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AN UPDATE OF *PROLAGUS MICHAUXI* LÓPEZ-MARTÍNEZ, 1975 (PROLAGIDAE, LAGOMORPHA) FROM THE PLIOCENE OF SÈTE, SOUTHERN FRANCE

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Abstract: *Prolagus michauxi* López-Martínez, 1975 (Prolagidae, Lagomorpha) is one of the best known and most widespread species of its genus. It was described from Sète, a karst filling located in southern France that has yielded a rich fauna of micromammals. Its age is estimated between 3.5–3.0 Ma. This study provides as complete as possible a picture of the cranial and dental morphology by the analysis of the characters and their variation. Usually, the cranial and postcranial material is poorly represented in the fossil record, and thus little studied. Abundance of cranial and dental remains in Sète is an exception and allows for a better characterisation of *P. michauxi*. Detailed comparisons with contemporary species show its great resemblances with *P. sorbinii* Masini, 1989 from Italy with regard to dental features, but it differs by the characters of the cranium and the mandible. It is well known that the Alpine uplift and the progressive aridification of the Mediterranean region since the terminal Miocene (Messinian) have led to the fragmentation of habitats and, as far as the genus *Prolagus* is concerned, to the occurrence of numerous speciations. To adapt to these new conditions, some Mio-Pliocene species of *Prolagus*, in particular *P. michauxi*, have developed an enlarged premolar foramen next to upper cheek teeth and numerous foramina on the hard palate that allow for better thermoregulation. The fragmentation of habitats may also explain a great variation in dental morphologies in various Pliocene species whose geographical range extends from Portugal to Ukraine and Asia Minor, and also to North Africa. Indeed, *P. michauxi* is abundantly represented in the Iberian Peninsula and the Maghreb. Also, it was reported from several sites in Greece and Asia Minor, but the material is scarce, which makes the identifications uncertain.

Key words: Lagomorpha, Prolagidae, *Prolagus*, Sète, Pliocene, systematics, dispersal, adaptation

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Introduction

In her doctoral thesis defended at the University of Montpellier II on the fossil lagomorphs of southwestern Europe, López-Martínez (1974) described several new species of *Prolagus* Pomel, 1853, and among others *Prolagus michauxi* López-Martínez, 1975. The year after, she published a note in the Bulletin de la Société géologique de France (López-Martínez and Thaler 1975) to officially define these new species. The type material of *P. michauxi* comes from the karst deposits of Sète (Hérault, southern France) and consists of a skull, several mandibles and isolated teeth. Later on, this species was reported from numerous localities from Portugal to Turkey. The NOW Community Database, consulted on October 2, 2024 enumerate 61 records of *P. michauxi*, of which 45 are in Spain, the others in Italy (1), Greece (6), Turkey (3), Morocco (5) and Algeria (1). Several other sites with *P. michauxi* or *P.* cf. *michauxi* are not listed in this Database, and surprisingly neither Sète which is the type locality of the species. According to the same database, the ages of these records extend from early Turolian to early Villanyian, ca. between 8.5–3.0 Ma. What does such spatial and temporal dispersion hide? Is it a species well-adapted to temperate climates of the Mediterranean coasts, as suggested by López-Martínez (2002) or a catch-all species that includes all fossils with some resemblance to those of Sète?

In the meantime, a prolagid from Italy was defined as a new species, *P. sorbinii* Masini, 1989; it resembles in size and dental morphology *P. michauxi*, but differs in some characteristics of its skull. Initially *P. sorbinii* was considered endemic to Italy (Masini 1989, Angelone 2007). Later on, other *Prolagus* remains from Italy, the Balkans and Anatolia, initially attributed to *P. michauxi* or cf. *michauxi*, were referred to this species. On the other hand, Fejfar et al. (2006: 98) estimated that "The material from Gundersheim 4 match well with another species *Prolagus michauxi* of the similar Ruscinian sites in Spain and France (López-Martínez 1989); this contemporaneous form is probably synonymous with the taxon described by Heller [i.e., *Prolagus bilobus*

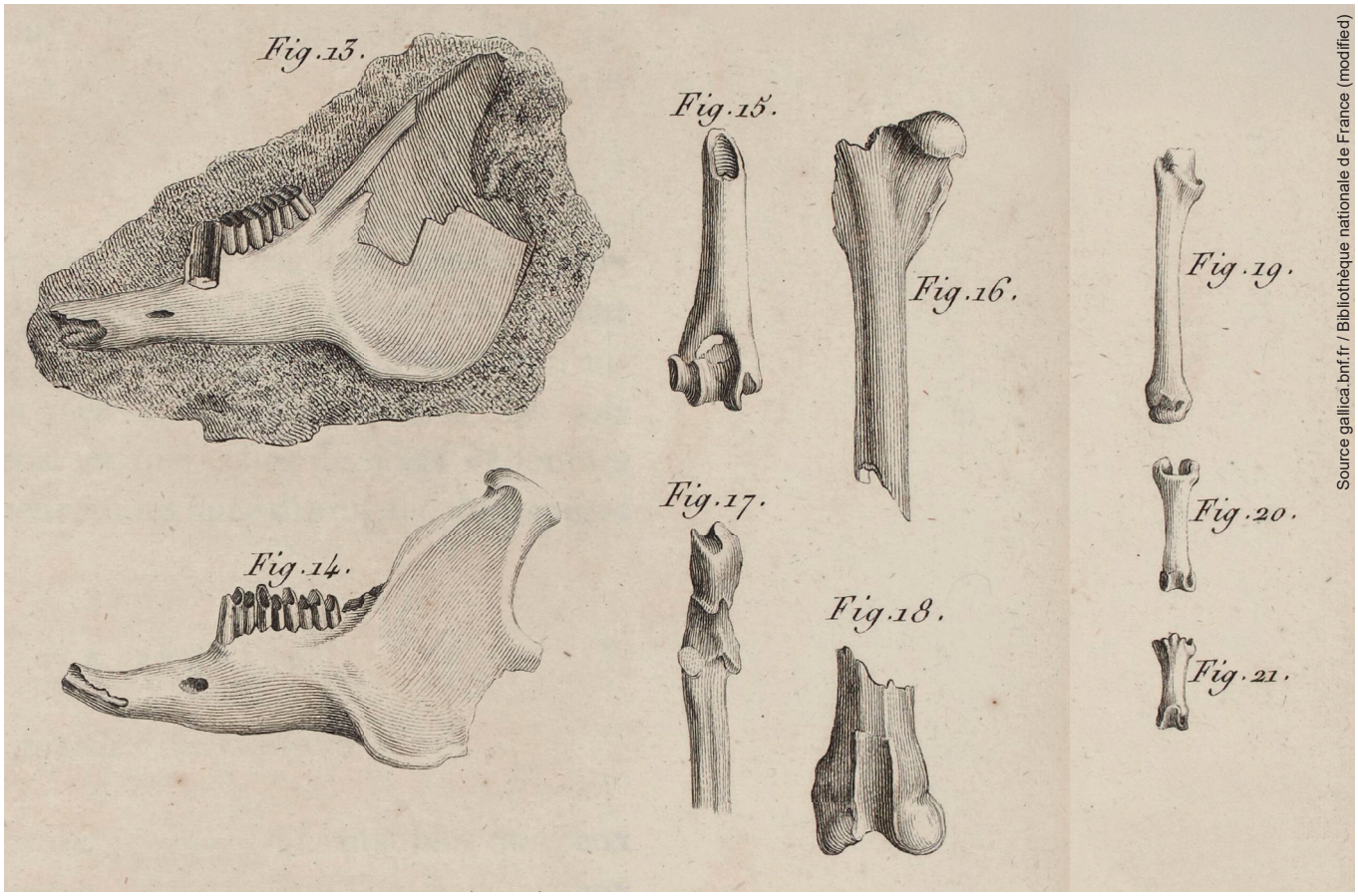
Heller, 1936]". At present, it is particularly confusing to know whether (i) the specific distinction between these three species is justified; (ii) if it is the case, what are the clear morphological criteria to characterize each of them; (iii) if all records reported to *P. michauxi* are justified.

In the context of recent developments in the knowledge of the Late Miocene and Pliocene Prolagidae, the attribution of new discoveries to one or another *Prolagus* species of this period has become problematic, partly due to the insufficient definition of the species themselves. The aim of the present study is to define *P. michauxi* by a thorough study based on more abundant material than when it was initially described.

The type locality of *P. michauxi* is an ossiferous breccia located on the seashore at the small peninsula of Cape Lazaret, at the foot of Mont Saint-Clair on which the town of Sète is founded. The precise geographical coordinates of the site are kept secret by the University of Montpellier II to prevent pillaging. In his work on "Recherches sur les Ossemens fossiles de Quadrupèdes, Volume 4, 1812", Georges Cuvier is probably the first author to talk about the ossiferous breccias of "Cette" and to describe the first remains of small mammals including a *Lagomys* illustrated by two hemimandibles and several postcranial bones (Text-fig. 1). He specified that there are fissure fillings with a reddish cement breccia, mixed with various bones of small and some large mammals among which the remains attributed to *Lagomys* are particularly abundant.

Jules de Christol (1802–1861) studied geological context, sedimentary characteristics and fossil content of various ossiferous breccias along the northern and western Mediterranean coasts. In his memoire, Christol (1834: 11) noted that "A Cette, on remarque que les parois des fentes qui contiennent les brèches sont recouvertes de stalactites, et alors le ciment, étant pénétré d'infiltrations de calcaire spâthique, est devenu très-solide; mais, dans quelques cavités de la même localité, où les stalactites ne se sont pas formées, la brèche osseuse est un limon argileux très rouge, susceptible d'être facilement pétri dans les doigts, et entièrement semblable à celui qui se forme actuellement. Ce limon contient autant d'ossemens que la brèche solide". However, he does not give any list of taxa represented in this breccia.

Marcel de Serres (1780–1862) was also interested in the breccia fillings of southern France. For that of Sète, in the third edition of his work on Cavernes à Ossements (Serres 1838: 183), he specifies that "Les débris de rongeurs sont de beaucoup plus abondants dans les brèches de Sète, surtout ceux qui se rapportent aux lièvres et aux lapins. Il existe au moins deux races de ces derniers: les uns de la taille de nos lapins, et d'autres d'un tier plus petits. On y voit également des campagnoles et d'autres espèces de rats". Ellenberger (1953) carried out a detailed study of the karst system of the Sète region and concluded that the bone breccias of Sète are part of a network of ancient caves that were decapitated by marine erosion due to the rise of sea level during the Pleistocene. Thaler (1955a, b, 1966) began an intensive exploitation of this filling and published the first results on its fauna. The abundance of small vertebrate remains is the result of the accumulation of owl pellets (Thaler 1966).



Text-fig. 1. Two hemimandibles and several postcranial bones from Cette (present name Sète) illustrated by Cuvier (1812: pl. II) as belonging to *Lagomys* (now referred to *Prolagus*).

