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## Quaternary fossil fish from the Kibish Formation, Omo Valley, Ethiopia

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## ABSTRACT

The late Quaternary Kibish Formation of the Omo Valley, southwestern Ethiopia, preserves environments reflecting a history of fluctuations in the level of nearby Lake Turkana over the past 200,000 years. The Kibish Formation has yielded a diverse mammalian fauna (as well as birds and crocodiles), stone tools, and the oldest anatomically modern *Homo sapiens*. Fish, the most common vertebrate fossils in this unit, are reported in this study. Catfish (especially clariids and *Synodontis*) and Nile perch (*Lates niloticus*) predominate, but the gymnarchid *Gymnarchus*, a cyprinid (*Barbus*), tigerfish (*Hydrocynus*), pufferfish (*Tetraodon*), and other catfish are also present. In total, nine teleost genera are found in the Kibish Formation, representing a subset of the 37 genera that constitute the modern Omo-Turkana ichthyofauna. Several taxa present in the modern fauna, including *Polypterus* and members of the family Cichlidae, are not found in the Kibish deposits. Most specimens are preserved as disarticulated or broken skeletal elements, but some preservation of articulated elements (e.g., sets of vertebrae, crania with lower jaws or cleithra) also occurs. Many of the catfish and Nile perch specimens are larger than the largest reported from the modern river or lake. Faunas of Kibish Members I and III closely resemble one another; the fauna from Member IV contains only the three most common taxa (*Clarias*, *Synodontis*, *Lates*), though this may result from insufficient sampling. Barbed bone points have been collected from the upper part of the formation, indicating a long association between the human inhabitants and the fish fauna of the Omo Valley.

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## Introduction

The Quaternary Kibish Formation of the Omo Valley, southwestern Ethiopia, has yielded a diverse mammalian fauna, stone tools, and other artifacts, as well as the oldest anatomically modern *Homo sapiens* (Howell, 1968; Day, 1969; McDougall et al., 2005). These deposits, preserving mainly deltaic and lacustrine environments (Butzer and Thurber, 1969; McDougall et al., 2005; Brown and Fuller, 2008), represent the youngest part of a series of rocks documenting changes in depositional environment throughout the Plio-Pleistocene in response to fluctuations in the level of nearby Lake Turkana (Brown et al., 1970; Butzer, 1976; Feibel, 1988).

The Kibish Formation is divided into four geologic members on the basis of disconformities; three of these (Members I, III, and IV) bear fossils. Members I and III are mainly composed of deltaic deposits, whereas Member IV may represent open-water (lacustrine) conditions (Butzer, 1969; Butzer et al., 1969). Each member was deposited rapidly; deposition was followed by a period of erosion and incision prior to deposition of the next member (Butzer, 1976; McDougall et al., 2005). Radiometric dating of tuffs within this sequence has established a depositional chronology and facilitated

stratigraphic correlations (McDougall et al., 2005). A tuff within Member I has been dated to ~200 ka, and the Member III tuff dates to ~100 ka (McDougall et al., 2005). On the basis of <sup>14</sup>C dating of mollusc shell, Member IV is thought to have been deposited sometime between ~3000 and 10,000 years ago (Butzer et al., 1972; Brown and Fuller, 2008).

Fish are the most common vertebrate fossils in the Kibish Formation and are also found in older Omo Group deposits (Arambourg, 1947), including the Mursi (pers. obs.) and Shungura [Greenwood, 1976b; Howell et al., 1987 (after Boaz, 1982)] formations. Little work has been done on Omo Group fish faunas. However, fossil fish from contemporaneous deposits in East and West Turkana have been better studied (e.g., Thomson, 1966; Schwartz, 1983; Feibel, 1988; Stewart, 2002; the fossil record of Neogene freshwater fish in Africa was comprehensively reviewed by Stewart, 2001).

The modern fish fauna of Lake Turkana has also been relatively well studied (e.g., Hopson and Hopson, 1982). Interesting features of this fauna, especially when considered relative to those of other East African Rift Lakes, include the low level of endemism and lack of diversification among endemic forms. These features are thought to result from repeated contacts between the Omo-Turkana Basin and the Nile system, most recently in the Holocene (Greenwood, 1976a; Adamson et al., 1980; Hopson and Hopson, 1982).

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The Omo River is the link between Lake Turkana and the Nile, yet its fish fauna is relatively poorly known. Although older collections were made (e.g., Boulenger, 1906; 1909–1916), the classic work on Omo River fishes was done as part of the “Mission Scientifique de l’Omo” (Pellegrin, 1935). The most recent compilation of the modern Omo-Turkana fish fauna is more than ten years old (Leveque et al., 1991), and at least five new species have been discovered in this system since (Dgebuadze et al., 1994; Golubtsov and Berendzen, 1999).

Documenting the ichthyofauna from the Kibish Formation is a step towards fleshing out our knowledge of the Plio-Pleistocene fish faunas of the Omo-Turkana Basin. This information may help document hydrographic connections and provide clues as to the environments preserved and the paleoecology of the region. The presence of technologies associated with fishing in Members III and IV of the Kibish Formation also indicates that this fauna may have been an important food source for humans living in the Omo Valley at this time.

## Methods

### Fossil collection and identification

Fossil fish material was collected from Members I, III, and IV of the Kibish Formation (Member II did not contain fossils). Several specimens in exceptional condition were collected during the 2002 field season; intensive collection of fish material occurred during the 2003 field season. Most material was collected by surface prospecting, though some identifiable material also came from screening at archaeological excavations associated with the Kibish project. Because fish are the most common vertebrate fossils in the Kibish Formation and the fish assemblage was dominated by only a few taxa, I limited collections to readily identifiable elements, and did not exhaustively collect every element representing the most common taxa (e.g., *Lates* vertebrae). A total of 337 individual specimens (NISP) were collected.

Specimens were identified using preexisting fossil material in the National Museum of Ethiopia, modern skeletal and preserved material from the University of Michigan Museum of Zoology, and figures from the literature. I also skeletonized fish caught in the Omo River near camp and used these for comparison with fossil material. All fossil material was deposited in the National Museum of Ethiopia (NME), Addis Ababa, with the other fossils from the Kibish Formation. The fish fossils are organized by locality. Each specimen is labeled with a provisional identification and provenience data, including GPS coordinates and stratigraphic position within the Kibish Formation.

