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## NOTE

# CHAD: DISCOVERY OF A VERTEBRATE FAUNA CLOSE TO THE MIO-PLIOCENE BOUNDARY

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## INTRODUCTION

Since 1994 the "Mission Paleoanthropologique Franco-Tchadienne" (M.P.F.T.) has conducted several seasons of field research in the Djurab desert of northern Chad, resulting in the discovery of more than one hundred Mio-Pliocene vertebrate fossil sites. The discovery in the Koro Toro region (KT12; Brunet et al., 1995, 1996) of a new species of australopithecine associated with a fauna estimated biochronologically at around 3.0 to 3.5 Ma, as well as that of a second site with primitive hominids (KT13; Brunet et al., 1997a), led us to focus our efforts on older sedimentary levels. Work in the Kollé region (KL) yielded a fauna with a biochronological age between 4 and 5 Ma (Brunet et al., 1998). Further to the west, Kossom Bougoudi (KB; 16°20'N; 18°40'E), an area of scattered dunes, produced a very rich fauna indicating a still older age than Kollé (Fig. 1). Because of the importance of sites of this age in understanding the environments of the earliest hominids, and due to their scarcity in Africa, the focus of this paper is on the environment and faunas of KB.

The site of Kossom Bougoudi was first discussed by Y. Coppens and initially attributed to a biostratigraphic unit termed "niveau type Bochianga" that characterizes lower Pleistocene levels with *Anancus* and lacking elephants (Coppens, 1967a, b). Later, this level was attributed to the Kolinga 1 zone, characterized by several taxa including Stegotetrabelodontinae, *Stegodon, Primelephas, Anancus, Hipparion, Libytherium, Hexaprotodon,* and *Elephas,* and dated between 4 and 5 Ma (Coppens, 1972; Coppens and Koeniguer,1976).

### Sedimentary Environment

In this region of little or no relief the geomorphological monotony is relieved only by the movement of dunes and sand-storms. However in the KB area the presence of many small buttes (around 5 m height) allows reconstruction of a lithological succession, from bottom to top (Fig. 2), of lower green sandstone (3.0 m), green silty clay (1.2 m), and upper green sandstone (0.6 m); this sequence is either covered by or episodically interstratified with white diatomites (0.2 m). The sandstones are little or poorly cemented, without oblique stratification but strongly channeled. They are often markedly heterogranular with an abundant supporting matrix. Frequent desiccation cracks in the sandstones and upper parts of the silty clay reflect repeated, probably seasonal, drying episodes. The fossil vertebrate remains are mainly concentrated in the sandstones. In regional context this sequence is a consequence of repetitive climatic fluctuation between environments of ephemeral streams and of lakes (Brunet et al., 1997b). These environmental fluctuations help to explain why vertebrate fossils, and notably mammals, are almost always restricted to sandstones. Various kinds of insect bioturbations, particularly dung beetle nests (Duringer et al., in press) and termite nests, are omnipresent, also mainly in the sandstones.

### Environmental Reconstruction and Biogeography

Preliminary identifications list 55 taxa (Table 1). Fossils are known almost entirely from lower and upper green sandstones. Because there are no obvious evolutionary differences between the two levels, we regard the two assemblages as representing a single fauna.

Silicified wood with many xylem vessels of large diameter represents a liana. The liana-like character is compatible with the presence of gallery forest bordering a stream or lake.

The two fish families most commonly represented are the Latidae (Perciformes) and the Ariidae (Siluriformes). The Perciformes need oxygenated water, and the recovery of several articulated skeletons of Latidae indicate fish trapped by more or less rapid falls in water levels (Van Neer and Gayet, 1988). While the Siluriformes prefer relatively deep water, some of the Mochokidae and Bagridae can live in ponds while the Clariidae, dwellers of shallow water, can tolerate anoxic conditions or survive outside water (Daget, 1954).

Among lacertilians, *Python sebae* prefers aquatic and swampy habitats; *Varanus niloticus* is a semi-aquatic lizard. The biodiversity of crocodilians is great. The generalist *Crocodylus lloydi* occupied the niche of living large predators such as *C. niloticus.* Remains of Gavialidae are rare and suggest a generalist-fish eater, while the common ***Euthecodon*** cf. *brumpti* is strictly a fish-eater.

