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EARLY PLIOCENE LAGOMORPHS FROM TOLLO DE CHICLANA-1B (GUADIX BASIN, SPAIN): NEW PERSPECTIVES ON THE EVOLUTION AND THE PALEOBIOGEOGRAPHY OF LATE NEOGENE WESTERN EUROPEAN LAGOMORPHA

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Abstract. The continental record of the Guadix Basin (southern Spain) documents a fundamental time-window for the evolution of leporids and prolagids. Here we provide the first attempt of a taxonomic revision of the lagomorphs of the Guadix Basin (*Prolagus* aff. *michauxi*, *Trischizolagus* aff. *crusafonti*, and *Oryctolagus* cf. *laynensis*), evidencing that, at least in southern Spain, the accepted taxonomic model should be reconsidered in light of a possible partly endemic evolutionary history of lagomorphs during the latest Miocene and Pliocene. Actually, our data highlight that there was a limited interchange between southern Iberian lagomorphs and those of the rest of western Europe at least since the late Turolian (MN13). Dispersals were instead active, in the early part of the MN13, from southern Iberia to northern Africa, a new territory where prolagids and leporids underwent local radiation and evolution.

INTRODUCTION

The Iberian Peninsula is a key area for lagomorph evolution during the latest Miocene-Pleistocene. In particular, the Iberian Peninsula should be the area in which, during that time interval, originated the modern rabbit, and where the last non-insular prolagid survived (López Martínez 2001, 2008).

Southern Iberian Peninsula is remarkably rich in continental fossils, and small mammals very densely cover a time span from MN12 to MN17 (García-Alix et al. 2008a; Minwer-Barakat et al. 2012a, and references therein). Recent systematic studies addressed mostly rodents and eulipotyphlans, whereas lagomorphs have so far lacked a thorough revision. Such revision is envisaged not only to fill the gap in systematic studies, but more importantly because the time span covered by the

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southern Iberian Peninsula fossil record is of fundamental importance for the evolution of European lagomorphs, e.g., the last adaptive radiation and/or species differentiation of *Prolagus*, and the rise of *Oryctolagus* against the background decline of *Trischizolagus*. Both processes took place around MN15.

The rich assemblage from the Tollo de Chiclana-1B (TCH-1B, MN15b) in the Guadix Basin represents the starting point of a revision of the lagomorph species of the latest Miocene-Pliocene of southwestern Europe, a due update after 50 years from the last efforts on the topic (considering López Martínez's two Ph.D. Theses on the issue dating back respectively to 1974 and 1977 – the former unpublished, and the latter published in 1989). Special attention is dedicated to *Prolagus michauxi*, a problematic taxon of putative MN13-15 Euro-Anatolian distribution (see Angelone 2007), and to the investigation of the p3 phylogenetic morphoclines in leporids. In a wider framework, this research represents another tile to update the taxonomy of MN15 lagomorphs, and to evaluate the impact of climate, geography, and ecology on their distribution started by Čermák (2009), Čermák & Angelone (2013), Čermák & Wagner (2013), Čermák et al. (2021).

GEOLOGICAL SETTING

The Guadix Basin (Fig. 1.1) is an intramontane basin established in the Late Miocene, the infill of which covers the contact between the Internal and External zones of the Betic Cordillera, in southern Spain (Viseras et al. 2005). Its sedimentary infill comprises a first stage of marine sedimentation (Tortonian), a second phase corresponding to a regression during the latest Tortonian, and a third phase of continental sedimentation (late Turolian-Late Pleistocene) which ended with a stream piracy process that caused the change of the basin from endorheic to exorheic (Calvache & Viseras 1997; Soria et al. 1998; García-García et al. 2009; Minwer-Barakat et al. 2012b).

The section of Tollo de Chiclana is situated in the central sector of the Guadix Basin, between the village of Villanueva de las Torres and the Negratín Dam (Fig. 1.2). In this area, distal alluvial and fluvial deposits crop out, alternating with lacustrine carbonates. The section includes three fossiliferous levels, corresponding to dark clays rich in organic matter: Tollo de Chiclana-1, -1B and -3 (TCH-1, TCH-1B and TCH-3), which were respectively assigned to the late Ruscinian, latest Ruscinian, and early Villányian (Fig. 1.3). Particularly, the level TCH-1B has yielded abundant and diverse rodent and insectivore remains, which have been studied in detail in previous works (Minwer-Barakat et al. 2004, 2005, 2008a, b, 2010; Furió et al. 2007; García-Alix et al. 2007, 2008b).

