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ARTICLE

NEW CICHLID FOSSILS FROM THE MIDDLE-LATE MIOCENE ALKALINE LAKES OF AFRICA

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ABSTRACT—The African Cichlidae *Oreochromis* (*Alcolapia*) and *Oreochromis amphimelas* can survive in extremely alkaline environments and represent the only known modern alkaliphilic cichlid fish found in Africa. The presence of fossil cichlids from the Miocene of central Kenya (Tugen Hills) that are morphologically similar to *Oreochromis* (*Alcolapia*) has been noted in previous works, but the conclusions remained tentative. The purpose of this study is to examine newly discovered fossil cichlids from the Tugen Hills and to compare their osteology with that of extant *Oreochromis* (*Alcolapia*). This is performed based on a comprehensive collection of comparative material, using microscopy and computed microtomography (µCT). We provide a revised diagnosis for the genus †*Rebekkachromis*, and revise its systematic relationships by assigning it to the Oreochromini (rather than to the Etiini). Two new species of †*Rebekkachromis* are described, i.e., †*R. valyricus*, sp. nov., and †*R. vancouveringae*, sp. nov., and a morphologically diverse assemblage of co-occurring †*Rebekkachromis* specimens is documented. Moreover, we found that †*Rebekkachromis* had three sensory canal pores (instead of four) on the lower arm of the preopercle, a feature that distinguishes both the modern *Oreochromis* (*Alcolapia*) and our fossil specimens from almost all other modern African cichlid fish. Our new data indicate that alkaliphile cichlids similar to *Oreochromis* (*Alcolapia*) were present in Central Kenya about 10–13 Ma ago and that the ability of African cichlid fishes to thrive in highly alkaline waters had already developed by that time.

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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

Cichlid fishes (Cichlidae) are a family comprising over 1,700 valid species worldwide (Fricke et al., 2019) and are widely cited as an iconic example of adaptive diversification (Seehausen, 2006; Futuyma and Kirkpatrick, 2017). Cichlids are classified into four subfamilies, the Indian/Sri Lankan/Malagasy Etroplinae (16 spp.), the Malagasy Ptychochrominae (16 spp.), the Neotropical Cichlinae (>560 spp.), and the African/Middle Eastern Pseudocrenilabrinae (>1,100 spp.) (Fricke et al., 2019) (Fig. 1). The largest clade within the Pseudocrenilabrinae (Dunz and Schliewen, 2013), the haplotilapiines, accounts for more than 90% of all African cichlid species (Froese and Pauly, 2019) and is divided into 22 tribes based on morphological and molecular data (Dunz and Schliewen, 2013).

The most geographically widespread haplotilapiine tribes, and one of the most species-rich, are the Oreochromini, which includes more than 60 species in nine genera (Froese and Pauly, 2019) and its members can be found in rivers and lakes all over Africa (Trewavas, 1983; Schwarzer et al., 2009; Dunz and Schliewen, 2013). *Oreochromis* Günther, 1889 is the most speciose oreochromine genus, with 37 species (Froese and Pauly, 2019). It includes the four species sometimes referred to as 'soda tilapias,' which belong to the subgenus *Alcolapia* Thys van den Audenaerde, 1968, i.e., *Oreochromis* (*Alcolapia*) *grahami* (Boulenger, 1912), *O.* (*Alcolapia*) *alcalica* (Hilgendorf, 1905), *O.* (*Alcolapia*) *ndalalani* (Seegers and Tichy, 1999) and *O.* (*Alcolapia*) *latilabris* (Seegers and Tichy, 1999) (see Tichy and Seegers, 1999; Ford et al., 2016; Ford et al., 2019).

The ability to adapt to life in the alkaline-saline conditions found in 'soda lakes' (salinity >5‰, pH >9; e.g., Schagerl and Renaut, 2016) is one aspect of cichlid evolution that has attracted particular interest (Onyango and Kisia, 2007; Kavembe et al., 2016). Although most cichlids are freshwater fish, members of all cichlid subfamilies exhibit resistance to increased salinity (Ward and Wyman, 1977; Reinthal and Stiassny, 1991; Martinez-Palacios et al., 1996; Oldfield, 2004; Langston et al., 2010). However, only

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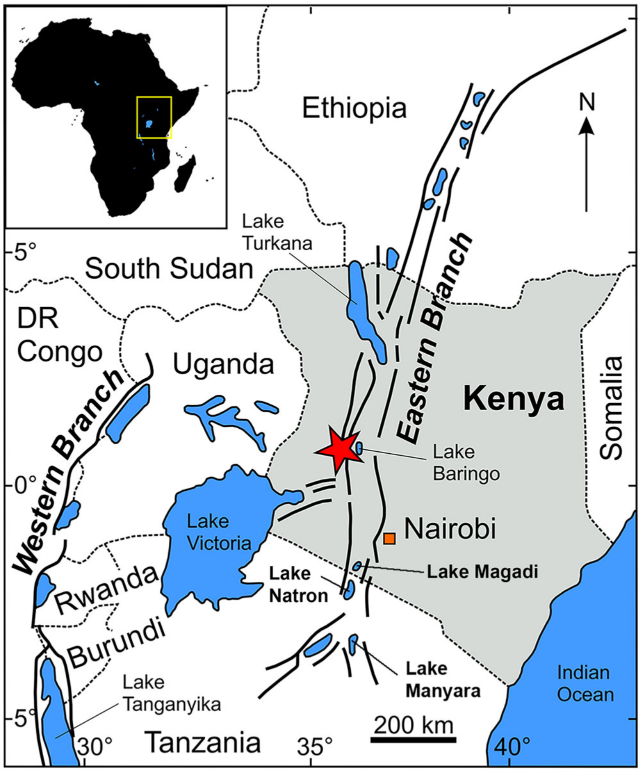

FIGURE 1. Sketch map of East Africa. The star marks the study area in the Tugen Hills. Map modified from Kiage and Liu (2009) and Penk et al. (2019), with the permission of Elsevier.

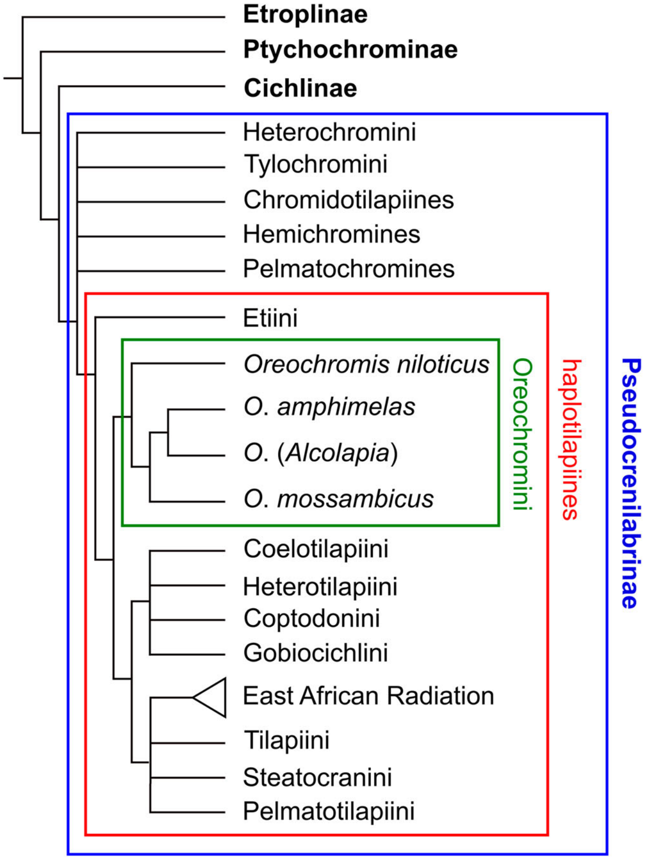

FIGURE 2. Simplified composite phylogeny depicting the relationships among the Cichlidae, based on Schwarzer et al. (2009), Dunz and Schliewen (2013), Irisarri et al. (2018), Schedel et al. (2019), and Ford et al. (2019). Note that the clade referred to as the East African Radiation itself encompasses numerous tribes and it has been collapsed.

the four aforementioned soda cichlids, living today in lakes Magadi and Natron, and the closely related species *Oreochromis amphimelas* (Hilgendorf, 1905) from the nearby Lake Manyara (Fig. 1), are known to endure extreme soda conditions (Ford et al., 2019), making them the only known modern alkaliphile cichlid fish.

Alcolapia was originally defined by Thys van den Audenaerde (1968) as a subgenus of *Tilapia* Smith, 1840 and later described as a subgenus of *Oreochromis* based on morphological data (Trewavas, 1983; Seegers and Tichy, 1999). *Alcolapia* was raised to genus status in Seegers et al. (1999), but subsequent molecular phylogenetic analyses supported its placement within *Oreochromis* (Nagl et al., 2001; Schwarzer et al., 2009; Dunz and Schliewen, 2013; Kavembe et al., 2013; Matschiner et al., 2017; Ford et al., 2019) (Fig. 2). However, not much is known about the emergence of cichlids in alkaline environments in the geological past. Van Couvering (1982) described †"*Sarotherodon*" *martyni* from the Middle Miocene (≈12 Ma) of the Ngorora Formation in the Tugen Hills of Central Kenya (Fig. 1). She assigned this species to the genus *Sarotherodon* Rüppell, 1852 because she assumed a close affinity between her fossil specimens and the modern alkaliphile cichlids, which at that time were classified in this genus. However, she also pointed out that "a detailed comparison of the osteology" between her fossils and the modern alkaliphile cichlids "has yet to be made" (Van Couvering, 1982:89). Furthermore, Van Couvering (1982) implied that †"*S.*" *martyni* lived under alkaline conditions (pH about 9–10), as the mineral analcime, which is indicative for high alkalinity (Hay, 1966, 1970), was abundant in the Miocene sediments that yielded this fossil species. More recently, another fossil species, †*Oreochromimos kabchorensis* Penk, Altner, Cerwenka, Schliewen, and Reichenbacher, 2019, characterized by a morphology intermediate between that of *Oreochromis* (*Alcolapia*) and all other *Oreochromis*, was described from the Ngorora Formation of the Tugen Hills (Penk et al., 2019). However, Penk et al. (2019) were cautious not to directly suggest a relationship with *Oreochromis* (*Alcolapia*) pending further information.

New fossil cichlid material collected from alkaline paleoenvironments of the middle Miocene Ngorora Formation in the Tugen Hills offers a new opportunity to examine the emergence of cichlids in alkaline lakes. Several of these new specimens have yielded excellent microtomography (μCT) data, which has allowed us to study structures that are otherwise difficult to observe in fossils. The specific objective of this paper is to describe a morphologically diverse new fossil cichlid fauna, including the introduction of two new species, and to compare their osteology with that of extant *Oreochromis* (*Alcolapia*).

Geological Setting and New Fossil Sites

The Tugen Hills in Central Kenya is a mountain range that lies within the eastern branch of the East African Rift System (EARS) (Fig. 1). The rocks exposed in the Tugen Hills originated during the formation of the Central Kenya Rift section of the EARS during the Miocene and Pliocene. Volcanic rocks testify to periods of enhanced tectonic activity, while fluvial and lacustrine sediments accumulated when volcanism had effectively ceased and only occasional ash falls occurred (Bishop and Chapman, 1970; Bishop and Pickford, 1975; Rasmussen et al., 2017).

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The fossils studied here were recovered from the middle to upper Miocene Ngorora Formation in the Tugen Hills. The study area is located in the Baringo District, ca. 30 km northwest of Lake Baringo (Fig. 1). The Ngorora Formation comprises volcaniclastic rocks and tuffs alternating with fluvial and lacustrine, mostly siliciclastic sediments and paleosols; it reaches a thickness of 365 m and can be subdivided, from bottom to top, into the five lithostratigraphic members A to E (Bishop and Pickford, 1975; Rasmussen et al., 2017). The rocks of the Ngorora Formation were deposited in the Ngorora Basin, which can itself be partitioned into a northern (Kabasero sub-basin, area I) and a southern area (Kapkiamu sub-basin, area II) (Bishop and Pickford, 1975; Rasmussen et al., 2017:fig. 2). Apart from abundant finds of fossil mammals, turtles, crocodiles and plants, the Ngorora Formation hosts a fossil-fish *Lagerstätte*, characterized by numerous assemblages of cichlid fish fossils, especially in the sediments comprising the Members C to E of the Kapkiamu sub-basin (Bishop and Pickford, 1975; van Couvering, 1982; Rasmussen et al., 2017; Altner et al., 2017; Kevrekidis et al., 2019; Penk et al., 2019).

The fossil cichlid fishes described here were collected from the Ngorora Formation during field campaigns in the Tugen Hills in 2011 (site Terenin) and 2014 (site Yatianin). Terenin (GPS coordinates 0°48.284′N, 35°48.936′E, 1842 m above sea level) is situated south west of the small village of Bartabwa in the Kabasero sub-basin, whereas Yatianin (0°43.986′N, 35°46.904′E, 1405 m above sea level) is located ca. 20 km south of Terenin in the Kapkiamu sub-basin. Terenin represents Member A of the Ngorora Formation according to Pickford et al. (2009), whereas Yatianin belongs to the uppermost part of Member C of the Ngorora Formation according to Rasmussen et al. (2017). Using the stratigraphic scheme of Rasmussen et al. (2017), the stratigraphic age of Terenin is ca. 13 Ma and that of Yatianin ca. 12 Ma. At both sites, the fossils with which we are concerned were collected from silicified, white to light grey, laminated diatomites. For a more detailed description of the Yatianin section see Rasmussen et al. (2017), for Terenin no further data are available.

MATERIALS AND METHODS

Material

Comparative Extant Material—We used this set of comparative material to examine characters that are also discernible in our fossils, but whose taxonomic or systematic utility has not been previously assessed: (1) the numbers of sensory canal pores on the preopercle were determined for 231 species representing all cichlid subfamilies and all African tribes (Table S1). These data were drawn from the literature (164 species), from specimens preserved in alcohol or formaldehyde from the collection of the SNSB-Bavarian State Collection of Zoology in Munich (97 species), from bone preparations from the collections of the Bavarian State Collection of Anthropology and Paleoanatomy in Munich (15 species) and from a µCT scan of *O.* (*Alcolapia*) *grahami*. (2) X-ray images of 1301 formalin-fixed specimens of Pseudocrenilabrine cichlids from all tribes were inspected (Table S2) in order to assess the range of intra- and interspecies variation of two particular characters – the fusion pattern of the hypural plates, and the number of supraneurals. The number of supraneurals was recognizable in all but two of these individuals. The fusion pattern of the hypural plates was discernible in over 90% of the specimens. (3) The number of lateral-line tubules on the lacrimal was surveyed for almost all species of the tribe Oreochromini (59 out of 63, Table S3). The data were compiled from the literature (59 species), and from specimens preserved in alcohol or formaldehyde from the SNSB-Bavarian State Collection of Zoology in Munich (14 species).

Fossil Material—The material from the Yatianin site consists of remains of 23 individuals, here numbered OCO-11-1 to -23. Eleven of these are almost complete, six preserve the head and anterior portions of the body, and in the rest the caudal fin and some posterior portions of the body can be discerned. Eleven slabs were recovered from the site Terenin, which contained isolated or partially articulated bones and one articulated postcranial skeleton (numbers OCO-683-11 to OCO-692-11, OCO-773-11). Furthermore, the holotype of †*Rebekkachromis ngororus* (OCO-3-3a, b), which is the type species of †*Rebekkachromis*, was reexamined. All specimens are currently housed in the Department of Earth and Environmental Sciences at the Ludwig-Maximilians-Universität München, and will be transferred to Kipsaraman, Baringo County, Kenya, when the planned Baringo County Geopark is established.

Methods

Measurements, Meristics, and Osteology—The fossils were measured with digital sliding calipers and measurements were rounded to the nearest 0.1 mm. For each fossil specimen from Yatianin, the relative body proportions were calculated after normalization to standard length (SL). The meristic counts of vertebrae include the terminal centrum; abdominal vertebrae are characterized by the absence of a closed hemal arch. Dorsal and anal fin ray counts included every discernible ray associated with a pterygiophore; because the last two rays of the dorsal and anal fin share one pterygiophore, they were counted as one ray. Circuli were counted on the posterior lateral field of the scale. A dagger symbol (†) denotes extinct taxa. For details on the preparation and optical imaging of fossils see Supplemental Data.

