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†*TUGENCHROMIS PICKFORDI*, GEN. ET SP. NOV., FROM THE UPPER MIOCENE—A STEM-GROUP CICHLID OF THE ‘EAST AFRICAN RADIATION’

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ABSTRACT—The highly diverse tropical freshwater fish family Cichlidae is sparsely represented in the fossil record. Here we describe the new cichlid †*Tugenchromis pickfordi*, gen. et sp. nov., from the Upper Miocene (9–10 Ma) of central Kenya. The new taxon possesses a unique combination of characters, including six lateral line foramina on the lacrimal, three lateral line segments, cycloid scales, and a low number of vertebrae (29), dorsal fin spines (13), and dorsal soft rays (9). Its lacrimal morphology and tripartite lateral line suggest an affinity with the present-day Lake Tanganyika tribes Ectodini and Limnochromini, and thus with members of the ‘East African Radiation’ among the African cichlids. To further elucidate the relationships of †*T. pickfordi*, we used a comprehensive comparative data set comprising meristic data from all present-day tribes of the ‘East African Radiation.’ Principal coordinates analyses support links between the fossil and Ectodini + Limnochromini, and additionally with modern Haplochromini. We conclude that †*T. pickfordi* could be an extinct lineage within the ‘most ancient Tanganyika tribes,’ or a stem lineage of the ‘ancient Tanganyika mouthbrooders.’ A direct relationship to the Haplochromini is unlikely because its members do not exhibit the derived characteristics of the lacrimal as seen in †*T. pickfordi*. Because Lake Tanganyika is located in the western branch of the East African Rift System, †*T. pickfordi* from the eastern branch supports the ‘melting-pot Tanganyika hypothesis,’ which posits that the cichlids of modern Lake Tanganyika are derived from riverine lineages that had already diversified prior to the lake formation.

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SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP.

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INTRODUCTION

The Cichlidae are an extremely diverse tropical family of mainly freshwater fishes, comprising about 220 genera and at least 1696 species (e.g., Kolm et al., 2006; Fitzsimmons and Watanabe, 2010; Eschmeyer and Fong, 2016). Based on morphological and molecular data, four subfamilies can be recognized: Cichlinae (distributed in South, Central, and North America), Etoplinae (restricted to South Asia and Madagascar), Pseudocrenilabrinae (restricted to Africa and the Middle East), and Ptychochrominae (limited to Madagascar) (Cichocki, 1976; Stiassny, 1991; Chakrabarty, 2004; Sparks and Smith, 2004; Smith et al., 2008). Because

Cichlidae are extraordinarily species-rich, often highly specialized in ecology and behavior (e.g., parental care, mouthbrooding), and show a broad spectrum of trophic adaptations, they represent one of the most intensively studied fish groups and have long been used as model organisms for the study of speciation and adaptive evolution (e.g., Kocher, 2004; Seehausen, 2006; Genner et al., 2007). However, their fossil record is scanty and this makes it difficult to explore their evolutionary history over long time scales.

The Pseudocrenilabrinae (African cichlids) represent the most species-rich subfamily of the Cichlidae. Based on molecular phylogenetics, they can be separated into 27 lineages comprising around 150 genera and more than 1100 described species (e.g., Stiassny et al., 2007; Schwarzer et al., 2009; Eschmeyer and Fong, 2016). According to Schliewen and Stiassny (2003), Schwarzer et al. (2009), Schwarzer (2011), and Dunz and Schliewen (2013), the haplotilapiines represent a major clade among the Pseudocrenilabrinae, comprising a total of 22 lineages, among which the ‘East African Radiation’ (EAR) is the most speciose subclade (Fig. 1A–B).

The cichlids assigned to the EAR are characterized by a high capacity for rapid speciation and adaptive radiations, and most are endemic to the Great Lakes of the Rift Valley—Tanganyika, Malawi, and Victoria (e.g., Meyer et al., 1990; Sturmbauer and Meyer, 1993; Moran et al., 1994; Sturmbauer et al., 1994; Loh et al., 2013). However, some

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groups assigned to the EAR are not restricted to the Great Lakes but occur in rivers and lakes across East and Central Africa; the majority of these are riverine members of the Haplochromini (see Fig. 1B), besides a few species of the

Lamprologini (Schelly and Stiassny, 2004). The remaining tribes of the EAR are endemic to the Lake Tanganyika drainage and comprise the Boulengerochromini, Bathybatini, Trematocarini, Eretmodini, Benthochromini, Cyprichromini,

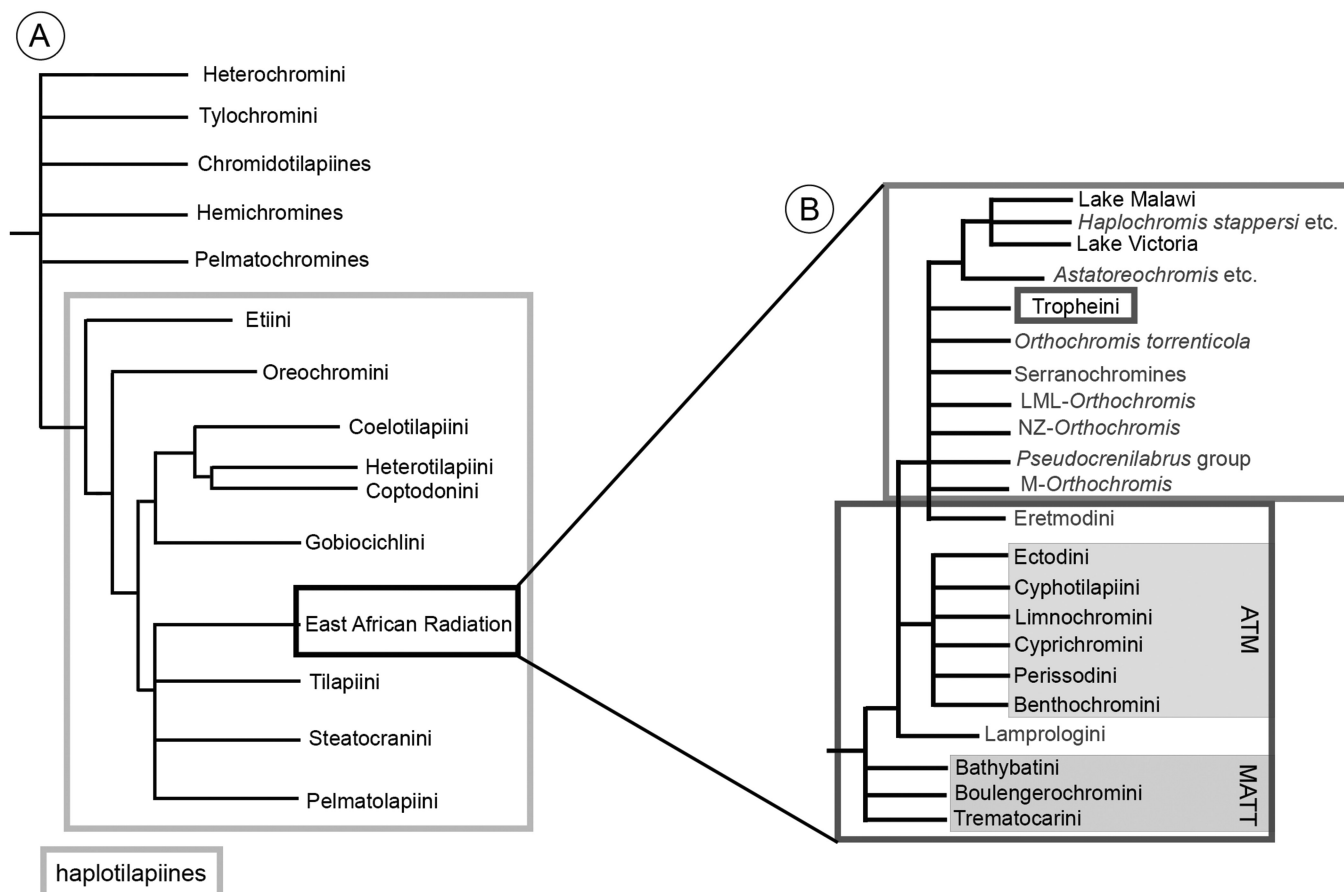


FIGURE 1. **A**, simplified composite phylogenetic tree depicting possible relationships among the Pseudocrenilabrinae, based on Schwarzer et al. (2009) and Dunz and Schliwen (2013). **B**, strict consensus phylogenetic tree illustrating possible relationships within the 'East African Radiation'; tree was compiled using the 'compute consensus' option of PAUP. Sources: Neighbor-joining consensus tree based on mitochondrial and nuclear genetic data (amplified fragment-length polymorphism [AFLP]; Weiss et al., 2015:fig. 3), and maximum likelihood tree based on mitochondrial and nuclear genetic data (Meyer et al., 2015:fig. S1); only nodes with a bootstrap support >50 were considered. **Abbreviations:** ATM, ancient Tanganyika mouthbrooders; MATT, most ancient Tanganyika tribes; M-*Orthochromis*, Malagarasi *Orthochromis* from the rivers Malagarasi, Luiche, and Rugufu; LML-*Orthochromis*, *Orthochromis* from the Luapula-Mweru system and the Lualaba/Congo system; NZ-*Orthochromis*, northern Zambian *Orthochromis* from northern Zambia; see Weiss et al. (2015) and Meyer et al. (2015) for further explanations. Lineages that include riverine taxa are depicted in purple font. The blue frames encompass tribes endemic to Lake Tanganyika (except for the riverine group within the Lamprologini). The red frame encloses all lineages of the Haplochromini. **C**, illustration of a generalized cichlid depicting all morphometric measures (arrows) used in this study. **Abbreviations:** BL, body length; h, minimal body height; H, maximal body height; H2, body height at origin of anal fin; IA, length of anal fin base; IC, length of caudal fin; ID, length of dorsal fin base; lpc, length of caudal peduncle; IV, length of pelvic fin; IVbs, length of pelvic fin base; V-A, distance between pelvic fin origin and anal fin origin.

Perissodini, Cyphotilapiini, Limnochromini, Ectodini, and Tropheini (Fig. 1B).

According to Weiss et al. (2015), the contemporary cichlid fauna of Lake Tanganyika comprises four major groups: (i) the ‘most ancient Tanganyika tribes’ (Boulengerochromini, Bathybatiini, Trematocarini); (ii) Lamprologini and Eretmodini; (iii) the ‘ancient Tanganyika mouthbrooders’ (Benthochromini, Cyprichromini, Perissodini, Cyphotilapiini, Limnochromini, Ectodini); and (iv) the Tropheini, a subgroup of the Haplochromini. It should be noted that virtually no other Haplochromini are found in Lake Tanganyika, whereas members of the other subgroups of the tribe have diversified into the major species flocks of Lake Malawi and Lake Victoria, as well as several riverine lineages.