The faunal assemblage of the TCH-1B site includes the species *Stephanomys donnezani* (Depéret, 1890), *Castillomys crusafonti* Michaux, 1969, *Apodemus atavus* Heller, 1936, *Occitanomys brailloni* Michaux, 1969, *Rhagapodemus frequens* Kretzoi, 1959, *Mimomys hassiacus* Heller, 1936, *Blancomys meini* Adrover, 1986, *Trilophomys vandeweerdi* Brandy, 1979, *Pliopetaurista pliocaenica* (Depéret, 1890), *Eliomys intermedius* Friant, 1953, *E. truci* Mein & Michaux, 1970, *Asoriculus gibberodon* (Petényi, 1864), *Paenelimnoecus pannonicus* (Kormos, 1934), and *Archaeodesmana brailloni* (Rümke, 1985). Particularly, the presence of the murid *S. donnezani* and the arvicolid *M. hassiacus*, together with the absence of the arvicolid *Mimomys stehlini* Kormos, 1931 (a good marker of the early Villányian, which appears upwards in the section in the level TCH-3) allow assigning TCH-1B to the end of the Ruscinian, unit MN15b (Minwer-Barakat et al. 2008b, 2012a).

MATERIAL AND METHODS

The studied material is curated in the Departamento de Estratigrafía y Paleontología, Universidad de Granada (Spain).

The image documentation was acquired by drawings taken with a camera lucida mounted on a Leica MS5 binocular microscope (Prolagidae), and photos (Leporidae). Measurements were taken on the camera lucida drawings and converted by means of a graphical scale (Prolagidae) or using a digital caliper and an ocular micrometer on a binocular microscope (Leporidae). All measured data are given in millimeters [mm]. Prolagid teeth nomenclature and metrics follow Angelone & Sesé (2009). For leporids, dental terminology, metrics, and morphotype classification used to describe teeth follow Sych (1965), Palacios & López Martínez (1980), Fladerer (1987), Fladerer & Reiner (1996), and Čermák et al. (2015). The original scheme of P2 morphotypes by Fladerer & Reiner (1996), originally used for *Hypolagus*, was extended here adding the BMR-morphotype "C" (characterized by a very long hypoflexus), to apply also to advanced/modern taxa of Leporidae.

Interspecific comparisons were made by direct physical revision of type materials (°) or other materials (*), or on a bibliographical basis; if not specified, the bibliographical source corresponds to the one in which the species was erected.

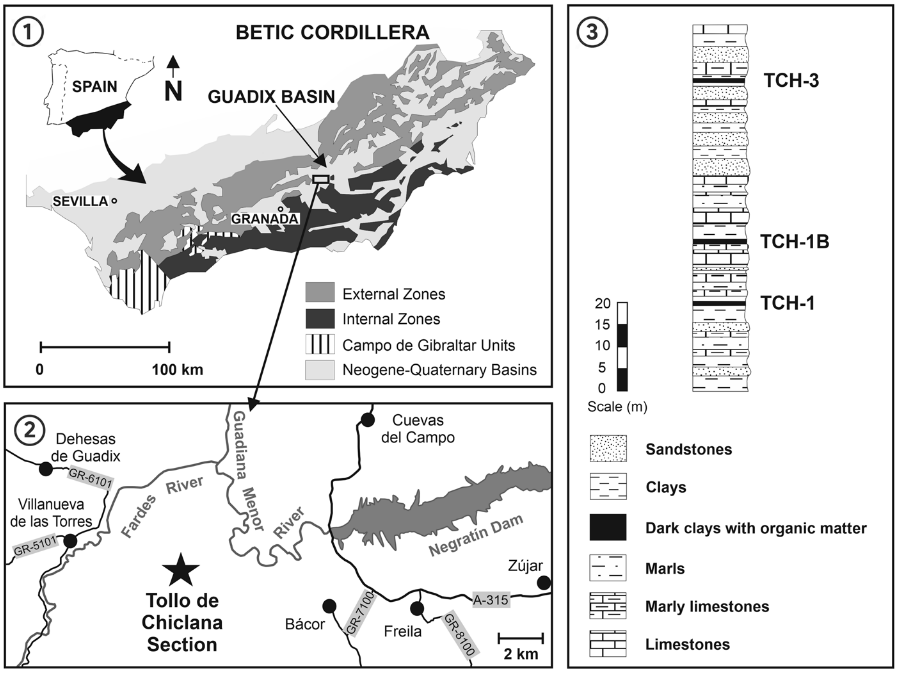

Fig. 1 - Geographic and geological context of the Tollo de Chiclana-1B (TCH-1B) fossil site. (1) Location map of the Guadix Basin in the context of the Betic Cordillera (southern Spain); (2) geographic location of the Tollo de Chiclana section, marked with a star; (3) stratigraphic column of the Tollo de Chiclana section and position of the fossil-bearing levels TCH-1 (late Ruscinian), TCH-1B (latest Ruscinian), and TCH-3 (early Villányian). Modified from Minwer-Barakat et al. (2012a).

