The importance of articulated skeletons in the identification of extinct taxa: new fossils of cichlids from the Miocene of Kenya and clupeids from the Miocene of Greece (Teleostei)

Dissertation zur Erlangung des Doktorgrades
an der Fakultät für Geowissenschaften
der Ludwig-Maximilians-Universität München

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München, 28. September 2020

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Tag der mündlichen Prüfung: 08.02.2021

Statutory declaration and statement

I hereby confirm that my Thesis entitled "Fossil fishes from terrestrial sediments of the Miocene of Africa and Europe", is the result of my own original work. Furthermore, I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the Ludwig-Maximilians-Universität München.

München, 21.09.2020
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Abstract

Fishes are important components of aquatic faunas, but our knowledge on the fossil record of some taxa, relative to their present diversity, remains poor. This can be due to a rarity of such fossils, as is the case for the family Cichlidae (cichlids). Another impediment is the rarity of well-preserved skeletons of fossil fishes. This becomes even more problematic for taxa whose modern representatives are challenging to distinguish based on osteological data, as is the case for the cichlids and also for the representatives of the family Clupeidae (clupeids: herrings, shads and allies). Our limited understanding of the past diversity of these taxa hinders efforts to address questions regarding their evolution. In this study, new material of well-preserved and articulated skeletons of fishes belonging to the aforementioned families is presented.

There are few areas in Africa with sediments that could hold fossils of freshwater fishes. Recently, however, the Ngorora Formation at the Tugen Hills area in Kenya has been recognized as a conservation and concentration Lagerstätte, furnishing complete skeletons of cichlids dating to the middle-late Miocene. For some of these fossils, the use of µCT technology allowed the imaging of anatomical details which would otherwise be hard or impossible to observe. Material from three new localities is presented: from the sites Rebekka (ca. 11 Ma), Yatianin (ca. 11 Ma) and Terenin (ca. 13 Ma). Based on this material, four new species of fossil cichlids, placed in one new genus, †*Rebekkachromis*, are described.

In the course of this project, new data on the osteology and dentition of modern cichlids were collected and/or compiled and presented, concerning 1) the size of the oral teeth relative to their position on the jaws, 2) the number of sensory canal pores on the preopercle, 3) the number of lateral-line tubules on the lacrimal, 4) the number of supraneural bones and 5) the fusion pattern of hypural plates. The results of these investigations corroborate the use of the above-mentioned characters for taxonomic purposes, as the intraspecific variation is very low. At the same time, they allowed the examination of the systematic relationships of the fossil fishes from the Tugen Hills. The results regarding the placement of oral teeth in the mouth helped establish that †*Rebekkachromis* is a haplotilapiine genus.

The most notable and unexpected result from these investigations, however, was that the species of the modern subgenus of alkaliphile cichlids *Oreochromis* (*Alcolapia*) have three sensory canal pores on the lower branch of their preopercle, as does †*Rebekkachromis*, unlike any other haplotilapiine known to date. This new evidence, together with other meristic and morphological characters (e.g. the minute scales on the nape, throat and belly), indicates a strong resemblance of †*Rebekkachromis* to *Oreochromis* (*Alcolapia*). This observation

provided further support to the idea that the middle-upper Miocene sediments of Tugen Hills hold not only the earliest haplotilapiine, but more precisely the earliest oreochromine cichlids.

Because of the high concentration of fishes in the Tugen Hills, we can make inferences not only about individual species, but also about the communities of the fishes that lived in those lakes. For instance, the consistent absence of accompanying fauna and flora in the examined sites, together with the geological context of the Tugen Hills, indicate that †*Rebekkachromis* was living in alkaline lakes. The modern alkaliphile cichlids of the subgenus *Oreochromis* (*Alcolapia*) live further south, close to the border of Kenya with Tanzania. As tectonism and volcanism proceeded with a north-to-south direction along the East African Rift System, it makes sense that alkaliphile cichlids developed in the same direction.

Furthermore, the genus †*Rebekkachromis* seems to have included a diverse morphogroup of related cichlid species. The occurrence of different species, and/or intermediate forms between those species, living in the same paleolakes may indicate the presence of species flocks. The paleolakes in the Tugen Hills seem to have favored the development of species flocks, as attested by the presence of other possible species flocks in the upper Miocene of the same area.

The last section of this Thesis concerns fishes from a different continent and family, but within a similar timeframe. Well-preserved skeletons of clupeids were recovered from a new terrestrial locality, dating to the late Miocene of the Serres Basin in Northern Greece. These fossils represent a new species that cannot be attributed to any of the modern clupeid genera, but which has the least differences with *Hilsa*, a genus known from the Indo-West Pacific. The new fossil species was tentatively attributed to the fossil genus †*Pseudohilsa*, known from the middle Miocene of Azerbaijan. †*Pseudohilsa*, together with some other fossils attributed to "*Hilsa*" from the middle Pliocene of Abkhazia in the Black Sea region, might indicate that fishes similar to the modern-day genus *Hilsa* were once living in the Eastern Paratethys realm and its successors. The new fossil species from Greece are therefore the first *Hilsa*-lookalikes known from the Mediterranean Basin.

The results of this Thesis highlight the importance of localities which furnish well-preserved and articulated skeletons, which are necessary to investigate the systematics of fossil fishes. The new osteological data on modern cichlids presented in this study demonstrated the potential of morphological characters to inform us about the relationships of fossil fishes. This work enriches our knowledge of the past diversity of African cichlids and clupeids from the Balkans, with the description of new taxa and inferences about their environment and distribution.

Zusammenfassung

Fische sind ein wichtiger Bestandteil der aquatischen Fauna, allerdings ist unser Wissen über deren Fossilbericht in Relation zur ihrer heutigen Diversität noch sehr spärlich. Dies kann an der Seltenheit von solchen Fossilien liegen, wie im Falle der Familie der Cichlidae (Cichliden, Buntbarsche). Ein weiteres Hindernis stellt die Rarität von gut erhaltenen Fischskelett-Fossilien dar. Diese Problematik verschärft sich in Bezug auf jene Taxa, deren moderne Vertreter nur schwer durch, auf osteologisch basierende, Merkmale zu unterscheiden sind. Dies ist der Fall bei Cichliden und auch bei der Familie der Clupeidae (Clupeiden: z.B. Heringe). Unser begrenztes Wissen über die einstige Diversität dieser Taxa beeinträchtigt Bemühungen die Fragen zu ihrer Evolution zu beantworten. In dieser Arbeit wird neues Material von gut erhaltenen Skelettfossilien der bereits genannten Familien vorgestellt.

Es sind nur wenige Gebiete in Afrika, die Sedimente aufweisen, welche Fossilien von Süßwasserfischen enthalten können. Vor kurzem jedoch wurde die Ngorora Formation im Gebiet der Tugen Hills in Kenya als Konservat- und Konzentratlagerstätte erkannt, welche vollständige Skelette von Cichliden enthält, die auf das mittlere bis späte Miozän datiert werden können. Für einige dieser Fossilien konnte die Anwendung von µCT anatomische Details ans Tageslicht bringen, welche ansonsten nur schwer oder gar nicht erfasst hätten werden können. Material aus drei neuen Lokalitäten wird vorgestellt: Aus dem Aufschluss Rebekka (ca. 11 Ma), Yatianin (ca. 11 Ma) und Terenin (ca. 13 Ma). Auf Grundlage dieses Materials wurden vier neue Arten von Cichliden beschrieben und einer neuen Gattung (†*Rebekkachromis*) zugeordnet.

Im Zuge dieses Projekts wurden neue Daten über die Osteologie von rezenten Cichliden gesammelt und/oder zusammengestellt und vorgestellt in Bezug auf 1) die Größe der oralen Zähne in Bezug auf ihre Position in den Kiefern, 2) die Anzahl der „sensory canal pores“ (Sinnes-Kanal-Poren) auf dem Vordeckel (Präoperkulum), 3) die Anzahl der Poren der Seitenlinie auf dem Tränenbein, 4) die Anzahl der supra-neuralen Knochen und 5) die Verschmelzung der hypuralen Platten. Die Ergebnisse dieser Studien bestätigen den Gebrauch der vorhin genannten Merkmale für taxonomische Zwecke, da deren intraspezifische Variation sehr gering ist. Gleichzeitig erlauben die Ergebnisse eine Untersuchung der systematischen Beziehungen von fossilen Fischen aus den Tugen Hills. Die Ergebnisse bezüglich der Positionierung der oralen Zähne im Mund, halfen †*Rebekkachromis* als eine haplotilapiine Gattung zu etablieren. Das bemerkenswerteste und unerwartetste Ergebnis dieser Studie, jedoch war, dass eine rezente Art der alkaliphilen Untergattung des Cichliden *Oreochromis* (*Alcolapia*) drei Sinnes-Kanal-Poren auf ihrem Vordeckel aufweist, genau wie †*Rebekkachromis*, und im Gegensatz zu jedem anderen bekannten Haplotilapiinen. Dieser neue

Befund, zusammen mit anderen meristischen und morphologischen Merkmalen (z. Bsp. den winzigen Schuppen im Nacken, am Hals und am Bauch), deuten auf eine starke Ähnlichkeit mit *Oreochromis* (*Alcolapia*) hin. Diese Beobachtung stützt zusätzlich die Idee, dass die mittel- bis spät-miozänen Schichten der Tugen Hills nicht nur die ältesten Haplotilapiine enthalten, sondern, genauer gesagt, die ältesten oreochrominen Cichliden.

Aufgrund der hohen Konzentration von Fischen in den Tugen Hills, können wir nicht nur Schlussfolgerungen bezüglich der einzelnen Species ziehen, sondern auch bezüglich ganzer Fischgemeinschaften, die in diesen Seen gelebt haben. Zum Beispiel deutet die immer fehlende begleitende Fauna und Flora der Paläo-Seen der Tugen Hills darauf hin, dass †*Rebekkachromis* in alkalischen Seen gelebt hat. Die modernen alkaliphilen Cichliden der Untergattung *Oreochromis* (*Alcolapia*) leben weiter südlich, nahe der Grenze Kenias zu Tanzania. Da Tektonik und Vulkanismus entlang des Ostafrikanischen Graben von Nord nach Süd progradierten, ist es sinnvoll, dass sich alkaliphile Cichliden in derselben Richtung entwickelten.

Zudem scheint es, dass †*Rebekkachromis* eine diverse morphologische Gruppierung von nahverwandten Cichliden umfasst. Das Vorkommen von verschiedenen Arten und/oder Zwischenformen von Arten, die im selben Paläosee lebten, weisen eventuell auf einen Artenschwarm („species flock“) hin. Die Paläoseen in den Tugen Hills schienen die Entwicklung von Artenschwärmen gefördert zu haben, wie es durch die Anwesenheit anderer Artenschwärme aus dem oberen Miozän aus der gleichen Gegend bereits gezeigt wurde.

Der letzte Teil der Studie beffast sich mit Fische von einem anderen Kontinent und aus einer anderen Familie, jedoch aus der selben Zeit. Gut erhaltene Skelette von Clupeiden wurden aus einer neuen terrestrischen Lokalität geborgen, die auf das späte Miozän des Serres Becken in Nord Griechenland datiert wird. Diese Fossilien stellen eine neue Art dar, welche sich keiner rezenten Gattung von Clupeiden zuordnen lässt, jedoch die wenigsten Unterschiede zu *Hilsa* aufweist, eine Gattung die aus dem Indo-West-Pazifik bekannt ist. Die neue fossile Art wurde vorläufig der fossilen Gattung †*Pseudohilsa* zugeordnet, die aus dem mittleren Miozän Azerbaijans bekannt ist. Das Vorkommen von †*Pseudohilsa*und andere Fossilien aus dem Pliozän in Abchasien (Region am Schwarzen Meer), die zu „*Hilsa*“ zugeordnet wurden, , könnten drauf hinweisen, dass Fische, die stark der rezenten Gattung *Hilsa* ähneln, sowie deren Nachfolger einst im Gebiet der Östlichen Paratethys gelebt haben könnten. Darum stellen die Fossilien aus Griechenland das erste *Hilsa*-Pendent aus dem Mediterranen Becken dar.

Die Ergebnisse dieser Arbeit heben die Bedeutung dieser Lokalitäten hervor, welche gut erhaltene und artikulierte Fossilien führen. Diese Fossilien sind essenziell für systematische

Untersuchungen von fossilen Fischen. Die neuen osteologischen Daten von modernen Cichliden aus dieser Arbeit demonstrierten das Potential von morphologischen Merkmalen, die uns Informationen über die Beziehungen von fossilen Fischen geben. Diese Arbeit bereichert unser Wissen über die vergangene Diversität von Afrikanischen Cichliden und Clupeiden aus dem Balkan mit Beschreibungen von neuen Taxa und Schlussfolgerungen über deren Umwelt und deren Verbreitung.

TABLE OF CONTENTS

1. Introduction

1.1. Pisces

The modern fishes form a diverse (ca. 35,600 species) paraphyletic group comprising all non-tetrapodomorph Craniata, such as the jawless hagfishes (82 species) and lampreys (47 species), the cartilaginous Chondrichthyes (e.g., sharks, skates and rays, ca. 1300 species), the lobe-finned Sarcopterygii (8 species, excluding tetrapods) and the bony fishes or Actinopterygii (the rest) (Fricke et al., 2020). Fishes comprise more than half of all vertebrates and exhibit a wide variety of adaptations regarding their morphology, physiology, behavior and the habitats they occupy (Helfman et al., 2009; Nelson et al., 2016). Fishes originated in the early Cambrian (Benton, 2014) and today occupy habitats in all continents, from the bottom of the oceans to the lakes in high mountains. The Actinopterygii are made up, in terms of species numbers, almost entirely of the Teleostei (Fricke et al., 2020). The three major taxa that constitute the Teleostei are the Elopomorpha, which are sister to the Osteoglossomorpha plus Clupeocephala (Betancur et al., 2017). The Clupeocephala are distinguished in two clades, the Otomorpha (=Otocephala) and the Euteleostomorpha (=Euteleostei) (Betancur et al., 2017). The fossil fishes examined in this Thesis belong to each of the latter two clades, each explained below.

The extant Otomorpha comprises about 11,000 species, 1,500 genera and 90 families (Arratia, 2018). The Otomorpha comprises the Clupeomorpha (herrings, anchovies and allies), and their sister Ostariophysi plus the deep-sea Alepocephaliformes (e.g., Betancur et al., 2017; Straube et al., 2018). The Otomopha are mostly freshwater fishes with the exception of Alepocephaliformes and most Clupeomorpha (e.g., Nelson et al., 2016; Arratia, 2018).

One of the most species-rich Euteleostomorpha taxa are the Percomorphaceae (=Percomorpha) (Betancur et al., 2017), with over 13,000 species recognized to date (Nelson et al., 2016). The relationships between several percomorph taxa still need to be resolved, but, according to the latest classification, are distinguished into nine supraordinal groups (=series) (Betancur et al., 2017). One of these series is the Ovalentaria which comprises 45 families, such as the damselfishes and clownfishes (Pomacentridae, 422 species), Old World silversides (Atherinidae, 78 species), pupfishes (Cyprinodontidae, 103 species), mullets (Mugilidae, 79 species), convict blennies (Pholidichthyidae, 2 species) and cichlids (Cichlidae, >1700 species) (Betancur et al., 2017; Fricke et al., 2020). The latter two families, although morphologically different, are considered sister taxa based on molecular data, forming the order Cichliformes (Betancur et al., 2017).

1.2. Cichlidae

About 5% of all fish species (1727 species) belong to the family Cichlidae making this the third largest family of fishes, after the Gobiidae (1923 species) and Cyprinidae (1754 species) (Fricke et al., 2020). They are mostly tropical fishes, living in freshwaters; a few can survive in brackish or fully marine conditions (Martinez-Palacios et al., 1996; Oldfield, 2004; Langston et al., 2010). They are small to moderately-sized fishes, most ranging between 5–50 cm and present a variety of body types (Nelson et al., 2016). There is a variable degree of sexual dimorphism and many species are brightly colored, a trait playing an important role in reproduction (Fryer and Iles, 1972; Hemdal, 2003; Oconner, 2012). The majority of species are most active during the day (Helfman et al., 2009).

They are distinguished by their single nostril on each side of the head and a divided lateral line (Skelton, 2001; Nelson et al., 2016). The dorsal and, to a lesser extent, the anal fin have broad bases and are composed of a spiny and a soft-rayed part (Skelton, 2001; Nelson et. al., 2016). The pelvic fins are placed forwards, approximately under the pectoral fins (Skelton, 2001; Nelson et. al., 2016). The jaws are protrusible and the dentary and the premaxillary may bear teeth of variable morphology (Fryer and Iles, 1972; Motta, 1994). Some teeth e.g., are unicuspid, bicuspid or tricuspid (Fryer and Iles, 1972; Kullander, 1998; Takahashi, 2003). The unicuspid teeth may be conical or flattened and the lobes of the bi- and tricuspid teeth may be equal in size or different (Fryer and Iles, 1972; Kullander, 1998; Takahashi, 2003). A key innovation, which may have contributed to the evolutionary success of the cichlids, is the possession of robust pharyngeal jaws, which also bear teeth (e.g., molariform, unicuspid, bicuspid) and help in processing the food (Fryer and Iles, 1972; Liem, 1973; Mabuchi et al., 2007).

Because of their coloration, small size, interesting mating behaviors (e.g. mouthbrooding) and their ability to thrive in captivity, they are some of the most popular aquarium species (Nelson et al., 2016). Their importance as a food source increases rapidly, with cichlids being the second most caught group of fishes in inland waters by weight and a single genus, *Oreochromis*, forming over 10% of the world's aquaculture production (FAO, 2020). Their propensity to radiate has also made them some of the most popular taxa to study among evolutionary biologists (Seehausen, 2006; Futuyma and Kirkpatrick, 2017; McGee et al., 2020) (see more in the section 1.2.2.).

1.2.1. Systematics of the Cichlidae

Cichlids are distinguished into four subfamilies, the Indian/Sri Lankan/Malagasy Etroplinae (16 species), the Malagasy Ptychochrominae (16 species), the Neotropical subfamily Cichlinae (568 species) and the African/Middle Eastern Pseudocrenilabrinae (1,127 species) (Fricke et al., 2020). The monophyly of these families is well supported by molecular data (e.g., Sparks and Smith, 2004; Smith et al., 2008; Irisarri et al., 2018), but not by morphological data (e.g., Stiassny, 1991; Kullander, 1998). The Pseudocrenilabrinae are divided in 27 major lineages and tribes (e.g., Stiassny, 1990; Dunz and Schliewen, 2013; Schwarzer et al., 2015; Irisarri et al., 2018). Several of these tribes were initially diagnosed based on morphological evidence (Poll, 1986; Takahashi, 2003), and the monophyly of most of these tribes was later corroborated by molecular studies (e.g., Dunz and Schliewen, 2013; Irisarri et al., 2018; Schedel et al., 2019). Few morphology-based phylogenetic studies have focused so far in elucidating the relationships between these tribes/lineages and with limited success (Stiassny, 1991; Takahashi, 2003). Molecular evidence point to the monotypic tribe Heterochromi being the sister taxon to the rest of the Pseudocrenilabrinae (e.g., Keck and Hulsey, 2014; Irisarri et al., 2018). The largest clade among Pseudocrenilabrinae are the haplotilapiines, which include 22 tribes/lineages (e.g., Dunz and Schliewen, 2013 and references therein). Haplotilapiines are a group which is well supported by molecular data (e.g., Schwarzer et al., 2009; Dunz and Schliewen, 2013; Irisarri et al., 2018; Schedel et al., 2019) and distinguished by a single morphological synapomorphy shared by most of its members, i.e. the presence of tricuspid teeth in the inner rows of the oral dentition (Schliewen and Stiassny, 2003; Dunz and Schliewen, 2013).

1.2.2. Diversity and diversification in Pseudocrenilabrinae

Cichlids fishes live throughout the rivers and lakes of Africa, and most of their diversity is concentrated in East Africa (Fryer and Iles, 1972; Stiassny and Meyer, 1999). The Lakes which have been formed by the activity of the East African Rift System are hotspots of cichlid diversity, with the three larger ones, Lakes Tanganyika, Victoria and Malawi (Nyasa) holding hundreds of endemic species each (e.g., Fryer and Iles, 1972; Coulter, 1991; Stiassny and Meyer, 1999; Turner et al., 2001). Lake Tanganyika is the most ancient and most diverse, hosting Pseudocrenilabrinae cichlids from 16 tribes (Fryer and Iles, 1972; Coulter, 1991; Meyer et. al., 2015; Ronco et al., in press). In contrast, the tribe Haplochromini dominates Lakes Malawi and Victoria (Fryer and Iles, 1972; Greenwood 1980; Stiassny and Meyer, 1999; Salzburger et al., 2005). Many of these cichlids show convergences in morphological features, regarding their body proportions and/or structures related to feeding, e.g., jaws or lips (Fryer and Iles, 1972; Kocher et al., 1993; Stiassny and Meyer, 1999; Rüber and Adams, 2001).

Cichlids are prone to form species flocks, i.e. groups of species which share a common ancestry and live sympatrically (Greenwood, 1984a), especially when they find themselves in lakes (Meyer, 2005; Seehausen, 2015; Salzburger, 2018). These species flocks can vary widely with regards to species numbers, from the large species flocks inhabiting the Lakes Victoria and Malawi to smaller radiations, such as the soda tilapias of the Lakes Natron and Magadi (Seegers and Tichy, 1999; Verheyen et al., 2003). A major issue in cichlid research is whether these species flock evolved really in sympatry or if they are congregations of species which developed in geographical isolation, e.g., in different rivers or lake sub-basins, and met later (Kornfield and Smith, 2000; Salzburger and Meyer, 2004; Genner et al., 2015; Weiss et al., 2015). Ecological opportunities, such as the formation of a new lake, a new trophic resource, the absence of other competing species and/or predators or the development of new traits that allow the exploit of a new niche may promote speciation and the formation of species flocks (Liem, 1973; Wagner et al., 2014; Schluter, 2000; Seehausen, 2015).

1.2.3. Resistance to alkalinity

Cichlid species from all subfamilies have been reported to have increased tolerance to increased salinity (Ward and Wyman, 1977; Reinthal and Stiassny, 1991; Martinez-Palacios et al., 1996; Oldfield, 2004; Langston et al., 2010; Ai et al., in press), but only a few species of the genus *Oreochromis* have been known to be able to tolerate increased salinity and alkalinity. These alkaliphile cichlids are the four species of the subgenus *Oreochromis* (*Alcolapia*), which live in the Lakes Magadi and Natron, as well as their close relative, *Oreochromis amphimelas* inhabiting Lake Manyara (Trewavas, 1983; Seegers and Tichy, 1999; Tichy and Seegers, 1999; Kavembe et al., 2016; Ford et al., 2019). These species have developed several behavioral and physiological adaptations to cope with the alkaline environment, for example they are the only fishes that excrete urea instead of ammonia (Wood et al., 2002)

1.2.4. Paleobiogeography and the fossil record in Cichlidae

The fact that different cichlid subfamilies occur in different landmasses which split off from Gondwana has led some to hypothesize that this distribution might be due to vicariance, which would suggest a Cretaceous age for these subfamilies (Stiassny, 1991; Streelman et al., 1998; Farias et al., 1999; Farias et al., 2000). However, the oldest cichlid fossils come from the Eocene of Tanzania (Murray, 2000, 2001a) and some younger fossils from the Eocene of

Argentina (Malabarba et al., 2006; Malabarba et al., 2010; Perez et al., 2010). A competing hypothesis is that of dispersal, in which cichlids originated much later and then spread to other continents (Lundberg, 1993; Murray, 2001b). The existence of saline-tolerant cichlids (see section “Resistance to alkalininity”) makes this hypothesis plausible. In addition, the latest molecular clock analyzes date the split between the sister-groups Cichlinae and Pseudocrenilabrinae after the breakup of South America and Africa, thus favoring this hypothesis (Matschiner, 2019).

However, the lack of reliable fossils makes testing any biogeographical scenarios challenging. Before the start of the current project of our team, led by Prof. Dr. Bettina Reichenbacher, which examined the fossil cichlids from the Tugen Hills, Kenya, there were less than 20 fossil cichlid species known (Altner et al., 2017). As shown and discussed in the following chapters, these studies resulted in the description of several new species and genera (Altner et al., 2017; Penk et. al., 2019; Kevrekidis et. al. 2019; Altner et al., 2020 a, b; Kevrekidis et al., 2020), significantly increasing our knowledge regarding the paleontology of cichlids.

1.3. Clupeomorpha

Clupeomorphs are small to moderate-sized fishes (<1 m and most <0.5 m) with a fusiform body, almost always living in schools and feeding mostly on plankton (Whitehead, 1985). The majority of the species are marine, living near coastal areas, but many are anadromous and some are adapted to fully freshwater conditions (Nelson et al., 2016). They lack bright coloration, usually being countershaded, with silvery flanks and a dark dorsum (Longhurst, 1971). The majority of species are most active during the night (Helfman et al., 2009). In most species there is no pronounced sexual dimorphism (Whitehead, 1985). Clupeomorphs lack hard spines on their fins. They have a short, single dorsal fin which is placed about the middle of the body (e.g., Grande 1985; Whitehead, 1985; Nelson et al., 2016). The pelvic fin is usually inserted under or near the beginning of the dorsal fin and the caudal fin is forked (e.g., Grande 1985; Whitehead, 1985; Nelson et al., 2016). The jaws are not protrusible (e.g., Nelson et al., 2016). The mouth may bear small conical teeth in the jaws and other bones that make up the roof of the mouth such as the vomer, the palatines the endopterygoids and ectopterygoids, but in several species the teeth are absent (e.g., Whitehead, 1985; Sato, 1994). Some lineages (†Ellimmichthyiformes, Denticipitoidei, see section 1.3.1. for the systematics within the Clupeomorpha) have a complete lateral line, but in the Clupeoidei the lateral line is reduced or absent.

Because they are mostly schooling fishes, the modern Clupeomorphs are easy to catch with nets (Whitehead, 1985), which made them one of the most commercially important fishes throughout human history (Coull, 1993). In 2018 only five clupeomorph taxa, the anchoveta, (*Engraulis ringens*), the Atlantic herring (*Clupea harengus*), the European pilchard (*Sardina pilchardus*), the Japanese anchovy (*Engraulis japonicus*) and the sardinellas nei (*Sardinella* spp.) accounted for ca. 17% of the global marine capture production (FAO, 2020). Due to their anadromous way of life, clupeid species such as the Pacific herring (*Clupea harengus*) play an important ecological role in energy and nutrient transfer between marine and coastal or inland ecosystems and have been characterized as cornerstone resources (Willson et al., 1998).

1.3.1. Systematics of the Clupeomorpha

The Clupeomorpha are divided in the fossil †Ellimmichthyiformes and the extant Clupeiformes (e.g., Grande, 1985; Murray and Wilson, 2013; Nelson et al., 2016). The Clupeiformes comprise the Denticipitoidei and Clupeoidei (Grande, 1985; Nelson et al., 2016). There is only one family in the Denticipitoidei, Denticipitidae, with a single species, *Denticeps clupeoides* Clausen 1959 (Grande, 1985; Nelson et al., 2016). The Clupeoidei include several families, such as the Pristigasteridae (longfin herrings, 39 species), the Engraulidae (anchovies, 164 species), the Chirocentridae (wolf herrings, 2 species) and the Clupeidae (shads, sardines, menhadens, and pilchards, 211 species) (Fricke et al., 2020). This classification is based mostly on morphological characters (Nelson, 1970; Grande, 1985; Whitehead, 1985; Nelson et al., 2016) but more recent molecular studies dispute the monophyly of the latter two families, as e.g., they place the Chirocentridae within the Clupeidae (Wilson et al., 2008; Li and Ortí, 2007; Lavoué et al., 2007, 2010, 2013; Queiroz et al., 2020). Other molecular studies point to the existence of one or two additional lineages from the taxa included in the Clupeidae, the Dussumieriidae and/or the Spratelloididae (Li and Ortí, 2007; Lavoué et al., 2013, 2014, 2017; Bloom and Lovejoy, 2014; Bloom and Egan, 2018). However, there is no consensus regarding the relationships between these families, based either on morphological (e.g., Grande, 1985; Di Dario, 2009; Patterson and Johnson, 1995; Miyashita, 2010) or molecular evidence (e.g. Li and Ortí, 2007; Lavoué et al., 2013; Bloom and Egan, 2018).

Within the family Clupeidae, morphological and molecular studies have indicated the presence of several subfamilies, such as the Dussumieriinae, the Pellonulinae, the Ehiravinae, the Dorosomatinae the Clupeinae and the Alosinae (e.g., Grande, 1985; Whitehead, 1985; Lavoué et al., 2014). However, as noted above, it is not clear yet, based on molecular studies, not only which taxa should be included in the Clupeidae, but also whether these subfamilies are valid or which taxa should be included in each subfamily (e.g., Lavoué et al., 2013, 2014; Bloom and Egan, 2018). There is only one morphological phylogeny with an emphasis on the Clupeidae so far, presented in the unpublished Thesis of Sato (1994). This study corroborated the monophyly of the Clupeidae, but not of the subfamilies Dussumieriinae, Clupeinae and Alosinae (Sato, 1994).

1.3.2. Adaptations and characteristics of the Clupeomorpha

Clupeomorpha have an otophysic connection with their swimbladder (Grande, 1985). A pair of ducts from the swimbladder penetrate the exoccipital and expand in bony bullae inside the skull forming a pair of bullae in the prootic and usually one additional pair of bullae in the pterotic as well (Blaxter et al., 1981; Blaxter and Hunter, 1982). Inside these bullae, a membrane separates the gas by the inner ear fluid (Blaxter et al., 1981; Blaxter and Hunter, 1982). This system seems to facilitate hearing and the detection of water movements, both valuable abilities for the schooling and highly predated upon Clupeomorpha (Blaxter et al., 1981; Whitehead, 1985). The bullae are also in contact with the recessus lateralis (Blaxter et al., 1981; Blaxter and Hunter, 1982), a space in the cranium where the lateral line canals of the head (infraorbital, supraorbital, temporal and preopercular sensory canals) converge (Grande, 1985), forming the so-called acousticolateralis system (Blaxter et al., 1981). Clupeiformes are able to detect higher frequencies than other fishes (Mann et al., 2005; Ladich and Schulz-Mirbach 2016), and a few, such as the American shad (*Alosa sapidissima*) can detect ultrasounds (Mann et al., 1998, 2001). This ability seems to be related with predator avoidance, as e.g., *Alosa sapidissima* exhibits avoidance or defensive behavior when exposed to ultrasounds (Mann et al., 1998; Popper et al., 2004).

Another characteristic of Clupeomorpha is the possession of scutes, i.e. hardened modified scales along the midline of the body (Grande, 1985; Whitehead, 1985; Nelson et al., 2016). In dorsoventral view, these scutes seem like a very elongated ovoid with pointed ends and they may possess a shallow keel. They are attached to the body by means of long ascending arms, and extend in the ventral region from the isthmus to the anus and, in some fossil and recent species, also in the predorsal region (Grande, 1985; Whitehead, 1985; Murray and Wilson, 2013). The ancestral condition seems to be the one where the ventral margin is covered by scutes, from the gular region to the beginning of the anal fin (Lavoué et al., 2014). Some taxa, such as the Chirocentridae or the Dussumieriinae have reduced or lost, respectively, most of their ventral scutes, other than the one directly in front of the pelvic fin i.e. the pelvic scute

(Grande, 1985; Whitehead, 1985). Additionally, the pelvic scute of the Dussumieriinae is W-shaped (Grande, 1985; Whitehead, 1985).

1.3.3. (Paleo)biogeography and the fossil record of the Clupeomorpha

In the following section, only the fossil record of skeletal remains and not that of otoliths is considered, as the latter is not the object of the present study. The oldest otomorph known to date is †*Tischlingerichthys* from the Upper Jurassic marine sediments from Bavaria, Germany (Arratia, 1997; Arratia and Schultze, 2015). The earliest clupeomorph fossils date to the Early Cretaceous of the Mediterranean, East Asia, and North and South America (e.g., Chang and Grande, 1997; Murray and Wilson, 2013; Alvarado-Ortega, 2014; Vernygora et al., 2016; Boukhalfa et al., 2018; dos Reis Polck et al., 2020). The hotspot of clupeoid diversity today is in the Indo-West Pacific region, hosting more than 50% of all species (Nelson et al. 2016). Lavoué et al. (2013) estimated that the center of origin of the Clupeoidei must have been the precursor of this region in the eastern Tethys Sea during the Early Cretaceous. Fossils of similar age found outside of this region seem to contradict this idea though, so this issue remains open (e.g., De Figueiredo, 2009a, b; Forey et al., 2003).

The †Ellimmichthyiformes went extinct in the Eocene (Grande, 1985; Nelson et al. 2016; Marramà et al., 2019), but the Clupeiformes exist to date. There is only one known fossil Denticipitoidei species (Greenwood 1960, 1984b). Even though the Clupeoidei are known from the Early Cretaceous, most fossil species and genera are known from the Oligocene and the Miocene (Grande, 1985). Whether that was a time period of intense speciation for the clupeoids or if this is due to a strong preservation bias, is unknown.

The majority of the described fossil clupeoids belong to the Clupeidae (Grande, 1985). The families Chirocentridae and Pristigasteridae have no known fossil representatives and there is only a handful of species of Engraulidae known to date, from the Eocene to the Pliocene (Landini and Menesini, 1978; Grande and Nelson, 1985; Yabumoto, 1988; Marramà and Carnevale, 2016). The rarity of the fossil representatives of these families may be due to a preservation bias (Grande and Nelson, 1985), as these fishes live in high energy environments, though that is not always the case (Whitehead et. al., 1988).

Another important note is that most of the fossil clupeoid taxa are known from the sediments of Europe, North Africa and North America (Grande, 1985). Modern clupeoids live in all the seas of the world except Antarctica (Whitehead, 1985, Whitehead et. al., 1988), (though there is one clupeid fossil from the Paleocene of Antarctica, see Jerzmańska, 1991).

The distribution of the fossil taxa is in contrast with the current distribution of clupeoids, a fact which might indicate the presence of a sampling bias in favor of these regions.

