THE RELATIONSHIP BETWEEN *TILAPIA NIGRA* (GÜNTHER) AND *T. MOSSAMBICA* PETERS IN THE EASTERN RIVERS OF KENYA

BY

P. J. P. WHITEHEAD

*Ministry of Forest Development, Game & Fisheries, Kenya**

(With 8 figures in the text)

In the Athi river, Kenya, an upper river population of cichlid fishes has been described as *Tilapia nigra*, closely resembling *T. mossambica* in the lower Athi, but distinguished by a higher anal spine count (four to six as against three, rarely four, spines). Field studies indicated a steady increase in anal spine numbers with altitude, and a slight overlap is found in morphometric and meristic characters between the two species. *T. nigra* is however geographically isolated from *T. mossambica* in the Athi river by the Lugards Falls, and the consequent reproductive isolation, coupled with meristic and colour differences, is here considered indicative, if not of complete, at least of incipient speciation.

CONTENTS

INTRODUCTION

Tilapia nigra (Günther) was previously the only cichlid fish known from the Athi river, Kenya (Trewavas 1937), but subsequent collections from the lower reaches of this river have included specimens with three anal spines, and these

*Present address: Department of Zoology, British Museum (Natural History)

were considered to be *T. mossambica* Peters (Whitehead 1954). In the Tana river (see Fig. 1) *T. mossambica* is common in the lower reaches, and *T. nigra* has been recorded from a tributary higher up (Whitehead 1959 a). Specimens originally named *T. nilotica* (L), *T. nyirica* Lönnberg and *Chromis spilurus* Günther (from the southern Eusso Nyiro*, Mwangadan and Simba rivers) were all considered to be *T. mossambica* by Trewavas (*loc. cit.*). There are no other cichlids in the Athi or Tana rivers, except as recent introductions.

T. nigra and *T. mossambica* closely resemble each other, but the former has been described as having four or five spines in the anal fin, never three, whereas three is the rule in *T. mossambica*. There are however records of four-spined *T. mossambica* (e.g. one out of ten specimens from the Eusso Nyiro—Trewavas, *loc. cit.*) but hitherto such four-spined *T. mossambica* have been considered rare individual variants, and the use of anal spine counts as a means of distinguishing between the two species has been a useful one. But in the lower thirty miles of the Athi river, trapping records have shown that, although three-spined fishes predominate, four-spined fishes comprise up to 25 per cent. of the population (Whitehead 1954). This high proportion implied that *T. nigra* was present. Now however, breeding experiments have shown that four-spined lower Athi fishes can produce both three- and four-spined progeny (but never five), whereas three-spined fishes have never been produced by four- and five-spined *T. nigra* derived from other parts of the Athi river. I conclude that the lower Athi fishes belong to a population of *T. mossambica* in which the four-spined variant is unusually common.

There is however a population of *T. mossambica* in the pools below Buffalo Springs (affluent to the Eusso Nyiro near Isiolo) in which four-spined fishes comprised 36 per cent in a count of ninety fishes. This is the only other population of *T. mossambica* known where the four-spined variant is so abundant. A four-spined population of *T. mossambica*-like fishes is found in the Rovuma river, but their identity has not yet been established.

Stocks of *T. nigra* have been held at the Inland Fishery Research Station at Sagana, Kenya, since 1952. These fishes were ultimately derived from the upper reaches of the Athi river, perhaps about twenty years ago, and were transferred from dam to dam until eventually reaching Sagana. The Sagana population, like that in the upper Athi river, contains a majority of five-spined fishes, but four-spined fishes may comprise up to 20 per cent of the population. Since the two species occur in the same river system, and appear to overlap in the middle reaches of the river, the problem arose whether the two were in fact specifically distinct, and if so, what criteria could be used to distinguish four-spined individuals of each. There is some evidence that anal spine numbers tend to increase as one proceeds up the Athi river, and in ponds the two 'species' have readily hybridized. But on the Athi river, Lugards Falls provide a distinct break between the two populations, three-spined fishes not

---

* There are two Eusso Nyiro rivers in Kenya (the name is derived from the Masai and means a muddy river). The southern Eusso Nyiro runs within the Rift Valley, passes just to the west of Lake Magadi, and empties into the northern end of Lake Natron. All other references in this paper are to the northern Eusso Nyiro, an eastward-flowing river to the north of the Tana river (see map), which becomes lost in the Lorian Swamp.
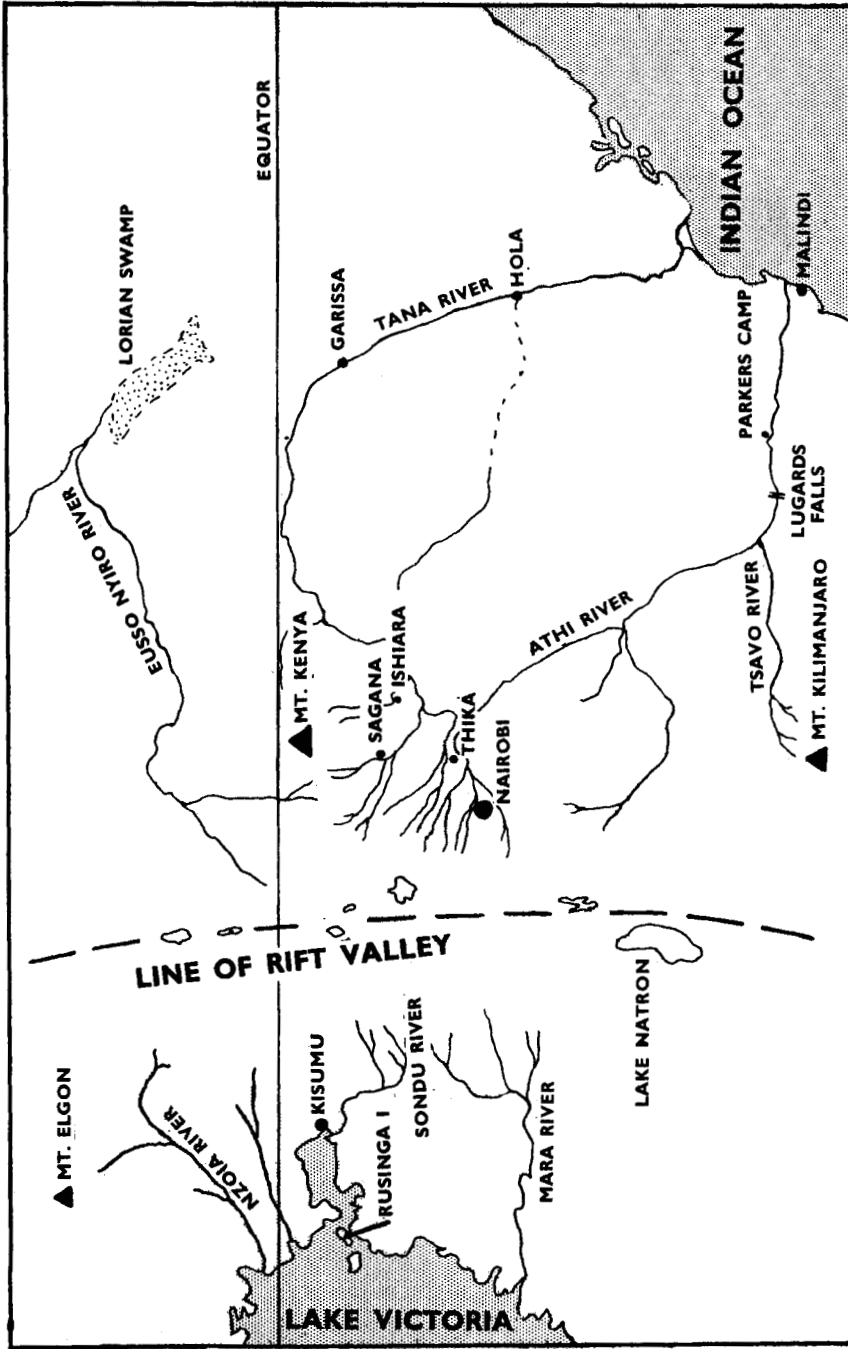
Fig. 1—Sketch map showing main river systems in Kenya.

occurring above the falls, and five-spined fishes rapidly becoming absent below the falls.

From the evidence presented here, I lean to the view that *T. nigra* should be treated for the time being as a valid species, distinct from *T. mossambica*, and hereafter reference to a fish as *T. nigra* or *T. mossambica* implies that it satisfies one or other of these two groups of criteria :

T. nigra : four, five or six anal spines, and not less than sixteen dorsal spines (two exceptions to the latter out of about five hundred fishes) ; male breeding colours as described for *T. nigra* ; ultimately derived from the upper Athi river (above Lugards Falls).

T. mossambica : three anal spines or a member of a population in which three-spined fishes predominate, and not more than 18 dorsal spines ; male breeding colours as described for *T. mossambica* ; ultimately derived (in my material) from the lower reaches of the Athi or Tana rivers.

The presence of more than three anal spines has been considered of some systematic importance in several cichlid genera, including *Tilapia*, and indeed the generic status of *Astatoreochromis* of Lake Victoria rested until recently mainly on this one character (Greenwood 1959). Boulenger (1916) acknowledged the three-spined condition as primitive, but he did not place great systematic importance on increased anal spination, certainly not as a sole generic character. In the same paper he regarded four and five-spined *Tilapia* from the upper Athi river merely as a variety of *Tilapia nilotica*. On the other hand Hubbs (1918) believed increased spination in that case sufficient cause to give the Athi fishes specific status. The present work strongly suggests that the transition from three to five anal spines is a significant one, but that the intermediate four-spined condition is often misleading from a systematic point of view since it is shared in varying degrees by both *T. nigra* and *T. mossambica*. Had *T. nigra* not been so closely related to *T. mossambica* and had the two been separated by a more complete geographical barrier, then the discrepancy in anal spination would have seemed even more significant. But while four other species of *Tilapia* usually have four anal spines, the upper Athi population represent the only known case where the five-spined condition can predominate and six-spined fishes are found. *T. mossambica* has a wide distribution on the eastern side of Africa, but even four-spined fishes are unusual.

Because of the value of anal spine numbers, both as a taxonomic and a simple field guide, this aspect has been particularly studied in the *nigra-mossambica* complex of eastern Kenya. The following comparison has reduced specific differences between the two species to the four criteria listed above, of which coloration is the most definitive. There are also slight differences in the degree of allometry shown by the proportions of the premaxilla and the caudal peduncle, but these are less readily defined. Since the two species will interbreed in ponds, and may well do so in nature, the justification for believing that they are genetically isolated rests on distributional grounds. Further work, especially on the Tana river, may show this assumption to be false, the two forms showing at most incipient speciation which in the Athi river has been reinforced by a physical barrier, Lugards Falls. The present results are therefore an assessment of the problem rather than a final verdict.

A COMPARISON BETWEEN *T. NIGRA* AND *T. MOSSAMBICA*

Distribution

T. mossambica is a widespread species, occurring in most of the eastward-flowing rivers of Africa, from the Webi Shebeli in the north, to East London in the south (as *T. natalensis* M. Web.). Further, since making a mysterious appearance in E. Java in 1939 (Shuster 1952), this fish has now virtually encircled the globe, having been introduced for fish culture purposes in almost every part of the East and West Indies, as well as in India, Pakistan, Hawaii and some of the southern states of America (Chimitz 1955). It is now one of the principal species used at the Fish Culture Research Station at Malacca (Hickling 1959), and also at several smaller stations in the West Indies.

