Musteloidea (Carnivora, Mammalia) from the Late Miocene of Venta del Moro (Valencia, Spain)

Musteloidea (Carnivora, Mammalia) del Mioceno Superior de Venta del Moro (Valencia, España)

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ABSTRACT

The purpose of the present work is to describe the Musteloidea from the Late Miocene locality of Venta del Moro (Valencia, Spain). We have identified the following species: *Martes ginsburgi* nov. sp., *Lutra affinis* Gervais, 1859, *Plesiogulo monspessulanus* Viret, 1939 and *Promephitis alexejewi* Schlosser, 1924. Besides *Plesiogulo monspessulanus* which was already described in this locality and in Las Casiones (MN 13, Teruel Basin), we are approaching an unedited Musteloidea assemblage from the Miocene of the Iberian Peninsula. The m1 of *Martes ginsburgi* nov. sp. is similar in size and morphology to the Asian species of the genus, *M. anderssoni* and *M. zdanskyi*, but it differs in having a very wide M1 with a developed lingual platform. The presence of *Lutra affinis* is the third register of this species in the fossil record, since it was only previously known from the Pliocene of Montpellier (France) and the terminal Miocene of Maramena (Greece). *Promephitis alexejewi* is the first appearance of this species in Europe, which has been only registered until now in several localities of Mongolia and China. It differs from the rest of *Promephitis* species in the possession of a narrower m1, with a very sectorial trigonid.

Keywords: Mammalia, Carnivora, Musteloidea, *Martes*, *Lutra*, *Plesiogulo*, *Promephitis*, Venta del Moro, Spain, Upper Miocene

RESUMEN

Se describen los Musteloidea procedentes del Mioceno terminal (MN13) de Venta del Moro (Valencia, España). Se han determinado los siguientes taxones: *Martes ginsburgi* nov. sp., *Lutra affinis* Gervais, 1859, *Plesiogulo monspessulanus* Viret, 1939 y *Promephitis alexejewi* Schlosser, 1924. Exceptuando a *P. monspessulanus*, que ya se ha citado también en la MN13 de Las Casiones (Teruel), se trata de una asociación inédita en el Mioceno de la Península Ibérica. *Martes ginsburgi* nov. sp. se asemeja en talla y morfología del m1 a las especies asiáticas del mismo género *M. anderssoni* y *M. zdanskyi*, pero se diferencia de ellas por la posesión del un M1 muy ancho, con una plataforma lingual muy desarrollada. La presencia de *Lutra affinis* supone la tercera cita de esta especie en el registro fósil, ya que sólo se conocía en el Plioceno de Montpellier (Francia) y en el Mioceno terminal de Maramena (Grecia). *Promephitis alexejewi* supone la primera cita para Europa de esta especie registrada hasta ahora sólo en dos yacimientos de Mongolia y China. Se diferencia del resto de especies afines por la posesión de un m1 más estrecho, con trigónido muy sectorial.

Palabras clave: Mammalia, Carnivora, Musteloidea, *Martes, Lutra, Plesiogulo, Promephitis,* Venta del Moro, España, Mioceno Superior

Introduction

Venta del Moro (province of Valencia, Spain) is one of the most interesting mammal localities of the Miocene in the Iberian Peninsula. The numerous campaigns of excavation undertaken since 1970 have not only provided a rich vertebrate assemblage, but also a good collection of inverte-

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brates and plants (Aguirre *et al.*, 1973; Morales & Aguirre, 1976; Morales, 1984; Montoya *et al.*, 2006). The mammal association dates the deposits in the Upper Turolian (MN13, M3), and age estimation obtained from paleomagnetic information places it around 5.8 m.y. (Opdyke *et al.* 1997), but more recently Dam et al (2006) have dated the M3 unit in 6.05 Ma.

The European continental mammal faunas of the western Mediterranean were characterized during the Late Miocene by the arrival of a considerable number of Asian and African immigrants. In the Iberian Peninsula, this dispersal event began with the M2-M3 local zones that correspond to the lower part of MN13 mammal biozone (Made *et al.*, 2006). This event is named the "second Messinian mammalian event (MME-2) " or the " *Paraethomys* event " by Agustí *et al.* (2006).

Besides the Musteliodea, the carnivore association of Venta del Moro also consists of the families Canidae (*Eucyon debonisi*), Ursidae (*Agriotherium roblesi*), Hyaenidae (*Thalassictis* aff. *hyaenoides*) and Felidae (*Felis* sp., *Fortunictis* sp., *Paramachaerodus maximiliani* and *Amphimachairodus giganteus*). More information about its mammal association can be found in Morales *et al.* (1980), Morales (1984), Pickford *et al.* (1993, 1995), Made & Morales (1999), Montoya *et al.* (2006; 2009), Pesquero *et al.* (2007) y Salesa *et al.* (2010).

In the rich collections obtained during the first years of excavations in the locality, between 1970 and 1980, very few fossils assignable to Musteloidea were recovered. Furthermore, in the first papers where the carnivores of Venta del Moro were studied, only an undetermined Mustelidae and an incomplete upper carnassial determined as *Plesiogulo monspessulanus* were described by Morales & Aguirre (1976) and Morales (1984).

In 1995, the locality was reopened and since then annual campaigns of excavation have been carried out. These campaigns have provided an important fossil collection among which are the fossils here studied (Montoya *et al.* 2006). With new fossils of *Plesiogulo*, other specimens of three taxa of Musteloidea were also recovered. The principal aims of this work are focused in the classification of these specimens.

The first abbreviation consists of the catalogue number of the Museu de Geologia de la Universitat de València. The second one is the field number.

MGUV: Museu de Geologia de la Universitat de València, Burjassot

MNCN: Museo Nacional de Ciencias Naturales, Madrid

Systematic Palaeontology

Order Carnivora Bowdich, 1821: 33
Superfamily Musteloidea Fischer de Waldheim, 1814: 372
Family Mustelidae Fischer de Waldheim, 1814: 372
Subfamily Mustelinae Fischer de Waldheim, 1814: 372
Genus *Martes* Pinel, 1792: 55

Martes ginsburgi nov. sp. (Fig. 1)

Type locality: Venta del Moro, Upper Miocene, Upper Turolian, MN13.

Holotype: MGUV-15857 VV-10983: left hemimandible fragment with p4-m1; MGUV-16128 VV-10998: right hemimandible fragment with p3-m1; MGUV-19616 VV-11759: cranial fragment with left P4-M1; MGUV-15856 VV-10974: left upper canine. Most likely associated elements might belong to the same individual. Stored in the Museu de Geologia de la Universitat de València (Burjassot, Spain).

Etymology: in memory of Dr Léonard Ginsburg.

Diagnosis: *Martes* with the same size of the extant *Martes martes* and *Martes foina*. P4 is robust with a very developed protocone. M1 narrow (antero-posterior length) and very broad (labial-lingual width), with much developed lingual platform and a reduced metacone. m1 shows a concave lingual wall and a convex labial wall, a broad talonid and a quite high and lingually expanded metaconid. p4 is short and high, with a well developed posterior cusp.