### Collection and preparation of modern comparative material

Relatively few comparative skeletons are available for modern eastern African freshwater fishes, making identifications of fossil specimens challenging (Greenwood, 1974; Van Neer, 1993). Fish used to produce modern comparative material were caught from the Omo River near camp (5°23'42"N, 35°55'03"E) using hooks and lines; most fishing activity occurred around dusk. Once caught, fish were assigned to species, measured (standard length, or SL), photographed, gutted, and filleted. For skeletonization, filleted fish were placed in containers (plastic wash basins or food tins) filled with river water and left in a sunny spot within sight of camp. Screen was wrapped around the top of the containers to keep animals out. Water was changed each morning. Nearly complete or complete disarticulation and complete skeletonization usually occurred in three to five days, and remains were largely odor free. On the last day of soaking, clean water from camp was used in lieu of muddy river water whenever possible. A small amount of bleach

may be added to the water on the last day, though I did not use bleach in producing these skeletons. Sixteen skeletons representing five species (SL ranging from ~20 cm to ~1 m) were made in this fashion, and were deposited in the University of Michigan Museum of Zoology (UMMZ) fish collection or the NME (Table 1).

## Material

Infraclass TELEOSTEI  
Order MORMYRIFORMES  
Family GYMNARCHIDAE  
*GYMNARCHUS* Cuvier, 1829  
*GYMNARCHUS NILOTICUS* Cuvier, 1829

*Specimens.* Kibish Member I: 10 oral teeth; Kibish Member III: 1 oral tooth

*Gymnarchus* oral teeth vary in shape (Kibish material includes teeth with both square and triangular outlines), but are identifiable by the possession of distinct serrations not present in teeth of other mormyrid genera (Boulenger, 1906; pers. obs.). *Gymnarchus niloticus* is the only extant species in this genus, and is present in the modern Omo-Turkana Basin (Fig. 1A).

Order CYPRINIFORMES  
Family CYPRINIDAE  
*BARBUS* Cuvier and Cloquet in Cuvier, 1816  
*BARBUS* sp.

*Specimens.* Kibish Member I: 1 pharyngeal tooth; Kibish Member III: 3 pharyngeal teeth.

Cyprinids possess teeth only on their fifth ceratobranchials, the lower pharyngeal bones. These teeth occlude with a keratinous basioccipital pad during food processing. *Barbus* is represented by five species in the modern Omo-Turkana Basin, all of which possess robust pharyngeal teeth (Fig. 1B). Cyprinid teeth are distinctive, and isolated teeth can be used for species identification.

CYPRINIDAE indet.

*Specimens.* Kibish Member I: 1 pharyngeal tooth.

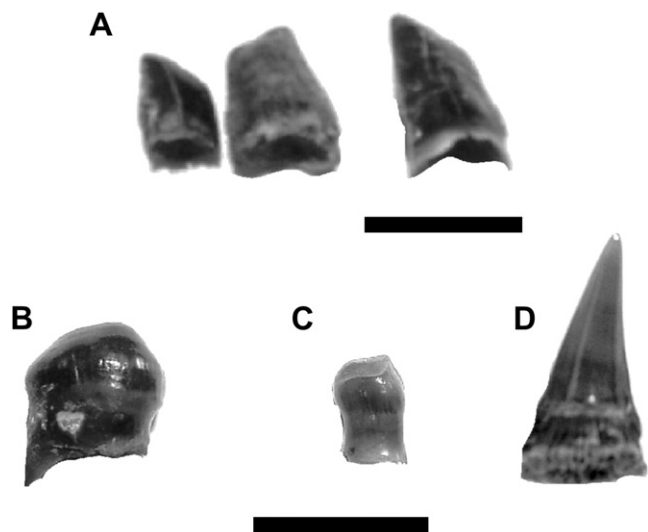
This tooth may come either from *Barbus* or from the cyprinid species *Labeo*, which is represented in the modern Omo-Turkana Basin by three species (Fig. 1C).

Order CHARACIFORMES  
Family ALESTIDAE

**Table 1**

Modern fish caught from the Omo River near camp during January and February 2003

Species	SL (mm)	Designation
<i>Alestes baremose</i>	290	NME
<i>Andersonia leptura</i>	200	NME
<i>Andersonia leptura</i>	260	NME
<i>Andersonia leptura</i>	250	UMMZ 241264
<i>Clarias lazera</i>	680	UMMZ 241266
<i>Clarias lazera</i>	720	UMMZ 241266
<i>Clarias lazera</i>	1000	NME
<i>Synodontis schall</i>	210	NME
<i>Synodontis schall</i>	240	NME
<i>Synodontis schall</i>	240	UMMZ 241265
<i>Synodontis schall</i>	360	UMMZ 241265
<i>Synodontis schall</i>	?	NME
<i>Synodontis schall</i>	?	NME
<i>Synodontis frontosus</i>	210	NME
<i>Synodontis frontosus</i>	230	UMMZ 241265
<i>Synodontis frontosus</i>	?	NME



**Fig. 1.** Fossil teleost teeth from the Kibish Formation: (A) *Gymnarchus* teeth, (B) *Barbus* pharyngeal tooth, (C) Cyprinidae indet. pharyngeal tooth, (D) *Hydrocynus* tooth. Scale bars are 0.5 cm (A) and 1 cm (B–D).

*HYDROCYNUS* Cuvier, 1817  
*HYDROCYNUS* sp.

*Specimens.* Kibish Member III: 1 oral tooth.

While the skeleton of *Hydrocynus* (the tigerfish) is rather delicate and rarely found in fossil assemblages (Stewart, 1997), the distinctive oral teeth more readily preserve (Fig. 1D). *Hydrocynus* possesses recurved caniniform teeth with distinctive crenulated bases. Many observations suggest that this fish replaces its entire dentition (all four jaw quadrants) simultaneously (Begg, 1972; Gaigher, 1975; Tweddle, 1982; Gagiano et al., 1996). Even fragments excluding the base can easily be distinguished from teeth of most other fishes (and from small crocodile teeth, which are round in cross section) on the basis of their labiolingual compression. This genus is represented by two species in the modern Omo-Turkana Basin: *H. forskahlii* and *H. vittatus* [this species includes *Hydrocynus lineatus*, as discussed by Hopson and Hopson (1982), as well as *Hydrocyon lineatus*, whose teeth were figured by Eastman (1917)]. Teeth in *Hydrocynus* may vary within individuals according to position along the jaw, and also may vary between (unicuspid and tricuspid) tooth generations. Tooth numbers have also been reported to vary between species (Brewster, 1986). However, it is unclear whether fossil teeth may be assigned to species on the basis of morphological criteria (see Greenwood, 1972; Stewart, 2001). Brewster (1986) suggested subsuming *H. vittatus* within *H. forskahlii*, which would mean that all modern *Hydrocynus* in the Omo-Turkana Basin belong to a single species. Her suggestion has not been uniformly followed in more recent literature.

