

African fishes

SIR — Meyer *et al.* conclude¹ that morphological diversification in flocks of cichlid fishes in Lake Victoria occurs without much molecular evolution. This agrees with our own data on hybrids between different species of cichlid fish from Lake Victoria, which can be bred easily over several generations²⁻⁴. In addition to the molecular data on mitochondrial DNA, our results show the genetic compatibility for the entire genome of some Lake Victoria 'haplochromines'.

But we disagree with Meyer *et al.*'s second conclusion that Lake Malawi species are more closely related to those of Lake Victoria than to those of Lake Tanganyika. We tested by hybridization the genetic compatibility of *Astatotilapia burtoni*, a riverine species from the Lake Tanganyika basin, with *Astatotilapia nubilus*, a riverine species from the Lake Victoria basin. The fertility of the hybrids between these species suggests that they are genetically almost as compatible as haplochromines from the Lake Victoria basin^{2,3}. Moreover, we also tried to breed hybrids between the monotypic genus *Astatoreochromis alluaudi* and several haplochromines of Lake Victoria. According to Meyer *et al.*, this species should be more closely related to Lake Victoria haplochromines than to those of Lake Tanganyika. We succeeded, however, in breeding only one hybrid population between *Astatoreochromis alluaudi* and *Astatotilapia 'black lividus'* (a so far undescribed species of Lake Victoria). These hybrids reproduced, but the eggs deteriorated before hatching. This is the only evidence for sterile hybrids that we have obtained so far. *Astatoreochromis alluaudis* is also the only species in Lake Victoria that stands out in its protein characteristics⁵.

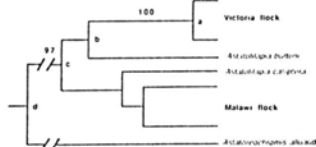
We believe that Meyer *et al.* should include molecular data from the riverine Lake Tanganyika haplochromine *A. burtoni* in their analysis. Their second conclusion will then be that some haplochromines of different lakes arose from more closely related riverine species; in other words, that segregation had started before the lakes formed. The major problem of the species flocks of the great African lakes is clearly how they have evolved and are maintained in sympatry,

while obviously relying exclusively on pre-mating barriers — a significant ethological problem in its own right⁴.

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MEYER *ET AL.* REPLY — Inferring relationships from patterns of hybridization is risky. The hybridization studies involving *Astatotilapia burtoni* males and *Astatotilapia nubilus* females produced only lethal hybrids². Females of *A. burtoni* mated rarely with males of *A. nubilus*, but produced viable hybrids². Numerous studies have shown that hybrid incompatibility, although usually correlated



Evolutionary tree based on comparisons of part of the control region of mtDNA. The region sequenced and the methods used are described by Meyer *et al.*¹. Bootstrap values appear above the two internal branches that are statistically significant (a–b and c–d). The distance from any node to the tips of the descendant branches are roughly proportional to the average number of base substitutional differences between species united by that node. The root of the tree (node d) was determined by using *Julidochromis* as an outgroup (see ref. 1). The two sequences of *Astatotilapia* have been deposited in Gen Bank with accession numbers X58151 (A.c.) and X58152 (A.b.).

with phylogenetic distance, is not an accurate metric for building trees and time scales.

In anticipation of questions about *Astatotilapia*'s phylogenetic status, one of us (A. M.) sequenced the most variable part of the control region of mitochondrial DNA from two key species, *A. burtoni* and *A. calliptera* (a non-endemic cichlid from Lake Malawi). Three *Astatotilapia* species from the Lake Victoria basin (*A. nubilus*, *A. elegans* and *A. piceatus*) had already been tested¹. The figure shows a tree relating the two new sequences to those of the species flocks in

Lake Victoria and Malawi as well as to *Astatoreochromis alluaudi*. The results confirm (with 97 per cent confidence) the hypothesis, suggested by interspecific hybridization studies, that *A. burtoni* is a closer relative of these flocks than is *Astatoreochromis*. This analysis also suggests (although not significant statistically) that *A. burtoni* is closer phylogenetically to the Lake Victoria flock than is the Lake Malawi flock.

Furthermore, and contrary to the hypothesis of Crapon de Caprona and Fritzsche above, the members of the Lake Victoria flock (including *A. nubilus*, *A. elegans* and *A. piceatus*) are more closely related to one another mitochondrially than to *A. burtoni*. The bootstrap value that shows the reality of the a–b lineage in the figure is 100 per cent. We infer that the Lake Victoria flock arose long after the splitting of the *A. burtoni* lineage from the a–b lineage. Our molecular estimate of the time of most recent common ancestry for the Lake Victoria flock is 200,000 years¹, which implies that the flock is younger than the lake (250,000 to 750,000 years old⁶). Thus, our results cast doubt on Crapon de Caprona and Fritzsche's model, above, according to which segregation occurred within the flock before the lake formed.

Another notable feature of the figure is

that *Astatotilapia* species are candidates for being the sister groups of both the Lake Victoria and Lake Malawi flocks. Although *Astatotilapia* is not a monophyletic group (mitochondrially), these particular species may be close in body plan and lifestyle to the ancestral state for these two flocks, and this may help to explain their ability to hybridize with distant relatives.

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SCIENTIFIC CORRESPONDENCE

1/4-7/8 350: 457-468