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Original article

Ichnological evidence of a Miocene rhinoceros bitten by a bear-dog (*Amphicyon giganteus*)

Rhinocéros du Miocène mordu par un chien-ours (*Amphicyon giganteus*) : preuves ichnologiques

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Abstract

A rhinocerotid hemimandible, the *Iberotherium rexmanueli zbyszewskii* holotype, was bitten by *Amphicyon giganteus,* a carnivore that could attack large prey and be an opportunistic scavenger as well. The large, young adult *Iberotherium* was not senile and may have been killed by a single individual or by a pack of *Amphicyon giganteus,* but disease or accident may also have caused its death. Alternatively, during a drought event, a dying or in harsh physical condition rhinoceros may have been overcome while seeking a water point where ambush would be possible. Death also may have been a consequence of a major flood. As decay progressed and the remnants were eventually deposited, parts could have been consumed by scavengers. After consumption, wet bone surfaces could undergo some corrosion. Fissures may have resulted from desiccation or mechanical stress. The hemimandible was abandoned after consumption and left exposed until new sands were deposited over it.

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Résumé

Une hémimandibule de rhinocéros adulte jeune, holotype de *Iberotherium rexmanueli zbyszewskii,* a été mordue par un *Amphicyon giganteus,* carnivore capable d'attaquer des proies de grande taille et d'être en même temps un charognard opportuniste. Cet individu d'*Iberotherium* peut avoir été tué par un seul individu ou par une bande. Pourtant la mort peut avoir résulté d'une maladie ou d'un accident. D'autre part, un rhinocéros mourant, en mauvaise condition physique (ou juste cherchant un point d'eau où une embuscade serait possible) pourrait avoir été tué lors d'un épisode de sécheresse. En outre, la mort peut avoir été la conséquence d'une crue importante. La décomposition des cadavres progressant, les restes auraient pu avoir été déposés et consommés par des charognards. À la suite, la surface des os pourrait avoir subi quelque corrosion. Des fissures pourraient avoir été produites par dessiccation. Il est possible aussi que des tensions mécaniques aient pu, en partie, en être responsables. L'hémimandibule en question a été abandonnée après consommation. Elle est restée exposée jusqu'à ce que de nouvelles masses de sables la recouvrent.

Resumo

Uma hemimandíbula de rinoceronte, holótipo de *Iberotherium rexmanueli zbyszewskii,* foi mordida por um *Amphicyon giganteus,* carnívoro capaz de atacar presas de grande porte e de, simultaneamente, ser um necrófago oportunista. O rinoceronte em causa, adulto mas não senil, pode ter sido morto por um só predador ou por um grupo de predadores. A morte pode, no entanto, ter resultado de doença ou acidente. Por outro lado, um rinoceronte moribundo, em má condição física (ou tão só à procura de um local com água, onde poderia sofrer emboscada) pode ter sido abatido no decurso de um episódio de seca. Além disso, a morte pode ter resultado de uma cheia importante. Ao progredir a decomposição de cadáveres, os restos teriam podido depositar-se e ser consumidos por necrófagos aproveitadores de carniça. Seguidamente, superfícies de osso sofreriam corrosão. A dessecação originaria fissuras; porém, podem ter resultado, em parte, de tensões mecânicas. A hemimandíbula, abandonada após consumo, ficou exposta até ser recoberta por novas massas de areia.

Keywords: Bite; Rhinocerotid; Amphicyonid; Miocene; Portugal

Mots clés : Morsure ; Rhinocérotidé ; Amphicyonidé ; Miocène ; Portugal

Palavras chave: Mordedura; Rinoceronte; Anficionídeo; Miocénico; Portugal

1. Introduction

In another paper (Antunes et al., 2006) we dealt with some ichnological evidence on lower, uppermost lower and early middle Miocene from the Lisbon Neogene series. That evidence concerned a few mammalian coprolites that had been trampled by a rhinoceros, by an *Anchitherium,* and by a small cervid. All show the corresponding footprints.