Studied material:

(*) MGUV-15856 VV-10974: left upper canine.
(*) MGUV-15857 VV-10983: fragment of left hemimandible with p4-m1.
(*) MGUV-16128 VV-10998: fragment of right hemimandible with p3-m1.
(*) MGUV-19616 VV-11759: cranial fragment with left P4-M1.
MGUV-19236 VV-12154: right M1.
MGUV-24321 VV-15333: fragment of left hemimandible with p4-m1.
(*): Associated elements, very probably belonging to the same individual.

Upper canine (VV-10974): Tooth of conical outline, with two edges: a gentle posterior one and a strong anterior-lingual edge, which turns in the base of the tooth into a weak posterior cingulum.

P4 (VV-11759): Compressed paracone and metastyle with continuous cristids, without any notch between them. The anterior cristid of the paracone is well defined and reaches an ante-
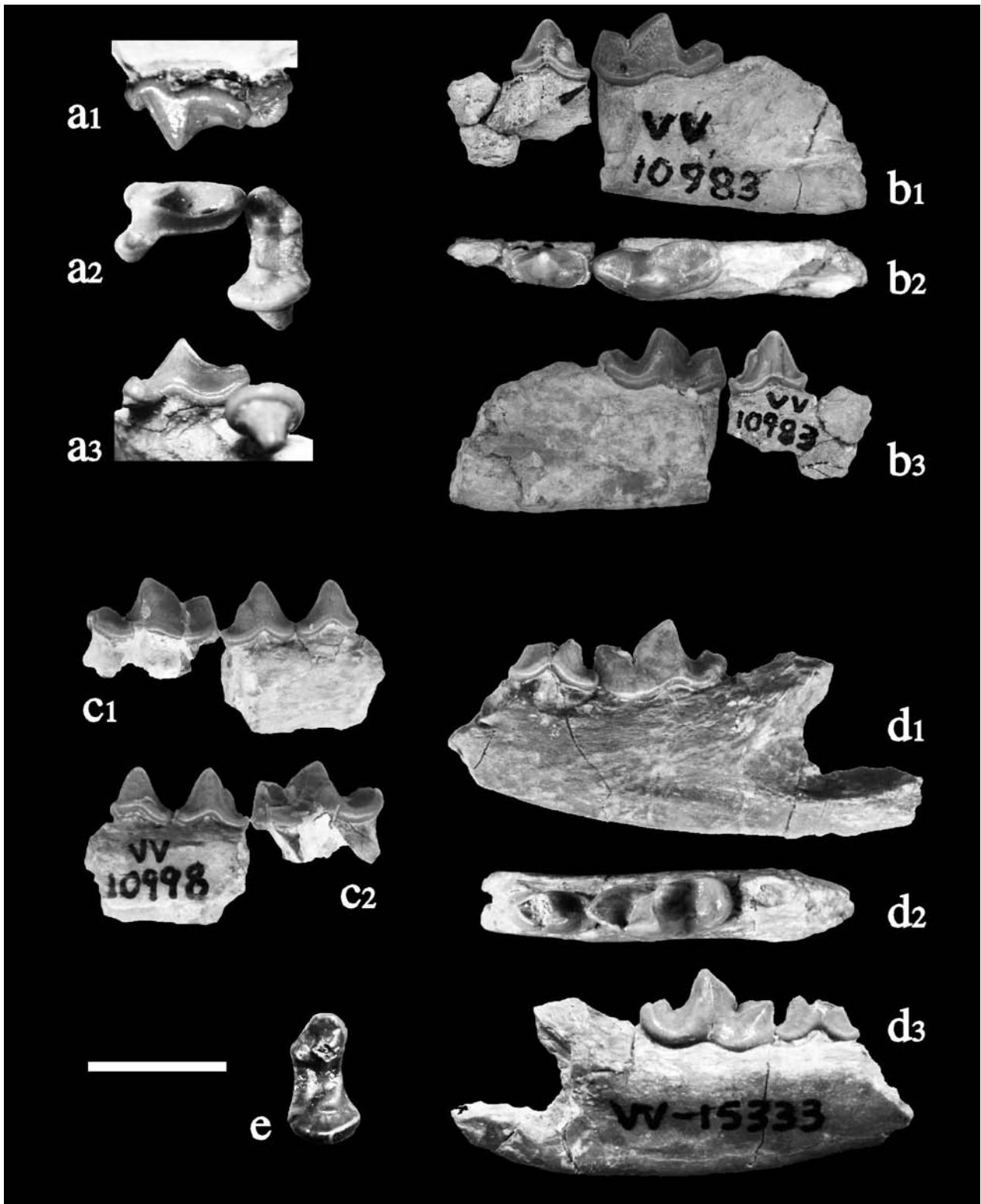
Fig. 1.—*Martes ginsburgi* nov. sp. from Venta del Moro (a to c, holotype); a, left P4-M1 (MGUV-19616 VV-11759); b, fragment of left mandible (MGUV-15857 VV-10983); c, fragment of right mandible (MGUV-19616 VV-11759); d, fragment of left mandible (MGUV-24321 VV-15333); e, right M1 (MGUV-19236 VV-12154); a1, b1 c1, d1, buccal views; a2, b2, d2, e, occlusal views; a3, b3, c2, d3, lingual views. Scale bar: 10 mm.

rior well-developed cingulum, similar to a small parastyle. A second very weak cristid, in anterior-lingual position, runs towards the base of the protocone. The protocone is dune-shaped, not very developed in size but very prominent and moved forward, with its anterior edge nearly at the same level as the anterior end of the tooth. There is a strong and continuous lingual cingulum and a very weak labial one.

M1 (VV-11759; VV-12154): Molar with a typical musteloid occlusal shape, with a narrower labial wall compared to the lingual one. The paracone is clearly larger than the metacone and has a well-developed stilar platform. The protocone shows a clear duniform shape, with a long and well-developed anterior cristid that extends towards the base of the paracone, and shows a small cusp towards the posterior edge. A great cingulum, with the shape of a striated platform, stands out in the lingual wall of the protocone. The specimen VV-12154 is somehow smaller and has smoother edges and reliefs, with a barely noticeable cingulum, whereas in the specimen VV-11759 the labial cingulum is well developed.

Hemimandible (VV-10983; VV-10998; VV-15333): p3 is smaller in length but nearly as high as p4. It does not show any accessory cusps, only two small protuberances or cingulum in the base of the anterior and posterior ends of the tooth. The p4 shows a well-developed anterior cristid that contacts the basal cingulum, which is stronger in the lingual wall. There is a high but not individualized accessory cusp in the posterior part of the premolar, and a small talonid with almost no relief.