As for Prolagidae, the comparisons were made with MN15 congeneric species of western and central Europe:

° *P. depereti* López Martínez in López Martínez & Thaler, 1975 from Perpignan (F) – Early Pliocene (MN15); collections – Musée de Confluences, Lyon.

P. ibericus López Martínez in López Martínez & Thaler, 1975 from Layna (ES) – Early Pliocene (MN15); collections – Université Claude Bernard-1 Lyon.

° *P. michauxi* López Martínez in López Martínez & Thaler, 1975 from Sète (FR) – Early Pliocene (MN15); holotype from original publication, plus elements from the type series illustrated by López Martínez (1974), and those curated in the Naturistorisches Museum Basel and the Université Claude Bernard-1 Lyon.

°* *P. bilobus* Heller, 1936 from Gundersheim sites (D) – Early Pliocene (MN15b); collections – Senckenberg Museum, Frankfurt am Main.

Further comparisons were made with samples attributed to:

Prolagus from Afoud 12-1 and 12-2 (MA) attributed by Dupré et al. (2022) and Mahboubi et al. (2022) to *P. michauxi* – Late Miocene (MN13); data taken from the above cited papers.

Prolagus from Lissasfa (MA) attributed by Sen et al. (2024) to *P. michauxi* – Miocene/Pliocene boundary (MN13/14); data from Sen et al. (2024).

Samples of *P. michauxi* from the MN13-MN15 of the Iberian Peninsula, namely El Arquillo, Librilla, Alcoy N, Gorafe 1-4, Gorafe 2+3 (ES); data from López Martínez (1989);

Prolagus cf. *michauxi* from Vendargues (F) – Early Pliocene (MN14); data from López Martínez (1977).

Prolagus aff. *ibericus* from Balaruc II (F) – Early/Late Pliocene (MN15/16) and Seynes (F) – Late Pliocene (MN16); data from López Martínez (1974).

As for dimensional comparisons, for the purpose of the individuation of spatio-temporal trends in the representants of the family Prolagidae in the Neogene of southwestern and south-central Europe, in addition to the samples above, the materials here examined were compared also with:

* *P. sorbinii* Masini, 1989 from Brisighella 25 (I) – Late Miocene (MN13); collections – Museo di Storia Naturale (Geology and Palaeontology Section), University of Florence.

° *P. italicus* Angelone, 2008 from Montagnola Senese (I) – Pleistocene (MN17); collections – Dipartimento di Scienze della Terra, Università di Siena.

As for Leporidae comparisons were made with:

Alilepus turolensis López Martínez, 1977 from El Arquillo (ES) – Late Miocene (late Turolian, MN13).

° *Alilepus meini* Angelone & Rook, 2011 from Ribardella (I) – Late Miocene (late Turolian, MN13); collections – Museo di Storia Naturale (Geology and Palaeontology Section), University of Florence.

° *Nuralagus rex* Quintana et al., 2011 from Punta Nati 6 (ES, Minorca) – late Neogene (post-Messinian, Pliocene); collections – Museu de l'Institut Català de Paleontologia Miquel Crusafont (Sabadell).

° *Sardolagus obscurus* Angelone et al., 2018 from Monte Tuttavista (I, Sardinia) – Early Pleistocene (MN17-MQ1); collections – Laboratorio di Paleontologia, Dipartimento di Scienze, Università Roma Tre.

Afrolagus pomeli Sen & Geraads, 2023 from Ahl al Oughlam (MA, Casablanca) – Pliocene/Pleistocene boundary

Hypolagus peregrinus Fladerer & Fiore, 2003 from Monte Pellegrino (I, Sicily) – Early Pleistocene.

* *Hypolagus petenyii* Čermák & Fladerer in Čermák, 2009 from Host'ovce 2 (SK), Ivanovce 1 (SK), Měňany 3 (CZ); Pliocene (late Ruscinian – early Villányian, MN15b-16a); collections – temporarily in the Institute of Geology of the Czech Academy of Sciences, v. v. i. (Prague).

Hypolagus balearicus Quintana et al., 2010 from Caló d'en Rafelino (ES, Mallorca) – earliest Pliocene?; collections – Institut Mediterrani d'Estudis Avançats (Esporles).

° *Serengetilagus praecapensis* Dietrich, 1941 from Laetoli (TA) – Pliocene; collections – Museum für Naturkunde (Berlin).

° *Pliopentalagus dietrichi* (Fejfar, 1961) from Ivanovce (SK), Muselievo (BG), and Budăi (MD) – see Čermák & Wagner (2013) for details; Early Pliocene (late Ruscinian, MN15b).

Trischizolagus crusafonti (Janvier & Montenat, 1971) from La Alberca (ES) – Late Miocene (MN13).

