Journal of Vertebrate Paleontology 23(3):508–516, September 2003
© 2003 by the Society of Vertebrate Paleontology

OREOCHROMIS LORENZOI, A NEW SPECIES OF TILAPIINE CICHLID FROM THE LATE MIOCENE OF CENTRAL ITALY

GIORGIO CARNEVALE, CHIARA SORBINI, and WALTER LANDINI
Dipartimento di Scienze della Terra, Università di Pisa, via S. Maria, 53, 56126 Pisa, Italy, landini@dst.unipi.it

ABSTRACT—A new species of tilapiine cichlid, *Oreochromis lorenzoi*, is described from the late Miocene (Messinian) of central Italy. This species is represented by four articulated specimens and a caudal region of a fifth individual. *Oreochromis lorenzoi*, sp. nov. is the earliest confirmed representative of the genus *Oreochromis*, and it is the first European fossil cichlid. *Oreochromis lorenzoi* and additional examples from other fossil fishes provide evidence of faunal exchanges between Africa and the northern coasts of the Mediterranean during the Miocene. Paleoenvironmental implications are also discussed.

INTRODUCTION

The family Cichlidae is one of the most speciose perciform families with more than 1,400 described species. Together with Labridae (including Scaridae and Odacidae), Pomacentridae, and Embiotocidae, the cichlids are included in the suborder Labroidei (Liem and Greenwood, 1981; Stiassny and Jensen, 1987). They live in brackish and freshwater environments of Africa, Madagascar, the Neotropics, the West Indies, the Middle East, Southern India, and Sri Lanka. Monophyly of this family is currently recognized (Liem and Greenwood, 1981; Stiassny, 1981) and several authors consider cichlids as sister-taxon of other labroid families (Stiassny and Jensen, 1987). These fishes have long fascinated ichthyologists and evolutionary biologists (Fryer et al., 1983; Futuyma, 1998). The center of this attraction is the explosive, adaptively multiradiate speciation in the Great Lakes of Africa, where these fishes are greatly represented with a conspicuous number of taxa (Greenwood, 1973). This dramatic radiation is one of the macroevolutionary episodes in vertebrate history, involving the proliferation of numerous distinct lineages occupying a diversity of trophic levels over a geologically short length of time (Carroll, 1997).

Paradoxically, considering the explosive speciation, cichlids are conservative in underlying anatomy (Stiassny, 1991), undergoing a modest genetic differentiation (Meyer, 1993). Despite their taxonomic differentiation, large structural modification or bauplan reorganization are not easily recognizable. The ecological and evolutionary success of cichlids has been attributed to breeding behavior, color-based sexual selection, niche partitioning, and trophic polymorphism (Kornfield and Smith, 2000). An incredible variety of diets and adaptations is justified by the morphopotentiality of the pharynx (Liem, 1973, 1980; Lauder, 1983), which represents an amazing key innovation (sensu Lauder, 1981).

Fossil cichlids are known from many Tertiary localities of Africa, the Near East, the Antilles, and South America. The oldest cichlids have been found in the Eocene sediments of Mahenge, Tanzania (Murray, 2000, 2001a), but the origin of this family is more ancient, probably localized in the Cretaceous (Stiassny, 1991; Kumazawa et al., 1999) or early in the Cenozoic (Murray, 2001b; Vences et al., 2001).

In the 1980s some cichlid remains were found in Miocene deposits of central Italy (Fig. 1). These fishes were reported by Sorbini (1988:pl. 38, fig. 1) and Landini and Sorbini (1989:fig. 6), who preliminarily described the fossils as indeterminate Tilapiini. One of these fishes (MCSNV T1097) was also figured in Frickhinger (1991:863) and erroneously considered of Pliocene age.

Tilapiine cichlids are today distributed in Africa, Israel, Syria, and Iran, while fossil remains are known from the Cenozoic and Quaternary of the African Plate (White, 1937; Greenwood, 1974; Van Couvering, 1982; Trewavas, 1983). More recently, Gaemers (1989) erected the tilapiine cichlid genus *Eurotilapia*, based on otoliths and teeth from the Miocene of Germany, Moravia and Switzerland. These remains were later considered by the same author as belonging to a channid (Gaemers, 1990).

Identification of fossil cichlids is often very difficult because of fragmentation and crushing of the specimens. Furthermore, many diagnostic characters at the species level are based on color patterns, rarely preserved on fossils. Among the ten synapomorphies of cichlids, recognized among others by Stiassny (1991), six correspond to soft anatomy and the remaining four to delicate structures such as microbranchiospines or elements from the branchial skeleton that have little chance to fossilize. More recently, some fossil cichlids have been restudied after a new survey of cichlid osteology (Casciotta and Arratia, 1993; Murray and Stewart, 1999) and several diagnostic characters, easily recognizable on fossils, have been listed.

The objectives of this paper are to describe and reanalyze the fossil tilapiine cichlids from the Miocene of central Italy. Paleoecology and paleobiogeography are also discussed.

MATERIALS AND METHODS

Five fossil specimens have been studied: two complete skeletons (MSF26, MSF207) and one incomplete skeleton preserved in plate and counterplate (MGPC21812a, MGPC21812b) from Borgo Tossignano, one complete skeleton in plate and counterplate (MCSNV T1097/MCSNV T1098) from Monte Castellaro, and one incomplete skeleton in plate and counterplate (MSF3/MSF3.1) from Brisighella. All the specimens, except MSF3/MSF3.1, measure from 52 mm to 84.5 mm standard length. Specimen MSF3/MSF3.1 is the largest one. This specimen lacks the anterior part of the body and the estimated total length reached about 420 mm. No differences have been found to distinguish the specimens and thus are all considered as belonging to the same species of fish. Also, the largely incomplete specimen MSF3/MSF3.1 shows an identical pattern of squamation.

Measurements on all the specimens have been taken using a dial calipers. All extinct taxa are marked with daggers (†) preceding their names.

Drawings were made using a WILD type 181300 microscope with camera lucida. ‘‘Kukri’’-shaped pharyngeal teeth were

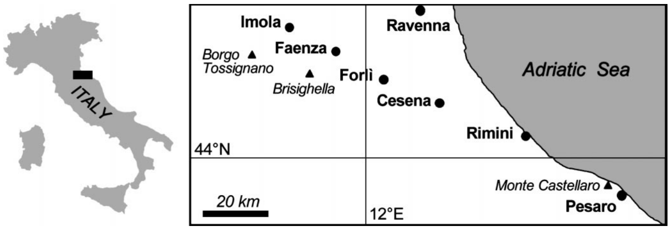

FIGURE 1. Topographic map showing, with solid triangles, the sites where the specimens of †*Oreochromis lorenzoi* were collected.

photographed using a JEOL JSM-5200 SEM, and scales were photographed using a WILD Photomakroskop M400.

Institutional Abbreviations—Museo Civico di Storia Naturale, Verona (**MCSNV**); Museo di Geologia e Paleontologia ''G. Capellini'' Università di Bologna (**MGPC**); Museo Civico di Scienze Naturali, Faenza (**MSF**).

