

## The aardvark from the Miocene hominoid locality Çandır, Turkey

With 4 figures, 2 plates

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### Abstract

The aardvark species *Orycteropus seni* is based on a mandible from the Middle Miocene of Çandır. This specimen and a metapodial are described and the evolution of the aardvarks is discussed. The Early Miocene African genus *Myorycteropus* may have given rise to three lineages. Within Africa, it may have given rise to the Middle Miocene *Orycteropus chemeldoi*. Following a dispersal to the Indian Subcontinent it gave rise to the Middle to Late Miocene *O. browni* lineage, which possibly gave rise to the Late Miocene *Leptorycteropus guilielmi*. Following a dispersal to Anatolia, it gave rise to the Middle Miocene to Recent lineage *Orycteropus seni* - *O. pottieri/mauritanicus* - *O. gaudryi/depereti* - *O. crassidens* - *O. afer*. If this is correct, the lineage leading to the living species, moved out of Africa during the early Middle Miocene and back into Africa during the early Late Miocene. A similar pattern has been proposed to have occurred in other taxa, including hominids. The mandibular morphology, the presence of large functional canines and the relatively large cheek teeth in the fossil forms support Patterson's (1975) idea that the typical tooth structure of the Tubulidentata did not evolve as a response to a myrmecophagous diet and that aardvarks are not complete myrmecophages, but omnivores. This is particularly so for the fossil forms, including *O. seni* from Çandır.

**Keywords:** Tubulidentata, Orycteropodidae, *Orycteropus seni*, phylogeny, evolution, Miocene, Çandır, Turkey, ecology, myrmecophagy.

### Zusammenfassung

Die Erdferkelart *Orycteropus seni* basiert auf einer Mandibel des Mittleren Miozäns von Çandır. Dieses Exemplar und ein Metapode werden beschrieben und die Evolution der Erdferkel wird diskutiert. Die früh Miozäne afrikanische Gattung *Myorycteropus* scheint der Ursprung von drei Evolutionsreihen zu sein. Innerhalb Afrikas kann es im Mittel Miozän zu der Art *Orycteropus chemeldoi* evoluiert sein. Nach einer Ausbreitung auf den Indischen Halbkontinent evoluierte es zu der Mittel- bis Spätmiozänen Linie *O. browni*, welche wiederum den Ursprung für die Spätmiozäne Linie *Leptorycteropus guilielmi* bildete. Nach einer Ausbreitung nach Anatolien bildete es den Ursprung für die Mittelmiozäne bis rezente Linie *Orycteropus seni* - *O. pottieri/mauritanicus* - *O. gaudryi/depereti* - *O. crassidens* - *O. afer*. Wenn diese Hypothese korrekt ist, dann sollte die Linie, die zur rezenten Art führt, Afrika während des Frühmiozäns verlassen haben und später, während des frühen Spätmiozäns, wieder zurückgekehrt sein. Ein ähnliches Modell wurde auch für andere Taxa (z. B. die Hominiden) vorgeschlagen. Die Mandibulärmorphologie, die Anwesenheit großer funktioneller Eckzähne und die relativ großen Molaren unterstützen Patterson's (1975) Idee, nach der die typische Zahnstruktur der Tubulidentata nicht als Antwort auf Myrmecophagie zu verstehen ist und die Erdferkel keine ausschließlichen Myrmecophagen sind, sondern Omnivoren. Das gilt im Speziellen für die fossilen Formen, einschließlich *O. seni* von Çandır.

**Schlüsselwörter:** Tubulidentata, Orycteropodidae, *Orycteropus seni*, Phylogenie, Evolution, Miozän, Çandır, Türkei, Ökologie, Myrmecophagie

## Introduction

The Middle Miocene locality of Çandır is well known for its hominoid remains currently assigned to *Griphopithecus* (ANDREWS et al. 1996, GÜLEÇ & BEGUN this volume), and abundant fauna (SICKENBERG et al. 1975 and chapters in this volume). The locality has been assigned to the Middle Miocene, neogene mammal unit MN6, usually in a position above Paşalar (e.g. DE BRUIJN et al. 1992). Few arguments have been given for the age of the locality relative to that of other Anatolian and European localities and possibly the first discussion on its age, based on a detailed study of a large amount of material, suggested Çandır to be younger than İnönü I and Paşalar (VAN DER MADE 1996). All three localities have *Orycteropus*, but the best material is from Çandır.

Antbears or aardvarks (from the Dutch "aardvarken", meaning literally "earth pig") belong to the Tubulidentata. There is one living species, *Orycteropus afer*, living in Africa. It eats termites and a particular type of fruit

*Cucumis humifructus* (PATTERSON 1975). The origin of the order is not well known and various fossil forms from the paleogene of America and Europe have been assigned to this order. However, these alleged relationships have either been proved to be non-existent, or are still debated. The oldest tubulidentates that are universally accepted are from the early Miocene of Africa and belong to the species *Orycteropus minutus* PICKFORD, 1975 and *Myorycteropus africanus* MACINNES, 1956. During the Middle Miocene, the genus dispersed from Africa. The fossils from Çandır, Paşalar and İnönü I represent, along with some specimens from the Chinji Formation, the oldest *Orycteropus* outside Africa.

It is the aim of this paper to describe the specimens from Çandır, and to discuss evolution and biogeography of the aardvarks.

## Materials and methods

### Measurements and their abbreviations

All measurements are in mm, unless otherwise indicated. Measurements of the metapodial are as in suoids VAN DER MADE (1996). The use and value of DAP' and DT' are discussed elsewhere (VAN DER MADE 1996 1998, etc.).

- DAP = antero-posterior diameter (or in teeth, the length).
- DAP' = DAP of a tooth expressed as a percentage of the DAP of the first molar.
- DAPp = DAP of the proximal part of a bone.
- DT = maximum transverse diameter.
- DT' = DT of a tooth expressed as a percentage of the DT of the first molar.
- DTa = DT of the anterior lobe of a tooth.
- DTd = DT of the distal part of a bone.
- DTp = DT of the posterior lobe of a tooth or DT of the proximal part of a bone.
- L = length of a bone.

## Material studied

The material from Çandır is compared to material from other localities studied in the following institutes. The abbreviations will be used for reference in the text.

- MTA = Maden Tetkik ve Arama (Geological Survey of Turkey) Ankara.
- NNML = Nationaal Natuurhistorisch Museum Leiden.
- FISF = Forschungs-Institut Senckenberg, Frankfurt.
- BSPHGM = Bayerische Staatssammlung für Paläontologie und Historische Geologie, München.

## Description and comparisons

- Tubulidentata HUXLEY, 1872
- Orycteropidae GRAY, 1821
- Orycteropus* GEOFFROY, 1795
- Orycteropus seni* TEKKAYA, 1992

- 1975 *Orycteropus* sp. – SICKENBERG et al.: 23, 25.
- 1990 *Orycteropus* sp. – FORTELIUS: 479-480, Figure 1.
- 1992 *Orycteropus seni* n. sp. – TEKKAYA: 275-289, photograph 1, figure 3.
- 1992 *Orycteropus* sp. – TEKKAYA: photograph 3.

Holotype: 2532 a left mandible with  $M_{1,3}$ , kept in the MTA.

Type locality: Çandır, Turkey.

Age of the type locality: Middle Miocene, MN 6.

Diagnosis: Species of *Orycteropus* intermediate in size between *M. africanus* and *O. pottieri*, with the symphysis starting about 27 mm before the first molar.

Remarks: The original spelling of the species name has been changed according to the nomenclatorial rules.

Material: 2532 - left mandible with  $M_{1,3}$ ;  $M_1$  10.6 x 4 - 6.4 (DAP x DTa - DTp),  $M_2$ : 11.3 x 6.4 - 6.7,  $M_3$ : 8.1 x 5.6 - 4.8. Depth x width of the mandible, below  $P_3$ : 11.8 x 6.1, below  $P_4$ : 14.6 x 6.6, below  $M_1$ : 16.3 x 7.9, below  $M_2$ : 17.9 x 9.2, below  $M_3$ : 18.0 x 9.1.

AÇHÜ 1063 - right second metatarsal; DAPp = 14.9, DTp = 8.9, L = 58.4, DAPd = 9.6, DTd = 11.1.

These specimens are stored in the MTA.

Description and comparison: The mandible is slender and elongate (Plate 1). It is broken where the symphysis starts, 26.8 mm anterior to the first molar. The lower border of the mandible turns a little downward in the area where the symphysis starts. At this point the depth of the mandible is still considerable. These features suggest a well developed symphysis. The alveoli of the premolars are not easily visible; the mandible is possibly compressed here. A possible alveolus for a canine is visible on the buccal side at the level where lingually the symphysis starts. In *Myorycteropus africanus* the symphysis seems to start below the anterior part of the  $P_3$  or posterior part of the  $P_2$  (MACINNES 1956, Plate 1, figs. 3-

4). The symphysis in *Orycteropus pottieri* OZANSOY, 1965 from Sinap starts below the posterior part of the canine or below the first premolar, or 22 to 26.7 mm anterior to the first molar (MNHN, MTA). In a mandible of *Orycteropus gaudryi* Major, 1888 from Muğla (MTA) it is below the canine and 34.1 mm anterior to the  $M_1$ .