The megadiversity of the Pseudocrenilabrinae and especially of the EAR contrasts with their comparatively meager fossil record. Cichlid fossils from Africa and Arabia include

some completely preserved skeletons, but most are represented by isolated elements, and thus their affinities remain largely intractable (see also Stewart, 2001; Otero, 2010). In all, a total of 17 fossil cichlid species have been described from Eocene to Pliocene sediments of Africa and Arabia (Table 1). The objective of this study is to describe a newly discovered fossil cichlid specimen from the upper Miocene Ngorora Formation (Central Kenya, East African Rift System) and to investigate its phylogenetic position based on osteological characters and a newly assembled comparative data set derived from modern African cichlids.

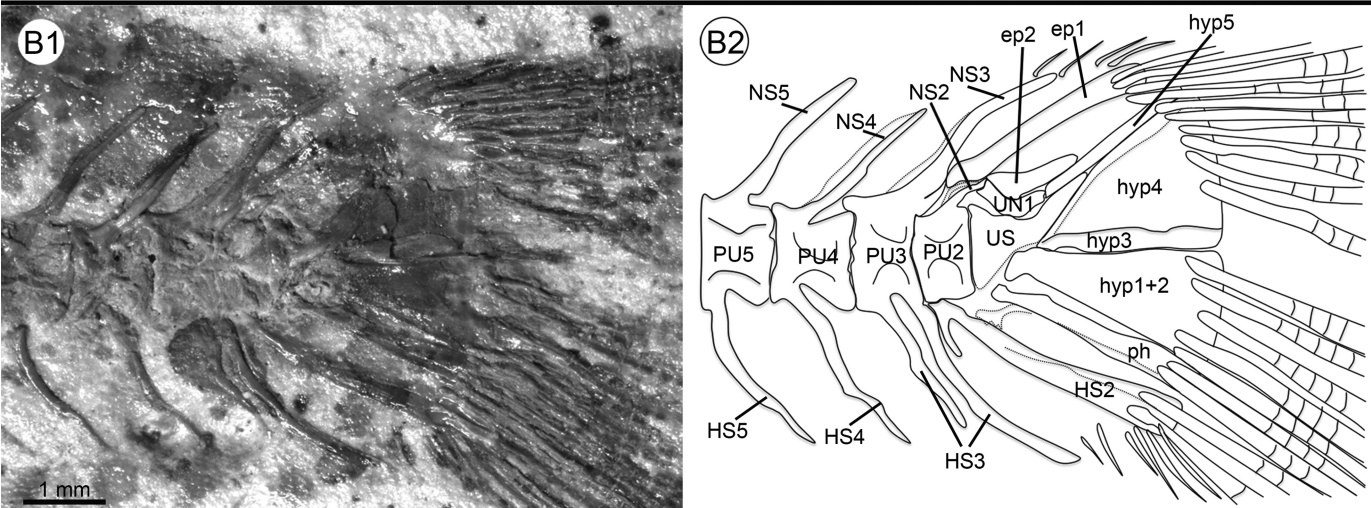
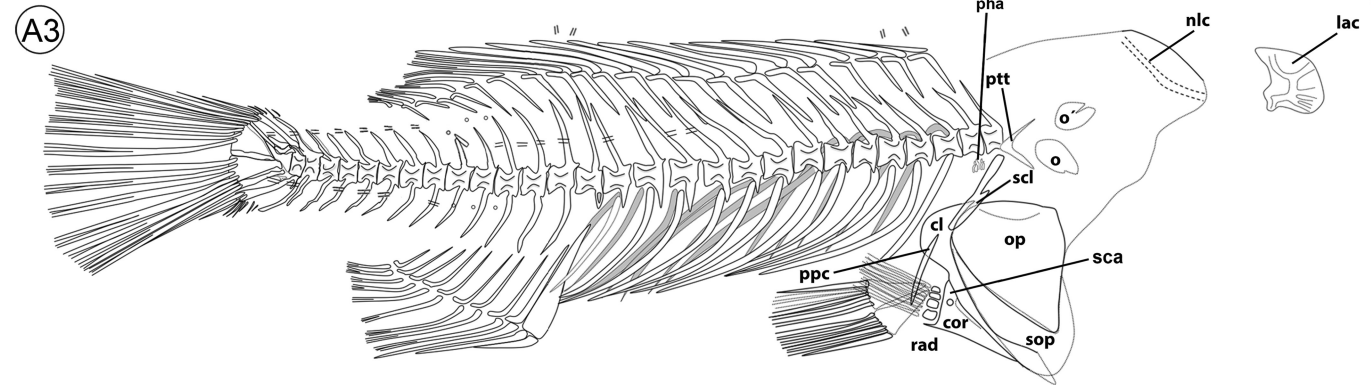
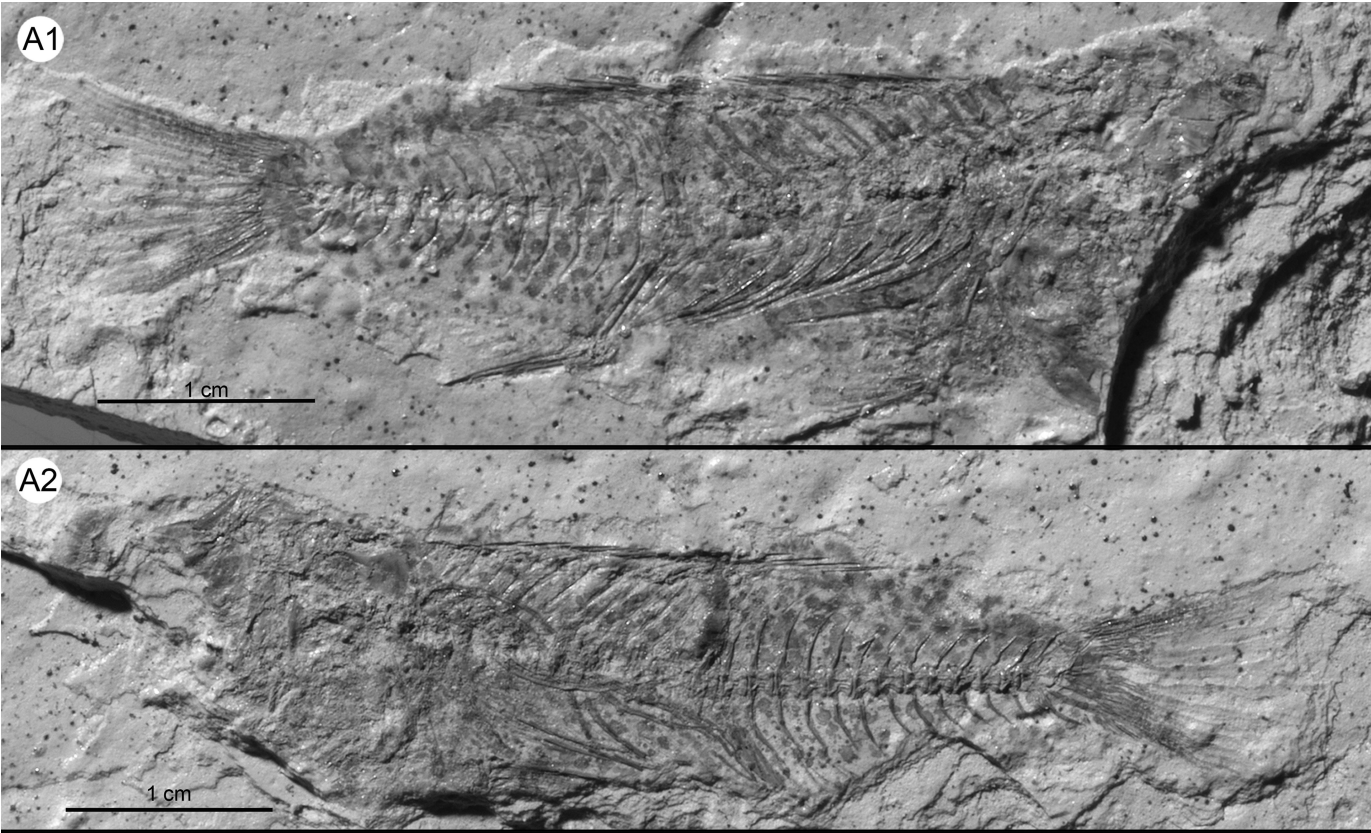
Geological Setting

Study Site—The single individual with which this study is concerned was collected at the Waril site (0°40′56.21″N;

TABLE 1. Eocene to Pliocene fossil cichlid species from Africa and Arabia that are based on articulated skeletons and their putative phylogenetic placement according to the literature.

Proposed assignment of previous authors	Fossil cichlid species	Eocene	Oligocene	lower Miocene	Middle–upper Miocene	Upper Miocene	Lower Pliocene
Murray, 2000:fig. 11: Based on the cladogram of Lippitsch (1995, 1998) close to Cyprichromini (= EAR tribe); Murray, 2001:fig. 3: Not resolved	† <i>Mahengechromis brachycranium</i> Murray, 2000	~46 Ma					
	† <i>Mahengechromis curvifrons</i> Murray, 2000	~46 Ma					
	† <i>Mahengechromis ellipticus</i> Murray, 2000	~46 Ma					
	† <i>Mahengechromis plethos</i> Murray, 2000	~46 Ma					
	† <i>Mahengechromis rotundus</i> Murray, 2000	~46 Ma					
Lippitsch and Micklich, 1998: Heterochromini	? <i>Heterochromis</i> sp. Lippitsch and Micklich, 1998		33.9–23.0 Ma				
Lippitsch and Micklich, 1998: Close to Tilapiini	Tilapiini Group 2 Lippitsch and Micklich, 1998		33.9–23.0 Ma				
Lippitsch and Micklich, 1998: Haplochromine assemblage	Tilapiini Group 3 Lippitsch and Micklich, 1998		33.9–23.0 Ma				
Van Couvering, 1982: Close to <i>Pelmatochromis</i> or <i>Paratilapia</i>	† <i>Macfadyena dabanensis</i> Van Couvering, 1982		33.9–23.0 Ma				
Van Couvering, 1982: Close to Tropheini	† <i>Kalyptochromis hamulodentis</i> Van Couvering, 1982		33.9–23.0 Ma				
Van Couvering, 1982: Close to Haplochromini, <i>Cichla</i> , or <i>Hemichromis</i>	† <i>Nderechromis cichloides</i> Van Couvering, 1982			23.0–16.0 Ma			
Van Couvering, 1982: Close to <i>Pelmatochromis</i>	† <i>Palaeofulu kuluensis</i> Van Couvering, 1982			23.0–16.0 Ma			
Van Couvering, 1982: Oreochromini	† <i>Oreochromis martyni</i> (Van Couvering, 1982)				16.0–5.3 Ma		
Van Couvering, 1982: Close to <i>Pelmatochromis</i> or <i>Tilapia</i> , or Haplochromini	† <i>Palaeochromis darestei</i> Sauvage, 1907					11.6–5.3 Ma	
	† <i>Palaeochromis roussetti</i> Sauvage, 1907					11.6–5.3 Ma	
Carnevale et al., 2003: Oreochromini	† <i>Oreochromis lorenzoi</i> Carnevale et al., 2003					11.6–5.3 Ma	
Murray and Stewart, 1999: Oreochromini	† <i>Oreochromis harrisae</i> Murray and Stewart, 1999						4.4–4.3 Ma

Extinct species are marked with †.