Anatomical Abbreviations—**1st v**, first vertebra; **br**, branchiostegal rays; **ch**, ceratohyal; **cl**, cleithrum; **den**, dentary; **e**, epural; **fr**, frontal; **hyo**, hyomandibula; **hyp**, hypural; **ior**, infraorbital bones; **lac**, lachrymal; **op**, opercle; **phy**, parhypural; **pmx**, premaxilla; **pop**, preopercle; **psph**, parasphenoid; **ptt**, posttemporal; **qu**, quadrate; **scl**, supracleithrum; **sn**, supraneural; **soc**, supraoccipital; **sop**, subopercle; **sy**, symplectic; **un**, uroneural.

SYSTEMATIC PALEONTOLOGY

Subdivision TELEOSTEI sensu Patterson and Rosen, 1977
Order PERCIFORMES sensu Johnson and Patterson, 1993
Suborder LABROIDEI sensu Stiassny and Jensen, 1987
Family CICHLIDAE Gill, 1872
Tribe TILAPIINI Trewavas, 1983
Genus *OREOCHROMIS* Günther, 1880
Subgenus *OREOCHROMIS* sensu Trewavas, 1983
†*OREOCHROMIS* (*OREOCHROMIS*) *LORENZOI*, sp. nov.
(Figs. 2–7; Table 1)

Sorbini L. (1988):26, pl. 38
Landini and Sorbini (1989):287–292, pl. 1

Holotype—MSF26, a complete specimen which preserves the diagnostic characters (Fig. 6A).

Additional Specimens—MSF207 (paratype; Fig. 6B); MSF3/MSF3.1 (Fig. 7A, B); MCSNVT1097/MCSNVT1098 (paratype) (Fig. 6C, D); MGPC21812a/MGPC21812b (paratype; Fig. 6E, F).

Locality and Horizon—†*Oreochromis lorenzoi* is known only from the Miocene deposits of the Gessoso-Solfifera Formation. As reported by Landini and Sorbini (1989), the fossils have been collected from three localities of eastern-central Italy (Fig. 1) (Brisighella, Borgo Tossignano, Monte Castellaro) where this formation outcrops. The Gessoso-Solfifera Formation dates back to the upper Miocene, Messinian, and consists of sixteen evaporite cycles (Vai and Ricci Lucchi, 1977; Marabini and Vai, 1985; Vai, 1997), all included in the ''lower evaporite'' Mediterranean Messinian lithostratigraphic unit (see, e.g., Hilgen et al., 1995). The most ancient specimen (MSF3/MSF3.1) comes from the euxinic layers of the basal evaporite cycles of Monticino Quarry (approximatively 6 Ma; see e.g., Krijgsman et al., 1999), near the town of Brisighella, while the others are from the marly and clayey interstrata of the upper evaporite cycles outcropping near Borgo Tossignano and Monte Castellaro.

Diagnosis—Differs from other *Oreochromis* (*Oreochromis*) by the unique combination of vertebral (30), dorsal (XV+12), and anal (IV+8) formulae.

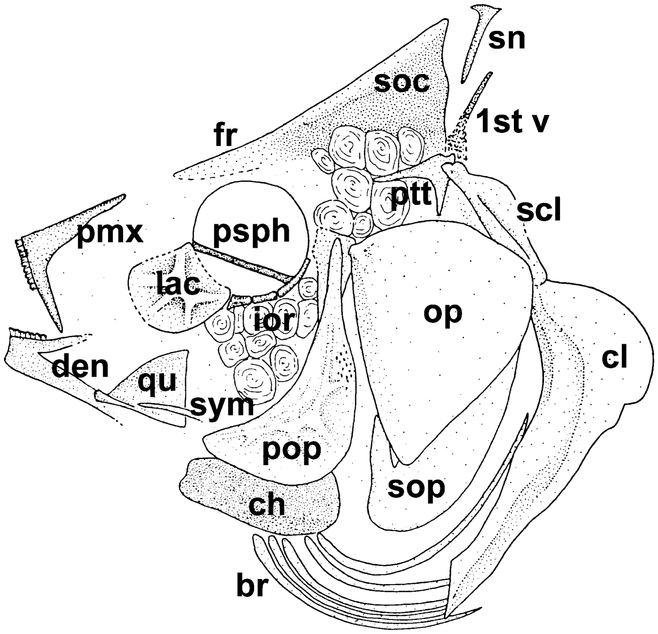

FIGURE 2. †*Oreochromis lorenzoi* labeled reconstruction of head and pectoral girdle.

Discussion—†*Oreochromis lorenzoi* shows a number of characters diagnostic of Tilapiini, including: cycloid scales, general body shape, and presence of ''kukri''-shaped pharyngeal teeth. Within Tilapiini, this species also shows several characters diagnostic of the genus *Oreochromis*, including: acute notch in the posteroventral edge of the cleithrum dorsal plate; predorsal bone sharply angled; granulation pattern of the scales; scales on belly smaller than flank scales; lachrymal of moderate depth. The inclusion of the species in the subgenus *Oreochromis* is justified by the presence of the following features: scaleless lachrymal with five lateral line openings; four anal fin spines. Following the data reported in Trewavas (1983), †*Oreochromis lorenzoi* is very similar in meristic characters to *Oreochromis leucostictus*, *Oreochromis shiranus*, and *Oreochromis spilurus* based on the number of dorsal and anal fin spines. However, none of the species shows a similar combination of vertebral and dorsal and anal fin formulae. Therefore, †*Oreochromis lorenzoi* differs from all other living and fossil described species of the genus *Oreochromis*.

Etymology—The specific epithet ''lorenzoi'' honors the late Dr. Lorenzo Sorbini, Director of the Museo Civico di Storia Naturale of Verona, in recognition of his contribution to the knowledge of the Miocene cichlids here described.

Description

Measurements for †*Oreochromis lorenzoi* are summarized in Table 1. †*Oreochromis lorenzoi* is a deep-bodied cichlid. The shape and body contours (Fig. 3A, B) are very similar to those of several other species of the genus *Oreochromis*. The profile of the head is slightly convex. The caudal peduncle is short and deep.

Neurocranium—In general the bones of the skull are extensively crushed and difficult to interpret. Of the skull roof only small portions of the frontals are visible on MSF207 (Fig. 2).

