

Fossil Fish from the Nile River and Its Southern Basins

Kathlyn M. Stewart

Abstract The differing composition of the modern Nile River system fish faunas reflects the tectonic and climatic changes which occurred throughout the Cenozoic, particularly the late Cenozoic. The pre-Pliocene fish taxa were widespread ('nilotic') and fairly uniform in composition, with some of the earliest records of several families recorded in the Nile Valley. However geomorphological and climatic changes in much of Plio-Pleistocene northern and eastern Africa severely changed the hydrology of these areas, and the fish faunas of the Nile's southern basins experienced considerable immigration and disappearances. Exchange of fish between basins apparently occurred, particularly between the Nile and Lakes Albert and Turkana. The high humidity of the early Holocene resulted in expanded lakes and rivers, leading to exchanges between the Nile and the saharan and sahelian zones. The Nile and two of its large basins now have a fish fauna with a primarily 'nilotic' distribution, while three other basins whose faunas were isolated in the Holocene have largely endemic faunas.

1 Background

Examination of the present day fish faunas of the Nile River and its drainage system demonstrates several anomalies, among them: the modern fish fauna of the main Nile River has a significantly different composition from those of Lakes Edward and Lake Victoria, although both lakes are connected to the Nile; Lake Turkana's modern fauna is very similar to that of the Nile River although it has not been connected to the Nile for thousands of years; Lake Tana is the source for the Blue Nile, but has a fauna very different from the Blue Nile (Daget et al., 1984, 1986, 1991). These anomalies, however, are not seen in the Miocene-aged faunas from the Nile and its basins; the faunas are extremely similar (at a generic level) (Arambourg & Magnier, 1961; Gaudant, 1987; Greenwood, 1951, 1973, 1974; Greenwood & Howes, 1975; Murray, 2004; Murray & Attia, 2004; Priem, 1914, 1920; Roberts,

K.M. Stewart (✉)

Canadian Museum of Nature, P.O. Box 3443, Station D, Ottawa, K1P 6P4, Canada
e-mail: kstewart@mus-nature.ca

1975; Robinson & Black, 1974; Stewart, 1990, 2003a; Van Couvering, 1977, 1982; Van Neer, 1992, 1994; Vignaud et al., 2002).

The differing composition of the Nile system fish faunas is very much tied to geomorphological changes which occurred throughout the Cenozoic, particularly in the late Cenozoic. Prior to the late Miocene, much of the African continent was a plateau, with few topographical barriers, and a network of rivers and basins which probably allowed movement of a relatively uniform and widespread fish fauna (Beadle, 1981; McCauley et al., 1982, 1998). During the latest Miocene, however, the lowering of the Mediterranean Sea led to the strengthening of the Nile River, while in Pliocene and Pleistocene central and eastern Africa, large-scale earth movements and volcanism occurred in association with the formation of the African Rift System (Adamson & Williams, 1980; Bishop, 1967; Hsü et al., 1977; Said, 1981, 1993). These forces created new barriers and basins, dramatically changing the hydrology of northern, central and eastern Africa.

This paper reviews the origins and distribution of the fossil fish in the Nile River and its four large southern lakes – Albert, Edward, Victoria, Tana – plus Lake Turkana to which it was recently connected. The data indicates that the Nile River taxa remained fairly uniform throughout the later Cenozoic, but in the southern basins the fish faunas underwent major changes in association with the dramatic geomorphological changes.

As Greenwood (1976a) stated over 30 years ago, the main problem in describing the evolutionary and biogeographic relationships of African fossil fish is that ‘few fossil remains are identified to the species level.’ The fossil record now is certainly richer than when Greenwood wrote, however most identifications are still at the level of genus, leaving the evolutionary story incomplete until more intact fossils are recovered. Further, the fossil fish record is very much biased by differential preservation and recovery of taxa. Those taxa with large, robust elements, e.g., *Lates*, are much better represented as fossils than fish such as *Citharinus*, which has elements and teeth with poor preservation potential. The more recent use of sieves during fossil recovery has resulted in a more diverse taxa, particularly of smaller and less robust fish, however most small-sized fish or those with less robust elements are virtually invisible in the fossil record.

2 The Nile River

Varying numbers exist for the number of fish taxa in the present-day Nile River *sensu lato* (including the main Nile, Victoria, Albert, White and Blue Nile), but based on Lévêque (1997) there are 127 species and 27 families; including the Claroteidae makes 28 families (Mo, 1991). Twenty of these families have a fossil record in the main Nile River valley, while the White, Victoria and Albert Nile have poor fossil records and knowledge of their modern faunas is also sparse.

According to Lévêque (1997), 27 fish species are endemic to the Nile River, while ten others are restricted to the Nile River and the rivers of eastern Africa. A full 87 species (70%) have a “nilotic” distribution, defined here as dispersion

across the present saharan and sahelian zones, and including the Nile River system, the Niger River system, the Senegal River system and the Lake Chad basin. These waterways are at present separated by vast areas of desert and some highlands. The discontinuous dispersal of these faunas suggests common waterways in the past which connected these basins.

One period of faunal dispersion was during the Holocene, a time of high humidity and productive waterways across the saharan and sahelian zones of Africa. There is considerable fossil evidence that a mature, relatively uniform nilotic fauna existed at this time along the Nile River valley and across northern Africa, with sites ranging from the Nile valley westwards to Arouane, in northern Mali. These sites contained a diversity of fish taxa, including large Nile perch and catfish, and other aquatic fauna such as hippopotami and crocodiles, indicating large, permanent waterways (Daget, 1959, 1961; Petit-Maire et al., 1983; Van Neer, 1989).

However, there must also have been *previous* dispersions of a uniform fish fauna, because many of the same taxa are found in pre-Holocene fossil sites across northern, eastern and central Africa (few fossil sites exist in western Africa, and southern African fish have a different history). Many of the earliest or near-earliest records for this fauna are found in fossil sites along the present Nile River valley.

The fossil record for this fauna essentially begins with the recovery of eight families from the highly fossiliferous Eocene and Oligocene deposits in the Fayum Depression, about 100km southwest of modern Cairo (Fig. 1). Previously in the Cenozoic the Tethys Sea had intermittently covered northern Egypt and most fish faunas were marine. Four endemic freshwater families (Protopteridae, Polypteridae, Gymnarchidae and Alestidae), and four other families (Clupeidae, Cichlidae and Latidae) are reported from the Fayum (Table 1). All are present in the modern Nile.

Two archaic genera – the protopterid *Protopterus* (lungfish), belonging to a group dating back to the Devonian, and polypterid *Polypterus*, a primitive, fleshy finned fish showing some similarities to ancient palaeonisciforms (Carroll, 1988) – have fossil records from the Cretaceous to the Oligocene. The two modern lungfish species now in the Nile River – *Protopterus aethiopicus* and *P. annectens* – were first identified in Oligocene deposits north of Fayum in what is now the western Nile valley (Greenwood, 1974; species identification is “cf”). Such species longevity indicates considerable conservatism of these taxa.

The earliest known gymnarchid teeth have been recovered from the Birket Qarun Formation (late Eocene) at Fayum (A. Murray, personal communication; personal observation), and are identical to those of modern *Gymnarchus niloticus*, an eel-like mormyroid which uses an electrical field to sense its environment. Surprisingly, while *Gymnarchus* is present in the Nile and has a modern nilotic distribution, it has no fossil record in the Nile River between the Oligocene and the Holocene. This lack may be due to sampling or preservational bias, but gymnarchid teeth are robust and distinctive, so its absence may be real.

Multi-cusped alestid teeth are reported from the Jebel Qatrani Formation (late Eocene and Oligocene) at Fayum, which are similar to teeth of modern *Alestes* and *Brycinus* species present in the Nile River (Murray, 2004; Roberts, 1975; Van Couvering, 1977). Earlier alestid teeth have been reported from other

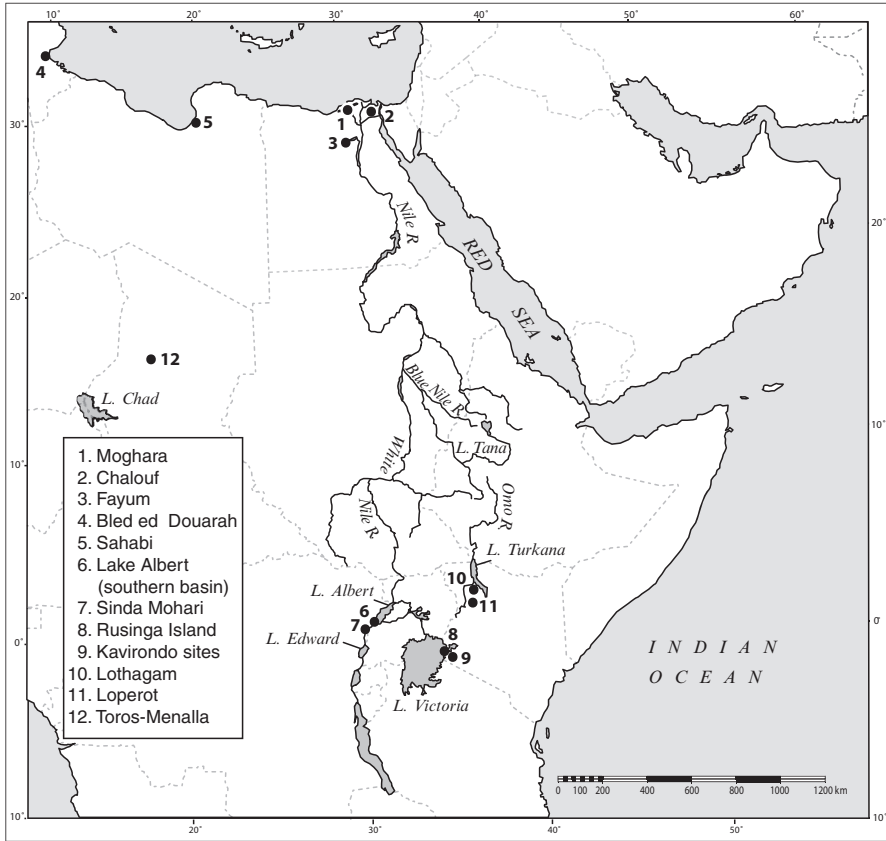


Fig. 1 Map of Eocene/Oligocene, early and late Miocene sites mentioned in text and/or tables

northern African sites, including in Morocco, and dating from the Cretaceous to the Oligocene. These reports indicate the widespread dispersion of this endemic family already in the early Cenozoic. While Alestidae are present in the modern Nile, similar to *Gymnarchus*, this family has no fossil record in the Nile River valley between the Oligocene and the Pleistocene.

