



Systematic palaeontology (vertebrate palaeontology)

A new species of *Deinsdorfia* (Soricidae, Insectivora, Mammalia) from the Pliocene of Spain

Marc Furió^{a,*}, Pierre Mein^b

^a Institut Català de Paleontologia, Universitat Autònoma de Barcelona, c/Escola Industrial 23, Sabadell 08201, Barcelona, Spain

^b Laboratoire de paléoenvironnements et paléobiosphère, université Claude-Bernard (Lyon-1), 2, rue Dubois, 69622 Villeurbanne cedex, France

Received 14 March 2008; accepted after revision 21 May 2008

Available online 10 July 2008

Presented by Philippe Taquet

Abstract

A new species of *Deinsdorfia* is defined using new material coming from the karstic fissure infilling of Almenara-Casablanca 4 (Castelló, Spain), which shows important differences with the rest of the previously known species of the genus. The definition of a new species is supported by the characters found in extra material coming from the localities of Valdeganga, in the Albacete Province (Spain). The stratigraphical occurrence of this genus of pigmented-toothed shrews reinforces the idea of the Iberian Peninsula as a sink area during the Pliocene, where some Central-European soricids expanded their distribution. Most of those migrations or distributional expansions coincide with moments of climatic changes in the northern hemisphere. **To cite this article: M. Furió, P. Mein, C. R. Palevol 7 (2008).**

© 2008 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

Résumé

Une nouvelle espèce de *Deinsdorfia* (Soricidae, Insectivora, Mammalia) du Pliocène d'Espagne. Une nouvelle espèce de *Deinsdorfia* est créée pour le matériel provenant du remplissage karstique d'Almenara-Casablanca 4 (Castelló, Espagne), montrant des différences significatives avec les autres espèces connues de ce genre. Un matériel complémentaire provient de divers sites de Valdeganga (Albacete, Espagne). Cette nouvelle espèce de musaraigne à dents colorées du Pliocène supérieur confirme le rôle de refuge de la péninsule Ibérique lors des phases de migration ou d'expansion territoriale des Soricidae européens, liées à des variations climatiques. **Pour citer cet article : M. Furió, P. Mein, C. R. Palevol 7 (2008).**

© 2008 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

Keywords: *Deinsdorfia doukasi* nov. sp.; Spain; Almenara-Casablanca; Valdeganga; Pliocene glaciation

Mots clés : *Deinsdorfia doukasi* nov. sp.; Espagne; Almenara-Casablanca; Valdeganga; Glaciation Pliocène

* Corresponding author.

E-mail address: marc.furio@icp.cat (M. Furió).

1. Introduction

During the Pliocene, the global gradual cooling trend was interrupted several times by climatic optima and glaciations peaks, thus precluding the regular Later Pleistocene icing pulses [17]. Such climatological changes had consequences on the terrestrial ecosystems of the northern hemisphere, causing some biogeographical changes and faunal turnovers in the European lands. Due to their requirements of feeding supply and their high metabolic rates, the subfamily Soricinae (i.e. the red-toothed shrews) was one of the most affected groups of mammals. Some studies on different genera suggest that they modified their geographical ranges during this period driven by the derived major shifts on the environments [20,21,23,29]. Good evaluation of the palaeobiogeography of the Soricinae can potentially provide essential clues to approach some palaeoenvironmental parameters. However, the models based on this group of micromammals are of difficult construction because shrews are usually scarce within the vertebrate fossil assemblages, and most of the finds correspond to isolated dental elements, making it difficult to identify the taxon for non-specialized palaeontologists. Consequently, several faunal lists of Pliocene fossil sites refer to them as Soricinae indet. or, in worst cases, as *Sorex* sp., assuming that the subfamily was strictly represented by the most frequent genus of red-toothed shrews nowadays. It is noteworthy that imprecise taxonomical identifications can easily lead to wrong conclusions on the real diversity and biogeography of the soricines during the Pliocene.

This problem strongly concerns the shrews of the extinct genus *Deinsdorfia*, because their isolated teeth can be easily misidentified as belonging to *Sorex*. Not by chance, these genera are included in the same tribe (the Soricini), and consequently both share important characters as expected for close relative taxa. In fact, most of the *Deinsdorfia* finds were formerly identified as *Sorex*, due to the absence of a solid taxonomical framework on European fossil shrews until the 1980s decade. The evolution of general knowledge on this genus, and how it has been changing since it was originally described, is a good demonstration that problems on taxonomy and nomenclature can have important effects in other palaeontological fields. Actually, the history of the nomenclature related with *Deinsdorfia* was somewhat complex, and it influenced not only the concept, but also the number of species and the consequent vision of their geographical distribution along the geological time.

The first description of a species of the genus was made by Heller [9], who defined '*Sorex*' *fallax* from the Early Pliocene site of Gundersheim (Germany). Almost three decades later, Sulimski [28] described the species '*Sorex*' *hibbardi* from the Polish site of Weze, without noticing any kind of relationship with the material from Gundersheim. One year later, Heller [10] defined *Deinsdorfia franconica*, a new genus and species, based on a toothless right mandible from the Early Pleistocene site of Deinsdorf (Germany). Based on the drawing of the posterior view of the condyles in this latter work, Fejfar [6] pointed out that this species should be included into the tribe Soricini. However, Repenning [19] referred to *D. franconica* as *Neomyini incertae sedis*, while '*Sorex*' *hibbardi* was ascribed to the Soricini, also as *incertae sedis*.

The taxonomy of '*Sorex*' *hibbardi* was revised ten years later, when Jammot [13] included the species in the genus *Parapetenya*. This new genus was created to allocate two more species, '*Sorex*' *kretzoi* and '*Blarinella*' *kormosi*. Both species, as well as '*S.*' *hibbardi*, had been previously considered to be of difficult ascription [19], and some reservations existed on their tribal assignation. Jammot was of the opinion that the creation of the genus *Deinsdorfia* was abusive given the absence of an original diagnosis, and he synonymized *D. franconica* with '*Sorex*' *hibbardi*. It is to be noted that Jammot was the first who noticed the similarity between the toothless mandible described by Heller in 1963 [10] and the fossil remains of '*Sorex*' *hibbardi* described by Sulimski [28].

The taxonomical position of the species was again subject of discussion in 1984, when Reumer [20] established the most widely accepted classification of European fossil soricids to date. Reumer did not mention the work of Jammot, and so his proposals were developed absolutely independently. This led to two important changes. On the one hand, the three species previously included in the genus *Parapetenya* by Jammot [13] were ascribed to three different genera: *Sulimskia kretzoi*, *Zelceina kormosi*, and *Deinsdorfia hibbardi*. *Sulimskia* was so different from the other two that it was even included in a distinct tribe, the Blarinini. On the other hand, Reumer [20] did not consider *Deinsdorfia* as an invalid genus, but he included the species '*Sorex*' *hibbardi* created by Sulimski [28] in it. Despite of being replaced with its corresponding senior synonym (i.e. *D. hibbardi*), *D. franconica* stayed as the type species of the genus *Deinsdorfia*, in good following of the ICZN (see article 67.1.2 of the current version).

After solving those systematic problems concerning synonymy and taxonomy, Reumer [20] also named two

new species for the genus, *D. kordosi* and *D. janossyi*. Reumer was not only meritorious of having fixed the exact criteria to recognize the genus, but also of having discriminated different species within it. From then onwards, all other authors joined his vision and some of them found evidences to discriminate new representatives within the genus. Thus, Rzebik-Kowalska [22] described two new species on the basis of some Polish remains, *D. reumeri* and *D. insperata*. A new species, *D. kerkhoffi*, was also defined by Reumer in Doukas et al. [5], based on the material found in the Mio-Pliocene Greek locality of Maramena. Finally, in a last contribution to the knowledge of the genus, Dahlmann and Storch [4] re-examined the original material of '*Sorex*' *fallax*, establishing that the species should actually be included in *Deinsdorfia*.

It is noteworthy that the prolonged uncertainty on the taxonomy of *Deinsdorfia* resulted in considering it as a monospecific genus for a long time, because most of the '*Deinsdorfia*-like' finds were identified as the species '*hibbardi*'. Among other examples, this was the case of Spain, where the scarce findings of this genus did not permit the recognition of any significant difference to describe a new species. Consequently, the specimens recovered at that time were automatically assigned to the single species of the genus. However, new findings from the karstic infilling of Almenara-Casablanca 4 (MN 16, Late Pliocene) demonstrate that the Spanish material of *Deinsdorfia* was different from all the previously known species of the genus elsewhere. Reevaluation and comparison of the material from the Valdeganga section, quoted as *Parapetenya hibbardi* in Mein et al. [15], support this vision.

