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MORPHOMETRIC AND ALLOZYME VARIATION IN NATURAL POPULATIONS AND CULTURED STRAINS OF THE NILE TILAPIA *OREOCHROMIS NILOTICUS* (TELEOSTEI, CICHLIDAE)

EMMANUEL J. VREVEN([1]), BÉATRICE ADÉPO-GOURÈNE([2]), JEAN-FRANÇOIS AGNÈSE([2,3]) AND GUY G. TEUGELS([1])*

([1])Musée Royal de l'Afrique Centrale, Laboratoire d'Ichtyologie, B-3080 Tervuren, Belgium.
([2])Centre de Recherches Océanologiques, ORSTOM, Laboratoire de Génétique, BP V18, Abidjan, Cote d'Ivoire
([3])CNRS, UPR 9060, Université Montpellier II, F-34095 Montpellier cedex 5, France.
e-mail: teugels@africamuseum.be

Abstract. Morphometric and allozyme variation of nine natural populations and three cultured strains of *Oreochromis niloticus* has been studied. Natural populations from West Africa and the Nile, identified as the same subspecies, *O. niloticus niloticus*, differed significantly. The Nile populations are genetically closer to the population from Lake Edward, identified as *O. niloticus eduardianus*. Morphological differences were observed between natural populations and their cultured strains. These are undoubtedly related to ecophenotypic influences, because cultured strains are genetically related to their natural parental populations.

Key words: *Oreochromis niloticus*, natural populations, cultured strains, morphometry, allozymes, Africa.

INTRODUCTION

The Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758) is endemic to Africa but has been introduced in many parts of the world for aquaculture. In particular the subspecies *O. niloticus niloticus* is one of the most cultured freshwater fishes with an estimated production of 426,773 mt in 1994 (Garibaldi, 1996).

The meristic and morphometric characters of this subspecies that are available in local faunal guides generally refer to local populations (e.g. DAGET, 1954 for specimens originating from the Upper Niger). TREWAVAS (1983) presented comparative data for specimens originating from throughout the major part of its distribution but these are based on relatively small samples. GOURÈNE & TEUGELS (1993) examined the morphometrics of cultured strains and noted differences between them. An overall comparison of the data published is difficult if not impossible as different characters were employed and their definition is not always identical.

Several authors have published on allozyme variation especially of cultured stocks of *O. niloticus* (e.g. BASIAO & TANIGUCHI, 1983; MCANDREW & MAJUMDAR, 1983; SEYOUM

& KORNFIELD, 1992). MACARANAS *et al.* (1995) compared allozymes of Asian farmed strains and several wild African populations. ROGNON *et al.* (1996) compared allozymes in cultured strains and in some natural West African populations. AGNÈSE *et al.* (1997) studied allozymes in natural populations from all over the distribution range of the species.

Herein is offered the first attempt to qualify and compare the morphometric and allozyme variation in the same material of *O. n. niloticus*. This forms part of an ongoing program on the characterization of natural populations and cultured strains of species used in aquaculture in West Africa and the Nile, in order to increase their production on the basis of rational use of genetic resources.

MATERIAL AND METHODS

Eight natural populations of *O.niloticus niloticus*, one natural population of *O. niloticus eduardianus* and three cultured strains were examined. All these were collected in Africa between August 1993 and December 1994 (Table I, Fig. 1). Natural populations were identified morphologically according to TREWAVAS (1983). The cultured strains originate from a natural population from the Volta basin (Volta strain), a crossbred of natural populations from the Volta basin and Lake Edward (Bouake strain) and natural populations from the Nile near Cairo and Lake Manzalla (Quarun strain).