In Kenya, *T. mossambica* has been recorded in the Eusso Nyiro, in the Tana system from sea level to Garissa and again in the Thuchi, a tributary of the Tana at about 3000 feet, in the Athi river below Lugards Falls, in the Voi river at Voi, in the Maji Chumvi river, and in salt pans ten miles north of Malindi. Trewavas (*loc. cit.*) records specimens from the Mwangadan and Simba rivers, the latter a tributary of the Athi. (The Athi river here refers to the river from source to sea and thus includes the 'Sabaki' and 'Galana', terms occasionally used to describe the lower hundred miles of the Athi.) *T. mossambica* has been little used in ponds and dams in Kenya, exceptions being some small ponds near Kilifi (Coast Province) and several experimental irrigation plots on the Hola (Galole) Irrigation Scheme on the Tana river.

T. nigra has a more restricted range, being found mainly in the Athi system above Lugards Falls. Specimens have however been examined from the Thuchi river. This species was first used for fish culture purposes in 1922 (Copley 1958) and has since been stocked into a large number of dams and ponds throughout the country, mainly in areas to the east of the Rift Valley, but also within the Lake Victoria drainage basin. It was introduced into Lake Naivasha in 1926, and from there into Lake Bunyoni in Uganda, where it was apparently ousted by *T. nilotica* (Lowe 1958). It was also introduced (unsuccessfully) into the Belgian Congo (De Bont 1948), and has been used in South Africa. It is the principal species studied at the Inland Fishery Research Station at Sagana (see van Someren 1960).

Lowe (1955) examined specimens of *Tilapia* collected from the Pangani river in Tanganyika and believed some to be *T. nigra*. However, she mentions reports that this species was stocked into streams flowing from the southern side of Mount Kilimanjaro, and thus into the Pangani system. It is likely therefore that *T. nigra* is indigenous to the Athi and Tana rivers only.

Anal spines

Morphology

In both *T. nigra* and *T. mossambica* the first two anal spines are carried on the same interhaemal pterygiophore. Thereafter each pterygiophore carries a single spine or branched ray except the last, which sometimes bears two small branched rays. Apart from the first and last pterygiophores, the remainder show a close similarity in shape, although the articular head becomes progress-

ively smaller in the posterior pterygiophores. Thus the addition of an extra spine does not normally involve structural alteration of the pterygiophore, but the articular head may be larger.

Spines and branched rays also show a basic morphological similarity. But whereas the branched rays are clearly double units, whose proximal ends fit laterally on either side of the articular head of the pterygiophore, the spines are fused along their entire length and appear as single bones. Differentiation
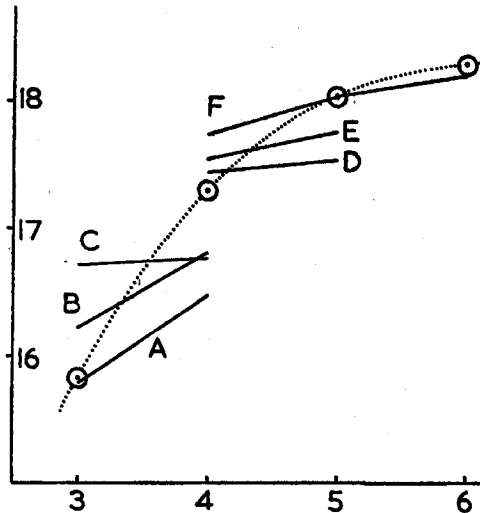

Fig. 2—Correlation between anal spine numbers (abscissa) and average dorsal spine numbers found in each anal spine group (ordinate).

A. 244 *T. mossambica* from the lower thirty miles of the Athi river.
B. 198 *T. mossambica* from Parkers camp, about sixty miles up the Athi river.
C. 91 *T. mossambica*, F_1 generation bred at Sagana from parents derived from the lower thirty miles of the Athi river.
D. 31 *T. nigra* from the Makindu and Isavo rivers, tributary to the Athi river about 130 miles from its mouth. (Figures from Boulenger, 1916.)
E. 54 *T. nigra* from just above Lugards Falls (about 100 miles up the Athi river).
F. 356 *T. nigra* from pond populations at Sagana.
    Dotted curve, the averages for samples A, C and F. For explanation see text.

between spines and soft rays would thus seem to be one of degree, depending on the rays themselves and not on the pterygiophores. But where spines are missing (see below), their place is always taken by a branched ray, and where the first two spines are missing there are always two branched rays articulating with the first pterygiophore ; loss of the first spine only however, does not apparently involve the replacement by a soft ray.

In rare cases, unusual spine counts may result from abnormal development of spines and pterygiophores. Thus in the only three-spined *T. nigra* discovered at Sagana, the spine lengths corresponded with those of the second, third and fourth spines of a normal fish of that size. Confirmation that the first and not the fourth spine was missing was obtained from the first pterygiophore, which carried a single spine, the articulation for the first (anterior)

spine being completely absent. The size and characteristic shape of this pterygiophore showed that it was in fact the first pterygiophore and not the second one. Similarly, in the case of three-spined fishes which appeared amongst stocks of *T. nigra* at the Mwea-Tebere Rice Irrigation Scheme near Sagana, dissection showed that the first and not the fourth spine was missing.

Table 1. Percentage frequency occurrence of four-, five- and six-spined *T. nigra* in Sagana ponds.

	Pond						
	A 1	A 2	A 3	A 4	A 5	Stock B	Mean
4-spine	14·6	19·3	17·8	18·4	24·3	13·3	17·9
5-spine	83·3	80·0	82·2	80·4	74·8	84·4	80·8
6-spine		1·7		0·5	0·9	2·2	1·3

Ponds A 1–A 5 stocked with male fishes taken from Stock pond B. Sample from the latter contained 18% females.

In another specimen of *T. nigra* no anal spines were apparent. Dissection showed that the first pterygiophore carried a minute spine as well as two branched rays. The second pterygiophore, which itself was branched, carried a branched ray, as did the eight subsequent pterygiophores. One and two-spined *T. nigra* have been recorded. In one specimen the first three spines had been replaced by soft rays, but the fourth spine was present. The rare six-spined *T. nigra* are true six-spined fishes, that is, the first (double-headed) pterygiophore bears two spines as usual, and the additional spine is on the fifth pterygiophore. No cases have been found where the first pterygiophore is duplicated.

Table 2. Correlation between hard and soft rays in the anal fin.

(a) Hard rays against total anal rays (*T. nigra* and *T. mossambica*)

		total rays				
		11	12	13	14	15	Mean
	3	2	22	34			12·55
hard	4		11	26	79	10	13·70
rays	5				16	7	14·30
	6				3	2	14·40

(b) Hard rays against soft rays (*T. nigra* and *T. mossambica*).

		soft rays			
		8	9	10	11	Mean
	3	2	22	34		9.55
hard	4	11	26	79	10	9·70
rays	5		16	7		9·30
	6	3	2			8·40

(c) Hard rays against soft rays (F_1 of lower Athi *T. mossambica* grown at Sagana).

		soft rays	
		8	9	10	Mean
hard	3	2	22	34	9·55
rays	4	11	21		8·66

References to partly ossified anal rays (e.g. Lowe, 1955, p. 354) and occasional specimens at Sagana showing this condition, suggested that the addition of an extra spine might in some cases merely involve replacement of a soft ray by a hard one.   A direct, if loose, correlation exists between numbers of anal spines and total number of all anal rays (Table 2 *a*), suggesting addition of an extra ray in the higher spine groups rather than replacement of a soft ray by a spine.   This appears to be supported by the lack of correlation between hard and soft rays (Table 2 *b*), but in this case the range in numbers of soft rays may mask a direct correlation.   In the progeny of the three-spined *T. mossambica* bred at Sagana however, the inverse correlation (Table 2 *c*) indicates replacement of soft by hard rays in the four-spined individuals. Probably both methods of increase in spine numbers occur.

In a sample of 307 juvenile *T. mossambica* from the lower Athi river (11–43 mm total length), it was found that the fourth anal spine when present is not thickened in fishes below 15 mm, although its presence can usually be inferred by the absence of branching and the shortness of this ray relative to the adjacent branched ray.   In this sample the percentage of four-spined fishes in the forty-nine specimens under 15 mm was 8·2, while in the whole sample it was 16·6, suggesting that in fact the fourth spine was not always detectable in the smaller fishes.   In *T. nigra* however, a fourth spine is quite distinct at even 10 mm, whereas the fifth is sometimes doubtful.   Appearing late in ontogeny, the final spine may perhaps be more susceptible to environmental influence than the others.

Variations in anal spine numbers

T. mossambica

The proportion of three- to four-spined *T. mossambica* varies considerably in different parts of the Athi and Tana rivers.   At present no four-spined fishes have been recorded from the Tana below Garissa, but four-spined fishes from the lower Athi have been stocked into ponds at Hola and these will undoubtedly find their way into the Tana.

Basket-trap records over nine months in the lower thirty miles of the Athi river showed a 3 : 1 preponderance of three-spined fishes (Whitehead 1954). The two shoal together, and as noted above, 16 per cent of such a shoal were four-spined.   In the lakes which are connected to the river (either by streams or flooding) the proportion of four-spined fishes may be as high as 34 per cent. (44 fishes from Lake Mekimba) or as low as 0·2 per cent. (374 fishes from a pool connected to Lake Chem Chem).   Further up the Athi river, at Parkers Camp (see map), four-spined fishes actually predominated, with three-spined individuals comprising only 24 per cent of the population, and five-spined fishes occasionally being found.   There would therefore appear to be an increase in anal spine numbers further up the Athi river, as shown in Fig. 8.   The reasons for this are discussed later.

The high proportion of four-spined *T. mossambica* in Buffalo Springs has already been mentioned.   The presence of four-spined *T. mossambica* in the Eusso Nyiro may result from contamination by the Buffalo Springs population.

Ten four-spined *T. mossambica* from the lower Athi river were bred in a shallow ¼ acre pond at Sagana. Forty-one fry were examined, of which 23 per cent had four anal spines and the rest had three. In another pond three-spined *T. mossambica* from the lower Athi were bred, and of fifteen fry recovered, all but one had three anal spines. In a similar experiment carried out previously, four-spined fry comprised 19·7 per cent of the 700 juveniles examined, but on draining the pond a four-spined female *T. nigra* was discovered and it is not certain whether this fish influenced the results. That four-spined lower Athi fishes can produce three-spined progeny is significant since this is not the case with the upper Athi fishes.

If the results of the third breeding experiment were influenced by the female *T. nigra*, then the other two experiments show that the maintenance of the four-spined variant in the lower Athi is dependent on the presence of four-spined fishes, i.e. on a genetic factor.

T. nigra

In the Sagana ponds, five-spined fishes comprise about 80 per cent of the population, the remainder being four-spined, with about 1 per cent six-spined individuals, as shown in Table 1. Natural populations of *T. nigra* have been sampled in several areas, and some dams stocked with *T. nigra* have also been examined.

