Ciências da Terra (UNL)	Lisboa	Nº 15	pp. 161-172 2 Tabs., 2 Pl.	2003

The last Anthracothere *Brachyodus onoideus* (Mammalia, Artiodactyla) from westernmost Europe and its extinction

Miguel Telles Antunes [1, 2, 3] **& L. Ginsburg** [1, 4]

Projecto "POCTI/36531/PAL/2000 – Studies on Portuguese Paleontology (Post-Paleozoic)". Fundação para a Ciência e a Tecnologia/ Ministério da Ciência e das Universidades.

1. Academia das Ciências de Lisboa. 2. European Academy of Sciences, Arts and Humanities, Paris.
3. Centro de Estudos Geológicos, Faculdade de Ciências e Tecnologia da UNL, 2829-516 Caparica, Portugal. mta@fct.unl.pt 4. Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, 8 rue Buffon, 7005 Paris, France.

Abstract

Key-words: Anthracotheriidae; *Brachyodus onoideus*; lower Miocene; Western Europe; Portugal.

This paper deals with *B. onoideus* specimens from Portugal. This species occurs in the Lisbon area (in the upper part of the lower Miocene, ca.18 to 17.6 Ma) in a very accurate stratigraphic framing (age, lithostratigraphic, climatic and palaeoecologic control being most complete). Some mandibular dental size variation, sex characters, functional interpretation, ecology and predation, chemical corrosion, and extinction are discussed.

Resumo

Palavras-chave: Anthracotheriidae; *Brachyodus onoideus*; Miocénico inferior; Europa ocidental; Portugal.

Esta nota trata de espécimes de *B. onoideus* recolhidos em Portugal. A espécie ocorre na parte superior do Miocénico inferior da região de Lisboa (ca.17.6 Ma a 18 Ma), em enquadramento estratigráfico particularmente preciso e sob quase completo controlo litostratigráfico, cronológico, climático e paleoecológico. Variações de tamanho dos dentes mandibulares, caracteres sexuais, interpretação funcional, ecologia e predação, corrosão, bem como a extinção são discutidos.

1. Introduction

Brachyodus onoideus (Gervais, 1859) is the last european Anthracothere. The type was collected at Eggenburg, Austria (Depéret, 1895). The species is known from the upper part of the European Lower Miocene, from Austria to Portugal.

In France, *Brachyodus onoideus* was referred to by authors among which Stehlin (1907), Mayet (1908), Richard (1948) and Ginsburg (1989). It is common in the lower part of the "Sables de l'Orléanais" (Loire basin), and at the continental "molasses", "niveau II= niveau du calcaire de Herret", according to Crouzel (1957).

In Spain, data about *Brachyodus onoideus* are very scarce and concern the Navarra region (Golpe, 1975, p. 42).

In Portugal, the same species occurs in the Upper Burdigalian of the Lower Tagus basin, IVb local unit, near Lisbon (Zbyszewski, 1949; Antunes, Addendum *in* Antunes *et al.*, 1996).

Other lower Miocene *Brachyodus* species are known from Egypt (Fourtau, 1920). The genus still lived in

Eastern Africa during Middle Miocene (MacInnes, 1951). Anthracotheriids, represented by *Merycopotamus*, survived in Tunisia until Upper Miocene (Black, 1972). Hence *Brachyodus* is present in Africa at about the same times as in Europe, albeit with a major difference: some genera from the same family persisted much later.

Merycopotamus and other genera have been found in Asia (Pinjor Formation, Siwaliks area) until the Pleistocene (Colbert, 1935). The Asian situation is therefore quite similar to the African one. A closely related to *Brachyodus* form, i.e. *Parabrachyodus hyopotamoides* (Lydekker, 1883), occurs among the Bugti Hills fauna (levels 4 and 5) in Central Pakistan, Lower Miocene (Welcomme *et al.*, 1997). This fauna was ascribed to MN3b and basal MN4. Age is therefore very close to that of the latest European *Brachyodus* (Welcomme & Ginsburg, 1997).

The appearance and especially the intriguing extinction of *Brachyodus onoideus* are important data as far as Western Europe is concerned. Extinction is a very useful tool in mammal biochronology. Those events will be discussed under the light of the lower Tagus basin data, where interbedding of marine and continental levels allows a very accurate stratigraphic framing (and a most complete age, climatic and palaeoecologic control).

2. Age

All specimens were found in sands from the IV b unit ("Areias e argilas da Quinta do Bacalhau") from the Lisbon Miocene series.

At our present state of knowledge it would be difficult to have a more accurate set of age data. In the Lower Tagus basin there is a succession of marine transgressive sedimentary infillings whose lateral and vertical relationships have been recognized in detail (Antunes *et al.*, 1996; Antunes *et al.*, 1996; Antunes *et al.*, 2000). These have been dated:

- isotopically (K-Ar on glauconites, Sr on Pectinid and Oyster shells, sometimes also on Foraminifera tests) for each suitable level.
- by magnetostratigraphy whenever possible.
- by planktic Foraminifera;
- by Ostracoda;
- by Palinology (pollen & spores, Dinoflagellata);
- by Calcareous nannoplankton.

