Eucyon debonisi n. sp., a new Canidae (Mammalia, Carnivora) from the latest Miocene of Venta del Moro (Valencia, Spain)

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ABSTRACT

A new species of canid (*Eucyon debonisi* n. sp.) is described from the late Miocene of Venta del Moro (Valencia, Spain). The new species is smaller than all the other *Eucyon* species, excepting *E. intrepidus* from the late Miocene of Lukeino (Kenya). *Eucyon debonisi* n. sp. is characterized by the greater size of the M2 in relation with the M1, showing comparable morphology with *E. monticinensis*, but this new species has a stronger parastyle, a less developed lingual cingulum and a more closed valley in the talon of the M1. Besides, it has a more slender dentition and mandible than *E. monticinensis* and possesses a diastema between p1 and p2 and between p2 and p3. Excepting the problematic *Canis cipio* from the middle Turolian locality of Concud (Spain), *E. debonisi* n. sp. represents the first modern canid that reached western Europe.

KEY WORDS
Mammalia,
Carnivora,
Canidae,
Eucyon,
Venta del Moro,
Spain,
late Miocene,
late Turolian,
new species.

RÉSUMÉ

Eucyon debonisi n. sp., *un nouveau canidé (Mammalia, Carnivora) du Miocène terminal de Venta del Moro (Valence, Espagne).*
Une nouvelle espèce de canidé (*Eucyon debonisi* n. sp.) du Miocène supérieur de Venta del Moro (Valence, Espagne) est décrite. La nouvelle espèce est plus petite que toutes les autres espèces d'*Eucyon*, à l'exception d'*E. intrepidus* du Miocène supérieur de Lukeino (Kenya). *Eucyon debonisi* n. sp. se caractérise par la grande taille de la M2 par rapport à la M1 et montre une morphologie comparable à celle d'*E. monticinensis*. Cependant, cette nouvelle espèce a un parastyle plus marqué, un cingulum lingual moins développé et une vallée plus fermée dans le talon de la M1. De plus, elle possède une dentition et une mandibule plus minces qu'*E. monticinensis* ainsi qu'un diastème entre la p1 et la p2 et entre la p2 et la p3. À l'exception de l'espèce problématique *Canis cipio* du Turolien moyen espagnol, *E. debonisi* n. sp. représente le premier canidé moderne ayant atteint l'Europe occidentale.

INTRODUCTION

The late Miocene locality of Venta del Moro (province of Valencia, Spain), in the Cabriel Basin, is one of the most interesting sites from the Spanish Neogene fossil record. It contains an abundant and diversified mammalian fauna, associated to the remains of many other groups, from plants (pollen and macro-flora) to a diverse number of invertebrates and non-mammal vertebrates (Montoya *et al.* 2006). Dated as late Turolian (MN13, M3), with an estimated age of approximately 5.8 Ma (Opdyke *et al.* 1997), this locality was proposed as the reference level for the Ventian mammal age (Aguirre *et al.* 1976; Alberdi *et al.* 1977; Morales 1984). This denomination has fallen into disuse in the past years, but it was used to refer to the upper part of biozone MN13, a period of time in which a large number of non-European groups of mammals arrived to western Europe, such as camels and hippos (Morales 1984; Pickford & Morales 1994; Pickford *et al.* 1993, 1995; Agustí *et al.* 2006; Made *et al.* 2006).

Among these non-European immigrants, one of the most interesting groups are the first modern canids, not including the problematic *Canis cipio* Crusafont, 1950 from the MN12 localities Concud and Los Mansuetos, Spain (Pons & Crusafont 1978). Excluding the latter, the classification of these canids has been very controversial, as they have been named firstly as *Nyctereutes* cf. *donnezani*

and *Canis* sp. by Morales & Aguirre (1976) then as *Nyctereutes* aff. *donnezani* and *Vulpes* sp. (Morales 1984) and finally as "*Canis*" cf. *monticinensis* by Rook (1992). Later, "*Canis*" *monticinensis*, along with other related species, was included in the genus *Eucyon* Tedford & Qiu, 1996, an opinion accepted in the most recent articles (Made *et al.* 2006; Spassov & Rook 2006; García 2008).

Intensive excavations have been carried out since 1995 in the locality of Venta del Moro with satisfactory results (Montoya *et al.* 2006). A large amount of new remains of canids, some of them very complete and well preserved, have been found. The main objective of this paper is to describe them and to specify their systematic classification.

SYSTEMATICS

Order CARNIVORA Bowdich, 1821
Family CANIDAE Fischer de Waldheim, 1817
Genus *Eucyon* Tedford & Qiu, 1996

Eucyon debonisi n. sp.

Nyctereutes cf. *donnezani* – Morales & Aguirre 1976: 34, pl. 1, figs 1-5.

Canis sp. – Morales & Aguirre 1976: 38, pl. 1, figs 6-8.

TABLE 1. — Measurements (in mm) of the upper dentition of *Eucyon debonisi* n. sp. from Venta del Moro (Spain). Abbreviations: **L**, length; **W**, width; **MMr**, length of the molar row; **PPr**, length of the premolar row.

Specimen	LC	WC	LP2	WP2	LP3	WP3	LP4	WP4	LM1	WM1	LM2	WM2	PPr	MMr
MGUV 14780							14.9	6.6	10.7	12.1	6.9	8.9		18.3
MGUV 14781			7.6	2.5	9.1	3	13.7	6.4	10.2	11.7	6.8	9.5	35.7	16.7
MGUV 14752dext	7		8.1	2.7	9.4	3.2	14.3	7.1	11.4	13.2	7.5	10	34.6	19.1
MGUV 14752sin					9.3		15.3	7	11	13.5	7.4	10		18.6
MGUV 14786							13.6	6.5						
MGUV 14784									9.7	11				
MGUV 14785											6.4	8.7		
MGUV 14346									10.4	12.1				
MGUV 14777											6.3	9.5		
MGUV 14368									10.5	13.3				
MGUV 14309									10.4	13				
MGUV 18472							15.4	7						
MGUV 14778	7.1	5.4												
MGUV VV-14889									10.4	12.4				
MGUV VV-14988											6.2	9.5		
MNCN-VM 1									11.3	12.7	6.9	9.2		18.1
MNCN-VM 2							14.5							
MNCN-VM 3					9	3.4								
MNCN-VM 5							16.6							

Nyctereutes aff. *donnezani* – Morales 1984: 30, fig. 10, pl. 2, fig. 3.

Vulpes sp. – Morales 1984: 33, fig. 11, pl. 2, fig. 2.