The supraoccipital is preserved on MSF207. The supraoccipital crest (Fig. 2) is convex posteriorly and greatly resembles that of *Oreochromis niloticus* (Murray and Stewart, 1999:fig. 3A). The relationship of the supraoccipital to the surrounding

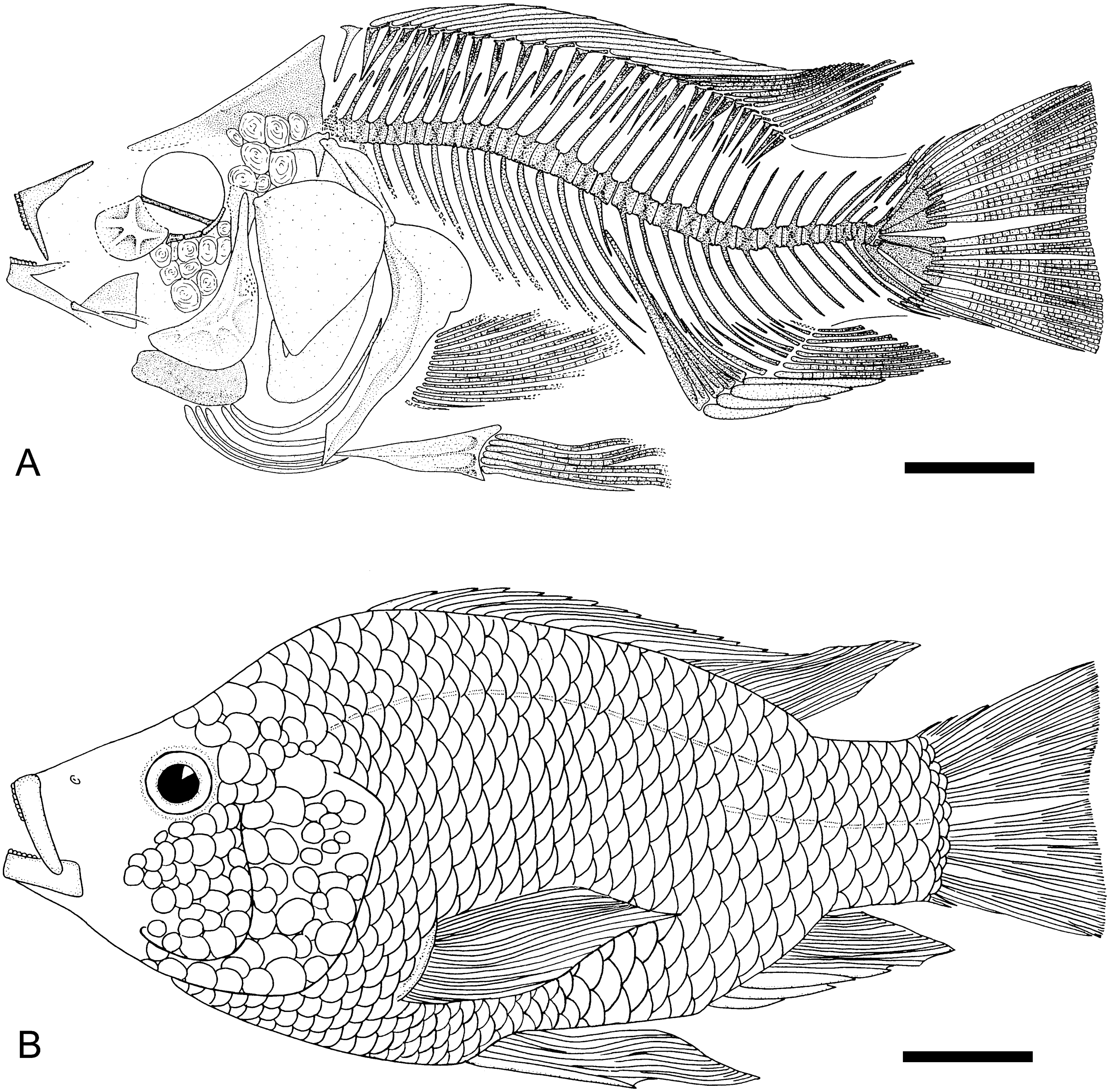

FIGURE 3. †*Oreochromis lorenzoi*, **A**, reconstruction of the skeleton. **B**, reconstruction of the scale pattern. Scale bars equal 1 cm.

bones is not clear because of the preservation of the specimens. Ventral to the supraoccipital, the lateral sensory canal of the pterotic is partially preserved on MSF207.

The parasphenoid is exposed in the lower third of the orbit (Fig. 2).

Infraorbitals—Four infraorbitals are visible on MGPC21812b. The fifth infraorbital and the dermosphenotic are badly damaged. The lachrymal is large, subrectangular in outline (Fig. 2), and reaching nearly 16% of the head length. This bone has five sensory canal pores disposed in the same pattern as in many other tilapiines (Vandewalle, 1972; Stiassny, 1991; Murray and Stewart, 1999). Infraorbitals two through four are tubular, thin, and subrectangular in shape (Fig. 2).

Jaws and Suspensorium—In the upper jaw, the ascending arm of the premaxilla appears slightly longer than the dentigerous arm. The dentigerous arm of this bone bears many bicuspid and tricuspid teeth (Fig. 4A, B). Of the lower jaw, the dentary is visible on MSF207, while part of the articular is preserved in MCSNVT1097. The lower jaw teeth are similar to those of the premaxilla (Fig. 4A, B).

The quadrate and the symplectic are visible on MCSNVT1097, but poorly preserved (Fig. 2). The dorsal portion of the hyomandibula is present on MSF207 (Fig. 2), and greatly resembles that of *Oreochromis niloticus* and †*Oreochromis harrisae* (Murray and Stewart, 1999:figs. 3D, 4).

Opercular Series—The preopercle is present on MSF26 and MGPC21812b. In both specimens this bone is exposed in medial view, showing the lateral sensory canal and pores (Fig. 2).

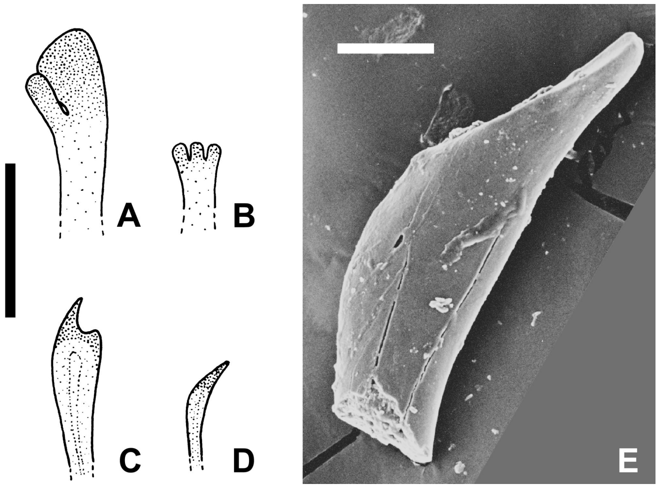

FIGURE 4. Teeth of †*Oreochromis lorenzoi* **A**, bicuspid jaw tooth in frontal view. **B**, tricuspid jaw tooth in frontal view. **C**, pharyngeal tooth in lateral view. **D**, kukri-shaped pharyngeal tooth in lateral view. Black scale bar equals 1 mm. **E**, SEM photograph of a kukri-shaped pharyngeal tooth in lateral view. White scale bar equals 50 μm.