Trischizolagus maritsae Bruijn et al., 1970 from Maritsa (GR, Rhodes) – Late Miocene/?Early Pliocene (MN13/?14).

Trischizolagus dumitrescuae Radulesco & Samson, 1967 from Măluşteni (RO) and Bereşti (RO) – Early Pliocene (MN14b-15a).

* *Trischizolagus gambariani* (Melik-Adamyan, 1986) from Nurnus (AM), data taken from Melik-Adamyan (1986) and Tepe Alagöz (TR; Čermák et al. 2019) – Early Pliocene (MN14, Ruscinian).

Trischizolagus raynali (Geraads, 1994) from Grotte des Rhinocéros (MA, Casablanca) – Early/Middle Pleistocene; Sen et al. (2024).

Trischizolagus meridionalis Sen & Geraads, 2023 from Ahl al Oughlam (MA, Casablanca) – Pliocene/Pleistocene boundary.

Oryctolagus laynensis López Martínez, 1977 from Layna (ES) – Early Pliocene (MN15).

° *Oryctolagus valdarnensis* (Weithofer, 1889) from Valdarno (I) and Pirro Nord (I) – Early Pleistocene; collections – Basel Naturhistorisches Museum and Museo di Storia Naturale (Geology and Palaeontology Section), University of Florence.

Oryctolagus giberti De Marfà, 2008 from Cueva Victoria (ES) – Early Pleistocene.

Oryctolagus lacosti (Pomel, 1853) from Perrier-Étouaries (FR), Saint Vallier (FR), and El Carmel (ES) – Early–Middle Pleistocene (MN17-MQ2); López Martínez (1989), De Marfà (2009), and De Marfà & Mein (2007).

Abbreviations

Dental structures, measurements and statistics. 'a'-'e' – leporid p3 hypoconid morphotypes (sensu Čermák 2009); A0-A1 – leporid p3 morphotypes based on presence/absence of anteroroflexid (sensu Čermák et al. 2015); AA – partial width; BMR – leporid buccal mesial reentrant (mesoflexus) of P2; d3, d4 – deciduous teeth; dx – right; I/i – upper and lower incisors; CV – coefficient of variation; L – length; LL – lingual lobe (hypercone) of P2; M/m – upper and lower molars; N – number of specimens; OR – observed range; P/p – upper and lower premolars; PH – hypoflexus depth; PR1-PR3 – leporid p3 morphotypes based on the occurrence of morphostructures between trigonid and talonid (sensu Čermák et al. 2015); sin – left; TH – distal hypercone length; W – width; Want – anteroloph width; Wg – width of internal fault in leporid I1; Wpost – posteroloph width; Wtrig – trigonid width; Wtal – talonid width; $\bar{x}$ – mathematic mean.

Institutions and localities abbreviations. ICP-Sabadell – Museu de l'Institut Català de Paleontologia Miquel Crusafont in Sabadell; ISE-Montpellier – Institut des Sciences de l'Évolution de Montpellier; MDC-Lyon – Musée de Confluences Lyon; MNHN-Paris – Musée National d'Histoire Naturelle de Paris; NHM-Basel – Naturhistorisches Museum Basel; TCH-1B – Tollo de Chiclana-1B; UCB-Lyon – Université Claude Bernard Lyon 1.

Country abbreviations. According to ISO 3166-1 alpha-2 codes.

Systematic paleontology

Order **Lagomorpha** Brandt, 1855
Family Prolagidae Gureev, 1960
Genus *Prolagus* Pomel, 1853

Prolagus aff. ***michauxi*** López Martínez in López Martínez & Thaler, 1975

Fig. 2-3

Prolagus* aff. *michauxi					
		N	**$\bar{x}$**	**OR**	**CV**
p3	L	41	1.83	1.40-2.13	9.45
	W	31	2.04	1.21-2.47	13.68
d3	L	10	1.18	1,04-1.35	9.21
	W	9	0.89	0.74-1.23	17.67
d4	L	1	-	1.14	-
	W	1	-	0.80	-
P2	L	29	1.24	0.89-1.45	10.22
	W	26	1.94	1.34-2.36	12.04
P3	L	36	1.57	1.23-1.83	10.57
	W	30	2.21	1.63-2.88	13.62
P4	L	26	1.32	1.04-1.50	9.09
	AA	19	2.35	1.46-2.88	13.02
	PH	23	1.18	0.58-1.53	16.63
	TH	29	0.77	0.54-0.92	11.19
M1	L	14	1.37	1.10-1.46	7.58
	AA	11	2.36	1.96-2.71	9.97
	PH	12	2.24	1.79-2.58	12.14
	TH	15	0.71	0.56-0.77	7.76
M2	L	23	1.25	0.98-1.35	7.36
	AA	21	2.12	1.75-2.42	9.18
	PH	21	2.04	1.58-2.35	10.48
	TH	23	0.62	0.44-0.71	9.47

Tab. 1 - Teeth measurements (in mm) of *Prolagus* aff. *michauxi* from the Pliocene (MN15b) locality TCH-1B (Guadix Basin, Spain).