35°43'7.43"E), located in the Kerio Valley, to the west of the Tugen Hills in the Central Kenya Rift Valley (Fig. S1). The fish-bearing sediments are tuffaceous lacustrine siltstones. Waril is part of the Ngorora fish Lagerstätte and can be assigned to the upper Miocene (9–10 Ma) based on lithostratigraphy and the presence of an equid in a paleosol above the lacustrine sediments (Pickford, 1978; Jacobs, 2002; Rasmussen et al., 2017). Ancient Lake Waril was a comparatively deep and alkaline lake, and the climate in the area was seasonally dry (Pickford, 1978; Jacobs, 2002; Kingston et al., 2002; Tiercelin and Lezzar, 2002; Bonnefille, 2010; Bamford et al., 2013; Rasmussen et al., 2017).

MATERIALS AND METHODS

Fossil Material—The material consists of a single skeleton in part and counterpart (OCO-5-22/OCO-5-35). It is deposited in the Museum in Kipsaraman, Kenya, which is affiliated with the National Museum in Nairobi. Prefix OCO for Orrorin Community Organization.

Comparative Material—Because information on the meristics and osteology of African cichlids is rather limited, a new comparative data set has been assembled for this study. Taking into account the fact that the new fossil displays a lacrimal with six lateral line tubules (see below), a feature only known for the present-day Lake Tanganyika tribes, the data set focuses on representatives of these tribes as well as on members of the tribe Haplochromini (see Supplementary Data 1) because of their close phylogenetic relation to the present-day Lake Tanganyika cichlids (Meyer et al., 2015; Weiss et al., 2015; Fig. 1B). In total, the data set comprises 227 species (23 lineages, 96 genera, 763 specimens), representing all tribes and almost all genera of the present-day Lake Tanganyika cichlids as well as all lineages of the Haplochromini (according to Schwarzer et al., 2009; Dunz and Schliwien, 2013; Weiss et al., 2015) (Supplementary Data 1).

The data set for the 'most ancient Tanganyika tribes' (sensu Weiss et al., 2015; Fig. 1B) is nearly complete, except *Trematocara caparti* Poll, 1948a. An almost complete data set is also available for the Eretmodini, the exception here being *Eretmodus marksmithi* Burgess, 2012. The data set for the remaining groups (Lamprologini, 'ancient Tanganyika mouthbrooders' sensu Weiss et al., 2015) is less complete, but all genera are included, with the sole exception of *Baileychromis* Poll, 1986. The data set for the Haplochromini does not include the genera *Chilotilapia* Boulenger, 1908, *Cyclopharynx* Poll, 1948b, *Docimodus* Boulenger, 1897, *Gephyrochromis* Boulenger, 1901, *Interochromis* Yamaoka, Hori, and Kuwamura, 1988, *Iodotropheus* Oliver and Loiselle, 1972, *Microchromis* Johnson, 1975, *Pharyngochromis* Greenwood, 1979, and *Pseudosimochromis* Nelissen, 1977. We follow the genus concept of Van Oijen (1996) for the genus *Haplochromis*.

Morphological Studies—Adherent sediment particles were carefully removed from the fossil skeleton using a needle. Osteological, meristic, and morphometric characters of the fossil were examined using a stereomicroscope equipped with a digital camera. Scanning electron microscopy (SEM) images of pharyngeal teeth isolated from the fossil were prepared using a LEO 1430VP at 15 kV, and picture quality was enhanced using PhotoShop CS6. Radiographs were produced for each individual included in the comparative data set using a Faxitron UltraFocus LLC X-ray unit and served as the basis for investigation of the osteological and meristic characters of each specimen.

Morphometric measurements (see Fig. 1C) and meristic counts follow Barel et al. (1977). Measurements were taken to the nearest 0.01 mm in ImageJ 1.49v. Counts of vertebrae include the terminal centrum; abdominal vertebrae are characterized by the absence of a closed hemal arch (according to Barel, 1977). Dorsal and anal fin ray counts included every discernible ray, regardless of whether or not it was associated with a pterygiophore. Measurements on the fossil were standardized based on the body length, i.e., the distance from the posterior margin of the operculum to the posterior margin of the hypural plate (Fig. 1C; see also Van Couvering, 1982). Interpretation of osteological characters follows Van Couvering (1982), Poll (1986), Lippitsch (1995, 1998), Kullander (1998), and Takahashi (2003a, 2003b).

Statistical Analyses—We conducted a principal coordinates analysis (PCoA) in the program PAST 3.10 (Hammer et al., 2001) based on the characters noted in the fossil and inspection of the same characters in the comparative data set. Characters used as variables included counts of spines and rays in the dorsal and anal fins, counts of abdominal, caudal, and total vertebrae, number of predorsals, and the position of the vertebra associated with the pterygiophore of the last dorsal fin spine. The PCoA is a statistical tool for multivariate analysis, which visualizes group differences, as well as individual outliers based on similarities or dissimilarities in the data set. Unlike principal components analysis (PCA), PCoA produces a distance matrix by pairwise comparison of the individual characters and therefore yields more reliable results in the case of missing data (Hammer and Harper, 2006; Leyer and Wesche, 2007).

Institutional Abbreviations—NHMUK (formerly BMNH), Natural History Museum, London, U.K.; ZSM, Bavarian State Collection of Zoology, Munich, Germany.

SYSTEMATIC PALEONTOLOGY

CICHLIDAE Bonaparte, 1835

PSEUDOCRENILABRINAE Fowler, 1934

†*TUGENCHROMIS*, nov. gen.

Generic Diagnosis—Lateral line on the trunk divided into three segments, two of which are posterior lateral lines. One posterior segment positioned ventrally, the other dorsally to the anterior lateral line segment. This is a condition not seen in any other cichlid genus.

Etymology—'Tugen' refers to the 'Tugen Hills' (named after the local people, i.e., the 'Tugen,' a subgroup of the Kalenjin ethnic group), in which the type locality of the new fossil taxon is located. The Greek word 'Chromis' (χρῶμις) is a name used by the Ancient Greek and was applied to various fish. It is a common second element in cichlid genus names. *Tugenchromis* is masculine.

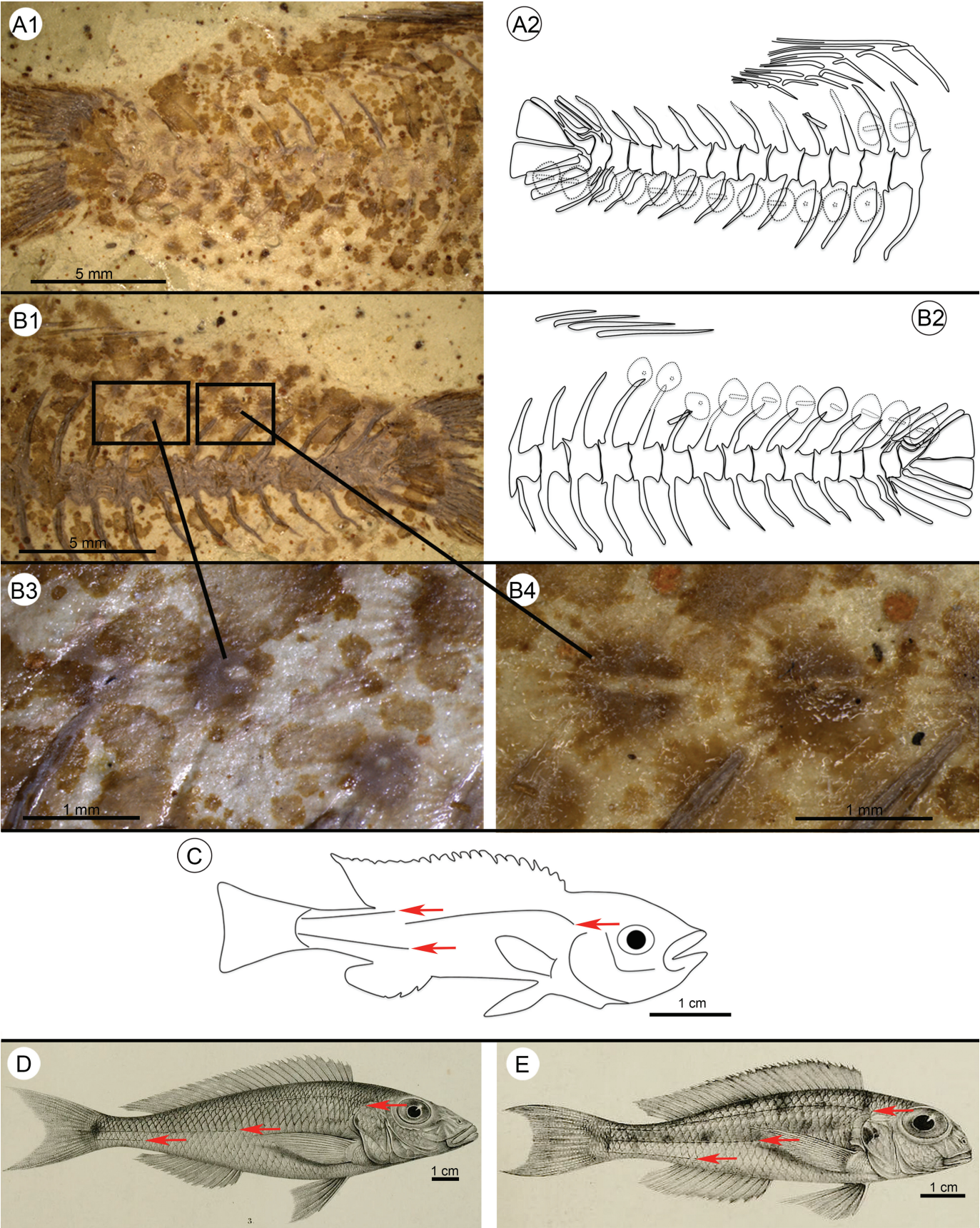
Type Species—†*Tugenchromis pickfordi*, sp. nov.

†*TUGENCHROMIS PICKFORDI*, sp. nov.
(Figs. 2–4)

Holotype—OCO-5-22/35, partially complete skeleton in part and counterpart (Fig. 2A1–A3), approximately 60 mm total length, 33.5 mm body length.

Diagnosis—As for genus.

←FIGURE 2. †*Tugenchromis pickfordi*, gen. et sp. nov. **A1–A2**, holotype in part (OCO-5-35) and counterpart (OCO-5-22); **A3**, right lateral view of the specimen (shading refers to ribs from the left side of the specimen); **B1**, caudal skeleton of †*T. pickfordi*, gen. et sp. nov. (OCO-5-22); **B2**, reconstruction of caudal skeleton in left lateral view. **Abbreviations:** **cl**, cleithrum; **cor**, coracoid; **ep**, epural; **hs**, hemal spine; **hyp**, hypural plate; **lac**, lacrimal; **nlc**, neurocranial lateral line canal; **ns**, neural spine; **o**, otolith; **op**, operculum; **ph**, parhypural; **pha**, pharyngeal teeth; **ppc**, postcleithrum; **pft**, posttemporal; **pu**, preural centrum; **rad**, radials; **sca**, scapula; **scl**, supracleithrum; **sup**, suboperculum; **us**, urostyle; **un1**, uroneural 1; =, tubular lateral line scale; °, pitted lateral line scale.