Furthermore, some regression events are marked by fluviatile beds that yielded large and small mammals, reptiles, etc. as well as plant remnants.

An earlier event at about 20-20.5 Ma is marked (among others) by the presence of *Brachyodus intermedius*. The same event was followed by the most important Burdigalian transgression at ca. 19.7 to 18 Ma, and that by still another continental event corresponding to the IVb stratigraphic unit, marked by two remarkable chronostratigraphic data:

- the first occurrence by immigration of the Gomphotheres;
- and the last appearance of *Brachyodus onoideus*, whose remnants were never found in later beds as in the rich, overlying Va unit sites.

The IVb sands with *Brachyodus onoideus* and the corresponding continental episode lasted sometime between 18 and 17.6 Ma.

All *Brachyodus onoideus* specimens have been collected in sandpits at or near Lisbon since the late 1930's until the cohercive closing of all commercial sand exploitations in that area in 1967.

Georges Zbyszewski and Octávio da Veiga Ferreira carried on much collecting for the Serviços Geológicos de Portugal (now Instituto Geológico e Mineiro). One of us (M.T.A.) also collected vertebrate fossils at the sandpits between 1957 and 1967.

The concerned sites are: (a) Quinta da Noiva (QN), eastern side of Avenida Gago Coutinho (formerly, Avenida do Aeroporto); (b) another sandpit about 200 m South of Quinta da Noiva (SQN), eastern side of Avenida Gago Coutinho; (c) Areeiro da Barbuda (AB), southern part of the Avenida Gago Coutinho's eastern side; (d) Quinta dos Paiois Vermelhos (PV), close by Azinhaga das Teresinhas, eastern side of Avenida Gago Coutinho; (e) Quinta do Narigão (QNa), western side of Avenida Gago Coutinho; and still westwards (f) Santa Luzia (SL); (g) Quinta da Carrapata (QC), where the LNEC (Laboratório Nacional de Engenharia Civil) has later been built; (h) Quinta do Correio-Mór, near Pote de Água (CM); (i) Quinta do Trindade, also near Pote de Água (QT).

3. Inventory, systematics, measurements

The accounted for specimens belong (a) to the collection Geologic Museum of the Instituto Geológico e Mineiro in Lisbon - those referred to by Zbyszewski (1949), except for the canine, p.36-37 and Pl.IX, fig.78 (ibid.) that actually belongs to *Amphicyon olisiponensis* Antunes & Ginsburg, 1977 (Ginsburg & Antunes, 1995, p.8); and (b) the M. T. Antunes collection.

The still earlier, late 19th century collecting at Horta das Tripas, in Lisbon, described by F. Roman (1907) and reported by him to *Brachyodus onoideus* has since been reported to another species, *B. intermedius*, and will not be included in this list.

Systematics

Under a systematic viewpoint, the material under study belongs in a single species:

Class	MAMMALIA Lin., 1758
Order	ARTIODACTYLA Owen, 1848
Suborder	SUIFORMES Jaekel, 1911
Infraorder	BUNOSELENODONTIA Weber, 1904

Superfamily Anthracotheroidea Gill, 1872
Family Anthracotheriidae Gill, 1872
Subfamily Bothriodontinae Scott, 1941
Genus *Brachyodus* Depéret, 1895

Brachyodus onoideus (Gervais, 1859)

Main references concerning Portugal

- not *Brachyodus onoideus in* Roman, 1907, pp. 45-50 (a smaller sized form from Horta das Tripas, Lisbon, lowermost Miocene, MN3 later reported to *Brachyodus intermedius*).
- *Brachyodus onoideus*, *in* Zbyszewski, 1949, pp. 33-38.
- *Brachyodus onoideus*, *in* Antunes, 1984, p. 307, 321.
- *Brachyodus onoideus*, *in* Antunes, 1996, p. 72 (*in* Antunes *et al.*, 1996).

Skull and dental material

The here adopted reference criterium is as follows: maxillary (upper) teeth in capital letters, mandibular (lower) ones in minuscule letters; D, or d, upper and lower deciduous teeth; the following number (1-4) indicates the order among milk teeth, premolars (P, p) and molars (M, m). For dental measurements, see Table 1; for dental length and width variation, see Table 2.

Upper dentition

Decidual dentition

- Complete right DP3, QN. Reference: Zbyszewski, 1949, p. 36, Pl. IX fig. 77 and 77a.

MANDIBLES AND MANDIBULAR DENTITION

The mandibles present a prominent, downwards extending angulus not so developped as in hippopotamuses.