"*Canis*" cf. *monticinensis* – Rook 1992: 153.

Eucyon cf. *monticinensis* – Spassov & Rook 2006: 130.

HOLOTYPE. — MGUV 14780 (VV-1549), fragment of right maxilla with P2, P4-M2; MGUV 14781 (VV-1624), fragment of left maxilla with I3-M2; MGUV 14779 (VV-1522), right mandible with p2-p3. Associated elements, very probably belonging to the same individual. Stored in the Museu de Geologia de la Universitat de València.

ETYMOLOGY. — In honour to Prof. Louis de Bonis, in recognition of his important contribution to the knowledge of the fossil carnivores.

LOCALITY AND AGE. — Venta del Moro, province of Valencia, Spain. Late Miocene, late Turolian (MN13).

DIAGNOSIS. — *Eucyon* of small size, with slender mandible and dentition; M1 with generally strong parastyle; strong lingual cingulum that closes completely the valley present in the talon. Mono-cuspidated inferior premolars, except p4 that possesses distal cusps; m2 with a wide trigonid, without paraconid, narrow talonid with a very weak entoconid.

DIFFERENTIAL DIAGNOSIS. — *Eucyon debonisi* n. sp. is smaller than all the other *Eucyon* species excepting *E. intre-pidus* Morales, Pickford & Soria, 2005 (= *E. minimus* Haile-Selassie & Howell, 2009). The differences with *E. davisi* (Merriam, 1911) are, the greater size of the M2 in relation with the M1, the more developed cingulum and the presence of a valley in the talon of the M1. When compared with *E. monticinensis* (Rook, 1992) this new species has a stronger parastyle but a less developed lingual cingulum and a more closed valley in the talon of the M1. Besides, it has a more slender dentition and mandible than *E. monticinensis* and possesses a diastema between p1 and p2 and between p2 and p3. It differs from *E. marinae* Spassov & Rook, 2006 in the absence of a distal cuspid in the p3. The m1 of *E. debonisi* n. sp. differs from those of *E. intrepidus* and *E. wokari* García, 2008 in the more simple morphology of the talonid, that remains undivided.

MATERIAL EXAMINED. — All the studied specimens are stored in the two following Spanish institutions: Museu de Geologia de la Universitat de València (Burjassot)-Venta del Moro (MGUV-VV) and Museo Nacional de Ciencias Naturales (CSIC, Madrid)-Venta del Moro (MNCN-VM).
MGUV 14779, 14780, 14781 (VV-1522-1549-1624) (holotype), fragment of right mandible with p2-p3, fragment of right maxilla with P2, P4-M2, fragment of left maxilla with I3-M2; MNCN VM-1, fragment of maxilla with incomplete P2 and P3 (Morales & Aguirre 1976: pl. 1, fig. 2); MNCN VM-2, right P4 (Morales & Aguirre 1976: pl. 1, fig. 3); MNCN VM-3, fragment of right maxilla with M1-M2 (Morales & Aguirre 1976: pl. 1, fig. 1); MNCN VM-4, fragment of mandible with p3 and incomplete

TABLE 2. — Measurements (in mm) of the lower dentition of *Eucyon debonisi* n. sp. from Venta del Moro (Spain). Abbreviations: **L**, length; **W**, width; **mmr**, length of the molar row; **ppr**, length of the premolar row.

Specimen	Lc	Wc	Lp1	Wp1	Lp2	Wp2	Lp3	Wp3	Lp4	Wp4	Lm1	Wm1	Lm2	Wm2	ppr	mmr
MGUV 14787			3.7	2.2	6.6	3							7.5	5.4	33.9	22.5
MGUV 14788									10.3	3	15.4	6.6	8.6	6.6		24.5
MGUV 14779					8.1	2.9	8.9	3							32.8	21.5
MGUV 14753					7.9	2.6	8		9	3.1	14.7	5.8				
MGUV 18474											16.9	6.4				
MGUV 14782											15	5.8				
MGUV 19623													7.6	5.5		
MGUV 18473											15.6	6.3				
MGUV 14791											16	6.6				
MGUV VV-14601											16.2	6.6				
MGUV 18471	6.3	4.4														
MGUV 19185					7.6	2.9										
MGUV 14755									8.7	2.9						
MGUV 14754					7.3	2.7										
MGUV VV-14793											17.2	6.5				
MGUV VV-14906													7.9	5.7		
MGUV VV-15125											16	6.3				
MGUV VV-14788									10.7	4.1						
MNCN-VM 15							8.5	3.2								
MNCN-VM 4							7.8	2.8	8.7		15					
MNCN-VM 50											16.7	6.6				
MNCN-VM 51											16.9	6.6				

m1 (Morales & Aguirre 1976: pl. 1, figs 4, 5); MNCN VM-5, right P4 (Morales & Aguirre 1976: pl. 1, fig. 8); MNCN VM-15, right p3; MNCN VM-50, rigth m1 (Morales 1984: pl. 2, fig. 2); MNCN VM-51, left m1 (Morales 1984: pl. 2, fig. 3); MGUV 14752 (VV-9248), maxilla with both dental series; MGUV 14753 (VV-9325), fragment of left mandible with p2-m1; MGUV 14777 (VV-75), left M2; MGUV 14778 (VV-793), right upper canine; MGUV 14782 (VV-2148), right m1; MGV 14784 (VV-4187), left M1; MGUV 14785 (VV-4312), left M2; MGUV 14786 (VV-4352), right P4; MGUV 14787 (VV-4515), left mandible with p1-p2 and m2; MGUV 14788 (VV-5315), fragment of right mandible with p4-m2; MGUV 14791 (VV-7100), left m1; MGUV 14793 (VV-8150), incomplete left m1; MGUV 18471 (VV-12464), left lower canine; MGUV 18472 (VV-12493), left P4; MGUV 18473 (VV-13282), right m1; MGUV 18474 (VV-13284), right m1; MGUV 19179 (VV-14346), right M1; MGUV 19180 (VV-14368), left M1; MGUV 19181 (VV-14309), right M1; MGUV 19623 (VV-12736), right m2; MGUV VV-14601, left m1; MGUV VV-14713, right p3; MGUV VV-14788, p4; MGUV VV-14793, right m1; MGUV VV-14889, left M1; MGUV VV-14906, right m2; MGUV VV-14988, left M2; MGUV VV-15125, right m1; MGUV 15753 (VV-9568), left astragalus; MGUV 19183 (VV-13763), left calcaneus; MGUV 19184 (VV-14181), right calcaneus; MGUV VV-14624, right navicular.