The m1 is a long carnassial, in which both the paracone and the protocone are located in the same plane; the protoconid is clearly higher, especially in the specimen VV-15333. The metaconid is quite reduced, and attached to the protoconid but not exceeding its posterior edge. The posterior cristid of the metaconid extends throughout all the lingual edge of the talonid, almost like a cingulum, reaching the posterior edge of the tooth, where it touches the base of the hipoconid. In the base of the lingual side of the talonid there is a slight cingulum, clearly perceptible in the specimen VV-15333. In this last specimen, the hipoconid is conical and well individualised, with a weak anterior cristid. On the other hand, in VV-10983 the hipoconid shows a well-developed anterior cristid and a weak posterior cristid, which gives this cusp an elongated shape.

Discussion

The systematics of the genus *Martes* is especially complex, partly due to its ample fossil record. Thus, more than a dozen fossil species are represented in the European Miocene faunas (Ginsburg, 1999), from the Lower Miocene of Wintershoft-West, with *Martes laevidens* Dehm, 1950, to the Mio-Pliocene transition of Maramena with *Martes lefkonensis* Schmidt-Kittler, 1995. There is also a vast representation of this genus in the Asian and North American faunas (Teilhard de Chardin and Leroy, 1945; Andersson, 1970). Many of these fossil species were defined based on fragmentary and sometimes not very significant material; size being

one of the most frequent criteria for specific differentiation.

The association of lower and upper dentition of this mustelid in Venta del Moro, allows us to exclude the majority of the species defined in the genus *Martes*, especially those prior to the Upper Miocene. In these forms the lingual and labial wall is displayed in a rectilinear disposal in which the metaconid is quite close to the protoconid. In the species from Venta del Moro, and in the extant species of *Martes* (*Martes martes*, *Martes foina* and *Martes pennati*), the labial wall tends to be semicircular, and the lingual one concave and discontinuous, due to the lingual displacement of the metaconid base. As a consequence, all these species have a very typical occlusal morphology in the m1. There are other fossil forms with the same m1 morphology, as *Martes anderssoni* Schlosser, 1924 from the Latest Miocene/Earliest Pliocene of Ertemte (Inner Mongolia) and *Martes zdanskyi* Teilhard de Chardin and Leroy, 1945 from the Villafranquian of China. In addition, these two species possess a similar size in the m1 (Table 1).

Both *Martes melibulla* Petter, 1963 and *Martes basilii* Petter, 1964 belong to this morphologic group, though their size is somehow larger than these last species. Upper dentition is unknown in any of these two species so the comparisons are restricted to the lower dentition, which is morphologically more homogeneous than the upper one. *M. basilii* and *M. melibulla* differ slightly from the species of Venta del Moro in the most rectilinear lingual and labial profile of the walls of m1; additionally, *M. melibulla* seems to have a shorter talonid in the m1. *Martes lefkonensis* Schmidt-Kittler, 1995 may also belong to this group of species, but its size is somewhat smaller than that of Venta del Moro. Another group of Late Miocene species still retain the more conservative morphology in the m1, as it is the case of *Martes paleosinensis* Zdansky, 1926 and *Martes lydekkeri* Colbert, 1933, hence they can be easily distinguished from the Venta del Moro species.

The form of Venta del Moro resembles *Martes anderssoni* and *Martes zdanskyi*; However, it differs in the morphology of the M1 from the first species. According to Schlosser (1924), in *Martes anderssoni* "the short, but very broad M1 has a nearly trapezoidal outline, but its inner border is semicircular, whilst the anterior and posterior margin are parallel and nearly straight". The molar was figured by Schlosser (1924, Pl. 1, fig. 14), it adjusts perfect-

Table 1.—**Measurements (in mm) of the dentition of Musteloidea from Venta del Moro. L, length; W, width**

		C sup		P4		M1		p3		p4		m1		m2	
		L	W	L	W	L	W	L	W	L	W	L	W	L	W
Martes ginsburgi nov. sp.	VV-10974	4,5	3.2												
	VV-11759			8.9	5.7	5.4	8.3								
	VV-12154					4.5	8.1								
	VV-10983									5.8	2.9	9.6	4.0		
	VV-10998							4.9	2.5	5.7	2.8	10.5	4.0		
	VV-15333								6.6		3.0	9.8	4.1		
Lutra affinis	VV-2381							7.7	3.8						
	VV-10547											11.4	5.7		
Plesiogulo monspessulanus	ZV-215	25.0	—												
	VV-16615							12.1	9.0	16.2	10.6	33.6	12.0 c.a.		
Promephitis alexejewi	VV-14292			6.0 c.a.	—										
	VV-8477											10.4	4.3	3.1	3.7
	VV-12895							3.0	2.1			10.5	4.4	3.5	3.8
	VV-12896							3.1	2.0	3.3 c.a.	—				

ly to the aforementioned description, and highlights an important difference between the Asian and the Spanish forms. If the association of lower and upper dentition, proposed by Schlosser (1924) for *Martes anderssoni* is correct, the above-mentioned species might be closer to *M. paleosinensis* than western Europe forms here discussed, as Andersson (1970) already suggested.

The m1 of *Martes zdanskyi* Teilhard and Leroy, 1945 from the Villafranquian of China is also similar in size and morphology to the species from Venta del Moro. However, the morphology of its M1 is very close to the extant species of *Martes*, especially to *Martes martes*, as Teilhard de Chardin and Leroy (1945) indicated, and therefore different from the form of Venta del Moro. Definitively, the martes of Venta del Moro seems different enough from all the other species here discussed as to propose the specific name of *Martes ginsburgi* nov. sp.

As for the extant forms, the new species is quite similar to *Martes martes*, though it differs in the absence of the cristid in the posterior base of the metaconid of the m1 and in the more slender morphology of the M1. Morphologically *Martes* aff. *anderssoni* Petter, 1967 (= *Martes* aff. *andersoni*) from the Vallesian of Can Ponsich is quite close to *M. ginsburgi* nov. sp., especially concerning the occlusal shape of the m1 and M1. However, there are differences between both forms that must be annotated; the protocone of the M1 in *M.* aff.

anderssoni is more developed, almost semi-circular and contacts a small metaconule that is attached to the metacone. Whereas in *M. ginsburgi* nov. sp. there is no trace of a metaconule and the protocone is less extensive and remains much separated from the metacone. The m1 of *M.* aff. *anderssoni* possesses a less developed talonid than the m1 of *M. ginsburgi* nov. sp., so its lingual wall has a less concave occlusal profile and a more slender general aspect. Petter (1967) expressed the view that the form Can Ponsich was intermediate between *Martes munki* Roger, 1900 and *Martes anderssoni*, this could apply to the size, but morphologically both species are quite different.

Finally, in the Venta del Moro specimen VV-12154, a right M1 is smaller and morphologically slightly different from the M1 of the holotype of *Martes ginsburgi* nov. sp., but the information is insufficient to know whether it belongs to a different species or it may represent intraspecific variability.

Genus *Plesiogulo* Zdansky, 1924: 38

Plesiogulo monspessulanus **Viret, 1939** (Fig. 2)

Studied material:

MNCN ZV-215: left P4 with broken protocone.