1.4. Significance of this study

Fishes are important components of aquatic faunas in terrestrial settings, but our knowledge on the fossil record of some taxa, such as the families Cichlidae and Clupeidae, is wanting. It is therefore important to increase our understanding on their past diversity, which could also help us address questions pertaining to their evolution. In this Thesis, new well-preserved fossil skeletons of cichlids and clupeids are described. For some of the fossils, the use of μCT technology allowed the imaging of details of their anatomy which are usually difficult to discern. Regarding extant cichlids, new compilations of data on their osteology are presented, which help us better investigate the systematics of their fossil relatives. Our knowledge on the past diversity of these fishes is enriched with the addition of new taxa and the suggested interpretations of their paleoenvironment and/or distribution.

1.5. Aims and outline of Thesis

1.5.1. Aims

The aims of this Thesis are a) to describe new fossil fish taxa from the middle-late Miocene of Kenya and Greece, b) to examine the distribution and taxonomic utility of some osteological characters and, c) to propose new ideas, based on our results, on the evolution and biogeographic history of these fishes.

1.5.2 Overview of manuscripts

Chapter 2 is a taxonomic study of fossil cichlids from the lacustrine sediments of the uppermost middle or lowermost upper Miocene (c. 11 MYA) site Rebekka, Ngorora Formation, Baringo County, Kenya. These new fossils are distinguished by all other known cichlid genera by the possession of two supraneurals and robust tricuspid oral teeth. Therefore, a new genus, †*Rebekkachromis* gen. nov., was raised to accommodate the fossil cichlids, including two new species, †*R. ngororus* sp. nov. and †*R. kiptalami* sp. nov. At the time these fossils were described, the possession of tricuspid teeth in the inner rows of the dentition made them the earliest known Haplotilapiini cichlids.

In Chapter 3 the diagnosis of the genus †*Rebekkachromis* is revised and expanded to include the new material from two additional sites of the Ngorora Formation, namely Yatianin and Terenin. The taxonomic utility of some characters is (re)evaluated and the distribution of these characters among extant African cichlids is determined. Based on our new dataset, †*Rebekkachromis* seems to resemble morphologically the modern alkaliphile cichlids of the genus *Oreochromis,* subgenus *Alcolapia*. Two new species of †*Rebekkachromis* are raised from the site Yatianin, †*R. valyricus* and †*R. vancouveringae* and several other specimens with different mixes of characters are described. The geological context and the absence of other macrofossils from the three sites examined in this project (Rebekka, Yatianin, Terenin) is congruent with the environment of an alkaline lake.

Chapter 4 is about fossil clupeid fishes of the family Clupeidae from the new upper Miocene locality "Aidonochori A" in the Serres Basin, Northern Greece. These fossil clupeids are distinguished by a new combination of characters, and therefore placed in a new species. This new species does not match any of the existing genera, thought it is least dissimilar to the genus *Hilsa*, which today lives in the Indo-West Pacific. The new fossil clupeids are tentatively attributed to the fossil genus †*Pseudohilsa* from the middle Miocene of Azerbaijan, making them the first clupeids which look similar to *Hilsa* from the Mediterranean Basin.

1.5.3. Author contributions

Chapter 2: Charalampos Kevrekidis, Martina Valtl, Stefanie B. R. Penk, Melanie Altner, Bettina Reichenbacher *Rebekkachromis* nov. gen. from the middle–upper Miocene (11 MYA) of Central Kenya: the oldest record of a haplotilapiine cichlid fish. CK conducted the observations, analyzed and interpreted the data and drafted the manuscript. MV and MA conducted a preliminary investigation of the fossil. MA and SBRP took the X-rays which were used to survey of the morphology of the supraneurals of the extant cichlids and SBRP contributed also to the processing of these results. BeRei supervised the entire study. CK, MA, SBRP and BeRei contributed to discussions and the final manuscript. Manuscript published in Hydrobiologia 83: 239–64. Doi: https://doi.org/10.1007/s10750-018-3715-8

Chapter 3: Charalampos Kevrekidis, Bernhard Ruthensteiner, Alexander F. Cerwenka, Stefanie B. R. Penk, Bettina Reichenbacher. New cichlid fossils from the middle-late Miocene alkaline lakes of Africa: CK conducted the observations, analyzed and interpreted the data and drafted the manuscript. SBRP contributed to the collection of data regarding the first infraorbital. BeRu and AFC performed the computed microtomography on the specimens. BeRei supervised the entire study. All the authors contributed to discussions and the final manuscript. Manuscript published at the Journal of Vertebrate Paleontology 40 (4). Doi: https://doi.org/10.1080/02724634.2020.1805621

Chapter 4: Charalampos Kevrekidis. A new species of clupeid fish from the upper Miocene of Northern Greece: CK conducted the observations, analyzed and interpreted the data and wrote the manuscript. Manuscript to be submitted to Acta Paleaeontologica Polonica.

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Results

The following subchapters are presented in the form of scientific articles.

2. *Rebekkachromis* nov. gen. from the middle–upper Miocene (11 MYA) of Central Kenya: the oldest record of a haplotilapiine cichlid fish

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Abstract

The fossil record of cichlids is sparse, and every new discovery can provide new insights into the evolutionary history of this speciose freshwater fish family. In this article, we describe †*Rebekkachromis* gen. nov. from the middle-to-late Miocene (c. 11 MYA) of the Central Kenya Rift within the East African Rift system. †*Rebekkachromis* is represented by two species that differ from all other fossil and extant African cichlids, except *Etia*, in possessing the unique character combination of two supraneural bones and a set of robust tricuspid oral teeth in the outer row of the dentition. Furthermore, †*Rebekkachromis* exhibits the only proposed morphological synapomorphy of the Haplotilapiini, namely the presence of tricuspid teeth in the inner row of the oral dentition. We show that †*Rebekkachromis* constitutes the oldest reliably identified fossil record of a haplotilapiine. The evolution of cichlid fishes possessing tricuspid teeth in the rivers and lakes of the Central Kenya Rift during the middle-to-late Miocene could have been facilitated by volcanic activity, as repeated ash falls may well have fostered the growth of algae and in particular diatoms. These fishes could thus have had a major advantage, because they could exploit the newly available, rich food resources.

2.1. Introduction

Cichlidae (Cichliformes) constitute one of the most speciose families of vertebrates, with about 1700 extant species having been recognized to date (Nelson et al., 2016; Eschmeyer and Fong, 2018). They are small-to-medium-sized fishes (mostly <80 cm), which can be recognized by, among other features, the presence of a bipartite lateral line, a single nostril on each side and a single dorsal fin comprising a relatively large number of spines and rays (e.g. Carpenter and Niem, 2001; Kullander, 2003). They exhibit a variety of morphological and behavioral specializations, such as bright colouration, pharyngeal jaws and mouthbrooding (e.g. Kocher, 2004; Seehausen, 2006; Genner et al., 2007). Most species inhabit tropical freshwater environments, although some are found in brackish waters (e.g. Kullander, 1998). More than two-thirds of all the known living species are endemic to Africa and parts of the Middle East (e.g. Salzburger, 2009), and these are placed in the monophyletic subfamily Pseudocrenilabrinae (e.g. Sparks and Smith, 2004).

Most pseudocrenilabrine species are found in the African Great Lakes region, notably lakes Tanganyika, Victoria and Malawi, and they constitute an iconic example of adaptive radiation owing to their diversity and adaptability (e.g. Salzburger and Meyer, 2004; Seehausen, 2006; Koblmüller et al., 2008, 2010; Salzburger, 2009; Takahashi and Koblmüller, 2011; Meier et al., 2017). The Haplotilapiini is the most speciose lineage of the pseudocrenilabrines and has a pan-African distribution (e.g. Schwarzer et al., 2009); it includes nine tribes plus the lineage that gave rise to the East African Radiation, which encompasses a further 13 tribes (Schwarzer et al., 2009; Dunz and Schliewen, 2013; see Fig. 1). However, species diversity is not evenly distributed among the Haplotilapiini. Thus, the tribe Etiini, which is sister to all other haplotilapiine clades, comprises a single extant species, *Etia nguti* Schliewen and Stiassny, 2003 (Schliewen and Stiassny, 2003). By contrast, the Haplochromini in Lake Victoria may include more than 700 species (Meier et al., 2017).

However, regardless of their present diversity, our knowledge of fossil cichlid species from Africa, Europe, the Neotropics, and the Near East is limited (e.g. Van Couvering, 1982; Perez et al., 2010; Altner et al., 2017). Isolated bones, jaws or teeth are relatively common, but cannot be securely assigned to any of the modern cichlid genera or lineages (e.g. Lippitsch and Micklich, 1998; Otero et al., 2015; Murray et al., 2017). Cichlid fossils that are based on articulated skeletons are particularly rare, and only 18 fossil cichlid species, from the Eocene to the Pleistocene, have been described so far from Africa and adjacent areas (see Altner et al., 2017 for a complete list). But even in the case of articulated skeletons, their further classification is difficult, as a phylogenetic framework for the extant African cichlids based on comprehensive sampling of taxa and morphological characters is still lacking. Existing classification schemes depend largely on soft-tissue or delicate hard-part characters (e.g. Cichocki, 1976; Greenwood, 1978; Stiassny, 1991; Casciotta and Arratia, 1993a; Kullander, 1998, 2003; Takahashi, 2003), and these characters are rarely preserved in fossils (e.g. Van Couvering, 1982; Casciotta and Arratia, 1993b).

One of the few areas worldwide known to have yielded exceptionally well preserved cichlid fossils are the Miocene sediments of the mountainous Tugen Hills in Central Kenya (Van Couvering, 1972, 1982; Rasmussen et al., 2017). In this region, the middle-toupper Miocene Ngorora Formation has recently been characterized as a fossil fish *Lagerstätte*, in particular for cichlid fossils (Rasmussen et al., 2017). The timespan represented by the Ngorora Formation covers a period of major rifting activity in East Africa and corresponds to the supposed onset of diversification of the modern cichlid fauna (Koblmüller et al., 2008; Danley et al., 2012). It thus covers a crucial phase in the evolution of cichlids.

The objective of this study is to present new fossil cichlids from the Ngorora Formation, including a new genus represented by two new species and one specimen left in open nomenclature. The new fossils all possess the only proposed morphological synapomorphy of the Haplotilapiini, i.e. tricuspid teeth in the inner row of their dentition (Schliewen and Stiassny, 2003), and thus constitute the oldest reliably identified fossil record of a haplotilapiine yet discovered. Furthermore, evidence is presented that document its affinity with the monotypic tribe Etiini.

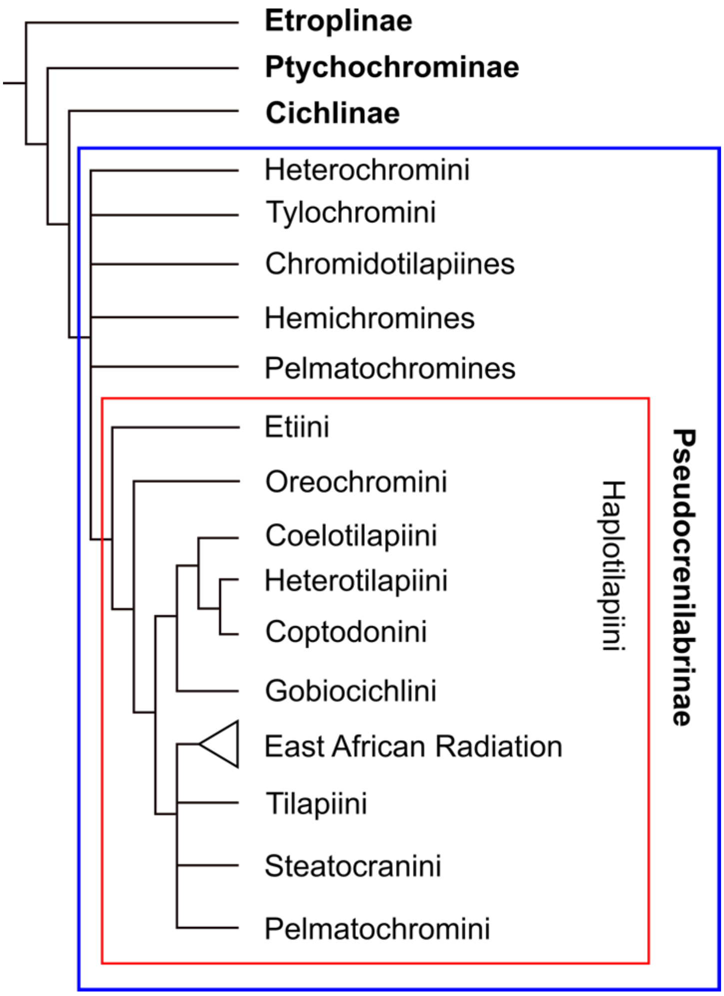

Figure 1. Simplified composite cladogram depicting possible relationships among the Cichlidae, based on Sparks and Smith (2004), Schwarzer et al. (2009) and Dunz and Schliewen (2013). The clade of the East African Radiation has been collapsed, as it contains numerous tribes.

2.1.1. Geological setting

The Tugen Hills in Central Kenya reach a maximum height of 2400 m and the range extends for about 100 km N–S. This area is tectonically situated within the Gregory Rift, which is part of the eastern branch of the East African Rift System, and stretches over 900 km from Lake Turkana (4°30´N) to northern Tanzania (2°S) (Smith, 1994; Hautot et al., 2000; Rasmussen et al., 2017). The Tugen Hills expose volcanic rocks alternating with fluvial and lacustrine sediments, and represents one of the most complete Miocene-to-Pliocene successions in Africa (Hill, 2002). The Ngorora Formation, which yielded the new cichlid fossils described in this study, covers the timespan between c. 13.3 and 9 MYA (Rasmussen et al., 2017). The rocks of the Ngorora Formation itself consist mainly of volcanic tuffs interleaved with fluvial or lacustrine silts and clays (Bishop and Chapman, 1970; Bishop and Pickford, 1975). The palaeoenvironmental settings it documents include lakes and floodplains that developed in a highly dynamic environment characterized by ongoing tectonic activity and frequent explosive volcanism (Rasmussen et al., 2017).

2.1.2. Study site

The study site is the Rebekka section, which is located near the Rebekka School in the Tugen Hills, west of the towns of Kamelon and Kipsaraman in Baringo County, Kenya. The section is a natural outcrop in a gorge and exposes about 11 m of siltstone and sandstone, which are followed by about 30 m of alluvial fan deposits. A map and a stratigraphic log of the section are provided in Rasmussen et al. (2017:figs. 2, 8). According to Rasmussen et al. (2017), the Rebekka section corresponds to the uppermost middle or lowermost upper Miocene (c. 11 MYA). Complete fish fossils have been recovered exclusively from the bottom of the section, from a green-to-grey, laminated siltstone with some brown-coloured lapilli. The lamination of the siltstone, together with the fact that complete fish fossils are found in it, suggest anoxic water at the bottom of a lake, while the lapilli inclusions indicate volcanic influences.

2.2. Materials and methods

2.2.1. Fossil material

The material described here consists of three articulated specimens, each of which is preserved in part and counterpart (indicated as a and b, respectively). All fossil specimens are laterally compressed; the slab against which the right side of the fish is pressed is termed the ‘‘right slab’’ and its counterpart is the ‘‘left slab’’; bones from both flanks can be found on each slab, depending on the precise plane of cleavage. The collection numbers are OCO-3-3a-b, OCO-3-4a-b and OCO-3. The prefix OCO stands for ‘Orrorin Community Organisation’. The specimens are currently housed at the Department of Earth and Environmental Sciences, Ludwig-Maximilians University Munich. They will be deposited in Kipsaraman, Baringo County, Kenya, as soon as the new Baringo County Geopark has been established.

2.2.2. Comparative material

Sixteen formalin-preserved specimens of *Etia nguti* Schliewen and Stiassny, 2003, deposited in the Bavarian State Collection of Zoology, Munich, Germany (ZSM- 039623_1 to 5, ZSM-043183_n27, -n28, ZSM- 029429; ZSM-P029430_1 to 5; ZSM-029431_1, -2, ZSM-036648); X-rays from 44 species representing nine haplotilapiine tribes (see Online Resource 2).

2.2.3. Methods

The fossil specimens were treated with Mowilith (a polyvinyl acetate) diluted in acetone, and were prepared under a stereoscopic microscope (Leica M165 C), using fine carbide needles (0.17–1 mm in diameter) which were mounted on mechanical pencils for ergonomic reasons. Areas of special interest (e.g. head, caudal fin) were drawn in Inkscape (http:// inkscape.org) based on composite microphotographs (stacked and stitched together in Adobe Photoshop, https://www.adobe.com/products/photoshop.html) taken using a Leica M170 HD camera mounted on the same microscope.

X-rays of formalin-fixed specimens of the comparative material were taken at the Bavarian State Collection of Zoology in Munich with a Faxitron UltraFocus digital X-ray cabinet.

Measurements were taken digitally in ImageJ (https://imagej.nih.gov/ij/) from photographs in the case of fossils, or from the X-rays in the case of the extant specimens. Measurements are shown in Fig. 2. Tests for allometric effects were done with the program Past3 (https://folk.uio.no/ohammer/past/). All measurements were compared pairwise with the standard length. Both sets of measurements were log– log transformed and linearly regressed by the least squares method. The bootstrapped (N = 1999) 95% confidence intervals of the slope were determined and examined to ascertain whether they included the expected slope of one (1).

Counts of vertebrae include the terminal centrum; abdominal vertebrae are characterized by the absence of a closed haemal arch (according to Barel et al., 1977). Dorsal and anal fin ray counts included every discernible ray associated with a pterygiophore; since the last two rays of the dorsal and anal fin share one pterygiophore, they were counted as one ray. The terminology of specific features of the bones (e.g. processes, crests) is illustrated in Fig. 2b.

2.2.4. Abbreviations

Abbreviations for measurements (Fig. 2a). SL, standard length; BL, body length; HL, head length; prD, predorsal distance; prV, prepelvic distance; prA, preanal distance; Llj, length of lower oral jaw; ED, horizontal eye diameter; pro, preorbital distance; HD, head depth; H1, maximum body height (usually just behind the head); H2, maximum body height at anal fin origin; h, minimum body height at the level of the caudal peduncle; lpc, length of caudal peduncle; pD, postdorsal distance; LA, length of anal fin base; LD, length of dorsal fin base; LDsp, length of spinous dorsal fin base; LDrs, length of soft dorsal fin base.

Anatomical abbreviations. aa, anguloarticular; br, branchiostegal rays; c 5, fifth ceratobranchial; cl, cleithrum; co, coracoid; dent, dentary; dpcl, dorsal postcleithrum; ecp, ectopterygoid; enp, entopterygoid; ep, epural (number); fr, frontal bone; gra, gill rakers; H, hypural plate (number); hb, hyoid bar; hm, hyomandibular; hp, hypurapophysis; hs, haemal spine of preural centrum (number); iop, interopercle; le, lateral ethmoid; mx, maxilla; na, nasal; ns, neural spine of preural centrum (number); op, opercle; ph, parhypural; plcr, principal caudal rays; pmx, premaxilla; pop, preopercle; prcr, procurrent caudal rays; ps, parasphenoid; ptt, posttemporal; pu, preural centrum (number); q, quadrate; rart, retroarticular; s, symplectic; sc, scapula; snr, supraneurals; soc, supraoccipital crest; sop, subopercle; stg, stegural; u, urostyle; uh, urohyal; vo, vomer; vpcl, ventral postcleithrum.

2.3. Results

2.3.1. Variation of selected characters in extant haplotilapiine cichlids

To provide a context for the taxonomic assignment of the fossils described below, the dentition of six *Etia* individuals was studied, and the maximum width of every exposed tooth was measured (Fig. 3a–c and Online Resource 1). Tooth width generally declines from the outer to the inner rows, and also towards the lateral edges of the mouth (Fig. 3b), and the difference in width between the largest and the smallest teeth may be up to 100% in large (>100 mm) specimens. The smaller specimens (<50 mm) show a greater degree of variability, with the largest teeth being around 2.5–3 times wider than the smallest (but those are the ‘‘outliers’’ in any case). As a result, there is usually some overlap in size between the smallest teeth of the outer row and the largest teeth of the inner row(s) of the same jaw (upper or

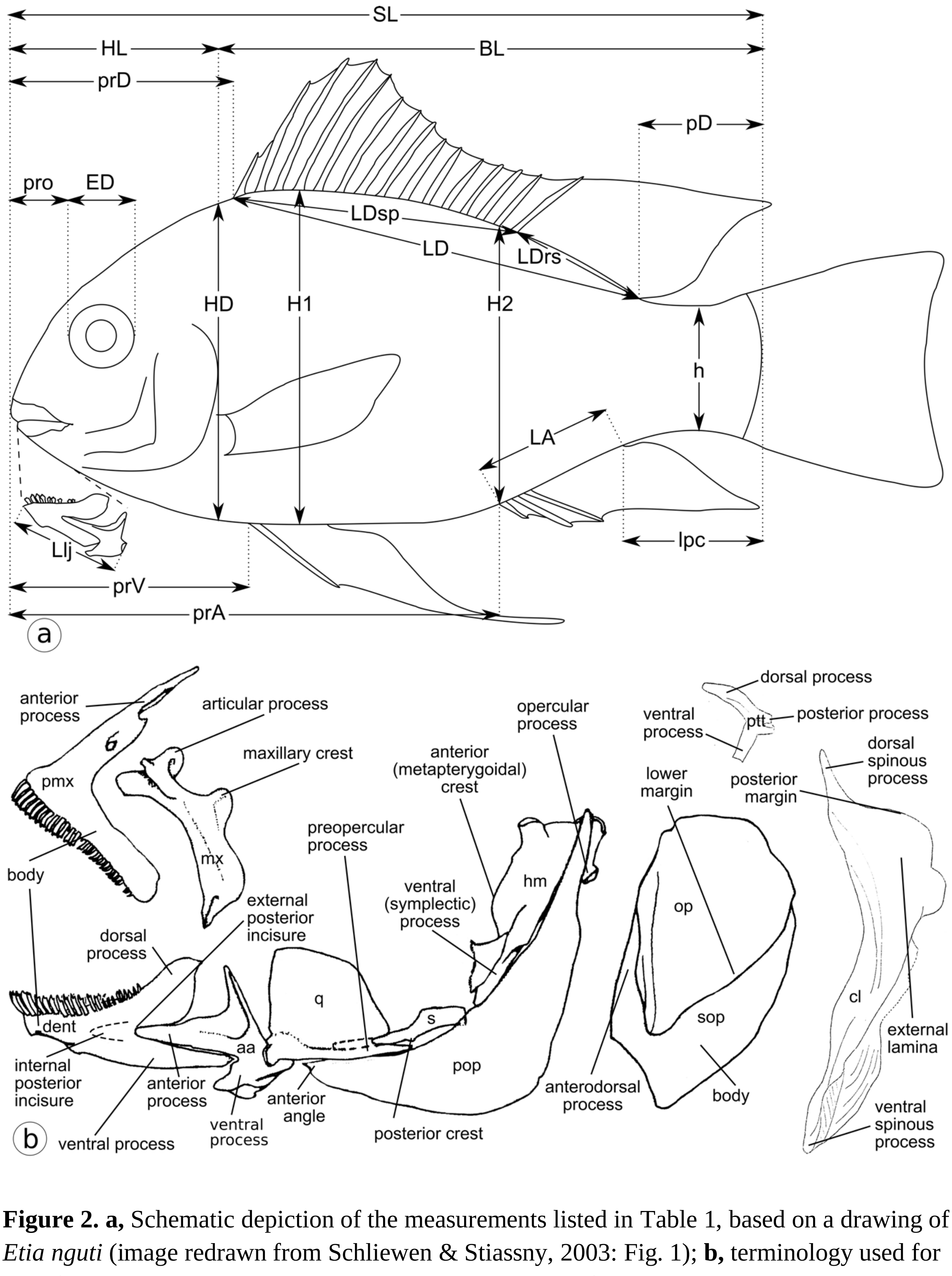

Figure 2. a, Schematic depiction of the measurements listed in Table 1, based on a drawing of *Etia nguti* (image redrawn from Schliewen & Stiassny, 2003: Fig. 1); **b,** terminology used for specific bones in the osteological descriptions (drawings of cleithrum and postcleithrum are modified after Van Couvering,1972, the rest of the bones are modified after Oliver, 1984). For explanation of the abbreviations, see ‘‘Materials and methods’’ section.

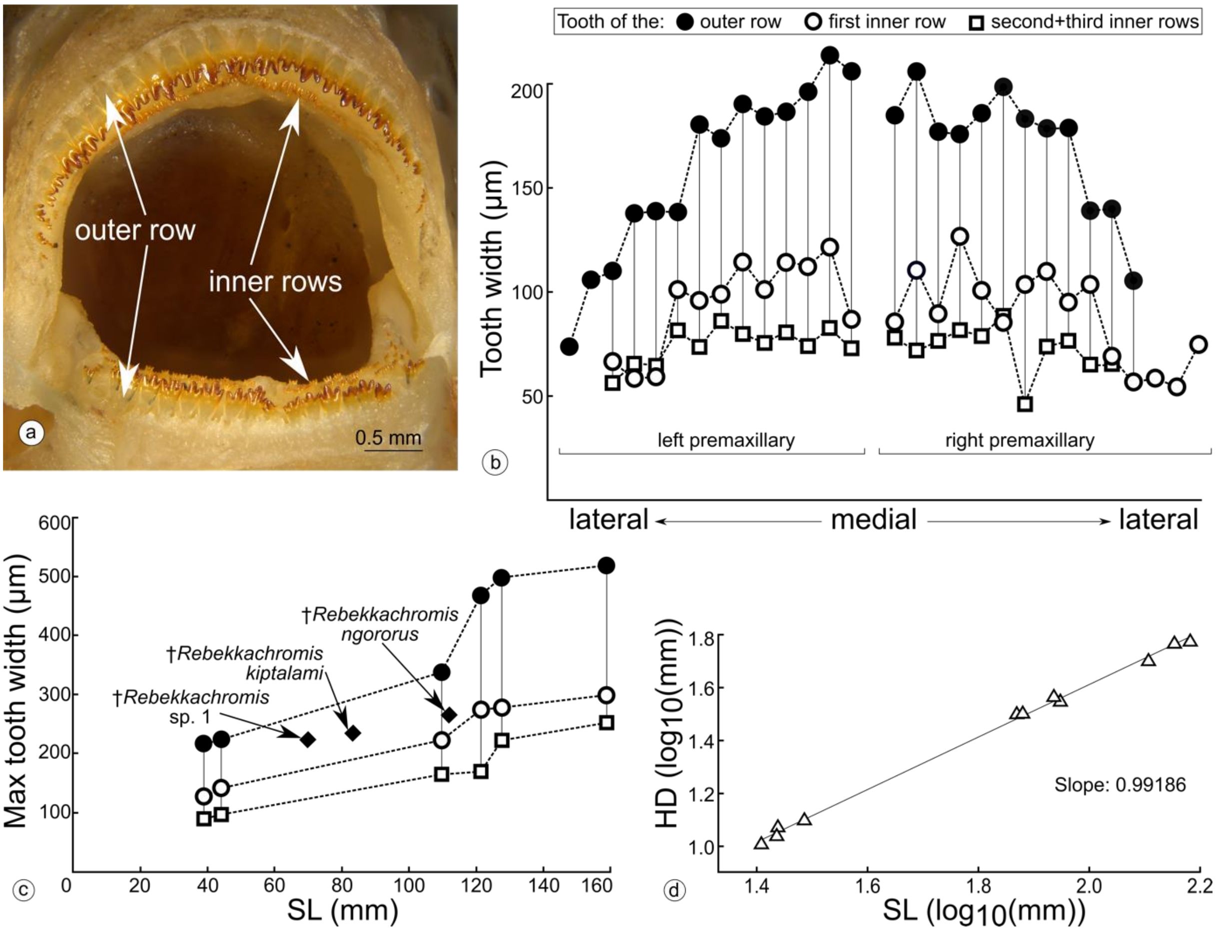

Figure 3. Comparison between the dimensions of the oral teeth of *Etia* and †*Rebekkachromis* gen. nov.; **a,** Dentition of a young *Etia nguti* (ZSM-043183_n27, SL = 44 mm) showing tricuspid and a few bicuspid teeth in the outer row of its dentition and exclusively tricuspid teeth in the inner rows; **b,** Tooth widths of all the teeth of the upper jaw of a young *Etia nguti* (ZSM-043183_n28, SL = 39.2 mm), each dot (black disc, white disc, white square) represents the row in which a tooth is situated (outer, first inner, second + third, respectively); **c,** Graph of the maximum transversal width of the teeth of *E. nguti* relative to SL, compared to the widest tooth found in each specimen of †*Rebekkachromis* (dots of different colours denote rows as in b); **d,** log–log graph of the head depth (HD) to standard length (SL)in *E. nguti*, with the line fitted by the ordinary least-squares method

lower) (Fig. 3b). On average, teeth from the upper jaw are wider than those of the lower jaw (Fig. 3a; Online Resource 1). The teeth in the inner rows are always tricuspid. Most of the teeth in the outer row are tricuspid in younger specimens (<45 mm SL, see Fig. 3a), and these are partially replaced by bicuspid teeth in older individuals (>50 mm) (see also Schliewen and Stiassny, 2003).

In addition, the number and morphology of the supraneural bones and possible anomalies were studied, based on X-rays from 44 species representing nine haplotilapiine tribes (Online

Resource 2). As expected from previous works, a single supraneural is usually present in all species except in *Etia nguti*, which possesses two supraneurals. Apart from the only example of *Oreochromis tanganicae* Günther, 1894, which we examined, on the order of 10% of the specimens of *Tilapia baloni* Trewavas and Stewart, 1975 and *T. sparrmanii* Smith, 1840 studied show a reversion to two supraneural bones. In the specimens of *T. baloni* and *T. sparrmanii*, the second supraneural is much smaller than the first and placed posteroventrally to it. In the single specimen of *O. tanganicae*, the second supraneural is not only smaller than the first, but is also placed posterodorsally to the latter, and its ventral tip seems less ossified than the dorsal tip. Furthermore, the relative length of the supraneural(s) is rather consistent within a species, and only a few individuals have supraneurals which, compared with the rest of their species, are significantly reduced in size [e.g. *Oreochromis amphimelas* (Hilgendorf, 1905)]. The inclination of the supraneural (anteriorly, posteriorly), its degree of convexity (bent or straight), as well as the presence and position (anteriorly, posteriorly, absent) of overhanging crests at its dorsal end, are variable (Online Resource 2).

Lastly, the pattern of allometry during growth in *Etia* was examined. Eleven *Etia* specimens were selected to cover a range from sexually immature to large adult individuals (26–152 mm, see Schliewen and Stiassny, 2003). The measurements BL, pro, LD and LDsp scaled hyperallometrically with SL, while prD, prV, ED, LDpr scaled hypoallometrically. All other measurements (HL, PrA, Llj, HD, H1, H2, h, pD, lpc, LA) scaled isometrically (see Fig. 3d for HD, and Online Resource 3 for the rest).

2.3.2. Systematic Palaeontology

Cichlidae Bonaparte, 1835
Pseudocrenilabrinae Fowler, 1934
Haplotilapiini Schliewen and Stiassny, 2003

†*Rebekkachromis* Kevrekidis, Valtl and Reichenbacher, gen. nov.

Generic Diagnosis—†*Rebekkachromis* differs from all other fossil and extant African cichlid species, except *Etia* Schliewen and Stiassny, 2003, in that it possesses the unique combination of two supraneural bones and robust tricuspid oral teeth in the outer row of the dentition. However, it also differs from *Etia* in the following characters: (i) the spines of the dorsal fin of †*Rebekkachromis* increase in length from the first to the last, whereas those of *Etia* generally become progressively shorter posterior to the third or fourth spine (Fig. 2a); (ii) in

†*Rebekkachromis,* unlike *Etia*, the pelvic fin does not reach the point of insertion of the anal fin, and the dorsal and anal fins do not extend to the posterior end of the hypural plates; (iii) the third and fourth hypurals are fused in †*Rebekkachromis*, but are separate in *Etia*; (iv) †*Rebekkachromis* has a vertebrae count of about 30 vs. 26 in *Etia*.

Etymology—‘‘Rebekka-’’ refers to the type locality of this genus, which is named after the nearby Rebekka School near Kipsaraman (Baringo County) in the Tugen Hills, Kenya. Historically, ‘‘-chromis’’ is a common second element in many cichlid genera and is derived from the ancient Greek word ‘‘χρόμις’’, meaning marine fish. Gender masculine.

Type Species—†*Rebekkachromis ngororus*, sp. nov.

†*Rebekkachromis ngororus* Kevrekidis, Valtl and Reichenbacher, sp. nov.

(Figures 4, 5; Online Resources 4, 5, and so on.)

Holotype—OCO-3-3a, b. A nearly complete skeleton in part and counterpart (Fig. 4a, b).

Diagnosis—Same as for the generic diagnosis. In addition, (i) the anterior angle of the preopercle is rounded and (ii) the spines of the third preural vertebra do not reach the procurrent rays (Figs. 4d, 5).

Etymology—The name ‘‘*ngororus*’’ refers to the Ngorora Formation, where the specimen was found.

Type locality and age—Kenya, Tugen Hills, Ngorora basin, Ngorora Formation, site Rebekka (0°44.772′N, 35°47.1366E), 11 MYA.

General description—Approximately 135 mm in total length and 112 mm standard length (Table 1). The head is large, comprising about 41% of standard length. The mouth is slightly open. The body is nearly straight. Most of the bones of the skeleton, particularly those of the head, are on the right slab (Fig. 4a); in the left slab (Fig. 4b) several bones can be recognized, mostly by their impressions in the sediment. The skeleton is nearly completely preserved, except for the ventral- and dorsalmost parts of the head, which broke off and were lost during the excavation.

Neurocranium—Fragments of the frontal bones are discernible, but their precise outline is not clear, because the neurocranium is crushed. The straight, elongate anterior part of the parasphenoid is recognizable, as is the triangularly shaped nasal.