2. Material and methods

2.1. Measures and description

The dental and the mandibular elements were described and measured following the nomenclature and methods detailed in Reumer [20]. Measures of the material from Almenara-Casablanca 4 were taken using a Nikon Measuroscope 10 optic calliper connected to a digital monitor Nikon SC-112. The material from Valdeganga 2 and 3 was measured using a Microscope Leitz Ortholux with a platinum ultrapack.

2.2. Storage of the material

The holotype and the paratypes of *Deinsdorfia doukasi* nov. sp. are stored at the Institut Català de Paleontologia (Sabadell, Barcelona, Spain). The rest of

the material from Almenara-Casablanca 4 is stored at the Museo de Geología de la Universidad de Valencia (Valencia, Spain). The material from Valdeganga 2 and 3 belongs to the collection of the second author, and it is physically kept at 'Université Claude-Bernard Lyon-1' (Lyon, France).

2.3. Geological and geographical setting

Almenara-Casablanca 4 (Castelló province, eastern coast of Spain) corresponds to a karstic fissure infilling at 40 m above sea level (lat. 39.755°N; long. 0.199°W). Valdeganga 2 and 3 (Albacete province, Spain) correspond to lignitic-marl levels in a section mainly dominated by lacustrine limestones placed at about 670 m above sea level (lat. 39.142°N; long. 1.675°W).

3. Systematic palaeontology

Order Soricomorpha Gregory, 1910

Family Soricidae Fischer von Waldheim, 1817

Subfamily Soricinae Fischer von Waldheim, 1817

Tribe Soricini Fischer von Waldheim, 1817

Genus *Deinsdorfia* Heller, 1963

Deinsdorfia doukasi nov. sp. (Figs. 1–3 and Tables 1–3)

Derivatio nominis: in honour of Prof. Constantin S. Doukas (Univ. Athens), who has been dedicating his entire professional career to the study of fossil insectivores.

Holotype: (Fig. 1) 1 right hemimandible with complete dentition (IPS-5951).

Paratypes: (Fig. 2) 1 left I1 (IPS-43685), 1 left P4 (IPS-43680), 1 right M1 (IPS-43681), 1 left M2 (IPS-43682), 1 left i1 (IPS-43683), 1 right m2 (IPS-43684), 1 left m3 (IPS-43686).

Type locality: Almenara-Casablanca 4 (Castelló, Spain).

Extra material referred: 2 right i1, 1 fragment of left i1, 1 fragment of right m2, 1 right I1, 2 left I1, 1 right M1, 2 right M2 (1 fragmented).

Geological age: Late Pliocene (Early Villafranchian), MN 16.

Other studied localities:

Valdeganga 2 (Albacete, Spain; Late Pliocene, Early Villafranchian, MN 16 [2]).

Referred material: Collection P. Mein, 'Université Claude-Bernard Lyon-1'.

1 broken right i1, 1 right a1, 3 left m1 (+ 1 broken), 2 right m1 (+ 2 broken), 2 left m2, 2 right m2, 4 left m3, 2 right m3, 1 broken left I1, 1 right A1, 1 right P4

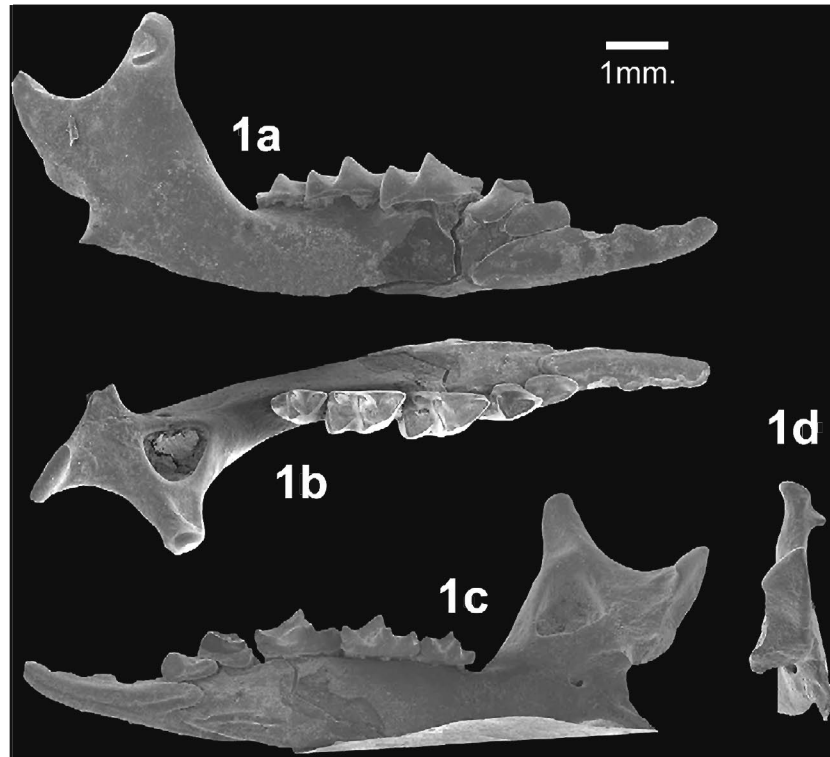


Fig. 1. Holotype of *Deinsdorfia doukasi* nov. sp. from Almenara-Casablanca 4. 1, IPS-5951, right hemimandible with the complete dental row (a, labial view; b, occlusal/dorsal view; c, lingual view; d, posterior view).

Holotype de Deinsdorfia doukasi nov. sp. d'Almenara-Casablanca 4. 1, IPS-5951, hémimandibule droite avec rangée dentaire complète (a, vue labiale; b, vue occlusale/dorsale; c, vue linguale; d, vue postérieure).

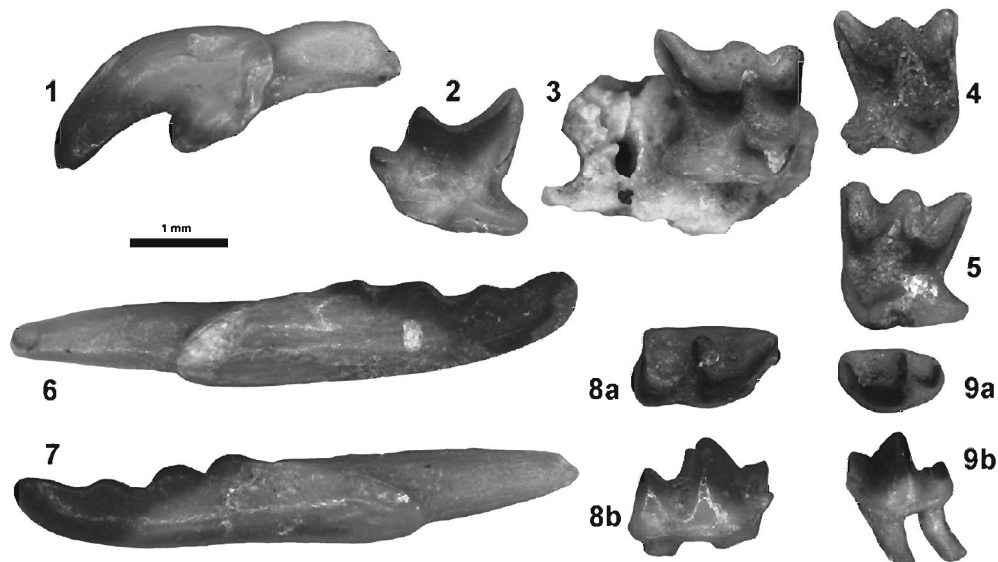


Fig. 2. Dental elements of *Deinsdorfia doukasi* nov. sp. from Almenara-Casablanca 4. 1, IPS-43685 (paratype), left I1; 2, IPS-43680 (paratype), left P4; 3, IPS-43681 (paratype), right M1; 4, ACB4-375, right M2; 5, IPS-43682 (paratype), left M2; 6, ACB4-379, right i1; 7, IPS-43683 (paratype), left i1; 8, IPS-43684 (paratype), right m2 (a, occlusal view, b, labial view); 9, IPS-43686 (paratype), left m3 (a, occlusal view; b, labial view).