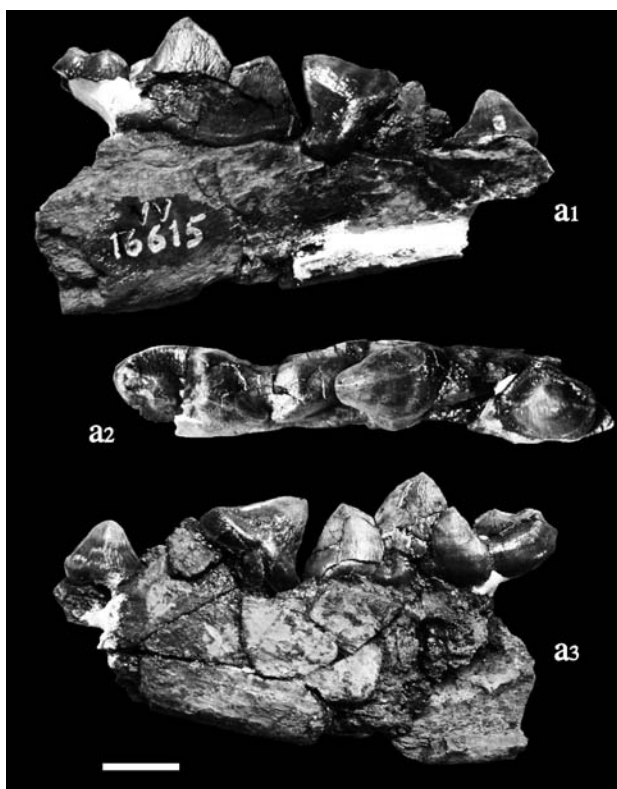MGUV-18608 VV-13331: part of the lingual wall of right M1.

Fig. 2.—*Plesiogulo monspessulanus* Viret, 1939 from Venta del Moro. Fragment of right mandible (MGUV-24585 VV-16615); a1, buccal view; a2, occlusal view; a3, lingual view. Scale bar: 10 mm.

MGUV-19233 VV-12431:Right I1 or I2.

MGUV-19626 VV-12424: P1 (?)

(*) MGUV-24585 VV-16615: right hemimandibule with p3-m1.

(*) MGUV-24586 VV-16905: right lower canine.

(*): Associated elements, probably belonging to the same individual.

I1 or I2 (VV-12431): The anterior wall is very high and the lingual cingulum is very developed.

P1 (?) (VV-12424): Small tooth, with only one root and a low and oval section, which shows an almost continuous crista.

P4 (ZV-215): This specimen is broken and has lost the protocone, and both the paracone and the metacone present a strong wear. It is a very robust tooth, with a short metacone. There is a well-marked lingual cingulum, along the base of the metacone, which disappears suddenly where the paracone meets the metacone, the precise spot where a soft invagination marking the beginning of the protocone is located. Though the protocone is broken, we can infer that it was small, very individualized, with only one root, and was placed right opposite the paracone. From this latter cusp two cristas arise, a very weak lingual one, which should have marked the anterior limit of the protocone, and an anterior one, slightly labial, fusing a basal anterior cingulum and becoming slightly more prominent at this point.

M1 (VV-13331): It consists only of the anterior half of the lingual wall. Only the musteloid morphology and its big size can be observed.

Lower canine (VV-16905): It is very badly preserved. We can only mention its robustness, the presence of two soft edges in anterior-lingual and posterior positions, and wrinkled enamel.

Hemimandible (VV-16615): We can say very little about the jawbone since it is completely broken and very badly preserved. The p3 is a robust and short tooth. The crown is of simple morphology, with only one cusp, but with a strong posterior-lingual expansion. It exhibits wrinkled enamel. The p4 is a massive tooth, with a minuscule paraconide and a highly reduced talonid. It is a robust tooth with only one cusp and hyenid-like morphology. It possesses strong labial and very soft lingual cingula. The anterior and posterior cristids are well developed.

The m1 is a robust carnassial, it has a low paraconid with an oblique anterior cristid, the posterior cristid is short and the lingual one is not very developed. The protoconid is higher than the paraconid, the metaconid is small and not projected backwards. The talonid is short, with a low and peripheral hipoconid, which encloses the central valley reaching the posterior cristid of the metaconid. No entoconid is individualized. A small cristid is placed between the anterior cristid of the hipoconid and the posterior base of the protoconid.

Discussion

The genus *Plesiogulo* groups species of large to very large size, with osteological and dental characteristics similar to the current wolverine, *Gulo gulo*, and with some species significantly exceeding its size. The earliest record of the genus comes from the Middle Miocene (MN6) Paçalar (Turkey) (Schmidt-Kittler, 1976). *Plesiogulo* had a wide distribution in Eurasia during the Late Miocene and Pliocene (see Rook *et al*., 1991), reaching Africa during the end of the Miocene (Haile-Selassie *et al*., 2004, Morales *et al*., 2005) and North America, which is one of the characteristic taxa of the Late Hemphillian (Harrison, 1981; Qiu, 2003).

The genus *Plesiogulo* was established by Zdansky (1924) for *Lutra brachygnathus* Schlosser (1903) from China. Viret (1939) created the species *P. monspessulanus* from the material from the Pliocene of Montpellier, characterized by a large size and relatively long and sharp m1, and a much reduced metaconid fused to the protoconid. Later, Teilhard de Chardin (1945) distinguished among the Chinese populations three different forms of *P. brachygnathus:* "*forme minor*", "*forme crassa*" and "*forme major*", primarily because of differences in size. Kurtén (1970) made a revision of the genus, and raised the *"formes"* of Theilhard through the

rank of species, *P. brachygnathus* remained valid and created the new species *P. praecocidens*. Hendey (1978) described the material from the lower Pliocene of Langebaanweg (South Africa) which he attributed to *P. monspessulanus*, and did not admit the validity of *P. major*, which he considered as a junior synonym *P. monspessulanus*. Harrison (1981) reviewed material of *Plesiogulo marshalli* from North America, and created the new species *P. lindsayi*, which is comparable in size to *P. monspessulanus*. Morales (1984) and Alcalá *et al.* (1994) quoted for the first time the presence of *P. monspessulanus* at two Upper Turolian Spanish localities, Venta del Moro and Las Casiones. Recently, Haile-Selassie *et al.* (2004) and Morales *et al.* (2005) have studied fossils of *Plesiogulo* in the Uppermost Miocene of Africa, coming in the first case from Lemudong'o, Kenya, and Middle Awash, Ethiopia, and in the second case, from the Lukeino formation, Kenya. Interestingly, both correspond to two different forms, one of great size, for which Haile-Selassie *et al.* (2004) created the new species *P. botori*, and another of the small size, identified by Morales *et al.* (2005) as *P. praecocidens*.

Plesiogulo has been registered in different localities from Eurasian Late Miocene and Pliocene, see for example Petter (1963), Koufos (1982), Rook *et al.* (1991), Sotnikov (1995) and Ginsburg (1999).