The oldest African records of the large perch *Lates* (*L. qatraniensis*), of the family Cichlidae (cf *Tylochromis*), and of the Oligocene freshwater clupeomorph *Chasmoclupea aegyptica* were also reported from the Fayum's early Oligocene Jebel Qatrani Formation (Murray, 2004; Murray & Attia, 2004; Murray et al., 2005). *Lates* has a widespread fossil record in all but southern Africa throughout the Neogene. The modern cichlid *Tylochromis* is present in West Africa and the Congo basin, but not in eastern or northern Africa. Its Oligocene presence in northern Africa (Fayum) suggests that it had a more widespread presence at that time. *Chasmoclupea* was preserved in fluvial deposits, although clupeomorphs are usually found in marine sediments. *Chasmoclupea* is extinct; only one clupeid (*Alosa fallax*) is now present in the Nile River estuaries.

Table 1 African freshwater fish from the Eocene, Oligocene, early and late Miocene, listed by age and site. Data from Arambourg and Magnier, 1961; Gaudant, 1987; Greenwood, 1951, 1973, 1974; Greenwood and Howes, 1975; Murray, 2004; Murray and Attia, 2004; Murray et al., 2005; Priem, 1914, 1920; Roberts, 1975; Robinson and Black, 1974; Stewart, 2003a; Van Couvering, 1977, 1982; Van Neer, 1994; Vignaud et al., 2002

Sites → Taxa ↓	Eocene/ Oligocene			Early Miocene →			Late Miocene →				
	Fayum	Moghara	Chalouf	Gl. Zelten, Sahabi	Bled ed Douarah	Toros Menalla	Southern L. Albert ^a	Victoria Basin ^b	Loperot	Lothagam	
<i>Protopterus</i> cf <i>annectens</i>	X										
<i>Protopterus</i> cf <i>aethiopicus</i>	X						X	X	X	X	
<i>Protopterus</i> sp.				X	X	X		X	X	X	
<i>Polypterus</i> sp.											
<i>Chasmodon</i> sp.	X										
<i>Heterotis</i> sp.											
<i>Gymnarchus</i> cf <i>niloticus</i>							X			X	
<i>Gymnarchus</i> sp.						X				X	
Gymnarchidae	X										
<i>Hydrocynus</i> sp.						X	X			X	
<i>Sindacharax lepersomei</i>							X			X	
<i>S. lothagamensis</i>										X	
<i>Sindacharax</i> sp.						X				X	
<i>Alestes/Brycinus</i>							X			X	
Alestidae	X										
<i>Distichodus</i> sp.							X			X	
Characiformes									X		
<i>Labeo</i> sp.							X				
<i>Barbus</i> sp.											
Cyprinidae									X		

(continued)

Table 1 (continued)

Sites → Taxa ↓	Eocene/ Oligocene			Early Miocene →			Late Miocene →			
	Fayum	Moghara	Chalouf	Gl. Zelten, Sahabi	Bled ed Douarah	Toros Menalla	Southern L. Albert ^a	Victoria Basin ^b	Loperot	Lothagam
Aff. <i>Bagrus</i>										X
<i>Bagrus</i> sp.			X							
<i>Clarotes</i> sp.				X			X			X
<i>Auchenoglanis</i> sp.							X			
<i>Clarias</i> sp.			X	X	X					X
Clariidae							X			
<i>Synodontis</i> sp.			X	X			X	X		X
Mochokidae							X			
Siluroidea/Siluriformes				X	X		X	X	X	
<i>Semlikitchthys</i>							X			
cf. <i>Semlikitchthys</i>										X
<i>Lates niloticus</i>										X
<i>Lates cf niloticus</i>					X					X
<i>L. qatramiensis</i>	X									
<i>Lates</i> sp.		X		X	X		X	X		X
Latidae										
cf. <i>Tylochromis</i>	X									
Cichlidae							X	X	X	
Percoidae										X

^a Includes Sindia Mohari.^b Includes Rusinga Island, Kavirondo.

The early and late Miocene sites of Moghara (Priem, 1920) and Chalouf (Priem, 1914) respectively, are located near the present-day Nile delta (Fig. 1). Their faunas are small, but contain the earliest African remains of the endemic catfish *Synodontis* and *Bagrus*, the cyprinid *Barbus* and an early record for the clariid *Clarias* (Table 1). All are reported from other Miocene sites in northern and eastern Africa, and all are present in the modern Nile. *Synodontis* is a small mochokid catfish which is speciose in the modern Nile. *Barbus* is suggested to have entered Africa from Saudi Arabia in the early Miocene (Otero, 2001). Modern *Clarias* is an airbreather which can live up to 18 hours out of water, can use its pectoral fins to “walk” between waterways, and is tolerant of deoxygenated waters; this may explain its ubiquity in African fossil sites.

A recent look at the *Lates* specimens from Moghara indicates that some elements almost certainly belong to *Semlikiichthys* (pers. obs; A. Murray pers. comm.), a large extinct percoid related to *Lates* (Otero & Gayet, 1999), while other elements are probably *Lates*. *Semlikiichthys* is also identified or tentatively identified at other Miocene sites (Stewart, 2003a) and several Pliocene sites (discussion below) (Tables 1 and 2). Many of the genera/families just described are also known from other northern African Miocene-aged sites, including Bled ed Douarah, Tunisia (Greenwood, 1973), Gebel Zelten, Libya (Arambourg & Magnier, 1961), Sahabi (Gaudant, 1987) and Toros-Menalla, Chad (Vignaud et al., 2002) (Fig. 1; Table 1), as well as in several sites in central and eastern Africa (discussed below). The widespread distribution of these genera and/or families at that time suggests a common waterway across northern Africa. Possible evidence for this waterway comes from radar imaging data and field studies in the eastern Sahara (Issawi & McCauley, 1992; McCauley et al., 1982; McCauley et al., 1998). These suggest that intermittently from the Oligocene until the Middle Miocene (ca 40 to 15 mya), streams flowed south and west from the Red Sea Mountains through what is now Egypt into the Sudan and Libya. About 25 mya, increased uplift of the Red Sea mountains resulted in the strengthening of several of these rivers, and there is evidence that one or more major river systems were flowing as far west as the Chad Basin, and into the Niger Basin. These rivers would have acted as conduits for the Miocene (and possibly Oligocene) fish fauna, from the Red Sea Mountains across northern Africa, resulting in widespread distribution of many of the same genera and species.

In the latest Miocene (ca 6–5 my), drying of the Mediterranean Sea basin and its rapidly lowering level altered the course of the “Nile”, then a stream flowing in the vicinity of its present valley (Butzer, 1980). As the sea level fell (the Messinian Salinity Crisis) (Hsü et al., 1977), the “Nile” presumably strengthened, partly through stream capture, and became a larger more powerful drainage. This powerful river must have allowed the movement of fish in a north/south direction, which eventually opened up faunal exchange between the Nile and the southern/eastern basins.

The earliest large and diverse freshwater fish fauna which can be attributed to the “new” main Nile is from Wadi Natrun, an important late Pliocene site located on the western edge of the modern Nile delta (Fig. 2). The fish have been studied by a variety of scientists throughout the twentieth century (Greenwood, 1972; Stromer,

Table 2 African freshwater fish from the early and late Pliocene, listed by age and site. Data from Feibel, 1988, 1994; Greenwood, 1972; Greenwood and Howes, 1975; Schwartz, 1983; Stewart, 1990, 2003a, b; Stewart and Murray, in press; Stromer, 1914; Van Neer, 1992, 1994; Weiler, 1926; White, 1926

Sites→ Taxa↓	Early Pliocene→					Late Pliocene→				
	Southern L. Albert ^a	East Turkana	Kanapoi	Lothagam	Wadi Natrun	Southern L. Albert ^b	Lusso, L. Edward	East Turkana	Lothagam	Omo River
<i>Dasyatis africana</i>								X		
<i>Protopterus</i> sp.	X			X	X			X	X	
<i>Polypterus</i> sp.		X	X	X	X			X	X	X
<i>Heterotis</i> sp.				X					X	
<i>Hyperopisus</i> sp.	X		X		X	X		X		
? <i>Hyperopisus</i>					X		X			
<i>Gymnarchus</i>										
<i>niloticus</i>		X						X		
<i>Gymnarchus</i> cf. <i>G.</i>	X									
<i>niloticus</i>										
<i>Gymnarchus</i> sp.			X	X			X	X	X	
<i>Banocharax</i> sp.	X						X	X		
<i>Hydrocynus</i> sp.	X	X	X	X	X	X	X	X	X	
<i>Sindacharax mutetii</i>			X	X				X	X	
<i>S. howesi</i>			X					X	X	
<i>S. deserti</i>				X	X			X	X	
<i>S. greenwoodi</i>				X				X	X	
<i>S. lepersonnei</i>	X					X				
<i>S. lothagamensis</i>			X	X						
<i>S. omoensis</i>			X	X			X	X	X	X
<i>Sindacharax</i> sp.		X	X	X			X	X		
<i>Alestes/Brycinus</i>	X						X			
<i>Brycinus</i>			X				X	X		
<i>macrolepidotus</i>										
<i>Distichodus</i> sp.	X	X	X	X			X			
<i>Gen. et sp. nov.</i>							X			
Characiformes							X			X