µCT—All slabs bearing fossil fishes were first X-rayed (FaxitronUltraFocus, SNSB-Bavarian State Collection of Zoology, Munich) in order to determine which specimens had the highest contrast between the bones and the surrounding sediment, as well as to identify potential sources of artifacts (e.g., concretions, other bones or skeletons underlying the specimens in question). Six specimens were selected for µCT scanning with a Phoenix Nanotom m (GE Sensing & Inspection Technologies GmbH). Details on the scanning process can be found in Appendices S2 and S3.

Institutional Abbreviations—**OCO**, Orrorin Community Organisation; **SAPM**, Bavarian State Collection of Anthropology and Paleoanatomy, Munich, Germany; **ZSM**, SNSB-Bavarian State Collection of Zoology, Munich, Germany.

RESULTS

Notes on the Morphology of *Oreochromis* (*Alcolapia*)

As mentioned above, our analysis of extant taxa focused on the characters that are also discernible in our fossils. Based on the µCT data for *Oreochromis* (*Alcolapia*) *grahami* (Supplemental Data), the lacrimal (= first infraorbital) is followed by a small second infraorbital (io2) with two openings (Fig. 3A, B). Behind the latter, at the posteroventral corner of the eye, is a long infraorbital (io3) with three to four openings; this is in turn separated from the dermosphenotic (io4) by a small gap (Fig. 3B). The preopercle displays three sensory canal pores on the lower arm and at least two sensory canal pores on the upper branch, including the terminal pore (Fig. 3C). The urohyal has a very small dorsal spine, which is directed anteriorly (Fig. 3D) – not posteriorly as in other species of *Oreochromis* (Fig. 3E). The ventral process of the anguloarticular is perforated by a canal. The hyomandibula has a convex anteroventral flange.

Based on the information obtained from X-ray images and alcohol-preserved specimens of all four species of *Oreochromis* (*Alcolapia*), the orientation of the supraneural bone ranges from

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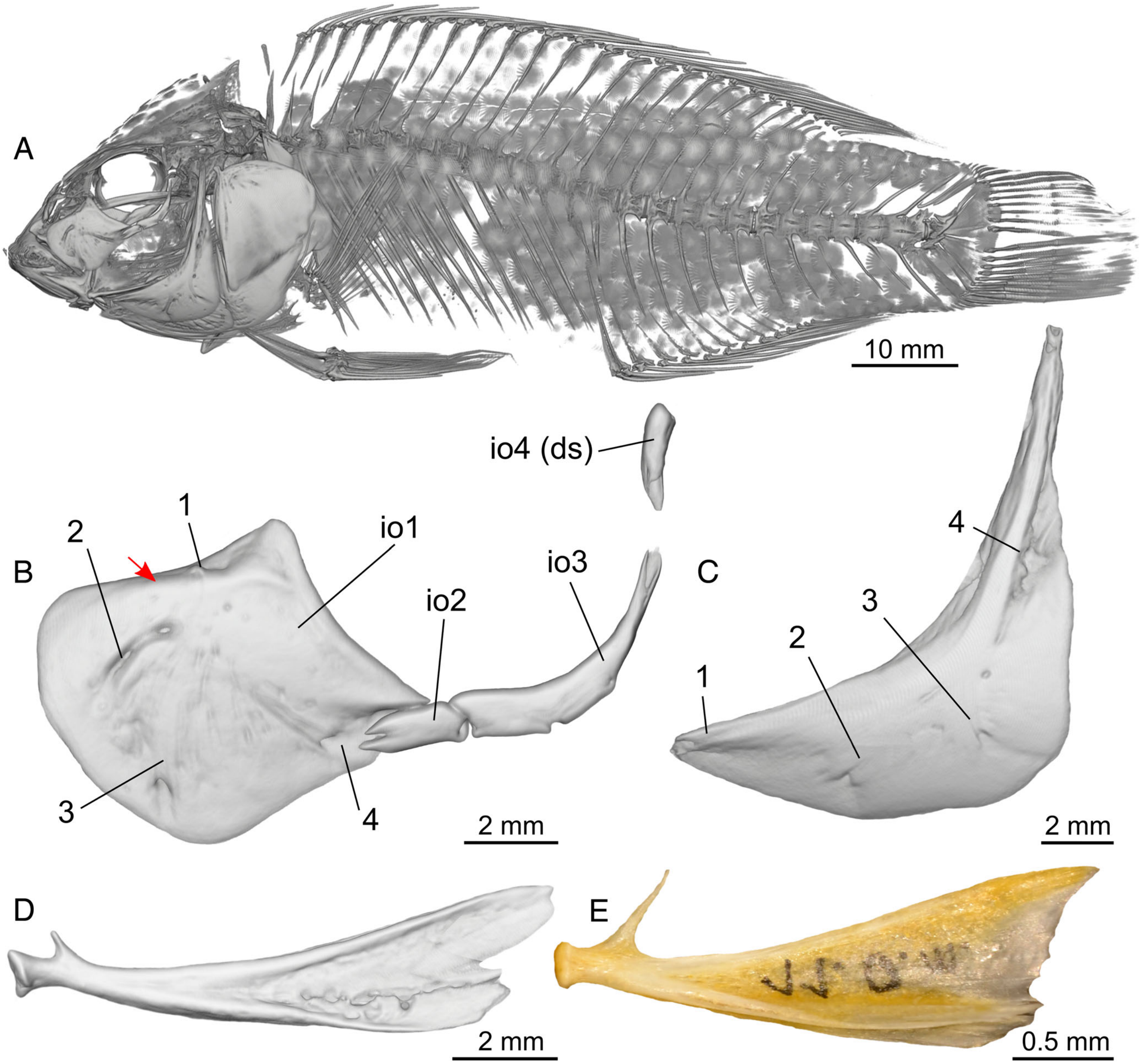

FIGURE 3. **A**–**D**, µCT data volume rendering of *Oreochromis* (*Alcolapia*) *grahami* (ZSM 25618). **A**, whole specimen; **B**, infraorbitals; **C**, preopercle, reversed; **D**, urohyal; **E**, photograph of urohyal of *Oreochromis niloticus* (Linnaeus, 1758) (SAPM 01887). The photograph in **E** was provided by M. Altner. All bones are depicted in lateral view; numbers denote the lateral-line tubules of the lacrimal and the sensory canal pores on the preopercle, the red arrow denotes the anterior ridge. **Abbreviations**: **io**, infraorbital; **ds**, dermosphenotic.

sharply angled relative to the vertical level (with the ventral tip facing anteriorly) to upright (see also Penk et al., 2019). The hypural plates of the caudal skeleton are not fused with the urostyle; the hypurapophysis of the parhypural is well developed. The scales on the throat and belly are minute (see also Penk et al., 2019); the scales on the nape are intermediate in size between the minute scales of the throat and those of the flank; and two longitudinal scale rows appear between the upper lateral line and the dorsal fin (Fig. 3A).

Variation of Selected Characters in Extant African Cichlids

The only criteria that permit one to analyze species diversity in fossil faunas are morphological characters that are known to exhibit low intraspecific variability. Here we have evaluated the taxonomic and systematic utility of four characters that are discernible in our fossils and for which only little information on their variation was available. Based on our comparative dataset of extant cichlid species, their intraspecific and interspecific variation, and their range of variation within a tribe were assessed in order to substantiate their use for taxonomic and systematic purposes. The traits selected for this analysis are: (1) the number of sensory canal pores on the lower arm of the preopercle; (2) the fusion pattern of the hypural plates; (3) the number of supraneural bones; and (4) the number of lateral-line tubules on the lacrimal.

With regards to trait 1, virtually all members of the African subfamily Pseudocrenilabrinae have four sensory canal pores on the lower arm of the preopercle (Stiassny, 1991; Takahashi, 2002; see

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here Fig. 4A, B and Table S1). *Oreochromis* (*Alcolapia*) is the sole extant haplotilapiine taxon that has three sensory canal pores in this position (Fig. 3C), and only one other Pseudocrenilabrine taxon possesses this character, namely the chromidotilapiine *Congochromis* (see Stiassny and Schliewen, 2007; Table S1). Cichlinae have mostly three sensory canal pores on the lower arm of the preopercle (Kullander, 1986, 1998; see here Fig. 4C, D) and the examined Etroplinae and Ptychochrominae have four (Table S1).

As to the fusion pattern of the hypural plates (trait 2), the X-rayed specimens could be classified into four categories (relative frequencies based on our comparative dataset are given in parentheses): all hypurals separated (50.2%), hypurals 1 and 2 fused (2.4%), hypurals 3 and 4 fused (6.3%), hypurals fused in pairs, i.e., 1 and 2, and 3 and 4 fused (41.1%) (Table S2). Fusion between hypurals 2 and 3 may occasionally occur, but was difficult to diagnose from the X-rays and is not considered here. Within a given species, the variability was low, with most specimens falling into a single category; only occasionally were a few individuals assigned to a different category (Table S2). Intratribal diversity was also low, with specimens from a given tribe falling into one or at most two categories (Table S2).

The same set of X-rayed specimens was used to assess the stability of the number of supraneural bones (trait 3; Table S2). Here we focused on species which usually have either one supraneural or none. Only eight species (*Trematocara kufferathi* Poll, 1948, *T. marginatum* Boulenger, 1899, *T. nigrifrons* Boulenger, 1906, *T. stigmaticum* Poll, 1943, *Bathybates fasciatus* Boulenger, 1901, *B. graueri* Steindachner, 1911, *B. vittatus* Boulenger, 1914, *Orthochromis* sp. *"Igamba"*) show any variability in this regard, and the first four of these (for which ten or more specimens were available) have an 'abnormal' number of supraneurals in ⩽10% of cases (Table S2).

The number of lateral-line tubules on the lacrimal (trait 4) was surveyed for almost all (59 out of 63) species of the tribe Oreochromini. Except for the alkaliphile species, all species usually have five lateral-line tubules on the lacrimal; only some specimens of *Oreochromis niloticus* (Linnaeus, 1758) and one of the examined specimens of *Iranocichla hormuzensis* Coad, 1982 have four. *Oreochromis amphimelas*, *O.* (*Alcolapia*) *alcalicus*, and *O.* (*Alcolapia*) *latilabris* have four lateral-line tubules, *O.* (*Alcolapia*) *grahami* has mostly four (exceptionally five) lateral-line tubules (see also Trewavas, 1983; Seegers and Tichy, 1999). The condition in *O.* (*Alcolapia*) *ndalalani* seems to be mixed. According to Seegers and Tichy (1999) there are four lateral-line tubules in this species, but two out of the three examined alcohol-preserved specimens have five lateral-line tubules and in one specimen there is a left/right asymmetry between four and five lateral-line tubules (see Table S3).

SYSTEMATIC PALEONTOLOGY

CICHLIDAE Bonaparte, 1835
PSEUDOCRENILABRINAE Fowler, 1934
OREOCHROMINI Dunz and Schliewen, 2013
†*REBEKKACHROMIS* Kevrekidis, Valtl, and Reichenbacher, 2019

Type Species—†*Rebekkachromis ngororus* Kevrekidis, Valtl, and Reichenbacher, 2019.

Included Species—†*Rebekkachromis ngororus* Kevrekidis, Valtl, and Reichenbacher, 2019; †*R. kiptalami* Kevrekidis, Valtl, and Reichenbacher, 2019; †*R. valyricus* Kevrekidis and Reichenbacher, sp. nov.; †*R. vancouveringae* Kevrekidis and Reichenbacher, sp. nov.

Occurrence—Ngorora Formation (middle–upper Miocene), Tugen Hills, Kenya.

Revised Diagnosis—Distinguished from all other African cichlids by the combination of the following traits: presence of tricuspid and/or unicuspid oral teeth in the inner and outer rows of its dentition, preopercle with six pores (three on the lower and three on the upper branch), slender urohyal lacking an anterodorsal projection, unicuspid to bicuspid pharyngeal dentition, one or two supraneurals, about 30 vertebrae including the urostyle, spines of the dorsal fin increasing in length from the first to the last, anal fin not extending beyond the posterior end of the hypural plates, scales cycloid, scales of the throat, belly, and nape minute relative to the flank scales.

Remarks—†*Rebekkachromis* forms a distinct morphogroup, based on the characters mentioned in its revised diagnosis. Certain characters which were included in the original diagnosis of †*Rebekkachromis* are modified here (i.e., the presence of two supraneural bones) or excluded (the fusion of the hypural plates) to accommodate the new fossil material (Figs. 5–6; Tables 1–2; Tables S6–8). This revision renders †*Rebekkachromis* much more diverse than previously thought.

In the descriptions of the new fossils, we emphasize characters such as the fusion pattern of the hypurals (Vandewalle, 1973), the number of supraneural bones (Kevrekidis et al., 2019), and the number of lateral-line tubules on the lacrimal, the taxonomic and systematic utility of which has previously been demonstrated for cichlids (Trewavas, 1983; Takahashi, 2003a, 2003b; Altner et al., 2017, 2020; Penk et al., 2019), and is supported by the new results presented here (Tables S1, S2). Further taxonomically informative characters that can be recognized in the studied fossils are the shape of the preopercle (Dierickx et al., 2017), the relative depth of the head (e.g., Poll, 1986), the granulation type of the flank scales (Lippitsch, 1990, 1992) and whether the neural and hemal spines of the preural centrum 3 support the procurrent rays (Sebilia and Andreata, 1991).

†*REBEKKACHROMIS VALYRICUS* Kevrekidis and Reichenbacher, sp. nov.
(Figs. 5A, 7A, 8A–B, 9A, 10A)

Holotype and Single Specimen—OCO-11-19a, b.

Etymology—The specific epithet "valyricus" refers to the imaginary city of Valyria from the series of epic fantasy novels by George R. R. Martin "A Song of Ice and Fire." It was located near a chain of volcanic mountains. The presence of dragons and volcanism-related ore deposits allowed Valyria to flourish and dominate its world. Valyria was destroyed by events linked to volcanism and tectonics, resulting in the loss of its unique culture and biodiversity.

Occurrence—The Yatianin site (≈12.1 Ma), uppermost middle Miocene of the Ngorora Formation, Tugen Hills, Kenya.

Diagnosis—Differentiated from all other †*Rebekkachromis* species by partial fusion between hypurals 2 and 3. Differentiated from †*R. vancouveringae*, sp. nov. by lacrimal with four lateral-line tubules (vs. five). Differentiated by rounded slender tip of lower preopercle arm from †*R. ngororus* (vs. rounded wide) and †*R. kiptalami* (vs. pointed slender). Differentiated by two separate supraneurals from †*R. kiptalami* (two fused supraneurals) and †*R. vancouveringae*, sp. nov. (one supraneural). Differentiated by a deeper head from †*R. kiptalami* (33% of SL vs. 26%). Differentiated from †*R. ngororus* by spines of the third preural vertebra that extend to procurrent caudal rays (vs. not) and by possession of granules on posterior field of scale, covering an area of ca. 70° from focus (vs. granules and tubercles in †*R. ngororus*).

Neurocranium—Taking the ventral edge of the parasphenoid as the relative horizontal plane, the ratio of the neurocranial length (basioccipital to vomer) to the neurocranial height (supraoccipital crest to parasphenoid) is ca. 2:1. The supraoccipital crest is straight, low-angled, pointed and posteriorly concave. Anterodorsally, this crest and the frontal are almost on the same plane, and they form an angle of about 30° with the parasphenoid.

