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The first fossil shellear and its implications for the evolution and divergence of the Kneriidae (Teleostei: Gonorynchiformes)

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Abstract

A new genus and species of shellear (Gonorynchiformes: Kneriidae), †*Mahengichthys singidaensis*, is described from the Eocene Mahenge deposits in Tanzania, Africa. This work represents the first record of a fossil kneriid gonorynchiform fish. Previously, all gonorynchiform fossils have been attributed to either the families Chanidae or Gonorynchidae, with some taxa incertae sedis. We explore the phylogenetic position of †*Mahengichthys singidaensis* within the gonorynchiforms, utilizing parsimony and maximum likelihood methodologies that incorporate both morphological and molecular data. Our results indicate that †*Mahengichthys singidaensis* is a kneriid gonorynchiform within the tribe Kneriini, which includes the extant genera *Kneria* and *Parakneria*. This phylogenetic work provides a framework for estimating the divergence times of the Kneriidae for the first time using Bayesian methodology with calibrations that include information regarding extinct kneriids. We infer that the exclusively freshwater family Kneriidae most likely diverged and diversified during the Cretaceous to Paleogene in Sub-Saharan Africa, following the continent's separation from South America.

Introduction

The order Gonorynchiformes includes seven extant and approximately seventeen extinct genera of fishes that exhibit incredible morphological diversity, with the clade dating back to the Early Cretaceous (FARA et al. 2010, POYATO-ARIZA et al. 2010a). There are three monophyletic families of gonorynchiform fishes, including the predominantly marine families Chanidae and Gonorynchidae, and the exclusively freshwater family Kneriidae distributed throughout Sub-Saharan Africa. While currently there is a general consensus regarding the monophyly of the order and each family, the relationships of the families to one another remains controversial, with conflict between molecular (LAVOUÉ et al. 2005, LAVOUÉ et al. 2012) and morphological (e. g., GRANDE & POYATO-ARIZA 1999, POYATO-ARIZA et al. 2010b) hypotheses. At present, the majority of previously described extinct genera are attributed to the families Chanidae and Gonorynchidae, with a few genera recognized as *incertae sedis* within the order (e. g., †*Halecopsis*, †*Apulichthys*). The only family that lacks a fossil representative is the exclusively freshwater family Kneriidae.

In this study we describe the first fossil specimens of an extinct kneriid species collected in the fossil deposits of the ancient maar lake of Mahenge in Tanzania, Africa. The Cenozoic Mahenge deposits are considered to be one of the most important freshwater fish localities in Africa (GREENWOOD 1974, MURRAY 2000a, KAISER et al. 2006) due to the excellent preservation of the specimens, and the diversity of fish fauna previously described. Many taxa important to our broader understanding of teleostean relationships have been described from this locality, including the clupeid †*Palaeodenticeps tanganikae* GREENWOOD, 1960, two osteoglossomorphs †*Singida jacksonoides* GREENWOOD & PATTERSON, 1967, and †*Chauliopareion mahengeense* MURRAY & WILSON, 2005, a siluriform from the genus *Chrysichthys* (MURRAY 2003a), a characiform †*Mahengecharax carrolli* MURRAY, 2003b, and various cichlid taxa (e. g., GREENWOOD 1960, GREENWOOD & PATTERSON 1967, MURRAY 2000b) including the extinct genus †*Mahengechromis* MURRAY, 2000b, which are among the oldest cichlid fossils currently described from Africa. Additional material from the locality remains to be described, including non-cichlid percomorph taxa (KAISER et al. 2006).

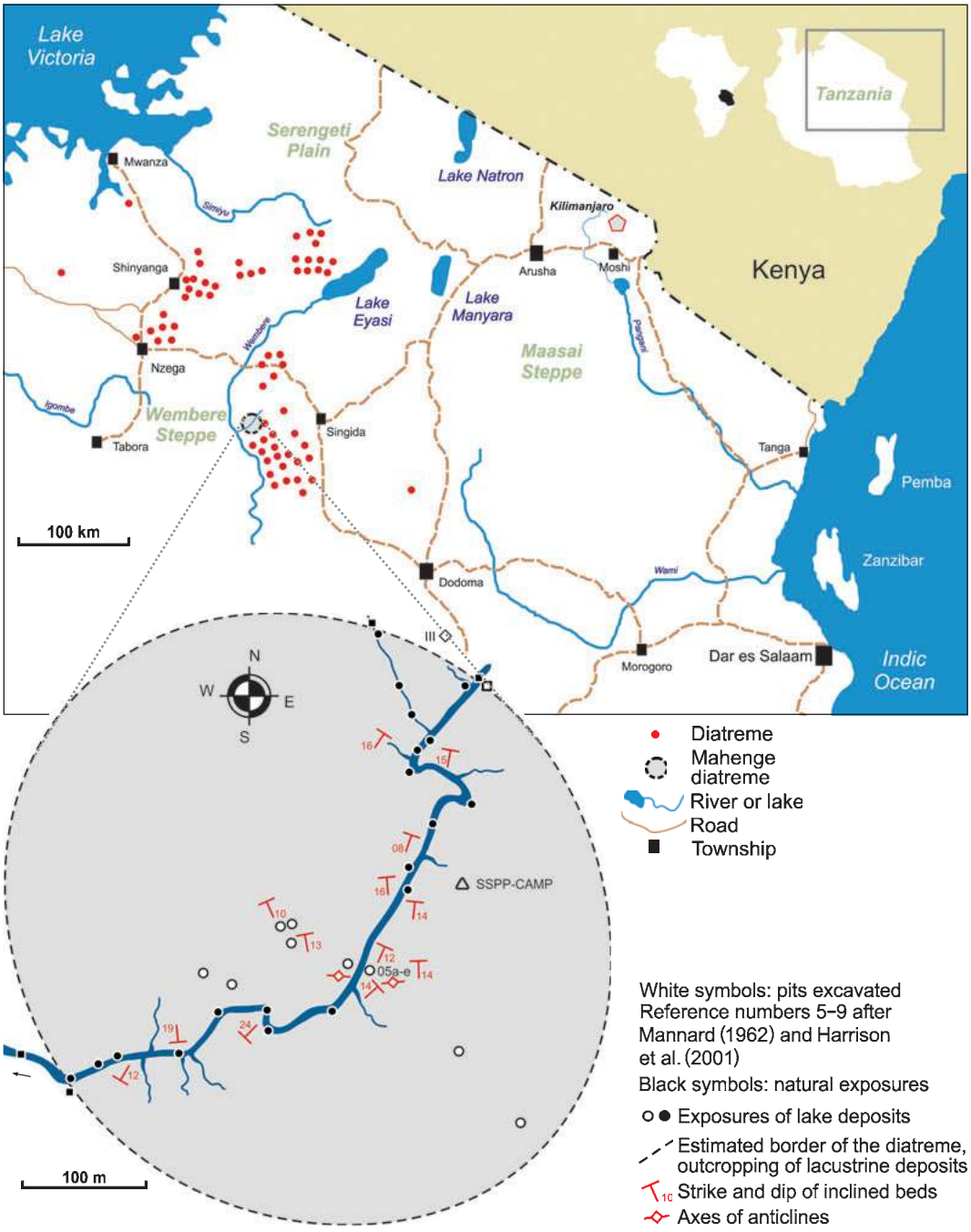
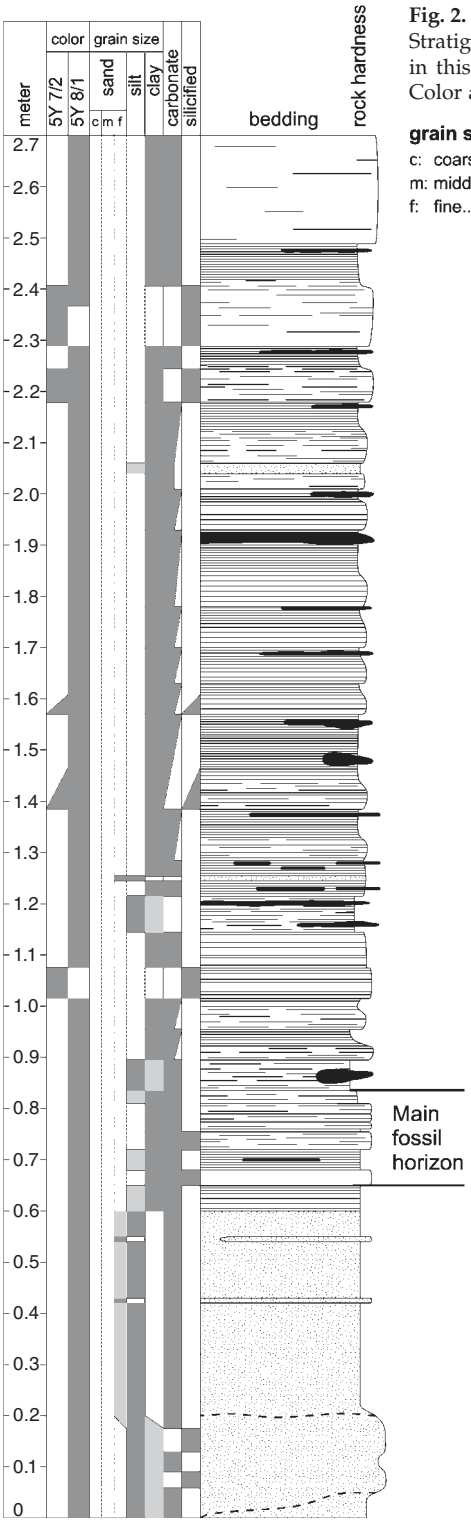


Fig. 1.
Diatreme fields in North-Central Tanzania. The Mahenge formation is found west of Singida. Enlarged map of the Mahenge diatreme includes excavation localities and natural outcrops. Modified from KAISER et al. (2006).



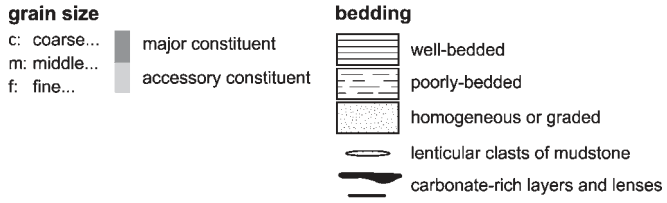


Fig. 2.
Stratigraphic section of pit 05c, where the fossil specimens discussed in this paper were recovered. Modified from KAISER et al. (2006). Color after Munsell® 1975.

The goals of this study include: (1) provide a thorough morphological diagnosis and description of the kneriid fossil material from Mahenge, (2) test the systematic placement of this species within the Gonorynchiformes using morphological and molecular data with a total evidence approach, and (3) synthesize fossil and molecular information to investigate the divergence times of the Gonorynchiformes. Below we further discuss the importance, flora and fauna, stratigraphy, and geologic age of the Mahenge deposits, and provide an overview of the evolutionary relationships within the family Kneriidae.

The Fossil-Lagerstätte of Mahenge: Stratigraphy and age

The Mahenge locality (4°47'50.2" S; 34°15'54.5" E; Fig. 1) is situated near the village of Mwaru and 65 km west of the town of Singida in north-central Tanzania (MANNARD 1962). Outcrops of lacustrine sediments indicate that the Eocene maar crater-lake was approximately 400 m in diameter. Fossil specimens recovered at this site are notable for their excellent preservation, and the lack of bioturbation indicates the lake possessed stable stratification of the water column with anoxic conditions near the sediment surface (HERENDEEN & JACOBS 2000, HARRISON et al. 2001, KAISER et al. 2006).

The Mahenge maar lake deposits have been critical in studying the evolution of Paleogene ecosystems in Africa, the origins of Malagasy biota, and have provided the first representatives of several modern groups of plants and vertebrates (e. g., bats, GUNNELL et al. 2003) in the fossil record of Sub-Saharan Africa (KAISER et al. 2006). The 2002 excavations at Mahenge (Tanzania) led by Thomas Kaiser (KAISER et al. 2006) as part of the Sub-Sahara-Paleogene-Project (SSPP), recovered more than 1900 vertebrate, plant and trace fossils. Fishes represented 51 % of the specimens collected, with 36 % of the material collected belonging to plant remains. The fossil flora, in addition to the sedimentological data, indicates that the Mahenge Lake had a dry climate with pronounced seasonality (KAISER et al. 2006).

The natural exposures at Mahenge are located along the cutback of the Luwala River, which crosses the crater from NE to SW. The main excavation efforts of the SSPP were concentrated in the center of the maar (pits 5 and 6

of MANNARD 1962 and HARRISON et al. 2001). The reference profile was composed of the main section in the center of the former lake, a sequence of 3.80 m of fossiliferous lake sediments. Despite diagenetic dolomitization, sedimentary fabrics are well preserved, and the overall sedimentation rate in the lake centre is estimated at 0.93 mm/year (KAISER et al. 2006). The base of the section documented so far is constituted by 1.10 m of basal lacustrine sediments that have never been exposed prior to 2002. This base consists of calcareous mudstones, silicified mudstones, and sandy siltstones (Fig. 2).

Previously recovered fish fauna from Mahenge led GREENWOOD & PATTERSON (1967) to suggest a Paleogene (probably Oligocene) age for the deposits. A kimberlite near Nzega, 120 km to the west of Mahenge, yielded U-Pb dates of 52.2 and 53.2 Ma, and fission track dates of 54.3+14 Ma and 51.1+3.8 Ma (DAVIS 1977, NAESER & MCCALLUM 1977, HAGGERTY et al. 1983), indicating an early Eocene (Ypresian) age. HARRISON et al. (2001) reported a middle Eocene (Lutetian) $^{206}Pb/^{238}U$ age of 45.83 ± 0.17 Ma from a single zircon crystal, which was recovered from the stream bed at Mahenge in 1996. The crystal is hypothesized to be from the eruption that created the maar lake, and is therefore slightly older than the lake itself (HARRISON et al. 2001, KAISER et al. 2006). Maar lakes in Europe and Africa have demonstrated that accumulation of lacustrine sediments quickly begins following the initial formation of the crater (LORENZ 1973, SMITH 1986, RAYNER & MCKAY 1986, RAYNER 1987, GIRESSE et al. 1991, CORNEN et al. 1992). Based on this information, HARRISON et al. (2001) estimate that the fossils recovered from the Mahenge maar sediments are approximately 45–46 Ma old.

Evolutionary history of the family Kneriidae

Prior to this study, the shellears (Kneriidae) were composed of five extant genera (approximately 31 species) including *Cromeria*, *Grasseichthys*, *Kneria*, *Parakneria*, and *Phractolaemus* (e.g., GRANDE & POYATO-ARIZA 1999, POYATO-ARIZA et al. 2010b). Hypotheses regarding the evolutionary relationships among genera within the kneriids have been conflicting (e.g., FINK & FINK 1996, LAVOUÉ et al. 2005, POYATO-ARIZA et al. 2010b, LAVOUÉ et al. 2012), in particular with regards to the phylogenetic position of the paedomorphic taxa *Cromeria* and *Grasseichthys* (Fig. 3). Within Kneriidae, there is a strong consensus for a subfamily Phractolaeminae *(Phractolaemus)* + subfamily Kneriinae clade *(Cromeria*, *Grasseichthys*, *Kneria*, *Parakneria)* as seen in Figure 3. The monotypic *Phractolaemus ansorgii* was previously classified in the family Phractolaemidae by NELSON (2006); however, we place *Phractolaemus* in the family Kneriidae with the other African freshwater gonorynchiforms, as was also recognized by POYATO-ARIZA et al. (2010b). While POYATO-ARIZA et al. (2010b) recovered *Cromeria* and *Grasseichthys* as sister taxa within Kneriinae based on morphological data (Fig. 3B), the molecular studies of LAVOUÉ et al. (2005, 2012) recovered *Cromeria* as the sister group to a clade that included *Grasseichthys* sister to *Kneria* + *Parakneria* (Fig. 3A). BRITZ & MORITZ (2007) suggested that the phylogenetic position of *Cromeria* and *Grasseichthys* might be difficult to ascertain within Kneriinae as a result of the reductive nature of paedomorphism and the possibility of convergence as a result of miniaturization.

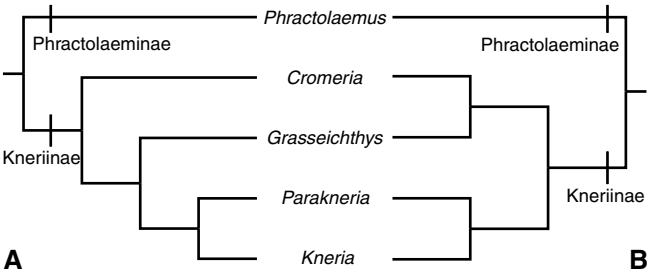


Fig. 3.
Hypotheses of phylogenetic relationships of the family Kneriidae. **A,** based on morphological data (after POYATO-ARIZA et al. 2010b). **B,** based on mitogenomic data (after LAVOUÉ et al. 2012).

Material and methods

Material examined

Specimens examined in this study were loaned from the following institutions: **BMNH,** Natural History Museum, London, United Kingdom; **CAS,** California Academy of Sciences, San Francisco, California, USA; **FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **KUNHM,** Division of Fishes, Natural History Museum, Lawrence, Kansas, USA; **MB,** Museum für Naturkunde, Leibnitz-Institut für Evolutions- und Biodiversitäts-

forschung, Berlin, Germany; **USNM**: Smithsonian Institute and United States National Museum, Washington, D.C., USA. Throughout this paper a † symbol indicates that a taxon is extinct. Fossil specimens examined in this study are discussed in the Systematic Paleontology section (diagnoses and description). Extant gonorynchiform specimens used for comparative studies with fossil material are listed below:

Chanos chanos: CAS (SU) 35075, 1 skl (skeleton), disarticulated bones, braincase of 148 mm length; KUNHM 39848 to 39894, day-to-day series of about 200 specimens from about 4 to 10 mm notochordal length and from 7 to 83.5 mm standard length (SL); KUMNH 40365, 2 skl, 370 and 376 mm SL and 4 c&s (cleared and stained specimens), 150, 180, 330, and 400 mm SL.

Gonorynchus abbreviatus: CAS 30993, 1 c&s, 150 mm SL; FMNH 76476, 1 c&s disarticulated specimen.

Kneria katangae: BMNH 1976.10.20.116-135, c&s, 41 mm SL. *Kneria wittei*: BMNH 1976.10.20.142-159, c&s, 51 mm SL.

Parakneria ladigesi: KUMNH 41054, 1 ethanol specimen, 91.3 mm Sl. *Parakneria* sp.: BMNH 2009.4.7.1-10, c&s, 40 mm SL.

Phractolaemus ansorgii: KUMNH 41050, 1 ethanol specimen, 92 mm Sl; USNM 203419, c&s, 113 mm SL.

The fossil specimens were mechanically prepared as a result of their preservation conditions. Different stereomicroscopes with different resolution power (Wild M4 and MZ8) were used in this study. Photographs were taken with a Canon EOS XSi digital SLR camera with 65 mm (f/2.8 1–5×) and 100 mm (F/2.8L) macro lenses. Extant gonorynchiforms used for comparative study were cleared and stained for both cartilage and bone following the methods described in ARRATIA & SCHULTZE (1992).

Terminology

The terminology of the skull roof bones follows the osteological homology criteria outlined in SCHULTZE (2008) and WILEY (2008), with traditional terminology presented in parentheses the first time a bone is cited. The organ associated with the opercular bones is identified here under the traditional terminology "opercular organ" rather than the modified terminology of the "opercular apparatus" (sensu GRANDE & YOUNG 1997). Here we use the term "opercular apparatus" to describe all bony elements of the opercular region. The anterior membranous outgrowth present in the anterior part of the hyomandibula is used here to identify the entire outgrowth, whereas the name metapterygoid process of the hyomandibula is restricted to the antero-ventral process at the anteroventral region of the membranous outgrowth. Names of vertebral elements, vertebral types, and caudal endoskeletal elements follow SCHULTZE & ARRATIA (1989), ARRATIA & SCHULTZE (1992), ARRATIA et al. (2001). Names and abbreviations used in the identification of different fin rays follow those of ARRATIA (2008).

Phylogenetic methodology

Morphological data. For this study, material of †*Mahengichthys singidaensis* n. gen. n. sp. was coded for 128 characters described by POYATO-ARIZA et al. (2010b) in their analysis of extant and extinct gonorynchiform evolutionary relationships. This dataset was chosen because it currently represents the most comprehensive morphological phylogenetic study that includes extant and extinct gonorynchiform taxa, and it has been modified from previous studies (e.g., GRANDE & POYATO-ARIZA 1999) to address additional character coding suggestions based on further morphological investigations (DAVIS & MARTILL 1999, BRITZ & MORITZ 2007, DIETZE 2007).

Taxonomic sampling included representatives from all extant gonorynchiform genera and fossil taxa included in the study of POYATO-ARIZA et al. (2010b). The analysis of POYATO-ARIZA et al. (2010b) identified several extinct genera that they excluded from their systematic study (†*Halecopsis*, †*Apulichthys*, †*Lecceichthys*, and †*Sorbininardus*) as a result of taxonomic uncertainty or excessive missing data as a result of preservation. In a separate analysis, POYATO-ARIZA et al. (2010b) included these taxa and found their systematic placement to be uncertain among other gonorynchiforms, although overall relationships among and within the three main gonorynchiform lineages (Chanidae, Gonorynchidae, Kneriidae) did not change. For this study the problematic genera were not included. Modifications during this study to characters and/or state coding are described below, including the deletion of two characters from our analysis for a total of 128 characters (Appendix 1). For an abbreviated list of character states and descriptions please see POYATO-ARIZA et al. (2010b) and Appendix 2 herein. Character numbers in parentheses refer to the number from POYATO-ARIZA et al. (2010b) when different from this study.

The following characters from POYATO-ARIZA et al. (2010b) have being modified from their original coding as detailed below**.**

7: Brush-like cranial intermuscular bones absent [0] or present [1]. *Chanos* was coded as lacking brush-like cranial intermuscular bones in POYATO ARIZA et al. (2010a: app. 2). However, we observed that *Chanos* has brush-like intermuscular bones, so it is coded here as having state 1 (see ARRATIA & HUAQUIN 1995: fig. 3A; and large specimens studied here).

