The oldest fossil cichlids (Teleostei: Perciformes): indication of a 45 million-year-old species flock

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Five closely related species of fossil cichlids collected from an Eocene site in Tanzania, East Africa, represent the oldest known cichlids. The specimens are whole-body, articulated fishes that are extremely well preserved and, therefore, have the potential to add to our knowledge of the history of this family. Modern cichlids are particularly well known for the numerous species flocks of the East African Great Lakes. A great deal of research is ongoing regarding all aspects of the fishes in these flocks, including their evolutionary history. The new collection of fossils reported here is interpreted as representing a species flock that arose in a small crater lake. These fossils indicate that cichlids' ability to form species flocks evolved early in the history of this family.

Keywords: Cichlidae; species flock; Eocene

1. INTRODUCTION

There are an estimated 1300 or more species in the family Cichlidae, which are found predominantly in Central and South America and Africa (Nelson 1994), the majority of which have radiated rapidly in the East African Great Lakes forming numerous species flocks (Meyer 1993). While other species flocks are known, East African cichlid fishes are the classic examples. Recent molecular work has shown the super-species flocks in Lakes Victoria and Malawi to be monophyletic (Meyer 1993; Booton *et al.* 1999), but the relationships of many other cichlids are still not well known (Kornfield & Parker 1997), although new information is continually being added (e.g. Streelman *et al.* 1998; Farias *et al.* 1999). There has been extensive research on the phylogenetic relationships, behaviour, evolution and all aspects of cichlid biology by many authors. However, one area in which knowledge is still critically lacking is the fossil record.

2. FOSSIL CICHLIDS

A new collection of fossil cichlids was recently recovered from Mahenge in the Singida region of Tanzania (figure 1). The Mahenge site has been interpreted as being a small, approximately circular lake of ca. 400 m diameter that formed in the crater of a kimberlite intrusion (Mannard 1962) and probably persisted for between ca. 8000 and 22 000 years (Harrison *et al.* 2001). Mannard (1962) sent some of the fossils from the Mahenge site to P. H. Greenwood at the Natural History Museum in London. Based on the ichthyofauna, Greenwood (1960) originally suggested the Mahenge specimens to be Late Tertiary period in age but, after further study, this was revised and given an older Oligocene age (Greenwood & Patterson 1967). Geological evidence gives an Eocene age for the site. Kimberlites from elsewhere in the Singida field have been dated to between 51 and 54 million years (Myr) using U–Pb and fission track dating (Harrison

et al. 2001). In 1996, the Wembere–Manonga Palaeontological Expedition, which was led by Dr T. Harrison of New York University, excavated the deposits at Mahenge and, in the process, collected zircon from the pipe for radiometric dating. Analysis of the zircon established a $^{206}\text{Pb}/^{238}\text{U}$ date for the formation of the lake of 46.0 ± 0.3 Myr ago, thereby placing Mahenge in the mid-Eocene period (Harrison *et al.* 2001). Modern studies of crater lakes formed in a similar fashion have indicated that the lake at Mahenge could have formed and been completely filled with sediments soon after the kimberlite intrusion (Hawthorne 1975; Smith 1986) and, therefore, that the fossils would not be much younger than the kimberlite intrusion itself. The cichlids from this site therefore predate the next oldest known cichlid fossils by at least 15 Myr.

Although an Early Cretaceous origin has been suggested for cichlids (Stiassny 1991), this hypothesis seems to be based on the assumption that a fully marine environment would have been a barrier to cichlid dispersal and, therefore, that the common ancestry of South American and African faunas would date back prior to the separation of these continents by the Atlantic Ocean ca. 120 Myr ago. However, some cichlids inhabit marine environments (e.g. Myers 1949; Greenwood 1994), which indicates that marine waters are not a barrier to cichlid dispersal. Farias *et al.* (1999) also supported an Early Cretaceous origin based on a sister-group relationship between African and neotropical taxa, each of which formed a monophyletic group in their analysis. However, regardless of whether the African cichlids are a monophyletic group or are paraphyletic (e.g. Stiassny 1991), the phylogenetic relationships equally support the migration of a lineage from Africa to the neotropics after separation of the two continents. The timing of the separation of South America from Africa therefore does not determine a latest date of origin for the Cichlidae.

Lundberg (1993) also argued against a Cretaceous age of origin as being far too old based on the fossil record. The two cichlid fossils previously credited with being the oldest are *Macracara prisca* from Brazil and an undescribed specimen from Italy. The Italian fossil is poorly preserved and is not confirmed as belonging to the Cichlidae

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Figure 1. Map of Tanzania with the location of the Mahenge crater lake deposits indicated.