In stead of having a crown, the molars have a tubulidentate structure. The molars have two lobes (see Plate 1). There are small anterior dipping facets over the anterior half of the first lobes and horizontal facets over the rest of the teeth. The molars are larger than those of *M. africanus* from the lower Miocene of Rusinga and Mwangano, *Orycteropus* sp. from the Chinji Formation and *O. browni* COLBERT, 1933 from the Dhok Pathan Formation (Figure 1). The molars are smaller than those of *O. crassidens* MACINNES, 1956 from the Pleistocene of Rusinga and are close to or in the lower range of *O. mauritanicus* ARAMBOURG, 1959 from the Vallesian of north Africa, *O. pottieri* from the Vallesian of Sinap and *O. gaudryi* from the Turolian of Samos. The  $M_2$  of *Orycteropus chemeldoi* PICKFORD, 1975 is more elongate than of the other species.

The second metatarsal (Plate 2) is roughly similar to that of a recent *Orycteropus*. Compared to a subadult specimen of recent *O. afer* in the NHML, the specimen is around 30% smaller. There is much less difference in size of the teeth of *O. seni* and *O. afer*. The distal articulation facet has a relatively small DAPd and relatively great DTd compared to the recent specimen.

**Results and Discussion:** The mandible is the holotype of *Orycteropus seni* TEKKAYA, 1992. The only other specimen from Çandır is the metapodial. Other material that probably belongs to the same species is from Paşalar (FORTELIUS 1990) and a single phalanx from İnönü I in the MTA (TEKKAYA 1992, Figure 3). A mandible without teeth from Belometchetskaia, assigned to *Orycteropus* sp. (GABUNIA 1956), tapers more towards anterior than in the specimens from Çandır, Sinap and Muğla. The specimen from Belometchetskaia is reported to have 6 antemolars. In early *Orycteropus*, the canine can still be easily recognized and there are no incisors. For these reasons, the identity of the Belometchetskaia specimen is considered here as dubious.

There are two molars from Paşalar that might either be  $M_1$  or  $M_2$ ; in the former case they are in the lower range *O. gaudryi* and close to the lower range of *O. pottieri*. In the latter case, their DAP is just outside the ranges, but still close to the DAP of the  $M_2$  of the type of *O. seni*. The fact that all these Middle Miocene specimens are small might be an indication that the *Orycteropus* from this time was smaller than the later *O. pottieri*. A smaller average size might be a justification for the species *O. seni*; no morphological features allow a clear separation from *O. pottieri*. The separation from *O. chemeldoi* is easier. The latter species has very elongate  $M_2$  (Figure 1) and a relatively small  $M_1$  (Figure 2).

Bearing in mind that cursorial species tend to have

metatarsals with distal pulleys with relatively small DT and large DAP, the proportions of the specimen from Çandır suggests the species would be less cursorial. However, the material is very limited. Several generic names have been introduced for aardvarks: *Myorycteropus* MACINNES, 1956 (type species *M. africanus*) and *Leporycteropus* PATTERSON, 1975. PICKFORD (1975) did not recognize *Myorycteropus*, but PATTERSON (1978) insisted that the genus is valid. In view of the differences in the postcranial skeleton described by MACINNES (1956) and PATTERSON (1975), *Myorycteropus* is recognized here.

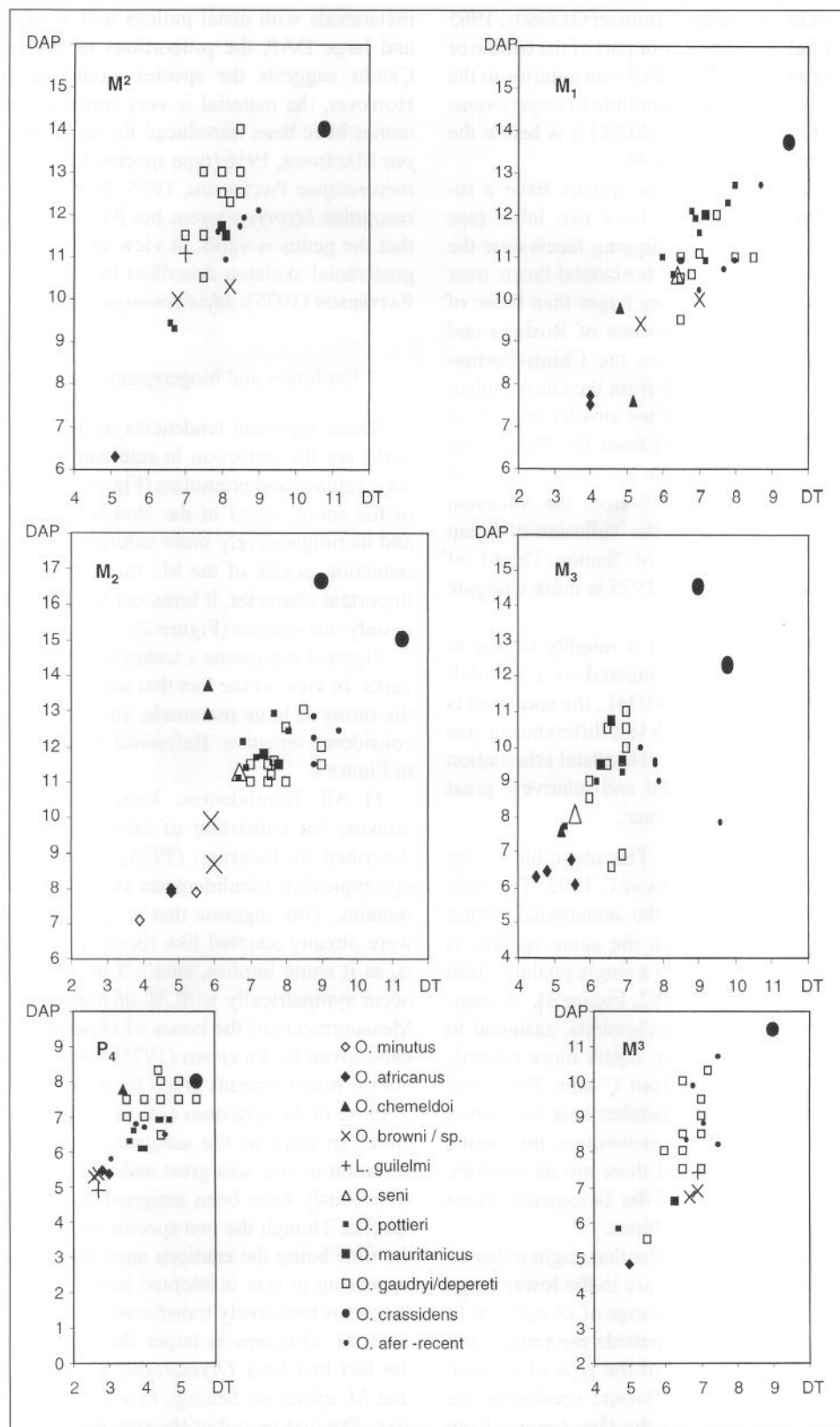
#### Evolution and biogeography of the aardvarks

Some important tendencies in the evolution of aardvarks are the reduction in size and number of the incisors, canines and premolars (Figure 3) and the elongation of the snout, noted in the elongation of the symphysis and its progressively more anterior position. Though the reduction in size of the  $M_3$  might be expected to be an important character, it turns out that it is clearly reduced in only one species (Figure 2).