13: Relative position of postparietal bones [parietals of traditional terminology].
The presence or absence of independent postparietal bones (parietal bones of traditional terminology) in kneriids is controversial. They have been reported as present in *Kneria wittei* by FINK & FINK (1996), but have been reported as lost in other studies (e. g., LENGLET 1974, GRANDE 1994). Distinct postparietal bones were observed in *K. wittei* of about 15 mm (GRANDE & POYATO-ARIZA 1999); however, they indicated that in specimens larger than 30 mm the postparietals were lost (GRANDE & POYATO-ARIZA 2010: 11, please note the original description in GRANDE & POYATO-ARIZA 2010 lists specimen sizes of 150 and 300 mm, which were confirmed as typos by GRANDE pers. comm.).
For this study we felt that the coding of this character by POYATO-ARIZA et al. (2010b: app. 2) was in need of further investigation. *Kneria* and *Parakneria* are coded as having a lateroparietal cranium (postparietal bones completely separated from each other by the supraoccipital [State 2]). However, we observe that *Kneria* and *Parakneria* do not have independent ossifications that can be identified as postparietals. See diagnostic characters of Kneriinae (POYATO-ARIZA et al. (2010b: 315). Consequently, we code this character as non-applicable (**–**) for *Kneria* and *Parakenia* and the fossil kneriid studied herein.

14: Postparietal portion of the supraorbital canal absent [0] or present [1].
Chanos was interpreted as lacking a postparietal [parietals of traditional terminology] portion of the supraorbital canal and coded as "0" in POYATO-ARIZA et al. (2010b: app. 2). However, the parietal branch of the supraorbital canal pierces the postparietal bone in juvenile specimens of *Chanos*, and the branch is reduced and difficult to observe in adults (ARRATIA & BAGARINAO 2010: fig. 3.6). *Chanos* is coded as possessing State 1 in our matrix.
Kneria and *Parakneria* were coded as State 0 by POYATO-ARIZA et al. (2010b); however, we have recoded this character as non-applicable because these genera lack postparietal bones [parietals of traditional terminology].

16: Supraoccipital crest small, short in lateral view [0] or long and enlarged, projecting above occipital region and first vertebrae, forming a vertical, posteriorly deeply pectinated blade [1]. The presence of a small crest or its absence is a controversial issue for certain gonorynchiforms (see BRITZ & MORITZ 2007 and POYATO-ARIZA et al. 2010b). For this study we modified State 0 to read: "supraoccipital crest small, short in lateral view or absent".

18: Mesethmoid wide and short [0] or long and slender, with anterior elongate lateral extensions [1] or large, with broad posterolateral wing-like expansions [2] or elongate and thin [3]. We find this character difficult to interpret because of the subjectivity of the qualitative descriptions (e. g., short, long, thin). For example, our observations of *Kneria* and *Parakneria* disagree with the interpretation that both genera have a long and slender mesethmoid. In the specimens we examined, the mesethmoid is observed as short. In addition, we observe variation in mesethmoid morphology in the specimen of *Parakneria* used in this study, and in illustrations presented in GRANDE & POYATO-ARIZA (2010: fig. 1.1F–G). Thus we code this feature as polymorphic with State 1 and 2. Because of the observed variability we believe this character is in need of further reexamination using multiple specimens of each species.

47: Interhyal present [0] or absent as an independent ossification [1]. The genera *Chanos*, *Kneria* and *Parakneria* are coded as having an interhyal [0]. We disagree with this coding because an independent bony interhyal is absent in all three genera; therefore, we code these taxa as State 1 in this study (MABEE et al. 2011, Character 52; http://www.morphbank.net/myCollection/?id=471267).

53: Shape of opercular bone in lateral view: rounded/oval [0] or triangular [1]. The genera *Kneria* and *Parakneria* were coded as State 0 by POYATO-ARIZA et al. (2010b); however, we have observed in the specimens examined here and the illustrations available in the literature (e. g., GRANDE & POYATO-ARIZA 2010) that both *Parakneria* and *Kneria* have an almost square opercle. Because shape characters are difficult to evaluate because of subjectivity, we added a third character state: "squarish or square [2]". The fossil specimens examined in this study and *Parakneria* possess a square opercular bone [2], and *Kneria* was coded as polymorphic (State 0 and 2) because of the observed variation. We suggest that this character should be revisited in future studies when more specimens of the same species and also other species are available.

73: Second abdominal centrum: as long as the first [0] or shorter than the first [1].
Parakneria and *Kneria* are coded as having a second abdominal centrum as long as the first centrum [0]. However, the second centrum may be longer (a state that it is not listed) or shorter than the first one in *Kneria wittei* (GRANDE & ARRATIA 2010: fig. 2.8A–B), depending on the sex of the specimens. The information for the fossil is not available. We prefer to delete this character from the analysis because, at least in *Kneria*, this character appears to be sexually dimorphic and is in need of further investigation.

88 (89): Lateral line and supracleithrum: supracleithrum pierced through dorsal region [0]; supracleithrum pierced all through its length [1]; lateral line does not pierce supracleithrum [2]. According to the material studied here, the lateral line does not pierce the supracleithrum in *Kneria* and *Parakneria* [2]. In contrast, it was coded as "0" by POYATO-ARIZA et al. (2010b).

94 (95): Neural arch and spine of preural centrum 1: both well developed, spine about half as long as preceding ones [0]; arch complete and closed, spine rudimentary [1]; arch open, no spine [2]. Both halves of the neural arch of preural centrum 1 protect the neural cord and either close above it or may stay open, and a spine may be absent or present (see ARRATIA 2010: fig. 13A,B; ARRATIA et al. 2001). *Kneria* is coded as 1, but *Parakneria* and *Chanos* are coded as 2 in POYATO-ARIZA et al. (2010b: app. 2). However, there is variation in *Parakneria* because contrary to the material described in GRANDE & ARRATIA (2010), the specimen studied here is observed with character state 1. Consequently, we code *Parakneria* as polymorphic with states 1 and 2. We code *Chanos* as possessing state 1, with a rudimentary spine.

104 (105): Hypural 5 of comparable size to preceding ones [0] or considerably larger [1]. The presentation of State 0 is unclear; commonly in teleosts hypural 5 is smaller than the preceding hypurals 4 and 3. This is the condition present in the fossil kneriid described herein as well as in most other Gonorynchiformes. A hypural 5 that is broader distally, and consequently larger than hypurals 4 and 3, is found only in *Phractolaemus* (e. g., among the fishes studied by POYATO-ARIZA et al. 2010b: app. 2); but *Grasseichthys gabonensis* can also have a hypural 5 distally expanded and larger than hypurals 4 and 3 (MONOD 1968: figs. 268–270). A hypural 5 distally broader than hypurals 3 and 4 is present in *Cromeria occidentalis* (BRITZ & MORITZ 2007: fig. 12), whereas hypural 5 is as broad as hypural 4 in *Cromeria nilotica* (BRITZ & MORITZ 2007: fig. 6) and slightly smaller in *Cromeria nilotica occidentalis* (MONOD 1968: fig. 267). *Grasseichthys* and *Cromeria* were coded as "0" by POYATO-ARIZA et al. (2010b: app. 2), a coding that should be revised when more material is available. We have slightly modified the presentation of this character:
"Hypural 5: smaller in size than hypurals 4 and 3 [0]; larger than hypurals 4 and 3 due to its distal expansion [1]."

(106): Hypural 5 (plus 6 if present) and second ural centrum separated [0] or articulating [1]. This character implies that a second ural centrum (diural terminology) should be present. However, a separated element identified as a second ural centrum is observed only in some of the fossil gonorynchiforms (e. g., †*Gordichthys* POYATO-ARIZA 1996; DIETZE 2007: fig. 10). Among the studied gonorynchiforms, only †*Gordichthys* presents the apomorphic state (POYATO-ARIZA et al. 2010b). The fossil kneriid studied here does not have a separate second ural centrum (see descriptions below) nor do most gonorynchiforms (see for instance GRANDE & ARRATIA 2010: figs. 2, 10B, 2,11A–F, 2.12A–H). Additionally, the second ural centrum of the diural terminology may correspond to different ural centra of the polyural terminology and consequently these centra may not necessarily be homologous (see SCHULTZE & ARRATIA 1989 and SCHULTZE & ARRATIA this volumen for further information). Considering the potential for homology problems involved, and that this character is not phylogenetically informative for this set of taxa, we have not included it in this study.

Molecular data. Whole mitogenome sequence data for extant gonorynchiform fishes were combined with the modified morphological dataset of POYATO-ARIZA et al. (2010b) to create a total evidence dataset. Mitogenome sequences for extant gonorynchiform fishes and outgroup taxa were recovered from previous studies (e. g., SAITOH et al. 2003, ISHIGURO et al. 2003, LAVOUÉ et al. 2005, LAVOUÉ et al. 2008, LAVOUÉ et al. 2012), with taxa and GenBank accession numbers listed in Table 1. Mitogenomes were aligned using the program MAFFT v6 with default parameters (KATOH 2008) for a total of 16219 base pairs, including: 2 ribosomal RNA genes (2848 bps), 13 protein-coding genes (11514 bps), 22 transfer RNA genes (1688 bps), and the control region (168 bps). While the fossil taxa are missing mitogenome information, previous works have indicated that using a combination of morphological and molecular information under a total evidence approach can provide a robust hypothesis of systematic placement for taxa that only have morphological data (EGGE & SIMONS 2009).

Phylogenetic analyses of morphological and total evidence data. Likelihood analyses of the morphological dataset and the total evidence dataset were conducted in GARLI v2.0 (ZWICKL 2006). Ten separate analyses were conducted for both the morphological and total evidence datasets, and the tree having the best likelihood score for each is presented here (see below) to evaluate evolutionary relationships. For the morphological dataset, a single partition was used under the MK (Markov) model for morphological data as recommended by LEWIS (2001). All morphological characters are treated as unweighted, with each site variable at equal rates. Polymorphisms are treated as missing data in the likelihood analysis. Five partitions were employed in the total evidence analysis, including the previous morphological partition and four mitogenome partitions with a partition each for the rRNA genes (2848 bps, GTR+I+Γ), protein-coding genes (11514 bps, GTR+I+Γ), tRNA genes (1688 bps, GTR+I+Γ), and control region (168 bps, HKY+I+Γ). The general time-reversible model that accounts for invariable sites and a gamma distribution (GTR+I+Γ) was selected by jMODELTEST v.0.1.1 (POSADA 2008) as the best fitting model under the Akaike information criteria (AIC) for three of the four mitogenome partitions. A nonparametric bootstrap analysis (FELSENSTEIN 1985) was performed for both datasets with 100 random pseudoreplicates using the recommended default settings in the GARLI manual.

Parsimony analyses were also performed in PAUP* (SWOFFORD 2000) on the morphological dataset with a heuristic search (1000 random addition sequence replicates) and tree-bisection-reconnection branch swapping. As with the likelihood analysis, all characters were unweighted and unordered. Nonparametric bootstraps (FELSENSTEIN 1985) were performed with 1000 pseudoreplicates. For all analyses of morphological and total evidence datasets, †*Diplomystus*, *Brycon*, and *Opsariichthys* were included as outgroup taxa. These taxa were also the outgroups for previous morphological studies (GRANDE & POYATO-ARIZA 1999, POYATO-ARIZA et al. 2010b).

Estimation of divergence times from molecular data. Simultaneous topology and divergence time estimation was performed with the Bayesian method BEAST v.1.6.1 (DRUMMOND & RAMBAUT 2007) with the same partitions and models for the mitogenome as discussed above for the likelihood analyses. Mean substitution rates were estimated under a relaxed uncorrelated lognormal clock that allows for independent rates to vary across branches. Four separate analyses were performed with 30 million generations each, sampling trees and parameters every 10000 generations. Stationarity was assessed using the program Tracer v1.5 (RAMBAUT & DRUMMOND 2007), and the first ten percent of total generations sampled from the combined four independent runs were discarded as burn-in. The remaining 11800 post-burn-in trees were used to compile the maximum clade credibility (mean heights) tree and posterior probabilities. All parameters possessed ESS's >200, which indicates the analyses satisfactorily sampled the posterior distributions of each parameter. Divergence time estimations were performed twice, once under the hypothesis that the paedomorphic taxa *Cromeria* and *Grasseichthys* form a clade within Kneriidae as suggested by previous morphological studies (e.g., GRANDE & POYATO-ARIZA 1999, POYATO-ARIZA et al. 2010b), and once without any constraints on evolutionary relationships, as previous studies based on mitogenomes alone have not recovered *Cromeria* and *Grasseichthys* as a clade (e.g., LAVOUÉ et al. 2005, LAVOUÉ et al. 2012).

Table 1.
Taxa sampled for whole mitochondrial genomes that were included in the combined total evidence maximum likelihood analysis and Bayesian divergence time estimation.

Order	Family	Species	Accession
Amiiformes		*Amia calva*	AB042952
Hiodontiformes		*Hiodon alosoides*	AP004356
Elopiformes		*Elops hawaiensis*	AB051070
Gonorynchiformes	Chanidae	*Chanos chanos*	AB054133
	Gonorynchidae	*Gonorynchus greyi*	AB054134
		Gonorynchus abbreviatus	AP009402
	Kneriidae	*Kneria* sp.	AF007278
		Parakneria cameronensis	AF007279
		Cromeria occidentalis	AF007275
		Cromeria nilotica	AP011560
		Grasseichthys gabonensis	AF007277
		Phractolaemus ansorgii	AF007280
Clupeiformes		*Denticeps clupeioides*	AP007276
Cypriniformes	Cyprinidae	*Opsariichthys bidens*	DQ367044
		Carassius auratus	NC006580
	Catostomidae	*Moxostoma poecilurum*	NC008674
Gymnotiformes		*Brachyhypopomus pinnicaudatus*	AP011570
Siluriformes		*Corydoras rabauti*	NC004698
Characiformes		*Chalceus macrolepidotus*	NC004700
Salmoniformes		*Oncorhynchus mykiss*	NC001717
Aulopiformes		*Aulopus japonicas*	NC002674
Myctophiformes		*Neoscopelus microchir*	AP002921
Polymixiiformes		*Polymixia lowei*	NC003181
Beryciformes		*Hoplostethus japonicas*	NC003187
Perciformes		*Morone saxatilis*	HM447585

Five actinopterygian fossil calibrations were assigned based on the oldest known fossil of each clade discussed below. All calibrations were assigned a lognormal prior to allow for a hard minimum age that was assigned *a priori*.

Neopterygii (C1): The node representing the most recent common ancestor (MRCA) of the neopterygians was given a minimum age of 284 million years ago (Ma) based on the fossil taxon †*Brachydegma caelatum*, with a soft upper age of 422 Ma based on the actinopterygian fossil taxon †*Andreolepis hedei*, as recommended by ALFARO et al. (2009). The lognormal prior was given an offset of 284 Ma, with a standard deviation of 1.0 and a mean of 2.967.

Euteleostei (C2): The MRCA of the Euteleostei+Ostarioclupeomorpha was dated at a minimum age of 150 Ma based on the stem euteleostean lineage †*Leptolepides sprattiformis* (ARRATIA 1997, 1999). The conservative soft upper age was set to 220 Ma (standard deviation of 1, mean of 2.289), based on the fossil taxon †*Pholidophorus latiusculus*, the stem teleost lineage in ARRATIA's (2000, 2001) phylogenetic study of lower teleost relationships.

Acanthomorpha (C3): The node representing the acanthomorphs was assigned a minimum age of 95 Ma based on **fossil taxa associated with *Polymixia*** and the beryciform taxa †*Hoploteryx lewesiensis* and †*Hoploteryx simus* (PATTERSON 1993). A conservative soft upper bound was set to 150 Ma (standard deviation of 1, mean of 2.047).

Chanidae (C4): The earliest fossil taxon currently belonging to the family Chanidae is †*Rubiesichthys*, with the minimum age of the family dated to 140 Ma (e.g., FARA et al. 2007, FARA et al. 2010, POYATO-ARIZA et al. 2010a). A conservative soft upper bound of 220 Ma was used (standard deviation of 1, mean of 2.422).

Kneriini (C5): Prior to this work there were no fossil taxa associated with the family Kneriidae. Based on the work presented here, we calibrated the node for the tribe Kneriini to a minimum age of 46 Ma, with a conservative soft upper bound of 220 Ma (standard deviation of 1, mean age of 3.199).

Systematic Paleontology

Teleostei MÜLLER, 1845 (sensu ARRATIA 1999)
Ostarioclupeomorpha ARRATIA, 1997
Order Gonorynchiformes (sensu ROSEN & GREENWWOD 1970)
Family Kneriidae (sensu GRANDE & POYATO-ARIZA 1999)

Mahengichthys n. gen.

Diagnosis (based on a unique combination of characters; unique characters among kneriids are identified with an asterisk [*])**.** Kneriids with no cranial fontanelles in skull roof. Postparietal bones [traditional parietals] absent as distinct ossifications. Quadrate-mandibular articulation occurring below anterior half of orbit. Dentary forming large and deep coronoid process. Enlargement of angulo-articular to be longer than dentary. Neural arches, except those of last preural vertebrae, touching or having overlapping contact with adjoining arches antero-posteriorly. Four or five sigmoidal supraneural bones located between occiput and dorsal pterygiophores [*]. Long neural and haemal spines extending to margins of body. Series of large and well-ossified epicentral bones extending to origin of pelvic fin. First anal pterygiophore long and curved, nearing ventral surfaces of vertebral centra [*].

Etymology. Derived from the name of the Mahenge locality in Tanzania, Africa, where the specimens were collected, and *-ichthys* (Greek) for fish.

†*Mahengichthys singidaensis* n. sp.
Figs. 4–16

Diagnosis. Same as generic diagnosis (monospecific genus).

Etymology. The specific name *singidaensis* refers to the town of Singida in Tanzania, Africa, near the fossil locality where the fossil fishes were recovered.

Holotype. MB.f.19057a/b (field-number MA5F2A2a/b), complete specimen preserved in part and counterpart (Fig. 4A,B); head with broken bones; part of postcranial skeleton three-dimensionally preserved.

Paratypes. MB.f.19058 (field-number MA5cF2A165), complete specimen preserved in part and counterpart (Fig. 4C); head poorly preserved; part of postcranial skeleton three-dimensionally preserved. MB.f.19059a/b

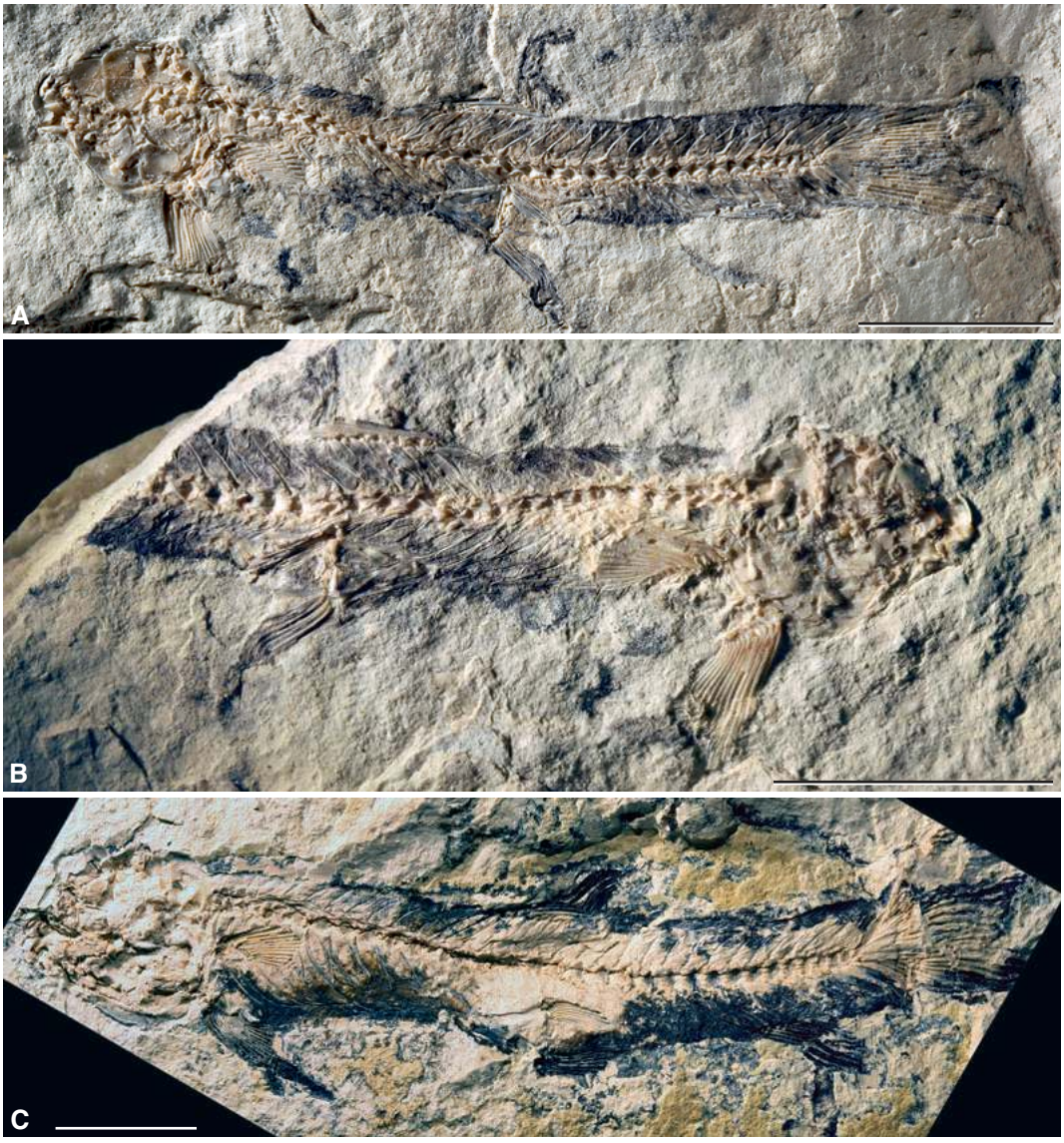


Fig. 4.
†*Mahengichthys singidaensis* n. gen. n. sp. in lateral view, Eocene of Mahenge, Tanzania, Africa. **A,** holotype (MB.f. 19057a). **B,** holotype (MB.f.19057b). **C,** paratype (MB.f.19058). Scales = 1 cm.

(field-number MA5c2H171a/b), incomplete specimen missing the body posterior to the pelvic fins; specimen preserved in part and counterpart (Fig. 5C). MB.f.19060a/b (field-number MA5cF2A823a/b, complete specimen with poorly preserved head. MB.f.19061a/b (field-number MA6cF2H1950a/b), complete specimen preserved in part and counterpart; the specimen is poorly preserved; however, bones are preserved three-dimensionally in the caudal fin. MB.f.19062 (field-number MA5dF2I752), complete specimen preserved as imprint.