Order SILURIFORMES  
Family BAGRIDAE  
BAGRIDAE indet.

*Specimens.* Kibish Member III: 5 dorsal spine bases; Kibish Member I: 1 pectoral spine base.

I assigned these spines to the family Bagridae on the basis of the serration patterns and morphology of the base (Gayet and Van Neer, 1990). Fossil bagrids were previously identified from the Omo Valley by Arambourg (1947), and *Bagrus* is common in modern Lake Turkana (Stewart, 2002).

Family CLARIIDAE  
*CLARIAS* Scopoli, 1777  
*HETEROBRANCHUS* Geoffroy Saint-Hilaire, 1809  
*CLARIAS* sp. or *HETEROBRANCHUS* sp.

*Specimens.* Kibish Member I: 2 cranial fragments, 1 mesethmoid fragment, 1 partial neurocranium; Kibish Member III: 1 articular, 1 cranial fragment, 1 mesethmoid, 1 mesethmoid fragment, 6 headplates, 1 headplate including partial mesethmoid and vomerine toothplate, 1 pectoral spine base, 1 premaxilla with toothplate; Kibish Member IV: 1 posterior and anterior ceratohyal, 2 headplates with vomerine toothplate, 1 premaxilla.

Two extant genera of clariids (*Clarias* and *Heterobranchus*) are present in the modern Omo-Turkana Basin; these genera are easily distinguishable from one another by the presence of a large adipose fin behind the dorsal fin in *Heterobranchus* (Hopson and Hopson, 1982; Agnese and Teugels, 2001). However, osteological differences between the genera are minimal, though differences in some skeletal elements have been mentioned in the literature [e.g., urohyals (Greenwood and Todd, 1970), pectoral spines (Greenwood, 1972; von den Driesch, 1983; Gayet and Van Neer, 1990), supraorbitals, opercula, dentaries, cleithral elements (von den Driesch, 1983), and palatines (Stewart, 2002)]. Most of the Kibish material consists of headplate fragments (the most commonly preserved clariid elements in many eastern African fossil assemblages and identifiable by their granulated surface; e.g., Van Neer, 1993) and cannot be assigned confidently to genus (Fig. 2). In modern settings, however, *Clarias* is much more common than *Heterobranchus* (Stewart, 2002: 32 species vs. four species in Africa according to Agnese and Teugels, 2001). Several individuals of *Clarias lazera* (and none of *Heterobranchus*) were caught in the Omo River during the 2003 field season and skeletonized.

Family MOCHOKIDAE  
*SYNODONTIS* Cuvier, 1817  
*SYNODONTIS* sp.

*Specimens.* Kibish Member I: 1 basioccipital region, 3 partial neurocrania, 1 complete neurocranium, 1 complete neurocranium with articulated cleithrum, 11 pectoral spine bases, 2 pectoral spine bases with cleithral articulations, 21 pectoral spine fragments, 2 dorsal spine fragment, 5 dorsal spine bases; Kibish Member III: 1 dorsal spine base, 1 dorsal spine articulation, 8 partial neurocrania, 5 pectoral spine bases, 2 pectoral spine bases with cleithral articulation, 11 pectoral spine fragments.

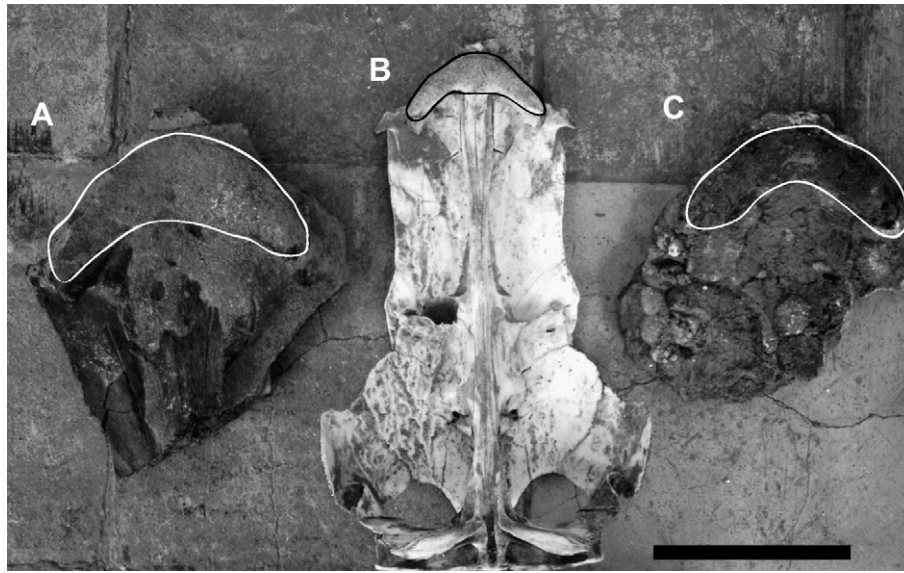
*SYNODONTIS?*

*Specimens.* Kibish Member III: 1 dorsal spine (heavily weathered), 1 pectoral spine with cleithral articulation; Kibish Member IV: 1 pectoral spine base, 3 pectoral spine fragments.

*Synodontis* is a diverse (>100 species) catfish genus restricted to Africa. There is conflict in the literature as to whether *Synodontis* species may be distinguished osteologically. Greenwood (1959: 40–41) discussed distinguishing species of *Synodontis* based on aspects of the cleithrum and dorsal spines, but stated that “no trenchant specific characters were observed in the pectoral spines of the extant species examined” (p. 41). Von den Driesch (1983) mentioned that several species of *Synodontis* from Egypt may be distinguished based upon “the toothing of the back and pectoral fin spines and the form of the caudal plate of the cleithrum” (p. 99); however, she did not provide the criteria used. A morphometric analysis of *Synodontis* species from Egypt suggests that discrimination is possible on the basis of skull measures (Mekawky and Mahmoud, 1992), but this study did not investigate spines.

