region. This leaves only the subgeneric characters—the genital tassel, the dentition, non-enlargement of the jaws in mature fishes and possibly a common pattern of mating pits—to unite the Malawi flock with species outside the lake, and we must assume that colonization of the lake by the ancestral species was rapidly followed by meristic and proportional changes.

The Rukwa basin is part of the same section of the Rift Valleys as Lake Malawi, from which it is now separated by the Rungwe volcanic mountains. *Oreochromis (Nyasalapia) rukwaensis* and the related *O. (Ny.) macrochir*, or their common ancestor would seem to be the most likely sister-species of the Malawi flock.

The colonization of lakes must have occurred simultaneously with their formation from the rivers that supplied them. Even in the short space of time needed to form a manmade lake changes in habits have been observed in the fish species involved. In Lake Volta, for example, *Schilbe mystus* and *Eutropius niloticus* were observed to become more specialized than they were in the river (Lowe-McConnell, 1975, quoting Petr, 1967 & 1968), taking advantage of the abundance of *Povilla* larvae in the wood of drowned trees.

The crater-lake Barombi-Mbo (see p. 75) is supplied by a stream about 3 km long believed once to have been part of the Meme River. Rivers in this region are subject to alternate spates and shrinkages. The first colonization may have occurred during an unusually high spate, followed by a period of relative isolation. A species probably of the lineage of *Sarotherodon melanotheron* or *S. galilaeus* on entering the lake might well specialize on phytoplankton, a resource, however, in which the lake is not rich. Growth would be poor and might result in a big head and lean body, the food-catching apparatus increasing in relative size with reduced expenditure on bones and teeth. Hence the reduced dentition and narrow pharyngeal bone in *S. linnellii*. Whatever governs the timing of the breeding cycles in the river might operate differently in the lake. After an interval of decades or even centuries a subsequent exceptional spate might induce a new wave of colonization by the same species from the river, the individuals of which would find a situation not identical with that found by the first wave. They must adapt both to new physical conditions and to the presence of a resident population. There is no reason at this latitude why their breeding cycles should coincide, and whatever heritable differences developed between the two would therefore be maintained and, once initiated, would probalby be increased by the mutual influence of these related but not identical populations. Two sympatric sister-species, *S. linnellii* and *S. caroli* would be rapidly established. This is an extension of the 'character-displacement' theory (Brown & Wilson, 1956).

A *Sarotherodon* with the heavy and finely toothed pharyngeal bones of *S. galilaeus* might on the other hand specialize in another part of the feeding spectrum of this species, namely detritus feeding. The detritus of the new crater lake would not be very rich and among other resources *S. steinbachi* has perfected a method of feeding on the interstitial organisms of the fine sand (see p. 81). It can be recognized immediately by its method of feeding, projecting the upper jaw downwards and using it to sweep sand into the mouth. The sand is ejected by way of the operculum after it has been chewed between the pharyngeal bones. That the uniquely massive pharyngeal bones would rapidly develop in relation to this method of feeding (Fig. 29) cannot be doubted with the example of *Astatoreochromis alluaudi* in mind (Greenwood, 1965*a*). How this and other morphological features became established in the genome is another quesion. *S. steinbachi* has no rivals in the lake in the use of interstitial food resources, although it may be found with others feeding on the detritus lying on the surface of encrusting sponges.

A hypothesis or model of this kind might 'explain' all the differentiation of the eleven endemic cichlids of this small and young crater-lake, given two or three founder-species. If the founders were all tilapiines, as the basic morphology would suggest, this would involve reversion to insectivory with the appropriate predacious morphology on the part of *Konia* and *Stomatepia*. Yet no other extra-lacustrine ancestors or sister-species have been found for these species. If they were indeed evolved from herbivorous or microphagous tilapiines this would be the only known example of the permanent abandonment of its specialized condition by a tilapia. See Trewavas *et al.*, 1972.

For the two related species of Lake Jipe a similar hypothesis is put forward; namely two colonizing events, separated by a period of allopatric change, and followed by sympatric divergence (p. 374).

In the vast area of the Malagarazi River, swamps and delta there would be opportunity in dry periods for a species to segregate into subpopulations, which might diverge in habits while their breeding cycles would become non-synchronous. On coming together again differences of habit and associated structures would be enhanced as they avoided competition. If this interpretation is correct, the similarity of *O. malagarasi* to its allopatric sister-species *O. upembae*, and the striking difference between it and its sympatric sister-species *O. karomo* well illustrate the power of allopatry (or allotopy) followed by sympatry (or syntopy) versus allopatry alone as an agent of speciation. Nevertheless, sympatric species-groups may also, at least in the early stages of diversification, exhibit very narrow differences both in structure and ecology (Marsh *et al.*, 1981; Van Oijen, 1982, *Neth. J. Zool.* **32**: 336; and work on Hawaiian fruit flies).

Allopatric species

Apart from these examples of sympatric speciation, within the respective genera or subgenera the differentiation of the species is evidently allopatric. Table 116 shows that the tilapias are represented in most localities by a single species of each of one to six genera or subgenera. Apparent exceptions to this are explicable by two space-saving imperfections in the table:

1. *Tilapia* is less fully analysed in the table than the mouth-brooding genera. Thys (1968*b*) recognized six subgenera of substrate-brooding *Tilapia* and three of these have been tabulated here with subgenus *Tilapia* under one heading.
2. In the table some of the areas grouped as one comprise more than one river-system.

Particular explanations are:

1. The very similar species *Oreochromis (O.) mossambicus* and *O. (O.) placidus* occur together from the Lower Zambezi southwards to Sodwana, but *O. placidus* extends farther northwards, *O. mossambicus* farther southwards, a distribution that has the appearance of an allopatric beginning with secondary overlap. Each of these two has an allopatric related species. *Oreochromis mortimeri* represents *O. mossambicus* in the Middle Zambezi, and *O. shiranus* replaces *O. placidus* in the Upper Shiré, Lake Malawi and Lakes Chilwa and Chiuta. The relationship further shows that *O. shiranus* probably entered Lake Malawi from the south and became sympatric with the

species-flock of subgenus *Nyasalapia* only when Lake Malawi expanded southwards in the Pleistocene.

2. *Oreochromis (O.) niloticus* and *O. (O.) aureus* live together in part of their respective areas. A suggested explanation of this is offered on page 139.

3. *Tilapia ruweti* occurs with *T. sparrmanii* in part of the wide area of the latter. In spite of their resemblances they may have separate origins; some features of *T. ruweti* led Poll & Thys (1965) originally to describe it in *Pelmatochromis. Tilapia baloni,* not included in the table, takes the place of *T. sparrmanii* as partner to *T. ruweti* in the upper reaches of the Luongo River in the Mweru catchment area.

4. The three species of *Tilapia* in Liberia and Sierra Leone are allopatric within the area, except that *T. (Heterotilapia) buttikoferi* and *T. (Coptodon) louka* are found in the same river system in Sierra Leone.

5. The five species of *Tilapia (Coptodon)* in northwest Cameroun are allopatric within the area.

6. The phyletic and ecological relationships of *Sarotherodon occidentalis* and *S. caudomarginatus* are not well known. The presence of both *S. occidentalis* and *S. galilaeus* in the Corubal River represents overlap, possibly secondary, of their respective distributions.