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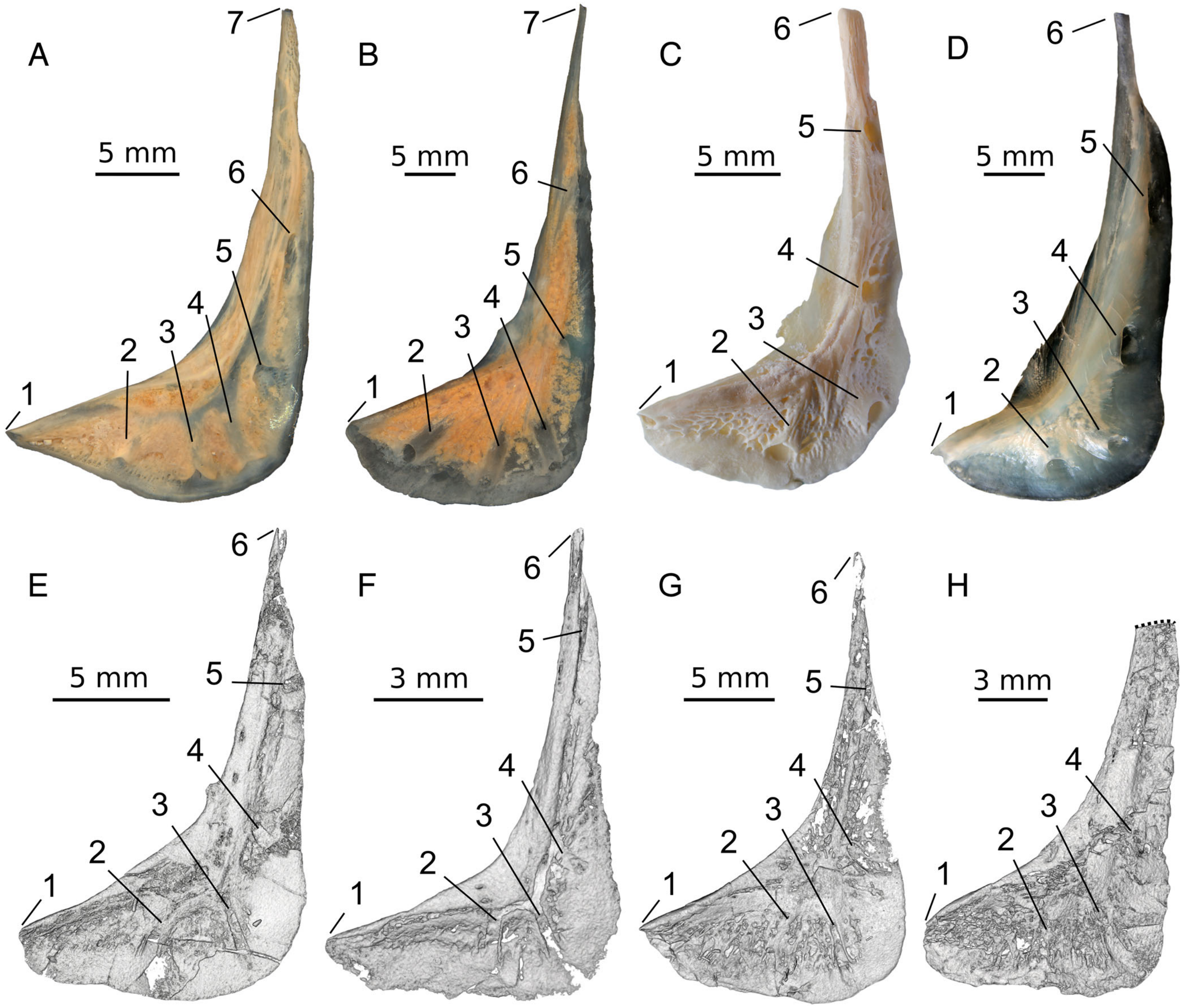

FIGURE 4. Preopercles of cichlids from the right side in lateral view, anterior is to the left. **A**, *Oreochromis andersonii* (Castelnau, 1861), Pseudocrenilabrinae, SAPM-PI-01875; **B**, *Cyphotilapia frontosa* (Boulenger, 1906), Pseudocrenilabrinae, SAPM-PI-02994; **C**, *Cichlasoma* sp., Cichlinae, SAMP-PI-00901; **D**, *Hypselecara temporalis* (Günther, 1862), Cichlinae, SAMP-PI-00904; **E**, †*Rebekkachromis vancouveringae* sp. nov., OCO-11-4; **F**, †*Rebekkachromis* sp., OCO-11-9; **G**, †*Rebekkachromis* sp., OCO-11-20; **H**, †*Rebekkachromis* sp., OCO-11-14. **A**–**D** are prepared bones, **E**–**H** are volume-rendered µCT data. Photographs **A** and **B** were provided by M. Altner. Numbers denote the sensory canal pores of the preopercle, dotted lines denote a fracture and an uncertain outline.

The parietal crest begins approximately at the middle of the orbit, slightly anteriorly to the third neurocranial sensory canal pore. The parasphenoid is straight and slender. The suture between the vomerine shaft and the parasphenoid is straight (Appendix S3). The exoccipital foramen is absent.

Primary Lateral Line Elements—The lacrimal is deeper than wide (ratio = 1.2:1) and has four lateral-line tubules of uniform width (Fig. 7A; Fig. S1C). It is broadly rectangular, with a concave anterior margin, convex ventral and posterior margins, and a straight dorsal margin. The anterodorsal spur of the lacrimal is robust, with a rounded tip. The anteroventral ridge, a structure which does not bear a lateral-line tubule, is prominent (Fig. S1C; for comparison see Fig. S1A, B). Taking the dorsal margin as the relative horizontal level, the first lateral-line tubule of the lacrimal faces anteriorly, the second anteroventrally, the third posteroventrally, and the fourth posterodorsally.

Posteriorly to the lacrimal, at the posteroventral angle of the orbit, is a long infraorbital with a short ventral flange. This bone has three openings, two at the extremities and one in the middle (Fig. 7A), and is followed by a gap (that might have been filled by a bone which is not preserved). The last infraorbital, the dermosphenotic, is tiny (Fig. 7A).

The lateral extrascapular has a robust posterior arm with three foramina on its medial side, which increase in size posteriorly (Fig. 8A, B). Almost at a right angle to the posterior arm there is a shorter, slenderer dorsal branch that does not appear to be open, and a very short anteroventral process (Fig. 8A, B). The nasal (Fig. 7A) has two sensory canal pores and is medially constricted.

Jaws—The body of the premaxilla is curved. The length ratio of the dentigerous arm of the premaxilla to the ascending arm is 1.3:1 and the angle between them is ca. 75° (Fig. 7A). On the

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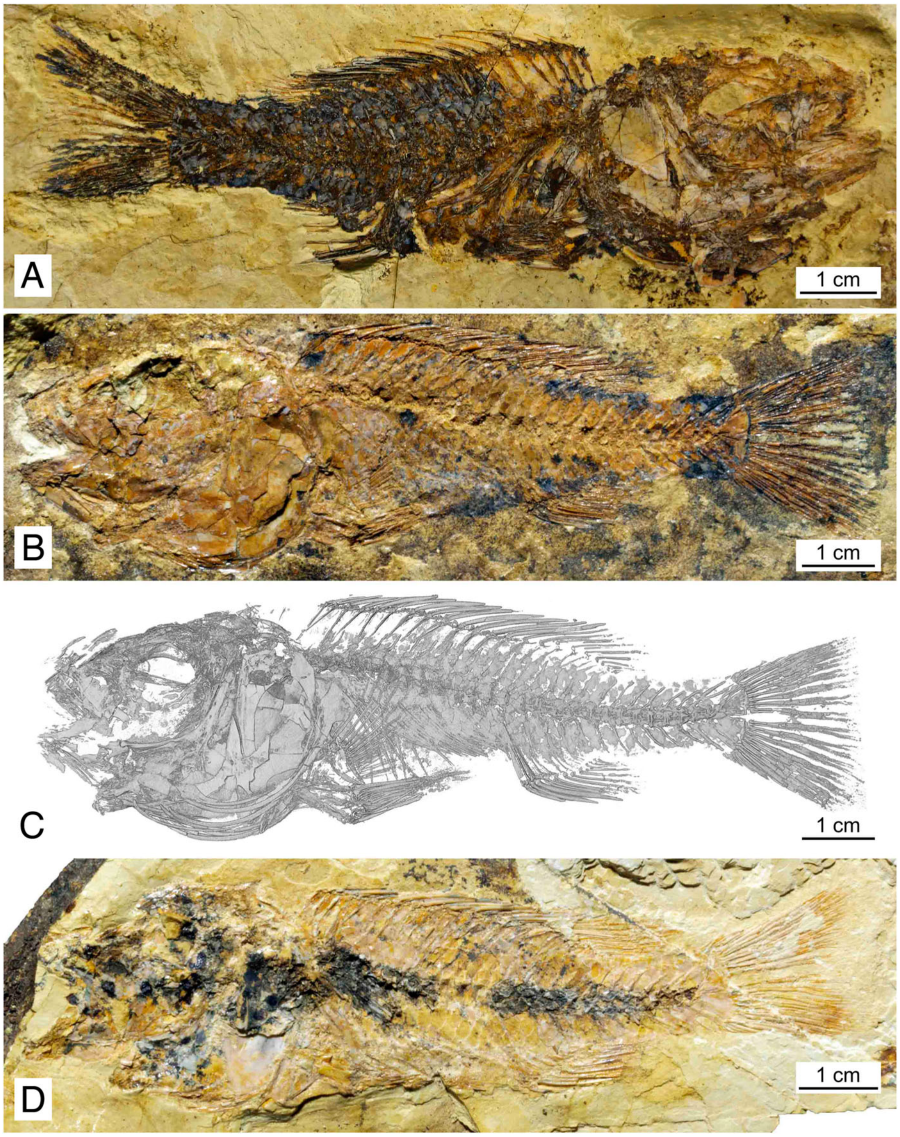

FIGURE 5. Skeletons of fossil cichlids from the Yatianin site. **A**, holotype of †*Rebekkachromis valyricus*, sp. nov., OCO-11-19b, in medial view; **B**, holotype of †*R. vancouveringae*, sp. nov., OCO-11-4b, in medial view; **C**, μCT data volume rendering of B in lateral view; **D**, †*Rebekkachromis* sp., OCO-11-13a, in medial view.

ascending arm there is a well-developed articular process, placed slightly lower than, and well separated from the ascending process. The wing at the dorsal ridge of the maxilla has a 'bell-like' shape. The angle between the anterior and posterior parts of the maxilla is ca. 140°. The dentary has at least four sensory canal pores (Appendix S3). The angle between the dorsal and anterior processes of the anguloarticular is 60°, as is that between the anterior and ventral processes (Fig. 7A). The dorsal process of the anguloarticular is slender and slightly curved. The ventral process forms an elongate parallelogram and is perforated by two sensory canal pores. The process at the posterior end of the articular facet of the anguloarticular is prominent. The retroarticular is almost triangular (Fig. 7A).

On the premaxilla and the dentary there are numerous (more than 30 in all) relatively broad tricuspid teeth of various sizes, distributed over most of the dentigerous arms of these bones (Fig. 9A). For example, on the anterior part of the premaxilla a 'large' tooth with a transverse width of 182 μm appears right next to a tooth that is only 101 μm wide (see Fig. 9A). The two lateral cusps are smaller than the median cusp, and all cusps have rounded tips. The crown of the teeth, and especially the median cusp, is curved lingually. Based on the alveoli of the dentary, there must have been at least two rows of teeth; an outer one with large tricuspid teeth and one or more inner row (s) with smaller tricuspid teeth.

Suspensorium and Opercular Series—The maxillary process of the palatine is flattened dorsoventrally and the mesethmoid process is either lacking or very weakly developed. The posterior and dorsal margins of the palatine form an angle of ca. 120°. The preopercle (height-to-length ratio 1.5:1) has a rounded ventral margin and a rounded but slender tip (see Fig. 7A). There are six sensory canal pores on the preopercle, three on the vertical arm and three on the horizontal (Fig. 7A; Appendix S3). The anterior end of the interopercle is positioned slightly ahead of the anterior end of the preopercle. The symplectic comprises a mediolaterally flattened posterior part and a 'rod-shaped' anterior part, rather like an inverted 'rifle,' and its posteroventral margin is smooth. The quadrate has a straight posteroventral process.

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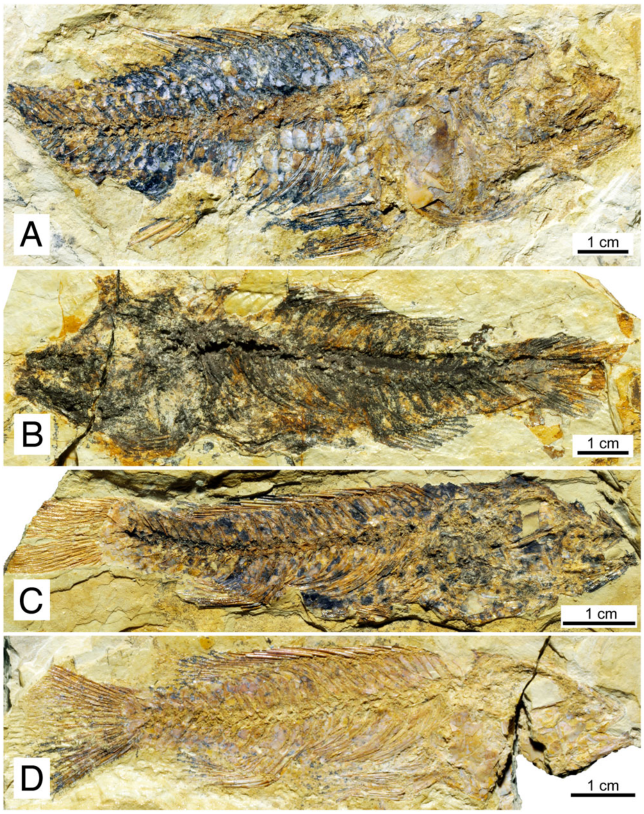

FIGURE 6. Skeletons of fossil cichlids from the Yatianin site, in medial view. **A**, †*Rebekkachromis* sp., OCO-11-20; **B**, †*Rebekkachromis* sp., OCO-11-14b; **C**, †*Rebekkachromis* sp., OCO-11-9b; **D**, †*Rebekkachromis* sp., OCO-11-21.

The hyomandibula (height-to-length ratio 2.6:1) has a robust ventral process and a prominent flange, and is not notched between the anterior and posterior condyles. The metapterygoid is moderately deep and posteriorly has a prominent, right-angled process. The opercle (height-to-length ratio 1.4:1) has a convex dorsal and posterodorsal margin and a concave posteroventral margin; the ventral angle is 53°; the subopercle is broad (Fig. 7A).

Hyoid and Branchial Arches—The anterior part of the urohyal is slender and elongate and lacks a dorsal spine (Fig. 7A). The maximum angle between the dorsal and ventral margins of the urohyal is 20°. The hyoid bar exhibits a medial constriction, but retains a robust neck, after which it expands in both directions, notably more on the ventral side. Five branchiostegal rays can be recognized on each side. A few ceratobranchials, together with their gill filaments, are preserved. The pharyngeal teeth are unicuspid to weakly bicuspid (Fig. 9G). They have one major cusp, which is straight or slightly hooked. In bicuspid teeth, the gap is concave, and the minor cusp is poorly developed.

Vertebral Column—There are at least 28 (estimated 29) vertebrae in total; at least 13 abdominal (estimated 14) and 15 caudal vertebrae. At least 12 pairs of pleural ribs are discernible, the last on the final abdominal vertebra. The prezygapophyses of the first vertebrae are located proximally to the centra. The hemal spines of the first caudal vertebrae are not significantly wider than the rest. There are two, 'wedge-shaped,' supraneurals (Fig. 8A, B). The anterior supraneural has a slightly expanded dorsal tip, whereas the posterior one is shorter and thinner. Both supraneurals are inclined, with the ventral tip pointing anteriorly, forming an angle of ca. 45° relative to the vertical level (Fig. 8A, B). As a result, the ventral tip of the posterior supraneural ends anteriorly to the first neural spine.

Pectoral and Pelvic Girdles and Fins—The angle between the dorsal and ventral processes of the posttemporal is 60°. This bone has three sensory canal pores (Appendix S3) and a low spine on its ventral process (Fig. 8A, B). The posteroventral border of the cleithrum forms a rounded right angle (Fig. 7A). There is no notch ventral to this angle (Fig. 7A) and the ventral process of the bone is pointed. The dorsal postcleithrum is slender, with a thickened anterior margin. The ventral postcleithrum is curved, mediolaterally compressed dorsally, tapers to a point ventrally and does not have an anteriorly directed spine. Parts of the supracleithrum, the scapula and the radials are also visible. The pectoral fin comprises at least 11 rays. The pelvic fin is supported by broad and long basipterygia, their anterior tips extending under the subopercle. Each supports one spine and five rays, which seem to terminate anterior to the origin of the anal fin.

Dorsal and Anal Fins—There are 13 spines and 9 rays of the dorsal fin. These elements are each supported by one pterygiophore, except for the last two rays, which share a pterygiophore. The first pterygiophore of the dorsal fin has no anteriorly directed projection and inserts into the space between the neural spines of vertebrae 1 and 2. The length of the dorsal spines increases from the first to the last. The rays of the dorsal fin do not extend beyond the last vertebra.