Locality	Anal spines			Percentage	Total
	4	5	6	five-spined	
Athi river at Yatta	8	141	2	93	151
Lake Naivasha	15	81	3	82	99
Small dam at Solai	24	86		78	110
Athi river at Athi River town	4	8		66	12
Thuchi river	1	2		66	3
Athi above Lugards Falls	44	32		42	76

Boulenger (1916) recorded 48·5 per cent five-spined fishes, and the remainder four-spined, out of 31 *Tilapia* from the Makindu and Isavo rivers, tributary to the Athi. These fishes were *T. nigra*, as shown by their dorsal spine numbers (Fig. 1 and Table 3) and lateral line scale counts (See p. 619).

The proportion of five-spined fishes in the Yatta sample is rather higher than that of Sagana, but the Lake Naivasha sample is very similar, and in both six-spined fishes occur. Comparing the Yatta sample with that taken immediately above Lugards Falls, it appears that the proportion of four-spined individuals decreases further up the Athi river (the sample at Athi River town is too small for comparison).

A 4 : 1 preponderance of five-spined fishes appears to be the general rule, but the method by which this balance is maintained is not known. A few single-pair crosses between four- and five-spined *T. nigra* have been made at Sagana, giving the following results.

Parental spine numbers	Progeny		Total
	Percentage five-spined	Percentage four-spined	
5 × 5	62	38	63
5 × 5	14	86	57
4 × 5	39	61	18
4 × 4	6	94	67

The high proportion of four-spined progeny in all but the first cross is contrary to the predominance of five-spined fishes in the ponds and elsewhere (the parents were derived from the Sagana ponds). The 4×4 cross does
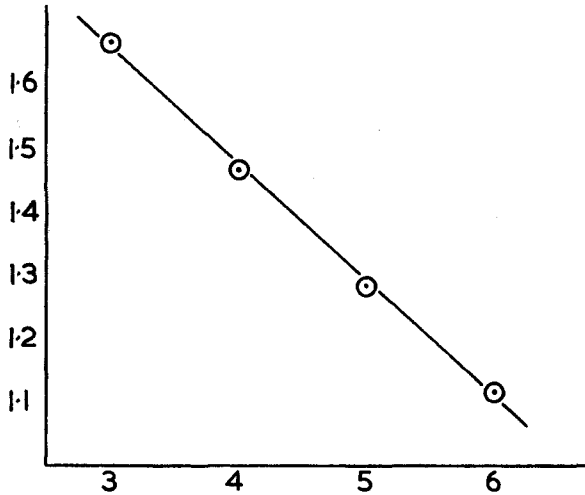

Fig. 3—Correlation between anal spine number (abscissa), and

$$\log_e \left(\frac{\text{mean dorsal spine number}}{\text{anal spine number}} \right),$$

(ordinate), for 626 specimens of T. nigra and T. mossambica (see Table 4).

suggest single gene inheritance, and none of the five-spined parents is known to have been homozygous, but as noted below, the situation may be further complicated by the influence of exogenous factors such as temperature.

Dorsal spines

Numbers of dorsal spines are higher in *T. nigra* than in *T. mossambica* (Table 3). Modal numbers are eighteen for *T. nigra* and sixteen for lower Athi *T. mossambica*, but there is considerable overlap and also some variation in different parts of the Athi river. No specimens of *T. mossambica* with nineteen dorsal spines have been found (540 fishes examined), and in only two specimens of *T. nigra* (out of 487) were there less than sixteen dorsal spines. Of 1012 fishes examined, and distinguished on characters other than dorsal spine counts, mean numbers were under seventeen for *T. mossambica* and over seventeen for *T. nigra* (see Table 3).

Table 3 shows that in both the three- and the four-spined groups of *T. mossambica*, and again in the four- and the five-spined groups of *T. nigra*, there is a tendency for higher mean numbers of dorsal spines further up the Athi river, similar to the trend found in anal spine numbers.

As in the case of the anal fin, an attempt was made to correlate hard and soft rays in the dorsal (Table 5). There is an indication that hard rays may

Table 3—Variations in numbers of dorsal spines in *T. nigra* and *T. mossambica* from various localities in Kenya.

Anal spine count	Species, locality	Dorsal spine count						Mean	Total
		14	15	16	17	18	19		
3	*T. mossambica* (Lower 30 miles of Athi river)	4	47	158	10	—	—	15·79	219
3	*T. mossambica* (Parkers Camp)	1	2	26	11	1	—	16·22	41
3	*T. mossambica* (Ishiara)	—	—	2	5	—	—	16·70	7
3	*T. mossambica* (F$_1$ bred at Sagana)	—	1	33	24	1	—	16·71	58
4	*T. mossambica* (Lower 30 miles of Athi river)	—	—	13	12	—	—	16·48	25
4	*T. mossambica* (F$_1$ bred at Sagana)	—	—	10	21	2	—	16·76	33
4	*T. mossambica* (Parkers Camp)	—	2	39	104	12	—	16·80	157
4	*T. nigra* (Upper Athi*)	—	—	—	9	7	—	17·44	16
4	*T. nigra* (Above Lugards Falls)	—	—	—	13	16	—	17·55	29
4	*T. nigra* (Sagana ponds)	1	1	13	24	136	9	17·73	184
4	*T. nigra* (Athi River town)	—	—	—	1	3	—	17·75	4
4	*T. nigra* (Yatta, Athi river)	—	—	—	—	2	—	18·00	2
5	*T. nigra* (Upper Athi*)	—	—	—	7	8	—	17·53	15
5	*T. nigra* (Above Lugards Falls)	—	—	—	6	19	—	17·76	25
5	*T. nigra* (Yatta, Athi river)	—	—	—	1	17	7	18·00	25
5	*T. nigra* (Athi River town)	—	—	—	—	8	—	18·00	8
5	*T. nigra* (Sagana ponds)	—	—	8	33	83	38	18·04	162
6	*T. nigra* (Sagana ponds, L. Naivasha & Yatta)	—	—	—	1	10	4	18·20	15
6	*T. nigra* (Dam at Njoro, 7,000 ft.)	—	—	—	—	—	2	19·00	2

* Figures from Boulenger (1916).

Table 4. Correlation between numbers of anal and dorsal spines in *T. mossambica* and *T. nigra* together from all localities. See graph, Figure 2.

		Dorsal spines								
		14	15	16	17	18	19	Total	Mean	$\log_e \dfrac{\text{mean dorsal}}{\text{anal}}$
Anal spines	3	4	50	169	15			238	15·82	1·6620
	4	1	1	26	36	136	9	209	17·30	1·4633
	5			8	33	83	38	162	18·04	1·2831
	6				1	10	6	17	18·29	1·1151

Table 5.   Correlation between hard and soft rays in dorsal fin in *T. nigra.*

		soft rays					
		8	9	10	11	Mean	Total
Hard	16			1		10·00	1
rays	17			8	6	10·40	14
	18			89	28	10·20	117
	19	1	1	1		9·00	3

Table 6—Correlation between soft rays in the anal and the dorsal in *T. nigra.*

		Dorsal soft rays			
		9	10	11	Mean
Anal soft rays	9		12	5	10·29
	10	1	68	17	10·16
	11		8	2	10·20
Mean		10·00	9·95	9·87	

replace soft ones in the 19-spined fishes, but insufficient specimens have been examined.

Enlargement of the jaws

Enlargement of the jaws in large males has been considered a characteristic of *T. mossambica* and not of *T. nigra*, the enlargement being less extreme and not a sexual character in the latter species (Trewavas 1937).   At Sagana however,
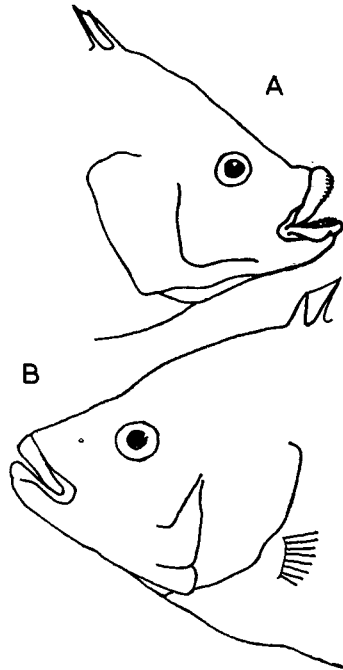
Fig. 4—Elongation of the upper jaw in *T. nigra.*

A.   Extreme condition in male of 305 mm total length.
B.   Female of 354 mm showing no obvious elongation.

large male *T. nigra* over 300 mm total length show extreme enlargement of the upper jaw (Fig. 4A), and some enlargement can be seen in fishes over 200 mm. Enlargement is not found in female *T. nigra*. In the largest female examined (354 mm) the snout and jaw profile did not differ from that found in smaller females and juveniles (Fig. 4B).

Enlargement of the upper jaw is due to elongation of the premaxilla, the horizontal ramus showing positive, and the vertical ramus (the pedicel) showing negative, allometry with standard length (or head length—see Table 8 and Fig. 7). Elongation starts much earlier in *T. mossambica* however and the vertical ramus shows more pronounced negative allometry than is found in *T. nigra* (Table 7). In the same table there is some indication that the lower jaw is slightly larger in *T. mossambica* and it too may show positive allometry.

Lowe (1955) has shown that a similar elongation occurs in *T. girigan*, *T. pangani*, and to a lesser extent in *T. jipe* also, species which are closely related to *T. mossambica*. She suggested that elongation may be partly a growth and partly a sexual character, and this is borne out in *T. nigra* by premaxilla measurements of a female of 282 mm standard length (Table 8). The premaxilla proportions of this fish resemble those of a male of about 170 mm but the horizontal ramus is longer, and the vertical ramus shorter, than would be expected in males of a smaller size.

Elongation does not appear to have an obvious functional significance, and would even appear to hinder grazing activities, although it may assist in nest-building, particularly since this is undertaken by the male. *T. nigra* filter feeds, but also browses on epiphytic algae, but in large males showing extreme elongation of the jaws, the upper and lower teeth cannot be apposed and indeed in some cases the mouth cannot be closed completely.

Dentition

A further characteristic of *T. mossambica* is the simplification of the teeth in the upper and lower jaws, especially in the outer series, the teeth becoming conical. This condition is even more marked in *T. m. korogwe*, where it occurs also in females (Lowe 1955). At Sagana, male *T. nigra* develop unicuspid, conical teeth, but this has been found in only the largest females (over 250 mm standard length). Like elongation of the jaws, simplification of the teeth appears to be partly a growth and partly a sexual character. Since female *T. nigra* do not engage in nest-building activities, simplification of the jaw teeth probably does not result from attrition, particularly since the median teeth are the last to be affected.

Conical teeth are usually found in the outer series of teeth in both jaws in male *T. nigra* and *T. mossambica* of about 180 mm standard length, the simplification starting at the lateral edges of the jaw and progressing towards the centre. Later, at about 250 mm, the inner rows of teeth also become conical again starting from the edges. The degree of simplification varies between individuals, as Fryer (1957) found with the Lake Nyasa cichlid, *Gephyrochromis lawsi* Fryer, in which simplification occurred in some populations but not in

others. In large males, showing extreme enlargement of the jaws, the function of the outer rows of teeth is not obvious, the majority being directed forwards (see Fig. 4A).

