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ALESTID (CHARACIFORMES: ALESTIDAE) FISHES FROM THE LATE OLIGOCENE NSUNGWE FORMATION, RUKWA RIFT BASIN, OF TANZANIA

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ABSTRACT—Alestidae is a clade of African characiform fishes including 19 extant genera and approximately 105 species that are known from Afro-Arabia, with records reported from the Eocene-Oligocene Jebel Qatrani Formation of Egypt, the Eocene Mahenge crater lake of Tanzania, and early Oligocene to Miocene sites on the Arabian Plate. Here we report the first record of alestid fishes from the late Oligocene Nsungwe Formation in the Rukwa Rift Basin of southwestern Tanzania. The Nsungwe alestid sample is composed of 92 teeth spanning a range of sizes and morphologies. Teeth are examined with regard to cusp number and organization, tooth position and replacement, and in the context of alestid jaw organization using modern, comparative representatives. Results suggest that at least two alestid taxa are represented in Nsungwe Formation localities. *Hydrocynus* teeth exhibit a single, conical cusp. Several of these specimens preserve a mesiodistally expanded crown and concave surface on the lingual aspect of the tooth. A second, unnamed taxon, with three morphological variants, is distinguished from *Hydrocynus* based on a multicuspid morphology of fully erupted teeth. The presence of these taxa in the late Oligocene of Africa below the equator provides key insights into the biogeography of the clade.

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INTRODUCTION

The teleost order Characiformes is a clade of about 1600 species of ostariophysan fishes that are found primarily in freshwater environments of Africa, and in South and Central America. Well-known extant characiforms include piranhas and tetras. Alestidae is a family of African characiforms commonly known as robber fish, composed of 19 extant genera with roughly 105 species, making it the most speciose African characiform family (Nelson, 2006; Eschmeyer and Fong, 2010). Although recent studies have consistently recovered a monophyletic Alestidae, the higher-level relationships of this family among Characiformes remain unclear (Dahdul, 2010). Debate also persists regarding whether this group is a trans-Atlantic clade (Arroyave and Stiassny, 2011; Oliveira et al., 2011). Today, alestids thrive in rivers and along coastal waters of western Africa, with representatives recovered from the fossil record of continental Africa as early as the Eocene (Dahdul, 2010).

Here we report the first record of alestid fishes from the late Oligocene Nsungwe Formation in the Rukwa Rift Basin of southwestern Tanzania (Fig. 1). Nsungwe Formation localities are radiometrically dated to around 25 Ma, and they have revealed a diverse vertebrate fauna including mammals, birds, crocodylians, lepidosaurs, anurans, and multiple clades of fishes, together with a number of novel invertebrate taxa (Stevens et al., 2005, 2006, 2009a, 2009b, 2013; Feldmann et al., 2007;

Roberts et al., 2010; McCartney et al., 2014; Blackburn et al., 2015). The specimens described herein were collected from localities sampling fluvial and shallow lacustrine paleoenvironments.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, U.S.A.; ANSP, Academy of Natural Sciences of Drexel University, Philadelphia; RRB, Rukwa Rift Basin Project, Ohio University, Athens, Ohio, U.S.A., and Tanzania Antiquities Division, Dar es Salaam, Tanzania.

MATERIALS AND METHODS

All fossil alestid specimens described herein were collected from the late Oligocene Nsungwe Formation in the Rukwa Rift Basin of southwestern Tanzania. Casts of the fossils are held at Ohio University and are available for study upon request; original fossils are the property of the Tanzania Antiquities Division. The fossils were mechanically prepared using a needle by S. Egberts. All comparative materials examined were previously cleared and stained skeletons stored in glycerol or alcohol. Teeth were magnified on a Nikon stereomicroscope bundled with Spot Advanced software (version 3.5.8) and photographed using a Spot Insight QE Color camera (model 4.2, image resolution 2048 by 2048) at different focal points, creating image stacks of four to nine pictures per specimen. A focused photomontage was then compiled from image stacks using Helicon Focus (version 5.3.4) in order to generate the figure plate. On each specimen, the following measurements were made using Spot Advanced: cusp height (the distance between the tooth base and the highest cusp tip, in mm) and tooth breadth (the mesiodistal tooth dimensions, in mm). Most Nsungwe alestid teeth are well preserved