(Frickhinger 1995). The Brazilian fossil, which is from Maranhão, is a cichlid, but is of questionable age. Maranhão was given an Early Tertiary date (Woodward 1939) based on the assumed presence of the Eocene clupeid genus *Knightia*. However, that genus is not represented at Maranhão (Grande 1985). The date of the site has more recently been given variously as Miocene (Frickhinger 1995) and possibly Pliocene (Schaeffer 1947; Grande 1985) and the fossil is now listed in an extant genus as *Geophagus priscus* (Casciotta & Arratia 1993; Frickhinger 1995). After excluding these two questionable records, the previously oldest known members of the family Cichlidae are described species from Oligocene deposits in East Africa and Saudi Arabia (Van Couvering 1982; Micklich & Roscher 1990; Casciotta & Arratia 1993) and undescribed remains from Oman (Thomas *et al.* 1999). The family Cichlidae may only have originated in the Tertiary period.

3. THE CICHLIDS OF MAHENG

The Mahenge cichlids are not only remarkable for their age, but also for their superb state of preservation. Many of the known cichlid fossils are isolated bones and incomplete specimens or are referable to extant genera (Greenwood 1974; Van Couvering 1982; Murray &

Figure 2. Photographs of six of the cichlid specimens from Mahenge illustrating the range of body form. The specimens, which are identified by the prefix 'WM' in reference to the collecting expedition Wembere–Manonga, are the property of the National Museum of Tanzania. (a) WM 019/96, (b) WM 215/96, (c) WM 405/96, (d) WM 072/96, (e) WM 472/96 and (f) WM 399/96. The scale bar is given in centimetres.

Figure 3. Phylogeny of the Cichlidae based on Lippitsch's (1995, fig. 2, 1998, fig. 4) cladograms of relationships. Position A is the most-derived placement for the Mahenge species based on the lack of advanced state for the pattern of the frontal canal pores (they have both a left and right pore zero rather than a single median pore) (see Stiassny 1991). Position B is the most basal position based on the possession of a single pre-dorsal (=supraneural) bone. The scale characteristics from Lippitsch (1993, 1995) indicate that the Mahenge cichlids are positioned at C (see Murray 2000).

Stewart 1999), which contributes little information on the early history of the family.

Characteristics that have been used to support the monophyly of the Cichlidae, such as details of the jaw musculature and the presence of microbranchiospines on the gill arches (e.g. Stiassny 1981), are not preserved in fossils. However, the Mahenge specimens can be included in this family based on the structure of the lower pharyngeal jaw, the interrupted lateral line, the form of the scales and scale covering and meristic characteristics such as the number of vertebrae, fin spines and fin rays.

The specimens, which range in size from 29 to 63 mm standard length, all have three spines and nine rays in the anal fin, 15 spines and eight or nine rays in the dorsal fin, a single pre-dorsal bone, a principal caudal fin ray count of 17 and between 22 and 26 vertebrae. In specimens with the pharyngeal and jaw teeth preserved, the teeth are unicuspid with a slightly hooked tip. The bodies are covered with ctenoid scales, which are slightly smaller on the chest than the flank. Cycloid scales cover most of the skull bones.

Greenwood (1960) originally examined a few, less well-preserved specimens and suggested that the Mahenge specimens belonged to a single species that might be similar to *Haplochromis bloyeti* (which has since been transferred to the genus *Astatotilapia*) (Wickler 1963). Upon

examination of two further specimens, Greenwood & Patterson (1967) suggested that the affinities might be with *Hemihaplochromis multicolor*, which is now recognized in *Pseudocrenilabrus* (Greenwood 1989). *Pseudocrenilabrus multicolor* and *Astatotilapia bloyeti* are both considered to be generalized haplochromines, in both anatomy and ecology. The Mahenge cichlids apparently represented a generalized or primitive species in Greenwood's (1960) view.

The cichlid specimens from the much larger 1996 collection (figure 2) represent at least five different species based on osteological characteristics such as the shape of the supraoccipital, frontal, opercular and hyomandibular bones (Murray 2000). Fryer *et al.* (1983) pointed out that different fossil species might be proposed when in fact they are merely two or more morphs of the same species. In cichlids, these morphs are for the most part distinguished by morphological differences in the teeth and jaws that are associated with different food types or environments (e.g. Greenwood 1965; Liem & Kaufman 1984; Meyer 1992; Huyseune 1995; Smits *et al.* 1996). The Mahenge cichlids are uniform in tooth type and there is little variation in the upper and lower jaws or the visible pharyngeal bones and teeth. The teeth, particularly on the pharyngeal jaws, would be expected to show variation if these cichlids were different morphs of

the same species with different food sources. Therefore, there is no evidence that phenotypic plasticity has affected the determination of the number of Mahenge species.

