Journal of African Earth Sciences 54 (2009) 62–74

Contents lists available at ScienceDirect

Journal of African Earth Sciences

journal homepage: www.elsevier.com/locate/jafrearsci

First description of a Pliocene ichthyofauna from Central Africa (site KL2, Kolle area, Eastern Djurab, Chad): What do we learn?

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ARTICLE INFO

Article history:
Received 10 July 2008
Received in revised form 4 March 2009
Accepted 13 March 2009
Available online 21 March 2009

Keywords:
Ichthyofauna
Pliocene
Chad
Palaeoenvironments
Paleobiogeography
Central Africa

ABSTRACT

This is the first extensive study of a freshwater fish fauna from a Pliocene site in Central Africa, based on fossils collected at the KL2 site in the fossiliferous area of Kolle (Lower Pliocene, Chad). A relatively high fish diversity is revealed, confirming the presence of 19 taxa: Polypteriformes, Polypteridae (*Polypterus* sp.); Osteoglossiformes, Osteoglossidae (*Heterotis* sp.), Mormyriformes, Gymnarchidae (*Gymnarchus* sp. cf. *niloticus*); Cypriniformes, Cyprinidae (*Labeo* sp.); Characiformes, Alestidae (*Hydrocynus*; Alestinae type *Alestes*/*Brycinus*; *Sindacharax* sp. cf. *deserti*, *Sindacharax* sp.), Distichodontidae (*Distichodus* sp.); Siluriformes, Ariidae (cf. *Calarius*), ?Bagridae (cf. *Bagrus*), Claroteidae (cf. *Clarotes*), Mochokidae (*Synodontis* sp.), Clariidae (*Clarias* sp. or *Heterobranchus* sp.); Perciformes family indet. (*Semlikiichthys* sp. cf. *darsao*), Latidae (*Lates* sp. cf. *niloticus*), Cichlidae indet., and Perciformes indet.; Tetraodontiformes Tetraodontidae (*Tetraodon* sp.). The aquatic environment corresponding to the fossil fish assemblage might be a floodplain crossed by well-oxygenated open waters. Compared with a contemporaneous East African region, the mid-Pliocene Chadian fish diversity reveals a certain endemicity, while connections between the Niger and the Chadian basin are suspected because of the presence of a freshwater ariid fish in Kolle.

1. Introduction

Chad is a key region in understanding early hominid geographic history, owing to its far west location from the Rift Valley and the occurrence of fossil hominids, i.e. *Australopithecus bahrelghazali*, a Pliocene australopithecin from Koro Toro (Brunet et al., 1995) and *Sahelanthropus tchadensis*, the oldest known ancestor from the Late Miocene deposits of the Toro-Menalla area (Brunet et al., 2002, 2005). More generally, the four Miocene and Pliocene Chadian fossiliferous areas discovered by the MPFT are the only ones in Central Africa to yield Neogene vertebrates (Fig. 1). In these respects, their study helps to understand the environmental frame of the hominid evolution. So far, the extensive study of Late Miocene ichthyofauna from Toro-Menalla has revealed a high diversity including several new taxa and provided information on the aquatic environment, notably at the hominid site (Otero et al., 2006, 2007, 2008, accepted for publication). In contrast, the fish remains yielded by the Pliocene Chadian fossiliferous areas from a more eastern part of the Djurab (Fig. 1) remain mostly unknown. A faunal list was only established from a preliminary review of the fish material in Kossom Bougoudi (Brunet et al., 2000).

Here, we focus on the area of Kolle, through the extensive study of the fish remains from site KL2 (Fig. 1). This study provides the first available data on a freshwater ichthyofauna from Central Africa during the Pliocene. The area, dated by cosmogenic nuclide (Lebatard et al., 2008), was found to be of an age consistent with the biochonological estimated ages (Brunet et al., 1998). In their paper describing the Kolle area, Brunet et al. (1998) noted a mammal association with a relatively low aquatic dependency. Even one of the two recorded hippos may have hardly been linked with water and was more likely a forest-dweller. According to these authors, other mammals, such as proboscideans, suids, giraffids and maybe bovins, point towards woodland, while rhinocerotids, equids, kobs and sivathers may have favoured grasslands. The aquatic component of the environment is documented by the diverse crocodylian fauna which includes three taxa and the strictly ichthyophagous *Euthecodon* (Brunet et al., 1998). Together with this original mosaic of environments, the Kolle mammalian fauna is characterized by a certain degree of endemicity which seems to have affected the Chadian basin since the foundation of the Pliocene (e.g. Boisserie et al., 2003; Lehmann et al., 2004). In this paper, we describe and

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doi:10.1016/j.jafrearsci.2009.03.004