Type locality and age. Mahenge, about 65 km west from Singida, Tanzania. Middle Eocene (Lutetian), 45 to 46 Ma (KAISER et al. 2006).

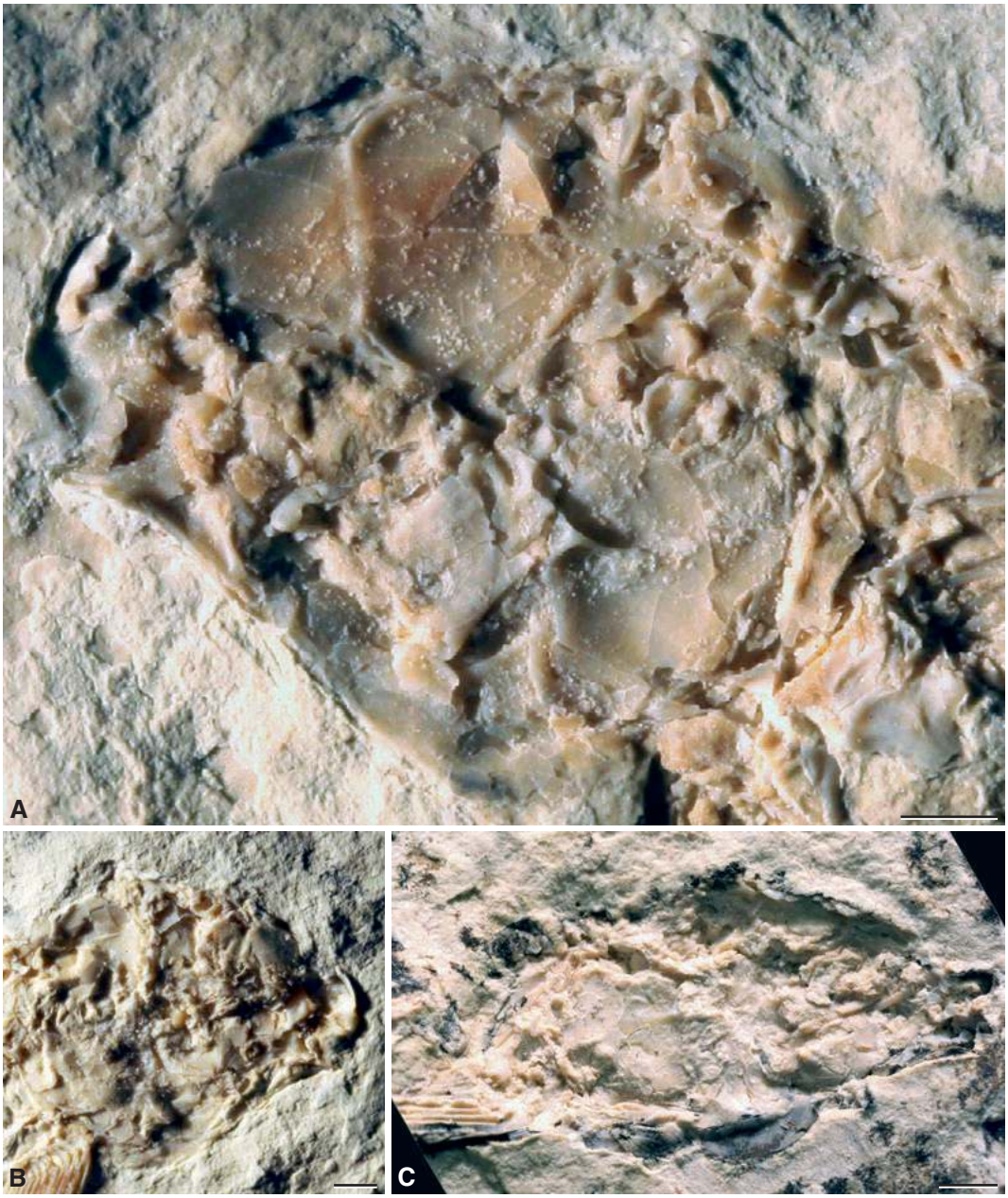


Fig. 5.
†*Mahengichthys singidaensis* n. gen. n. sp. **A,** cranial bones in dorso-lateral view (holotype MB.f.19057a). **B,** cranial bones in lateral view (MB.f.19057b). **C,** cranial bones in lateral view (MB.f.19059a). Scales = 1 mm.

Description

The fossil kneriid is a relatively small fish with the maximum total length of the specimens described herein of 72 mm, with 61 mm as the maximum standard length. The head is ~21 % of standard length. The caudal peduncle is almost as deep as the rest of the body (Fig. 4A–C). The dorsal fin is positioned close

to the midpoint of standard length (~47–52 % of SL), whereas the pelvic fins are positioned posterior to the mid-point of standard length (~55.5–60 % of SL). The origin of the anal fin is posteriorly placed, close to the caudal fin (~81–90 % of SL). We assume that the body was not extremely laterally compressed, but slightly rounded, based on the length of the ribs that are strongly curved ventrally.

Braincase. In general the skull bones are partially destroyed, especially those of the cheek region. Although several bones are three-dimensionally preserved, they remain difficult to interpret because some are partially broken and preserved in their inner view.

The skull roof (Fig. 5A–C) of †*Mahengichthys singidaensis* is more similar in its pattern, proportions, and shapes of bones to that of *Kneria wittei* as studied here than to that of *Parakneria* (see GRANDE & POYATO-ARIZA 2010: fig. 11F). The main element of the skull roof (Fig. 5A,B) is the parietal bone [= frontal bone of traditional terminology], which is slightly expanded postero-laterally in its postorbital region and narrows slightly anteriorly. A straight suture joins left and right parietals. The anterior margin of the parietal bone is almost straight, its orbital margin is slightly concave, and its posterior margin narrows posteriorly ending in a truncated triangle. The supraorbital canal runs very close to the lateral margin of the bone and it does not have sensory tubules with the exception of the epiphyseal one, which extends medially to join its counterpart and form a continuous epiphyseal bar. The supraorbital canal does not produce a parietal branch.

The parietal [= frontal of traditional terminology] bones suture anteriorly with an apparently broad mesethmoid, which seems to be as broad as the anterior margins of the parietals. The right part of the mesethmoid is better preserved and produces an antero-laterally directed process that is truncated distally.

A small, almost triangular autosphenotic sutures with the parietal at the corner of the orbital margin. Postero-laterally the parietal sutures with the pterotic that forms the lateral border of the skull roof and carries the otic canal closer to its lateral margin and the extrascapular canal posteriorly. The identification of bones just posterior to the pterotic and supraoccipital is difficult because some of them are displaced and others damaged. Postparietal [traditional parietal] bones are absent.

Circumorbital series. All circumorbital bones are damaged, making a description impossible.

Upper Jaw. The upper jaw (Fig. 6) is represented by the premaxilla and maxilla, which are incompletely preserved in most specimens. Both bones are preserved in medial view in the holotype. The premaxilla is narrower at its proximal region and expands postero-laterally, being almost rounded posteriorly. Its postero-ventral margin is not clearly observed in any specimen, so we are unable to ascertain whether the bone is prolonged postero-ventrally as observed in *Chanos*. The maxilla is thick and heavily ossified at the region of its proximal articulation and expands slightly posteriorly; however, other bones obscure its distal border. Both the premaxilla and maxilla lack teeth.

Lower jaw. The lower jaw (Fig. 6) is formed by an edentulous dentary anteriorly, a long angulo-articular posteriorly, and a retroarticular at the postero-ventral corner. The dentary is very narrow near the symphysis, with the antero-dorsal margin of the bone projecting abruptly in a broadly rounded dorsal margin that forms the coronoid process of the jaw. The

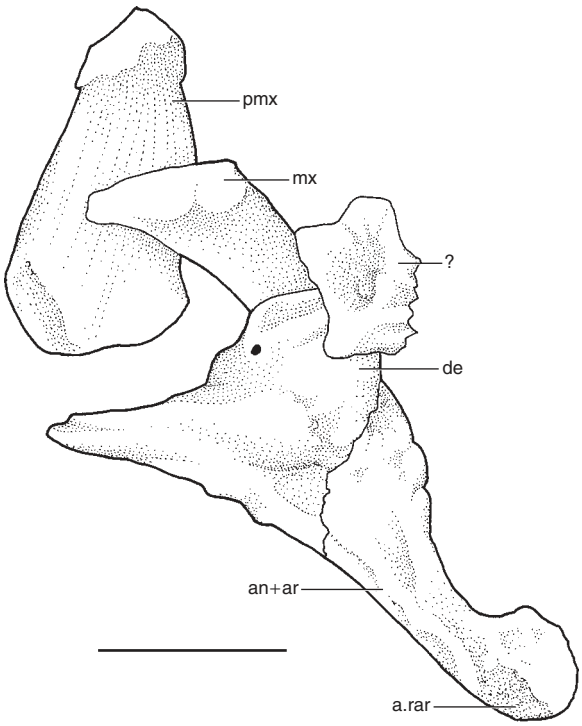


Fig. 6.
†*Mahengichthys singidaensis* n. gen. et n. sp. (holotype MB.f. 19057a). Jaws in medial views. Scale = 1 mm. Abbreviations: **an+ar**, angulo-articular; **a.rar**, articular surface for retroarticular; **de**, dentary; **mx**, maxilla; **pmx**, premaxilla.

dentary is narrow ventro-medially, with an expanded platform that is not as developed as the platform that forms the anterior part of the bone in *Kneria* and *Parakneria*. As shown by the holotype, the coronoid process of the jaw is formed by the dentary alone; the antero-dorsal part of the angulo-articular does not reach the highest point of the coronoid process. There is no evidence of a "leptolepid" notch, like the notch present in *Chanos* and extinct chanids, in the antero-dorsal margin of the dentary.

An almost straight suture joins the dentary and the elongate angulo-articular, with the latter bone being longer than the dentary. The angulo-articular narrows posteriorly to form the articular facet for the quadrate. Posterior to the facet, the angulo-articular projects as an almost rounded and moderately large post-articular process.

The retroarticular is not preserved in the holotype MB.f.19057a, but the articular surface for the bone is clearly observed at the postero-ventral region of the angulo-articular. Remnants of the retroarticular are found in the counterpart MB.f.19057b. According to the position of its articular surface, we infer that the retroarticular was not included in the articular facet for the quadrate.

A mandibular sensory canal has not been observed. Absence of the mandibular canal is a character of Recent kneriids as well as *Gonorynchus*, and is interpreted as a synapomorphy of Gonorynchoidei (POYATO-ARIZA et al. 2010b).

Palatoquadrate and suspensorium. Most of the palatoquadrate and suspensorium is hidden by more external bones or the bones are broken so that a detailed description is not possible. The large, almost rhomboidal hyomandibula is preserved in medial view in the holotype (Fig. 7), and is incompletely preserved in lateral view in MB.f.19059a. It has a moderately narrow antero-dorsally inclined dorsal region that articulates with the neurocranium throughout two articular facets. The hyomandibula is heavily ossified at its dorsal and posterior regions, whereas it presents an expanded membranous outgrowth antero-ventrally, and extending the dorsoventral length of the bone, a common feature also present in *Chanos* (e. g., ARRATIA 1992: fig. 7B). A large anterior membranous outgrowth, the metapterygoid process, projects in an antero-ventral direction but is not as acute as that of Recent kneriids and *Chanos* (ARRATIA 1992: fig. 7B; GRANDE 1994: figs. 15, 17; BRITZ & MORITZ 2007: fig. 18C). In contrast, a marked notch separates the antero-dorsal region of the hyomandibula and the metapterygoid process in gonorynchiforms such as *Cromeria* and *Grasseichthys* (e. g., GRANDE 1994: fig. 8, BRITZ & MORITZ 2007: figs. 10A, 15A). A well-defined posterior process with the articular condyle for the opercle is not present, so that the opercle and the body of the hyomandibula articulate directly, contrary to the situation in other kneriids with a well-defined articular process.

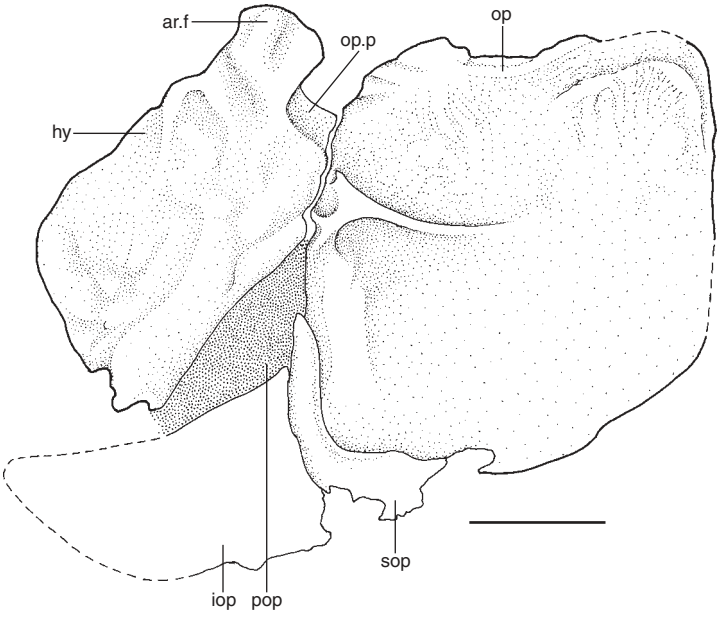


Fig. 7.
†*Mahengichthys singidaensis* n. gen. n. sp. (holotype MB.f.19057a). Hyomandibula and opercular bones in medial view. Abbreviations: **ar.f**, articular facet for opercular process of hyomandibula; **hy**, hyomandibula; **iop**, interopercle**;** **op**, opercle; **op.p**, opercular process of hyomandibula; **pop**, section of preopercle; **sop**, subopercle.

Opercular and branchiostegal series. Some opercular bones (Fig. 7) are best preserved in the holotype. However, in this specimen the interopercle is incomplete. A description of the preopercle cannot be provided because only fragments are preserved in different specimens.

The squarish opercle (Fig. 7) has a slightly straight dorsal margin and its internal surface

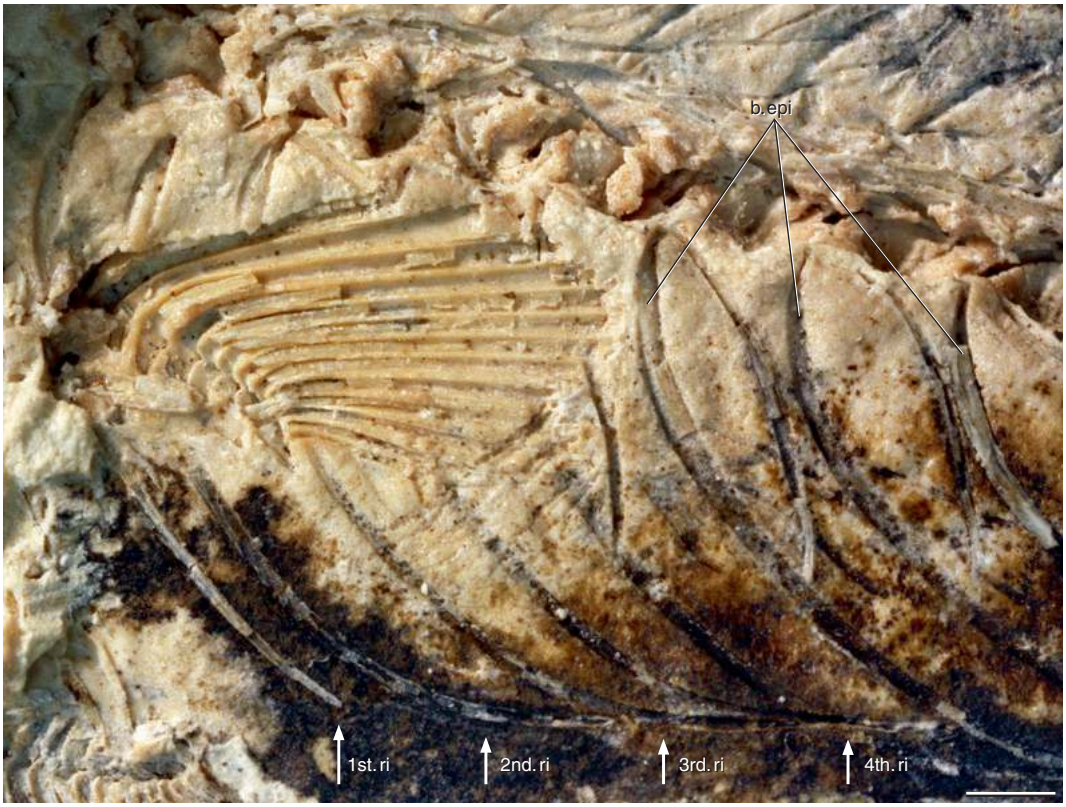


Fig. 8.
†*Mahengichthys singidaensis* n. gen. n. sp. (MB.f.19058). Part of anterior body illustrating 1st rib, other ribs, epicentrals, and pectoral fin. Abbreviations: **b.epi**, epicentral bones; **ri**, ribs; **1st.ri–4st.ri**, first to fourth rib.

shows some thicker regions close to the postero-dorsal margin of the bone. This may be an indication of the presence of the opercular organ that is found in Recent kneriids lying on the external wall of the opercle. The opercular organ is well developed in males and less developed in females (GRANDE & YOUNG 1997). The articular facet for the hyomandibula and its associated medial crest that projects posteriorly at about the mid surface of the opercular bone are similar to those found in similar positions in Recent kneriids. The subopercle is narrow, with a very well-developed and heavily ossified antero-dorsal process. The interopercle, which is broken in the holotype, is a large, slightly triangular bone missing its anterior region. In specimen MB.f.19059, the interopercle is an elongate, narrow, triangular bone that resembles the interopercle of *Parakneria* examined in this study (e.g., GRANDE & POYATO-ARIZA 2010: fig. 1.5D). A postero-dorsal process has not been observed at the posterior region of the opercle. At least two elongate branchiostegal rays are preserved in the holotype.

Vertebral column. The vertebral column (Fig. 4, 8–11) is represented by approximately 35 vertebrae including the terminal compound centrum, of which 11 or 12 are caudals. The centra are preserved three-dimensionally, with the ossified lateral walls of the centra often broken. The centra (Fig. 9A,B) are formed only by thin-walled autocentrum surrounding a moderately broad notochordal canal. The most anterior abdominal centra (Figs. 4, 8, 10) are slightly smaller than centra approaching the caudal region. Each neural arch is fused to its centrum throughout the vertebral column (Figs. 9A,B, 11). The lateral surfaces of the centra are preserved. They seem to be smooth and lack ridges, grooves or other kinds of ornament, with the exception of the posterior caudal centra described below. Despite size differences among them, the centra are as long as the neural arches, which are broad and with enlarged antero-dorsal processes (Figs. 9A,B, 11). The anterior and posterior margins of the neural arches are in contact and in some cases even

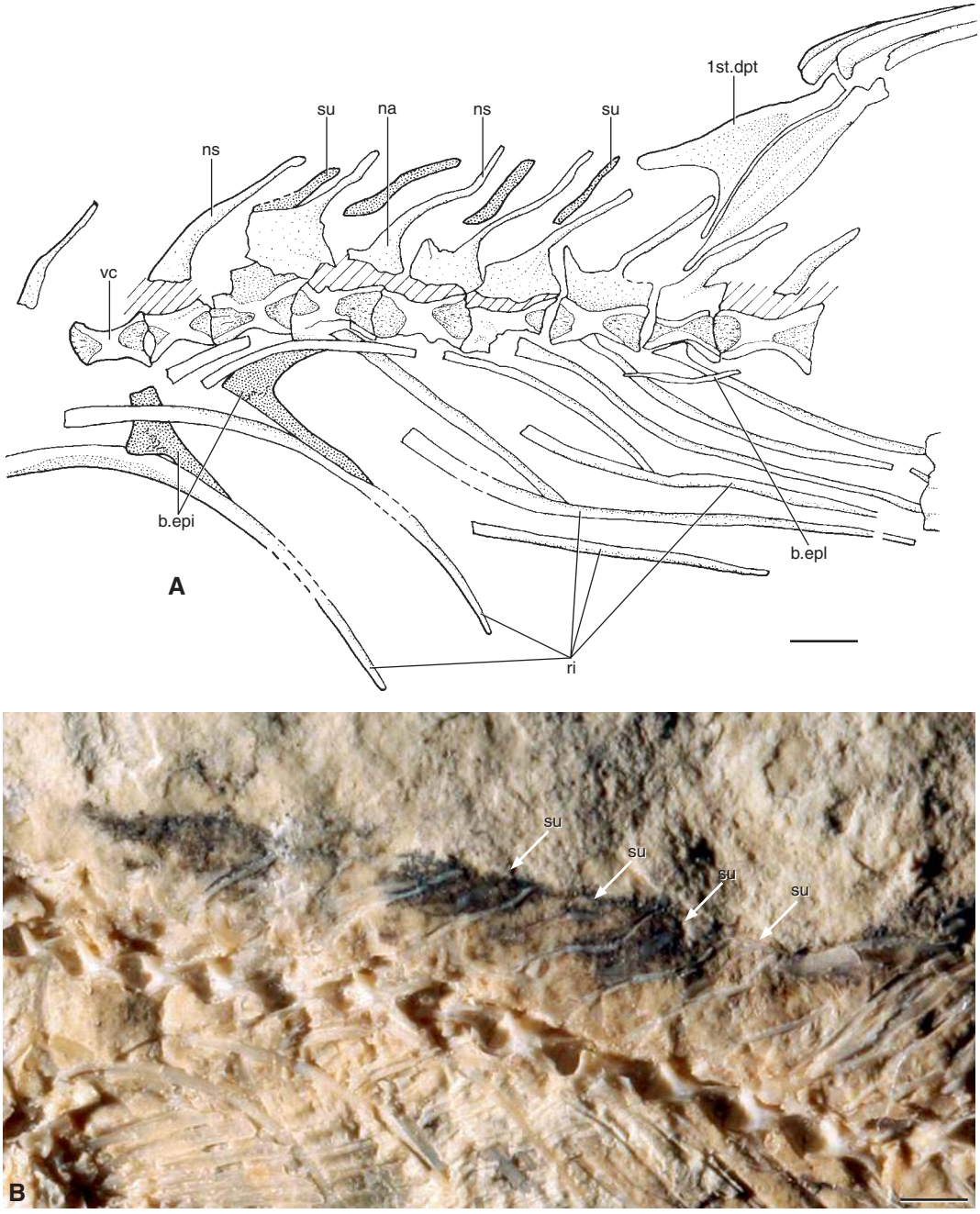


Fig. 9.
†*Mahengichthys singidaensis* n. gen. n. sp. (holotype MB.f.19057a). **A,** drawing of most anterior abdominal vertebrae, first two dorsal pterygiophores, and other elements associated to the vertebral column in lateral view. **B,** photograph. Scales = 1 mm. Abbreviations: **b.epi**, epicentral bones; **b.epl**, epipleural bones; **na**, neural arch; **ns**, neural spine; **su**, supraneural; **vc**, vertebral centrum; **1st.dpt**, first dorsal pterygiophore; **ri**, ribs.

overlap the adjoining arch. The thin, narrow neural spine is positioned closer to the posterior margin of the neural arch than to the anterior margin; in contrast, the spine is positioned approximately at the mid region of the neural arch in the most anterior abdominal vertebrae in *Kneria* and *Parakneria* specimens examined here (e.g., GRANDE 1994: fig. 5). The neural spines of the most anterior abdominal vertebrae are short and increase in length caudally.