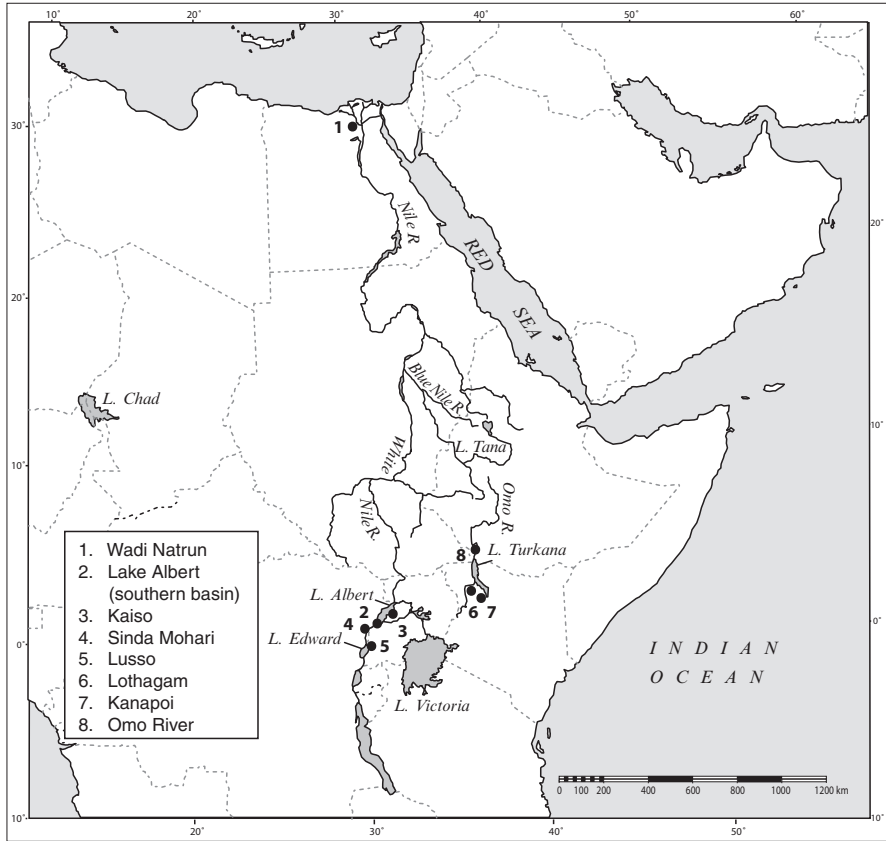


Fig. 2 Map of early and late Pliocene sites mentioned in text and/or tables

1914; Weiler, 1926) (Table 2). The site was formed during a series of marine transgressions alternating with fluvial sediments (El-Shahat et al., 1997), and while it contains some marine fish, most are freshwater. This freshwater fauna consists of several genera not recorded in previous “Nile” sites, but which are known from other Miocene northern and eastern African sites (Tables 1 and 2).

One of the more intriguing aspects of the Wadi Natrun fauna are three extinct taxa (Greenwood, 1972): the characiform *Sindacharax deserti*, a mormyrid *?Hyperopisus* and *Semlikiichthys*, the large percoid first recorded in early Miocene Moghara. *Sindacharax* has uniquely ridged molariform teeth, which differ from *Alestes*’ cusped teeth, for crushing hard objects, probably molluscs. *S. deserti* is also known from late Pliocene Lakes Albert and Turkana, indicating a connection between these basins. The last known record of *Sindacharax* is about 700,000 years ago, in the Turkana basin (Feibel, 1988). The extinct taxon *?Hyperopisus* is also represented by very large crushing-type teeth, which show considerable similarity to the much

smaller teeth of the modern mormyrid, *Hyperopisus. Semlikiichthys* seems to have disappeared at the same time as the molluscivore fish (discussion below), which may have been its chief prey.

The modern Nile fauna is dominated by the Mormyridae, Cyprinidae, Mochokidae and Cichlidae, and all are present at Wadi Natrun (Greenwood, 1972) The mormyrid *Hyperopisus* is a monotypic genus (*H. bebe*) present in the modern Nile, with a nilotic distribution. It is known from widespread early Pliocene sites in northern, central and eastern Africa. The cyprinids *Labeo* and *Barbus* have a modern African and Asian distribution; both are in the modern Nile. Both have a widespread Pliocene distribution.

No fish faunas have been reported from the main Nile Valley in the early Pleistocene, a period when the Nile may have ceased to flow until the middle Pleistocene (Said, 1981, 1993). Isolated *Lates niloticus* vertebrae were recovered in middle/late Pleistocene deposits of the White Nile near Malakal, Sudan (Fig. 3)

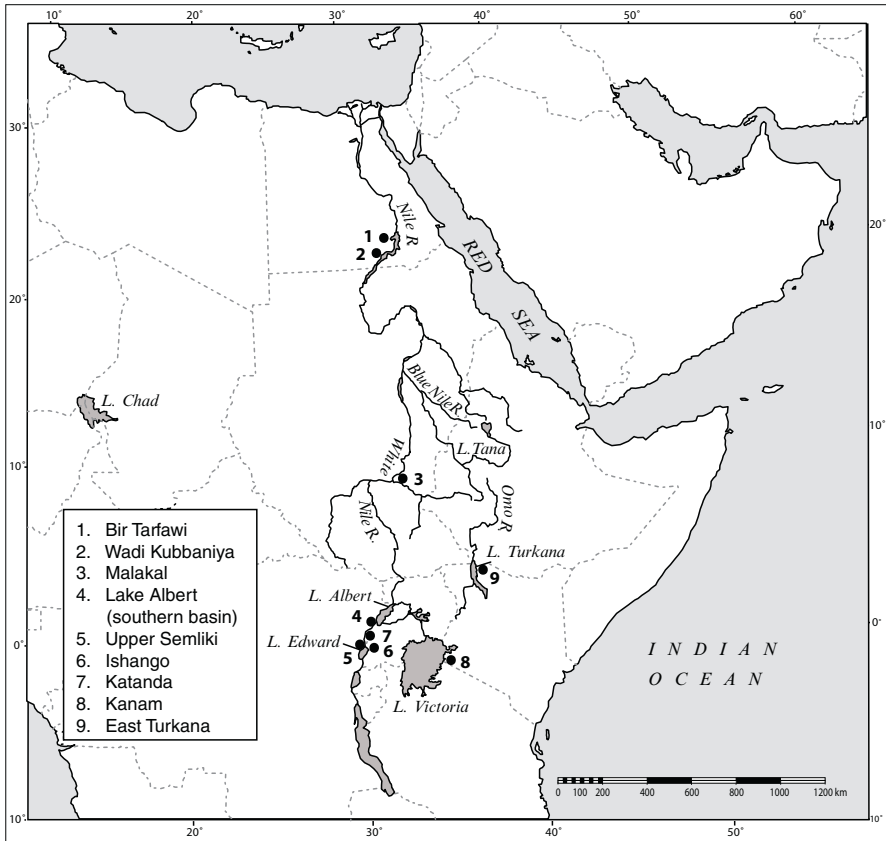


Fig. 3 Map of early, middle and late Pleistocene sites mentioned in text and/or tables

(Williams et al., 2001), indicating the presence of a reasonably large well-oxygenated body of water in this area. A much larger fauna is known from Bir Tarfawi in southern Egypt, now located in the middle of desert (Fig. 3). It dates to about 125,000BP, and contains mormyrids, *Alestes* or *Brycinus*, *Bagrus*, *Clarias*, *Synodontis*, *Lates niloticus* and Tilapiini (Table 3) (Van Neer, 1993). All but *Alestes/Brycinus* are known from Wadi Natrun. Alestidae were first recorded in the Paleogene Fayum deposits, but they have no Nile River record until Bir Tarfawi, surprising, as they were widespread in pre-Miocene northern Africa; their small teeth may have precluded recovery.

The later Pleistocene was also a time of drought, seemingly through northern and eastern Africa, including the Nile. Between 40,000 and 25,000BP, extensive evaporates along the White Nile suggest that major contributions of water from Lakes Albert and Victoria were rare or even non-existent (Adamson & Williams, 1980; Lamb et al., 2007) drastically reducing some sections of the Nile. There is also evidence from Lakes Albert and Victoria that very low lake levels prevented overflow into the White Nile prior to 11,500 years ago (Talbot et al., 2000), and similarly that low lake levels in Lake Tana prior to 15,000 years ago reduced outflow through the Blue Nile (Lamb et al., 2007), again reducing flow in the Nile (see discussion below).

Unfortunately there is little faunal evidence to determine if and which species was lost at this time. Virtually all known sites during this period are archaeological in origin, meaning taxa were biased to human selection. Accordingly, several late Pleistocene fishing sites along the Nile, with primarily *Clarias* remains, provide little insight into diversity of taxa at this time. However the late Pleistocene archaeological sites from Wadi Kubbania and northern (Nubian) Sudan along the main Nile (Fig. 3) contain *Bagrus*, *Synodontis*, *Tilapia* and *Lates* (Table 3), which show taxonomic continuity from the Mio-Pliocene and into the Holocene (Gautier & Van Neer, 1989). The fauna also includes the earliest records of the catadromous eel *Anguilla anguilla*, *Barbus bynni* and *Clarias* cf *garipepinus*, all of which inhabit the modern Nile. *Clarias* is tolerant of de-oxygenated waters, while *Barbus* and *Lates* are not, so presumably the Nile or its tributaries retained some areas of well-oxygenated water. Of note is the absence of *Sindacharax*, *?Hyperopisus* and *Semlikiichthys* from the middle and late Pleistocene sites of Bir Tarfawi and the Wadi Kubbania sites. Their last known presence in the main Nile was in the late Pliocene at Wadi Natrun. Possibly during the extreme drought of the early Pleistocene, these taxa disappeared from the river. The specialized teeth of the former two genera may have reduced their ability to adapt to a different diet.