The species coexisting as geographically defined groups are described by Ruwet, Voss & Hanon (1976) as 'complementary species'. In the table they may be read off horizontally, while a vertical reading of the columns provides lists of vicariating and related species.

Lake Tanganyika

Among the riddles of the fish fauna of Lake Tanganyika is the relationship of its one endemic tilapiine species (see pp. 24 & 501). The two non-endemic species, it is generally believed (Poll, 1956*b*: 12, 28; Thys, 1963: 594), entered the lake secondarily: *Tilapia rendalli* when it overflowed by the Lukuga to join the Lualaba; and *O. niloticus* when the Ruzizi River connected Lake Kivu and Lake Tanganyika, both late Quaternary events (Grove, 1981 quoting Hecky & Degens, 1973). *Oreochromis (Neotilapia) tanganicae* has no obvious nearly related species either to the west or to the east of Lake Tanganyika, whereas the lake forms a barrier between the sister-species *O. (Ny.) upembae* and *O. (Ny.) malagarasi,* as it does between species pairs of other genera (*Serranochromis* and *Orthochromis*), and between populations of about nine species of non-cichlid groups (Lowe-McConnell, 1975: 153) in the Malagarazi and the Zaire.

In the present obscurity of its extralacustrine relationships *O. (Ne.) tanganicae* is at one with most other species of the great flock of endemics in Lake Tanganyika.

Species and subspecies

It is often questionable whether the members of a vicariating series of populations should be classified as species or subspecies. Thus the series of brackish water populations of *Sarotherodon* along the West African coast are here treated as subspecies of *S. melanotheron* although Thys (1971) treated them as species. In the case of *S. m. nigripinnis* and *S. m. melanotheron* the distinction is only statistical and the geographical dividing line is not clear. *S. m. leonensis* is distinguished by the melanin pattern of mature fishes, but sufficient material of neighbouring populations is not available for comparison. The most northerly population of this series appears to have less melanin than the others but vestiges of the pattern are occasionally discernible. One new subspecific name is given to a population in this series that requires further study. Collectively these populations are well characterized as a species.

Within the subgenus *Oreochromis,* where sexual dichromatism is the rule, I have been influenced by this character. When this is similar in two populations I have allowed it to over-ride

Table 116. Outline natural distribution of species of subgenera of *Tilapia*, the genus *Sarotherodon* and the two main subgenera of *Oreochromis*. See also text, pp. 21–23 Figs 11 & 12. The asterisk signifies brackish water. In *Tilapia* there are more lineages than are indicated by the three subgenera and some of them, e.g. *T. (Heterotilapia) buttikoferi* and *cessiana*, are placed in the column headed '*T. (Tilapia)*', but between brackets. Brackets also indicate three monotypic subgenera of *Oreochromis* and the doubtful position of '*O*'. *schwebischi*. Some species of narrow local distribution are omitted (*Tilapia guinasana*, *baloni*, *rheophila*, *walteri*).

	T. (Tilapia)	*T. (Coptodon)*	*T. (Pelmatolapia)*	*Sarotherodon*	*O. (Oreochromis)*	*O. (Nyasalapia)*
Kenya, coastal	—	—	—	—	*spilurus*	—
Tanzania						
Lower Pangani	—	—	—	—	*korogwe*	—
Upper Pangani system	—	—	—	—	*pangani* *jipe* *hunteri*	—
Wami	—	—	—	—	*u. hornorum*	—
Rufigi & Mbemkuru	—	—	—	—	*u. urolepis*	—
Ruvuma	—	—	—	—	*placidus ruvumae*	—
Lower Zambezi to Sodwana; Lower Shiré; Limpopo	*sparrmanii*	*rendalli*	—	—	*p. placidus* *mossambicus*	—
Middle Zambezi	*sparrmanii*	*rendalli*	—	—	*mortimeri*	—
Kafue, Upper Zambezi, Okovango, Cunene	*sparrmanii* *ruweti*	*rendalli*	—	—	*andersonii*	*macrochir*
Bangweulu	*sparrmanii*	*rendalli*	—	—	—	*macrochir*
Lake Malawi basin	*sparrmanii*	*rendalli*	—	—	*shiranus*	*squamipinnis* flock
Lake Mweru basin Lufira R.	*sparrmanii* *ruweti*	*rendalli*	—	—	—	*macrochir* *salinicola*
Upembe & Lualaba R.	*sparrmanii* *ruweti*	*rendalli*	—	—	—	*upembae*
Lake Rukwa	—	—	—	—	—	*rukwaensis*
Malagarazi	—	—	—	—	—	*malagarasi* *karomo*
Lake Victoria	—	—	—	—	*esculentus*	*variabilis*

	T. (Tilapia)	_T. (Coptodon)_	_T. (Pelmatolapia)_	_Sarotherodon_	_O. (Oreochromis)_	_O. (Nyasalapia)_
Lower Quanza & Bengo	—	*_guineensis_	_cabrae_	—	—	_angolensis_
Lower Zaire	—	—	_cabrae_	*_melanotheron_ _gal. boulengeri_	—	*_lepidurus_
Zaire central basin	—	_congicus_	—	—	—	—
Chiloango	—	*_guineensis_ _tholloni_	_cabrae_	*_melanotheron_	(_schwebischi_)	—
Gabon & South Cameroon	_margaritacea_	*_guineensis_ _tholloni_ _ogowensis_ _nyongana_	_cabrae_	*_melanotheron_ _mvogoi_	(_schwebischi_)	—
NW Cameroon	—	*_guineensis_ _cameronensis_ _camerunensis_ _kottae_ _bemini_	_mariae_	*_melanotheron_ _galilaeus_ the species-flock of Barombi-Mbo (p. 75)	—	—
Cross River to Volta (Guinean)	—	*_guineensis_	_mariae_	*_melanotheron_ _galilaeus_	—	—
Pra R., Lake Bosumtwi, to coastal rivers of Ivory coast	_busumana_	*_guineensis_ _discolor_	_mariae_	*_melanotheron_ _g. multifasciatus_	—	—
Liberia, western Ivory Coast & Sierra Leone	(_buttikoferi_) (_cessiana_) (_joka_)	*_guineensis_ _louka_	_brevimanus_	*_melanotheron_ _tournieri_ _caudomarginatus_ _occidentalis_	— —	— —
Corubal R.	(?)	*_guineensis_	?	*_melanotheron_ _caudomarginatus_ _occidentalis_ _galilaeus_	—	—
Gambia	—	*_guineensis_	—	*_melanotheron_ _galilaeus_	_niloticus_	

Table 116. (cont.)