Pharyngeal dentition is identical in the two species, although there is some individual variation in the shape and size of the toothed area and proportions of the lower pharyngeal bone. In small fishes under 100 mm total length the
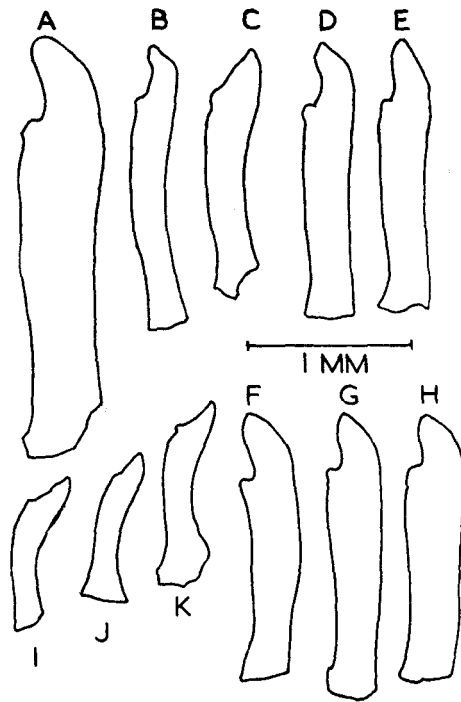

Fig. 5—Lower pharyngeal teeth in *T. mossambica* and *T. nigra*.

T. nigra 320 mm total length. A, Posterior tooth ; B, Middle tooth ; C, Anterior tooth. *T. nigra* 192 mm total length. D, E and F, Posterior teeth ; I and J, Anterior teeth. *T. mossambica* 195 mm total length. G and H, Posterior teeth ; K, Anterior tooth.

(From camera lucida drawings.)

posterior edge of the toothed area tends to be slightly indented, but in specimens over 200 mm this edge becomes straight or even a little convex in outline. The anterior teeth in the lower pharyngeal are hook-shaped and often unicuspid, but the second (anterior) tooth cusp becomes progressively more developed in the posterior series of teeth (Fig. 5). This cusp may become reduced in very large fishes, but there is no simplification comparable to that found in the jaw teeth.

In shape, size and numbers, the micro-gillrakers are identical in the two species (Whitehead 1959 b).

Lateral line scale counts

Comparison between Sagana and lower Athi river fishes shows that *T. nigra* may have a slightly higher lateral line scale count than *T. mossambica*, although the difference is small and insufficient numbers of fishes have been examined.

	29	30	31	32	33	Total
T. mossambica						
Lake Chem Chem	1	37	10			48
F₁ of lower Athi fishes grown at Sagana..		1	9			10
Parkers Camp, lower Athi		5	12			17
T. nigra						
Athi, just above Lugard Falls		5	7	1		13
Athi river at Yatta		2	3	5		10
Sagana fish ponds....................			30	27	1	58
Makindu and Isavo rivers (Boulenger, 1916)................................		1	20	10		31

Mean values for the seventy-five *T. mossambica* examined are 30·40, and for eighty-one *T. nigra*, 31·34. As in other meristic characters, there is considerable overlap, and again a tendency, in both species, for higher counts to be found higher up the Athi river, with a maximum at Sagana. Also, although the sample is small, the F₁ *T. mossambica* have higher counts than the lower Athi population from which their parents were derived.

Body proportions

Slight differences have been found in certain body proportions between *T. nigra* and *T. mossambica* (Table 7). Since many of the characters listed are liable to intraspecific variations due to allometry, sexual dimorphism and growth conditions, only pond-grown males of the same size group have been selected for measurement. Even so, the difference shown in relative body depth can probably be attributed to better growing conditions in the *T. nigra* pond.

The most noticeable difference between males of the two species lies in the proportions of the premaxilla, as discussed earlier, although in this size range the longer bone in *T. mossambica* is not yet associated with a markedly longer snout. The measurements show however that the preorbital depth is smaller in *T. mossambica*, and coupled with the shorter pedicel of the premaxilla, this may account for the slightly shorter head in *T. mossambica*. The lower jaw is a little longer in *T. mossambica*.

A further difference lies in the porportions of the caudal peduncle, which is slightly longer in *T. mossambica*. This difference has been found in all size groups and in fishes from different localities (see Fig. 6), but again some overlap occurs. The graph shows that peduncle length exhibits positive allometry with standard length. Peduncle depth is similar in the two species.

In all other respects the body proportions of the two species are identical.

Table 7—Proportional measurements of *Tilapia nigra* and *T. mossambica*

As a percentage of standard length		*T. mossambica* ex Sabaki river	*T. nigra* ex Sagana ponds
Head length		32·2 (33·4) 34·9	33·5 (34·1) 35·2
Body depth		39·3 (41·2) 43·0	41·7 (44·2) 48·0
Snout length		11·0 (11·6) 12·7	10·9 (11·8) 12·8
Eye diameter		6·7 (7·4) 7·7	6·8 (7·3) 7·9
Interorbital width		11·7 (12·2) 12·7	12·1 (12·8) 13·5
Post-occular distance		14·7 (15·1) 15·9	14·8 (15·4) 16·3
Pre-orbital depth		6·2 (6·5) 6·8	6·2 (7·0) 7·6
Lower jaw length		11·7 (13·5) 15·2	11·1 (12·1) 12·8
Lower pharyngeal bone	length	10·4 (11·1) 11·6	10·9 (11·2) 11·4
	width	10·4 (10·9) 11·4	10·2 (11·0) 11·5
Snout to dorsal		33·4 (34·4) 36·3	35·2 (36·4) 37·0
Snout to anal		40·0 (41·1) 42·6	41·1 (42·1) 43·2
Pectoral length		34·2 (36·6) 38·8	36·4 (39·5) 41·0
Anal spine length	3rd	12·1 (13·1) 14·8	—
	4th	14·1 (15·6) 16·9	11·7 (12·6) 13·6
	5th	—	14·3 (15·5) 17·1
	6th	—	(16·0)
Caudal peduncle	length	11·7 (13·6) 15·1	10·0 (11·7) 12·9
	depth	14·9 (15·9) 16·5	15·5 (16·1) 17·0
Premaxilla	length	11·0 (12·3) 13·4	8·9 (9·3) 9·9
	height	5·9 (6·9) 7·4	6·3 (7·8) 8·7
Lower pharyngeal	$\dfrac{\text{length}}{\text{depth}}$	0·89 (1·03) 1·20	0·97 (1·01) 1·08
Premaxilla	$\dfrac{\text{length}}{\text{depth}}$	1·54 (1·68) 2·05	1·08 (1·20) 1·42
Caudal peduncle	$\dfrac{\text{length}}{\text{depth}}$	0·74 (0·86) 0·96	0·63 (0·73) 0·77
Lateral line scales		30–31	31–32
Gillrakers on lower part of 1st arch		15–18	16–18
Size range (total length in mm)		145–154	146–156
No. of fishes		10	10

Measurements made on mature male fishes grown in ponds at Sagana. Means shown in brackets.

Table 8—Allometric changes in the proportions of the premaxilla in male *T. nigra.*

Standard length	Premaxilla		
	$\dfrac{Length}{S.L.} \times 100$	$\dfrac{Height}{S.L.} \times 100$	$\dfrac{Length}{Height} \times 100$
112	8·25	8·25	100
133	8·85	8·70	98
144	9·00	8·10	90
146	8·90	7·50	84
147	9·20	7·80	85
150	9·40	8·00	85
156	9·90	7·70	80
172	10·20	7·50	74
*282	11·00	7·50	68
175	11·70	7·40	63
180	11·40	8·10	71
183	11·50	6·60	57
200	N R	N R	62
252	12·30	6·70	55
260	N R	N R	62
305	12·40	7·50	60

* Female *T. nigra* included for comparison. Elongation of snout noticeable in specimens over 175 mm standard length.
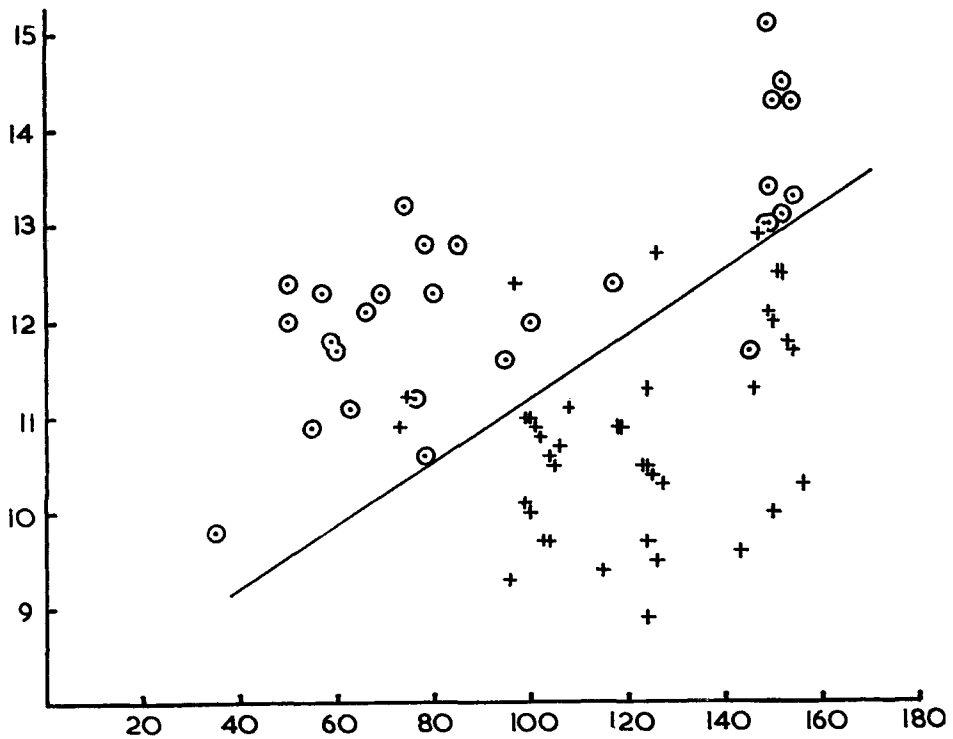

Fig. 6—Scatter diagram showing relatively longer caudal peduncle in *T. mossambica* (○) compared with *T. nigra* (+). Abscissa, standard length in mm ; ordinate, caudal peduncle length as a percentage of standard length. Diagonal line suggests division between species.
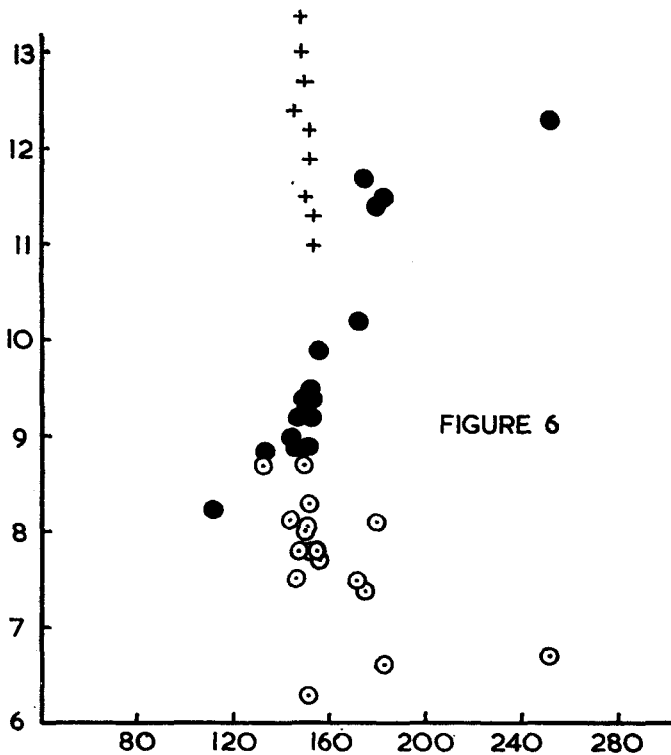
Fig. 7—Scatter diagram showing allometry in proportions of premaxilla in *T. nigra*. Abscissa, standard length in mm ; ordinate, premaxilla height and length as a percentage of standard length. Premaxilla lengths for *T. mossambica* shown for comparison.   ● premaxilla length for *T. nigra*.   ☉ premaxilla height for *T. nigra*.   + premaxilla length for *T. mossambica*.