The Holocene onset of rains and humidity, and new inflows from the southern lakes strengthened the Nile River, and many Holocene archaeological faunas are reported from the main Nile Valley (and across the saharan and sahelian zones). The early Holocene Wadi Howar sites (Fig. 4; Table 4) (Van Neer & Uerpmann, 1989) include three taxa of fish *Heterotis niloticus*, *Barbus bynni* and *Lates niloticus*, all of which are present in the modern Nile. These sites are located on dry or seasonal wadis which could not today sustain any of these fish, all of which

Table 3 African freshwater fish from the early, middle and late Pleistocene, listed by age and site. Data from Arambourg, 1947; Brooks et al., 1995; Feibel, 1988; Greenwood, 1959, 1968, 1976b; Greenwood and Howes, 1975; Schwartz, 1983; Stewart, 1990; Trewavas, 1937; Van Neer, 1986, 1993, 1994

Sites→ Taxa↓	Pleistocene→									
	Early Pleistocene→					Middle Pleistocene				
	Southern Lake Albert	Upper Semliki River	East Turkana	Omo River	Bir Tarfawi	Wadi Kubbamiya	Nubian Sudan	Ishango	Katanda	
<i>Dasyatis africana</i>			X							
<i>Protopterus cf P. aethiopicus</i>							X	X		
<i>Protopterus</i> sp.		X					X	X		
<i>Polypterus bichir</i>				X						
<i>Polypterus</i> sp.			X					X		
<i>Anguilla anguilla</i>			X			X				
<i>Heterotis</i> sp.			X						X	
<i>Hyperopisus</i> sp.	X		X							
? <i>Hyperopisus</i>		X								
Mormyridae					X				X	
<i>Gymnarchus niloticus</i>						X				
<i>Gymnarchus</i> sp.		X							X	
<i>Bunocharax</i> sp.	X									
<i>Hydrocynus</i> sp.	X	X								
<i>S. greenwoodi</i>				X						
<i>Sindacharax</i> sp.		X					X			
<i>Alestes/Brycinus</i> sp.		X								
<i>Distichodus</i> sp.		X								
<i>Citharinus</i> sp.		X								
<i>Labeo</i> sp.										
<i>Barbus cf altianalis</i>								X		
<i>B. bynni</i>						X		X (cf)		
<i>Barbus</i> sp.	X	X					X	X	X	

(continued)

Table 3 (continued)

Sites→ Taxa↓	Early Pleistocene→			Middle Pleistocene				Late Pleistocene→		
	Southern Lake Albert	Upper Semliki River	East Turkana	Omo River	Bir Tarfawi	Wadi Kubbaniya	Nubian Sudan	Ishango	Katanda	
<i>Bagrus</i> sp.		X		X	X	X	X	X	X	
<i>Clarotes laticeps</i>				X						
<i>Clarotes</i> sp.		X	X					X		
<i>Auchenoglanis</i> sp.		X								
<i>Clarias gariepinus</i>						X(cf)		X		
<i>Clarias</i> sp.		X	X	X	X		X	X	X	
Clariidae	X									
<i>Synodontis cf schall</i>								X		
<i>Synodontis cf frontosus</i>								X		
<i>Synodontis</i> sp.	X	X	X	X	X	X	X		X	
cf <i>Semlikiichthys</i>		X								
<i>L. niloticus</i>		X		X	X					
<i>Lates cf L. niloticus</i>	X							X		
<i>Lates</i> sp.		X	X				X	X	X	
<i>Tilapia</i> sp.								X		
Tilapiini					X					
Cichlidae		X	X	X					X	
<i>Tetraodon</i> sp.	X		X							



Fig. 4 Map of Holocene sites mentioned in text and/or tables

need permanent, oxygenated waters. Three extensive Holocene faunas from Abu Darbein, El Damer, and Aneibis, located along the Nile near the junction of the Nile and Atbara Rivers (Haaland & Magid, 1995; Peters, 1995), contain 21 genera with 16 named to species (Fig. 4; Table 4); all are in the modern Nile River. Continuity from the Pleistocene to the present Nile is seen with the species *Anguilla anguilla*, *Barbus bynni* and *Clarias cf gariepinis*, and the genera *Bagrus*, *Synodontis* and *Tilapia*. The taxa *Gymnarchus niloticus*, *Distichodus* sp. and *Tetraodon lineatus* are new appearances in the Holocene Nile, and may demonstrate emigration from other lakes or rivers. They are present in the modern Nile, but have no Nile Mio-Pleistocene fossil record, although all preserve well as fossils. A possible source of these immigrants is the Turkana basin, where they were recorded in the Pleistocene, and may have entered the Nile in the Holocene high water periods. Alternatively they could have come indirectly from the Niger or other western basins, but the Turkana route is shorter and more direct (via the Sobat and Pibor Rivers).

Table 4 African freshwater fish from the Holocene, listed by age and site. Data from Van Neer, 1988; Van Neer and Uerpmann, 1989; Marshall and Stewart, 1995; Peters, 1995; Phillipson, 1977; Robbins, 1974; Stewart, 1989

Sites→ Taxa ↓	Holocene→			
	Nile River near Atbara River	Wadi Howar sites	Gogo Falls	Turkana Basin sites
<i>Protopterus aethiopicus</i>	X			
<i>Protopterus</i> sp.				
<i>Polypterus bichir</i>				
<i>Polypterus</i> sp.	X			
<i>Anguilla anguilla</i>				
<i>Heterotis niloticus</i>	X	X		
<i>Hyperopisus bebe</i>	X			
<i>Mormyrops anguilloides</i>	X			
Mormyridae	X			X
<i>Gymnarchus niloticus</i>	X			
<i>Gymnarchus</i> sp.				
<i>Hydrocynus</i> sp.	X			X
<i>Alestes/Brycinus</i> sp.	X			X
<i>Distichodus</i> sp.	X			
<i>Citharinus</i> sp.	X			
Characiformes	X			
<i>Labeo</i> sp.	X			X
<i>Barbus cf altianalis</i>				
<i>B. bynni</i>		X		
<i>Barbus</i> sp.	X		X	X
Cyprinidae				
<i>Bagrus bayad</i>	X			X
<i>B. docmak</i>	X			
<i>Bagrus</i> sp.	X		X	X
<i>Clarotes laticeps</i>	X			
<i>Clarotes</i> sp.				
<i>Auchenoglanis</i> sp.	X			
<i>Heterobranchus</i> sp.	X			
<i>Clarias gariepinus</i>				
<i>Clarias</i> sp.	X		X	X
Clariidae	X			
<i>Synodontis schall</i>	X			X
<i>S. serratus</i>	X			
<i>S. sorex</i>	X			
<i>S. batensoda</i>	X			
<i>S. membranaceus</i>	X			
<i>Synodontis</i> sp.	X		X	X
<i>Malapterurus electricus</i>	X			
<i>Lates niloticus</i>	X	X		
<i>Lates cf niloticus</i>				
<i>Lates</i> sp.				X
<i>Tilapia</i> sp.				
Tilapiini	X			
Cichlidae			X	X
<i>Tetraodon lineatus</i>	X			X

3 Fish of the Nile's Southern Basins: Lakes Albert, Edward, Victoria, and Turkana

The fossil fish faunas of the southern Lakes Albert, Edward, Turkana, and to a lesser extent, Lake Victoria, are extensive compared to that of the Nile River. Detailed analysis of these faunas is ongoing and provides considerable insights both into the evolution of the African faunas, and into geomorphological changes which occurred in central and east Africa during the Plio-Pleistocene (Greenwood, 1974; Stewart, 2001). However, because the known connections of the basins with the Nile River are fairly recent, my discussions will be limited to a brief outline of their past faunas and their possible exchanges and/or influences on the Nile fauna.

3.1 Lake Albert

Modern Lake Albert is connected to the White and main Nile through the Albert Nile. Its fish fauna reflects this direct connection: all of its 14 families are present in the modern Nile. Of its 48 species (Witte, 2009), 30 are shared with the Nile (Greenwood, 1966), while 6 are endemic, and the others have a more restricted distribution. Twelve of Lake Albert's present-day 14 families have a fossil record. Lake Albert was initially formed as a shallow basin in the Middle/Late Miocene. At this time Africa was still a plateau, and rifting and uplift had not yet disrupted rivers which flowed westwards (the present day Kafu, Katonga and Kagera) across the Albert, Edward and Victoria basins and probably into the Congo basin (Cooke, 1958; Bishop, 1965; Bishop & Trendall, 1967). The Albert basin filled from these rivers, and provided colonizing opportunities for their fish. The Late Miocene fauna, from the southern Albert basin, including Sinda Mohari (Van Neer, 1992, 1994), overlaps completely with the Miocene northern African faunas, containing all but one of the genera/families reported (Table 1; Fig. 1), plus additional taxa. This overlap indicates that, through connecting waterways, the same northern African Miocene fauna was also distributed through central and eastern Africa (see also Lake Turkana).

Because of Lake Albert's position between the Nile and the vast fish faunas of the Congo River basin, it may have acted as a conduit for taxa between these systems.

Three taxa in the lake's Miocene deposits are not recorded in Mio-Pliocene northern Africa, including the citharinid *Distichodus*, a large characoid with bifurcate teeth, the cyprinid *Labeo*, and the catfish *Auchenoglanis*. *Labeo* and *Distichodus*, and to a lesser extent *Auchenoglanis*, are very speciose in the modern Congo basin, with several endemic species, and may therefore be emigrants from the Congo basin via the westward flowing rivers. The extinct, large *Sindacharax lepersonnei*, may also have derived from the Congo basin, or is endemic to Lake Albert, as it is not known elsewhere in Africa.