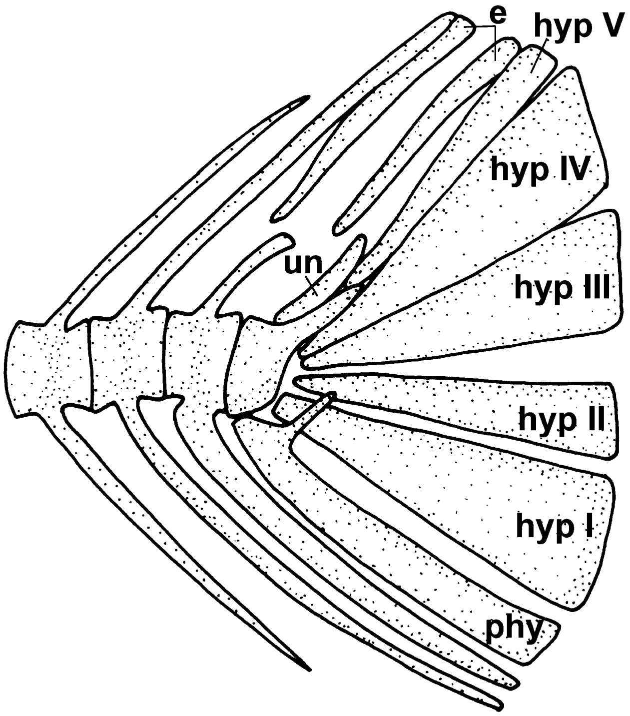

FIGURE 5. †*Oreochromis lorenzoi*, reconstruction of caudal skeleton.

The opercle has a posterodorsal excavation (Fig. 2), similar to that of *Oreochromis niloticus* and †*Oreochromis harrisae*, figured in Murray and Stewart (1999). Subopercle and interopercle are preserved as impressions on MSF26.

Gill Arches—The ceratohyal is clear on specimen MCSNVT1097 (Fig. 3). Anteriorly, the suture with the hypohyals is difficult to interpret. There are five branchiostegal rays. Only the fifth branchiostegal ray articulates with the epihyal.

Of the pharyngeal jaws only the teeth are preserved (Fig. 4C, D, E). The teeth of both upper and lower pharyngeal jaws are unicuspid. There are many ''kukri''-shaped teeth (Fig. 4D, E) in the anterior field of the lower pharyngeal jaw. These teeth were named by Greenwood (1987) for their resemblance to the blade of a ''kukri,'' the Nepalese knife much favored as a weapon by Gurkha soldiers. As reported by the same author (Greenwood, 1987), these teeth are found in most Tilapiini, with the exception of the genera endemic to the Cameroonian lake Barombi Mbu (*Myaka*, *Konia*, *Stomatepia*, and *Pungu*).

Vertebral Column—The vertebral column has a total of 30 vertebrae (16 abdominal plus 14 caudal). The two anteriormost centra are partially missing. On the anterior articular surface, each of the centra has little dorsal zygapophyses. The centra bear some lateral fossae. As in many other teleosts, the first two centra lack pleural ribs. There are 13 pleural ribs which articulate ventrally on the centra.

Median Fins and Supports—The caudal fin is moderately forked with subequal lobes. †*Oreochromis lorenzoi* has 17 principal rays with 15 branched. There are at least three upper and three lower procurrent rays. The caudal skeleton (Fig. 5) is well preserved and strongly resembles the generalized cichlid type illustrated by Vandewalle (1973). Five hypurals are present on each specimen. This number is considered primitive in cichlids (Vandewalle, 1973), and more generally in Perciformes (Rosen and Patterson, 1969). There are two epurals and a single uroneural. The parhypural bears a well-developed spine on its dorso-lateral surface.

The dorsal fin consists of 15 spines followed by 12 soft rays. These are supported by 26 pterygiophores. A slender, autogenous middle radial is present in fin-ray supports. †*Oreochromis lorenzoi* has a single predorsal bone which angles sharply, similar to that of *Oreochromis niloticus* and †*Oreochromis harrisae* described in Murray and Stewart (1999). A single predorsal bone is typical of African cichlids excepted *Tylochromis* and *Heterochromis* (Stiassny, 1991).

The anal fin is supported by 12 pterygiophores and contains four spines followed by 8 soft rays.

Paired Fins and Supports—The posttemporal is clearly visible in MGPC21812a. The angle between the upper and the lower arm is the same as in †*Oreochromis harrisae* and *Oreochromis niloticus* (Murray and Stewart, 1999:figs. 3, 4). Posteriorly, this bone overlaps the dorsal portion of the supracleithrum (Fig. 2). The supracleithrum is visible in MSF26 and MGPC21812a. The outline of this bone greatly resembles that of *Oreochromis niloticus* (Murray and Stewart, 1999:fig. 3E). The ventral end of the supracleithrum overlaps the dorsal end of the cleithrum (Fig. 3). The cleithrum appears to be very similar to that of *Oreochromis niloticus* illustrated in Murray and Stewart (1999). The *Oreochromis* acute notch is present in the posteroventral edge of the dorsal plate of this bone (Fig. 2). Scapulae, coracoids, and radial bones of the pectoral fins are not preserved in any of the examined specimens. At least 14 pectoral fin rays are preserved. The pelvic fin consists of one spine and five soft rays.

Scales—All the examined specimens have well-preserved squamation. The scales are large and nearly circular in outline. There are 32–38 circuli and 13 interradial spaces on each scale. On the caudal field, the scales show the type 3 granulation pattern (see Lippitsch, 1990). Lippitsch (1990) also observes this granulation pattern in *Oreochromis mossambicus*.

On the dorsal part of the head there are scales from the interorbital space backwards. The predorsal squamation resembles the biserial arrangement (sensu Lippitsch, 1990). As in other cichlids the snout and the lower jaw are scaleless. One series of scales is located in the space between the orbit and the dorsal part of the preopercle. Many opercular, subopercular and interopercular scales are visible. The posterodorsal corner of the opercle is scaleless (Fig. 3B).

The flanks and the caudal area are fully scaled (Fig. 7C, D). The upper lateral line is preserved on MSF26 and consists of