However some other specimens give us a glimpse of other mammalian predation activities. We will deal here with a rhinoceros hemimandible that reveals many bite marks by a carnivore.

The specimen was collected by M.T. Antunes ca. 1960 at a commercial sandpit at Casal das Chitas, near Charneca do Lumiar in the northern outskirts of Lisbon. The site disappeared a long time ago, owing to the enlargement of the Lisbon Airport westwards. It had been found in coarse, fluviatile sands from the Lisbon series' Vb unit, the "Areias do Vale de Chelas". The

age is MN5 mammal-zone, ca. 15.8 Ma, Langhian (lower middle Miocene), based on the mammalian fauna and also on its position in the series where it is intercalated between marine levels that have been accurately dated both by planktic foraminifera and Sr isotopes (Antunes, 2000).

2. Description

The specimen is a left hemimandible with P4-M3, the last molar being somewhat broken in its distal 2d loph. The rear part, including the ascending branch, was lost by accident during the collecting process. Also lost as a consequence of bites, is the symphysial and ramus portion in front of the last premolar.

The moderate abrasion status of all teeth and especially that of the last molar shows that this hemimandible belonged to a young adult, not a senile individual.

It was described by Antunes and Ginsburg (1983: 37–38) as the holotype of a new subspecies, *Gaindatherium (Iberotherium) rexmanueli* Antunes and Ginsburg, 1983 *zbyszewskii* Antunes and Ginsburg, 1983. However, its generic status has meanwhile been revised. As the relationship with *Gaindatherium* could not be confirmed, the subgenus *Iberotherium* was elevated to generic rank. Accordingly the corresponding taxon became referred to as *Iberotherium rexmanueli zbyszewskii* (Antunes and Ginsburg, 2000a).

However, in our preceding papers where this taxon was dealt with, there was no reference to the bite-induced modifications that affected the specimen.

A lot of teeth imprints are well marked on the bone, always with some loss of bony matter (Fig. 1). Some weak traces are conspicuous on the external surface of a cast (Fig. 2). These

Fig. 1. Young adult, incomplete left hemimandible with P4-M3, severely bitten by a large carnivore mammal, probably an *Amphicyon giganteus.* External view.
Figures: Rhinocerotidae – *Iberotherium rexmanueli zbyszewskii* (Antunes and Ginsburg, 1983). Type specimen of the subspecies.
Fig. 1. Hémimandibule gauche incomplète avec P4-M3 d'un adulte jeune, mordue par un mammifère carnivore de grande taille, probablement par un *Amphicyon giganteus.* Vue externe.
Figures : Rhinocerotidae – *Iberotherium rexmanueli zbyszewskii* (Antunes et Ginsburg, 1983). Spécimen type de la sous-espèce.

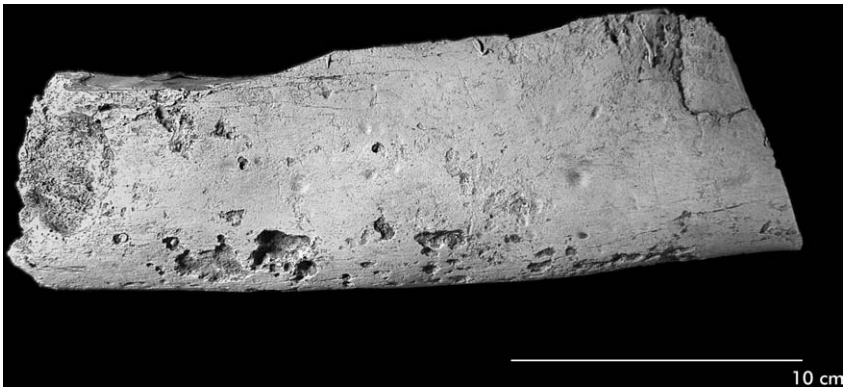

Fig. 2. External view of cast to show bite marks.
Fig. 2. Vue externe d'un moulage pour montrer des empreintes des morsures.

impressions may be interpreted as the result of shallow bites that were weakened (or partly absorbed) by soft parts, i.e. the flesh.