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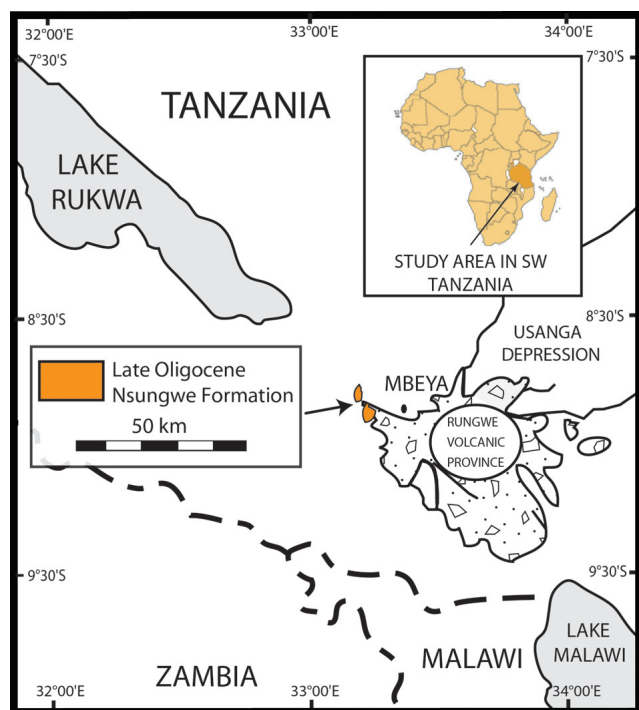


FIGURE 1. Map of the study area in southern Tanzania.

and present clean surfaces for measurement, although some exhibit discontinuities that precluded precise measurements. Representative teeth are illustrated in Figure 2, and additional specimen images are available on Morphobank.org, project no. 843.

Fossil specimens were represented by isolated teeth that were grouped for analysis based on number and arrangement of cusps. Teeth were assigned to taxon based on number and configuration of cusps, and tooth position in the jaw (i.e., dentary or premaxillary, inner or outer row, and mesial or distal within tooth row) was assessed based on tooth curvature, relative cusp height, and cusp arrangement, using comparisons with extant taxa (Appendix 1). Teeth bearing both labial and lingual cusps with ridges extending from one cusp to the next were considered inner premaxillary. Cusp number, tooth height, and tooth arrangement have previously been used in differentiation and description of alestids (Zanata and Vari, 2005; Stiassny and Mamonekene, 2007; Mirande, 2010). Although the majority of alestids exhibit three or more cusps on adult teeth, certain genera maintain a pattern of single cusps from early stages of life through maturity (Zanata and Vari, 2005). Smaller, unicuspid teeth may characterize fishes of diminutive body size (Zanata and Vari, 2005), but cusp pattern may also be indicative of age, species-level variation, or differences in feeding ecology.

SYSTEMATIC PALEONTOLOGY

CHARACIFORMES sensu Nelson, 2006
 ALESTIDAE sensu Murray and Stewart, 2002
HYDROCYNUS Cuvier, 1816
HYDROCYNUS sp.
 (Fig. 2A–C)

Referred Specimens—RRBP 10046B, 10084A, 11030, 11215, 11416, 12165.