Decidual dentition

- Fragment of left hemimandible of a very young individual with the nearly complete dp4 and part of the m1 (germ), SL (Plate 1, fig. 1-3).

Adult dentition

- Mandible without symphysis, comprising the nearly complete left hemimandible with p1-m3 (Plate 1, fig. 4-6), and a fragment of the very incomplete right one with m2-m3 (Plate 1, fig. 7), QC.
- Right hemimandible with p1-m3, much ferruginous/ quartz gangue, PV.
- Right hemimandible with the distal root of p3, the incomplete p4 and m1 to m3, QNa. Reference: Zbyszewski, 1949, pp. 35-36, Pl.VIII, fig.75, 75a-b.
- Mutilated right hemimandible with rather abraded p4 to m3 (Plate 1, fig. 8), QC, 11/ Aug./ 1964.

The concerned sites are: Quinta da Noiva (QN); Quinta dos Paiois Vermelhos (PV); Quinta do Narigão (QNa); Santa Luzia (SL); Quinta da Carrapata (QC). (3) Measurements according to Zbyszewski (1949, p. 35).

Larger differences in length have only been found in the last premolars (p3, p4) and the first molars (m1, m2). The observed maximum difference (for m1) is a mere 11.5%.

Table 1

Brachyodus onoideus from Lisbon area, IVb unit - Dental crown measurements (in mm):
- Mandibular teeth (dp4, p1-p4, m1-m3), maximum length (L) and max. width (W); - Molar series length (m1-m3); - Post-canine series length (p1-m3). Abbreviations: F., fragment; hem., hemimandible; I, individual; r., rigth; l., left; for the sites' toponyms, see Chapter 2; *, less accurate, approximative or estimated measurement; i., incomplete; {branches of the same mandible.

Specimen, site, sex?	L W	dp4	p1	p2	p3	p4	m1	m2	m3	m1-m3	p1-m3
F. l. hem., SL	L	40.8					-				
	W	18.4					-				
{L.hem.,QC. male?	L		12.2	24.9	28.8	*26.1	32.6	37.8	*51.4	*122	212
	W		9.8	15.9	18.7	-	24.3	26.9	28.0		
{F.r.hem., QC.	L							36.5	51.5		
	W							21.9	28.3		
R.hem., PV. Fem.?	L		11.8	23.4	26.5	26.5	28.9	34.1	52.7	117	206
	W		*6.0	14.9	17.2	19.9	21.1	28.4	27.1		
R. hem., QNa	L					**·28**	**·33**	**·40**	**·56**		
(Zby., 1949), male?	W					**·21**	**·24**	**·27**	**·28**		
F.r.hem.,QC. Fem?	L					29.0	29.8	34.1	50.1	116	
	W					22.6	23.4	27.4	27.1		
F. r. hem., QN	L										
	W										

Table 2

Brachyodus onoideus from Lisbon area, IVb unit Differences in dental crown measurements (See Table 1)
Larger ≈ Smaller + x %

Teeth	N	Length	N	Width
p1	2	12.2 • 11.8 + 3.5%	2	9.8 • *6.0 + *40% (not significant)
p2	2	24.9 • 23.4 + 6%	2	15.9 • 14.9 + 6%
p3	2	28.8 • 26.5 + 8%	2	18.7 • 17.2 + 8%
p4	4	29.0 • 26.5 + 8.5%	3	22.6 • 19.9 + 12%
m1	4	32.6 • 28.9 + 11.5%	4	24.3 • 21.2 + 13%
m2	6	37.8 • 34.1 + 10%	6	28.4 • 21.9 + 23%
m3	6	52.7 • 50.1 + 5%	6	28.3 • 27.1 + 4%
m1-m3	4	*122 • 116 + *5%		
p1-m3	3	212 • 206 + 3%		

Limb bones

FORE LIMB

Humerus

- Left humerus without its proximal part, otherwise well preserved (Plate 2, fig. 9), SQN.

Radius

- Incomplete right radius (Plate 2, fig. 10), PV. Max. ant.- post. diameter of the proximal articular surface, 39; ant.- post. x transverse diam. circa the middle of the diaphysis, 32.6 x 41.7.

Carpals

- Complete right lunare, QN. Reference: Zbyszewski, 1949, p. 37, Pl. IX, fig. 80, 80a, QNa.

- Complete left centrale, SQN. Max. height, 50; max. width, 46 (approx.).

Metacarpals

- Incomplete right metacarpal III (lacking distal extremity), AB. Proximal transversal width, 48.8; minimum width of the diaphysis, 37.0; minimum anterior-posterior length of the diaphysis, 26.0.

- Complete right metacarpal IV (Plate 2, fig. 11 – 14), QN. Max. length, 185; proximal transversal width, 46.6; prox. ant.- post. diam., 47.7; minimum width of the diaphysis, 39.5; minimum anterior-posterior length of the diaphysis, 24.3; distal transversal width, 47.0; distal ant.- post. diam., 40.6.