Most of the imprints are near the lower border of the hemimandible on its external surface, and on the lower border itself. In some parts, bone has been quite deeply perforated. At one area, bone has clearly been partly stripped-off. These imprints were produced by the incisors of a scavenging predator. There are others on the inner surface that are not so deep, including two arched imprints that may correspond to incisor bites. Some less clear traces away from the borders may have resulted from the action of rear teeth, especially the carnassials.

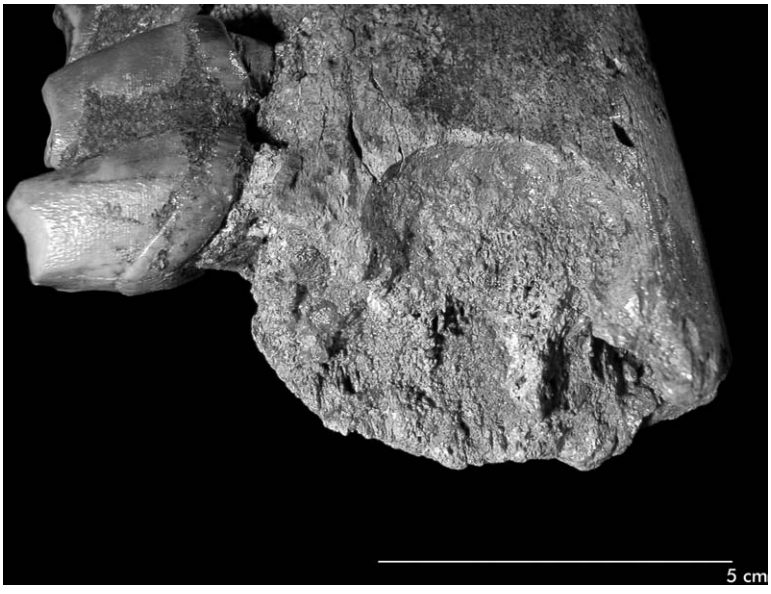

Fig. 3. Enlarged, unretouched photo to show the imprint of the symphysial region of the predator's mandible. Compare with figure 4.
Fig. 3. Photo agrandie, non retouchée, pour montrer l'empreinte de la région symphysaire de la mandibule du prédateur. À comparer avec la figure 4.