Description—Specimens attributed to *Hydrocynus* are conical teeth that taper from the base to the apex of the crown,

producing a pointed and unicuspid tooth. Two specific morphs are noted. The first morph tapers with a linear slope, with equal narrowing on each side of the tooth in both labial and lingual views (Fig. 2A–B). These specimens have a slightly detectable tooth crown curvature, the convex labial surface more prominent than the concave lingual surface. These specimens measure approximately 1.5 mm in height and 0.75 mm across the widest surface. The second morph exhibits a more prominent tooth crown curvature (Fig. 2C) and may represent a mesially positioned tooth. As in the first form, these specimens exhibit an evenly sloping concave lingual tooth surface and convex labial tooth surface, yet teeth in the second group have a more defined lingual slope that begins approximately one-third of the way from the base/crown margin. Specimens of the second morphology are somewhat smaller than those in the first form, measuring approximately 1.0 mm in height and 0.5 mm across widest surface.

Two specimens, RRBP 10084A and 10046B (Fig. 2A), exhibit a constriction on the mesiodistal sides of the crown, causing the crown to overhang the tooth base. Specimens RRBP 11030, 11215, 11416, and 12165 do not exhibit a clean surface where the crown would have ankylosed to the jaw elements and therefore comments regarding the conclusive absence or presence of constriction at the base of the tooth cannot be made.

Remarks—These new specimens bear strong resemblance to teeth previously attributed to mature *Hydrocynus* (Murray et al., 2010; fig. 4C–D). Specifically, Nsungwe specimens of this conical, unicuspid morphotype demonstrate wide proximal crowns that are notched just above the distal portion of the base, contributing to a constriction below the crown. The presence of a crenulated base in Nsungwe teeth (Fig. 2C) indicates that despite its small size, the tooth was mature and was shed naturally (see Murray et al., 2010). The larger teeth (RRBP 10046B, 11416) presumably derive from more mature individuals in the sample and exhibit a notched base that is more prominent than the notched bases of the smaller teeth.

Nsungwe teeth attributed to *Hydrocynus* exhibit a unique labiolingual pattern of curvature that distinguishes them from other morphotypes preserved in the sample. Unicuspid teeth are attributed to the Alestid genera *Clupeocharax*, *Lepidarchus*, and *Hydrocynus* (Zanata and Vari, 2005). *Clupeocharax* and *Lepidarchus* have a unicuspid dentition throughout ontogeny, whereas the unicuspid nature is an ontogenetically secondary condition of *Hydrocynus* (Zanata and Vari, 2005). *Clupeocharax* and *Lepidarchus* are both monospecific genera, and the unicuspid nature of their dentition may reflect their small body size (Murray, 2004b). The unicuspid teeth from Nsungwe are most likely attributable to mature individuals of *Hydrocynus*, as development in this taxon is characterized by a multicusp first set of teeth that later gives way to unicuspid replacements (Brewster, 1986; Trapani et al., 2005).

The Nsungwe *Hydrocynus* teeth are considerably smaller than in modern species, such as the extant tigerfish, *H. vittatus*. Although it is difficult to infer the size of individuals based on isolated teeth, mature teeth of Nsungwe *Hydrocynus* sample compare favorably in size with immature individuals of *H. vittatus* (287 ± 13 mm fork length; Gagiano et al., 1996) but not mature individuals (males >451 mm and females >522 mm total length; Gerber et al., 2009). It is tempting to suggest the presence of a smaller species or population of exclusively immature individuals, but specimens hail from well-sorted coarse-grained sandstones and therefore may simply reflect depositional environment.

CHARACIFORMES sensu Nelson, 2006
 ALESTIDAE sensu Murray and Stewart, 2002
 (Fig. 2D–N)