- Incomplete left metacarpal V, QN. Proximal ant.-post. diameter, 35.9; minimum width of the diaphysis, 31.0; minimum ant.-post. length of the diaphysis, 22.5.

- Incomplete right metacarpal V, Qna, 1967 (bitten by a large Carnivore, see Chapter 6). Ant.-post. diameter, 40.6; transverse articular width, 35.2; distal width, 39.2.

Phalanxes

- 1st phallanx from the hand, SQN. Max. length, 69.0; proximal ant.-post. diam., 38.9; distal ant.-post. diam., 30.4.

HIND LIMB

Femur

- Incomplete, very mutilated distal part of femur, side not stated, CM. Reference: Zbyszewski, 1949, p. 37, Pl. IX, fig. 83. No meaningful measurements can be taken.

- Left femur without its proximal part, otherwise well preserved, QNa. Max. length as preserved (less than the real max. length), 474.2 mm; max. distal width, 149.5 mm; smallest width about the middle of the diaphysis, 67.4 mm.

Patella

- Left, almost complete patella, QC. Max. width, 64.0.

Tibia

- Left tibia, ca. 1/2 distal part, SQN. Max. distal width, 94.3 mm.

- Mutilated distal part of right tibia, QT. Reference: Zbyszewski, 1949, p. 37. No meaningful measurements can be taken.

- Right tibia, ca. 1/3 distal part, QNa. Max. distal width, 96.5 mm.

Astragalus

- Complete left astragalus, QNa. Reference: Zbyszewski, 1949, p. 38, Pl. X, fig. 85, 85a, 85b, 85c. Maximum heigth, 130; "largeur maximum dans l'axe du condyle: 87 mm" (Zbyszewski, *id.*).

- Complete right astragalus, QNa, 1959. Max. heigth, 123.4; distal diameter (transverse measurement), 77.8.

- Complete right astragalus, SQN. Max. heigth, 124.2; transverse distal diameter, 76.1.

Calcaneus

- Almost complete left calcaneus, QC. Total length, 251; width at the sustentaculum tali level, - not taken (incomplete); max. ant.-post. diam. at the same level, 84.7.
- Much mutilated right calcaneus, SQN.

Metatarsals

- Complete left metatarsal (? III), QN. Reference: Zbyszewski, 1949, p. 22, Pl. V, fig. 38, ascribed to *Brachypotherium aurelianense* (?) (actually, *Diaceratherium aurelianense*). Max. length, 185; prox. width, 49; ant.-post. prox. diam., 50; distal width, 52; ant.-post. distal diam., 41.
- Somewhat mutilated left metatarsal IV, QN. Reference: Zbyszewski, 1949, p. 22, Pl. V, fig. 30 and 30a, also ascribed to *Brachypotherium aurelianense*. Max. length, 150; prox. width, 30; ant.-post. prox. diam., 35; distal width, 48; ant.-post. distal diam., 34.

Phalanxes

- 1st phallanx from the foot, QC, July 1965. Max. length, 72.0; proximal width, 43.6; proximal ant.-post. diam., 35.5; distal width, 35.3; distal ant.-post. diam., 20.0.
- 1st phallanx from the foot, QC, November 1967. Max. length, 61.8; proximal width, 44.6; proximal ant.-post. diam., 35.7; distal width, 36.0; distal ant.-post. diam., 20.8.

FORE LIMB or HIND LIMB

- 2d phallanx, QNa, 1967. Max. length, 47.0; proximal width, 45.8; proximal ant.-post. diam., 31.8; distal width, 43.6; distal ant.-post. diam., 26.4.
- sesamoid bone, QC, 08/ July/ 1965. Max. heigth, 44.5.

4. Description and functional interpretation

Most skeletal parts of *Brachyodus onoideus* have been described. It therefore is not especially useful to describe the specimens under study, except for some features that simultaneously seem meaningful and have not been accounted for (or just were undervalued).

The *Brachyodus onoideus* were large, heavy, robust animals. They still kept cursorial-type, not "columnar" limbs as in the Proboscideans. They show instead that there were marked angles between propodial and metapodial segments of both limbs, i.e. between humerus and radius+ulna, or femur and tibia+fibula. Metapoda are robust and rather long, not at all shortened as in the hippopotamuses.

As an overall view, the skeleton of *Brachyodus onoideus* seems to point out to basically terrestrial animals. They certainly were much less aquatic-adapted than hippos even if probably living (as indicated by other, ecologic data) in swamps or close by rivers, in areas with a dense plant-covering.

The peculiar, intense enamel ornementation is present both in the Anthracotheriids and the hippopotamuses but not in Suids and Tayassuids. This seems to point out to close relationships between Anthracotheriids and Hippopotamids, although this known for long interpretation is open to discussion (see Pickford, 1989).