Jaws—The body of the right premaxilla is preserved in dorsoventral view, and part of the left premaxilla lies posterior to it. Fragments representing the posterior and anterior portions of the left maxilla are preserved; judging from the orientation of the left fragment,

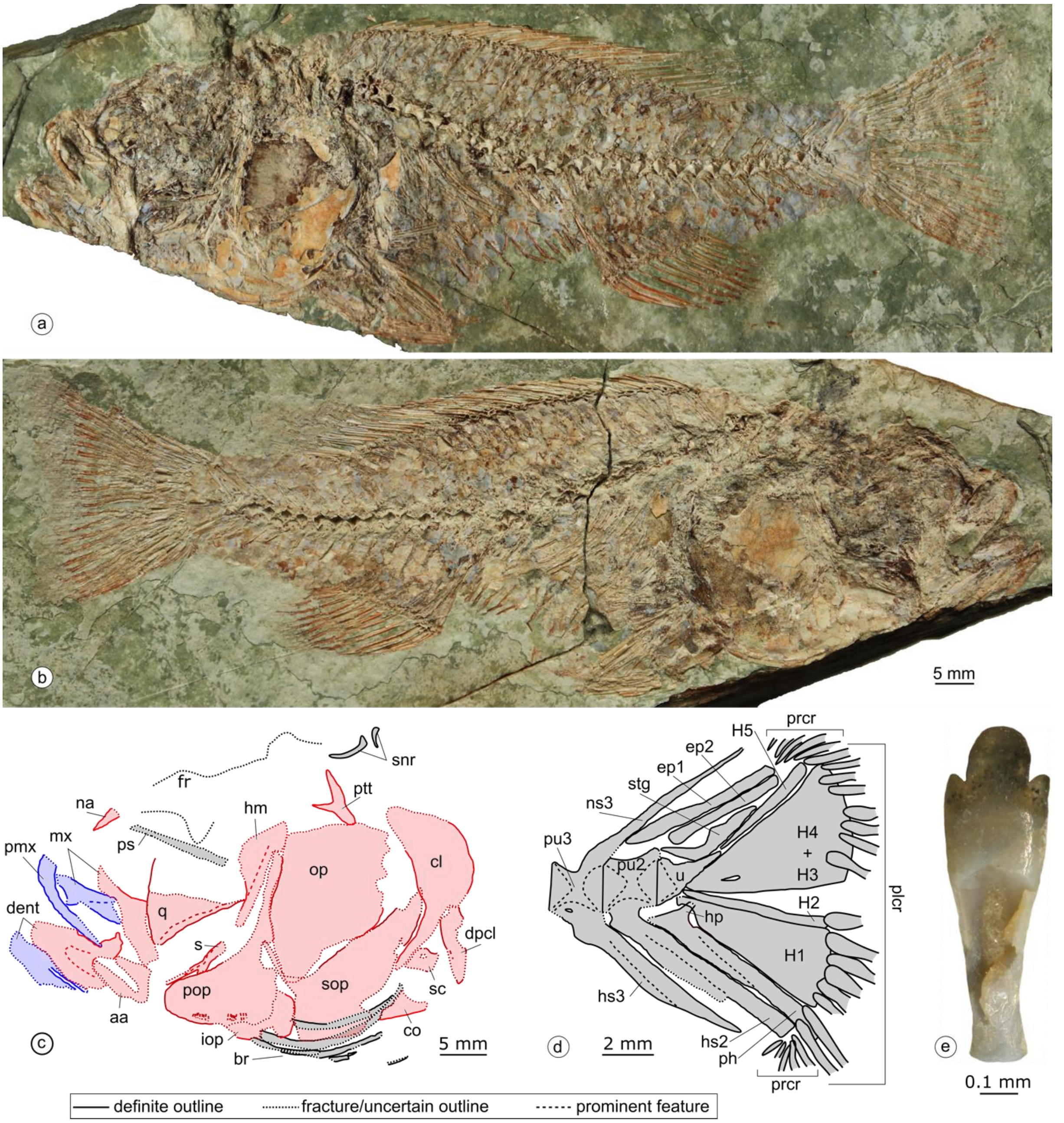

Figure 4. a, b, Holotype of †*Rebekkachromis ngororus* sp. nov. preserved on the right (a) and the left (b) slab; **c,** composite drawing of the most important bones of the head (blue denotes that the depicted elements come from the right slab, red from the left); **d,** drawing of the caudal fin; **e,** isolated tricuspid tooth, probably from the outer row of the dentition. For abbreviations of bones, see ‘‘Materials and methods’’ section.

these two parts must have formed an angle of 150°. Based on a fragment of the right maxilla that is flipped upside-down, so that its lateral side is exposed on the right slab, it is evident that the anterior portion is almost as long as the posterior and has a prominent ridge running from the ventral to the dorsal margin, probably terminating under the maxillary crest. The latter is convex posteriorly and concave anteriorly. Immediately in front of the right premaxilla are 11 isolated tricuspid teeth. Given their position and the fact that their distal portions are all directed ventrally, they most probably derive from one of the premaxillae. Their maximum width is 259µm, and their maximum width to maximum length ratio is about 0.3. The median cusp has a rounded outline and is notably wider and higher than the other two (Fig. 4e).

Both left and right dentary bones are well preserved, except for the posteriormost parts of the dorsal and ventral processes. Both anguloarticulars are in anatomical connection with the dentaries; only an anterior fragment of the anterior process of the right anguloarticular is preserved, but the length of the dentary-anguloarticular can be estimated from the left anguloarticular, of which the posterior part is better preserved. On this basis, the distances from the anterior tip of the dentary to the beginning of the internal posterior incisure, and to the external posterior incisure roughly correspond to 30 and 51%, respectively, of the entire dentary-anguloarticular length (Llj, see Fig. 2a).

Suspensorium and opercular series—Part of the left quadrate is discernible, with a robust preopercular process. The left symplectic is very well preserved. The posterior one-third of the bone is broad and mediolaterally flattened. The ventral margin is slightly convex, while the dorsal margin dips sharply one-third of the way from the posterior end, so that the anterior portion of the bone is rod-shaped. A thin groove begins at the dorsolateral margin of the posterior third of the symplectic and becomes more prominent anteriorly. The symplectic has a prominent posterior crest, which is convex posteriorly and concave anteriorly. The left hyomandibular has a long and robust ventral (symplectic) process and an anterior (metapterygoidal) crest which curves gently upwards, and the hyomandibular's opercular process is in contact with the opercle.

The left preopercle (length-to-height ratio = 0.6) has a rounded anterior angle (Fig. 5) and is ornamented with short radiating striae near its ventral margin. The interopercle is rounded posteriorly, and extends behind the preopercle. The opercle (length-to height ratio = 0.7) has an irregular pentagonal shape, and the ventral part of the anterior margin meets the lower margin at an angle of 60°. The body of the subopercle is preserved, along with a fragment of the anterodorsal process; together they form an angle of about 85°.

Hyoid and branchial arches—Fragments of five left branchiostegal rays are visible. Above them is another branchiostegal ray, probably from the right side.

Vertebral column—There are at least 28 and more probably 29 vertebrae, of which 13 are abdominal and 16 caudal. The exact number of abdominal vertebrae is not clear, as the first few are crushed and overlap with the bones of the head. There are more than nine pairs of ribs, but no epineurals are discernible. There are two supraneural bones. The anterior one is long and convex anteriorly (Figs. 4c, 5). The second supraneural is about one-third the length of the first and convex anteriorly (Figs. 4c, 5).

Pectoral girdle and fins—Both posttemporal bones are preserved and are Y shaped (only the left is shown in Fig. 4c for reasons of simplicity). The posterior process is short and stub shaped; the dorsal process is longer and more robust than the ventral process, and they form an angle of about 70°. The supracleithrum is not discernible. The cleithrum is a bent bone with a rounded and low dorsal spinous process, a broad external lamina and a convex posterior margin; most of the ventral half of the bone is missing. Under the external lamina of the cleithrum, part of the left dorsal postcleithrum is visible. It is a broad bone, with a heavily ossified anterior margin, and it tapers gently to a rounded ventral spinous process.

The exact shape of the scapula is not clear, but it appears to be quadrilateral and has a prominent foramen. A triangular fragment of the coracoid is visible, but it provides no further information. The pectoral fin comprises more than ten rays.

Pelvic girdle and fins—The basipterygia are broad and are oriented at approximately 45° to the horizontal plane. Their tips are not visible, as they extend under the subopercle. In each pelvic fin, there is one spine and five rays, which do not reach the anal fin (Fig. 5).

Dorsal and anal fins—In both fins, the rays do not extend to the level of the hypural plates. The dorsal fin comprises 13 spines and ten rays. These elements are each supported by one pterygiophore, except for the last two rays, which share a pterygiophore (and are therefore counted here as one ray). The length of the dorsal spines generally increases from the first to the last. The pterygiophore of the last dorsal spine is associated with the 12th vertebra.

The anal fin has three spines and nine rays. Most of these elements are supported by one pterygiophore each, except the first two spines and the last two rays (counted as one), which share a single pterygiophore. The spines increase in length posteriorly, as do the first six rays, while the remainder show a progressive decrease in length.

Caudal endoskeleton and fin—There are 16 (8 upper, 8 lower) principal rays, of which the uppermost and lowermost are unbranched, and about ten (5? upper, 5 lower) procurrent rays. The haemal spine of the third preural vertebra is about twice as broad as the corresponding neural spine, and neither reaches the procurrent rays. The parhypural is a long robust bone, its proximal end extending almost to the second preural centrum and urostyle (Fig. 4d). The parhypural has a broad hypurapophysis that extends laterally to the proximal tip of hypural 1, but its exact length is not known because it is broken. The bodies of both the

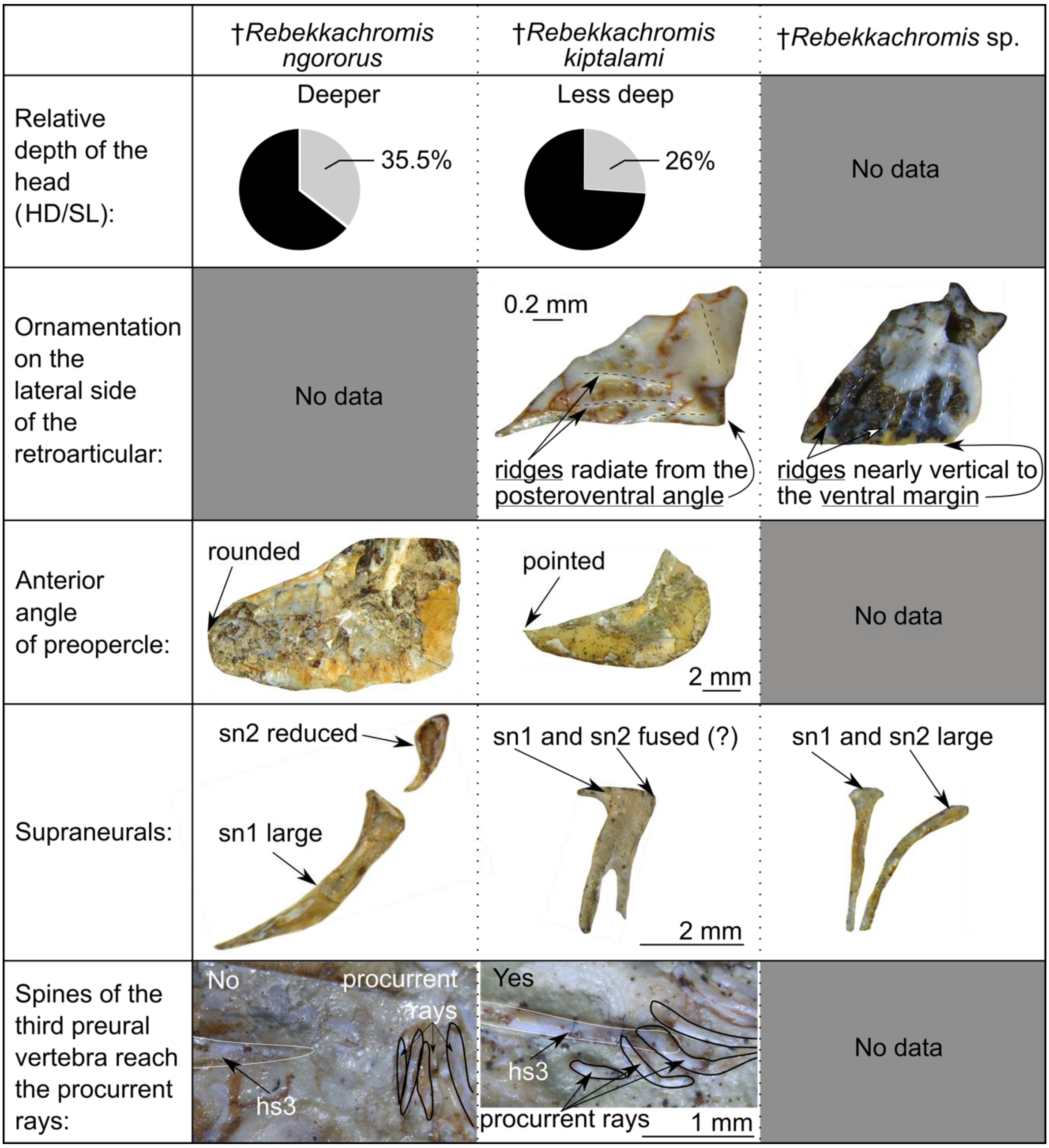

Figure 5. Summary of the main differences between the fossil species of †*Rebekkachromis* gen. nov. The retroarticular of †*Rebekkachromis* sp. and the photo of the procurrent rays of †*R. ngororus* are inverted for easier comparison with the rest. For the abbreviations of the bones, see ‘‘Materials and methods’’ section.

parhypural and the haemal spine of the second preural vertebra are made up of tubular bone, which gradually transitions into a thin bony flap anteroventrally.

The ventral margin of hypural 1 is excavated proximally (Fig. 4d). Hypural 2 is slender. The diastema, which is 1.4 mm wide, begins at 16% of the distance between the proximal and distal tips of the hypurals. Hypurals 3 and 4 are represented by a single robust bone, with a

Table 1. Meristic counts for the fossils and, for comparison, the extant *Etia nguti*. An asterisk (*) indicates data from Schliewen and Stiassny (2003).

Characters	†*Rebekkachromis ngororus* (OCO-3-3a, b)	†*Rebekkachromis kiptalami* (OCO-3-6a, b)	†*Rebekkachromis* sp. 1 (OCO-3-4a, b)	*Etia nguti* (n=8)
Total of vertebrae (abdominal, caudal)	29? (13?, 16)	30 (14, 16)	22+ (30 est.) (14, 10+)	26 (14, 12)
Position of vertebra associated with last dorsal fin spine	12? (not last abdominal)	14 (last abdominal)	14 (last abdominal)	14 (last abdominal)
Dorsal fin formula (spines, rays)	XIII, 10	XIV, 9	XIII, 10	XV, 9
Anal fin formula (spines, rays)	III, 9	III, 9	III, 7	III, 6-7
Pelvic fin formula (spines, rays)	I, 5	I, 5	I, 4+	?
Pectoral fin rays	10+?	15+?	13?	15
Principal caudal fin rays (upper + lower)	16 (8 + 8)	16 (8 + 8)	—	16 (8, 8)*
Procurrent caudal fin rays (upper + lower)	10? (5?, 5)	12 (6, 6)	—	10-11 (5-6, 5)
Gill rakers of the lower limb of the first gill arch	—	14? (not certain if this is the first gill arch)	—	14-16*
Branchiostegal rays	4 or 5	—	4?	5*

small suture in the proximal part. Hypural 5 is club shaped, and its proximal end is near the urostyle (Fig. 4d).

The ventral margin of the stegural is thickened and the dorsal margin is thin. Proximally, the stegural seems to be L shaped. Both epurals are rod shaped, but epural 1 is longer than epural 2 and extends further ventrally; also, the dorsal margin of its proximal half is expanded and thinner than the rest of the bone.

Squamation—Cycloid scales cover the body from behind the orbit to the end of the hypural plates. In the posterior portions of the scales, there are 8–16 circuli, which branch into up to 50–60 in the middle of the scale, and anteriorly there are 13–16 radii. Medially, the centre of the scales is granulated. The posteriormost nine scales of the upper lateral line are visible, the last of which is situated between the neural spines of the first and second caudal vertebrae. The upper lateral line is separated from the dorsal margin of the body by two or three scale rows. Longitudinally, immediately above the vertebral column, there are around 29 scales, and seven to eight scales vertically separate the upper lateral line from the beginning of the anal fin. In most extant cichlids, the posteriormost scales located in the middle of the body form the lower lateral line. The body of the specimen examined here is split along the sagittal (median) plane, and on both slabs, these scales are concealed by the vertebrae. Consequently, it is not possible to recognize the lower lateral line.

†*Rebekkachromis kiptalami* Kevrekidis, Valtl and Reichenbacher, sp. nov.

(Figures 5, 6; Online Resources 6, 7)

Holotype—OCO-3-6a, b. A nearly complete skeleton in part and counterpart (Fig. 6a, b).

Diagnosis—Same as for the genus, and it differs from †*R. ngororus* in the following characters: (1) the anterior angle of the preopercle is pointed, and (2) the spines of the third preural vertebra reach the procurrent rays (Fig. 6d).

Etymology—Species named in honour of Lukas and Nancy Kiptalam, in recognition of their great support of our fieldwork in the Tugen Hills.

Type locality and age—Same as for †*R. ngororus*.

General description—The total length of the holotype (OCO-3-6a, b) is approximately 105 mm and the standard length 85 mm. The mouth is closed, the body is straight and the head has a triangular shape. On the right slab (Fig. 6a) most of the dorsal margin of the posterior portion is missing, while on the left slab (Fig. 6b), the most notable absences are the ventral margin of the head and most of the anal fin.

Neurocranium—The frontal is crushed, but parts of it are still discernible. The slender parasphenoid is preserved in its entire length. It is not keeled and its ventral margin is almost straight. The pharyngeal apophysis is very weak and at least its anterior half is composed entirely of the parasphenoid. The vomer is slightly displaced from its original position, and its margins have the following configuration: acutely angled anteriorly, straight dorsally, convex posteriorly and concave ventrally. In front of the vomer, there is a nasal bone, seen possibly in lateral view, since it appears slender and elongate. Anterior to the orbit is a fragment of the right lateral ethmoid.

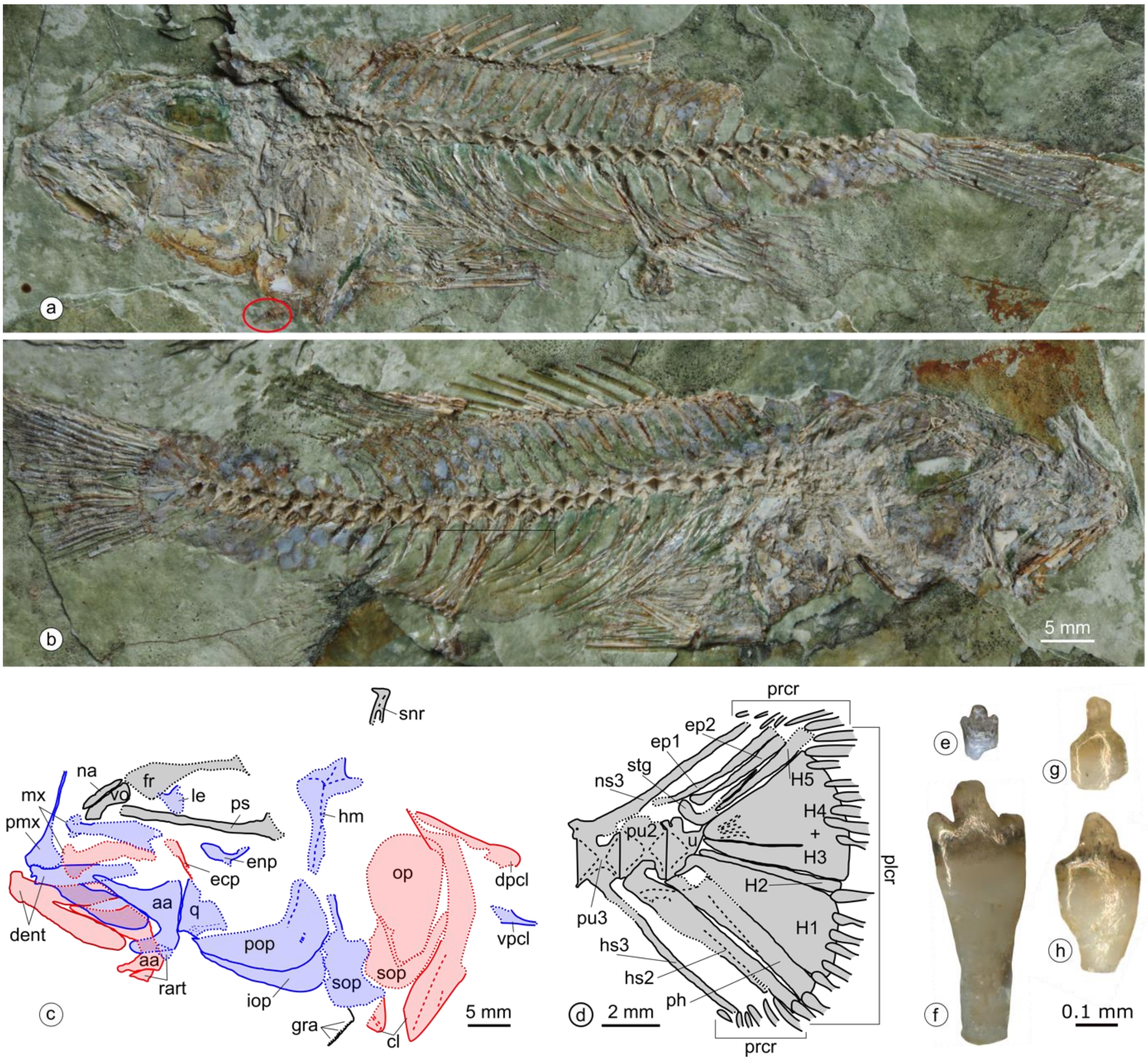

Figure 6. a, b, Holotype of †*Rebekkachromis kiptalami* sp. nov. preserved on the right slab (a, the red circle denotes the protruding ceratobranchial with the gill rakers) and the left slab(b); **c,** Composite drawing of the most important bones of th ehead from both slabs; **d,** Drawing of the caudal fin; **e,** Small tricuspid oral tooth, from one of the inner rows; **f ,** Large tricuspidoral tooth, probably from the outer row; **g, h,** Large oral teethwith single prominent cusp. Colours and dash styles of the drawn lines as in Fig. 4. For the abbreviations of the bones, see ‘‘Materials and methods’’ section.

Jaws—The slender anterior process and the anterior angles of the left and right premaxillae are recognizable. Fragments of both left and right maxillae are preserved. They show a well-developed articular process and an angle of 130° between their anterior and posterior parts. Left and right dentaries and anguloarticulars are joined to each other and appear to be preserved in their original anatomical connection, along with the left retroarticular. The posterior tip of the ventral process of the dentary is rounded, and the length of the internal posterior incisure is equivalent to 28% of the total dentary-anguloarticular length (Llj, see Fig.

2a). The anguloarticular has a slender anterior process and an elongate ventral process, which forms an angle of about 48° with the anterior process; the dorsal process is not discernible. The retroarticular is roughly triangular, with the posterior and ventral margins being roughly equal in size (Figs. 5, 6c). Four or five ridges radiate from the posteroventral angle of the retroarticular on its lateral surface (Figs. 5, 6c). Its posterior margin is almost straight, except for the lower third, which is excavated. Between the anterior tip of the dentaries and the premaxillae, there are numerous tricuspid teeth, which resemble those of †*R. ngororus* (Fig. 6e, f). The largest tricuspid tooth is 227µ wide, which is 33% of its total length, and the smallest is 91µm wide. Both large and small (i.e. less than half the width of the large) tricuspid teeth are found at the anterior part of the premaxilla. In addition, there are a few teeth with one protruding cusp; the largest of these is 203µm wide (Fig. 6h). They are anteroposteriorly flattened and have a wide base, while the distal portion tapers sharply to end in a prominent, rounded cusp, which is very similar to the medial cusp of the tricuspid teeth (Fig. 6g, h).

Suspensorium and opercular series—The anteroventral corner of the right quadrate forms a distinct projection. Fragments of the ecto- and entopterygoids as well as the hyomandibular are discernible. The preopercle has a pointed anterior angle (Figs. 5, 6c). Parts of the right (not drawn in Fig. 6c) and the left opercle and both subopercula are preserved, and it is estimated that the anteroposterior length of the opercle is about 70% of its maximum dorsoventral length.

Hyoid and branchial arches—The branchial arches are compacted under the opercle and therefore no details can be seen. However, a single ceratobranchial protrudes ventral to the head and bears 14 short gill rakers (Fig. 6a, c).

Vertebral column—There are 30 vertebrae in total, 14 abdominal and 16 caudal. There is a single supraneural element which splits into two branches ventrally and has a prominent overhanging crest anterodorsally (Figs. 5, 6c). It is not clear whether this is one bifurcated bone or two supraneural bones which were fused together. The latter scenario is favoured here, because the bone is much wider anterodorsally than is usual for cichlid supraneural bones, and there is a low crest running from the top of the bone up to the fork.

Pectoral girdle and fins—The left cleithrum is a broad, bent bone with a pointed ventral tip. The left dorsal postcleithrum is displaced dorsally from its original position and it is probably flipped upsidedown. If so, then the anterior margin is straight, except for its lowermost part, which is slightly expanded and rounded. The upper- and lowermost parts of the right ventral postcleithrum are missing, but it is evident that the bone was expanded dorsally, tapering to a tubeshaped lower part. There are at least 15 rays on the pectoral fin.

Pelvic girdle and fins—The basipterygia are poorly preserved, but they are broad, triangular bones that extend for some distance under the cleithrum. The pelvic fins have one spine and five rays, terminating before the anal fin.

Dorsal and anal fins—There are 14 spines in the dorsal fin and nine rays; only the most proximal parts of the last five rays are preserved. The pterygiophore of the last dorsal spine is associated with the 14th vertebra, which is also the last abdominal vertebra. There are three spines and nine rays in the anal fin. Other features of the dorsal and anal fins of †*R. kiptalami* resemble those of †*R. ngororus,* as described above.

Caudal endoskeleton and fin—In number, the principal caudal fin rays are identical to those of †*R. ngororus,* and the parhypural, hypurals 2 and 5, and the second epural are configured as in †*R. ngororus*. There are six procurrent caudal rays in both the upper and the lower series. The haemal spine of the third preural vertebra is almost as thick as the corresponding neural spine, and both are in contact with the procurrent rays (Fig. 5). The haemal spine of the second preural vertebra is distally bifurcated, which might represent a developmental anomaly. Hypural 1 has a straight ventral margin. There is no diastema between hypurals 2 and 3, but it cannot be excluded that this is a taphonomic artefact. Hypurals 3 and 4 are fused together only in their distal thirds. The stegural seems to be proximally hook shaped. Epural 1 is rod-like throughout its length, with no proximal expansions.

Squamation—The scales are cycloid and resemble those of †*R. ngororus,* but they are sparser and less well preserved. They extend from just behind the orbit (at least) and cover the hypural plates. Posteriorly there are five to eight circuli and anteriorly 10–13 radii. The middle and posterior central portions of their medial side are granulated, but this granulation does not reach the posterior margin. The last scale of the upper lateral line lies between the fourth and fifth caudal vertebra; besides that, no more than four other scales of the upper lateral line are preserved. The scales of the lower lateral line are obscured, as in the specimen of †*R. ngororus*.

†***Rebekkachromis*** **sp.**

(Figures 5, 7; Online Resources 8, 9)

Specimen—OCO-3-4a, b. Skeleton in part and counterpart (Fig. 7a, b).

Locality and age—Same as for †*R. ngororus.*

Remark—The condition of this specimen does not permit it to be attributed to a species, but it is believed to belong to the genus †*Rebekkachromis* because all the parts that are well preserved (supraneurals, dentition, pelvic fin, dorsal spines, estimated vertebrae number) show the diagnostic features of the genus. It is described here since it provides additional information on the osteology of the genus †*Rebekkachromis*.

General description—The preserved length is about 60 mm. The mouth is slightly open and the dorsal and ventral outlines of the head are straight. This specimen lacks the caudal fin and its head is cleaved along the mid-sagittal plane, unlike all other specimens recovered from this locality, where most of the bones of the head are on one or other of the slabs. Therefore, it is difficult to discern the outer surfaces of most bones, but some bones are better preserved than in the two species of †*Rebekkachromis* described above, e.g. the dorsal postcleithrum. Moreover, the orientation of the plane of cleavage reveals structures which are usually obscured, such as the pharyngeal teeth (Fig. 7f, g) and the branchial bar (Fig. 7c).

Neurocranium—The supraoccipital crest is low and forms a prominent concavity posteriorly. Parts of the frontal and the parasphenoid are discernible. The dorsal and ventral margins of the vomer appear to be straight and run almost parallel, and the anterior end is rounded. Behind the vomer and above the parasphenoid a fragment of the right lateral ethmoid can be seen.

Jaws—The right premaxilla is quite well preserved and its entire anterior ramus is about as long as the body of that bone. The lower left dentary is in place and probably in connection with the corresponding anguloarticular. The left retroarticular is connected to the anguloarticular and is ornamented with five nearly vertical ridges, which are situated above the ventral margin on its lateral side (Fig. 5). Numerous tricuspid teeth (Fig. 7d, e) are preserved in the mouth region, the largest of which measures 218µm in width and the smallest 99µm. Large and very small teeth are found side-by-side on the premaxillary, and especially in its anteriormost part.

Suspensorium and opercular series—The symplectic is partially preserved but may be flipped upside-down. Its elongate anterior portion curves ventrally, forming an angle of about 140° with the posterior, expanded part. Fragments of the left interopercle and subopercle are visible, but convey little information.

Hyoid and branchial arches—The right hyoid bar is discernible and comprises the anterior and posterior ceratohyals, and probably also the dorsal and ventral hypohyals, although exact delimitation of these bones is difficult. At least four branchiostegal rays can be

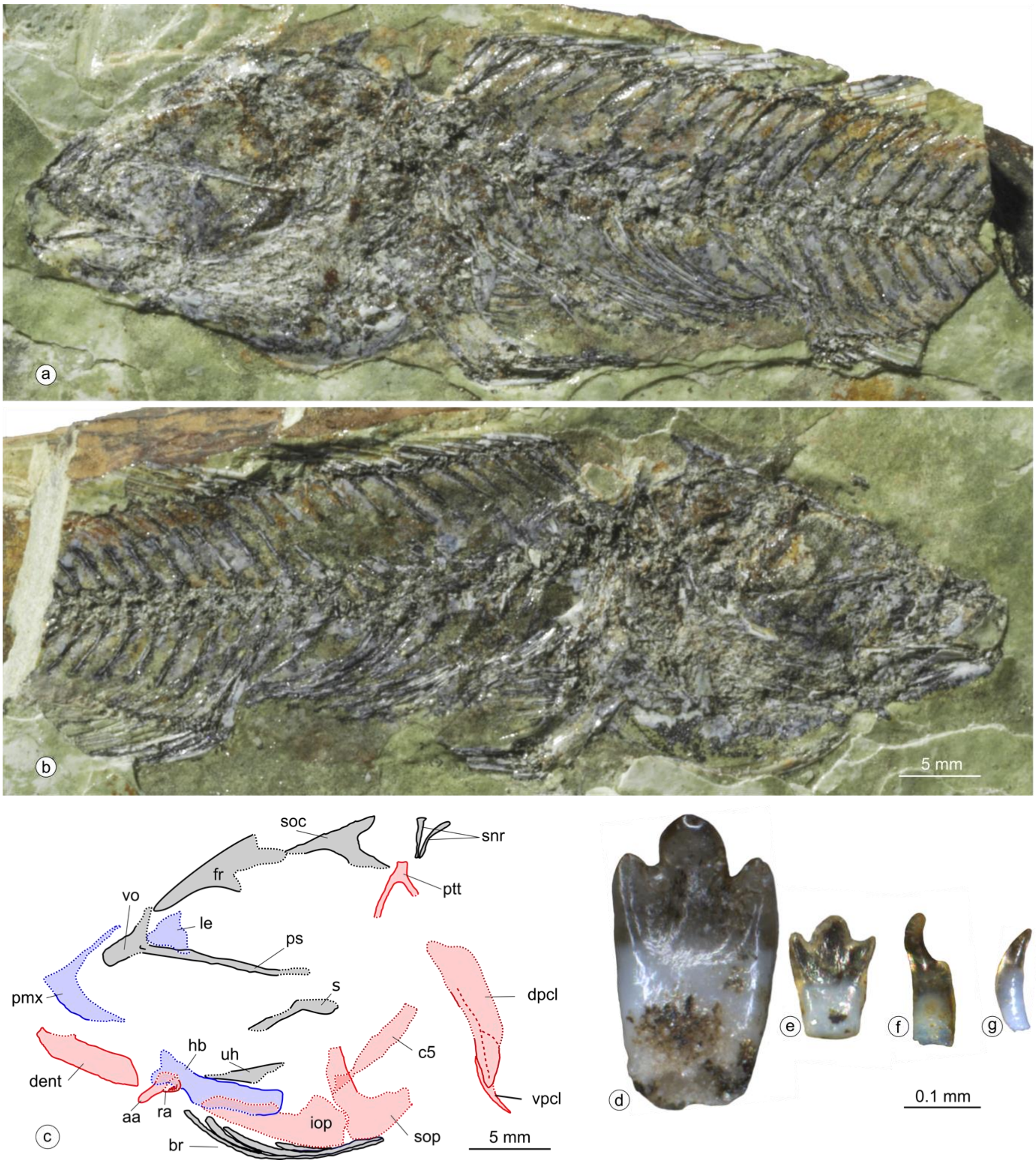

Figure 7. a, b, Specimen of †*Rebekkachromis* sp. preserved on the right (a) and the left (b) slab; **c,** composite drawing of the most important bones of the head from both slabs; **d,** large tricuspid oral tooth, probably from the outer row; **e,** small tricuspid oral tooth from one of the inner rows; **f,** bicuspid pharyngeal tooth; **g,** unicuspid ‘‘kukri-shaped’’ pharyngeal tooth. Colours and dash styles of the drawn lines as in Fig. 4. For the abbreviations of the bones, see ‘‘Materials and methods’’ section.

discerned below it. Behind the hyoid bar is a fragment of the central portion of the urohyal, dorsal and ventral margins of which form an angle of 17°. The left ceratobranchial 5 appears to have a ventral tip which is slightly expanded in the sagittal plane. There are numerous hook-shaped bicuspid (Fig. 7f) and ‘‘kukri’’-shaped (sensu Greenwood, 1987), unicuspid pharyngeal teeth (Fig. 7g) concentrated in two pockets above ceratobranchial 5; judging from their placement, they probably represent epibranchial teeth.