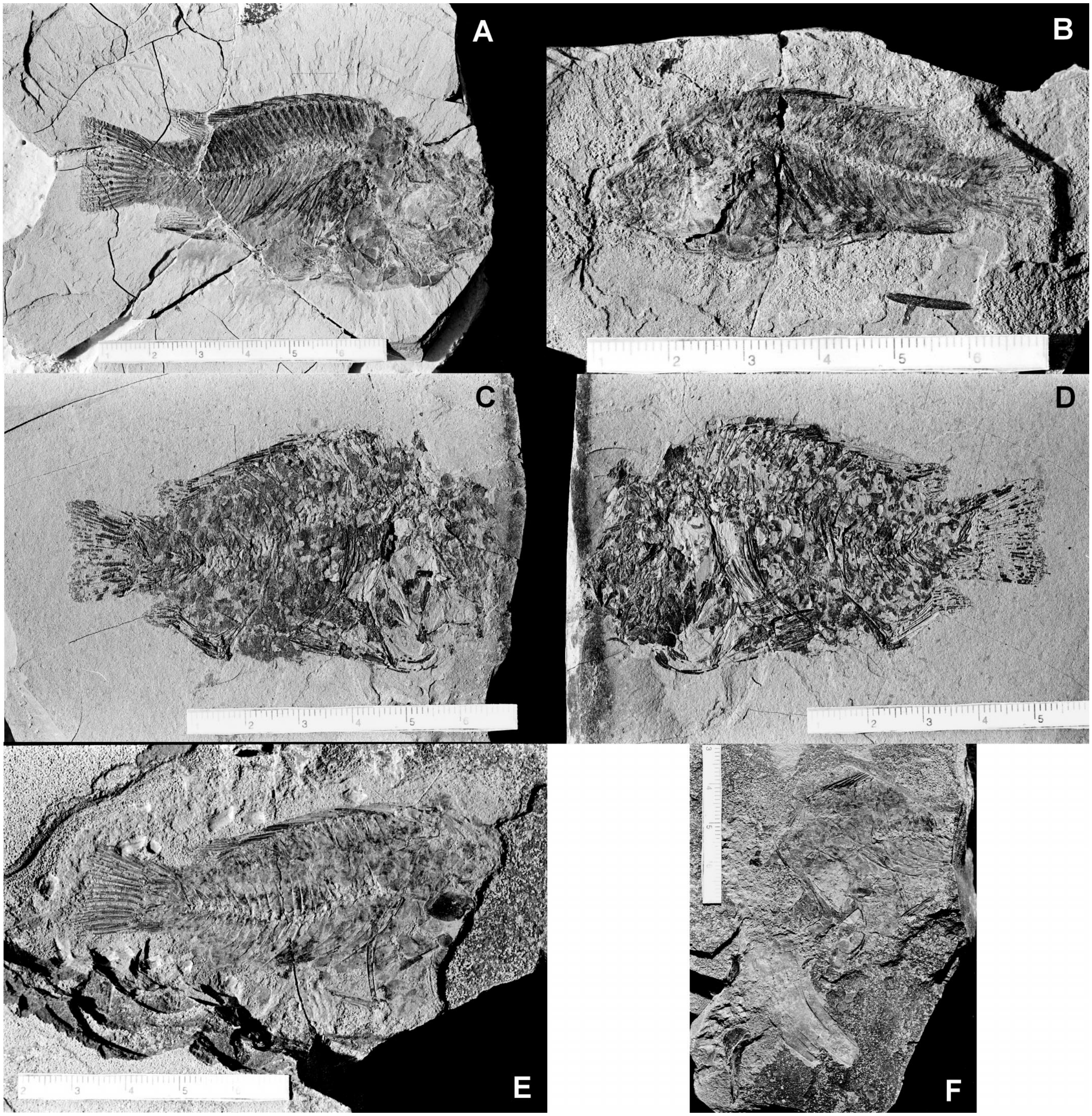

FIGURE 6. †*Oreochromis lorenzoi*, photographs of type specimens. **A**, holotype, MSF26, scale bar equals 6 cm. **B**, paratype, MSF207, scale bar equals 6 cm. **C**, paratype, T1098 (counterpart of T1097), scale bar equals 6 cm. **D**, paratype, T1097 (counterpart of T1098), scale bar equals 5 cm. **E**, paratype, MGPC21812a (counterpart of MGPC21812b), scale bar equals 5 cm. **F**, paratype, MGPC21812b (counterpart of MGPC21812a), scale bar equals 4 cm.

at least 15 scales. The lower lateral line is not preserved in any of the examined specimens. Between the dorsal fin and the upper lateral line there are two to three scale rows.

Scale size is different on different parts of the axial body. The dorsum and belly scales are small with respect to those of the flanks. Scales on the caudal peduncle are similar in size to those of the flanks. There are two rows of small scales between caudal rays that are preserved on MSF3/MSF3.1 and MGPC21812a. The dorsal and anal fins are scaleless.

DISCUSSION

As reported by Landini and Sorbini (1989), many fossil fishes associated with †*Oreochromis lorenzoi* have been collected at Brisighella, Borgo Tossignano, and Monte Castellaro. These faunas show a good structural variability. In particular, the Borgo Tossignano ichthyofauna strongly differs from those of Brisighella and Monte Castellaro. The Borgo Tossignano ichthyofauna is constituted of euryhaline (†*Aphanius crassicaudus*) and