The appearance of 13 “new” taxa in early Pliocene southern Albert deposits (Van Neer, 1992, 1994) (Table 2; Fig. 2) suggests new inflow/outflows in the lake, possibly resulting both from large-scale tectonic movements in the Pliocene, and from a humid period where expanded lakes and rivers must have facilitated exchange of fish faunas: Lakes Turkana, Chad, and Manonga, are all reported as much expanded at this time (Feibel, 1988; Griffin, 2006; Harrison, 1997). The appearance of *Sindacharax deserti*, *Bagrus*, *Lates niloticus* and *Tetraodon* suggests a connection with the Turkana basin, the only other early Pliocene fauna which contains all four taxa. Depending on the location of the pre-rift watershed, western flowing rivers may have linked both basins. Alternatively, new indirect connections with the Nile may have occurred, although the Wadi Natrun fossil record does not contain all these taxa. Additionally, the appearance of *Tetraodon* and the extinct *Chrysichthys* in Pliocene Lake Albert may indicate a connection with the Congo basin, as neither taxon has a fossil record in northern Africa, and both are very speciose in the modern Congo basin; *Tetraodon* has five species, while *Chrysichthys* has 16 species (Daget et al., 1986, 1991).

The “new” extinct taxa reported from early Pliocene southern Lake Albert – *Bunocharax*, a large characoid with robust jaws and large molariform teeth, *Nkondobagrus longirostris*, a bagrid with similarities to the modern catfish *Bagrus*, and *Chrysichthys macrotis*, a bagrid catfish similar to the modern genus (Van Neer, 1994), plus *S. lepersonnei* and *Semlikiichthys* provide an intriguing look at a fauna which no longer exists, but which inhabited the Albert and Edward basins, and to a lesser extent the Turkana basin and the Nile River. The extinct taxa were large fish, growing over a half a meter. At least six taxa (including two from Lake Edward, described below) had robust, molariform teeth, with such morphology suggesting a specialized trophic niche of mollusc eating. Teeth of these taxa show considerable wear, with ridges and cusps often completely worn away, and there is considerable pitting of the occlusal surface. These characters are consistent with a diet of crushing hard objects. Several of the extant taxa also were adapted for mollusc-eating. Pliocene fossil deposits in the Albert and Edward basins contain millions of mollusc shells, providing food for the large number of molluscivores, both extinct and extant.

Fossil faunas are, unfortunately, virtually unknown from the Congo basin, which due to its proximity and connection to Albert via western rivers, may also have shared this fauna. The disappearance of huge numbers of molluscs in the Pleistocene (Van Damme & Van Doclaer, 2009) may be linked to the disappearance of many of the molluscivore fish, which may have been too specialized to adapt to another diet. The diets of the other extinct taxa – *Semlikiichthys*, *Nkondobagrus* and *Chrysichthys macrotis* – are unknown, but modern *Chrysichthys auratus*, in the Nile, also preys mainly on molluscs. Relatives of the other two taxa are piscivores, and probably preyed on the large populations of molluscivore fish. By the late Pliocene in southern Albert and the Kaiso sites, all but *Bunocharax* and *Chrysichthys* have disappeared from the Albert basin.

The early Pleistocene fauna is the last large fauna known from Lake Albert (Van Neer, 1994) (Table 3; Fig. 3). It again shows several additions and disappearances

compared to the Pliocene faunas, probably resulting from tectonic changes in the Western Rift. Most of the molluscivores have disappeared. When the early Pleistocene fauna is compared with the fauna of present-day Lake Albert, it appears that several genera disappear during the Pleistocene, including *Bunocharax* (extinct), *Clarotes* and *Tetraodon*. This may be due to two long periods of very low lake levels between 25,000 and 12,500 BP (Beuning et al., 1997), or between 40,000 and 25,000 BP, when extensive evaporates along the White Nile suggest that major contributions of water from Lake Albert and Victoria were rare or even non-existent (Adamson & Williams, 1980).

The similarity between the modern Nile River and Lake Albert faunas, and the lack of Albert endemics, reflects their present day connection. Without late Pleistocene fossils, it is impossible to know how many taxa in the modern lake derive from its pre-Holocene fauna, particularly after drought in the Pleistocene. Modern Albert taxa not present in the Nile but shared with Lake Victoria, like *Barbus neu-mayeri* (De Vos & van den Audenaerde, 1990), may reflect a late Pleistocene connection which no longer exists (Murchison Falls is a barrier to fish movement via the Victoria Nile). Fish which occur in both the Nile and Congo basins, e.g., *Xenomystus nigri* (Roberts, 1992) may have entered the Albert basin from the Congo in the Mio-Pliocene and later entered the Nile.

3.2 Lake Edward

Modern Lake Edward is connected to Lake Albert via the Semliki River, and then indirectly to the White Nile. Its fish fauna is isolated from Lake Albert and the Nile, as the Semliki River rapids are a barrier to fish. Lake Edward has only eight families of fish, which contain 81 species, of which 56 are endemic. Few species are shared with the Nile River. Of the 81 species, 74% are cichlid, and about half are endemic (Snoeks, 2000). A composition dominated by endemic cichlids has clearly neither had a recent connection with the Nile, which has only eight cichlid species, nor is it a characteristic nilotic fauna. Edward's past fauna, however, had considerable overlap with the Nile system, bearing little resemblance to its modern fauna.

None of Lake Edward's late Pliocene ten genera occur in the modern lake (Table 2; Fig. 2). The fauna, from the Lusso site, contains a mix of taxa seen in the northern African Miocene sites (*Gymnarchus*, *Hydrocynus*, *Alestes*, *Sindacharax*, *Synodontis* and *Lates niloticus*), as well as four extinct taxa. Surprisingly, the fauna differs considerably from the geographically close Lake Albert taxa, suggesting the two faunas are not connected, similar to today (Table 2). Of the four extinct taxa, one is probably shared with Lake Albert (*Bunocharax*, rare at Edward), one with the Nile (?*Hyperopisus*) and two known only in Lake Edward (*Gen et sp. nov.* and *Sindacharax* sp.). *Gen et sp. nov.* is yet another probable characid with flat crushing teeth (Stewart, 1990).

The appearance of nine "new" taxa in extensive early and late Pleistocene faunas from the Upper Semliki, Ishango and Katanda (Table 3; Fig. 3) suggest

a new connection with either the Nile system or the Turkana basin. This connection may perhaps have been via Lake Albert, although the very different compositions of the Albert and Edward faunas make this unlikely. Continuing and severe tectonic movements could have created new indirect connections with the Turkana basin or the Nile, particularly as the existence of the White Nile is now documented (e.g., Williams et al., 2003).

Lake Edward is the only one of the Nile's southern lakes to have a detailed record of late Pleistocene faunal change. Very dramatic changes to the extensive Pleistocene Lake Edward fauna are recorded in the well-stratified Ishango archaeological site, where later Pleistocene levels contain large amounts of volcanic ash. These ash levels are followed by levels with drastic reductions in the fish taxa (Greenwood, 1959; Stewart, 1989). Apparently the ash, resulting from eruptions from nearby Mt Katwe, blanketed the lake and exterminated those fish most reliant on well-oxygenated waters, including *Lates niloticus*, *Barbus bynni* and *Synodontis*.

The modern Lake Edward fauna is very different from its late Pleistocene fauna, its immediate post-Katwe ash fauna, and the modern Nile and Lake Albert faunas. It does however resemble the modern fauna of Lake Victoria, in that both are heavily dominated by cichlids, with cyprinids, catfish and mormyrids (Victoria) next most common (Greenwood, 1966). Clearly Lake Edward's fauna has not been connected with the Nile since the Katwe eruption. There is some evidence that Lake Edward was connected with Lake Victoria in the latest Pleistocene (Bishop & Trendall, 1967), and this is the main source of its modern fauna.

3.3 Lake Victoria

Most geological data indicate that the present-day Lake Victoria basin was formed only in the late Pleistocene, after a period of desiccation (Beadle, 1981), although recent molecular data from modern cichlid flocks suggest that at least part of the basin has sustained enough water to support cichlids since much earlier (Verheyen et al., 2003; see also Lehman, 2009). The modern lake is indirectly connected to the Albert Nile via the Victoria Nile and Lake Albert, a connection which probably opened about 11,500 years ago (Talbot et al., 2000). However Lake Victoria's fish fauna is isolated from Lake Albert due to Murchison Falls on the Victoria Nile, which is a barrier to fish movement. Lake Victoria contains 12 fish families, and between 238 to 288 species (Lévêque, 1997), over three quarters of which are cichlids, most endemic, followed by cyprinids, clariids and mormyrids. As a footnote, many of these species have disappeared due to the introduction in the 1950s and 1960s of the large and piscivorous *Lates niloticus* (Pringle, 2005; Witte et al., 2000). Despite its indirect connection to the Nile, Lake Victoria's modern fauna is very dissimilar to that of the Nile. Its fauna is, however, similar taxonomically to that of both Lake Edward, with which it may have been connected in the Late Pleistocene (Bishop & Trendall, 1967) and/or earlier, and to Lake Kivu,

a small lake to the south of Lake Edward but no longer connected with it. Recent DNA evidence indicates Lake Victoria's haplochromine cichlids derived from Lake Kivu possibly 100,000 years ago (Verheyen et al., 2003) when the two lakes were somehow connected.