Parapophyses have not been observed on the most anterior abdominal vertebrae; however, ventro-lateral parapophyses fused to the centra and articulating with ribs have been observed on the last few abdominal vertebrae. The ribs are heavily ossified, long, narrow, markedly curved, and reaching the latero-ventral part of the walls of the body cavity (Fig. 8).

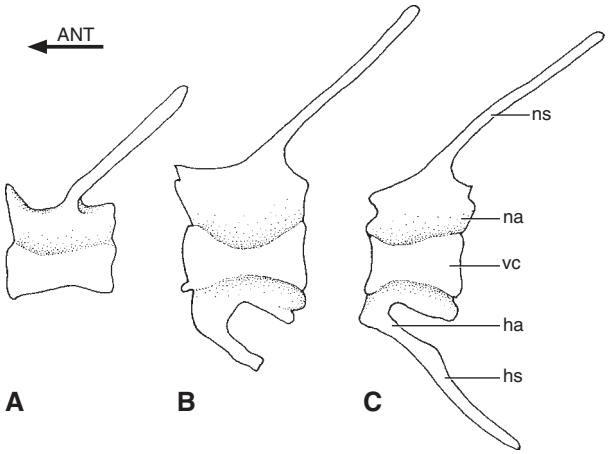


Fig. 10.
Diagramatic representation of different types of vertebrae in †*Mahengichthys singidaensis* n. gen. n. sp. **A,** anterior abdominal vertebrae. **B,** posterior abdominal region. **C,** midcaudal region. Abbreviations: **ha**, haemal arch; **hs**, haemal spine; **na**, neural arch; **ns**, neural spine; **vc**, vertebral centrum.

The posterior few caudal centra have a longitudinal caudal crest that separates a dorsal and a ventral fossa formed in the lateral wall of each centrum. Although the caudal centra decrease in size posteriorly, their neural and haemal arches are as long as the centrum and the arches are observed touching or overlapping each other. The neural and haemal spines are thin, elongate, and slightly inclined toward the horizontal. While the neural spines attach to the posterior half of the neural arch, the haemal spines attach to the anterior half of the haemal arch, especially in the most anterior caudal vertebrae.

Intermuscular bones. It is unclear whether supraneurals are present in the anterior-most abdominal region, but four or five thin, slightly sigmoidal supraneurals (Figs. 4, 8, 9), are positioned between the neural spines anterior to the first dorsal pterygiophore. The supraneurals seem to be short in the holotype (Figs. 4A,B, 9), but they are slightly longer in MB.f.19058 (see Fig. 4C).

A series of thin, moderately long epineural bones lying lateral to the neural arches is observed in specimen MB.f.19058 (see Fig. 4C). The epineurals extend along the abdominal region to the region below the dorsal fin; broken intermuscular bones are seen in the epaxial caudal region as far as the preural region, but it is difficult to find the limit where the epineural bones are replaced by elongate intermuscular bones with numerous projections that are broken in the fossils.

A series of heavily ossified, large epicentrals is observed along the abdominal region to a point in line with the pelvic fin (see Figs. 8, 9A,B). The ventral section of the first epicentrals is as long as the ribs. These large epicentrals are easily observed between the cleithrum and below the dorsal fin; in front of the dorsal fin they become smaller and thinner and it is difficult to distinguish them. There are broken, thin bones lying below the last abdominal vertebrae, in between ribs, and also along the caudal region. We interpret these remnants as belonging to the epipleural series.

Brush-like cranial intermuscular bones have not been observed and we interpret them as to be absent in the fossil kneriid described herein. They are also absent in *Kneria* and *Parakneria*.

Paired fins. The pectoral girdle is damaged in most specimens so its description is incomplete. A displaced, short, stout supracleithrum is observed in the holotype. The cleithrum as preserved in the holotype (Fig. 4A,B, is well ossified, massive, and expanded posteriorly. Four radials are preserved in specimen MB.f.19058 (Fig. 4C). The most anterior radial is slightly triangular and is the smallest, whereas the other three are longer, the largest being the most medial one. This arrangement is like that in recent kneriids.

The pectoral fins (Figs. 4, 12) have a low position on the body, closer to the ventral margin of the body than to the middle. The fins are moderately long, but not extending beyond the origin of the pelvic fins. There are 15 pectoral rays preserved in the holotype, but 14 rays in MB.f.19058. The most anterior pectoral rays have longer bases than the most posterior one. All rays are segmented and branched distally.

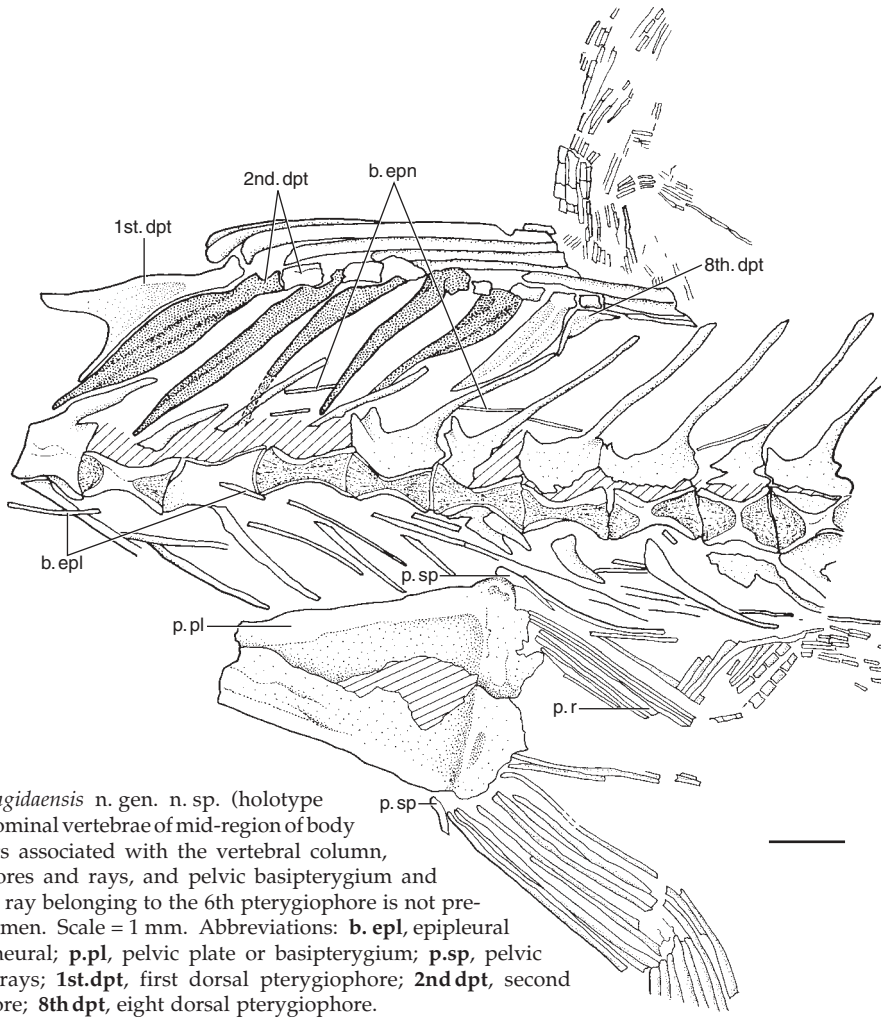


Fig. 11.
†*Mahengichthys singidaensis* n. gen. n. sp. (holotype MB.f.19057a). Abdominal vertebrae of mid-region of body and other elements associated with the vertebral column, dorsal pterygiophores and rays, and pelvic basipterygium and rays. Note that the ray belonging to the 6th pterygiophore is not preserved in this specimen. Scale = 1 mm. Abbreviations: **b. epl**, epipleural bones; **b.epn**, epineural; **p.pl**, pelvic plate or basipterygium; **p.sp**, pelvic splint; **p.r**, pelvic rays; **1st.dpt**, first dorsal pterygiophore; **2nd dpt**, second dorsal pterygiophore; **8th dpt**, eight dorsal pterygiophore.

Each pelvic plate or basipterygium is large, well ossified, triangular, and lacks anterior or lateral processes (Figs. 4, 13). The basipterygia are thicker caudally, especially at the postero-lateral border where the fin articulates. A short, broad, well-ossified postero-medial process is present in each basipterygium. A similar morphology is present in recent *Kneria* and *Parakneria* examined here. There are eight pelvic rays and a short splint in most specimens where the rays are preserved. Specimen MB.f.19060 has a splint plus 7 rays The pelvic rays have short bases followed by many short segments, and they are branched distally.

Dorsal and anal fins. The short-based dorsal fin is positioned at about half of the standard length, slightly anterior to the level of the origin of the pelvic fins (Fig. 4). The dorsal fin is higher than long, with the first principal ray (segmented but unbranched) slightly shorter than the second and the third, and the last few rays about ¼ the length of the longest principal ray. In all specimens where the rays can be counted, 9 or 10 rays are present (two small procurrent rays plus 7 or 8 principal rays).

The dorsal fin (Fig. 9, 11) is supported by long proximal radials and middle radials. Distal radials have not been observed due to conditions of preservation. The first dorsal pterygiophore is bifurcated, with an anterior shorter projection and a long, lanceolate one that extends ventrally. Other pterygiophores are also lanceolate and elongate with the exception of the last one, which is considerable smaller and triangular.

The anal fin (Figs. 4, 14) is short, with one or two procurrent rays and six principal rays. The first

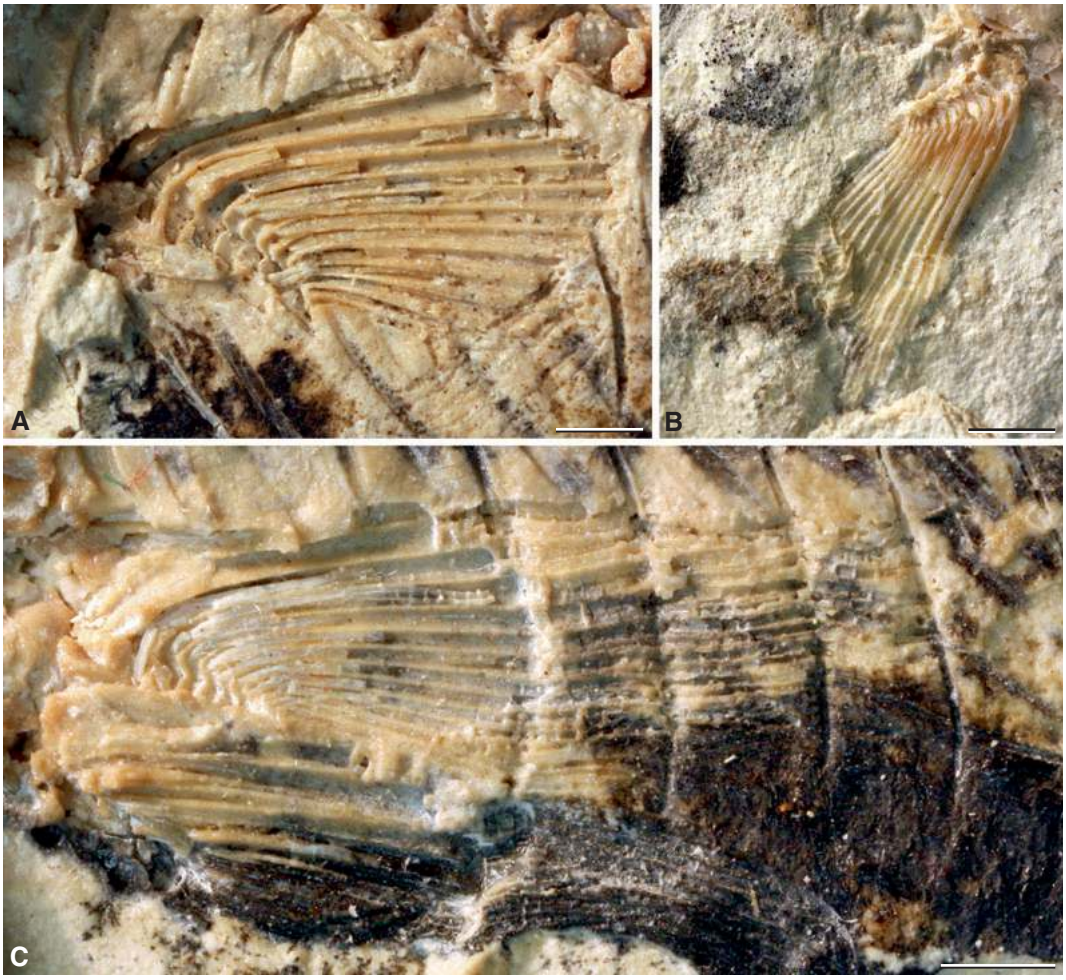


Fig. 12.
†*Mahengichthys singidaensis* n. gen. n. sp. Pectoral fins. **A,** imprint of pectoral fin including radials and rays (paratype MB.f.19058). **B,** paratype MB.f.19057b. **C,** MBf.19059a. Scales = 1 mm.

two anal pterygiophores are markedly bent and elongated and reach close to the vertebral centra. Other pterygiophores are considerably smaller.

Caudal fin. The caudal fin (Figs. 4, 15, 16C) is lacking the distal tips of the principal rays in all specimens where the fin is preserved. In addition, in two specimens the endoskeleton is partially preserved as an imprint but in others the bones are preserved three-dimensionally. The preserved rays in the holotype indicate the presence of a forked tail (Fig. 4A).

Three preural centra and the compound terminal centrum (Figs. 15, 16C) support the caudal rays. Parts of the preural vertebrae are incompletely preserved in the holotype, but the preserved elements confirm the presence of well-ossified vertebral centra fused to the neural and haemal arches, including the haemal arch of preural centrum 2. It has been hypothesized that the compound centrum is formed by the fusion of preural centrum 1 and at least ural centra 1 and 2 (polyural terminology; SCHULTZE & ARRATIA 1989, ARRATIA 2010, SCHULTZE & ARRATIA this volume). Other independent ural centra have not been observed associated with the dorsal hypurals. A neural arch and a short neural spine are present as part of the compound terminal centrum.

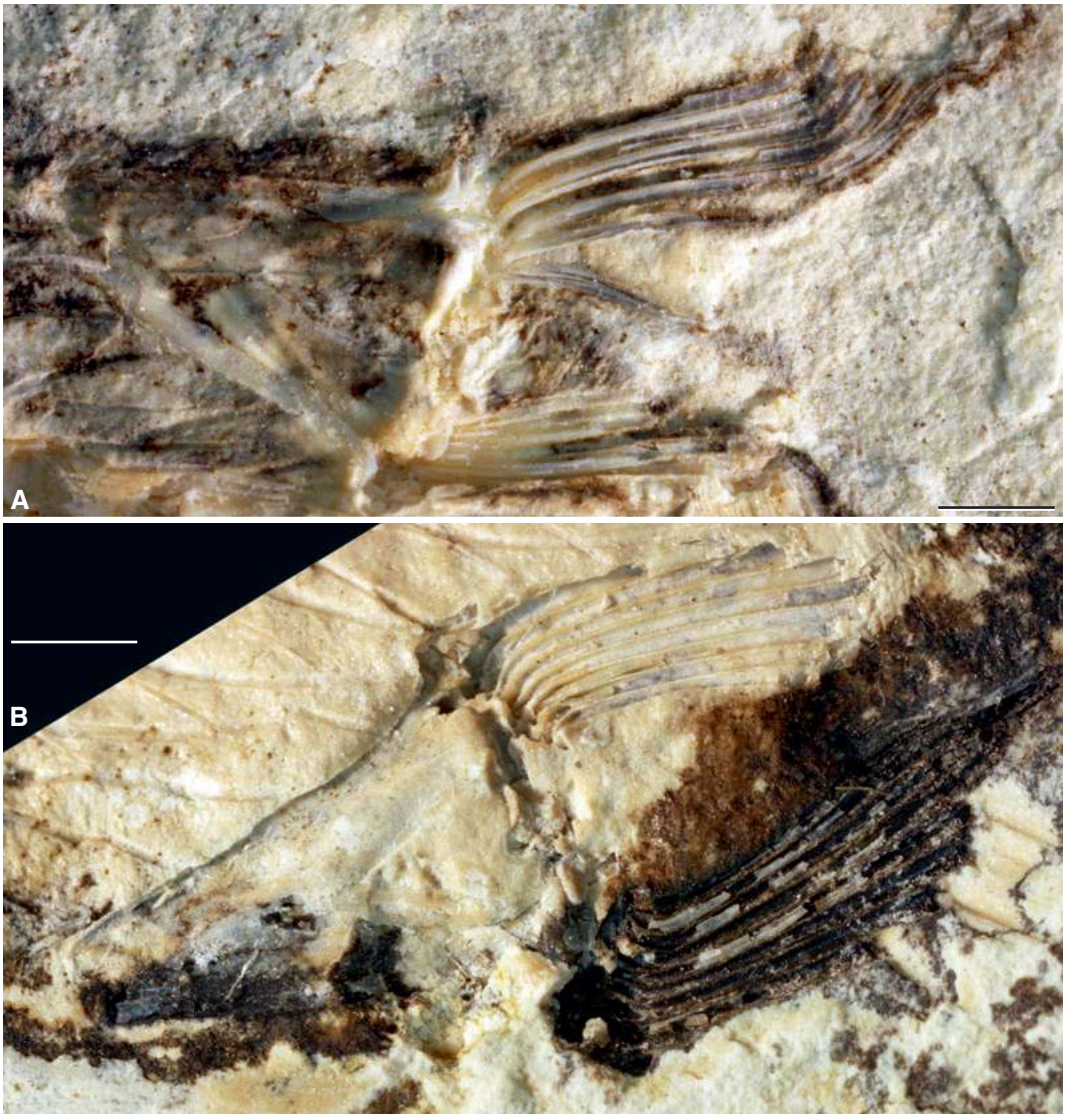


Fig. 13.
†*Mahengichthys singidaensis* n. gen. n. sp. Pelvic fins. **A,** MB.f.19057a. **B,** MB.f.19058. Scales = 1 mm.

Two elongate epurals are observed. The anterior one is larger and thicker than the posterior one in the holotype (Fig. 15A), features that can be due to preservation because in specimen MB.f.19061a/b, both epurals almost fill the space between the posterior margin of the neural spine of preural centrum 2 and the pleurostyle (Fig. 15B). The pleurostyle or uroneural is fused to the compound centrum forming a compact structure. The elongate pleurostyle seems to be narrower in the holotype than in specimen MB.f.19058.

The haemal spine of preural vertebra 4 is comparatively narrower than those of the haemal spines 3 and 2 (Fig. 15). The haemal spine of the compound centrum or parhypural is as broad as haemal spine 2. The arch of the parhypural is apparently not fused to the compound centrum in the holotype, but it is fused with the compound centrum in MB.f.19061. There are six hypurals (Fig. 15A). Hypural 1 seems to be narrower at its mid length and then expanded distally (holotype and specimen MB.f.19058). Hypural 1 reaches the compound centrum in the holotype (Fig. 15); however, hypural 1 does not reach the wall of the

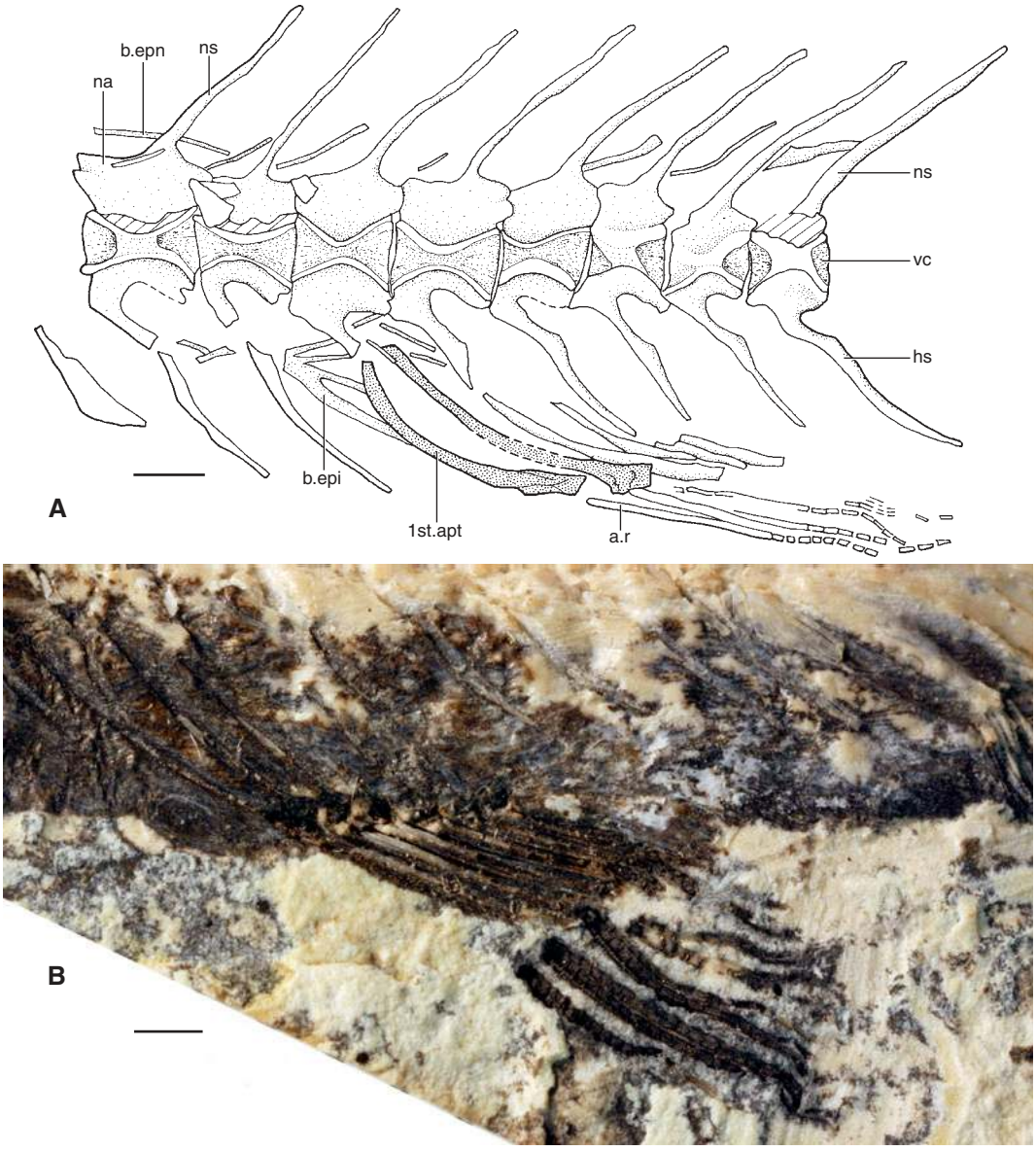


Fig. 14.
†*Mahengichthys singidaensis* n. gen. n. sp. Caudal vertebrae and anal fin. **A,** MB.f.19057a. **B,** MB.f.19058. Scales = 1 mm. Abbreviations; **1st.apt**, 1st anal pterygiophore; **a.r**, anal ray; **b.epi**, epicentral bones; **b.epn**, bony epineurals; **hs**, haemal spine; **na**, neural arch; **ns,** neural spine; **vc**, vertebral centrum.

compound centrum in specimen MB.f.19061a/b, but is separated from the centrum as in extant kneriids. Hypural 3 is incompletely preserved in the holotype; however, it is even broader than hypural 2 in specimen MB.f.19058. Hypurals 4 to 6 decrease in size dorsally. An elongate separation or diastema is observed between hypurals 2 and 3.