In the second half of the 20th century, numerous studies on the micromammals of Sète, often combined with those of neighboring sites, made it possible to draw up a detailed faunal list for this site. For rodents, the most up-to-date list is that of Bachelet (1990a): *Blancomys neglectus*, *Trilophomys pyrenaicus*, *Ruscinomys europaeus*, *Cricetus angustidens*, *Mimomys occitanus*, *Mimomys capettai*, *Micromys praeminutus*, *Occitanomys brailloni*, *O. ellenbergeri*, *Stephanomys donnezani*, *Paraethomys jaegeri*, *P. meini*, *Castillomys crusafonti*, *Apodemus gorafensis*, *A. dominans, A. jeanteti*, *Eliomys intermedius.*

Regarding the age of the fauna, the authors agree that it dates from the Late Pliocene. For Chaline and Laurin (1986), who analyzed the gradual evolution of a *Mimomys* lineage, the age of Sète must be 3.2 Ma. By regression analysis applied to several rodent lineages (Murinae and Arvicolinae) and taking into account the progressive increase in size between two reference points, Bachelet (1990b) calculated an age of 3.36 Ma. Michaux et al. (1997) place Sète between the Mont-Hélène and Seynes deposits, and assign a numerical age of 3.5 Ma. Aguilar et al. (2002, 2007) have rejuvenated this age to about 3 Ma in comparative studies of Pliocene micromammal faunas from southern France.

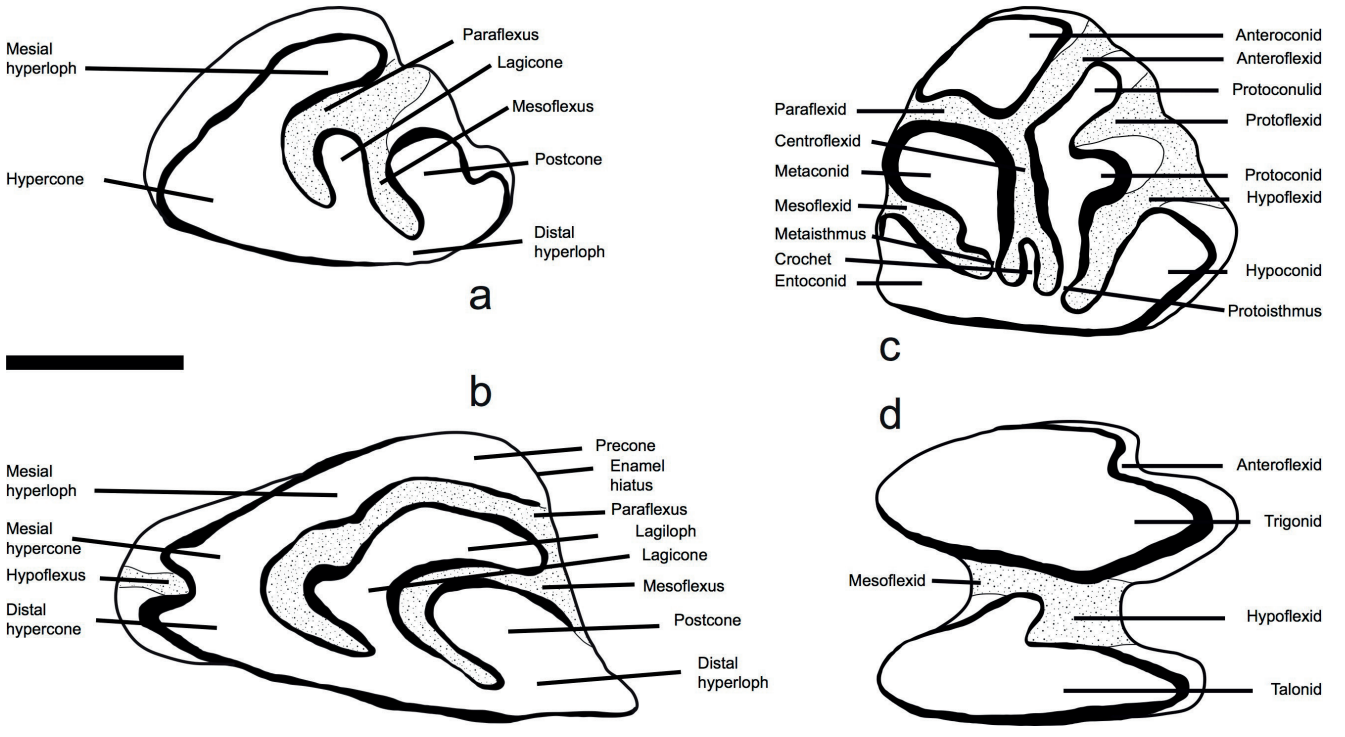
Material and methods

The lagomorph fossils of Sète here studied came from two collections: the type material used by López-Martínez (1974) in the Muséum National d'Histoire Naturelle of Paris, and an unstudied collection preserved at the Université Claude Bernard-Lyon 1 in Villeurbanne.

For the comparison of cranial characters, we used the figures and descriptions of Dawson (1969) for *Prolagus sardus* (Wagner, 1829) from Sardinia, unpublished cranial fragments of the same species from Corsica and preserved in the paleontology collections of the Paris Museum, as well as the material of Lortet (1872) from the Bastia bone breccia preserved in the Conservation Center of the Confluences Museum in Lyon. Most species of *Prolagus* are known only by their dentition and in the best cases their mandible. Among the exceptions is *P. oeningensis* (König, 1825) whose type specimen is a slab on which the skull is seen in lateral view; unfortunately, it is badly crushed, not allowing to appreciate its characters. Also, Masini (1989) described the new species *Prolagus sorbinii* based on a partial skeleton, the cranium of which is exposed in ventral view on a clay slab, allowing comparison of some characters with that of *P. michauxi* of Sète.

We preferred to illustrate all teeth with drawings, rather than with photos, for a better expression of dental features. All drawings have been made by the author with a camera lucida mounted on a Leica M3Z binocular microscope. In all illustrations of cheek teeth, the mesial side is toward the top of the page, enamel is represented in black, dentine in white and cement with dots. The dashed lines indicate the deepest part of the grooves on the occlusal surface which actually correspond to the direction of transverse grinding movements.

All measurements are in millimeters. They were taken with a Mitutoyo measuring equipment on the occlusal surface of teeth, and they indicate maximum length and width of teeth in the sagittal and transverse axes, from the external margin of enamel. This does not always correspond to the greatest length or width of teeth, since in many lagomorphs



Text-fig. 2. Dental terminology used in the present study to describe teeth of *Prolagus* (modified after López-Martínez and Thaler 1975, López-Martínez 1989). a: left P2, b: left P3, c: right p3, d: right m1. Enamel is represented in black, dentine in white, and the cement covered parts are dotted. Scale bar = 1 mm.

there is, as a rule, an additional coat of cement of variable thickness. The terminology for skull osteology follows Wible (2007) updated by Wolniewicz and Fostowicz-Frelik (2021), and for dental characters López-Martínez (1974, 1989) (Text-fig. 2). Upper/lower milk teeth are abbreviated as D/d, premolars as P/p, and molars as M/m. The general term of "lower molariforms" is used for p4–m1.

Systematic palaeontology

Order Lagomorpha Brandt, 1855
Family Prolagidae Gureev, 1960

Genus *Prolagus* Pomel, 1853

***Prolagus michauxi* López-Martínez, 1975**

Nomenclatural remark. López-Martínez (1974) has described several new species, including *Prolagus michauxi*, in her unpublished doctoral dissertation, supervised by her professor L. Thaler. The year after López-Martínez and Thaler (1975) published a paper in which all species newly named in the PhD thesis of López-Martínez were officially named. Although this note is co-authored by N. López-Martínez and L. Thaler, it is specified on p. 852 that the author of the new species is indeed N. López-Martínez.

Holotype. Partly damaged cranium CB.UMSL-l001. This specimen number was given by López-Martínez (1974) and López-Martínez and Thaler (1975) when the type material was stored in the collections of University of Montpellier. Later on, the type material was transferred to Museum National d'Histoire Naturelle in Paris where it is currently preserved as "Braillon collection", and the new number of the type skull is MNHN.F.STB212.

Type locality. Sète (Hérault, France, MN 15).

Original diagnosis. "*Prolagus* de taille plus grande que *P. oeningensis*, plus petite que *P. sardus*. Il a le conduit maxillo-incisif fermé à l'extérieur, et une P2 supérieure évoluée comme *P. sardus*, mais le crâne a un seul trou incisif, et les molaires supérieures ont des fossettes comme *P. oeningensis*. Le museau court, le foramen prémolaire très grand, les rangées supérieures divergentes, les arcs zygomatiques larges et saillants, et la P/3 inférieure large, à crochet fréquent et à robuste protoconulide, ce sont des caractères nouveaux" (López-Martínez and Thaler 1975: 856).

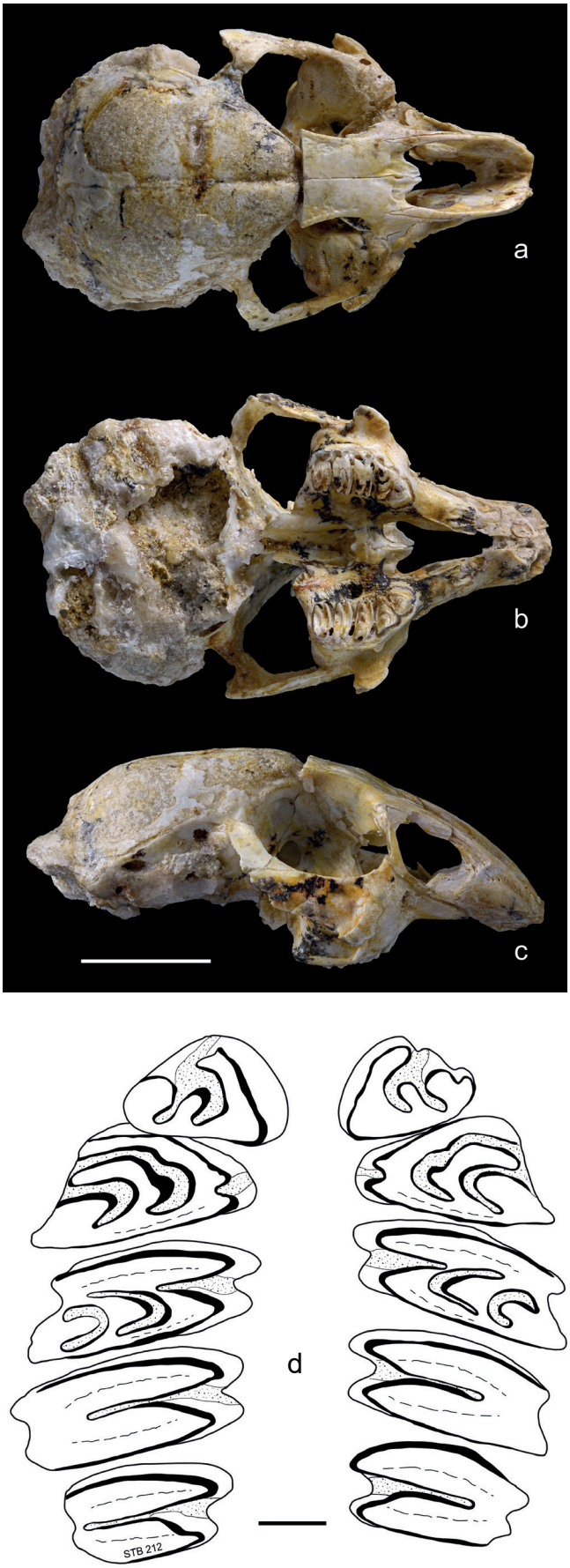
Emended diagnosis. A species of *Prolagus* of moderate size, with a short snout, upper diastema hollowed, the orbit broad and rounded, its anterior border above the p3, cranial profile arched, a little relapse before the occipital crest. Incisive foramen simple and starts between the second incisors. Toothrows arched and widened backwards. Premolar foramen large and situated next to P4 or P4/M1 septum. Mandible with diastema shorter than alveolar length, high ascending ramus, and weak masseteric crest. P2 with a moderately developed mesial hyperloph with or without enamel hiatus. Upper molars with a deep hypoflexus and occasional enamel island. p3 of variable morphology, longer than wide, anteroconid as big as or even bigger than the metaconid, often angulate bearing buccal or lingual fold, and displaced lingually; protoconulid as thick as the protoconid in most specimens, crochet is absent in almost half p3s, and when present it may be residual or moderately developed, often situated next to metaisthmus, but rarely at the bottom of centroflexid. p4, m1 and m2 have a well-defined notch on the mesial side of talonid, m1 and m2 have trigonid depressed mesiobuccally or a shallow anteroflexid in some specimens.