Dentition de Deinsdorfia doukasi nov. sp. d'Almenara-Casablanca 4. 1, IPS-43685 (paratype), I1 gauche; 2, IPS-43680 (paratype), P4 gauche; 3, IPS-43681 (paratype), M1 droite; 4, ACB4-375, M2 droite; 5, IPS-43682 (paratype), M2 gauche; 6, ACB4-379, i1 droite; 7, IPS-43683 (paratype), i1 gauche; 8, IPS-43684 (paratype), m2 droite (a, vue occlusale; b, vue labiale); 9, IPS-43686 (paratype), m3 gauche (a, vue occlusale; b, vue labiale).

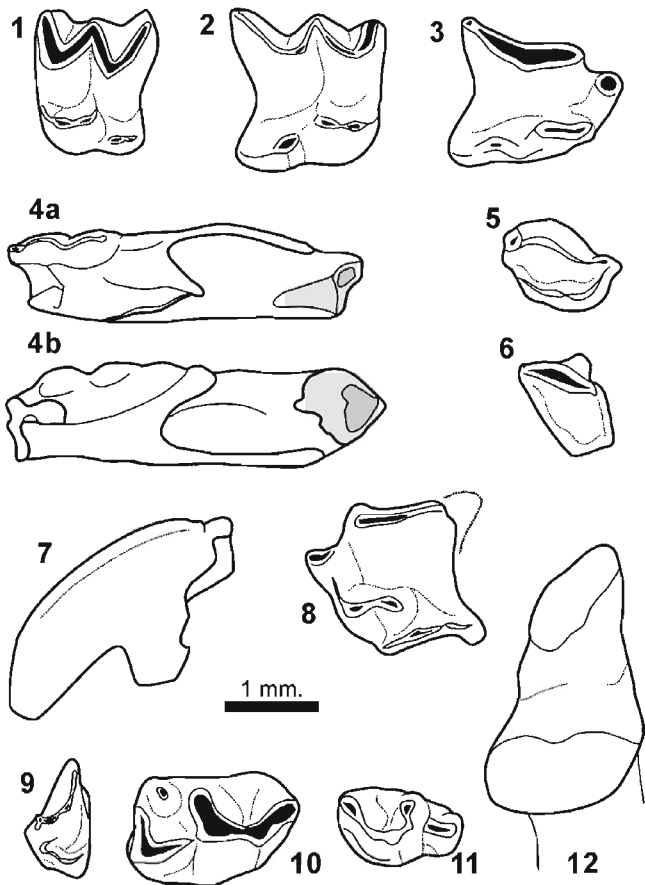


Fig. 3. Dental elements of *Deinsdorfia doukasi* nov. sp. from Valdeganga 2 (1 to 6) and Valdeganga 3 (7 to 11). 1, FSL-66209, left M2; 2, FSL-66208, right M1; 3, FSL-66207, right P4; 4, FSL-66212, broken right i1; 5, FSL-66211, left A1; 6, FSL-66214, left a1?; 7, FSL-66216, broken left I1; 8, FSL-66217, broken left P4; 9, FSL-66218, right M3; 10, FSL-66219, right m1; 11, FSL-66220, left m3; 12, FSL-66221, right mandibular condyle in posterior view.

Dentition de Deinsdorfia doukasi nov. sp. de Valdeganga 2 (de 1 à 6) et Valdeganga 3 (de 7 à 11). 1, FSL-66209, M2 gauche; 2, FSL-66208, M1 droit; 3, FSL-66207, P4 droite; 4, FSL-66212, i1 droite cassée; 5, FSL-66211, A1 gauche; 6, FSL-66214, a1? gauche; 7, FSL-66216, I1 gauche cassée; 8, FSL-66217, P4 gauche cassée; 9, FSL-66218, M3 droite; 10, FSL-66219, m1 droite; 11, FSL-66220, m3 gauche; 12, FSL-66221, condyle mandibulaire droit en vue postérieure.

(+ 1 broken), 2 broken left P4, 1 left M1, 1 right M1 (+ 3 broken), 1 left M2, 1 right M2.

Valdeganga 3 (Albacete, Spain; Late Pliocene, Late Villafranchian, MN 17 [2]).

Referred material: (Collection P. Mein, Université Claude-Bernard Lyon-1).

1 right hemimandible broken (missing all teeth), 1 left broken i1, 1 right broken i1, 1 left a1?, 1 left p4, 2 left m1, 1 right m1, 3 left m2 (+ 1 right broken), 1 right m3, 1 left m3, 1 left I1, 1 left P4, 1 right M3.

Synonymy

Parapetenya hibbaridi (SULIMSKI), in: Mein et al. [15], p.116 (Valdeganga 2).

Table 1

Measurements (mm) of the dental and mandibular elements of *Deinsdorfia doukasi* nov. sp. from Almenara-Casablanca 4
Mesures (mm) des éléments dentaires et mandibulaires de *Deinsdorfia doukasi* nov. sp. d'Almenara-Casablanca 4

Element	Parameter	min	mean	max	sd	n
I1	LT	0.82	0.92	1.02	0.141	2
	L	2.13	2.14	2.15	0.014	2
	H	1.25	1.31	1.36	0.077	2
P4	PE		1.19			1
	LL		1.30			1
	BL		1.70			1
	W		1.42			1
	M1	PE	1.17	1.18	1.19	0.014
M1	LL	1.32	1.42	1.51	0.134	2
	BL		1.56			1
	AW	1.42	1.46	1.50	0.056	2
M2	PW		1.57			1
	PE	1.03	1.05	1.07	0.028	2
	LL	1.21	1.27	1.32	0.078	2
	BL	1.28	1.33	1.40	0.061	3
	AW	1.52	1.53	1.54	0.014	2
M2	PW		1.43		0.000	2
	i1	L	4.04	4.11	4.18	0.070
a1	L		1.00			1
	p4	L		1.10		1
m1	L		1.61		1	
	TRW		0.80		1	
m2	TAW		0.85		1	
	L	1.38	1.42	1.45	0.049	2
m2	TRW	0.83	0.86	0.88	0.035	2
	TAW	0.76	0.81	0.86	0.050	3
	m3	L	1.03	1.08	1.12	0.063
m3	W	0.62	0.65	0.67	0.035	2
	Mandible	L		5.75		1
Mandible	H		4.11		1	
	Lm1-m3		4.04		1	
Mandible	HC		2.53		1	
	LUF		1.15		1	
Mandible	LLF		1.29		1	

Parapetenya hibbaridi (SULIMSKI), in: Mein et al. [15], p.118 (Valdeganga 3).

Deinsdorfia hibbaridi (Sulimski, 1962), in: Rzebik-Kowalska [24], p.53 (Valdeganga 2 and 3).

Deinsdorfia aff. *kordosi* REUMER, 1984, in: Furió et al. [7], p. 269 (Almenara-Casablanca 4).

Deinsdorfia hibbaridi (Sulimski, 1962), in: Van den Hoek Ostende and Furió [11], p. 270 (Valdeganga 1, referring to Valdeganga 2).

Deinsdorfia aff. *kordosi* Reumer, 1984, in: Van den Hoek Ostende and Furió [11], p. 271 (Almenara-Casablanca 4).

Deinsdorfia hibbaridi (Sulimski, 1962), in: Van den Hoek Ostende and Furió [11] p. 274 (Valdeganga 3).