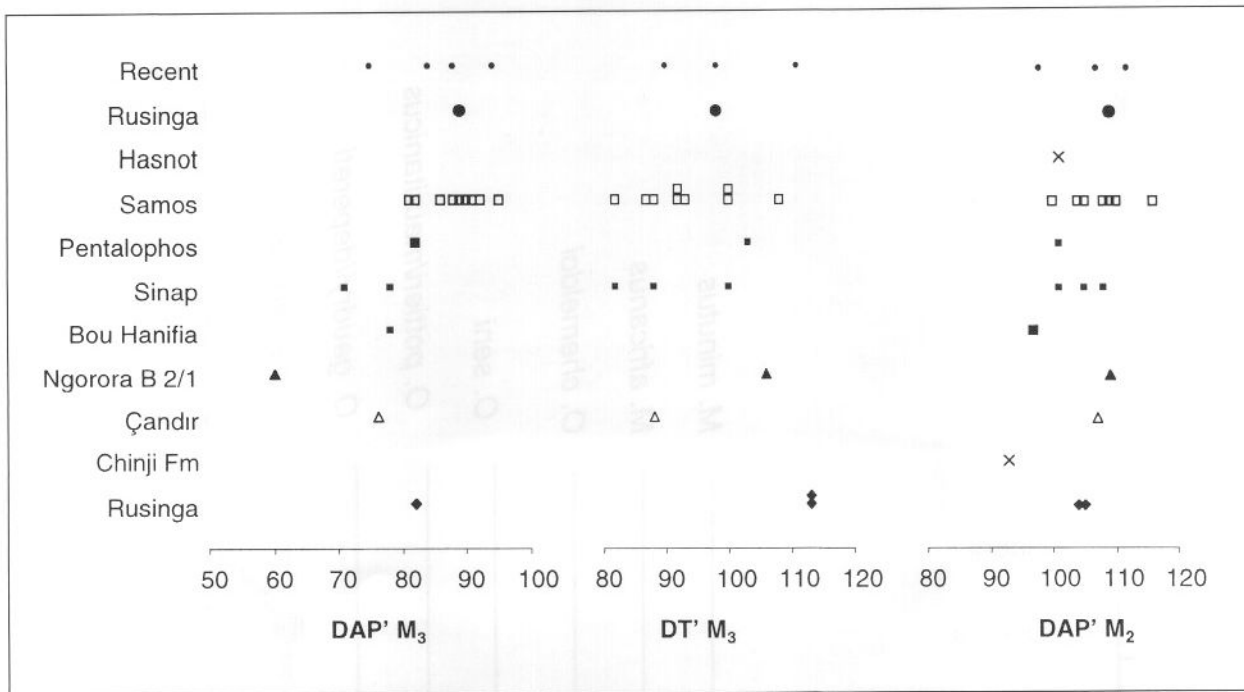
Figure 4 represents a tentative phylogeny of the aardvarks. In view of the fact that aardvark fossils are among the rarest of large mammals, such a phylogeny must be considered tentative. Reference is made to the numbers in Figure 4.

1) All Tubulidentata known share teeth without crowns, but consisting of tubules. Postcranial remains described by PICKFORD (1975) show that the morphology typical of tubulidentates is already present in these remains. This suggests that at least in part, these forms were already adapted like recent aardvarks. *O. minutus* is, as its name implies, small. The species is reported to occur sympatrically with *M. africanus* (PICKFORD 1975). Measurements of the bones of *O. minutus* from Mwangano given by PICKFORD (1975) suggest a small animal, but the measurements given for the teeth are very similar to those of *M. africanus* ( $M_2$  in Figure 1). This suggests either an error in the assignation of the teeth, or that variation in size was great and that other samples might erroneously have been assigned to a large and a small species. Though the two species may have coexisted, for the time being the cautious approach of a single lineage increasing in size is adopted here. This implies that the species is tentatively transferred to *Myorycteropus*.

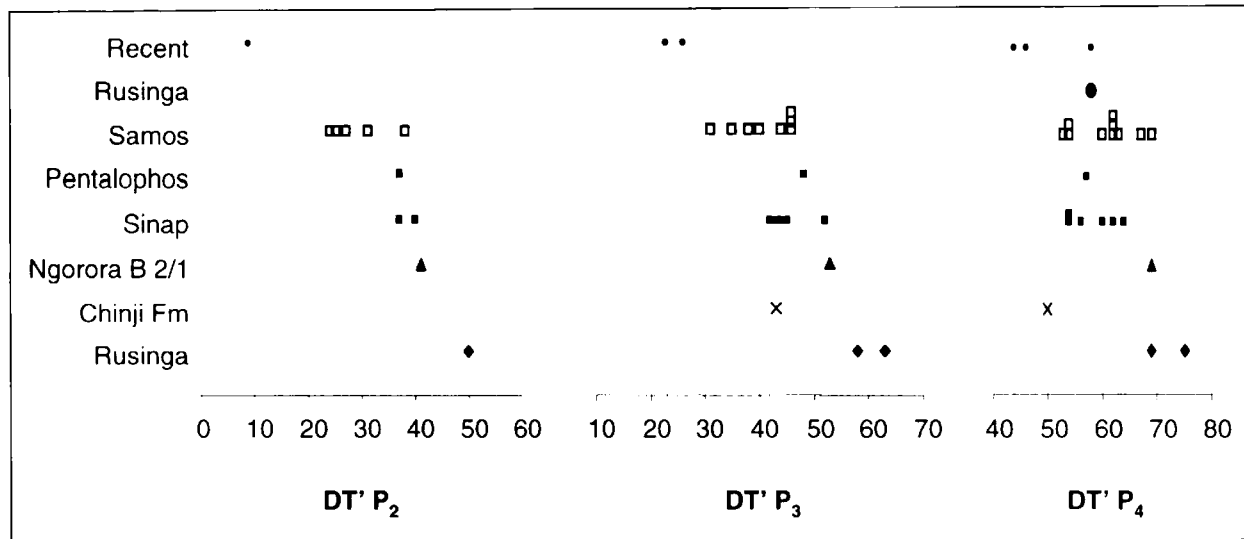
2) *M. africanus* is larger than *M. minutus*. This and the fact that later *Orycteropus* are still larger, suggests that *M. africanus* belongs to a lineage that increased in size. The first record of the symphysis is in *M. africanus* from Rusinga, and it appears to start below the posterior part of the  $P_2$  or anterior part of the  $P_3$  (MACINNES 1956, Plate 1, Figures 3-4), in spite of the fact that reconstructions of this specimen show an anteriorly positioned and elongate symphysis (MACINNES 1956, Figure 1; PICKFORD 1975, Figure 7). This position may well be primitive for the whole order, since it is common in other orders as



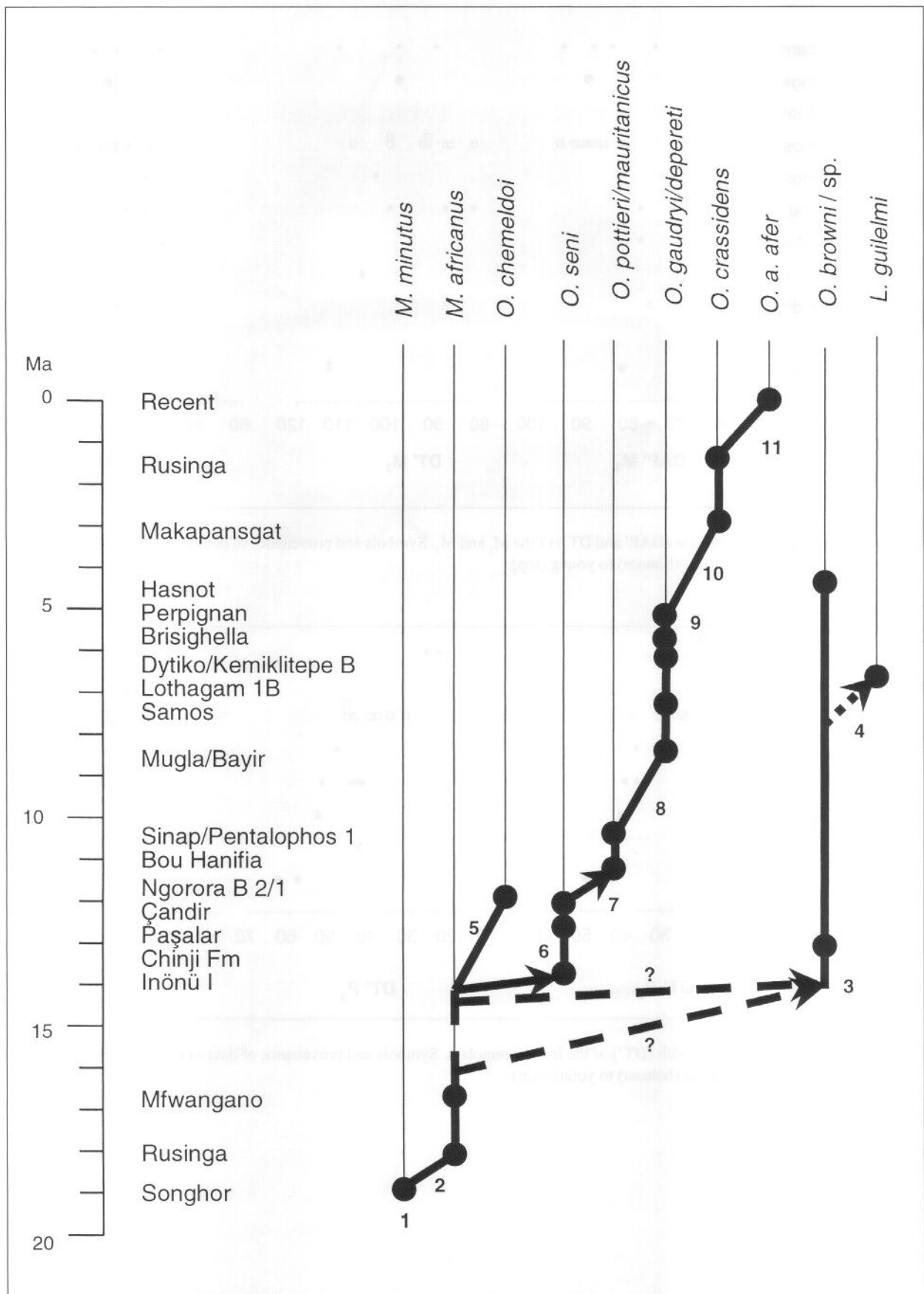
**Fig. 1:** Bivariate plots of the lower cheek of *Orycteropus*. *M. minutus* from Songhor (PICKFORD 1975); *M. africanus* from Rusinga (MACINNES 1956); *O. chemeldoi* from locality 2/1 in the Ngorora Formation, member B (PICKFORD 1975), *Orycteropus* sp. from the Chinji Formation and *O. browni* from Hasnot (PICKFORD 1978); *Leptorycteropus guilelmi* from Lothagam I (PATTERSON 1975); *O. seni* from Çandır (MTA), *Orycteropus pottieri* from Sinap (MTA) and Pentalophos (DE BONIS et al. 1994); *O. mauritanicus* (DE BONIS et al. 1994); *Orycteropus gaudryi* from Samos (COLBERT 1941), Dytiko, Kemiklitepe (DE BONIS et al. 1994), Muğla and Bayir (MTA); *O. afer crassidens* from the Pleistocene of Kiahera, Rusinga (MACINNES 1956) and Makapansgat (KITCHING 1963); Recent *Orycteropus afer* (NNML; FSSF).