TABLE I

List of natural populations and cultured strains examined of Oreochromis niloticus

	coordinates	*N (Morphometry)*	*Standard Length (mm)*	*N (allozyme study)*	*Abbreviation*
Natural Populations					
Dagana, Senegal	±16°31'N-15°30'E	18	77.4-252.6	63	DAG
Selingue, Mali	±11°37'N-8°14'E	24	95.0-138.5	58	SEL
Bamako, Mali	±12°39'N-8°00'E	17	73.5-219.4	22	BAM
Battor, Ghana	±6°04'N-0°25'E	7	180.0-252.4	7	BAT
Lake Chad, Chad	±13°20'N-14°00'E	20	140.6-279.3	22	CHA
N'Djamena, Chari, Chad	±12°07'N-15°03'E	17	97.9-156.9	30	SEL
Cairo, Nile, Egypt	±30°02'N-31°15'E	17	136.9-246.7	18	CAI
Lake Manzalla, Egypt	±31°15'N-32°00'E	16	122.1-178.0	30	MAN
Lake Edward, Uganda	±0°25'S-29°30'E	28	152.9-223.9	30	EDW
Cultured Strains					
Bouake strain		29	95.0-138.5	55	BKE
Volta strain		32	101.0-136.8	50	VOL
Quarun strain		20	154.7-225.5	20	QUA

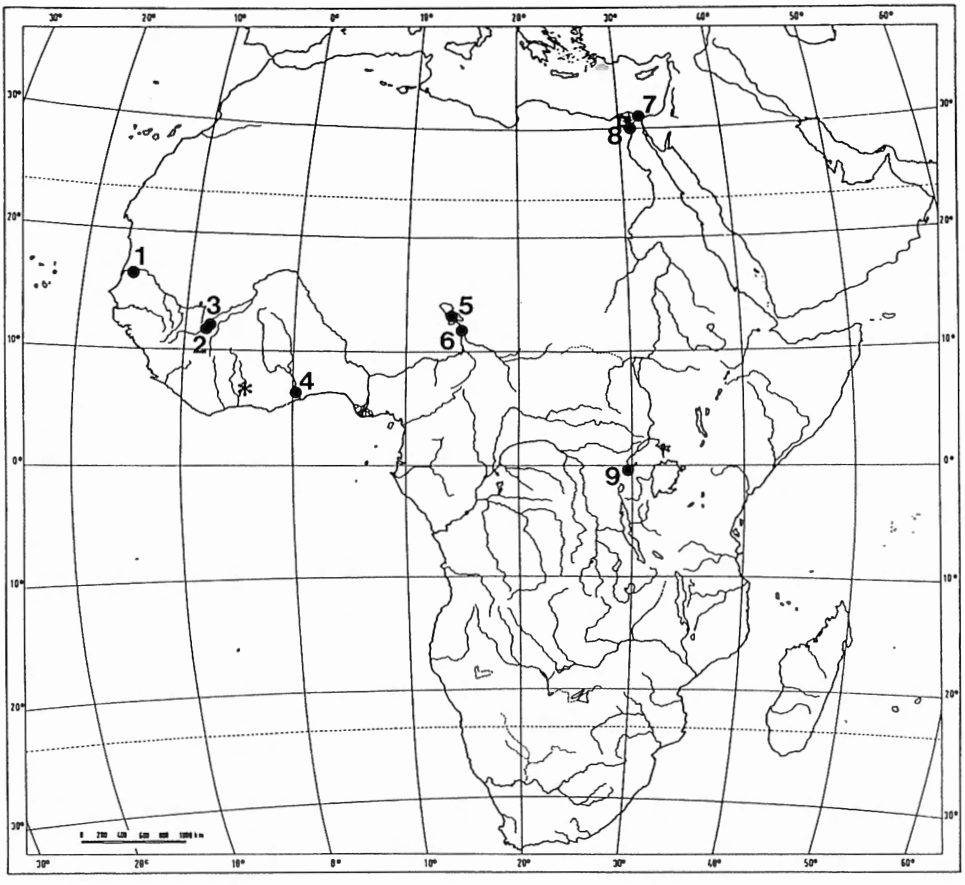

Fig. 1. – Geographical distribution of the natural populations and cultured strains examined of *O. niloticus*. 1 = Dagana (Senegal); 2 = Selingue (Mali); 3 = Bamako (Mali); 4 = Battor (Ghana); 5 = Lake Chad (Chad); 6 = N'Djamena (Chad); 7 = Lake Manzalla (Egypt); 8 = Cairo (Egypt); 9 = Lake Edward (Uganda). * = Bouake and Volta strains (= Quarun strain).