The anal fin has three spines and eight rays. Except for the first two spines and the last two rays, which share a single pterygiophore, all other elements are supported by one pterygiophore each. The pterygiophores are directed anteriorly; they are not expanded and one or two pterygiophores are associated with each hemal spine. The first pterygiophore is associated with caudal vertebrae 1 and 2. The anal fin spines increase in length posteriorly. The rays of the anal fin do not extend beyond the last vertebra.

Caudal Endoskeleton and Fin—The caudal fin is subtruncate to emarginate (Fig. 5A). There are 16 (8 upper, 8 lower) principal rays – of which the upper- and lowermost are unbranched – and at least 11 (6 upper, 5 + ? lower) procurrent rays (Fig. 10A). The hemal and neural spines of the preural vertebra 3 are fused with it, and their distal tips support the procurrent rays. The preural vertebra 2 has a neural arch, but there is no neural spine. The hemal spine of the preural vertebra 2 is autogenous, or at most only partially fused with the centrum. The dorsal end of the parhypural lies ventrally to the preural centrum 2 and the urostyle. The parhypural has a well-developed hypurapophysis. The ventral margin of hypural 1 is excavated proximally. The anterior halves of hypurals 2 and 3 are fused, forming a 'U'-shaped junction and a broad diastema posteriorly (Fig. 10A). In contrast, hypurals 4 and 5 are separate bones. The urostyle extends posterodorsally to hypural 5, the latter being 'club-shaped'. There is one autogenous 'L'-shaped uroneural, which begins above the urostyle. Two long epurals are found anterior to it; their ventral ends lie dorsal to the preural centrum 2 and they extend to the upper procurrent rays.

Squamation—All scales are cycloid. On the head region, scales can be securely identified at least on the cheek, as well as on the sub- and interopercles. The rest of the body is covered with scales. Above the vertebral column, posteriorly to the opercle and anteriorly of the urostyle, there is a series of 27 scales. The scales on the nape, and to a lesser extent those on the throat, are smaller than those on the flanks.

The scales on the flank, situated ventrally to the vertebral column and between the pectoral and anal fins, are nearly circular. One of the largest preserved flank scales has 20 circuli on its posterior lateral field (Fig. 11A, B, see Fig. 11A for terminology). Many of these circuli branch at least twice at the anterior lateral field. On the anterior field of the flank scales there are 10 to 12 radii (see Fig. 11C). On the posterior field of the flank scales the circuli break up, first into tubercles and then into small,

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TABLE 1. Meristic counts and morphometric measurements of all species of †*Rebekkachromis* and all specimens of †*R.* sp. from the site Yatianin.

	†*Rebekkachromis ngororus* (n = 1)	†*R. kiptalami* (n = 1)	†*R. valyricus* sp. nov. (n = 1)	†*R. vancouveringae* sp. nov. (n = 1)	†*R.* sp. Yatianin (n = 21)
Total vertebrae (abdominal, caudal)	29? (13?, 16)	30 (14, 16)	29? (14?, 15)	31 (15?, 16)	29–31 (14–16, 15–16)
Dorsal fin formula (spines, rays)	XIII, 10	XIII, 9	XIII, 9	XIII, 9 or 10	XII–XV, 8–11
Anal fin formula (spines, rays)	III, 9	III, 9	III, 8	III, 9	III, 7–10
Pectoral fin rays	10+	15+?	11+	15	15
Pelvic fin rays	I, 5	I, 5	I, 5	I, 5	I, 5
Number of supraneurals	2	2	2	1	1 or 2
Scales, transverse from hypural plates to opercle	29	—	27	—	26?–27?
Standard length (SL, mm)	112.6	85.3	88.2	98.7	70.3–117.5
Total length (%SL)	—	—	121.2	117.7	121.5–122.2
Preanal distance (%SL)	67.9	69.2	68.5	67.4	67.7–73.4
Prepelvic distance (%SL)	40.1	44.4	42.5	43.3	41.4–49.3
Predorsal distance (%SL)	38.4	38	41.2	40.6	38.8–40.7
Head length (%SL)	40.5	37.5	40.6	40.3	36.4–43.6
Horizontal eye diameter (%SL)	9.1	7.5	8.2	10.4	7.8–12.4
Preorbital distance (%SL)	11.8	15.1	16.8	14.6	11.1–17.0
Length of lower oral jaw (%SL)	9.1	7.5	13.8	15.4	13.4–19.3
Head depth (%SL)	35.5	26.0	32.9	34.5	29.2–36.6
Maximum body height at anal fin origin (%SL)	25.1	19.5	25.7	20.0	16.2–26.3
Minimum body height at the level of the caudal peduncle (%SL)	11.5	10.4	12.6	12.0	10.4–13.0
Postdorsal distance (%SL)	17.1	17.7	17.3	19.5	17.0–22.1
Length of caudal peduncle (%SL)	19.4	18.1	22.3	20.9	20.1–25.1
Length of anal fin base (%SL)	13.1	14.9	12.9	11.3	10.8–13.7
Length of dorsal fin base (%SL)	43.1	42.9	42.3	40.8	40.6–44.1
Length of spinous dorsal fin base (%SL)	27.5	28.7	29.5	28.2	28.3–32.3
Length of soft dorsal fin base (%SL)	12.9	15.5	12.4	12.7	11.7–16.5

Data for †*Rebekkachromis ngororus* and †*R. kiptalami* from Kevrekidis et al. (2019). The system of morphometric measurements is according to Kevrekidis et al. (2019). A plus (+) sign indicates certainty that there should be more elements of that feature in the fossil, but are not recognizable due to the incomplete preservation of the specimens. A question mark (?) indicates that the count is an estimate, whenever this is possible. If it is not possible to give an estimate, a question mark follows the plus sign (+ ?). Raw data of measurements are available in Table S6.

irregularly disposed granules (type 2 or 4, see Lippitsch 1990). The area covered by these granules forms a solid angle of ca. 70° from the focus of the scale, which is itself free of such granules (see Fig. 11C). The medial surface of the flank scales bears traces of the circuli and prominent granules, mostly on the central region of the scale (see Fig. 11D). Apart from those on the flank, scales generally bear only uninterrupted circuli.

The scales of the belly are much smaller than those of the flank (= 'minute') and only have circuli, lacking any other ornamentation. The transition from the scales of the flank to those of the belly is quite abrupt. The scales immediately anterior to the anal fin are similar in size to those of the flank. The dorsal and anal fins lack scales, whereas the anterior portions of the rays of the caudal fin possess them. Between two neighboring principal rays, there are two rows of small scales and three to four rows in the diastema.

Rebekkachromis valyricus possesses a bipartite lateral line, separated from each other by two scale rows. All lateral line scales are perforated by canals. The upper lateral line ends between the last abdominal and the first caudal vertebrae. Dorsally to its last scale, there are two more scale rows. Between the anal fin origin and the upper lateral line there are nine to ten scale rows.

†*REBEKKACHROMIS VANCOUVERINGAE* Kevrekidis and Reichenbacher, sp. nov.

(Figs. 4E, 5B, C, 7B, 8C, D, 9C, 10B, 11B)

Holotype—OCO-11-4a, b.

Occurrence—The Yatianin site (≈12.1 Ma), uppermost middle Miocene of the Ngorora Formation, Tugen Hills, Kenya.

Diagnosis—Differentiated from all other †*Rebekkachromis* species based on fusion pattern of hypurals (H1 + 2, H3, H4) and presence of one supraneural (vs. two). Further differentiated from †*R. valyricus*, sp. nov., by lacrimal with five lateral-line tubules (vs. four), by rounded slender anterior tip of lower preopercle arm from †*R. ngororus* (rounded wide) and †*R. kiptalami* (pointed slender), by deeper head from †*R. kiptalami* (34.5% of SL vs. 26%), and from †*R. ngororus* also by spines of the third preural vertebra that extend to procurrent rays (vs. not) and by possession of granules on ca. 70° field from focus (vs. granules and tubercles).

Etymology—Named in honor of the paleontologist Dr. Judith Anne Harris Van Couvering, who performed the first detailed studies of fossil cichlids from the Tugen Hills.

Description—In general the osteology of †*Rebekkachromis vancouveringae* is similar to that of †*R. valyricus.* In the following, we focus on those characters that distinguish this species from †*R. valyricus.*

The vomer (not discernible in †*R. valyricus*), has a rounded rostral tip in dorsal view, and dips ventrally in lateral view. The lacrimal has five lateral-line tubules of uniform width (Fig. S1D). If the dorsal margin is taken as the relative horizontal level, the first lateral-line tubule faces anteriorly, the second anteroventrally, the third posteroventrally, the fourth posteriorly, and the fifth posterodorsally. The rest of the lacrimal and the other infraorbitals resemble those of †*R. valyricus.* However, an 'extra' bone can be discerned in †*R. vancouveringae* (Fig. 7B). This elongate element lies between the long infraorbital with three openings and the dermosphenotic, and has two openings at its extremities and a ventral flange.

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TABLE 2. Comparison between species and selected specimens of †*Rebekkachromis*.

Species/Specimen	Supraneurals	Hypurals	Granulation on scales	100*HD/SL	Preopercle shape	Number of lateral-line tubules on the lacrimal	Spines of the third preural vertebra reaching procurrent rays
†*Rebekkachromis ngororus*	2	H1, H2, H3+4	Granules and tubercles	35,5	Rounded wide	–	no
†*Rebekkachromis kiptalami*	2 (fused)	H1, H2, H3+4	–	26	Pointed slender	–	yes
†*Rebekkachromis valyricus* sp. nov. (OCO-11-19)	2	H1, H2+3, H4	Granules in ca. 70° field	32,9	Rounded slender	4	yes
†*R. vancouveringae* sp. nov. (OCO-11-4)	1	H1+2, H3, H4	Granules in ca. 70° field	34,5	Rounded slender	5	yes
†*R.* sp. (OCO-11-13)	2	All separate	Granules in ca. 70° field	33,8	Rounded slender	4	–
†*R.* sp. (OCO-11-9)	1	H1+2, H3 +4	–	29,2	Rounded slender	4	–
†*R.* sp. (OCO-11-21)	2	H1+2, H3, H4	–	30,2	–	4	–
†*R.* sp. (OCO-11-20)	1	H1+2, H3, H4	Tubercles, 110° field	34,7	Pointed wide	4	–
†*R.* sp. (OCO-11-14)	1	H1+2, H3, H4	–	33,3	Rounded wide	5	yes

The sensory canal pores of the dorsal, posterior, and anteroventral processes of the lateral extrascapular are open; the dorsal process of the lateral extrascapular is longer than the posterior process and equally wide (Fig. 8C, D). The medial extrascapular is short and tube-like (Fig. 8C, D).

Only two sensory canal pores are visible on the dentary and are located on its anterior half. The retroarticular is ornamented laterally with more than two bony ridges, which radiate from the posterior angle of the bone, as in †*R. kiptalami* (Kevrekidis et al. 2019:fig. 5). The premaxilla and the dentary bear numerous broad tricuspid teeth (Fig. 9C), some large (180–196 µm) and some notably smaller (about 100 µm). These teeth resemble those of †*R. valyricus*, but in some teeth at least one of the lateral cusps is more or less fused with the median cusp (Fig. 9C). Furthermore, a few detached conical unicuspid teeth with curved tips were recovered from the dentary (Fig. 9C). Based on the alveoli present on the dentary, there must have been at least two rows of teeth, possibly an outer one with large tricuspid and unicuspid teeth and one or more inner row(s) with smaller tricuspid teeth. The morphology of the pharyngeal teeth ranges from slightly hooked to 'beveled' (sensu Barel 1976). In the latter type, the major cusp has one side straight or slightly inclined, whereas the other side is shallowly incurved.

There is a single wedge-shaped supraneural with a slight spur at its anterodorsal edge (Fig. 8C, D). Bones that were not preserved (or not discernible) in †*R. valyricus*, but are present in †*R. vancouveringae* include small epineurals associated with the first seven vertebrae, and a total number of 15 pectoral fin rays. In the caudal fin skeleton, hypurals 1 and 2 are fused, whereas hypurals 3, 4, and 5 are clearly separated from each other (Fig. 10B). In the head region, scales can be securely identified on the nape, the cheek, the opercle, and the sub-, inter- and preopercle.

†*REBEKKACHROMIS* spp.

For 21 specimens from the site Yatianin, only some of the taxonomically important characters described above are discernible (Table 2, Fig. S2). These specimens reveal a striking variability with respect to the fusion of their hypural plates and oral dentition (amongst others), but overall their skeleton conforms to the general characteristics of †*Rebekkachromis*, as described for †*R. valyricus*. Additions and/or differences from this norm are noted below. The five best-preserved specimens are described separately; they are distinguished from each other and from the nominal species of †*Rebekkachromis* by at least one or two taxonomically important characters (Table S8), but none of them is well preserved enough to justify the introduction of additional new species.

Specimen OCO-11-13—(Figs. 5D, 7C, 9D, 10C, 11C; Fig. S1E). This specimen resembles †*R. valyricus* with regards to the number of supraneurals, the granulation of the scales, the relative head depth, the preopercle shape and the number of lateral-line tubules on the lacrimal. It differs from †*R. valyricus* in having all the hypural plates of the caudal fin separate from each other (vs. hypurals 2 and 3 fused) and because the supraneurals are positioned almost upright (vs. inclined).

The rays of the dorsal fin reach the posterior end of the hypural plates (Fig. 5D). The oral dentition is dominated by shouldered unicuspid teeth, except for two adjacent tricuspid teeth on the anterior tip of the dentary (Fig. 9D). The glossohyal, which was not recognizable in any of the other specimens, is triangular and dorsoventrally flattened (Fig. 7C). The dorsal process of the lateral extrascapula is open. In the head region, at least the cheek and the opercle bear scales.

Specimen OCO-11-9—(Figs. 4F, 6C, 7E, 9B, 10D; Fig. S1H). This specimen resembles †*R. valyricus* with regards to the preopercle shape and the number of lateral-line tubules on the lacrimal. It differs from †*R. valyricus* in having hypural plates 1 and 2, as well as 3 and 4, fused (vs. hypurals 2 + 3 fused) and in possessing one supraneural (vs. two).

The oral dentition of this specimen comprises large and small tricuspid teeth (Fig. 9B). The dorsal process of the lateral extrascapula is open. The rays of the dorsal fin reach the posterior end of the hypural plates (Fig. 6C).

Specimen OCO-11-21—(Figs. 6D, 7F, 9E; Fig. S1I). This specimen resembles †*R. valyricus* with regards to the number of supraneurals and the number of lateral-line tubules on the lacrimal. It differs from †*R. valyricus* in having hypural plates 1 and 2 fused (vs. hypurals 2 + 3 fused).