Vertebral column—There are 14 abdominal and more than 10 caudal vertebrae. The supraneurals are long, slender and of nearly equal length; the first supraneural is straight and the second is bent, with the convex side facing anteriorly (Figs. 5, 7c).

Pectoral girdle and fins—The dorsal and ventral processes of the posttemporal form an angle of 60°. Dorsally, the left dorsal postcleithrum is incomplete, but seems to have a rounded tip, after which it broadens sharply. This bone is long and broad (max depth/max length = 0.22), consisting mostly of flat, thin bone, except for the anterior margin, which is heavily ossified, forming a hollow tube that runs along its entire length. The distal tip of the dorsal postcleithrum is oar shaped with a pointed tip, and it overlaps the dorsal part of the left ventral postcleithrum. The ventral postcleithrum is half the length of the dorsal postcleithrum and is curved and anteriorly convex. Dorsally it is broad, while its ventral half is conical and tapers to a pointed tip. There are at least 13 rays in the pectoral fin.

Pelvic girdle and fins—The basipterygia are long, triangular bones that extend to the gill cover. The pelvic fin has one spine and at least four rays, and it terminates before the beginning of the anal fin.

Dorsal and anal fins—The dorsal spine has 13 spines and ten rays, and the pterygiophore of the last dorsal spine is associated with the 14th vertebra, which is the last abdominal vertebra. The anal fin has three spines and seven rays. The distal ends of the dorsal and anal fins are not preserved, but otherwise the structure of these fins is the same as in †*R. ngororus*.

Squamation—The body is covered with cycloid scales, beginning behind the middle of the orbit. Posteriorly they have 11–16 circuli that branch into as many as 30 in the middle portion, and more than eight radii anteriorly. The scales between the head and the beginning of the pelvic fin, and those behind the supraoccipital crest are smaller than the rest. The anterior scales of the upper lateral line are not visible, but the last eight are recognizable; the last one is located between the neural spines of the first and second caudal vertebrae. The scales of the lower lateral line are obscured, as in †*R. ngororus*.

Comparisons—The ridges on the lateral side of the retroarticular have a different orientation from those of †*R. kiptalami* (Fig. 5), but the retroarticular is not preserved in †*R. ngororus*. In addition, †*Rebekkachromis* sp. has two clearly separate supraneurals (Figs. 5, 7c), the first of which does not differ much from that of †*R. ngororus*. If the reduced second supraneural seen in †*R. ngororus* is an aberration and not the rule for this species, then †*Rebekkachromis* sp. may be attributable to †*R. ngororus*.

2.4. Discussion

2.4.1. Comparisons between the fossil specimens

Morphometrically, the two named species of †*Rebekkachromis* are similar, with 15 out of 18 measurements, normalized to SL, differing by less than 5% (Table 1, Online Resource 3). The three remaining normalized measurements, of which the differences between the two species exceed the aforementioned value, are all related to depth, namely head depth (HD; 9.5%), maximum body height (H1; 10.4%) and maximum body height at anal fin origin (H2; 5.7%). It is worth noting that these are the only normalized measurements that fall outside the measured range of the examined *Etia* specimens (Online Resource 3). However, since each species of †*Rebekkachromis* is represented by only one specimen, the degree of intraspecific variability cannot be determined for these species at the moment. In addition, although HD, H1 and H2 are isometrically linked to SL in *Etia* (Fig. 3d, Online Resource 3), this may have not have been the case in †*Rebekkachromis*, and thus we cannot exclude the possibility that the observed morphometric differences between †*R. ngororus* and †*R. kiptalami* resulted from allometric growth. Not only is †*R. ngororus* larger than †*R. kiptalami* (SL = 112 vs 85 mm), but there is also some evidence that this difference in size could be related to age: the maximum number of circuli on the scales of the former is double than that of the latter (16 vs. 8).

There are other differences between the fossil specimens of which the taxonomic importance cannot be fully evaluated. For example, the two equally long supraneurals of †*Rebekkachromis* sp. (Figure 5) resemble those of *Etia* (Online Resource 2). However, it is not clear if the fusion of the two supraneurals of †*R. kiptalami* (Fig. 5), or the reduced posterior supraneural of †*R. ngororus* (Fig. 5), are the normal states for the respective species or whether these cases represent developmental anomalies. No fusion or bifurcation has been observed in the *Etia* specimens of our comparative sample, but the reduced posterior supraneural of †*R. ngororus* is reminiscent of the atypical second supraneural found in some individuals of the *Tilapia baloni*, *T. sparrmanii* and *Oreochromis tanganicae* (Online Resource 2) specimens examined. Nevertheless, given that the two species of †*Rebekkachromis* and also †*Rebekkachromis* sp. possess two supraneurals, it seems likely that their presence is normative for this fossil taxon and not an exceptional state, as for the aforementioned extant haplotilapiines.

Moreover, †*R. ngororus* and †*R. kiptalami* show two main differences that support our taxonomic interpretation that they represent distinct species. One difference is that the neural and haemal spine of PU 3 each support procurrent rays in †*R. ngororus*, whereas this is not the case in †*R. kiptalami* (Fig. 5). Interspecific variation in relation to this character has been reported in cichlid species by Sebilia and Andreata (1991). Based on their results, the aforementioned difference between the two fossil species of †*Rebekkachromis* can be interpreted as taxonomically significant.

The second main difference between †*R. ngororus* and †*R. kiptalami* is the shape of the anterior angle of the preopercle (rounded vs. pointed, see Fig. 5). A similar difference has been used to distinguish three different species of haplotilapiines, belonging to different genera (Dierickx et al., 2017). Consequently, the difference in the anterior angle of the preopercle also appears compatible with the identification of two different fossil species.

2.4.2. Interpretation of the dentition in †*Rebekkachromis*

In cichlids that have multiple rows of teeth in the oral dentition, most of the teeth in the inner row(s) are about half the size (or less) of those in the outer row (e.g. Trewavas, 1973; Tichy and Seegers, 1999; see Online Resource 1). As noted above (see ‘‘Variation of selected characters in extant haplotilapiine cichlids’’), size alone does not suffice to assign a tooth to a row, as the teeth of the outer row found nearer the lateral extremities of the mouth are similar in size to the medially located teeth of the inner row(s) (Fig. 3b; Online Resource 1). The smallest tricuspid teeth in †*R. kiptalami* and †*Rebekkachromis* sp. are less than half the size of their largest teeth (Figs. 6e vs. f and 7e vs. d, respectively) and both are found side-by-side in the anterior part of the premaxillaries. Therefore, the smallest teeth in these fossil species most likely come from one of the inner rows and the largest from the outer row.

Moreover, the comparative material implies that *Etia nguti* of comparable standard length has inner row teeth (which are all tricuspid) that are significantly smaller than the largest tricuspid teeth seen in †*Rebekkachromis* (see Fig. 3c), further supporting the notion that †*Rebekkachromis* had tricuspid teeth in the outer row of its dentition.

In addition, †*R. kiptalami* also has large teeth that have a single protruding cusp (see Fig. 6g, h). The single cusp of these teeth might be the result of the wearing out of lateral cusps, as can be expected in teeth of the outer row (see Trewavas, 1973). The implication is that these ‘‘unicuspid’’ teeth also come from the outer row.

2.4.3. Classification at family level

Crown Cichlidae are defined by a number of synapomorphies which either refer to soft-tissue characters or to hard-tissue characters that are rarely fossilized (see Stiassny, 1991; Casciotta and Arratia, 1993b). Nevertheless, the caudal skeleton of †*Rebekkachromis* exhibits several characters which, in combination, are diagnostic for the family Cichlidae (see Barel et al., 1976; Sebilia and Andreata, 1991; Takahashi and Nakaya, 2002). These are: seven branched fin rays in each lobe, five hypurals, two epurals, a free first stegural, a second preural vertebra lacking a neural spine but with a neural arch, and a third preural centrum fused to its haemal spine. Moreover, Cichlidae possess a divided lateral line that is characterized by an upper segment, which runs above the vertebral column, and a lower one located at the level of the vertebral column (Webb, 1990). In our †*Rebekkachromis* specimens, the lower segment cannot be discerned owing to the preservation state of the relevant body parts, but the upper lateral line segment is clearly detectable.

2.4.4. Classification at subfamily level

Based on molecular data, four subfamilies can be recognized within the Cichlidae: the Etroplinae (limited to Madagascar and Southern Asia), the Ptychochrominae (restricted to Madagascar), the Pseudocrenilabrinae (restricted to Africa and the Middle East), and the Cichlinae (restricted to the Neotropics) (Cichocki, 1976; Stiassny, 1991; Sparks and Smith, 2004; Smith et al., 2008; see here Fig. 1). The Etroplinae are the sister taxon to the rest of the cichlids. The next node is the split between the Ptychochrominae and the sister taxa Pseudocrenilabrinae and Cichlinae (Sparks and Smith, 2004).

The Malagasy/Indian/Sri Lankan subfamily Etroplinae is well defined based on 31 morphological characters (Sparks, 2008). At least five of these characters are clearly visible in †*Rebekkachromis*. According to Sparks (2008), etroplines have a deeply keeled parasphenoid (vs. nearly straight in †*Rebekkachromis*), the symplectic bears serrations along its ventrocaudal margin (vs. smooth), the ventral spinous process is peglike (vs. pointed), ‘‘the anterior anal fin pterygiophores insert into slots formed by laminar expansion of the anterior haemal spines’’ (vs. not), and ‘‘the anterior anal fin pterygiophores are compressed and dorsocaudally directed’’ (vs. not compressed and anteriorly directed). Therefore †*Rebekkachromis* cannot be considered to be a member of the Etroplinae.

The three fossil species of †*Rebekkachromis* all have tricuspid oral teeth in both the outer and inner rows of their dentition. Consequently, †*Rebekkachromis* cannot be a representative of the Malagasy subfamily Ptychochrominae, whose members display bicuspid or unicuspid teeth in their oral dentition; tricuspid teeth have not been observed in these taxa so far (Reinthal and Stiassny, 1997; Sparks and Reinthal, 2001; Stiassny and Sparks, 2006; Sparks, 2008).

There are no known morphological synapomorphies that define the Neotropical subfamily Cichlinae (Kullander, 1998; Sparks and Smith, 2004; see also Smith et al., 2008). However, Neotropical cichlids may have unicuspid, bicuspid or spatulate, blade-like teeth but, for all their diversity, no known extant or fossil Neotropical cichlid has tricuspid teeth in the inner or outer row of the dentition (Casciotta and Arratia, 1993b), with the sole exception of *Herotilapia* Pellegrin, 1904 (see McMahan et al., 2015). †*Rebekkachromis* is clearly dissimilar from *Herotilapia*, since the latter is diagnosed by the possession of many (10–13) anal fin spines and the association of five anal fin pterygiophores with the first haemal spine (see Schmitter-Soto, 2007). In conclusion, there are no firm grounds for placing †*Rebekkachromis* in the Cichlinae.

The last cichlid subfamily, the Pseudocrenilabrinae from Africa and Arabia, is also diagnosed based on characters of bones which are usually not preserved well enough, if at all, in fossils, e.g. the entopterygoid or the first epibranchial bone (see Stiassny, 1990, 1991). Nevertheless, within the Pseudocrenilabrinae, the monophyly of their largest lineage, the Haplotilapiini, is supported both by molecular analyses and the ‘‘presence of a tricuspid inner row dentition’’ (Schliewen and Stiassny, 2003, p. 69; see also Schwarzer et al., 2009; Dunz and Schliewen, 2013). Since †*Rebekkachromis* possesses this character, it can be assumed to be a haplotilapiine and a member of the Pseudocrenilabrinae.

2.4.5. Tentative classification within the Haplotilapiini

Within the Haplotilapiini the standard configuration is one supraneural bone and the only species with a normative set of two supraneurals is *E. nguti* (Schliewen and Stiassny, 2003). The two species and the additional specimen of †*Rebekkachromis* possess two supraneurals as well, and it therefore seems likely that their presence is normative for this fossil taxon and not an abnormal state, as in the case of some of the examined extant haplotilapiines (see the section ‘‘Comparisons between the fossil specimens’’). The possession of two supraneurals may therefore imply an affinity between †*Rebekkachromis* and *E. nguti.*

Moreover, the dentition of †*Rebekkachromis* may provide additional support for this hypothesis. Among the Haplotilapiini (see Fig. 1), the Oreochromini, Coelotilapiini, Heterotilapiini, Tilapiini, Steatocranini and Pelmatolapiini have mainly unicuspid and/or bicuspid oral teeth in the outer row of their oral dentition (Dunz and Schliewen, 2013; not enough information is available to specify the disposition for the remaining tribes). However, several haplotilapiine species, which are not closely related to each other, can also show tricuspid teeth in the outer row, as in †*Rebekkachromis*. Among these are *Etia nguti* (see above and Schliewen and Stiassny, 2003), some species of Oreochromis (see Tichy and Seegers, 1999), and also some species of *Petrochromis* (Tropheini, East African Radiation clade, see Yamaoka, 1983a). Generally, these teeth vary greatly in their shapes and proportions. The teeth of †*Rebekkachromis* are quite robust and this seems in conformity with the diagnosis of the genus *Etia*. According to Schliewen and Stiassny (2003, p. 63), *Etia* is ‘‘distinguished from all remaining African cichlids by the possession of some, or all, robust tricuspid teeth in the outer row oral dentition (vs. an unicuspid, bicuspid, or slender shafted, tricuspid outer row dentition)’’ (Schliewen and Stiassny, 2003, p. 63). Nevertheless, the utility of the morphology of cichlid teeth for cladistic purposes has not yet been thoroughly investigated, and thus additional data are necessary before the systematic placement of †*Rebekkachromis* can be reliably inferred. Until such time as the relationships of African cichlids are resolved based on morphological characters, †*Rebekkachromis* will be referred to as comparable to (‘‘cf.’’) Etiini.

2.4.6. Comparisons with previously described fossil cichlids

In the following, †*Rebekkachromis* is compared with previous descriptions of Pseudocrenilabrinae or Pseudocrenilabrinae- like fossil species that were based on articulated skeletons and also with some disarticulated remains that were left in open nomenclature. The comparison is presented in chronological order, from the Eocene to the Miocene.

From the middle Eocene (c. 46 MYA) of Tanzania five species of the genus †*Mahengechromis* Murray, 2000 have been described (Murray, 2000). They all have one supraneural, unicuspid oral teeth, ctenoid scales on their bodies and a comparatively small number of vertebrae (Murray, 2000, 2001a). They are thus very different from †*Rebekkachromis*, and their systematic placement within the Pseudocrenilabrinae is uncertain (Murray, 2001b). Isolated pharyngeal jaws with molariform teeth from the middle Eocene (c. 37–39 MYA) of Dur At-Talah, Libya (Otero et al., 2015) and the upper Eocene-lower Oligocene (33.77–35.12 MYA) of Fayum, Egypt (Murray, 2002) have been interpreted as possible members of the Tylochromini among the Pseudocrenilabrinae.

†*Macfadyena dabanensis* Van Couvering, 1982, from the Oligocene of the Daban Beds in Somalia, has two supraneural bones, but the oral teeth are conical and unicuspid, and no fusion is noted between hypurals 3 and 4 (Van Couvering, 1982). From the Upper Daban Series, the same author also refers to two additional, very incomplete specimens (C76109 and C76110), termed ‘‘form C’’ (Van Couvering, 1982). Specimen C76109 seems to have had two

supraneurals, but both specimens have ctenoid scales. Specimen C76110 has four spines on its anal fin, which itself extends beyond the beginning of the caudal fin, contrary to what is seen in †*Rebekkachromis*.

From the Oligocene–Miocene of Jordan a skeleton of a putative cichlid was described by Weiler (1970). According to its description (Weiler, 1970), it seems that neither its oral teeth nor its supraneurals are preserved, and it has a very low vertebra count, i.e. 23, relative to †*Rebekkachromis*. Some isolated tricuspid teeth were recovered from the same area (Weiler, 1970: plate 10, Figs. 15–17), but, as already noted by the author, they differ considerably from the tricuspid condition seen in modern African cichlids, and it is not possible to decide whether or not they represent cichlids.

From the Baid Formation of SW Saudi Arabia, which is probably lower Miocene in age (see Murray et al., 2017), at least three fossil fish species were reported based on incomplete specimens (Lippitsch and Micklich, 1998). According to the authors ‘‘the inclusion of the specimens into the family Cichlidae seems justified, but the final proof is still lacking’’. One species was referred to as a possible representative of the Heterochromini, because it most probably possesses two supraneurals and ctenoid scales. The second species displays cycloid scales on the soft rayed part of the dorsal fin, a condition not observed in †*Rebekkachromis,* and the number of anal fin spines is ?3 and 5 (Lippitsch and Micklich, 1998). The third species has ctenoid scales and probably separated hypural plates (Lippitsch and Micklich, 1998, p. 187). In conclusion, all three species clearly differ from †*Rebekkachromis*.

The basalmost Miocene (Lamitina beds, c. 22 MYA) of Uganda has furnished disarticulated remains of two or three species referred to as cf. *Pelmatochromis* (Van Couvering, 1982). The teeth that were recovered are all unicuspid. A lacrimal bone with six foramina is illustrated (Van Couvering, 1982: p. 37, Fig. 15c) but not described. Since no articulated bones were recovered from this locality (see Van Couvering, 1982), this lacrimal cannot be positively identified as belonging to a cichlid.

The lower Miocene Turkana Grits (17.5 ± 0.9–16.7 ± 0.8 MYA) near Loperot, Kenya have yielded several isolated bones of putative cichlids, as well as unicuspid to weakly tricuspid teeth and stout bicuspid teeth (Van Couvering, 1982). This tooth morphology is different from that seen in †*Rebekkachromis* (see Figs. 4e, 6e, f, 7d, e).

A further fossiliferous deposit from Kenya is the lower Miocene Kulu Formation (17–15 MYA, see Peppe et al., 2009, 2011). Four species have been reported (Van Couvering, 1982): †*Kalyptochromis hamulodentis* Van Couvering, 1982 was described based on a single specimen; it has two supraneurals, 30 vertebrae and cycloid scales. However, it differs from

†*Rebekkachromis* in a number of characters, such as the possession of seven or more branchiostegal rays, four or five anal fin spines and the fact that the only oral tooth recovered is bicuspid, with two equal cusps. The second species from the Kulu Formation is †*Nderechromis cichloides* Van Couvering, 1982. It differs from †*Rebekkachromis* in having conical unicuspid oral teeth and ctenoid scales. The third species, †*Palaeofulu kuluensis* Van Couvering, 1982, is similar to †*Rebekkachromis*, as it has two supraneurals, cycloid scales, and similar counts of rays in the dorsal (XII–XVI, 7–13) and anal (III–IV, 6–10) fins, as well as similar numbers of vertebrae (25–29) and branchiostegal rays (5). Nevertheless, it clearly differs from †*Rebekkachromis* in that the oral dentition consists of ''leaf-shaped'' unicuspid teeth in both the outer and inner rows, and only a few of these have a small second cusp. The fourth species is based on a partially articulated skeleton, termed ''form A'' by Van Couvering (1982). It has tricuspid teeth with equal cusps in the outer row of its dentition, and bicuspid teeth with unequal cusps in the inner row. This tooth disposition is again distinct from that of †*Rebekkachromis*.

The Kirimun Beds, near Kirimun, Kenya, probably belong to the middle Miocene (Van Couvering, 1982). Only isolated bones of fossil cichlids were recovered from these and described in open nomenclature as ''Cichlidae indeterminate—Group A'' by Van Couvering (1982). In addition, unicuspid, bicuspid and tricuspid teeth of putative cichlids were reported and found to be similar to the types described from Loperot (Van Couvering, 1982).

The middle-to-upper Miocene Ngorora Formation (13.3–7.8 MYA) has been described recently as a fossil fish *Lagerstätte*, with an abundance of fossil cichlids (Rasmussen et al., 2017). †*Sarotherodon martyni* Van Couvering, 1982 comes from the older part (≈ 12 MYA) of this formation. It shows similarities with †*Rebekkachromis* with respect to its meristic and morphometric parameters, and has one or two tricuspid teeth in the outer row of its dentition. However, there are clear differences between these two taxa. According to the description in Van Couvering (1982), the rest of the oral teeth from the outer row of †*S. martyni* are unicuspid, as are all of the teeth of the inner rows; moreover, †*S. martyni* has only one supraneural, and no fusion between hypurals 3 and 4 is mentioned. A further species recovered from the Ngorora Formation, albeit from the younger part (10–9 MYA), is †*Tugenchromis pickfordi* Altner, Schliewen, Penk and Reichenbacher, 2017. No oral teeth from this fish were recovered, but it clearly belongs to a lineage other than †*Rebekkachromis*, as it has only one supraneural and a tripartite lateral line, and hypurals 1 and 2 are fused, as are hypurals 3 and 4 (Altner et al., 2017).

The genus †*Palaeochromis* Sauvage, 1907 from the Seybouse Gypsiferous Marls of the upper Miocene ([7 MYA) of Algeria was re-examined by Van Couvering (1982) and comprises two species. †*Palaeochromis rouselleti* Sauvage, 1907 has bicuspid and tricuspid oral teeth and †*P. darestei* Sauvage, 1907 has leaf-shaped unicuspid and tricuspid oral teeth. These teeth are not illustrated in the published studies by Van Couvering (1982) and Sauvage (1907, 1910), and their dimensions and placement in the mouth are not known. Both species have one supraneural.

The upper Miocene sediments of the Sahabi Formation from Sahabi, Libya have yielded, among other vertebrates, isolated bones of fishes (Argyriou et al., 2012; Argyriou, 2014). From Member U-1 of this formation (Messinian, ca. 6.8 Ma, Boaz et al., 2008), an anguloarticular vertebra and a second vertebra have been attributed to cichlids (Argyriou, 2014). The anterior vertebrae of the †*Rebekkachromis* specimens are not well preserved, so they cannot be compared with the vertebra from Sahabi, but the anguloarticular from Sahabi seems to be different from those from Rebekka. Judging from the description and the figure (Argyriou, 2014:figs. 3–18), the anterior process of the anguloarticular of †*R. kiptalami* is more slender in form than that of the specimen from Sahabi, and the ventral process of the same bone is more elongate (both in †*R. kiptalami* and †*R*. sp.) and forms a more acute angle with the anterior process (in †*R. kiptalami*, condition unknown in †*R*. sp.) than that from Sahabi, which is almost vertical.

†*Oreochromis lorenzoi* Carnevale, Sorbini and Landini, 2003 was described from the upper Miocene (≈ 6 MYA) of the Gessoso-Solfifera Formation, Italy based on five complete or partial skeletons. It has one supraneural, cycloid scales, and its meristic counts are similar to those of †*Rebekkachromis* (Carnevale et al., 2003). It possesses numerous bicuspid and tricuspid oral teeth, the latter having cusps of equal length and thus differing from the tricuspid teeth of †*Rebekkachromis*. In addition, †*O. lorenzoi* is a deep-bodied cichlid (see figures in Carnevale et al., 2003), while †*Rebekkachromis* has a relatively slender body shape.

2.4.7. Reflections on the evolutionary history of the African cichlids

Species of African cichlids have been used as models in numerous studies designed to test the principles of speciation and theories of adaptive radiation (e.g. Seehausen, 2006). The evidence suggests that rapid and extensive speciation was related to intralacustrine allopatric divergence between habitat specialists in the large rift lakes, and that sympatric speciation may also have contributed to the species diversity in both large and small lakes (e.g. Turner et al., 2001). However, little is known as to when in the geological past speciation processes accelerated within the African Cichlidae, where this happened, and which mechanisms might have played a role. Here we show that the fossil record of cichlids from Africa, together with the results from this study, may offer a unique opportunity to address these issues from a palaeontological viewpoint. However, in this context it is also necessary to consider potential factors that may have prevented— or promoted—the preservation of freshwater fishes as fossils. As outlined by Otero (2010), two main types of sedimentary basins existed in Africa during the Miocene, namely (i) endorheic basins (e.g. Chad Basin), where shifts in climate and precipitation controlled the sedimentation; and (ii) basins that developed in the context of rifting (e.g. East African Rift Valley). Furthermore, other environments such as large floodplains vs. small lakes are also unequally preserved in the fossil record (Otero, 2010).

Nevertheless, the evidence suggests that a comparatively uniform Miocene fish fauna lived in the tropical rivers of North and Western Africa, and that extended and interconnected drainage systems existed in these parts of Africa at that time (Beadle, 1962, 1974; Otero and Gayet, 2001; Stewart, 2001; Murray et al., 2017). In contrast, the Pliocene freshwater fish faunas provide evidence for the emergence of distinct ichthyoprovinces, which in turn points to the development of new hydrological patterns that were related to the creation of the East African Rift valleys and subsequent volcanic activity (Roberts, 1975; Banarescu, 1995; Otero et al., 2009a, b, 2010a, b).

Notably, fossils of cichlids are relatively scarce in Oligocene to Pliocene freshwater fish assemblages from Africa (Fig. 8a). In addition, they are difficult to assign at the systematic levels of modern tribes or genera, because no matrix for phylogenetic analyses that is applicable to fossil material has yet been developed for them (see above) and little is known about the range of their osteological variation (see Trewavas, 1973). Morphological similarities between a given cichlid fossil and a modern tribe or genus have resulted in the tentative assignment of a number of fossil forms (e.g. Van Couvering, 1982; Micklich and Roscher, 1990; Lippitsch and Micklich, 1998), but it is not yet possible to rigorously evaluate whether these interpretations hold true. To cite Murray et al. (2017), ‘‘… it is generally not possible to determine which different cichlid taxa inhabited the various African Cenozoic sites.’’

However, the presence of tricuspid teeth in the inner row of the oral dentition, which has been suggested as a synapomorphy for the Haplotilapiini (see above and Schliewen and Stiassny, 2003), can be detected in well preserved fossils such as †*Rebekkachromis* gen. nov.

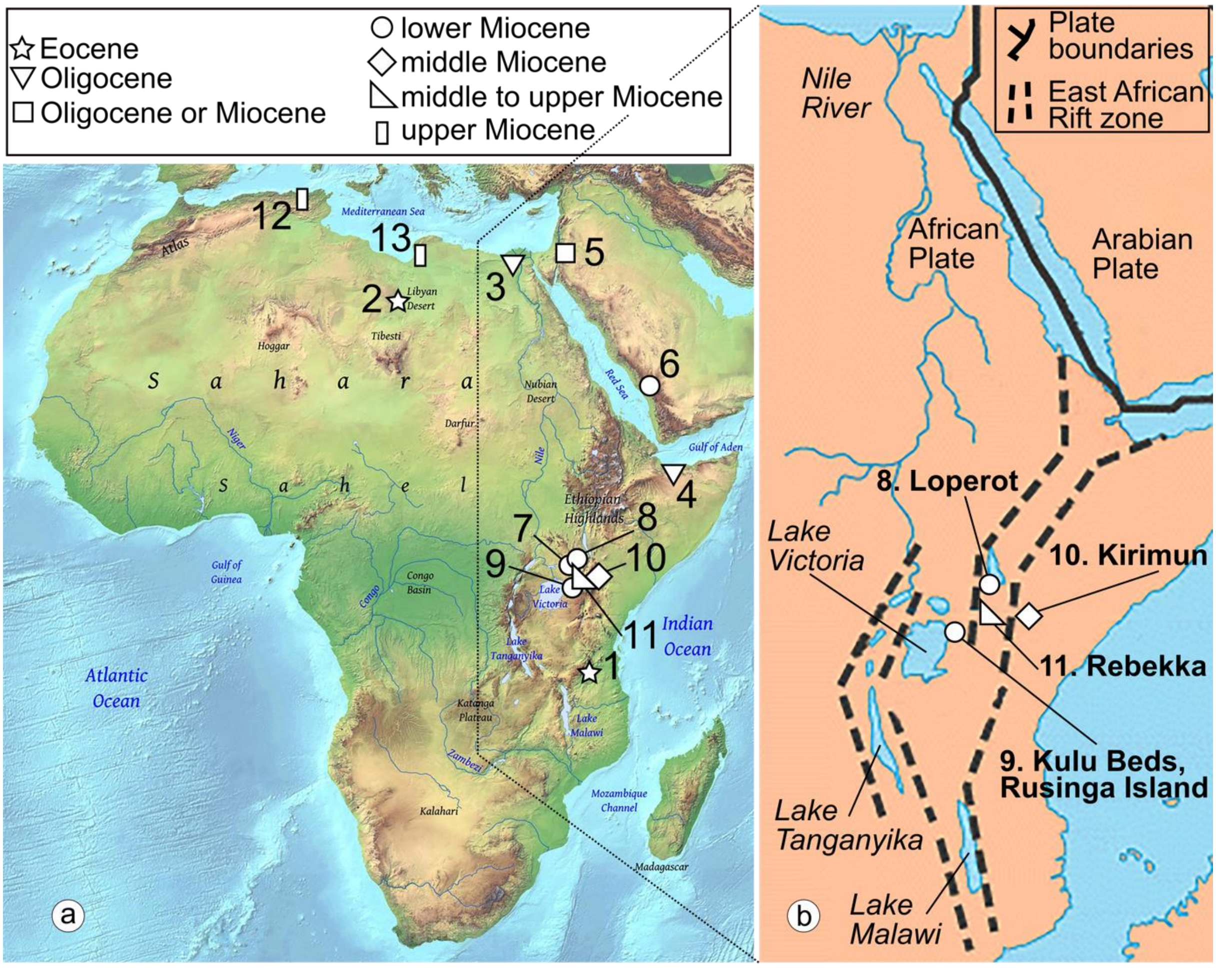

Figure 8. a, Map of Africa showing the distribution of the Eocene, Oligocene and Miocene localities that have yielded fossil cichlids based on articulated skeletal material (locs. 1, 4–6, 9, 11, 12) an disolated bones or dentition (2, 3, 7, 8, 10, 13); **b,** close-up of the East African Rift system depicting only those Miocene localities that have delivered cichlid fossils with tricuspid dentition: Loperot and Kirimun have yielded only isolated tricuspid teeth (Van Couvering, 1982); the Kulu Beds from Rusinga Island and Kapkiamu in the Tugen Hills delivered skeletal material having tricuspid teeth solely in the outer row of their dentition (‘‘form A’’ and †*Sarotherodon martyni*, see Van Couvering, 1982), and the Rebekka site (this study) is the single locality where tricuspid dentition could be recognized as belonging to the inner row of the dentition. Code for localities: 1 Mahenge, Tanzania (Murray, 2000); 2 Dur At-Talah, Libya (Otero et al., 2015); 3 Fayum, Egypt (Murray, 2002); 4 SE’ of Berbera, Somalia (Daban Fm, Van Couvering, 1982); 5 N’ of Shobak, Jordan (Weiler, 1970); 6 Ad Darb, Saudi Arabia (Baid Fm, Lippitsch and Micklich, 1998); 7 E’ of Bukwa, Uganda (Lamitina Beds, Van Couvering, 1982); 8 near Loperot, Kenya (Turkana Grits, Van Couvering, 1982); 9 Rusinga Island, Kenya (Kulu Fm, Van Couvering, 1982); 10 Kirimun, Kenya (Kirimun Beds, Van Couvering, 1982); 11 Tugen Hills, Kenya (Kapkiamu Shales, Van Couvering, 1982; Waril, Ngorora Fm, Altner et al., 2017; Rebekka, Ngorora Fm, this study); 12 near Guelma, Algeria (Seybouse Marls, Van Couvering, 1982); 13 Sahabi, Libya (Argyriou, 2014) Map sources: http://www.freeworldmaps.net/africa/ (a); https://upload.wikimedia.org (b)

(see Figs. 6, 7). It is notable that none of the comparably well preserved cichlid fossils known from the Eocene, Oligocene and lower to middle Miocene appear to have possessed this character (see above). The first record of tricuspid teeth—in the outer and not in the inner row of the oral dentition—refers to ‘‘form A’’ from the lower Miocene of Rusinga Island, Kenya (Van Couvering, 1982; see here Fig. 8a, b). Van Couvering (1982) also reported finds of isolated tricuspid teeth from Loperot (lower Miocene) and Kirimun (middle Miocene; see here Fig. 8b). Judging from her illustrations (Van Couvering 1982:fig. 35.1–2), these teeth are similar to those of the haplotilapiines, but it cannot be determined whether they are from the inner row of the oral dentition. †*Rebekkachromis* therefore represents the oldest haplotilapiine in which the synapomorphy ‘‘tricuspid teeth of the inner row’’ is definitely present and its age of c. 11 MYA can thus serve as minimum age for this clade.

To elucidate where the haplotilapiines might have emerged, the fossil record of Eocene to Miocene African cichlids has been plotted on a map (Fig. 8a). As explained above, the pattern obtained is certainly biased by the uneven distribution of appropriate sediments and also by unequal sampling efforts. But it is interesting that †*Rebekkachromis* comes from the Tugen Hills in the Central Kenya Rift valley, i.e. from the East African Rift System (Fig. 8b). During the middle and upper Miocene, the region of the Tugen Hills experienced high levels of volcanic activity with repeated ash falls (e.g. Hill, 2002) that led to—among other environmentally significant effects—mass kills of cichlid fishes (Rasmussen et al., 2017). In addition, based on fossil pollen grains and spores, it can be inferred that the area of the Tugen Hills was a wooded grassland or grassy woodland during the middle Miocene (13–12 MYA), whereas the same area was almost barren of vegetation in the middle-to-upper Miocene (12–10 MYA) (Rasmussen et al., 2017). The latter finding may be biased by taphonomic factors, but the discovery of certain mammalian fossils (a suid and an equid) also point to an increasingly drier climate at this time (Rasmussen et al., 2017). Thus, rising levels of aridity, together with the destructive influence of ash falls on soils and land plants (see Ayris and Delmelle, 2012), was probably responsible for the disappearance of the earlier vegetation. It can therefore be argued that, in the middle-to-late Miocene lakes of the Central Kenya Rift valley, the availability of plant debris, a favoured food for cichlid fishes, must have been very limited. The Rebekka site, for instance, has yielded exclusively fungal spores, and not a single pollen grain (Rasmussen et al., 2017).