5. Dental size variation and sex

The hemimandibles from the IVb unit from Lisbon show some differences in size and in dental measurements (Table 1). For dental length, the maximum differences are ca. 11.5% for m1; and for width, 23% for m2 (Table 2). Of course, the small number of specimens is restrictive and wear may affect measurements, even if not very much.

We may therefore conclude that there are no major size variations. The variation in dental mandibular morphology, size and proportions is moderate.

However, mandibular remains reveal differences that are of interest. Some mandibles are much stronger than other ones. As an example, the mandible from Quinta da Carrapata, 04/ Oct./ 1966 is much stronger than the hemimandible from Quinta dos Paiois Vermelhos. The right hemimandible fragment from Quinta da Carrapata, 11/ Aug./ 1964 may compare with the latter. The main differences lie in:

- the robustness of the mandibular bone;
- the stronger crests for muscular insertions.

Taking into account the differences between stronger and weaker mandibles, some differences concerning the teeth seem correlative. Each jugal tooth is somewhat longer and broader, the m1-m3 series and the entire series p1-m3 being longer too.

Hence there are differences that may be ascribed to sex, the robust form corresponding to males and the weaker to females.

6. Ecology and predation, chemical corrosion

The lowland areas of an alluvial plain close by a large river (that anticipated, with differences, the extant Tagus) certainly supported a richer mammalian life than the surrounding, open and drier extensions beyond it.

Brachyodus onoideus was one of the dwellers of such an alluvial plain. Even if it is not clear that they were more or less semiaquatic, they could (as other mammals) be drowned by intensive, sudden floods among other causes.

The adult *Brachyodus* would have been a difficult prey owing to their large size, even for the largest contemporary carnivores: either the often huge, long-snouted crocodilians (*Tomistoma lusitanica*) or the biggest mammalian carnivores as *Amphicyon olisiponensis*.

Necrophages preyed upon corpses; a metapod from QN shows clear bite imprints of a canine and jugal teeth that by their large size seem to have been produced by *Amphicyon olisiponensis* (or much less probably by the Ursids known in the IVb unit: *Hemicyon* cf. *stehlini* and *Plithocyon antunesi*, see Ginsburg & Antunes, 1995).

Some remnants could be exposed after at the sandy banks or bars and suffer intensive chemical corrosion that indeed did occur. If buried, the preservation of bones could be easier. Iron deposition (as goethite) cemented quartz (and other) grains into hard coatings on the bones. This suggests strongly contrasting seasons and ferralithic processes. Plant evidence seems to corroborate this.

Palaeobotanic data and especially foliar physiognomy and morphology point out to low mountain, warm temperate to subtropical forests under rainy to seasonally dry conditions not far from the river (Pais, 1986; Ginsburg & Antunes, 1995; Antunes *et al.*, 1999).

On the other hand, small mammals correspond to several ecologic niches: forest as well as open country or even steppe (Antunes *et al.*,1999). These would surround the richer in plant covering areas (gallery-forests?) by the river, which probably were more appropriate for *Brachyodus onoideus*.

7. The origin and extinction of *Brachyodus onoideus*

At the present state of knowledge, *Brachyodus onoideus* seems to be an european direct descendant from another European species, the Lowermost Miocene *Brachyodus intermedius* Mayet, 1908.

We do not know for sure what has been the cause (or causes?) of the *Brachyodus onoideus* rather sudden demise and extinction, even in areas where the species was well established as in Lisbon. That is but a particular case of a much broader and impressive phenomenon, v.g. their extinction everywhere at about the same time in later Lower Miocene. Some hypotheses may be advanced.

Brachyodus onoideus is poorly known in Spain, and only seems common in the Lower Tagus basin in Portugal. At those times, the central part of the Peninsula certainly comprised extensive, more or less dry plateaux and mountains far away from the sea. Climate conditions would have been milder along the western, Atlantic slope.

Even if the next eusthatic rise of the sea level at about 17 Ma dramatically changed local environments, there is no hint that this kind of suitable environments could not just shift to not so far away areas (maybe 50 km upstream or so). Climatic conditions still were subtropical to tropical. Mammalian fauna was rich. Environmental changes related to marine transgression probably had some influence, but do not convincingly account for the *Brachyodus onoideus* extinction in the concerned area, much less at the whole geographic range of the species that comprised both Europe and Asia.

We therefore have to look elsewhere for another explanation. Geologically speaking, nothing seems to account for such extinction. Under a biologic viewpoint, the sole major event that occurred by those times was the arrival of the Gomphotheres. Concurrence yes, may be a valid explanation, because of the immigration of successful continental immigrants from Africa in large numbers, harshly competing for plant food resources with the less fortunate former dwellers.