On both upper and lower jaws, the anterior teeth are predominantly tricuspid, of large and small size (Fig. 9E). Posteriorly, the lateral cusps undergo progressive reduction such that the teeth

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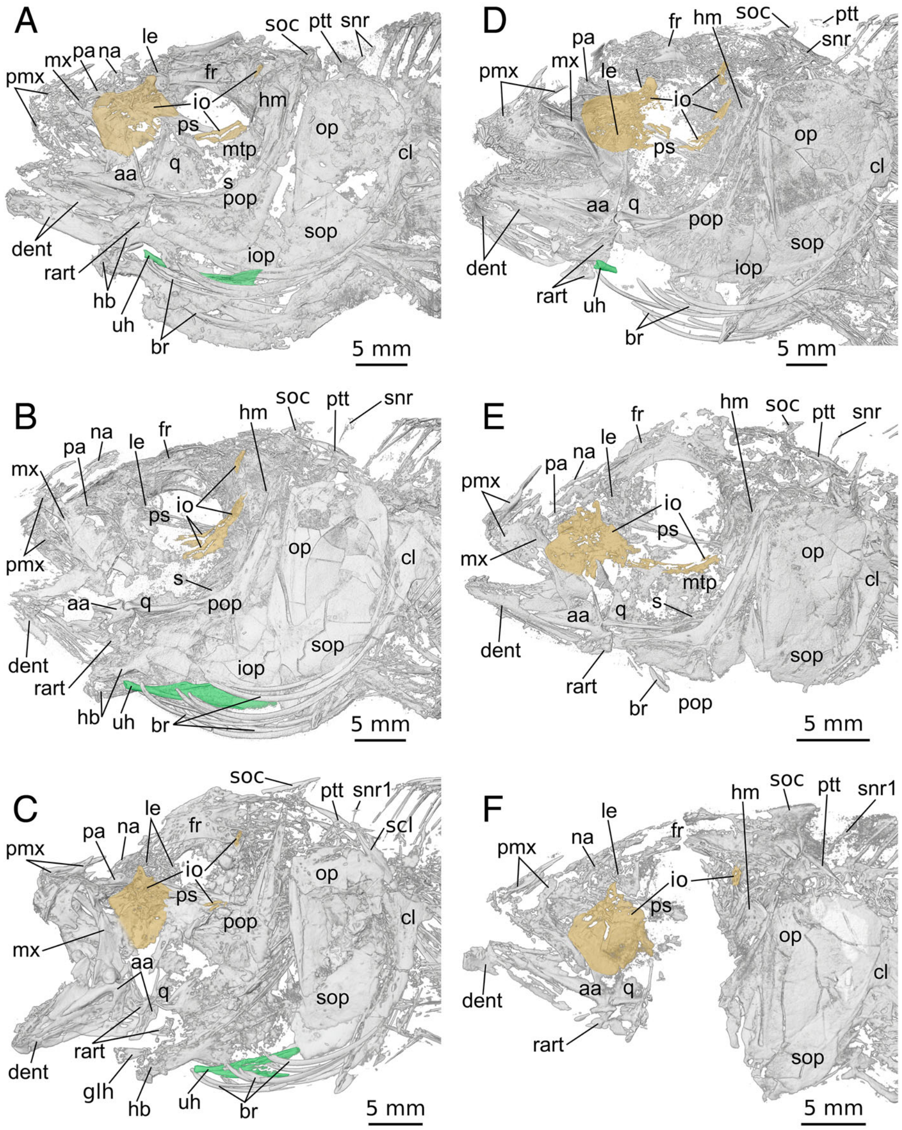

FIGURE 7. µCT data volume renderings of the head region of specimens from the Yatianin site in lateral view. **A**, †*Rebekkachromis valyricus*, sp. nov., OCO-11-19; **B**, †*R. vancouveringae*, sp. nov., OCO-11-4; **C**, †*Rebekkachromis* sp., OCO-11-13, **D**, †*Rebekkachromis* sp., OCO-11-20; **E**, †*Rebekkachromis* sp., OCO-11-9b; **F**, †*Rebekkachromis* sp., OCO-11-21. The infraorbitals are marked in yellow, the urohyal in green. **Abbreviations**: **aa**, anguloarticular; **br**, branchiostegal rays; **cl**, cleithrum; **dent**, dentary; **fr**, frontal; **hb**, hyoid bar; **hm**, hyomandibula; **glh**, glossohyal; **io**, infraorbitals; **iop**, interopercle; **le**, lateral ethmoid; **mtp**, metapterygoid; **mx**, maxilla; **na**, nasal; **op**, opercle; **pa**, palatine; **pmx**, premaxilla; **pop**, preopercle; **ps**, parasphenoid; **ptt**, post-temporal; **q**, quadrate; **rart**, retroarticular; **s**, symplectic; **snr**, supraneural; **soc**, supraoccipital crest; **sop**, subopercle; **uh**, urohyal.

become shouldered unicuspids. The dorsal process of the lateral extrascapula is open. The rays of the dorsal fin do not reach the posterior end of the hypural plates (Fig. 6D).

Specimen OCO-11-20—(Figs. 4G, 6A, 7D, 9F, 11E, F; Fig. S1F). This specimen resembles †*R. vancouveringae* with regards to the number of supraneurals, the granulation of the scales, the fusion pattern of the hypurals, and the relative head depth. It differs from †*R. vancouveringae* in having four lateral-line tubules on the lacrimal (vs. five), a pointed and wide lower arm of the preopercle (vs. rounded slender) and scales with tubercles on a ca. 110° field on the posterior field (vs. granules on a 70° field).

The dentary has at least five sensory canal pores. All teeth are unicuspid, and their tips curve lingually (Fig. 9F). Most are conical and a few are slightly bucco-lingually compressed. The teeth are disarticulated, but judging from the well-preserved alveoli of the premaxilla and the dentary, there is one outer row of large, widely spaced teeth, and two to three inner rows of closely spaced, smaller teeth (Fig. 9F). The dorsal process of the lateral extrascapula is open. In the head region, scales can be securely identified at the nape, the cheek, the opercle, and the subopercle. Small scales are present at least on the chest.

Specimen OCO-11-14—(Figs. 4H, 6B, 9F; Fig. S1G). This specimen resembles †*R. vancouveringae* with regards to the number of supraneurals, the fusion pattern of the hypurals, the relative head depth, the number of lateral-line tubules on the lacrimal and in having the spines of the third preural vertebra reaching the procurrent rays. It differs from †*R. vancouveringae* in having a rounded and wide lower arm of the preopercle (vs. rounded slender).

The oral dentition of this specimen is conical unicuspid and resembles that of OCO-11-20. The dorsal process of the lateral extrascapula is open.

Other Specimens from Yatianin—Sixteen cichlid specimens from Yatianin, which are even more fragmentary than the specimens described above, are depicted in Figure S2. Their squamation resembles that of †*R. valyricus.* All other discernible characters are summarized in Tables S6–S8. All specimens whose dentition is preserved (nine in all) exhibit tricuspid and shouldered unicuspid teeth. The pharyngeal teeth can be distinguished in seven individuals (OCO-11-2, OCO-11-3, OCO-11-10, OCO-11-12, OCO-11-15, OCO-11-18, and OCO-11-23) and they all are uni- to bicuspid. Three specimens clearly exhibit

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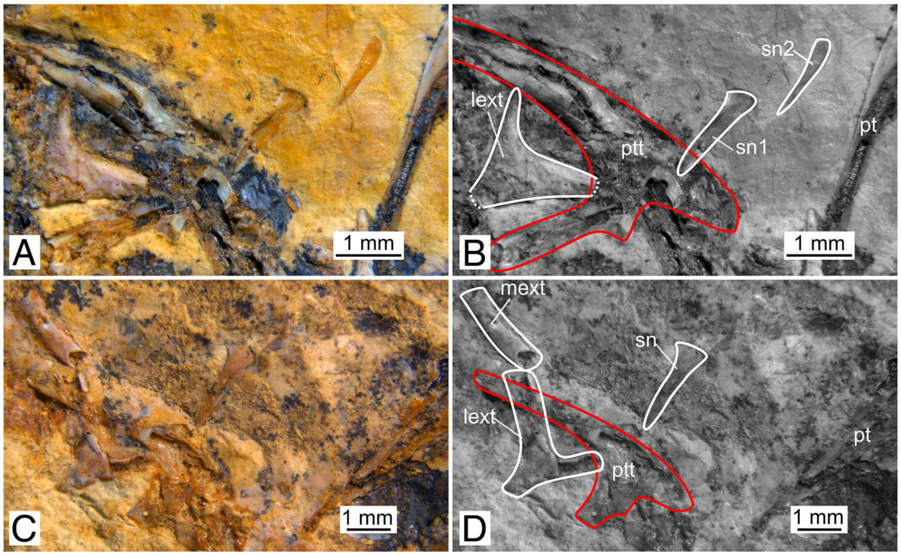

FIGURE 8. The nape of fossil cichlids from the Yatianin site, anterior is to the left. **A**, **B**, †*Rebekkachromis valyricus*, sp. nov., OCO-11-19a; **C**, **D**, †*R. vancouveringae* sp. nov., OCO-11-4b. **Abbreviations**: **lext**, lateral extrascapular; **mext**, medial extrascapular; **pt**, pterygiophore; **ptt**, post-temporal; **sn (1, 2)**, supraneural (first, second).

one supraneural and two others have at least one. In six of the 16, hypurals 1 and 2 are fused, whereas in four others all hypurals are separated. The remaining six specimens lack a caudal fin. The anal fin never extends to the hypural plates. In three specimens the dorsal fin rays reach the hypural plates and in another three specimens this is not the case.

Specimens from Terenin—One partial skeleton and several partially articulated or isolated bones of cichlids, all of which are in excellent condition, were recovered from the Terenin locality (Fig. 12; Fig. S3). No other macrofossils are known from this site. An attempt to differentiate between species was not made, owing to the high incompleteness of the material. On a dentary bone a recurved shouldered unicuspid tooth from the outer row of its dentition is seen (Fig. 12A). Several other teeth are preserved in the alveoli, but their crowns are broken (Fig. 12B). The outer row has wider teeth than the inner series, of which there are two or three. There are five sensory canal pores on the dentary (Fig. 12A). A fifth ceratobranchial (lower pharyngeal jaw) is preserved in excellent detail and is seen from the ventral side (Fig. 12C). No foramina are present, and the suture is straight. The urohyal is slender and has no anterodorsal projection (Fig. 12D). The anterior ceratohyal deepens sharply posteriorly (Fig. 12E). The scales are cycloid and devoid of granulation, and the lateral line is divided (Fig. S3A) The preopercles have three sensory canal pores on the lower arm and three more on the upper arm (Fig. S3B–D). Several caudal fins in various states of preservation were also found. They resemble that of †*R. valyricus* and show variations in hypural fusion patterns (H1 + 2 and/or H3 + 4). Because of the similarity of the cichlids from Terenin to those from Rebekka and Yatianin, the specimens from Terenin are also attributed to †*Rebekkachromis* sp.

†*REBEKKACHROMIS NGORORUS* Kevrekidis, Valtl, and Reichenbacher, 2019

μCT data of the type specimen of †*Rebekkachromis ngororus* (OCO-3-3) (Fig. 13A) from the site Rebekka revealed that the urohyal lacks an anterodorsal projection (Fig. 13B). The scales are similar to those of †*Rebekkachromis* sp. OCO-11-20 (Fig. 13C), but there is also some granulation present near the focus. Based on microscopical observations, the left preopercle has three sensory canal pores on the lower arm (Fig. 13D). The ventralmost sensory canal pore on the upper arm is identifiable.

DISCUSSION

Taxonomy and Systematics

Delimitation of Fossil Cichlid Species—In cichlid paleontology, a conservative approach in delimiting taxa is unavoidable, because modern African cichlids are frequently distinguished based on color patterns or characters that are never or hardly ever fossilized (e.g., Poll, 1986; Trewavas, 1983; Greenwood, 1989; Casciotta and Arratia, 1993). Murray (2000) described five different species from the Eocene of Mahenge, Tanzania, based on differences in the shape and proportions of some bones of the head, e.g., the opercle, the anguloarticular, and the hyomandibula. Such characters have considerable taxonomic potential (Murray and Stewart, 1999; Dierickx et al., 2017), but the fossils described here show a greater degree of homogeneity in these characters. Therefore, our fossils cannot be further distinguished on this basis. Furthermore, in the case of many other characters of known taxonomic value, variation due to factors such as ontogeny and sex must be considered. An abundant set of complete skeletons is needed to justify the use of such characters, which is why we refrain from using them to distinguish additional species from the site Yatianin. In the following, we discuss examples of such characters:

The shape and distribution of the oral teeth (e.g., Trewavas, 1983; Poll, 1986; Takahashi, 2003a) are subject to change throughout ontogeny, and cichlids can change the type of their oral teeth when they are close to sexual maturity (e.g., Trewavas, 1983; Schliewen and Stiassny, 2003). Furthermore, it is known that in older, larger specimens (particularly males) of *Sarotherodon*, *Oreochromis*, and *Oreochromis* (*Alcolapia*) some or all teeth can be unicuspid, as a result of abrasion or replacement (Trewavas, 1983), whereas younger individuals have bicuspid or tricuspid teeth. Among the studied material, the specimens OCO-11-20 and OCO-11-14, which were determined as †*Rebekkachromis* sp., have exclusively conical unicuspid teeth (Fig. 9F; Table 2). They are also slightly larger than the rest and OCO-11-20 has the highest number of circuli on its scales among all studied specimens (Fig. 11B, OCO-11-14 does not have well preserved scales).

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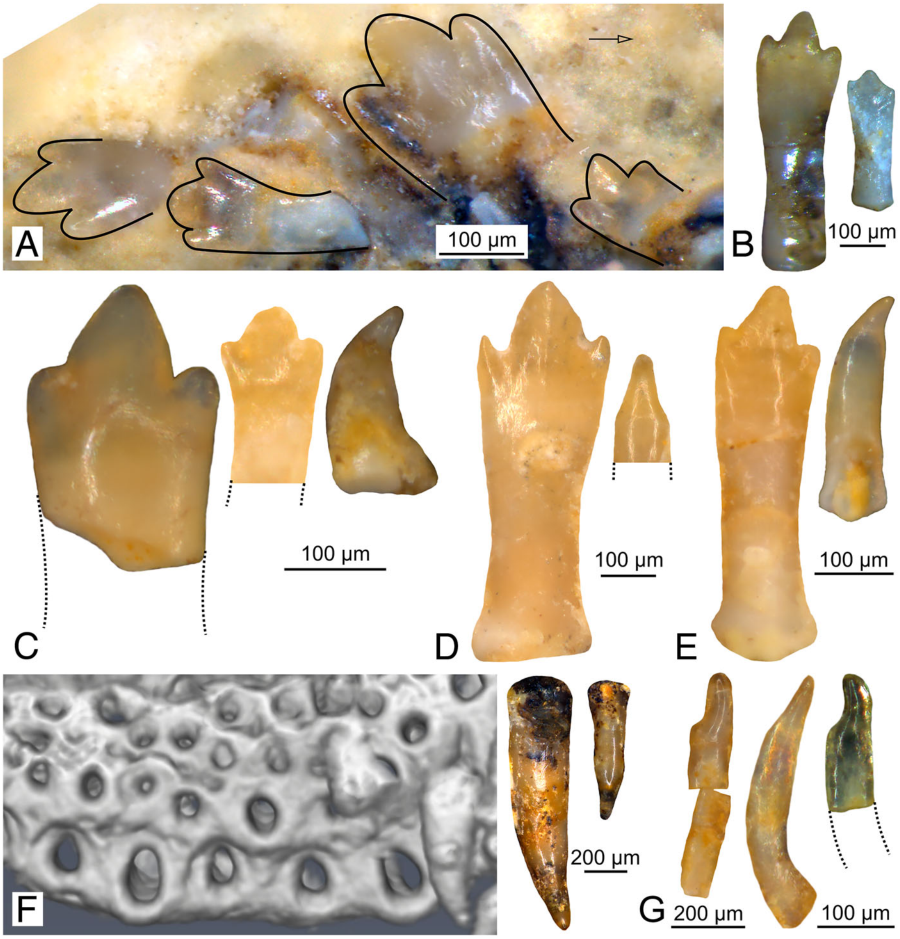

FIGURE 9. Teeth of fossil cichlids from the Yatianin site. **A**, †*Rebekkachromis valyricus*, sp. nov., large and small tricuspid teeth from the anterior tip of the lower oral jaw, OCO-11-19b; the arrow on the right points anteriorly. **B**, †*Rebekkachromis* sp., left: large tricuspid, right: small tricuspid teeth from the anterior tip of the lower oral jaw, OCO-11-9; **C**, †*R. vancouveringae*, sp. nov., left: large tricuspid, middle: small tricuspid, right: recurved conical unicuspid teeth from the anterior tip of the lower oral jaw, OCO-11-4b; **D**, †*Rebekkachromis* sp., left: large tricuspid, right: small, shouldered unicuspid teeth from the anterior tip of the lower oral jaw, OCO-11-13a; **E**, †*Rebekkachromis* sp., left: large tricuspid, right: small, weakly shouldered unicuspid teeth from the anterior tip of the lower oral jaw, OCO-11-21; **F**, †*Rebekkachromis* sp., left: μCT data volume rendering of the alveoli and unicuspid tooth of the anterior part of the premaxilla, OCO-11-20; large conical (middle) and smaller shouldered unicuspid (right) tooth, both from the anterior part of the upper oral jaws, OCO-11-14; **G**, pharyngeal teeth, left: bicuspid, middle: bevelled unicuspid, right: hooked bicuspid. Continuous lines denote definite outlines, dotted lines indicate that the tooth is fractured and its outline is uncertain.

Therefore, the dentition of these two specimens may be a result of their age.

Differences regarding the extension of the rays of the dorsal and anal fins relative to the base of the caudal fin, as noted here, might reflect sexual dimorphism. The posterior tips of the dorsal and anal fins are more pointed and longer in the males of some oreochromine cichlids, e.g., in *Sarotherodon galilaeus* (Linnaeus, 1758), *Oreochromis aureus* (Steindachner, 1864), and *O. mossambicus* (Peters, 1852) (see Chervinski, 1965; Trewavas, 1983; Oliveira and Almada, 1995), which use them against other males during competitive displays (Oliveira and Almada, 1995). Since all the species of †*Rebekkachromis* are represented by one individual each, this character cannot be used here to distinguish between the sexes.