Etymology—Species named in honor of the paleontologist Martin Pickford in recognition of his outstanding contributions to the geology and paleontology of East Africa.

Locality, Horizon, and Age—Outcrop Waril (0°40'56.21"N; 35°43'7.43"E) in Central Kenya; Ngorora Formation, Member E; late Miocene (9–10 Ma) (see Rasmussen et al., 2017).

DESCRIPTION

General Description—A slender, laterally compressed cichlid of small size with three sequences of trunk lateral lines (Figs. 2A1–A3, 3A1–B2, C). The body is preserved in lateral view, whereas the head, which is incomplete, is preserved in dorso-lateral view. The lacrimal clearly displays a lateral line branched into six tubules. The species is additionally characterized by a unique combination of meristic characters including 29 (14 + 15) vertebrae, a dorsal fin formula of XIII,9, and an anal fin formula of III,9. The scales are large and cycloid, the number of scales in the longitudinal line is approximately 30. Measurements of the holotype are summarized in Table 2.

Neurocranium—The nasals, frontals, and eyes are not preserved. The occipital region is severely crushed, but imprints of oval sagittal otoliths with a prominent rostrum and a small antirostrum are recognizable (Fig. 2A1–A3). The pterotic is partly preserved and shows canals that probably represent the neurocranial lateral line canals (NLCs) (Fig. 2A1–A3). The lacrimal shows the lateral line branching into six tubules and is almost as deep as it is wide (2.47 × 2.79 mm), its ventral and posterior outline is convex, and the dorsal and anterior contours are rather straight (Figs. 2A1–A3, 4A1–A2).

Jaws and Teeth—Approximately 130 slender teeth are present, ranging in size from 0.21 to 0.23 mm in length and 0.03 to 0.06 mm in width. Some are unicuspid and hook-like with a shoulder; others are simple unicuspid (Fig. 4C–F). Based on their positions between the supracleithrum and the first vertebra, we consider these teeth to be pharyngeal. No bicuspid or tricuspid teeth are preserved. Jaw teeth and bones are not preserved.

Suspensorium and Hyoid Arches—The large and approximately triangular operculum is robust, its dorsal, anterior, and posterior borders are convex, and the articulation process is small (both parts; Fig. 2A1–A3) and lacks scales. The posterior part of a large and rounded suboperculum is visible below the operculum (Fig. 2A1–A3). Other bones of the suspensorium are not preserved.

Vertebral Column—The vertebral column contains 29 (14 + 15) vertebrae. The first two and the last two vertebrae are short (length-to-height ratio = 0.6–0.8). The neural spine of the first vertebra is not recognizable. The neural spines are short at the anterior end of the vertebral column and become more elongated posteriorly, reaching their maximum length at the level of the end of the spinous part of the dorsal fin (vertebrae 6–20) before shortening again along the caudal peduncle. The hemal spines show a similar pattern, with long spines at the origin of the anal fin becoming progressively shorter towards the caudal fin (Fig. 2A1–A3). There are probably 12 (at least 11) pairs of robust ribs that reach the margin of the abdominal cavity and are connected to the centra by strong parapophyses. The first pair of ribs originates on the third vertebra (Fig. 2A1–A3). Epineurals and supraneurals/predorsals are not discernible.

Median Fins and Support Structures—The caudal skeleton is similar to that of other members of the Cichlidae. Five hypural plates (Hyp1–5) are recognizable, and the diastema between

Hyp1+2 and Hyp3 is almost closed. Hyp1+2 and Hyp4 are large and triangular, Hyp3 is comparatively thin and appears to be separated from Hyp4 by a fine suture, and Hyp4 presents a crest-like thickening on its dorsal outline. Hyp5 is long and slender and reaches uroneural 1 proximally; it is separated from Hyp4 by the stegural. A long and widened parhypural, almost reaching the terminal centrum, is present, whereas a hypurapophysis is not recognizable (Fig. 2B1–B2). Two epurals are visible. The one positioned between the neural spines of PU3 and PU2 is long and broad, whereas the other, located on top of uroneural 1 between the neural spine of PU2 and hypural plate 5, is very short. None of these structures is fused with the stegural. Two preural vertebrae (PU2, PU3) contribute to the caudal endoskeleton. The PU2 has a strongly reduced neural spine, whereas its hemal spine is autogenous, broad, elongate, and displays a long, slender anterior process. The neural spine of PU3 is not reduced, and its hemal spine is duplicated. The caudal fin is truncate to subtruncate and comprises 16 (8 + 8) segmented principal rays, of which the uppermost and lowermost are unbranched. The principal rays are supported by epural 1, hypural plates 1–5, the parhypural, and the hemal spine of PU2 (Fig. 2B1–B2). Seven short, unbranched procurent rays are present both dorsally and ventrally and are supported by epural 1, the neural spine of PU3, and the hemal spine of PU2.

The dorsal fin consists of 13 spines and nine rays (Table 2). The lengths of the spines increase from the first to the last spine. Each spine and each ray (apart from the last ray) is supported by an elongate and thin pterygiophore, and each pterygiophore is associated with its individual interneural space (Fig. 2A1–A3). The first pterygiophore inserts into the interneural space of vertebrae 1 and 2, whereas the last pterygiophore associated with a spine inserts behind the neural spine of vertebra 13 (Fig. 2A1–A3). The pterygiophores of the rays become progressively shorter caudally.

The anal fin consists of three spines, which increase in length from spine I to spine III, and nine branched rays. The first two spines share one pterygiophore, whereas the third spine and the branched rays are each supported by a single pterygiophore, except for the last ray. All pterygiophores shorten progressively towards the caudal fin (Fig. 2A1–A3).

Paired Fins and Support Structures—Imprints of nine pectoral fin rays are visible. The cleithrum is a robust slightly bent bone, with the upper part anteriorly expanded and the lower part partially covered by the suboperculum (Fig. 2A1–A3). The supracleithrum is long, straight, and dorsorostrally tapered (Fig. 2A1–A3). Above this bone the posttemporal is visible; it is crushed but seems to be widely forked with equal arms. A long and slender postcleithrum extends from the anterior expansion of the cleithrum downwards to the pectoral fin rays and partially overlaps with the basipterygium (Fig. 2A1–A3). The scapula seems to be rectangular and has a large foramen; a coracoid is visible as an imprint underneath the scapula and cleithrum. Four rectangular radials are present, the ventral-most being the largest and the dorsal-most the smallest.

The pelvic fins are set low, and each is composed of a strong spine and five branched rays that do not reach the anal fin (Fig. 2A1–A3). The pelvic fin spine presents lateral and medial processes for articulation with the pelvic bone. The basipterygia are triangular in shape (Fig. 2A1–A3); the proximal tip is not recognizable.

←FIGURE 3. **A1–C**, part and counterpart of the caudal portion and complete reconstruction of †*Tugenchromis pickfordi*, gen. et sp. nov., showing the pattern of the three lateral line (trunk canal) segments. **A1–A2**, segment of the posterior trunk canal extending below the vertebral column and also below the anterior canal segment (OCO-5-35); **B1–B2**, additional segment of the posterior trunk canal above the vertebral column (OCO-5-22); **B3–B4**, close-up views of pitted and tubular lateral line scales. **C–E**, tripartite lateral line pattern in Ectodini and the new fossil cichlid. **C**, †*T. pickfordi*, gen. et sp. nov.; **D**, *Grammatotria lemairii*; **E**, *Xenotilapia sima*. Arrows indicate the three trunk canal segments. Panels **D** and **E** modified from Boulenger (1899).

TABLE 2. Morphometric measurements and meristic counts of †*T. pickfordi*.

Character	mm	% of BL
Dimension		
Body length	33.47	—
Maximum body height	12.50	37.3
Maximum body height at anal fin origin	10.55	31.5
Length of dorsal fin base	23.04	68.8
Length of anal fin base	6.14	18.3
Length of pelvic fin	6.61	19.7
Length of pelvic fin base	1.85	5.5
Distance between pelvic fin base and anal fin base	14.49	43.3
Minimum body height	4.48	13.4
Length of caudal fin	10.65	31.8
Length of caudal peduncle	10.95	32.7
Meristics		
Dorsal fin	XIII,9	
Anal fin	III,9	
Pectoral fin	9+	
Pelvic fin	I,5	
Caudal fin	7 + 8 + 8 + 7	
Vertebrae	29 (14 + 15)	

Squamation—Cycloid scales are visible on the flanks and the peduncle (Figs. 2A1–A2, 3A1–B4, 4H1–H2) and are especially well preserved on the caudal peduncle along the lateral line (Figs. 2A1–A2, 3A1–B4). Some scales are present along the base of the soft-rayed part of the dorsal fin. Whether these scales are displaced or not cannot be determined with certainty. Scales carry approximately nine to 13 radii and are longer in the vertical axis (= scale width, 1.09–1.38 mm) than the horizontal (= scale length, 1.0–1.19 mm; Fig. 4G1–H2). Approximately 30 scales can be discerned in the longitudinal row.

The lateral line (= trunk canal according to Webb, 1990) is divided into three segments along the body:

- (i) The anterior segment consists of at least 14 lateral line scales, 11 of which have a tubular opening. Ten of the 14 lateral line scales form a row that extends across the middle of the neural spines of vertebrae 11–18 (Figs. 2A1–A3, 3A1–A2, 3C). The first two scales in this row are tubular, and these are followed by two normal scales (without a sensory opening), one with a tubular opening, one normal scale, and then four scales, each with a tubular opening. The remaining lateral line scales are dislocated. Two of them appear above the first two spines of the dorsal fin, and two are positioned above spines 9 and 10 of the dorsal fin.