Unfortunately Lake Victoria has a poor fossil record of both cichlids and non-cichlids, with fossils known only from Early Miocene deposits on Rusinga Island and from Kavirondo sites near present day Winam Gulf (Greenwood, 1951) (Fig. 1). These deposits contained taxa with widespread Miocene occurrence, including *Protopterus*, *Polypterus*, *Synodontis* and *Lates* (Table 1); *Lates* has only been recently introduced to the modern lake, while the other three genera are present in small numbers. The Miocene Victoria lake or series of lakes dried out, and, like Lake Albert, was traversed by westward flowing rivers. A Plio-Pleistocene cichlid recovered near Kanam – *Oreochromis spilurus* – is now only found in eastern flowing rivers, suggesting the watershed was further west than at present (Trewavas, 1937). The DNA evidence linking the modern Victoria cichlids with those from Lake Kivu suggests the two lakes were connected in some way in the late Middle Pleistocene until the Late Pleistocene (Verheyen et al., 2003). Little is then known about the morphology of the Victoria basin until the latest Pleistocene, when tectonic tilting led to overflow of the present basin indirectly into the White Nile (Talbot et al., 2000), although barriers prevent movement of fish. Fish faunas from Holocene sites located on inflowing rivers to Lake Victoria contain genera represented in the modern lake. The best documented of these is from the Middle Holocene site of Gogo Falls (Fig. 4), located on the Guja River (Robertshaw, 1991), containing mormyrids, *Barbus*, *Bagrus*, *Clarias*, *Synodontis* and indeterminate cichlids (Marshall & Stewart, 1995) (Table 4).

3.4 Lake Turkana

Lake Turkana was last connected to the White Nile via the Lotigipi Swamps, and the Sobat and Pibor Rivers in the humid early and middle Holocene (Adamson & Williams, 1980; Johnson, 2009), but subsequently drought has reduced the lake level so that overflow cannot occur. The mainly swampy ground and deserts between the modern lake and the Nile are a barrier to fish, leaving the Turkana fauna isolated from the Nile. The fauna of modern Lake Turkana reflects the recent Nile connection, as its 18 families are all shared with the Nile, as are about 35 of its 51 species (Lévêque, 1997).

The earliest remains from Turkana are from the early Miocene site of Loperot, and from a large and diverse late Miocene fauna from Lothagam, both in the western Turkana basin. The Lothagam fauna contains 11 extant genera, all present in the modern lake (Stewart, 1997, 2003a) (Fig. 1; Table 1). This taxa largely duplicates the taxa from other reported Miocene sites, especially Lake Albert, which has a very similar fauna. Lothagam contains the earliest confirmed record of *Lates niloticus*, which is subsequently widespread in Plio-Pleistocene sites.

While the extensive Turkana basin Pliocene and Pleistocene faunas contain much of the Miocene taxa (Figs. 2 and 3; Tables 2 and 3) new apparently endemic species (four new *Sindacharax* species and a new species of *Lates* [Stewart, 2003a, b; Stewart and Murray, 2008]) from the Lothagam, Kanapoi and Omo River sites suggest the early Pliocene lake (Feibel, 1988) was isolated for a period of time. The recovery of the widespread *Brycinus macrolepidotus* is its earliest record, and it also may have evolved in the isolated Pliocene lake (Stewart, 2003b). The appearance of *Sindacharax deserti* in the Pliocene Lothagam, Kanapoi and Ekora (a Pliocene-aged site near Kanapoi) deposits coincides with its appearance in Pliocene Nile River deposits (Wadi Natrun), and in Pliocene Lake Albert deposits. Evidence of expanded lakes and rivers in the early Pliocene (e.g., Lakes Turkana, Chad, Manonga [Feibel, 1988; Griffin, 2006; Harrison, 1997]) suggest that new in/outflows were probably created; additionally the newly strengthened Nile River had emerged. The distribution of *S. deserti* may signify an exchange of fauna between these basins. The brackish-water stingray *Dasyatis* is present in late Pliocene until early Pleistocene deposits, indicating a connection between the paleolake and the Indian Ocean. *Dasyatis* was apparently able to colonise the lake and maintain a breeding population during this period (Feibel, 1994). In the late Pleistocene, *Sindacharax* and *Semlikiichthys* disappear; the last evidence of *Sindacharax* is 700,000 years BP (Feibel, 1988). There is evidence of drought in the late Pleistocene, but it is not known how low the lake levels were, and lack of late Pleistocene sites to indicate which taxa survived.

Modern Lake Turkana may be a model of what happened during Pleistocene aridity. At present the lake level is declining, which concentrates the lake waters, making them highly saline (it has the highest salinity of the large Rift lakes). Several mormyrid species, which possess an electro-sensory system, were recorded in the lake in the early twentieth century, but are now rarely found in the lake and have apparently moved into the Omo delta area and river, where the water is fresher (discussion in Beadle, 1981). Unfortunately the fossil record is not extensive enough to test this model.

In the pluvial early and middle Holocene, three Turkana basin sites (Koobi Fora sites: Stewart, 1989; Lowasera: Phillipson, 1977; Lothagam: Robbins, 1974) contain evidence of a diverse fauna – eleven genera plus mormyrids and cichlids – which are all in modern Lake Turkana and in the modern Nile (Hopson & Hopson, 1982) (Fig. 4; Table 4). The sites date between about 9,500 to 4,500 BP and suggest that the connection with the Nile had already been established. Surprising is the number of endemic species in the lake – 10 (Hopson & Hopson, 1982) – probably due to its isolation from the Nile River since the early to middle Holocene. Two closely related species – *Lates macrophthalmus* and *L. longispinis* in Lakes Albert and Turkana respectively, are an example of the rapid rate of latid endemism in the Holocene lakes following connection to the Nile: both species are assumed to have evolved from *L. niloticus*, which entered the lakes from the Nile in the early to middle Holocene, meaning an evolution of only about 5,000 to 9,000 years (Greenwood, 1976c).

3.5 *The Blue Nile and Lake Tana*

Compared to the main and White Nile Rivers, there is a paucity of data on the Blue Nile River and its fauna. The modern fauna includes about 46 species, with most apparently downstream of Roseires. Most genera are shared with the modern Nile (Greenwood, 1976a). Lake Tana, from which the Blue Nile arises, has an interesting fauna quite different from the Blue Nile (Vijverberg et al., 2009). The lake has about 28 species of fish, of which 18 are endemic to the lake. It also has a well-studied *Barbus/Labeobarbus* species flock (De Graaf et al., 2007) and a genus, *Nemacheilus* (Greenwood, 1976a), known only in Europe and Asia. The endemism and species-flock reflect Lake Tana's isolation from the Blue Nile, due to a basalt flow 30km downstream from its outflow.

I know of no reported pre-Holocene faunas for the Blue Nile or Lake Tana. The lack of a fossil record is unfortunate because the past history of Lake Tana's *Barbus* and *Labeobarbus* species flock would be of great evolutionary interest. DNA analysis suggested that the evolution of one *Barbus* species from another occurred <16,000 years ago, after the most recent formation of the lake (De Graaf et al., 2007).

A Holocene fauna was dug from the Sheikh Mustafa site on the Blue Nile, dating to about 7,930 BP. It consisted virtually completely of *Clarias* (Chaix, 2003; Fernandez, 2003), which is now present in the Blue Nile.

4 Conclusions

Differences in the modern fish faunas of the Nile River and its southern basins reflect their fossil history in conjunction with geomorphological changes. The fossil fish record essentially begins in the Eocene and Oligocene deposits of the Fayum, Egypt, where eight families including four endemics – Protopteridae, Polypteridae, Gymnarchidae, Alestidae, Clupeidae, Cichlidae, Latidae and Channidae – have some of their earliest records. All of these families and some genera are present in the modern Nile River, possibly suggesting continuity from the early/middle Cenozoic to the present.

Descendants of these families were part of a uniform Miocene fauna which was apparently widespread across northern, eastern and probably western Africa, including the present Nile valley area, and the Albert, Victoria and Turkana basins. This fauna was possibly dispersed by Miocene rivers flowing west across the present Sahara from the Red Sea mountains, with connections to inflows to the lake basins. The emergence of a strengthened Nile River in the latest Miocene provided a north/south waterway for the further movement of fish. The Nile Valley's Pliocene Wadi Natrun fauna shows continuity with the widespread Miocene taxa, which continues through the late Cenozoic.

In contrast, Pliocene and Pleistocene faunas from Lakes Albert, Edward and Turkana, and what little we know of Victoria and Tana, show ongoing disappearances

and new immigration of taxa, resulting from tectonic and climatic events at this time. In the humid early Pliocene there is evidence of faunal exchanges with the appearance of the extinct *Sindacharax deserti*, ?*Hyperopisus* (not in Turkana) and *Semlikiichthys* at the Albert and Turkana basins and the Nile River. In this humid period Lake Albert may have acted as a conduit between the Congo and Nile systems for faunal exchange. In contrast, the aridity and drought of the early and late Pleistocene in many areas eliminated several taxa, including those now extinct, and probably forced others into refuges.

A period of humidity and extensive waterways in the early and middle Holocene allowed the movement of fish faunas between the Nile River and the saharan and sahelian zones. The Nile River and two of its large basins (Lakes Albert and Turkana) now have a fish fauna with a primarily 'nilotic' distribution, while three other basins (Lakes Edward, Victoria and Tana), whose faunas were isolated in the late Pleistocene and Holocene, have largely endemic faunas.

The fossil record for Nile River fish can be frustrating in its lack of fish identified to the species level. While it contributes to the history of modern Nile taxa at a generic level, it has little to offer on the evolution of the Nile's endemic species, and has obvious limits to its inferences on biogeography. Nevertheless the fossil record is far richer than it was thirty years ago, and can answer more questions about evolution and biogeography than in the past.

Acknowledgements I thank Henri Dumont for inviting me to submit a manuscript to 2009. Thanks to Alison Murray and Olga Otero for discussions on relating to Nile fish distribution and biogeography. My thanks also to two anonymous reviewers for their helpful comments on the draft of this paper.