Coloration

No colour differences have been found between the juveniles or the females of the two species. There are however important differences in the breeding coloration of mature males, and the difference is maintained even when the two species are grown under identical conditions in the ponds at Sagana.

T. nigra : The following description is based on males over 200 mm standard length from the Sagana ponds. 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 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 on posterior angle of operculum, slightly smaller than eye diameter ; 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 spinous portion ; bright blue on upper half of spinous portion ; 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 fins, fin rays vermillion, fin membrane colourless.

In large male *T. mossambica* from the lower Athi the general body colours are similar but with the following important differences. The blue on the dorsal and anal fins is much more brilliant, and the yellow on the flanks, especially near the base of the anal fin, is much brighter. In addition, there are varying degrees of red, red-purple, or even a bronzed-purple, on the upper lip, throat, cheeks, operculum, at the base of the pectoral fins, and occasionally in the centres of the scales for some distance along the flanks. Not all these areas are necessarily so coloured, but this has not been found in *T. nigra* (except rarely a dull purple flush appears on the operculum of recently killed fishes).

The red colour in *T. mossambica* is brought out very clearly under aquarium conditions, and small fishes of only 40 mm have shown it when confined to small tanks. It is also shown by F_1 *T. mossambica* grown at Sagana and so is evidently not dependent on the warmer water conditions of the lower Athi or Tana.

In this connection, the Buffalo Springs population of *T. mossambica* should be mentioned. These fishes are small and show breeding colours at about 100 mm total length. The general body colour, especially on the lower parts of the flanks, is a dusty grey-blue, as is the upper lip, although the lower lip is white. The blue of the dorsal, anal and pelvic fins is not so bright as in either *T. nigra* or *T. mossambica*, but the lappets and the tip of the caudal are red. In many ways the colour differences are greater between these fishes and *T. mossambica*, than between the latter and *T. nigra*, and since colour is here cited as a major difference between *T. nigra* and *T. mossambica*, it might seem unjustified to include the Buffalo Springs fishes in *T. mossambica*. However, no proportional or meristic differences have been found by which the Buffalo Springs fishes can be separated, and until live specimens of *T. mossambica* from the Eusso Nyiro can be examined, I regard the Buffalo Springs fishes as exhibiting a colour form conditioned mainly by isolation in an extremely shallow and restricted environment. The dusty-blue colour of the lower flanks is also found in two other small fishes living in restricted (and in this case alkaline) environments, *Tilapia percivali* Blgr. and *T. grahami* Blgr.

Vision is probably the dominant sensory modality in breeding behaviour in fishes (Aronson 1957), and in the cichlid fishes coloration has been increasingly recognised as a useful systematic guide. Thus in *Tilapia*, male breeding colours may provide an important means of advertising breeding grounds (Lowe 1959), and coupled with territorial behaviour, may assist in keeping sympatric species separate (Lowe 1956). In some mouth-brooding species at least, the female appears to select the male, and not *vice-versa*, so that male reproductive patterns are probably the main releaser preventing cross-breeding (Baerends & Baerends-van Roon 1950 ; Lowe 1956). Thus *T. saka* Lowe and *T. squammipinnis* (Günther) of Lake Nyasa, while morphologically almost identical,

differ in colour, especially male breeding dress, as well as in breeding sites and season (Lowe 1953). On the other hand Lowe (1959) later found that two other species in Lake Nyasa have breeding colours similar to *T. saka*, and she felt that it is more likely that breeding place and other aspects of morphology keep these three species separate. Also, two sympatric species in Lake Jipe have remarkably similar breeding colours and nests (Lowe 1953), and Baerends & Baerends-van Roon (*loc. cit.*) suggest that in aquaria sex recognition by the male may depend rather on the smaller size of the female than on colouration.

From the conflicting evidence it would seem that coloration is an isolating (and thus specific) character only when in conjunction with other aspects of breeding biology, ethology, breeding sites and seasons. In the present case, coloration differences between *T. nigra* and *T. mossambica* have not prevented cross-breeding, presumably because their breeding biology is very similar. In the case of crosses between *T. nigra* and *T. leucosticta* Trewavas (reported erroneously as *T. nigra* and *T. zillii*—Whitehead 1960) even more striking colour differences are found in breeding males.

It is worth noting that the 'Malayan *T. mossambica*' which sired Hickling's (1960) hybrids, showed a black male breeding dress. These fishes, derivatives of the original E. Java stock, have been acclimatized in Malaya since about 1942. While this suggests caution in placing too much emphasis on coloration, particularly in a wide-spread species such as *T. mossambica*, the importance of colour differences probably increases the closer the two forms are geographically.

Salinity tolerance

T. mossambica is a euryhaline species, reported to survive in salinities of as much as 69 parts per mille and to be able to breed in water of 30–48 parts (Vaas & Hofstede 1953). Three-spined *T. mossambica* have been caught in salt pans and pools filled by spring tides near Gongoni, ten miles north of Malindi, where salinities of 40 parts per mille have been found. The Zanzibar species of *Tilapia* has been successfully reared in marine fish ponds where salinities equal those of the sea (Talbot & Newell 1957).

Salinity tolerance may be a character possessed by *T. mossambica* and not *T. nigra*. Thus Lowe (1955) reports that the closely related *T. pangani* does not survive the transfer into seawater lagoons.

THE ZONE OF OVERLAP

On the Athi river the two species appear to overlap in a stretch of about fifty miles below Lugards Falls. Since there are no clear-cut morphological differences, it is not possible to say for certain that genetic mixing occurs, although it would seem likely. Above the falls no three-spined fishes were found. The falls are a series of rapids, but in one place there is a steep drop of about twelve feet which appears to be a barrier to the upstream migration of *Tilapia* although large *Barbus* are said to ascend it. Of eleven fishes caught immediately below the falls, three had four anal spines and the rest had five. It would appear that *T. nigra* from above the falls are occasionally washed over and have established a population below. But judging from the very small proportion of five-spined fishes (0·7 per cent) found at Parkers Camp, forty

miles downstream, *T. nigra* either does not penetrate far down the river or else does not maintain its identity for very long. The results of hybridization between the two species (see below) provide a possible explanation for the
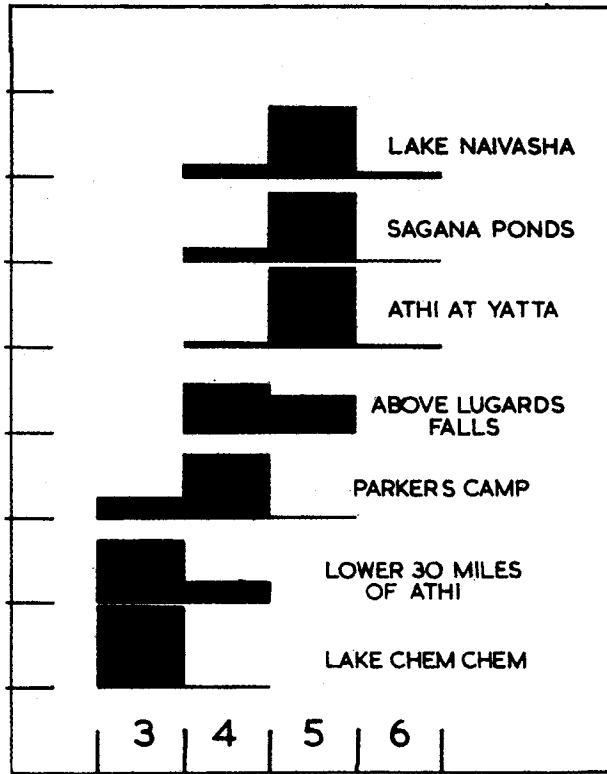

Fig. 8—Percentage frequency occurrence of three- to six-spined fishes in samples from the Athi river, Sagana and Lake Naivasha. Lower three histograms, *T. mossambica*, although a few *T. nigra* are present in the Parkers Camp sample. Remainder *T. nigra*. Figures taken from Table 9.

rarity of five-spined fishes since only one out of 155 hybrids had five anal spines. The high porportion of four-spined fishes at Parkers Camp (75 per cent) may also be due to hybridization since four-spined fishes predominated in the pond

Table 9—Percentage occurrence of three- to six-spined fishes in samples of *T. mossambica* and *T. nigra* from various localities on the Athi river, at Sagana and in Lake Naivasha. See also Fig. 8.

	Percentage frequency				
	3	4	5	6	Total
Lake Chem Chem	99·8	0·2	—	—	374
From traps in lower 30 miles of Athi river	75·0	25·0	—	—	311
Parkers Camp on Athi river	24·0	75·3	0·7	—	666
Just above Lugards Falls	—	58·0	42·0	—	76
Makindu and Isavo rivers*	—	51·5	48·5	—	31
Athi river at Yatta....................	—	5·3	93·4	1·3	151
Sagana ponds.........................	—	17·9	80·8	1·3	448
Lake Naivasha	—	15·2	81·8	3·0	99

* Based on figures given by Boulenger, 1916.

cross.   However, the influence of exogenous factors cannot be discounted and there is no definite evidence that the Parkers Camp fishes result from crossing.

Caudal peduncle lengths were measured in small samples of fishes from Parkers Camp and from above Lugards Falls (Fig. 9).   Peduncle lengths are plotted as a percentage of standard length, as in Fig. 6, and the diagonal used in the latter to separate the two species has been superimposed.   All but two of the Parkers Camp *T. mossambica* lie above the line, and these two were four-spined fishes and may thus have been *T. nigra*.   Two of the *T. nigra* from above Lugards Falls are above the line, but as Fig. 6 shows, there is some overlap between the species.   Unfortunately there is a size discrepancy between the two samples in Fig. 9 and it cannot be said whether the Parkers Camp *T. mossambica* would remain distinct as regards peduncle proportions in the smaller size groups.
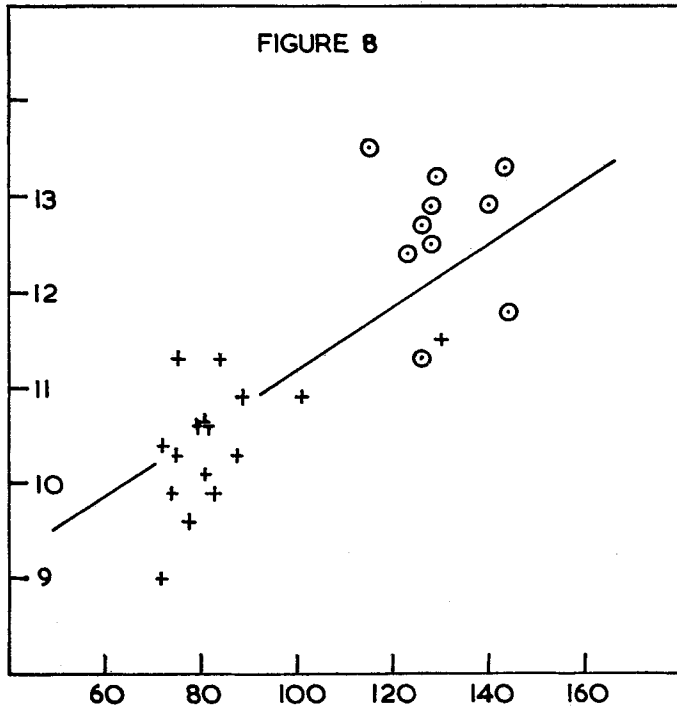

Fig. 9—Scatter diagram showing caudal peduncle length as a percentage of standard length (ordinate), against standard length (abscissa).   ⊙ *T. mossambica* from Parkers Camp, Athi river. + *T. nigra* from immediately above Lugards Falls.   (Diagonal line superimposed from Fig. 6.)