*Synodontis* was the most commonly caught fish from the Omo River during our field season. The crania and axial skeletons of all





**Fig. 2.** Ventral views of (A, C) fossil clariid partial crania and (B) modern *Clarias lazera* cranium. Vomerine tooth patches are outlined to show their relative size. The specimen shown in B is from a fish approximately 1 m SL. Scale bar = 10 cm.

specimens appeared indistinguishable (from each other and from the fossils; Fig. 3), but size and patterning of serrations on the spines of the dorsal and pectoral fins indicates two species. Although it has been noted that, within a species, serration patterns of the pectoral spines may vary ontogenetically, and even between individuals of the same size [Greenwood, 1966; Van Neer, 1994a; compare Fig. 1 (#8) of Gayet and Van Neer (1990) with Fig. 2 of Luff and Bailey (2000)], I found two types of spines in individuals of similar size, with no intermediates. Covariation between serration patterns on dorsal and pectoral spines corroborates the hypothesis that there are two species. These likely correspond to *S. schall* and *S. frontosus*, which are the only two *Synodontis* species that inhabit the Omo-Turkana Basin. One species had spines identical to those pictured in the literature for *S. schall* (e.g., von den Driesch, 1983;

Luff and Bailey, 2000). Pectoral and dorsal spines from modern individuals from the Omo River are figured and described in Figs. 4 and 5. Others have suggested criteria for distinguishing dorsal spines of *S. schall* and *S. frontosus*, including cross-sectional shape (Greenwood, 1959) and flaring of the articular area (Schwartz, 1983). I found it difficult to see these distinctions in the Kibish material, and I assigned fossil dorsal and pectoral spines to *Synodontis* sp.

Other Kibish *Synodontis* material includes well-preserved neurocrania, some with cleithra still articulated. Several blocks full of *Synodontis* material were also recovered from one locality (Fig. 6A). *Synodontis* was the second most common taxon (and the most common siluriform taxon) in the Kibish Formation. In addition, individuals were typically much smaller than those of other siluriform taxa.

#### Family SCHILBEIDAE

*SCHILBE* Oken, 1817

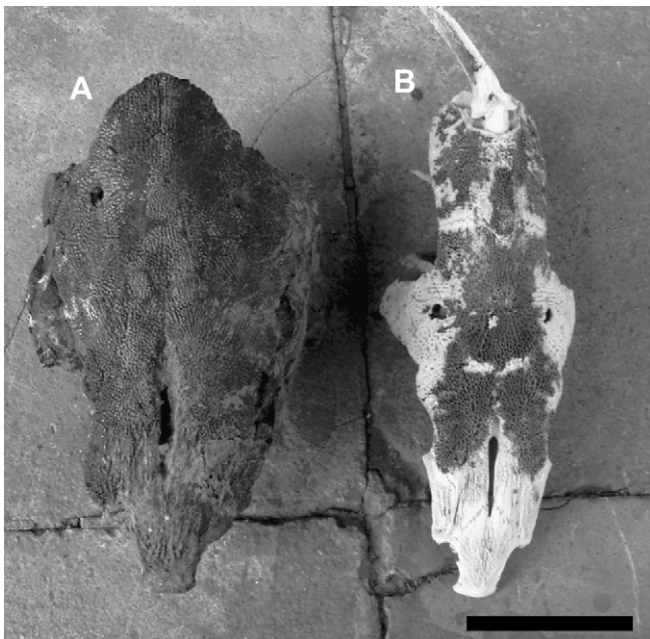
*SCHILBE URANOSCOPUS* Ruppell, 1832

**Specimens.** Kibish Member III: 1 cranial fragment including mesethmoid, 1 cranium with articulated jaws.

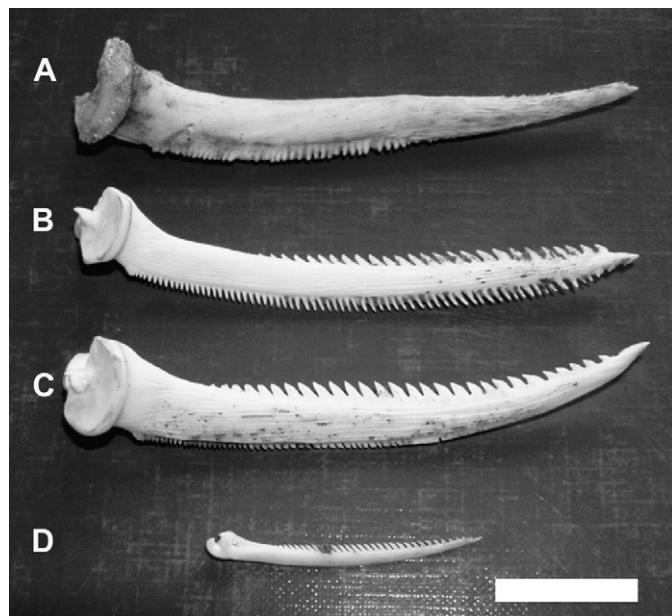
The fossil record for *Schilbe* is very poor (Stewart, 2001), with the only reports of fossil material from Miocene Chiando Uyoma deposits in Kenya (Schwartz, 1983) and from the late Miocene Upper Nawata Formation at Lothagam (Stewart, 2002). I have attributed two specimens from Kibish Member III to this genus, including an exceptionally well-preserved cranium with jaws articulated and teeth still attached. In particular, the texture of the bone, shape of the mesethmoid, and extreme dorsoventral compression of the skull, as well as its overall resemblance to modern comparative material, led to its identification as *Schilbe*. *Schilbe uranoscopus* is the only extant species present in the Omo-Turkana Basin.

SILURIFORMES indet.

**Specimens.** Kibish Member I: 1 pectoral spine base, 1 pectoral spine base with cleithral articulation, 1 vomer; Kibish Member III: 2 cleithrum fragments, 5 dorsal spine bases, 3 dorsal spines, 1 pectoral spine base, 2 pectoral spine fragments, 3 spine fragments, 1



**Fig. 3.** (A) Fossil and (B) modern *Synodontis* skulls. Scale bar = 5 cm.



**Fig. 4.** Pectoral spines of modern Omo River catfish: (A) *Clarias lazera*, (B) *Synodontis schall*, (C) *Synodontis frontosus*, and (D) *Andersonia leptura*. Scale bar = 2 cm. *Clarias lazera* lacks all but a few tiny serrations on its concave edge (this species also lacks dorsal spines). *Andersonia leptura*, which was not found in the fossil assemblage, lacks serrations on its convex edge. The two species of *Synodontis* can be distinguished by the pattern of serrations on their convex edges. *Synodontis frontosus* possesses fewer, small serrations that end approximately halfway along the length of the spine; *S. schall* possesses more pronounced serrations that continue to the spine tip. These two species also differ in their dorsal spines.

vertebra; Kibish Member IV: 2 cranial fragments, 1 dorsal spine tip (weathered), 1 pectoral spine fragment.