MEASUREMENTS
See Tables 1 and 2.

DESCRIPTION
MGUV 14779, 14780, 14781 (VV-1522-1549-1624), holotype (Fig. 1)
Slender P4, with a well-individualized protocone. Continuous and strong lingual cingulum. Very smooth labial cingulum. It has a quite marked mesial crista in the paracone with a thick base but not so prominent as a real parastyle. Strong mesial cingulum, wide in its labial edge. Sharp paracone. The M1 has a smooth medial inflexion in the buccal wall, a well-marked inflexion in the distal wall and a convex mesial wall. The paracone has a pyramidal shape, and a weak lingual crista. Dune-shaped protocone, fused to the paraconule and metaconule, thus closing completely the central valley. The lingual cingulum is quite developed, displaced towards the distal part and fused to the base of the metaconule and the paraconule closing a deep valley between them. The molar is surrounded by a moderate cingulum in which a strong parastyle stands out. In occlusal view, the M2 shows
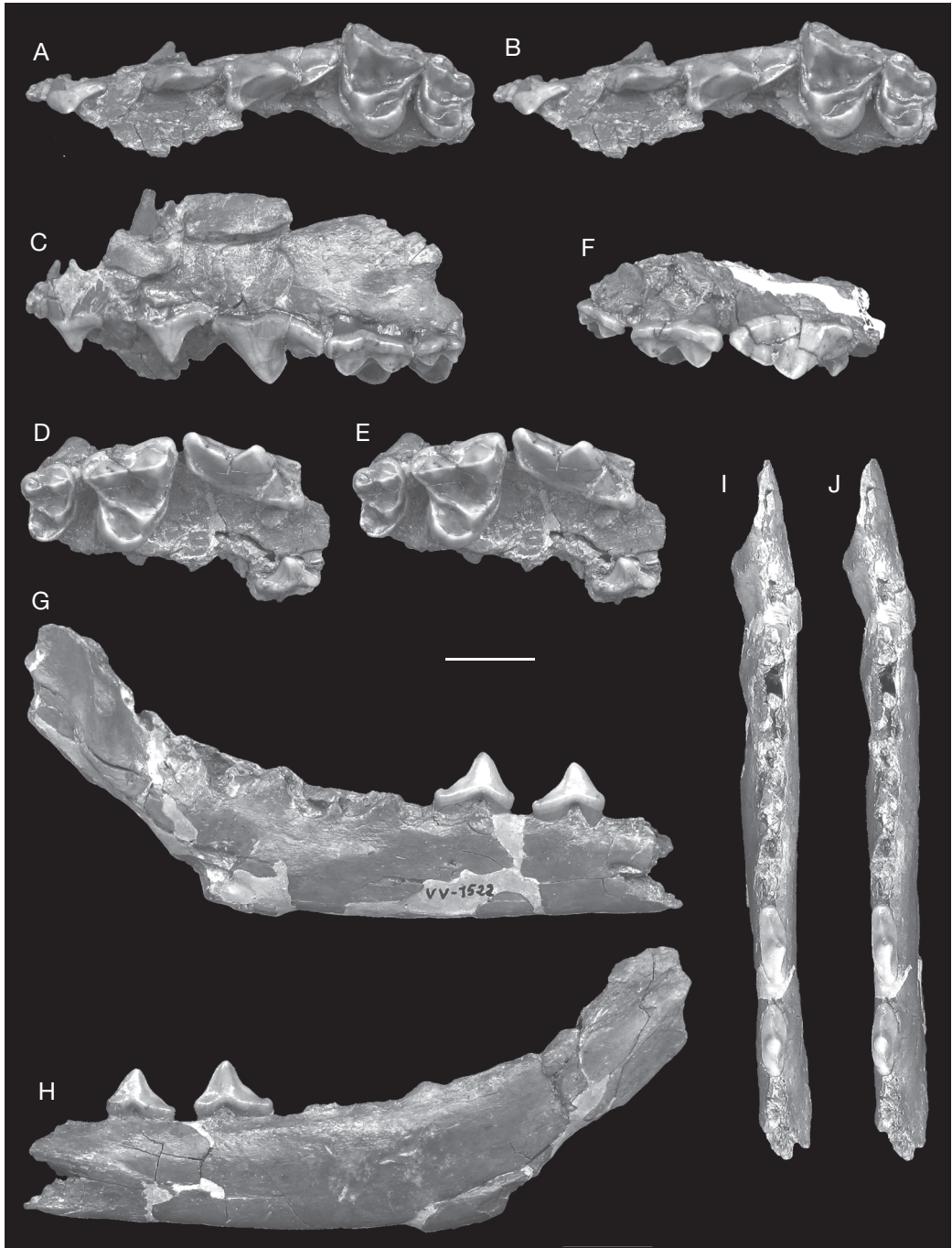
Fɪɢ. 1. — Holotype of *Eucyon debonisi* n. sp. from Venta del Moro (Spain): **A**-**C**, fragment of left maxilla with P2-M2 (MGUV 14781); **D**-**F**, fragment of right maxilla with P2 and P4-M2 (MGUV 14780); **G**-**J**, right mandible with p2-p3 (MGUV 14779); **A**, **B**, **D**, **E**, **I**, **J**, stereo-photographs of occlusal views; **C**, **F**, lateral views; **G**, buccal view; **H**, lingual view. Scale bar: 10 mm.
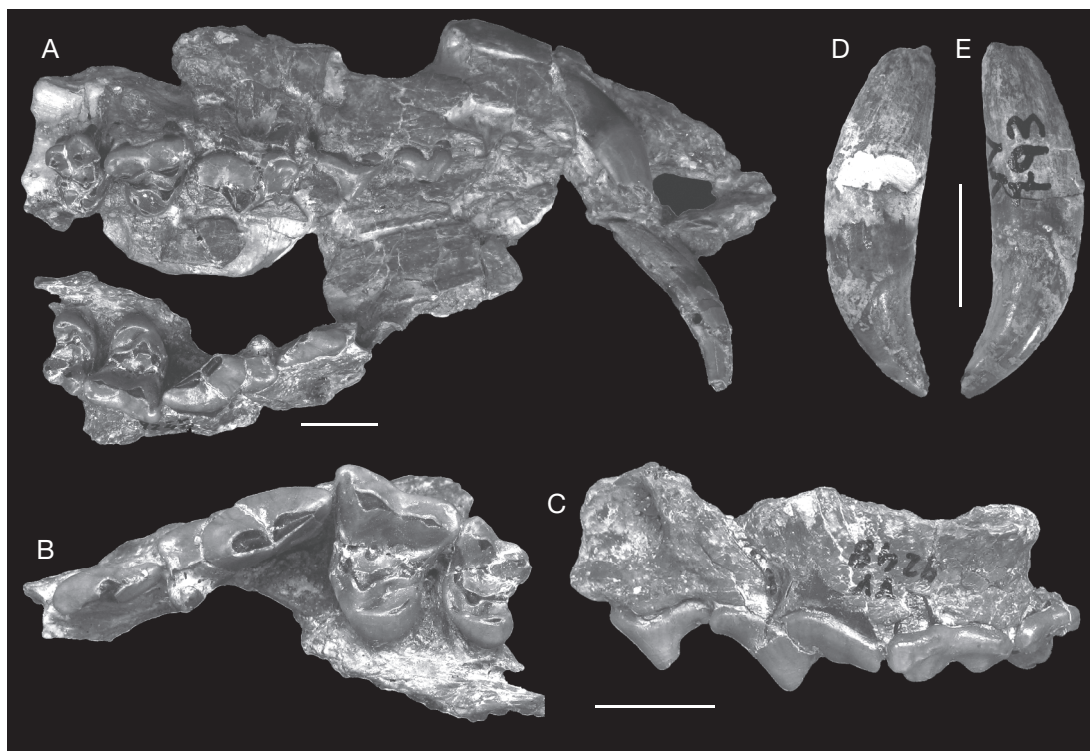
Fɪɢ. 2. — *Eucyon debonisi* n. sp. from Venta del Moro (Spain): **A-C**, maxilla with both dental series (MGUV 14752); **B, C**, detailed views of the left maxilla with P3-M2; **D, E**, right upper canine (MGUV 14778); **A**, ventral view; **B**, occlusal view; **C**, lateral view; **D**, lingual view; **E**, buccal view. Scale bars: 10 mm.