The potential for overestimating the number of species represented by fossil specimens based on a morphological species definition is further countered by the fact that many cichlid species are distinguished by biologists based on colour patterns, behaviour and habitat preference. None of these characteristics is represented in the fossil record. Dorit (1990) discussed the question of whether the true range of species present in the fossil record could be distinguished. He concluded that the number of species in a fossil assemblage would be underestimated compared with a similar assemblage of extant species. It is more likely that the number of species recognized in a fossil assemblage such as that of Mahenge will be fewer than probably actually existed. In addition, the excavated area of the crater lake at Mahenge represents less than 0.1% of the surface area of the lake. It is likely that the number of cichlid species has been both underestimated and undersampled.

4. EOCENE SPECIES FLOCK

The concept of cichlid subgroups has changed since Greenwood's (1960) work on these fossil cichlids. Several lineages are now recognized in addition to the traditional 'haplochromine/tilapiine' dichotomy (e.g. Stiassny 1991). There are few osteological or other characteristics known for cichlids that are applicable to fossils (the number of pre-dorsal bones, the pattern of the frontal canal pores and a suite of scale characteristics). Each of these characteristics indicates a different placement within the family for the Mahenge cichlids (figure 3). However, these species do seem to belong in a basal position and cannot be included in any of the haplochromine genera.

However, do the Mahenge crater lake cichlids comprise a species flock? Greenwood (1984) suggested that, in order to identify groups of organisms as species flocks, the members must be monophyletic and endemic to a circumscribed geographical area. Other potential fossil species flocks have been reported, such as that of semionotid fishes from the Early Jurassic Towaco Formation, Newark Basin (McCune 1987) and percoid fishes from the Eocene Messel Formation (Micklich 1996). Recent lepidological studies (Lippitsch 1993, 1995, 1998) have shown that scale characteristics have the potential to be exploited in characterizing genera of cichlids. Although Lippitsch (1993) listed 96 scale and squamation characteristics, only 42 of these can be determined from the Mahenge fossil material. The Mahenge cichlids share the same character state for all 42 characteristics. The scale criteria indicate that these fish were closely related and they have therefore been described within a single genus (Murray 2000).

With regard to endemism, it is probable that the Mahenge species, which were adapted to lacustrine habitats in an isolated crater lake, would be endemic to this locality, although the nature of the fossil record precludes certainty. The close relationships of these cichlids with one another based on scale and squamation characteristics and the isolated nature of this lake indicate that these species may have formed an Eocene crater lake cichlid species flock.

Modern crater lakes containing cichlid species flocks, including Barombi Mbo and Bermin (Cameroon), also contain non-cichlid fishes (e.g. Stiassny *et al.* 1992), as is the situation at Mahenge. There are representatives of four non-cichlid taxa that are also known from the Mahenge deposits. These are two described species, the osteoglossomorph *Singida jacksonoides* (Greenwood & Patterson 1967) and the clupeomorph *Palaeodenticeps tanganyikae* (Greenwood 1960), along with an undescribed catfish (Siluriformes cf. Mochokidae) and a second osteoglossomorph. As with modern cichlid species flocks, the flock at Mahenge formed in the presence of non-flocking fishes.

The ability of cichlids to form species flocks has been accredited to intrinsic factors of the fish, including behaviour, leading to sympatric speciation or to extrinsic factors, such as the extensive shorelines of the Great Rift Lakes favouring isolation of populations, leading to micro-allopatric speciation (Greenwood 1964; Liem 1973; Fryer 1977; Dominey 1984; Owen *et al.* 1990; Verheyen *et al.* 1996; Seehausen *et al.* 1997). The nature of a small crater lake indicates that the Mahenge cichlids may have speciated sympatrically as has been suggested for other crater lake cichlid flocks (Schliewen *et al.* 1994).

Not only are the Mahenge cichlids the oldest known species but, as a potential flock, they are the oldest record of any kind of species flock formation in the Cichlidae. Species flocks in lacustrine habitats have been described for tilapiine and haplochromine cichlids from extant populations in Africa and a 'riverine flock' of cichlids has been described from South America (De Lucena & Kullander 1992). Other fossil cichlids from an Oligocene lake in Saudi Arabia were considered as belonging to several different lineages and, therefore, do not constitute a species flock (Lippitsch & Micklich 1998). The Mahenge cichlids provide the first fossil evidence to indicate that the ability of the cichlids to form species flocks arose prior to 40 Myr ago.

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