#### Order PERCIFORMES

##### Family LATIDAE Jordan, 1923

*LATES* Cuvier in Cuvier and Valenciennes, 1828

*Specimens.* Kibish Member I: 1 dentary fragment, 20 fin spine bases, 2 fin spine fragments, 4 fin spines, 1 neurocranium, 1 palatine, 1 premaxillary fragment, 1 premaxilla, 29 vertebrae, 2 vomers;

Kibish Member III: 2 cleithral fragments, 6 dentaries, 2 dentary fragments, 5 fin spine bases, 10 fin spine fragments, 2 fin spines, 1 partial neurocranium, 4 neurocrania, 3 palatine fragments, 35 vertebrae, 1 vomer; Kibish Member IV: 1 dentary, 10 fin spine bases, 1 partial neurocranium, 1 premaxilla, 11 vertebrae, 1 vomer.

*Lates* was the most abundant fish taxon in the Kibish Formation, and was well represented by jaws, crania, fin spines, and vertebrae. Modern Lake Turkana has two *Lates* species, *L. niloticus* and *L. longispinnis*, but the latter is only present in the Holocene. In Plio-Pleistocene deposits, both *L. niloticus* and *Semlikiichthys* are present (Greenwood, 1976c; Harrison, 1991; Stewart, 2002). Osteological variability in *L. niloticus* is pronounced (Van Neer, 1987).

A fairly substantial number of fin spines were recovered. Distinguishing fin spines from Nile perch and tilapiine cichlids may be difficult (e.g., Van Neer, 1994a, b), though some differences are illustrated in Figure 6.3 of Gautier and Van Neer (1989). It may also be possible to distinguish these two species based on size, but Nile perch in the Kibish deposits ranged widely in size (neurocrania, for example, ranged from less than 10 cm to nearly 1 m in length; Fig. 6B). Comparison of Kibish fossils with modern comparative material led me to refer all these spines to *Lates*. In addition, many were found associated with other *Lates* material.

#### Order TETRAODONTIFORMES

##### Family TETRAODONTIDAE

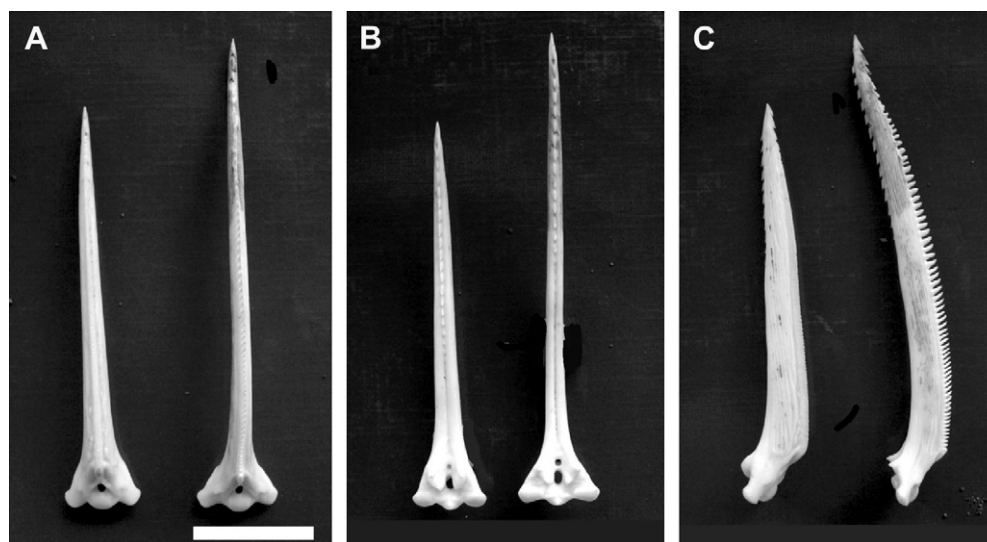
*TETRAODON* Linnaeus, 1758

*TETRAODON* sp.

*Specimens.* Kibish Member I: 1 toothplate; Kibish Member III: 1 toothplate.

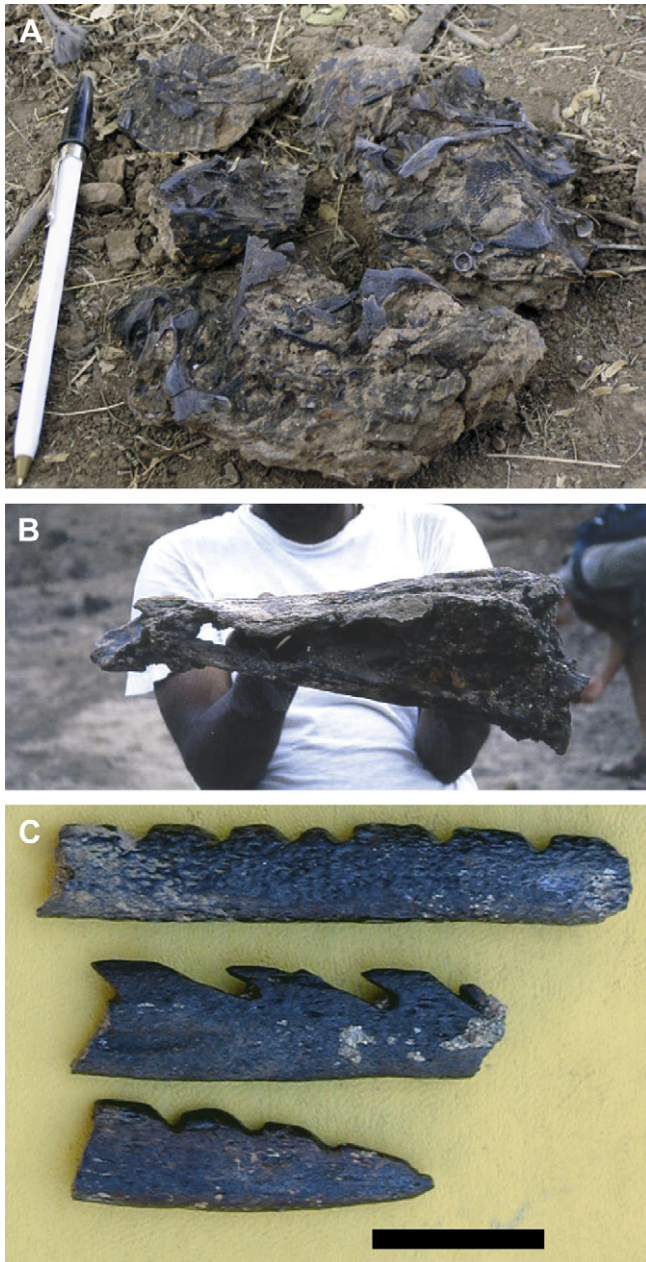
*Tetraodon*, a freshwater pufferfish, inhabits shallow water and eats mainly molluscs (Hopson and Hopson, 1982; Van Neer, 1994a). Its robust toothplates are most likely to preserve as fossils. *Tetraodon* has also been reported from the Lake Albert–Lake Edward rift (Van Neer, 1994a), Koobi Fora (Schwartz, 1983), and Lothagam (Stewart, 2002). One species, *Tetraodon lineatus*, is currently found in the Omo-Turkana Basin, though two species were present in the Plio-Pleistocene.