The caudal fin presents 13 or 14 dorsal procurrent rays, 19 principal rays (10 in the dorsal lobe and 9 in the ventral one), and about 7 or 8 ventral procurrent rays. The first and last principal rays are thicker than other principals, with many short segments, and the joints between segments are slightly Z-like as in

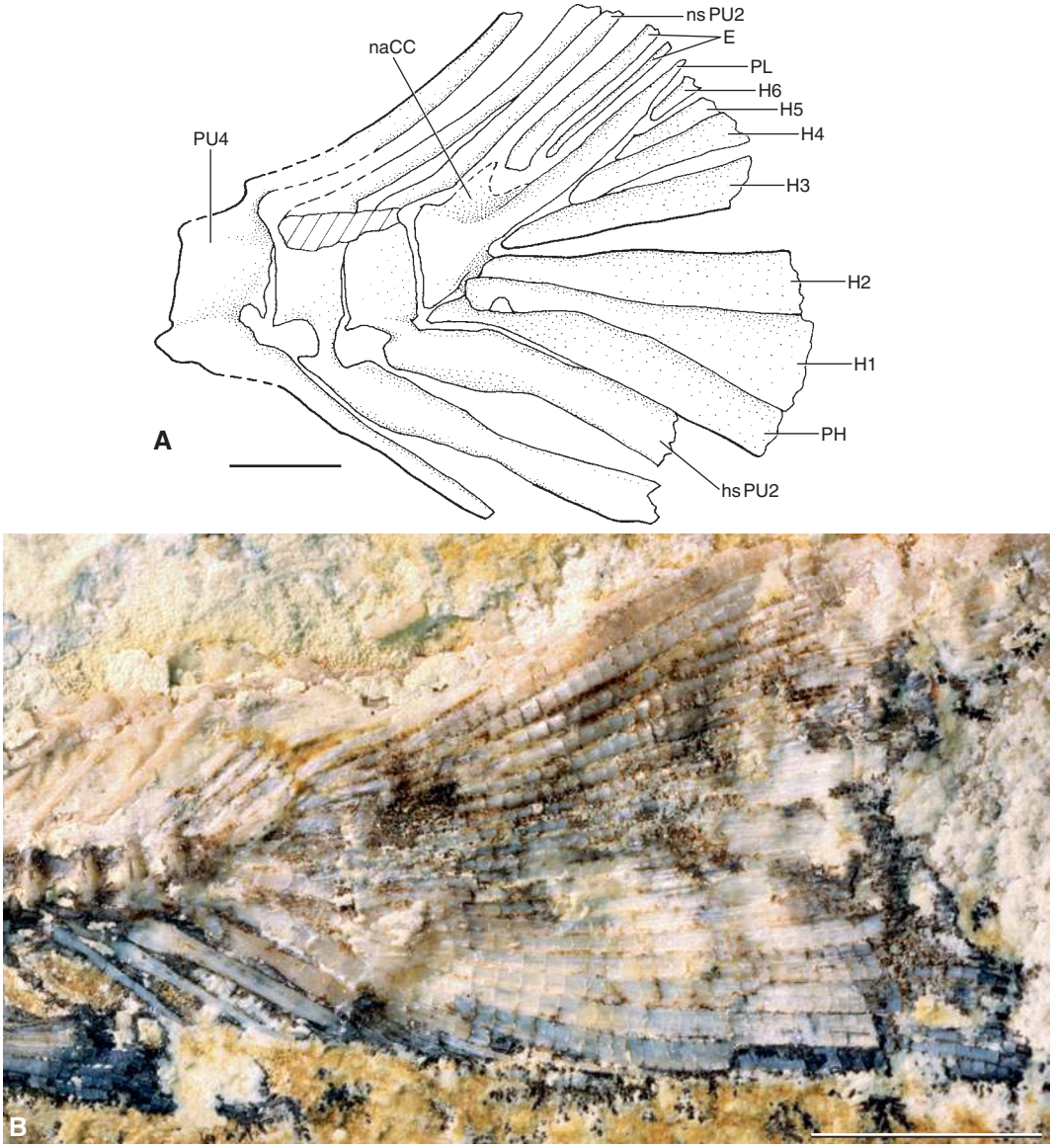


Fig. 15.
†*Mahengichthys singidaensis* n. gen. n. sp. **A,** restoration of caudal endoskeleton in lateral view based on holotype MB.f.19057a. **B,** caudal skeleton and fin of MB.f.19061a. Scales = 1 mm. Abbreviations: **E**, epurals; **H1–6**, hypurals 1–6; **hsPU2**, haemal spine of preural centrum 2; **naCC**, neural arch of compound terminal centrum; **nsPU2**, neural spine of preural centrum 2; **PH**, parhypural; **PL**, pleurostyle; **PU4**, preural centrum 4.

other primitive fossil (ARRATIA 2008) and extant forms (e. g., *Elops* and *Megalops* ARRATIA 2009: fig. 15). In extant *Kneria* and *Parakneria*, the segmentation of the first and last principal rays is almost straight.

Scales. Remnants of scales are observed in between the neural and haemal spines, especially in the caudal region, where the long longitudinal ridges characterizing the scales are preserved (Fig. 16C). Radii in the anterior field of the scales have not been observed. The density of the ridges makes it impossible to observe isolated scales, only the imbricated squamation.

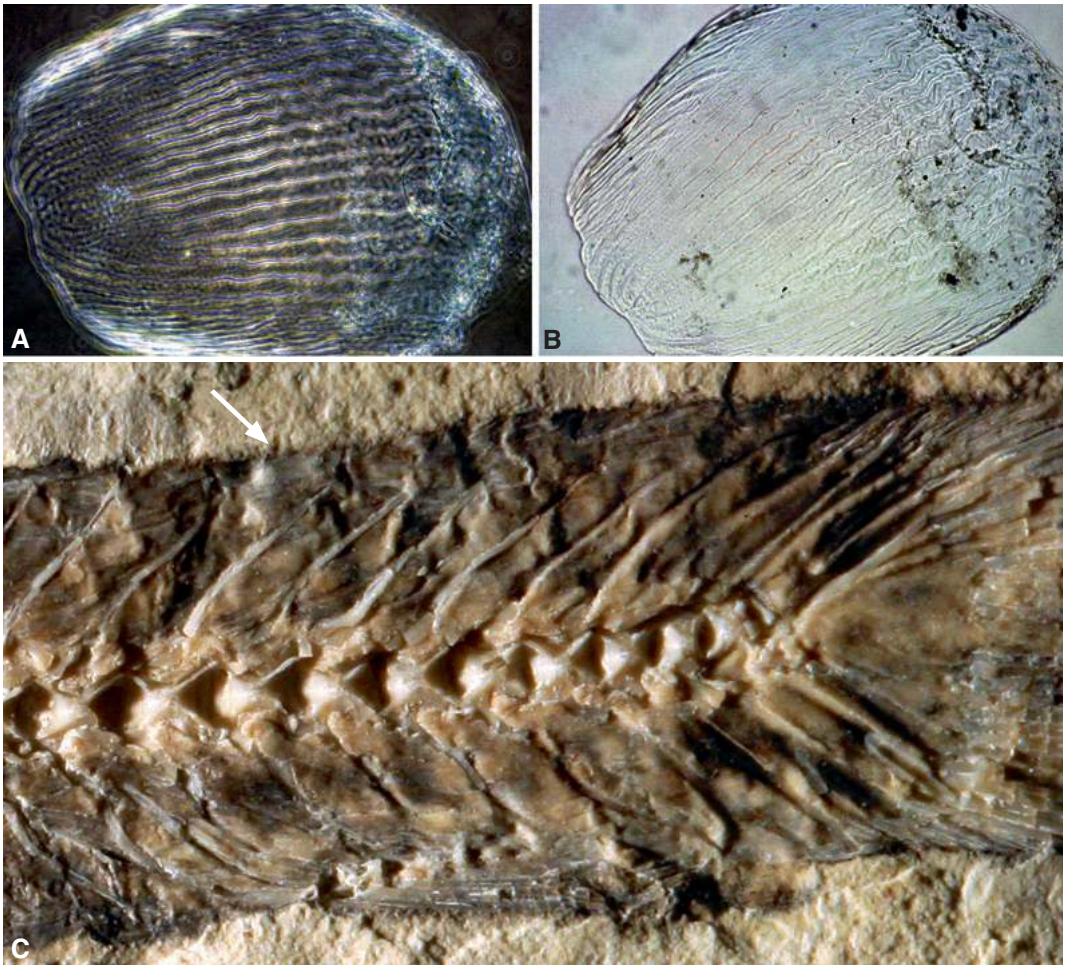


Fig. 16.
A, B, scales of Recent *Kneria* showing the characteristic ridged pattern of the surface (BMNH 1976.10.20.142-159). **C,** caudal region of the holotype MB.f.19057a. Arrows point to the ridged pattern of the scales. Scales = 1mm.

The fossil scales resemble those present in Recent kneriids, especially *Kneria* species with longitudinal ridges, which become slightly undulating in the middle field of the scales (see Fig. 16A,B). In *Parakneria*, long, almost straight longitudinal ridges are placed near the dorsal and ventral borders of the scales, but the ridges in the middle field are wavier than in *Kneria*. No radii are observed in the scales of tribe Kneriini, while they are present in *Phractolaemus* (KUMNH 41050), which in addition present large scales without longitudinal ridges.

The structure of the scales in the fossil and recent kneriids is interpreted here as a potential synapomorphy of this tribe. The scale morphology within the family and other gonorynchiforms is in need of further study.

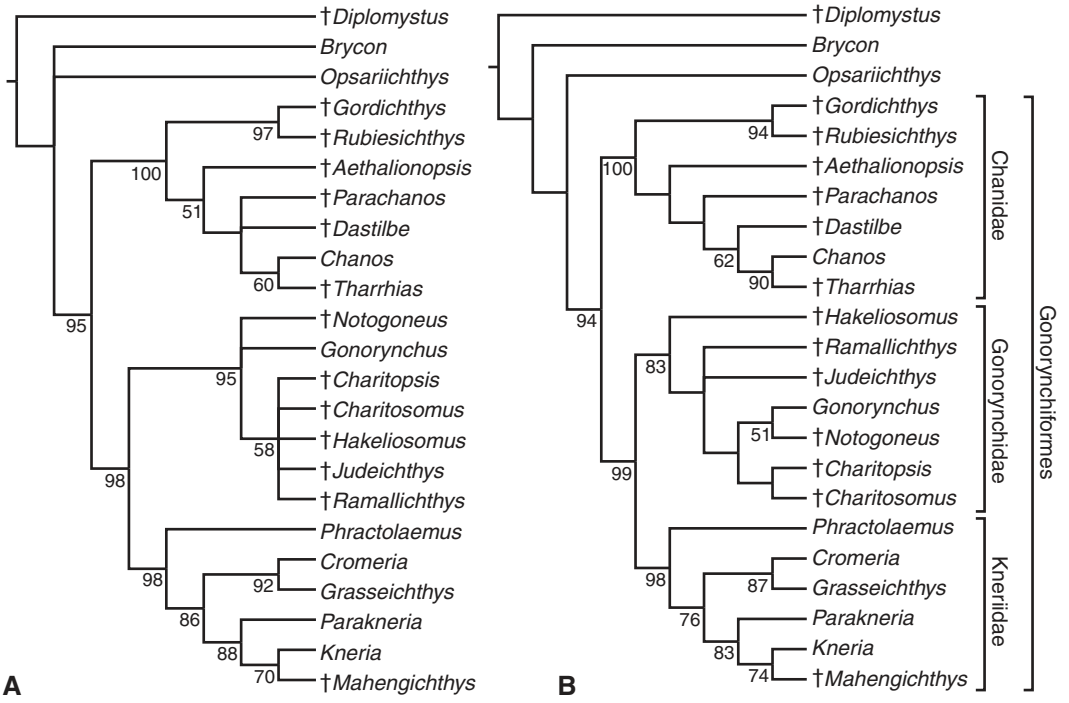


Fig. 17.
Relationships of the Gonorynchiformes based on parsimony (**A**) and maximum likelihood (**B**) analyses of 128 morphological characters modified from POYATO-ARIZA et al. (2010b). Numbers below nodes denote bootstrap values, with only values greater than 50 shown. Results from parsimony analysis (A) are presented as a strict consensus of 25 equally parsimonious trees (232 steps).

Phylogenetic relationships

Morphological data. Figure 17 shows the strict consensus of 25 equally parsimonious trees from the maximum parsimony analysis (Fig. 17A), and the optimal maximum likelihood (Fig. 17B) topology for gonorynchiform fishes based on the modified morphological data of POYATO-ARIZA et al. (2010b). For parsimony, of the 128 morphological characters, 87 were phylogenetically informative (tree length of 232, consistency index of 0.707, retention index of 0.081). In both analyses there is strong bootstrap support for the monophyly of the Gonorynchiformes and of each of the three families (Chanidae, Gonorynchidae, Kneriidae). Relationships among gonorynchiform families were identical to results of POYATO-ARIZA et al. (2010b) for both methods, with Chanidae sister to a clade of Kneriidae + Gonorynchidae. Evolutionary relationships within the family Kneriidae are identical between the two methodologies (Fig. 17A,B). The subfamily Phractolaeminae *(Phractolaeumus)* was recovered as the sister group to a well-supported subfamily Kneriinae. The paedomorphic *Cromeria* and *Grasseichthys* were recovered as sister taxa with high bootstrap support (tribe Cromerini) with both methodologies. This clade is sister to a strongly supported tribe Kneriini, which includes *Parakneria* as the sister group to a clade of *Kneria* + †*Mahengichthys singidaensis*.

Total evidence. The maximum likelihood phylogeny for a combined morphological (Appendix 1) and molecular (Table 1) analysis is shown in Figure 18. As with the morphological data alone, there is strong bootstrap support for the monophyly of the Gonorynchiformes and all families. However, the relationships among families differ from the morphological analysis, with Gonorynchidae sister to Chanidae + Kneriidae. This result is consistent with the findings of LAVOUÉ et al. (2005, 2012) that were based on mitogenomic data alone. The family Kneriidae is again composed of subfamily Phractolaeminae *(Phractolaeumus)* sister to a well-supported subfamily Kneriinae. The tribe Cromerini *(Cromeria* and *Grasseichthys)* is recovered

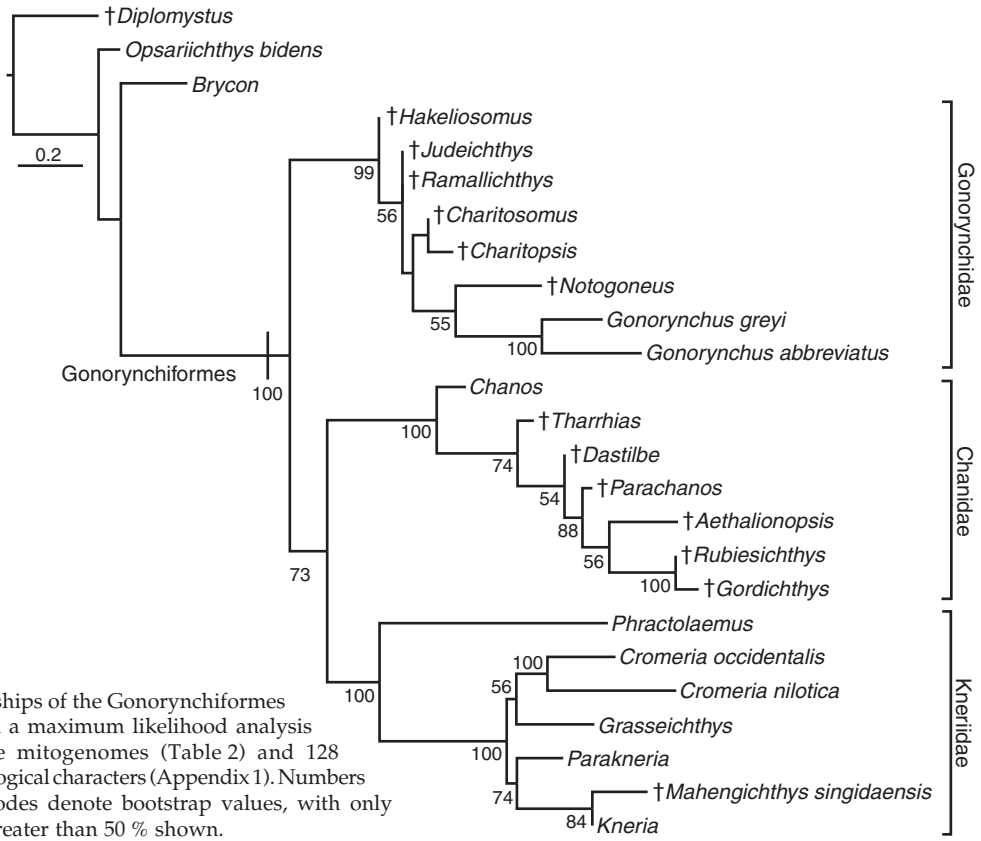


Fig. 18.
Relationships of the Gonorynchiformes based on a maximum likelihood analysis of whole mitogenomes (Table 2) and 128 morphological characters (Appendix 1). Numbers below nodes denote bootstrap values, with only values greater than 50 % shown.

with weak-moderate bootstrap support, while the tribe Kneriini *(Kneria*, *Parakneria*, and †*Mahengichthys singidaensis)* has strong support. The fossil kneriid †*Mahengichthys singidaensis* is again recovered as the sister lineage to the extant genus *Kneria*, within the Kneriini.

Evolution and divergence of the Kneriidae. The Bayesian time trees, based on a synthesis of divergence estimates from mitogenomic data and fossil calibrations, are shown in Figures 19 and 20. Information regarding the divergence times of lineages of Gonorynchiformes can be found in Table 2. The highest posterior densities (HPD) refer to the interval of age ranges from which 95 % of all sampled ages were found during the divergence analysis. Comparisons to the divergence estimates for gonorynchiforms from previous studies that did not include calibration information for the family Kneriidae based on fossil specimens described herein are also included in Table 2. Our first hypothesis (Table 2A) of divergence time estimations is reconstructed with the tribe Cromerini *(Grasseichthys* + *Cromeria)* constrained to be monophyletic (Fig. 19), as indicated by the optimal results of our likelihood total evidence study that incorporated both mitogenomic and morphological information (Fig. 18). Our second hypothesis (Table 2B) does not include a constraint on the monophyly of Cromerini, as mitogenome data alone does not recover this clade in previous studies (LAVOUÉ et al. 2005, LAVOUÉ et al. 2012). The order Gonorynchiformes is estimated to have diverged during the Jurassic (Figs. 19, 20; Table 2A,B), with the most recent common ancestor of the families Chanidae + Kneriidae also diverging during this time. Our results indicate that the genus *Gonorynchus* diverged during the Late Cretaceous to Paleogene (Figs. 19, 20; Table 2A, B). The family Kneriidae most likely diverged during the Late Jurassic to Early Cretaceous, with the subfamily Kneriinae diverging in the Late Cretaceous to the Paleocene Epoch of the Paleogene (Figs. 19, 20, Table 2A, B). During the Late Cretaceous to Paleogene, both tribes Kneriini and Cromerini are already established (Figs. 19, 20; Table 2A, B). When Cromerini are constrained to be monophyletic, the tribe's estimated divergence age is slightly older than that of Kneriini (Fig. 19, Table 2A).

Discussion

Based on our descriptions and subsequent phylogenetic analysis, we indicate that †*Mahengichthys singidaensis* is the first known fossil representative of the gonorynchid family Kneriidae. POYATO-ARIZA et al. (2010b) suggested that while gonorynchiforms in general have expansive fossil records, fossil representatives of the exclusively freshwater kneriids have previously been difficult to recover as a result of poor fish preservation in central and Sub-Saharan Africa, and scarce field work in Cenozoic African localities. The Mahenge formation is well known for its excellent preservation of whole to completely articulated fish specimens (e.g., GREENWOOD & PATTERSON 1967, MURRAY 2003b, KAISER et al. 2006), and is located within the present distribution of extant taxa for the family Kneriidae. Specimens of †*Mahengichthys singidaensis* are unambiguously identified as a member of the Gonorynchiformes by the following synapormorphies: postparietal bones [= parietal bones] reduced or absent, premaxilla rounded and lacking an ascending process, neural arch of first vertebra contacting occipital region, rib on third vertebra slightly shorter and broader than following ribs, and intermuscular bones represented by epineurals, epicentrals, and epipleurals.