Diagnosis (Fig. 4)

Table 2

Measurements (mm) of the dental elements of *Deinsdorfia doukasi* nov. sp. from Valdeganga 2

Mesures (mm) des éléments dentaires de *Deinsdorfia doukasi* nov. sp. de Valdeganga 2

Element	Parameter	min	mean	max	sd	n
P4	PE		1.32		0.000	2
	LL		1.44			1
	BL	1.72	1.80	1.89	0.070	5
	W		1.45		0.000	2
M1	PE	1.24	1.25	1.26	0.014	2
	LL	1.47	1.53	1.59	0.060	3
	BL		1.52			1
	AW	1.45	1.48	1.50	0.025	3
M2	PW		1.64			1
	PE	0.96	1.02	1.07	0.078	2
	LL	1.06	1.13	1.19	0.092	2
	BL	1.21	1.23	1.25	0.028	2
M3	AW		1.46			1
	PW	1.32	1.36	1.39	0.049	2
	L		0.55			1
	W		1.00			1
p4	L		1.52			1
m1	L	1.63	1.66	1.69	0.022	5
	TRW	0.76	0.83	0.87	0.050	5
	TAW	0.83	0.86	0.92	0.035	5
m2	L	1.42	1.43	1.45	0.015	4
	TRW	0.80	0.83	0.85	0.021	4
	TAW	0.79	0.82	0.85	0.028	4
m3	L	1.04	1.09	1.21	0.064	6
	W	0.58	0.62	0.67	0.029	6

Table 3

Measurements (mm) of the dental of *Deinsdorfia doukasi* nov. sp. from Valdeganga 3

Mesures (mm) des éléments dentaires de *Deinsdorfia doukasi* nov. sp. de Valdeganga 3

Element	Parameter	min	mean	max	sd	n
I1	LT		0.68			1
	L		1.81			1
	H		1.37			1
P4	PE		1.30			1
	LL		1.50			1
	BL		no			0
	W		1.47			1
p4	L		1.47			1
m1	L	1.59	1.67	1.73	0.074	3
	TRW	0.86	0.90	0.94	0.040	3
	TAW	0.89	0.93	1.01	0.067	3
m2	L	1.37	1.46	1.55	0.127	2
	TRW	0.82	0.88	0.96	0.072	3
	TAW	0.83	0.88	0.94	0.057	3
m3	L	1.19	1.20	1.23	0.023	3
	W	0.60	0.65	0.70	0.050	3

Deinsdorfia species with very elongated intermedial dental elements (P4, M1, p4 and m1) (Fig. 4a); very thin tip of the coronoid process (Fig. 4b); low ascending ramus compared with a rather enlarged horizontal ramus; mental foramen very reduced, and long-distanced from the posterior part of the mandible, placed under the talonid of m1; p4 big and rather stout; i1 without bulbous cuspules and always missing a well-marked cingulum at the buccal base of the crown (Fig. 4c); m1 with a very open trigonid valley due to a long paralophid; very elongated P4, with a protocone and hypocone crest-shaped; P4 similar in size to M1; M1 and M2 with distinctive isolated hypocones (Fig. 4d); long metacrest in M1, but M2 rather symmetrical, with a non-reduced posterior margin (Fig. 4e); I1 with a quite long apex, never fissident; all teeth with dark-red to black stain.

Differential diagnosis

Deinsdorfia doukasi nov. sp differs from all the other species of *Deinsdorfia* by its thinner tip of the coronoid process, by its short ascending ramus compared to the length of the horizontal ramus (only similar in size to *D. hibbardii*), and except for *D. kordosi* and *D. fallax*, by its extremely long paralophid of the m1. It has a shorter lower molar row than *D. kerkhoffi*, but longer than any other known *Deinsdorfia* species (Fig. 5). It differs from all other species of *Deinsdorfia*, except for *D. fallax*, by the retention of isolated hypocones in M1 and M2. In addition, it can be specifically distinguished from each one of the other known *Deinsdorfia* species by the following characters.

Deinsdorfia doukasi nov. sp differs from *D. janossyi* by having a more pointed tip of the coronoid process, by lacking a concave anterior margin of the ascending ramus, by having a more elongated a1, and by having a shorter parastylar crest on P4. It differs from *D. kordosi* by having a P4 with a less enlarged parastylar crest but more posteriorly elongated protocone, by having an M1 with a metaloph finishing close to the base of the metacone, and by having a less reduced posterior margin of the M2. It differs from *D. fallax* by the retention of metalophs in the M1 and M2 clearly oriented towards the bases of their corresponding metacones, by its shorter apex of the I1 and by its longer m1. It differs from *D. reumeri* by lacking bulbous parts in the i1 (cuspules or apex), by having a thinner tip of the coronoid process, by showing a softer impression of the external temporal fossa, and by having a longer m1. It differs from *D. insperata* by having longer lower dental elements with no significant undulations in their buccal cingula and by having a smaller and more anteriorly placed mandibular foramen. It differs from *D. kerkhoffi* by having more reduced posterior dentition (specially the talonid of m3),

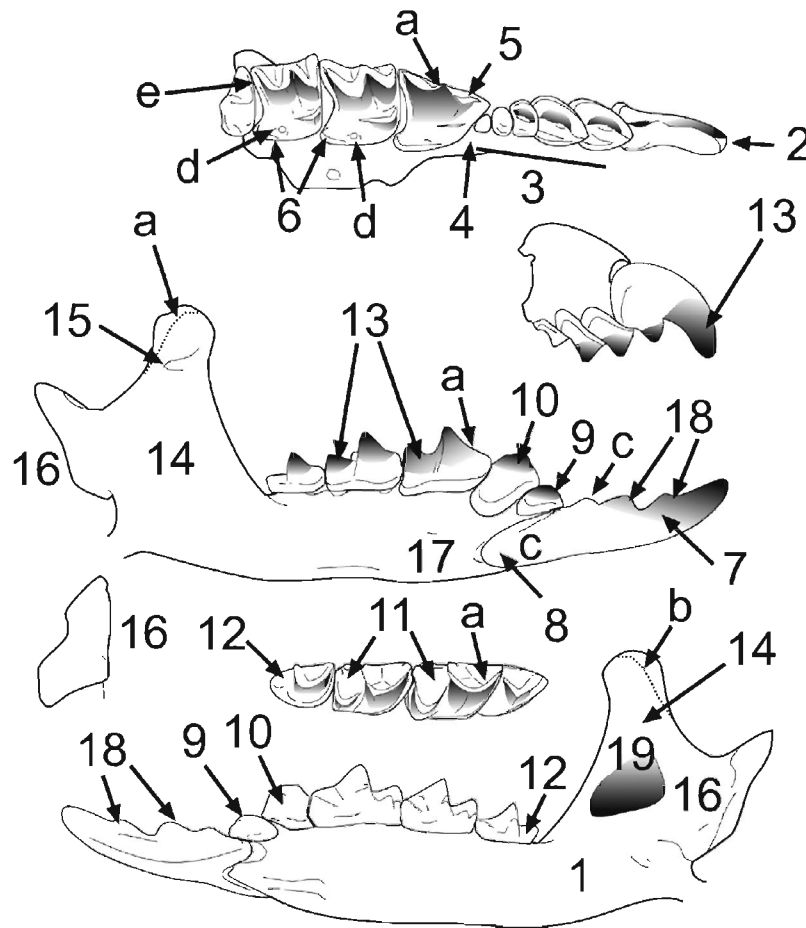
***Deinsdorfia doukasi* nov. sp.**

Fig. 4. Specific characters of *Deinsdorfia doukasi* nov. sp. Generic traits (according to Reumer [20]) are arrowed with a number, while the specific ones are signalled with a letter. Middle-sized Soricini (1); non-fissident upper incisor (2); five upper antemolars (3), in which the A5 is placed lingually of the parastyle of P4 (4); P4 with extremely elongate parastyle and high parastylar crest (5); hypocones and hypoconal flanges in the upper molars reduced and small (6); lower incisor tricuspidate (7) and reaching as far backwards on the buccal side of the mandible as p4 (8); a1 small (9); p4 large (10); m1 and m2 with short talonids (11), m3 with a small, usually single-cuspid talonid (12). The teeth are stained red (13). Ramus short and stout with a low coronoid process (14); well-developed coronoid spicule (15); condyle comparatively large (16); mental foramen below the talonid of m1 (17). Other characters specified for the genus are: cusplules of the i1 asymmetric and tilted anteriorly (18); reduced internal temporal fossa (19). The specific characters are indicated in the text.

Caractères spécifiques de Deinsdorfia doukasi nov. sp. Les caractères génériques (selon Reumer [20]) sont signalés par un numéro, et les caractères spécifiques par une lettre. Soricini de taille moyenne (1); incisive supérieure non fissidente (2); cinq antémolaires supérieures (3), dans lesquelles A5 est placé lingualemment par rapport au parastyle P4 (4); P4 avec un parastyle très allongé et une crête parastylaire haute (5); hypocônes et flancs hypocônax des molaires supérieures réduits et petits (6); incisive inférieure tricusplulée (7), se développant vers l'arrière sur le côté buccal de la mandibule comme p4 (8); a1 petit (9); p4 grand (10); m1 et m2 avec des talonides courts (11), m3 avec un talonide court, à une seule cusplide généralement (12). Les dents sont pigmentées en rouge (13). Ramus mandibulaire court et massif, avec un processus coronoïde bas (14); spicule coronoïde bien développée (15); condyle comparativement grand (16); foramen mental sous le talonide de m1 (17). Les autres caractères spécifiés pour le genre sont: cusplules de i1 asymétriques et inclinées antérieurement (18); fosse temporelle interne réduite (19). Les caractères spécifiques sont indiqués dans le texte.

by its smaller dimensions in the lower dentition and mandible, and by having a thinner tip of the coronoid process. It differs from *D. hibbardi* by having slightly bigger dimensions of the teeth, by not having bulbous cusplules in the lower incisor, by not presenting a cingulum at the posterior buccal margin of i1, and by having a reduced talonid in the m3.