	T. (Tilapia)	*T. (Coptodon)*	*T. (Pelmatolapia)*	*Sarotherodon*	*O. (Oreochromis)*	*O. (Nyasalapia)*
Senegal R.	—	**guineensis* *zillii*	—	**melanotheron* *galilaeus*	*niloticus* *aureus*	—
Chad basin, Benue, Middle & Upper Niger, Volta	—	*zillii* *dageti*	—	*galilaeus*	*niloticus* *aureus*	—
Lower Nile, Israel coastal	—	*zillii*	—	*galilaeus*	*niloticus* *aureus*	—
Jordan Valley	—	*zillii*	—	*galilaeus*	*aureus*	—
Lake Albert	—	*zillii*	—	*galilaeus*	*niloticus* *leucostictus*	—
Lake Turkana	—	*zillii*	—	*galilaeus*	*niloticus*	—
Ethiopian lakes	—	—	—	—	*niloticus*	—
Lake Baringo	—	—	—	—	*niloticus*	—
Lake Edward/George	—	—	—	—	*niloticus* *leucostictus*	—
Lake Kivu	—	—	—	—	*niloticus*	—
Lake Tanganyika	—	*rendalli*	—	—	*niloticus*	—
Lake Tanganyika	—	—	—	—	O. (*Neotilapia*) *tanganicae*	—
Singida, Kitangiri, Eyasi, Manyara	—	—	—	—	O. (*Vallicola*) *amphimelas*	—
Lake Magadi,	—	—	—	—	O. (*Alcolapia*)	—

meristic differences. Thus, *O. spilurus spilurus* and *O. s. niger*, known to hybridize in nature, have been treated as subspecies because no difference was reported in male territorial coloration (but see p. 241). Where territorial coloration is distinctive it has been regarded as indicative of a degree of reproductive isolation and the respective populations have been treated as species. Examples are *O. mossambicus* and *O. mortimeri*, respectively of the Lower and Middle Zambezi, and *O. mossambicus* and *O. spilurus*. The black body and fins and white lower parts of the head in male *O. mossambicus* distinguish it from these otherwise very similar forms.

The adjacent geographical areas of *O. mossambicus* and *O. mortimeri* are separated by the Cabora Bassa Falls, between the Middle and Lower Zambezi. Formerly the Middle Zambezi was not favourable ecologically to populations of *O. mortimeri* (Jackson, 1961*a*), but the formation of the barrage-lake above the dam at Cabora Bassa has converted the Middle Zambezi into an environment in which *O. mortimeri* has increased in numbers (Jackson & Rogers, 1976). This may bring about the meeting of the two forms, a meeting that has already been achieved in some localities by indiscriminate stocking of both species. it remains to be seen whether this will result in blurring the differences between them or whether one will oust the other by ecological selection.

What is recorded here is the position during recent decades when the species were being studied.

Oreochromis mossambicus and *O. spilurus*, between which the male coloration is almost the only distinction, are separated by the coastal region of Tanzania, the provinces of *O. urolepis* and *O. korogwe*. The two latter differ from them in male coloration and meristic characters (Table 76) and *O. urolepis* also in the pharyngeal dentition. More strikingly, *O. urolepis hornorum* has been found to have a different sex-determining mechanism, revealed when males of this form were mated with females of *O. mossambicus* (see p. 288) or *O. spilurus niger* (p. 257) with the production of an all-male F_1. *Oreochromis mossambicus* and *O. spilurus* are unlikely to come together except by human agency. If this should take place it is difficult to predict the result.

Two long-term studies have been made of mixed populations in a free ecological situation, one of *O. s. niger* and *O. leucostictus* in Lake Naivasha (p. 257), the other of *O. niloticus* and *O. macrochir* in Lake Itasy, Madagascar (p. 451). Both involved well-defined, unrelated species; *O. niloticus* and *O. macrochir* have been placed in separate subgenera.

Both introductions were followed by a period in which the two species and a series of intermediate forms, deemed hybrids, were found in each lake, but the final result was the elimination of one species and the hybrids (or all but a few), and the dominance of the other species (or a phenetically indistinguishable form). This result was brought about by ecological selection in each case, but there was also evidence in Lake Itasy that the fecundity of the hybrids was reduced (Daget & Moreau, 1981).

No similar study has been made of hybrid populations of more closely related species. Results are unpredictable and would depend on the environmental factors and the autoecology of the species concerned. No decision as to their taxonomic relationships should be made on immediate success of interbreeding in a pond or tank. Multiple factors in a free ecological situation may reveal unexpected divergences in the course of several generations.

The value of coloration as a guide to specific distinction and the limited value of metameric numbers is demonstrated by the two similar, and partially sympatric species, *O. niloticus* and *O. aureus*. That these were separate species was recognized by field workers on features of coloration not available to systematists who relied on preserved specimens. When the colour characters were recognized as specific, meristic ranges formerly attributed to variation were found to have two corresponding modes (Table 48). and specific transferrins and esterase were found (Avtalion, 1982) (see p. 20).

Aquarium experiments have shown that when several of each of *O. niloticus* and *O. aureus* are together, assortative mating occurs, although they are capable of interbreeding if they have no other choice. The two species are sympatric in parts of their ranges and there they do not mix. (Reproductive isolation has elsewhere been found to be enhanced between sympatric populations of two forms. See Dobzhansky, 1970: 380.) Here reproductive compatibility is also limited by the fact that the sex-determining mechanism differs as between the two species. The same difference exists between *O. niloticus* and *O. urolepis hornorum*, which when hybridized produce an all-male F_1. Females of *O. mossambicus* and *O. spilurus niger* may be mated with *O. u. hornorum* with the same result; and the same is true of each of the pairs whose history has been followed in Lake Itasy and Lake Naivasha, where they were introduced.

Although introgressive hybridization may follow in all these cases, the result is not, as at least one fish-farmer (I. S. C. Parker, pers. commn) has suggested, a population differing in no important respect from the two parent species. Lovshin (1982) claims to have some evidence that there is a degree of inhibition against matings between female *O. niloticus* and male *O. u. hornorum*, the number of hybrid young produced being lower than would be expected from the same number of adults of either pure species. He suggests some behavioural or chemical barrier.

In some instances the decision to give specific or subspecific rank to populations is more arbitrary. The ranking of *O. upembae* and *O. malagarazi* as two species, separated geographically by Lake Tanganyika, should not obscure their close relationship (cf. Poll, 1951: 112, 137). And *O. spilurus percivali* is a population with striking differences from the population of *O. s. spilurus* in the Northern Uaso Nyiro from which it is believed to have originated.

An example of a colour difference being outweighed by meristic identity is the treatment here of the population of an island crater lake in Lake Turkana, origin of the syntypes of '*Tilapia vulcani*'. This population is found to share with that of the main lake two differences from *O. n. niloticus*, namely a modal XVI dorsal spines (XVII in *O. n. niloticus*) and more slender teeth in the jaws and pharynx (Figs 54 & 61). It differs from the main lake population in the intense blue-black colour of adult males (dark iridescent green in the main lake), a larger head (Table 42), longer fin-spines and leaner body. The broader bands of teeth, more of which become tricuspid, continue to an extreme a trend seen in the main lake (Fig. 54). These features are paralleled elsewhere, cf, the large head and dark colour of *O. (Ny.) lidole* in the crater-lake Chungruru and the large head long fin-spines and lean body of the starved population that yielded the syntypes of '*T. eduardiana*' (p. 156–7). The nature of the dentition is no doubt conditioned by the diet. This is unknown, but by analogy may be predicted to depend on epilithic growths. These considerations, together with the short past and probably impermanent future of the isolation of the crater-lake A, have influenced me in extending the coverage of the name *vulcani* to the whole population of Lake Turkana as a subspecies of *O. niloticus,* on the assumption that the undoubted peculiarities of the crater-lake population have not become genetically based.