Twenty five measurements were taken on each specimen, for the morphometric analysis, using dial calipers (Fig. 2). Eight meristic counts were made on each fish: number of gill rakers on the lower part (cerato- + hypobranchial) of the first branchial arch; number of gill rakers on the complete first branchial arch; number of dorsal spines; number of soft dorsal-fin rays; number of anal spines; number of soft anal-fin rays; number of scales on the lower lateral line and number of scales on the upper lateral line. Due to preservation, it was not possible to obtain a complete data set for the meristic counts for some of the specimens. The results were evaluated by principal component analysis (PCA) using the CSS: STATISTICA package (Statsoft, versions 3.1 and 4.5). Only those specimens for which a complete data set was available were used in these analyses. Data were log transformed to fullfill the criteria of normality. The covariance matrix was used. As suggested

by HUMPHRIES *et al.* (1981) and BOOKSTEIN *et al.* (1985) the first principal component was interpretated as a size factor and the other components as shape factors, independent of size. Therefore the first principal component was not used.

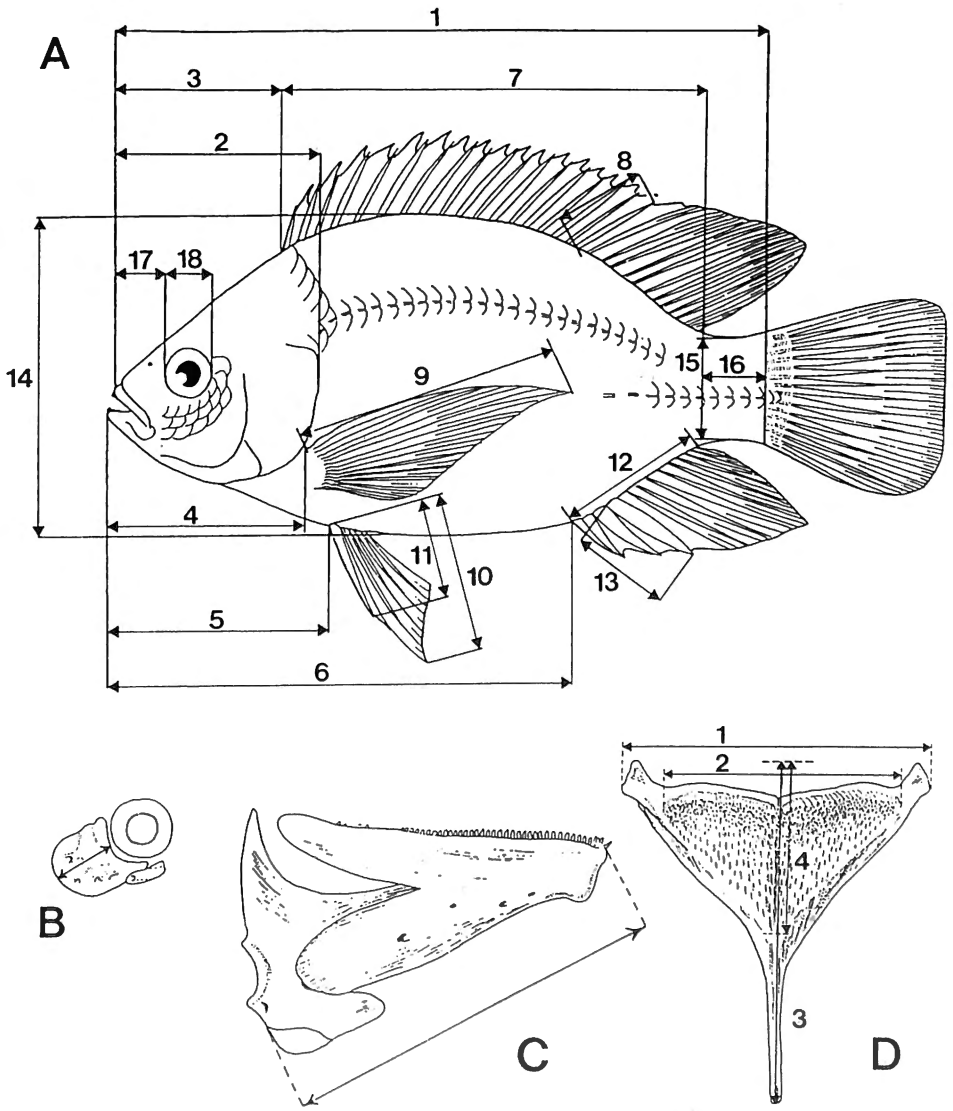

Fig. 2. – Measurements taken on the *O.niloticus* specimens. (A) 1. standard length (SL); 2. head length (HL); 3. predorsal length; 4. prepectoral length; 5. prepelvic length; 6. preanal length; 7. dorsal-fin length; 8. dorsal-spine length; 9. pectoral-fin length; 10. pelvic-fin length; 11. pelvic-spine length; 12. anal-fin length; 13. anal-spine length; 14. body depth; 15. caudal-peduncle depth; 16. caudal-peduncle length; 17. snout length and 18. eye diameter; (B) preorbital-bone depth; (C) lower-jaw length and (D) 1. total pharyngeal-bone width; 2. toothed pharyngeal-bone width; 3. total pharyngeal-bone length and 4. toothed pharyngeal-bone length.

For the allozyme variation, specimens were kept at -20°C for a few days and then stored at -80°C for later analysis. Standard horizontal starch gel (12%) electrophoresis was carried out to investigate the products of 25 loci. The stain protocols and buffers used were those described in POUYAUD & AGNÈSE (1995) and PASTEUR *et al.* (1987). The nomenclature is that proposed by SHAKLEE *et al.* (1990). The allozymic data were analysed with the phylogenetic software programme PHYLIP (PHYLIP software package, Felsenstein, version 3.5). A total of 100 randomly modified frequency matrices were obtained using the program SEQBOOT to build a genetic network. These matrices were then transformed into Nei's (1978) genetic distance matrices using the GENEDIST program. The corresponding trees were built by neighbourjoining by the program NEIGHBOR and summarized into a single tree using CONSENSE (bootstrapping).