Phylogenetic position of †*Mahengichthys singidaensis* and the evolutionary relationships of Kneriidae

Our likelihood analyses with both morphological and total evidence approaches indicate that †*Mahengichthys singidaensis* is a kneriid taxon with strong support as a member of the tribe Kneriini, which includes the extant genera *Kneria* and *Parakneria* (Figs. 17A,B, 18). Morphological synapomorphies uniting †*Mahengichthys singidaensis* within the family Kneriidae, for characters that could be observed in the available specimens, include (see appendix 1 in POYATO-ARIZA et al. 2010b, **indicates homoplasy): presence of wings on lateral ethmoids (19[1]), absence of mandibular sensory canal (32**[1]), presence of postero-dorsal ascending process of interopercular bone (67[1]), and anterior neural arches contacting with no overlap (77**[1], 78 in POYATO-ARIZA et al. 2010b). Synapomorphies that support the position of †*Mahengeichthys singidaensis* within subfamily Kneriinae include: postparietals [= parietals of traditional terminology] absent as independent ossifications (15[3]), mesethmoid long and slender, with anterior elongate lateral extensions (18[1]), and articular head of hymandibular bone double, with anterior articular surface separate from posterior articular surface (45**[1]). Synapomorphies that support placement within tribe Kneriini include: shape of opercular bone in lateral view squarish or square (53[2]), first six anterior epicentral bones highly modified and larger than posterior ones (83[1], 84 in POYATO-ARIZA et al. 2010b), and lateral line not piercing supracleithrum (88[2], 89 in POYATO-ARIZA et al. 2010b).

The phylogenetic position of †*Mahengichthys singidaensis* within the tribe Kneriini is well supported across all analyses performed herein (Figs. 17–18). Both the morphological and total evidence analyses

Table 2.
Divergence time estimates for Gonorynchiformes in millions of years ago (Ma), with the range of estimates representing a 95 % interval of sampled ages. Divergence time estimates from this study include two hypotheses. In the first one, the tribe Cromeriini is constrained to be monophyletic (A), as inferred from the total evidence analysis. In the second, no constraints are placed on monophyly within the family Kneriidae (B). The two separate estimates from LAVOUÉ et al. (2012) refer to their two reconstruction methods in the absence of fossil kneriid information. The first included a narrow range between minimum and upper ages for priors (A), and the second included a more conservative range of ages (B).

Clade	This study		LAVOUÉ et al. 2012		NAKATANI et al. 2011
	A	B	A	B	
Neopterygii	316–285	320–285	n.a.	n.a.	n.a.
Teleostei	272–193	285–199	n.a.	n.a.	n.a.
Gonorynchiformes	185–147	193–147	145–120	265–175	280–230
Gonorynchus	85–29	85–26	75–20	125–25	n.a.
Families Chanidae + Kneriidae	171–141	177–141	122–110	230–135	260–210
Family Kneriidae	152–107	160–110	110–71	198–103	212–152
Subfamily Kneriinae	93–58	96–63	67–31	114–49	n.a.
Tribe Kneriini	78–48	70–47	45–12	75–20	n.a.
Tribe Cromeriini	87–52	n.a.	n.a.	n.a.	n.a.

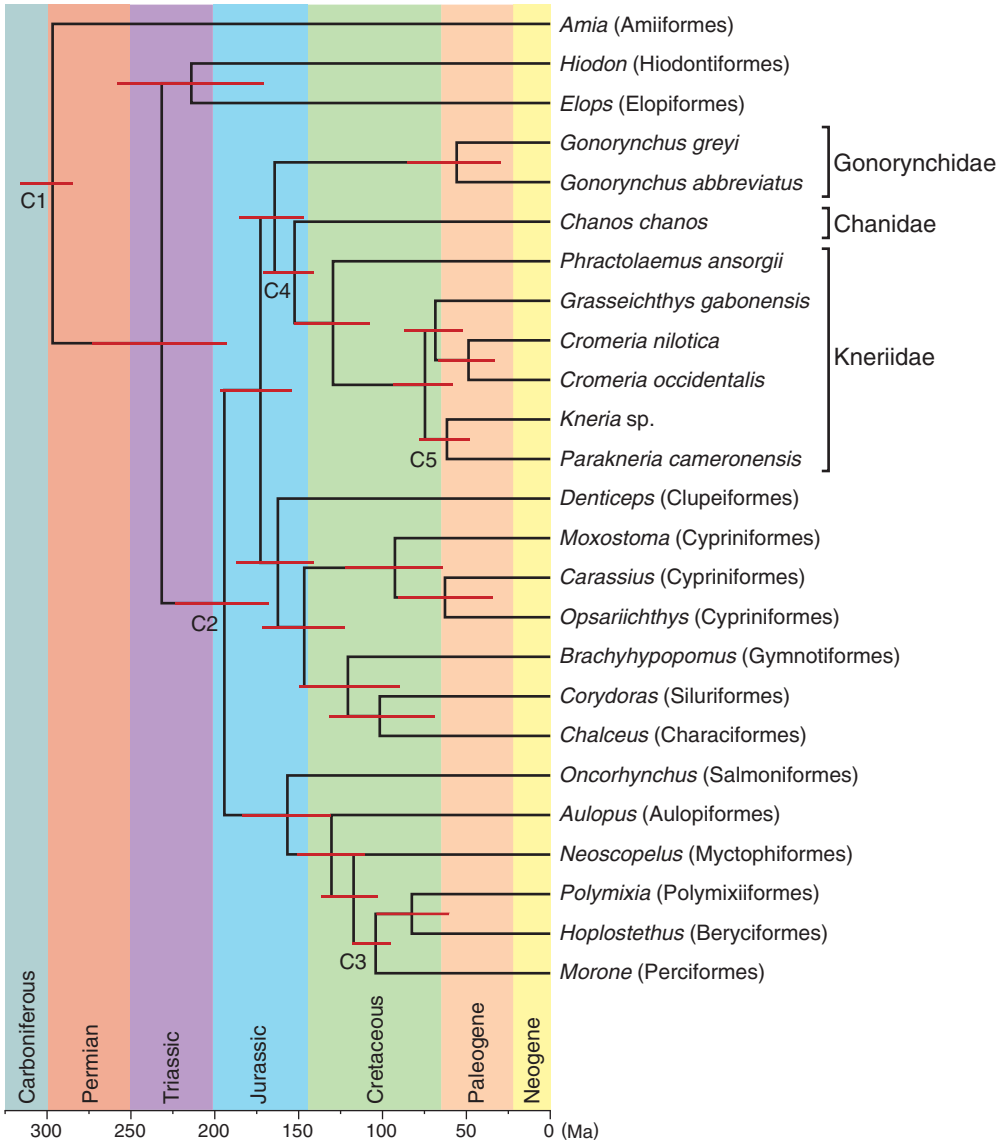


Fig. 19.
Divergence time estimations for the Gonorynchiformes where tribe Cromeriini *(Cromeria + Grasseichthys)* is constrained to be monophyletic as inferred by the total evidence analyses (Fig. 18). Red bars denote 95 % or higher posterior densities (Table 2). All nodes possessed posterior probabilities greater than 95 %. Please refer to Materials and Methods for information regarding node calibrations.

strongly support the monophyly of the family Kneriidae, with *Phractolaemus* as the sister group to a well-supported subfamily Kneriinae (Fig. 21). These results are consistent with previous phylogenetic hypotheses (e.g., GRANDE & POYATO-ARIZA 1999, LAVOUÉ et al. 2005, POYATO-ARIZA et al. 2010b, LAVOUÉ et al. 2012). Within Kneriinae, there is strong support for the monophyly of the tribe Kneriini *(Parakneria*, *Kneria*, and †*Mahengichthys singidaensis)* across all analyses herein (Fig. 21).

The evolutionary relationships of the genera *Grasseichthys* and *Cromeria* within Kneriinae have been the focus of recent controversy, primarily regarding the use of reductive characters as character states in

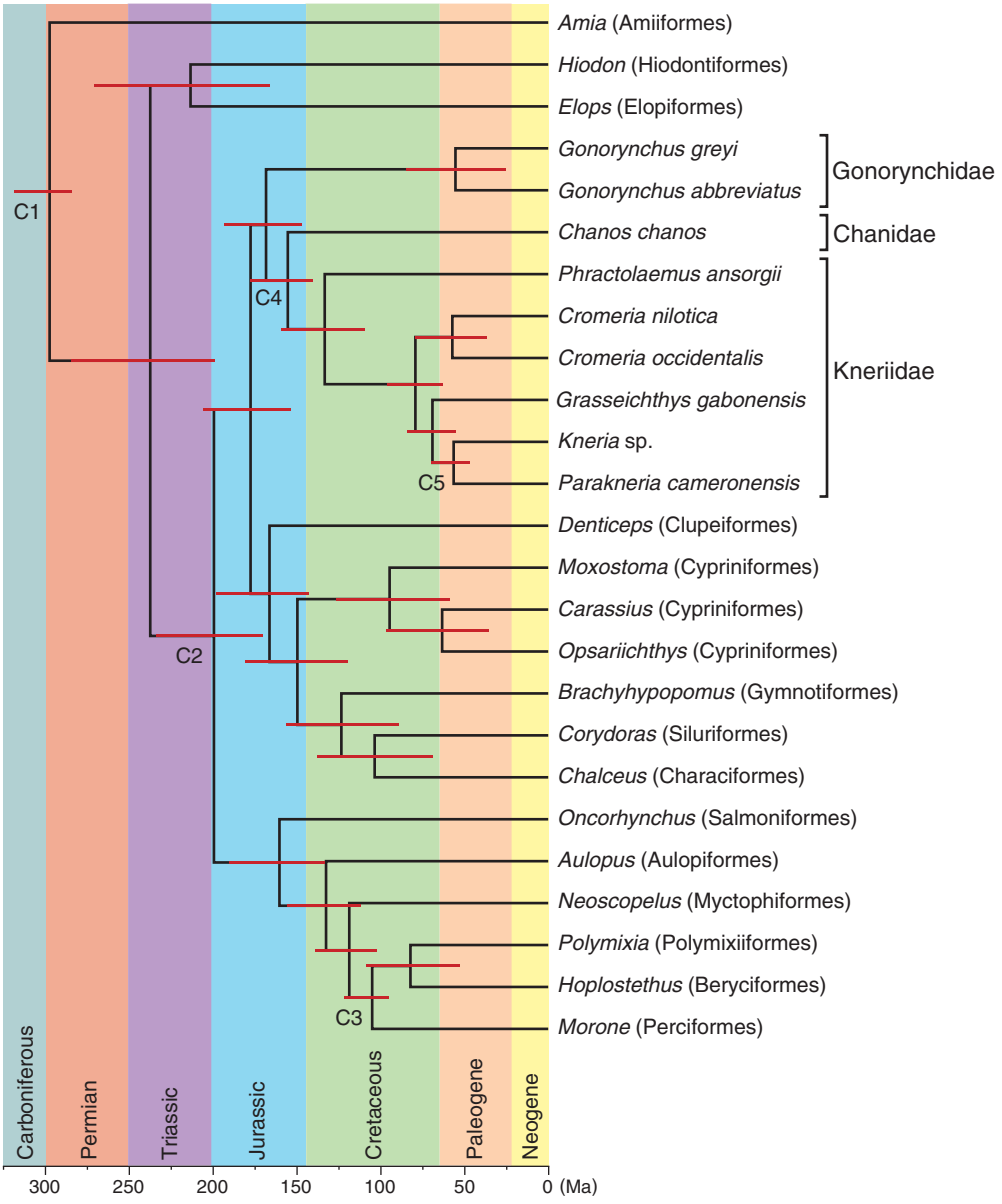


Fig. 20.
Divergence time estimations for the Gonorynchiformes where tribe Cromeriini *(Cromeria + Grasseichthys)* is not constrained to be monophyletic. Red bars denote 95 % higher posterior densities (Table 2). All nodes possessed posterior probabilities greater than 95 %. Please refer to Materials and Methods for information regarding node calibrations.

morphological phylogenetic reconstructions of relationships. Previous morphological systematic studies (GRANDE & POYATO-ARIZA 1999, POYATO-ARIZA et al. 2010b) recovered *Cromeria* and *Grasseichthys* as sister groups (Cromeriini) within Kneriinae; however, BRITZ & MORITZ (2007) argued that the characters supporting this clade are largely reductive in nature (e. g., lack of body scales, loss of interhyal [but see comments on character 47, p. 330], loss of nasal bones), with no unambiguous derived states uniting this

clade. POYATO-ARIZA et al. (2010b) suggested that reductive characters could be synapomorphies if they are indicative of a common ancestry, which is accurate. BRITZ & MORITZ's (2007) detailed anatomical study of the paedomorphic taxa indicated that the reductive cranial anatomy varies considerably between the two genera, but they did not conduct a phylogenetic hypothesis to further examine the evolutionary relationships of the family.

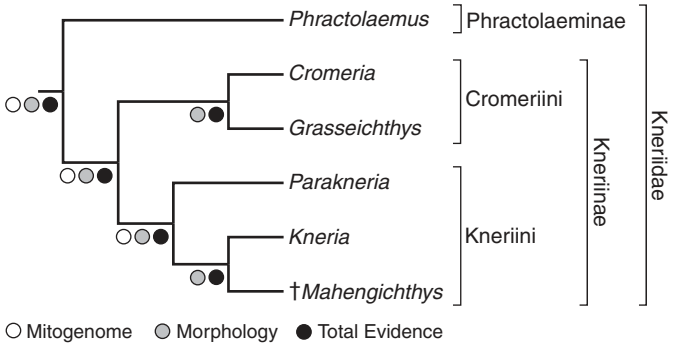


Fig. 21.
Evolutionary relationships of the family Kneriidae, summarized from the results of analyses herein and the previous morphological work by POYATO-ARIZA et al. (2010b) and mitogenomic work of LAVOUÉ et al. (2005, 2012). Circles by nodes indicate that the clade was well supported by mitogenomic, morphological, and total evidence analyses.

The morphological matrix presented by POYATO-ARIZA et al (2010b) represents the most comprehensive study incorporating extinct and extant gonorynchiform taxa, and unsurprisingly we recover a well-supported Cromeriini with our analyses utilizing their characters, albeit slightly modified (Figs. 17–18). Previous phylogenetic studies based on mitogenomic data alone (e.g., LAVOUÉ et al. 2005, LAVOUÉ et al. 2012) do not recover a monophyletic Cromeriini, and instead hypothesize that *Cromeria* is the sister lineage to *Grasseichthys* + Kneriinae. However, when mitogenomic data were included in our total evidence analysis, we again recover a well-supported monophyletic tribe Cromeriini. LAVOUÉ et al. (2012) investigated the character evolution of 22 reductive/absent characters discussed in BRITZ & MORITZ (2007), and identified that under the hypothesis of a monophyletic Cromeriini, seven (DELTRAN) or eleven (ACCTRAN) of these reductive/absent characters would be interpreted as synapormorphies for the tribe. The remaining eleven reduced or absent characters are autapomorphic. The results from our study support the monophyly of the Cromeriini and suggest that these reduced and absent characters (GRANDE & POYATO-ARIZA 1999, BRITZ & MORITZ 2007, POYATO-ARIZA et al. 2010b) are most likely the result of shared ancestry, although we believe further molecular (particularly nuclear genes) and developmental morphological work is needed to further explore paedomorphism in the Kneriidae.

Comments on †*Mahengichthys singidaensis* and paedomorphism

Specimens of †*Mahengichthys singidaensis* described here do not show any evidence of cranial miniaturization, and the specimens themselves are considerably larger than observed sizes for miniaturized fishes (e.g., WEITZMAN & VARI 1988, BRITZ et al. 2009, BRITZ & CONWAY 2009). As discussed previously, †*Mahengichthys singidaensis* shares a number of synapomorphies with the Kneriinae, and our results further indicate that this taxon is more closely related to the extant non-paedomorphic genus *Kneria*. It is interesting, however, that all fossil specimens of †*Mahengichthys singidaensis* collected to date possess elongated neural and haemal spines that extend to the margins of the body, a morphology that is also present in the paedomorphic taxa *Grasseichthys* and *Cromeria* (BRITZ & MORITZ 2007), but not in *Kneria* and *Parakneria*. Also of note is that †*Mahengichthys singidaensis* differs from extant kneriids in the number of supraneurals, possessing four to five, while extant kneriids have only one (86[0], 87 in POYATO-ARIZA et al. 2010b).

Temporal divergence of the Kneriidae with comments on historical biogeography

The age of the Mahenge deposits, approximately 46 Ma, suggests that the family Kneriidae is minimally of Eocene age, although the phylogenetic position of †*Mahengichthys singidaensis* within the tribe Kneriini indicates that the family itself is likely older than the Eocene. Previous studies that estimated the divergence times of the Gonorynchiformes and the family Kneriidae (e.g., NAKATANI et al. 2011, LAVOUÉ et al. 2012) did not include fossil calibration information for the Kneriidae, as this is the first study to identify and describe a kneriid from the fossil record. LAVOUÉ et al. (2012) calibrated their gonorynchiform divergence-time estimates with two different calibration-prior schemes in an attempt to account for their lack of kneriid fossil calibrations; the first was a narrow exponential prior with a hard minimum age and

a soft upper age that was 15 % greater than the minimum age (Table 2, reconstruction 1), and the second was a more conservative uniform prior with only a hard minimum age and a maximum upper estimate of 271 Ma that corresponded to estimated divergence times from additional divergence-time studies of Ostariophysi in SAITOH et al. (2011) and NAKATANI et al. (2011). (Table 2, reconstruction 2). LAVOUÉ et al. (2012) also included only two fossil calibrations, both from the family Chanidae, and only a single outgroup taxon (the cypriniform *Carassius auratus*).

Our divergence-time estimates for gonorynchiform fishes are the first to include information regarding the fossil record of the Kneriidae, with four additional conservative fossil calibrations distributed across the evolutionary history of actinopterygian fishes (Figs. 18–19; please see Materials and Methods for detailed calibration and prior information). In general, our divergence-time estimates for the Gonorynchiformes and the major gonorynchiform lineages fall in between the two divergence-time reconstructions of LAVOUÉ et al. (2012), and are considerably younger than other mitogenomic divergence-time studies of ostariophysans (Table 2). While the oldest fossil taxa associated with Gonorynchiformes are known from the Early Cretaceous, such as †*Rubiesichthys* and †*Gordichthys* (e. g., WENZ, 1984, FARA et al. 2007, FARA et al. 2010, POYATO-ARIZA et al. 2010a), our study suggests that the Gonorynchiformes first diverged during the Jurassic (Figs. 19–20, Table 2), and most likely in a marine environment (NAKATANI et al. 2011). Previous studies have suggested that the broad geographic distribution (predominantly Tethys Ocean) of fossil gonorynchiform taxa in the families Chanidae and Gonorynchidae, in combination with their occurrences in the fossil record during the Early and Late Cretaceous, indicates that major lineages of gonorynchiform fishes were well established by the Early Cretaceous (e. g., GRANDE, 1999; POYATO-ARIZA et al. 2010a). Our divergence-time estimates support this hypothesis, with all three families of gonorynchiform fishes estimated to have diverged between the Jurassic and the Late Cretaceous (Figs. 18–19; Table 2).

All extant members of the family Kneriidae are exclusively freshwater fishes distributed throughout Sub-Saharan Africa. It is therefore unsurprising that the first fossil Kneriid is identified from a freshwater lake habitat located in Tanzania. Our results indicate that the common ancestor of the family Kneriidae most likely invaded freshwater systems of Africa sometime during the Late Jurassic to Early Cretaceous, subsequently diversifying throughout Sub-Saharan Africa. During the initial time of estimated divergence for the family, Africa was still directly connected to South America, with the two landmasses beginning to "unzip" approximately 130 Ma ago (ALI & KRAUSE 2011). However, the subfamily Kneriinae is estimated to have diverged and diversified during the Late Cretaceous (Figs. 18–19, Table 2), following the complete separation of Africa and South America. During the Paleogene, the major lineages of the subfamily Kneriinae are estimated to have already diverged, including the paedomorphic tribe Cromeriini and the tribe Kneriini.

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References

ALI, J. R., & KRAUSE, D. W. (2011): Late Cretaceous bioconnections between Indo-Madagascar and Antarctica: refutation of the Gunnerus Ridge causeway hypothesis. – Jour. Biogeo. **38**: 1855–1872.

ALFARO, M. E., SANTINI, F., BROCK, C., ALAMILLO, H., DORNBURG, A., RABOSKY, D. L., CARNEVALE, G., HARMON, L. J. (2009). Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. – Proc. Nat. Acad. Sci. **106**: 13410–13414.

ARRATIA, G. (1992): Development and variation of the suspensorium of primitive Catfishes (Teleostei: Ostariophysi) and their phylogenetic relationships. – Bonner Zool. Monogr. **32**: 1–149.