In the current state of knowledge, the large-sized forms of *Plesiogulo* are included in the species' *P. monspessulanus* (Eurasia and Africa), *P. lindsayi* (North America) and *P. botori* (Africa). According to Harrison (1981), *P. lindsayi* is characterized by the presence of a relatively wide m1, with a strong metaconid, unlike *P. monspessulanus*, whose m1 always shows a more elongated morphology and a very small or virtually absent metaconid. *P. botori* differs from these other two species in its larger size and slight morphological differences in both P4 and M1 (Haile-Selassie *et al.*, 2004).

The form from Venta del Moro is a quite large *Plesiogulo*. Morales (1984) already indicated that it is a slightly larger form than the specimens from South Africa; therefore, our material is placed even above the maximum values of P. *monspessulanus* (including *"P. major"*). This could suggest a relationship with *P. botori* from contemporary levels of Africa, considered by Haile-Selassie *et al.* (2004) as the largest species of the genus. Unfortunately, the fossils here studied do not allow a good morphological comparison with the African species, since only

its upper dentition is known and we have not yet recovered complete upper teeth from Venta del Moro. In addition, the clearly elongated morphology in the m1 here studied, with a very small metaconid are diagnostic characters of *P. monspessulanus*. Therefore, considering the absence of the upper dentition from our site, or the lower dentition of *P.botori*, we consider it more prudent to determine the *Plesiogulo* of Venta del Moro as *P. monspessulanus*, species already recorded in Spain from the upper Turolian of Las Casiones, Teruel (Alcalá *et al.*, 1994).

There have been several hypotheses on the degree of phylogenetic relationship between *Plesiogulo* and the extant *Gulo*. Kurtén (1970) in his revision of *Plesiogulo* considered this as the predecessor of *Gulo*, whereas Hendey (1978) rejected this possibility, due to geographic reasons and due to the different morphology of p2, which is single-rooted in *Plesiogulo* and double-rooted in *Gulo*. Other authors, such as Sotnikov (1995) also oppose to considering the family relationship. Ginsburg & Morales (1992) described the genus *Iberictis*, Lower Miocene (MN4) of Spain and France, whose upper dentition is very close to *Plesiogulo*. In the opinion of these authors, also expressed in Alcalá *et al.* (1994), extant *Gulo* and *Mellivora* must have originated from a line of Mellivorinae from the lower and middle Miocene, including genus *Laphictis* and *Ischyrictis*, which have a more conservative dentition morphology, while *Plesiogulo* would derive from *Iberictis* or other related form, forming a separate phylogenetic lineage, without extant representatives.

Subfamily Lutrinae Bonaparte, 1838: 111
Genus *Lutra* Brunnich, 1772: 34
***Lutra affinis* Gervais, 1859** (Fig. 3)

Studied material:

MGUV-15775 VV-2381: left p4.

MGUV-15855 VV-10547: fragment of right hemimandible with m1.

p4 (VV-2381): It is an elongated premolar with a strong development of the talonid. The posterior accessory cusp is very developed. A cingulum surrounds the base of the tooth, though it becomes very weak towards the middle of the lingual face and is especially strong in both posterior and anterior sides.

m1 (VV-10547): The talonid is very developed, broader and only slightly shorter than the trigonid. The cusps of the trigonid are arranged in a V-shape. The paraconid and the metaconid are similar in size, though the protoconid is higher. The talonid
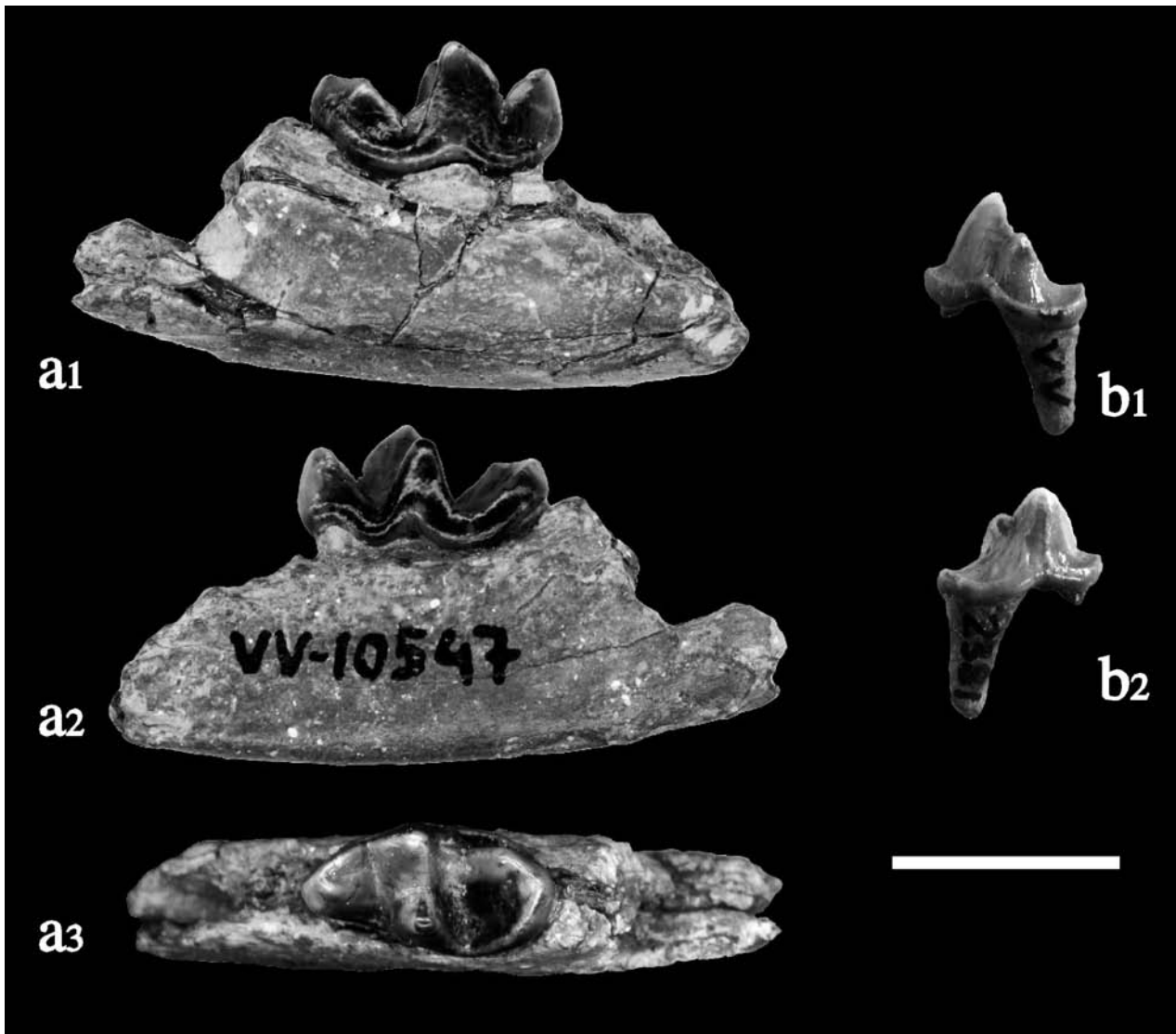
Fig. 3.—*Lutra affinis* Gervais, 1859 from Venta del Moro; a, fragment of right mandible (MGUV-15855 VV-10547); b, left p4 (MGUV-15775 VV-2381); a1, b1, buccal views; a2, b2, lingual views; a3, occlusal view. Scale bar: 10 mm.

presents a narrow and bevelled hipoconid, followed by a minuscule hipoconulid and a strong cristid that is directed towards the base of the metaconid. In lingual view, the valley of the talonid is similar in depth to the valley of the trigonid. A cingulum is developed only at the base of the labial wall of the tooth.