RESULTS

Morphometric variation

Natural populations from West Africa, Egypt and Lake Edward

Principal component analysis on 25 metric variables performed on 142 specimens of *O.niloticus* belonging to 9 natural populations is illustrated in Fig. 3. PCI accounts for 96.0%, PCII for 1.0 % and PCIII for 0.6% of the observed variance. All specimens from Egypt (Cairo and Lake Manzalla) and Lake Edward, except one, are located on the negative sector of the second component, while the majority of specimens from West Africa are located on the positive sector of this component. The latter is defined mainly by the caudal peduncle length, the toothed pharyngeal bone length and width. Interestingly, the Bamako specimens hardly overlap with the specimens from Selingue; both localities are situated on the Upper Niger in Mali (Fig. 1). All other West African populations are largely overlapping and cannot be distinguished from each other on the second or the third component.

All natural populations and the Bouake strain

The plot of a principal component analysis on 25 metric variables for 169 specimens of *O.niloticus* belonging to 9 natural populations and the cultured Bouake strain is given in Fig. 4a. PCI accounts for 96.2%, PCII for 1.0% and PCIII for 0.8% of the observed variance. The cultured strain results from an interbreeding between specimens from the Volta basin and Lake Edward. This is however not discernible from the results obtained: a slight overlap is noted between the Bouake strain and the Battor (Volta) population, but the Bouake strain is completely separated from the population of Lake Edward. The latter is almost entirely located on the negative sector, while all Bouake specimens are situated on the positive sector of the second component, which is defined mainly by the toothed pharyngeal bone length, the anal spine length and the body depth.

All the natural populations, the Bouake and the Volta strains

Fig. 4b illustrates the plot of a principal component analysis on 25 metric variables for 200 specimens of *O.niloticus* belonging to 9 natural populations and two cultured strains.

PCI accounts for 95.8%, PCII for 1.0% and PCIII for 0.8% of the observed variance. The Volta strain, descending from a natural population of the Volta basin, only slightly overlaps with the Battor (=Volta) population. Interestingly, the Volta strain almost completely overlaps with the Bouake strain.