a similar shape to that of M1, with a strong stylar platform. The cingulum has a moderate size, even in lingual view, where a shallow and plain valley is present. The P3 has an elongated crown, narrow, and with only one cusp. The mesial crista is displaced towards the lingual part. The distal crista ends in a tiny basal cusp. It has very smooth cingula. The P2 is similar in shape to the P3. The P1 has just one root, with a strong internal cingulum and a small distal cusp. The mesial crista is also located in the lingual border.

The mandible has rodent tooth marks and lacks all the teeth excepting the p2 and the p3. The p2 is separated by a diastema from the p3 and from the canine. Both premolars are similar in shape, but the p2 is smaller and more vertical than the p3. It possesses a quite vertical mesial cristid, wide in its base, while the distal cristid is more enlarged. The p3 lacks a distal

accessory cuspid, but has a small cuspid at the base of the distal cristid. The cingula are very smooth.

MGUV 14752 (VV-9248), maxilla with both dental series (Fig. 2A-C)
The infraorbital foramen is located at the level of P3. The canine has a moderate size and a sharp distal edge. The molars are larger and quite more worn than those of the holotype. When compared with the holotype, the P4 has a strong cingulum, with a wider mesial corner. The M1 has a very strong parastyle and the M2 possesses a higher labial cingulum.

MGUV 14753 (VV-9325), left hemimandible with p2-m1 (Fig. 3G-I)
The p2 has only one cuspid with a quite vertical mesial cristid that turns to be slightly wider towards

its base. It has a large distal cristid that, instead of a distal cuspid, has a slight incision marking a change (from more to less steep) in the slope. The p3 is broken, but a small cuspid in the distal part of the talonid can still be observed. The p4 is narrow, with a high principal cuspid and a vertical mesial cristid in which the basal end has turned slightly wider. The distal cuspid is high and strong, and has a well-developed talonid that has a low central cuspid. The m1 has a high protoconid, which possesses a small disto-buccal cristid. The paraconid has a vertical mesial cristid, and although the metaconid is broken, its large size can be deduced. The talonid is well developed and the hypoconid, which has a pyramidal shape, runs in a parallel way to the mesio-distal molar axis. The distal cristid of the hypoconid ends in a small hypoconulid. The entoconid is quite small and is well separated from the hypoconid. Its mesial cristid is elongated and possesses an individualized cuspid.

MGUV 14787 (VV-4515), very well-preserved left hemimandible with p1, p2 and m2 (Fig. 3A-C)
The mandibular body is very slender and shows a broken angular process. Its shape differs only slightly from the European fox (*Vulpes vulpes* Linnaeus, 1758). The p1 is quite reduced and isolated by diastemas. The p2 is poorly preserved and is also separated from the p3 by another diastema. The m2 has a wide trigonid, mesio-buccally expanded; the cingulum is only present at the base of the protoconid. This molar lacks the paraconid, and only a small lump is present instead. The metaconid is as high as the protoconid but the latter is wider. The talonid is a simple and narrow cuspid, with a moderate hypoconid and a very small entoconid.

MGUV 15753 (VV-9568), left astragalus (Fig. 4E-H)
Measurements: proximo-distal length = 20 mm, latero-medial length = 12.3 mm, dorso-plantar length = 10.3 mm.

The trochlea bears two high lips separated by a deep valley that runs from the proximo-plantar edge to the disto-dorsal neck. The neck is quite elongated towards the medio-distal part and ends in the facet for the navicular. This facet is smooth, convex, and oval-shaped, with its major axis running from the latero-dorsal vertex to the medio-plantar one. The facet for the calcaneus has two different surfaces, the larger one being located just on the opposite part of the trochlea for the tibia, whereas the smaller one is placed on the lateral tip of the distal end of the facet for the navicular. The latter is a small facet, which hardens the articulation between the astragalus and the calcaneus, thus avoiding lateral movements between them.

This astragalus has been compared with those from *E. davisi* (Harrison 1983) and *E. monticinensis* (Rook *et al.* 1991). They seem to be quite similar in shape but both species are clearly larger than *E. debonisi* n. sp.

MGUV 19183 (VV-13763) left calcaneus and MGUV 19184 (VV-14181), right calcaneus (Fig. 4A-D)
Measurements: left calcaneus, proximo-distal length = 31.3 mm, latero-medial length = 11.3 mm, dorso-plantar length = 11.9 mm; right calcaneus, proximo-distal length = 32.1 mm, latero-medial length = 12 mm, dorso-plantar length = 12.4 mm.