Bird remains also demonstrate the presence of aquatic habitats. Among Ciconiidae, is a new very large species of *Jabiru.* This extant stork prefers aquatic habitats and eats mainly fish (Del Hoyo et al., 1992).

For Mammals, a new species of Tubulidentata is represented by the first complete skeleton from the African Neogene. At KB, this form is associated with a rich insect fauna, notably Hodotermitidae represented

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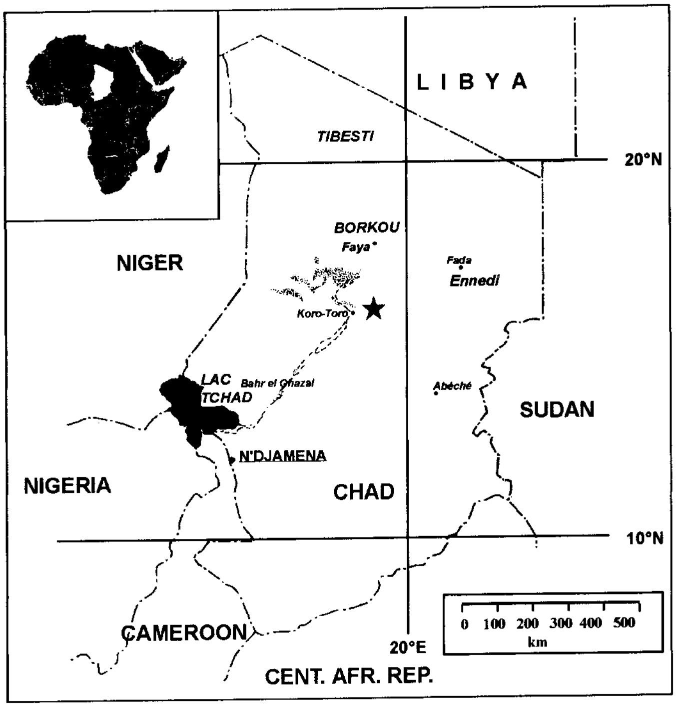

FIGURE 1. Kossom Bougoudi (black star), location map.

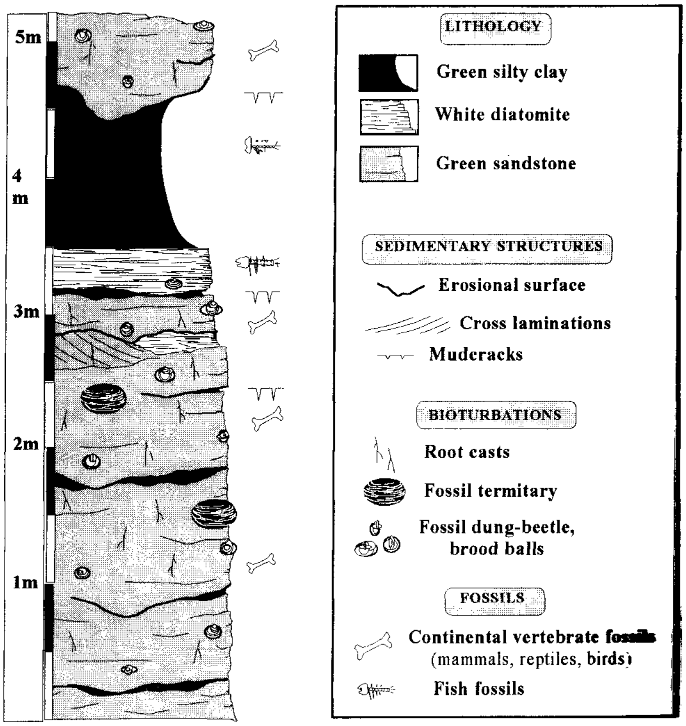

FIGURE 2. Kossom Bougoudi, geologic section.