Referred material: 1 fragm. mand. dx with m1-2 (TCH-1B 1352); 5 d3 sin (TCH-1B 1336-1340); 5 d3 dx (TCH-1B 1341-1345); 1 d4 sin (TCH-1B 1346); 29 p3 sin (TCH-1B 1123-1130, TCH-1B 1132-1141, TCH-1B 1150-1152, TCH-1B 1154-1158, TCH-1B 1160-1162, TCH-1B 1349-1351); 36 p3 dx (TCH-1B 1099-1122, TCH-1B 1131, TCH-1B 1142-1149, TCH-1B 1153, TCH-1B 1159, TCH-1B 1348); 27 P2 sin (TCH-1B 1174-1187, TCH-1B 1192-1202, TCH-1B 1205-1206; 22 P2 dx (TCH-1B 1163-1173, TCH-1B 1188-1191, TCH-1B 1203-1204, TCH-1B 1207-1211); 20 P3 sin (TCH-1B 1233-1251, TCH-1B 1255); 25 P3 dx (TCH-1B 1212-1232, TCH-1B 1252-1254, TCH-1B 1256); 23 P4 sin (TCH-1B 1265-1284, TCH-1B 1291-1292, TCH-1B 1295); 17 P4 dx (TCH-1B 1257-1264, TCH-1B 1285-1290, TCH-1B 1293-1294, TCH-1B 1347); 7 M1 sin (TCH-1B 1296-1302); 7 M1 dx (TCH-1B 1304-1309, TCH-1B 1333); 16 M2 sin (TCH-1B 1303, TCH-1B 1310-1322, TCH-1B 1334-1335); 10 M2 dx (TCH-1B 1323-1332).

Measurements: see Tab. 1.

Age: MN15b, Pliocene.

Occurrence: TCH-1B, Guadix Basin, Granada, Spain.

Description

d3 (Fig. 2.19-22). In unworn specimens, the anteroconid is divided in two cusps which completely merge with wear. An additional cusp is present on the labial side of the anteroconid; such cusps may