TELEOSTEI indet.



**Fig. 5.** Dorsal spines of modern Omo River *Synodontis* species: (A) anterior view, (B) posterior view, (C) side view (anterior is to the right). Scale bar = 2 cm. In each panel, *S. frontosus* is shown on the left and *S. schall* is on the right. Both species possess approximately 10–20 serrations on the concave (posterior) edge of the spine, but whereas *S. frontosus* lacks all but a few serrations on its convex (anterior) edge, *S. schall* possesses 55–75 pronounced serrations running the entire length of the spine. It should be emphasized that these ranges may not hold for very small or very large fish.





**Fig. 6.** (A) Blocks containing concentration of *Synodontis* bones; (B) large *Lates* cranium found in Member IV; (C) examples of barbed bone points found in Members III and IV. Scale bar in C = 2 cm.

**Specimens.** Kibish Member I: 1 cleithrum, 1 neurocranium, 1 opercula, 1 toothplate, 11 vertebrae; Kibish Member III: 1 cranial fragment, 1 dentary with articular, 2 neurocrania, 1 premaxillary fragment, 5 toothplate fragments; Kibish Member IV: 1 dentary.

## Discussion

### Composition of the fauna

Presence/absence data for fish genera in fossiliferous members of the Kibish Formation are shown in Table 2. Composition of the fauna (grouped by order) is shown in Fig. 7. Percentages indicate numbers of individual specimens (NISP). Although there were some concentrations of fish bones apparently from single individuals within the Kibish deposits, calculating minimum

numbers of individuals (MNI) would have given values similar to NISP due to the highly fragmented and scattered nature of most of the material, as well as the large number of localities from which material was collected. If anything, exhaustive collection of all fish remains and calculation of MNI values would have increased the percentage of the fauna represented by the most common taxa.

The Kibish assemblage is dominated by perciforms (consisting exclusively of *Lates niloticus* and constituting 47.1% of the fauna) and siluriforms (39.6%). *Synodontis* (61% of Kibish siluriform specimens) and clariids (15%) dominate the catfish fauna. Other ostariphsans (characiforms, cypriniforms) make up less than 2% of the total fauna, mormyriiforms (represented by *Gymnarchus* teeth) 3.3%, and tetraodontiforms (represented by *Tetraodon* toothplates) less than 1%.

Kibish Members I and III, the most completely sampled units, are similar in both taxonomic composition (Table 2) and frequencies (Fig. 7B, C). Only the three most common taxa (*Lates*, *Synodontis*, and *Clarias*) were collected from Member IV; this may reflect a change in environments, undersampling, or some combination of the two.

Of 37 genera documented in the modern Omo-Turkana Basin (including Lake Turkana; this list was compiled from Boulenger, 1906; Pellegrin, 1935; Hopson and Hopson, 1982; Leveque et al., 1991; Dgebuadze et al., 1994; Golubtsov and Berendzen, 1999), I have identified nine in the Kibish deposits. Catfish are the best represented, with four genera identified in the Kibish deposits and 10 (or nine if *Clarias* and *Heterobranchus* are grouped) in the modern fauna. Groups particularly poorly represented include cypriniforms (one of seven genera), characiforms (one of six genera), and cichlids (zero of five genera). However, these comparisons may not be entirely fair, as the Kibish deposits do not preserve the full range of environments present in the basin. I did not assign any of the material to new or extinct taxa; the Kibish fauna looks very much like the modern fauna, which is not surprising given its young age.

### Taphonomy

Most fish material in the Kibish Formation is preserved as isolated, often broken single skeletal elements, though some preservation of articulated elements (e.g., sets of vertebrae, crania with jaws or cleithra attached) also occurs. Most of the damage to some specimens appears to have occurred only after postburial subaerial exposure. Disarticulation of fish material may result from predation or from postmortem flotation, transport, and scavenging (Elder and Smith, 1988). However, at least some of the material must have experienced rapid burial and mineralization, as evidenced by teeth preserved in sockets in a large specimen of the catfish *Schilbe*. This is unusual because the attachment of these teeth consists of unmineralized collagen; teeth would be expected to be lost during decomposition. (For comparison, no modern catfish caught from the Omo River survived the skeletonization process with teeth intact.) Fish in intermittently flooded environments may survive aquatic transport and scavenging and be rapidly buried if they are trapped by desiccation after one flood event and buried by the onset of the next (Smith et al., 1988).

All material, including material from Member IV (possibly as young as 3,000 years) is completely fossilized. Most of the fossil material is dark gray or black in color; Stewart (1991) noted that fish remains in Lake Turkana begin to change from white to pale brown within 18 months. In addition, several small blocks full of *Synodontis* material attest to several different modes of preservation (Fig. 6A).