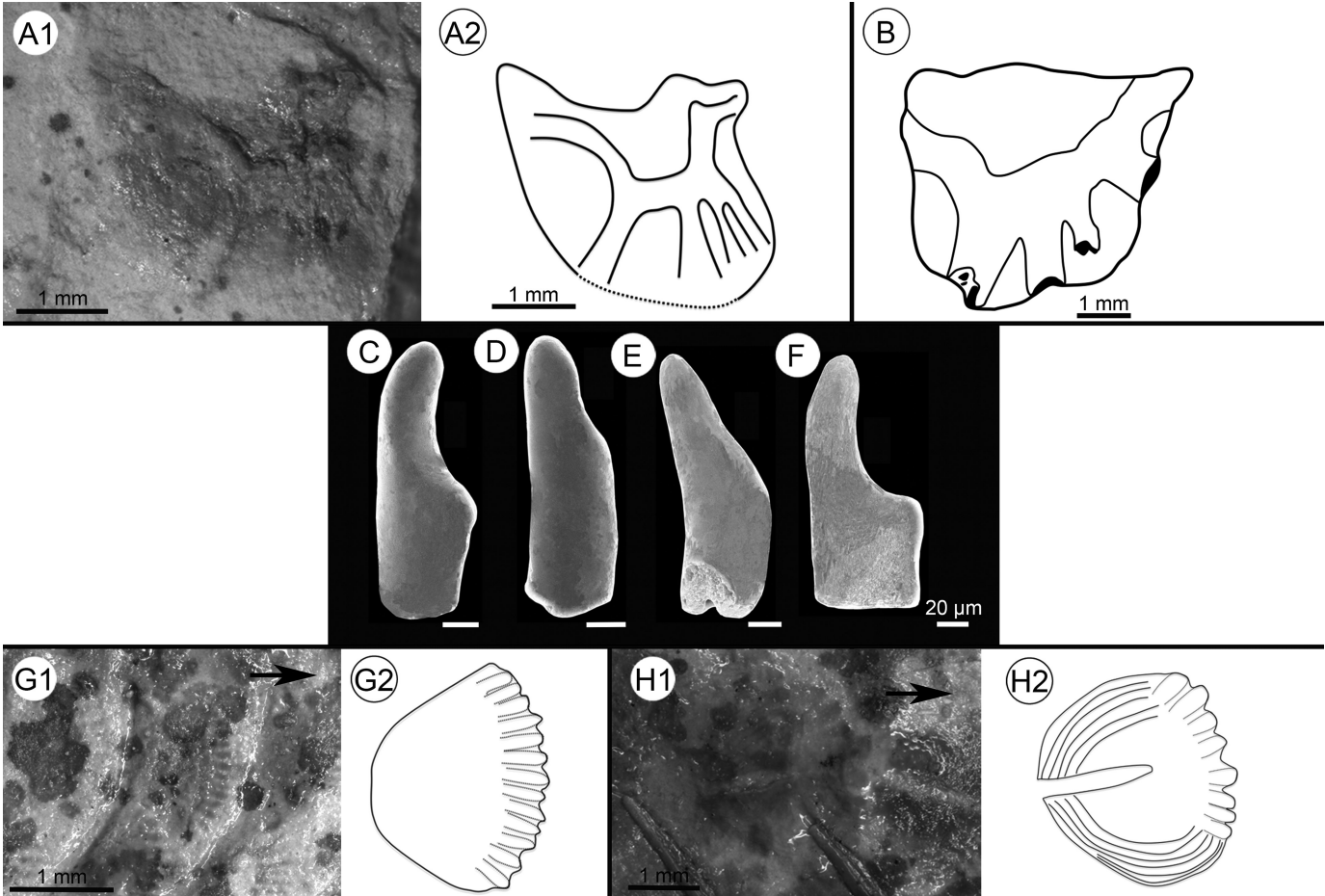


FIGURE 4. **A1–A2**, lacrimal of †*Tugenchromis pickfordi*, gen. et sp. nov. (OCO-5-22), showing the lateral line branched into six tubules; **B**, lacrimal of cf. *Pelmatochromis* spp. (redrawn after Van Couvering, 1982); **C–F**, SEM images of pharyngeal teeth of †*T. pickfordi*, gen. et sp. nov. (OCO-5-22); **C**, hook-like unicuspid tooth with shoulder; **D**, simple unicuspid tooth; **E**, simple unicuspid tooth; **F**, hook-like unicuspid tooth with shoulder; **G1–H2**, scales of †*T. pickfordi*, gen. et sp. nov.; **G1–G2**, flank scale with 13 radii (OCO-5-35); **H1–H2**, lateral line scale with tubular opening on peduncle; circuli are also discernible (mirror image; OCO-5-22). The arrows point anteriorly.

- (ii) Of the two posterior segments, one is positioned below the anterior trunk canal segment and separated from it by a vertical gap of two scale rows (Figs. 2A1–A3, 3A1–A2, 3C). It consists of 12 scales arranged in a row that extends across the middle of the hemal spines from vertebra 18 to the terminal centrum. The first three scales are pitted, the fourth is normal, and then follow three scales with a tubular opening, two normal scales, and again two scales with a tubular opening. The first pitted scale ‘overlaps’ with the last tubular scale of the anterior trunk canal segment (with a gap of two scale rows in between), and also with the first pitted scale from the second posterior trunk canal segment (with a gap of one scale row in between; see below).
- (iii) The second segment of the posterior trunk canal is positioned dorsally and posterior to the anterior segment and separated from it by a single scale row. It consists of 10 scales arranged in a row that projects just above the neural spines of the caudal vertebrae (from vertebra 18 to the terminal centrum). This row starts with three pitted scales, which are followed by seven scales with a tubular opening (Figs. 2A1–A3, 3B1–C).

Statistical Analysis

A PCoA based on nine meristic characters was carried out on the entire comparative data set (all data are provided in the Supplementary Data 2). We restricted this analysis to the cichlids of the ‘East African Radiation’ (see Fig. 1B) because a ‘lateral line on anteriormost infraorbital [lacrimal] branched into six tubules’

sensu Takahashi (2003b:368) is not present in any other African or non-African cichlid (Cichocki, 1976; Trewavas, 1983a; Stiassny, 1991; Kullander, 1998; Takahashi, 2003a).

In the PCoA, we distinguished four groups, following Weiss et al. (2015) and Meyer et al. (2015), i.e., the ‘most ancient Tanganyika tribes,’ the Lamprologini + Eretmodini, the ‘ancient Tanganyika mouthbrooders,’ and the Haplochromini (Fig. 5). The data show that †*T. pickfordi* falls within the 95% confidence ellipses of the ‘ancient Tanganyika mouthbrooders’ and the Haplochromini (Fig. 5). In all analyses, the PCoA strongly suggests that the character set found in †*T. pickfordi* is distinct from those of the members of the ‘most ancient Tanganyika tribes,’ and also from the Eretmodini and the Lamprologini. We performed a second PCoA with †*T. pickfordi* and the ‘ancient Tanganyika mouthbrooders’ alone (Fig. S2A). Now †*T. pickfordi* falls close to the 95% ellipses of the Ectodini and Limnchromini (Fig. S2A). In a further PCoA, †*T. pickfordi* was analyzed with all Haplochromini (Fig. S2B). Here †*T. pickfordi* lies within the 95% ellipses of the Haplochromini of Lake Victoria, the Pseudocrenilabrus Group, the Serranochromines, and the riverine Haplochromini (Fig. S2B).

DISCUSSION

Systematic Demarcation

Relationships of †*T. pickfordi* to the Cichlidae—Diagnostic characters for the family Cichlidae have been compiled by Fujita (1990), Sebilja and Andreatta (1991), Carpenter (2001), Takahashi and Nakaya (2002), and Nelson (2006). †*Tugenchromis pickfordi* can be securely identified as a member of the Cichlidae, based on its possession of the following combination

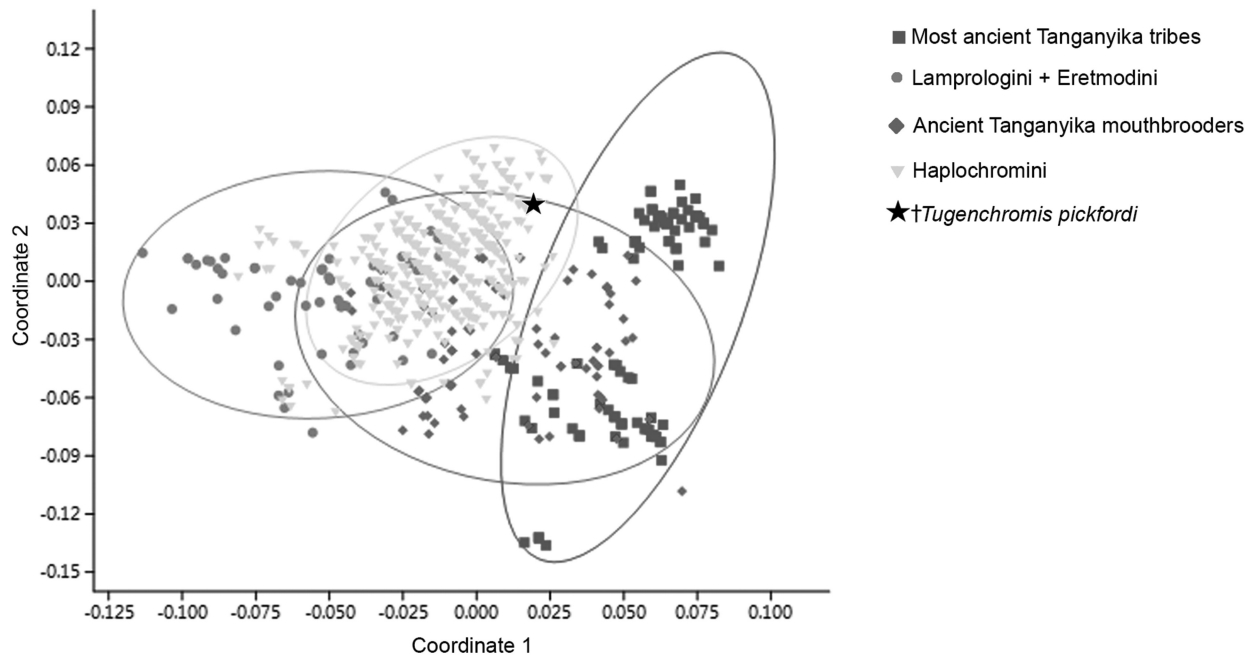












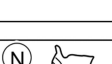










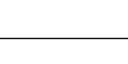





FIGURE 5. Principal coordinates analysis (PCoA) scatter plot based on nine meristic characters of †*Tugenchromis pickfordi*, gen. et sp. nov., and the four major cichlid groups of the ‘East African Radiation,’ indicated with different symbols and colors (N = 764; see Supplementary Data 2 for raw data). Species score limits are visualized as 95% confidence ellipses. Coordinate 1 vs. Coordinate 2. Coordinate 1 explains 50.96% and Coordinate 2 explains 36.85% of the variation.

of characters: number of principal caudal fin rays (8 + 8) (Fig. 2A3), pelvic fin formula (I,5) (Fig. 2A3), caudal skeleton with five hypurals, two epurals and free first uroneural, PU2 without neural spine but with neural arch and autogenous

hemal spine, and PU3 with non-autogenous hemal spine (Fig. 2B1–2). Moreover, Cichlidae possess a divided lateral line that is characterized by an anterior and a posterior trunk canal segment, with the anterior one positioned dorsally to the