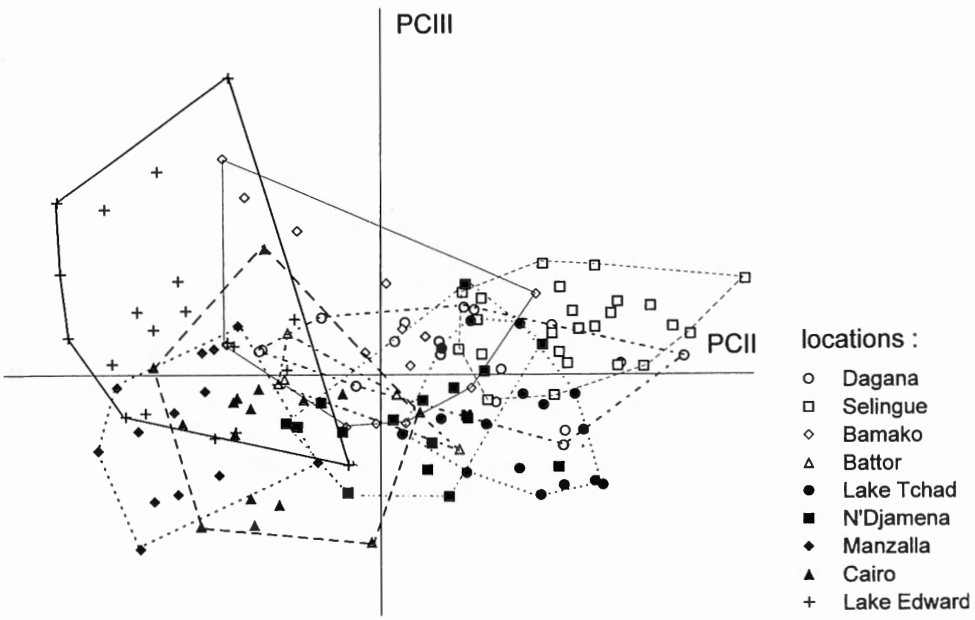

Fig. 3

Fig. 3. – Plot of a principal component analysis on log tranformed data of 25 metric variables for 142 specimens of *O.niloticus* originating from 9 natural populations from West Africa, the Nile and Lake Edward. For locality data see Table I.

Fig. 4. – (a) Plot of a principal component analysis (PCA) on log transformed data of 25 metric variables for 169 specimens of *O.niloticus* originating from 9 natural populations from West Africa, the Nile and Lake Edward and the cultured Bouake strain. The populations of Battor, Lake Edward (natural populations) and Bouake (cultured strain) are outlined. (b) Plot of a PCA on log transformed data of 25 metric variables for 200 specimens of *O.niloticus* from 9 natural populations from West Africa, the Nile and Lake Edward and the cultured Bouake and Volta strains. The populations of Battor (natural population) and Volta (cultured strain) are outlined. (c) Plot of a PCA on log transformed data of 25 metric variables for 220 specimens from 9 natural populations from West Africa, the Nile, Lake Edward and the cultured Bouake, Volta and Quarun strains. The populations of Cairo and Manzalla together (natural population) and Quarun (cultured strain) are outlined. Dagana (○); Selingue (□); Bamako (◇); Battor (△); Lake Tchad (●); N'Djamena (■); Manzalla (◆); Cairo (▲); Lake Edward (+); Bouake strain (✳); Volta strain (○) and Quarun strain (□). For locality data see Table I.