The calcaneus is quite elongated, especially the distal third of the bone, between the posterior articular surface for the astragalus and the distal end (facet for the cuboid). Both the lateral and medial faces are quite smooth and straight, with a very small lateral development of the trochlear process and reduced sustentaculum tali when compared with other carnivores. The articular surfaces for the astragalus are very similar to those of *Canis aureus* Linnaeus, 1758. However, the distal part of the posterior articulation surface is much more concave and the anterior articulation surface is larger than in this species. The calcaneal tuberosity is quite robust, and has a shallower groove for the large terminal tendons of the muscles soleus and gastrocnemius, when compared with the studied canids.

The calcaneus of *E. debonisi* n. sp. has been compared with that of *E. davisi* (Harrison 1983), and apart from being smaller, it shows some differences. The trochlear process and the groove in the calcaneal tuberosity are more developed in *E. davisi*, whereas the articulation surfaces for the astragalus are quite more elongated in *E. debonisi* n. sp.
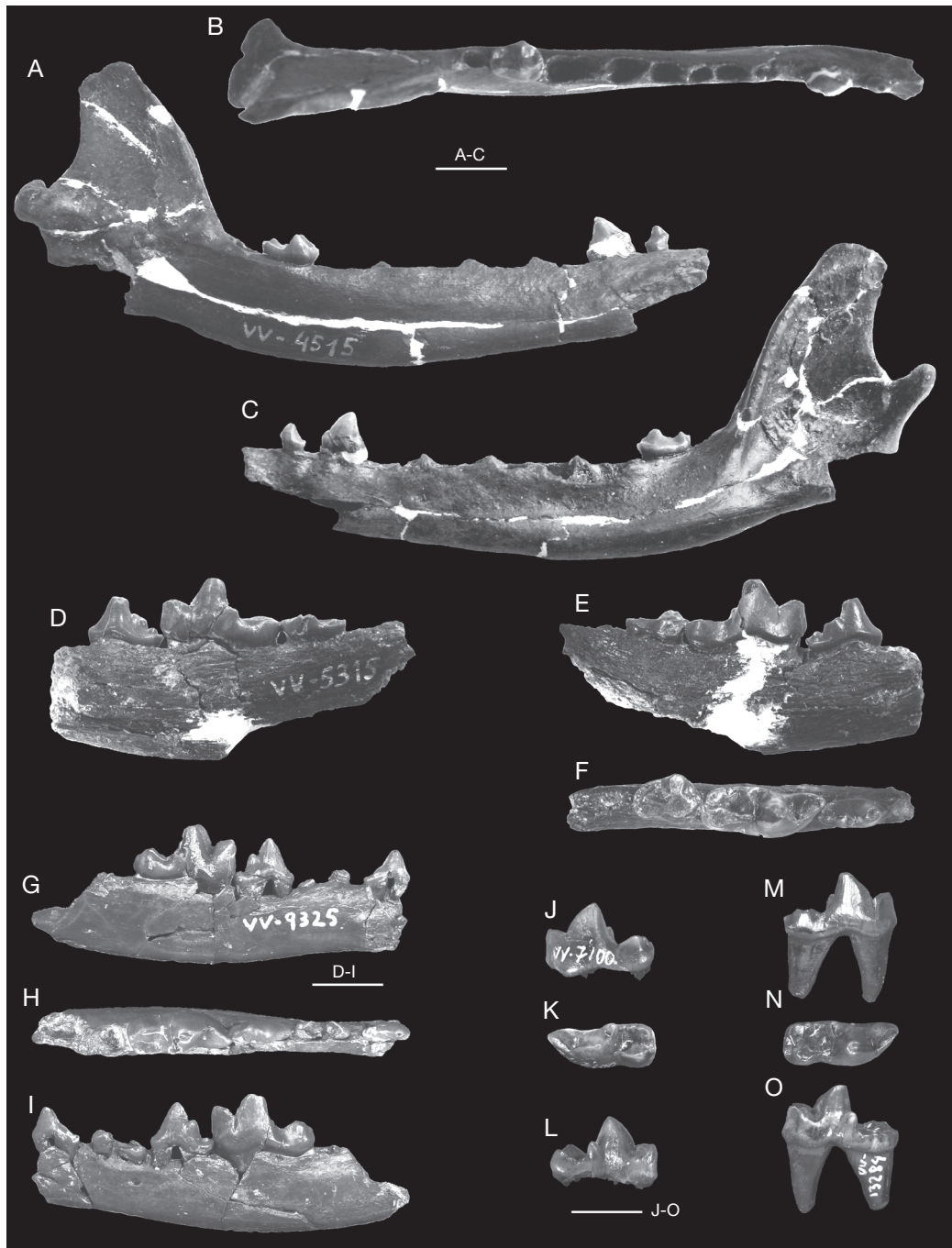
Fig. 3. — *Eucyon debonisi* n. sp. from Venta del Moro (Spain): **A-C**, left hemimandible with p1, p2 and m2 (MGUV 14787); **D-F**, fragment of right hemimandible with p4-m2 (MGUV 14788); **G-I**, fragment of left hemimandible with p2-m1 (MGUV 14753); **J-L**, left m1 (MGUV 14791); **M-O**, right m1 (MGUV 18474); **A**, **D**, **G**, **L**, **O**, lingual views; **B**, **F**, **H**, **K**, **N**, occlusal views; **C**, **E**, **I**, **J**, **M**, buccal views; Scale bars: 10 mm.

MGUV VV-14624, right navicular (Fig. 4I, J)
Measurements: proximo-distal length = 7.4 mm, latero-medial length = 10.6 mm, dorso-plantar length = 9.6 mm.

This is a quite cubic bone, with a concave proximal surface and a straight distal one. The facet for the astragalus is somehow more circular than that of the studied extant canids. This is a consequence of the weaker development of the latero-plantar notch. It has smooth medial and dorsal surfaces, while both the lateral and especially the plantar parts are much rougher. The facet for the cuboid is a small rounded smooth surface located in the lateral part of the bone that is distally projected. In the plantar facet there is a quite developed and rounded tuberosity for the attachment of the ventral calcaneus-navicular and ventral naviculo-cuneiform ligaments.