	Taxon	Vertebrae	Dorsal fin formula	Anal fin formula	scales	#Lt	Lacrimal	
Tanganyika cichlids, 6 tubules on lacr.	† <i>T. pickfordi</i>	29	XIII/9	III/9	cycloid	6		
	Ectodini	31–38	XI–XIX/10–19	II–III/6–18	ctenoid	4–7		
	Limnochromini	29–35	XIV–XVIII/8–12	III/7–9	ctenoid	5–6		
	Perissodini	33–38	XIV–XX/10–15	III/8–13	cycloid	5–6		
	Eretmodini	30	XXI–XXV/2–7	III/6–8	ctenoid	5–6		
	Lamprologini	28–38	XVI–XXIV/6–12	IV–X/4–9	ctenoid	3–7		
	Bathybatini	34–41	XIII–XVIII/13–18	III/12–19	cycloid	5–6		
Tanganyika cichlids, < 6 tubules on lacr.	Tropheini	30–34	XVI–XXII/5–11	III–VI/5–9	ctenoid	5		
	Benthochromini	36–38	XVII–XIX/11–13	III/9–11	ctenoid	5		
	Cyphotilapiini	30–33	XVI–XIX/8–10	III/7–8	ctenoid	5		
	Cyprichromini	35–38	XII–XVIII/10–18	III/7–13	ctenoid	4–5		
	Trematocarini	28–31	IX–XII/10–14	III/7–12	cycloid	3–5		
	Boulengerochromini	34	XV–XVII/14–16	III/8–11	cycloid	5		
Non-Tanganyika Haplochromini	<i>M-Orthochromis</i>	30–37	XVI–XXII/8–11	III/7–11	ctenoid	5		
	<i>LML-Orthochromis</i>	28–33	XVI–XXI/7–10	III/6–8	ctenoid	5		
	<i>NZ-Orthochromis</i>	30–34	XVI–XIX/8–11	III/6–9	ctenoid	5		
	<i>O. torrenticola</i>	31–32	XVII–XVIII/10	IV/7–9	ctenoid	5		
	<i>O. machadoi</i>	29–32	XV–XVII/9–11	III–IV/6–9	ctenoid	5		
	<i>H. vanheusdeni</i>	29–31	XV–XVIII/8–10	III/6–9	ctenoid	5		
	<i>Pseudocrenilabrus</i> -Group	26–30	XIII–XVI/8–11	III/6–10	ctenoid	4–5		
	V-Haplochromini	26–32	XIII–XVIII/6–11	II–IV/6–13	ctenoid	5		
	M-Haplochromini	27–36	XII–XIX/7–13	III–IV/6–12	ctenoid	5		
	Serranochromines	26–37	XIII–XVIII/6–14	III/5–13	ctenoid	5		
	R-Haplochromini	26–33	XIV–XX/6–11	III–VII/4–9	ctenoid	5		

posterior and separated from it by a vertical gap of at least two scale rows (Webb, 1990). A divided lateral line is also present in the fossil (Figs. 2A3, 3; see also below).

Relationships of *†T. pickfordi* to the Cichlid Subfamilies—Previously suggested synapomorphies characterizing the different subfamilies and tribes within the living Cichlidae are related to soft tissue characters, the pharyngeal apophysis, details of the epibranchial bones, microstructures of scale surfaces, squamation patterns, lateral line foramina on the head, and other delicate structures (e.g., Regan, 1920a, 1922; Greenwood, 1978; Lippitsch, 1990, 1995; Stiassny, 1991; Casciotta and Arratia, 1993; Kullander, 1998, 2003). However, the major focus of these studies was to clarify the phylogenetic relationships within a specific subfamily. Furthermore, the position of *Heterochromis*, either within the Neotropical Cichlinae or within the African Pseudocrenilabrinae, could not be determined (see Sparks, 2008, and references therein). As a result, a matrix based on morphological characters that would allow confident attribution of our fossil to one of the four subfamilies is not available. However, the character ‘lacrima with six lateral line tubules’ is a unique synapomorphy in some lineages of the haplotilapiines. Because this synapomorphy is also present in *†T. pickfordi*, the new fossil taxon can be recognized as a member of the subfamily Pseudocrenilabrinae. The placement of *†T. pickfordi* within the African cichlids is additionally supported by its late Miocene age, because the split between African cichlids and the Malagasy, Indian, and South American cichlids is thought to have occurred in the Eocene, at the latest (Murray, 2001; Azuma et al., 2008; Friedman et al., 2013).

Relationships of *†T. pickfordi* within the Pseudocrenilabrinae—Most of the African cichlid tribes and lineages have been defined based on unique combinations of morphological characters (e.g., Poll, 1986; Dunz and Schliwen, 2013), but phylogenetic hypotheses for their interrelationships rest solely on molecular data (e.g., Koblmüller et al., 2008; Schwarzer et al., 2009; Meyer et al., 2015). One reason for this is our still limited knowledge of the osteology of African cichlids, although the homoplasy of several characters also plays a role (Stiassny, 1991). As for the family Cichlidae, no character-state matrix for phylogenetic analyses of interrelationships within the Pseudocrenilabrinae that is applicable to fossils has yet been developed. Moreover, the type specimen of *†T. pickfordi* lacks the head, which further restricts the number of morphological characters available. However, based on the lacrima morphology, meristic traits, and lateral line pattern, it is nevertheless possible to infer

the probable systematic affinities of *†T. pickfordi* within the Pseudocrenilabrinae.

Relationships of *†T. pickfordi* with Lake Tanganyika Cichlids—As mentioned above, the character state ‘lacrima with six tubules,’ as seen in *†T. pickfordi*, is not present in any cichlids other than a few lineages of the ‘East African Radiation’ (Cichocki, 1976; Kullander, 1998; Stiassny, 1991; Takahashi, 2003a; Trewavas, 1983a). In fact, it is restricted to six Lake Tanganyika tribes, i.e., the Bathybatini, Perissodini, Limnochromini, Ectodini, Lamprologini, and Eretmodini (Takahashi, 2003a) (see Fig. 6). In addition, both the rounded trapezoid shape of the lacrima and the arrangement of the tubules seen in *†T. pickfordi* are reminiscent of Limnochromini (Fig. 6). Comparison of meristic characters in *†T. pickfordi* with the six aforementioned Lake Tanganyika tribes reveals a close similarity to Ectodini and Limnochromini; only the number of vertebrae is slightly lower in the fossil compared with the Ectodini (29 vs. 31–38) (Fig. 6).

Both Ectodini and Limnochromini have ctenoid scales, whereas cycloid scales are present in *†T. pickfordi*. Cycloid scales occur in almost all non-haplotilapiine Pseudocrenilabrinae (Tylochromini, species of *Hemichromis*, chromidotilapiines, and species of *Pelmatochromis* and *Pterochromis*), but also in several tribes of the haplotilapiines (e.g., Tilapiini, Steatocranini, Pelmatilapiini, Boulengerochromini, Bathybatini, Trematocarini, Perissodini) (Lippitsch, 1995, 1998; Dunz and Schliwen, 2013; Fig. 6). Among the six Lake Tanganyika tribes discussed above, only Bathybatini and Perissodini possess cycloid scales (Poll, 1986; Lippitsch, 1998), and the latter is closely related to Ectodini (Weiss et al., 2015). It thus appears that *†T. pickfordi* presents a unique mosaic-like character set, combining traits found in four modern Lake Tanganyika tribes (Ectodini, Limnochromini, Bathybatini, and Perissodini; Fig. 7).

Another striking feature of *†T. pickfordi* is the presence of a tripartite lateral line. Among Pseudocrenilabrinae, a three-fold division of the lateral line system is known exclusively from two genera of the Ectodini, i.e., *Xenotilapia* Boulenger, 1899a, and *Grammatotria* Boulenger, 1899a (e.g., Pellegrin, 1904; Poll, 1986). Phylogenetic relationships within the Ectodini remain poorly resolved in molecular phylogenies based on either mitochondrial or nuclear DNA (Koblmüller et al., 2004; Weiss et al., 2015). It thus remains uncertain whether or not the emergence of an additional (third) trunk canal segment occurred only once within the Ectodini. Moreover, there is a notable difference between *†T. pickfordi* and *Grammatotria/Xenotilapia* in the position of the additional (third) trunk canal segment. In the latter, it lies below the posterior trunk canal segment (Poll, 1986),

←FIGURE 6. Meristic counts, scale types, and lacrima morphology of *†Tugenochromis pickfordi*, gen. et sp. nov., and representatives of all cichlid lineages of the ‘East African Radiation.’ Meristic counts from this study (see Supplementary Data 2), Weber (1897), Trewavas (1935, 1964, 1983b), Greenwood (1956a, 1956b, 1957, 1959, 1960, 1962, 1967, 1973, 1979, 1980, 1989, 1993), Greenwood and Gee (1969), Greenwood and Barel (1978), Hoogerhoud and Witte (1981), Witte and Witte-Maas (1981), Poll (1986), Winemiller and Kelso-Winemiller (1991), Bowers and Stauffer (1993), Stauffer and Van Snik (1996), Stauffer et al. (1997), De Vos and Seegers (1998), De Zeeuw et al. (2000), Black (2010), Oliver and Arnegard (2010), and Konings and Stauffer (2012). Note that some of these publications do not specify whether the total/caudal count of vertebrae includes the urostyle or not. Scale type from this study and Poll (1986). Lacrima morphology from this study (A, J, N–S), Cichocki (1976) (T), Liem (1978) (M), Oliver (1984) (V, W), Anker (1986) (U), and Takahashi (2003a) (B–I, K–L). Species from which lacrimas are illustrated are indicated by capital letters: A, *†T. pickfordi* (OCO-5-22); B, *Ectodus descampsi* Boulenger, 1898; C, *Greenwoodochromis christyi* (Trewavas, 1953); D, *Xenochromis hecki* Boulenger, 1899b; E, *Eretmodus cyanostictus* Boulenger, 1898; F, *Variabilichromis moorii* (Boulenger, 1898); G, *Bathybates minor* Boulenger, 1906; H, *Lobochilotes labiatus* (Boulenger, 1898); I, *Benthochromis tricoti* (Poll, 1948a); J, *Cyphotilapia* sp. (ZSM 043240_P-AA-0999); K, *Cyprichromis microlepidotus* (Poll, 1956); L, *Trematocara marginatum* Boulenger, 1899a; M, *Boulengerochromis microlepis* (Boulenger, 1899a), scale bar for lacrima not known, TL of specimen 16 cm; N, *Orthochromis malagaraziensis* (David, 1937) (ZSM 041469_DRC-2011+1029); O, *Orthochromis stormi* (Boulenger, 1902) (ZSM 042318); P, *Orthochromis* sp. Mambili (ZSM uncatalogued specimen); Q, *Orthochromis torrenticola* (Thys van den Audenaerde, 1963) (ZSM 038201_Uli-LUB 2008+008); R, *Orthochromis machadoi* (Poll, 1967) (BMNH 1984.2.6.116-131_2); S, *Haplochromis vanheusdeni* Schedel, Friel and Schliwen, 2014 (ZSM 043134); T, *Pseudocrenilabrus philander* (Weber, 1897); U, *Haplochromis elegans* Trewavas, 1933; V, *Maylandia (Pseudotropheus) zebra* (Boulenger, 1899c); W, *Serranochromis macrocephalus* (Boulenger, 1899b). **Abbreviations:** ATM, ‘ancient Tanganyika mouthbrooders’; lacr., lacrima; LML-*Orthochromis*, Luapula-Mweru system and Lualaba/Congo *Orthochromis*; #Lt, number of lateral line tubules on the lacrima; M-Haplochromini, Haplochromini of Lake Malawi; M-*Orthochromis*, Malagarasi *Orthochromis*; MATT, ‘most ancient Tanganyika tribes’; n.a., not available; NZ-*Orthochromis*, northern Zambian *Orthochromis*; R-Haplochromini, riverine Haplochromini; V-Haplochromini, Haplochromini of Lake Victoria. All scale bars equal 5 mm.