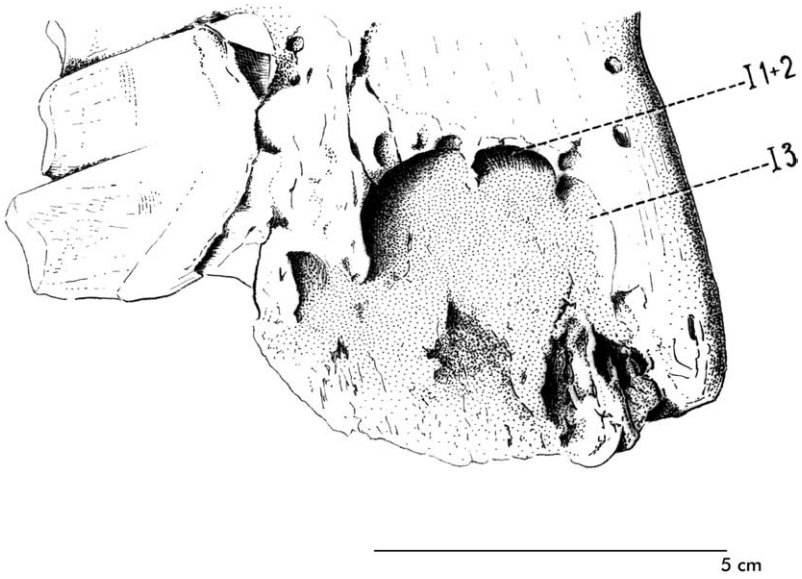

Fig. 4. Drawing of the same view as figure 3, to show the excavations made by the predator's incisors on the bone; those from the left side (to the right in the drawing) correspond to I1 and I2 and distally to I3. Vestigial septa corresponding to spaces between teeth separate the excavations made by the right and left incisors, and especially by the left incisors I1+I2 and I3.
Fig. 4. Même dessin de la figure 3 montrant les dépressions produites sur l'os par les incisives du prédateur ; celles du côté gauche (à droite) correspondent mésialement à I1, I2 et I3. Des septes vestigiaux correspondant aux intervalles entre les dents séparent les cavités pour les incisives droites et gauches, aussi bien que, du côté gauche, la cavité la plus mésiale pour I1 et I2 de celle pour la I3.

Besides these imprints, there is a major imprint near the symphysis (Figs. 3 and 4). This imprint even shows the bone-moulded cavities that were produced by the incisors (3 on both sides), but it does not so clearly show those that resulted from the canines. The septa between the incisor roots are not preserved with the exception of the faint base that remains between I2 and I3; there is no recognizable trace of the less developed, more mesial septum that separates the roots of I1 and I2.

Bone, even if strong, has been deeply crushed and carved, much of it being ripped-off. The symphysis has largely been lost. However, the carnivore was not able to crush enough to expose the mandibular channel that would provide access to nutrient-rich marrow.

The hemimandible also presents some faint, corrosion marks on its internal (lingual) surface. Fissures can be seen on the outer (labial) surface, though less so on the inner and especially on the lower border.

3. Discussion

One important consideration is the predator's identification. It obviously was a large-sized mammal. We infer only one large animal because overall the imprints are very similar. Nothing suggests they could have been produced by more than one individual or more than a single species.

Although huge crocodilians as *Tomistoma lusitanica* were found nearby, their different teeth and trace pattern would be easy to recognize.

Among the contemporary, sufficiently large-sized Carnivora there is only *Dinocyon* that remains totally unknown from this basin and *Amphicyon.* Only one species ascribed to the latter genus has been recorded from the early middle Miocene Vb unit in the Lisbon area, i.e. *Amphicyon giganteus* (Schinz, 1825), while the presence of *Amphicyon major* has not been confirmed (Ginsburg and Antunes, 1995).

The mandible from the *Amphicyon major* female skeleton from Sansan (Sa 844, collected in 1964 by Bergounioux and Crouzel and displayed at the Galerie de Paléontologie, Muséum national d'Histoire naturelle, Paris) perfectly fits, especially into the major and more pronounced bite. In particular, the 50.8 mm distance measured between the points of the mandible canines is striking as they look rather compatible with the traces under study.

We tried to measure the distance between the points of mandible canines of the predator based on the corresponding traces (Fig. 5). However this proved to be difficult and quite confusing because there are too many imprints. Furthermore canine traces from the same bite may produce differently developed marks, some deeper than others.

Shape can also vary from the more common nearly circular pattern where the impression resulted from a single impact to a larger, more complex shape, where the canine point evidently scratched the bone surface to a variable extent and direction. How to recognize the pair of imprints from the same bite?

On the other hand, the carved imprint of the symphysial part of the predator's mandible is much larger than that of a male Iberian wolf from Northern Portugal, *Canis lupus signatus*