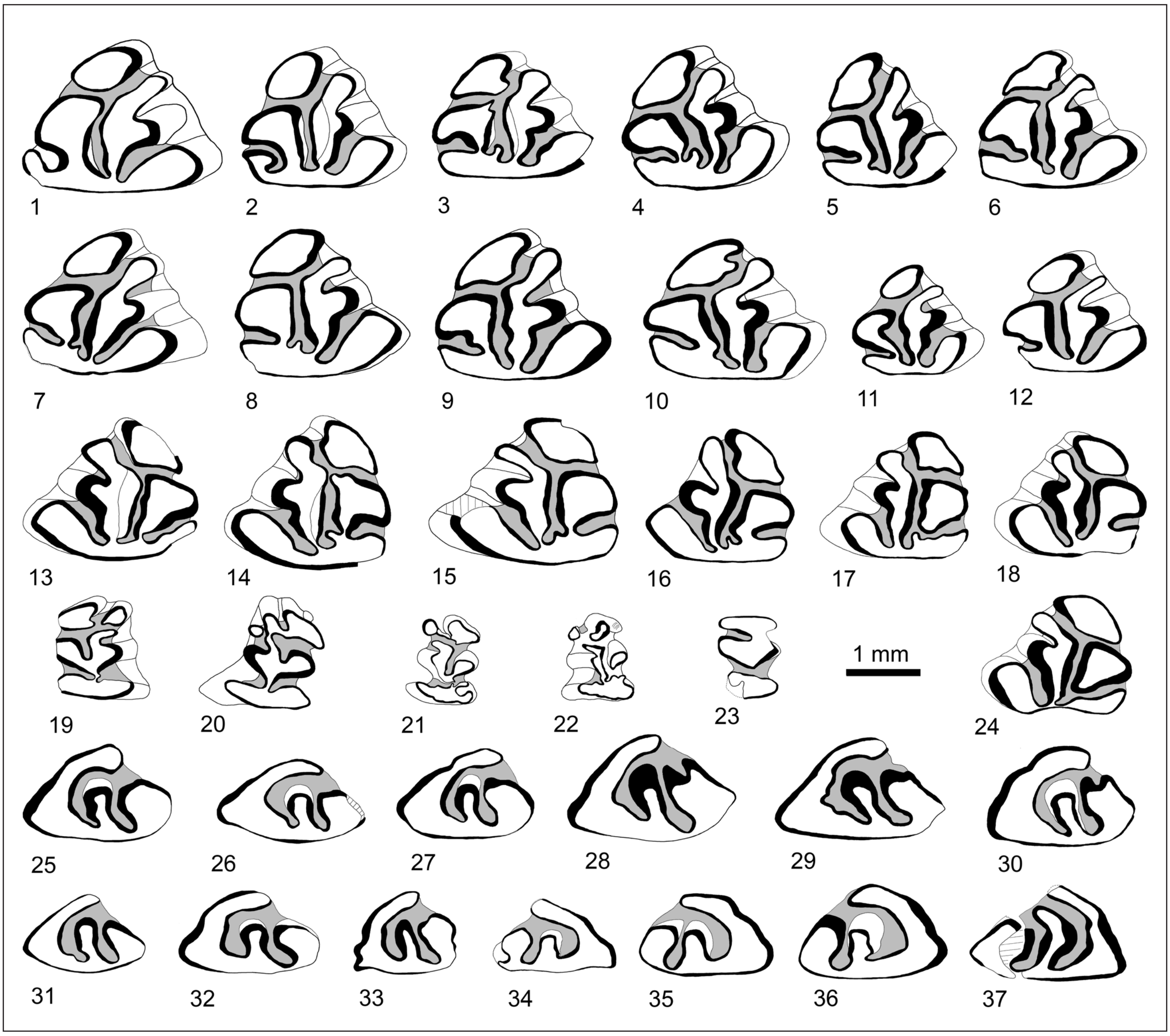

Fig. 2 - Occlusal morphology of premolars p3 and P2, and of and lower milk teeth (d3, d4) of *Prolagus* aff. *michauxi* from the Pliocene (MN15b) locality TCH-1B (Guadix Basin, Spain). (1) p3 dx TCH-1B 1099; (2) p3 dx TCH-1B 1103; (3) p3 dx TCH-1B 1106; (4) p3 dx TCH-1B 1107; (5) p3 dx TCH-1B 1109; (6) p3 dx TCH-1B 1142; (7) p3 dx TCH-1B 1114; (8) p3 dx TCH-1B 1110; (9) p3 dx TCH-1B 1118; (10) p3 dx TCH-1B 1131; (11) p3 dx TCH-1B 1115; (12) p3 dx TCH-1B 1117; (13) p3 sin TCH-1B 1127; (14) p3 sin TCH-1B 1136; (15) p3 sin TCH-1B 1123; (16) p3 sin TCH-1B 1124; (17) p3 sin TCH-1B 1130; (18) p3 sin TCH-1B 1139; (19) d3 sin TCH-1B 1341; (20) d3 dx TCH-1B 1336; (21) d3 dx TCH-1B 1339; (22) d3 dx TCH-1B 1338; (23) d4 dx TCH-1B 1346; (24) p3 sin TCH-1B 1129; (25) P2 sin TCH-1B 1199; (26) P2 sin TCH-1B 1196; (27) P2 sin TCH-1B 1197; (28) P2 sin TCH-1B 1175; (29) P2 sin TCH-1B 1179; (30) P2 sin TCH-1B 1195; (31) P2 sin TCH-1B 1181; (32) P2 sin TCH-1B 1200; (33) P2 sin TCH-1B 1182; (34) P2 dx TCH-1B 1170; (35) P2 dx TCH-1B 1163; (36) P2 dx TCH-1B 1164; (37) P2 dx TCH-1B 1211.

connect with wear to the anteroconid by means of an enamel strip first and later by a dentine+enamel bridge. A further additional cusp is present labially at the basis of the crown in 2 out of 10 specimens. The anteroconid is connected to the metaconid complex only in one extremely worn specimen (Fig. 2.20). In 3 relatively unworn specimens the metaconid is isolated, whereas protoconid+protoconulid are connected through a protoisthmus to the entoconid; in other 2 specimens with the same stage of wear, the metaconid is instead fused to the protoconid+protoconulid on the distal side, whereas an extremely deep centroflexid separates them in the mesial and central part. The entoconid is deeply indented in early stages of wear, and its enamel is quite wavy.