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whereas it is positioned above this segment and also above the anterior segment in †*T. pickfordi* (Figs. 2A1–A3, 3). As a result, it is not unambiguously clear whether the third trunk canal segment of the fossil taxon is homologous to the third segment seen in modern *Xenotilapia* and *Grammatotria*.

In summary, if only the character state ‘lacrima with six lateral line tubules’ is considered a synapomorphy, then †*T. pickfordi* could represent an extinct lineage within the ‘most ancient Tanganyika tribes’ (Fig. 7B). Alternatively, if the combination of the character states ‘lacrima with six lateral line tubules,’ ‘cycloid scales,’ and ‘presence of tripartite lateral line’ is considered synapomorphic, then †*T. pickfordi* can be positioned as a stem lineage of the ‘ancient Tanganyika mouthbrooders’ (Fig. 7C).

Relationships of †*T. pickfordi* with Haplochromini—If the meristic characters of the Haplochromini and †*T. pickfordi* are compared, overlap is recognizable in all of them (Fig. 6). This similarity in the meristic values is mirrored in the PCoA, which places †*T. pickfordi* within the 95% confidence ellipses of this tribe (Fig. 5). The Haplochromini are nested phylogenetically within the diversity of the Lake Tanganyika tribes (Meyer et al., 2015; Weiss et al., 2015) (Fig. 1B). They may have emerged around 5 Ma according to Koblmüller et al. (2008) and Friedman et al. (2013). They may also be substantially older, according to the estimates of Genner et al. (2007) who proposed ages of 8.9 Ma (fossil-based calibration) or 19.5 Ma (Gondwana-based calibration) for them. This means that the Haplochromini may or may not be younger than †*T. pickfordi*; therefore, we cannot exclude a close relationship of †*T. pickfordi* to the Haplochromini, if only meristic characters are considered. However, the Haplochromini do not show the derived character state ‘lacrima with six lateral line tubules’ as seen in †*T. pickfordi* and the six tribes of the ‘East African Radiation’ as discussed above.

Comparisons with Previously Described Fossil Cichlids

Most fossil cichlids from Africa and Arabia, and the single Pseudocrenilabrinae-like cichlid that has been found in Europe (*Oreochromis lorenzoi* Carnevale et al., 2003), can be distinguished from †*T. pickfordi* based on their meristic counts or osteological characters (Table 3). In the following comparison, we consider all previously described fossil cichlids from Africa, Saudi Arabia, and Europe that display at least some of the characters that are preserved in †*T. pickfordi*. We have not used an elevated number of anal spines (more than 3) to discriminate between †*T. pickfordi* and other fossil cichlids here, because cichlids may show intraspecific variation for this character (see Trewavas, 1983a, on several species of *Oreochromis*).

†*Tugenochromis pickfordi* can be clearly differentiated from the fossil remains of a possible member of *Tylochromis* (cf. *Tylochromis* Regan, 1920b) described from Libya and Egypt by Otero et al. (2015) and Murray (2002, 2004), respectively, based on its slender pharyngeal teeth (vs. molariform in cf. *Tylochromis*). Counts of dorsal spines and vertebrae that differ from those of †*T. pickfordi* have been reported for †*Mahengechromis* spp. Murray, 2000, unidentified fossils referred to as ‘Form B’ Van Couvering, 1982, †*Kalyptochromis hamulodentis* Van Couvering, 1982, *Oreochromis lorenzoi* Carnevale et al., 2003, *Tilapia nigra* Trewavas, 1937, and *T. crassispina* Arambourg, 1947 (see Table 3 for details and references). *Oreochromis harrisae* Murray and Stewart, 1999, *Tilapia fossilis*, and *T. melanopleura* White, 1937, possess a larger number of dorsal spines than †*T. pickfordi* (15 vs. 13), whereas their numbers of vertebrae are either unknown or slightly lower than the count for †*T. pickfordi* (27 vs. 29).

All other fossil cichlid species from North and East Africa (Van Couvering, 1982) and from Saudi Arabia (Weiler, 1970;

Lippitsch and Micklich, 1998) share some characters with †*T. pickfordi*. Low numbers of dorsal fin spines comparable to that seen in †*T. pickfordi* (13) have been reported for †*Macfadyena dabanensis* Van Couvering, 1982 (14), unidentified cichlids termed ‘Form C’ (14) and ‘Form D’ (13) (Van Couvering, 1982), †*Nderechromis cichloides* (14), †*Palaeofulu kuluensis* Van Couvering, 1982 (12–16), †*Palaeochromis roussetti* Sauvage, 1907 (13–14), †*P. darestei* Sauvage, 1907 (12–14), ?*Heterochromis* sensu Lippitsch and Micklich, 1998 (13–14), and undetermined cichlids described by Weiler (1970) (12). Among these species, †*M. dabanensis*, ‘Form C,’ †*P. kuluensis*, and ?*Heterochromis* most probably have two predorsal bones (Van Couvering, 1982; Lippitsch and Micklich, 1998) and are therefore unlikely to be closely related to the Lake Tanganyika tribes (to which †*T. pickfordi* is assigned; see above), which generally have only one predorsal (this study). Moreover, ?*Heterochromis* sensu Lippitsch and Micklich, 1998, shows ctenoid rather than cycloid scales. ‘Form D’ can be separated from †*T. pickfordi* by its low number of vertebrae. †*N. cichloides* has more soft rays in the median fins than †*T. pickfordi* (A: 10–12 vs. 9 and D: 13 vs. 9), and its scales are ctenoid (Van Couvering, 1982; vs. cycloid in †*T. pickfordi*). In †*Palaeochromis roussetti* and †*P. darestei*, the scale type and pharyngeal dentition are similar to those of †*T. pickfordi*, but the numbers of vertebrae are different (25–26 vs. 29 in †*T. pickfordi*) and the body of †*T. pickfordi* is more elongate (Sauvage, 1910). The undetermined cichlids described by Weiler (1970) can also be separated from †*T. pickfordi* based on their vertebral count (23 vs. 29).

It is more difficult to conclusively distinguish between †*T. pickfordi* and several fossil cichlids described in open nomenclature, because their lateral line and meristic counts are not known. Among these latter forms are ‘Tilapiini Group 2’ and ‘Tilapiini Group 3’ from the Oligocene of Saudi Arabia (Lippitsch and Micklich, 1998) (Table 3). Given their older age (Oligocene) and their geographical origin (Saudi Arabia), it is unlikely that †*T. pickfordi* represents the same taxon as either ‘Tilapiini Group 2’ or ‘Tilapiini Group 3.’ In addition, ‘Tilapiini Group 3’ has ctenoid scales, whereas the scales of †*T. pickfordi* are exclusively cycloid. In ‘Tilapiini Group 2,’ Lippitsch and Micklich (1998) observed scales on the soft-rayed part of the dorsal fin. †*Tugenochromis pickfordi* may also possess a row of scales on the soft-rayed part of the dorsal fin, but these scales could also be dislocated in our specimen.

Further cichlid fossils in open nomenclature have been described by Van Couvering (1982). These include ‘Form A’ from the Oligocene in Somalia and several Miocene taxa from Kenya, i.e., ‘?Tilapia Cichlidae Form A,’ ‘Cichlidae Form C,’ ‘Cichlidae Form D,’ ‘Cichlidae spp. Group A,’ and ‘Cichlidae spp. Group B’ (Table 3). Here again, given the Oligocene age of ‘Form A,’ this taxon most probably does not correspond to †*T. pickfordi*. Moreover, of the Miocene taxa from Kenya, ‘Cichlidae Form D’ can be clearly differentiated from †*T. pickfordi*, because it possesses molariform (vs. slender in †*T. pickfordi*) pharyngeal teeth. Similarly, the pharyngeal teeth of ‘Cichlidae spp. Group A’ and ‘Cichlidae Form C’ differ from those of †*T. pickfordi*. The remaining Miocene taxa from Kenya (‘?Tilapia Cichlidae Form A,’ ‘Cichlidae spp. Group A,’ ‘Cichlidae spp. Group B’), all of which are incompletely preserved, share with †*T. pickfordi* the slender pharyngeal teeth and/or the cycloid scales and could possibly represent the latter.

Two further species deserve special consideration. The first is †*Oreochromis (Sarotherodon) martyni* (Van Couvering, 1982), which, like †*T. pickfordi*, was recovered from the Ngorora Formation of the Tugen Hills, albeit in a slightly older stratigraphic context (middle Miocene). The meristic counts for both are quite similar, but †*O. (Sarotherodon) martyni* has a divided lateral line of the general cichlid type (Van Couvering, 1982) and can therefore be definitively distinguished from †*T. pickfordi*.

TABLE 3. Summary table of relevant characters of the fossil specimen and all previously described African, Saudi Arabian, and European fossil cichlids, where at least some of these characters are preserved.