Skeletal-element preservation in different taxa shows distinct patterns. Preservation of siluriform material (Fig. 8A) is biased toward durable spines (67.4% of specimens) and crania (25.8% of

**Table 2**  
Representation of teleost genera in the Mursi Formation

Genus	Kibish Member I	Kibish Member III	Kibish Member IV
<i>Gymnarchus</i>	X	X	
<i>Barbus</i>	X	X	
<i>Hydrocynus</i>		X	
<i>Clarias</i>	X	X	X
<i>Schilbe</i>		X	
<i>Bagrus</i>	X	X	
<i>Synodontis</i>	X	X	X
<i>Lates</i>	X	X	X
<i>Tetraodon</i>	X	X	

specimens), and against elements of the axial skeleton (<1% of specimens). Poor preservation of siluriform vertebrae appears to be a common phenomenon and has been documented both in natural (Van Neer, 1986) and culturally derived (Stewart and Gifford-Gonzalez, 1994) assemblages. The reason for such poor preservation is unknown, but may result from intrinsic qualities of the bone (e.g., density; Stewart, 1991) combined with—in cultural contexts—susceptibility to cooking methods such as roasting (Stewart and Gifford-Gonzalez, 1994). In *Lates* (Fig. 1B), the skeleton is more evenly represented, though axial elements including vertebrae (47.7%) and fin spines (33.8%) constitute the bulk of the material. As mentioned, exhaustive collection would have resulted in even higher representation of these elements. Other taxa are most frequently, often solely, represented by teeth.

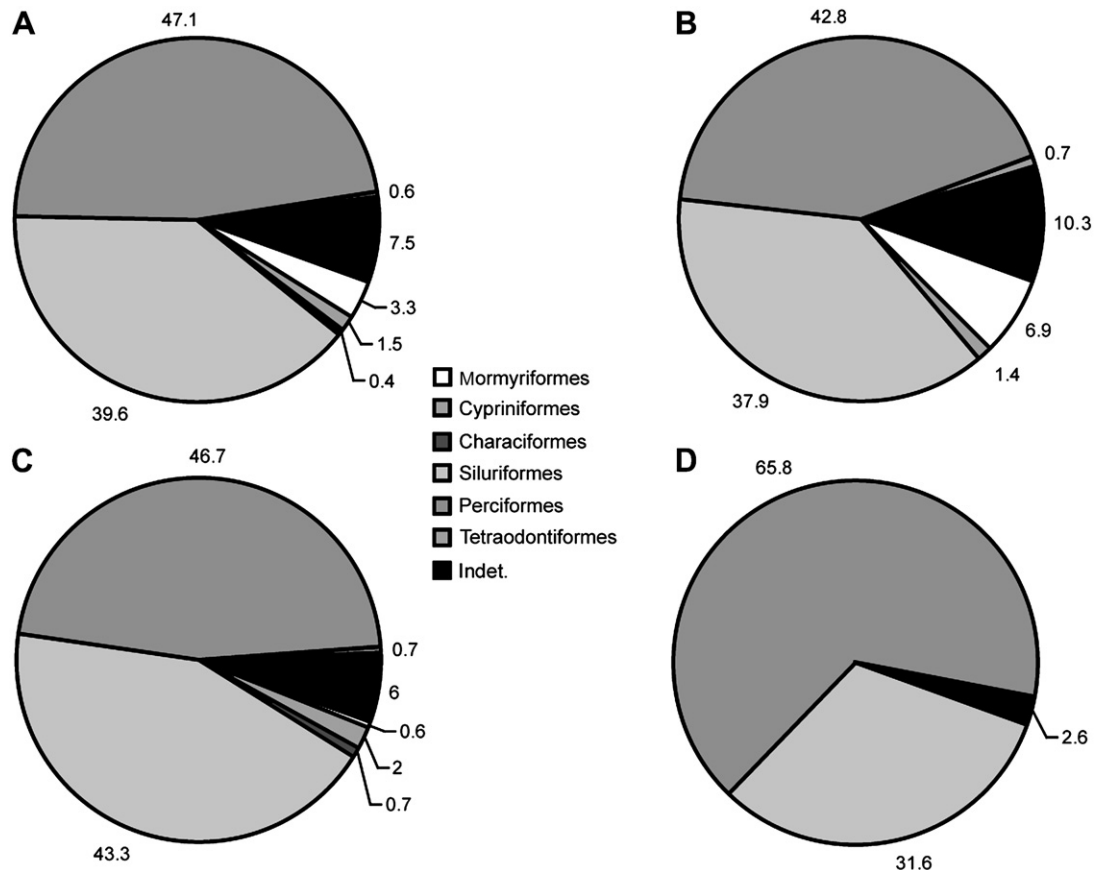
Smith et al. (1988) and Stewart (1991) suggested several factors that may mediate survivability of fish material, including body size and bone density. These factors appear to play roles in the Kibish

fish assemblage. Much of the material comes from individuals with large body size (especially clariids and Nile perch), and many species with fragile skeletons (e.g., cypriniforms, characiforms) show minimal preservation except for teeth. One exception is *Synodontis*, which is a very common fossil despite its small body size. However, the cranial elements and spines that constitute the bulk of the material from this taxon are extremely durable.

#### Paleoecology

Reconstructing the paleoecology of the Kibish ichthyofauna is complicated by a number of factors common to many fossil fish assemblages. While different sets of taxa have distinct prey and habitat preferences, taphonomic features (see above), ecological features (e.g., ontogenetic variability in habitat usage, seasonal fluctuations in available habitat and predatory behavior), and the variability of environments preserved over time may all serve to mute a paleoecological signal.

The Kibish Formation preserves mainly deltaic (or, in Member IV, lacustrine) environments (Butzer, 1969; Butzer and Thurber, 1969; McDougall et al., 2005). The fish fauna is consistent with this, containing mainly taxa found in shallow water, though the specific habitat preferences of certain species differ. In particular, species like *Gymnarchus* and *Clarias* are found in swampy water, whereas species like *Hydrocynus* and *Lates* prefer open, well-oxygenated water (Winemiller and Kelso-Winemiller, 1994; Stewart, 2002). Clariids, which are air-breathing catfishes, have high tolerance for low-oxygen environments, whereas *Lates* cannot tolerate such environments (Gautier and Van Neer, 1989; Schofield and Chapman, 1999).



**Fig. 7.** Ordinal taxonomic composition of the fauna (based on NISP) from (A) the entire Kibish assemblage, (B) Kibish Member I, (C) Kibish Member III, and (D) Kibish Member IV.

