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Short Note

The oldest known *Massoutiera* (Rodentia: Ctenodactylinae)

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The Ctenodactylidae Gervais 1853 is a family of rodents characterized by a hystricomorphous skull and a sciurognathous lower mandible. It comprises four subfamilies, of which only the Ctenodactylinae are extant. The Ctenodactylinae are known from the Early Miocene to Recent and include 22 species distributed in 14 genera. The four extant genera (*Pectinator* Blyth 1856, *Massoutiera* Lataste 1885, *Felovia* Lataste 1886 and *Ctenodactylus* Gray 1830) are restricted to areas in north equatorial Africa (Figure 1).

The reference to a possible Pliocene representative of *Pectinator* in Asia (see for instance McKenna and Bell 1997: p. 190) probably comes from Darlington (1957: p. 392). However, this was based on Hinton (1933), who described a fossil lower jaw from India as *Pectinator sivalensis*. This material was transferred by Black (1972) to the fossil genus *Sayimys*. Elsewhere, Jaeger (1970: p. 921) cited a “Ctenodactylidae gen. et sp. nov. cf. *Felovia*” from the Early Pleistocene locality of Irhoud Ocre (Jbel Irhoud, Maroc). On the basis of this material, he later named the species *Irhoudia bohlini* (Jaeger 1971). Supposedly based on the studies of previous authors (Joleaud 1935, Arambourg 1949, 1952, Arambourg and Coque 1958), Le Houérou (1995: p. 60, 1997: p. 629) mentioned the presence of *Ctenodactylus gundi* at the Early Pleistocene (~2.5 Ma, see Gibbard et al. 2010) locality of Ain Brimba (Tunisia). Nevertheless, none of the cited publications indicated the presence of *Ctenodactylus* at this locality, and thus this record appears dubious (see also Coque 1962). Jaeger (1975: p. 7) merely listed Ctenodactylidae indet. at the same site. For extrinsic reasons (age), it is likely that this material actually belongs to the genus *Irhoudia*, which is found in the Upper Miocene of Algeria (Jaeger 1977: p. 93, Coiffait-Martin 1991), in the Plio-Pleistocene of Tunisia (Jaeger 1975, Mein and Pickford 1992) and in some Moroccan sites dating from the Mio-Pliocene to the Early Pleistocene (Jaeger 1971, Raynal et al. 1999, Geraads 1995, 1998, 2002). Although the extant ctenodactylines have usually been considered to be known only from the Holocene (Wood 1977, Nowak 1999: p. 1622, they are now noted at the Late Pleistocene site of the Grotte des Pigeons (*Ctenodactylus* spp.; Taforalt, Morocco) (Bouzouggar et al. 2007).

They are also recorded at the Holocene sites of Redeyef (Table Sud and Table Redeyef, Gafsa, Tunisia) (Vaufrey 1955: p. 394) and Ti-n-Thora (Tadrart Acacus, Libya). The latter specimens are the subject of the present paper. They are described and compared with recent ctenodactylines, and their systematic verification is evaluated below.

The sites of Ti-n-Thora started being excavated during the 1960s and continued during the 1970s and 1980s (Barich 1987a, Di Lernia and Garcea 1997). Three localities are known at Ti-n-Thora: Ti-n-Thora East, Ti-n-Thora North, and Ti-n-Thora Two Caves (Gautier and Van Neer 1982, Barich 1987a,b, Gautier 1987). These localities have been dated by radiocarbon at the institute of geochemistry of the Sapienza Università di Roma by G. Belluomini (Belluomini and Manfra 1987, see also Barich 1984, 1987c). The oldest locality is Ti-n-Thora Two Caves, which has been dated from 9350 ± 110 to 8230 ± 50 BP (7400 ± 110 to 6280 ± 50 BC), followed in age by Ti-n-Thora East from 9080 ± 70 to 7330 ± 80 BP (7130 ± 70 to 5380 ± 80 BC) and by Ti-n-Thora North from 7070 ± 60 to 5260 ± 130 BP (5120 ± 60 to 3310 ± 130 BC).

Ti-n-Thora East was the richest locality from a faunal viewpoint and it has yielded most of the ctenodactyline remains, which were initially identified as *Ctenodactylus* sp. by Cassoli and Durante (1974). In 1982, Gautier and Van Neer reidentified the Libyan gundi material as *Massoutiera mzabi*. However, this was not based on a detailed morphological study of the specimens. Based on the distribution of modern ctenodactylines, Gautier and Van Neer (1982) assumed that only *Ctenodactylus gundi* and *Massoutiera mzabi* could have been present at Ti-n-Thora (*Ctenodactylus vali* was frequently used as a subspecies of *Ctenodactylus gundi* at that time; see for instance Ranck 1968). As the material from Ti-n-Thora is closer in size to *Massoutiera mzabi* than to *Ctenodactylus gundi*, they concluded that they were dealing with the former. However, it has not been proven that the difference in size between *Ctenodactylus vali* (which is smaller than *Ctenodactylus gundi*; George 1982) and *Massoutiera mzabi* is significant.