All mature male three- and four-spined fishes at Parkers Camp showed the typical *T. mossambica* colouration, and a breeding male with five anal spines caught immediately below Lugards Falls showed the *T. nigra* coloration. None of the five-spined fishes from Parkers Camp were mature.

There appears to be another zone of overlap at Ishiara on the Thuchi river. Three-, four-, and five-spined fishes were found, but the first two conformed in proportional measurements to *T. mossambica*, and the last to *T. nigra*.   Grand

Falls evidently does not act as the barrier between the two species on the Tana river since Ishiara is some distance above this.

THE HYBRIDS OF *T. NIGRA* AND *T. MOSSAMBICA*

A shallow 1/4 acre pond at Sagana was stocked with female *T. nigra* from the Sagana stock ponds and male *T. mossambica* derived from the lower twenty miles of the Athi river. The males all had three anal spines, while the females had four or five. Breeding occurred within a month and many broods of fry were produced, so there is evidently no physiological barrier between the two species under pond conditions.

Of 157 fry examined, all had four anal spines except for one with five and one with three (the latter was a true three-spined fish, with two spines articulating with the first pterygiophore). This very high proportion of four-spined fishes may be another example of the intermediacy which Hubbs (1940) believed to be a general rule in fish hybrids (see also Hubbs & Johnson 1943, andHubbs 1955). The dorsal spine numbers also appear to be intermediate, 63 percent of the hybrids having seventeen spines and the rest eighteen. It is however possible that the lower temperatures at Sagana have influenced meristic characters (see next section) and in effect have masked the *T. mossambica* influence. It is therefore unwise to look for intermediacy in this cross, unless perhaps the cross were carried out under intermediate environmental conditions. It might be said however, that intermediate conditions occur in the Parkers Camp region, where the predominance of four-spined fishes may well be due to hybridization.

Sex ratios in the hybrids were strongly biased, 84 per cent of the ninety fishes examined being males. The fishes were sexed on the appearance of the genital papilla, but all doubtful specimens and all females were confirmed by macroscopic inspection of the gonads. In all cases the gonads appeared perfectly normal. Hickling (1960) found strongly skewed sex ratios (96–100 per cent males) in crosses between the Malayan strain of *T. mossambica* and the Zanzibar species of *Tilapia* in ponds at Malacca. Such skewed sex ratios have also been reported in sunfishes (*Lepomis* spp.) by Hubbs & Hubbs (1933), Hubbs (1955) and Gordon (1957), and males predominated in the cross *T. nigra* × *T. leucosticta* mentioned earlier. In two natural populations of *T. mossambica* the sex ratio was 1 : 1 (47 : 46 fishes from Lake Chem Chem, and 100 : 99 fishes from Parkers Camp). There does however seem to be a tendency for male *T. nigra* to predominate in ponds in Sagana (van Someren 1953), but not to the extent shown by the hybrids.

In lateral line scale counts the hybrids are nearer to *T. nigra*. Of twenty counts made, all had thirty-one scales except one with thirty-two. But in length of caudal peduncle, twelve fishes measured all lay above the diagonal (and in most cases well above) shown in Fig. 6. and thus conformed to *T. mossambica*, as also did the single five-spined hybrid.

One male hybrid showed the red *T. mossambica* breeding coloration faintly on the operculum, but the specimens were small and this was the only fish seen with even faint breeding colours.

THE INFLUENCE OF TEMPERATURE ON SPINE NUMBERS

The influence of certain environmental conditions on meristic characters, especially during sensitive periods of ontogeny, is now well established in some holarctic fishes. Racial and even supposedly specific differences have been shown to be phenotypically determined in some cases. Since *T. nigra* and *T. mossambica* differ in several meristic characters (those of the former usually being the higher of the two), and since they occupy different zones in the Athi river, it is possible that the differences are to some extent phenotypic.

One of the chief differences between Sagana and the upper Athi river (above 4000 feet) on the one hand, and the lower reaches of the Athi and Tana rivers on the other, is probably temperature, perhaps the most important factor influencing meristic counts (Tåning 1946). In the lower Athi, thirty miles from its mouth, water temperatures averaged 28·1 °C during a period of nine months (Whitehead 1954). At Sagana, ponds 2 to 3 feet in depth have given mean maximum and minimum readings of 25·9 and 23·5°C, while the mean values for shallow ponds of about 1 foot in depth were 27·6 and 21·7°C respectively. In the stock ponds, from which fishes for spine counts were mainly derived, the pond bottoms shelve to about eight feet, and maximum water temperatures are probably lower. Maximum temperatures in the very shallow spawning ponds (6 to 9 inches deep) are usually about five degrees higher than in the ponds 2 to 3 feet deep, although minimum temperatures are depressed.

The increase in dorsal and anal spine numbers further up the Athi river (see Fig. 8, Table 9 and Table 3) may be correlated with lower water temperatures. The striking rise in numbers of dorsal spines in lower Athi *T. mossambica* bred at Sagana (Table 3 and Fig. 2) is hard to account for in any other way. It is possible that this may also account for the high proportion of four-spined fishes at Parkers Camp, but Lugards Falls is only forty miles above this and it seems unlikely that the temperature difference between the two localities (if there is one at all) could account for the very different composition of the two samples, as shown in Fig. 8. It seems more likely that the progressive decline in numbers of four- and five-spined fishes below Lugards Falls is due to diminishing numbers of *T. nigra* (or perhaps hybrids).

There is however more likelihood that temperature has influenced the results of crosses between four- and five-spined *T. nigra* in the spawning ponds since the temperature difference between these and the deep stock ponds must be considerable. In the herring, Blaxter (1957) found incubation temperature to be the most consistent factor influencing myotome counts, which he considered correlated with vertebral numbers. He could find no obvious effect of parental numbers of vertebrae on the offspring, nor any apparent influence of race on the counts. Certainly the high proportion of four-spined progeny in the Sagana crosses is at variance with the apparently stable 4 : 1 predominance of five-spined fishes in the stock ponds.

Tåning (1952), working on the sea trout, obtained lowest average numbers of vertebrae at incubation temperatures of about 6°C, while lower as well as higher temperatures led to higher average numbers. On the other hand the reverse was true for numbers of rays in the dorsal, pectoral and anal fins, the highest average values being obtained at intermediate temperatures.

In the case of *T. nigra* and *T. mossambica*, lower spine counts certainly appear to be correlated with higher water temperatures, but few collections have been made in localities which are colder than Sagana, and it cannot be said whether meristic characters will again show lower values. Accurate mean temperatures are not known for the localities cited below, but in Kenya lower mean air temperatures are generally found at higher altitudes. In Lake Naivasha (6000 feet, i.e. 2000 feet higher than Sagana) the proportion of four- to five-spined *T. nigra* is very similar to that at Sagana (from whence the fish were derived). Worthington & Ricardo (1936) record surface temperatures of between 20 and 24°C in February during the hot season. In a small dam at Solai in the Rift Valley (5400 feet), 78 per cent of the 110 fishes examined had five anal spines, again similar to Sagana. On the other hand, in a small dam at Njoro (7000 feet) six-spined fishes were reported as common, whereas at Sagana they comprise about 1 per cent of the population. It may be significant that six-spined fishes made up 3 per cent of ninety-nine specimens examined from Lake Naivasha.

Although there is some indication that exogenous factors, mainly temperature, influence spine counts, the rather distinct break between the populations of *Tilapia* above and below Lugards Falls argues that the meristic differences between *T. nigra* and *T. mossambica* have some genotypic basis also, encouraged by isolation of *T. nigra* above the falls.

CORRELATION BETWEEN DORSAL AND ANAL SPINE NUMBERS

When all available specimens of *T. nigra* and *T. mossambica* are considered, there appears to be a relationship between dorsal and anal spine numbers such that an increase in one is accompanied by an increase in the other (Table 4). Using the formula,

$$r = \frac{\dfrac{xTyx}{N} - (XY)}{\sigma x \sigma y}$$

the high value of $r = 0.77$ has been obtained, where x denotes anal, and y dorsal spines. The relationship is not however a direct one, dorsal spines increasing progressively less the higher the number of anal spines (dotted curve in Fig. 2). An almost exact straight line relationship does exist when average dorsal spine numbers, divided by anal spine numbers, is plotted as a logarithm (to the base e) against anal spine numbers (Fig. 3 and Table 4). By analogy with body proportions, such a relationship might be termed *allomery* (in this case negative), i.e. the progressive numerical change in a meristic character in relation to another meristic character, as a means of comparing races or populations within a cline.

Dorsal and anal spine numbers may be intrinsically linked, so that dorsal spines may be capable of increasing (due to environmental influences) up to a certain limit, beyond which further increase may be prevented until another anal spine is added. Again, the relationship between the numbers of spines in the two fins may reflect different degrees in their response to the same extrinsic factor.

41*

No correlation was found between soft dorsal and soft anal rays in 113 specimens of *T. nigra* from the Sagana ponds (Table 6).

<div align="center">FOUR-SPINED SPECIES OF *TILAPIA*</div>

The majority of *Tilapia* species have three anal spines, but four (or more) anal spines have been described as normal in the following species.

    T. nigra, upper Athi and Tana rivers, Kenya.

    T. placida Trewavas, lower Zambezi system.

    T. hunteri (Günther), endemic to Lake Chala, Tanganyika.

    T. shirana Blgr., endemic to Lake Nyasa.

    T. jipe Lowe, endemic to Lake Jipe (Pangani system) Tanganyika.

Lowe (1955) has shown that four anal spines occur occasionally in *T. mossambica korogwe*, found in the Korogwe fish ponds connected with the Pangani river, but she does not mention four-spined *T. m. mossambica* from that area. Vaas & Hofstede (1952) failed to find a four-spined *T. mossambica* in over five hundred specimens examined from thirty localities in Indonesia, and neither did Jubb (1958) in the Zambezi system.

Collections of *T. hunteri* from Lake Chala have shown that in fact fishes with three anal spines may predominate (Lowe 1955).

Trewavas (1937) believed *T. browni* Nichols, based on a single four-spined specimen from the Webi Shebeli, to be a variant of *T. mossambica*, and tells me that subsequent collections from another tributary of this river have included two further fishes, both with three anal spines. In the same paper she places " *T. browni* of Fowler " from the Athi river with *T. nigra*.