4. Description

4.1. Mandible

The coronoid process is relatively low compared to the total length of the mandible. The coronoid spicule is well marked and it is placed near the tip of the coro-

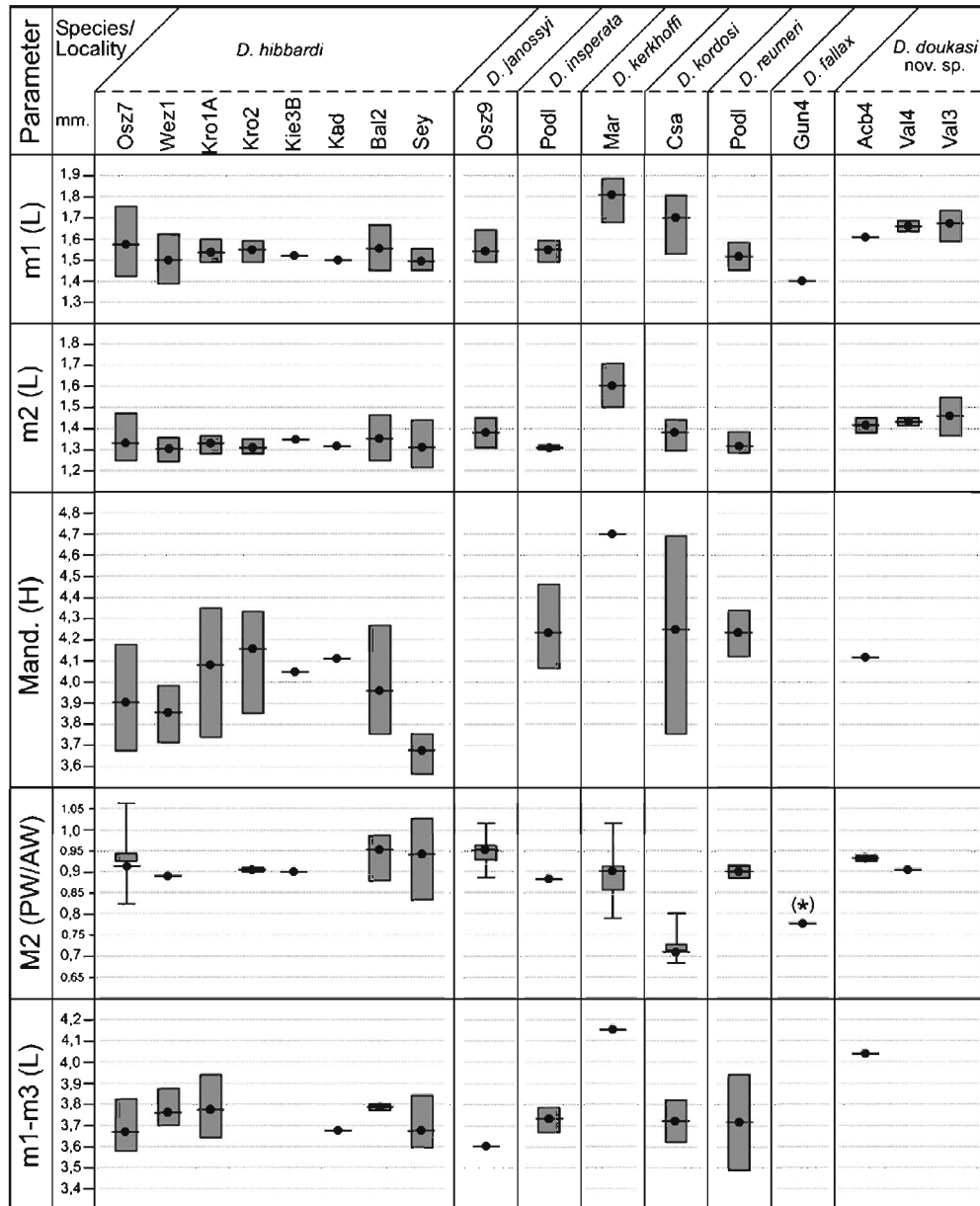


Fig. 5. Ranges of the dental and mandibular measurements in different species of *Deinsdorfia*. Specimens from Almenara-Casablanca 4, Valdeganga 2 and 3, Balaruc 2 and 3, Seynes have been measured following Reumer [20]. The rest of the data has been taken from Reumer [20], Rzebik-Kowalska [22], Doukas et al. [5] and Dahlmann and Storch [4]. (The symbol * indicates that the measurement has been taken from the illustrated specimen.)
*Rangs des mesures dentales et mandibulaires de différentes espèces de Deinsdorfia. Les spécimens d'Almenara-Casablanca 4, Valdeganga 2 et 3, Balaruc 2 et Seynes ont été mesurés selon Reumer [20]. Les autres données sont issues de Reumer [20], Rzebik-Kowalska [22], Doukas et al. [5] et Dahlmann et Storch [4]. (Le symbole * indique que la mesure a été prise à partir du spécimen figuré).*

noid process. In posterior view, this tip is tilted towards the labial side. The condyle is big compared with the posterior side of the mandible. The morphology of the condyle is the typical one for the Soricini, showing a lower facet larger than the upper one, extended to the lingual side. Both facets are separated by a long interarticular area. The mandibular foramen is relatively small and it is placed below the middle of the internal temporal fossa. This fossa has a triangular shape with rather curved

sides and angles, and it is not higher than the condyle. The ventral side of the horizontal ramus is straight along its whole length. The angular process is not preserved in the only specimen available.

4.2. *il*

These teeth are tricusplated. The pigmentation affects completely the anterior part of the tooth and the

tips of all its cuspules. In the mandible, it reaches labially the p4, but it only arrives underneath the a1 lingually. There is no clear cingulum running the base of the crown in any of the lower incisors found.

4.3. a1

The tooth is unicusped, slightly elongated anteroposteriorly, and a bit longer than the p4. Only the higher part of the cusp is pigmented. A small cingulum covers the base of its lingual side.

4.4. p4

This tooth has a clearly delimited re-entrant valley, opening to the lingual side. A small cingulum is visible at the base of this face. Labially, the tooth sinks under the m1 until the middle of its trigonid. The tip of the tooth is pigmented.

4.5. m1

This tooth is by far the largest tooth of the mandible. The trigonid is considerably longer than the talonid. The protoconid is the highest cusp. The paralophid runs from the protoconid to the paraconid, making a small inflexion half-way both cusps. The trigonid angle is very open. The talonid is short. The entoconid crest is consequently short, but relatively high and thick. The entostylid is quite reduced. In labial view the posterior face is slightly convex. In unworn specimens from Valdeganga 2, the oblique crest of the m1 does not reach the posterior face of the trigonid, but it finishes in a small cuspule, leaving a little notch that connects the talonid basin with the labial face.

4.6. m2

The tooth is similar to the m1, but smaller. The trigonid is not as long as it is in m1, and consequently the paralophid makes a stronger inflexion. This inflexion corresponds to the lowest point of the crest that joins protoconid and paraconid. The pigmentation on the talonid is only present on the hypoconid, while it surrounds all the highest part of the labial surface of the trigonid. The unworn m2 from Valdeganga 2 show the same peculiarity as their corresponding m1 in their oblique crests.

4.7. m3

Paraconid, protoconid, and metaconid have similar heights. The talonids are reduced to a comma-shaped

crest. In one of the two specimens available, this crest is strongly inflexed lingually, thus giving a general aspect of an open talonid basin. In the material from Valdeganga 2, the occlusal outline of the talonid in m3 is somewhat reduced in dimensions, and in some specimens it bends slightly towards the labial side.

4.8. I1

The apex of this tooth is not fissident. The darker pigmentation covers the anterior part of the apex, but it progressively fades posterodorsally. The talon is also slightly stained. The dorsal margin of the crown is slightly curved, while the posterior margin is more abruptly inflexed. A poorly-defined broad cingulum is present at the labial base of the crown.