Tables for the identificaion of the species of *Sarotherodon* and *Oreochromis*. Mode of use and degree of validity

The Tables 117, 118 & 119 on pages 522 to 533 have an advantage over the dichotomous key in that related species are grouped together. The individuals to be identified should first be assigned to a subgenus (pp. 24–30). If the fish has been captured in waters not affected by introductions by man, the choice is narrowed by the locality and Table 116 may first be consulted. There are now, however, few river-systems in Africa that have not been contaminated by introductions and this clue is also useless for species acquired for stocking ponds in other continents.

In Kenya, for example, the tilapias naturally occurring in rivers flowing to the Indian Ocean are *O. s. spilurus* and *O. s. niger*, the former in the shorter rivers and lower reaches of the longer, the latter in the Athi above Lugard's Falls and in the upper tributaries of the Tana. But lakes, ponds and dams have been stocked with *O. s. niger* and also with *Tilapia zillii*. Inadvertently with *T. zillii* came *O. leucostictus*, ultimately from Lake Albert, but via fishponds at Kajansi in Uganda and Kisumu in Kenya. There is probably no river system in Kenya in which a population of pure *O. s. niger* can now be found, and *O. s. spilurus* can be expected to be pure only in such eastern rivers as do not include stocked dams.

Oreochromis niloticus, which formerly was absent from Lake Victoria, has now been introduced there from both Lake Albert and Lake Turkana. Species exported from Israel to the Americas and elsewhere may include not only the two native Levantine forms *O. niloticus* and *O. aureus* and hybrids of these, but also *O. niloticus* of African origins*.

In southern Africa *O. mossambicus* and *O. mortimeri* cannot easily be distinguished except in the territorial phase of the male, and young *O. placidus* have superficially only a fourth anal spine to distinguish them from both these. Here also original geographical limits have been blurred or destroyed by stocking and by the creation of man-made lakes. In such lakes new conditions may cause the merging of formerly distinct breeding locations and seasons, with resulting hybridization of related forms.

Colour differences are often difficult to establish because of the range of colour-changes in individuals. They are most likely to be valid between breeding males, but the males of several species become almost completely black in full territorial phase. Colours produced by pigments other than melanin are lost in preserved fishes.

Proportional differences are subject to allometry. For most species only individuals of about 100 mm SL and over have been used in the tables, but in *O. (Alcolapia) alcalicus*, where this size is rarely attained, most fishes used were under 100 mm. No account of allometry has been taken in the tables, and although maximum values for depth of preorbital bone and lower jaw characterize groups of species, it is well when using these to turn to the list of material of the species chosen to see what range of size was available.

Differences in pharyngeal bones are best appreciated by reference to the illustrations.

The combinations of characters in the columns, taken in conjunction with the illustrations and followed by checking the full descriptions should lead to correct determinations. But imported pond fishes may have passed through the establishments of more than one fish-culturist. Their original features may have become modified and hybridization, inadvertent or deliberate, may have occurred.

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*Israeli exporters are now giving reliable details of stock supplied.

Table 117

Genus *SAROTHERODON* (part)

Species	*melanotheron*	*mvogoi*	*galilaeus*
Pages	41–70	70–74	94–123
Habitat (FW=fresh water)	brackish estuaries & lagoons	FW	FW, except Nile delta
Natural geographical area	Zaire to Senegal Fig. 11	Upper parts of rivers Nyong, Ntem, Ivindo & Ja	Jordan Valley, Nile, Chad, West Africa, NW Cameroon, Upper & Lower Zaire Figs 36, 43
Depth % SL	37·0–51·5(54)	39·0–47·0	43·0–56·5
Scales lat. line	27–30	27–30	(28) 29–32
Depth preorb. % hd.	24·0–32·5	28·0–32·0	19·5–29·5
Lower jaw % hd.	27·0–34·5	24·0–29·5	28·0–32·5
Pharyngeal			
L. % hd.	31·6–37·0	35·9–39·0	32·3–43·5
mean	34·02	(N=3)	37·6 (*g. multifasciatus* 39·7)
blade/dent.	0·9–2·2	1·6–2·0	1·0–2·0 (1·15–2·2)
Lower gill-rakers	(12, 13) 14–19	19–23	19–26 (27)
Shape caudal margin	Emarginate	Emarginate	Emarginate
Other markers	Irregular black patches characteristic of populations or irregular bars (Figs. 17 & 22)	Pink spots on flank-scales	Plain grey or yellowish or with vertical bars of irregular outline; caudal margin pink

Table 117 (cont.)

Genus *SAROTHERODON* (cont.)

Species	*lohbergeri*	*steinbachi*	*linnellii*	*caroli*
Pages	75–79	79–83	84–93	84–93
Habitat (FW = fresh water)	FW	FW	FW	FW
Natural geographical area	Lake Barombi Mbo, Cameroon			
Depth % SL	37·0–45·0	39·5–45·5	38·5–40·0	38·5–45·0
Scales lat. line	30–31(32)	30–33	30–32	30–32
Depth preorb. % hd.	17·5–24·0	20·0–26·0	17·5–24·5	19·0–26·0
Lower jaw % hd.	26·5–32·0	26·0–31·0	32·0–37·5	32–36
Lower gill-rakers	14–17	19–23	15–18	17–20
Pharyngeal L. % hd.	33·0–39·0	40·0–49·5	35·1–40·2	35·9–40·5
mean	36·2	(N = 3)	37·1	38·3
blade/dent.	1·08–1·6	0·9–1·2	0·8–3·0	2·2–3·0
Shape caudal margin	Emarginate	Emarginate	Truncate or very slightly emarginate	Truncate
Other markers	Silver-grey; mid-lateral black stripe interrupted on anterior part of caudal peduncle	Pearly in life, grey as preserved	Grey or green; black patches on lower parts of head	Grey with darker smudges or green

Table 117 (cont.)

Genus ***SAROTHERODON*** (concl.)

Species	*occidentalis*	*caudomarginatus*	*tournieri*
Pages	128–134	134–138	124–128
Habitat (FW = fresh water)	FW or slightly brackish	FW	FW
Natural geographical area	Liberia to Casamance R.	Liberia to Guinée	Cavally, Cess and St John rivers
Depth % SL	45·0–51·0	46·0–49·0	46·0–56·5
Scales lat. line	30–32	31–34	27–29
Depth preorb. % hd.	21·5–33·0	26·5–29·0	22·0–29·0
L. lower jaw % hd.	27·5–34·5	28·5–34·5	29·5–35·5
Lower gill-rakers	22–27	18–24	16–20
Pharyngeal			
L. % hd.	34·2–38·3	37·2 & 38·8	39·5
mean	37·04		
blade/dent.	1·1–1·45	1·3 & 1·4	1·96
Shape caudal margin	Emarginate	Deeply emarginate	Emarginate
Colour markers	General yellow colour	Infolded skin above upper lip bright yellow	Grey vertical bars on body

Table 118

Genus *SAROTHERODON* or *OREOCHROMIS*?