Other species of *Tilapia* in which four-spined individuals have been recorded include *T. leucosticta* Trewavas from Lakes Edward and George (Trewavas 1933), and *T. esculenta* Graham and *T. variabilis* Blgr. from Lake Victoria (Lowe 1957). Trewavas (1937) doubted Boulenger's (1915) record of a four-spined *T. variabilis*, which was probably based on a specimen recorded by Pellegrin (1905) as *T. galilaea*. Later however she examined this specimen in the Paris Museum and found that it was indeed a four-spined *T. variabilis* (personal communication). I have examined a four-spined *T. zillii* from stock introduced in Lake Victoria and have seen a four-spined individual from a Zanzibar population of a species allied to *T. mossambica*. Boulenger's (1916) Athi river four and five-spined *T. nilotica* were undoubtedly *T. nigra*, as noted earlier.

Four-spined *Tilapia* have also been found as fossils in the Lake Victoria region. Trewavas (1937) referred Pleistocene fossils from the Rawe Fish Beds to *T. nigra*, while Greenwood (1951) considered Miocene fossils from Rusinga Island to be most closely related to *T. mossambica* (and especially to the type specimens of *Chromis spilurus* Günther from the Tana system). Amongst the Miocene fossils only two had four anal spines, and may have been aberrant forms, but in ten Pleistocene fishes where spine counts were possible, all had four spines.

Four-spined fishes now occur in localities to the east of the Kenya Rift Valley but including Lake Nyasa (whose faunal affinities are all with those of the

eastern rivers—Brooks 1950). They occur as aberrant forms, as regular variants, or as distinct species, and in most cases appear to be related to *T. mossambica*. Three of the four-spined species show elongation of the jaws, a *mossambica* character (*T. nigra*, *T. jipe* and *T. shirana*). Trewavas (1941) and Lowe (1959) consider *T. shirana* to belong to the *T. mossambica* group ; *T. jipe* also resembles *T. mossambica*, as do the two three-spined Pangani species, *T. pangani* and *T. girigan*, both of which show elongation of the jaws. Sexual dimorphism as regards size is a further character of the *T. mossambica* group, and it is found in *T. nigra* (Brown & van Someren 1953 ; van Someren & Whitehead 1960), *T. shirana* (Lowe 1953), as well as in *T. jipe*, *T. girigan* and *T. pangani* (Lowe 1955). *T. placida* resembles both *T. mossambica* and *T. shirana* ; Jubb (1958) states that apart from the anal spines, formalin-preserved specimens of *T. placida* cannot be separated from *T. mossambica*, although the body depths which he tables are greater than any I have found in either *T. mossambica* or *T. nigra*. The relationships of *T. hunteri* are how-ever very imperfectly known.

The capacity to produce four spines in the anal fin appears to be exceptional outside the *mossambica* group of *Tilapia*, which at the present time is found to the east of the Rift Valley. Four-spined species now occur in relatively small and isolated localities, and in many cases the species are endemic to that area, suggesting that the four-spined condition has arisen independently several times. The four-spined condition was evidently present in Miocene times, and has perhaps remained a latent possibility, capable of dominating a population when isolated under certain environmental conditions. The Buffalo Springs population may represent an initial stage in differentiation from the *mossambica* stem, the upper Athi *T. nigra* a later stage where differences other than anal spination have evolved. The final stage may be shown by *T. shirana*, now geographically isolated from *T. mossambica*.

DISCUSSION

This study has been concerned with the relationship between *Tilapia nigra* and its nearest relative, the fishes in the lower Athi and Tana rivers referred to as *T. mossambica*. The conclusion that the upper river fishes are specifically distinct from the lower river fishes largely depends on the definition given to the term species, and particularly the weight attached to geographical factors in providing reproductive isolation, as opposed to physiological ones. Species are here regarded as the largest assemblages of forms capable (or potentially so) of actively sharing a common gene pool under natural conditions and as a result sharing one or more genotypically determined unique morphological features. Smaller groupings (subspecies, etc.) share a part but not the whole of the common gene pool actually available to them ; larger units (genera, etc.) have only a small part of the gene pool reproductively available. Physiological incompatibility achieves the most permanent isolation of the gene pool. Other types of isolation depend to a greater or lesser extent on environmental factors for their efficiency in producing reproductive isolation. Where there is no physiological barrier, the isolation of species must be seen as a result, not so much of particular characteristics of the organism itself, but of interdependent

organism-environment relations. The status of the upper Athi population of *Tilapia* has been examined in this light.

The differences separating *T. nigra* from the lower Athi *T. mossambica* involve body proportions, meristic counts, coloration, and distribution in the eastern rivers of Kenya. In the first two categories, sufficient overlap exists that occasional specimens could be assigned to either species, although this might be expected in a cline. There is however an indication that environmental factors, if suitably manipulated, might over many generations narrow or perhaps even eventually eliminate certain meristic differences. Colour appears to be a more trenchant character, but is only useful as a diagnostic character where sexually active male fishes are concerned, and it does not appear in preserved specimens. The two species occupy different zones of the Athi and Tana rivers, but these zones overlap at Ishiara on the Tana, and at Lugards Falls on the Athi. Finally the ease with which the two hybridize in ponds suggests that the same happens in nature, and some evidence of this is deduced from the Parkers Camp fishes.

Thus it might be said that the justification for keeping the upper Athi population of *Tilapia* distinct at species level rests solely on grounds of nomenclatural convenience. But species have been defined as genetically ' closed ' systems, as opposed to the open systems of demes, races, isolates, varieties or subspecies (Dobzhansky 1958). From the evidence available, I regard *T. nigra* as just such a closed system, for although gene exchange is possible (perhaps probable) between the two species, the exchange takes place in one direction only as a result of the Lugards Falls barrier. The gene pool of *T. nigra* is thus isolated from that of *T. mossambica*, and the latter, although probably contaminated by *T. nigra* in the lower Athi and perhaps Tana rivers, is elsewhere quite discreet.

It might also be argued that, while the upper Athi *T. nigra* population is geographically isolated and thus uncontaminated by its nearest relative *T. mossambica*, nonetheless the differences between the two species amount to no more than phenotypic variation due mainly to the colder conditions of the upper river. Thus the correlation found between anal and dorsal spine numbers apparently shows no discontinuity when the two species are combined (Fig. 3). But such would be expected in any Artenkreis where two closely related species are considered. There is also the very significant rarity of five-spined fishes at Parkers Camp (0·7 per cent of a large sample) to be accounted for, compared with the predominance of such fishes at a point just above Lugards Falls, only forty miles upstream. Such a sharp break in the relative abundance of four and five-spined fishes, coupled with the absence of three spined fishes above the Falls, certainly argues that the three and the five-spined fishes belong to two different genetic groups and are not merely eco-phenotypes.

Speciation involves the evolution of a reproductive isolating mechanism severe enough to continue perfecting itself. In most cases this involves genetically determined incompatibility. But where two populations are isolated geographically it is impossible to say exactly at what point speciation has occurred. Artificial removal of the barrier sometimes results in rapid hybridization between two well-defined species, but this cannot be taken to invalidate

one of them. Thus rainbow and cut-throat trout have crossed in some N. American rivers, while hybridization has occurred between carp and goldfish in Lake Erie even though the latter two fishes overlap in their natural range without crossing. Evidently, the physiological barrier is by no means the essential correlate of speciation, merely its most extreme form. The overwhelming majority of species have been defined with genetical incompatibility merely an assumption, although one that is often found in investigated cases.

The present case may represent incipient allopatric speciation, where two populations show some genetic divergence but are still capable of crossing when the geographical barrier is removed. In the same way, *T. nigra* and *T. leucosticta* are not incapable of hybridizing, and the hybrids, although predominantly males, are fully capable of breeding (unpublished observations). *T. mossambica* will cross with *T. andersoni* Castelnau (M. A. Mortimer, personal communication), and it has been reported that *T. nilotica* (L) and *T. galilaea* (Artédi) have also crossed (Yashouv and Chervinsky 1959). Lowe (1958) suspected other *Tilapia* hybrids as a result of introductions of several species into ponds and lakes in Uganda. Evidently the efficacy of the complicated breeding patterns in *Tilapia* as a means of preventing cross-breeding are sometimes upset when environmental conditions are altered. This seems to suggest both that isolating mechanisms are evolved and are efficient only within a particular set of environment-organism relations, and that physiological incompatibility may in many cases come much later in the process of speciation.

From the evidence I conclude that at the present time the upper Athi population of *Tilapia* represents a closed gene system which shows differences from its nearest geographical relative which cannot be entirely ascribed to phenotypic variation. Furthermore, the principal difference, the possession of more than four anal spines, is significant because it is unique in this genus. I therefore consider that *T. nigra* should at the present time retain specific rank.

The lower Athi *Tilapia* have throughout been referred to *T. mossambica*, and indeed in all morphometric characters they accord well with descriptions of that species (except of course in the higher proportion of four-spined individuals). But in coloration, and especially that of breeding males, they appear to differ, lacking the overall black colour and having yellow on the flanks. Since coloration has been used as a diagnostic feature in redefining *T. nigra*, some consideration should be given it in dealing with the lower Athi *T. mossambica*. It is unlikely that *T. mossambica* (*sensu strictu*) has never colonized the Athi or Tana rivers, being found in rivers to the north and south, so that the lower Athi population at least may be considered to be one which has diverged from the original stock, a divergence probably attributable in part to contamination by *T. nigra*. The Pleistocene fossils found near Lake Victoria show that a *T. nigra*-like form had been differentiated at that time, but it is difficult to say whether the upper river fishes then contaminated those of the lower reaches, or whether there was from earlier times a genetic potentiality in the original *T. mossambica* stock for producing more than three anal spines and that this later became accentuated in the upper river population. In the case of a river fish, its pattern of distribution is almost linear, so that the inter-

face between two populations occupying adjacent zones is very small compared with the distance between the extreme limits of the two. Gene diffusion would thus be necessarily slow, and partially isolated lakes of riverine origin (such as Lake Chem Chem) would be expected to show little contamination. It is suggested (see below) that the Tana river population of *T. nigra* was derived from that of the upper Athi relatively recently, and the apparent lack of four-spined *T. mossambica* in the lower Tana may reflect just this slow process of diffusion.

In the Donyo Sabuk and Thika areas the Athi and Tana rivers are separated by less than two miles, and the drainage pattern of the tributaries of the two rivers draining the Aberdare Mts. strongly suggests river capture and resultant exchange of faunae.

The high proportion of four-spined *T. mossambica* in the lower Athi is in striking contrast to their rarity or absence in other river systems. The lower Athi population might be considered a distinct variety or subspecies on the basis of both anal spination and coloration, as might also the Buffalo Springs fishes, but more information is required of typical populations before this can be established with certainty. The Buffalo Springs fishes are clearly derived from *T. mossambica* of the Eusso Nyiro ; the high proportion of four-spined fishes does not seem to have arisen from contamination by *T. nigra* since the latter is not known from this river. Although 3,000 feet above sea level, the Isiolo district is hot and dry, so that the four-spined condition is not a result of cold temperatures, but more likely the result of isolation in a restricted environment. These fishes differ from *T. mossambica* of either the Athi or the Tana rivers in possessing a dusty blue colour on the flanks and having rather shorter dorsal spines. In both these characters they strongly resemble *T. percivali* Blgr., a small species found in the springs near Chanler's Falls, about twenty miles further down the Eusso Nyiro. No four-spined individuals have been found amongst the latter species. On the other hand the rather dark blue, almost black colour of large males of the Buffalo Springs population hints at a closer affinity with *T. mossambica sensu strictu* than with the Athi and Tana specimens. The Buffalo Springs population may represent an early stage in the differentiation of a four-spined species, at present partially isolated and perhaps capable of contaminating the *T. mossambica* of the Eusso Nyiro.