by fossil termitaries, nests of Hymenoptera (solitary wasps), and brood nests of Scarabaeidae (Duringer et al., in press). In Lagomorpha, the presence of a less robust, less advanced *Serengetilagus* hare in Chad is thus compatible with an earlier age for KB than Laetoli. Because of these differences from the Laetoli specimen (McInnes, 1951; Erbajeva and Angermann, 1983) the Chadian hare is provisionally named *Serengetilagus* aff. *precapensis*. Among the Rodentia, Sciuridae are represented by a ground squirrel of the genus *Xerus*. The small size of the skull, associated with bunodont low-crowned teeth with poorly developed anterolophs and posterolophs, suggests a new species distinct from the lineage *X. janenschi-X. inauris* from Laetoli and Olduvai (Denys, 1987, 1990), but less evolved than *X. erythropus* from Omo members B and C (Wesselman, 1984). In Carnivora, *Dinofelis* sp. smaller than the Langebaanweg species (Hendey, 1974), is closer to *D. diastemata* from the French Pliocene (Piveteau, 1948). While the hunting hyena, *Lycyaena* sp. differs in only a few features from *L. chaeretis* from Pikermi (Gaudry, 1862–1867).

Among the Equidae, two species of *Hipparion* (middle and large size) are present. Lower teeth are all caballine or at least caballoid. Ectostylids are almost invariably present. The large form is known notably from a very large anterior cranium with a preorbital fossa far anterior to the orbit and very well defined behind. The only two skulls of similar size known elsewhere with a similarly placed but antero-posteriorly shorter fossa are from Samos (Forsten, 1983, fig. 2-S). All other very large skulls with preorbital fossae are Vallesian. There are no similar crania in the Plio-Pleistocene of Africa, although there are large crania without fossae (Hadar), or with fossae, but smaller (Langebaanweg, Ekora).

The Proboscidean teeth indicate significant diversity with probably four species coexisting: (1) *Anancus kenyensis* "simple morph" (sensu Tassy, 1986); (2) *Stegodon kaisensis* "Nkondo stage" (sensu Tassy, 1994); (3) *Primelephas* aff. *gomphotheroides* close to *Primelephas* from Lukeino (Tassy, 1986) and Lothagam 1 (Maglio, 1973); and (4) a primitive Elephantine represented by a d3 more derived than *Stegotetrabelodon orbus* from Lothagam (Maglio and Ricca, 1977). The teeth from this fourth species resembles those of *Primelephas gomphotheroides* from Lukeino (Tassy, 1986), with two more derived features, thinner lamellae and higher laminar index (8.4 vs. 7.0).

Five families of Artiodactyla are recognized. Despite their scarcity, remains of two suid taxa could be present, while the particularly numerous remains of Hippopotamidae belong to a single species. The Chadian Camelidae is among the oldest known from Africa. This form differs from living *Camelus* in its large size, robusticity, well developed p3 and p4, and the low obliquity of the 3rd lobe of m3. All these characters recall *Paracamelus* but this genus, very poorly known in Eurasia (Zdansky, 1926; Khaveson, 1954; Pickford et al., 1995), has never been reported from Africa. *Paracamelus* is referenced for the first time in China (ca. 5 Ma) as an immigrant from North America (Tedford et al., 1991). Bovidae has a tribal representation unique in Africa: (1) almost all the material comprises Reduncini and Hippotragini; (2) Antilopini and Bovini are rare; and (3) Tragelaphini and Alcelaphini are absent. *Kobus* nov. sp. readily distinguished by the well curved frontal and diverging horn cores (large at the base and crescent shaped towards the tip) from *Kobus* nov. sp. B from KT13 (Brunet et al., 1997a), but closer to *Redunca* aff. *darti* from Sahabi (Lehmann and Thomas, 1987). However, the relatively small horn cores, their cross section, the curvature of the cranial vault and the basioccipital also resemble *Kobus subdolus* Gentry, 1980 from Langebaanweg which however has a less derived dentition. Hippotragini (genus and species aff. *Protoryx* sp.) is characterized by vertically oriented horn cores, a little divergent at the base, with clear basal helicoidal torsion in anterior view and marked anterior curvature at mid-length. These characters are present in the modern *Hippotragus*. However, the primitive dentition (cusps little pinched, pillars little projecting, caprine folds weak or absent) and, above all, the very narrow anterior cranium and occipital separated into two lateral planes, are reminiscent of the *Protoryx-Pachytragus* group, which is not known in Africa after the beginning of the Late Miocene.