Differential diagnosis. *Prolagus michauxi* is a moderate sized species and differs in that from the large Plio-Pleistocene species known in Italy and Spain. Among the contemporaneous species, *P. crusafonti* López-Martínez, 1975 and *P. ibericus* López-Martínez, 1975 differ from the prolagid of Sète in having P2 without mesial hyperloph, and p3 with a small anteroconid. *Prolagus bilobus* Heller, 1936 is larger, its p3 is elongated and bears a strong crochet at the bottom of centroflexid. *P. latiuncinatus* Angelone et Čermák, 2015 from Polgardi 2 in Hungary has p3 short and wide, with a well-developed crochet at the bottom of the centroflexid and no enamel hiatus on the mesial hyperloph of P2. The type material of *P. sorbinii* Masini, 1989 is different from *P. michauxi* in having elongated muzzle that gradually widens backwards towards the anterior zygomatic process, whilest it is rather squarish on the cranium of Sète, larger premolar foramen, a high body mandible and wide ascending ramus on the mandible, although its dentition displays similar features, unless for new materials referred to this species from several other Italian localities.

Material. Material from Sète in the collections of the Paris Museum: In addition to the type cranium, the type material consists of 19 fragments of maxillae (5 adults and 14 juveniles) bearing various cheek teeth or simply edentulous (STB299–307, STB353–356, STB900–905), three upper incisors (STB914–916), 15 isolated P3s (STB318–332), 27 P4s (STB333–352, STB358-364), 31 upper molars (STB365–390, STB906–913), two almost complete hemimandibles (STB213 and 308), 15 fragmentary hemimandibles (three adults and 12 juveniles) bearing various cheek teeth (STB309–317, STB917–922), two lower incisors (STB923–924), 10 isolated p3s (STB925–934) 12 lower cheek teeth (STB935–946).

Material from Sète in the collections of the Université Claude Bernard-Lyon 1 (UCBL-FSL): 9 fragments of maxillae (6 adults and 3 juveniles) bearing various cheek teeth or simply edentulous (540436–540443, 540466), a first upper incisor (540434), a second upper incisor (540535), 7 isolated P2s (540366–540370, 540445, 540464–540465), 20 P3s (540371–540387, 540444, 540446), 16 P4s (540388–540401, 540447–540448), 47 upper molars (540402–540433, 540449–540463), nine fragments of hemimandibles bearing various cheek teeth (540345–540353), 26 p3s (540327–540344, 540354–540360, 540365), four lower molariform teeth (540361–540364).

Description. **Cranium** (Text-figs 3, 5a). In dorsal view, the cranium displays three parts: short muzzle (see



Text-fig. 3. a–d: Cranium (holotype, CB.UMSL-l001) of *Prolagus michauxi* López-Martínez, 1975 from Sète in dorsal (a), ventral (b) and lateral (c) views and occlusal view of right and left cheek teeth of this cranium (d). Scale bars are 10 mm for the cranium, and 1 mm for the dentition.

below), maxillary-frontal complex bearing cheek teeth, and braincase. The nasal bones are not preserved, but their imprint on the premaxillae and frontals show that they were of almost equal width from front to back and barely flared midway. Their distal imprint on the frontals slightly exceeds the level of the mesial margin of zygomatic arches. The posterodorsal process of premaxilla punches distally into the frontal well beyond the distal limit of the nasals. The frontomaxillary suture is sinuous and is located just before the middle of the orbits. The zygomatic arches widen backwards. The frontal is rather flat, but its distal part is not preserved; consequently, its distal extension and its suture with the parietals cannot be observed. Behind the frontals the cranial roof is stripped of its bone, exposing the braincase, which is drop shaped.

In lateral view, the roof of the cranium displays a regular dorsal convexity from incisors up to the occipital bone, but a sudden break about four millimeters before the occipital crest. Such a break in the profile of the roof is not observed in *P. sardus* of which several skulls are known (for instance Dawson 1969, Wilkens 2005, 2012). The upper diastema makes a sharp angle in front of P2. The maxillary fenestration is large and limited distally by a narrow anterior orbital rim. The infraorbital foramen is small and situated just anterior to the level of P2. The orbital fossa is somewhat larger than in *P. sardus*, its basal margin rounded, and its mesial rim is above the P2/P3 limit.

In ventral view, the part of the cranium behind the posterior zygomatic processes is stripped of its bone, and only the volume of the braincaise is preserved. The first striking feature of the Sète cranium is its short muzzle. To assess this feature, we compared the length of the diastema between I2 and P2, with the length of the alveoli of P2–M2 (Tab. 1). On the Sète cranium, these two lengths are identical. In *P. sardus*, the muzzle is longer, the diastema being 114 % (n = 6) compared to the alveolar length. The muzzle is well delimited from the rest of the skull by a bend between the maxilla and the zygomatic process of the maxilla. This bend is clearly less marked in *P. sardus* and *P. sorbinii*. The tooth rows are arched and spread out distally. The mesial zygomatic process is strong and clearly detaches from the maxilla. The incisive foramen is simple, starts mesially between the I2s, more anteriorly than in *P. sardus*. The palatal vacuities enlarge distally and end at the level of the P2/P3 septum. The hard palate is short; its anterior process is clearly stronger than the posterior process. The choanae begin at the P4/M1 boundary and are moderately wide. The zygomatic arches are much more spaced than in *P. sardus*, and consequently the shape of the orbital fossa in basal view is trapezoidal on the Sète cranium, while it is rather rectangular in *P. sardus*. Also, the shape of the braincase is globular on the Sète specimen, but progressively widened backwards in *P. sardus.* On the palate, the premolar foramen is large, almost round in shape, and it is located opposite the distal part of the P4 in six specimens, while in three other cranial fragments this foramen extends in front of the P4/M1 boundary.

Mandible (Text-figs 4, 5b, c). Over 20 specimens more or less complete are preserved. The diastema is short (average 6.4 mm, n = 10), shorter than p3–m2 alveolar length (average 8.0 mm, n = 10). The ventral margin of the body

Table 1. Measurements of cranium and mandible for *P. michauxi* of Sète, *P. sorbinii* from Monte Castellaro (Italy), *P. sardus* from Corsica and Sardinia and *Prolagus* sp. from Beremend 26 and 39 (Hungary). All measurements are in millimetres.

Measurements	*P. michauxi* Sète	*P. sorbinii**	*P. sardus***	*P. bilobus**** Gundersheim-Findling	*Prolagus* sp.**** Beremend 26 and 39
Length cranium (without I)	>41	50	52.5	–	–
Length nasal	>10	–	–	–	–
Length muzzle	10.1	13.8	–	–	–
Width zygomatics distal	23.8	>26	–	–	–
Width min interorbitary	6.1	–	–	–	–
Width braincase	>21	? 31.0	–	–	–
Orbite length	10.4	–	–	–	–
Orbite height	8.3	–	–	–	–
Length upper diastema right	7.8–8.6	10.9–12.0	–	–	–
Alveoli P2–M2 length	8.4	9.5	–	–	–
P2–M2 length	7.8	9.0	10.6	–	–
Choanae width	3.1	deformed	–	–	–
Hard palate min length	2.2	deformed	–	–	–
Mandible total L (without i)	31.5	34.0	–	–	–
Diastema length	6.4 (4)	7.9	–	5.75	8.2
p3–m2 alveolar length	8.0 (4)	8.8	–	7.95	9.2
p3–m2 length	7.8	8.6	10.2	–	6.1
Body height max	8.0	11.0	–	6.5	8.2
Body height under m2	6.7	9.2	–	6.23	7.9
Ascending ramus height	20.4	21.8	–	25.4	21.4
Angle body-ramus	120°	110°	120–135°	130°	115°

*Masini 1989, **Tobien 1935, ***Čermák et al. 2021

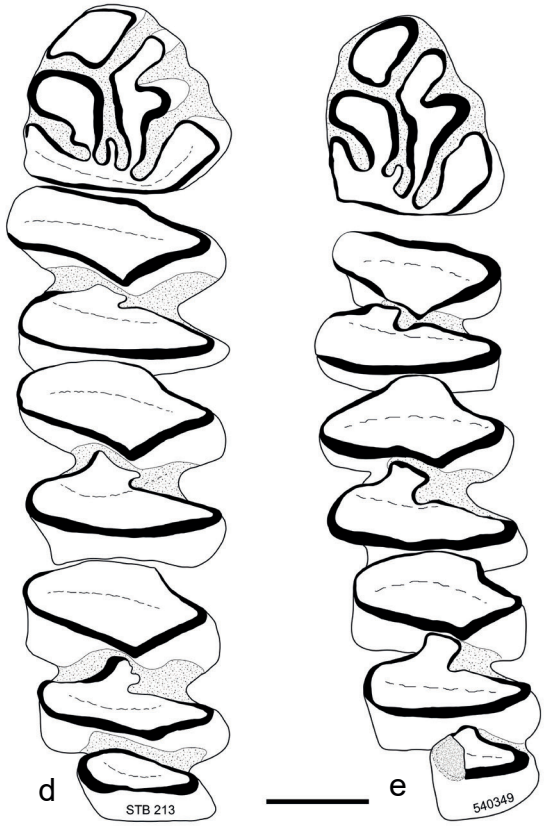
is moderately curved under cheek teeth, but depressed backward at the limit of body-ascending ramus. The mesial mental foramen is small, situated under the mesial edge of p3, while the distal mental foramen is large and situated beneath the m1–m2 contact, close to the ventral margin. The masseteric fossa is not well delimited mesially, the angular process is strong, and distally hook-shaped. The ascending ramus is high, and the angle between the alveolar line and the mesial margin of the ascending ramus is 120°. The coronoid process is reduced to an extra curvature on the mesial margin of the ascending ramus. The articular surface on the articular process is teardrop-shaped, facing forward. In lingual view, the mandibular body is smooth and flatter than in buccal view. The articular surface of the symphysis extends backwards less than half of the diastema. The mylohyoid line continues under the entire dental row close to the ventral margin, and it rises slightly under the molars. The mandibular foramen is large, situated below the level of alveolar line and well behind the m2, directly above the ventral swelling between the body and angular process. Between the mandibular foramen and the articular process the ascending ramus has a large depression (pterygoid fovea in Wible 2007, and Wolniewicz and Fostowicz-Frelik 2021), well defined anteriorly but open posteriorly.