References

- Adamson D. & F. Williams, 1980. Structural geology, tectonics and the control of drainage in the Nile basin. In M. A. J. Williams & H. Faure (eds), *The Sahara and the Nile*, pp. 225–252. Balkema, Rotterdam.
- Arambourg C., 1947. Contribution à l'étude géologique et paléontologique du Bassin du lac Rodolphe et de la Basse Vallée de l'Omo. Deuxième partie. Paléontologie. Mission scientifique de l'Omo, 1932–1933. Tome I. Géologie-Anthropologie. *Museum National d' Histoire Naturelle Paris* 3: 229–562.
- Arambourg C. & P. Magnier, 1961. Gisements de vertébrés dans le bassin tertiaire de Syrte (Libye). *Comptes Rendus de l' Académie des Sciences, Paris* 252: 1181–1183.
- Beadle L. C. 1981. *The Inland Tropical Waters of Africa*. Second Edition. London, New York, Longman, 475 pp.
- Beuning K. R. M., M. R. Talbot & K. Kelts, 1997. A revised 30,000-year paleoclimatic and paleohydrologic history of Lake Albert, East Africa. *Palaeogeography Palaeoclimatology Palaeoecology* 136: 259–279.
- Bishop, W. W., 1965. Quaternary geology and geomorphology in the Albertine Rift Valley, Uganda. *Geological Society of America Special Paper* 84: 293–320.
- Bishop, W. W. & A. F. Trendall, 1967. Erosion-surfaces, tectonics and volcanic activity in Uganda. *Quarterly Journal of the Geological Society of London* 488: 385–420.

- Brooks, A. S., D. Helgren, J. S. Cramer, A. Franklin A, W. Hornyak, J. M. Keating, R. G. Klein, W. J. Rink, H. Schwarcz, J. N. L. Smith, K. M. Stewart, N. E. Todd, J. Verniers & J. E. Yellen, 1995. Dating and context of three Middle Stone Age sites with bone points in the Upper Semliki Valley, Zaire. *Science* 268: 548–553.
- Butzer, K. W., 1980. Pleistocene history of the Nile Valley in Egypt and Lower Nubia. In M. A. J. Williams & H. Faure (eds), *The Sahara and the Nile*, pp. 253–280. Balkema, Rotterdam.
- Carroll, R. L., 1988. *Vertebrate Paleontology and Evolution*. New York, Freeman.
- Chaix, L., 2003. La faune des sites mésolithiques et néolithique de la zone du Nil Bleu (Soudan Main). *Complutum* 1, 14: 373–396.
- Cooke, H. B. S., 1958. Observations relating to Quaternary environments in East and Southern Africa. *Transactions of the Geological Society of South Africa* 60, Annex:1–74.
- Daget, J., 1959. Restes de Poissons du Quaternaire saharien. *Bulletin de l' IFAN A* 21: 1105–1111.
- Daget, J., 1961. Restes de Poissons du Quaternaire saharien. *Bulletin de l' I.F.A.N. A* 23: 182–191.
- Daget, J, J. P. Gosse & D. T. van den Audenaerde T (eds), 1984. Check-list of the Freshwater Fishes of Africa Vol 1. Royal Museum of Central Africa, Tervuren.
- Daget, J., J. P. Gosse & D. T. van den Audenaerde (eds), 1986. Check-list of the Freshwater Fishes of Africa, Vol. 2. Royal Museum of Central Africa, Tervuren.
- Daget J, J. P. Gosse, G. G. Teugels & D. T. van den Audenaerde (eds), 1991. Check-list of the Freshwater Fishes of Africa Vol. 4. Royal Museum of Central Africa, Tervuren.
- De Graaf M., H.-J. Megens, J. Samallo & F. A. Sibbing, 2007. Evolutionary origin of Lake Tana's (Ethiopia) small *Barbus* species: indications of rapid ecological divergence and speciation. *Animal Biology* 57: 39–48.
- De Vos L. & D. T. van den Audenaerde, 1990. Petits *Barbus* (Pisces, Cyprinidae) du Rwanda. *Revue d'Hydrobiologie Tropicale* 23: 141–159.
- El-Shahat A., S. N. Ayyad & M. A. Abdalla, 1997. Pliocene facies and fossil contents of Qaret El-Muluk formation at Wadi El-Natron depression, Western Desert, Egypt. *Facies* 37: 211–224.
- Feibel, C. S., 1988. Paleoenvironments of the Koobi Fora Formation, Turkana Basin, Northern Kenya. Ph. D. Thesis, University of Utah, Salt Lake City, Utah.
- Feibel, C. S., 1994. Freshwater stingrays from the Plio-Pleistocene of the Turkana Basin, Kenya and Ethiopia. *Lethaia* 26: 359–366.
- Fernandez, V. M., 2003. Four thousand years in the Blue Nile: paths to inequality and ways of resistance. *Complutum* 14: 409–425.
- Gaudant, J., 1987. A preliminary report on the osteichthyan fish-fauna from the Upper Neogene of Sahabi, Libya. In N. T. Boaz, A., El-Arnautl, A. W. Gaziry, J. de Heinzelin, & D. D. Boaz (eds), *Neogene Paleontology and Geology of Sahabi*, pp. 91–99. AR Liss, New York.
- Gautier, A. & W. Van Neer, 1989. Animal remains from the Late Paleolithic: the sequence at Wadi Kubbaniya. In F. Wendorf, R. Schild & A. E. Close (eds), *The Prehistory of Wadi Kubbaniya*, Vol. 2, pp. 119–170. Southern Methodist University Press, Dallas.
- Greenwood, P. H., 1951. Fish remains from Miocene deposits of Rusinga Island and Kavirondo Province, Kenya. *Annals and Magazine of Natural History* 12: 1192–1201.
- Greenwood, P. H., 1959. Quaternary Fish Fossils. Parc National Albert, Mission J. de Heinzelin de Braucourt (1950), Fascicule 4,1: 1–80.
- Greenwood, P. H., 1966. *The Fishes of Uganda*. Uganda Society, Kampala.
- Greenwood, P. H., 1968. Fish remains. In F. Wendorf (ed.), *Prehistory of Nubia*, pp. 100–109. Southern Methodist University, Dallas.
- Greenwood, P. H., 1972. New fish fossils from the Pliocene of Wadi Natrun, Egypt. *Journal of Zoology London* 168: 503–519.
- Greenwood, P. H., 1973. Fish fossils from the Late Miocene of Tunisia. *Notes du Service de Géologie Tunis* 37: 41–72.
- Greenwood, P. H., 1974. Review of Cenozoic freshwater fish faunas in Africa. *Annals of the Geological Survey of Egypt* 4: 211–232.

- Greenwood, P. H., 1976a. Fish Fauna of the Nile. In J. Rzóška (ed.), *The Nile, Biology of an Ancient River*, pp. 127–141. Junk, The Hague.
- Greenwood, P. H., 1976b. Notes on *Sindacharax* Greenwood and Howes, 1975, a genus of fossil African characid fishes. *Revue de Zoologie et Botanique Africaine* 90: 1–13.
- Greenwood, P. H., 1976c. A Review of the Family Latidae (Pisces, Perciformes). *Bulletin of the British Museum (Natural History) (Zoology)* 29: 1–81.
- Greenwood, P. H. & G. J. Howes, 1975. Neogene fossil fishes from the Lake Albert-Lake Edward rift (Congo). *Bulletin of the British Museum (Natural History) (Geology)* 26: 72–127.
- Griffin, D. L., 2006. The late Neogene Sahabi rivers of the Sahara and their climatic and environmental implications for the Chad Basin. *Journal of the Geological Society* 163: 905–921.
- Haaland, R. & A. A. Magid, 1995. *Aqualithic Sites along the Rivers Nile and Atbara, Sudan*. Alma Mater Verlag, Bergen.
- Harrison, T., 1997. Introduction: Paleontological and Geological Research in the Manonga Valley, Tanzania. In T. Harrison (ed.), *Neogene Paleontology of the Manonga Valley, Tanzania*, pp 2–44. Plenum, New York.
- Hopson, A. J. & J. Hopson, 1982. The fishes of Lake Turkana with a description of three new species *Alestes ferox* sp. nov., *Alestes minutus* sp. nov., (Pisces: Characidae) and *Barbus turkanae* sp. nov. (Pisces: Cyprinidae). In A. J. Hopson (ed.), *Lake Turkana: A Report on the Findings of the Lake Turkana Project 1972–1975*, Vols. 1–6, pp. 283–347. Overseas Development Administration, London.
- Hsü, K. J., L. Montadert, D. Bernoulli, M. B. Cita, A. Erickson, R. E. Garrison, R. B. Kidd, F. Mèlierés, C. Müller & R. Wright, 1977. History of the Mediterranean salinity crisis. *Nature* 267: 399–403.
- Issawi, B. & J. F. McCauley, 1992. The Cenozoic rivers of Egypt: the Nile problem. In: R. Friedman & B. Adams (eds), *The Followers of Horus: Studies Dedicated to Michael Allen Hoffman 1944–1990*, pp. 121–138. Egyptian Stud Association Publication 2, Oxbow Books, Oxford.
- Lamb, H. F., C. R. Bates, P. V. Coombes, M. H. Marshall, M. Umer, S. J. Davies & E. Dejen, 2007. Late Pleistocene desiccation of Lake Tana, source of the Blue Nile. *Quaternary Science Review* 26: 287–299.
- Lévêque, C., 1997. *Biodiversity dynamics and conservation: the freshwater fish of tropical Africa*. Cambridge University Press, Cambridge.
- Marshall, F. B. & K. M. Stewart, 1995. Hunting, fishing and herding pastoralists of western Kenya: the fauna from Gogo Falls. *Archaeozoologia* 7: 7–29.
- McCauley, J. F., G. G. Schaber, C. S. Breed, M. J. Grolier, C. V. Haynes, B. Issawi, C. Elachi & R. Blom, 1982. Subsurface valleys and geoarchaeology of the Eastern Sahara revealed by Shuttle Radar. *Science* 218: 1004–1020.
- McCauley, J. F., C. S. Breed, B. Issawi, G. G. Schaber, M. El-Hinnawi & A. El-Kelani, 1998. Spaceborne Imaging Radar (SIR) geologic results in Egypt (a review: 1982–1997). In G. M. Naim (ed.), *Proceedings of the Egyptian Geological Survey Centennial Conference, 1996*, pp. 489–527. Special Publication, Geological Survey of Egypt 75.
- Mo, T., 1991. Anatomy, Relationships, and Systematics of the Bagridae (Teleostei: Siluroidei) with a Hypothesis of Siluroid Phylogeny. Koeltz, Koenigstein.
- Murray, A. M., 2004. Late Eocene and early Oligocene teleost and associated ichthyofauna of the Jebel Qatrani Formation, Fayum, Egypt. *Palaeontology* 47: 711–724.
- Murray, A. M. & Y. S. Attia, 2004. A new species of *Lates* (Teleostei:Perciformes) from the lower Oligocene of Egypt. *Journal of Vertebrate Paleontology* 24: 299–308.
- Murray, A. M., E. Simons & Y. S. Attia, 2005. A new clupeid fish (Clupeomorpha) from the Oligocene of Fayum, Egypt, with notes of some other fossil clupeomorphs. *Journal of Vertebrate Paleontology* 25: 300–308.
- Otero, O., 2001. The oldest-known cyprinid fish of the Afro-Arabic plate, and its paleobiogeographical implications. *Journal of Vertebrate Paleontology* 21: 386–388.
- Otero, O. & M. Gayet, 1999. *Semlikichthys* (Perciformes incertae sedis), genre nouveau, et position systématique nouvelle pour *Lates rhachirhynchus* Greenwood and Howes, 1975, du Plio-Pleistocene Africain. *Cybiurn* 23: 3–27.