Species	*schwebischi*
Pages	489–495
Habitat	FW
Geographical area	Ogowe, Chiloango and Niari Kouilou
Depth % SL	42·5–49·5
Scales lat. line	28–30
D. preorb. % hd.	20·0–29·5
Lower jaw % hd.	28·5–38·5
Lower gill-rakers	21–25
Pharyngeal	
L. % hd.	35·5–40·0
mean	38·31
blade/dent.	1·2–1·85
Anal spines	III
Other markers	Ventral scales not very small; profile of head concave in mature males D XIV–XVI 12–13

Table 119

Genus *OREOCHROMIS*

Subgenus *Oreochromis* (part): species in which the jaws are not enlarged in mature males. Caudal truncate.

Species	*niloticus*	*aureus*	*esculentus*	*leucostictus*
Pages	140–193	193–208	209–221	221–230
Habitat (FW = fresh water)	FW, except Nile delta	FW, except Nile delta	FW	FW
Natural geographical area	Senegal to Gambia, Volta to Chad, Nile, Ethiopia, Baringo Fig. 51	Jordan Valley Senegal, Niger, Chad, Nile delta	Lake Victoria	Lakes Albert, Edward/George
Depth % SL	36·5–50·0	35·0–49·0	(37·8)40·5–45·5	38·5–47·0
Scales lat. line	(31)32–33(34)	30–33	(31)32–34(35)	28–31
Depth preorb. % hd.	16·0–22·0	16·0–23·0	16·0–21·0	18·0–23·5
L. lower jaw % hd.	29·0–36·0	29·5–37·0	31·0–35·0(36·5)	29·5–34·0
Lower gill-rakers	(18,19)20–26 (27,28)	18–22	15–21	19–23
Pharyngeal				
L. % hd.	28·0–33·4	23·8–31·1	(30)33·0–38·0	28·8–36·6
mean	29·8–32·1*	27·68	33·62	32·74
blade/dent.	0·56–1·55	0·70–1·36	1·4–2·3	1·3–3·0
Anal spines	III	III	III	III(IV)
Other markers	C with regular vertical stripes in most populations Margin of D grey or black	C with less regular markings. D and C in ♂ with red margins	Breeding ♂ red and black D without red margin	Dark olive green with many white or greenish spots. Breeding ♂ with D margin dark green or red

*In samples from different populations

Table 119 (cont.)

Genus *OREOCHROMIS*

Subgenus *Oreochromis* (part): species in which the jaws are enlarged in mature males. Caudal truncate.

Species	*s. spilurus*	*s. niger*	*korogwe*	*u. urolepis*	*u. hornorum*
Pages	231–250	251–260	271–276	276–291	276–291
Habitat	fresh to salt water	FW	fresh to brackish	fresh (to brackish?)	fresh to brackish
Natural geographical area	Coastal rivers of Kenya and Somalia	Athi R.	Lower Pangani	Rivers Rufigi, Kingani and Mbemkuru	Wami system and Zanzibar
Depth % SL	37·0–46·5	38·0–54·0	37·0–45·5	41·5–48·0	38·0–45·5
Scales lat. line	29–31	30–32	29–31	30–31	30–32
Depth preorb. % hd.	17·0–22·0	16·5–23·5	19·5–24·5	23·0–28·5	20·0–25·0
Lower jaw % hd.	33·0–43·0	33·0–45·0	35·0–45·0	31·5–47·0	33·0–50·0
Lower gill-rakers	16–19	15–19	14–16(17)	20–25(27)	18–26
Pharyngeal	N=15				
L. % hd.	29·6–34·3		25·7–31·5	28·2–34·6	25·6–33·5
mean	31·6		28·06	31·6	30·07
blade/dent.	0·6–1·5		0·9–1·3	0·9–1·3	0·8–1·3
Anal spines	III (IV)	IV–VI	III–IV	III	III
Other markers	Yellow-buff with orange lappets and blue lower fins. Breeding ♂ often blue with black fins	As *s. spilurus*	Grey or dark green. Ripe ♂ with D margin red and dark bars on lower half of body	♀ and non-breeding ♂ with 2-4 mid-lateral blotches. ♂ dark to near black, with red D margin and upper half of C	♀ as *urolepis*, breeding ♂ black with narrow red D margin

Table 119 (cont.)

Genus *OREOCHROMIS*

Subgenus *Oreochromis* (continued): further species in which the jaws are enlarged in mature males. Caudal truncate.

Species	*mossambicus*	*mortimeri*	*andersonii*	*p. placidus*	*p. ruvumae*
Pages	292–315	316–323	323–331	333–340	340–342
Habitat	FW to sea water	FW, salt-tolerant	FW	FW (and brackish?)	FW and brackish
Natural geographical area	Lower Zambezi, Limpopo and eastern rivers southwards Fig. 78	Middle Zambezi & tributaries	Upper Zambezi, Kafue, Okavango, Cunene	Lower Zambezi to Sodwana Fig. 78	Ruvuma R. Fig. 78
Depth % SL	36·0–49·5	39·0–46·0 (51·5)	39·0–50·5	37·0–53·5	34·0–41·0
Scales lat. line	30–32	30–32	31–35	30–32	30–32
D. preorb. % hd.	20·0–22·7 (24·5)	19·0–24·0	18·0–25·0	19·5–25·0	18·5–23·0
Lower jaw % hd.	32·0–45·5	32·0–44·0 (46)	29·0–36·0(42)	30·5–42·0	30·0–37·0 (41·5)
Lower gill-rakers	(14,15)16–19 (20)	16–20	(20)21–25 (27)	16–20	16–18
Pharyngeal L. % hd.	28·1–33·8	29·0–31·0	28·5–36·0	28·2–35·0	33·0 & 33·3
mean	31·15	29·9	31·6	30·8	(N=2)
blade/dent.	0·7–1·35	0·7–1·5		0·6–1·15	0·85
Anal spines	III	III	III	IV(V)	(III) IV
Other markers	Breeding ♂ black, with white lower parts of head and red margins of D and C	Breeding ♂ dark purple to black. D and C with red margin	2-4 mid-lateral black spots; D & C red-edged or C & A with red more extensive D XVI–XVIII 11–14	No white lower parts of head in breeding ♂	

Table 119 (cont.)

Genus *OREOCHROMIS*

Subgenus *Oreochromis* (continued): further species in which the jaws are enlarged in mature males. Caudal truncate.

Species	*s. shiranus*	*s. chilwae*	*p. pangani*	*p. girigan*	*jipe*
Pages	343–356	348–356	358–363	358, 363–6	366–369
Habitat	FW	Alkaline water	FW	FW	FW
Natural geographical area	Lake Malawi Upper Shire	Lake Chilwa	Upper Pangani	Lake Jipe	Lake Jipe
Depth % SL	36·0–45·0	39·5–49·5	(33)35·5–42·0	37·0–43·5	34·0–40·5
Scales lat. line	31–32(33)	31–32(33)	33–36	33–36	33–36
D. preorb. % hd.	20·5–27·5	18·5–24·0	20·5–25·0	18·5–23·0	19·0–22·0
Lower jaw % hd.	33·0–44·5	29·0–41·5	30·0–41·0	30·0–36·0 (40)	28·5–33·5
Lower gill-rakers	16–21	16–19	16–21	17–20	18–22
Pharyngeal L. % hd.	29·5–32·0	29·0–34·0	28·2–30·3	28·0–30·8	32·7–36·5
mean	31·7	31·8	29·2	29·8	34·5
blade/dent.	0·8–1·26	0·9–1·2	1·0–1·3	0·4–0·8	0·8–1·4
Anal spines	(III)IV(V)	(III)IV	III	III	III or IV(V)
Other markers	Olive green, yellow ventrally	Silvery, darker above.	Pectoral 29–37% SL	Pectoral (30)32–37·5	Pectoral 34–41·2% SL
	Males darker to black, with orange lappets	Males darker to nearly black, with red lappets	Scales with dark centres and golden-yellow edges		
			Phar. teeth moderate	Phar. teeth coarse	Caudal fin with dark vertical stripes. Phar. teeth very fine

Table 119 (cont.)