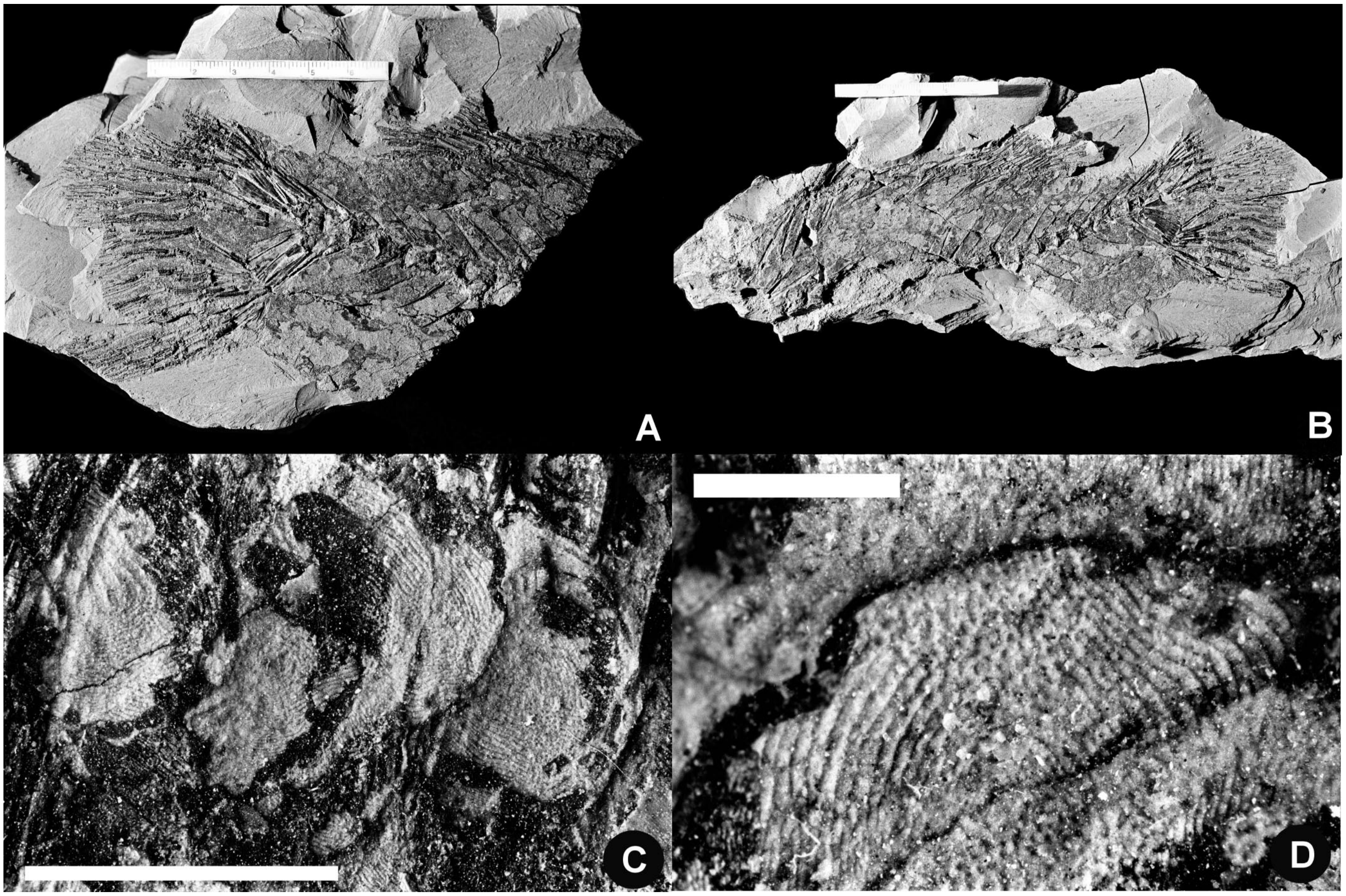

FIGURE 7. †*Oreochromis lorenzoi* **A**, photograph of MSF3.1 (counterpart of MSF3) scale bar equals 6 cm. **B**, photograph of MSF3 (counterpart of MSF3.1), scale bar equals 6 cm. **C**, photograph of flank scales on specimen T1097, scale bar equals 5 mm. **D**, detail of a flank scale on specimenT1097, scale bar equals 1 mm.

migratory (*Atherina boyeri*) taxa, while the Monte Castellaro fish fauna consists of both euryhaline (†*Aphanius crassicaudus*, *Atherina boyeri*, †*Gobius ignotus*, *Lates niloticus*, *Harengula* sp.) and stenohaline (*Epinephelus* sp., *Scorpaena* sp., *Spratelloides gracilis*, *Zeus faber*) taxa, and that from Brisighella mainly consists of stenohaline (*Sarda* sp., *Trachurus* sp.) taxa.

The structural differences among these three ichthyofaunas are clearly related to the depositional environments. The Brisighella ichthyofauna, which mainly consists of stenohaline taxa, has been found in basal evaporite cycles of Monticino Quarry and represents a coastal community, similar to those found today along the Egyptian Mediterranean coasts (Landini and Sorbini, 1989). The Borgo Tossignano and Monte Castellaro ichthyofaunas, instead, have been found in the upper evaporite cycles, which correspond to coastal lagoonal environments (Marabini and Vai, 1985) with a salinity more (Monte Castellaro) or less (Borgo Tossignano) like that of seawater.

Considering †*Oreochromis lorenzoi* from an ecological point

TABLE 1. Measurements for †*Oreochromis lorenzoi*. Except for standard length and total length, all measurements are as percentage of standard length.

	MSF26	MSF207	MGPC21812	T1097/T1098
Total length	88 mm	60 mm	99 mm	83 mm
Standard length	74 mm	52 mm	84.5 mm	65 mm
Body depth	44.6	40.4	40.2	55.4
Caudal peduncle height	18.9	13.5	14.2	23.1
Caudal peduncle length	12.2	9.6	13	13.8
Head length	43.2	34.6	40.2	36.2
Head height	?	36.5	35.5	?
Preorbital distance	14.9	15.4	15.4	15.4
Orbital diameter	10.8	11.5	10.1	?
Pectoral fin length	?	?	17.8	15.4
Last dorsal spine length	17.6	13.5	13.6	16.9
Soft dorsal height	16.2	13.5	10.7	10.8
4th anal spine length	16.2	10.8	?	16.9
Lower jaw length	?	27.8	?	?

of view, a high degree of ecological plasticity is inferred. The association with migratory, euryhaline, and fully marine fishes suggests a behavior similar to that observed for *Oreochromis mossambicus* (Heemstra, 1986; Miyazaki et al., 1996). Similar to *O. mossambicus*, †*Oreochromis lorenzoi* probably was a freshwater species, which migrated into coastal lagoons, estuaries, and shallow marine environments.

The presence of †*Oreochromis lorenzoi* is indicative of warm conditions. The occurrence of cichlids in the northern Mediterranean area, associated with other taxa of Nilotic-Sudanian affinity, such as *Lates niloticus* (see Carnevale and Landini, 2001), suggests the existence of thermo-xeric conditions in Messinian times. These findings reinforce the hypotheses of Suc and Bessais (1990), based on pollen analysis.

Remains of fossil *Oreochromis* are known from a few Pliocene and Quaternary localities of Africa (Trewavas, 1983; Murray and Stewart, 1999; Tichy and Seegers, 1999). Furthermore, in agreement with Murray and Stewart (1999), the Miocene †*Sarotherodon martyni* could be considered to belong to the genus *Oreochromis* (see the description of Van Couvering, 1982). However, the lack of a systematic revision of †*Sarotherodon martyni* justifies the consideration that †*Oreochromis lorenzoi* represents the earliest confirmed member of the genus *Oreochromis*.

Based on the present geographic distribution, the African origin of this genus is clearly evident. The affinity of †*Oreochromis lorenzoi* to *Oreochromis leucostictus*, *Oreochromis shiranus*, and *Oreochromis spilurus* suggests close relationships with the area of distribution of these species, which are restricted to drainage basins of East Africa, from Somalia to Mozambique. The presence of cichlids in the northern Mediterranean during the Miocene is particularly significant from a biogeographic point of view. These findings support the hypothesis of faunal exchange between Eurasia and the African Plate. The faunal exchanges between the African Plate and Eurasia began in the middle Miocene (Adams et al., 1983) and correspond to the first mammalian migration between the two continents (Rögl and Steininger, 1983). A contemporaneous ichthyological bidirectional migration has been recently stressed by Otero and Gayet (2001). After a survey of the European late Miocene fossil record, a number of African taxa, such as clariids, characids, and latids (Deperet, 1890; Thenius, 1952; Antunes, 1989; Antunes et al., 1995; Gayet and Otero, 1999; Otero and Sorbini, L., 1999; Carnevale and Landini, 2001; Otero, 2001) have been observed. The European occurrence of this number of fresh and brackish water fishes of Nilotic affinity suggests the existence of close relations between this northern migratory pulse and climatic conditions. Greenwood (1974) describes many typical Nilotic fish faunas from the Miocene of Maghreb, today replaced by a typical Eurasian freshwater fauna, coexisting with an impoverished African biota (see also Sorbini and Tirapelle Rancan, 1980). Thus, a nearly uniform climatic continuity could be assumed along the Mediterranean coasts in the Late Miocene.

If the relationships of †*Oreochromis lorenzoi* are correct, its presence in the Mediterranean could be explained by an expanded area of distribution of this group of species, today restricted to East Africa. This hypothesis is supported by the probable assignment (Trevawas, 1983) of the Pliocene fossil teeth from Jordan Valley, originally described by Avnimelech and Steinitz (1952), to the species *Oreochromis spilurus*. A wider distribution of these fishes was probably related to the hydrographical influences of the Miocene rifting phases, which created the link between East Africa and the Nile. In the development towards an asymmetrical half-graben geometry (Bosworth, 1985; Ebinger et al., 1984; Rosendahl, 1987), only the East African drainage basins are involved in the rifting. A relation between East African rifting and fish distribution has been pointed out by Roberts (1975) and Greenwood (1983).

