XVth International Congress of Zoology, Sect. II, Paper 2

EVOLUTION AND SPECIATION IN THE *HAPLOCHROMIS* (PISCES, CICHLIDAE) OF LAKE VICTORIA

P. H. GREENWOOD

British Museum (Natural History) and East African Fisheries Research Organization, Jinja, Uganda

THE species flock of cichlid fishes in Lake Victoria comprises two endemic *Tilapia*, about seventy endemic *Haplochromis* and four endemic monotypic genera with strong *Haplochromis* affinities. In addition there are six *Haplochromis* and one monotypic genus with a somewhat wider distribution; however, only one of these species, the nilotic *H. multicolor*, extends beyond the Edward–Victoria drainage basins. The smaller *Haplochromis* species flocks in Lakes Edward and Kivu are closely related to that of Victoria, but even including these species the whole complex shows less taxonomic, morphological and ecological diversity than the flocks of *Haplochromis* and *Haplochromis*-like species in Lake Nyasa.

Despite the narrow range of diversity in the *Haplochromis* of Lake Victoria, most of the species are biologically valid. Until recently fifty-five species were recognized, but as a result of intensive field studies at least fifteen more species must be added. Some of these are new and others are species which previously were sunk in synonymy. In many cases it was found that morphologically identical species had distinctive male breeding coloration and that they could also be distinguished on ecological criteria, particularly the type of substrate to which the species was confined.

Variation in such characters as scale-numbers, gill-raker and fin-ray counts is restricted to very narrow limits; indeed, the range for the entire flock may be encompassed by a single species. As Regan first showed, the greatest structural diversity is found in the dentition; this in turn is indicative of adaptive radiation towards specialized feeding habits. Associated with these dental characters there is considerable variation in syncranial architecture.

Ecologically, the flock is characterized by intra-generic diversity in feeding habits and a wide intra-specific tolerance of different habitats.

From the morphological and anatomical viewpoints, the seventy *Haplochromis* may be divided into two major but interconnected groups, in each of which the range and nature of dental specialization is slight. One group comprises the non-piscivorous species and the other the piscivorous species. Within each group there has evolved a number of structurally specialized lines, each composed of a few species showing increasingly specialized dentition and skull structure. If these sub-groups were not so clearly linked to the main body of anatomically

uniform species, they could be recognized as distinct genera. The presence of several species apparently showing ancestor–descendant relationships is a striking feature of the flock.

Four major theories have been advanced to explain the means whereby the flock was evolved; hitherto there has been no ecological information to employ in these arguments.

The earliest theory was that of "explosive", sympatric speciation (with which may be included Regan's idea of evolution by habitudinal segregation); it was postulated before the genetical mechanism of speciation was fully appreciated and can no longer be considered tenable.

There is no evidence to support the concept of multiple colonization of the lake by species from affluent rivers. The adaptively multi-radiate lacustrine *Haplochromis* species in Lake Victoria stand in marked contrast to the taxonomically and ecologically uniform *Haplochromis* in any river system. Except for a few of the most generalized endemic species, the nearest relatives of the Lake Victoria *Haplochromis* occur in the lake itself.

Microgeographical isolation by ecological barriers probably gave rise to some species, but it cannot be considered an important evolutionary factor because so few species are confined to any particular habitat. Most species show a distinct preference for either a firm or a soft substrate, but they will occur in a variety of habitats (e.g. bays, gulfs and exposed coasts) provided the substrate is suitable. The most obvious ecological differences within the flock are the feeding habits of various species-groups; there is no indication that any food source is so distributed that microgeographical isolation could influence the evolution of trophic groups. It is a characteristic of the flock that several species with the same feeding habits occur in any one area. The large number of predatory species (over 40% of the total) may be partly responsible for this phenomenon in that they could keep the density of the prey-species at a level where interspecific competition for food would be minimized. Evidence favouring the origin of some species by microgeographical isolation is provided by several pairs of morphologically similar species, one member occurring offshore over a mud-bottom and the other inshore over a firm substrate. The soft-substrate species may have evolved from populations which left the inshore regions to avoid competition for food or for breeding sites.

The fourth theory, which incorporates the available geological history of the lake, envisages evolution and speciation taking place when the lake was broken up into a number of smaller lakes, either through climatic changes or earth movements. The related *Haplochromis* of Lakes Victoria, Edward and Kivu accord well with this theory of lake contraction and expansion, as does the presence of five species common to both Edward and Victoria. Since Victoria occupies an expansive and shallow basin, as compared with Lakes Edward and Kivu, it would appear to

provide greater physiographical opportunities for fractioning. This in turn may account for its greater number of endemic species. Each lake possesses a species flock showing clear division into the basic trophic groups of predatory, insectivorous, mollusc-eating and algal-grazing species, but in Victoria there has been far more speciation within the groups. Populations isolated for relatively short periods of time could be expected to diverge only slightly in morphological and ecological characters, thus accounting for the taxonomic and bionomic picture which has emerged from the field study of Lake Victoria *Haplochromis* species.