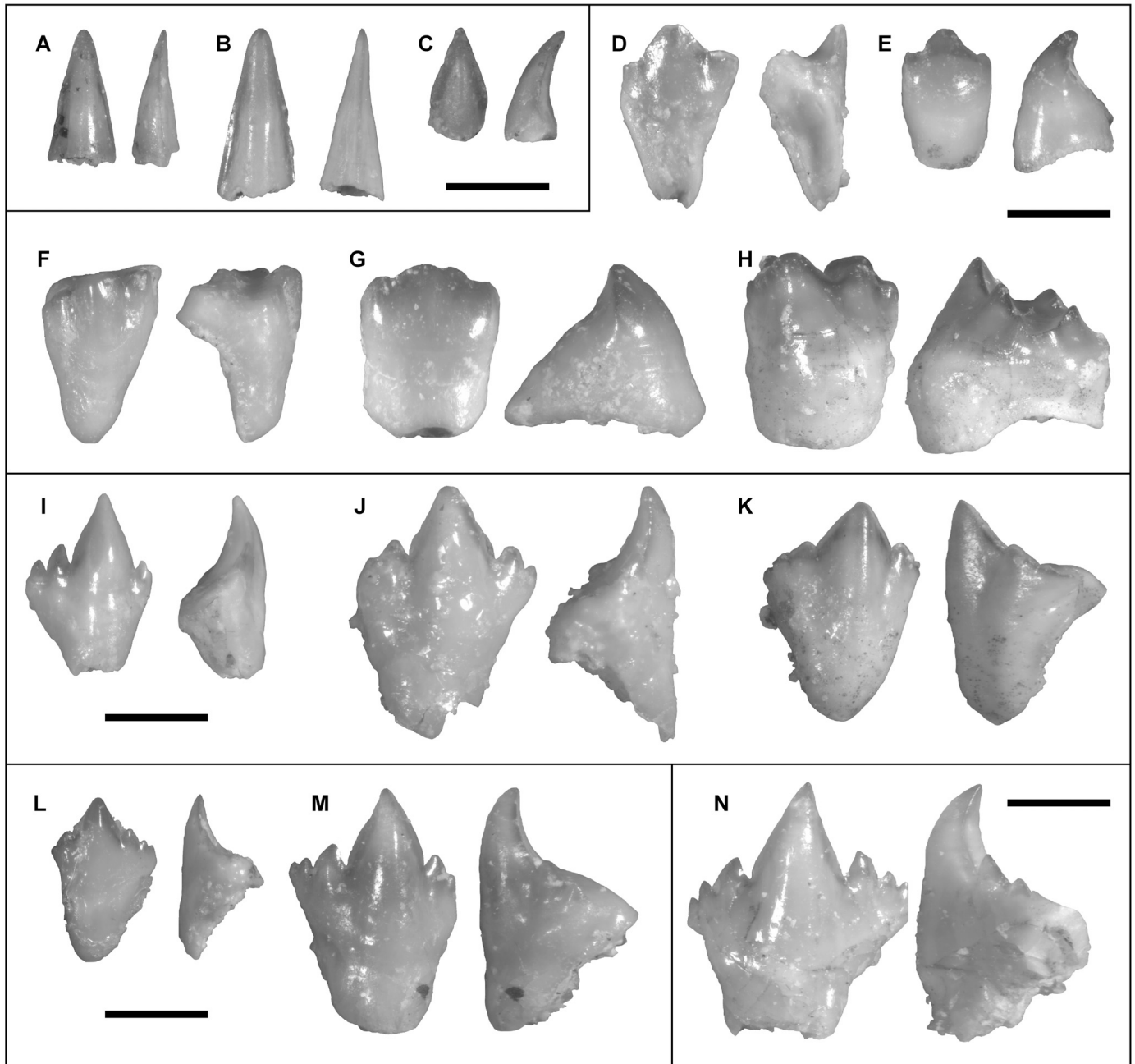


FIGURE 2. Exemplar RRBP specimens from the Nsungwe Formation in labial (left) and profile (right) views. (A–C) *Hydrocynus* (one cusp); A, 10046B; B, 11416; C, 12165; (D–E) Morphology A (three-cusped outer premaxillary teeth); D, 09487C; E, 10137B; (F–H) Alestidae (four cusps); F, outer premaxillary tooth, 10159; G, outer premaxillary tooth, 12499; H, inner row premaxillary tooth, 10079A; I, dentary tooth, 09248A; (J–K) Morphology B (five-cusped dentary teeth); J, 09201B; K, 07624; (L–M) Alestidae (six-cusped dentary teeth); L, 09316A; M, right tooth, 08261A; (N) Morphology C (seven-cusped dentary tooth), 11087A. Scale bars equal 1 mm.