p3 (Fig. 2.1-18, 24). 47 analyzable specimens, of which 6 young/unworn; overall shape in adult individuals characterized by W>L; large, triangular shaped anteroconid, shifted lingually with respect the mesio-distal axis of the tooth, as large or larger than the metaconid (~30-35%); ⅓ of adult individuals presents on the anteroconid a notch of variable depth on the labial side, whereas the other ⅔ present also a slightly bent enamel on the distal side; juveniles show a triangular anteroconid though with less angular edges, or a tilted oval shape, though in most cases presenting the labial notch. The metaconid is triangular, rarely quadrangular, the enamel on its labial side smooth or wavy; particular features are the isolation of the metaconid in more than 10% of specimens, and the noticeable incidence (>50%) of a spur on its labio-distal part, in correspondence of the connection with the metaisthmus. The metaisthmus width is extremely variable, from very thick to extremely thin, to bottlenecked; its general outline is mainly U-shaped (i.e., with parallel sides); the tubular U-shape can be slightly bent towards the distal side, and in a few specimens (3/47 individuals) the mesoflexid is J-shaped; the mesoflexid orientation is variable (perpendicular to the mesio-distal axis or tilted towards the distal side); in most cases (70%) the mesial side of the metaflexid is deformed by a notch, whereas the distal side, i.e., the one corresponding to the mesial side of the entoconid, is predominantly smooth (42/47 individuals). The entoconid, whose length is about ¼ of L (measure taken on the lingual edge in order to avoid the bias due to the variable inclination of the mesoflexid), has no enamel hiatus. The crochet is present in half of the sample; it may be medium-sized to large (~30% of the sample), or very reduced (~20%), and its size is not related to its position in the centroflexid. Centroflexid and protoflexid are extremely deep, reducing the distal part of the tooth to a mere strip. The protoisthmus is thin, often bottlenecked (~45%). The hypoconid is quite bulky and protruding labially. Protoconid of medium size and relatively long. The protoconulid can be very massive (22/47 specimens) or relatively thin, however in both cases it is quite often enlarged on the labial tip; the orientation of the protoconulid with respect to the protoconid is extremely variable and their connection may be characterized by a spur.

d4 (Fig. 2.23). The sole available specimen has a massive anterior lobe, a paraflexid slightly exceeding the longitudinal axis of the tooth, and no centroflexid. The trigonid is an isosceles triangle, and the talonid has a very simple shape and contour, without notches or extroflexions.

P2 (Fig. 2.25-37). Long mesial hyperloph, covering the lagicone (~30% of the sample) or part of the postcone, also in juveniles; hiatus variable (70% of available specimens has no enamel hiatus); the connection of the mesial hyperloph with the precone is sharply bent in ~70% of cases. Both paraflexus and mesoflexus are very deep, though the mesoflexus is deeper, almost reaching the distal edge of the tooth; the paraflexus is bent labially, whereas the mesoflexus can be straight to strongly bent labially. A characteristic undulation of the enamel of variable amplitude may be present along the linguodistal side of the paraflexus (~60%). The lagicone does not mesially exceed the postcone and shows a lingual undulation of the enamel in ~50% of cases. An incipient lagiloph is present in some individuals, and one specimen has a developed lagiloph plus a centrocone (Fig. 2.37). The postcone is variable in size and shape (triangular or quadrangular), usually not exceeding the lagicone mesially; quadrangular postcones may be indented mesially by a notch (~45% of the sample).

P3 (Fig. 3.1-10). No enamel hiatus on the precone, which is often enlarged with respect to the mesial hyperloph; the mesial hyperloph covers the centrocone and the complete postcone, i.e., reaching on the labial side the junction of the postcone with the cement. The mesial hypercone is shorter than the distal one. The hypoflexus is absent (and thus the mesial hypercone is fused with the distal one) in 4 over 37 specimens, whereas in the rest of the specimens the hypoflexus may vary from shallow to deep and V-shaped, to very deep and U-shaped; U-shaped hypoflexa may upturn mesially. Para- and mesoflexus are deep, almost reaching the distal border of the tooth; distally, the paraflexus prolongs in direction of the mesoflexus tightening the base of the lagicone. The connection lagicone-centrocone is often marked by a sharp bending of the enamel strip. The centrocone reaches the labial edge of the tooth in ~45% of the specimens. The postcone is roughly quadrangular and bears a mesial notch of variable depth in 50% of the specimens.

P4 (Fig. 3.11-19). Short mesial hyperloph, with distal enamel band sharply bending at ~40° at ⅓ (or rarely at ½) of its length from the lingual tip (PH); the bending determines the hypoflexus (which penetrates the tooth for ~50% of AA) to be V-shaped at the lingual edge and then to become U-shaped labially; the hypoflexus does not