Dentition. The first upper incisors (I1) are elongated mediolaterally, but short anteroposteriorly. The mesial groove forms an open V displaced medially. The enamel is thin and covers the anterior face and partially the lateral face. This incisor has two pulp cavities. The second upper incisor (I2) is ellipsoid in outline and placed distomedially to I1. Its medial wall is less rounded than its lateral wall.

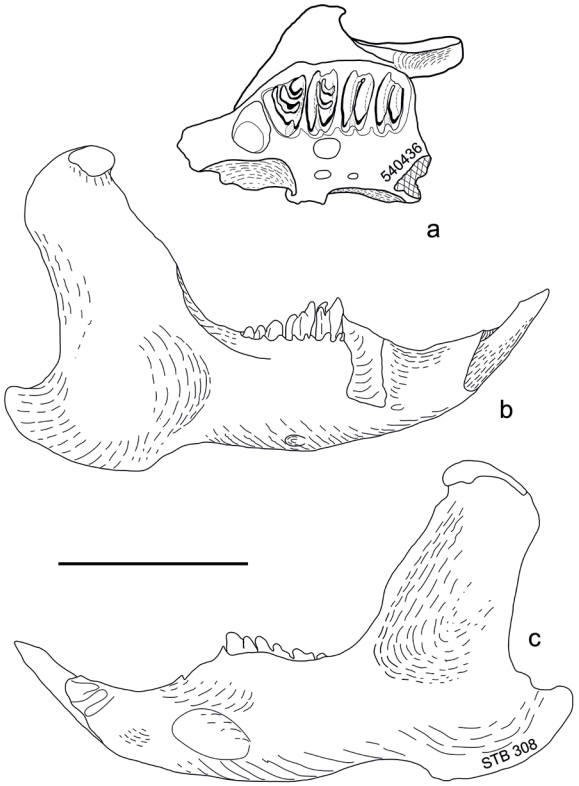
The P2 is represented by 10 specimens, three of which are on the maxilla with other cheek teeth. It is displaced lingually relative to P3. The mesial hyperloph covers part of the mesial face, but does not exceed the level of the mesoflexus buccally. Its buccal end may be with or without enamel hiatus. The mesoflexus and paraflexus, as well as the lagicone that separates them, are oblique on eight P2s, but rather rectilinear on two others. The lagicone is always thinner than the postcone. One P2 has a small additional groove that cuts into the postcone.

The P3 is known by 42 specimens. The buccal face may be more (36) or less (6) oblique, but in all specimens the distal hyperloph is very sharp. The mesial hyperloph have enamel hiatus in only three P3s. The angle between the lagicone and lagiloph is more or less sharp in 28 specimens, while in 14 others there is no angle. The lagiloph does not reach the buccal margin on 24 P3s out of 42. The hypoflexus may be absent (3), short and V-shaped (29) or narrow and quite deep (10), and when it exists it is filled with cement. The postcone has an ellipsoid outline. The enamel is thick around the cusps, but thin along the lophs.

The P4 has mesial and distal lophs of approximately equal width (see Tab. 2). The hypoflexus extends buccally slightly beyond the lingual margin of the paraflexus. The paraflexus is a J-shaped and its mesial part is oblique, while



Text-fig. 4. ***Prolagus michauxi*** **López-Martínez, 1975 from Sète. a–d: right hemimandible in dorsal (a), buccal (b) and medial (c) views and occlusal view of its dentition p3–m2 (d). e: occlusal view of right p3–m2 of the hemimandible UCBL-FSL.540349. The collection number of specimens is indicated on the drawings. Scale bars are 10 mm for the mandible, and 1 mm for the dentition.**



Text-fig. 5. ***Prolagus michauxi*** **López-Martínez, 1975 from Sète. a: fragment of cranium bearing P3–M2 in ventral view. b–c: right mandible bearing p4–m2 in buccal (b) and medial (c) views. The collection number of specimens is indicated on the drawings. Scale bar = 10 mm.**

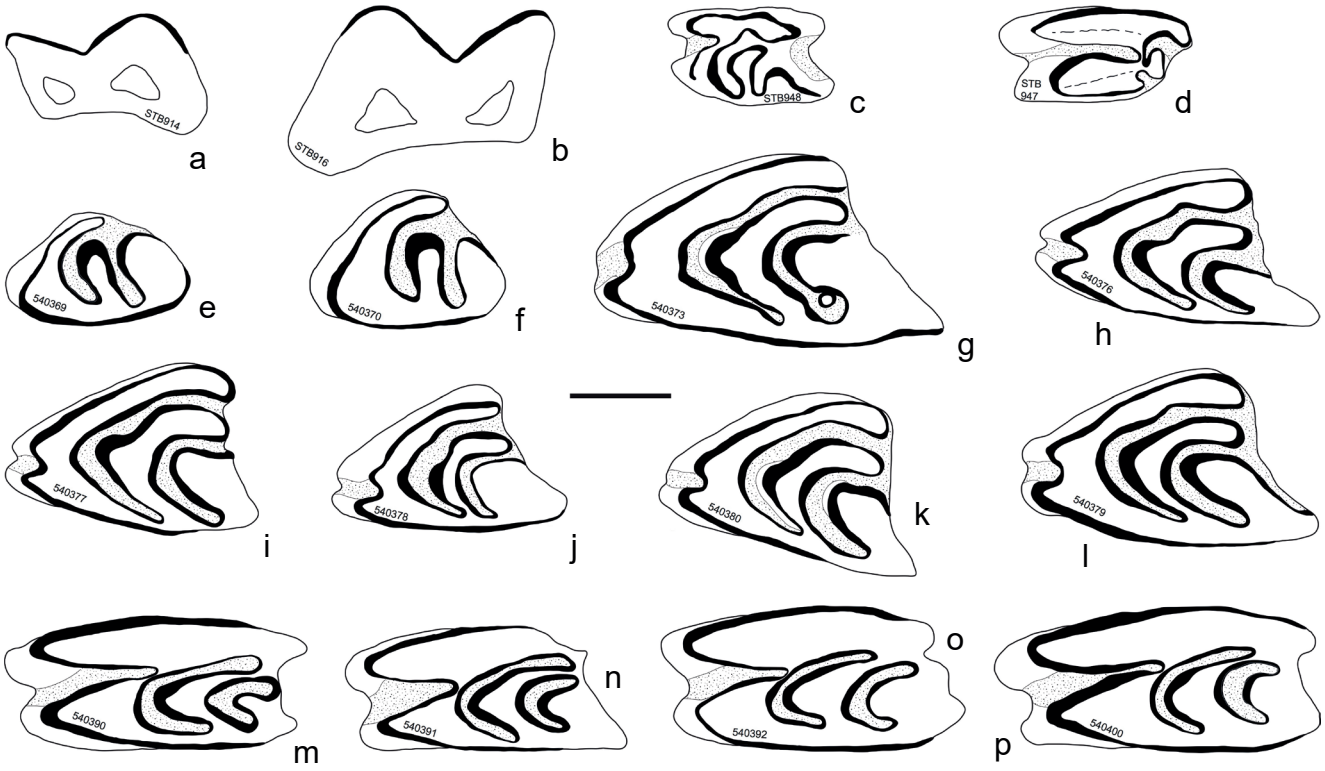
the mesoflexus, always isolated, has a horseshoe shape.

The M1 and M2 have a deep hypoflexus that cuts into the occlusal surface for more than two-thirds of its width. Eight M1s have a small round or ellipsoid enamel island, while 21 others are devoid of it. No M2 has this structure.

Most p3s (35) have an elongated occlusal outline (length > width), but four p3s which are slightly wider than long. In all p3s the anteroconid is more or less shifted lingually, and in 17/35 p3s it is almost longitudinally aligned with the metaconid and entoconid. It is larger than the metaconid (16/35), similar in size (16/35) or even smaller (3/35). Its outline is ellipsoid (13/35) or rather angular (28/35), leaning towards the metaconid, and in 16 cases it bears a buccal depression or indentation. The metaconid is in most cases pear-shaped with its tail attached to the entoconid by a narrow enamel band (the metaisthmus), except in four specimens which have metaconid isolated. At any case, its buccal edge is rather strait along the centroflexid, while the lingual edge is rounded. The protoconulid may be as thick as the protoconid (24/35) or thinner (11/35). The protoisthmus is thin in most p3s, except in five of 35 specimens its thickness exceeds 0.2 mm. The mesoflexid is rather narrow, slightly oblique (30) or strongly bent backwards (5); two p3s of 35 have mesoflexid closed (Text-fig. 6). The crochet is lacking in 16 p3s, barely developed (residual) on 12, but strong on 7 others. When present, it may be at the bottom of the centroflexid (2/19) or next to the metaisthmus (17/19). The entoconid is as thick as the hypoconid (23/35) or rather thin

Table 2 Measurements of upper and lower teeth of *Prolagus michauxi* from Sète (Hérault, France). N = number of specimens, ant = anterior, post = posterior. All measurements are in millimetres.

Upper teeth	N	Length		Width ant		Width post	
		Range	Mean	Range	Mean	Range	Mean
Incisor	6	1.04–1.51	1.2	1.67–2.28	1.97	–	–
P2	9	0.96–1.29	1.12	1.66–2.12	1.83	–	–
P3	38/37	1.28–1.90	1.62	2.02–3.31	2.64	–	–
P4	39/38/38	1.17–1.70	1.38	2.15–3.37	2.6	2.01–3.21	2.56
M1	65	1.10–1.72	1.36	1.77–3.45	2.61	1.72–3.21	2.4
M2	11	1.17–1.63	1.36	2.33–3.06	2.57	1.76–2.81	2.19
Lower teeth	**N**	**Length**		**Width ant**		**Width post**	
		Range	**Mean**	**Range**	**Mean**	**Range**	**Mean**
incisor	2	2.16–2.18	2.17	1.21–1.24	1.23	–	–
p3	29/34	1.63–2.33	1.91	1.48–2.10	1.77	–	–
p4	15	1.40–1.87	1.63	1.58–2.10	1.82	1.50–2.06	1.79
m1	8	1.55–1.90	1.71	1.54–2.03	1.78	1.55–2.00	1.82
m2	8	2.14–2.69	2.34	1.46–1.91	1.73	1.43–1.78	1.65