Tricuspid teeth situated in the inner row of the dentition of modern cichlids are used for grazing on diatoms and/or for browsing on multicellular filamentous algae (e.g. Yamaoka, 1983b; Streelman and Albertson, 2006). While growth of higher (vascular) plants was obviously inhibited in the Tugen Hills during the middle-to-late Miocene, the repeated ash falls might have fostered the growth of algae and in particular diatoms by providing abundant amounts of silica and other nutrients to the water bodies (see Kurenkov, 1966 and Abella, 1988 for modern analogues). Cichlid fishes that possessed tricuspid teeth at that time could thus have had a major advantage because they could exploit the newly available, rich food resources.

However, these considerations must remain tentative because of the uneven preservation of fossil freshwater fish assemblages across Africa (see above and Otero, 2010). It is not possible at present to pinpoint exactly the emergence of the Haplotilapiini, but it seems justified to suggest that by the late Miocene they were already abundant in the Central Kenya Rift. Their tricuspid teeth in the inner row can be viewed as a key innovation because this character probably led to a new feeding behaviour, which has remained characteristic for many of the African cichlids up to the present (Streelman and Albertson, 2006). The development of this key character may then have led to subsequent, rapid species diversification and to the evolution of the modern haplotilapiine tribes. Although this assumption needs to be tested by further work on the Miocene African cichlids, it is fully consistent with the recent discovery of †*Tugenchromis* from the upper Miocene (10–9 MYA) of the Tugen Hills, as its putative phylogenetic position lies within the tribes of the East African Radiation (see Altner et al., 2017). In conclusion, the scenario proposed here could serve as another example of how localized and short-lived ecological conditions can open a window of opportunity that triggers an adaptive explosion which may encompass a whole continent (see Joyce et al., 2005).

2.5. Conclusions

As noted above, the first fossil records of the Haplotilapiini could date back to the early Miocene, but †*Rebekkachromis* gen. nov. from the middle-to-late Miocene is the earliest confirmed representative of the haplotilapiines that has come to light. It is therefore suggested that the minimum age constraint for the Haplotilapiini in molecular dating studies should be set at 11 MYA, which is the age of the beds from which †*Rebekkachromis* gen. nov. was recovered.

In addition, the outcome of our study raises the question of whether the cichlid fossils that predate the first haplotilapiines belong to other, extant or extinct, non-haplotilapiine lineages. Another issue that arises is whether non-haplotilapiine lineages were more diverse in the past than they are today and whether they radiated. If so, what might have driven their decline, e.g. climate change or competition?

The high degrees of homoplasy between the cichlids and the vagaries of preservation mean that it may prove impossible to answer these questions with any degree of certainty. Be that as it may, the next step in this quest must be the construction of a solid phylogenetic framework for the extant Pseudocrenilabrinae incorporating morphological characters that can be applied to fossils.

Acknowledgements

The Research Authorization (NCST/ RCD/12B/012/54) was provided by the National Council for Science and Technology (Nairobi). We are very grateful to W. Moturi, J. M. Mironga and K. N. N. Ondimu (all of the Faculty of Environment andResources Development, Egerton University) for their essential scientific and logistic support. We owe our deep gratitude to M. Pickford and B. Senut (Musée National d'Histoire Naturelle, Paris, France), to the members of the Orrorin Community Organization who helped in all aspects of the fieldwork, and to all the other Kenyan residents and politicians who assisted on our project and provided support. We are much indebted to S. Sónyi (Bavarian State Collection for Paleontology and Geology, Munich, Germany) for the preparation of the fish fossils in the field. We are grateful to U. Schliewen and F. Schedel (both Bavarian State Collection of Zoology, Munich, Germany) for providing X-rays and for their constructive discussions. We are grateful to D. Neumann (Bavarian State Collection of Zoology, Munich, Germany) and J. Maclaine (Natural History Museum, London, U.K.) who facilitated access to specimens of extant species. We are grateful to G. Wörheide, the Director of the Bavarian State Collection for Palaeontology and Geology, for his kind support. Finally, we acknowledge the constructive comments of two anonymous reviewers. This research was funded by the German Research Foundation (grant RE 1113/18–1-2).

2.6. Supplementary Material

Available at https://link.springer.com/article/10.1007/s10750-018-3715-8#Sec20

2.7. References

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3. 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 fishes 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 cooccurring †*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.

3.1. 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 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

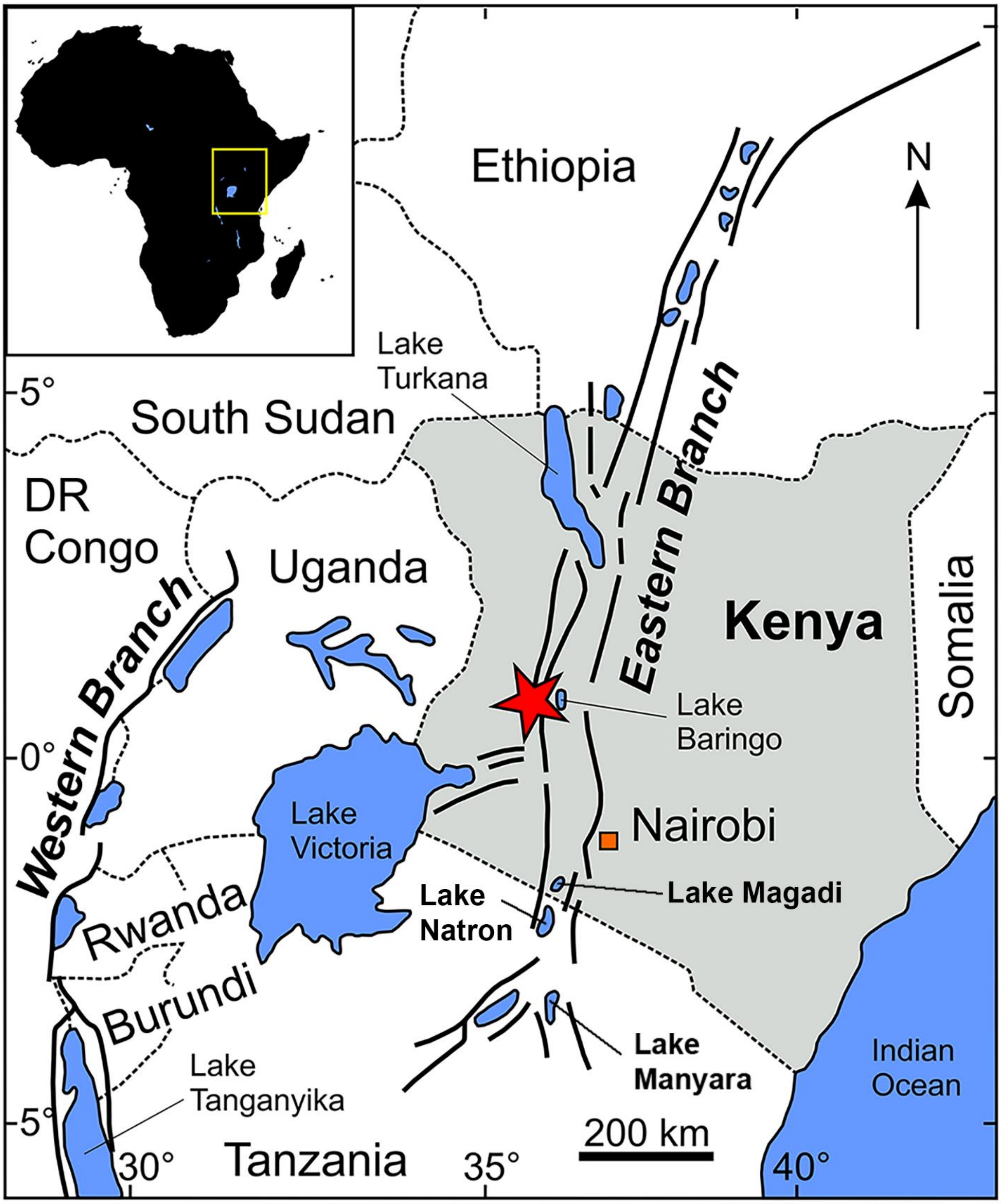

Figure 1. Sketch map of East Africa. The star marks the study area. Map modified from Kiage and Liu (2009) and Penk et al. (2019), with the permission of Elsevier.

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;

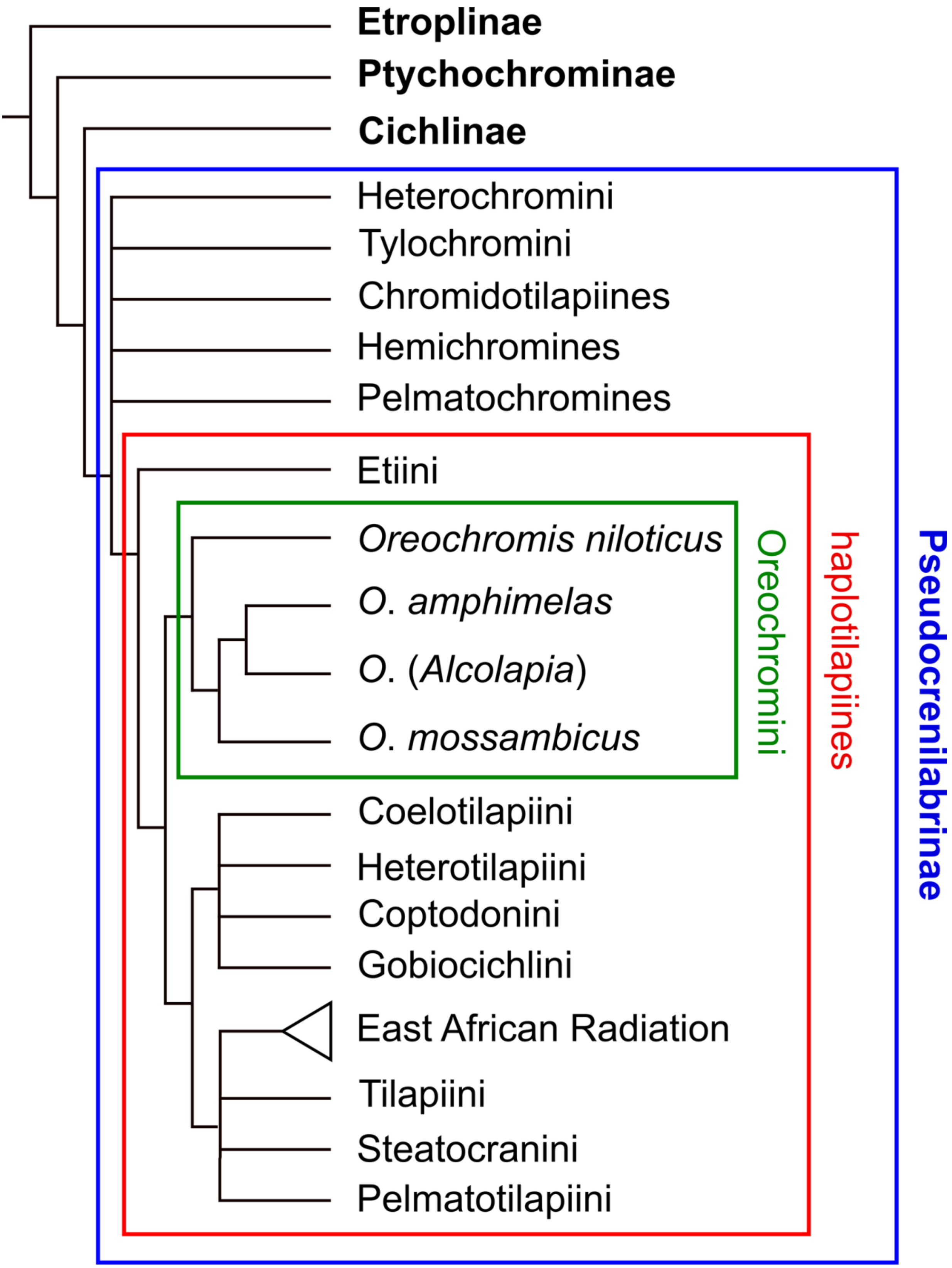

Figure 2. Simplified composite phylogeny depicting the relationships among the Cichlidae, based on Schwarzer et al. (2009), Dunz and Schliewen (2013), Irisarri et al. (2018), Schedel et al. (2019), and Ford et al.(2019). Note that the clade referred to as the East African Radiation itself encompasses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

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 to 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*).

3.1.1. 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). 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 palaeosols; 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 SW of the small village of Bartabwa in the Kabasero subbasin, 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.

3.2. Materials and methods

3.2.1. 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 was 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.

3.2.2. 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 haemal 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.

3.3. Results

3.3.1. 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 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).

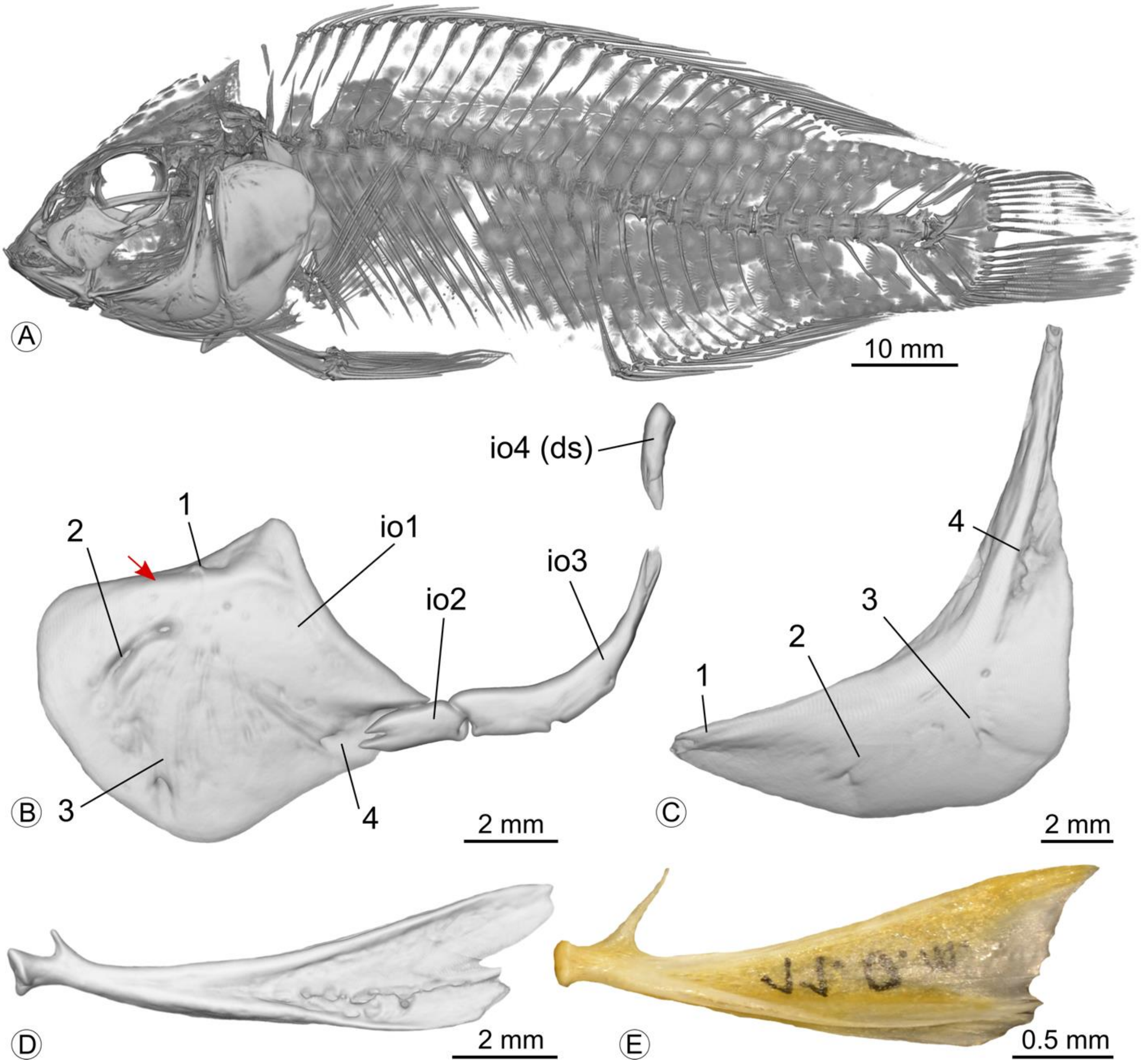

Figure 3. A–D, µCT data volume rendering of *Oreochromis* (*Alcolapia*) *grahami* (ZSM 25618). **A,** whole specimen; **B,** infraorbitals; **C,** preopercle,reversed; **D,** urohyal; **E,** photograph of urohyal of *Oreochromis niloticus* (Linnaeus, 1758) (SAPM 01887). The photograph in E was provided 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.

3.3.2. 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 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 $\leqslant$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*)

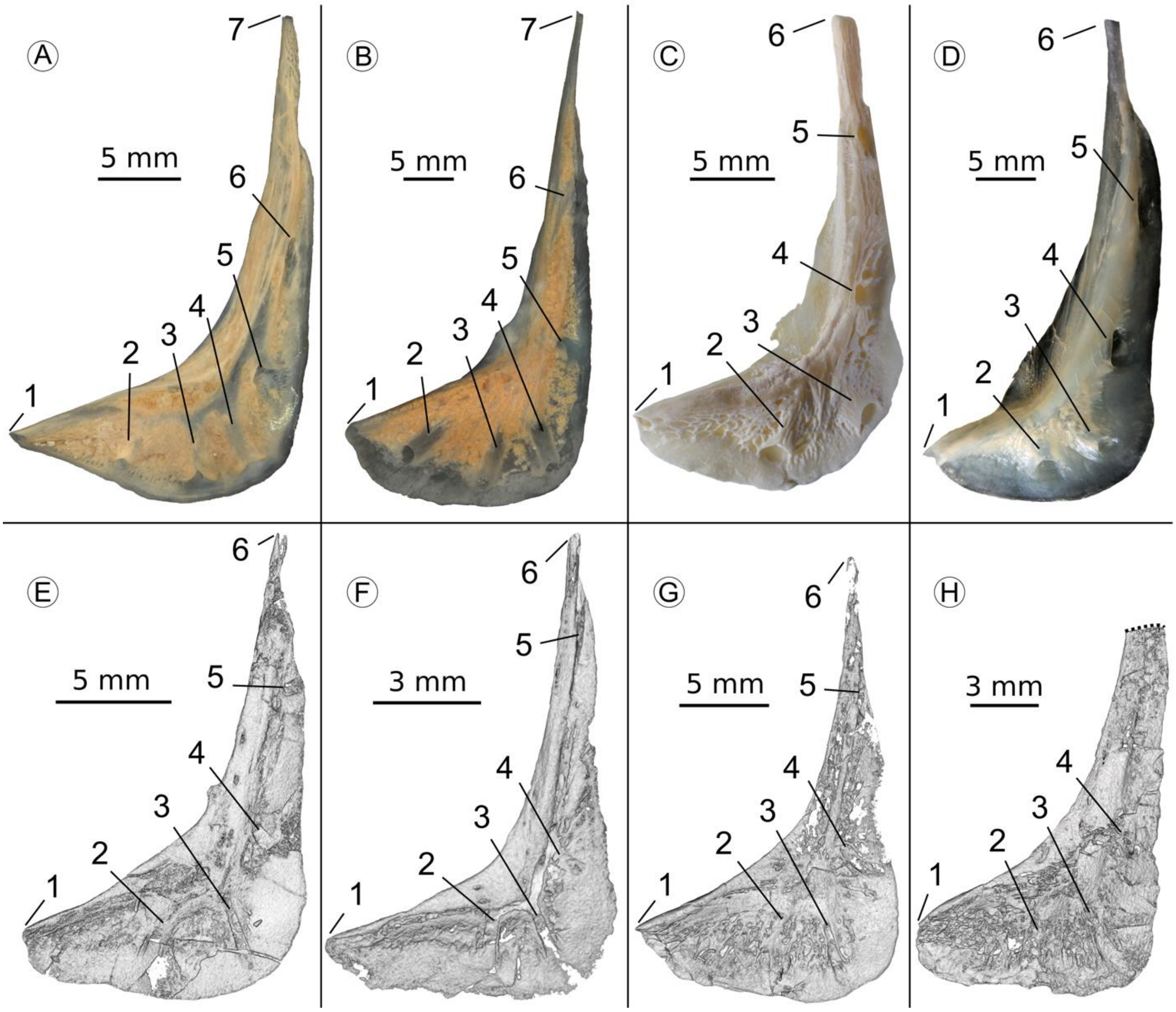

Figure 4. Preopercles of cichlids from the right side in lateral view, anterior is to the left. **A,** *Oreochromis andersonii* (Castelnau, 1861), Pseudocrenilabrinae, SAPM-PI-01875; **B,** *Cyphotilapia frontosa* (Boulenger, 1906), Pseudocrenilabrinae, SAPM-PI-02994; **C,** Cichlasoma sp., Cichlinae, SAMPPI-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.

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).

3.3.3. 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 haemal 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—Site Yatianin (≈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. 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.

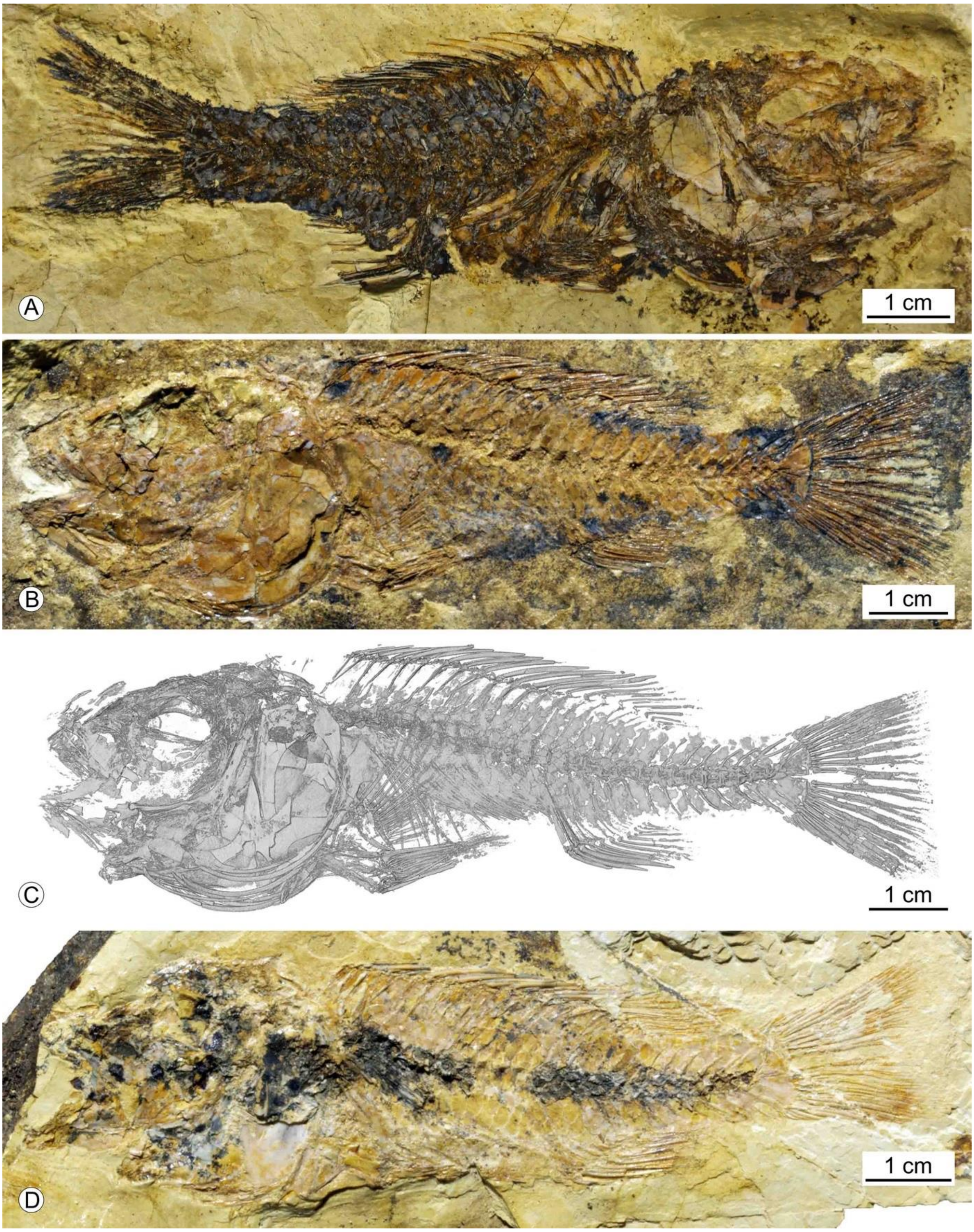

Figure 5. Skeletons of fossil cichlids from the site Yatianin. **A,** holotype of †*Rebekkachromis valyricus*, sp. nov., OCO-11-19b, in medial view; **B,** holotype of †*R. vancouveringae*, sp. nov., OCO-11-4b, in medial view; **C,** μCT data volume rendering of B in lateral view; **D,** †*Rebekkachromis*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

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 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 ‘belllike’ 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.

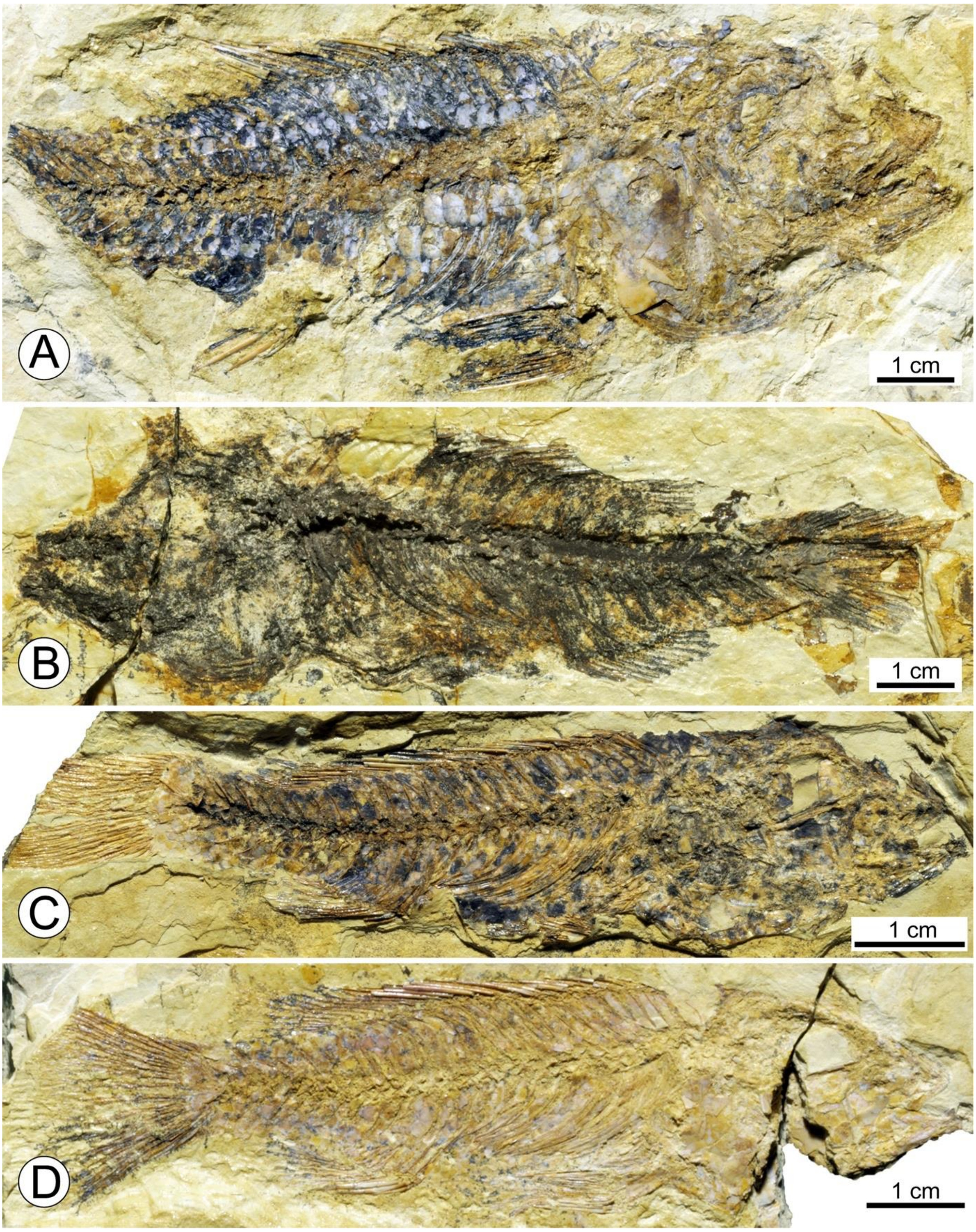

Figure 6. Skeletons of fossil cichlids from the site Yatianin, in medial view. **A,** †*Rebekkachromis* sp., OCO-11-20; **B,** †*Rebekkachromis* sp., OCO-11-14b; **C,** †*Rebekkachromis* sp., OCO-11-9b; **D,** †*Rebekkachromis* sp., OCO-11-21.

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.

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 haemal 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,

Table 1. Meristic counts and morphometric measurements of all species of †*Rebekkachromis* and †*R*. sp. from the site Yatianin. 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 Suppl. Data 2, Table S5.

	†*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 transversal 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

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 haemal 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 haemal 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 haemal 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 welldeveloped 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

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

Species/ Specimen	Supraneurals	Hypurals	Granulation on scales	100*H D/SL	Preopercle shape	Number of sensory canal pores 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 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, 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—Site Yatianin (≈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.

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

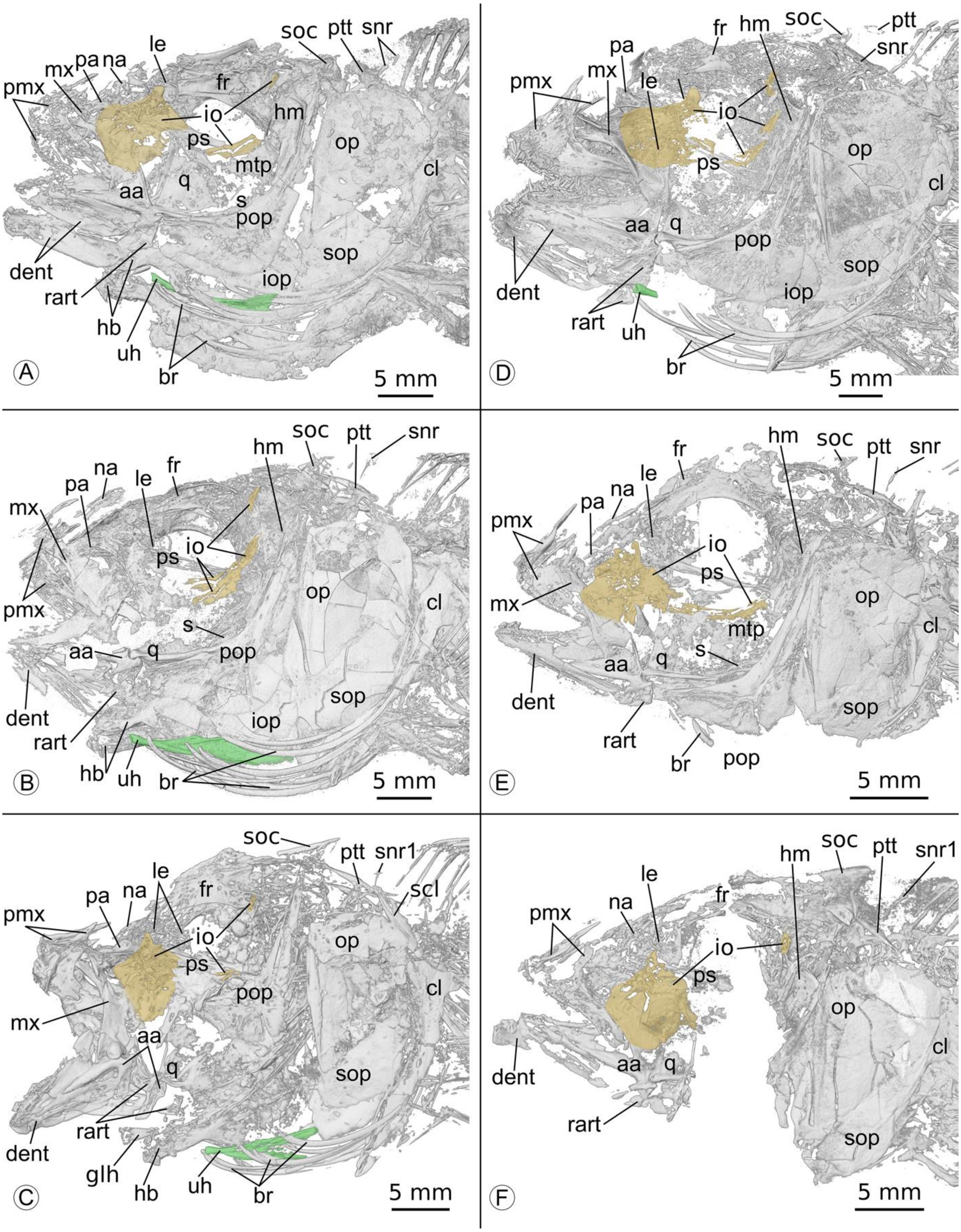

Figure 7. µCT data volume renderings of the head region of specimens from the site Yatianin in lateral view. **A,** †*Rebekkachromis valyricus*, sp. nov., OCO-11-19; **B,** †*R. vancouveringae*, sp. nov., OCO-11-4; **C,** †*Rebekkachromis* sp., OCO-11-13, **D,** †*Rebekkachromis* sp., OCO-11-20; **E,** †*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.