**Fig. 2:** The variation in relative size (DAP' and DT') of the  $M_2$  and  $M_3$ . Symbols and provenance of data as in figure 1. The localities are in approximate order from old (bottom) to young (top).



**Fig. 3:** The variation in relative width (DT') of the lower premolars. Symbols and provenance of data as in figure 1. The localities are in approximate order from old (bottom) to young (top).



**Fig. 4:** Stratigraphic distribution of different tubulidentates. Localities and their approximate ages in Ma on the left. Thick lines indicate possible ancestor-descendant relationships and arrows indicate possible dispersal events. See discussion in text.

well. This specimen, and specimens of *O. pottieri* show this even better, indicating that incisors must have been reduced in size or that they were already completely lost. The snout must have been narrow. All later aardvarks have smaller anterior premolars (Figure 3). The skeleton of *M. africanus* shows that it was more adapted to digging than the living species (MACINNES 1956; PATTERSON 1975). *O. gaudryi* is close to the living species in its morphology, while *Leptorycteropus* is even less adapted to digging. Either *M. africanus* belongs to a lineage different of that of the other species, or the adaptation to digging became less pronounced during the course of evolution. During the Middle Miocene, three different lineages existed, which may have evolved from *M. africanus* (increasing the size and losing the extreme adaptation to digging), or from a similar form that never was strongly adapted to digging (*O. minutus?*).

3) The early Indian *Orycteropus* seems to have been progressive in the degree of reduction of the size of the premolars (Figure 3). Nothing is known about its canines. In fact, there is very little material (PICKFORD 1978) and consequently, these forms are badly known. On the basis of Late Miocene remains, two species, *O. browni* and *O. pilgrimi*, have been named (COLBERT 1933; see also LEWIS 1938), but they have been synonymized (PICKFORD 1978). The much older material from the Chinji Formation might be suspected to represent a different species, and is referred to *Orycteropus* sp. by Pickford (1978), but the material is so incomplete that no clear differences can be observed. Irrespective of age, the forms from the Indian Subcontinent have a similar size; they are larger than *M. africanus* and smaller than *O. seni* and *O. pottieri* (Figure 1). It has been postulated that around 14 Ma there was a dispersal event of *Orycteropus* to Anatolia and to the Indian Subcontinent. This is in accordance with the first appearances of *Orycteropus* in these areas (unpublished material in BSPHGM). In this case, size decrease must have occurred in the Indian Subcontinent. However, an alternative scenario is that while increasing in size, the ancestral African lineage gave first rise to an Indian branch (there was faunal exchange around 16.5 Ma ago and possibly again around 15.5 Ma ago) and later to *O. seni* in Anatolia (around 14 Ma ago), while the African forms evolved into *O. chemeldoi*. [Editors' note: the older age for Çandir preferred in Begun et al., (this volume) obviates the need to postulate two dispersal events from Africa. Larger *Orycteropus seni* could have evolved from smaller Siwaliks *Orycteropus*).

4) *Leptorycteropus guillemi* PATTERSON, 1975 has relatively small premolars, ie. its molars are in the lower extreme of the range of *O. gaudryi*, whereas the premolars are much smaller (Figure 1). In tooth proportions it seems to be like the Indian forms. The retention of a canine and the backward position of the symphysis in *L. guillemi* exclude *O. gaudryi* as a potential ancestor and the  $M^3$  of normal size seems to exclude *O. chemeldoi*, which has a reduced  $M_3$ . Very tentatively the species is related here to

*O. browni*. If such a relationship can be demonstrated, it should be considered either to include the Indian forms in *Leptorycteropus*, or include *L. guillemi* in *Orycteropus*. *Leptorycteropus* is much less adapted to digging than the living species (PATTERSON 1975).

5) The African *O. chemeldoi* follows *M. africanus* in time, but no character is known that relates it to any particular species of aardvark, save for size, which places it along with most other species between *M. africanus* and *O. crassidens*. Generic assignation is maintained here as in the original description. It is a medium sized species with very elongate  $M_2$  (Figure 1) and  $M_3$  of very reduced size (Figure 2). Both characters seem to be unique and derived, precluding the species from being ancestral to later species. The mandible was reconstructed with a very elongate anterior part, as in living *Orycteropus* (PICKFORD 1975, Figure 7). However, as argued here, this morphology evolved much later, and there is no reason to believe that the symphysis in *O. chemeldoi* was much different from that in *M. africanus* and *O. pottieri*. The species is known from the Ngorora Formation, member B and from Fort Ternan (PICKFORD 1975).

6) Probably around 14 Ma ago, when intense faunal exchange occurred between the various land masses in the Old World, *Orycteropus* dispersed into Anatolia (VAN DER MADE 1999). Like all species younger than *M. africanus*, *O. seni* is larger than *M. africanus*. [Editors' note: this evolutionary patterns holds even with the older age of Çandir preferred in BEGUN et al. (this volume).]

7) *O. pottieri* is larger than *O. seni*. Material from Sinap includes very good specimens of the mandibular symphysis. It is still robust and is placed as much forward as in the older specimens from Çandir and Rusinga. The canine is still large and is a peg-like tooth, like the premolars, but slightly larger than the first premolar and higher crowned than all the premolars. It is placed far forward and both canines must have been very close together, nearly touching. Wear facets indicate that the tooth was functional and that there were an upper first premolar and canine. The symphyseal area is narrow, but not to the same degree as in living aardvarks. There are no incisors. The presence of functional canines and the relatively short snout at this stage is interesting in view of PATTERSON's (1975) idea that aardvarks were initially not, or not so, heavily dependent on myrmecophagy.

The species *O. mauritanicus* has been named from Bou Hanifia, but the available material does not seem to present important differences with *O. pottieri*. It differs however from *O. chemeldoi*, which has the unique derived characters of the elongate  $M_2$  and the much reduced  $M_3$ . The facts that *O. mauritanicus* is very close to, or even synonymous with, *O. pottieri*, and that no possible late Early or Middle Miocene African ancestral form is known suggest that early Late Miocene *Orycteropus* dispersed again into Africa. Material from the Kakara Formation assigned to *O. cf. chemeldoi* (PICKFORD 1994) might well represent *O. mauretanicus* or *O. pottieri*.

8) In *O. gaudryi*, the symphysis is placed more forward and the anterior premolars are strongly reduced in size (Figure 3). Functional canines and first premolars were not present anymore. The relative length of the third molar is slightly reduced (Figure 2). Morphologically this species is already very close to the living species. SONDAAR (1971) found size differences in *Orycteropus* from different quarries in Samos. However, the data presented here do not show evidence of different sizes during the late Miocene of the area. *O. gaudryi* is also reported from Maragheh (MAJOR 1893).