Taxon	Reference	Age	Locality	Pd	V	D	A	Scales	Pharyngeal teeth	LL	L _r	#L _t
† <i>Tugenochromis pickfordi</i>	This study	Upper Miocene	Waril, Kenya	1	29	XIII,9	III,9	Cycloid	Unicuspid	3	30?	6
† <i>Mahengechromis</i> spp.	Murray (2000)	Eocene	Mahenge, Tanzania	1	22–25	XV,8–9	III,8–10	Ctenoid	Unicuspid	2	30	4–5
cf. <i>Tylochromis</i>	Murray (2002)	Upper Eocene	Jebel Qatrani Fm., Egypt	—	—	—	—	—	Molariform	—	—	—
cf. ? <i>Tylochromis</i>	Otero et al. (2015)	Upper Eocene	Dur At-Talah, Libya	—	—	—	—	—	Molariform	—	—	—
† <i>Macfaduena dabanensis</i>	Van Couvering (1982)	Oligocene	Daban Beds, Somalia	2	27	XIV,9	III,10?	—	Bicuspid	1+	—	—
Form A				—	—	—	—	Cycloid	Uni-, bi-, tricuspid	—	—	—
Form B				—	15+	XI?,13	III?,10	Cycloid	Uni- and bicuspid	2	22	—
Form C				2?	27?	XIV,6+	IV,7	Ctenoid	—	—	—	—
Form D				—	24	XIII,11	VI,12	? cycloid	—	—	—	—
† <i>Kalyptochromis hamulodentis</i>		Lower Miocene	Kulu Fm., Kenya	2	30	XVII,10	IV,12	Cycloid	Unicuspid	—	—	—
† <i>Nderechromis cichloides</i>				—	—	XIV,13	III,10–12	Ctenoid	Bicuspid	—	—	—
† <i>Palaeofulu kulensis</i>				2	25–29	XII–XVI,7–13	III,7–10	Cycloid	Bicuspid	2	—	4–5
? <i>Tilapia</i> , Cichlidae Form A			Kulu Fm., Kenya	—	—	—	—	Cycloid	Bicuspid	—	—	—
<i>Pelmatochromis</i> sp.			Lamitina Beds, Uganda	—	—	—	—	Cycloid	Bicuspid	—	—	6
Cichlidae Form C		Lower Miocene	Turkana Grits, Kenya	—	—	—	—	Cycloid	Bicuspid	—	—	—
Cichlidae Form D		Lower Miocene	Turkana Grits, Kenya	—	—	—	—	Cycloid	Molariform	—	—	—
† <i>Oreochromis martyni</i>		Middle–upper Miocene	Ngorora Fm., Kenya	1	27–29	XIII–XIV,9–11	III,7–11	Cycloid?	Uni- and bicuspid	2	—	—
Cichlidae spp. Group A		Middle Miocene	Kirimun Beds, Kenya	—	—	—	—	—	Bicuspid or round and flat	—	—	—
Cichlidae spp. Group B				—	—	—	—	Cycloid	—	—	—	—
† <i>Palaeochromis roussetti</i>		Upper Miocene	Seybouse Valley, Algeria	1	25–26	XIII–XIV,?9–14	III,8	Cycloid or ctenoid	Uni- and bicuspid	—	—	—
† <i>Palaeochromis darestei</i>				1	25–26	XII–XIV,10–16	III,9–10	Cycloid	Uni- and bicuspid	2	—	—
? <i>Heterochromis</i>	Lippitsch and Micklich (1998)	Oligocene	Ad Darb, Baid Fm., Saudi Arabia	1+	—	XIII–XIV,13+	IV–V,–	Ctenoid	—	—	—	—
Tilapiini Group2				—	—	—	III?V–	Cycloid	—	—	—	—
Tilapiini Group3				—	—	—	IV,–	Ctenoid	—	—	—	—
Cichlidae indet.	Weiler (1970)	Oligocene–Miocene	Wadi Araba, Jordan	—	23	XII,5–9?	III,8	Cycloid	—	—	—	—
† <i>Oreochromis lorenzoi</i>	Carnevale et al. (2003)	Upper Miocene	Gessoso-Solfifera Fm., Italy	1	30	XV,12	IV,8	Cycloid	Unicuspid, kukri	2	26?	5
† <i>Oreochromis harrisiae</i>	Murray and Stewart (1999)	Lower Pliocene	Middle Awash, Ethiopia	1	—	XVI?,11?	—	Cycloid	Unicuspid	2	31	5
† <i>Tilapia fossilis</i>	White (1937)	Upper Pleistocene	Ashanti, Lake Bosumtwi, Ghana	—	27	XV,12	III,7–8	Cycloid	Unicuspid	2	—	—
† <i>Tilapia melanopleura</i>				—	—	XV?,–	III,12?	Cycloid	Uni- and bicuspid	2	—	—
† <i>Tilapia nigra</i>	Trewavas (1937)	Lower Pleistocene	Kavirondo Province, Kenya	—	29–30	XVII,9–11	IV,9–10	—	—	—	30–32	—
† <i>Tilapia crassispina</i>	Arambourg (1947)	Lower Pleistocene	Omo Valley, Kenya	—	30	XVI,–	III,8	Cycloid	Unicuspid	—	35?	—

Extinct species are marked with †. **Abbreviations:** A, anal fin formula; D, dorsal fin formula; LL, number of lateral line segments; L_r, scales in longitudinal row; #L_t, number of tubules on the lacrimal; Pd, number of predorsals; Scales, scale type; V, number of vertebrae. Fossil taxa are arranged in accordance to the author.

The second taxon of interest here is cf. *Pelmatochromis* spp. Van Couvering, 1982, found in the lower Miocene of Uganda. This fossil cichlid has been described on the basis of disarticulated bones; hence, no meristic counts are known. However, it features a lacrimal with the same overall shape as that of †*T. pickfordi* and also the six foramina seen in †*T. pickfordi* (Table 3; Fig. 4A1–B), and both forms have cycloid scales. Most other characters of cf. *Pelmatochromis* spp. refer to the head and therefore cannot be compared with †*T. pickfordi*. However, the presence of leaf-shaped unicuspid pharyngeal teeth in †*T. pickfordi* can be ruled out. These considerations, together with its lower Miocene age, make it unlikely that cf. *Pelmatochromis* spp. sensu Van Couvering (1982) is the same species as †*T. pickfordi*.

Evolutionary History of the Lake Tanganyika Cichlids

The temporal relationship between cichlid diversification in the East African Rift Valley and the colonization of Lake Tanganyika is the subject of controversy and ongoing discussion. Problems in interpreting the evolutionary history of the cichlids of Lake Tanganyika have arisen from discordances between phylogenetic trees constructed on the basis of mitochondrial vs. nuclear markers, incomplete taxon sampling, uncertainty with respect to the geological age of Lake Tanganyika itself, and the paucity of cichlid fossils from Africa with unambiguous phylogenetic placement (Meyer et al., 2015; Weiss et al., 2015). Estimates of the geological age of the Lake Tanganyika Basin range from 5.5 to 14.5 Ma, depending on the methods used. Cohen et al. (1993) extrapolated Pleistocene sedimentation rates to the Miocene and concluded that the Lake Tanganyika Basin formed 9–12 Ma. A slightly older age (14.5 Ma) was proposed on the basis of combined litho- and biostratigraphic data (Roller et al., 2010), whereas a drastically younger age (5.5 Ma) has been suggested based on thermochronology (Spiegel et al., 2007; Bauer et al., 2010). Previous studies dealing with molecular data and cichlid diversification have generally accepted the age suggested by Cohen et al. (1993), which has led to the widespread assumption that the cichlids of Lake Tanganyika must have originated about 9–12 Ma ago (Salzburger et al., 2005; Day et al., 2008; Sturmbauer et al., 2010; Koblmüller et al., 2008).

In a recent study, Weiss et al. (2015) presented both mitochondrial and nuclear DNA data based on a comprehensive sample of taxa including all Lake Tanganyika cichlid lineages (sensu Poll, 1986; Nishida, 1991; Meyer, 1993), as well as potential precursor lineages. Their analyses suggested that some Tanganyika lineages exhibit a mosaic genomic structure, most probably due to repeated hybridization, introgression, and gene flow from riverine cichlids and from other Tanganyika lineages (see also Clabaut, 2005; Meyer et al., 2015). Furthermore, Weiss et al. (2015) recognized four major groups among the Lake Tanganyika cichlid fauna, which appear to have originated from four different founder lineages. These groups are (i) the ‘most ancient Tanganyika tribes,’ (ii) Lamprologini and Eretmodini, (iii) the ‘ancient Tanganyika mouthbrooders,’ and (iv) Tropheini. Our study shows †*T. pickfordi* to be morphologically intermediate between the Limnochromini and Ectodini (see above), both of which belong to the ‘ancient Tanganyika mouthbrooders’ (Fig. 6). The presence of cycloid scales in †*T. pickfordi* (vs. ctenoid scales in Limnochromini and Ectodini) shows that it shares a character state with other ‘ancient Tanganyika mouthbrooders’ (e.g., Perissodini) and perhaps even with members of the ‘most ancient Tanganyika tribes’ (e.g., Bathibatini; Figs. 6, 7). Therefore, we have suggested that †*T. pickfordi* may represent either an extinct lineage within the ‘most ancient Tanganyika tribes’ (Fig. 7B) or a stem lineage of the ‘ancient Tanganyika mouthbrooders’ (Fig. 7C).

Because Lake Tanganyika is located in the western branch of the East African Rift System (EARS), the discovery of a potential precursor of Tanganyika cichlids from the late Miocene in the eastern branch of the EARS (Central Kenya Rift) supports the ‘melting-pot Tanganyika hypothesis’ (Weiss et al., 2015). This hypothesis suggests that precursor lineages of the modern Lake Tanganyika cichlids originated in rivers and wetlands prior to the formation of the lake, and possibly in areas beyond the boundaries of the present-day Lake Tanganyika drainage. In other words, the primordial Lake Tanganyika was initially colonized by an already diversified cichlid fauna.

The geological age of †*T. pickfordi* can serve in future studies as a new minimum age for the lineage that gave rise to the ‘ancient Tanganyika mouthbrooders’ or, alternatively, for the ‘most ancient Tanganyika tribes.’ Molecular clock analyses have resulted in highly variable node-age estimates for the origin of Lake Tanganyika cichlid lineages, depending on the calibration point used (cichlid fossils, break-up of Gondwana, or formation of the Tanganyika Basin). These dates range from younger than 12 Ma (formation of the Lake Tanganyika Basin; e.g., Koblmüller et al., 2008) to 20–26 Ma (fossil; Schwarzer et al., 2009) to 22–51 Ma (Gondwana; Genner et al., 2007). If †*T. pickfordi* is a stem lineage of the ‘ancient Tanganyika mouthbrooders,’ then the split between the ‘most ancient Tanganyika tribes’ and the Lamprologini/Eretmodini lineages must date back to at least 9 million years, whereas the ‘ancient Tanganyika mouthbrooders’ had not necessarily radiated within the lake at that time.

Furthermore, the site ‘Waril’ in the Central Kenya Rift, where †*T. pickfordi* was discovered, and the fossil’s inferred phylogenetic relationships support the existence of an ancient hydrological connection (e.g., via a proto-Malagarasi River) between the Central Kenya Rift and Lake Tanganyika, as proposed in previous geological studies (Coulter, 1991; Cohen et al., 1997; Goodier et al., 2011). This connection was probably disrupted in the initial stages of rifting—close to, or coincident with, the ‘Nyanja event,’ i.e., the initial flooding of the Lake Tanganyika Basin (Rosendahl, 1988), which, according to Cohen et al. (1993), occurred around 9–12 Ma (see also Lezzar et al., 1996; Cohen et al., 1997). This scenario is compatible with our data, because the lake sediments in which †*T. pickfordi* was found are 9–10 Ma old. It should also be noted in this context that a Miocene trans-African east-west directed hydrological network has previously been suggested for the Upper Nile and the Chad Basin (Otero et al., 2009; Day et al., 2013; Pinton et al., 2013).

CONCLUSION

Based on lacrimal morphology and meristic data derived from all present-day cichlids of the ‘East African Radiation,’ we propose that the newly discovered cichlid fossil from the upper Miocene of Central Kenya either represents a stem lineage of the ‘ancient Tanganyika mouthbrooders’ or an extinct lineage within the ‘most ancient Tanganyika tribes.’ This result implies that the use of a comprehensive set of comparative material derived from extant cichlids may make it possible to phylogenetically place other fossil cichlids with greater confidence in future studies.

Apart from a lower Miocene cichlid from Uganda (cf. *Pelmatochromis* spp.), none of the previously described fossil cichlid taxa from Africa, Arabia, and Europe possess distinctive similarities to †*T. pickfordi*. This indicates that the Ngorora fish Lagerstätte in Central Kenya may provide an unrivalled window into the evolutionary history of African cichlids, particularly into the origin of the ‘East African Radiation,’ i.e., the megadiversity of the present-day cichlids in Lake Tanganyika, Lake Malawi, and Lake Victoria.

Furthermore, the new fossil provides additional support for the presence of an ancient east-west connection (e.g., proto-

Malagarasi River) between the Central Kenya Rift and Lake Tanganyika, which is consistent with previous assumptions regarding the hydrological networks across East and Central Africa during the Miocene.

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