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

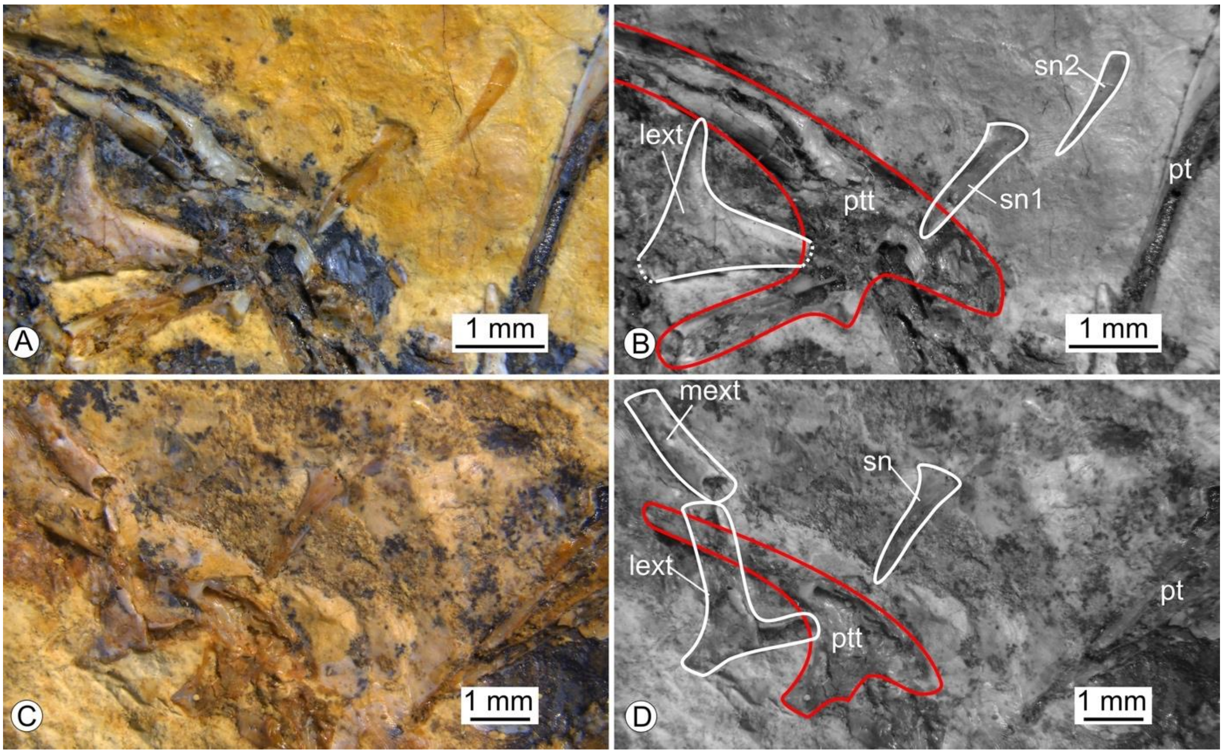

Figure 8. The nape of fossil cichlids from the site Yatianin, anterior is to the left. **A, B,** †*Rebekkachromis valyricus*, sp. nov., OCO-11-19a; **C, D,** †R. *vancouveringae* sp. nov., OCO-11-4b. Abbreviations: lext, lateral extrascapular; mext, medial extrascapular; pt, pterygiophore; ptt, post-temporal;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

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 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

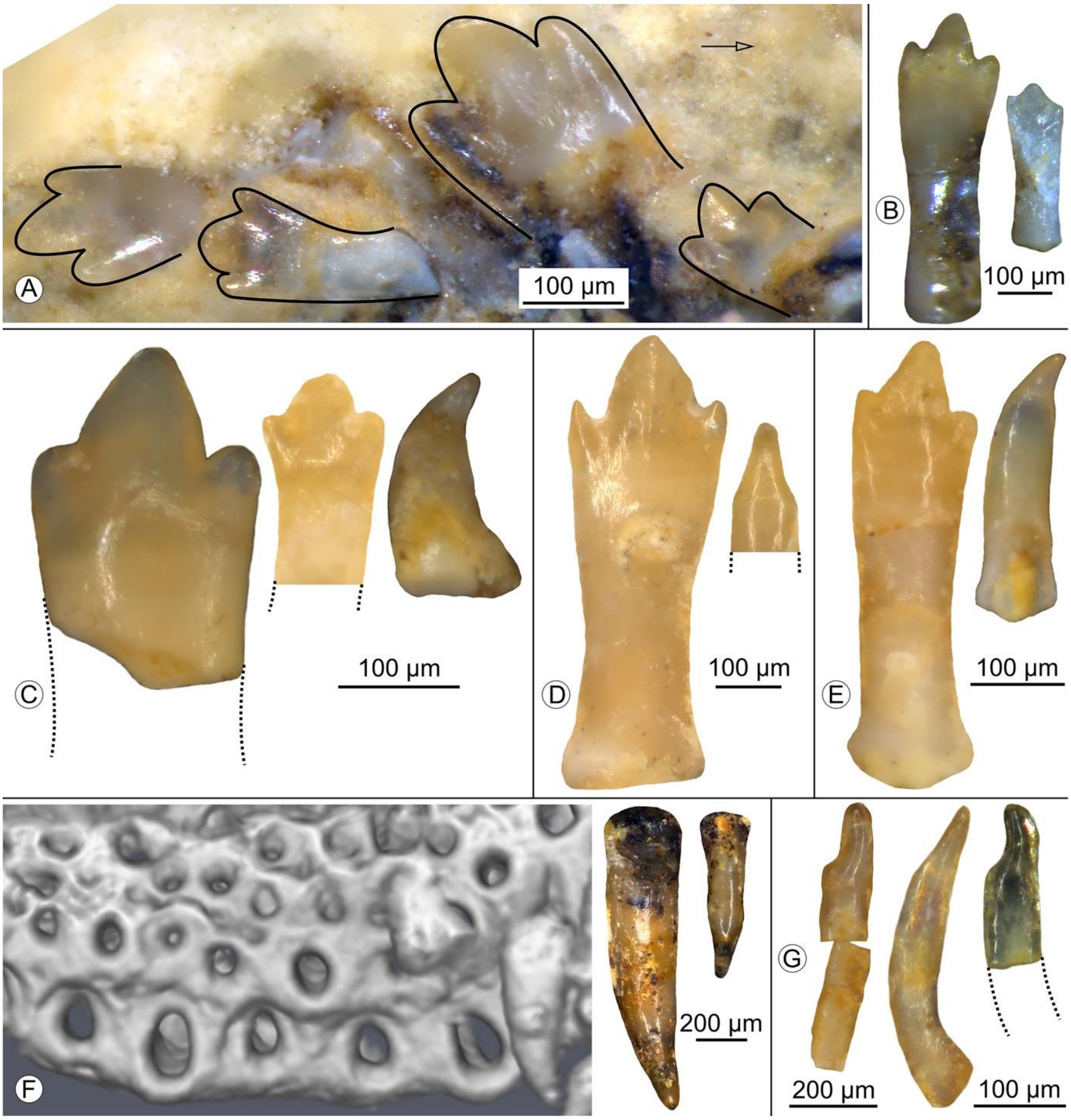

Figure 9. Teeth of fossil cichlids from the site Yatianin. **A,** †*Rebekkachromis valyricus*, sp. nov., large and small tricuspid teeth from the anterior tip of the lower oral jaw, OCO-11-19b; the arrow on the right points anteriorly. **B,** †*Rebekkachromis* sp., left: large tricuspid, right: small 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.

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 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 foramens 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.

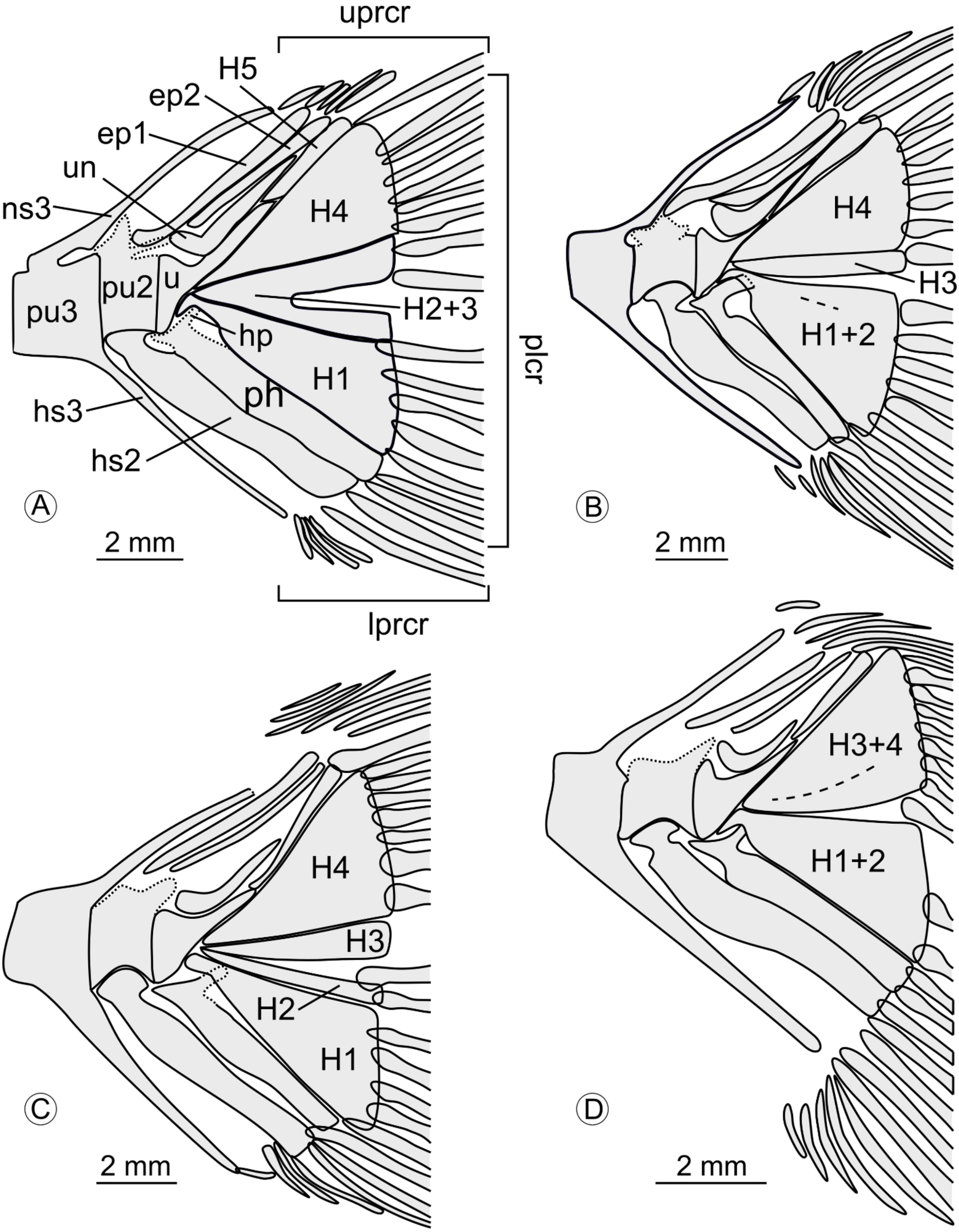

Figure 10. Schematic drawings of the caudal fins of fossil cichlids from the site Yatianin. **A,** †*Rebekkachromis valyricus,* sp. nov., OCO-11-19; **B,** †*R. vancouveringae,* sp. nov., OCO-11-4; **C,** †*Rebekkachromis* sp., OCO-11-13; **D,** †*Rebekkachromis* sp., OCO-11-9. Continuous lines denote a definite outline, dotted lines indicate that the outline is uncertain. Abbreviations: ep, epural; H, hypural plates; hp, hypurapophysis; hs, haemal 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.

3.4. Discussion

3.4.1. 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 -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). 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

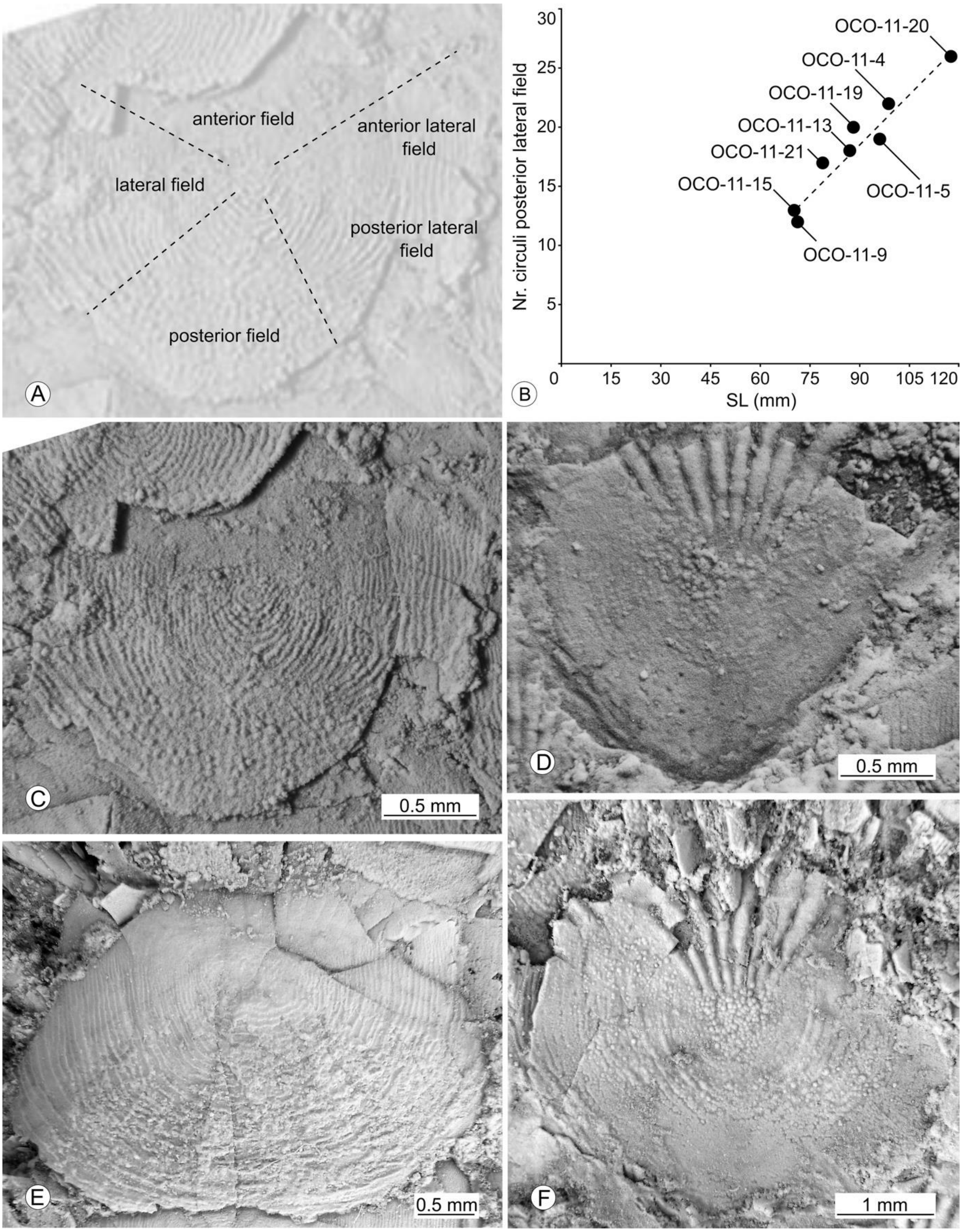

Figure 11. Flank scales of fossil cichlids from the site Yatianin, anterior is to the top. **A,** terminology; **B,** scatter plot of the number of circuli on the posterior lateral field relative to standard length (SL); **C,** †*Rebekkachromis* sp., OCO-11-13, lateral view; **D,** †*R. vancouveringae*,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

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 for the site Yatianin 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, 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

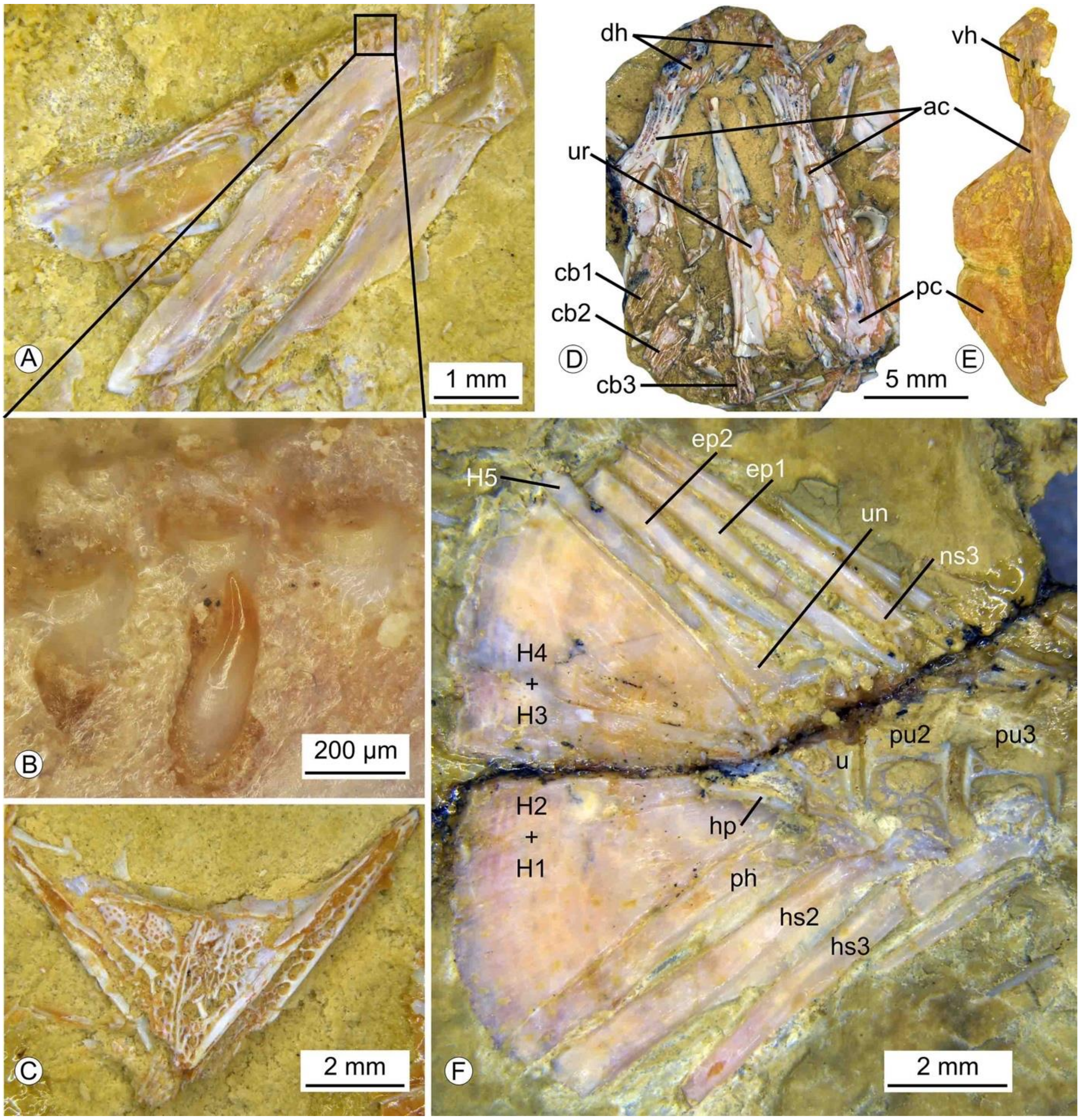

Figure 12. Skeletal elements of †*Rebekkachromis* sp. from the site Terenin. A, left and right dentary, OCO-688-11; B, same individual, complete recurved, shouldered unicuspid tooth, and lingually some teeth with broken crowns; C, fifth ceratobranchial (lower pharyngeal jaw), ventral view, OCO-678-11; 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, haemal spine of preural centrum; ns3, neural spine of preural centrum 3; pc, posterior ceratohyal; ph, parhypural; plcr, principal caudal rays; pu, preural centrum; u, urostyle; un, uroneural; ur, urohyal; vh, ventral hypohyal.

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 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*-

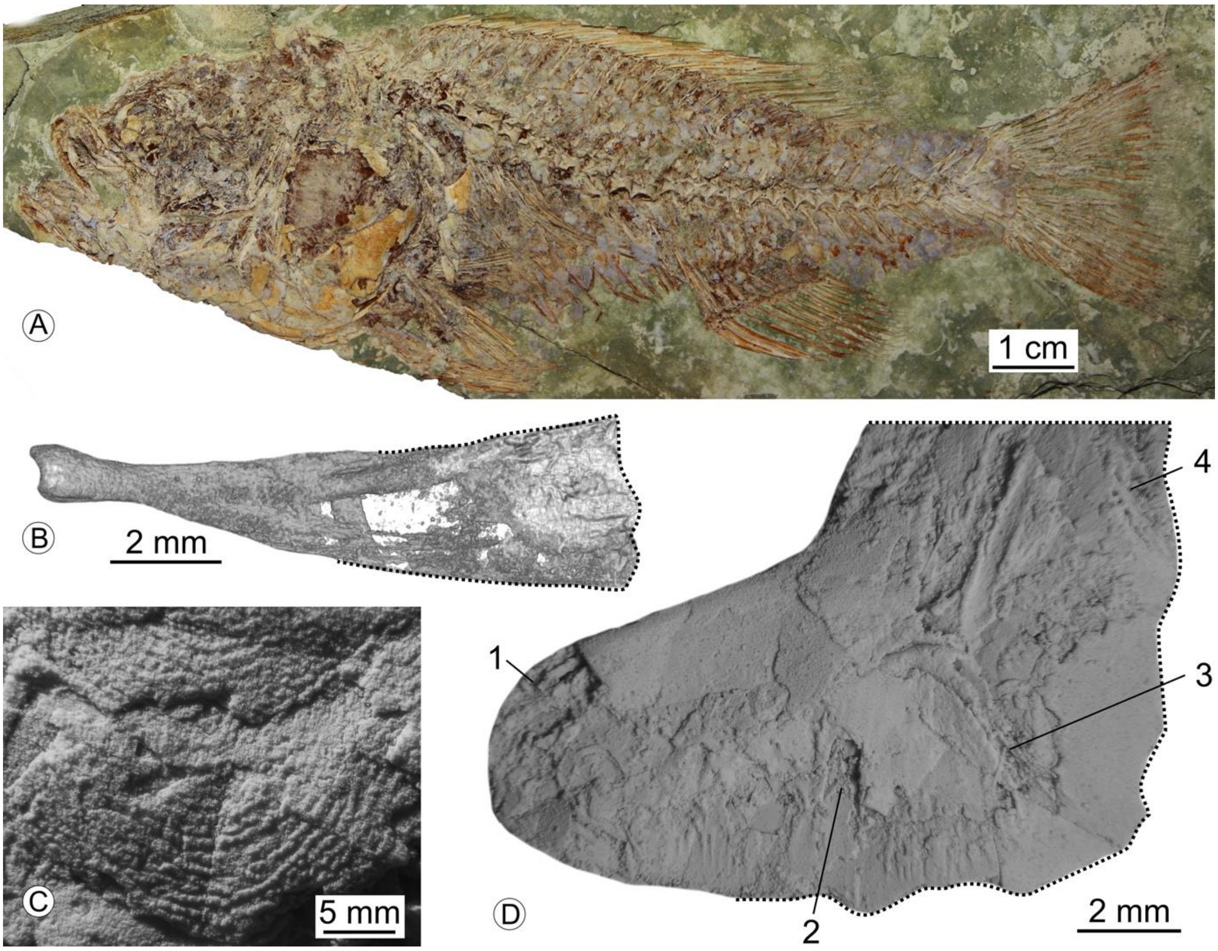

Figure 13. †*Rebekkachromis ngororus* from the site Rebekka, OCO-3-3a. **A,** complete skeleton of the holotype; **B,** urohyal, reversed; **C,** imbricate cycloid scales, anterior on top; **D,** preopercle, in lateral view. C and D are coated with ammonium chloride. Numbers denote the sensory canal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

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 *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 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 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 fanglike dentition and the high number of vertebrae (33) (amongst others; see Altner et al., 2020). The three species of the †*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).

3.4.2. †*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 (HCO3 – , CO32–), 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 (NaAlSi2O6·H2O) 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).

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, 1983:384; 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.

3.4.3. A nascent species flock?

The propensity of cichlids to form species flocks, especially in lakes, has been studied extensively (e.g., Greenwood, 1984a; 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 site Yatianin.

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 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).

3.4.4. 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.

3.5. 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 diagnosis 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 morphology-based phylogeny for Pseudocrenilabrinae cichlids based on characters that can be applied to fossils.

Acknowledgments

The Research Authorization (NCST/RCD/12B/012/54) was provided by the National Council for Science and Technology (Nairobi). We are very grateful to W. Moturi, J. M. Mironga and K. N. N. Ondimu (all of the Faculty of Environment and Resources Development, Egerton University) for their essential scientific and logistical support. We owe our deep gratitude to M. Pickford and B. Senut (Musée National d'Histoire Naturelle, Paris, France), to the members of the Orrorin Community Organization who helped in all aspects of the fieldwork, and to all the other Kenyan residents and politicians who assisted on our project and provided support. We are much indebted to S. Sónyi (Bavarian State Collection for Palaeontology and Geology, Munich, Germany) for the preparation of the fish fossils in the field.We are grateful to M. Altner (Ludwig-Maximilians- Universität München, Munich, Germany) for constructive criticism and for providing a crucial part of the X-rays. We thank G. Arratia (Kansas University, Lawrence, U.S.A.), A. Bannikov (Russian Academy of Science, Moscow, Russia), G. Carnevale (Università di Torino, Turin, Italy), M. Dohrmann and C. Gierl (both Ludwig-Maximilians-Universität München, Munich, Germany), T. Přikryl (Czech Academy of Sciences, Prague, Czech Republic), F. Schedel and U. Schliewen (both ZSM, Munich, Germany) for constructive discussions. We are grateful to J. Maclaine (Natural History Museum, London, U.K.), D. Neumann (ZSM, Munich, Germany), and H. Obermaier (SAPM, Munich, Germany) for facilitating access to specimens of extant species. We thank M. Kottelat (Delémont, Switzerland and Lereve Kong Chian Natural History Museum, Singapore) and K. Polatidis (University of Western Macedonia, Florina, Greece) for helping us to formulate the Latin names of the new species. We are grateful to G. Wörheide (Bavarian State Collection for Palaeontology and Geology, Munich, Germany) for his kind support. We thank P. Hardy (Düsseldorf, Germany) for critical reading of the manuscript. This manuscript benefited greatly from the constructive comments of the reviewers, Alison Murray (University of Alberta, Canada) and one more anonymous reviewer. We thank W. Orsi and the LMU Mentoring program for providing funding to make this article open access. The research was funded by the German Research Foundation (grant RE 1113/18–1-2).

3.6. Supplementary Material

Supplemental Data 1, DOI: 10.6084/m9.figshare.11688936
Supplemental Data 2, DOI: 10.6084/m9.figshare.12977540
Supplemental Data 3, DOI: 10.6084/m9.figshare.11604483

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4. A new species of clupeid fish from the upper Miocene of Northern Greece

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Abstract

Much remains to be known on the past diversity and evolutionary history of the Clupeidae (herrings, shads and allies), owing to the frequently subtle differences between modern taxa and the moderate preservational quality of several fossils. In this study, new material of fossil clupeids is described, from a new locality from the upper Miocene of the Serres Basin, Northern Greece. The examined fossils are well-preserved articulated skeletons, exhibiting features such as a small size (<150 mm in standard length), slender body, two pairs of bullae, at least six frontoparietal striae, mouth terminal, two supramaxillae, five branchiostegal rays, ten supraneurals, 40–42 vertebrae, eight or nine pelvic fin rays, 17 rays in the dorsal and 16–19 rays in the anal fin, last two fin rays of the anal fin not elongate, two epurals, dorsal scutes absent, 21–23 strong ventral scutes with ascending arms. The new fossils cannot be attributed to any modern genus, though they show the least differences with the monotypic genus *Hilsa*, which today inhabits the Indo-West Pacific. Comparisons with fossil taxa from the Cenozoic indicate that the new fossils constitute a new species which is tentatively attributed to the fossil genus *Pseudohilsa*. Clupeids reportedly similar to the modern-day *Hilsa* have been previously described from the Pliocene of the Black Sea and the middle Miocene of the Caspian Sea, but this is the first time that such a fossil clupeid is described from the Mediterranean.

4.1. Introduction

The teleost cohort Otomorpha comprises almost a third of all living fish species. They are distinguished in the Clupeomorpha (e.g., anchovies and herrings, >400 modern species), and Ostariophysi (>10,000 modern species) plus the deep-sea Alepocephaliformes (ca. 140 modern species) (Betancur et al., 2017; Straube et al., 2018; Fricke et al., 2020). The Ostariophysi comprise the orders Cypriniformes (caprs), Siluriformes (catfishes), Characiformes (characins), Gonorynchiformes (milkfishes) and Gymnotiformes (neotropical knifefishes), and both their fossil and extant representatives have gathered considerable scientific attention regarding their diversity, biogeographic history and evolution (Briggs, 2005; Chen et al., 2013; Nelson et al., 2016; Betancur et al., 2017). On the contrary, the Clupeomorpha have received less attention, with the last major work on this taxon published 35 years ago (Grande, 1985). The Clupeomorpha include the extinct †Ellimmichthyiformes and the Clupeiformes, which survive to date (e.g., Grande, 1985; Murray and Wilson, 2013; Nelson et al., 2016). The largest family within the Clupeiformes, in terms of species, is the Clupeidae (Fricke et al., 2020).

The fishes of the family Clupeidae (e.g., herrings, sardines, shads and menhadens) are some of the most intensely commercially exploited fishes worldwide (FAO, 2020). Clupeids, which are comprised of almost 200 species (Fricke et al., 2020) distributed worldwide, are medium-sized fishes, usually in the 15-25 cm range (e.g., Whitehead, 1985). The majority of clupeids are coastal pelagic fishes, forming schools and feeding on plankton (e.g., Whitehead, 1985; Nelson et al., 2016). Their tolerance to low salinities allows several species to be anadromous and about 10% of all species are predominantly freshwater (Nelson et al., 2016). Some features that characterize, but are not limited to, this family (see section "Systematic discussion to the level of family") are: the possession of an otophysic connection, where the swimbladder extends in the skull to reach the inner ear, forming one or two pairs of bullae in the neurocranium; the presence of one or more scutes along the ventral midline; single unpaired fins with soft rays, the dorsal fin located approximately at the middle of the body; a near or complete lack of a lateral line on the body and the possession of two elongate postcleithra (e.g., Grande, 1985).

Little is known about the evolutionary history of clupeids, even though dozens of fossil species have been described to date (e.g., Grande, 1985). There are several reasons for this apparent antithesis; clupeids are not only numerous, but many are also morphologically similar to each other (Whitehead, 1985), meaning that there are frequently few characters to differentiate between modern taxa. Additionally, several fossil clupeid taxa have been described based on fossils which have not retained many of taxonomically important characters (Grande, 1985).

In this paper, new material of fossil clupeids is described from the new site "Aidonochori A", from the Late Miocene of the Serres Basin, Northern Greece. The fossils from this site are preserved as complete and well-preserved skeletons, preserving many details of their anatomy. The main goals of this study are a) to describe a new species of clupeid fish and b) to examine the relationships of the fossils from the site "Aidonochori A" with other modern and fossil clupeids.

Figure 1. Geographic overview of **a,** the placement of the Strymon-Serres Basin in Northern Greece (red rectangle) and **b,** the southern part of this Basin. The red star denotes the fossiliferous locality "Aidonochori A". Images from https://www.google.de/maps, ©2020TerraMetrics, Kartendaten; ©Google, Mapa GIsrael.

4.1.1. Geographical and geological setting

The Serres Basin in Greece is part of the broader Strymon-Serres Basin, which has a NW-SE direction and is run by the Strymonas River (Struma in Bulgarian) in southwestern Bulgaria and northern Greece. At its southernmost part, the Strymonas River is joined by the Angitis River and pours into the Northern Aegean Sea (Fig. 1). The Serres Basin is part of the Serbo-Macedonian Massif and is filled with Neogene-Quaternary sediments ca. 2000–3000 m thick, the oldest of which date to the middle-late Miocene (Psilovikos and Karystineos, 1986; Karistineos and Ioakim, 1989; Zagorchev, 2007; Tranos et al., 2011). The Neogene deposits of the Strymonas-Serres Basin contain marine, terrestrial and brackish sediments (Psilovikos and Karystineos, 1986; Ioakim et al., 2005). Because of the complex paleogeographical history and uncertainties with regards to dating, the stratigraphy and paleoecology of the Serres Basin are matters of ongoing research (Syrides, 1995; Ioakim et al., 2005; Pimpirev and Beratis, 2010).

The "Aidonochori A" locality is right next to the village of Aidonochori, situated at the southwest margin of the Strymonas-Serres Basin, at the foothills of Kerdilio Mountain. The fossils are found in a layer composed of silty marls ca. half a meter thick. The fossiliferous layer is exposed on two sides, which meet each other; one is a roadcut and the second is the wall near the top of a gorge. The sediment contains mica and carbonate. The fossils were collected in 1997 by the private researcher and collector Nikos Bacharidis. Only fossils of clupeid fishes have been recovered so far from this locality, lying in several superimposed layers. A study of the stratigraphy and age of the locality is pending, but according to Prof. Dr. G. Syrides who visited the locality in 2015, the geological context of the area indicates an upper Miocene age (Syrides, 2015, pers. comm.).

4.2. Materials and Methods

4.2.1. Materials

The studied material belongs to the Laboratory and Museum of Geology and Palaeontology of the Aristotle University of Thessaloniki (LGPUT). A total of five fossil individuals were examined from the "Aidonochori A" locality. For specimens LGPUT ADS 001, 002 and 004 only the slab with the right side of the fish was recovered, while for LGPUT ADS 005 both slabs are available. Specimen LGPUT ADS 003 is on the same slab as ADS 002 and consists of an isolated neurocranium, seen in ventral view.

4.2.2. Methods

Microscopic observations were performed with a stereomicroscope (Leica M165 C) mounted with a digital camera (Leica M170 HD). The specimens were prepared with fine carbide needles (0.17–0.5 mm in diameter) and treated with the acrylic resin Paraloid B-72. The identification of the fossil bones was facilitated by the osteological descriptions and drawings of Phillips (1942), Grande (1985), Sato (1994), Segura and Díaz de Astarloa (2004) and Di Dario (2009); with regards to the general osteology of teleosts see Schultze (2008), Arratia (2008), Schultze and Arratia (2013). The caudal vertebrae are characterized by the presence of a closed haemal arch, and identified by the presence of ventrally projecting haemapophyses. Vertebrae counts include the first preural vertebra, which is fused to the urostyle, and fin ray counts include all rays, except for the two last rays of the dorsal and anal fins which are borne by one pterygiophore. Measurements were taken with digital sliding calipers and rounded to the nearest 0.1 mm.