Referred Specimens—Outer row premaxillary teeth: RRBP 05242, 07572, 08152, 08162B, 09201C, 09341, 09377B, 09487C, 10079D, 10137A, 10137B, 10159, 11124B, 11206A, 11247A, 11522, 11529, 11559C, 12499, 12562B. Inner row premaxillary teeth: RRBP 10079A, 10079C, 11258, 12113. Dentary teeth, Morphology A: RRBP 05261, 07624, 08363D, 08465E, 09082, 09085, 09111B, 09185A, 09201A, 09201B, 09248A, 09324, 09398A, 09463A, 09463C, 09464D, 10019D, 10034F, 10034K, 10079B, 10118T, 10199C, 11141A, 11175B, 11212A, 11212C, 11224, 11288B, 11323, 11349, 11513, 11530, 12298, 12567; Morphology B: RRBP 07461, 07475, 07602, 07613, 08261A, 09132,

09238A, 09316A, 09316B, 09316C, 09505B, 10019E, 10034B, 10046C, 10066I, 10079E, 10087, 10094, 11435A, 11435B, 12154, 12333A; Morphology C: RRBP 07475, 09201E, 10019O, 10066B, 10066C, 11087A, 11419A, 11419B.

Description—A total of 88 Nsungwe Formation specimens are referred to the characiform family Alestidae. Among other factors, all specimens were referred to Alestidae based on having outer premaxillary or outer dentary teeth with three to seven cusps, a diagnostic character of the family to the exclusion of *Hydrocynus* (Zanata and Vari, 2005; Miranda, 2010), and a group of inner row premaxillary teeth that

exhibit a unique four-cusp morphology. The cusp tips are sharp, bearing a characteristic amber color, whereas the base of the tooth is broadly expanded lingually, and ivory in color. Although depositional environment is known to alter pigmentation in certain vertebrate fossils (e.g., Dumont et al., 2014), some extant alestids notably exhibit pigmented tooth crowns (e.g., ANSP 38609, 38704, 66421). Therefore, the pigmentation could be inherent to the dental enamel and enameloid layers known to exist in recent actinopterygians (Sasagawa et al., 2009).

The teeth in the Nsungwe sample exhibit notable variation in cusp number and shape. In teeth with different cusp numbers, crowns are convex labially and concave lingually (Fig. 2D–K). The descriptions of the Nsungwe alestid specimens are classified first based on tooth position (outer row premaxillary, inner row premaxillary, and dentary). Within those classifications are subdivisions of morphologies based on cusp number.

Outer Premaxillary Row—Thirteen low-crowned outer premaxillary teeth bearing three and four cusps have been recovered in the Nsungwe sample to date (Fig. 2D–G). Three-cusped teeth range in overall tooth height from 1.02 to 1.96 mm and overall tooth breadth from 0.62 to 1.65 mm. Tricuspid teeth exhibit a large central cusp flanked by a smaller cusp on either side, giving such teeth a relatively symmetrical appearance in labial view. In profile view, smaller cusps are situated lingual to the prominent median cusp. Seven teeth with four cusps were recovered. Most of the four-cusped teeth do not exhibit a single prominent cusp. Instead, these teeth have two similarly sized cusps on either side of the midline, flanked by smaller cusps mesially and distally, producing a fairly symmetrical tooth. Four-cusped specimens range in overall (cusp + root) height between 0.94 and 2.24 mm and in maximum breadth from 0.46 to 1.98 mm.

Inner Premaxillary Row—Five teeth exhibiting this morphology have been recovered in the Nsungwe sample to date, and these teeth bear between five and eight cusps (Fig. 2H). Tooth crowns on inner row premaxillary teeth bear both labial and lingual cusps with ridges extending from one cusp to the next, forming a ring-like orientation of cusps. Cusps are not completely separated from one another and often join together, contributing to variability in cusp number.

Dentary Teeth—Sixty-four teeth with five to seven cusps were recovered (Fig. 2I–N).