9) During the latest Miocene (MN 13-14) *Orycteropus* dispersed into Italy and France (ROOK & MASINI 1994). The French material was named *O. depereti* HELBIG, 1933, but is very similar to *O. gaudryi*. It is not clear for how long an isolated European lineage may have existed, or whether there was a single species with a circum-Mediterranean distribution.

10) *Orycteropus crassidens* is much larger than *O. gaudryi/depereti*. It is slightly larger than the recent *Orycteropus afer*, but has much larger teeth. The differences in tooth size are such that the taxon should be recognized at the specific level; moreover, larger teeth in a skull of the same size is a morphological difference.

11) The living species *O. afer* reduced the size of its teeth relative to the remaining parts of the skull and body.

#### A peculiar biogeographic pattern

Whereas during the late Early and early Middle Miocene, dispersals of African taxa into Eurasia were common, during the Late Miocene dispersals into Africa were far more common and involve bovids (VRBA 1996) and suids, as well as many other taxa (VAN DER MADE 1998, 1999). The peculiar phenomenon that a lineage first dispersed during the Middle Miocene out of Africa, evolved and dispersed during the early Late Miocene again into Africa, is known or assumed for several taxa.

It is assumed that, *Tetralophodon* and *Anancus* evolved outside Africa from elephantoids that dispersed from Africa; the former dispersed 10.5 Ma ago and the latter 8.0-7.5 Ma ago back into Africa (KALB et al. 1996).

*Giraecopithecus* or *Ouranopithecus* evolved from a form that dispersed from Africa, but in its turn, may be ancestral to the African great ape and human clade (ANDREWS et al. 1996; BEGUN et al. 1997). Since these forms went extinct in Europe during the Vallesian, their dispersal into Africa should have been not later than the end of the Vallesian.

A slightly different case is that of the Tetraconodontinae. *Conohyus* evolved from the Indian *Sivachoerus* after it dispersed into Europe. During the early Late Miocene *Conohyus* dispersed into Africa giving rise to *Nyanzachoerus*. *Conohyus* seems to have dispersed once more during the Late Miocene into Africa and *Sivachoerus* seems

to have done so twice (VAN DER MADE 1998). These dispersals formed parts of several dispersal events involving other taxa as well, and may have been around 11, 10.4, 7.7 and 6.3 Ma ago (VAN DER MADE 1998, 1999).

The possible relationship between *O. browni* and *L. guillemi* would imply a dispersal from the Indian Subcontinent to Africa during the late Miocene, not later than some 7.7 Ma ago. The dispersal of *O. pottieri/mauritanicus* into Africa must have been some 11 Ma ago.

Though many of the taxa involved are not particularly well known, it seems that evidence is growing that it is a common phenomenon that during the late Early and early Middle Miocene lineages dispersed from Africa or the Indian Subcontinent in a northward direction, while their descendants dispersed into Africa during the Late Miocene.

#### Ecomorphology

All tubulidentates are interpreted to be adapted in different degrees to fossorial habits, *Leptorycteropus* less and *Myorycteropus* more than *Orycteropus* (PATTERSON 1975: 224). The retention of functional teeth, the size of the mandible, the position of the mandibular condyle far above the occlusal plane and the presence of a high ascending ramus led Patterson to consider at least some aardvarks as omnivores, rather than as complete myrmecophages. The retention of functional teeth was explained by the fact that the living species, *O. afer*, is known to eat a subterranean fruit, *Cucumis humifructus*, also known as „the aardvark cucumber“.

It has been assumed that even the earliest tubulidentates had an elongate symphysis that was placed far forward (eg. reconstructions by PICKFORD, 1975, Figure 7). However, the symphyses of the older species are much shorter, much more robust and placed less forward than in the living species; the total length of the part of the mandible in front of the  $M_1$  is some 5 cm in the Vallesian *O. pottieri* (three specimens in the MNHN: Yas 43, 2052, 2053) and twice that in the recent taxon. In the specimens of *M. africanus* from Rusinga and *O. seni* from Çandır, the beginning of the symphysis is situated much more posterior than in *O. afer* and in a similar position to that in *O. pottieri*.

*Orycteropus pottieri* does not have lower incisors, but has a canine that is larger than the  $P_{1-3}$ , with a tip that reaches above the occlusal surface of the cheek teeth (MNHN 2052). The tooth was certainly functional.

As PATTERSON (1975) noted, the height of the condyle above the occlusal surface increases through time. Several specimens of *O. pottieri* from Sinap (MNHN) preserve condyles. The condyle is a well developed structure with an articular surface with a width of about 13 mm. I took two measurements: the distance between the posterior edge of the condyle and the anterior surface of the  $M_1$  measured along the occlusal surface of the and

the elevation of the condyle above the occlusal plane. In two specimens the measurements are respectively 78 and 32 mm and 72 and 28 mm. In the living species, they are 104 and 40 mm, 95 and 49 mm and 89 and 43 mm in three adult and 77 and 46 mm in a juvenile specimen in the NNML. The indices are respectively 2.44 and 2.57 versus 2.60, 1.94, 2.07 and 1.67. The averages of these figures suggest that the condyle did become relatively lower, not higher. There is however much variation, probably partially ontogenetic. Whereas the data show that in any case the condyle was well elevated above the occlusal surface, one should be cautious with the interpretation of an evolutionary tendency.

The observation that the teeth of the recent species are small relative to the post cranial skeleton suggests that the importance of teeth became reduced in the recent species. Though the range of variation is not known in the fossil forms and has not been studied in the recent forms, the reduced DAPd relative to the DTd in the metapodial of *O. seni* suggests a less cursorial adaptation.

The observations on mandibular and canine morphology and on relative molar size support PATTERSON'S (1975) interpretation that the tubulidentates, and certainly the fossil forms, are omnivores and not complete myrmecophages. Preserved mandible morphology in *O. seni* is similar to that of *O. pottieri* and suggests that the presence of this species does not necessarily indicate the presence of large colonies of termites in Çandır.

The tubulidentates appear to have dispersed out of Africa in a step wise fashion: around 16.5 to 14 Ma ago into Pakistan and Anatolia, some 10 Ma ago into Greece, and around 5-6 Ma ago into Italy and France, followed by an extinction some 5 Ma ago apparently everywhere outside Africa. Although, the appearance in Greece later than in Anatolia might be due to an incomplete record, this pattern is likely to be related to the changing geography and changing distribution of favorable habitats. The availability of appropriate foods is an important component of a favorable habitat. The study of the paleodistribution of termites and other insects that have large colonies and of subterranean fruit similar to *Cucumis humifructus* might shed light on both tubulidentate evolution and ecology, as well as on the paleoenvironment of the areas where fossil tubulidentates are found.

#### Acknowledgements

I thank Prof. Erksin GÜLEÇ for inviting me to study and describe material from Çandır and for financial support that I received through her. I thank the following persons for permission to study material, for help during my work in their institutes and for any other type of help: M. BASTIR, D. BEGUN, A. CADEE, Ç. ERTÜRK, J. FRANZEN, K. HEISSIG, G. SARAC, S. SEN, CH. SMEENK, E. ÜNAY. This study benefitted from support by project PB96-1026-C03-02 of the DGES and the "Unidades Asociadas" program of the DGICYT.