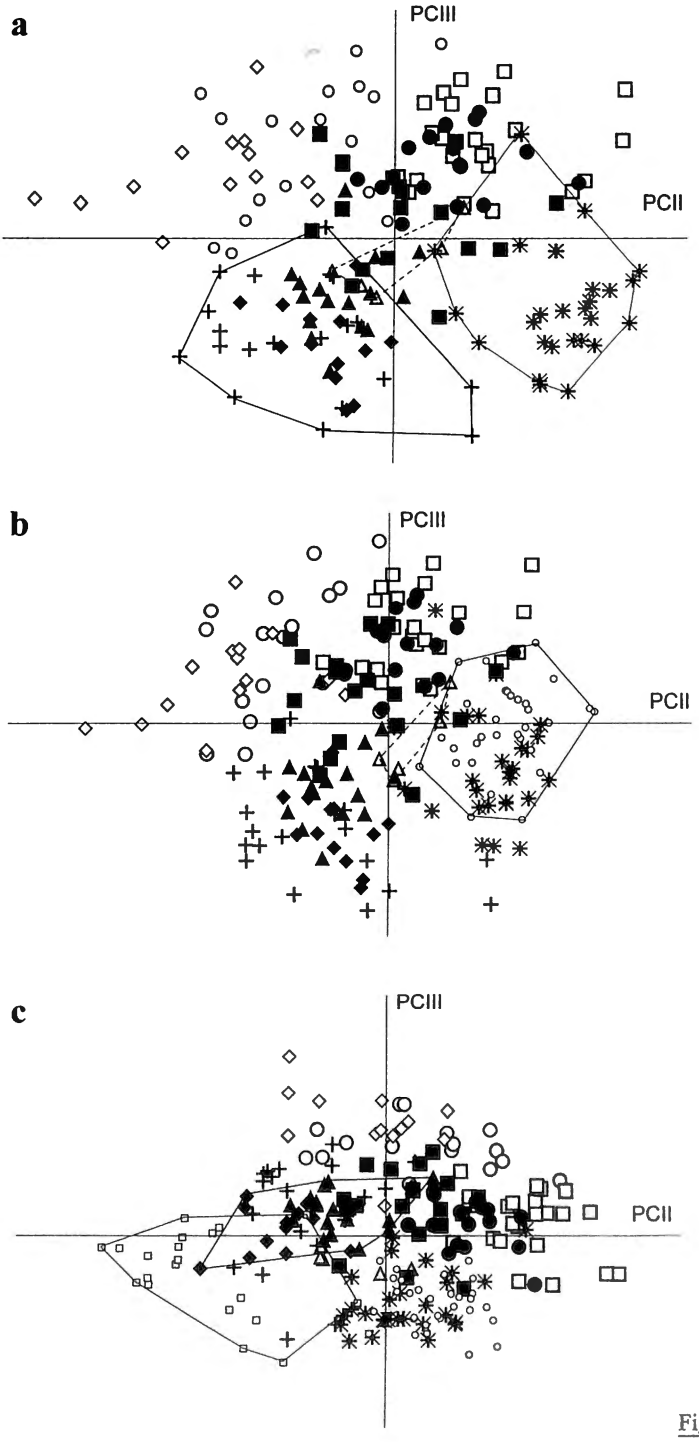

Fig. 4

All natural populations, the Bouake, Volta and Quarun strain

Fig. 4c shows the plot of a principal component analysis on 25 metric variables for 220 specimens of *O.niloticus* belonging to 9 natural populations and three cultured strains. PCI accounts for 95.1%, PCII for 1.1% and PCIII for 1.0% of the observed variance. Only a small part of the Lake Manzalla and Cairo specimens overlap with the Quarun strain polygone. Noteworthy in this figure is that most of the specimens belonging to cultured strains are located on the negative sector of the third component, while the majority of specimens from natural populations are situated on the positive sector of this component. The third component in this analysis is defined mainly by the lower jaw length, the body depth and the pelvic fin length.

Allozyme variation

Thirteen of the 25 loci studied were polymorphic (Table 2). The rate of observed heterozygosity (H) was between 0.01 (Lake Edward) and 0.047 (Quarun) and the rate of observed polymorphism (P95%) between 0.04 (Niger River at Selingue and Lake Edward) and 0.16 (Quarun). The values are comparable to those obtained in previous studies of natural *O. niloticus* populations (Seyoum & Kornfield, 1992) even if the loci analyzed were not the same as in the present study. Cultured strains did not show lower H and P values than natural populations, indicating that they did not loose genetic polymorphism.

The populations are clustered in two major genetic groups (Fig. 5). One cluster is composed of the natural populations from the Nile drainage (Manzalla, Cairo and Lake Edward) with two cultured strains (Quarun and Bouake). The second major group is composed of the West African natural populations (Dagana, Selingue, Bamako, N'djamena, Chad and Volta) with one cultured strain (Volta).