Morphology A (Fig. 2I–K) comprises 36 five-cusped teeth that exhibit one prominent cusp, and four smaller cusps. Nineteen of the five-cusped teeth recovered to date are roughly symmetrical, with a larger central cusp flanked by two smaller cusps mesially and distally. All five-cusped teeth vary in overall height of the entire tooth from 0.81 to 2.44 mm and maximum breadth of the entire tooth from 0.64 to 1.77 mm. Exemplar specimens exhibiting this symmetrical morphology include RRBP 09201B (Fig. 2J). Seventeen of the five-cusped teeth exhibit a large, off-center prominent cusp, with one smaller cusp located on the mesial side and three consecutively smaller cusps on the distal side (RRBP 07624; Fig. 2K). There is no notable size contrast between the symmetrical and asymmetrical morphologies.

Morphology B comprises 21 six-cusped teeth (Fig. 2L–M). The teeth in this sample are further divided into two categories: symmetrically cusped teeth (five specimens) and asymmetrically cusped teeth (16 specimens). Symmetrical teeth exhibit a large central cusp flanked mesiodistally by two cusps on one side and three on the other, which are approximately equal to one another in surface area. Asymmetrical teeth in this sample have a larger mesial than distal cusp region flanking the large prominent cusp (Fig. 2M). Six-cusped teeth range in overall height from 0.87 to 2.36 mm and maximum breadth from 0.64 to 1.83 mm. Asymmetrical teeth tended to be slightly larger than symmetrical teeth.

Morphology C comprises eight seven-cusped teeth (Fig. 2N). All of these teeth exhibit the same general structure, with three cusps flanking either side of a larger central cusp. These teeth range in overall height from 1.94 to 2.51 mm and maximum breadth from 1.29 to 2.08 mm. Six- and seven-cusped teeth are generally larger than teeth with fewer cusps.

Remarks—In the consideration of alestid fossil dentition, *Alestes* and *Brycinus* are often grouped together (e.g., *Alestes/Brycinus*, Stewart, 2001, 2009; Murray and Stewart, 2002) because their teeth are very similar, and taxonomically, all *Brycinus* species were once included in *Alestes*, and some fossil forms have been reassigned to †*Sindacharax* or †*Bunocharax* (see Stewart, 2001). We do not consider the Nsungwe specimens to represent †*Sindacharax*, because teeth of that genus differ from the Nsungwe teeth in both size and cusp morphology. Teeth of †*Sindacharax* are at least 10 times larger than the new specimens, they have a lower cusp profile, and their cusp rows are more numerous but less symmetrical than our specimens (Greenwood and Howes, 1975). Instead, we consider the Nsungwe morphologies to bear closest resemblance to those of *Alestes/Brycinus* and *Micralestes*.

Phylogenetic analyses of Alestidae indicate that several species of extant *Alestes* form a monophyletic group that is the sister taxon to *Hydrocynus* (Murray and Stewart, 2002). More recently, morphology-based (Zanata and Vari, 2005) and molecular (Arroyave and Stiassny, 2011; Oliviera et al., 2011) phylogenetic studies support this idea. Furthermore, several species of *Brycinus* form a clade, although resolution is poor (Zanata and Vari, 2005). Character transformations that describe those relationships include a number of bony and soft tissue apomorphies, including the relative position of dentition on jaw elements, but not a specific description of teeth (Murray and Stewart, 2002). Species keys have aided in understanding alestid relationship and include within them dental characters separating *Alestes* from *Brycinus*, because they are of moderate or massive size, respectively (Myers, 1929). Furthermore, although increases in tooth height and breadth in *Alestes* are correlated with cusp number, *Micralestes* specimens are easily distinguished from *Alestes* teeth by a larger number of cusps, and by their consistently more symmetrical shape (pers. observ., W.N.S.). In particular, mesial teeth of the dentary in extant *Micralestes* appear to be relatively symmetrical, whereas more distal teeth in the dentary exhibit only slight asymmetry such that the mesial-most smaller cusps flanking the prominent central cusp are either fewer in number or more crowded relative to those cusps distal to the large cusp (Stiassny and Mamonekene, 2007).