As a result, seven characters were considered here as taxonomically relevant to discriminate among †*Rebekkachromis* (Table 2). However, †*R. valyricus*, †*R. vancouveringae* and each of the five specimens described separately as †*Rebekkachromis* sp. (OCO-11-13, OCO-11-9, OCO-11-21, OCO-11-20, and OCO-11-14) exhibits a different combination of these seven characters (Table 2). As explained above, it appears not appropriate to introduce new species for the †*Rebekkachromis* sp. specimens because of their incomplete preservation. Nevertheless, the number of two species from the Yatianin site should be considered as a minimum and additional well-preserved material from this site might elevate this number.

Systematics of †*Rebekkachromis* at the Level of Tribe—†*Rebekkachromis* has already been established as a haplotilapiine African cichlid, based on the possession of tricuspid teeth in the inner rows of its oral dentition (Kevrekidis et al., 2019). The newly described characters (pertaining e.g., to the urohyal, vomerine-parasphenoid suture and squamation, see 'Systematic Discussion' in Supplemental Data) support the previous assignment of †*Rebekkachromis* up to the level of the lineage of the haplotilapiines.

†*Rebekkachromis* was originally referred to as being "comparable to (cf.) Etiini" in Kevrekidis et al. (2019:56). However, the additional fossil specimens and the μCT data presented enable us to expand the definition †*Rebekkachromis* and to describe an array of previously unknown characters (e.g., six sensory canal pores on the preopercle, small scales on the nape, urohyal lacking an anterodorsal spine). As a result, its systematic placement can now be undertaken with greater confidence. A morphological phylogeny comprising all pseudocrenilabriine lineages recognized today is currently lacking, but the published information on their morphology, combined with the new data presented here, is sufficient to permit systematic inferences.

The number of lateral-line tubules on the lacrimal is an established character for the systematics of cichlids (Trewavas, 1983; Takahashi, 2003a, 2003b). Intraspecific and intrageneric variation of this character, as well as left-right asymmetry, has been previously noted (Greenwood, 1989; Trewavas, 1983; Penk et al., 2019) but seems not to occur regularly. Among the extant haplotilapiines, a lacrimal bone with four lateral-line tubules, as seen in most specimens of †*Rebekkachromis*, is found only in the Cyprichromini, Trematocarini, Lamprologini, Ectodini, Oreochromini,

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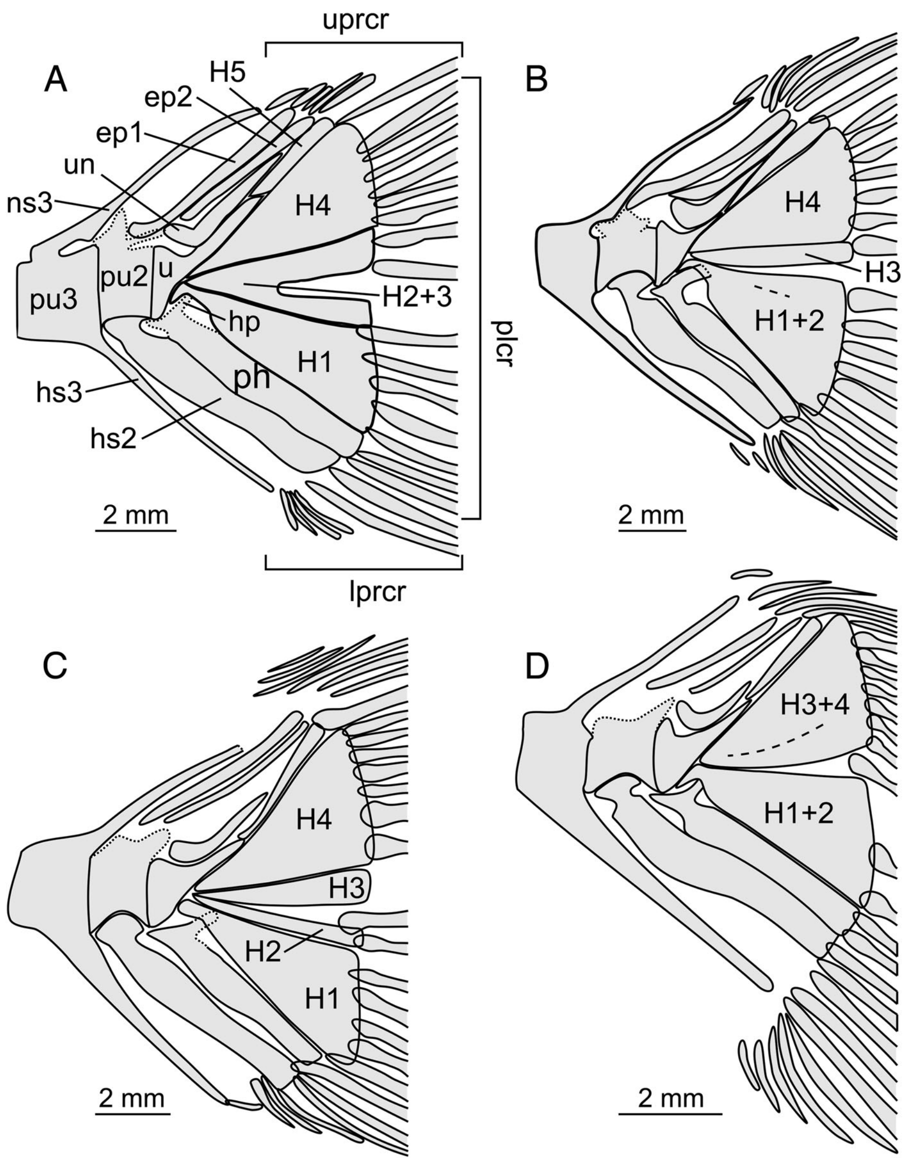

FIGURE 10. Schematic drawings of the caudal fins of fossil cichlids from the Yatianin site. **A**, †*Rebekkachromis valyricus*, sp. nov., OCO-11-19; **B**, †*R. vancouveringae*, sp. nov., OCO-11-4; **C**, †*Rebekkachromis* sp., OCO-11-13; **D**, †*Rebekkachromis* sp., OCO-11-9. Continuous lines denote a definite outline, dotted lines indicate that the outline is uncertain. **Abbreviations**: **ep**, epural; **H**, hypural plates; **hp**, hypurapophysis; **hs**, hemal spine of preural centrum; **lprcr**, lower procurrent caudal rays; **ns3**, neural spine of preural centrum 3; **ph**, parhypural; **plcr**, principal caudal rays; **pu**, preural centrum; **u**, urostyle; **un**, uroneural; **uprcr**, upper procurrent caudal rays.

and in the haplochromine *Pseudocrenilabrus*-group (Takahashi, 2003b; Altner et al., 2017; Penk et al., 2019; Altner et al., 2020). In addition, a lacrimal with four lateral-line tubules has been reported for two extinct cichlid genera from the Miocene of the Tugen Hills, i.e., †*Oreochromimos* (see Penk et al., 2019) and †*Warilochromis* (see Altner et al., 2020), and is also known for a further new cichlid taxon from the same area (Altner and Reichenbacher, 2020). †*Rebekkachromis* is very similar to †*Oreochromimos*, which is why we can refer here to the systematic discussion of Penk et al. (2019) why †*Oreochromimos* can be assigned to the Oreochromini. In addition, some characters only or better discernible in †*Rebekkachromis* (e.g., processes of the anguloarticular), partially through the use of µCT imaging, add further support why †*Rebekkachromis* cannot belong to the following tribes: (1) Cyprichromini: according to Takahashi (2003a) characterized by a forked caudal fin (vs. subtruncate to emarginate in †*Rebekkachromis*) and ctenoid scales at midbody (vs. exclusively cycloid). (2) Trematocarini: according to Poll (1986) characterized by a head which is not covered by scales (vs. covered by scales in †*Rebekkachromis*); expanded cephalic sensory canal pores (see also Takahashi, 2003a) (vs. not expanded); exclusively unicuspid conical teeth (vs. unicuspid and tricuspid); a short upper lateral line, lower lateral line absent (vs. two ordinary lateral lines). According to Stiassny (1981), the dorsal process of the anguloarticular has a laterally expanded posterior border (vs. slender, unexpanded dorsal process). (3) Lamprologini: according to Stiassny (1997) characterized by a notched head of the hyomandibula (vs. not notched in †*Rebekkachromis*); more than three anal fin spines (see also Takahashi, 2003a) (vs. three anal fin spines); fusion between hypurals 3 and 4 and the urostyle (vs. no fusion between hypurals and urostyle, fusion between hypurals 3 and 4 variable); usually unicuspid inner row teeth and large, fang-like canines in the outer row (vs. unicuspid and tricuspid, no canines); a reduction in the number of infraorbitals (vs. at least three to four infraorbitals including the lacrimal); ctenoid scales (see also Lippitsch, 1998; Takahashi, 2003a) (vs. exclusively cycloid); an abrupt change to small scales above the upper lateral line (vs. gradual); a cheek lacking scales (vs. scaled cheek). (4) Ectodini: according to Greenwood (1983) characterized by a palatine whose posterior and dorsal margins

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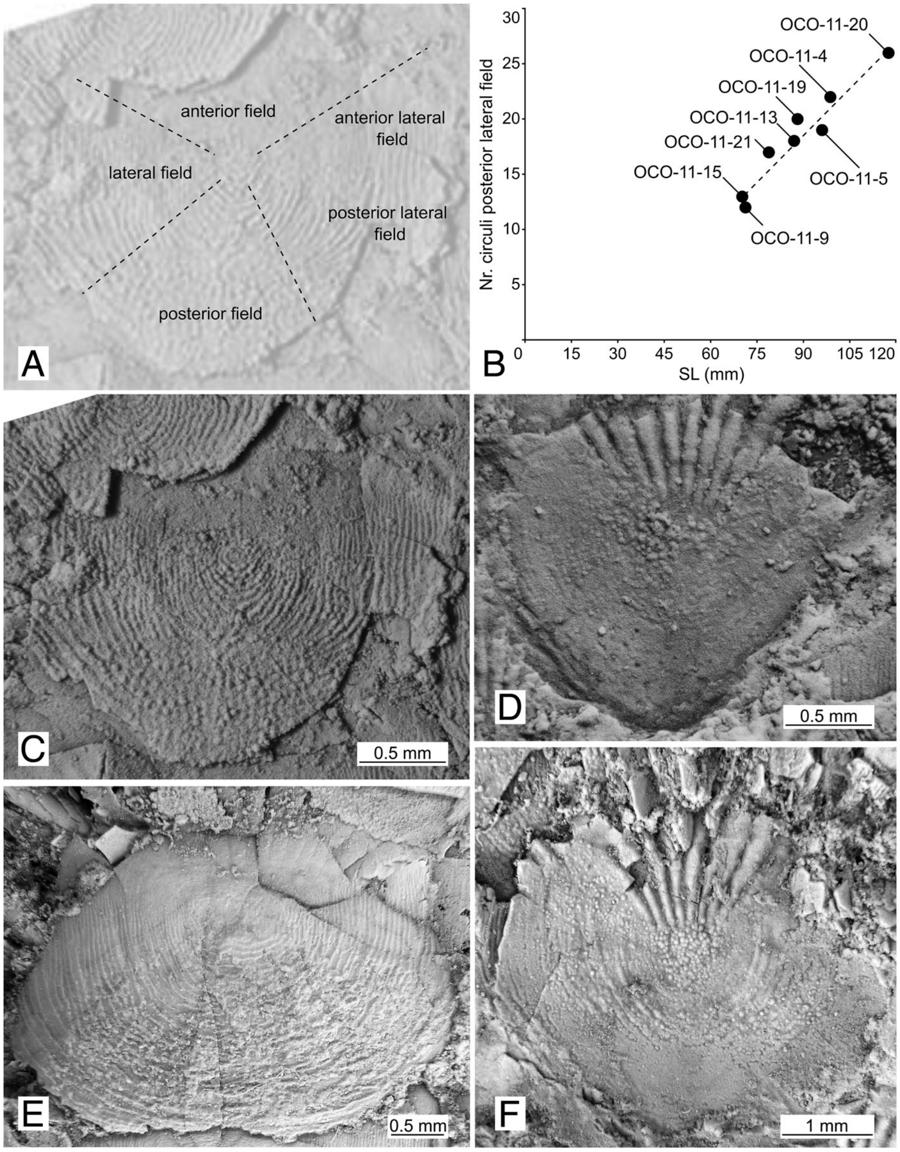

FIGURE 11. Flank scales of fossil cichlids from the Yatianin site, anterior is to the top. **A**, terminology; **B**, scatter plot of the number of circuli on the posterior lateral field relative to standard length (SL); **C**, †*Rebekkachromis* sp., OCO-11-13, lateral view; **D**, †*R. vancouveringae*, sp. nov., OCO-11-4, medial view; **E**, †*Rebekkachromis* sp., OCO-11-20, lateral view; **F**, same individual, medial view. Coated with ammonium chloride.

form a 90° angle (vs. 120° in †*Rebekkachromis*); a distinct process at the posterodorsal corner of the operculum (vs. convex dorsal margin); an elongate lacrimal (see also Takahashi 2003b) (vs. rectangular); the dorsal process of the anguloarticular has a posteriorly expanded border (see also Liem, 1981) (vs. not expanded). Ectodini also possess ctenoid scales (Lippitsch, 1998; Takahashi, 2003a) (vs. exclusively cycloid). (5) The Haplochromini and the Oreochromini are morphologically very diverse tribes and it is not easy to tell them apart exclusively based on hard-part characters (see Takahashi, 2003b; Altner and Reichenbacher, 2020). The Haplochromini however, including those of the *Pseudocrenilabrus*-group, are characterized by the possession of, at least some, ctenoid scales (Greenwood, 1989; Lippitsch, 1993, 1997, 1998).

In conclusion, according to the results of the present study and also taking into account that the probably related †*Oreochromimos* has been classified as a member of the Oreochromini (Penk et al., 2019), †*Rebekkachromis* can be attributed to this tribe as well. The main difference between †*Rebekkachromis* and other members of the Oreochromini is that †*Rebekkachromis* has one or two supraneurals (vs. one), although exceptions may occur (only one of the examined extant Oreochromini specimens had two supraneurals, see Table S2 and Kevrekidis et al., 2019).