COMPARISONS

Eucyon debonisi n. sp. exhibits a smaller dentition than *E. davisi* (type species of the genus), except in M2. Differences regarding *E. davisi* are rather clear; remarkably in the upper dentition we noticed that the P4 is more gracile in the Spanish species (Fig. 5), meaning a lesser development in the size of the protocone. Nevertheless, compared to the M1, the M2 of *Eucyon debonisi* n. sp. are clearly larger (Fig. 6). Several differences are also found in the M1, mainly regarding the strength of the cingulum and the development of the talonid valley, being these stronger in *E. davisi* than in *E. debonisi* n. sp. As to the lower dentition, the talonid of the m1 in *E. debonisi* n. sp. is close to that of *E. davisi*. However, in several specimens of the latter species (UCMP112197) the structure of the talonid is simpler, also the talonid valley is continuous to the distal edge, whereas in Venta del Moro this is closed due to the closeness between the entoconid and the hypoconid and also to the presence of two small cuspids located in the distal edge of the tooth. In fact, the new material found in Venta del Moro shows that *Eucyon debonisi* n. sp. is close to *E. monticinensis*, differing from the Italian species in a smaller and gracile dentition (Figs 6; 7). The only known mandible of *E. monticinensis* is remark-
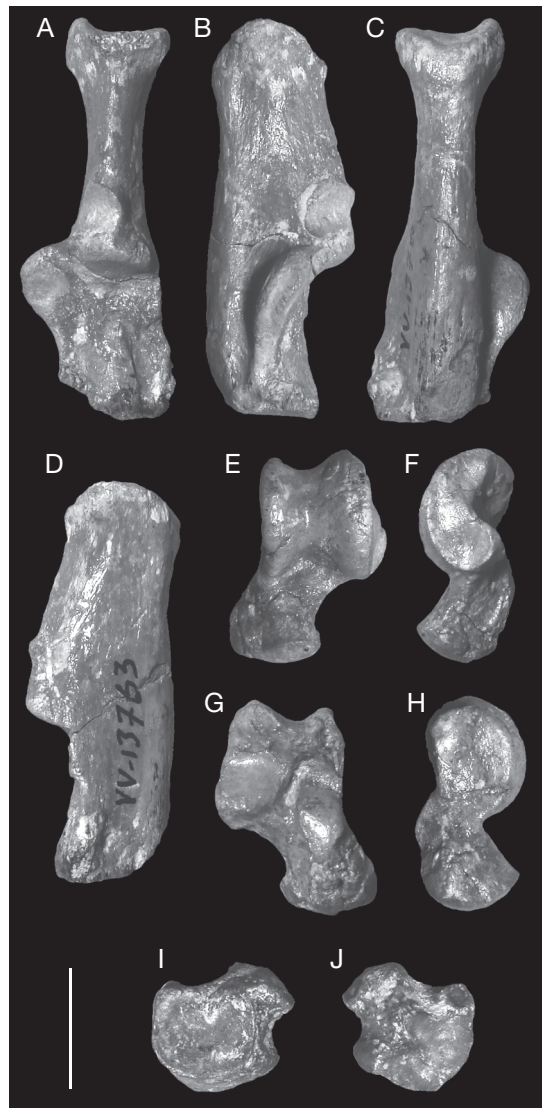

FIG. 4. — *Eucyon debonisi* n. sp. from Venta del Moro (Spain): **A-D**, left calcaneus (MGUV 19183); **E-H**, left astragalus (MGUV 15753); **I, J**, right navicular (MGUV VV-14624); **A, E**, dorsal views; **B, H**, medial views; **C, G**, plantar views; **D, F**, lateral views; **I**, proximal view; **J**, distal view. Scale bar: 10 mm.

ably more robust than that from Venta del Moro; furthermore, it lacks a diastema between p1-p2 and between p2-p3, whereas these are noticeably perceptible in *E. debonisi* n. sp.

Likewise, the M1 of *E. monticinensis* has a stronger lingual cingulum, more closed central valley and
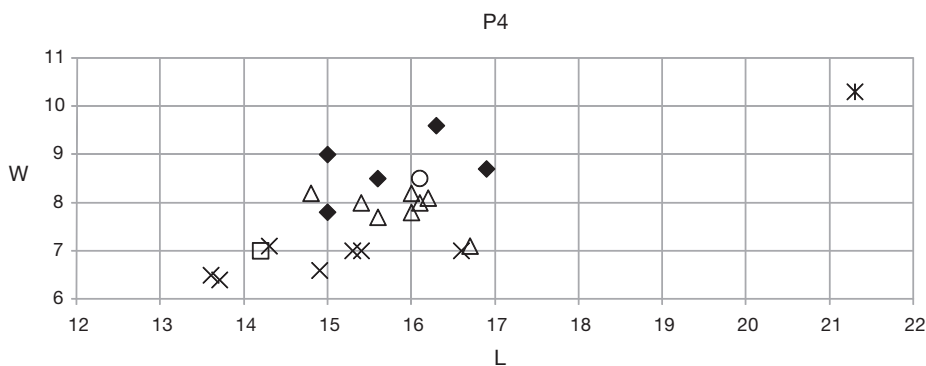
P4

Fig. 5. — Bivariate plot of the P4 of different *Eucyon* Tedford & Qiu, 1996 species and *Canis cipio* Crusafont, 1950. Data, in part, from Crusafont (1950), Martin (1973), Hendey (1974), and Tedford & Qiu (1996). Abbreviations: **L**, length; **W**, width. ○, *E. adoxus* Martin, 1973; ✖, *C. cipio* Crusafont, 1950; ✕, *E. debonisi* n. sp.; △, *E. davisi* (Merriam, 1911); ◆, *E. zhoui* Tedford & Qiu, 1996; □, *Eucyon* sp.

a weaker parastyle than the M1 from Venta del Moro. The talonid of the m1 is quite similar in both *E. debonisi* n. sp. and *E. monticenensis*, even though the latter lacks distal cuspids to the hypoconid and entoconid. As regards *Eucyon marinae* from the Mongolian Pliocene (Ruscinian/Lower Villafranchian), described by Spassov & Rook (2006), differences regarding size are remarkable, substantially larger in the Mongolian species. On the other hand, it also presents greater strength and development in the distal cuspids of the p4 and p3. On the contrary, the m1 of *E. debonisi* n. sp. and *E. marinae* are closely related, including a similar morphological pattern for the talonid of this molar (Spassov & Rook 2006: fig. 4). Comparison to other Eurasian species such as *E. zhoui* Tedford & Qiu, 1996 or *E. minor* (Teilhard de Chardin & Piveteau, 1930) proves more difficult. Tedford & Qiu (1996) pointed out that the main distinction between *E. zhoui* and *E. davisi* lies in the proportions of the cranium, showing overlapping with the dental dimensions of the two species, both presenting a larger size than *E. debonisi* n. sp.