Genus *OREOCHROMIS*

Subgenera:	*Oreochromis* (concl.)	*Alcolapia*	*Vallicola*
Species	*hunteri*	*alcalicus*	*amphimelas*
Pages	369–373	375–391	375–7, 391–404
Geographical area	Lake Chala, Kilimanjaro	Lakes Natron and Magadi	Lakes Manyara, Eyasi, Kitangiri and Singida
Habitat	FW	warm alkaline waters	fresh and alkaline waters
Depth % SL	30·5–34·4	29·0–39·0	31·5–40·0
Scales lat. line	34–38	25–30	30–34
D. preorb. % hd.	20·5–22·0	17·0–24·0	12·5–16·5
Lower jaw % hd.	31·0–36·0	30·0–38·0	32·5–37·0
Lower gill-rakers	18–21	9–14	12–16
Pharyngeal			
L. % hd.	30·8 & 33·5	(27·5)29·2–36·5	29·1–32·1
mean	(N=2)	31·3	30·84
blade/dent.	1·0–1·45	1·3–2·1(3)	1·1–1·98
Anal spines	III	(II)III	III
Other markers	Scales of chest & belly very small. Length of caudal ped. 1·2–1·4 times its depth. Microbranchiospines pres. D XVI–XVII 11–13	Scales of chest & belly very small usually non-imbricating. P. not more than 28% SL. No micro-branchiospines D IX–XIII (XIV) 11–15	Scales of chest & belly very small. P. 23–32% SL. Upper profile concave in large fishes. No microbranchiospines D XII–XIV 11–12

Table 119 (cont.)

Genus *OREOCHROMIS*

Subgenus *Nyasalapia* (part): Anal spines III. Males with genital tassel.

Species	*lepidurus*	*angolensis*	*macrochir*	*variabilis*
Pages	409–411	405–409	435–453	412–422
Habitat	Brackish?	FW (and brackish)	FW	FW
Natural geographical area	Lower Zaire	Lower Quanza and Bengo	Upper Zambezi, Okavango, Cunene, Kafue, Bangweulu, Mweru basin & Lufira, Lulua, Luembe.	Lakes Victoria and Kyoga and associated rivers
Depth % SL	38·5–48·0	38·0–44·0	43·0–56·0	39·0–47·0
Scales lat. l.	29 or 30	29–32	(29)30–33	31–33
D. preorb. % hd.	20·5–24·5	18·0–22·0	20·0–27·0	18·5–26·0
Lower jaw % hd.	30·0–34·0	29·0–34·0	27·0–36·0	27·0–35·0
Lower gill-rakers	19–24	21–26	20–26	17–23
Pharyngeal				
L. % hd.	34·3 & 38·3	37·2–39·8	31·5–38·0	32·0–35·5
mean	(N=2)	38·3	35·58	33·55
blade/dent.	2·0 & 2·3	1·1–1·9	1·0–1·9	1·0–1·5
Interorb. w.	36·2–42·0	33·0–41·3	34·5–48·0	38–48
Caudal	Densely scaly in adult, with reticulate pattern	Not densely scaly; truncate	Not densely scaly; truncate	Not densely scaly; no vertical stripes
Other markers		Pelvic fin, as well as D, C & A with white spots. Flank with iridescent spots	Head green, in males dark, iridescent	

Table 119 (cont.)

Genus *OREOCHROMIS*

Subgenus *Nyasalapia* (part): Anal spines III. Males with genital tassel.

Species	*upembae*	*malagarasi*	*rukwaensis*	*karomo*
Pages	422–426	426–430	430–434	482–488
Habitat	FW	FW	FW	FW
Natural geographical area	Upembe region Lualaba & Luvua rivers	Malagarazi R. & swamps	Lake Rukwa basin	Malagarazi R. & swamps
Depth % SL	43·0–45·0	41·0–49·0	43·5–51·0	39·5–46·5
Scales lat. line	28–31	30–32	30–32	29–31
D. preorb. % hd.	19·0–24·0	20·0–23·5	20·0–26·0	20·5–24·5
Lower jaw % hd.	29·0–34·5	28·0–34·0	30·0–38·5	33·0–38·0
Lower gill-rakers	20–25	20–24	20–22	18–20
Pharyngeal L. % hd.	32·5–33·0	33·8–38·0	32·5–35·0	*c.*38·0
	(N=3)	(N=4)	(N=3)	(N=1)
mean blade/dent.	1·1–1·5	1·0–1·4	0·9–1·5	nearly 2
Interorb. w. % head	38·5–43·5	37·0–43·5	34·5–40·0	37·0–41·5
Other markers	Caudal scaly, with narrow vertical stripes	Caudal less scaly, with no melanin-pattern or faint reticulations	Caudal not scaly. Body without dark blotches, plain or with grey vertical bars	Caudal not scaly. Body with dark mid-lateral blotches. Teeth all tricuspid in adult
	2–4 large dark blotches along the flanks			

Table 119 (cont.)

Genus *OREOCHROMIS*

	Subgenus *Nyasalapia* (concl.)	Subgenus *Neotilapia*
	The Malawi flock. See pp. 457–481 for distinctions between the species.	*O. (Ne.) tanganicae* pp. 496–502
Habitat	FW	FW
Natural geographical area	Lake Malawi and Upper Shiré R.	Lake Tanganyika
Depth % SL	35·0–44·5	43·5–51·0
Scales lat. line	32–35	(31, 32)33(34)
D. preorb. % head	21·0–26·5	24·5–30·5
Lower jaw % head	30·0–39·5	31·0–38·0
Lower gill-rakers	17–22	22–26
Interorb. w. % head	44·0–55·5	39·0–46·0
Pharyngeal		
L. % head*	34·5–44·0	35·0–40·5
blade/dent.*	1·0–3·5	1·3–1·7
Caud. ped. l/d	1·0–1·5	0·7–1·0
Caudal fin	Scaly, emarginate	Not scaly, slightly emarginate
Teeth	Outermost bicuspid, but in large females with a varying admixture of tricuspids	All tricuspid in adults

* See Table 110.