4.3. Systematic paleontology

Superorder Clupeomorpha Greenwood, Rosen, Weitzman and Myers, 1966
Order Clupeiformes Bleeker, 1859
Suborder Clupeoidei Bleeker, 1859
Family Clupeidae Cuvier, 1816

†*Pseudohilsa*? *nikosi* Kevrekidis sp. nov.

Holotype—LGPUT ADS 001

Paratypes—LGPUT ADS 002, LGPUT ADS 003; LGPUT ADS 004, LGPUT ADS 005.

Etymology—Named in honor of Nikos Bacharidis, private researcher and fossil collector who discovered the locality and collected the material presented here, in recognition of his longstanding contribution to the development of paleontology in Greece.

Occurrence—Site "Aidonochori A" (40°50' 29"N, 23°43' 12"E) next to the village Aidonochori near Serres, Central Macedonia, Greece; upper Miocene.

Diagnosis—Distinguished from all other extant and fossil clupeid species by the following combination of features: small size (up to ca. 150 mm); maximum depth at about dorsal fin origin, 24–33% of standard length); head length ca. 32% of standard length; diameter of eye ca. 25% of head length; two pairs of bullae in its cranium; at least six frontoparietal striae; mouth terminal; two supramaxillae; lower jaw articulation at about middle of orbit; five branchiostegal rays; ten supraneurals; 40–42 vertebrae; pleural ribs to total vertebrae ratio 0.57–0.6; 15 rays in pectoral fin; eight or nine rays in pelvic fin, which originates under anterior third of dorsal fin base; 17 rays in dorsal fin; 16–19 rays in anal fin; two epurals; ca. 40 scales in a transverse row, no dorsal scutes; strong ventral scutes (4 at gular region, 11–12 prepelvic associated with ribs, 10–11 postpelvic).

General description—Slender-bodied fish, with a triangular head. The dorsal outline is almost straight and the ventral outline is slightly convex. In the following sections, the emphasis is placed on features or bones which are clearly discernible; structures that are badly preserved are noted as such or omitted from the description.

Neurocranium—The neurocranium is approximately triangular in lateral and ventral view. Some bones, particularly those behind the orbit, are crushed and their precise borders are difficult to discern. The basioccipital articulates with the first vertebra. The small supraoccipital forms the posterodorsal angle of the neurocranium. Anteriorly to that is the

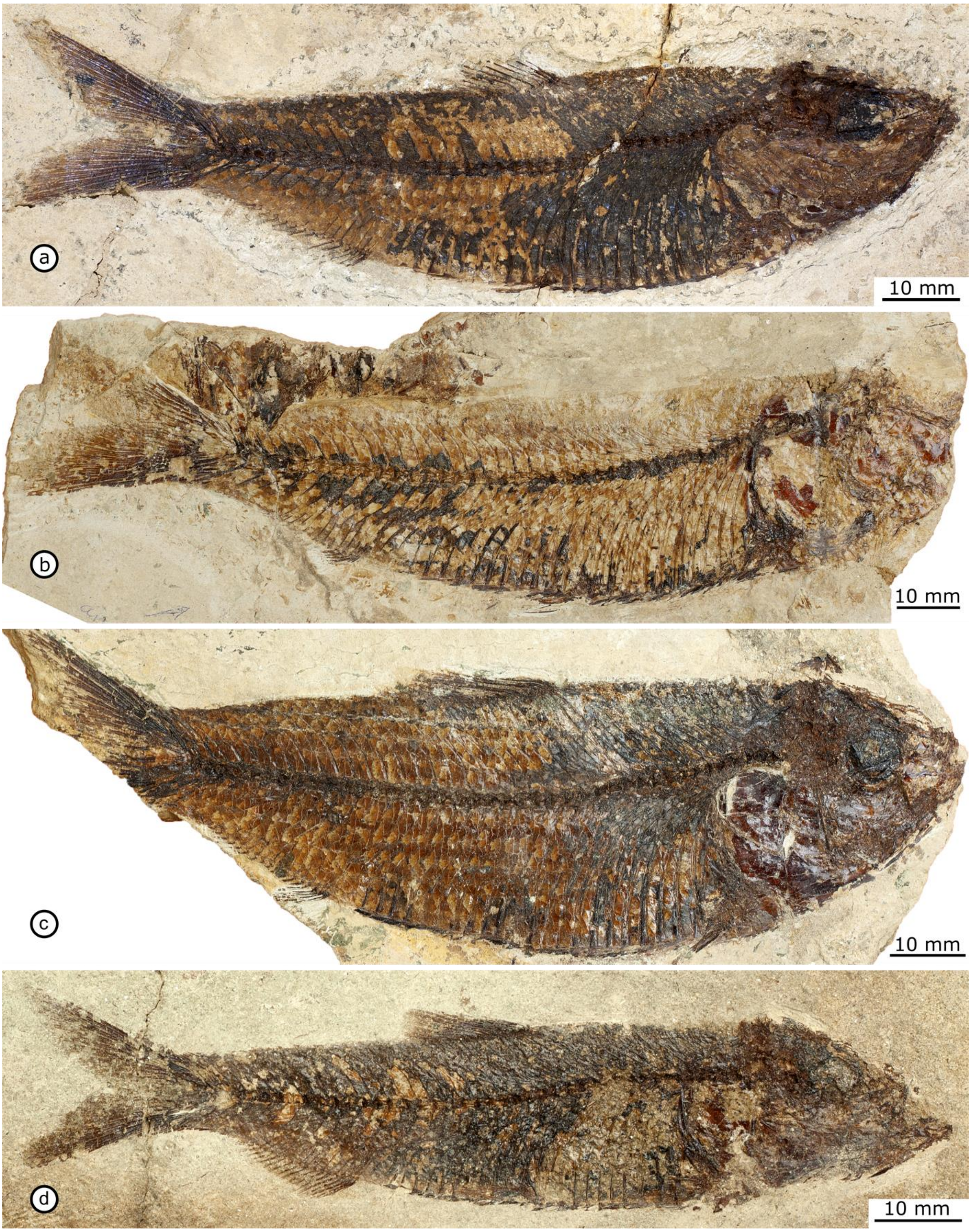

Figure 2. Skeletons of the clupeid †*Pseudohilsa*? *nikosi* sp. nov. **a,** specimen LGPUT ADS 001; **b,** specimen LGPUT ADS 002; **c,** specimen LGPUT ADS 004; **d,** specimen LGPUT ADS 005.

parietal (or postparietal, see Schultze, 2008), which is separated by the frontal bone (or parietal, see Schultze, 2008) by the oval temporal foramen. The temporal foramen does not seem to be

Table 1. Morphometric characteristics of †*Pseudohilsa*? *nikosi* from the site "Aidonochori A". Measurements are given in mm, in parentheses each measurement is given as a percentage of the standard length. A plus sign (+) denotes that the actual number must have been greater in the living fish.

	LGPUT ADS 001	LGPUT ADS 002	LGPUT ADS 004	LGPUT ADS 005
Standard length	99.3	119+ (estimated ca. 150)	111.6	88.3
Total length	118.6 (119%)	148+ (estimated ca. 180)	128+	102.3 (116%)
Body length	67.8 (68%)	87.3	77 (69%)	59.5 (67%)
Head length	31.5 (32%)	-	34.6 (31%)	28.8 (33%)
Head depth	24.9 (25%)	-	33.8 (30%)	22.7 (26%)
Preorbital distance	8.7 (9%)	-	8.6 (8%)	7.5 (8%)
Horizontal eye diameter	7.9 (8%)	-	8.1 (7%)	7.7 (9%)
Predorsal distance	50.7 (51%)	-	54 (48%)	44.7 (51%)
Postdorsal distance	36.3 (37%)	-	40.1 (36%)	31.9 (36%)
Prepelvic distance	52 (52%)	-	61 (55%)	46.1 (52%)
Postpelvic distance	46.8 (47%)	59.1	49.7 (45%)	41.9 (47%)
Preanal distance	75.8 (76%)	-	84.1 (75%)	65 (74%)
Postanal distance	10.8 (11%)	14	24.35 (22%)	11 (12%)
Body depth at dorsal fin origin	27.5 (28%)	-	36.4 (33%)	21 (24%)
Body depth at pelvic fin origin	24.9 (25%)	32.5	34.7 (31%)	20 (23%)
Body depth at anal fin origin	20.9 (21%)	-	27 (24%)	15.9 (18%)
Minimum body depth at the level of the caudal peduncle	11.2 (11%)	-	13.6 (12%)	8.9 (10%)

Table 2. Meristic characteristics of †*Pseudohilsa*? *nikosi* from the "Aidonochori A" site. A question mark (?) denotes uncertainty, a plus sign (+) that the actual number must have been greater in the living fish.

	LGPUT ADS 001	LGPUT ADS 002	LGPUT ADS 004	LGPUT ADS 005
Supraneurals	10	?	10	10
Branchiostegal rays	5	?	5	?
Vertebrae total (abdominal/caudal)	41 (16/25)	40 (16/24)	41 (16/25)	42 (17/25)
Pectoral rays	11+	11+	10+	15
Pelvic fin rays	7+	8 or 9	?	8
Dorsal fin rays	17	-	17	17
First pterygiophore of dorsal fin associated with vertebra	9		10	10
Anal fin rays	16	16	19	18
First pterygiophore of anal fin associated with vertebra	26	27	27	27
Scutes: Free prepelvic/ rib associated/ postpelvic scutes	3+?/11/10	4/12/11	?/11/11	?/11/11
Procurrent caudal fin rays (upper/lower)	8/8	-/5+	6+/6+	8/7
Principal caudal fin rays (upper/lower)	10/9	10/9	10/9	10/9
Epurals	2	-	2	2

overlain by any flange. The frontal bones are large and have an almost straight to slightly concave profile in lateral view (Fig. 3a). Posteriorly, on their dorsal surface, they are ornamented with more than six, prominent and reticulate, fronto-parietal striae (Fig. 3b–c). The frontals connect anteriorly with the mesethmoids and ventrally to the latter is the vomer, which appears toothless. Posteriorly to the vomer is the parasphenoid, a straight and slender bone. The parasphenoid doesn't seem to bear teeth and it projects at about the lower third of the orbit. The orbit is limited anterodorsally by the frontal bones and lateral ethmoids and posterodorsally by the frontal bones and sphenotics. Posteriorly to the sphenotics are the pterotics which bear the pterotic bullae. The bullae are easy to tell apart from the other structures of the head owing to their round shape and their characteristic, glassy and perforated texture (Fig. 3d). Anteroventrally to the pterotic bullae are the larger prootic bullae.

The specimen LGPUT ADS 003 is an isolated neurocranium in ventral view (Fig. 3e-f). In this specimen, the basioccipital is situated between the exoccipitals. Its posterior part, which would articulate with the first vertebra is discernible. The parasphenoid is missing and seems to have broken off. Anterolaterally to the exoccipitals are the pterotics, which bear the pterotic bullae. Anteriorly to the exoccipitals and the basioccipital are the prootics with the much larger prootic bullae. Anterolaterally to the prootics are the sphenotics. Anteriorly to the sphenotics and prootics are the large, broadly triangular frontal bones whose anterior portion is missing.

Circumorbital series—The orbit is rounded and occupies ca. 25% of the head's length. Five infraorbitals are discernible and they bear the infraorbital canal. Anteriorly, the first infraorbital is elongate, the second is shorter and the third is the largest of the series. The fourth and fifth infraorbitals are forming the postero-dorsal margin of the orbit, and they have a broadly rectangular shape (Fig. 3a). It is not clear if the sixth infraorbital (dermosphenotic) is present or not. A semicircular sclerotic bone is preserved at the upper half of the orbit.

Jaws—There is no sign of teeth in any of the jaws. The premaxilla is subtriangular and well ossified (Fig. 3a). The maxilla has a robust, rod-like anterior articular process and a flattened and curved posterior blade; the angle between these two parts is about 150°. From all the bones of the upper jaw, the maxilla reaches the farthest behind, at about the anterior third of the orbit. The posterior supramaxilla is paddle-shaped and the anterior supramaxilla is smaller and elongate. There is no sign of a hypomaxilla.

The dentary is broad and robust, with a well-developed ventral arm. Seen laterally, the dentary possesses a fossa near its tip. The mandibular canal is running longitudinally near the ventral margin of the bone. Posteriorly to the dentary is the anguloarticular, whose posterodorsal margin is straight (Fig. 3a). The retroarticular is not recognizable. The articulation of the lower jaw with the suspensorium is positioned approximately in the level of the middle of the orbit.

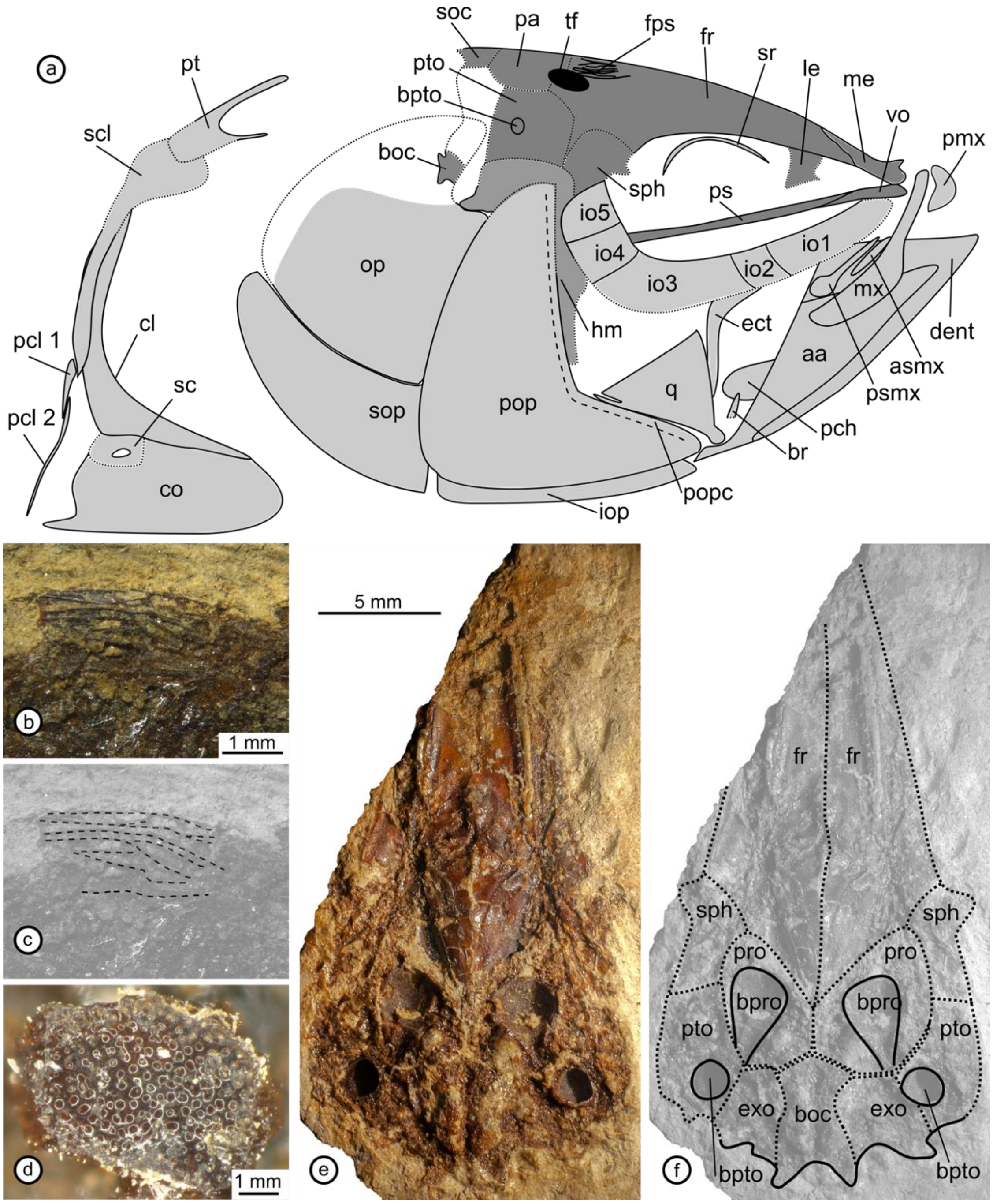

Figure 3. The neurocranium of †*Pseudohilsa*? *nikosi*. **a,** Schematic representation of the head and pectoral girdle of †*Pseudohilsa*? *nikosi*, based on all examined specimens, lateral view; **b,** the frontoparietal striae on the neurocranium of the specimen LGPUT ADS 005; **c,** same as previous, with frontoparietal striae drawn; **d,** fragment of bulla prootica from the specimen LGPUT ADS 004, showing the glassy and perforated texture of this structure; **e,** neurocranium of the specimen LGPUT ADS 003, ventral side; **f,** same as previous, with the neurocranial bones drawn. A full line denotes a definite outline of the bone, a dotted line an uncertain outline and/or a fracture and an interrupted line a prominent feature of the bone. With darker gray are depicted those structures placed most medially, to facilitate viewing. Abbreviations: aa, anguloarticular; asmx, anterior supramaxilla; boc, basioccipital; bpro, bulla prootica; bpto, bulla pterotica; br, branchiostegal ray; cl, cleithrum; co, coracoid; dent, dentary; ect, ectopterygoid; exo, exoccipital; fps, frontoparietal striae; fr, frontal bone; io, infraorbital; iop, interopercle; le, lateral ethmoid; me, mesethmoid; mx, maxilla; op; opercle; pch, posterior ceratohyal; pcl, postcleithrum; pmx, premaxillary; pop, preopercle; popc: preopercular canal; pro, prootic; ps, parasphenoid; psmx, posterior supramaxilla; pt, posttemporal; pto, pterotic; q, quadrate; sc, scapula; scl, supracleithrum; soc, supraoccipital; sop, subopercle; sph, sphenotic; sr, sclerotic ring; vo, vomer.

Suspensorium—The dorsal part of the hyomandibula is expanded; ventrally the hyomandibular shaft is long and almost straight and its ventral tip does not seem to reach the level of the quadrate (Fig. 3a). The quadrate is subtriangular, with approximately equal sides. The dorsoposterior process is strong and pointed, and dorsally the quadrate's margin is slightly concave, lacking an incision. The ectopterygoid, which appears toothless, is slender and the anterior and ventral arms form an oblique angle (ca. 120°).

Opercular series—The opercle has a straight anterior margin and a slightly convex ventral margin. It is smooth and bears no striations. The subopercle is broadly triangular, with a short and pointed anterodorsal process. The preopercle is wide, L-shaped, its upper arm longer than the lower arm and has a tapering and rounded anterior angle (Fig. 3a). The dorsal and ventral margins of the preopercle form a slightly acute angle (ca. 80°). The preopercular canal runs near the anterior and dorsal margins of the upper and lower arms of the preopercle respectively. The interopercle seems to be wider posteriorly and narrower anteriorly. Its anterior tip reaches approximately at the same level as the lower arm of the preopercle.

Hyoid and branchial arches—There are five branchiostegal rays attached to the ceratohyals. Under the bones of the opercular series are the ceratobranchials and/or hypobranchials and the epibranchials. These bones bear numerous gill rakers anteriorly. In at least one specimen (LGPUT ADS 005) there are more than 20 gill rakers at the second or third lower branchial arch, near the junction with the upper branchial arch.

Vertebral column and associated structures—There are 40–42 vertebrae, including preural centrum 1, and the closed haemal arches begin between the 16th or 17th vertebra (Table 2). The opercle covers the first five or five and a half vertebrae. The first 10 vertebrae are almost square, while the rest are more oblong. The neural arches are fused to their respective vertebral centra in the abdominal and caudal regions. In some vertebrae it is possible to discern that the prezygapophyses are more developed than the postzygapophyses. There are 24 ribs, starting from the third vertebra and ending on the 26th, which almost reach the ventral body margin. Therefore, the ribs-to-total number of vertebrae ratio is 0.57–0.6.

The epineural processes sprout from the neurapophyses until ca. the 20th vertebra and are free of the wall of the neural arch after that, as epineurals. The epipleurals are all free. The epineurals and the epipleurals are very thin and elongate. Each vertebra seems to be associated with an epineural and an epipleural; in the most anterior vertebrae these structures are harder to discern though. In the caudal region the epineurals and an epipleurals become progressively more strongly inclined. There are 10 posterodorsally inclined supraneurals, shaped as slender wedges with an expanded dorsal tip, which become slenderer posteriorly. Due to the preservation, the type of articulation of the ribs with the vertebrae and/or the parapophyses not discernible.

Pectoral and pelvic girdles and fins—Each posttemporal has a broad body and slender, rod-like dorsal and ventral arms, the dorsal longer than the ventral (Fig. 3a). The supracleithrum is broad dorsally and tapers ventrally. The cleithrum is long and robust, curving anteriorly at its ventral portion. Close to the cleithrum and ventrally to the supracleithrum there are two elongate postcleithra (Fig. 3a). The uppermost postcleithrum is the shortest and broadest, and below that there is one longer and slenderer postcleithrum, which almost reaches the ventral margin. Ventrally to the cleithrum and attached to it is the flat and thin coracoid, which is highly perforated. The anterior and ventral margins of the coracoid are convex, and posteroventrally the end of the coracoid is pointed. Postero-dorsally, between the cleithrum and the coracoid, is the scapula. The scapula is perforated by the scapular foramen and it articulates with the pectoral radials, which are crushed in our specimens. The pectoral fin is situated close to the ventral margin and has 15 rays.

The pelvic bones are long and triangular, reaching forward the length of four or five vertebrae. After the crushed radials come eight or nine pelvic fin rays (i7 or i8). The pelvic fin originates approximately under the 18th–19th vertebra and under the anterior third of the base of the dorsal fin.

Dorsal and anal fins—Both median fins have the following characters in common. They are subtriangular in shape (Fig. 2d), their pterygiophores decrease in size posteriorly and their fin rays increase in length until the third to fifth element and then progressively decrease, including the last two anal rays of the anal fin (Fig. 4). The pterygiophores are formed by the proximal radials which are possibly fused to the middle radials (see e.g., Grande, 1985:p.338 and 347) (Fig. 4); it is not clear if the distal radials are present or fused with some other element. The first two (procurrent) fin rays are the distally undivided and the second ray may or may not be segmented. The principal rays (sensu Arratia, 2008) begin from the third fin ray, which is segmented and undivided, and then continue to the last rays, which are segmented and divided.

The dorsal fin origin is placed about the middle of the body. It has 17 rays and an equal amount of pterygiophores (the last two rays are borne by the same pterygiophore and therefore counted as one). The pterygiophores of the extremities are modified. The anteriormost pterygiophore is a flattened and deep anteroventrally-facing keel and the posteriormost pterygiophore is a slender horizontally-oriented stay (Fig. 4a). The first pterygiophore is

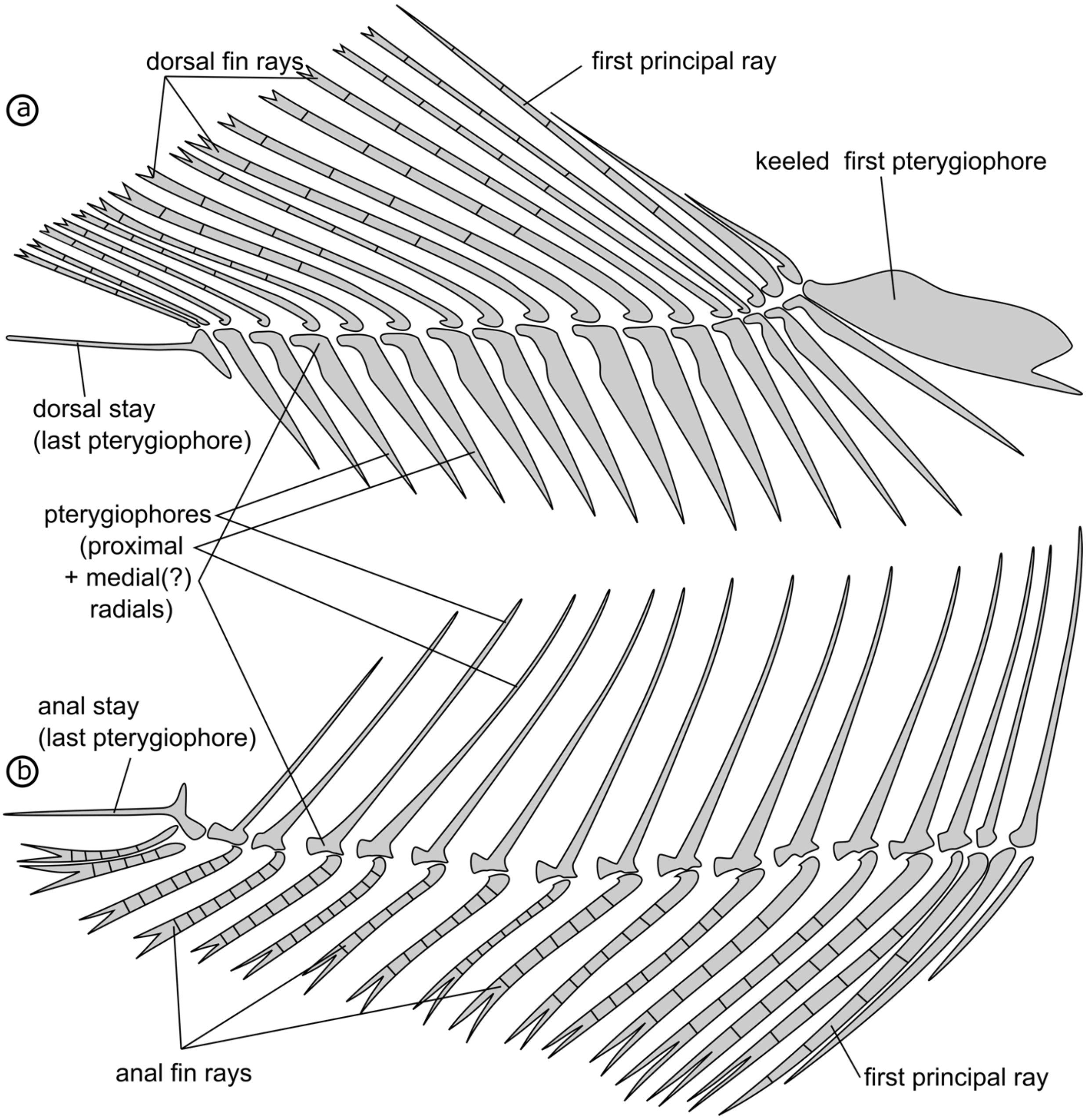

Figure 4. Schematic representation of the unpaired fins of †*Pseudohilsa*? *nikosi*, based on all examined specimens. **a,** dorsal fin; **b,** anal fin. Anterior is on the right; the fins are not in scale relative to each other.

associated with the neural spine of the ninth to the tenth vertebra. Between the projection of the end of the dorsal fin and the beginning of the anal fin there is a space of five vertebrae on the horizontal level. There are 16–19 anal fin rays supported by 15–18 pterygiophores (Fig. 4b). The first pterygiophore is unmodified, slender and elongate as the rest of the pterygiophores and it supports two rays, which are undivided distally. The same pterygiophore is associated with the haemal spine of the 26th or 27th vertebra. The last pterygiophore is modified to a slender horizontally-oriented stay and bears two fin rays, which are counted as one.

Caudal endoskeleton and fin—The caudal fin is forked, the longest principal rays almost three times the length of the shortest middle principal rays. There are ten principal and seven procurrent caudal fin rays in the upper lobe and nine principal and six to seven procurrent rays in the lower lobe (Fig. 5). The uppermost and lowermost principal rays are segmented and undivided, the rest of the principal rays are segmented and divided. The uppermost principal fin ray begins posteroventrally to the pleurostyle and the lowermost principal caudal fin ray reaches the hemal spine of preural vertebra 2. All except the anteriormost procurrent caudal rays are segmented. Anteriorly to the procurrent caudal rays of each lobe there is a caudal scute, which appears longer, flatter and unpaired, in contrast to procurrent rays. The basal segments of the two middle principal caudal fin rays bear small processes.

All the caudal fin rays are supported by the last four to five vertebrae. The first preural vertebra bears dorsally a neural arch and a short neural spine and dorsoposteriorly it is fused to the elongate first uroneural, or pleurostyle. Between the pleurostyle and the neural spine of the second preural vertebra there are two moderately elongate epurals. The parhypural, which is not fused to the first preural vertebra, and the haemal spine of the second and third preural vertebrae are more expanded and robust than the haemal spines of the other, anterior vertebrae. There are six hypurals, of which the first and third are expanded, the rest are narrower. The anterior end of hypural 1 is tapering to a hook-shaped process. The hypural 3 is posteroventrally notched, forming the hypural diastema. All hypurals are autogenous, with the exception of the hypural 2, which is fused to the ural centrum 2 (polyural terminology, see Schultze and Arratia, 2013). Posteriorly to the pleurostyle there is the elongate second uroneural.

Squamation—The scales are seen only from their medial side, and therefore their anterior side is exposed to the observer and not the posterior, the opposite of what happens when someone observes a fish exteriorly. Consequently, the sculpture on the lateral surface of the scales is not visible, except for some patches that are transparent enough to allow one to see through them the fine circuli on the lateral surface of the anterior field of the scales (Fig. 6a, b). There are about 40 scales in a transverse row along the body, from behind the head to the end of the hypural plates, and about 11 horizontal scale rows over the pelvic fin. The scales are imbricate and of similar size (Fig. 6a, b), with the posterior scales being somewhat smaller than the anterior ones. There are no lateral line scales.

Along the ventral midline of the body there is a series of scutes. There are ca. four free prepelvic scutes along the gular region, 11 to 12 prepelvic scutes each associated with the ventral portion of a pair of ribs and 11 postpelvic scutes, also associated with an equal amount

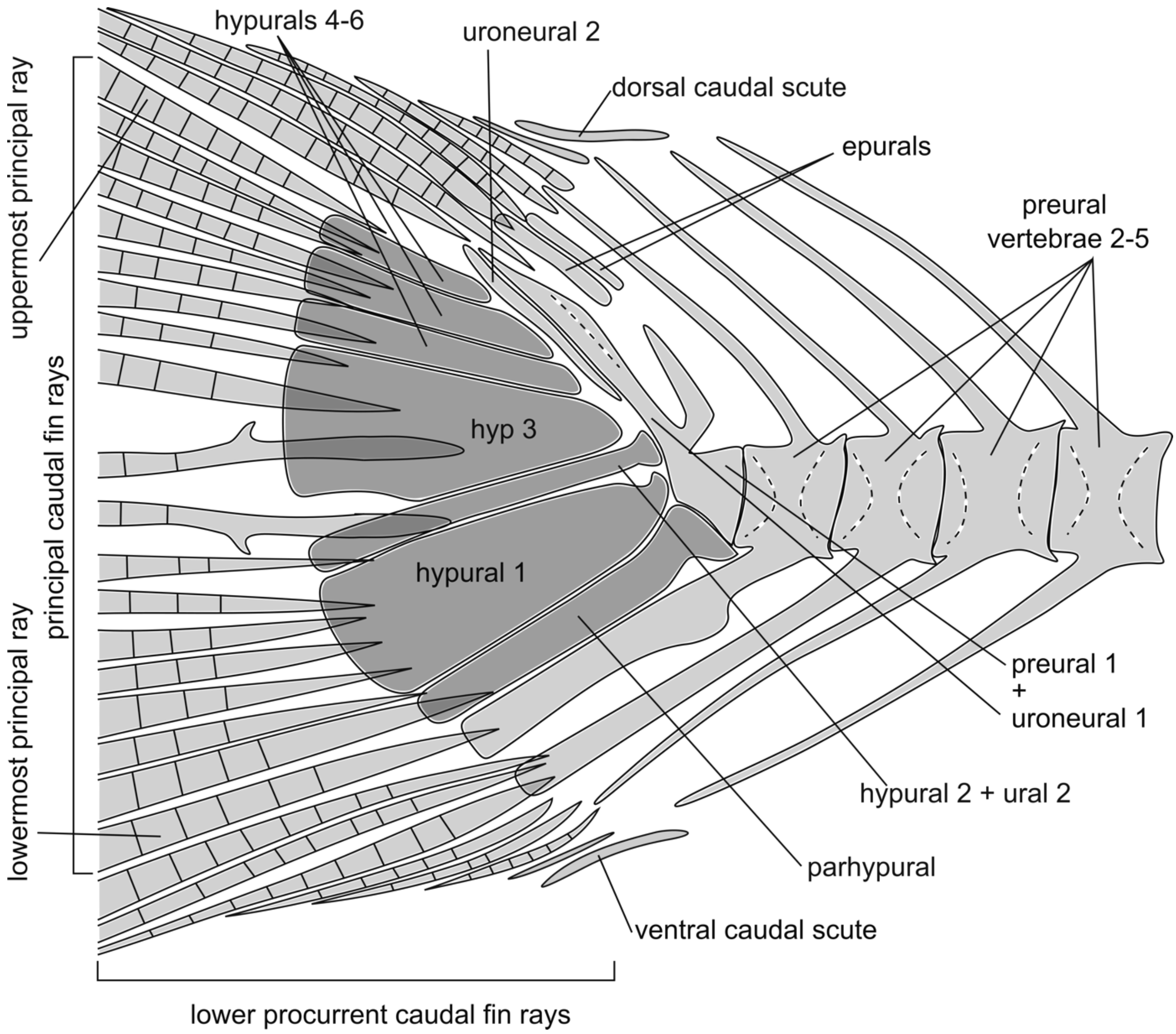

Figure 5. Schematic representation of the caudal fin of †*Pseudohilsa*? *nikosi*, based on all examined specimens. A full line denotes a definite outline of the bone, a dotted line an uncertain outline and/or a fracture and an interrupted line a prominent feature of the bone. With darker gray are depicted those structures placed most medially. Anterior is on the right; the arrangement of the caudal fin rays might have slightly differed in the live fish as the fossils show minor taphonomic alterations.

of pairs of ribs. The scutes are strong, with a sharp median keel which deepens posteriorly (Fig. 6c, d). The pelvic scute, meaning the scute which is directly in front of the insertion of the pelvic fin, is shaped similar to the rest. All the scutes, with the possible exception of the one directly below the pelvic fin, bear ascending arms. These arms are robust and long; the arms of the rib-associated prepelvic scutes reach to about 40% or more of the body cavity and the pelvic scute has the most prominent arms. In general, the ascending arms

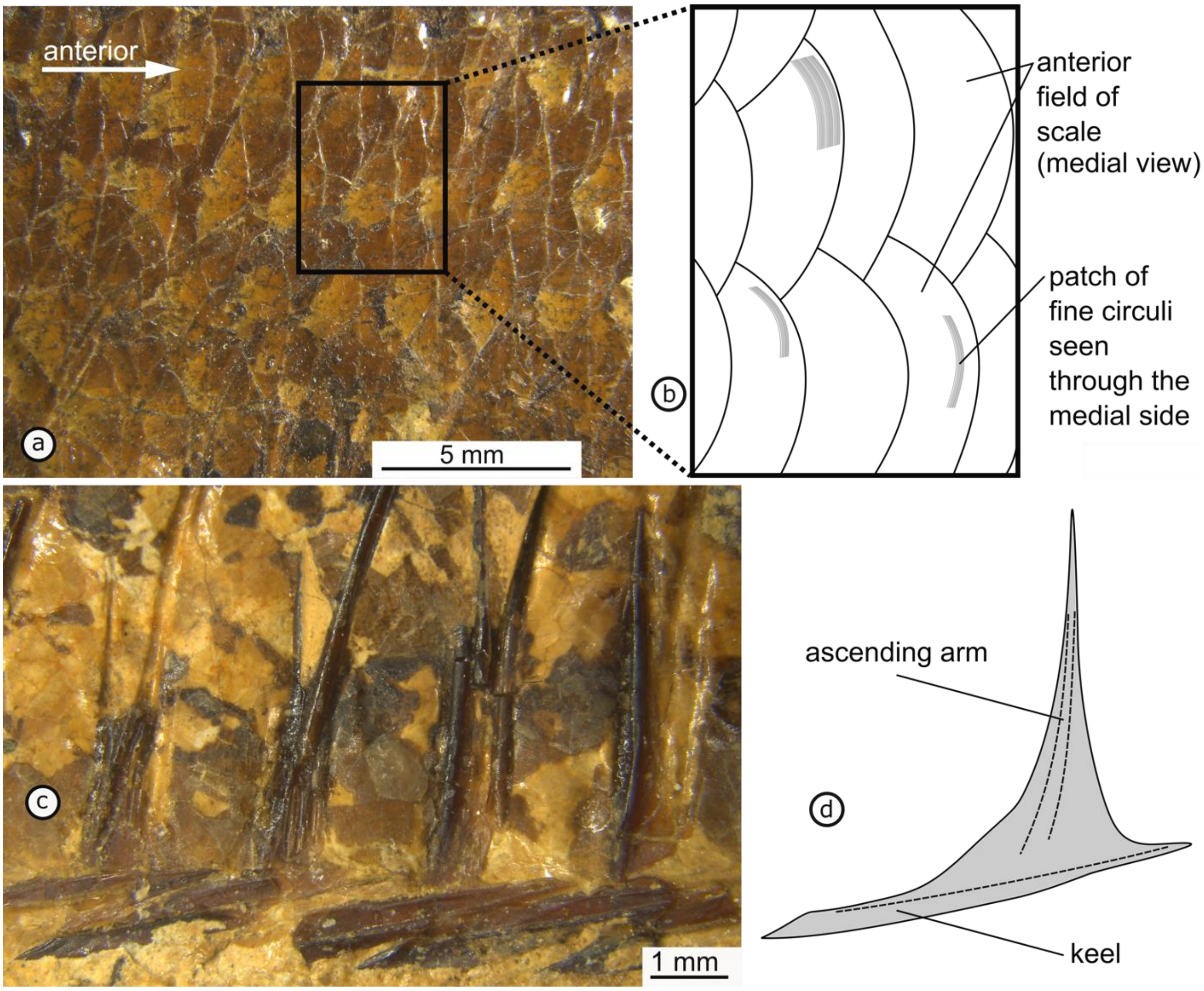

Figure 6. The squamation of †*Pseudohilsa*? *nikosi*. **a,** Flank scales of the specimen LGPUT ADS 004, in medial view; **b,** detail of same, schematic representation showing the circuli of the scales, image presenting only the green channel of the original photograph; **c,** postpelvic abdominal scutes of the specimen LGPUT ADS 002; **d,** Schematic representation of a scute of †*Pseudohilsa*? *nikosi*, based on all examined specimens. Anterior is on the right; a full line denotes a definite outline of the bone and an interrupted line a prominent feature of the bone.

are placed closer to the anterior end of the scute, except for the posteriormost postpelvic scutes where the ascending arms are placed closer to the posterior end. Predorsal scutes are absent.