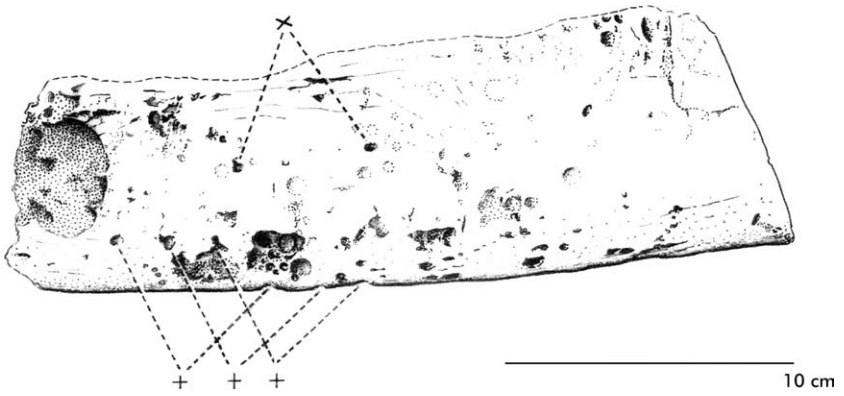

Fig. 5. Drawing from the cast (Fig. 2) to show especially some imprints and illustrate attempted interpretations: although the two imprints (x) above are closely similar, its distance (41 mm) is much too short to be compatible with the predator's symphysis as shown by its cast. Also shown are a few two-impression sets corresponding to a mandibular canine-point separation distance of ca. 50 mm; three are clearly shown (+), which are all very similar, with one canine imprint on the external surface and the corresponding other imprint from the same set on the lower border of the hemimandible. This suggests successive, more or less parallel bites made by the predator with the prey in about the same position. Photographs by Susana Rodrigues. Drawings by Miguel Telles Antunes.

Fig. 5. Dessin du moulage (Fig. 2) pour montrer quelques empreintes particulières et mettre en évidence les essais d'interprétation : malgré le fait que deux empreintes (x) soient très semblables, leur distance (41 mm) est trop courte pour être compatible avec la symphyse du prédateur telle qu'elle est révélée par la description. On montre également quelques paires d'impressions correspondant à une distance entre les pointes des canines mandibulaires d'environ 50 mm ; trois paires très semblables sont mis en évidence (+), avec les empreintes d'une canine sur la surface externe, et de l'autre de la même paire sur le bord inférieur de l'hémimandibule. Ces dernières paires suggèrent des morsures successives, plus ou moins parallèles, par le prédateur, et la proie presque dans la même position. Photographies de Susana Rodrigues. Dessins de Miguel Telles Antunes.

Cabrera, whose corresponding distance between canine points is ca. 42 mm. This is about the same as the distance between the more apparent pair of imprints, but that measurement (41 mm) is obviously too small for the size of the symphysis imprint and thus is not acceptable. Trying to find some likely sized pair of imprints, we may perhaps accept a value of about 50 mm for the predator's distance between canine points as compatible with the size of the symphysis imprint. Of course, we are aware this is not obvious, but nevertheless it may be a valid approach.

If this assumption is correct, as it then seems probable, the imprints shown by the specimen were produced by successive, more or less parallel bites while the prey was kept more or less in the same position (Fig. 5). This suggests that feeding by the large predator happened on the spot, on a still relatively complete corpse and not on parts that had been carried away.

All this enables us to conclude that the predator's size was about that of a brown bear: we measured ca. 60 mm for the distance between mandible canine points from a large, male *Ursus arctos* (Pales and Garcia, 1981: Plate 8, rostral view). It was indeed an *Amphicyon*. Its large size may point to a (female?) individual of none other than the then relict species *Amphicyon giganteus*.

On the other hand, in the same Vb unit, the amphicyonid *Pseudocyon sansaniensis* and both the ursids *Hemicyon sansaniensis parvus* Ginsburg and Antunes, 1995 and *Plithocyon antunesi* Ginsburg and Morales, 1998 were too small (Ginsburg and Antunes, 1995; Ginsburg and Morales, 1998).

Even if its presence is impossible for geographic reasons, a rather large species like the North American *Hemicyon ursinus* was also far too small. As estimed from a specimen kept at the Paris Muséum's Galerie de Paléontologie, the intercanine distance was measured as merely ca. 40 mm.