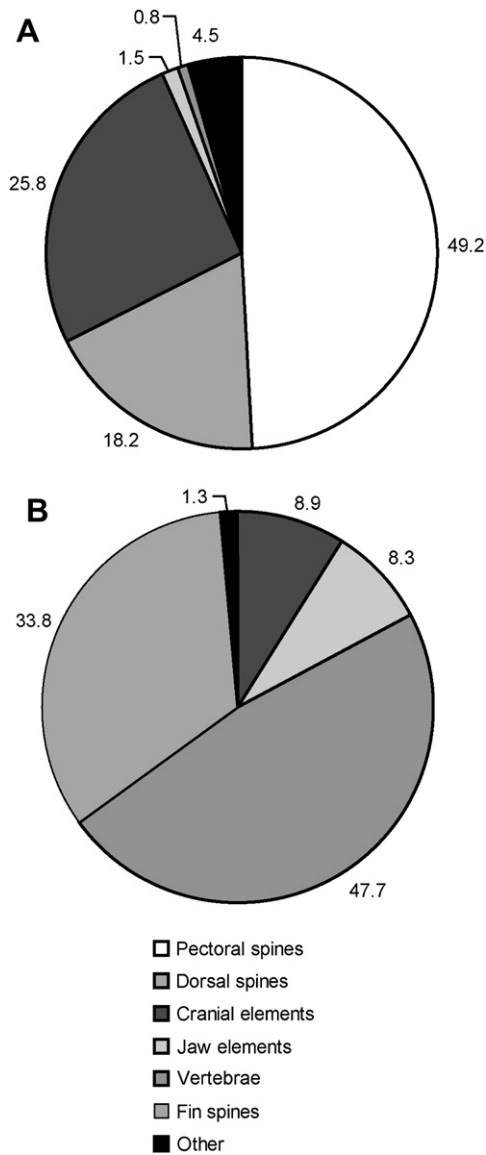


Fig. 8. Skeletal-element preservation in the Kibish fauna for (A) siluriforms and (B) *Lates*.

Size of fish preserved in a fossil assemblage may result from taphonomic factors, but also may provide clues to paleoecology. The clariids preserved in the Kibish fauna are almost without exception very large fish (Fig. 2). *Clarias* is generally bottom-dwelling and is both predator and scavenger (e.g., Olowo and Chapman, 1999); these individuals may have been too large to serve as prey for Nile perch, which is a gape-limited predator (Goudswaard and Witte, 1997), though crocodiles would not have such limitations. Thus, they may have shared more open environments with *Lates*, though they still would have returned to floodplain environments seasonally to spawn (see below).

*Synodontis* individuals from Kibish are uniformly small (<0.5 m length). These fish are dietary generalists, eating mainly invertebrates, and without strong habitat preferences (e.g., Sanyanga, 1998). Nile perch from Kibish range greatly in size (as inferred from crania and vertebrae). Ontogenetically, these fish switch their diets from one of mainly invertebrates at small size to piscivory at larger size, and move out into open water (Schofield and Chapman, 1999). Some of the Nile perch material is from extremely large individuals (Fig. 6B) and is similar to those seen in certain modern and other fossil assemblages (Thomson, 1966).

Surprising absences from the Kibish ichthyofauna include *Polypterus* and cichlids, especially tilapiines. Several explanations may account for these absences. In the case of *Polypterus*, its fragmented armored plates might have been confused with those of catfish. Alternatively, this taxon would not be found in even slightly saline environments (Stewart, 2002), and is often rare, as it is in the modern Omo-Turkana Basin. Cichlids are a more surprising absence. I might have mistaken fin spines for those of *Lates*, as mentioned above. But the teeth are distinctive and, though small, would not have been mistaken if found. It is possible that the relatively fragile skeletons of these fish were destroyed postmortem. It is also possible that the microenvironments the Kibish deposits sample did not contain cichlids, but this is unlikely, as Stewart (1991) found cichlids to be overrepresented in modern fishbone assemblages on the shores of Lake Turkana that were biased toward the littoral fauna. Another possibility is that the environments sampled by the Kibish Formation contained an abundance of small cichlids unlikely to preserve; this might reflect the openness of the environment (Schofield and Chapman, 1999). Finally, the lack of cichlids may be because fine-mesh screening was not employed in sampling, though I did look for small teeth and collected some from other species (e.g., *Gymnarchus*).

In sum, the species present and their frequencies and sizes indicate a mostly shallow environment for Members I and III, with fairly well-oxygenated conditions; perhaps a mix of fringe and channel environments within and around the delta. Kibish Member IV preserves only three taxa (*Clarias*, *Synodontis*, and *Lates*), and also contains most of the largest Nile perch individuals. Along with a molluscan fauna indicative of wave action (Van Damme and Gautier, 1972), the environment appears to have been more open water.

#### Human interaction with the fish fauna

As most of the Kibish fish material is present as isolated elements or scatters, and as signs of cultural modification are lacking (e.g., cut-marks, charring; Stewart, 1994; Stewart and Gifford-Gonzalez, 1994), there is no reason to believe that the material described here was procured or processed by humans. However, the presence of barbed bone points in Member IV (Fig. 6C; for description, see Brown, 1975) indicates that humans in the Omo Valley have a long history of fishing.

Barbed bone points similar to those from the Kibish Formation are found associated with other Middle Stone Age technologies, and often with processed fish material, throughout eastern and southern Africa (e.g., Robbins et al., 1994; Yellen, 1998). Points are reported as far back as 90 ka, at Katanda, Zaire, where they are associated with siluriform (*Clarias*, some *Synodontis*) material (Yellen et al., 1995).

Fish are generally considered to have been a seasonal food source, capable of being procured chiefly during the rainy season, when many species move onto the shallow floodplain to spawn (Stewart, 1994). Some species, including *Clarias*, may be hunted with bare hands at this time (Gautier and Van Neer, 1989; Stewart, 1994), though the large size of the individuals found in Kibish may have precluded this. Other species, like cichlids or the cyprinid *Barbus*, would require spears to catch (Stewart, 1994; Stewart and Gifford-Gonzalez, 1994).

One interesting question is whether humans living in the Omo Valley procured *Lates*, which, being an open-water fish, might have required rafts for its hunting (Van Neer, 1989). Currently, the local people use wooden dugout canoes to ferry across the Omo River; no trace of such canoes would remain in the archaeological record. However, Stewart and Gifford-Gonzalez (1994), in their study of modern Dassanetch fishing camps around Lake Turkana, noted that



Nile perch were often speared in channels and other shallow water, thus suggesting that rafts are not necessary.

Finally, on a purely speculative note, the resemblance between the form of many barbed bone points (both uniserial and biserial) and catfish spines may be purely coincidental. Alternatively, perhaps the spines impressed early hunters with their potential utility as flesh-piercing hunting implements. This may have come about through simple visual inspiration or—perhaps—more likely—through painful lesson.

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