# Why are there so many cichlid species?

The explosive speciation of cichlid fishes in the African great lakes has intrigued biologists for many decades. Interest was revitalized in 1996 after the publication in *Science* of geological data[1] indicating that the youngest lake, Lake Victoria, must have been completely dry during the most recent Ice Age – perhaps as recently as 12 400 years ago. This implies that the approximately 500 haplochromine cichlid species must have evolved within this extremely short timespan from a single ancestral species[2]. But even with lower estimates of species number and higher estimates of the age of the species flock, the haplochromine cichlids still present one of the most dramatic examples of speciation and diversification in vertebrates.

An old hypothesis – concerning the importance of temporary geographical isolation of cichlid fishes in satellite lakes around Lake Victoria for speciation of cichlid fishes[3] – is no longer much in favour[4,5]. Such satellite lakes only have very few species of cichlids and can therefore not explain the bulk of the speciation events in Lake Victoria. More specifically, this hypothesis cannot explain the large diversity of 'rock' species – since there are no rocky islands in these satellite lakes and each group of rock islands in Lake Victoria has its own species assemblage.

Seehausen *et al.*[6] have now put forward a persuasive hypothesis explaining the high frequency of speciation events that must have occurred. They show how sexual selection could be the driving force behind speciation in the haplochromine cichlids of Lake Victoria, because mate choice of females for differently coloured males maintains reproductive isolation between sympatric species and colour morphs. Females have a strong preference for males of a particular colour when light conditions are sufficiently good[7]. Males of sympatric, closely related species always differ in colour, one species having blue males, the other red or yellow males (females are usually inconspicuously coloured). This colour dichotomy of blue versus red/yellow also holds for conspecific male colour morphs that occur abundantly in the lake.

The colours of the males coincide well with the visual sensitivity of cichlids. Cichlid eyes have three retinal cone pigments and the greatest sensitivity is either for blue or for red and yellow. In deeper water, red/yellow is better visible than blue. Small evolutionary changes can modify the maximum sensitivity of the eye from red/yellow to blue and vice versa (polymorphism in colour vision is known in guppies[8]). Changes in colouration of the males happen frequently, judging from the large number of blue and red/yellow sibling species. If females prefer conspicuous males, individual variation in sensitivity for colours (in females) and in pigmentation (males) will lead to such a frequent occurrence of colour dichotomy (see also Refs 9,10).

Evidence for the importance of sexual selection for the maintenance of reproductive isolation comes from behavioural experiments in monochromatic light, which masks colour differences[8]. Under these light conditions, a breakdown of preferences for conspecific mates occurs. Sadly, important additional evidence comes from a recent loss of cichlid species in Lake Victoria. The increased turbidity of the water owing to human activities is causing a breakdown of reproductive barriers. Females can no longer distinguish males of sibling species from their own when visibility is poor and hybridize with males from other species[6,7]. Hybrids are fully fertile and therefore the species diversity of parts of Lake Victoria has seriously declined with increasing turbidity of the water. There is a great danger of further decline because of the continuing pollution.

Seehausen *et al.*'s hypothesis can explain allopatric speciation where, after allopatric divergence, incipient species later overlap in distribution. But their hypothesis also allows for fully sympatric speciation, solely by mate choice of the females – as in the models of Lande[11], Turner and Burrows[12] and Payne and Krakauer[13]. Spatial heterogeneity plays a role in the sympatric speciation scenario as well, because depth differences are correlated with differences in colour perception, which is relevant for mate preferences; speciation can only take off when novel 'compatible' male and female types (i.e. red males with females that prefer red males) temporarily stay together. Allopatric speciation of cichlid species will certainly have played a role in Lake Victoria, because of its size and diversity of habitats. However, the abundance of sympatrically occurring colour morphs as well as the common absence of mating barriers other than behavioural ones suggests that sympatric speciation has played an important role.

Seehausen *et al.*'s hypothesis[6] nicely augments a much older hypothesis on the speciosity of cichlid fishes. This much-discussed hypothesis was first proposed in 1973 by Liem[14], and bears on the importance of the versatile pharyngeal jaw apparatus in the evolution of cichlid fishes. A large number of speciation events and mating barriers produced by sexual selection is not enough to maintain species diversity. Species diversity is determined by the balance of the numbers of species that originate and go extinct. When, after speciation events, the new species are indistinguishable ecologically, species will be lost in a process akin to random drift[15]. However, the species will never be exactly similar ecologically, in which case the extinction process will be considerably more rapid, except when the differences lead to niche differentiation[16,17]. This niche differentiation has taken place in cichlids on a large scale, leading to a spectacular adaptive radiation. Adaptive radiation can only take place when species are splitting up repeatedly and mate recognition systems or other mechanisms are keeping the adaptively diverging populations apart[18]. Conversely, the many newly emerged species can only continue to coexist when adaptive radiation takes place. Thus, the origination of large numbers of species and a rapid adaptive radiation necessarily go together.