Finally, the behaviour of *Amphicyon* and its ecologic role may be discussed. We want to stress that large-sized but unspecialized carnivores like *Amphicyon* could probably attack rather large prey but were certainly also carrion-eater scavengers. At that times there were no carnivores, such as very large felids, whose roles would be quite like those of the lion and tiger today. In lower middle Miocene times and in the area studied, attacks on large mammals would have been carried out mostly by the most powerful carnivore, *Amphicyon giganteus*. This was the largest modern-type, fissiped carnivore of those times, 0.9 metres tall at the shoulder and more than 200 kg in weight, assuming it had an ursoid aspect (Guérin, 2003: 386). It would have preyed on giraffoids and other large mammals, and it was likely a scavenger also (Guérin, ibidem). Predation and/ or scavenging on a rhinoceros can be expected, as seems to be the case.

Of course, the latest creodont *Hyainailourus sulzeri* also still existed (Antunes and Ginsburg, 2000b). However this archaic beast was exceedingly rare, as only a single bone has been collected. It certainly exceeded *Amphicyon* in size, but was probably less agile. Its success was limited and only its huge size (exceeding 1 metre at the shoulder and 500 kg in weight) helped it against much more advanced competitors. Its African affinities are well-known. It migrated into Asia and Europe (lower Miocene) along with the Gomphothere mastodons (Proboscidea), while moving in the opposite direction the modern Carnivora penetrated into Africa and contributed to the extinction of the Creodonts, until then the prevailing African flesh-eaters.

Robust *Hyainailouros* dentition is quite similar from this viewpoint to that of hyenas which suggests a scavenger, bone-crushing regime. Size could enable *Hyainailouros* to prey on large

mammals, including rhinocerotids and occasional proboscideans (Guérin, 2003: 385). In the case, however, an eventual *Hyainailouros* interference is too unlikely.

The preceding case does not prevent us from regarding *Amphicyon giganteus* as the super-predator of those times, at the top of the trophic pyramid (Ginsburg and Antunes, 1995: 28–29) and occupying an ecological niche that was taken later by large felids. Of course, this certainly did not deny them opportunistic, scavenger, carrion-eater behaviour.

A rather similar situation has been described. An *Amphicyon giganteus* hemimandible from the early middle Miocene of Arrisdrift, Namibia (Morales et al., 1998: Pl. 4, Fig. 4a, b) shows such heavily abraded teeth (P4-M1-M2) that it certainly should very often have gnawed bones. This also points to scavenging. See also Morales et al. (2003).

In normal situations a full-grown, non senile rhinoceros is not an easy prey. So was the individual killed by *Amphicyon giganteus*? Was it killed by a single individual or by a pack of these carnivores? All this seems possible, but still other situations as disease or accident may have caused death.

Another hypothesis is that large herbivores such as *Iberotherium* were prone to suffer from drought. Let us stress that in western Europe, and in the Lisbon area in particular, there was a climate change towards aridity during early middle Miocene. Temperature and even more moisture decreased (Antunes, 2000: 347, Table 3). Hence it is not surprising that *Iberotherium* was quite scarce in Vb's times, and that a smaller immigrant from Asia, better adapted to savannah environments as *Hispanotherium* became by far the dominant rhinocerotid (Antunes and Ginsburg, 1983, 2000). Rhinocerotids better adapted to forest or humid environments as *Iberotherium* probably became rather rare. All these data suggest as a possible scenario that during a drought event an animal that was dying or in poor physical condition or just seeking a water-point, where ambush was possible, has easily been overtaken by carnivores.

Another possible hypothesis is death as a consequence of a natural catastrophic event such as a major flood. Even if some rhinocerotids can swim, they may drown in floods and floods certainly occurred, as indicated by sedimentary evidence. As our (M.T.A.) field observations have shown, animal corpses and displaced large logs underwent transportation, as well as clay balls, oyster shells and rock fragments that resulted from intensive erosion of nearby outcrops. Corpses could have been transported by running water, more easily after body cavities became filled with decomposition gases. When in waters, corpses could be lacerated by large-sized crocodilians. As decay progressed and the corpses (wether complete or not) were eventually deposited. Parts would be consumed by scavengers such as *Amphicyon giganteus* even if the latter were mostly hunters. Perhaps after consumption, immersed or simply wet bone surfaces could undergo some corrosion. Fissures couls have resulted from desiccation, as shown by the external surface of the hemimandible under study, even if mechanical stress during biting may account in part for it.