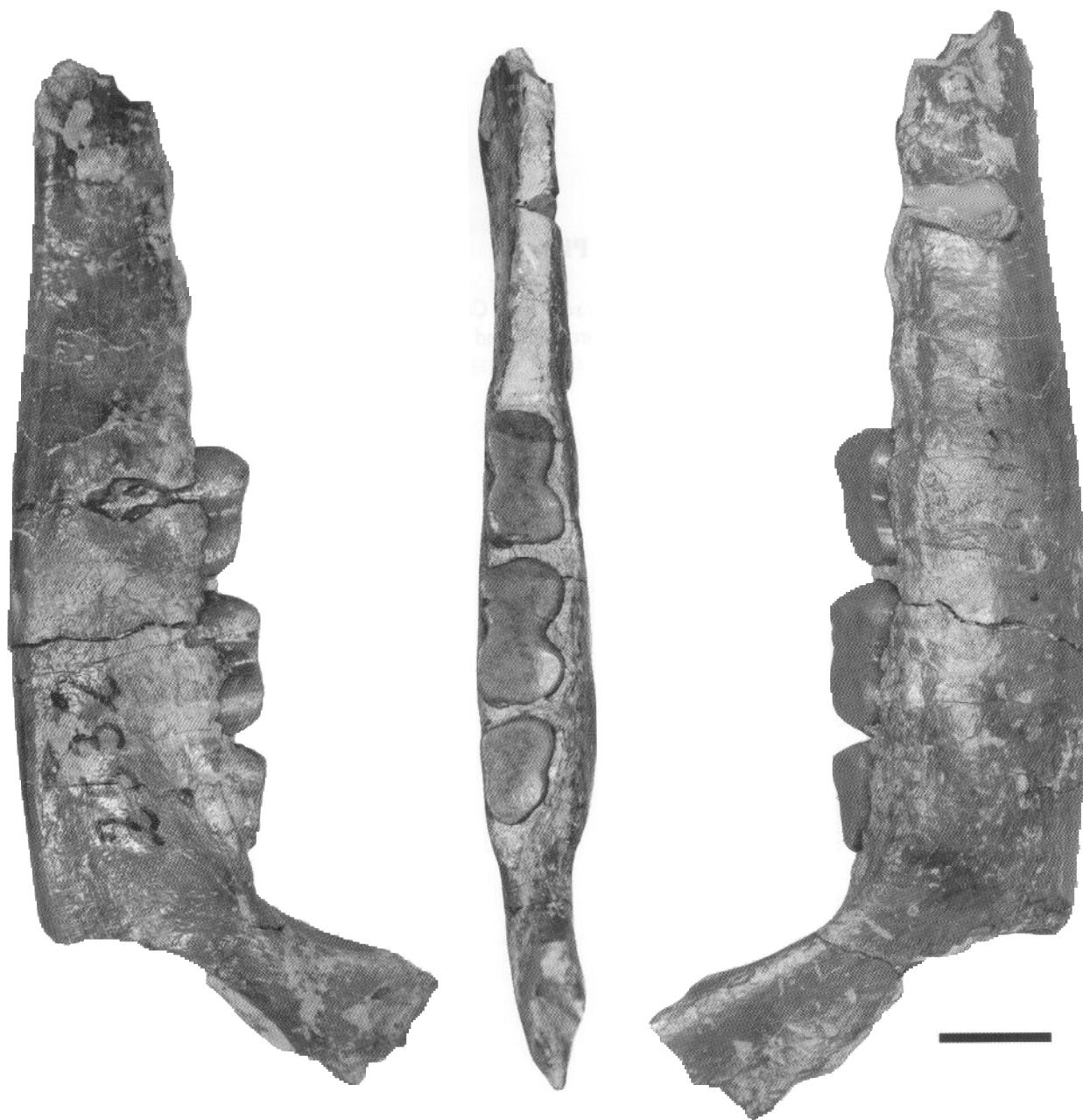
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## **Plates 1-2**

### **Plate 1**

Number 2532 – left mandible with  $M_{1-3}$  of *Orycteropus seni* from Çandır.  
From left to right: lingual, occusal and buccal views.



## Plate 2

AÇHÜ 1063 – right second metatarsal of *Orycteropus seni* from Çandır.  
From left to right: lateral, anterior, medial, posterior, proximal and distal views.



## Errata and reply to Guest Editor's notes

With 1 fig.

Jan VAN DER MADE

The "Instructions for authors" indicate that the correspondence between CFS and the authors of the articles is through the editor of a volume; this includes the correction of proofs. Unfortunately, I never received the print proofs of my papers on the aardvarks and suoids in the monograph on the geology and vertebrate paleontology of Çandır (VAN DER MADE 2003 a & b). As a consequence, some errors slipped through, which could have been corrected, and the photographs in the plates and many figures were reproduced much too large (up to more than twice as large as was the intention), resulting in figures A and E in Plate 4 (p. 177) being cut off. However, another result of my not receiving print proofs is the inclusion in the texts of these papers of notes by the guest-editors which contain irrelevant and even false information.

### Errata

Minor errors in the texts of both papers include:

- p. 134, right column, synonymy. "1992 *Orycteropus seni*", seni should be with s with a cedille.
- p. 136, first line figure caption. "lower cheek teeth" should be "cheek teeth".
- p. 140, left column, 2nd line from the bottom: "dispersd" should be "dispersed".
- p. 140, right column, line 7: "late Miocene" should be "Late Miocene".
- pp. 144–147, plates 1–2. The size of the scale bars is 1 cm.
- p. 151, middle of right column: "The tooth differs ... hypopreconulid)." This is a single sentence and not two sentences of two different paragraphs.
- p. 151, table 1. Figure caption: "Schizochocrus anatolien-sis" should be in italics.
- p. 151, table 1. The table is printed in a different way than submitted. The left  $I_1$  and its values moved to the right;

the values are DMD and DLL. The values given for the  $I_3$  and  $I^2$  are DMD and DLL.

p. 152, right column. A new paragraph should start with "The  $I_3$  tends ....".

p. 153, right column, discussion, last but one line of first paragraph. "its wide  $P_3$ " should be "its wide  $P^3$ ".

p. 155, table 2. A value given as 187.9 should be 17.9. Where "AÇH" is indicated, "AÇHÜ" should be indicated.

p. 156, table 2. "Fortsetzung" should be "Continuation". Where "AÇH" is indicated, "AÇHÜ" should be indicated.

p. 157, right column, line 8. "... crown of the  $C^m$  ..." should be "... crown of the  $C^f$  ...".

p. 158, table 3. A  $D^4$  and its values moved one column to the left (resulting in the value for DTa being given in the column for DAP, etc.). Where "AÇH" is indicated, "AÇHÜ" should be indicated.

p. 159, table 3. "Fortsetzung" should be "Continuation". Where "AÇH" is indicated, "AÇHÜ" should be indicated.

p. 159, table 3, line 29. MTA -- is a right maxilla with  $D^{3+4}$ . Everything in the line of the  $D^4$  has moved one column to the left.

p. 162, right column, line 3. *Lophidon* should be *Lophiodon*.

p. 164, left column, line 15. "... tend defend" should be "... tend to defend".

p. 164, right column, 4th line from the bottom. A new paragraph should start with "Certain ages ...".

p. 165, right column, 5th line from the bottom. *Tucroceros* should be *Turcoceros*.

pp. 172–173, plate 2. The scale bar represents approximately 1.25 cm.

pp. 176–177, plate 4. The scale bar represents approximately 2.5 cm, save for figure E, which is not to scale.

## Guest-editor's notes

A long time after the manuscripts were submitted to one of the guest-editors and about three years prior to publication, I was contacted by D. BEGUN, one of the guest-editors of the volume. He insisted very much on that I should place Çandır (and other Turkish localities, including Paşalar) in MN5 instead of MN6 and that these MN units should be much older than I assumed. In addition, he asked me to write sections on the ecology of the suoids and aardvarks, which I did. On the assignation of Paşalar and Çandır to MN units and the age of the MN units, we had a lengthy exchange of e-mails, in which I explained the arguments for my opinion in great detail, including the timing of the origin of *Listriodon* in Pakistan and its subsequent dispersal in Eurasia.

This intense exchange of e-mails, lasting for over a year, did not make me change the assignation of Çandır and Paşalar to MN units, since in my opinion no convincing reasons were offered for changing the widely accepted assignation to MN6. The ages of the MN units have been much debated for a decade since long palaeomagnetic sections in Spain suggested much younger ages for the MN 3-4, 4-5 and 5-6 transitions than previously believed (KRIJGSMAN et al. 1994 1996, DAAMS et al. 1999a 1999b). This coincided with correlations proposed on the basis of the evolution of the Suoidea (VAN DER MADE 1992 1996 1999). Though my manuscript contained already a paragraph that indicated the different views on the ages of the MN units (p. 164, right column, 4th line from the bottom, starting with "Certain ages ..."), I tried to satisfy BEGUN by adding in two places a reference to the final chapter by BEGUN et al., who favour the other view (p. 165, left column "but see BEGUN et al., this volume"; p. 166, left column "see BEGUN et al., this volume for an alternative interpretation"). Nevertheless, the guest-editors added in three other places comments in my texts. These notes are redundant and contain erroneous information while at least one of the guest editors knew that the information was erroneous. Though several other authors in the volume do not seem to favour the editor's views on the stratigraphy, no notes were inserted in their texts.

On page 139, the guest editors of the volume inserted two "editors' notes" in my text on "Evolution and biogeography of the aardvarks". One note merely states that an evolutionary pattern described on that page, even holds with the older age of Çandır preferred by the guest editors. If the difference of opinion in dating is irrelevant here, why still insert a note? The other comment is on a minor detail in aardvark evolution and biogeography, bringing the aardvarks a little more in line with the guest-editors ideas on general biogeography in relation to hominid dispersals and evolution.

On page 164, a study of listriodont evolution is cited (VAN DER MADE 1996), in which the sublophodont *Bunolistriodon guptai* is again considered as a valid species, different from, and giving rise to *Listriodon pentapotamia*.