Key to the species of *Sarotherodon*

1a	Lower gill-rakers 12–19 (20)		2
1b	Lower gill-rakers (18) 19–27		5
2a	Scales in lateral line series 27–30		3
2b	Scales in lateral line series 30–32		4
3a	Length of caudal peduncle 0·6–0·9 of its depth; usually black patches on head and body; brackish water in West Africa	***melanotheron***	p. 41
3b	Length of caudal peduncle 0·5–0·6 of its depth; no black patches, faint vertical bars on body; near border of Ivory Coast and Liberia, fresh water	***tournieri***	p. 124
4a	Silver-grey, with mid-lateral black band interrupted on anterior part of caudal peduncle; length of head 33·0–38·4% SL; teeth with slender shafts and broad crowns; in 4–7 rows; Barombi Mbo, Cameroon	***lohbergeri***	p. 75

4b Dark grey or green; length of head 37–45% SL; teeth very small, in 3–6 rows; Barombi Mbo, Cameroon . . . . ***linnellii*** p. 84

5a Caudal moderately emarginate or truncate 6

5b Caudal deeply emarginate. Guinée to Liberia . . . . ***caudomarginatus*** p. 134

6a Pharyngeal bones massive, median length of lower 40–50% length of head; Barombi Mbo, Cameroon . . . . ***steinbachi*** p. 79

6b Lower pharyngeal bone not longer than 43·5% length of head 7

7a Scales in lateral line series 27–30; length of head 33·6–39·5% SL; total D rays 24–27; Rivers Nyong, Ntem, Ivindo and upper Ja . . . . ***mvogoi*** p. 70

7b Scales in lateral line series (28) 29–32 8

8a Length of head 39–48% SL; toothed area of lower pharyngeal small, its length contained 2–3 times in that of blade; total dorsal rays 26–28; Barombi Mbo, Cameroon . . ***caroli*** p. 84

8b Length of head 31–39% SL; toothed area of lower pharyngeal broad 9

9a Total dorsal rays 27–30 (mode 28 or 29); upper profile of snout straight or slightly decurved; length of head 32·5–39% SL; widely distributed in the Levant, Nile system, West Africa excluding Sierra Leone and Liberia . . . . ***galilaeus*** p. 94

9b Total dorsal rays 29–31; upper profile of snout steeply decurved; length of head 31–35% SL; West Africa from the Casamance to St John rivers, Liberia . . . ***occidentalis*** p. 128

Key to the species of *Oreochromis*

Two populations are excluded from this key, namely *O. (Oreochromis) niloticus filoa* (p. 167) from hot springs near Addis Ababa, and *O. (Nyasalapia) salinicola* (p. 454) from saline springs in the Lufira basin. In some cases there may be two paths leading to one species.

1a Microbranchiospines present; 5 canal openings in the preorbital bone (Fig. 16) 2

1b No microbranchiospines; 4 openings in the preorbital bone (Fig. 131) (subgenera ***ALCOLAPIA*** and ***VALLICOLA***) 20

2a Genital papilla of male not prolonged into tubercles and filaments 3

2b Genital papilla of mature male prolonged into tubercles and filaments (subgenus ***NYASALAPIA***) 21

3a All teeth of jaws tricuspid with slender shafts in adults; scales of lateral line series usually 33; Lake Tanganyika (subgenus ***NEOTILAPIA***) . . . . ***tanganicae*** p. 496

3b Outermost teeth of jaws bicuspid or in adults with an admixture of tricuspids or unicuspids (subgenus ***OREOCHROMIS***) 4

4a Jaws of mature males not greatly enlarged, length of lower 29–37% length of head . . . 5

4b Jaws of mature males greatly enlarged, lower reaching maxima of 38–50% length of head . 9

5a Anal spines III 6

5b Anal spines III or IV, usually IV; caudal fin with vertical stripes; length of lower pharyngeal bone 32·7–36·5% length of head; Lake Jipe and (introduced) upper Pangani . . ***jipe*** p. 366

6a Scales in lateral line series 30–35, usually 32 or 33 7

6b Scales in lateral line series 28–31; no vertical stripes on caudal fin; white spots on body, especially above anal fin; basins of Lakes Albert and Edward/George; introduced into Lakes Victoria and Naivasha . . . . ***leucostictus*** p. 221

7a Caudal fin with regular vertical black stripes throughout its depth, only in Ethiopia often running into a reticulum in middle of fin; length of lower pharyngeal bone 28·0–33·4% length of head; depth of preorbital bone not exceeding 22% length of head; Soudanian subregion of West Africa; Yarkon River in Israel; Nile system including Lakes Albert, Edward/George, Turkana, Tsana; other Ethiopian lakes; Lakes Baringo, Kivu, Tanganyika; introduced into Lake Victoria and many other places . . . . ***niloticus*** p. 140

7b Caudal fin in adult without regular vertical stripes 8

8a Breeding male predominantly blue with red or pink margin to dorsal fin; margin of caudal fin bright pink; dorsal spines XV–XVII, mode XVI; length of lower pharyngeal bone 23·8–31·1% length of head . . . . ***aureus*** p. 193

8b Breeding male reddish, with extensive black markings and no red margin to dorsal fin; dorsal spines XVI–XVIII, mode XVII; lower pharyngeal bone (30) 33–38% length of head; Lake Victoria and (introduced) northern waters of Tanzania ***esculentus*** p. 209

8c Breeding male dark with red margins to dorsal, caudal and anal fins; females and non-breeding males with 3–5 conspicuous mid-lateral black blotches and a more dorsal series of 3–4; length of lower pharyngeal bone 28·6–36·0% length of head; Upper Zambezi, Kafue, Okavango and Cunene ***andersonii*** p. 323

9a Lower gill-rakers 14–20 (21); anal spines III–VI 10

9b Lower gill-rakers 18–26 (27); anal spines III 17

10a Anal spines IV–VI; Upper Athi system and upper tributaries of Tana, Kenya; introduced in many Kenyan farm dams ***spilurus niger*** p. 251

10b Anal spines IV, rarely III or V 11

10c Anal spines III or IV in about equal numbers; lower gill-rakers 14–16 (17); Lower Pangani in fresh or brackish water ***korogwe*** p. 271

10d Anal spines III, occasionally IV 13

10e Anal spines III 14

11a Caudal peduncle not longer than deep 12

11b Caudal peduncle longer than deep ***hunteri*** p. 369

12a Lower pharyngeal teeth fine (Fig. 44); Lake Malawi basin ***shiranus*** p. 343

12b Lower pharyngeal teeth coarser (Fig. 111); Rovuma River and lower parts of Zambesi; Lower Shiré, lower Sabi (Save) and eastern rivers southward to Sodwana (27°32´S) ***placidus*** p. 333

13a Lower gill-rakers 13–19; pectoral fin in fishes of 45–67 mmSL 31–41%SL; jaws slender (Fig. 86; coastal rivers of Kenya and Somalia ***spilurus spilurus*** p. 231

13b Lower gill-rakers 13–16; pectoral fin in fishes of 36–63 mmSL 28–34%SL; jaws stout (Fig. 86); pool near Northern Uaso Nyiro ***spilurus percivali*** p. 260

14a Scales in lateral line series 30–32; usual pattern of females and non-breeding males exhibiting a mid-lateral series of 3–5 blotches and a more dorsal of 3–4 15

14b Scales in lateral line series 33–36, each scale except the ventral rows with black and yellow parts, giving a brilliant spotted appearance 19

15a Lower gill-rakers 14–21; pharyngeal teeth fine (Figs 103 & 106) 16

15b Lower gill-rakers 18–27 17

16a Breeding males dark iridescent purple to nearly black, with red dorsal and caudal margins; Middle Zambezi and tributaries ***mortimeri*** p. 316