4.9. A1

The tooth is crossed by a central crest from the anterior to the posterior side. There is a strong cingulum surrounding the base of the labial face. The base of the lingual face presents a ridge with a small cuspule at its posterior extreme.

4.10. P4

The tooth is labiolingually compressed but mesiodistally elongated. The parastyle is small. The paracone is the tallest cusp. The protocone has the form of a small longitudinal ridge that finishes in a central position of the tooth and does not connect with the hypocone. The hypocone is visible as a slight elevation of the lingual cingulum rather than a real isolated cusp. The posterior emargination is moderated. The pigmentation strongly affects the paracone, but it fades out distally. A slight pigmentation covers the anterior part of the parastyle.

4.11. M1

The tooth is mesiodistally elongated due to the enlargement of the metacrest. The highest parts of the lingual face of the ectoloph are stained in a dark-red colouration. The lingual side of the protocone is slightly pigmented too. The posterior emargination is quite pronounced due to the unusual posterior development of the ectoloph and the hypoconal flange. The hypocone is preserved as a well-delimited small conical cusp.

4.12. M2

The M2 exhibits the same characters exposed for the M1, but its occlusal outline and ectoloph are quite more symmetrical. Anterior and posterior widths are consequently similar. The rest of the features closely fits the description of the M1. In the material from Valdeganga 2, the hypocone and the hypoconal flange of the M2 are less developed than in the material from ACB4. The occlusal outline is also quite square, although the anterior sides are slightly wider than the posterior ones.

4.13. M3

The only specimen available comes from Valdeganga 3. The tooth is very short in the anteroposteriorly direction. The protocone and the postmesocrista are much reduced, but still present. The paracone is the tallest cusp, and the paracrista is much longer than the paramesocrista.

5. Taxonomical remarks

The material from the Valdeganga section does not differ significantly from that other coming from Almenara-Casablanca 4. Although sizes are not definitively discriminant in that case, it is noteworthy that the lengths of isolated lower molars (m1 and m2) of the Spanish material show differences in their means by reaching slightly higher values than in the rest of the European species, except from the m1 and m2 of *D. kerkhoffi* and the m1 of *D. kordosi*, which are clearly longer (Fig. 5). The differences are more accentuated when the complete molar row lengths are considered. Unfortunately, within all the Spanish material available, only the specimen from Almenara-Casablanca 4 preserves the m1–m3 series, and therefore this character must be taken with some reservations. *Deinsdorfia doukasi* nov. sp. is more clearly identified as a distinct one when morphological traits are added to the measurements (see Figs. 1 and 5), because the ranges of the Spanish and the European material partially overlap in some cases.

Some reservations exist on the specific ascription of the material of *Deinsdorfia* from the southern France localities of Seynes and Balaruc 2. According to the drawing of *D. hibbardi* from Seynes illustrated in Jamnot [13], the tip of the coronoid process of the mandible is slightly thinner than the ones ascribed to the same species from Osztramos 7 and Csarnota 2 showed by Reumer [20]. This suggests that the material from Seynes actually belongs to *D. doukasi* nov. sp. More-

over, the M1 and the M2 of *D. hibbardi* from Balaruc 2 figured in [3] (Pl. 4, Fig. 2) show a similar development of the posterior emargination and of the shape of the hypocone, placing it closer to the new species than to the *D. hibbardi* specimens depicted by Reumer [20] from the Hungarian sites. Nevertheless, the measurements of *Deinsdorfia* from Seynes and Balaruc 2 stored in Lyons reach somewhat lower values in most of their dental and mandibular elements than those of *D. doukasi* nov. sp. from Almenara-Casablanca 4 and Valdeganga sites (Fig. 5). For these reasons, the material of *Deinsdorfia* from those sites can be tentatively ascribed to a transitional form between *D. hibbardi* and *D. doukasi* nov. sp., waiting for further research.

6. Discussion

The genus *Deinsdorfia* is restricted to the Pliocene of Europe. The older and the younger occurrences of the genus (i.e. previous and posterior to the Pliocene) are sparsely documented, and frequently the exact age of these sites is given with some reservations. The stratigraphical ranges of most of the known species are restricted to a few MN zones, or even just one (Fig. 6). The oldest record of the genus corresponds to *Deinsdorfia kerkhoffi*, only documented in the type-locality of Maramena (Greece), and chronologically ascribed to the Mio-Pliocene boundary (MN 13–14, [4]). According to the data available in Rzebik-Kowalska [22], *Deinsdorfia insperata*, *D. reumeri*, and *D. janossyi* are restricted to the beginning of the Early Pliocene (MN 14). In a similar way, the occurrence of *D. fallax* is limited to the late Early Pliocene (MN 15) site of Gundersheim [4], and *D. kordosi* covers a close range (Early Pliocene, MN 15). Nevertheless, in that second case, its chronological range possibly extends till the early Late Pliocene (MN16 *confer* citation from Rebelice Królewskie, Poland, [22]). The biostratigraphical range of *D. hibbardi* is consequently the larger within the genus, covering an interval comprised between the Early Pliocene and the Early Pleistocene. However, such a range must be accepted with some reservations, because some of the identifications were carried out when only this species of *Deinsdorfia* had been defined (see Introduction).

According to the available data about *Deinsdorfia*, the genus reached its widest spreading and diversification during the Early Pliocene. The transition from the Early Pliocene to the Late Pliocene apparently resulted in a noticeable impoverishment of its diversity. Given that the occurrences of *Deinsdorfia* in the Iberian Peninsula are

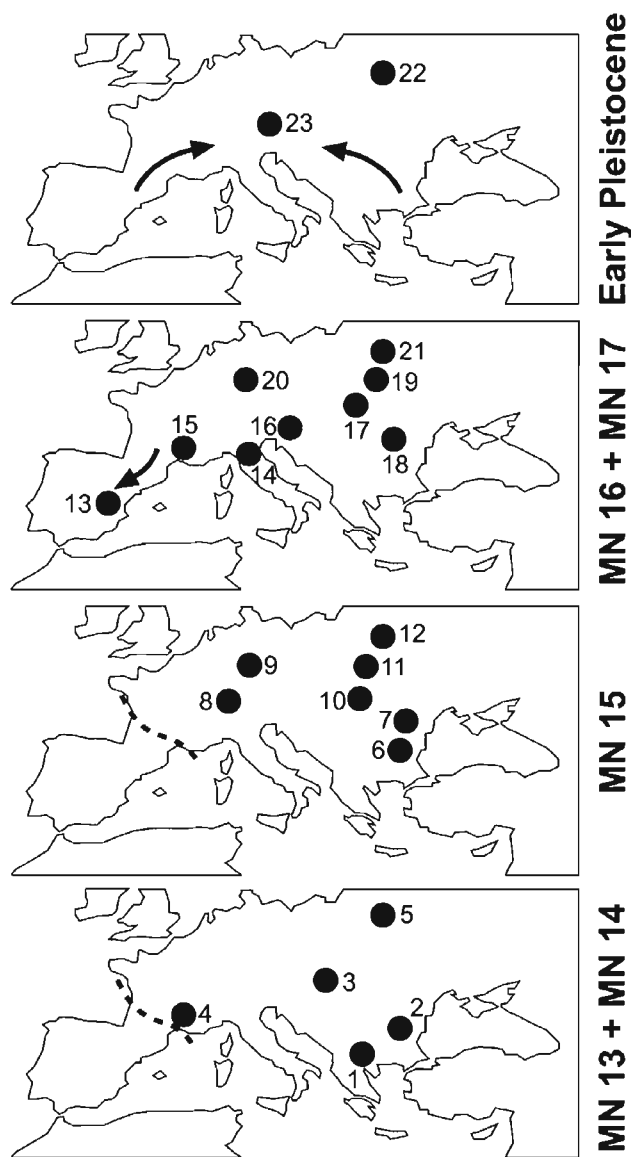
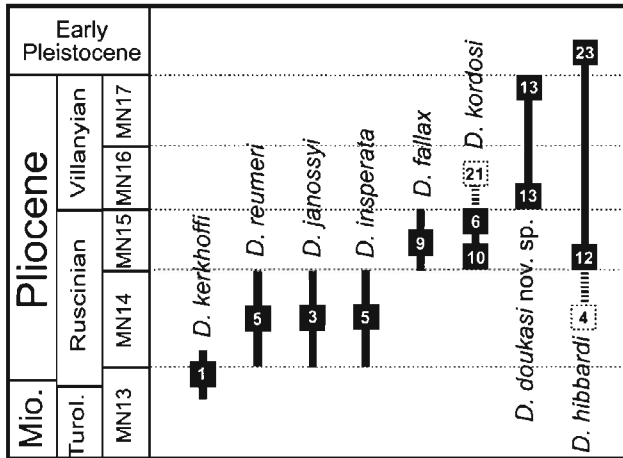


Fig. 6. Biochronological ranges of the known *Deinsdorfia* species and geographical distribution of the genus along the time. In the table above, the solid lines indicate the known temporal range, while dotted lines indicate possible extended ranges (cf. quotations). The oldest and the youngest record of each species are specified in black squares,

restricted to Late Pliocene localities [11], the extinction of some species of *Deinsdorfia* in the rest of Europe can be related to the migration of some representatives of the genus to Spain.