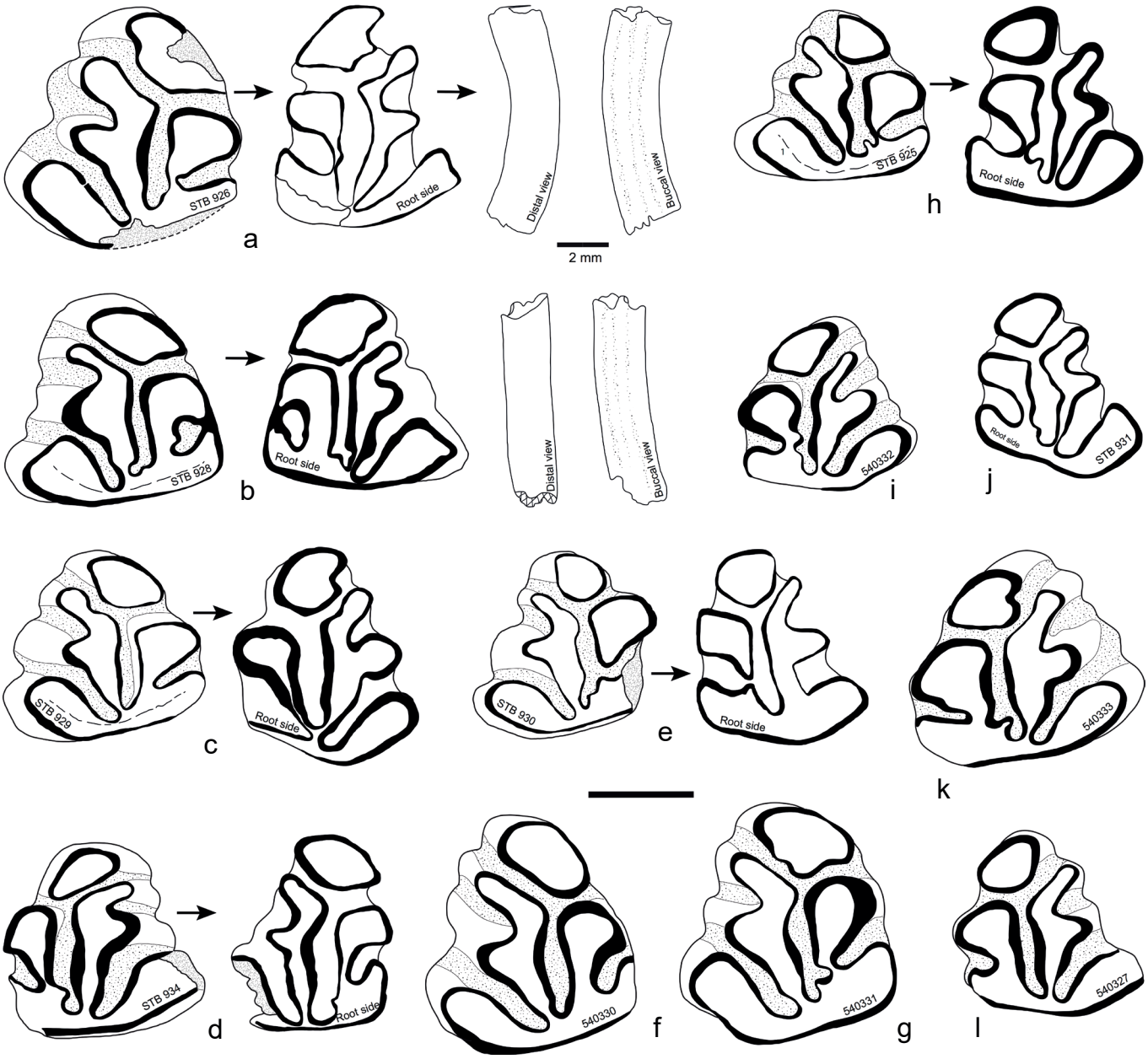
Text-fig. 6. Upper teeth of *Prolagus michauxi* López-Martínez, 1975 from Sète in occlusal view. a: section of a juvenile right upper incisor, b: section of a left upper incisor, c: left D3, d: left D4, e: left P2, f: left P2, g–l: left P3s, m–p: left P4s. The collection number of specimens is indicated on the drawings. Scale bar = 1 mm.

(12/35). It bears enamel hiatus on its lingual margin on 15 p3s.

The p4s, m1s and m2s have anteroflexid well marked in young individuals, which disappears or remains as a depression in adults. All p4s, m1s and m2s have a well-marked notch filled with cement on the mesiobuccal side of the talonid.

Discussion

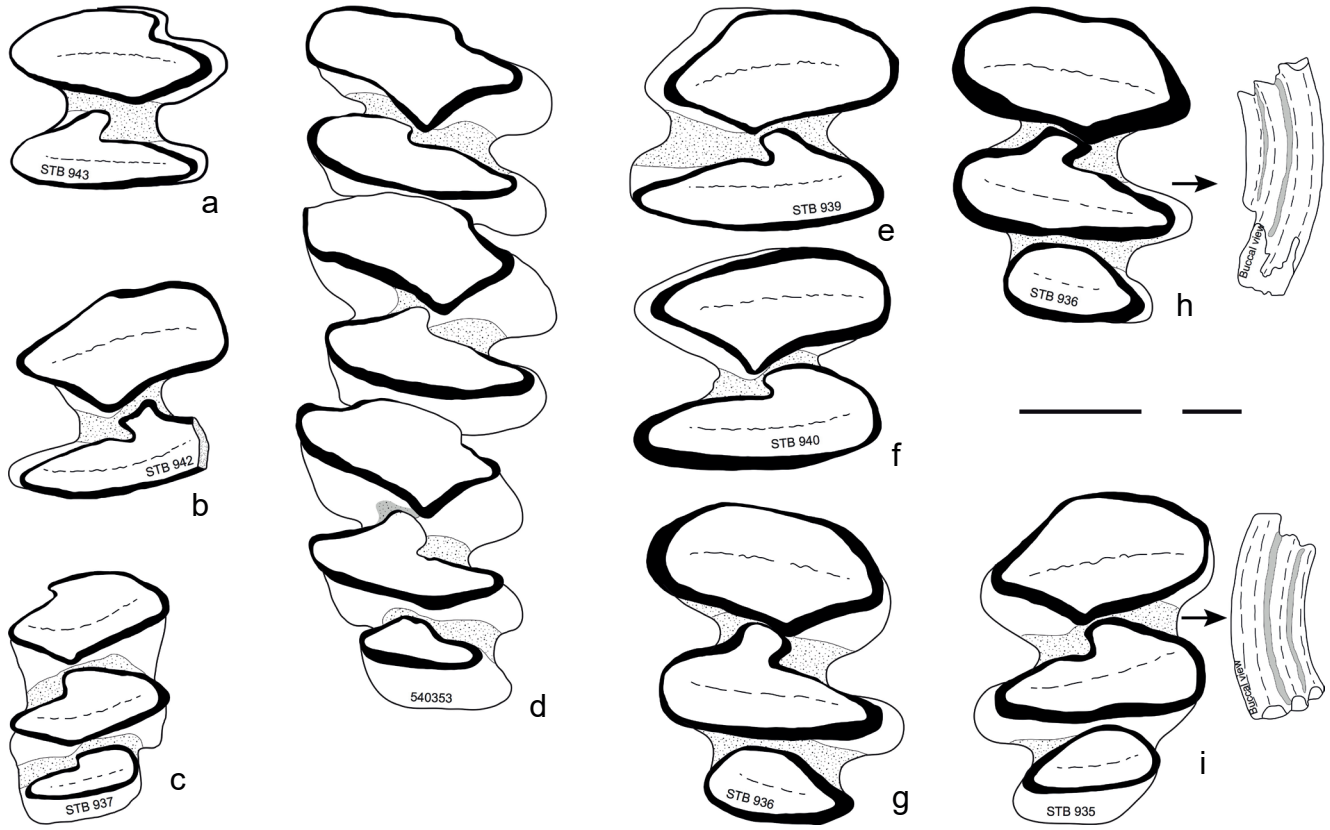
In the introduction to her doctoral thesis López-Martínez (1974: 8) noted that "The palaeontological study of lagomorphs is essentially based, like that of other groups of micromammals, on the morphology and variability of dental parts. They contain much more information than any other bony part of the body". Indeed, the abundance of dental remains in the fossil record has led students of lagomorphs to base the systematics of fossil taxa on dental characters, particularly those of P2 and p3, while the cranial and postcranial characters are generally neglected. Studies including cranial bones and postcranial elements are rare, and/or exceptionally reported in the definition of fossil lagomorph species. An exception is the mandible, which is better preserved and



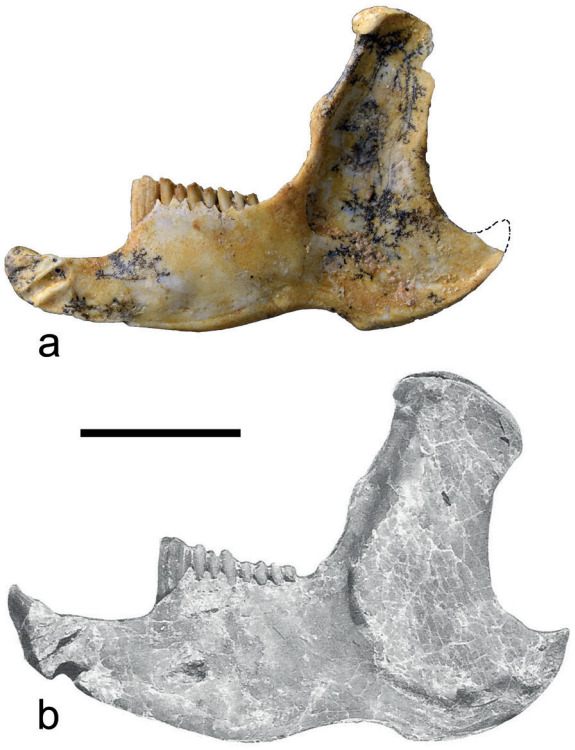
Text-fig. 7. Eight p3s of *Prolagus michauxi* López-Martínez, 1975 from Sète in occlusal and root views, and for (a) and (b) in distal and buccal views. a: left p3, b: left p3, c: left p3, d: right p3, e: left p3, f: left p3, g: left p3, h: left p3, i: right p3, j: juvenile right p3, k: right p3, l: right p3. The collection number of specimens is indicated on the drawings. Large scale bar for occlusal views = 1 mm; small scale bar for lateral views = 2 mm.

often described and illustrated. In this context *Prolagus michauxi* is an exception, because López-Martínez defined it from its skull and dentition altogether (López-Martínez 1974, 1989, López-Martínez and Thaler 1975).

More than twenty species have been reported to the genus *Prolagus* (López-Martínez 1989, 2002, Angelone and Čermák 2015, Čermák et al. 2021, Vasileiadou and Sylvestrou 2022). They are known in Europe from the Iberian Peninsula to Ukraine, in Asia Minor, and also in the Maghreb, for a time interval that extends from the later Lower Miocene (MN 3) to the Holocene (Dupré et al. 2022, Sen and Geraads 2023, Sen et al. 2024). For the comparison of *Prolagus michauxi* of Sète, we will only consider species from the latest Miocene and Pliocene, those having an average size close to that of *P. michauxi*, and some similarities in their dental and skull characters. Species from Early and Middle Miocene have archaic features (on the p3 small and round anteroconid, metaconid connected to the protoconid, on the P2 the absence of mesial hyporloph…), and they are not retained for comparison. Also, it seems useless to compare *P. michauxi* of Sète with the endemic species of Italy which have very large size and/or developed new characters such as the strong mesial hyperloph extended mesially and buccally on the P2, unusual enamel folds on the premolars and molars etc. (Mazza 1987, Angelone 2007, 2008a, Angelone et al. 2020). Also excluded are all *Prolagus* species having P2 without mesial hyperloph, which is a typical ancestral feature that some Late Miocene and Plio-Pleistocene species have preserved, such as *P. crusafonti* López-Martínez, 1975 and *P. ibericus* López-Martínez, 1975.