– (1997): Basal teleosts and teleostean phylogeny. Palaeo Ichthyologica **7**: 1–168.
– (1999): The monophyly of Teleostei and stem group teleosts. – In: ARRATIA, G. &. SCHULTZE, H.-P. (eds.): Mesozoic Fishes 2 – Systematics and Fossil Record: 265–334; München (Pfeil).
– (2000): New teleostean fishes from southern Germany and the systematic problems concerning the "pholidophoriforms". – Paläontol. Z. **74**(1/2): 113–143.
– (2001): The Sister-group of Teleostei: Consensus and Disagreements. – J. Vert. Paleontol. **21**(4): 767–773.
– (2008): Actinopterygian postcranial skeleton with special reference to the diversity of fin ray elements, and the problem of identifying homologies. – In: ARRATIA, G., SCHULTZE, H.-P. & WILSON, M. V. H. (eds.): Mesozoic Fishes 4 – Homology and Phylogeny: 49–101; München (Pfeil).
– (2009): Identifying patterns of diversity of the actinopterygian fulcra. – Acta Zoologica, Stock. 90 (Suppl. 1): 220–235.
– (2010): The Clupeocephala re-visited: Analysis of characters and homologies. – Rev. Biol. Mar. & Oceanogr. **45**(51): 635–657.
ARRATIA, G. & BAGARINAO, T. (2010): Early ossification and development of the cranium and paired girdles of *Chanos chanos* (Teleostei, Gonorynchiformes). – In: GRANDE, T., POYATO-ARIZA, F. J. & DIOGO, R.: Gonorynchiformes and Ostariophysan Relationships. A Comprehensive Review: 71–106; Enfield, NH (Science Publishers).
ARRATIA, G. & L. HUAQUÍN (1995): Morphology of the lateral line system and of the skin of diplomystid and certain primitive loricarioid catfishes and systematics and ecological considerations. – Bonner zool. Monogr. **36**: 1–110.
ARRATIA, G. & SCHULTZE, H.-P. (1992): Reevaluation of the caudal skeleton of certain actinopterygian fishes. III. Salmonidae. Homologization of caudal skeletal structures. – J. Morphol. **214**: 1–63.
ARRATIA, G., SCHULTZE, H.-P. & CASCIOTTA, J. (2001): Vertebral column and associates elements in dipnoans and comparison with other fishes. Development and homology. – J. Morphol. **250**(2): 101–172.
BRITZ, R. & CONWAY, K. W. (2009): Osteology of *Paedocypris*, a miniature and highly developmentally truncated fish (Teleostei: Ostariophysi: Cyprinidae). – J. Morphol. **270**(4): 389–412.
BRITZ, R., CONWAY, K. W. & RÜBER. L. (2009): Spectacular morphological novelty in a miniature cyprinid fish, *Danionella dracula* n. sp. – Proc. R. Soc. London B **276**(1665): 2179–2186.
BRITZ, R. & MORITZ, T. (2007): Reinvestigation of the osteology of the miniature African freshwater fishes *Cromeria* and *Grasseichthys* (Teleostei, Gonorynchiformes, Kneriidae), with comments on kneriid relationships. – Mit.. Mus. Nat.kd. Berl., Zool. Reihe **83**: 3–42.
CORNEN, G., BANDET, Y. GIRESSE, P. & MALEY, J. (1992): The nature and chronostratigraphy of Quaternary pyroclastic accumulations from Lake Barombi Mbo (West-Cameroon). – J. Volcanol. Geotherm. Res. **51**: 357–374.
DAVIS, G. L. (1977): The ages and uranium contents of zircon from kimberlites and associated rocks. – Carnegie Inst. Washington, Yearbk. **76**: 631–635.
DAVIS, S. P. & MARTILL, D. M. (1999): The gonorynchiform fish *Dastilbe* from the Lower Cretaceous of Brazil. – Palaeontology **42**: 715–740.
DAVIS, M. P. & FIELITZ, C. (2010): (2009): Estimating divergence times of lizardfishes and their allies (Euteleostei: Aulopiformes) and the timing of deep-sea adaptations. – Mol. Phyl. Evol. **53**(3): 1194–1208.
DRUMMOND, A. J. & RAMBAUT, A. (2007): BEAST: Bayesian evolutionary analysis by sampling trees. – BMC Evol. Biol. **7**: 214.
EGGE, J. J. D. & SIMONS, A. M. (2009): Molecules, morphology, missing data and the phylogenetic position of a recently extinct madtom catfish (Actinopterygii: Ictaluridae). – Zool. Jour. Linn. Soc. **155**: 60–75.
DIETZE, K. (2007): Redescription of *Dastilbe crandalli* (Chanidae, Euteleostei) from the Early Cretaceous Crato Formation of north-eastern Brazil. – J. Vert. Paleontol. **27**: 8–16.
FARA, E., GAYET, M. & TAVERNE, L. (2007): Les Gonorynchiformes fossiles: distribution et diversité. – Cybium **31**(2): 125–132.
FARA, E., GAYEY, M. & TAVERNE, L. (2010). The fossil record of Gonorynchiformes. – In: GRANDE, T., POYATO-ARIZA, F. J. & DIOGO, R. (eds.): Gonorynchiformes and Ostariophysan Relationships. A Comprehensive Review: 173–226; Enfield, NH (Science Publishers).
FELSENSTEIN, J. (1985): Confidence limits on phylogenies: an approach using the bootstrap. – Evol. **39**: 783–791.
FINK, S. V. & FINK, W.L. (1996): Interrelationships of ostariophysan fishes. – In: STIASSNY, M. L. J., PARENTI, R. L. & JOHNSON, G. D. (eds.): Interrelationships of Fishes: 209–249; San Diego (Academic Press).
GIRESSE, P., MALEY, J. & KELTS, K. (1991): Sedimentation and palaeoenvironment in crater lake Barombi Mbo, Cameroon, during the last 25,000 years. – Sediment. Geol. **71**: 151–175.
GRANDE, T. (1994): Phylogeny and paedomorphosis in an African family of freshwater fishes (Gonorynchiformes). – Fieldiana **78**: 1–20.

GRANDE, T. & ARRATIA, G. (2010): Morphological analysis of the gonorynchiform postcranial skeleton. – In: GRANDE, T., POYATO-ARIZA, F. J. & DIOGO, R. (eds.). Gonorynchiformes and Ostariophysan Relationships. A Comprehensive Review: 38–70: Enfield, NH (Science Publishers).
GRANDE, T. & POYATO-ARIZA, F. J. (1999): Phylogenetic relationships of fossil and Recent gonorynchiform fishes (Teleostei: Ostariophysi). – Zool. J. linn. Soc. **125**: 197–238.
– (2010): Reassessment and comparative morphology of the gonorynchiform head skeleton. – In: GRANDE, T., POYATO-ARIZA, F. J. & DIOGO, R. (eds.). Gonorynchiformes and Ostariophysan Relationships. A Comprehensive Review: 1–38; Enfield, NH (Science Publishers)
GRANDE, T. & YOUNG, B. (1997): Morphological development of the opercular apparatus in *Kneria wittei* (Ostariophysi: Gonorynchiformes) with comments on its possible function. – Acta Zool. (Stockholm) **78** (2): 145–162.
GREENWOOD, P. H. (1960): Fossil denticipitid fishes from East Africa. – Bull. Brit. Mus. (Natur. Hist.), Geol. **5**: 1–11.
– (1974): Review of Cenozoic freshwater fish faunas in Africa. – Annals Geol. Surv. Egypt **4**: 211–232.
GREENWOOD, P. H. & PATTERSON, C. (1967): A fossil osteoglossoid fish from Tanzania (E. Africa). – Zool. J. Linn. Soc. **47**: 211–223.
GUNNELL, G. F., JACOBS, B. F., HERENDEEN, P. S., HEAD, J. J., KOWALSKI, E., MSUYA, C. P., MIZAMBWA, F. A., HARRISON, T., HABERSETZER, J. & STORCH, G. (2003): Oldest placental mammal from Sub-Saharan Africa: Eocene microbat from Tanzania – evidence for early evolution of sophisticated echolocation: – Palaeontologia Electronica **5** (2): 1–10 (http://palaeo-electronica.org/2002_2/africa/main.htm).
HAGGERTY, S. E., RABER, E. & NAESER, C. W. (1983): Fission track dating of kimberlitic zircons. – Earth and Planetary Science Letters **63**: 41–50.
HARRISON, T., MSUYA, P., MURRAY, A. M., JACOBS, B. F., BÁEZ, A. M., MUNDIL, R. & LUDWIG, K. R. (2001): Paleontological investigations at the Eocene locality of Mahenge in North-Central Tanzania, East Africa. – In: GUNNEL, G. F. (ed.): Unusual Occurrences and Rarely Sampled Habitats: 39–74; New York (Kluwer Academic/Plenum Publishers).
HERENDEEN, P. S. & JACOBS, B. F. (2000): Fossil legumes from the middle Eocene (46.0 Ma) Mahenge flora of Singida, Tanzania. – Amer. J. Botany **87** (9): 1358–1366.
ISHIGURO, N. B., MIYA, M. & NISHIDA, M. (2003): Basal actinopterygian relationships: a mitogenomic perspective of the phylogeny of the "ancient fish". – Mol. Phyl. Evol. **27**: 476–488.
KAISER, T. M., ANSORGE, J., ARRATIA, G., BULLWINKEL, V., GUNNELL, G., HERENDEEN, P. S., JACOBS, B., MINGRAM, J., MSUYA, C., MUSOLF, A., NAUMANN, R., SCHULZ, E. & V. WILDE, V. (2006): The maar lake of Mahenge (Tanzania) – unique evidence of Eocene terrestrial environments in sub-Sahara Africa. – Z. Deut. Gesells. Geowissenschaf. **157** (3): 99–120.
KATOH T. (2008): Recent developments in the MAFFT multiple sequence alignment program. – Briefings in Bioinformatics **9**: 286–298.
LAVOUÉ, S., MIYA, M., SAITH, K., ISHIGURO, N. B., & NISHIDA, M. (2005): Molecular systematics of the gonorynchiform fishes (Teleostei) based on whole mitogenome sequences: implications for higher-level relationships within the Otocephala. – Mol. Phil. Evol. **37**: 165–177.
LAVOUÉ, S., MIYA, M., POULSEN, J. Y., MOLLER, P. R., & NISHIDA, M. (2008): Monophyly, phylogenetic position and inter-familial relationships of the Alepocephaliformes (Teleostei) based on whole mitogenome sequences. – Mol. Phyl. Evol. **47** (3): 1111–1121.
LAVOUÉ, S., MIYA, M., MORITZ, T., & NISHIDA, M. (2012): A molecular timescale for the evolution of the African freshwater fish family Kneriidae (Teleostei: Gonorynchiformes). – Ichthyol. Res. **59**: 104–112.
LENGLET. G. (1974): Contribution á l'étude ostéologique des Kneriidae. – Ann. Soc. Roy. Zool. Belgique 104: 51–103.
LEWIS, P. (2001): A likelihood approach to estimating phylogeny from discrete morphological character data, – Syst. Biol. **50** (6): 913–925.
LORENZ, V. (1973): On the formation of maars. – Bull. Volcanol. **37**: 183–204.
MABEE, P., GREY, E., ARRATIA, G., BOGUTSKAYA, N., BORON, A., COBURN, M., CONWAY, K., HE, S., NASEKA, A., RIOS, N., SIMONS, A., SZLACHCIAK, J. & WANG, Z. (2011): Gill arch and hyoid arch diversity and cypriniform phylogeny: Distributed integration of morphology and Web-based tools. – Zootaxa **2877**: 1–40.
MANNARD, G. W. (1962): The Geology of the Singida Kimberlite Pipes, Tanganyika. – Ph.D. Thesis, McGill University, Montreal, 348 pp.
MONOD, T. (1968): Le complexe urophore des poisons téléostéens. – Mem. Inst. Fond. Afrique Noire **81**: 705 pp.
MÜLLER, J. (1845): Über den Bau und die Grenzen der Ganoiden, und über das natürliche System der Fische. – Abh. Kgl. Akad. Wiss. Berlin **1845** (for 1844): 117–216.
MUNSELL, A. H. (1975): Soil Color Charts. – Baltimore: Munsell Color, Macbeth.
MURRAY, A. M. (2000a): The Paleozoic and Early Cenozoic fishes of Africa. – Fish and Fisheries **1**: 111–145.
– (2000b): Eocene cichlid fishes from Tanzania, East Africa. – J. Vert. Paleontol. **20** (4): 651–664.
– (2003a): A new species of catfish (Claroteidae, *Chrysichthys*) from an Eocene crater lake in East Africa. – Canad. J. Earth Sci. **40** (7): 983–993.

– (2003b): A new characiform fish (Teleostei: Ostariophysi) from the Eocene of Tanzania. ñ Canad. J. Earth Sci. **40** (4): 473–481.
MURRAY, A. M. & WILSON, M. V. H. 2005. Description of a new Eocene osteoglossid fish and additional information on *Singida jacksonoides* Greenwood and Patterson 1967 (Osteoglossomorpha), with an assessment of their phylogenetic relationships. – Zool. J. Linn. Soc. **144**: 213–228.
NAESER, C. W. & MCCALLUM, M. E. (1977): Fission-track dating of kimberlitic zircons. – Ext. Abstr., 2nd Int. Kimberlite Conf., American Geophysical Union (Washington, D.C.).
NAKATANI, M., MIYA, M., MABUCHI, K., SAITOH, K., & NISHIDA, M. (2011): Evolutionary history of Otophysi (Teleostei), a major clade of the modern freshwater fishes: Pangaean origin and Mesozoic radiation. – BMC Evol. Biol. **11**: 177.
NELSON, J. S. (2006): Fishes of the World. 4th ed., xix + 601 pp., Hoboken, NJ (John Wiley and Sons, Inc).
PATTERSON, C. (1993): Osteichthyes: Teleostei. – In: BENTON, M. J. (ed.): The fossil Record **2**: 621–656; London (Chapman & Hall).
PATTERSON, C. & JOHNSON, G. D. (1995): The intermuscular bones and ligaments of teleostean fishes. – Smithson. – Contrib. Zool. **559**: 1–85.
POLL, M. (1974): Kneriidae. – In: DAGET, J., GOSSE, J.-P. & THYS VAN DEN AUDENAERDE, D. F. E. (eds.): Check-list of the freshwater fishes of Africa (CLOFFA). ORSTOM, Paris and MRAC, Tervuren. Vol. **1**: 129–133.
POSADA, D. (2008): jModelTest: Phylogenetic Model Averaging. – Mol. Biol. Evol. **25**: 1253–1256.
POYATO-ARIZA, F. J. (1996): A revision of the ostariophysan fish family Chanidae, with special reference to the Mesozoic forms. – Paleo Ichthyologica **6**: 1–52.
POYATO-ARIZA, F. J., GRANDE, T. & DIOGO, R. (2010a): General overview of fossil and Recent Gonorynchiformes (Teleostei, Ostariophysi). – In: NELSON, J. S., SCHULTZE, H.-P. & WILSON, M. V. H. (2010b): Origin and Phylogenetic Interrelationships of Teleosts. Honoring Gloria Arratia: 269–293; München (Pfeil).
– (2010b): Gonorynchiform interrelationships: Historic overview, analysis, and revised systematics of the group. – In: GRANDE, T., POYATO-ARIZA, F. J. & DIOGO, R. (eds.): Gonorynchiformes and Ostariophysan Relationships. A Comprehensive Review: 227–337; Enfield, NH (Science Publishers).
RAMBAUT, A. & DRUMMOND, A. J. (2007): Tracer v1.4, Available from http://beast.bio.ed.ac.uk/Tracer
RAYNER, R. J. (1987): March flies from an African Cretaceous springtime. – Lethaia **20**: 123–127.
RAYNER, R. J. & MCKAY, I. J. (1986): The treasure chest of the Orapa diamond mine, Botswana. – Notes and Records **18**: 55–61.
ROSEN, D. E. & GREENWWOD, P. H. (1970): Origin of the Weberian apparatus and the relationships of the ostariophysan fishes. – American Museum Novitates **2428**: 1–25.
SAITOH, K., MIYA, M., INOUE, J. G., ISHIGURO, N. B. & NISHIDA, M. (2003): Mitochondrial genomics of ostariophysan fishes: perspectives on phylogeny and biogeography. – J. Mol. Evol. **56**: 464–472.
SAITOH, K., SADO, T., DOOSY, M. H., BART, H. L., INOUE, J. G., NISHIDAE, M., MAYDEN, R. L. & MIYA, M. (2011): Evidence from mitochondrial genomics supports the lower Mesozoic of South Asia as the time and place of basal divergence of cypriniform fishes (Actinopterygii: Ostariophysi). – Zool. Jour. Linn. Soc. **161**: 633–662.
SCHULTZE, H.-P. 2008. Nomenclature and homologization of cranial bones in actinopterygians. – In: ARRATIA, G., SCHULTZE, H.-P. & WILSON, M. V. H. (eds.): Mesozoic Fishes 4 – Homology and Phylogeny: 23–48; München (Pfeil).
SCHULTZE, H.-P. & ARRATIA, G. 1989. The composition of the caudal skeleton of teleosts (Actinopterygii, Osteichthyes). – Zool. J. Linn. Soc., London **97**: 89–231.
SCHULTZE, H.-P. & ARRATIA, G. (this volume): The caudal skeleton of basal teleosts, its conventions, and some of its major evolutionary novelties in a temporal dimension. – In: ARRATIA, G., SCHULTZE, H.-P. & WILSON, M. V. H. (eds.): Mesozoic Fishes 5 – Global Diversity and Evolution: 187–246; München (Pfeil).
SMITH, R. M. H. (1986): Sedimentation and palaeoenvironments of Late Cretaceous crater-lake deposits in Bushmanland, South Africa. – Sedimentology **33**: 369–386.
SWOFFORD, D. L. (2000): PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods). Computer Software Manual. – Sunderland, MA (Sinauer Associates).
WEITZMAN, S. H & VARI, R. P. (1988): Miniaturization in South American freshwater fishes; an overview and discussion. – Proc. Biol. Soc. Washington **101**: 444–465.
WENZ, S. (1984): *Rubiesichthys gregalis* n. g., n. sp., Pisces Gonorhynchiformes, du Crétace inférieur du Montsech (Province de Lérida, Espagne). – Bull. Mus. Natn. Hist. Natur. 4e sér., 6, sect. C (3): 275–285.
WILEY, E. O. (2008): Homology, identity and transformation. – In: ARRATIA, G., SCHULTZE, H.-P. & WILSON, M. V. H. (eds.): Mesozoic Fishes 4 – Homology and Phylogeny: 9–22; München (Pfeil).
ZWICKL, D. (2006): Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. – 125 pp. Unpublished Ph.D. thesis, University of Texas at Austin.

Appendix 1

Abbreviated list of 128 characters reproduced and modified herein from the investigation of POYATO-ARIZA et al. (2010b). Characters in parentheses refer to the character number in POYATO-ARIZA et al. (2010b) where they differ from this study.

1. Orbitosphenoid: present [0]; absent [1].
2. Basisphenoid: present [0]; absent [1].
3. Pterosphenoids: well developed and articulating with each other [0]; slightly reduced, not articulating anteroventrally but approaching each other anterodorsally [1]; greatly reduced and broadly separated both anteroventrally and anterodorsally [2].
4. Posterolateral expansion of exoccipitals: absent [0]; present [1].
5. Exoccipitals: posteriorly smooth with no projection above basiocipital [0]; with posterior concave-convex border and projection above basioccipital [1].
6. Cephalic ribs: absent [0]; present and all articulating with exoccipitals [1]; present and articulating with both exoccipitals and basioccipital [2].
7. Brush-like cranial intermuscular bones (sensu PATTERSON & JOHNSON 1995): absent [0]; present [1].
8. Nasal bone: small but flat [0]; just a tubular ossification around canal [1]; absent as independent ossification [2].
9. Frontals: wide all through most of their length, narrowing anteriorly to form triangular anterior border [0]; elongate and narrow except in postorbital region [1]; wide, anteriorly shortened, anterior border roughly straight [2]; roughly rectangular in outline, narrow throughout length [3].
10. Interfrontal fontanelle: absent [0]; present [1].
11. Frontal bones: paired in adult [0]; co-ossified, with no median suture [1].
12. Foramen for olfactory nerve in frontal bones: absent [0]; present [1].
13. Relative position of parietals: medioparietal (in full contact with each other along midline) [0]; mesoparietal [1]; lateroparietal (completely separated from each other by supraoccipital) [2].
14. Parietal portion of supraorbital canal: absent [0]; present [1].
15. Parietals: large [0]; reduced but flat and blade-like in shape [1]; reduced to canal-bearing bones [2]; absent as independent ossifications [3].
16. Supraoccipital crest: small, short in lateral view or absent [0]; long and enlarged, projecting above occipital region and first vertebrae, forming vertical, posteriorly deeply pectinated blade [1].
17. Foramen magnum: dorsally bounded by exoccipitals [0]; enlarged and dorsally bounded by supraoccipital [1]
18. Mesethmoid: wide and short [0]; long and slender, with anterior elongate lateral extensions [1]; large, with broad posterolateral wing-like expansions [2]; elongated and thin [3].
19. Wings (extensions) on lateral ethmoids: absent [0]; present [1].
20. Teeth in premaxilla, maxilla, and dentary: present [0]; absent [1].
21. Premaxilla: consisting of one solid portion [0]; premaxilla consisting of two distinct portions, with shorter, non-osseous element lying ventral to much longer osseous portion, which in turn articulates with maxilla [1].
22. Premaxillary "gingival teeth": absent [0]; present [1].
23. Premaxilla: small, flat and roughly triangular [0]; large, very broad, concave-convex, with long oral process [1]; narrow and elongated, its length more than one half length of maxilla [2].
24. Premaxillary ascending process: present [0]; absent [1].
25. Dorsal and ventral borders of maxillary articular process: straight or slightly curved [0]; very curved, almost describing an angle [1].
26. Maxillary process for articulation with autopalatine: absent [0]; present [1].
27. Posterior region of maxilla: slightly and progressively expanded to form thin blade, with roughly straight posterior border [0]; very enlarged, swollen to bulbous outline, with curved posterior border [1].
28. Supramaxilla(e): present [0]; absent [1].
29. Notch between dentary and angulo-articular bones: absent [0]; present [1].
30 (28). Articulation between dentary and angulo-articular: strong, dentary not V-shaped posteriorly [0]; loose, with posteriorly V-shaped dentary [1].
31. Notch in antero-dorsal border of dentary: absent [0]; present [1].
32. Mandibular sensory canal: present [0]; absent [1].
33. Inferior and superior enlarged retroarticular processeses of mandible: both absent [0]; inferior retroarticular process present, superior retroarticular process absent [1]; both inferior and superior retroarticular processes present [2].
34. Quadrate with: posterior margin smooth [0]; elongated forked posterior process [1].
35. Quadrate-mandibular articulation: below or posterior to orbit, no elongation or displacement of quadrate [0];

anterior to orbit, quadrate displaced but not elongate [1]; anterior to orbit, with elongation of body of quadrate instead of displacement [2].
36. Symplectic: elongated in shape but relatively short [0]; very long, about twice length that of ingroup [1]; absent as independent ossification [2].
37. Symplectic and quadrate: articulating directly with each other [0]; separated through cartilage [1]; no contact due to absence of symplectic [2].
38. Metapterygoid: large, broad, and in contact with quadrate and symplectic through cartilage [0]; reduced to thin rod [1].
39. Dermopalatine: present [0], absent [1].
40. A patch of about twenty conical teeth on endopterygoids and basibranchial 2: absent [0]; present [1].
41. Ectopterygoids: well developed, ectopterygoid overlapping with ventral surface of the autopalatine by at least 50 % [0]; well developed, with three branches in lateral view, reduced but direct contact with autopalatine [1]; reduced, articulating with ventral surface of autopalatine by at most 10 % through cartilage, resulting in loosely articulated suspensorium [2]; absent as distinct ossifications [3].
42. Teeth on vomer and parasphenoid: absent [0]; present [1].
43. Anterior portion of vomer: horizontal [0]; anteroventrally inclined, nearly vertical [1]; dorsally curved [2].
44. Spatial relationship between vomer and mesethmoid anteriorly: vomer and mesethmoid ending at about same anterior level [0]; mesethmoid extending anteriorly beyond level of anterior margin of vomer [1]; vomer extending anteriorly beyond level of anterior margin of mesethmoid [2].
45. Articular head of hyomandibular bone: double, with both articular surfaces placed on dorsal border of main body of bone [0]; double, with anterior articular surface forming separate head from posterior articular surface [1].
46. Metapterygoid process of hyomandibular bone: absent [0], present, anterior [1]; present, ventral [2].
47. Ossified interhyal: present [0]; absent as independent ossification [1].
48. Teeth on fifth ceratobranchial: present [0]; absent [1].
49. First basibranchial in adult specimens: ossified [0]; unossified [1].
50. Fifth basibranchial in adult specimens: cartilaginous [0]; ossified [1].
51. First pharyngobranchial in adult specimens: ossified [0]; unossified [1].
52. Size of opercular bone: normal, about one quater of head length [0]; expanded, at least one third of head length [1].
53. Shape of opercular bone in lateral view: rounded/oval [0]; triangular [1]; squarish or square [2].
54. Opercular spines: absent [0]; present [1].
55. Opercular apparatus on external surface of operculum: absent [0]; present [1].
56. Opercular borders: free from side of head [0]; partially or almost completely connected to side of head with skin [1].
57. Angle formed by preopercular limbs: obtuse [0]; approximately straight [1]; acute [2].
58. Posterodorsal limb of preopercular bone: well developed [0]; reduced, correlated with expansion of anteroventral limb that meets its fellow along ventral midline [1].
59. Ridge on anteroventral limb of preopercular bone: absent [0]; present [1].
60. Preopercular expansion: absent, preopercular not enlarged [0]; present, restricted to posteroventral corner [1]; present in posteroventral corner and part of posterodorsal limb [2]; present in anteroventral limb only [3].
61. Supraopercular bone: absent [0]; present as relatively large, flat bone [1]; present as tubular ossification(s) [2].
62. Spine on posterior border of subopercular bone: absent [0]; present [1].
63. Major axis of subopercular bone in lateral view: inclined [0]; subhorizontal [1]; subvertical [2].
64. Subopercular clefts: absent [0]; present [1].
65. Interopercular bone: relatively broad and positioned medioventral to preopercular bone [0]; reduced to long thin spine and positioned mediodorsal to preopercular bone [1]; reduced to long thin spine and positioned lateroventral to preopercular bone [2].
66. Spine on posterior border of interopercular bone: absent [0]; present [1].
67. Posterodorsal ascending process of interopercular bone: absent [0]; present [1].
68. Number of infraorbitals: five or more [0]; four [1]; three or fewer [2].
69. Infraorbital bones not including lacrimal: well developed [0]; reduced to small, tubular ossifications [1]; hypertrophied [2].
70. Lacrimal: flat and comparable in length to subsequent infraorbitals [0]; tube-like and extremely long, without keel [1]; flat, long, and large, with keel near lower edge [2]; long and large, with spines and crests [3].
71. Supraorbital: present [0]; absent [1].
72. Two anteriormost vertebrae: as long as posterior ones [0]; shorter than posterior ones [1].
73 (74). Autogenous neural arch anterior to arch of first vertebra: present [0]; absent [1].
74 (75). Neural arch of first vertebra and exoccipitals: separate [0]; in contact [1].
75 (76). Neural arch of first vertebra and supraoccipital: separated [0]; in contact [1].