Discussion

The dentition of Venta del Moro attributed to *Lutra affinis* shows a very similar morphology to that of the extant *Lutra lutra*, though it is smaller and possesses certain morphologic differences. The m1 is a clearly narrower tooth, specially the talonid. In *L. lutra* the talonid expands lingually from the posterior end of the metaconid base and labially from the contact between the protoconid and the hipoconid. However, the labial edge in the molar of Venta del Moro shows a clear convex morphology. In *L. lutra* the base of the paraconid is surrounded by a cingulum, whereas in the otter of Venta del Moro this character is absent both in the lingual face and in the anterior end of the paraconid. Additionally, the p4 of the otter of Venta del Moro differs from that of *Lutra lutra* in being narrower, with a stronger basal cingulum, a more sharp-pointed

principal cusp and a much better defined posterior accessory cusp, which is also located in a more labial position.

Lutra affinis was described by Gervais (1959) in the locality of (Sables de) Montpellier. But the best information about this species comes from the locality of Maramena (Greece), in which Schmidt-Kittler (1995) attributed both a complete jaw and two isolated m2 to this species. The dentition of Venta del Moro is slightly greater than that of Maramena, but it can fit perfectly into its variability range. We do not find significant morphological differences between these two forms, therefore we assign the dentition of Venta del Moro to *Lutra affinis*.

Lutra libyca Stromer, 1913, from the Pliocene of Garet el Muluk, is relatively close to these forms in size, but it differs morphologically both from *L. affinis* and *L. lutra*. The p4 in this North African species possesses a less-individualised accessory cusp than *L. affinis*, but not so reduced as in *Lutra lutra*. Furthermore, a very clear difference is that the talonid of m1 is notably broader than the ones in *L. affinis* and *L. lutra*. Other otters of the Mio-Pliocene of Africa are highly different from this European species, as is the case of *Torolutra ougandensis*, or the different species attributed to *Syvaonyx* and to *Enhidriodon* (Stromer, 1935; Hendey, 1978; Petter Morales *et al.*, 2005).

Family Mephitidae Bonaparte, 1845: 1
Genus *Promephitis* Gaudry, 1861: 722
Promephitis alexejewi Schlosser, 1924 (Fig. 4)

Studied Material:

MGUV-15776 VV-8477: fragment of right hemimandible with m1-m2.

(*) MGUV-19234 VV-12895: fragment of left hemimandible with p3 y p4 (broken), m1-m2.

(*) MGUV-19235 VV-12896: fragment of right hemimandible with canine, p3, p4 (broken) and m1.

MGUV-19617 VV-14292: left M1 with broken paracone.

MGUV-24319 VV-15302: fragment of left m1 with broken metaconid and talonid.

(*): Associated elements, probably belonging to the same individual.

Mandible (VV-12895, VV-12896): Although it is quite poorly preserved, we can clearly observe that the tooth series is shortened, and although there are three premolars (p2-p4), all are quite reduced. The canine is preserved only in VV-12896 but in very poor condition, yet it shows that it was tall, robust and disproportionately large compared to the premolar row. The p2 is not preserved, but there is an alveolus in VV-12896 between the p3 and the base of the canine, tiny in size, almost imperceptible and uniradiculated. There is no diastema, which accentuates the shortening of the premolar row. The p3 and p4 are of small size, and are imbricated, as in the current species *Conepatus humboldtii*, although the form of Venta del Moro shows a greater reduction in p2. The mandibular branch is high and robust, with thickened symphyseal area, apparently in relation to the enormous size of the canine.

m1 (VV-8477, VV-12895, VV-12896): Elongated tooth with slightly longer trigonid compared to the talonid. The trigonid is compressed transversely with a relatively high and sharp protoconid, with a cutting posterior cristid. The paracone is sharp, with a vertical cristid, the posterior cristid runs towards the anterior cristid of the protoconid, and no clear separation between both is perceptible, although the notch is still visible labially. The metaconid is small and sharp, and is slightly located posteriorly, well individualized, and deeply separated from the protoconid so that the posterior wall of trigonid has a deep vertical groove. The talonid is slightly wider than the trigonid and has a long and deep valley. The hypoconid is high and shows an anterior cristid, followed by the posterior cristid of the protoconid, and a well-marked posterior cristid that runs through the back edge of the tooth. In this cristid a small hypoconulid shows individualized in a posterolabial position. We can also observe an entoconid, smaller in size than the hypoconid, at the lingual edge of the talonid. In the specimen VV-8477 the entoconid is preceded by two additional smaller cusps, well distinct, which are located between the entoconid and the base of the metaconid. In contrast, in VV-12895 only an additional cusp can be observed anterior to the entoconid.

m2 (VV-8477, VV-12895): little can be said about the morphology of this tooth, due to poor preservation of the available specimen. It has a roughly circular contour, which shows a deep valley surrounded by poorly differentiated rounded cusps.

M1 (VV-14292): partially broken tooth. Neither the paracone nor the anterior stylar area are preserved. It shows a strong protocone with a curved semicircular shape and a postprotocristid extending towards the posterior edge of the tooth, where it contacts the base of the metacone. The metacone is robust though less developed than the protocone and shows no signs of metastyle or metaconules. The posterolingual talon is very strong and wide. The posterior edge of the tooth has a developed concavity situated between the posterior ends of the metacone and the talon. Besides the mentioned talon no cingula are distinguishable.