The striking diversity of feeding niches that characterizes cichlids of Lake Victoria[4,14,19] suggests that niche differentiation occurred by rapid specialization for different feeding niches. This implication is strengthened by the observation that sibling species are always characterized by small differences in feeding behaviour (Ref. 20, and N. Bouton, pers. commun.).

Recent support for Liem's[19] hypothesis comes from a comparison of the pharyngeal jaw apparatus in cichlid fishes with that of the presumed generalized percoid ancestors[21,22]. This comparison supports a hypothesis of Vermeij[23] that speciose taxa are characterized by more independent elements than taxa that are less speciose. A large number of independent elements increases the number of potential solutions for a particular biomechanical problem. Therefore, body plans with more independent elements can be more easily modified and diversified than those with fewer independent elements. During the evolution of the cichlid pharyngeal jaw apparatus, two decouplings have occurred[21]. These decouplings have increased the number of independent elements and, thus, the number of degrees of freedom of the cichlid pharyngeal jaw apparatus compared to that of generalized percoids.

There are two reasons why the flexible and versatile pharyngeal jaw apparatus of

  0169-5347/98/$19.00 PII: S0169-5347(97)01239-1 

cichlids promotes evolutionary diversification. First, it provides behavioural plasticity; second, it provides evolvability. Although cichlids usually act as specialists, occupying particular feeding niches, they can eat very diverse food items when necessary, albeit with lower efficiency. This is probably relevant right from the start of the speciation process, because if limiting similarity forces a polymorphic population towards diversification, this type of phenotypic plasticity immediately allows rapid shifts. Subtle niche shifts are not only necessary for sympatric speciation; in the case of allopatric speciation flexibility will be important as well – when a population becomes geographically isolated in a different habitat, the behavioural plasticity will help it to persist.

The second reason for the importance of the versatile pharyngeal jaw apparatus for evolutionary diversification is that quite small behavioural and morphological changes allow cichlids to specialize on different food items[14,21]. Moreover, phenotypic plasticity (including behavioural changes) permits changes in the right direction to occur. These phenotypic adaptations can subsequently be assimilated genetically, which confers great evolutionary potential.

It is essential to combine insights from different disciplines when analysing sympatric and parapatric speciation processes. Such speciation events can only have an influence on species diversity when reproductive barriers arise between different morphs and when disruptive selection occurs so that extinction because of limiting similarity is avoided[17]. In the case of the haplochromine cichlids of Lake Victoria, the following scenario can now be proposed by combining insights. Sexual selection for strikingly coloured males is the driving force behind the generation and reproductive isolation of colour morphs. Disruptive selection on feeding and other specializations promotes the divergence of these incipient species and the resulting niche shifts promote their coexistence. Rapid diversification is possible because of a pharyngeal jaw apparatus with a large number of independent elements that can easily be modified. This flexible pharyngeal jaw apparatus also allows behavioural flexibility which together with a capacity for learning makes cichlids unusually resilient against extinction. There are thus two selection processes acting together – a process of species splitting due to sexual selection and a process of adaptive radiation due to disruptive selection.

Integration of the theory of sexual selection and speciation with the theory of adaptive radiation exemplified by the cichlid story leads to a widening of Vermeij's concept[23]. Body plans of organisms with many independent elements not only allow diversification, but are more likely to allow rapid diversification when subjected to disruptive selection[18]. In addition, it is possible, at least in the case of cichlids, that such body plans allow wider behavioural plasticity. In this context we note that the bony fishes are both very speciose compared to other vertebrate classes and characterized by a particularly large number of loosely connected bony elements in their heads.

We now have a convincing scenario of the happy coincidence of mechanisms that led to the most explosive speciation and adaptive radiation in vertebrate evolution yet described. However, the increased turbidity of Lake Victoria is not only causing hybridization of species, but is – presumably – also preventing further speciation events. This pollution must be reduced if the evolution of the cichlid fauna is to continue along its intriguing path.