76 (77). Spine on the neural arch of first vertebra: present, well developed [0]; present but reduced [1]; absent [2].
77 (78). Anterior neural arches: no contact with adjoining arches [0]; contacting adjoining arches with no overlapping [1]; overlapping contact with adjoining arches [2].
78 (79). Unmodified neural arches anterior to dorsal fin in adults: fused to centra [0]; autogenous, at least laterally [1].
79 (80). Neural arches of vertebrae posterior to dorsal fin in adults: fused to centrum [0]; autogenous, at least laterally [1].
80 (81). First two anterior parapophyses: autogenous [0]; fused to centra [1].
81 (82). Rib on third vertebral centrum: similar to posterior ones [0]; widened and shortened [1]; modified into Weberian apparatus [2].
82 (83). Paired intermuscular bones consisting of three series: epipleurals, epicentrals, and epineurals: absent [0]; present [1].
83 (84). Anterior (first six) epicentral bones: unmodified, no differences in size from others [0]; highly modified, much larger than posterior ones [1]; epicentrals in anterior vertebrae absent [2].
84 (85). Size and arrangement of anterior supraneurals (whatever the number present): large, separate from each other if more than one supraneural present [0]; larger, in contact with neighbours if more than one supraneural present [1]; supraneurals greatly reduced in size [2].
85 (86). Posterior process on posterior border of first supraneural: absent [0]; present [1].
86 (87). Number of supraneurals: several supraneurals in a long series [0]; two or fewer supraneurals [1].
87 (88). Postcleithra: present [0]; absent [1].
88 (89). Lateral line and supracleithrum: supracleithrum pierced through dorsal region [0]; supracleithrum pierced throughout its length [1]; supracleithrum not pierced by lateral line [2].
89 (90). Fleshy lobe of paired fins: absent [0]; present [1].
90 (91). Caudal fin morphology: elongated, posteriorly forked [0]; higher than long, slightly incurved posteriorly [1]; crescent-shaped [2].
91 (92). Fringing fulcra in dorsal lobe of caudal fin: present [0]; absent [1].
92 (93). Caudal scutes: absent [0]; present [1].
93 (94). Ural centra, preural centrum one, and uroneural one: autogenous [0]; fused [1]; fused except for ural centrum two, which is autogenous [2].
94 (95). Neural arch and spine of preural centrum one: both well developed, spine about half as long as preceding ones [0]; arch complete and closed, spine rudimentary [1]; arch open, no spine [2].
95 (96). Uroneurals: arranged in a linear series [0]; arranged in a double series [1].
96 (97). Number of uroneurals: three [0]; two [1]; one [2].
97 (98). Anterior extent of first uroneural: to anterior end of first preural [0]; to anterior end of second preural [1]; to anterior end of third preural [2]; uroneural fused to caudal fin complex [3].
98 (99). Uroneural two and second ural centrum: in contact [0]; separated [1]; uroneural two absent [2].
99 (100). Parahypural and preural centrum 1: independent in adults [0]; fused only in large adults [1]; fused since early ontogenetic stages [2].
100 (101). Reduction in the number of hypurals: six [0]; fewer than six [1].
101 (102). Hypurals 1 and 2: independent [0]; partially fused to each other [1]; totally fused to each other [2].
102 (103). Hypural 1 and terminal centrum: articulating [0]; separated by a hiatus [1]; fused [2].
103 (104). Hypural 2 and terminal centrum: fused [0]; articulating [1].
104 (105). Hypural 5: smaller in size than hypurals 4 and 3 [0]; larger than hypurals 4 and 3 due to its distal expansion [1].
105 (107). Haemal arch and preural centrum 2: fused [0]; independent [1].
106 (108). Postero-lateral process of caudal endoskeleton: absent [0]; present [1].
107 (109). Scales on body: present [0]; absent [1].
108 (110). Type of scales: cycloid [0]; modified ctenoid [1].
109 (111). Lateral line: not extending to posterior margin of hypurals [0]; extending to posterior margin of hypurals [1].
110 (112). Intermandibularis: mainly attaching on dentary [0]; exclusively attaching on angulo-articular [1].
111 (113). Protractor hyoidei: not inserting on coronoid process [0]; inserting on coronoid process [1].
112 (114). Hyohyoideus inferioris of both sides: mostly overlapping each other [0]; mostly mixing mesially with each other [1].
113 (115). Hyohyoideus abductor: not attaching on pectoral girdle [0]; with significant part of its fibers attaching on pectoral girdle [1].
114 (116). Adductor profundus: not subdivided into different sections [0]; subdivided into different sections [1].
115 (117). Attachment of adductor profundus: on first pectoral ray only [0]; on first and second pectoral rays [1].

116 (118). Most lateral bundles of adductor mandibulae: inserting on mandible and/or primordial ligament [0]; attaching also, or even exclusively, on other bones such as maxilla or premaxilla [1].
117 (119). Position of adductor mandibulae A1-OST: mostly horizontal [0]; with peculiar anterior portion almost perpendicular to its posterior portion [1].
118 (120). Section A2 of adductor mandibulae: present [0]; absent [1].
119 (121). Several small tendons branching off from adductor mandibulae A2: absent [0]; present [1].
120 (122). Peculiar adductor mandibulae A1-OST-M: absent [0]; present [1].
121 (123). Direct insertion of adductor mandibulae A2 far anteriorly on anteromesial surface of dentary: absent [0], present [1].
122 (124). Dilatator operculi: mainly mesial and/or dorsal to adductor mandibulae A2 [0]; markedly lateral to A2 [1].
123 (125). Peculiar tendon of adductor mandibulae A2 running perpendicular to main body of this section and connecting it to anteroventral surface of quadrate: absent [0]; present [1].
124 (126). Distinct section A3 of adductor mandibulae: absent [0]; present [1].
125 (127). Adductor mandibulae Aω: present [0]; absent [1].
126 (128). Adductor arcus palatini: not inserting on preopercle [0]; inserting also on preopercle [1].
127 (129). Levator arcus palatini: not divided [0]; divided into two well differentiated bundles [1].
128 (130). Origin of dilatator operculi: on ventrolateral surface of neurocranium [0]; on dorsal margin of cranial roof [1].

Appendix 2

The morphological data matrix for 128 characters that have been modified herein from the investigation of POYATO-ARIZA et al. (2010b). Polymorphisms are indicated by a cell with more than one state. State N represents the character is not applicable. Characters in italics refer to the character number in POYATO-ARIZA et al. (2010b) where they differ from this study.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
†*Diplomystus*	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brycon	0	1	0	0	0	0	0	1	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Opsariichthys	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
†*Aethalionopsis*	?	?	?	?	?	?	?	0	0	0	?	2	1	1	0	?	0	?	1	0	?	1	?	0	1	1	1	0	0	?	0	0	0	1
Chanos	1	1	1	1	2	1	1	0	0	0	0	2	1	2	1	0	2	0	1	0	0	1	1	0	1	1	1	0	0	1	0	0	0	1
†*Charitopsis*	1	1	?	?	?	?	?	1	0	0	?	2	?	1	?	?	0	0	1	0	?	0	1	0	1	0	1	1	0	0	?	?	0	0
†*Charitosomus*	1	1	2	0	?	1	1	?	1	0	0	0	2	0	1	0	0	0	0	1	0	?	0	1	0	1	0	1	1	0	0	?	2	0	0
Cromeria	1	1	2	0	0	1	0	2	0	1	0	0	?	?	3	0	1	1	1	1	0	0	0	1	0	0	0	1	1	0	0	1	0	1	0
†*Dastilbe*	1	1	1	0	0	?	?	?	0	0	0	0	2	0	1	1	0	0	?	1	0	?	1	1	0	1	1	1	0	0	1	0	0	0	1
Gonorynchus	1	1	2	0	0	1	1	1	1	0	1	1	2	0	1	0	0	0	0	1	1	1	0	1	0	0	0	1	1	1	0	1	0	0	0
†*Gordichthys*	1	1	?	0	?	?	?	0	0	0	0	0	1	0	1	0	?	0	?	1	0	?	1	1	1	0	1	1	0	0	1	0	0	0	1
Grasseichthys	1	1	2	0	0	0	0	2	0	1	0	0	?	?	3	0	1	1	1	1	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0
†*Hakeliosomus*	1	?	?	0	0	?	?	?	1	0	0	0	2	0	1	0	?	0	0	1	?	?	0	1	0	1	0	1	0	0	0	?	1	0	0
†*Judeichthys*	1	1	?	0	?	1	1	?	1	0	0	0	2	0	1	0	?	0	0	1	0	?	0	1	0	1	0	1	1	0	0	?	1	0	0
Kneria	1	1	2	0	0	1	0	0	0	0	0	0	N	N	3	0	1	1	1	1	0	0	0	1	0	1	0	1	1	0	0	1	0	0	0
†*Notogoneus*	1	?	2	0	0	1	1	?	1	0	0	0	2	0	1	0	0	0	0	1	?	?	0	1	0	?	0	1	1	1	0	?	0	0	0
†*Parachanos*	?	?	?	0	?	?	?	1	0	0	0	0	2	0	1	?	?	0	?	1	0	?	1	1	0	1	1	1	0	0	?	0	0	0	1
Parakneria	1	1	2	0	0	1	0	0	0	0	0	0	N	N	3	0	1	12	1	1	0	0	0	1	0	1	0	1	1	0	0	1	0	0	0
Phractolaemus	1	1	2	0	0	1	0	1	2	0	0	0	?	?	2	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	2
†*Ramallichthys*	1	1	?	0	0	1	1	?	1	0	0	0	2	0	1	0	?	0	0	1	0	?	0	1	0	1	0	1	1	0	0	?	1	0	0
†*Rubiesichthys*	1	1	?	0	?	?	?	0	0	0	0	0	2	0	1	0	?	0	?	1	0	?	1	1	1	0	1	1	0	0	1	0	0	0	1
†*Tharrhias*	1	1	1	0	1	?	0	1	0	0	0	0	2	0	1	1	0	2	?	1	0	?	1	1	0	1	1	1	0	0	1	0	0	0	1
†*Mahengichthys*	?	?	?	?	?	?	0	?	0	0	0	?	N	?	3	0	?	1	1	1	0	0	0	1	0	?	?	1	0	1	0	1	0	?	0

	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70
†*Diplomystus*	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brycon	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Opsariichthys	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
†*Aethalionopsis*	1	0	0	?	0	0	?	?	?	0	?	?	?	?	?	?	1	0	0	0	?	1	0	1	1	1	0	0	0	0	0	0	0	0	0
Chanos	1	1	0	1	0	0	0	0	2	0	1	1	1	0	0	0	1	0	0	0	0	1	0	0	2	1	0	1	0	0	0	0	1	0	0
†*Charitopsis*	?	?	0	?	1	2	0	0	1	?	0	?	?	?	?	?	0	1	1	0	?	0	0	0	0	0	1	0	0	0	0	0	1	1	?
†*Charitosomus*	0	0	0	1	1	2	0	0	1	1	0	?	?	?	?	?	0	1	0	0	?	0	0	0	0	0	1	0	0	0	0	0	1	1	0
Cromeria	2	2	0	1	0	3	0	01	02	1	2	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	1	12	1	0
†*Dastilbe*	1	0	0	1	0	0	?	?	?	0	1	?	?	?	?	?	1	0	0	0	?	1	0	1	0	1	0	1	0	0	0	0	?	0	0
Gonorynchus	0	0	1	1	1	2	0	0	1	1	0	0	1	1	0	1	0	1	0	0	1	0	0	0	0	2	0	0	0	0	0	0	2	1	2
†*Gordichthys*	1	0	0	1	0	0	1	?	?	0	1	?	?	?	?	?	1	0	0	0	?	2	0	0	1	1	0	0	0	0	0	0	?	0	0
Grasseichthys	1	0	N	1	0	3	0	0	2	1	2	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	1	12	1	0
†*Hakeliosomus*	0	0	0	1	1	2	0	0	2	1	0	0	?	?	?	?	0	1	0	0	?	0	0	0	0	0	0	0	0	0	0	0	1	1	0
†*Judeichthys*	?	0	0	1	1	2	0	0	2	1	?	?	?	?	?	?	0	1	0	0	?	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Kneria	0	0	0	1	0	2	0	1	2	1	2	1	1	1	1	1	0	2	0	1	1	0	0	0	0	2	0	0	0	0	0	1	1	1	0
†*Notogoneus*	?	0	?	?	1	2	0	0	1	1	0	?	?	?	?	?	0	1	0	0	?	0	0	0	0	0	0	0	1	0	0	0	1	1	?
†*Parachanos*	1	0	0	?	0	0	?	?	?	0	1	?	?	?	?	?	1	0	0	0	?	1	0	1	1	1	0	1	0	0	0	0	?	0	0
Parakneria	0	0	0	1	0	2	0	1	2	1	2	1	1	1	1	1	0	2	0	0	1	1	0	0	0	2	0	0	0	0	0	1	1	1	1
Phractolaemus	2	2	0	1	0	2	0	2	2	0	2	0	1	1	0	1	0	0	0	0	1	0	1	0	3	1	0	0	0	1	0	1	1	2	0
†*Ramallichthys*	?	0	0	1	1	2	0	0	2	1	?	?	?	?	?	?	0	1	0	0	?	0	0	0	0	0	0	0	0	0	0	0	1	1	0
†*Rubiesichthys*	1	0	0	1	0	0	?	?	?	0	1	?	?	?	?	?	1	0	0	0	?	2	0	0	1	1	0	0	0	0	0	0	?	0	0
†*Tharrhias*	1	1	0	1	0	0	0	0	2	0	1	?	1	?	?	?	1	0	0	0	?	1	0	1	2	1	0	1	0	0	0	0	1	0	0
†*Mahengichthys*	?	?	?	1	0	?	0	?	?	1	?	?	?	?	?	?	1	2	0	?	?	?	?	?	?	?	0	?	0	0	0	1	?	?	?

	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104
†*Diplomystus*	?	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0		0	1	0	0	0	0	0	?	0		0	0	0
Brycon	0	1	1	0	0	1	0	0	0	1		2	0	0	1	0	0	0	0	0		1	0	1	1	0	0	3	1	2		0	1	0
Opsariichthys	0	1	1	0	0	1	0	0	0	1		2	0	0	1	0	0	0	0	0		1	0	1	1	0	1	3	1	0		0	0	0
†*Aethalionopsis*	0	?	?	?	?	?	?	1	1	0		?	?	0	?	?	0	?	?	0		0	1	0	1	0	0	?	1	0		0	0	1
Chanos	0	1	1	1	0	1	0	1	0	0		1	1	0	0	0	0	1	0	0		1	1	1	1	0	1	3	1	1		0	1	1
†*Charitopsis*	1	1	?	?	?	2	2	?	0	?		1	1	0	?	?	?	1	?	0		0	1	0	?	?	?	?	?	1	?	?	?	?	?
†*Charitosomus*	0	1	1	1	?	2	2	?	0	?		1	1	0	1	0	0	1	0	0		0	1	0	1	1	0	1	3	1	2	1	1	2	0
Cromeria	0	1	1	1	1	1	1	1	0	0	1	1	1	0	N	0	1	1	0	0	0	1	0	1	2	0	2	3	?	0	1	0	1	1
†*Dastilbe*	0	1	1	?	0	1	0	1	0	0		1	1	0	0	0	0	0	0	0		0	0	0	1	0	1	1	0	0	0	0	0	1
Gonorynchus	1	1	1	1	0	1	1	0	0	1		1	1	0	1	0	0	1	0	1	0	1	0	1	1	0	2	3	2	2	1	1	2	0
†*Gordichthys*	0	1	?	?	?	1	0	1	0	?		1	?	0	0	1	0	0	1	0	1	1	0	0	1	0	1	1	0	0	0	0	0	1
Grasseichthys	0	1	1	1	1	1	1	0	0	1		1	0	0	0	0	1	1	0	0	0	1	0	1	1	0	2	3	?	0	1	0	2	1
†*Hakeliosomus*	0	1	1	?	?	2	2	2	?	0	?	1	1	0	1	0	0	1	?	0	0	1	0	1	1	0	1	3	1	2	1	0	2	0
†*Judeichthys*	0	1	1	?	?	2	2	?	0	?		1	1	0	1	0	0	1	0	0	0	1	0	1	1	0	1	3	?	2	1	?	2	0
Kneria	0	1	1	1	1	1	1	0	0	1		1	1	1	0	0	1	1	2	0	0	1	0	1	1	0	2	3	?	0	0	0	1	1
†*Notogoneus*	1	1	1	1	?	0	0	0	0	1		1	1	0	0	0	0	1	0	0	0	1	0	1	1	0	1	3	0	0	1	0	0	1
†*Parachanos*	0	?	1	?	?	?	?	1	0	?		1	?	0	?	?	0	0	0	0	0	1	?	0	1	0	1	2	0	0	0	0	0	1
Parakneria	0	1	1	1	1	1	1	0	0	1		1	1	0	0	0	1	1	2	0	0	1	0	1	12	0	2	3	?	0	0	0	1	1
Phractolaemus	0	1	1	1	0	1	1	0	0	1		1	1	0	1	0	1	1	0	0	2	1	0	1	2	0	2	3	?	0	1	0	1	0
†*Ramallichthys*	0	1	1	?	?	2	2	?	0	?		1	1	0	1	0	0	1	0	0	0	1	0	1	1	0	1	3	1	2	1	1	2	0
†*Rubiesichthys*	0	1	1	?	?	1	0	1	0	?		1	?	0	0	1	0	0	?	0	0	1	0	0	1	0	1	1	0	0	0	0	0	1
†*Tharrhias*	0	1	1	1	0	1	0	1	0	0		1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	1
†*Mahengichthys*	?	1	1	1	?	1	1	0	0	?		1	1	1	?	?	0	1	2	?	0	1	0	1	1	0	2	3	?	0	0	0	1	1

	104 105	105 107	106 108	107 109	108 110	109 111	110 112	111 113	112 114	113 115	114 116	115 117	116 118	117 119	118 120	119 121	120 122	121 123	122 124	123 125	124 126	125 127	126 128	127 129	128 130
†*Diplomystus*	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Brycon	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	1
Opsariichthys	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
†*Aethalionopsis*	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chanos	0	1	1	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
†*Charitopsis*	?	?	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†*Charitosomus*	0	1	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cromeria	0	0	0	1	?	0	0	0	1	0	1	1	1	0	0	0	1	0	0	1	0	1	0	0	0
†*Dastilbe*	0	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Gonorynchus	0	0	0	0	1	1	0	1	1	0	1	1	1	0	0	0	0	1	0	0	0	1	1	0	0
†*Gordichthys*	0	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Grasseichthys	0	0	0	1	?	0	0	0	1	0	1	1	1	0	1	?	?	?	?	?	0	1	0	0	0
†*Hakeliosomus*	0	0	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†*Judeichthys*	0	1	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kneria	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	1	0	0	0	0	1	0	0	1
†*Notogoneus*	0	1	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†*Parachanos*	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Parakneria	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	1	0	0	0	0	1	0	0	0
Phractolaemus	1	0	0	0	0	0	1	0	1	0	1	1	1	1	0	1	1	0	0	0	0	1	0	0	0
†*Ramallichthys*	0	1	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†*Rubiesichthys*	0	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†*Tharrhias*	0	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†*Mahengichthys*	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

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