Text-fig. 8. Lower cheek teeth of *Prolagus michauxi* López-Martínez, 1975 from Sète. a: right m1, b: left p4, c: juvenile left m2, d: right p4–m2, e: left p4 or m1, f: left p4 or m1, g: right m2, h: right m2 in occlusal and buccal views, i: left m2 in occlusal and buccal views. The collection number of specimens is indicated on the drawings. Large scale bar for occlusal views = 1 mm; small scale bar for buccal views = 2 mm.



Text-fig. 9. Comparison of the mandibles of *Prolagus michauxi* from Sète (a) and that of *P. sorbinii* from Monte Castellaro (b) in their lingual views.

For most species of *Prolagus*, the cranium is not known except for *Prolagus oeningensis* (König, 1825), *P. sorbinii* Masini, 1989 and *P. sardus* (Wagner, 1829). The holotype of *P. oeningensis* is a partial skeleton represented on a slab where the skull is seen from the left lateral side. The illustrations and descriptions by König (1825) and later on by von Meyer (1845) are inadequate for comparison since the diagnostic features of the skull and dentition are not visible.

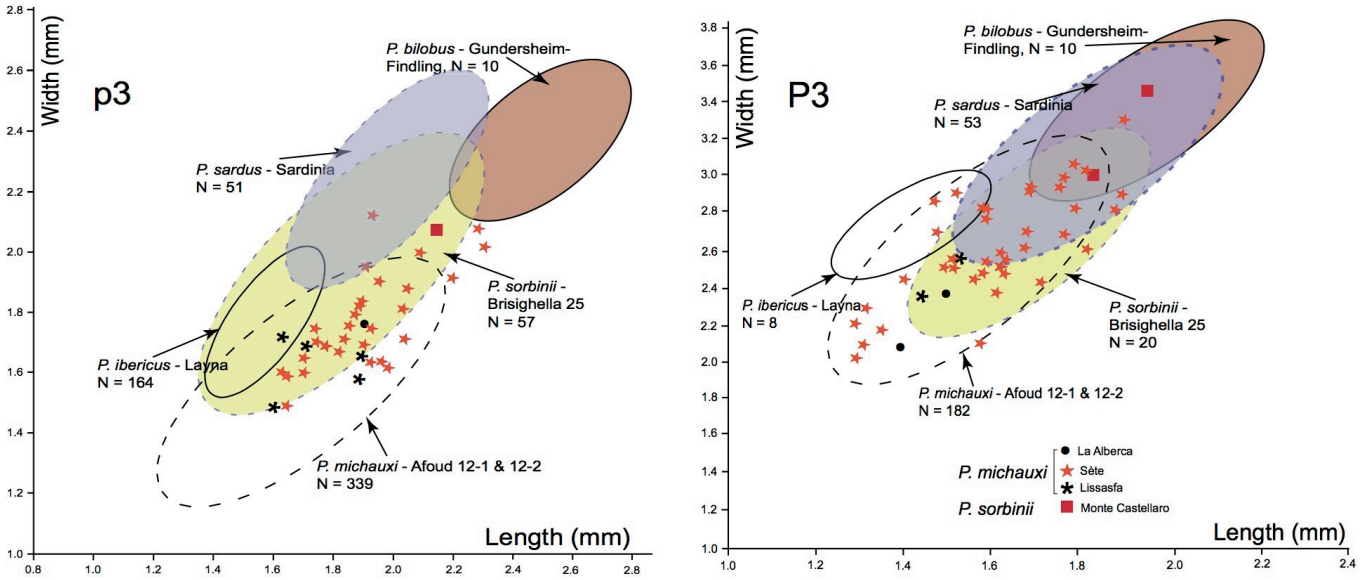
Masini (1989) described a new species, *Prolagus sorbinii*, based on a partial skeleton from Monte Castellaro in Italy, preserved on a clay slab. Later on, Angelone (2007), Angelone and Cavallo (2010), Angelone and Rook (2012) and Angelone et al. (2021) referred to this species several other findings (only teeth) from Mio-Pliocene localities of Italy. The type cranium from Monte Castellaro (Messinian, Italy) is displayed on ventral view, so it can only be compared with that of Sète on this part. Masini (1989: 300) noted that "The muzzle is narrow and fairly elongated, with a long premaxillar bone". The ratio of upper diastema/alveolar length, measured on the illustrations of this article is 114, similar to that of *P. sardus* (Tab. 1). In this character, it clearly differs from the cranium of Sète, which has a ratio of 100. However, as noted by Masini (1989: 300), the skull is crushed and "deformed, in particular the muzzle on the right side is broken at the sagittal plane and rotated", this preventing complete confidence in this ratio. Indeed, as much as the upper diastema appears long, the mandibular diastema is particularly short (L diastema 7.7 mm/L toothrow 8.8 = 88 %) according to the measurements published by

Masini (1989). In this species, the position of the incisive foramen is more distal than in *P. michauxi*, and it tends to be divided. The palatal vacuities on the *P. sorbinii* cranium seem narrower, but this cannot be ascertained because of the deformed state of the muzzle. Also in this species the premolar foramen is larger and situated next to P4, while in *P. michauxi* it lies more distally next to the second half of P4 or even a little behind (see Masini 1989: pl. 2, fig. 2, pl. 3, fig. 1).

Compared to the cranium of *P. sorbinii*, the specimen of Sète is different in having short muzzle (25 % of the total length of cranium versus about 29 % in *P. sorbinii* and 32 % in *P. sardus*), a better marked angle between the muzzle and the anterior process of zygomatic arc while in *P. sorbinii*, as well as in *P. sardus*, the sides of the muzzle gradually widen backwards to reach the anterior zygomatic processes, and the cranium of Sète has a larger braincase.

The mandible of *Prolagus sorbinii* has a high body and a wide ascending ramus, unlike that of *P. michauxi* which has a moderately high body and a narrow ascending ramus (Text-fig. 9). On the medial face a strong crest originating from the anterior part of the articular process descends towards the body and branches off backwards on the angular process to reach the distal edge of this process. Consequently, the pterygoid fovea and pterygoid fossa are well defined. They host the attachments of the lateral pterygoid muscle and the medial pterygoid muscle, respectively (Wible 2007). This crest and the fossae that it surrounds (Text-figs 4, 5, 9) are weakly defined on the medial face of the Sète mandibles.

In contrast to these differences in the cranium and mandible, the dentition of these two species is very similar in size and morphology (Text-fig. 10). Angelone et al. (2021: 114) note that "the salient features of *P. sorbinii* are to be found especially in the third lower premolar with anteroconid as large as the metaconid, V-shaped mesoflexid, thick entoconid with continuous enamel, reduced crochet and shifted towards the metaisthmus, not very elongated protoconulid; second upper premolar with mesial hyperloph and continuous enamel on the precone; third upper premolar with "short" centrocone and right-angled lagicone-lagiloph connection; fourth upper premolar with very long and oblique parafossette and "C" shaped mesofossette; upper molars with pits and very deep hypoflexus". All these characteristics are also shared by the specimens from Sète as described above. Angelone (2007, 2008a) and Angelone et al. (2021) mention a number of differences in the tooth morphology of *P. sorbinii* compared to *P. michauxi*: right angled lagicone/lagiloph connection on P3, parafossette very long, tending to curve upwards on P4, fossettes always present on M1 and M2, and on the p3 labial indentation of anteroconid absent or incipient, metaconid contour quadrangular, and entoconid without enamel hiatus. In addition to its type locality, dental remains from several Italian sites (several fissures at Brisighella, Velona, Ciabot Cagna, Borro Strolla BS-1 and BS-2, Solava, Case Inferno, Arcille) have been referred to this species (Masini 1989, Angelone 2007, 2008a, Abbazzi et al. 2008, Angelone et al. 2015, 2020, 2021). Despite the abundance of fossils attributed to this species, the frequency of dental characters remains at present practically unknown, except for the metaconid isolated on 15 % of the p3s of Brisighella 25 (n = 57; Angelone 2008a). As it appears above in the description of the teeth of *P. michauxi* of Sète, the characters of the dentition are subject to a large variation (Text-figs 3–8). If the cranium and mandible are missing, only the frequency of some dental characters is sufficient to distinguish species. Given the lack of knowledge on the frequency of discriminating dental characteristics, it does not seem obvious to distinguish *P. sorbinii* from *P. michauxi*.



Text-fig. 10. Scatterplot diagram comparing the lengths and widths of p3s and P3s of *Prolagus* from different localities. Data for *P. michauxi* of Sète, La Alberca and Lissasfa are our own measurements; data for *P. michauxi* of Afoud 12-1 and 12-2 are from Dupré et al. (2022); data for *P. ibericus* of Layna are from López-Martínez (1974); data for *P. sardus* from Angelone et al. (2008) based on the material from the karstic cavity VI-b6 of Monte Tuttavista in Sardinia; data for *P. bilobus* are from Čermák et al. (2021); data for *P. sorbinii* from Monte Castellaro (type locality) and from Brisighella 25 are from Angelone (2007). N = number of specimens.

However, given the differences observed in the cranium and mandible, these two species cannot be definitively synonymized.

Some other records from Greece (de Bruijn 1995), Bulgaria (Sen 2020), Moldova and Ukraine (Tesakov and Averianov 2002) and Turkey (Sen et al. 2019) have been referred to as *P. sorbinii* or *P.* cf. *sorbinii.* Furthermore, Tesakov and Averianov (2002) included in this species the remains from Greece and Turkey, initially identified as *P. michauxi* or *P.* cf. *michauxi*. Indeed, these authors considered all the Late Miocene-Pliocene prolagids from Southeastern Europe and Asia Minor to be assignable to *P. sorbinii*, as a counterpart of the western species of the same epoch that is *P. michauxi*. Angelone et al. (2021: 115) seem to agree with this statement: "*Prolagus sorbinii* is … also recognized in the southern Balkans and in Anatolia… Its paleobiogeographic path, however, was opposite to its taxonomic history: probably originating in the southern Balkans, this species dispersed towards the north and then west during the Messinian and managed to penetrate what today corresponds to north-western Italy and a part of central Italy thanks to the establishment of an emerged connection with the European continent".

Angelone (2008b) provided a quantitative approach using Fourier Analysis applied on p3 anteroconid contour of several *Prolagus* species. Her results indicate a closer relationship between *P. michauxi* and *P. sorbinii* with respect to the earlier species *P. oeningensis*. From this, she deduced that both species are derived from P. *oeningensis* through *P. crusafonti*, and that they had a parallel evolution during the latest Miocene and Early Pliocene. Such an assumption needs to be confirmed and reinforced by other morphological and phylogenetic analyses.

As noted above, Fejfar et al. (2006: 98) suggested that "*Prolagus michauxi* of the similar Ruscinian sites in Spain and France … is probably synonymous with the taxon described by Heller [i.e., *Prolagus bilobus*]". This suggestion cannot be retained. Čermák and Angelone (2013) and Čermák et al. (2021) provided a complete picture of this species with detailed studies of many Central European records. Comparison of the size and pattern of teeth clearly show that *P. bilobus* is different: it is larger than all the remains attributed to *P. michauxi* (Text-fig. 10), its p3 is elongated, has an anteroconid often smaller than the metaconid, less laterally stretched and less indented, a strong crochet on all p3s situated at the bottom of the centroflexid, not displaced next to the metaisthmus as in *P. michauxi*, a strong antero-external depression on the trigonid, and well-marked depression on the talonid of lower molariform teeth (see details in Čermák et al. 2021).