16b Breeding male black with white lower parts of head and red edges to dorsal and caudal fins; Lower Zambezi, Lower Shiré and fresh and brackish waters southwards to Algoa Bay; widely introduced ***mossambicus*** p. 292

17a Scales in lateral-line series 28–30, mode 29; dorsal spines XIV–XVI, mode XV; body without lateral blotches; Ogowe, Chiloango, Kouilou ***schwebischi*** p. 489

17b Scales in lateral-line series 30–32; dorsal spines XVI–XVIII, mode XVI or XVII 18

18a Soft anal rays 9–11, usually 10 or 11; depth of preorbital bone at SL over 240 mm more than 25% length of head; caudal fin with narrow black vertical stripes or with a dense covering of scales; eastern rivers of Tanzania from Wami to Mbemkuru ***urolepis*** p. 276

18b Soft anal rays 11–13, modes 11 or 12 in different populations; depth of preorbital not more than 25% length of head; caudal fin without vertical stripes or scaly covering; Upper Zambezi, Kafue, Okavango, Cunene ***andersonii*** p. 323

19a Pharyngeal teeth fine; anterior blade of lower pharyngeal as long as or longer than the median length of the dentigerous area; Pangani River ***pangani pangani*** p. 358

19b Pharyngeal teeth rather coarse (Fig. 124); anterior blade of lower pharyngeal shorter than median length of dentigerous area; Lake Jipe ***pangani girigan*** p. 363

20a Preorbital naked, deep, at SL 34–127 mm 17–24% length of head; lower gill-rakers 9–14; canals of lateral line system very narrow; Lakes Natron and Magadi, introduced into Lake Nakuru ***alcalicus*** p. 375

20b Preorbital scaly, narrow, at SL 57–269 mm 12–17% length of head; lower gill-rakers 12–16; canals of lateral line system well developed; Lakes Manyara, Eyasi, Kitangiri and Singida ***amphimelas*** p. 375

21a Teeth of jaws in adult all tricuspid with slender shafts 22

21b Most outer teeth in adults bicuspid 23

22a Teeth all approximately the same size; jaws produced, with broad dentigerous areas; females and non-breeding malesd with a series of 3–5 lateral blotches; Malagarazi system . . . . . . ***karomo*** p. 482

22b Inner teeth much smaller than outermost; jaws not produced; females and non-breeding males with vertical black bars on a silvery ground; Lake Malawi . . . . . . ***karongae*** p. 457

23a Caudal fin densely scaled in adult 24

23b Caudal fin not densely scaled 29

24a Length of caudal peduncle equal to or (usually) less than its depth; interorbital width 35·5–43·6% length of head 25

24b Lenth of caudal peduncle equal to or greater than its depth; interorbital width 44·6–55·5% length of head; females and non-breeding males usually with dark vertical bars on upper half of body; Lake Malawi basin 26

25a Total dorsal rays 25–27, mode 27; blade of lower pharyngeal bone 2·0–2·3 times the median length of the dentigerous area; caudal fin with reticulate pattern; Lower Zaire in brackish water . . . . . . ***lepidurus*** p. 409

25b Total dorasl rays 26–29, mode 28; blade of lower pharyngeal bone 1·1–1·5 times the median length of the dentigerous area; caudal fin with vertical stripes; Upemba region and Lualaba . . . . . . ***upembae*** p. 422

26a Breeding male black, with white margin to dorsal fin 27

26b Breeding male pale iridescent blue, with top of head and nape white . ***squamipinnis*** p. 457

27a Lower pharyngeal bone with long blade, 2·1–3·2 times the median length of the small dentigerous area . . . . . . ***lidole*** p. 457

27b Lower pharyngeal bone with a broad dentigerous area 28

28a Length of anterior blade of lower pharyngeal bone 1·3–2·1 times the median length of the dentigerous area; length of head 34·7–39·8% SL . . . . . . ***saka*** p. 457

28b Length of anterior blade of lower pharyngeal bone 1·0–1·7 times the median length of the dentigerous area; length of head 30·8–36·0% SL . . . . . . ***karongae*** p. 457

28c Length of anterior blade of lower pharyngeal bone 1·2–1·4 times the median length of the dentigerous area; length of head 37·6–40·5% SL; Lake Chungruru ***chungruruensis*** p. 465

29a In mature males outer teeth becoming unicuspid and the posterior upper teeth enlarged; mature males with white (as preserved) spots on pelvic fins; Quanza and Bengo rivers . . . . . . ***angolensis*** p. 405

29b In large males some outer teeth becoming unicuspid, but not enlarged; no white spots on pelvic fins 30

30a Females and non-breeding males plain or with 3–5 mid-lateral blotches, if not with maradadi colouring; interorbital width 37–48% length of head in fishes of 105–224 mm SL . . . 31

30b Adults without stripes or blotches except (in some) faint facultative vertical bars . . . 32

31a Lower gill-rakers 20–24, $\bar{x}=21\cdot1$ (Table 103); no maradadi individuals known; Malagarazi system. . . . . . ***malagarasi*** p. 426

31b Lower gill-rakers 17–23, $\bar{x}=19\cdot54$; some females with maradadi colouring (Fig. 148); Lake Victoria basin, Lake Kyoga complex and Victoria Nile . . . . . . ***variabilis*** p. 412

32a Interorbital width 34·6–40·1% length of head; profile straight; Lake Rukwa basin . . . . . . ***rukwaensis*** p. 430

32b Interorbital width 34·5–48·0% length of head; profile decurved, often steeply; Upper Zambezi, Okavango, Cunene, Kafue, Bangweulu Region; Luapula, L. Mweru, Lufira, some upper tributaries of the Kasai . . . . . . ***macrochir*** p. 435

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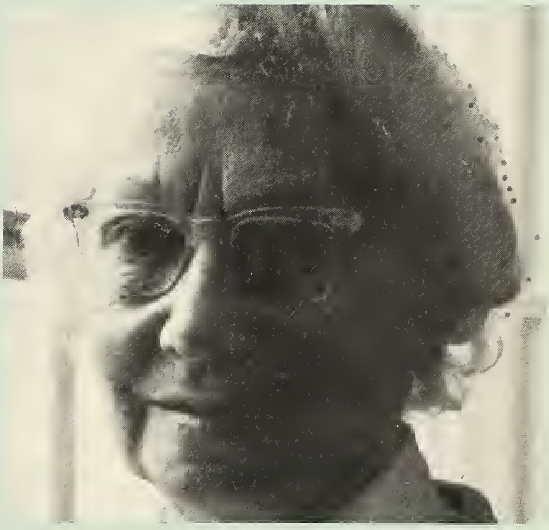

Dr Ethelwynn Trewavas has devoted much of her distinguished career in ichthyology to the study of cichlid fishes, and in particular the African tilapia species. Her appreciation of the importance of biological factors in the understanding of cichlid taxonomy has taken her into the field on several occasions, and has brought her into close contact with fish culturists and fishery workers. Thus, this monograph has been written with the problems of these workers, as well as those of museum-bound taxonomists, very much in mind.

Before her retirement in 1961 Dr Trewavas was Deputy Keeper of Zoology in the British Museum (Natural History), where for many years she was also curator of fishes, and where she has continued her researches into cichlid and other fishes long after her formal retirement.

Jacket design by Keith Whitehead