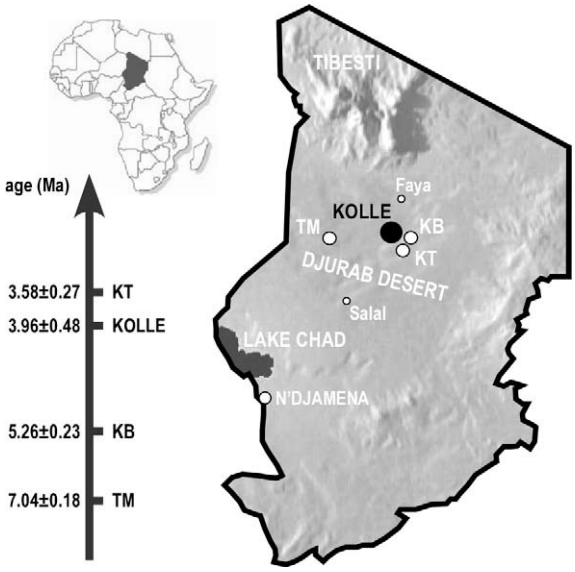

Fig. 1. Age and location of the fossiliferous area of Central Africa on a Recent topographical map. Dating from Lebatard et al. (2008).

attribute the fish remains from KL2. Following Fara et al. (2005), we have attempted to evaluate the influence of taphonomic imprint on the fossil ichthyofauna before discussion on the palaeoenvironment of the site and on the putative paleobiogeographic relationships of this Pliocene Chadian ichthyofauna.

2. Geological context

The formation in Kolle consists mainly of siliciclastic series dominated by weakly lithified sandstone interbedded with argillaceous mudstone and diatomite (Schuster et al., 2000; Duringer et al., 2000; Schuster, 2002). Cosmogenic nuclide dating of the lacustrine diatoms that overly the fossiliferous layers provided an age of 3.96 ± 0.48 Ma (Lebatard et al., 2008). The fossiliferous area of Kolle corresponds to marginal deposits of a great lake which may have occupied a large part of both north and south sub-basins of the Chad-Chari basin. Terrestrial vertebrates and fishes were buried in sands intercalated with clays (Fig. 2; Schuster et al., 2000; Schuster, 2002). Fishes were collected at six sites in the Kolle area (2, 5, 8, 11, 25, 27), but only in KL2 did the sampling campaign spend several weeks; material was collected both by walker-diggers and by sediment screeners. Hence, the fish diversity revealed in KL2 is much higher than in the other sites (notably because fish are frequently preserved as small isolated bones, teeth and scales) and legitimates an accurate study. The classic sedimentological study was duplicated by geophysical study of the sediment deposits. From these combined data, Schuster (2002) concludes that the site corresponds to a floodplain crossed by a contemporaneous stream channel. We observed differences in the fossil distribution between the two zones. The channel is much richer and preserved rather smaller remains whereas big fossils are found in the plain. The concentration of small material (including fish remains) is explained by concentration during the sedimentation as so often observed in channel deposits.

This different distribution of the fossils between the two zones is enhanced because (1) in the plain, the fossils are collected on the deflated surface so that the few smaller fossils that may have been present have for a long time been swept away by the wind, and (2) in the channel, we collected fossils on the surface and also by digging the sediment.

Fig. 2. View of the site KL2 with square sampling.

3. Material

Dozens of bones and hundreds of isolated teeth and ganoid scales were collected during field missions partly in 1998 and mostly in 1999. They are listed in Table 1. The sample number refers to the fossiliferous site and to the year of collection: e.g. KL2-99-025 is the 25th sample collected in 1999, at site 2 in the fossiliferous area called Kolle. After examination, the fish fossils collected by the MPFT will be housed in the collection of the CNAR (Centre National d'Appui à la Recherche, BP, 1228, N'Djaména, Republic of Chad).

The material for comparison is composed of Late Miocene fossils from Chad, described in Otero et al. (2006, 2007, 2008, accepted for publication), and of prepared dry-skeletons: the catfish *Clarotes laticeps* from the reference collection of Wim Van Neer (Institut des Sciences Naturelles, Brussels); the catfishes *C. laticeps* and *Heterobranchus* sp., from the dry-skeleton collection in the Natural History Museum (Zoology Department, London); and polypteriforms (*Polypterus bichir*, *Polypterus senegalus*), osteoglossiform (*Heterotis niloticus*), mormyriform (*Gymnarchus niloticus*), characiforms (*Hydrocynus brevis*, *Alestes* sp. cf. *baremoze*, *Brycinus macrolepidotus*), siluriforms (*Arius thalassinus*, *Bagrus bajad*, *Auchenoglanis biscutatus*, *Auchenoglanis occidentalis*, *Synodontis clarias*, *Synodontis schall*, *Clarias* sp. cf. *gariepinus*), perciforms (*Lates niloticus*, *Oreochromis niloticus*) and tetraodontiform (*Tetraodon lineatus*), from the reference collection of Olga Otero (iPHEP, Poitiers).

4. Systematic palaeontology

Super-division: Cladistia
Order: Polypteriformes
Family: Polypteridae
Polypterus St. Hilaire, 1802
Polypterus sp. (Fig. 3)

Description and attribution. The several rhomboid ganoid scales (Fig. 3a–c) belong to polypterid fishes (bichirs). The scales are from 5 to 10 mm in width. They typically show the articulation system with peg (dorsal) and socket (ventral), a strong anterior process and a cover layer of a peculiar type of enamel called ganoin. The external face may also exhibit smooth ridges such as those observed in part of the scales from KL2 (Fig. 3a and b). The lateral line opens on the scales in a groove ending in a posterior notch (Fig. 3b) or in a pore (Fig. 3c). The two cases are observed in the Late Miocene Chadian fossil species *Polypterus faraou* (Otero