Another middle-sized species comparable to *Prolagus michauxi* of Sète is *P. latiuncinatus* Angelone et Čermák, 2015 from Polgardi 2 in central Hungary. Its age is determined as late Turolian (MN 13) by the authors. Despite its size similarity, this species is different in having p3 generally short and wide (length/width ratio 91 %), constant presence of a drop-shaped and well-developed crochet at the bottom of the centroflexid in all p3s, and the lack of enamel hiatus on the mesial hyperloph of P2 (Angelone and Čermák 2015).

An interesting feature of the *Prolagus* cranium is the premolar foramen. In most species of *Prolagus*, the premolar foramen is small, i.e., its length does not exceed 0.5 mm, and it is located on the palate next to P3 or P4 (see Angelone and Sesé 2009, Angelone and Čermák 2015). Strangely, the endemic Italian species of *Prolagus* as well as *P. sardus* which became extinct in the Corso-Sardianian domain during historical times, have premolar foramen small (Mazza 1987, Angelone 2007, 2008a, Angelone et al. 2008, 2015). In a few species, namely in order of size importance *P. michauxi*, *P. sorbinii*, *P. ibericus* and *P. calpensis* Forsyth Major, 1905, it is significantly larger (over 0.5 mm), and its length almost equals that of P4. In addition, in these species it is located further back, facing the distal part of P4 or P4/M1 contact as seen in the first three species, or even medial to the M1 in *P. calpensis*. The foramen premolar on the cranium remains of Sète lies next the P4/M1 contact, it is larger than in all Miocene species of *Prolagus*, but smaller than that of *P. sorbinii*, *P. ibericus* and *P. calpensis*. Fostowicz-Frelik and Meng (2013) explored the variation of this foramen in several groups of lagomorphs and tried to identify its function. These authors noted that the genus *Prolagus* has the widest premolar foramen among lagomorphs. They also observed that it hosts "an offshoot of the infraorbital artery which descends in the antero-ventral direction and passes through the premolar foramen, … thus premolar foramen might have played the supporting role in blood supplementation" (Fostowicz-Frelik and Meng 2013: 11), and a better vascularization of the oral cavity. The enlargement of this foramen, paralelled with the increase of the number and size of palatal foramina, is "interpreted in terms of improved means of thermoregulation in species living in more arid and warmer conditions then their forest-dwelling ancestors. The animals could more effectively cool themselves by panting, due to increased blood flow through the mucous membranes in the oral cavity. It might have been an important adaptation in rather hot Mediterranean climate at that time" (Fostowicz-Frelik and Meng 2013: 13). This confirms the prediction of López-Martínez (2002) who noted that the formation of the Alpine barrier and the progressive aridification of the climate since the beginning of the Messinian fragmented the ecosystems and consequently favoured a greater speciation in *Prolagus* with the occurrence of local or endemic species adapted to the new climatic and environmental conditions along the northern and southern rims of Mediterranean. This is consistent with the high number of *Prolagus* species during the latest Miocene and Pliocene compared to older epochs.

Conclusions

This study has attempted to provide a picture as complete as possible of *Prolagus michauxi* López-Martínez, 1975 from its type locality of Sète. It is one of the most famous species of the genus *Prolagus*, since it was reported, right or wrong, from over sixty localities ranging from Portugal to Turkey, and also from North Africa, but more particularly from Spain. Although in some early works fossils dating from the early and middle Turolian have been erroneously referred to *P. michauxi*, the temporal extension of this species seems to be limited to the interval from the late Turolian to the early Villanyian, ca. 6–3 Ma. It is contemporaneus with

P. ibericus López-Martínez, 1975, known only in Spain, *P. sorbinii* Masini, 1989 best known from late Turolian and Ruscinian localities of Italy and *P. bilobus* Heller, 1936 which has a paleogeographical extent in Central Europe.

The type material of *P. michauxi* includes several cranial parts, mandibles and numerous isolated teeth. It is significantly abundant to present a reliable picture of the Sète population. The material displays a great size and morphological intra-population variability, in particular in the characters of its dentition.

The species closest to *P. michauxi* in size and dental characters is *P. sorbinii*. It was initially described from a partial skeleton on a clay slab from Monte Castellaro (Masini 1989). Later on, dental remains from several other Italian sites were referred to this species (Angelone 2007, Angelone et al. 2021, and references therein). Although the dental characters of this species fall within the variation observed in *P. michauxi* from its type locality of Sète, the characters of its skull and mandible from Monte Castellaro indicate a species with an elongated snout and a high-bodied mandible with a strong ascending ramus, very different from those of Sète. However, the variation of cranial and dental characters in this species is not well known, making the comparison insufficient. As noted by Angelone (2007: 411) "The holotype of *P. sorbinii* figured in Masini (1989) appears as a somehow weird individual, showing a mix of fully adult and juvenile characteristics". In addition, dental remains referred to this species from other similar aged Italian localities were not studied in detail to show intraspecific morphological variation. Also, some characters that Angelone (2007: 413) considered distinctive from that of *P. michauxi* (i.e., d3 with a slight enamel concavity on the entoconid lingual side; bulky P2, due to a strong verticalization of the first portion or the mesial hyperloph and postcone with external indentation; P3 with lagicone-lagiloph connection making almost a right angle, short centrocone not reaching the labial side of the tooth; P4 with long, verticalized parafossette sometimes enlarged at its labial end, and with occasional presence of an accessory enamel islet behind the metafossette) are also observed in the Sète population. As a result of the present morphological analysis and detailed comparisons, it appears that it is at present impossible to distinguish these two species based on the dental features and size.

Such an observation leads to propose two hypotheses: (i) either we maintain the two species as one being limited to western Europe and the Maghreb (*P. michauxi*) and the other to the Italian peninsula and south-eastern Europe (*P. sorbinii*), (ii) or we restrict the name of *P. sorbinii* to the type material from Monte Castellaro while waiting for more material and detailed morphological analysis of the remains from Italian localities allowing to evidence the frequency of characters and their possible differences from that of *P. michauxi*.

Another issue is in the attribution of the limited fossil samples from Greece, Bulgaria, Moldova, Ukraine and Turkey, which mainly consist of isolated teeth. For most of these records, the small number of specimens does not allow to appreciate the frequency of the discriminating characters, so attribution to *P. michauxi* or *P. sorbinii* can be reconsidered.

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References

Abbazzi, L., Benvenuti, M., Ceci, M. E., Esu, D., Faranda, C., Rook, L., Tangocci, F. (2008): The end of the Lago-Mare time in the SE Valdelsa Basin (Central Italy): interference between local tectonism and regional sea-level rise. – Geodiversitas 30(3): 611–639.

Aguilar, J.-P., Crochet, J. Y., Hebrard, O., Le Strat, P., Michaux, J., Pedra, S., Sigé, B. (2002): Les micromammifères de Mas Rambault 2, gisement karstique du Pliocène supérieur du Sud de la France: âge, paléoclimat, géodynamique. – Géologie de la France, 2002(4): 17–37.

Aguilar, J.-P., Lazzari, V., Michaux, J., Sabatier, M., Calvet, M. (2007): Lo Fournas 16-M (Miocène supérieur) et Lo Fournas 16-P (Pliocène moyen), nouvelles localités karstiques à Baixas, Sud de la France. Partie I – Description et implications géodynamiques. – Géologie de la France, 2007(1): 55–62.

Angelone, C. (2007): Messinian *Prolagus* (Ochotonidae, Lagomorpha, Mammalia) of Italy. – Geobios, 40: 407–421. https://doi.org/10.1016/j.geobios.2006.04.004

Angelone C. (2008a): *Prolagus italicus* n. sp. (Ochotonidae, Lagomorpha), a new Pliocene species of peninsular Italy. – Geobios, 41: 445–453. https://doi.org/10.1016/j.geobios.2007.12.001

Angelone, C. (2008b): Contribution of Complex Discrete Fourier Transform (CDFT) analysis to the systematics of the genus *Prolagus* (Ochotonidae, Lagomorpha, Mammalia). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 249(2): 129–138. https://doi.org/10.1127/0077-7749/2008/0249-0129

Angelone, C., Cavallo, O. (2010): A new look to *Prolagus* (Ochotonidae, Lagomorpha) from the late Messinian of Ciabót Cagna (Piedmont, NW Italy). – Rivista Italiana di Paleontologia e Stratigrafia, 116: 267–270. https://doi.org/10.13130/2039-4942/5954

Angelone, C., Čermák, S. (2015): Two new species of *Prolagus* (Lagomorpha, Mammalia) from the Late Miocene of

Hungary: Taxonomy, biochronology, and palaeobiogeography. – Paläontologische Zeitschrift, 89: 1023–1038. https://doi.org/10.1007/s12542-014-0247-z

Angelone, C., Čermák, S., Kotsakis, T. (2015): The most ancient lagomorphs of Sardinia: An overview. – Geobios, 48: 287–296. https://doi.org/10.1016/j.geobios.2015.06.002

Angelone, C., Čermák, S., Moncunill-Solé, B. (2021): I lagomorfi di Cava Monticino (Brisighella, Ra) [The lagomorphs of Cava Monticino (Brisighella, Ra)]. – In: Rook, L. (ed.), La fauna messiniana di Cava Monticino (Brisighella, RA). Memorie dell'Istituto Italiano di Speleologia, Ser. II, 37: 109–119. (in Italian)

Angelone, C., Moncunill-Solé, B., Kotsakis, T. (2020): Fossil Lagomorpha (Mammalia) of Italy: Systematics and biochronology. – Rivista Italiana di Paleontologia e Stratigrafia, 126(1): 157–187. https://doi.org/10.13130/2039-4942/13014

Angelone, C., Rook, L. (2012): Late Neogene and Quaternary lagomorphs from Tuscany: A revision based on specimens in Basel Naturhistorisches Museum and Florence University collections. – Swiss Journal of Palaeontology, 131: 127–145. https://doi.org/10.1007/s13358-011-0035-2

Angelone, C., Sesé, C. (2009): New characters for species discrimination within the genus *Prolagus* (Ochotonidae, Lagomorpha, Mammalia). – Journal of Paleontology, 8: 80–88. https://doi.org/10.1666/07-067R2.1

Bachelet, B. (1990a): Muridae et Arvicolidae (Rodentia, Mammalia) du Pliocène du sud de la France: Systématique, évolution et biochronologie; Ph.D. Thesis. – MS, Université des Sciences et Techniques du Languedoc, Montpellier, France, 211 pp., 19 pls. (copy in library of Muséum National d'Histoire Naturelle, Paris)

Bachelet, B. (1990b): Revision of the population of Arvicolids from the Pliocene fauna of Sète (Hérault, France). Evidence of the *Mimomys capettai* lineage. – In: Fejfar, O., Heinrich, W.-D. (eds), International symposium Evolution, phylogeny and biostratigraphy of arvicolids (Rodentia, Mammalia). Geological Survey/Pfeil Verlag, Prague/Munich, pp. 33–44.

Brandt, J. F. (1855): Beiträge zur nähern Kenntniss der Säugethiere Russland's. – Mémoires de l'Académie impériale des Sciences de Saint-Pétersbourg, Sér. 6, Sciences mathématiques, physiques et naturelles, T. 9, seconde partie: Sciences naturelles, 7: 1–365.

de Bruijn, H. (1995): The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian boundary (Neogene). 11. Lagomorpha (Mammalia). – Münchner Geowissenschaftliche Abhandlungen, Reihe A, 28: 133–136.