Systematics of †*Rebekkachromis* within the Extant Oreochromini—Among the nine extant genera of the Oreochromini, only *Oreochromis*, *O.* (*Alcolapia*), and *Iranocichla* may have four lateral-line tubules on the lacrimal (see Penk et al. 2019:fig. 11). However, as described in the Results, a number of four lateral-line tubules on the lacrimal was regularly found in *O. amphimelas*, *O.* (*Alcolapia*) *alcalicus*, and *O.* (*Alcolapia*) *latilabris*, and mostly also in *O.* (*Alcolapia*) *grahami.* Among the further species, only some specimens of *O. niloticus* and one of the examined specimens of *I. hormuzensis* had four lateral-line tubules on the lacrimal. Penk et al. (2019:fig. 11h) noted a strongly bent and anteriorly convex supraneural of *Iranocichla*, which is very different from the straight or only slightly curved supraneural of *Oreochromis* and †*Rebekkachromis* (Fig. 8). Accordingly, among the extant Oreochromini †*Rebekkachromis* is considered here as probably most closely related to

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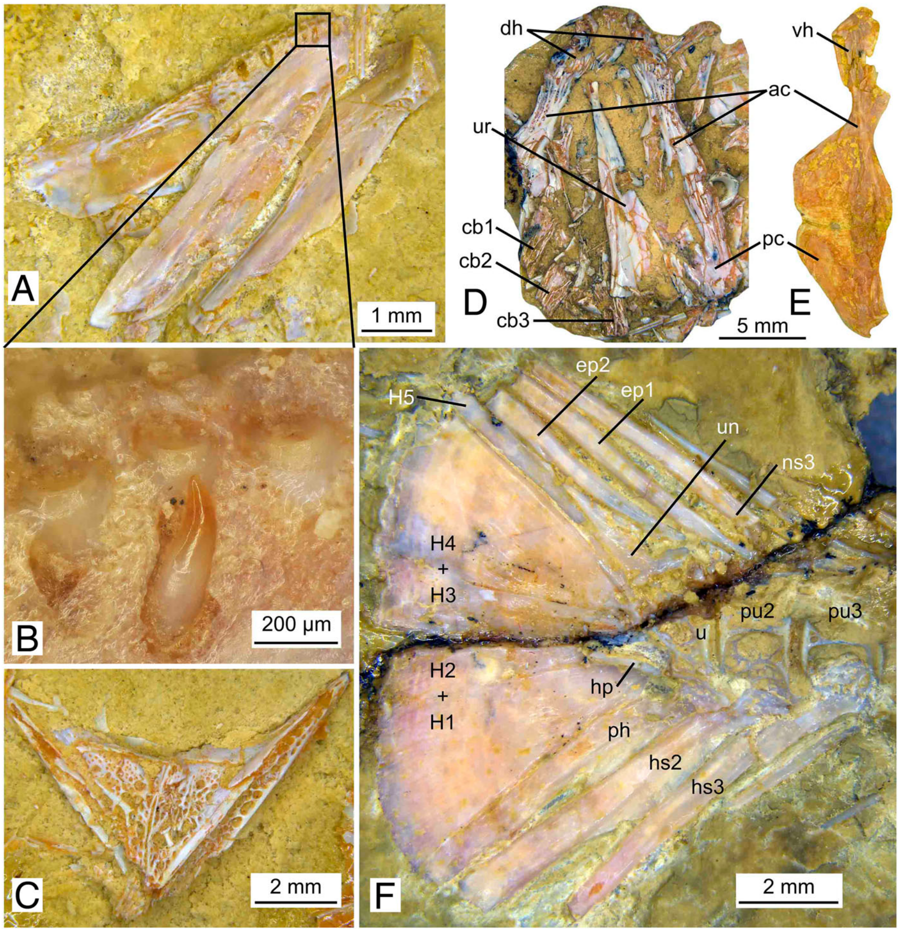

FIGURE 12. Skeletal elements of †*Rebekkachromis* sp. from the Terenin site. **A**, left and right dentary, OCO-688-11; **B**, same individual, complete recurved, shouldered unicuspid tooth, and lingually some teeth with broken crowns; **C**, fifth ceratobranchial (lower pharyngeal jaw), ventral view, OCO-678-11; **D**, bones of the hyoid and branchial complexes, dorsal view, anterior to the top (the urohyal is seen in lateral view, dorsal margin on the left), OCO-691-11; **E**, hyoid bar, OCO-689-11; **F**, caudal fin, OCO-773-11. **Abbreviations**: **ac**, anterior ceratohyal; **cb**, ceratobranchial; **dh**, dorsal hypohyal; **ep**, epural; **H**, hypural plates; **hp**, hypurapophysis; **hs**, hemal spine of preural centrum; **ns3**, neural spine of third preural centrum; **pc**, posterior ceratohyal; **ph**, parhypural; **plcr**, principal caudal rays; **pu**, preural centrum; **u**, urostyle; **un**, uroneural; **ur**, urohyal; **vh**, ventral hypohyal.

O. (*Alcolapia*). This assignment is reinforced by an additional line of evidence: †*Rebekkachromis* possesses three sensory canal pores on the lower arm of the preopercle (Figs. 4E–H, 13D; Fig. S3B–D) and the only other extant haplotilapiine group that possesses this character is *O.* (*Alcolapia*) (see Fig. 3C; Table S1).

Comparison of †*Rebekkachromis* with *Oreochromis* (*Alcolapia*) and Other *Oreochromis*—Apart from the new data presented here on the morphology of the hard parts of *O.* (*Alcolapia*) and other species of *Oreochromis*, data from the literature, particularly Murray and Stewart (1999), is used to further discriminate †*Rebekkachromis.* Murray and Stewart (1999) examined the osteology of five *Oreochromis* species (*O. aureus*, *O. mossambicus*, *O. niloticus*, *O. placidus*, and *O. urolepis*). The molecular phylogeny of Ford et al. (2019:fig. 1), which included the latter four species, suggests that they form a paraphyletic group with regards to *O.* (*Alcolapia*) (Fig. 2). These five species are hereafter referred to as '*Oreochromis* spp.' Though the osteology of other species of *Oreochromis* is not well studied, they are used here for tentative comparisons with †*Rebekkachromis.* They reveal that, in addition to the presence of five lateral-line tubules on the lacrimal (vs. mostly four in †*Rebekkachromis* and *O.* (*Alcolapia*)), and four sensory canal pores on the lower arm of the preopercle (vs. three in †*Rebekkachromis* and *O.* (*Alcolapia*)), the three following characters differentiate both †*Rebekkachromis* and *O.* (*Alcolapia*) *grahami* from *Oreochromis* spp. (sensu Murray and Stewart, 1999): (1) *Oreochromis* spp. has a supraoccipital crest with an enlarged posterior tip in dorsal view (Murray and Stewart, 1999:fig. 2), whereas in †*Rebekkachromis* and *O.* (*Alcolapia*) *grahami* this tip is tapered (Appendix S3);(2) *Oreochromis* spp. has an opercle with a posterodorsal excavation (Murray and Stewart, 1999:fig. 3b), whereas in †*Rebekkachromis* and *O.* (*Alcolapia*) *grahami* this area of the opercle is convex (Figs. 3A, 7); (3) *Oreochromis* spp. has an acute notch at the posteroventral edge of the dorsal plate of the cleithrum (Murray and Stewart, 1999:fig. 3c), whereas in †*Rebekkachromis* and *O.* (*Alcolapia*) *grahami* this notch is absent (Figs. 3A, 7).

In addition, three characters differentiate †*Rebekkachromis* from both *Oreochromis* spp. (sensu Murray and Stewart, 1999) and *O.* (*Alcolapia*) *grahami*: (1) *Oreochromis* spp. and *O.* (*Alcolapia*) have a dorsal process of the posttemporal with a rounded tip in dorsal view (vs. an angled tip in †*Rebekkachromis*) (Murray and Stewart, 1999:fig. 3f; see also this paper Appendix S3); (2) *Oreochromis* spp. and *O.* (*Alcolapia*) have a normative number of one supraneural (vs. one or two in †*Rebekkachromis*, Table S2); (3) *Oreochromis* spp. and *O.* (*Alcolapia*) have a urohyal with a small dorsal spine (vs. no spine in †*Rebekkachromis*, Figs. 3D, E, 7).

Overall, †*Rebekkachromis* is morphologically most similar to *Oreochromis* (*Alcolapia*), but in the absence of a phylogenetic study, the current taxonomic status of †*Rebekkachromis* as a separate genus is retained for now.

Comparison with Previously Described Cichlids from the Tugen Hills—The presence of complete skeletons of cichlid fishes was noted in the original description of the Ngorora Formation (Bishop and Chapman, 1970). The first cichlid from the

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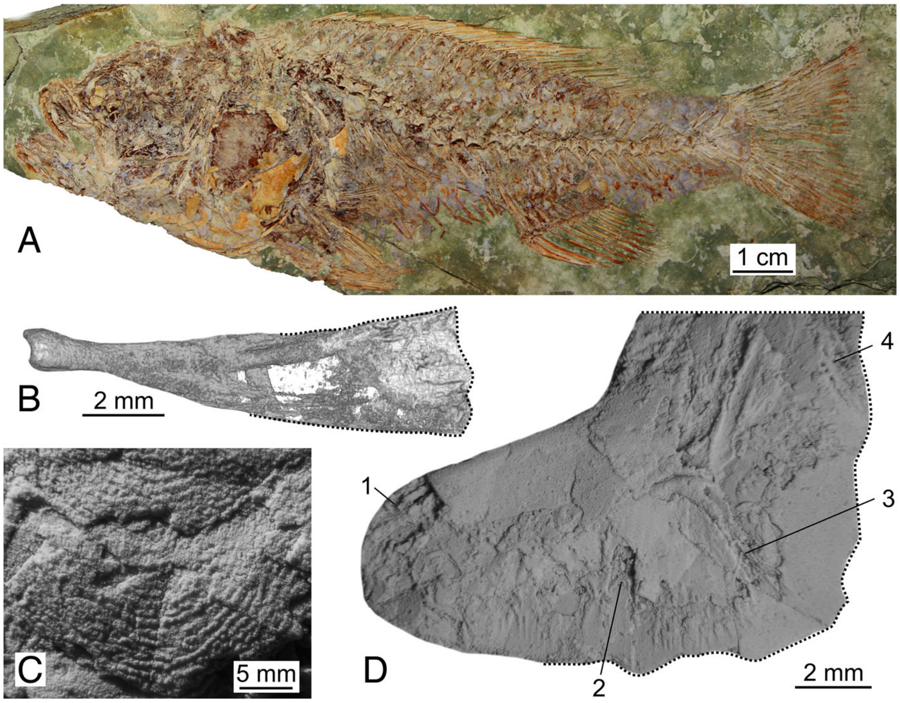

FIGURE 13. †*Rebekkachromis ngororus* from the Rebekka site, OCO-3-3a. **A**, complete skeleton of the holotype; **B**, urohyal, reversed; **C**, imbricate cycloid scales, anterior on top; **D**, preopercle, in lateral view. **C** and **D** are coated with ammonium chloride. Numbers denote the sensory canal pores of the preopercle, dotted lines denote a fracture and the outline is uncertain.

Tugen Hills that was described in detail was introduced as a new species and named "†*Sarotherodon martyni*" (Van Couvering, 1972, 1982). It had been collected from the Kapkiamu shales (≈12 Ma), which represent an equivalent of the Ngorora Formation (see Van Couvering, 1982). Van Couvering (1982) suggested a close affinity of her new species with the members of the "*Alcolapia*" group, *O.* (*Alcolapia*) *grahami*, *O.* (*Alcolapia*) *alcalicus*, and *Oreochromis amphimelas* (at that time all were referred to as *Sarotherodon*, see Introduction). She based this conclusion on the low meristic counts of †"*S.*" *martyni*, particularly with respect to the spines of the dorsal fin, and the presence of minute scales (or absence of scales) on the chest and belly (Van Couvering, 1982). †"*Sarotherodon*" *martyni* might be attributable to the genus *Oreochromis*, because the species of the "*Alcolapia*" group it resembles were transferred to this genus (Murray and Stewart, 1999).

Based on the text and the figures of the original description (Van Couvering, 1982:pl. 8, 9), several similarities between †"*S.*" *martyni* and †*Rebekkachromis* can be noted: the lacrimal is deeper than wide, and followed by some infraorbitals, at least one of which, at the posteroventral angle of the orbit, seems to have more than two openings. The preopercle of †"*S.*" *martyni* is described as having four sensory canal pores, "two of which open directly from the main canal and two by way of side branches" (van Couvering, 1982:84). It is possible that the two terminal sensory canal pores were not included in the count, which would mean that the total number of sensory canal pores might be six, as in †*Rebekkachromis*. However, †"*S.*" *martyni* differs from †*Rebekkachromis* by the possession of a mostly unicuspid dentition. Without a reexamination of the holotype of †"*S.*" *martyni*, which was not possible in the course of this work, it is impossible to conclude whether this taxon corresponds to *Oreochromis*, or to an extinct genus. Therefore we refer to it here as †"*S.*" *martyni*.

More recently, the extinct monotypic genus †*Oreochromimos,* represented by *Om. kabchorensis*, was described from the middle Miocene of the Ngorora Formation (≈12.5) Ma of the Tugen Hills (Penk et al., 2019). †*Oreochromimos* shares several similarities with †*Rebekkachromis* (Table S9), i.e., the lacrimal has four lateral-line tubules, a slender urohyal without an anterodorsal projection, the dorsal process of the anguloarticular is curved, the oral dentition comprises unicuspid and small tricuspid teeth, the meristic counts are similar, there is one supraneural, the head bears scales, the scales of the chest and belly are minute, and the squamation is cycloid (Penk et al., 2019). Penk et al. (2019) concluded that †*Oreochromimos* has a morphology intermediate between *Oreochromis* and "*Alcolapia*," based on meristic counts and squamation, and on osteological characters such as the lacrimal depth, the number of lateral-line tubules on the lacrimal, and the presence/absence of a notch on the cleithrum (see Penk et al., 2019:table 1). An important difference relative to †*Rebekkachromis* is the presence of a single club-shaped supraneural and four sensory canal pores (vs. three) on the lower arm of the preopercle, which is also the condition in *Oreochromis* (Table S9).

It is worth noting that the three studies that have independently examined multiple specimens of fossil cichlids from the Tugen Hills in detail (Van Couvering, 1982; Penk et al., 2019; this study) used different material, character sets, and methods, but all arrive at similar conclusions. These fossil taxa (†*Rebekkachromis*, †*Oreochromimos kabchorensis*, †"*Sarotherodon*" *martyni*) indicate that a diverse fauna of cichlids, distinguishable from, but morphologically similar to *Oreochromis* (*Alcolapia*), were abundant in the paleolakes of the Tugen Hills during the middle Miocene.

Finally, three further extinct cichlid genera are known from the upper Miocene site Waril (10–9 Ma), i.e., the monotypic genera †*Tugenchromis* Altner, Schliewen, Penk, and Reichenbacher, 2017 and †*Warilochromis* Altner, Ruthensteiner, and Reichenbacher, 2020, as well as †*Baringochromis* Alter and Reichenbacher, 2020 that is represented with three species (Altner and Reichenbacher, 2020). †*Tugenchromis pickfordi* was described based on a

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single specimen and has been proposed to be a member of the 'East African Radiation' clade; it has a tripartite lateral line and six lateral-line tubules on its lacrimal (Altner et al., 2017). It is thus clearly different from †*Rebekkachromis*. The single species of †*Warilochromis*, *W. unicuspidatus*, has been assigned to the tribe Haplochromini; it is clearly distinct from †*Rebekkachromis* because of its fang-like dentition and the high number of vertebrae (33) (amongst others; see Altner et al., 2020). The three species of †*Baringochromis* differ from †*Rebekkachromis* in the number of supraneurals (0–1 vs. 1–2), because the lacrimal is followed by five tubular infraorbitals (vs. probably not more than three), and because none of its tubular infraorbitals has more than two openings (vs. three) (amongst others; Altner and Reichenbacher, 2020).

Comparison with other Pseudocrenilabrinae Fossil Species—A comparison of †*Rebekkachromis* with other Pseudocrenilabrinae fossils was given by Kevrekidis et al. (2019). Where possible, this comparison is extended here in the light of the revised diagnosis of †*Rebekkachromis*.

The earliest cichlid found so far in Africa is the middle Eocene (ca. 46 Ma) †*Mahengechromis* Murray, 2000, from Tanzania (Murray, 2000). In addition to the differences described in Kevrekidis et al. (2019), †*Mahengechromis* is clearly distinct from †*Rebekkachromis* because its supraoccipital crest is high (vs. low), the urohyal bears a dorsal spine (vs. absent), and the preopercle has seven sensory canal pores (vs. six) (see Murray, 2000, 2001).

An early fossil member of the Pseudocrenilabrinae from the lower Oligocene (ca. 32 Ma) of eastern Europe (Bulgaria) is †*Rhodopotilapia gracialis* Kirilova and Georgiev, 2015. This species has two supraneurals, unicuspid pharyngeal teeth and cycloid scales (Kirilova and Georgiev, 2015). The head is not well preserved, but it differs from †*Rebekkachromis* in having a larger number of dorsal fin rays (16 vs. 8–11 in †*Rebekkachromis*), and a slightly lower number of vertebrae (27 vs. 29–31) (Kirilova and Georgiev, 2015).

†*Macfadyena dabanensis* Van Couvering, 1982, from the Oligocene Daban Beds in Somalia is differentiated from †*Rebekkachromis* by its high supraoccipital crest and its bicuspid to tricuspid pharyngeal teeth, in addition to the differences already stated in Kevrekidis et al. (2019).

†*Palaeofulu kuluensis* Van Couvering, 1982, from the Miocene Kulu Formation in Kenya (17–15 Ma) is similar to †*Rebekkachromis* in terms of meristics and squamation, but its oral teeth are unicuspid and 'leaf-shaped' (see Kevrekidis et al., 2019). In addition, its urohyal bears a prominent dorsal process (vs. absent) and the preopercle has four sensory canal pores on its lower arm (vs. three) (see Van Couvering, 1982:plates 5, 6; fig. 23).