With respect to the African species, recently described by Morales *et al.* (2005), García (2008) and Haile-Selassie & Howell (2009), comparisons are still limited due to the scarcity of the material available. Distinction between *E. debonisi* n. sp. and *E. wokari* García, 2008 from the Middle Awash Valley (Ethiopia) is substantially clear; the latter presents a talonid of m1 definitely of the type *Canis*, with robust

hypoconid and also the lingual cristid contacts the labial cristid of the entoconid. The talonid valley is split into two parts: a large mesial part and a small distal one where a tiny cuspid is noticed. Besides, an oblique cristid in the hypoconid is perceptible. The m2 of *E. wokari* differs from *E. debonisi* n. sp. in the presence of paraconid as well as in the greater development of the talonid size. In addition, the M1 of *E. wokari* is somewhat longer than the one in the species from Venta del Moro.

Morales *et al.* (2005), Howell & García (2007) and Haile-Selassie & Howell (2009) have recently recorded the presence of the genus *Eucyon* in stratigraphic levels of the late Miocene in Kenya and Ethiopia. One of the major characteristics of these African forms lies in their small size, markedly smaller than *Eucyon debonisi* n. sp. *Eucyon intrepidus*, defined in Lukeino (Morales *et al.* 2005) on the basis of two M1, is morphologically similar to *Eucyon* aff. *intrepidus* from Lemudong'o (Howell & García 2007), and as a matter of fact, García (2008) had already classified it as *E. intrepidus*. Among the material from Lemudong'o, there is an incomplete m1 with a well-preserved talonid even though it presents a slightly different morphology to the one observed in *E. debonisi* n. sp. In the Lemudong'o specimen both hypoconid and entoconid are innerly connected by a smooth transverse cristid which splits the talonid valley into two parts: a small distal and a greater mesial one. Traces of the presence of two tiny distal cuspids
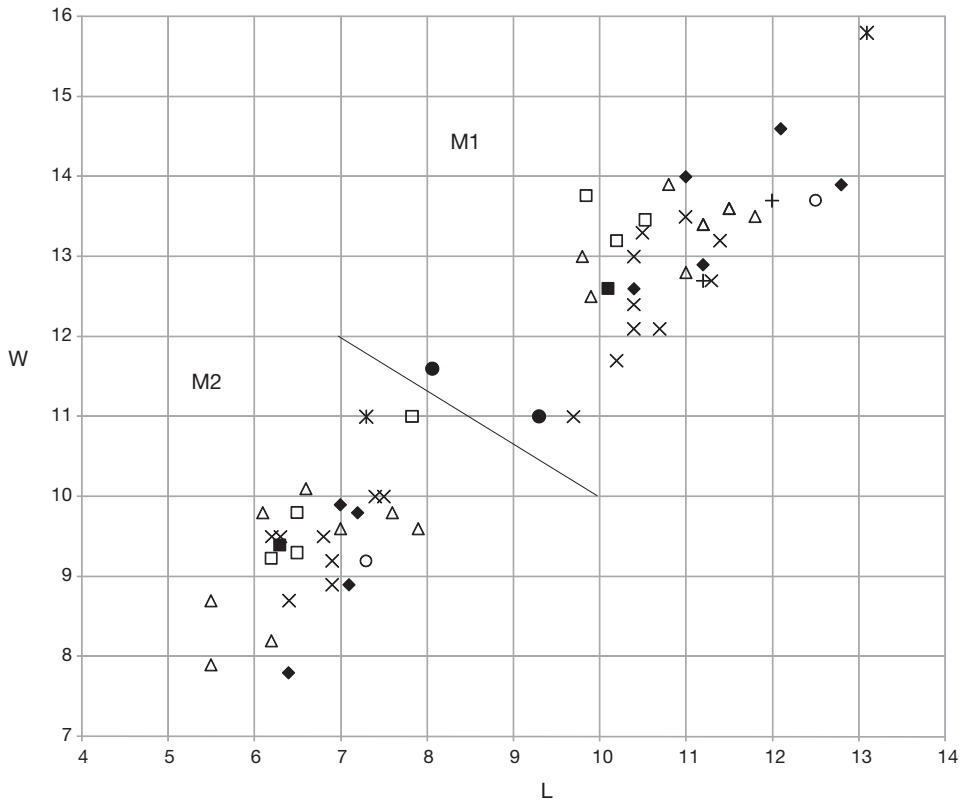
FIG. 6. — Bivariate plot of the M1 and M2 of different *Eucyon* Tedford & Qiu, 1996 species and *Canis cipio* Crusafont, 1950. Data, in part, from Crusafont (1950), Martin (1973), Hendey (1974), Rook (1992), Tedford & Qiu (1996), Morales *et al.* (2005) and García (2008). Abbreviations: **L**, length; **W**, width. ○, *E. adoxus* Martin, 1973; ✕, *C. cipio*; ✗, *E. debonisi* n. sp.; △, *E. davisi* (Merriam, 1911); ◆, *E. zhoui* Tedford & Qiu, 1996; □, *Eucyon* sp.; ●, *E. intrepidus* Morales, Pickford & Soria, 2005; +, *E. monticinensis* (Rook, 1992); ■, *E. wokari* García, 2008.

were found, but they are worn out and in fact their relevance is minimal. Apparently *E. wokari* García, 2008 exhibits this morphological pattern, but in this case the transverse cristids are markedly more developed, as it is the case regarding hypoconid and entoconid size.

Haile-Selassie & Howell (2009) have described an m1 as a new species of *Eucyon*, *E. minimus*. This determination is mainly based on the small size of the m1, the only specimen found, which theoretically is smaller than the m1 known in other *Eucyon* species. Nevertheless, there is an m1 with the broken paraconid in Lemudong'o having practically the same size as the Ethiopian species so both molars are morphologically very close. Even if no internal cristids are noticeable either in the hypoconid or

the entoconid (in the m1 from Lemudong'o, they are very weak), the talonid is split into two parts as it is the case in the Lemudong'o tooth. Also as the m1 from Lemudong'o is associated to an M1 presenting size and morphology close to that of *E. intrepidus*, it is most likely that *E. minimus* and *E. intrepidus*, from the African late Miocene, might be classified as a single species. Moreover, the priority would belong to *E. intrepidus*.