Although there are many evaporitic Messinian fish bed localities in the Mediterranean (Landini and Sorbini, 1992), it is interesting to note that all the specimens here illustrated have been found in the Periadriatic region. Following paleogeographic reconstructions (e.g., Vai, 1989), this area was characterized by a strong development of marginal and satellite basins, probably due to the synergistic effect of the drop of sea level and the intra-Messinian tectonic phase, that is a geodynamic pulse affecting the whole emerging Apennine orogen (Vai, 1987). This event consisted of a major thrusting and foredeep migration phase that allowed a large development of shallow-water biotopes (coastal lagoons, neritic environments, etc.) in this area, favouring the establishment of cichlids, while the colonization of other northern Mediterranean coastal areas was probably difficult.

ACKNOWLEDGMENTS

We would like to thank Gian Paolo Costa (Faenza), Marco Sami (Faenza), Carlo Sarti (Bologna), and Roberto Zorzin (Verona) for providing access to specimens in the MSF, MGPC, and MCSNV collections. We also thank Roberto Albani for assistance with SEM, Marcello Gini for photographs, and Federica Giudice for improvement of the English. This paper benefited from constructive comments by Alison M. Murray, Melanie L. J. Stiassny and Mark V. H. Wilson. This research was supported by MURST 40% funds.

LITERATURE CITED

Adams, C. G., A. W. Gentry, and P. J. Whybrow. 1983. Dating the tethyan terminal event. Utrecht Micropaleontological Bulletin 30: 273–298.

Antunes, M. T. 1989. Miocene catfishes (Ariidae, Bagridae) from Lisbon: a Nilotic (or Sudanian) type fauna. Ciências da Terra 10:9–22.

———, A. Balbino, and J. Gaudant. 1995. Découverte du plus récent Characiforme européen dans le Miocène Terminal du Portugal. Comunicaçoes Instituto Geológico e Mineiro 81:79–84.

Avnimelech, M., and H. Steinitz. 1952. On fish remains in the continental Neogene of the Jordan Valley (Israel). Eclogae Geologiae Helvetiae 44:444–447.

Bosworth, W. 1985. Geometry of propagating continental rifts. Nature 316:625–627.

Carnevale, G., and W. Landini. 2001. On the first occurrence of the genus *Lates* Cuvier and Valenciennes in the pre-evaporitic Messinian of the Mediterranean. Bollettino del Museo Civico di Storia Naturale di Verona 25:71–76.

Carroll, R. L. 1997. Patterns and Processes of Vertebrate Evolution. Cambridge University Press, Cambridge, 448 pp.

Casciotta, J., and G. Arratia. 1993. Tertiary cichlid fishes from Argentina and reassessment of the phylogeny of New World cichlids (Perciformes: Labroidei). Kaupia—Darmstädter Beiträge zur Naturgeschichte 2:195–240.

Deperet, C. 1890. Les animaux pliocènes du Roussillon. Mémoires de la Société géologique de France 3:1–195.

Ebinger, C. J., M. J. Crow, B. R. Rosendahl, D. A. Livingstone, and J. LeFournier. 1984. Structural evolution of Lake Malaŵi, Africa. Nature 308:627–629.

Frickhinger, K. A. 1991. Fossilien Atlas Fische. Mergus, Melle, 1,088 pp.

Fryer, G., P. H. Greenwood, and J. F. Peake. 1983. Punctuated equilibria, morphological stasis and the paleontological documentation of speciation: a biological appraisal of a case history in an African lake. Biological Journal of the Linnaean Society 20:195–205.

Futuyma, D. J. 1998. Evolutionary Biology. Sinauer, Sunderland, 751 pp.

Gaemers, P. A. M. 1989. The first cichlid (Perciformes, Pisces) from Europe: the new, fossil genus *Eurotilapia*, evidence from otolith and teeth. Annales du Muséum Royal d'Afrique Centrale, Sciences Zoologiques 257:109–116.

——— 1990. Current projects. Newsletter of Systematic Ichthyology 12:7.

Gayet, M., and O. Otero. 1999. Analyse de la paléodiversification des Siluriformes (Osteichthyes, Teleostei, Ostariophysi). Geobios 32: 235–246.

Gill, T. N. 1872. Arrangement of the families of fishes. Smithsonian Miscellaneous Collections 247:1–49.

Greenwood, P. H. 1973. Morphology, endemism and speciation in African cichlid fishes. Verhandlungen der Deutschen Zoologischen Gesellschaft 66:115–124.

——— 1974. Review of Cenozoic freshwater fish faunas in Africa. Annals of the Geological Survey of Egypt 4:211–232.

——— 1983. The zoogeography of African freshwater fishes: bioaccountancy or biogeography?; pp. 179–200 *in* R. W. Sims, J. H. Price, and P. E. S. Whalley (eds.), Evolution, Time and Space: The Emergence of the Biosphere. The Systematics Association Special Volume 23. Academic Press, London.

——— 1987. The genera of pelmatochromine fishes (Teleostei, Cichlidae). A phylogenetic review. Bulletin of the British Museum of Natural History (Zoology) 53:139–203.

Günther, A. 1880. Report on the shore fishes procured during the voyage of H. M. S. 'Challenger' in the years 1873–1876. Challenger Report of Zoology 1:1–82.

Heemstra, P. C. 1986. Cichlidae; p. 670 *in* M. M. Smith and P. C. Heemstra (eds.), Smiths' Sea Fishes. Springer-Verlag, Berlin.

Hilgen, F. J., W. Krijgsman, C. G. Langereis, L. J. Lourens, A. Santarelli, and W. J. Zachariasse. 1995. Extending the astronomical (polarity) time scale into the Miocene. Earth and Planetary Science Letters 136:495–510.

Johnson, G. D., and C. Patterson. 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal. Bulletin of Marine Science 52:554–626.

Kornfield, I., and P. F. Smith. 2000. African cichlid fishes: model systems for evolutionary biology. Annual Review of Ecology and Systematics 31:163–196.

Krijgsman, W., F. J. Hilgen, S. Marabini, and G. B. Vai. 1999. New paleomagnetic and cyclostratigraphic age constraints on the Messinian of the Northern Apennines (Vena del Gesso Basin, Italy). Memorie della Società Geologica Italiana 54:25–33.

Kumazawa, Y., M. Yamaguchi, and M. Nishida. 1999. Mitochondrial molecular clocks and the origin of euteleostean biodiversity: familial radiation of perciforms may have predated the Cretaceous/Tertiary boundary; pp. 35–52 *in* M. Kato (ed.), The Biology of Biodiversity. Springer-Verlag, Berlin.

Landini, W., and L. Sorbini. 1989. Ichthyofauna of the evaporitic Messinian in the Romagna and Marche regions. Bollettino della Società Paleontologica Italiana 28:287–293.

———, and ——— 1992. Données récentes sur les Téléostéens du Miocène et du Pliocène d'Italie. Geobios, Mémoire Spécial 14: 151–158.

Lauder, G. V. 1981. Form and function: structural analysis in evolutionary morphology. Paleobiology 7:430–442.

——— 1983. Functional design and evolution of the pharyngeal jaw apparatus in euteleostean fishes. Zoological Journal of the Linnaean Society 77:1–38.