- Peters, J., 1995. Mesolithic subsistence between the 5th and 6th Nile cataract: the archaeofaunas from Abu Darbein, El Damer and Aneibis (Sudan). In R. Haaland & A. A. Magid (eds), *Aqualithic Sites along the Rivers Nile and Atbara, Sudan*, pp. 178–244. Alma Mater Vorlag, Bergen.
- Petit-Maire, N., J. C. Celles, D. Commelin & M. Raimbault, 1983. The Sahara in northern Mali: man and his environment between 10,000 and 3,500 years bp. *African Archaeological Review* 1: 105–125.
- Phillipson, D. W., 1977. *Lowasera*. *Azania* 12: 1–32.
- Priem, R., 1914. Sur les poissons fossiles et, en particulier, des Siluridés du Tertiaire supérieur et des couches récentes d’Afrique. *Mémoires de la Société de Géologie de France* 21: 5–13.
- Priem, R., 1920. Poissons fossiles du Miocène de l’Égypte (Burdigalien de Moghara, “Désert lybique”). In R. Fourtau (ed.), *Contribution à l’étude des Vertébrés miocènes de l’Égypte*, pp. 8–15. Government Press, Cairo.
- Pringle, R., 2005. The origins of the Nile Perch in Lake Victoria. *Bioscience* 55: 780–787.
- Robbins, L. H., 1974. The Lothagam Site. East Lansing, Publications of the Museum, Michigan State University, Anthropology Series.
- Roberts, T. R., 1975. Geographical distribution of Africa freshwater fishes. *Zoological Journal of the Linnean Society* 57: 249–319.
- Roberts, T. R., 1992. Systematic revision of the old world freshwater fish family Notopteridae. *Ichthyological Exploration of Freshwater* 2: 361–383.
- Robertshaw, P., 1991. Gogo Falls: a complex site east of Lake Victoria. *Azania* 26: 63–195.
- Robinson, P. & C. C. Black, 1974. Vertebrate faunas from the Neogene of Tunisia. *Annals of the Geological Survey of Egypt* 4: 319–332.
- Said, R., 1981. *The Geological Evolution of the River Nile*. Springer, New York, 151 pp.
- Said, R., 1993. *The River Nile: Geology, Hydrology and Utilization*. Pergamon, New York, 320 pp.
- Schwartz, H., 1983. Paleoeology of Late Cenozoic fishes from the Turkana Basin, Northern Kenya. Ph. D. Thesis, University of California-Santa Cruz, Santa Cruz, California.
- Snoeks, J., 2000. How well known is the ichthyodiversity of the large East African lakes? *Advances in Ecological Research* 31: 17–38.
- Stewart, K. M., 1989. Fishing Sites of North and East Africa in the Late Pleistocene and Early Holocene. BAR International Series 521, Oxford.
- Stewart, K. M., 1990. Fossil fish from the Upper Semliki. *Virginia Museum of Natural History Memoirs* 1: 141–162.
- Stewart, K. M., 1997. A new species of *Sindacharax* (Teleostei: Characidae) from Lothagam, Kenya, and some implications for the genus. *Journal of Vertebrate Paleontology* 17: 34–38.
- Stewart, K. M., 2001. The freshwater fish of Neogene Africa (Miocene–Pleistocene): systematics and biogeography. *Fish and Fisheries* 2001, 2: 177–230.
- Stewart, K. M., 2003a. Fossil fish remains from Mio-Pliocene deposits at Lothagam, Kenya. In J. M. Harris & M. G. Leakey (eds), *Lothagam*, pp. 75–115. New York, Columbia University Press.
- Stewart, K. M., 2003b. Fossil fish remains from the Pliocene Kanapoi site, Kenya. In J. M. Harris & M. G. Leakey (eds), *Geology and Vertebrate Paleontology of the Early Pliocene Site of Kanapoi, Northern Kenya*, pp. 21–39. *Contributions to Science* 498, NHM, Los Angeles.
- Stewart, K. M. & A. M. Murray, 2008. Fish Remains from the Plio-Pleistocene Shungura Formation, Omo River basin, Ethiopia. *Geobios*.
- Stromer, E., 1914. Mitteilungen über Wirbeltierreste aus dem Mittelpliocän des Natrontales (Ägypten). 4. Fische: a) Dipnoi, *Protopterus*. *Zeitschrift der Deutschen Geologischen Gesellschaft zu Berlin* 66: 420–425.
- Talbot, M. R., M. A. J. Williams & D. A. Adamson, 2000. Strontium isotopic evidence for Late Pleistocene re-establishment of an integrated Nile drainage network. *Geology* 28: 343–346.
- Trewavas, E., 1937. Fossil cichlids from Dr. L.S.B. Leakey’s Expedition to Kenya 1934–35. *Annals and Magazine of Natural History* 10: 381–386.
- Van Couvering, J. A. H., 1977. Early records of freshwater fishes in Africa. *Copeia* 1: 163–166.

- Van Couvering, J. A. H., 1982. Fossil cichlid fish of Africa. Special Paper on Palaeontology 29, Palaeontological Association, London.
- Van Neer, W., 1986. Some notes on the fish remains from Wadi Kubaniya (Upper Egypt; Late Palaeolithic. In D. C. Brinkhuizen & A. T. Clason (eds), *Fish and Archaeology*, pp. 103–111. BAR International Series 294, Oxford.
- Van Neer, W., 1988. Fish remains from a Holocene site (84/13–9) in Wadi Howar, Sudan. *Archaeozoologia* 2: 339–348.
- Van Neer, W., 1989. Holocene fish remains from the Sahara. *Sahara* 2: 61–68.
- Van Neer, W., 1992. New Late Tertiary fish fossils from the Sinda region, Eastern Congo. *African Studies and Monographs Supplement* 17: 27–47.
- Van Neer, W., 1993. Fish remains from the last interglacial at Bir Tarfawi (eastern Sahara, Egypt). In F. Wendorf, R. Schild & A. E. Close (eds), *Egypt During the Last Interglacial. The Middle Paleolithic of Bir Tarfawi and Bir Sahara East*, pp. 144–155. Plenum, New York.
- Van Neer, W., 1994. Cenozoic fish fossils from the Albertine Rift Valley in Uganda. In B. Senut & M. Pickford (eds), *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Congo*. Vol. II. Palaeobiology, pp. 89–127. Centre International pour la Formation et les Echanges en Géosciences, Orleans.
- Van Neer, W. & H.-P. Uerpmann, 1989. Palaeoecological Significance of the Holocene Faunal Remains of the B.O.S.-Missions. In H.-P. Uerpmann & W. Van Neer (eds), *Forschungen zur Umweltgeschichte der Ostsahara*, pp. 307–341. Heinrich-Barth-Institut, Köln.
- Verheyen, E., W. Salzburger, J. Snoeks & A. Meyer, 2003. Origin of the Superflock of Cichlid Fishes from Lake Victoria, East Africa. *Science* 300: 325.
- Vignaud, P., P. Dourine, H. T. Mackaye, A. Likies, C. Blondel, J.-R. Boisserie, L. de Bonis, V. Eisenmann, M.-E. Etienne, D. Geraads, F. Guy, T. Lehmann, F. Lihoreau, N. Lopez-Martinez, C. Mourer-Chauviré, O. Otero, J.-C. Rage, M. Schuster, L. Viriot, A. Zazzo & M. Brunet, 2002. Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad. *Nature* 418: 152–155.
- Weiler, W., 1926. Mitteilungen über die Wirbelterreste aus dem Mittel pliozän des Natrontales (Aegypten). *Sitzungsberichte der Bayerischen Akademie für Wissenschaften* 3: 317–340.
- White, E. I., 1926. The geology and palaeontology of the Kairo bone beds. Part II. Paleontology – Pisces. Occasional Paper of the Geological Survey of Uganda 2: 45–52.
- Williams, M. A. J., D. Adamson, M. Talbot & P. Aharon, 2001. Quaternary lakes, paleochannels and dunes in the White Nile Valley. Abstract. Past Climate Variability Through Europe and Africa, August 27–31, 2001, Aix-en-Provence, France.
- Williams, M. A. J., D. Adamson, J. R. Prescott & F. R. Williams, 2003. New light on the age of the White Nile. *Geology* 31, 11: 1001–1004.
- Witte, F., B. S. Maku, J. H. Wanink, O. Seehausen, E. F. B. Katunzi, P. C. Goudswaard & T. Goldschmidt, 2000. Recovery of cichlid species in Lake Victoria: an examination of factors leading to differential extinction. *Reviews in Fish Biology and Fisheries* 10: 233–241.