The Seybouse Gypsiferous Marls of the late Miocene (>7 Ma) of Algeria have yielded two species assigned to the genus †*Palaeochromis* Sauvage, 1907 (Sauvage, 1907, 1910; Van Couvering, 1982), which have a dentition which differs from that seen in †*Rebekkachromis* (see Kevrekidis et al., 2019). Furthermore, †*Palaeochromis* differs from †*Rebekkachromis* in having a smaller number of vertebrae (25 or 26 vs. 29–31) and a larger number of dorsal fin rays (9–16 vs. 8–11) (Sauvage, 1910; Van Couvering, 1982).

Finally, †*Oreochromis lorenzoi* Carnevale, Sorbini and Landini, 2003 from the upper Miocene (≈6 Ma) of the Gessoso-Solfifera Formation, Italy (Carnevale et al., 2003) and †*O. harrisae* Murray and Stewart, 1999 from the lower Pliocene of Ethiopia (Murray and Stewart, 1999) are distinguished from †*Rebekkachromis* based on the presence of an acute notch on their cleithrum (vs. no notch) and the possession of bicuspid teeth (vs. unicuspid and tricuspid). Furthermore, †*O. lorenzoi* has four anal fin spines (vs. three) and four sensory canal pores on the lower arm of its preopercle (vs. three) (see Carnevale et al., 2003).

†*Rebekkachromis* and its Paleoenvironment

In this section we provide some background information about the characteristics of alkaline lakes and discuss the abiotic and biotic environment in which †*Rebekkachromis* lived.

Geochemistry of Alkaline Lakes—Saline-alkaline (soda) lakes are found today on every continent except Antarctica, but they are particularly numerous in East Africa, especially in the eastern branch of the East African Rift System (EARS) (Grant and Sorokin, 2011; Grant and Jones, 2016; Fazi et al., 2018) (see Fig. 1). There, tectonism has created several endorheic basins, from which water is lost mostly through evaporation (e.g., Schagerl and Renaut, 2016). Evaporation may increase the salinity of a lake, but volcanic activity, past or present, is crucial for enhanced alkalinity (Pecoraino et al., 2015). The weathering of volcanic rocks results in waters that are rich in sodium (Na^+) and bicarbonate and carbonate ions (HCO_3^-, CO_3^{2-}), and is responsible for the alkalinity of several lakes along the present-day eastern branch of the EARS (e.g., Pecoraino et al., 2015; Schagerl and Renaut, 2016; Fazi et al., 2018).

Analcime ($NaAlSi_2O_6{\cdot}H_2O$) is a silicate mineral that forms under highly alkaline conditions (Hay, 1966; Surdam and Sheppard, 1978) and thus can be used as an indicator of soda conditions when found in paleolake sediments (e.g., van Couvering, 1982; Rasmussen et al., 2017). Volcanism in the central portion of the Kenya rift, where the Tugen Hills are located, began ca. 17–15 Ma ago (e.g., Hill, 2002; Macgregor, 2015). Analcime is part of the clay mineral fraction in several beds of the middle to late Miocene (13.3–9 Ma) Ngorora Formation (Van Couvering, 1982; Renaut et al., 1999; Rasmussen et al., 2017), as well as in the underlying Tambach Formation (16–14 Ma, Renaut et al., 1999). This confirms previous conclusions that the paleolakes of the Tugen Hills, in which the sediments of the Ngorora Formation were deposited, must have been highly alkaline (see Bishop and Pickford, 1975; van Couvering, 1982; Renaut et al., 1999; Rasmussen et al., 2017).

Remarks on Taphonomy—The exceptional preservation of the fish found in the Tugen Hills might be attributable to anoxic conditions at the bottom of a lake (Rasmussen et al., 2017). In modern soda lakes, anoxia can be induced by chemical or thermal stratification (Melack and MacIntyre, 2016). Soda conditions might also promote fossilization by slowing down the decomposition of a fish carcass by bacteria (Gäb et al., 2020). In general, excellent preservation is an indicator that fish specimens were fossilized in situ and have not been transported over a long distance after death.

Accompanying Flora and Fauna—The goal of this section is to demonstrate that the taphocoenoses in which †*Rebekkachromis* is found are congruent with those of soda lakes, rather than freshwater lakes. Despite being considered extreme environments, soda lakes are among the most productive aquatic ecosystems on Earth (Oduor and Schagerl, 2007). Most primary production is due to alkaliphilic or alkali-tolerant cyanobacteria and eukaryotic algae, which are very abundant and diverse (Grant and Jones, 2016; Krienitz and Schagerl, 2016), unlike vascular plants (Kipkemboi, 2016). Although this microflora is a rich food source for consumers, only a few groups of zooplankton, macroinvertebrates, and vertebrates are adapted to tolerate highly alkaline conditions (Kavembe et al., 2016; Mengistou, 2016; Yasindi and Taylor, 2016). Lakes with low alkalinity and salinity, e.g., Lake Turkana, may host a more diverse macroflora and fauna (Kavembe et al., 2016; Kipkemboi, 2016) than the depauperate macrodiversity that is typical of lakes with more extreme conditions, e.g., Lakes Natron and Magadi (Melack, 1996). The only vertebrates known to inhabit the latter two are extremophile cichlids of *Oreochromis* (*Alcolapia*), as well as the lesser flamingo (Kavembe et al., 2016; Krienitz et al., 2016).

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The above-mentioned characteristics of modern soda lakes, particularly the most extreme ones, correspond well with the faunistic composition of the fossil sites of the Ngorora Formation. No macrofossils of plants or animals, apart from cichlids, have been recovered from Yatianin, Rebekka, Kabchore (Rasmussen et al., 2017), or Terenin. The absence of evidence for the existence of other macroorganisms is not necessarily evidence of absence, but the favorable conditions for fossilization in these sites and the autochthonous nature of the cichlid fauna indicate that it would be reasonable to expect a more diverse accompanying fauna, if one had existed there at that time. Therefore, the apparent in situ preservation of these fossils indicates a very impoverished macrofauna.

Fossil cichlids that are very different from *O.* (*Alcolapia*) and the Oreochromini have been described from the upper Miocene part of the Ngorora Formation (Altner et al., 2017, 2020), and fossils of a wider range of aquatic invertebrates and vertebrates, such as freshwater crabs, gastropods and bivalves, catfish, aquatic turtles, and crocodiles have also been reported (Bishop and Chapman, 1970; Bishop and Pickford, 1975). These localities may represent periods of permanent or seasonal high lake-water levels. The salinity and alkalinity of modern soda lakes recede when their volume increases, e.g., due to a wetter climate, making them habitable for a wider range of organisms (Oduor and Kotut, 2016). †*Rebekkachromis* might still have been able to survive in more moderate conditions because experiments show that *O.* (*Alcolapia*) can be conditioned to tolerate them (Wood et al., 2002).

Consequently, the absence of accompanying flora and fauna from the sites in which †*Rebekkachromis* has been found is wholly compatible with what is known from modern soda lakes. Therefore, stable soda conditions are likely to have been in place long before the death of these fish. Moreover, it appears more plausible that a disruption of the prevailing conditions in a soda lake (e.g., acidification brought about by ash falls from volcanic eruptions; see Rasmussen et al., 2017), rather than the induction of soda conditions, should have caused mass die-offs of fishes.

Alkaline Environment and Fish Size—Some morphological features of *O.* (*Alcolapia*) have been proposed to be related to the particular conditions of soda lakes. The 'small' size (80–100 mm) of fossil cichlids from the Tugen Hills has been suggested as a proxy for the alkalinity of the paleolakes (Bishop and Chapman, 1970; Bishop and Pickford, 1975). However, Trewavas (1983) rejected the notion that the small size of *O.* (*Alcolapia*) (SL≈ 40–80 mm, Trewavas, 1983, Seegers and Tichy, 1999) could be the result of the soda condition itself. Although there is no doubt that the size of *O.* (*Alcolapia*) is controlled largely by environmental factors, alkalinity and salinity are only two among several such factors. For example, when *A. grahami* was introduced into the soda Lake Nakuru in the 1950s and 1960s, it very quickly reached sizes up to twice those observed in its native Lake Magadi, although these two lakes have a similar pH value of about 10 (Vareschi, 1979; Trewavas, 1983). Hence, this marked change in size argues that alkalinity alone cannot determine size; other factors, e.g., temperature, or also the size of the lake, must be at work (Trewavas, 1983). Reduced predation has also been hypothesized to account for the growth of *A. grahami* to larger sizes (Maina et al., 2019). Therefore, the size alone of the fish inhabiting a paleolake cannot be regarded as a proxy for the alkalinity of the water.

This is additionally corroborated by fossil cichlids, possibly comparable to *Oreochromis* or *O.* (*Alcolapia*) *grahami*, which have been reported from the area around Lake Magadi. They have an early Holocene age, a time when the extreme soda conditions of today were not yet in place (White, 1953; Butzer et al., 1972; Whitehead, in Trewavas, 1983; Tichy and Seegers, 1999). These fossil cichlids were reported to reach greater sizes than modern *O.* (*Alcolapia*) (ca. 100 mm SL, Whitehead, in Trewavas, 1983:384; Tichy and Seegers, 1999) and this size is comparable to that of many cichlids from the soda paleolakes of Tugen Hills.

Alkaline Environment and Dentition—Species of *O.* (*Alcolapia*) are predominantly herbivorous and it seems that the depauperate macrodiversity of soda lakes prevents the evolution of other trophic adaptations (Ford et al., 2016). On the other hand, species of *O.* (*Alcolapia*) display an oral dentition (Tichy and Seegers, 1999) which is very different from that observed in some specialized feeders e.g., insectivorous cichlids (Fryer and Iles, 1972), but is reminiscent of the variable oral dentition of †*Rebekkachromis* (completely tricuspid, unicuspid, or mixed). On the other hand, there is little diversity in the pharyngeal teeth and jaw of *O.* (*Alcolapia*), presumably because once acquired, their food is of similar size and consistency and no further specialization is needed (Tichy and Seegers, 1999; Ford et al., 2016). Their pharyngeal teeth are 'kukri' unicuspid to hooked bicuspid (Tichy and Seegers, 1999; Seegers and Tichy, 1999) and †*Rebekkachromis* has a similar pharyngeal dentition. The lack of large flat molariform pharyngeal teeth that are more suitable for prey such as gastropods (Fryer and Iles, 1972) may be another indicator of the absence of such organisms from the soda paleolakes of the Ngorora Formation.

A Nascent Species Flock?

The propensity of cichlids to form species flocks, especially in lakes, has been studied extensively (e.g., Greenwood, 1984; Salzburger and Meyer, 2004), with the most iconic examples of cichlid species flocks being those of the Haplochromini of the Lakes Malawi and Victoria, with hundreds of species each. Members of the Oreochromini have also formed species flocks, especially in smaller lakes, e.g., the cichlids of the crater Lake Barombi Bo (Schliewen et al., 1994; Schliewen and Klee, 2004), or the modern alkaliphile cichlids of Lake Natron and Lake Magadi (e.g., Trewavas, 1983; Tichy and Seegers, 1999; Ford et al., 2015).

Lecointre et al. (2013) summarized the work of Ribbink (1984), Greenwood (1984) and Eastman and McCune (2000) and proposed five criteria to detect species flocks. The first three criteria (species diversity, endemicity, monophyly) were considered core characteristics of a species flock, whereas the other two criteria (habitat dominance in terms of biomass; ecological diversity) characterize a 'full flock' (Lecointre et al., 2013). Below, these criteria are considered for the cichlids from the Yatianin site.

Species Diversity—There are at least two †*Rebekkachromis* species known from Yatianin, and the discovery of more complete material would possibly allow the description of additional species. The presence of individuals which are similar but not identical to the named species indicates that the criterion about species diversity is at least partially satisfied.

Endemicity—†*Rebekkachromis* seems to be endemic for the middle to late Miocene of the Tugen Hills; however, the absence of sediments of the same age from other areas needs to be considered.

Monophyly—Species of †*Rebekkachromis* share a unique combination of features which are not usual among haplotilapiines (preopercle with three sensory canal pores on the lower arm, scales of the nape minute, urohyal lacking anterior spine), which points to a common ancestry.

Habitat Dominance—The absence of other macrofauna combined with the excellent preservation of cichlids indicate that in terms of animal or at least vertebrate biomass †*Rebekkachromis* was dominating its environment.

Ecological Diversity—†*Rebekkachromis* has a variable oral dentition (exclusively tricuspid, tricuspid + unicuspid) which might point to different food acquisition strategies. †*Rebekkachromis* is also diverse with regard to the fusion between hypurals of the

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caudal fin. The caudal fin is mainly involved in propulsion, but if and how the fusion between the hypural plates can be related to function has not yet been explored for cichlids.

In conclusion, †*Rebekkachromis* spp. from Yatianin could represent an early stage of differentiation and the idea that this assemblage represents a species flock in nascent state needs to be researched further. It is not always possible to establish endemicity in paleontology, but the criteria concerning monophyly and ecological diversity could be examined in future research. Species flocks "in the making" have been reported previously for killifishes from the upper Miocene of the Tugen Hills (Altner and Reichenbacher, 2015).

Origin and Dispersal Scenarios of †*Rebekkachromis*

As mentioned above ('Geochemistry of alkaline lakes'), both tectonism and volcanism can be responsible for the genesis of alkaline lakes. Tectonism and associated volcanism proceeded in East Africa with a general north to south direction (e.g., Macgregor, 2015). Volcanism along the eastern branch of the EARS began in the Turkana region in northern Kenya during the Eocene (ca. 35–40 Ma) (Furman et al., 2006), and reached other parts of northern Kenya (Morley et al., 1992), as well as the central Ethiopian Plateau, in the Oligocene (ca. 30 Ma) (Hofmann et al., 1997). In the early-to-middle Miocene (ca. 17–15 Ma), the central part of the Kenya Rift, where the Tugen Hills are situated, became volcanically active (Hill, 2002; Macgregor, 2015), and the Ngorora Formation documents the existence of alkaline lakes shortly afterward. In northern Tanzania, volcanism began in the late Miocene (ca. 8 Ma) (Dawson, 1992), and in the area of modern-day Lake Natron and Lake Manyara volcanic activity set in about 5 Ma (Foster et al., 1997). The lower Pleistocene Humbu and Moinik formations, deposited between 1.7 and 1.2 Ma, show evidence for the existence of alkaline lakes at that time (Dawson, 1992).

Because of the direction of volcanism, a north to south direction for the migration of alkaliphile cichlids in those areas is possible. As described above, cichlid fishes in alkaline lakes were present in the Tugen Hills since the middle Miocene (Bishop and Pickford, 1975; van Couvering, 1982; Renaut et al., 1999; Rasmussen et al., 2017). Consequently, alkaliphile cichlids could have evolved several million years before the formation of the Magadi-Natron-Manyara lake basins and much farther north. As the youngest part of the Ngorora Formation, known from the site Waril (9–10 Ma), revealed a different cichlid fauna (Altner et al., 2017, 2020; Altner and Reichenbacher, 2020), it seems possible that †*Rebekkachromis* became extinct in the Tugen Hills about 10 Ma.

CONCLUSIONS AND OUTLOOK

The four main results and conclusions of this paper are: (1) *Oreochromis* (*Alcolapia*) is distinguished from *Oreochromis* and all other haplotilapiine cichlids (except †*Rebekkachromis* and †*Baringochromis*) by the possession of three (vs. four) sensory canal pores on the preopercle. (2) The definition of the genus †*Rebekkachromis* is revised to include two new species described here. This genus was present in the Tugen Hills at least between 13–10 Ma. (3) †*Rebekkachromis* seems to form a distinct morphogroup, which most closely resembles *Oreochromis* (*Alcolapia*) among the extant African cichlids. Together, the fossil cichlids from the Tugen Hills, i.e., †*Rebekkachromis*, †*Oreochromimos kabchorensis*, and †"*Sarotherodon*" *martyni*, indicate that a morphologically wide array of *Oreochromis* (*Alcolapia*) 'look-alikes' were present in the paleolakes of the Ngorora Formation. (4) The alkaline paleolakes of the Tugen Hills in which †*Rebekkachromis* was living may have had a similarly impoverished macrofauna as the modern soda lakes of East Africa, which is indicated by the complete absence of such fossils in the †*Rebekkachromis*-bearing sediments.

These conclusions corroborate and complement the hypothesis of an early emergence of cichlids in alkaline lakes in the Tugen Hills during the middle Miocene. Examination of the relationship of †*Rebekkachromis* and other extinct African cichlids to modern cichlids in greater detail will require the construction of a morphological phylogeny for Pseudocrenilabrinae cichlids based on characters that can be applied to fossils.

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