Liem, K. L. 1973. Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. Systematic Zoology 22:425–441.

——— 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. American Zoologist 20:295–314.

———, and P. H. Greenwood. 1981. A functional approach to the phylogeny of the pharyngognath teleosts. American Zoologist 21:83–101.

Lippitsch, E. 1990. Scale morphology and squamation patterns in cichlids (Teleostei, Perciformes): a comparative study. Journal of Fish Biology 37:265–291.

Marabini, S., and G. B. Vai. 1985. Analisi di facies e macrotettonica della Vena del Gesso in Romagna. Bollettino della Società Geologica Italiana 104:21–42.

Meyer, A. 1993. Phylogenetic relationships and evolutionary processes in East African cichlid fishes. Trends in Ecology and Evolution 8: 279–284.

Miyazaki, H., T. Kancko, S. Hasegawa, and T. Hirano. 1998. Developmental changes in drinking rate and ion and water permeability during early life stages of euryhaline tilapia, *Oreochromis mossambicus*, reared in fresh water and sea-water. Fish Physiology and Biochemistry 18:277–284.

Murray, A. M. 2000. Eocene cichlid fishes from Tanzania, East Africa. Journal of Vertebrate Paleontology 20:651–664.

——— 2001a. The oldest fossil cichlids (Teleostei, Perciformes): indication of a 45 million-year-old species flock. Proceedings of the Royal Society of London, Series B 268:679–684.

——— 2001b. The fossil record and biogeography of the Cichlidae (Actinopterygii: Labroidei). Biological Journal of the Linnaean Society 74:517–532.

———, and K. M. Stewart. 1999. A new species of tilapiine cichlid from the Pliocene, Middle Awash, Ethiopia. Journal of Vertebrate Paleontology 19:293–301.

Otero, O. 2001. The oldest-known cyprinid fish of the Afro-Arabic Plate, and its paleobiogeographical implications. Journal of Vertebrate Paleontology 21:386–388.

———, and M. Gayet. 2001. Palaeoichthyofaunas from the lower Oligocene and Miocene of the Arabian Plate: palaeoecological and palaeobiogeographical implications. Palaeogeography, Palaeoclimatology, Palaeoecology 165:141–169.

———, and L. Sorbini. 1999. Étude systématique et anatomique du *Lates* (Perciformes, Latidae) du Messinien continental de Monte Castellaro, Italie. Considérations paléobiogéographiques. Studi e Ricerche sui Giacimenti Terziari di Bolca 8:29–42.

Patterson, C., and D. E. Rosen. 1977. A review of ichthyodectiform and other Mesozoic teleost fishes, and the theory and practice of classifying fossils. Bulletin of the American Museum of Natural History 158:81–172.

Roberts, T. R. 1975. Geographical distribution of African freshwater fishes. Zoological Journal of the Linnaean Society 57:249–319.

Rögl, F., and F. F. Steininger. 1983. Vom Zervall der Tethys zu Mediterran und Paratethys. Die Neogene Paläogeographie und Palinspastik des zirkum-mediterranen Raumes. Annalen Naturhistorisches Museum Wien 85:135–163.

Rosen, D. E., and C. Patterson. 1969. The structure and relationships of the paracanthopterygian fishes. Bulletin of the American Museum of Natural History 141:357–474.

Rosendahl, B. R. 1987. Architecture of continental rifts with special reference to East Africa. Annual Review of Earth and Planetary Sciences 15:445–503.

Sorbini, L. 1988. Biogeography and climatology of Pliocene and Messinian fossil fish of eastern-central Italy. Bollettino del Museo Civico di Storia Naturale di Verona 14:1–85.

———, and R. Tirapelle Rancan. 1980. Messinian fossil fish of the Mediterranean. Palaeogeography, Palaeoclimatology, Palaeoecology 29:143–154.

Stiassny, M. L. J. 1981. The phyletic status of the family Cichlidae (Pisces, Perciformes): a comparative anatomical investigation. Netherlands Journal of Zoology 31:275–314.

——— 1991. Phylogenetic intrarelationships of the family Cichlidae: an overview; pp. 1–35 *in* M. H. A. Keenleyside (ed.), Cichlid Fishes. Behaviour, Ecology and Evolution. Chapman and Hall, London.

———, and J. S. Jensen. 1987. Labroid intrarelationships revisited: morphological complexity, key innovations, and the study of comparative diversity. Bulletin of the Museum of Comparative Zoology 151:269–319.

Suc, J. P., and E. Bessais. 1990. Pérennité d'un climat thermoxérique en Sicile, avant, pendant, après la crise de salinitè messinienne. Comptes Rendus de l'Académie de Sciences de Paris 310:1701–1707.

Thenius, E. 1952. Welreste aus dem Unterpliocän des Wiener Beckens (Ein Beitrag zur Geschichte der Welse des europäischen Jungtertiärs). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 134:80–94.

Tichy, H., and L. Seegers. 1999. The *Oreochromis alcalicus* flock (Teleostei: Cichlidae) from lakes Natron and Magadi, Tanzania and Kenya: a model for the evolution of ''new'' species flocks in historical times? Ichthyological Exploration of Freshwaters 10:147–174.

Trewavas, E. 1983. Tilapiine Fishes of the Genera *Sarotherodon*, *Oreochromis*, and *Danakilia*. British Museum (Natural History), London, 583 pp.

Vai, G. B. 1987. Migrazione complessa del sistema fronte deformativo-avanfossa-cercine periferico: il caso dell'Appennino Settentrionale. Memorie della Società Geologica Italiana 38:95–105.

——— 1989. A field trip guide to the Romagna apennine geology. The Lamone valley. Bollettino della Società Paleontologica Italiana 28: 343–367.

——— 1997. Cyclostratigraphic estimate of the Messinian stage duration; pp. 463–476 *in* A. Montanari, G. S. Odin, and R. Coccioni (eds.), Miocene Stratigraphy: An Integrated Approach. Elsevier Science, Amsterdam.

———, and F. Ricci Lucchi. 1977. Algal crusts, autochthonous and clastic gypsum in a cannibalistic evaporite basin: a case history from the Messinian of Northern Apennines. Sedimentology 24: 211–244.

Van Couvering, J. A. H. 1982. Fossil cichlid fish of Africa. Special Papers in Paleontology 29:1–103.

Vandewalle, P. 1972. Ostéologie et myologie de *Tilapia guineensis* (Bleeker, 1862). Annales du Musée Royal de l'Afrique centrale, Sciences Zoologiques 196:1–50.

——— 1973. Ostéologie caudale des Cichlidae (Pisces, Teleostei). Bulletin Biologique de la France et de la Belgique 107:275–289.

Vences, M., J. Freyhof, R. Sonnenberg, J. Kosuch, and M. Veith. 2001. Reconciling fossils and molecules: Cenozoic divergence of cichlid fishes and the biogeography of Madagascar. Journal of Biogeography 28:1091–1099.

White, E. I. 1937. The fossil fishes of the terraces of Lake Bosumtwi, Ashanti. Bulletin of the Gold Coast Geographical Association 8: 47–58.

Received 30 January 2002; accepted 24 July 2002.

View publication stats