Finally, it is noteworthy to compare these forms to *Eucyon* sp. from Langebaanweg (South Africa) which is finely represented by cranial and post-cranial material not yet described in detail. Thus, the cranium matches the *Eucyon*'s characters pointed out by Tedfor & Qiu (1996), lacking "vulpine-crease". The Langebaanweg form shows a larger size
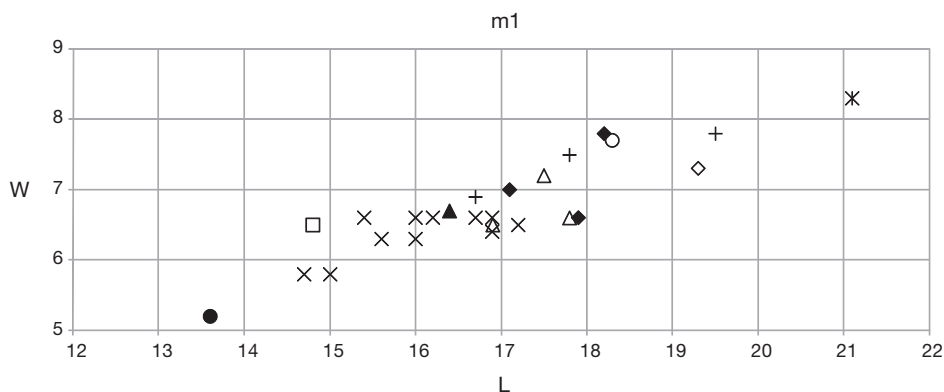
Fɪɢ. 7. — Bivariate plot of the m1 of different *Eucyon* Tedford & Qiu, 1996 species and *Canis cipio* Crusafont, 1950. Data, in part, from Crusafont (1950), Martin (1973), Rook (1992), Tedford & Qiu (1996), Morales *et al.* (2005), Spassov & Rook (2006) and Haile-Selasssie & Howell (2009). *Eucyon* sp. from Langebaanweg, dimension of the specimen PQ-L-31272, Iziko South African Museum, Cape Town. *Eucyon intrepidus* Morales, Pickford & Soria, 2005 = *E. minimus* Haile-Selassie & Howell, 2009. Abbreviations: **L**, length; **W**, width. ○, *E. adoxus* Martin, 1973; ✕, *C. cipio*; ✕, *E. debonisi* n. sp.; △, *E. davisi* (Merriam, 1911); ◆, *E. zhoui* Tedford & Qiu, 1996; □, *Eucyon* sp.; ●, *E. intrepidus*; +, *E. monticinensis* (Rook, 1992); ■, *E. wokari* García, 2008; ◇, *E. marinae* Spassov & Rook, 2006; ▲, *E. minor* (Teilhard de Chardin & Piveteau, 1930).

than that of *E. intrepidus* closely similar to that of *E. debonisi* n. sp. Interestingly, the width of the M1 is very much alike and even larger than the molars of *E. davisi* and *E. debonisi* n. sp. All the same, at least one of the M1 of *E. intrepidus* from Lukeino and the M1 from Lemudong'o are also very wide despite their smaller size. The P4 of Langebaanweg form is closely related to that of *E. debonisi* n. sp. due to the short development of the protocone. The m1 of *Eucyon* sp. from Langebaanweg lies close to the m1 from Lemudong'o and Ethiopia. Thus, the m1 of the SAM-PQ L31272 mandible exhibits a strong and elongated hypoconid clearly distinguished from the entoconid. Without doubt, such traits refer to the *E. debonisi* n. sp. form, but the South African form presents a very weak and somewhat obliquous buccal cristid in the ento-conid; even weaker than that of *E. intrepidus* from Lemudong'o. Nevertheless, despite its weakness, the talonid remains subdivided as it is the case in the *E. intrepidus* from Lemudong'o and in the *Eucyon minimus* from Ethiopia. This narrow and short distal valley is closed due to the presence of similar size hypoconulids and entoconulids.

In summary, we have found a rather similar pattern for these African *Eucyon*; however, there is evident variability, but in all the cases the talonid valley is split into two irregular parts. The same can be observed in *E. wokari*, but unlike this, the inner connection between the entoconid and the paraconid is very weak. Thus, *E. wokari* looks clearly linked to *Canis*, whereas the other African forms are more primitive as to their talonid morphology is con-cerned, however, they remain clearly distinguished from the typical morphology of Eurasian *Eucyon*. In any case, these remain fully differenciated from the morphology of the talonid of *Eucyon debonisi* n. sp. where the hypoconid and entoconid are located in the distal side, not allowing the development of a distal valley, regardless of its small size.

GENERAL DISCUSSION

The presence of Canidae in the Eurasian late Miocene has remained an utter rarity for a long time, leaving aside the controversial *Canis cipio* (Crusafont 1950) first discovered in the Concud site (Teruel, Spain) and later also found in Los Mansuetos, a site close to the former and nearly coetaneous (MN 12). *Canis cipio* is the largest by far of all the *Eucyon* species described up to now and this might be the reason why it is still considered controversial. A thorough research about these remains should be carried out,

however it is not the purpose of this study. Even though in a lesser way, Canidae remains from Venta del Moro, determined in the present study as *Eucyon debonisi* n. sp., have also been debatable. They had previously been classified as *Nyctereutes* aff. *donnezani* and *Canis* sp. (Morales & Aguirre 1976; Morales 1984), then, Rook (1992) classified them as *Canis* aff. *monticinensis*. Despite being Miocene, the Venta del Moro fauna, is clearly outstanding due to the presence of immigrants from various origins such as camels, hippopotami, bovini, *Agriotherium*, etc. (Pickford & Morales 1994; Made *et al.* 2006). Among these, *E. debonisi* n. sp. stands out as an immigrant from American origin whose age, as it is the case with some of the other mentioned taxa, is older than most of the similar species known in Eurasia. Very probably, this is due to the particularly rich geological record in Spain during the end of the Miocene. As we have already stated, *E. debonisi* n. sp. is closer to the Holarctic *Eucyon*, the only outstanding difference being its smaller size; although there are several features which might be considered primitive such as the relatively large size of the M2 compared to M1 and the tiny size of the accessory cuspids on the lower premolars. But as a matter of fact, this matches perfectly well the concept of *Eucyon* as a genus with primitive traits compared to *Canis*.

It would be thought-provoking to establish a direct link between *E. debonisi* n. sp. and African *Eucyon*, especially during such an exceptional time as the end of the Miocene when, as we mentioned above, plentiful of Eurasian immigrants are detected in Africa (Morales *et al.* 2005; Made *et al.* 2006). Without doubt, we need more evidence. Nevertheless, from the phylogenetic point of view, *E. debonisi* n. sp. might as well be the sister group of African eucyons. However, characters proving this relationship prove still scarce. On the other hand, the Mediterranean, even dried, might have acted as a tremendous barrier which limited direct connections between Africa and Mediterranean Europe. Most likely, the faunistic relationships between these two areas are easily understood in paleoclimatic terms related to temporal changes of the boundaries between biogeographical regions (Pickford & Morales 1994).

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