It is a well-known fact that the distribution of some European soricids has been latitudinally constrained. Latitudinal limitations, expansions and retractions of

respectively at the bottom and the top of its corresponding range bar. When only one record is available, the black square occupies an intermediate position of this bar. In the maps, the occurrences of similar age in the same country are symbolized by means of a single number. Dotted lines are in this case the deduced natural frontiers, and arrows symbolize the deduced expansions or retractions of the populations of the genus *Deinsdorfia*. MN 13/14: 1, Maramena (Greece); MN 14: 2, Dorkovo (Bulgary), 3, Osztramos 9 (Hungary), 4, Vendargues (France), 5, Podlesice (Poland); MN 15: 6, Muselievo (Bulgary), 7, Dranic (0, 2 and 3) (Romania), 8, Vue-des-Alpes (Switzerland), 9, Gundersheim 4 (Germany), 10, Csarnota 2 (Hungary), 11, Ivanovce (Slovakia), 12, Weze 1 (Poland); MN 16 and MN 17: 13, Valdeganga (2 and 3), Almenara-Casablanca 4, Barranco del Monte 1 (Spain), 14, Arondelli (Italy), 15, Seynes; Balaruc 2 (France), 16, Crnotice (Slovenia), 17, Osztramos 7 (Hungary), 18, Podari (Romania), 19, Hajnácka (Slovakia), 20, Deinsdorf, Frenchen (Germany), 21, Rebielice Królewskie 1A, 2, Kielniki 3B (Poland); Plio-Pleistocene: 22, Kadzielnia 1 (Poland); Early Pleistocene: 23, Deutsch-Altenburg 21 (Germany). Data taken from Rzebik-Kowalska [24], updated with references in Rzebik-Kowalska [25], Rzebik-Kowalska and Popov [26], Popov [18], Horáček et al. [12], Sabol et al. [27], Laplana-Conesa et al. [14].

Rangs biochronologiques des espèces connues de Deinsdorfia et distribution géographique du genre. Dans le tableau, les lignes continues indiquent le rang temporel connu, alors que les lignes pointillées indiquent une possible extension du rang (cf. citations). Les restes les plus anciens et les plus récents répertoriés pour chaque espèce sont spécifiés dans les cadres noirs, respectivement dans la partie inférieure et dans la partie supérieure de la barre de rang correspondant. Quand il y a seulement un enregistrement disponible, le cadre noir occupe une position intermédiaire de la barre. Sur les cartes, les occurrences d'un âge similaire dans le même pays sont symbolisées au moyen d'un nombre unique. Les lignes pointillées sont, dans ce cas, placées comme frontières naturelles déduites, et les flèches symbolisent des expansions ou des retractions déduites pour les populations du genre Deinsdorfia. MN 13/14: 1, Maramena (Grèce); MN 14: 2, Dorkovo (Bulgarie), 3, Osztramos 9 (Hongrie), 4, Vendargues (France), 5, Podlesice (Pologne); MN 15: 6, Muselievo (Bulgarie), 7, Dranic (0, 2 et 3) (Roumanie), 8, Vue-des-Alpes (Suisse), 9, Gundersheim 4 (Allemagne), 10, Csarnota 2 (Hongrie), 11, Ivanovce (Slovaquie), 12, Weze 1 (Pologne); MN 16 et MN 17: 13, Valdeganga (2 et 3), Almenara-Casablanca 4, Barranco del Monte 1 (Espagne), 14, Arondelli (Italie), 15, Seynes, Balaruc 2 (France), 16, Crnotice (Slovénie), 17, Osztramos 7 (Hongrie), 18, Podari (Roumanie), 19, Hajnácka (Slovaquie), 20, Deinsdorf, Frenchen (Allemagne), 21, Rebielice Królewskie 1A, 2, Kielniki 3B (Pologne); Plio-Pléistocène: 22, Kadzielnia 1 (Pologne); Pléistocène inférieur: 23, Deutsch-Altenburg 21 (Allemagne). Données prises à partir de Rzebik, Kowalska [24], actualisées avec les références de Rzebik, Kowalska [25], Rzebik, Kowalska et Popov [26], Popov [18], Horáček et al. [12], Sabol et al. [27], Laplana, Conesa et al. [14].

their geographical range due to climatic oscillations have been reported for *Amblycoptus* during the Late Miocene and the Early Pliocene [29], and for *Crocidura* and *Asoriculus* during the Pliocene and the Pleistocene [20,21,23]. According to the data of Minwer-Barakat et al. [16], *Blarinoides* seems to have occupied the Iberian Peninsula already in the Late Ruscinian, but only reached southern areas in the Villanyian (MN 16). In the opposite way, the African genus *Myosorex* limited its northern distribution to southern France [8]. During the colder periods of the Pliocene and the Pleistocene, the southern regions acted as a sink area for *Amblycoptus* and *Blarinoides*, but as refuge area for *Myosorex*, *Crocidura* and *Asoriculus*. Since *Deinsdorfia* did not disappear from Central Europe during all of the Pliocene, it can be considered an analogous case to that of *Amblycoptus* and *Blarinoides*.

Thus, beyond the specific characterization of *D. doukasi* nov. sp., the presence of *Deinsdorfia* in some Late Pliocene localities from Spain reports the evidence of its expansion towards southern European lands, coinciding with the transition from the Ruscinian to the Villanyian. Such boundary is characterized by the appearance of a latitudinal climatic gradient in the northern hemisphere [1] and its estimated correlation with the glacial event M2-MG2, comprised between 3.2 and 3.3 Ma. [17]. In the Iberian Peninsula, such an event is reflected as a noticeable turnover of the micromammalian faunas, in which the Arvicolidae took over the terrestrial ecosystems to the detriment of the Muridae [1]. In a similar way, it is deduced that the colder temperatures in the northern hemisphere pulled the populations of *Deinsdorfia* southwards.

7. Conclusions

The genus *Deinsdorfia* is a genus of pigmented-toothed shrews typical of the European Pliocene fossil record. However, the new Spanish form *D. doukasi* nov. sp. is actually restricted to the Villanyian (Late Pliocene). According to its fossil occurrences in the Iberian Peninsula, its biostratigraphical range is comprised between the MN 16 and the MN 17. Temporally, its arrival probably coincided with the mid-Pliocene cooling-event M2-MG2 dated at about 3.3 Ma. In the absence of documented Pleistocene fossil occurrences in Spain, it must be deduced that the intensified icing episodes of the Plio-Pleistocene transition forced its extinction in southwestern Europe. Soon after, during the Early Pleistocene, the genus became completely extinct in the rest of Europe.

Acknowledgements

The support of the Researching Hominid Origins Initiative (RHOI-HOMINID-NSF-BCS-0321893) is gratefully acknowledged. Generalitat Valenciana supplied the necessary funds to carry out the Almenara-Casablanca 4 fieldworks in 2004. M.F. acknowledges the work of Andrés Santos-Cubedo and Miguel Cubedo, who sorted the sediment from ACB-4 and found most of the studied material, and the motivation received from Francesc Gusi and Jordi Agustí to restart the studies on the ACB karstic complex. Special thanks are given to Meike Köhler for translating the texts in German, to the staff from Servei de Microscopia (Universitat Autònoma de Barcelona) for helping to take the SEM photographs of the holotype of *D. doukasi* nov. sp., and to an anonymous reviewer for the valuable comments he (or she) made to improve the contents and the expression of the first manuscript.