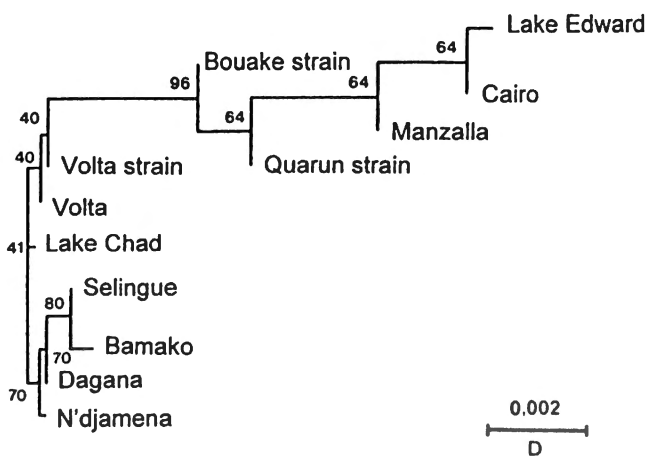

Fig. 5. – Consensus unrooted tree produced by neighbourjoining with the phylogenetic software PHYLIP for 9 natural populations and 3 cultured strains of *O. niloticus*. Number at each node indicates the percentage obtained using bootstrapping.

TABLE II

Allelic frequencies at polymorphic loci observed in 9 natural populations and 3 cultured strains of O. niloticus. *For abbreviations see Table I*

pop. locus	*DAG*	*SEL*	*BAM*	*BKE*	*VOL*	*BAT*	*CHA*	*NDJ*	*CAI*	*QUA*	*MAN*	*EDW*
AAT-2												
(N)	63	58	22	52	50	06	17	27	17	20	30	27
A	.52	.82	.93	.47	.34	.42	.44	.50	.06	.00	.02	
B	.48	.18	.07	.53	.66	.58	.56	.50	.94	1.00	.98	1.00
C												
AAT-3												
(N)	63	58	22	55	50	07	22	30	18	19	29	27
A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.97	.74	.88	1.00
B									.03	.26	.12	
ADH												
(N)	63	58	22	55	50	07	20	30	18	20	30	30
A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
B												
CK-1												
(N)	63	58	22	55	50	07	20	30	18	20	30	30
A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.98	1.00	1.00	1.00	1.00
B								.02				
CK-2												
(N)	63	58	22	55	50	07	20	28	18	20	30	30
A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.89	1.00	1.00	1.00	1.00
B								.11				
FBP-2												
(N)	63	57	22	55	50	07	21	30	18	20	30	28
A	1.00	1.00	1.00	.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.84
B				.01								.16
FH												
(N)	63	58	22	23	50	07	22	30	15	20	41	30
A	1.00	1.00	1.00	.44	1.00	1.00	1.00	1.00	.07	.55	.28	
B				.56					.93	.45	.72	1.00
IDHP-1												
(N)	62	58	22	55	50	07	22	30	18	20	30	30
A	.97	1.00	1.00	1.00	1.00	1.00	1.00	.98	1.00	1.00	1.00	1.00
B	.03							.02				
LDH-2												
(N)	62	58	22	55	50	07	20	30	18	20	30	30
A	1.00	1.00	1.00	1.00	.87	.86	1.00	1.00	1.00	1.00	1.00	1.00
B					.13	.14						
PGM												
(N)	62	58	22	55	50	07	20	30	17	20	30	30
A	1.00	1.00	1.00	1.00	1.00	1.00	.93	1.00	1.00	1.00	.97	1.00
B							.07				.03	
PT-1												
(N)	62	58	22	55	50	06	22	30	18	20	30	30
A	1.00	.99	.93	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
B		.01	.07									
PT-2												
(N)	62	56	18	52	50	06	22	30	18	20	30	30
A	1.00	.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
B		.01										
SOD												
(N)	62	58	22	55	50	07	22	30	18	20	30	30
A	.78	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.97	.93	.97	1.00
B	.22								.03	.07	.03	
A	1.2	1.1	1.2	1.1	1.1	1.1	1.1	1.2	1.2	1.2	1.2	1.0
$P_{95\%}$	8.0	4.0	8.0	8.0	8.0	8.0	8.0	8.0	8.0	16.0	8.0	4.0
$P_{99\%}$	16	4.0	8.0	8.0	12	8.0	8.0	16	16	16	20	4.0
H%	3.6	1.2	1.1	3.7	2.6	4.5	2.7	3.3	1.4	4.7	3.0	1.0