Finally, the perennial aquatic conditions are indicated by a flora record of liana-like leguminous plants and by a fauna with high biodiversity of fish of which certain (Perciformes of the genus *Lates*) usually live in oxygenated water of some depth. This perennial characteristic is equally documented by the abundance of aquatic reptiles. The presence of such a habitat is further documented by the aquatic birds and by the very large number of specimens of hippopotamid with a species which seems dependent upon forested habitats (Gèze, 1985). A wooded habitat is also supported by the Proboscidea, Suidae, Giraffidae, and Rhinocerotidae (represented only by the folivorous *Diceros* while the grazer *Ceratotherium* is absent). The hare, squirrel, aardvark, and hipparions indicate more open habitats, while the Reduncini (*Kobus*) and the Hippotragini (cf. *Protoryx*) are found in humid grassland.

A complementary approach to paleoenvironmental reconstruction is

TABLE 1. Kossom Bougoud: faunal list.

- FLORA
  - LEGUMINOSAE
    - (?) Papilionoideae indet.
- ARTHROPODA
  - COLEOPTERA
    - Scarabaeidae indet.(nests)
  - ISOPTERA
    - Hodotermitidae indet. (nests)
  - HYMENOPTERA
    - Hymenoptera indet. (nests)
- VERTEBRATA
  - TELEOSTEI
    - Characiformes
      - Characidae
        - *Hydrocynus* sp.
        - cf. *Sindacharax* sp.
    - Siluriformes
      - Bagridae
        - *Bagrus* sp.
        - *Clarotes* sp.
      - Ariidae
        - *Arius gigas*
        - Ariidae sp. nov.
      - Mochokidae
        - *Synodontis* sp.
      - Clariidae
        - *Clarias/Heterobranchus*
    - Perciformes
      - Latidae
        - *Lates niloticus*
      - Cichlidae
        - Cichlidae indet.
    - Tetraodontiformes
      - Tetraodontidae
        - Tetraodontidae indet.
  - REPTILIA
    - Testudines
      - Trionychidae
        - Trionychidae indet.
      - Testudinidae
        - Testudinidae indet.
    - Serpentes
      - Boidae
        - *Python* aff. *sebae*
    - Lacertilia
      - Varanidae
        - *Varanus* cf. *niloticus*
    - Crocodylia
      - Crocodylidae
        - *Crocodylus lloydi*
        - *Euthecodon* cf. *brumpti*
      - Gavialidae
        - Gavialidae gen. et sp. nov.
  - AVES
    - Ciconiiformes
      - Ciconiidae
        - *Ephippiorhynchus* nov.sp.
        - Ciconiidae indet.
      - Ardeidae
        - Ardeidae indet. (cf. *Ardea*)
    - Pelecaniformes
      - Phalacrocoracidae
        - *Phalacrocorax* sp. (same size as *P. carbo*)
    - Anseriformes
      - Anatidae
        - Anatidae indet.
  - MAMMALIA
    - Carnivora
        - Carnivora indet.
      - Hyaenidae
        - *Lycyaena* sp.
      - Felidae
        - *Dinofelis* sp.

TABLE 1. Continued.