The synonymies of the two species are given, the holotype of *B. guptai* is figured and the reasons for the evolutionary and biogeographic model are explained in great detail. In this study, the lophodont suid *Listriodon* is assumed to have originated around 13.8 Ma ago from the sublophodont *Bunolistriodon* in an area that includes Pakistan, after which it dispersed to Anatolia and other areas of Eurasia, evolving into the species *Listriodon splendens*. This scenario implies that Paşalar and Çandır should be younger than 13.8 Ma which would confirm the guest edition opinion and contradict mine. Two to three years previous to publication of the paper, this theme was discussed by BEGUN and me in a lengthy exchange of e-mails. Nevertheless, the guest-editors inserted a note in my text, citing a paper that indicates the appearance of *L. pentapotamia* around 16.9 and not 13.8 Ma. However, that paper (FLYNN et al. 1995) did not treat details of listriodont evolution, did not discriminate between *B. guptai* and *L. pentapotamia* and did not, and could not, cite VAN DER MADE (1996). All this should be very clear to at least one of the guest-editors.

The guest-editors have two final chapters in the volume, treating palaeoecology, stratigraphy and palaeobiogeography, where they could have developed their ideas on the evolution and biogeography of the aardvarks and suids, providing the arguments for their opinions. The privileged position of editor should not be used to insert false information in the text of authors who do not agree with the editor's point of view, nor for introducing any other kind of remarks with the aim to discredit an author. Neither should "editor's notes" be used as a gratuitous way to make propaganda for the editor's ideas at the cost of the work of other authors.

## The guest-editor's final chapter

One of the papers most frequently cited in the guest editor's final chapter (BEGUN et al. 2003) is VAN DER MADE (2003 b). However, this is a dubious honour.

BEGUN et al. (2003, p. 252 r) repeated the remark on the age of the origin of *Listriodon* in Pakistan which was put into my text at page 164 as a guest-editor's note. As pointed out above, the remark is erroneous and D. BEGUN should have known this.

BEGUN et al. (2003: 253, left, lines 16-20) state that VAN DER MADE (2003 b) considered Çandır younger than İnönü I, but that the "small sample from Çandır precludes a definitive judgement, as Van der Made himself notes." This probably refers to p. 158, right column, where it is clearly stated that there is much difference between the samples from İnönü and Paşalar, but where it is also stated that there might be overlap between the Paşalar and Çandır samples, if these samples were larger (which does not imply that there should be any doubt on that the average and extreme values in Çandır are higher). Unlike, what BEGUN et al. suggest, it was not stated that the small

sample size of Çandır precludes a definitive judgement of the age of Çandır relative to İnönü I. For many years I hold the opinion that İnönü I is older than Çandır on the basis of the *B. latidens* - *B. meidamon* lineage (VAN DER MADE 1993) and this has not changed. This opinion is not only based on the meso-distal diameter of the incisors, but also on their morphology and index, on the shape and size of the canines and the morphology and degree of elongation of the cheek teeth of *Bunolistriodon*, and the evolution of other mammal lineages.

BEGUN et al. (2003: 253, right, lines 2-5 from the bottom) state "Two of the suoid species are only known from Turkey (the exception being *Listriodon splendens*), ..." However, *Bunolistriodon meidamon* is also present in Prebreza in Serbia (FORTELIUS et al. 1996a 1996b, VAN DER MADE 1996, VAN DER MADE & RIBOT 1999). Prebreza is assigned to MN6 (MEIN 1975 1977 1990, DE BRUIJN et al. 1992) and its *B. meidamon* is more primitive than that from Çandır, supporting a correlation of Çandır to MN 6.

BEGUN et al. (2003: 256) stated: "While Çandır is said to be later than Sansan (VAN DER MADE, this volume), the incisors from both localities appear to be statistically indistinguishable in size (MADE, this volume, Figure 6). However, no incisors from Sansan appear in this figure, since it treats *Bunolistrion*, which is not present in Sansan. *Listriodon splendens* is present in both Sansan and Çandır, but there are no incisors of that species in Sansan, and accordingly such incisors do not appear in figures 7 and 8. Figures 2 and 3 treat the incisors of the Schizotherini and there incisors from Sansan and Çandır are compared. However, nowhere it is stated that the that the sizes of these incisors have any implications for age of Çandır relative to Sansan.

#### Çandır and Paşalar: assignation to MN units and age

The main conclusion of BEGUN et al. (2003) seems to be that Çandır (and Paşalar and İnönü I) are much older than previously thought.

BECKER-PLATEN et al. (1975) recognised a sequence of faunal units (Faunen Gruppen) for Turkey, each one called after a reference locality. Paşalar and Çandır were reference localities of subsequent units. Paşalar was correlated to Sansan and Prebreza and Çandır was correlated to La Grive M, Tung Gur, the middle series of the Oberen Süßwasser-Molasse and Belometchetskaia. Most or all later authors accepted Çandır being slightly younger than Paşalar. After MN units were introduced, Paşalar was usually placed low in MN 6 and Çandır higher in MN6 in general studies and in specialised ones (eg. MEIN 1975 1977 1990, DE BRUIJN et al. 1992, BERNOR & TOBIEN 1990, STEININGER et al. 1996, FORTELIUS et al. 1996a 1996b, VAN DER MADE 1996 1999a 1999b, RUMMEL 1998). This still seems to be the opinion of most persons who studied material from these localities, but not of BEGUN et al. (2003).

Most authors dealing with the fauna in the Çandır monograph either seem to be inclined to assign Çandır to MN6 (eg. NAGEL 2003: 113, VAN DER MADE 2003b) or leave the assignation to an MN unit open (eg. various chapters by GERAADS), while DE BRUIJN seems to be the only one who clearly prefers an assignation to MN5, and in this differs from his co-authors (2003: 66, right, line 9: "I (H.d.B.) am inclined ...."). BEGUN, et al. (2003) added very little positive to this opinion of DE BRUIJN, save for inflating the importance of arguments in favour of placing Çandır in MN5 and doing the opposite with arguments in favour of placing it in MN6.

The inflation of the importance of an argument is illustrated by BEGUN et al. (2003) stating that the *Democricetodon* and *Keramidomys*, described by DE BRUIJN et al. (2003), "suggest to them an earlier age for the site." However, as we have seen, it does not suggest this to *them*, but to DE BRUIJN (2003: 66, right, line 9: "I (H.d.B.) am inclined ....") and apparently not to (all of) his co-authors. The other main argument of BEGUN et al. (2003, p. 256 r) concerns the *Heteroprox* teeth from Çandır that are more primitive than those from Sansan. However, GERAADS (2003: 186 left), who described the teeth, assumed that the European and Turkish *Heteroprox* belonged to different lineages. So the relative state of evolution of the *Heteroprox* teeth cannot be used for correlation.

Half a tooth serves for a correlation, provided it is a correlation favored by BEGUN et al. (2003), whereas much larger samples are considered to be too small to be used in correlation, if they do not like the result. The *Bunolistriodon* lineage, discussed above, that places Paşalar and Çandır plainly in MN6 is considered to be based on samples that are too small for "definitive judgement". However, on page 260 (left, lines 6-7 from the bottom), the similarity of half a hominid tooth from Engelswies (MN5) to the Paşalar sample seems to be considered an argument for assigning Paşalar to MN5.

In their discussion, BEGUN et al. (2003) focussed much on the possibility that a taxon present in Çandır, is also present in MN5, but did not indicate that the taxon is also present in MN6. For instance, on p. 254 (left, lines 2-3) they stated: "while *Giraffokeryx* and *Hypsodontus*, both unknown from Western Europe but with records in Eastern Europe, have MN 5 distributions". However, these taxa are present in the MN 6 locality Prebreza (PAVLOVIĆ 1969), and do thus not provide a reason for placing Çandır in MN5.

The bovid *Turcoceros* might provide a new argument in the discussion on the age of Çandır. BEGUN et al. (2003: 254, left, lines 1-2) stated: "The genus *Turcoceros* is not known from Europe at all." Though part of the material was published as *Eotragus* (THENIUS 1951), *Turcoceros* is present in Mannersdorf and St. Margarethen, both MN 6 localities with *Listriodon splendens*.

BEGUN et al. (2003) ignored some of the arguments in favour of placing Çandır in MN6, represented others in an incorrect way (so that they do not appear good arguments) and inflated the evidence in favour of placing the locality

in MN5. If Çandır is accepted to be slightly younger than Paşalar, four to five suoid lineages suggest that these localities should be MN6 (Figure 1), and there is additional evidence from other groups.