Discussion

Promephitis represents the most widespread Old World genus of skunks, it has been registered since the Upper Miocene in Europe and West Asia, extended to the Pliocene in East Asia (He & Wang, 1991, Wang & Qiu, 2004). A revision of the systematics of the genus was published by Wang & Qiu (2004); according to these authors the dentition of the different species shows a great morphological similarity greatly hampering distinction between
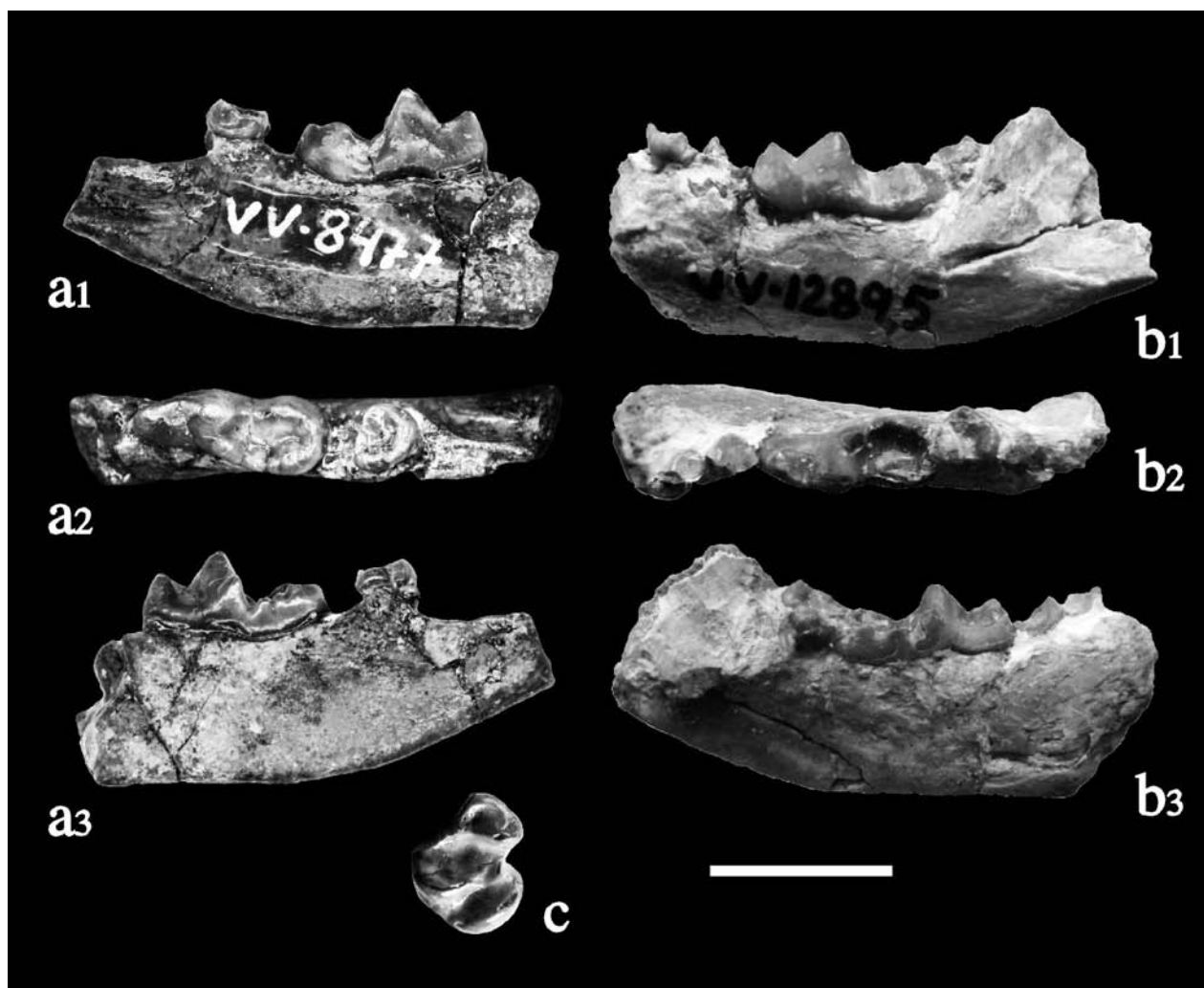
Fig. 4.—*Promephitis alexejewi* Schlosser, 1924 from Venta del Moro; a, fragment of right mandible (MGUV-15776 VV-8477); b, fragment of left mandible (MGUV-19234 VV-12895); c, left M1 (MGUV-19617 VV-14292); a1, b1, buccal views; a2, b2, c, occlusal views; a3, b3, lingual views. Scale bar: 10 mm.

them. Moreover, with few exceptions, the size of the dentition is included in a very limited range of variability. In fact, size range of the m1 of *Promephitis hootoni* (sensu Wang & Qiu, 2004) covers practically most of the identified species of the genus, this is at least true for *P. majori*, *P. quinensis*, *P. larteti*, the type of *P. hootoni* and *P. brevirostris*; and although there is no m1 to compare, *P. pritinidens* may also be included into the same size range. The exceptions are *P. parvus* somewhat smaller and *P. maxima* significantly larger.

Other two species fall outside the range occupied by *P. hootoni*, one is *P. maeotica* Alexejew, 1916 from the Turolian of Novo-Elisavetovka (Ukraine) only slightly greater than the maximum specimens

of *P. hootoni*. The second is *P. alexejewi* Schlosser, 1924 from the Late Turolian of Mongolia, somewhat larger than *P. maeotica*. Both species have been registered in other Chinese sites, *Promephitis cf. maeotica* by Zdansky (1937) from the Turolian of Shansi, that Wang & Qiu (2004) considered as a synonym of *P. hootoni;* and *Promephitis cf. alexejewi* from the Pliocene of Yushe Teilhard de Chardin & Leroy (1945), identification more or less accepted by Wang & Qiu (2004) as *P.* "*alexejewi*".