However we think there are not enough data for a more developed taphonomical discussion on corrosion or post-mortem weathering effects.

4. Conclusions

A rhinocerotid hemimandible ascribed to *Iberotherium rexmanueli zbyszewskii* from the lower middle Miocene Vb unit from Lisbon was bitten by a large carnivore.

Hyainailouros sulzeri can be eliminated as the bite's author. Exceedingly rare, it was not a serious competitor to *Amphicyon giganteus,* the predator that is inferred as responsible, maybe a female.

Large-sized but non-specialized carnivores like *Amphicyon* could probably attack large prey but certainly were also opportunistic, carrion-eater scavengers.

The large, young adult *Iberotherium* may have been killed by a single individual or by a pack of *Amphicyon giganteus,* but disease or accident cannot be excluded as causes of its death.

During a drought event, an animal that was dying or in poor physical condition, or just seeking a water point where ambush could be easy may have been overcome by carnivores.

There is still the possibility that death may have been a consequence of a catastrophic event such as major floods. Field data show that this is quite probable.

After consumption, immersion or simply wet bone surfaces could undergo some corrosion.

Fissures may have resulted from desiccation, but mechanical stress may partly account for it. The hemimandible had surely been abandoned after consumption and left exposed until new sands were deposited over it.

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References

Antunes, M., Telles, 2000. Miocene mammals from Lisbon and geologic age. A showcase for marine-continental correlations. Ciências da Terra (UNL) 14, 343–348.

Antunes, M., Telles, Balbino, A.C., Ginsburg, L., 2006. Miocene mammalian footprints on coprolites from Lisbon, Portugal. Annales de Paléontologie 92, 13–30.

Antunes, M., Telles, Ginsburg, L., 1983. Les Rhinocérotidés du Miocène de Lisbonne Systématique, écologie, paléobiogéographie, valeur stratigraphique. Ciências da Terra (UNL) 7, 17–98.

Antunes, M., Telles, Ginsburg, L., 2000a. Les Périssodactyles (Mammalia) du Miocène de Lisbonne. Ciências da Terra (UNL) 14, 349–354.

Antunes, M., Telles, Ginsburg, L., 2000b. Présence du Créodonte *Hyainailouros sulzeri* dans le Miocène du bassin du Bas Tage (Lisbonne, Portugal). Ciências da Terra (UNL) 14, 355–358.

Antunes, M., Telles, Ginsburg, L., 1995. Les Carnivores du Miocène de Lisbonne (Portugal). Annales de Paléontologie 81, 125–165.

Ginsburg, L., Morales, J., 1998. Les Hemicyoninae (Ursidae, Carnivora, Mammalia) et les formes apparentées du Miocène inférieur et moyen d'Europe occidentale. Annales de Paléontologie 84, 71–123.

Guérin, C., 2003. Palaeoecological study of Arrisdrift Mammals. Memoir Geological Survey Namibia 19, 385–388.

Morales, J., Pickford, M., Fraile, S., Salesa, M.J., Soria, D., 2003. Creodonta and Carnivora from Arrisdrift, early Middle Miocene of Southern Namibia. Memoir Geological Survey Namibia 19, 177–194.

Morales, J., Pickford, M., Soria, D., Fraile, S., 1998. New carnivores from the basal middle Miocene of Arrisdrift, Namibia. Eclogae Geologicae Helvetiae 91, 27–40.

Pales, L., Garcia, M.A., 1981. Atlas Ostéologique des Mammifères. II. Tête/ Rachis. Ceintures scapulaire et pelvienne/ Carnivores/ Homme. Éditions du CNRS, Paris.