Acknowledgements

This work has been supported by the PRAXIS XXI 2/ 2.1/ CTA/ 106/ 94 Project "Neogénico e Quaternário da Margem atlântica da Ibérica e transformações globais", and by the Project POCTI/ 1999/ PAL/ 36531 "Studies on portuguese Palaeontology (Post-Paleozoic)".

References

Antunes, M. T.; Legoinha, P.; Nascimento, A. & Pais, J. (1996) - The evolution of the Lower Tagus basin (Lisbon and Setúbal Peninsula, Portugal) from Lower to early Middle Miocene. *Géologie France*, 4: 59-77.

Antunes, M. T.; Pais, J.; Balbino, A.; Mein, P. & Aguilar, J.-P. (1999) - The Cristo Rei section (Lower Miocene)/ Distal fluviatile environments in a marine series, plant, vertebrate and other evidence, age. *Ciências Terra (UNL)*, 13: 141-155.

Black, (1972) - Review of fossil Rodents from the Neogene Siwalik beds of India and Pakistan. *Paleontology*, 15 (2): 238-266.

Colbert, E. H. (1935) - Distributional and phylogenetic studies on indian fossil Mammals. IV. The phylogeny of the indian Suidae and the origin of the Hippopotamidae. *Amer. Mus. Novitates*, 799: 1-24.

Crouzel, F. (1957) - Le Miocène continental du bassin d'Aquitaine. *Bull. Service Carte Géologique France*, 248, LIV: 1-264.

Depéret, C. (1895) - Ueber die Fauna von miocäne Wilbertieren aus der ersten Mediterranstufe von Eggenburg. *Sitzungsberichten Kaiserichte Akademie Wissenschaften Wien*, 104 (1): 395-416.

Fourtau, (1920) - Contribution à l'étude des Vertébrés miocènes de l'Égypte. *Geological Survey Egypt*: 1-121.

Ginsburg, L. (1989) - Les Mammifères des sables du Miocène inférieur des Beilleaux à Savigné-sur-Lathan (Indre-et-Loire). *Bull. Muséum national d'Histoire naturelle*, Paris, 4e. série, 11, C (2): 102-121.

Ginsburg, L. & Antunes, M. T. (1995) - Les Carnivores du Miocène de Lisbonne (Portugal). *Annales Paléontologie*, 81(3): 125-165.

Golpe-Posse, J. (1975) - Historia del conocimiento de los Suiformes de la Paleontología española. *Paleontología y Evolución*, XI: 1-52 + I-XVII.

MacInnes, D. G. (1951) - Miocene Anthracotheriidae from East Africa. *British Museum (Natural History)* Fossil Mammals of Africa, 4: 1-24.

Mayet, L. (1908) - Étude des Mammifères miocènes des sables de l'Orléanais et des faluns de la Touraine. *Annales l'Université Lyon*, Nouvelle série, I. Sciences, Médecine, 24: 1-336.

Pais, J. (1986) - Évolution de la végétation et du climat pendant le Miocène au Portugal. *Ciências Terra (UNL)*, Lisboa, 8: 179-191.

Pickford, M. (1989) - Update on hippo origins. *C. R. Acad. Sci. Paris*, 309, Série II: 163-168.

Richard, M. (1948) - Contribution à l'étude du Bassin d'Aquitaine. Les gisements de Mammifères tertiaires. *Mémoires Société Géologique France*, Paris, 380 p.

Roman, F. (1907) - Le Néogène continental de la basse vallée du Tage (rive droite)/ 1re partie - Paléontologie. *Commission Service Géologique Portugal*, Lisbonne, 88 p.

Stehlin, H. G. (1907) - Notices paléomammologiques sur quelques dépôts miocènes des bassins de la Loire et de l'Allier. *Bull. Soc. Géol. France*, Paris, 4e. série, 7: 525-550.

Welcomme, J.-L.; Antoine, P.-O.; Duranthon, F.; Mein, P. & Ginsburg, L. (1997) - Nouvelles découvertes de Vertébrés miocènes dans le synclinal de Derce Bugti (Balouchistan, Pakistan). *C. R. Acad. Sci. Paris*, Sciences de la Terre et des Planètes, 325: 531-536.

Welcomme, J.-L. & Ginsburg, L. (1997) - Mise en évidence de l'Oligocène sur le territoire des Bugti (Balouchistan, Pakistan). *C. R. Acad. Sci. Paris,* Sciences de la Terre et des Planètes, 325: 999-1004.

Zbyszewski, G. (1949) - Les Vertébrés du Burdigalien supérieur de Lisbonne. *Services Géologiques Portugal*, Lisbonne, 77 p.