References

- [1] J. Agustí, M. Garcés, J. M. Parés, Pliocene correlation between climatic change and mammalian succession in the Western Mediterranean, in: J.H. Wrenn, J.-P. Suc, S.A.G. Leroy (Eds.), *The Pliocene: Time of Change*, American Association of Stratigraphic Palynologists Foundation, Dallas, 1999, pp. 121–129.
- [2] H. de Bruijn, R. Daams, G. Daxner-Höck, V. Fahlbusch, L. Ginsburg, P. Mein, J. Morales with contribution of E. Heinzmann, D. F. Mayhew, A. J. Van der Meulen, N. Schmidt-Kittler, M. Telles Antunes, Report of the RCMNS working group on fossil mammals, *Reisenburg*, 1990, *Newslett. Stratigr.* 26 (2/3) (1992) 65–118.
- [3] J.-Y. Crochet, Insectivores pliocènes du Sud de la France (Languedoc-Roussillon) et du Nord-Est de l'Espagne, *Palaeovertebrata* 16 (1986) 145–171.
- [4] T. Dahlmann, G. Storch, Eine pliozäne (oberruscinische) Kleinsäugerfauna aus Gundersheim, Rheinhessen. 2. Insektenfresser: Mammalia, Lipotyphla, *Senckenb. Lethaea* 76 (1996) 181–191.
- [5] C.S. Doukas, L.W. van den Hoek Ostende, C.D. Theodoropoulos, J.W.F. Reumer, The vertebrate Locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 5. Insectivora (Erinaceidae, Talpidae, Soricidae, Mammalia), *Muench. Geowiss. Abh. A* 28 (2005) 43–64.
- [6] O. Fejfar, Die plio-pleistocene Wirbeltierfaunen von Hajnácka und Ivanovce (Slowakei), CSSR. V. *Allosorex stenodus* n.g. n.sp. aus Ivanovce A, *Neues Jahrb. Geol. Palaeontol. Abh.* 123 (3) (1966) 221–248.
- [7] M. Furió, A. Santos-Cubedo, J. Agustí, Pequeños mamíferos: Corredores, voladores y devoradores de insectos, in: F. Gusi (Ed.), *Roedores, monos, caballos y ciervos. Faunas fósiles de Casa Blanca-Almenara de 5 a 1 millones de años (Castellón)*, Diputació de Castelló, Castelló, 2005, pp. 265–280.
- [8] M. Furió, A. Santos-Cubedo, R. Minwer-Barakat, J. Agustí, Evolutionary history of the African soricid *Myosorex* (Insectivora, Mammalia) out of Africa, *J. Vertebr. Paleontol.* 27 (4) (2007) 1018–1032.

- [9] F. Heller, Eine oberpliocäne Wirbeltierfauna aus Rheinhessen, Neues Jahrb. Mineral. Geol. Palaeontol. Beil., Abt. B 76 (1936) 99–160.
- [10] F. Heller, Eine altquartäre Wirbeltierfauna des unteren Cromerium aus der nördlichen Frankenalb, Neues Jahrb. Geol. Paläontol. Abh. 118 (1) (1963) 1–20.
- [11] L.W. van den Hoek Ostende, M. Furió, Spain, in: L.W. van den Hoek Ostende, C.S. Doukas, J.W.S. Reumer (Eds.), The Fossil Record of the Eurasian Neogene Insectivores (Erinaceomorpha, Soricomorpha, Mammalia), Part I, Scripta Geol. (special issue 5), Naturalis, Leiden, 2005, pp. 149–284.
- [12] I. Horáček, A. Mihevc, N. Zupan Hajna, P. Pruner, P. Bosák, Fossil vertebrates and Paleomagnetism update of one of the earlier stages of cave evolution in the classical karst, Slovenia: Pliocene of Črnotice II site and Raciska Pecina, Acta Carsologica 36 (3) (2007) 453–468.
- [13] D. Jammot, Les Musaraignes (Soricidae, Insectivora) du Plio-Pleistocène d'Europe, PhD thesis, University of Dijon, France, 1977 (341 p.).
- [14] C. Laplana-Conesa, O. Amo Sanjuán, J. A. Andrés Moreno, N. López Martínez, A. Sánchez Marco, F. B. Sanchiz, M. I. Sanz Villar, P. Sevilla García, Primeros datos sobre el nuevo yacimiento de microvertebrados Barranco del Monte 1 (Plioceno Superior, Concud, Teruel), XX Jornadas de la Sociedad Española de Paleontología, abstracts volume, 2004, pp. 93–94.
- [15] P. Mein, E. Moissenet, G. Truc, Les formations continentales du Néogène supérieur des vallées du Jucar et du Cabriel au NE d'Albacete (Espagne). Biostratigraphie et environment, Doc. Lab. Géol. Fac. Sci. Lyon 72 (1978) 99–147.
- [16] R. Minwer-Barakat, A. García-Alix, E. Martín-Suárez, M. Freudenthal, *Blarinoides aliciae* sp. nov., a new Soricidae (Mammalia, Lipotyphla) from the Pliocene of Spain, C. R. Palevol. 6 (4) (2007) 281–289.
- [17] M. Mudelsee, M. E. Raymo, Slow dynamics of the Northern Hemisphere glaciation, Paleoclimatology 20, PA4022, doi:10.1029/2005PA001153.
- [18] V.V. Popov, Pliocene small mammals (Mammalia, Lipotyphla, Chiroptera, Lagomorpha, Rodentia) from Muselievo (North Bulgaria), Geodiversitas 26 (3) (2004) 403–491.
- [19] C.A. Repenning, Subfamilies and genera of the Soricidae, Geol. Surv. Prof. Pap. 565 (1967) 1–74.
- [20] J.W.F. Reumer, Ruscinian and Early Pleistocene Soricidae (Insectivora, Mammalia) from Tegelen (The Netherlands) and Hungary, Scripta Geol. 73 (1984) 1–173.
- [21] J. Rofes, G. Cuenca-Bescós, First evidence of the Soricidae (Mammalia) *Asoriculus gibberodon* (PETÉNYI, 1864) in the Pleistocene of North Iberia, Riv. Ital. Paleont. Stratigr. 112 (2) (2006) 301–315.
- [22] B. Rzebik-Kowlaska, Pliocene and Pleistocene Insectivora (Mammalia) of Poland. VI. Soricidae: *Deinsdorfia* HELLER, 1963 and *Zelceina* SULIMSKI, 1962, Acta Zool. Cracov. 33 (4) (1990) 45–77.
- [23] B. Rzebik-Kowlaska, Climate and history of European shrews (family Soricidae), Acta Zool. Cracov. 38 (1) (1995) 95–107.
- [24] B. Rzebik-Kowalska, Fossil History of Shrews in Europe, in: J. M. Wojcik, M. Wolsan (Eds.), Evolution of Shrews, Library of the Mammal Research Institute, Polish Academy of Sciences, Białowieza, vol. 1, 1998, pp. 23–92.
- [25] B. Rzebik-Kowalska, Romania, in: L.W. van den Hoek Ostende, C. S. Doukas, and J. W. S. Reumer (Eds.), The Fossil Record of the Eurasian Neogene Insectivores (Erinaceomorpha, Soricomorpha, Mammalia), Part I, Scripta Geol. Spec. Issue 5, Naturalis, Leiden, 2005, pp. 135–147.
- [26] B. Rzebik-Kowalska, V. V. Popov, Bulgaria, in: L.W. van den Hoek Ostende, C.S. Doukas, J.W.S. Reumer (Eds.), The Fossil Record of the Eurasian Neogene Insectivores (Erinaceomorpha, Soricomorpha, Mammalia), Part I, Scripta Geol. (special issue 5), Naturalis, Leiden, 2005, pp. 31–35.
- [27] M. Sabol, A. Durisova, M. Elecko, P. Holec, N. Hudácková, V. Konečný, M. Slamková, D. Vass, New data from the Early Villanyian site of Hajnácka I (Southern Slovakia), 18th International Senckenberg Conference, abstracts volume, 2004, pp. 61–62.
- [28] A. Sulimski, Supplementary studies on the insectivores from Weze 1 (Poland), Acta Palaeontol. Pol. 7 (3–4) (1962) 441–502.
- [29] J. Van Dam, Anourosoricini (Mammalia: Soricidae) from the Mediterranean region: a pre-Quaternary example of recurrent climate-controlled north-south range shifting, J. Paleontol. 78 (4) (2004) 741–764.