      - Canidae
        - Canidae indet.
    - Rodentia
      - Rodentia indet.
      - Sciuridae
        - *Xerus* sp. nov.
      - Muridae
        - *Arvicanthis* division
        - cf. Tachyoryctini indet.
    - Lagomorpha
      - Leporidae
        - *Serengetilagus* aff. *precapensis*
    - Tubulidentata
      - Orycteropodidae
        - *Orycteropus* sp. nov.
    - Perissodactyla
      - Equidae
        - *Hipparion* sp. nov. (large size)
        - *Hipparion* sp. (medium size)
      - Rhinocerotidae
        - cf. *Diceros* sp.
    - Proboscidea
      - Gomphotheriidae
        - *Anancus kenyensis* "*kenyensis* morph"
      - Elephantidae
        - *Stegodon kaisensis* "Nkondo stage"
        - Elephantinae primitive indet.
        - *Primelephas* aff. *gomphotheroides*
    - Artiodactyla
      - Suidae
        - *Nyanzachoerus kanamensis*
        - Suinae sp. nov.
      - Hippopotamidae
        - Hexaprotodon harvardi
      - Camelidae
        - *Paracamelus* sp.
      - Giraffidae
        - Giraffidae indet.
        - *Giraffa* cf. *jumae*
      - Bovidae
        - Bovidae indet. (cf. Aepyceros)
      - Reduncini
        - *Kobus* sp. nov.
      - Hippotragini
        - aff. *Protoryx* sp.
      - Antilopini
        - cf. *Antidorcas* sp.
      - Bovini
        - cf. *Simatherium* sp.

to measure stable carbon isotope ratios in the enamel of mammalian herbivores. Till now, 31 enamel fragments of herbivore teeth from KB (Table 2) have been analyzed (Bocherens et al., 1996; Zazzo et al., in press). The values of $\delta$ $^{13}$C vary between −10.2 and 1.3 ‰ with a mean value of 2.9 ± 3.2‰. In comparison, with measurements on living African fauna (Lee-Thorp and Van der Merwe, 1987) these values cover the range of feeding types from browsers to grazers. The lowest values were from giraffes while the highest were from bovids, hipparions, and *Anancus*. This supports the presence of forested areas. Values of $\delta$ $^{13}$C for herbivores from younger Chadian sites (KL and KT) are perceptibly higher, notably for the hominid sites (KT12 and KT13). These preliminary results point to environmental differences, and suggest the successive opening of habitats from KB through KL to KT.

TABLE 2. Carbon isotope values for herbivore tooth from Chadian Pliocene sites.

| Site | KB | KL | KT |
|---|---|---|---|
| n | 31 | 20 | 25 |
| $\delta$ $^{13}$C (average) | −2.9 ± 3.2 | −2.0 ± 2.1 | −0.1 ± 1.9 |
| Minimum | −10.2 | −5.6 | −5.4 |
| Maximum | 1.3 | 1.4 | 2.2 |

As with other Chadian Pliocene faunas (KT and KL; Brunet et al., 1995, 1997a, 1998) that from KB mostly comprises species common to other African faunas of the same age, but the approximately 10% new species suggest a certain provincialism. As at Kollé, this difference is also marked by the association of at least three proboscidean species and in particular the abundance of *Stegodon*, present in Uganda but rare in Ethiopia and absent in Kenya (Tassy, 1994).

## Biochronology

The primitive features of the two main bovid taxa (*Kobus*, sp. nov. and aff. *Protoryx*, sp.) are compatible with an early Pliocene age. Remember that Tragelaphini are unknown in Chad and that Alcelaphini do not become common until later in the Pliocene. The presence of *Paracamelus* also supports an early Pliocene age. The sole Tetraconodontinae *Nyanzachoerus kanamensis*, in the absence of other species of the genus, indicates an age between 4.5 and 5.5 Ma. Based on the Suidae, KB would be older than Lothagam Apak Member (5.0–4.72 Ma; Leakey et al., 1996) which has *N. kanamensis* and *N. jaegeri* but younger than Sahabi (between 5 and 6 Ma) with *N. syrticus* and *N. kanamensis* (Harrison and Baker, 1997). Hence, the association of *N. kanamensis* and *N. jaegeri* at Kollé (Brunet et al., 1998) indicates a younger age for this site. This seems well supported by the fact that an elephant (*Loxodonta*) is only known in the Kollé fauna. The "simple morph" of *Anancus kenyensis* is sole present at KB while it is associated with the "complex morph" at Kollé.

The current state of knowledge places the KB fauna older than the one from Kollé, with an age close to the Mio-Pliocene boundary, around 5 Ma. This is a crucial time period for understanding the environments of the first hominids.

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