4.4. Discussion

4.4.1. Systematic discussion down to the level of family

Most of the characters which might support the monophyly of Otomorpha are not identifiable in the examined fossils (e.g., silvery area at the anterior part of swim bladder, united cartilaginous basis for first and second hypurals, parietals fused with medial extrascapulars, early ossification of autopalatine, ossified epicentrals) (Arratia, 1999; Wiley and Johnson, 2010; Arratia, 2018; Straube et al. 2018). However, some characters which are characteristic for at least most Otomorpha are clearly discernible in our fossils, such as the fusion of haemal arches to centra anterior to the second preural centrum, a second hypural fused to the second ural centrum (polyural terminology, see Schultze and Arratia, 2013) and the presence of a pleurostyle (Arratia, 1999; Wiley and Johnson, 2010; Arratia, 2018; Straube et al. 2018).

The fossil fishes from the site "Aidonochori A" possess some typical characteristics of the superorder Clupeomorpha, meaning the presence of bullae in the skull, the possession of ventral scutes and an autogenous first hypural with a hooked anterior end (Grande, 1985; Fujita, 1990; Wiley and Johnson, 2010). The lack of a lateral line, the fusion of the first preural centrum to the first uroneural but not to the parhypural and a temporal foramen which does not seem to be overlain by any flange mean that the fossils should be assigned in the suborder Clupeoidei of the order Clupeiformes (Grande, 1985; Di Dario and de Pinna, 2006; Wiley and Johnson, 2010).

Based on anatomical characters, the Clupeoidei have been divided in the families Engraulidae (anchovies), the Chirocentridae (wolf herrings), the Pristigasteridae (longfin herrings) and the Clupeidae (herrings and allies) (Nelson, 1970; Grande, 1985; Whitehead, 1985). For the purposes of this study, this classification is followed. It is noted however, that there is no consensus regarding the relationships between these families based either on morphological (e.g., Grande, 1985; Di Dario, 2009; Patterson and Johnson, 1995; Miyashita, 2010) or molecular evidence (e.g. Li and Ortí, 2007; Lavoué et al., 2013; Bloom and Egan, 2018). Moreover, the monophyly of the Clupeidae is contested, e.g., because of the inclusion in this family, in some molecular studies, of the Chirocentridae (Wilson et al., 2008; Li and Ortí, 2007; Lavoué et al., 2007; Lavoué et al., 2010; Lavoué et al., 2013; Queiroz et al., 2020).

The Engraulidae can be excluded because they are characterized by having the tip of the maxilla and the lower jaw articulation being positioned well behind the eye (vs. at the level of the eye in the specimens from the site "Aidonochori A"), snout "pig-like", projecting anteriorly (vs. snout not projecting) and a high number of branchiostegals (7–19 vs. 5) (Ridewood, 1904; Whitehead, 1962; McAllister, 1968; Grande, 1985; Nelson et al., 2016). Additionally, the ratio of ribs-to-total number of vertebrae is too high for Engraulidae (up to 0.54 vs. 0.57–0.6, see Grande, 1985:pp. 263–264; Di Dario 2009). *Chirocentrus* Cuvier, 1816 is the only genus in the family Chirocentridae and is characterized by fang-like oral teeth (vs. absent), small scales (vs. normal), anal fin with many rays (>30 vs. <20), pelvic fin with six or seven rays (vs. eight or nine), eight branchiostegals (vs. five), lack of abdominal scutes (vs. fully scuted) and about 70 or more vertebrae (vs. 40–42) (McAllister, 1968; Grande, 1985; Whitehead, 1985; Nelson et al., 2016). Pristigasteridae clearly differ from the specimens from the site "Aidonochori A", because they too have more than 30 rays in the anal fin, the supraneurals are inclined vertically or anterodorsally (vs. posterodorsally), the postzygapophyses are larger than the prezygapophyses (vs. prezygapophyses larger, Fig. 5, see Di Dario, 2002) and they lack a notch at the third hypural (vs. notch present) (Wongratana,1980; Grande, 1985, Nelson et al., 2016). The Clupeidae is the only family that matches the fishes from the site "Aidonochori A" in all the above-mentioned characters and also is characterized by the presence of two long, rod-like postcleithra (Grande, 1985) as in the fossils (Fig. 3a).

4.4.2. Systematic discussion to the level of subfamily

There is currently no consensus regarding the systematics of Clupeidae at the level of subfamily, with different molecular phylogenies suggesting different groupings (e.g., Wilson et al., 2008; Lavoué et al., 2014; Bloom and Lovejoy, 2014). Here the classification presented in Nelson et al. (2016) is followed, in which the Clupeidae are distinguished in the subfamilies Dussumieriinae, Ehiravinae, Pellonulinae, Dorosomatinae, Clupeinae and Alosinae.

The Dussumieriinae are excluded because they possess only one, W-shaped, abdominal scute (vs. abdomen fully scuted in the specimens from the site "Aidonochori A") (Grande, 1985). Fishes of the subfamily Ehiravinae are small and paedomorphic (up to 50–60 mm vs. up to ca. 150 mm SL) (Nelson et al., 2016). The Ehiravinae and the Pellonulinae have lost the anterior supramaxilla (vs. present) and their ural centrum 2 (polyural terminology, see Schultze and Arratia, 2013) is fused to the compound first preural centrum plus the uroneural (Grande, 1985). In Dorosomatinae the last dorsal fin ray is elongate and filamentous (vs. short and lacking a filament) and/or the mouth is inferior to subterminal (vs. terminal) (Grande, 1985; Whitehead, 1985). The remaining two subfamilies, Clupeinae and Alosinae, are not distinguished by unambiguous synapomorphies that can be easily observed in fossils. For this reason, all modern and fossil genera attributed to either of these subfamilies are included in further discussions.

4.4.3. Comparison with modern genera

As noted above, molecular phylogenies have not yet converged on which genera should be included in either of the subfamilies Clupeinae or Alosinae. Here the classifications presented in Nelson et al. (2016) and Whitehead (1985) are followed, which were mostly based on morphological characters and assigned the most genera in both of these subfamilies. According to Whitehead's (1985) list there are 16 genera in Clupeinae (*Sprattus* Girgensohn, 1846; *Clupeonella* Kessler, 1877; *Sardina* Antipa, 1904; *Sardinops* Hubbs, 1929; *Harengula* Valenciennes, 1847 (see Cuvier and Valenciennes, 1847); *Opisthonema* Gill, 1861; *Herklotsichthys* Whitley, 1951; *Amblygaster* Bleeker, 1849; *Sardinella* Valenciennes, 1847 (see Cuvier and Valenciennes, 1847); *Clupea* Linnaeus,1758; *Escualosa* Whitley, 1940; *Platanichthys* Whitehead, 1968; *Ramnogaster* Whitehead, 1964; *Rhinosardinia* Eigenmann, 1912; *Lile* Jordan and Evermann, 1896; *Strangomera* Whitehead, 1964) and 7 in Alosinae (*Alosa* Linck, 1790; *Brevoortia* Gill, 1861; *Ethmidium* Thompson, 1916; *Ethmalosa* Regan, 1917; *Hilsa* Reagan, 1917; *Tenualosa* Fowler, 1933; *Gudusia* Fowler, 1911). Unless otherwise stated, the generic features described in Whitehead (1985) are used.

The genera *Sprattus* and *Clupeonella* are readily distinguished because they lack a pterotic bulla (vs. pterotic bulla present in the fishes from the site “Aidonochori A”, Fig. 3a, e, f). The presence of one or more dorsal scutes further excludes the genera *Herklotsichthys*, *Harengula*, *Ethmalosa*, *Ethmidium*, *Tenualosa* and *Opisthonema* (vs. no dorsal scutes, see Grande 1985:tables 9a and 10a). In the genera *Amblygaster* and *Sardinella* the last two anal fin rays are enlarged (vs. equal or shorter to the penultimate fin ray). *Sardina* and *Sardinops* have distinct bony ridges radiating downward on their opercle (vs. opercle smooth). The last dorsal fin ray in *Opisthonema* is elongate and filamentous (vs. equal or shorter to the penultimate fin ray). *Rhinosardinia* possesses a sharp spine on the anteroposterior part of the maxilla (vs. smooth, Fig. 3a). From the remaining genera the pelvic fin has less than eight rays in *Escualosa*, *Platanichthys*, *Ramnogaster*, *Lile* and *Brevoortia* (vs. eight or nine).

Gudusia is different than the fishes known from the site “Aidonochori A” because its pelvic fin inserts just before the dorsal fin (vs. slightly behind), and it also has a deep body (vs. slender), a preorbital length which is much shorter than the horizontal diameter of the eye (vs. roughly the same, Table 1) and many more scales in the lateral series (77–91 vs. ca. 40). *Clupea* and *Strangomera* have higher counts of supraneurals (15–19 and 15 respectively vs. 10), branchiostegal rays (8 and 7 respectively vs. 5, see also McAllister, 1968) and vertebrae (>50 and 44 respectively vs. 40–42). *Alosa* also possesses a higher number of branchiostegal rays (7–8 vs. 5, see also McAllister, 1968) and vertebrae (ca. 50 or more vs. 40–42) and often has a striated opercle (see also Svetovidov, 1963:p. 233). *Hilsa* has fewer predorsal bones (7 vs. 10), and a deep body (vs. slender).

Therefore, the here described fishes from the site “Aidonochori A”, cannot be attributed to any of the modern genera. They do, however, seem to have the least pronounced differences with *Hilsa*. *Hilsa* is genus that includes a single species, *Hilsa kelee* (Cuvier, 1829), also known as the Kelee shad.

4.4.4. Fossils attributed to Hilsa—Danil'chenko (1980) reassigned four species formerly placed in *Alosa* to *Hilsa*, namely †*H. elegans* (Gabelaia, 1976), †*H. oblonga* (Gabelaia, 1976), †*H. torosa* (Gabelaia, 1976), †*H. lata* (Gabelaia, 1976). According to Danil'chenko (1980) they come from the lower to middle Pliocene sediments of the region of Abkhazia, on the eastern coast of the Black Sea, in the South Caucasus. The delimitation of these species was based on meristic (e.g. number of vertebrae and fin ray counts of unpaired fins) and morphometric characters (e.g. body depth) (Gabelaia, 1976; Danil'chenko, 1980). These characters of the fossil "*Hilsa*" species are generally similar to those of the fossils from the site "Aidonochori A", but other taxonomically important characters are missing from the description of these species (e.g., presence/absence of frontoparietal striae, perforation of the scales, number of pelvic fin rays). It is therefore not possible to compare directly the fossils from the site "Aidonochori A" to these "*Hilsa*" specimens, or to be certain to which genus the latter belong. Moreover, the differences between these fossils from the region of Abkhazia are small and the validity of some of these species needs to be reconsidered.

4.4.5. Comparison of the herrings from the site "Aidonochori A" with fossil genera

In this section, the fishes from the site "Aidonochori A" are compared with extinct genera from the Cenozoic which are adequately described to allow comparisons with our specimens. Only genera attributed to the family Clupeidae, but not to the subfamilies Dussumieriinae, Ehiravinae, Pellonulinae and Dorosomatinae are considered. The differences with these fossil genera are described below. Unless otherwise stated, the data on the fossil genera come from the original descriptions. The fossil genera are presented from the oldest to the youngest.

i. †*Primisardinella* Danil'chenko, 1968; upper Paleocene of Turkmenistan; larger size (ca. 600 mm vs. up to ca. 180 mm total length in the fossils from the site "Aidonochori A"), last two anal rays enlarged (vs. equal or shorter to the penultimate fin ray) (see also Danil'chenko, 1980).

ii. †*Horaclupea* Borkar, 1973; upper Paleocene or lower Eocene (or Maastrichian, Upper Cretaceous, see Arratia et al. 2004) of Gujarat, India; lower number of vertebrae (30–35 vs. 40–42), lower number of dorsal fin rays (8 vs. 16–17).

iii. †*Eoalosa* Marramà and Carnevale, 2018; Eocene marine sediments of Monte Bolca, Italy; higher number of vertebrae (47 vs. 40–42), lower number of pelvic fin rays (seven vs. eight or nine).

iv. †*Bolcaichthys* Marramà and Carnevale, 2015; Eocene marine sediments of Monte Bolca, Italy; "pelvic-fin origin slightly in front of or behind the posterior end of the dorsal fin" (Marramà and Carnevale, 2015:p. 2) (vs. under the anterior third of the dorsal fin base), lower number of supraneurals (eight vs. ten), higher number of epurals (three vs. two).

v. †*Gosiutichthys* Grande, 1982; middle Eocene lacustrine sediments of Wyoming, U.S.A.; smaller fish (up to ca. 40 mm vs. up to ca. 150 mm), dorsal scutes present (6–13 vs. none), lower number of vertebrae (34–36 vs. 40–42), supraneural bones (6–7 vs. 10) pelvic fin rays (6–7 vs. 8 or 9), dorsal fin rays (9–10 vs. 16–17) and anal fin rays (9–12 vs. 16-19), higher number of branchiostegal rays (8 vs. 5).

vi. †*Marambionella* Jerzmanska, 1991; upper Eocene–lower? Oligocene of Seymour Island/Marambio, Antartica; higher number of vertebrae (ca. 49 vs. 40–42) and ventral scutes (19 prepelvic and 13 postpelvic vs. ca. 16 and 10–11).

vii. †*Chasmoclupea* Murray, Simons and Attia, 2005; lower Oligocene lacustrine sediments of Fayum, Egypt; lower number of pelvic fin rays (7 vs. 8 or 9), dorsal fin rays (12 vs. 16–17), higher number of supraneurals (13? vs. 10). From figures 1 and 2 of the original description, it can be seen that the ascending arms of the ventral scutes are very broad (vs. slender).

viii. †*Clupeops* Sauvage, 1880; Miocene of Drome, France; prominent teeth on premaxillary (vs. no teeth), 55 vertebrae (vs. 40–42).

ix. †*Moldavichthys* Baykina and Schwarzhans, 2017a; middle Miocene of Moldova; premaxilla and dentary toothed (vs. premaxilla and dentary toothless), opercle with radial ridges (vs. smooth), higher number of branchiostegals (seven to eight vs. five).

x. †*Karaganops* Baykina and Schwarzhans, 2017b; middle Miocene of Tambov, Russia; last two anal fin rays enlarged (vs. equal or shorter to the penultimate fin ray), higher number of branchiostegals (seven vs. five) and vertebrae (44–46 vs. 40–42).

xi. †*Pseudohilsa* Menner, 1949; Middle Miocene of Absheron peninsula, Azerbaijan; lower number of dorsal fin rays (10–13 vs. 16–17) (see also Danil'chenko, 1980).

xii. †*Ganolytes* Jordan, 1919 (including its junior synonyms †*Diradias* Jordan, 1924 and †*Xenothrissa* Jordan, 1925 according to David, 1943; upper Miocene marine sediments of California, U.S.A.; opercle strongly striated (vs. smooth), higher number of vertebrae (45–52 vs. 40–42) (see also David, 1943).

xiii. †*Eosardinella* Sato, 1966; upper Miocene marine sediments of NE Japan; a pair of "very pronounced" ridges on the operculum (vs. smooth), higher number of vertebrae (47 vs. 40–42).

xiv. †*Quisque* Jordan, 1920; upper Miocene marine sediments of California, U.S.A.; probably 9–10 dorsal scutes present (vs. none), lower number of vertebrae (30–32 vs. 40–42), dorsal fin rays (12 vs. 16–17) and anal fin rays (10 vs. 16–19), higher number of pelvic fin rays (ten vs. eight or nine) (see also Jordan, 1921).

xv. †*Sarmatella* Menner, 1949; upper Miocene of Croatia; last two anal fin rays enlarged (vs. equal or shorter to the penultimate fin ray), higher number of vertebrae (44–54 vs. 40–42) and branchiostegal rays (seven vs. five) (see also Baykina, 2013).

xvi. †*Xyne* Jordan and Gilbert, 1919 (†*Xyrinius* Jordan and Gilbert, 1919 referred to this genus, see David, 1943); upper Miocene marine sediments of California, U.S.A.; pelvic fin inserted slightly before dorsal fin (vs. under the anterior third of the dorsal fin base), preopercle with longitudinal ridges (vs. smooth), higher number of vertebrae (46–47 vs. 40–42) (see also David, 1943).

xvii. †*Austroclupea* Bardack, 1961; Miocene or Pliocene freshwater sediments of Argentina; large orbit fitting three times in head length (vs. about four times), lower number of vertebrae (35–37 vs. 40–42), pelvic fin rays (seven vs. eight or nine).

xviii. †*Paleopiquitinga* de Figueiredo 2010; Pliocene of NE Brasil; higher number of branchiostegal rays (seven vs. five), lower number of pelvic fin rays (seven vs. eight or nine), supraneural bones (eight vs. ten), epurals (one vs. two) and postpelvic scutes (eight vs. ten to eleven).

The genus which has the least amount of differences with the fossils from the site "Aidonochori A" is †*Pseudohilsa* (misspelled as "*Pseudochilsa*" in Grande, 1985). Menner (1949) raised this genus to accommodate the species †*Diplomystus brevicaudus,* described by Lednev (1914).

The assignment of this species in †*Diplomystus* by Lednev (1914) was done even though it lacked some typical characteristics of this genus, e.g, dorsal scutes. Apart from the lower number of dorsal fin rays, there are few other differences to set †*Pseudohilsa brevicauda* apart from †*Pseudohilsa*? *nikosi*, such as that the eye is ca. 33% of the head length (vs. ca. 25%) and that the pelvic fin is under the posterior half of the dorsal fin's base (vs. the anterior half) (Lednev, 1914; Danil'chenko, 1980). †*Pseudohilsa brevicauda* shares several similarities with †*Pseudohilsa*? *nikosi*, such as a similar standard length (ca. 100–150 mm), a slender body, a smooth opercle, absence of teeth, similar number of vertebrae (36–40 vs. 40–42 at †*Pseudohilsa*? *nikosi*), ten or eleven supraneurals, last two anal rays not enlarged, ca. 40 transverse scale rows, ca. 22 ventral scutes, half of which postpelvic (it is not clear if the scutes of the throat were taken into account) (Lednev, 1914; Danil'chenko, 1980). However, some important features of †*Pseudohilsa brevicauda* are not described in the available literature, such as the presence or absence of frontoparietal striae, the number of epurals, the number of branchiostegals and pelvic rays. For the reasons above, the specimens from the site "Aidonochori A" are placed tentatively in the genus †*Pseudohilsa* but in a separate species, †*Pseudohilsa*? *nikosi*.

4.4.6. Other fossil Clupeomorpha from Greece

The oldest Clupeomorpha fossil from Greece is †*Scombroclupea* sp. from the Upper Cretaceous (Maastrichian) near Karpenisi (Koch and Nicholaus, 1969). The only record of a clupeomorph fossil fish from northern Greece is a clupeid from the Pliocene of the Serres Basin (Weiler, 1943). This fossil has ca. 50 vertebrae (vs. 40–42 in †*Pseudohilsa*? *nikosi*) and a striated operculum (vs. smooth) and is therefore clearly different from those of †*Pseudohilsa*? *nikosi*. Based primarily on these characters, Weiler (1943) attributed this fossil to "*Caspialosa nordmanni*" (Antipa, 1904), a junior synonym of the extant *Alosa tanaica* (Grimm, 1901). Other fossil clupeomorphs from Greece have been described from the upper Miocene to Pliocene of Central Greece and Crete. They have been assigned to the extant genera *Alosa*, *Sardina* and *Spratelloides* (Gaudant 2001, 2004, 2014; Gaudant et al., 1994, 1997, 2005, 2006, 2010; Argyriou and Theodorou, 2011; Argyriou, 2021).

4.4.7. Paleoecological remarks

Systematic excavations for the fossil site "Aidonochori A" are still pending, but some preliminary remarks regarding the paleoecology can be made. The sediment is fine-grained, contains mica and carbonate. These characteristics, combined with the good state of preservation of the skeletons point to a terrestrial, low energy environment. It is unfortunately not possible to infer the salinity of this environment, as the clupeids are known to be euryhaline and no other fossils have been recovered from this locality so far.

The modern clupeid which seems to resemble †*Pseudohilsa*? *nikosi* the closest, *Hilsa kelee,* is a marine pelagic fish, which, as many other clupeids, lives in shoals and can tolerate very low salinities (Whitehead, 1985). The aforementioned characteristics are congruent with what is known for †*Pseudohilsa*? *nikosi* from the site "Aidonochori A", where multiple individuals have been recovered from sediments of terrestrial origin in close proximity to each other.

4.4.8. Paleobiogeographical remarks

The only occurrence of †*Pseudohilsa* so far has been from the middle Miocene of Absheron peninsula, Azerbaijan, near the Caspian Sea (Menner, 1949; Danil'chenko, 1980). Therefore, the fossils from the site "Aidonochori A" may help expand the distribution of this genus. It is also notable that these two occurrences are not very far in space and geological time.

Hilsa kelee lives in the Indian Ocean and the West Pacific (Whitehead, 1985). The fossils which have been implicitly (†*Pseudohilsa*) or explicitly presented as relating to *Hilsa* come from the Caspian Sea (†*Pseudohilsa brevicauda*; Menner, 1949; Danil'chenko, 1980), the Eastern Mediterranean †*Pseudohilsa*? *nikosi*) or the Black Sea (*H. elegans, H. oblonga, H. torosa* and *H. lata*; see Gabelaia, 1976; Danil'chenko, 1980). Their presence hints at the existence of *Hilsa*-lookalikes in Tethys and Paratethys during the middle Miocene–Pliocene and may suggest a local extinction of these fishes from the remnants of the Tethys and Paratethys at some point during the late Neogene or Quaternary.

A similar biogeographical scenario seems to have been the case for other clupeiform fishes such as *Spratelloides* or *Etrumeus*. These genera were present in the Neogene of the Mediterranean (e.g., Grande 1985; Gaudant et al., 1994, 2010; Gaudant 2004; Landini and Sorbini, 2005; Argyriou and Theodorou, 2011; Argyriou 2021), but subsequently went locally extinct and were known as having a mostly tropical distribution. They were, however, among the first fishes to invade again the Mediterranean Basin after the opening of the Suez Canal (Por, 1978; Golani, 1998), an invasion which might be facilitated by the current climate trend (Por, 2009).

Nevertheless, such biogeographical scenarios regarding †*Pseudohilsa*? *nikosi* ought to be treated with caution, until the affinities of this species are interpreted with confidence. In order to elucidate the possible relationships of the fossil *Hilsa* lookalikes with each other and modern *Hilsa*, further systematic studies are necessary.

4.5. Conclusions and Outlook

The clupeid fossil fishes from the upper Miocene site “Aidonochori A” are attributed to a new species, †*Pseudohilsa*? *nikosi*, owing to their unique morphology among fossil and extant clupeids. They are placed provisionally in the genus †*Pseudohilsa*, which is known from the middle Miocene of the Caspian Sea. Among extant clupeids, they seem to resemble morphologically *Hilsa kelee*, which has a tropical distribution in the Indo-West Pacific. The fossils attributed to †*Pseudohilsa*, as well as some fossils attributed to *Hilsa* from the middle Pliocene of the Black Sea are in need of revision, but it seems that clupeids resembling *Hilsa* were present in the Mediterranean and Paratethys during the Neogene. Future systematic studies of the fossils should help clarify the relationships between the aforementioned taxa and their biogeographical links.

Acknowledgements

I would like to thank Nikos Bacharidis for discovering the locality in Aidonochori, excavating the fossils and entrusting me with their study. I thank for her collaboration Prof. Dr. Evangelia Tsoukala, director of the Museum of Geology and Palaeontology of the Aristotle University of Thessaloniki. This study benefited from the discussions and suggestions of Dr. Gloria Arratia (University of Kansas, Lawrence, USA). I thank Prof. Dr. Bettina Reichenbacher for providing funding for this research (DFG grant Nr. 403523527) and her kind support.

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5. Conclusions and Outlook

In chapters 2 and 3, the fossil remains of cichlid fishes from the middle-upper Miocene Ngorora Formation from the Tugen Hills area, Kenya, were described. A new genus is raised to accommodate the described fossils, †*Rebekkachromis*. In the locality Rebekka (ca. 11 Ma), two species, †*R. ngororus* and †*R. kiptalami* were recognized. From the site Yatianin two more species, †*R. valyricus* and †*R. vancouveringae* were described and five other specimens show each a unique mixture of characters. Before the start of the investigations in the Tugen Hills, about 20 nominal species of African cichlids were known. Only as an outcome of examining these three localities from the Tugen Hills, about a quarter of new species were added to this list. This is a significant increase in our knowledge and it highlights the importance of the Tugen Hills as a source of information on the past diversity of cichlids.

Based on μCT and optical microscopy data, the fossils from the examined sites form a distinct morphogroup, with defining characters such as: a preopercle with three pores on the lower branch of this bone, a slender urohyal lacking an anterodorsal projection, similar meristic values, all scales cycloid and scales of the nape, throat, and belly minute relative to the flank scales. Owing to the co-occurrence of different species and morphs with intermediate characteristics, it is hypothesized that †*Rebekkachromis* in Yatianin might have been in the process of forming a nascent species flock.

In order to investigate the systematics of †*Rebekkachromis*, a survey of some osteological characters of modern cichlids was conducted by using optical microscopy, X-rays and data from the literature. The results of this exercise allowed the reconstruction of the dentition of †*Rebekkachromis* which helped establish †*Rebekkachromis* as a member of the haplotilapiines, the largest group among African cichlids. Based on other characters, such as the number of lateral-line tubules on the lacrimal, the number of supraneural bones and the number of sensory canal pores on the preopercle, the fossils were attributed to the tribe Oreochromini, which today has a pan African distribution. The new evidence presented here reinforce previous claims for a close morphological similarity of some cichlids from the Tugen Hills to the modern alkaliphile cichlids, belonging to the subgenus *Oreochromis* (*Alcolapia*). The geology and paleontology of the Ngorora Formation also indicate that these fossil cichlids used to live in alkaline waters. Thus, the sediments of the Ngorora Formation likely hold the only examples of fossil cichlids living in alkaline waters known to date.

The systematic investigations on the fossils of chapter 3 were greatly facilitated by the use of μCT technology. Compared to other methods, such as mechanical preparation of the fossils, μCT technology is costlier and harder to access, but at the same time faster and non-destructive, while offering us the chance to examine anatomical structures in great detail. In cases where μCT fails, other techniques, such as synchrotron technology, could be of help.

Chapter 4 concerns fishes from the locality “Aidonochori A”, from the Serres Basin in Northern Greece. The fossils from this locality resemble, but don’t quite fit, the modern genus *Hilsa*, known from the Indo-West Pacific. The clupeids from the locality “Aidonochori A” are tentatively placed in the fossil genus †*Pseudohilsa*, known from the middle Miocene of Azerbaijan, but to a different, new species. Though in need of revision, †*Pseudohilsa* and some fossils attributed to “*Hilsa*” from the Abkhazia in the Eastern Black Sea, may indicate that clupeids similar to the modern *Hilsa* were present in the Basins that made up the Paratethys; the fossils from the site “Aidonochori A” are the first *Hilsa*-lookalikes from the Mediterranean.

The new material of fossil skeletons allowed the description of structures which are not always recognizable in fossils. The next step in the study of the fossil representatives of both of these families should be the construction of phylogenies with a broad taxon sampling and which are based on morphological characters. The placement of fossils in a phylogenetic framework will allow us to interpret the relationships of the examined fossils in greater detail and it could also help answer many of the questions raised in this Thesis.

Acknowledgements

I am deeply indebted to Prof. Dr. Bettina Reichenbacher for her great support and her supervision. I am very thankful to the members of our working group for their support and collaboration, Dr. Melanie Altner, Dr. Christoph Gierl, Stefanie Bianca Ramona Penk, Dr. Martin Dohrmann, Eleni Charmpila. The help and collaboration of the people from the Zoological State Collection and the Anthropological and Paleoanatomical State Collection, Munich, has been essential to the completion of this project; I am grateful to Dr. Ulrich Schliewen, Dirk Neumann, Dr. Frederic Schedel, Nadine Usimesa Wingi, Dr. Bernhard Ruthensteiner, Dr. Alexander F. Cerwenka, (SNSB-ZSM), Dr. Henriette Obermaier, Dr. Nadja Pöllath, Britta Möllenkamp (SNSB-SAPM) as well as to Prof. Dr. Evangelia Tsoukala (LGPUT). I would like to thank all the Kenyan scientists, residents, and politicians who helped our group in fieldwork. I would like to thank René Neumaier, Domink Bastl, Elisabeth Lange, Stefan Sónyi, Judith Braukämper, Dr. Nora Dotzlerand, Dr. Tanja Schulz-Mirbach, Imelda Hausmann, Manuela Schellenberger, Britta Nüske-Illenberger, Monika Brinkrolf, Ella Schönhofer for technical support. I acknowledge for their support Prof. Dr. Gert Wörheide (LMU and SNSB-BSPG), PD Dr. Mike Reich, Prof. Dr. Michael Krings, PD Dr. Gertrud Rößner, Prof. Dr. Alexander Nützel (SNSB-BSPG), Prof. Dr. Dirk Erpenbeck, PD Dr. Oliver Voigt (LMU) and Spyros Karamoulas and Ariadni Karamoula. For discussions, suggestions and comments I thank Prof. Dr. Alison Murray (University of Alberta, Canada), Dr. Thodoris Argyriou (Muséum National d'Histoire Naturelle, Paris), Dr. Gloria Arratia (University of Kansas, Lawrence, USA). The moral support of Carolin Gut (LMU) through these years has been invaluable and crucial; lately also that of Margit Gut. I thank Nikos Bacharidis because, other than providing the specimens for chapter 4, is one of the main persons responsible for getting me into paleontology; my family’s support, moral and otherwise, is responsible for keeping me there. I thank Prof. William Orsi and the LMU Mentoring program for providing funding to make the article of chapter 3 open access. The research was funded by the German Research Foundation (DFG); chapter 2 and 3 were funded with the grant RE 1113/18–1-2 and chapter 4 with the grant RE 1113/24–1.