DISCUSSION

The morphometric analysis of the natural populations originating from West Africa did not reveal clear differences between them. The separation of the Selingue and Bamako populations, both from the Upper Niger, and isolated by a relatively short geographical distance (±110 km), is explained by the isolated position of the former which lives in a man-made lake. All the natural populations from West Africa originate from Sahelo-Sudanian river systems (Senegal, Niger, Volta and Chad) (TREWAVAS, 1983; LÉVÊQUE *et al.*, 1991). Climatological (extension and recession of water bodies) and geological (tectonic activities such as earth movements, faulting, volcanism, and erosion) events during the Late Quaternary largely explain the similarities in faunal composition between them and, in this case, between the natural populations of *O. niloticus* (HUGUENY & LÉVÊQUE, 1994). It should also be noted that during the rainy season, the upper reaches of most of these basins are in contact and faunal exchanges can occur.

According to TREWAVAS (1983), natural populations from the Lower Nile system in Egypt belong to the same subspecies as those from West Africa, *O. niloticus niloticus*. Morphometrically, however, the majority of specimens of both geographic regions can be distinguished from each other. Moreover, the Nile specimens are morphologically closer to the Lake Edward specimens, which, following TREWAVAS (1983) belong to another subspecies *O. niloticus eduardianus*. This is confirmed by the allozyme study. Therefore the subspecific status for the Nile specimens as defined by TREWAVAS (1983) is called into question; further research is necessary.

Morphologically, the parental populations (Volta and Lake Edward, in particular the latter) are markedly different from the Bouake strain. Genetically however, the Bouake strain possesses two specific alleles of the Lake Edward population (FBP-2*B and FH*B) although the specific allele of the Volta (LDH-2*B) could not be detected. This clearly demonstrates that the morphology of the cultured strain has been seriously influenced by conditions in captivity, resulting in a different phenotype.

Concerning the Volta strain, only a small overlap in external morphology is found with the parental population. The small sample size of the latter however, does not enable firm final conclusions concerning the degree of difference in external morphology between them. Genetically, the Volta strain possesses the Volta specific LDH-2*B allele. Further, the Volta strain has a slightly higher number of alleles per locus when compared with the natural Battor (Volta) population, which is probably due to the small sample size of the latter. On the contrary, the H value of the Volta strain is lower. Those two results indicate that there is probably inbreeding, as the consanguinity within a population does not affect the number of alleles of the populations but decreases the number of heterozygotes.

Regarding the Quarun strain, only few specimens overlap with the Manzalla and Cairo specimens (parental populations). Again captive conditions resulted in a different ecophenotype. Genetically the Quarun population is close to the Lake Manzalla and Cairo populations. These three samples possess AAT-3*B, an allele which is characteristic (private) for the Nile populations.

Genetic polymorphism between the three cultured strains and their parental populations was comparable. ROGNON *et al.*, 1996 observed that cultured strains of tilapia have

sometimes higher H and P values compared to wild populations. We suspect that they erroneously mixed the origin of cultured strains and wild populations because no alien allele has been found in these populations, which excludes the possibility of interbreeding.

Morphological differences between cultured strains of *O. niloticus* were already reported by GOURENE &TEUGELS (1993). An overall comparison of all natural populations and all cultured strains examined, showed also important morphological differences between both. It is thus obvious that in captivity the external morphology will be considerably influenced by environmental conditions. MEYER (1987) reported on phenotypic plasticity in a Neotropical cichlid, *Cichlasoma managuense* caused by differences in diet and possibly in feeding mode during ontogeny. Other factors however, such as the lack of currents in culture ponds, undoubtedly affect the external morphology; this is expressed, for example, in the difference in body depth. The degree to which captivity conditions affect the growth rate and thus the aquaculture productivity is presently being studied.

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