The differences between *P. maeotica* and *P. alexejewi* are scarce. Thus, Wang & Qiu (2004) suggested that the m1 of *Promephitis maeotica* is disproportionately wide. However, this view is not justified considering the size of the different species and
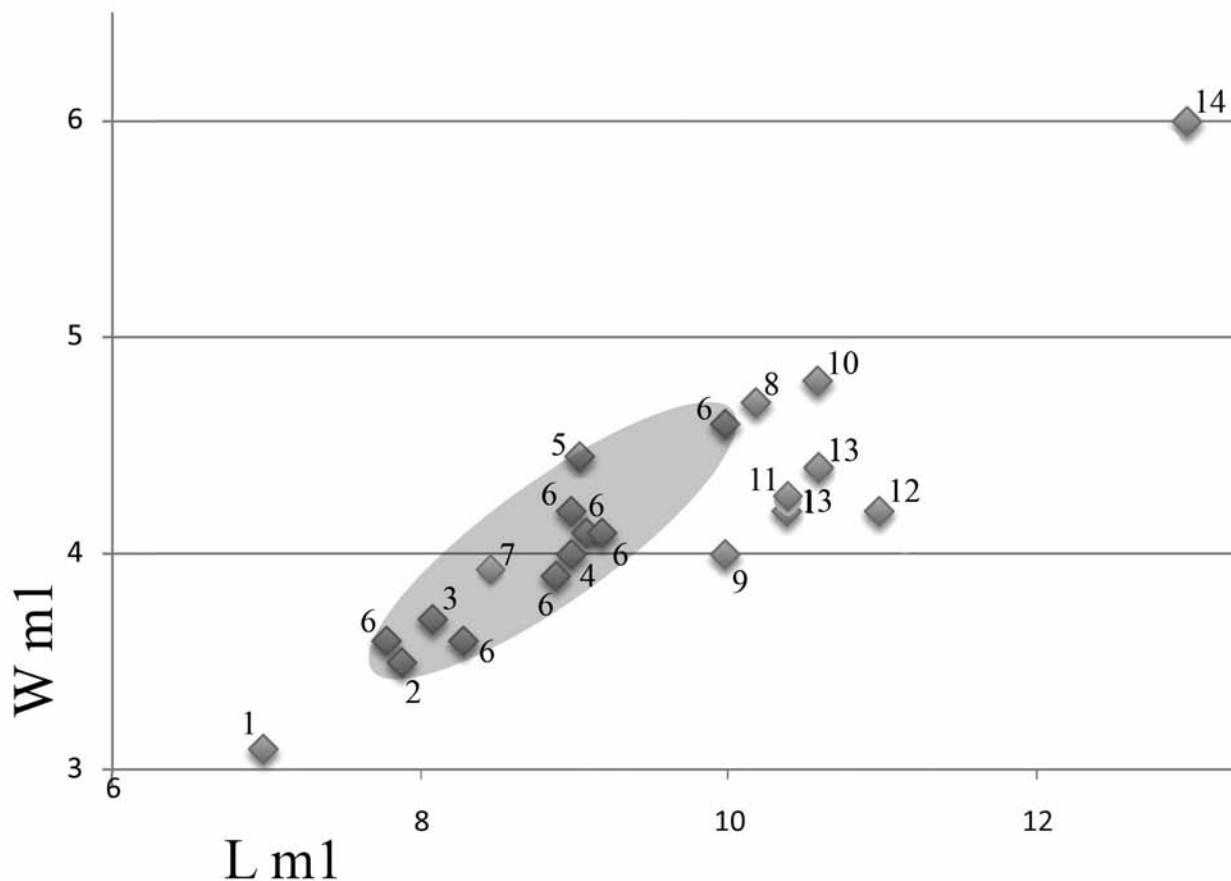
Fig. 5.—Length/width plot of the lower carnassial of *Promephitis*. 1.- *Promephitis parvus* Wang & Qiu (2004) from Dongxiang Formation (China). 2.- *Promephitis majori* Pilgrim (1933) from Samos (Grecia). 3.- *Promephitis qinensis* Wang & Qiu (2004) from Wangdaifuliang (China). 4.- *Promephitis brevirostris* Meladze (1967) from Bazalethi (Georgia). 5.- *Promephitis hootoni* Senyurek (1954) from Küçükyozgat (Turquía). 6.- *Promephitis hootoni* (several Chinese localities, see Wang & Qiu, 2004). 7. *Promephitis hootoni* from Akkasdagi, Turquía (De Bonis, 2005). 8.- Alexejew (1916) from Novo Elisavetovka, Odessa (Ukrania). 9.- *Promephitis* cf. *maeotica* from Yang-Mu-Kou (locality 49, Zdansky 1937). 10.- *Promephitis alexejewi* Schlosser (1924) from Ertemte, Inner Mongolia (China). 11.- *Promephitis alexejewi* from Ertemte (Additional m1 in Wang & Qiu, 2004). 12.- *Promephistis* cf. *alexejewi* from Yushê, China (in Teilhard de Chardin & Leroy, 1945). 13.- *Promephistis alexejewi* from Venta del Moro (Spain). 14 *Promephitis máxima* He & Huang (1991) from Jiangsu (China).

most likely this is a mistake. Likewise, these authors also note that the M1 of *P. maeotica* and *P. alexejewi* differ in size and proportions, especially in the transverse width (9.1 mm vs. 7.6),which makes it impossible to consider them as a single species. In addition, Wang & Qiu (2004) also suggested that the specimens attributed to *P. alexejewi* cannot belong to the same individual and, therefore, the possibility that they may belong to different species should be pondered. However, the proportions of the M1 of *P. maeotica* and *P. alexejewi*, examined from the figures of Alexejew (1916, fig. 2) and Schlosser (1924, fig. 31) show no significant differences and perhaps these differences in width between these two species might be more appropri-

ately considered a measurement error, or simply intraspecific variability. Moreover, Wang & Qiu (2004) have pointed out that "Recent screen washing yielded an additional m1, measuring 10.4 x 4.2 mm, from the type locality of *P. alexejewi*" this new molar has almost the same dimensions as the molars from Venta del Moro. Therefore, the material here studied and the new specimen of the type locality of *P.alexejewi*, along with *P. cf. alexejewi* and *P. cf. maeotica*, could constitute a relatively homogeneous group (characterized by less width of the lower carnassial, with a more sectorial trigonid) which could be defined as *Promephitis alexejewi* Schlosser, 1924. However, the m1 of *P. alexejewi* is slightly wider than the other forms of the group,

and a new review of the material described by Schlosser (1924) would be desirable. A second candidate to determine the forms of this group could be *P. maeotica*, whose morphological differences with *P. alexejewi* have already been mentioned. However, *P. maeotica* is also very close to *P. hootoni*, both sharing the same geographical area and being very close in age.

Conclusions

The musteloidea association of Venta del Moro, although with a limited diversity range, is quite new for the Spanish Turolian. *Lutra affinis* is registered for the first time in Spain, a species defined in the sands of Montpellier, also recognized in the Greek site of Maramena (Schmidt-Kittler, 1995). Fossil otters have been known in Spain since the Middle Turolian of Teruel basin, but only with species attributed to *Sivaonyx* (Alcalá, 1994, Morales *et al.*, 2005). *Plesiogulo monspessulanus* is the only one of the species described here which was already known in the locality of Venta del Moro, as it was also registered in Las Casiones site from the Late Turolian of Teruel Basin. The genus underwent a major radiation during the Late Miocene and early Pliocene, recorded throughout Eurasia, Africa and North America. Skunks were very well diversified in the Vallés-Penedés basin during the Vallesian (Petter, 1963, 1967), but they were certainly rare in the Turolian. In fact, besides the group now determined as *Promephitis alexejewi* in Venta del Moro, the only skunk previosly determined from the Spanish Turolian was in the locality of Crevillente 2 (Lower Turolian), classified as *Promephitis sp.* by Montoya (1994). Finally, the genus *Martes*, has been represented in the Spanish faunas since the Lower Miocene, and as was the case in other areas they were quite rare during the Turolian, in fact *Martes basilii* Petter (1964) was the only certain form determined to specific level. *Martes ginsburgi*, the new species, is so far the only occurrence of this genus from the Late Turolian of Spain. Certainly, some kind of taphonomic or environmental problems existed for the family Mustelidae in these Turolian faunas, in view of the scarce fossil record, likewise, this trend showed signs of great increase during the Pliocene, so with some rare exceptions, almost the entire family is missing (Fraile *et al.*, 1997).

Except in the case of *Plesiogulo monspessulanus* already registered in Las Casiones (Alcalá *et al.*,

1994), which belongs to the M2 zone of the MN13 (see Van Dam, 1997), the entry of the other three forms recorded in Venta del Moro may well be linked to the important dispersal event occurred during the transit between van Dam's M2 and M3 zones (see Made *et al.*, 2006), called "second Messinian mammalian event (MME-2)" or "Paraethomys event» by Agustí *et al.* (2006).

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