## Acknowledgements

We thank Menno Schilthuizen, Paul Brakefield, Hans Slabbekoorn, Jan Sevenster, Peter Mayhew, Niels Bouton and Olivier Glaizot for discussion and comments.

**Frietson Galis**

*Institute for Evolutionary and Ecological Sciences, University of Leiden, PO Box 9516, 2300 RA Leiden, The Netherlands*

**Johan A.J. Metz**

*Institute for Evolutionary and Ecological Sciences, University of Leiden, PO Box 9516, 2300 RA Leiden, The Netherlands and Adaptive Dynamics Network, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria*

## References

1 Johnson, T.C. *et al.* (1996) **Late Pleistocene desiccation of Lake Victoria and rapid evolution of cichlid fishes,** *Science* 273, 1091–1093

2 Meyer, T.D. *et al.* (1990) **Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondrial DNA sequences,** *Nature* 347, 550–553

3 Greenwood, P.H. (1965) **The cichlid fishes of Lake Nabugabo, Uganda,** *Bull. Br. Mus. Nat. Hist. (Zool.)* 25, 139–242

4 Kaufman, L.S., Chapman, L.J. and Chapman, C.A. (1997) **Evolution in fast forward: haplochromine fishes of the Lake Victoria region,** *Endeavour* 21, 23–30

5 Seehausen, O. (1996) *Lake Victoria Rock Cichlids. Taxonomy, Ecology and Distribution*, Verduyn Cichlids

6 Seehausen, O., van Alphen, J.J.M. and Witte, F. (1997) **Cichlid fish diversity threatened by eutrophication that curbs sexual selection,** *Science* 277, 1808–1811

7 Seehausen, O. and van Alphen, J.J.M. **The effect of male coloration on female mate choice in closely related Lake Victoria cichlids (*H. nyererei* complex),** *Behav. Ecol. Sociobiol.* (in press)

8 Archer, S.N. *et al.* (1987) **Visual pigment polymorphism in the guppy *Poecilia reticulata*,** *Vis. Res.* 27, 1243–1252

9 Endler, J.A. and Houde, A.E. (1995) **Geographical variation in female preferences for male traits in *Poecilia reticulata*,** *Evolution* 49, 456–468

10 Deutsch, J.C. (1997) **Colour diversification in Malawi cichlids: evidence for adaptation, reinforcement or sexual selection?** *Biol. J. Linn. Soc.* 62, 1–14

11 Lande, R. (1982) **Rapid origin of sexual isolation and character divergence in a cline,** *Evolution* 36, 1–12

12 Turner, G.E. and Burrows, M.T. (1995) **A model of sympatric speciation by sexual selection,** *Proc. R. Soc. London Ser. B* 260, 287–292

13 Payne, R.J.H. and Krakauer, D.C. (1997) **Sexual selection, space, and speciation,** *Evolution* 51, 1–9

14 Liem, K.F. (1973) **Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws,** *Syst. Zool.* 22, 425–441

15 Wright, S. (1931) **Evolution in Mendelian populations,** *Genetics* 16, 97–159

16 MacArthur, R.H. and Levins, R. (1967) **The limiting similarity, convergence and divergence of coexisting species,** *Am. Nat.* 101, 377–385

17 Meszéna, G. and Metz, J.A.J. **The role of effective environmental dimensionality, in** *Advances in Adaptive Dynamics* (Dieckmann, U. and Metz, J.A.J., eds), (in press)

18 Metz, J.A.J. *et al.* (1996) **Adaptive dynamics: a geometrical study of the consequences of nearly faithful reproduction,** in *Stochastic and Spatial Structures of Dynamical Systems* (van Strien, S.J. and Verduyn Lunel, S.M., eds), pp. 183–231, Elsevier

19 Liem, K.F. (1980) **Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes,** *Am. Zool.* 20, 295–314

20 Hoogerhoud, R.J.C., Witte, F. and Barel, C.D.N. (1983) **The ecological differentiation of two closely resembling Haplochromis species from Lake Victoria (*H. iris* and *H. hiatus*; Pisces, Cichlidae),** *Neth. J. Zool.* 33, 283–305

21 Galis, F. and Drucker, E.G. (1996) **Pharyngeal biting mechanics in Centrarchids and cichlids: Insights into a key evolutionary innovation,** *J. Evol. Biol.* 9, 641–670

22 Galis, F. (1996) **The application of functional morphology to evolutionary studies,** *Trends Ecol. Evol.* 11, 124–129

23 Vermeij, G. (1974) **Adaptation, versatility, and evolution,** *Syst. Zool.* 22, 466–477