One trend observed in the Nsungwe sample is a range in cusp number in conjunction with greater tooth height and breadth. This pattern is generally consistent throughout the entire Nsungwe Formation alestid sample: five-cusped teeth average 1.62 mm in overall height and 1.24 mm in maximum breadth, whereas six- and seven-cusped teeth average 2.02 mm in overall height and 1.42 mm in maximum breadth. It is not possible to confidently assign body size to the Nsungwe sample, because alestid teeth in close proximity to one another can be of different sizes. For example, in a single dental row preserved in cleared and stained specimens of the extant *Alestes kingsleyae* (e.g., ANSP 38609), larger teeth with more numerous cusps are often situated next to smaller teeth with fewer cusps.

The range in tooth size is also consistent with a developmental trend observed for many bony fishes (Trapani et al., 2005), including *Alestes stuhlmanni* (Murray, 2004b), a taxon known to express ontogenetic changes in its dentition. Changes in cusp number may take place during the development of replacement teeth as well, as observed in cleared and stained extant specimens. One individual of *Alestes kingsleyae* (ANSP 38069) exhibits five cusps on erupted teeth, yet replacement teeth still housed within the bone have a well-defined prominent cusp, with just

one cusp flanking either side. Similarly, in *Phenacogrammus ansgorii* (ANSP 38704), developing teeth located posteriorly in the jaw exhibit fewer cusps than erupted teeth. We apply a simplifying assumption that teeth recovered from the Nsungwe Formation represent the fully erupted, fully developed condition, and not an ontogenetic stage in the dentition.

CONCLUSION

A number of alestid fossils have been described from the Paleogene of Afro-Arabia, with records reported from the Eocene Mahenge crater lake of Tanzania (Murray, 2003), the Eocene-Oligocene Jebel Qatrani Formation of Egypt (Murray, 2004a), and early Oligocene to Miocene sites on the Arabian Plate (Otero and Gayet, 2001). The Nsungwe Formation localities in Tanzania provide the first late Oligocene record of subequatorial African alestids.

Many characiforms exhibit tightly packed, sharp-cusped teeth related to their feeding behavior, and alestids are no exception. Alestid specimens recovered from the late Oligocene Nsungwe Formation of Tanzania consist of isolated premaxillary and dentary teeth bearing between one and seven cusps, with no representation of bicuspid teeth. Teeth are strongly convex along the outer margin, and concave lingually.

Phylogenetic analyses of alestid relationships generally do not include dental characters, let alone the number of cusps or the teeth (Zanata and Vari, 2005). Yet, the characteristic tooth shapes makes it possible to refer Nsungwe Formation specimens minimally to the level of Alestidae, with morphology and cusp number further separating modern genera (Zanata and Vari, 2005; Dahdul, 2010). *Hydrocynus* exhibits changes in tooth form through ontogeny, beginning with unerupted multicusp teeth, which once lost are replaced with unicuspid teeth (Brewster, 1986; Trapani et al., 2005). Notably, the most complete characiform fossil from the Eocene of Tanzania, †*Mahengecharax* (Murray, 2003), was previously hypothesized as the sister taxon to Alestidae, yet does not preserve erupted dentition. Perhaps unerupted dentition can one day shed more light on its position within the alestid characiforms.

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APPENDIX 1. Comparative material.

- Alestes kingsleyae*, ANSP 38609, cleared and stained
Alestes liebrechtsii, AMNH 5931, dry skeleton
Alestopetersius hilgendorfi, ANSP 66421, cleared and stained
Brycinus imberi, ANSP 67250, cleared and stained
Bryconaeithiops sp., AMNH 227484, cleared and stained
Hydrocynus maxillosus, AMNH 17317, dry skeleton
Nannopetersius ansorgii, ANSP 38704, cleared and stained