The fossil *Tilapia* from Kanam, identified by Trewavas as *T. nigra*, all had four anal spines, although in one case a fifth ray may have been spinous too. In present-day populations of this species, five-spined fishes predominate, or at least make up the majority of the individuals. It is possible that increase in anal spination has been a progressive evolutionary trend, with five spines now predominating and six-spined fishes found occasionally. The Kanam fossils may be an early stage in this divergence, being fishes originally living in the upper reaches of an eastward-flowing river which later became isolated to the west of the present Rift Valley by river reversal consequent upon the rise of the eastern rift arch (as suggested by Kent, 1942).

The *mossambica*-like fishes found in Miocene deposits on Rusinga Island differ from *T. mossambica* in having rather fewer dorsal spines (13–14, as against (14) 15–17 (18) in the Athi and Tana river specimens). But the fact

that some specimens had four anal spines seems to strengthen the supposition that, if these fishes could be referred to *Tilapia*, then they belonged to the *T. mossambica* group. Later however, Greenwood (1960) felt that, on the basis of further material examined by E. Trewavas, as well as an examination of cichlid fossils from Tanganyika, some of the Rusinga fishes at least could be referred to *Haplochromis* or even *Pelmatochromis* on the characters preserved. Four anal spines are however extremely rare in *Haplochromis*. Unequivocal identification of these fossils is of great interest since they were found in association with fossils of two nilotic genera, *Lates* and *Polypterus*, now absent from the Lake Victoria region. In addition, nilotic fishes are also absent from the eastern river zone now inhabited by the *T. mossambica* group of *Tilapia* (except in the region of the Zambesi). Thus the present-day distribution of the nilotic fishes and the *T. mossambica* group is not contiguous, implying that the two have become dispersed on either side of a major water divide.

REFERENCES

ARONSON, L. R. (1957). Behaviour and parental behaviour. Chapter III: Part 3 in the *Physiology of fishes* **2**, Ed. M. E. Brown, New York: Academic Press.

BAERENDS, G. P. & BAERENDS-VAN ROON, J. M. (1950). *An introduction to the study of the ethology of cichlid fishes.* Leyden: E. J. Brill.

BLAXTER, J. H. S. (1957). Herring rearing—III. The effect of temperature and other factors on myotome counts. *Mar. Res. Dep. Agric. Fish Scotl.* No. I: 1–16.

BOULENGER, G. A. (1915). *Catalogue of the freshwater fishes of Africa in the British Museum (Natural History)* **3** : p. 168.

BOULENGER, G. A. (1916). On specimens of the perciform fish *Tilapia nilotica* with increased number of anal spines. *Proc. zool. Soc. Lond.*, 1916, 345–347.

BROOKS, J. L. (1950). Speciation in ancient lakes. *Quart. Rev. Biol.* **25**: 131–176.

BROWN, J. M. & VAN SOMEREN, V. D. (1953). New fish culture methods for *Tilapia* in East Africa. *Nature, Lond.* **172**: 330.

DE BONT, A. F. (1948). Fish farming in the Belgian Congo. *Nature, Lond.* **162** : 998.

CHIMITZ, P. (1955). Tilapia and its culture. *FAO Fish. Bull.* **8** (No. 1).

COPLEY, H. (1958). *Common freshwater fishes of East Africa.* London: Witherby.

DOBZHANSKY, T. (1958). Species after Darwin. Chapter 2 in *A century of Darwin.* Ed. S. A. Barnett, London: Heinemann.

FRYER, G. (1957). A new species of *Gephyrochromis* (Pisces, Cichlidae) from Lake Nyasa, with notes on its ecology and affinities. *Rev. Zool. Bot. afr.* **55**: 347–352.

GREENWOOD, P. H. (1951). Fish remains from Miocene deposits of Rusinga Island and Kavirondo Province, Kenya. *Ann. Mag. nat. Hist.* (12) **4** : 1192–1201.

GREENWOOD, P. H. (1959). The monotypic genera of cichlid fishes in Lake Victoria, Part II. *Bull. Brit. Mus. (nat. Hist.)* (Zool.) **5** : 165–218.

GREENWOOD, P. H. (1960). *Fossil denticipitid fishes from East Africa. Bull. Brit. Mus. (nat. Hist.* (Geol.) **5** : 1–11.

GORDON, M. (1957). Physiological genetics of fishes. Chapter X in *The physiology of fishes.* **2.** Ed. M. E. Brown. New York: Academic Press.

HICKLING, C. F. (1959). The Fish Culture Research Station, Malacca. *Nature, Lond.* **183** : 287–289.

HICKLING, C. F. (1960). The Malacca *Tilapia* hybrids. *J. Genet.* **57** : 1–10.

HUBBS, C. L. (1918). Notes on fishes from Athi river in British East Africa. *Field Mus. Publ. Zool.,* **12,** 9–16.

HUBBS, C. L. (1940). Speciation of fishes. *Amer. Nat.,* **74,** 198–211.

HUBBS, C. L. (1955). Hybridization between fish species in nature. *Syst. Zool.* **4** : 1–20.

HUBBS, C. L. & HUBBS, L. C. (1933). Increased growth, predominant malesness and apparent infertility of hybrid sunfishes. *Pap. Mich. Acad. Sci.* **17** : 613.

HUBBS, C. L. & JOHNSON, R. E. (1943). Hybridization in nature between species of catastomid fishes. *Contr. Lab. Vertebr. Biol.,* No. 22.

JUBB, R. A. (1958). A preliminary report on the collections of freshwater fishes made by the Bernard Carp expeditions to the Caprivi Strip, 1949, the lower Sabi river, 1950, and to Barotseland, 1952. *Occ. Pap. nat. Mus, S. Rhodesia* No. 22 b; 177–189.

KENT, P. E. (1942). The Pleistocene beds of Kanam and Kanjera, Kavirondo, Kenya. *Geol. Mag., Lond.* **79** : 117–32.

LOWE, R. H. (1953). Notes on the ecology and evolution of Nyasa fishes of the genus *Tilapia,* with a description of *T. saka* Lowe. *Proc. zool. Soc. Lond.* **122** : 1035–1041.

LOWE, R. H. (1955). New species of *Tilapia* (Pisces, Cichlidae) from Lake Jipe and the Pangani river, East Africa. *Bull. Brit. Mus. (nat. Hist.)* (Zool.) **2** : 349–368.

LOWE, R. H. (1956). The breeding behaviour of *Tilapia* species (Pisces: cichlidae) in natural waters: observations on *T. karomo* Poll and *T. variabilis* Blgr. *Behaviour* **9** : 140–163.

LOWE, R. H. (1957). Observations on the diagnosis and biology of *Tilapia leucosticta* Trewavas in East Africa. *Rev. Zool. Bot. afr.* **55** : 353–373.

LOWE, R. H. (1958). Observations on the biology of *Tilapia nilotica* Linné in East Africa. *Rev. Zool. Bot. afr.* **57** : 129–170.

LOWE, R. H. (1959). Breeding behaviour patterns and ecological differences between *Tilapia* species and their significance for evolution within the genus *Tilapia* (Pisces; Cichlidae). *Proc. zool. Soc. Lond.* **132** : 1–30.

PELLEGRIN, J. (1905). Mission scientifique de Ch. Alluaud en Afrique orientale.—Systématique. *Mem. Soc. zool. Fr.* **17** : 174–185.

SHUSTER, W. H. (1952). A provisional survey of the introduction and transplantation of fish throughout the Indo-Pacific region. *Proc. Indo-Pacific Fish. Counc. (3rd Meeting),* Thailand, 187–196.

TANING, A. V. (1946). Stage of determination of vertebrae in teleostean fishes. *Nature, Lond.* **157** : 594.

TANING, A. V. (1952). Experimental study of meristic characters in fishes. *Biol. Rev.* **27** : 170–193.

TALBOT, F. H. & NEWELL, B. S. (1957). A preliminary note on the breeding and growth of *Tilapia* in marine fish-ponds on Zanzibar Island. *E. Afr. Agric. J.* **22** : 118–121.

TREWAVAS, E. (1933). Scientific results of the Cambridge Expedition to the East African lakes, 1930–31.—11. The cichlid fishes. *J. Linn. Soc., Lond.* (Zool.) **38** : 309–341.

TREWAVAS, E. (1937). Fossil cichlid fishes of Dr L. S. B. Leakey's expedition to Kenya in 1934–35. *Ann. Mag. nat. Hist.* (10) **19** : 381–386.

TREWAVAS, E. (1941). Nyasa fishes of the genus *Tilapia* and a new species from Portuguese East Africa. *Ann. Mag. nat. Hist* (11) **7** : 294–306.

VAAS, K. F. & HOFSTEDE, A. E. (1953). Studies on *Tilapia mossambica* Peters (*ikan mudjair*) in Indonesia. *Contr. Inl. Fish. Res. Sta., Bogor* No. 1: 1–88.

VAN SOMEREN, V. D. (1953). Annual Report in *Review of Kenya Fisheries,* 1952. Kenya: Govt. Printer.

VAN SOMEREN, V. D. (1960). The Inland Fishery Research Station, Sagana, Kenya. *Nature, Lond.,* **186** : 425–426.

van Someren, V. D. & Whitehead, P. J. P. (1960).   The culture of *Tilapia nigra* (Günther) in ponds.   III—the early growth of males and females at comparable stocking rates, and the length/weight relationship.   *E. Afr. Agric. J.* **25** : 169–173.

Whitehead, P. J. P. (1954).   A report on the fisheries of the lower Athi (Sabaki) river, Kenya.   Unpublished report, *Ministry of Forest Development, Game & Fisheries, Nairobi, Kenya.*

Whitehead, P. J. P. (1959 a).   Notes on a collection of fishes from the Tana river below Garissa, Kenya.   *J. E. Afr. nat. Hist. Soc.* **23** : 167–171.

Whitehead, P. J. P. (1959 b).   The feeding mechanism of *Tilapia nigra*.   *Nature, Lond.* **184** : 1509–1510.

Whitehead, P. J. P. 1960.   Interspecific hybrids of *Tilapia*: *T. nigra* × *T. zillii*. *Nature, Lond.* **187** : 878.

Worthington, E. B. & Ricardo, C. K. (1936).   Scientific results of the Cambridge Expedition to the East African lakes, 1930–31.—No. 17.   The vertical distribution and movements of the plankton in Lakes Rudolf, Naivasha, Edward and Bunyoni.   *J. Linn. Soc., Lond.* (Zool.), **40,** : 33–69.

Yashouv, A. & Chervinsky, J. (1959).   Hybrids of *Tilapia nilotica* × *T. galilaea*.   *Nature, Lond.* **184** : 1739.