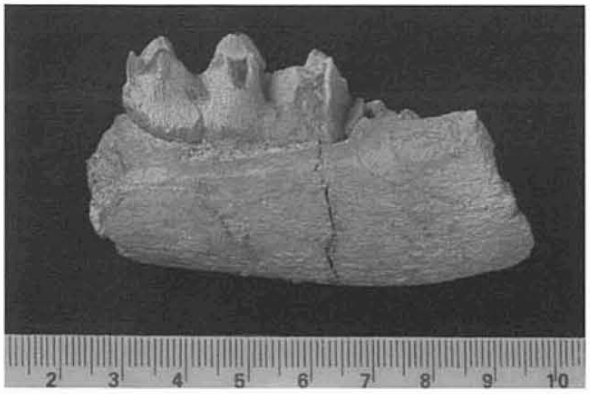
Plate 1

Brachyodus onoideus (Gervais, 1859)

Decidual dentition:
1 - 3 – Fragment of left hemimandible of a very young individual with the nearly complete dp4 and part of the m1 (germ), Santa Luzia sandpit. External/ labial (1), occlusal (2) and internal/ lingual (3) views.

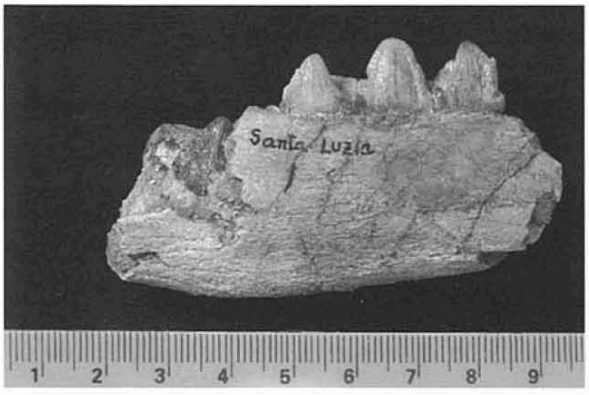
Adult dentition:
4 - 6 – Incomplete mandible without symphysis, Quinta da Carrapata. Nearly complete left hemimandible with p1-m3, external (4), occlusal (5) and internal (6) views;
7 – The same mandible, a fragment of the very incomplete right hemimandible with m2-m3. Occlusal view.
8 – Mutilated right hemimandible with rather abraded p4 to m3, Quinta da Carrapata. Occlusal view.