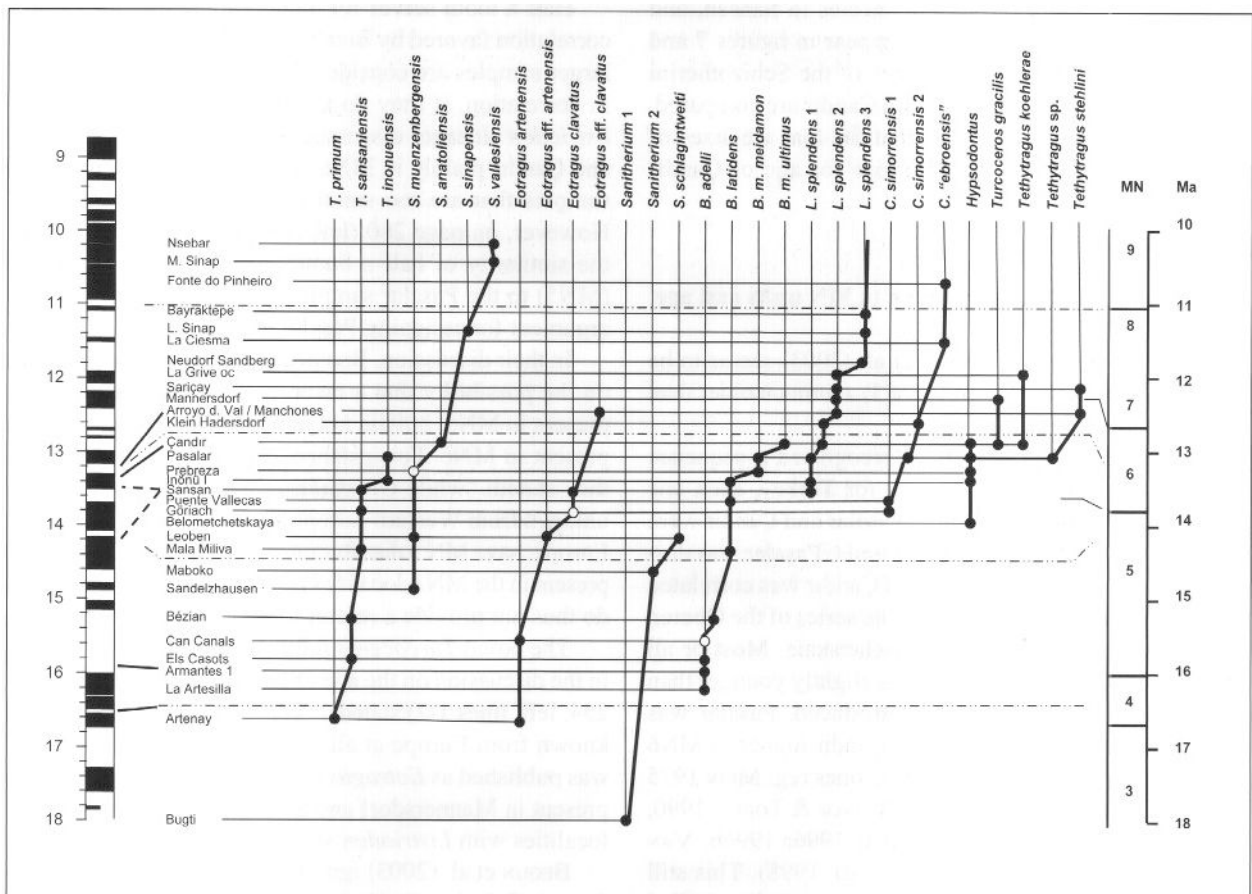
The age of the MN units, and thus of the localities assigned to them, is treated by BEGUN et al. in a similar way as the assignation of Paşalar and Çandır to MN units. Just an example. BEGUN et al. (2003: 258-259) on the one hand insist on a particular correlation of the Sansan palaeomagnetic section, but do not mention that nearly one third of this 46 m section is hiatus, and on the other hand discredit the Aragon and Vargas sections by stating that "The difficulty is that the Aragon and Vargas sections have gaps ...". The Aragon section has a gap of some 6 meters and a total length of 170 m (which is less than 4%), the Vargas section has a gap of some 10 m and a total length of 108 m (9%). It is obvious that there are problems in correlation, but a discussion of this type is not the way of resolving these problems. Neither does it seem useful to give great weight to correlations that consist of several steps (DAAMS & FREUDENTHAL 1981).

KRIGSMAN (2003), who studied palaeomagnetism in the Çandır section, presented two best fit correlations for Çandır to chrons C5ACn and C5ABn, resulting in the ages 14.1 and 13.5 Ma, respectively. Two alternative correla-

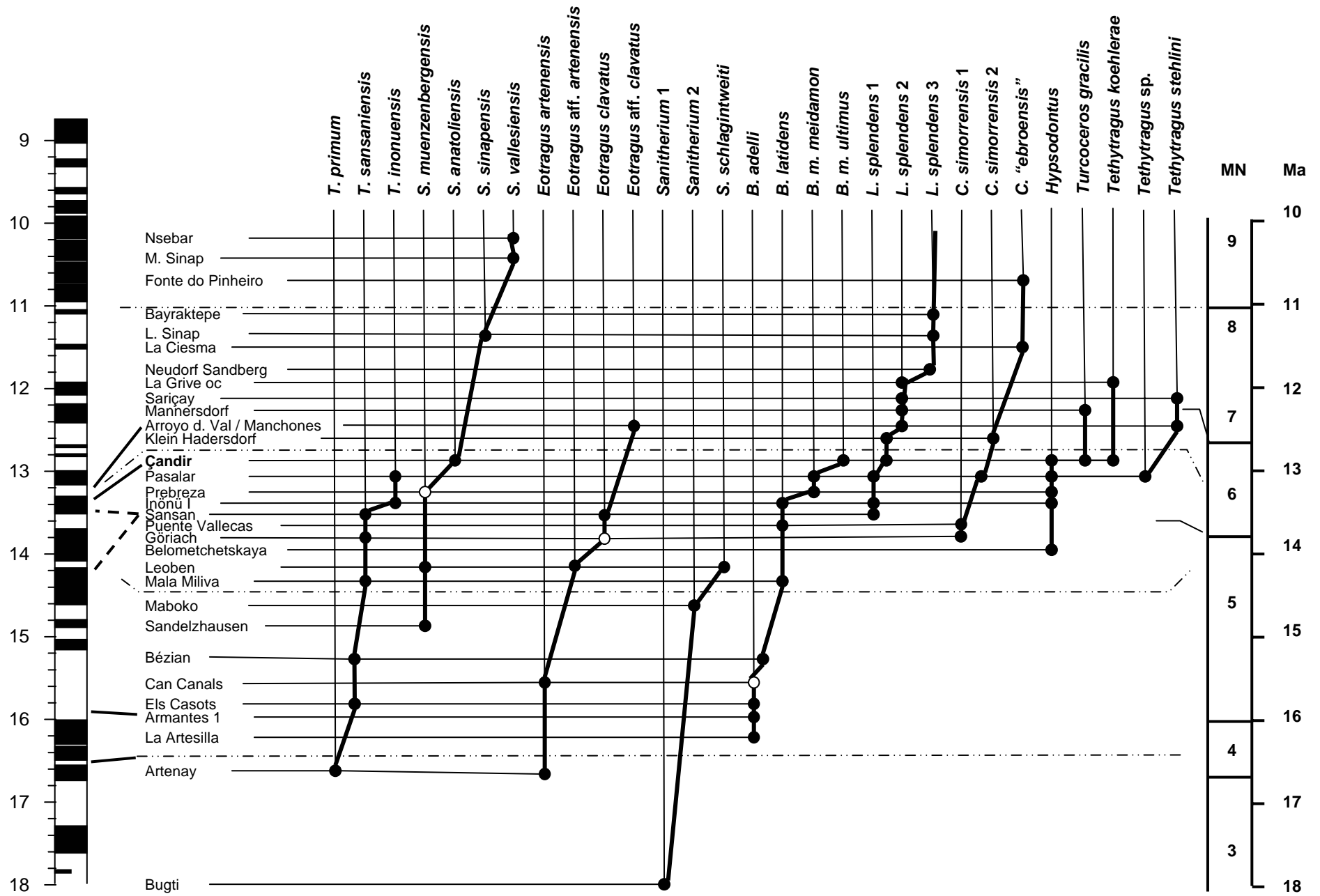
tions were offered, which assume that the sedimentary cyclicity in the Çandır section is related to precessional cyclicity, though this cannot be proven to be the case. These result in estimated ages of 16.3 and 16.5 Ma for the locality. Here it is considered that an age of 13.5 Ma is the more likely age for Çandır. Figure 1 shows the suoid and some bovid lineage studied by me and the correlations to the GPTS that are here considered more reliable and relevant. One of the changes with Figure 9 (VAN DER MADE 2003) is that Çandır is placed at 13.5 and not around 12.7 Ma. Also Aroyo del Val and Manchones are considered to be a little older. The model of evolution of these suoids and bovids and the correlations proposed fit very well the more reliable palaeomagnetic data.

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**Fig. 1:** Middle and Late Aragonian Suoidea and some of the Bovidae and their distribution in some of the localities. Modified from VAN DER MADE (2003b: Figure 9). Correlations to the GPTS according to DAAMS et al. (1999a 1999b).



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