Thus, a detailed study of this material is necessary to confirm or refute its attribution to *Massoutiera mzabi*. With this end in view, the cranial material available in the collections of the “Research Unit Palaeontology” of the Universiteit Gent (Belgium) under the number P2576 (three hemimandibles from the site of Ti-n-Thora East) was examined and compared with the specimens of the four extant genera of gundis housed in the collections of the Muséum national d’Histoire naturelle (Paris, France) and of the Museum für Naturkunde der Humboldt-Universität (Berlin, Germany).

The three Ti-n-Thora East hemimandibles (Figure 2) correspond to the 7th growth stage of Lataste (1885): adult indi-

Figure 1 Distribution of the extant Ctenodactylinae (IUCN 2010) and location of the localities of Ti-n-Thora (Libya).

viduals having jaws with the three molars, but lacking any trace of the premolars. The lower molars are rootless and hypsodont. They are bilobed (lacking any trace of metaflexid). The lobes are diagonal, particularly the anterior one, which is very oblique. The protoconid is hypertrophied and the ectolophid is very narrow. The hypoflexid is very deep and it is filled with cement. There is a significant size increase from the first lower molar (m1) to the third (m3). Except for *Massoutiera mzabi*, the specimens from Ti-n-Thora East differ from all the extant species of the Ctenodactylinae. For instance, they differ from *Ctenodactylus gundi* and *Ctenodactylus vali* in having cement on the labial embayment of the lower molars. This characteristic (among others such as the rootless and bilobed lower molars) also precludes its allocation to the genus *Pectinator*. Within the extant Ctenodactylinae, *Massoutiera mzabi* and *Felovia vae* are the taxa that are the most alike, especially regarding the lower molars. However, there are some differences that prevent the

allocation of the three mandibles of Ti-n-Thora East to the genus *Felovia* (e.g., they have no trace of a metaflexid, which is short, but still present, in the lower molars of *Felovia*). Thus, we confirm the suggestion by Gautier and Van Neer (1982) that the ctenodactylina specimens from Ti-n-Thora East belong to *Massoutiera mzabi*.

Massoutiera mzabi has a large, although spotty, geographical range: central and southwestern Algeria, southern Libya, eastern Mali, western Niger, and northwestern Chad (Figure 1). The fact that this species currently lives in the Acacus, as it did around 9000 BP, should not be taken as evidence of the same hyperarid climatic conditions as today. First of all, the studies carried out by Gouat et al. (1984) show that *Massoutiera mzabi* has a physiological and behavioral plasticity that allows it to adapt to a variety of environments. Therefore, this species can live not only in the most inhospitable of places but also in areas with a less extreme climate (e.g., Hoggar), where it co-occurs with a wide variety of animals (Gouat et al. 1984). In addition, the faunal association of Ti-n-Thora East, even though it records a large number of species adapted to arid conditions (*Procapra capensis*, *Paraechinus aethiopicus*, *Vulpes ruepelli*, *Gazella dama*, *Gazella dorcas*), also includes widely distributed taxa (*Hystrix cristata*, *Lepus capensis*, *Canis aureus*, *Felis silvestris*, *Galerella sanguinea*, *Herpestes ichneumon*), as well as species characteristic of savannah (*Panthera leo*, *Papio cynocephalus sensu lato*). All in all, the fauna of Ti-n-Thora resembles the fauna that currently (or until recently) dwells in areas of the transition zone between the Sahara desert and the tropical regions of Africa (Sahel), as well as the fauna present in the ecoregion of the Tibesti Mountains. Today, the semidesert/desert boundary in North Africa is located at approximately 30°N latitude (Schulz et al. 2009: p. 70, figure 1). The Sahel, which today is located around 18°N latitude, extended up to 23°N latitude during the African Humid Period (~11500–5500 BP) (Jolly et al. 1998, Claussen et al. 2002, Renssen et al. 2006, Schütt and Krause 2009). Similarly, in northern Africa, the semidesert/desert boundary is

Figure 2 *Massoutiera mzabi* from Ti-n-Thora (specimens P2576). (A) Right hemimandible with m1–m3 in occlusal view; (B) same specimen in medial view; (C) right hemimandible with m1–m3 in occlusal view; (D) left hemimandible with m1–m3 in occlusal view. Scale bar=4 mm.

expected to have progressed to the south, namely towards the Tadrart Acacus. Thus, it is likely that Ti-n-Thora 9000 BP was not a desert as is today but rather a semiarid zone.

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