PLATE 1

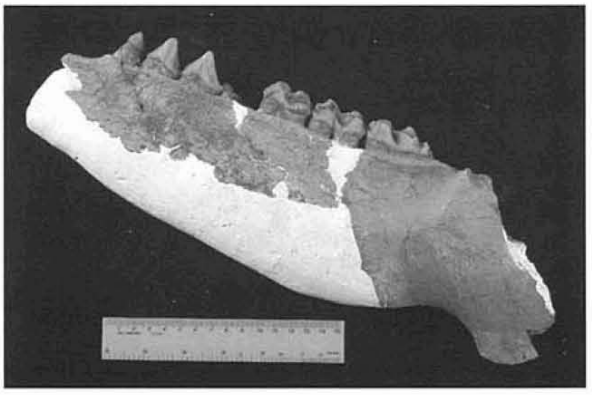


1

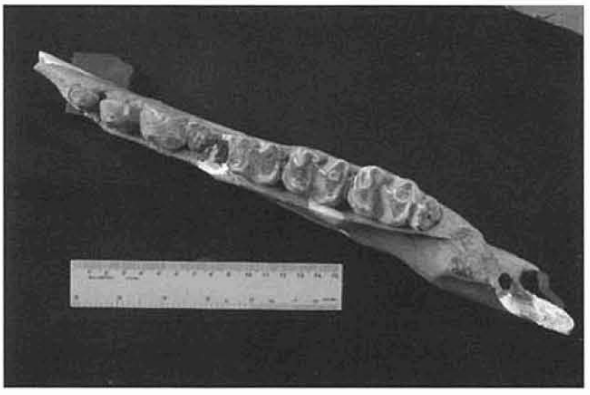
2



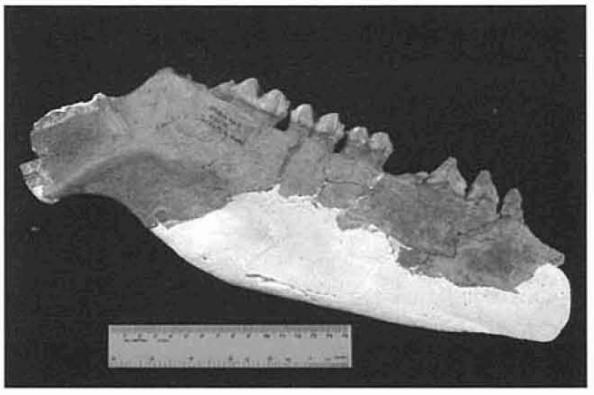
3



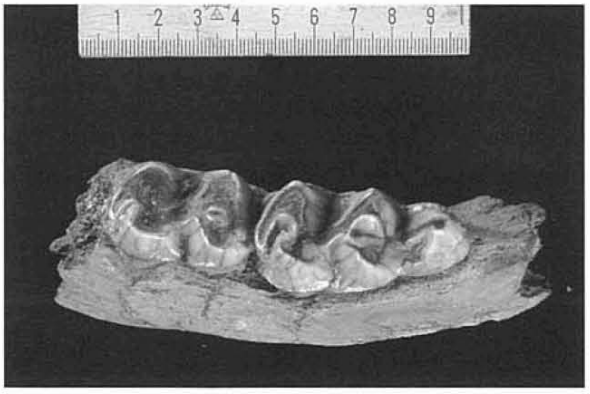
4



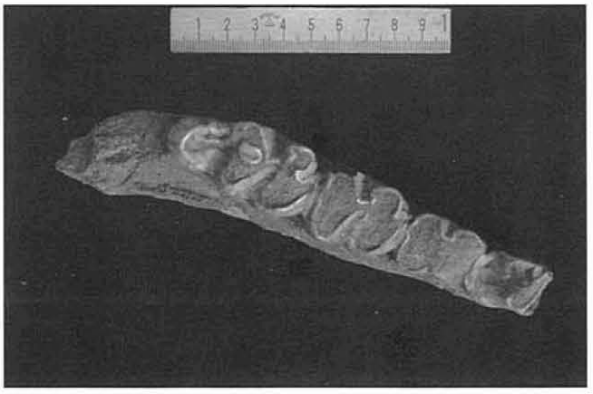
5



6



7



8

Plate 2

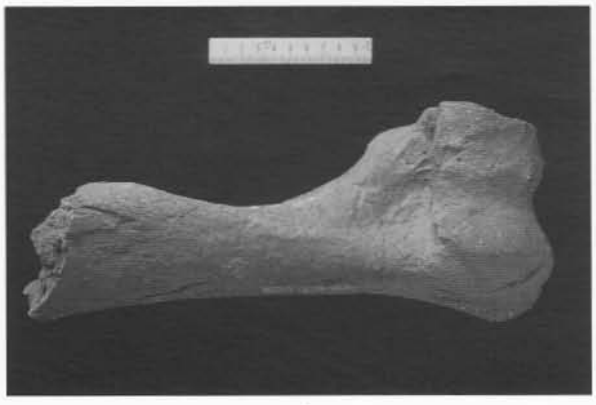
Brachyodus onoideus (Gervais, 1859)

FORE LIMB
Humerus
9 – Left humerus without its proximal part, 200 m South of Quinta da Noiva. Anterior view.
Radius
10 – Incomplete right radius, proximal part, Quinta dos Paiois Vermelhos. Anterior view.
Metacarpals
11 - 14 – Complete right metacarpal IV, Quinta da Noiva. Anterior (11), internal (12), posterior (13) and external (14) views.

HIND LIMB
Patella
15 – Left, almost complete patella, Quinta da Carrapata.
Astragalus
16 –

The concerned sites are: (a) Quinta da Noiva (QN), eastern side of Avenida Gago Coutinho (formerly, Avenida do Aeroporto); (b) another sandpit about 200 m South of Quinta da Noiva (SQN), eastern side of Avenida Gago Coutinho; (c) Areeiro da Barbuda (AB), southern part of the Avenida Gago Coutinho's eastern side; (d) Quinta dos Paiois Vermelhos (PV), close by Azinhaga das Teresinhas, eastern side of Avenida Gago Coutinho; (e) Quinta do Narigão (QNa), western side of Avenida Gago Coutinho; and still westwards (f) Santa Luzia (SL); (g) Quinta da Carrapata (QC), where the LNEC (Laboratório Nacional de Engenharia Civil) has later been built; (h) Quinta do Correio-Mór, near Pote de Água (CM); (i) Quinta do Trindade, also near Pote de Água (QT).

PLATE 2



9

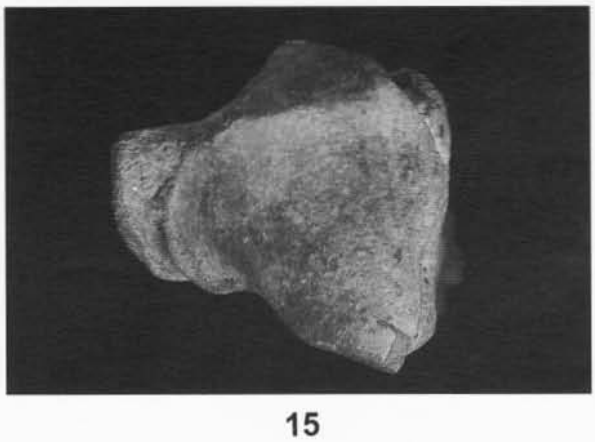
10

11

12

13

14



15

16