Čermák, S., Angelone, C. (2013): Revision of the type material of the Pliocene species *Prolagus bilobus* Heller, 1936 (Mammalia, Lagomorpha), with comments on the taxonomic validity of *P. osmolskae* Fostowicz-Frelik, 2010. – Bulletin of Geosciences 88(1): 45–50. https://doi.org/10.3140/bull.geosci.1369

Čermák, S., Angelone, C., Moncunill-Solé, B. (2021): *Prolagus* Pomel, 1853 (Lagomorpha, Mammalia) in the framework of the Pliocene faunal rearrangements in central Europe. – Comptes Rendus Palevol, 20(28): 597–617. https://doi.org/10.5852/cr-palevol2021v20a28

Chaline, J., Laurin, B. (1986): Phyletic gradualism in a European Plio-Pleistocene *Mimomys* lineage (Arvicolidae, Rodentia). – Paleobiology, 12(2): 203–216. https://doi.org/10.1017/S009483730001366X

de Christol, J. (1834): Observations générales sur les brèches osseuses. – F. Martel Aîné, Imprimeur de la Faculté des Sciences, Montpellier, 32 pp.

Cuvier, G. (1812): Recherches sur les ossemens fossiles de quadrupèdes, Tome Quatrième, Chapter "Sur les brèches osseuses". – Deterville, Paris, 38 pp., 2 pl.

Dawson, M. R. (1969): Osteology of *Prolagus sardus*, a Quaternary ochotonid (Mammalia, Lagomorpha). – Palaeovertebrata, 2: 157–190. https://doi.org/10.18563/pv.2.4.157-190

Dupré, S., Mahboubi, S., Guy, F., Surault, J., Benammi, M. (2022): Systematic palaeontology of Late Miocene lagomorphs from the Aït Kandoula Basin (Morocco). – Comptes Rendus Palevol, 21(40): 859–899. https://doi.org/10.5852/cr-palevol2022v21a40

Ellenberger, P. (1953): Sur les anciens grottes de la Corniche de Sète (cap de Lazaret) et leur faune villafranchienne. – Bulletin de la Société géologique de France, Sér. 6, 3(1-3): 85–98. https://doi.org/10.2113/gssgfbull.S6-III.1-3.85

Fejfar, O., Storch, G., Tobien, H. (2006): Gundersheim 4, a third Ruscinian micromammalian assemblage from Germany. – Palaeontographica, Abt. A, 278: 97–111. https://doi.org/10.1127/pala/278/2006/97

Forsyth Major, C. I. (1905): Rodents from the Pleistocene of the Western Mediterranean region. – Geological Magazine, 5(2): 462–467. https://doi.org/10.1017/S0016756800128390

Fostowicz-Frelik, Ł., Meng, J. (2013): Comparative morphology of premolar foramen in lagomorphs (Mammalia: Glires) and its functional and phylogenetic implications. – PLoS ONE, 8(11): e79794 (18 pp.). https://doi.org/10.1371/journal.pone.0079794

Gureev, A. A. (1960): Zaytseobtaznye (Lagomorpha) oligotsena Mongolii i Kazakhstana [Oligocene lagomorphs (Lagomorpha) from Mongolia and Kazakhstan]. – In: Flerov, K. K. (ed.), Tretichnye mlakopitayushchie, vypusk 4 [Tertiary Mammals, part 4]. Trudy Paleontologicheskogo institua [Paleontological Institute Transactions], 77: 5–34. (in Russian)

Heller, F. (1936): Eine oberpliozäne Wirbeltierfauna aus Rheinhessen. – Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, B, 76: 99–160.

König, C. D. E. (1825): Icones fossilium sectiles. Centuria Prima. – s. n., Londini, 4 pp., 19 pls. https://doi.org/10.5962/bhl.title.157008

López-Martínez, N. (1974): Évolution de la lignée *Piezodus-Prolagus* (Lagomorpha, Ochotonidae) dans le Cénozoïque d'Europe sud-occidentale; Ph.D. Thesis. – MS, Université des Sciences et Techniques du Languedoc, Montpellier, France, 165 pp., 18 pls. [copy in library of Muséum National d'Histoire Naturelle, Paris]

López-Martínez, N. (1989): Revisión sistemática y bioestratigráfica de los lagomorfos (Mammalia) del Terciario y

Cuaternario de España. – Memorias del Museo Paleontológico de la Universidad de Zaragoza, 3: 1–342. (in Spanish)

López-Martínez, N. (2002): Paleobiogeographical history of *Prolagus*, an European ochotonid (Lagomorpha). – Lynx, n. s., 32(2001): 215–231.

López-Martínez, N., Thaler, L. (1975): Biogéographie, évolution et compléments à la systématique du grouped'Ochotonidés *Piezodus-Prolagus* (Mammalia, Lagomorpha). – Bulletin de la Société géologique de France, Sér. 7, 17(5): 850–866. https://doi.org/10.2113/gssgfbull.S7-XVII.5.850

Lortet, L. C. E. (1872): Étude sur le *Lagomys Corsicanus* (Cuvier) de Bastia (Corse). – Archives du Muséum d'Histoire naturelle de Lyon, 1: 53–57. https://doi.org/10.3406/mhnly.1872.935

Masini, F. (1989): *Prolagus sorbinii* n. sp., a new ochotonid (Mammalia, Lagomorpha) from the Messinian of Italy. – Bollettino della Società Paleontologica Italiana, 28(2-3): 295–306.

Mazza, P. (1987): *Prolagus apricenicus* and *Prolagus imperialis*: Two new ochotonids (Lagomorpha, Mammalia) of the Gargano (Southern ltaly). – Bollettino della Società Paleontologica Italiana, 26(3): 233–243.

von Meyer, H. (1845): Zur Fauna der Vorwelt. Fossile Säugethiere, Vögel, und Reptilien aus dem Molasse-Mergel von Oeningen. – Verlag der S. Schmerberischen Buchhandlung (Nachfolger H. Keller), Frankfurt am Main, pp. 1–67, 11 pls.

Michaux, J., Aguilar, J.-P., Montuire, S., Wolff, A., Legendre, S. (1997): Les Murinae (Rodentia, Mammalia) néogènes du Sud de la France: Évolution et paléoenvironnements. – Geobios, 30(suppl. 1): 379–385. https://doi.org/10.1016/S0016-6995(97)80042-3

NOW Community (2024): New and Old Worlds Database of Fossil Mammals (NOW). Licensed under CC BY 4.0. Retrieved October 2, 2024 from http://doi.org/10.5281/zenodo.4268068

Pomel, A. (1853): Catalogue méthodique et descriptif des vertébrés fossiles découverts dans le bassin hydrographique supérieur de la Loire et de l'Allier. – J.-B. Baillière, Paris, 193 pp.

Sen, S. (2020): Lagomorphs (Mammalia) from the Early Pliocene of Dorkovo, Bulgaria. – Fossil Imprint, 76(1): 99–117. https://doi.org/10.37520/fi.2020.007

Sen, S., Geraads, D. (2023): Lagomorpha (Mammalia) from the Pliocene-Pleistocene locality of Ahl al Oughlam, Morocco. – Palaeobiodiversity and Palaeoenvironments, 103(3): 633–661. https://doi.org/10.1007/s12549-022-00569-5

Sen, S., Geraads, D., Pickford, M., Vacant, R. (2024): Pliocene and Pleistocene lagomorphs (Mammalia) from Northwest Africa: New discoveries. – Palaeobiodiversity and Palaeoenvironments, 104(2): 381–417. https://doi.org/10.1007/s12549-024-00605-6

Sen, S., Karadenizli, L., Antoine, P. O., Saraç, G. (2019): Late Miocene − early Pliocene rodents and lagomorphs (Mammalia) from the southern part of Çankırı Basin, Turkey. – Journal of Paleontology, 93(1): 173–195. https://doi.org/10.1017/jpa.2018.60

de Serres, M. (1838): Essai sur les cavernes à ossements et sur les causes qui les y ont accumulés. 3e édition. – J.-B. Baillière-Germer Baillière, Paris, XVI + 412 pp.

Tesakov, A. S., Averianov, A. O. (2002): *Prolagus* (Lagomorpha, Prolagidae) from the Pliocene of Moldova and Ukraine. – Paleontological Journal, 36(1): 80–86.

Thaler, L. (1955a): Présence de deux espèces éteintes de Rongeurs Cricetinés dans les brèches ossifères villafranchiennes de Sète. – Comptes rendus de l'Académie des Sciences de Paris, 240: 1255–1257.

Thaler, L. (1955b): Sur l'âge pliocène de la faune des grottes du Lazaret (Sète, Hérault). –Comptes rendus de l'Académie des Sciences de Paris, 241: 433–435.

Thaler, L. (1966): Les rongeurs fossiles du Bas-Languedoc dans leurs rapports avec l'histoire des faunes et la stratigraphie du Tertiaire d'Europe. – Mémoires du Muséum National d'Histoire Naturelle, N. S., Sciences de la Terre, 17: 1–295.

Tobien, H. (1935): Über die pleistozänen und postpleistozänen Prolagusformen Korsikas und Sardiniens. – Berichte der Naturforschenden Gesellschaft zu Freiburg in Brisgau, 34: 253–344.

Vasileiadou, K., Sylvestrou, I. (2022): The fossil record of hares, rabbits, and pikas (Mammalia: Lagomorpha) in Greece. – In: Vlachos, E. (ed.), Fossil Vertebrates of Greece, Vol. 1. Springer, Cham, pp. 611–637. https://doi.org/10.1007/978-3-030-68398-6_16

Wagner, R. (1829): Beiträge zur Geschichte der fossilen Thiere. – Isis von Oken, 22(1): 1132–1141.

Wible, J. R. (2007): On the cranial osteology of the Lagomorpha. – Bulletin of Carnegie Museum of Natural History, 39: 213–234. https://doi.org/10.2992/0145-9058(2007)39[213:OTCOOT]2.0.CO;2

Wilkens, B. (2005): Osservazioni sulla presenza in epoca recente del prolago sardo a Tavolara secondo le notizie di Francesco Cetti [Observation on the recent presence of *Prolagus sardus* at Tavolara according to the report of the naturalist Francesco Cetti]. – In: Fiore, I., Malerba, G., Chilardi, S. (eds), Atti 3° Convegno Nazionale di Archeozoologia (Siracusa, 3-5 novembre 2000). Instituto Poligrafico e Zecca dello Stato, Roma, pp. 217–222. (in Italian)

Wilkens, B. (2012): Archeozoologia. Il Mediterraneo, la storia, la Sardegna [Archaeozoology. The Mediterranean, history, Sardinia]. – Edes, Editrice Democratica Sarda, 163 pp. (in Italian)

Wolniewicz, A. S., Fostowicz-Frelik, Ł. (2021): CT-Informed skull osteology of *Palaeolagus haydeni* (Mammalia, Lagomorpha) and its bearing on the reconstruction of the early lagomorph body plan. – Frontiers in Ecology and Evolution, 9: 634757 (24 pp.). https://doi.org/10.3389/fevo.2021.634757