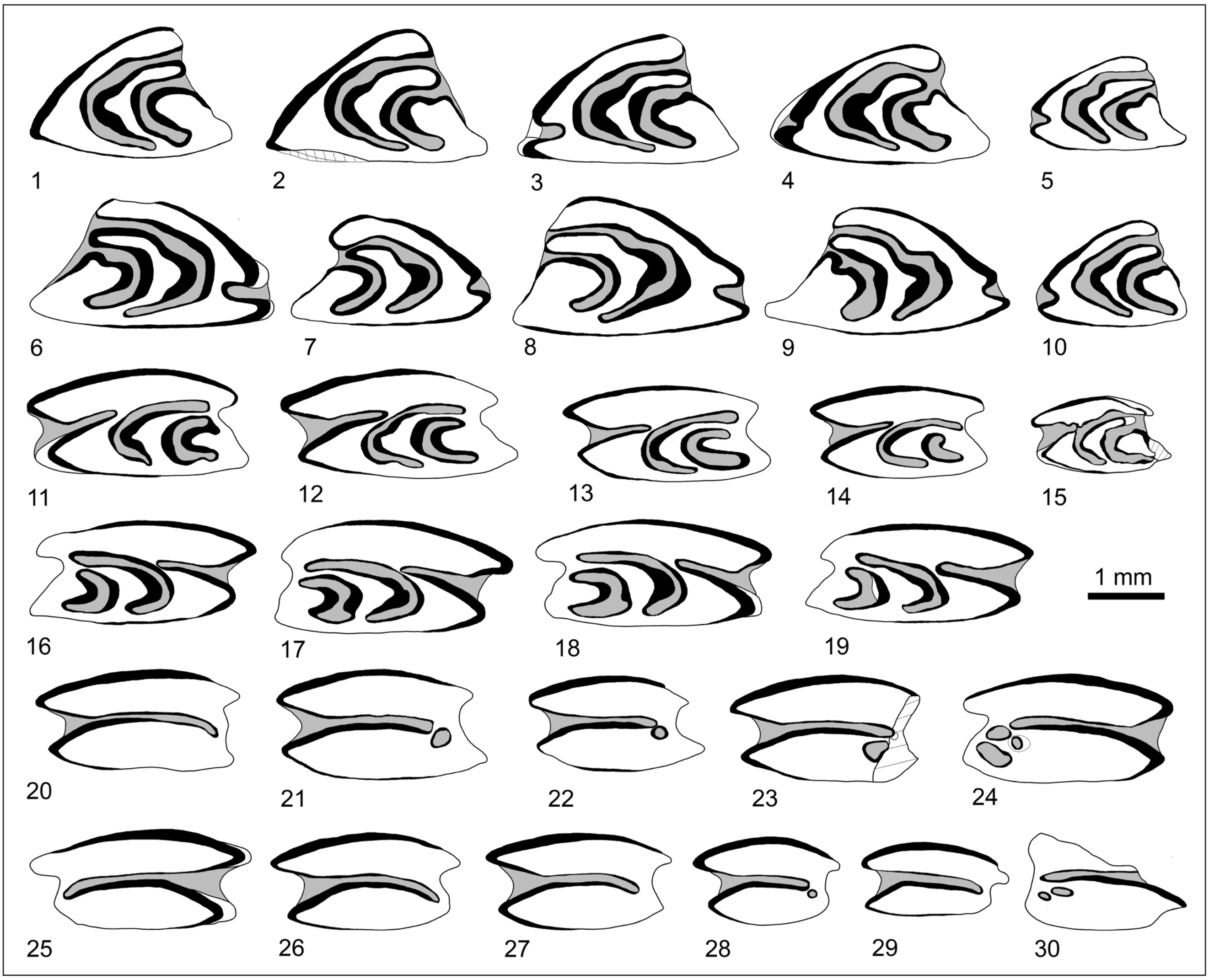

Fig. 3 - Occlusal morphology of upper teeth P3-M2 of *Prolagus* aff. *michauxi* from the Pliocene (MN15b) locality TCH-1B (Guadix Basin, Spain). (1) P3 sin TCH-1B 1212; (2) P3 sin TCH-1B 1219; (3) P3 sin TCH-1B 1216; (4) P3 sin TCH-1B 1221; (5) P3 sin TCH-1B 1217; (6) P3 sin TCH-1B 1241; (7) P3 dx TCH-1B 1234; (8) P3 dx TCH-1B 1236; (9) P3 dx TCH-1B 1238; (10) P3 dx TCH-1B 1223; (11) P4 sin TCH-1B 1268; (12) P4 sin TCH-1B 1269; (13) P4 sin TCH-1B 1270; (14) P4 sin TCH-1B 1267; (15) P4 sin TCH-1B 1266; (16) P4 dx TCH-1B 1263; (17) P4 dx TCH-1B 1257; (18) P4 dx TCH-1B 1261; (19) P4 dx TCH-1B 1262; (20) M1 sin TCH-1B 1297; (21) M1 sin TCH-1B 1299; (22) M1 sin TCH-1B 1296; (23) M1 sin TCH-1B 1302; (24) M1 dx TCH-1B 1306; (25) M2 sin TCH-1B 1327; (26) M2 sin TCH-1B 1312; (27) M2 sin TCH-1B 1310; (28) M2 sin TCH-1B 1334; (29) M2 dx TCH-1B 1322; (30) M1 dx TCH-1B 1305.

stretch perpendicularly to the mesio-distal axis of the tooth, but curves mesially; the parafossette has the mesio-labial branch very long, parallel to the AA axis, and covering the mesofossette. The mesofossette is C-shaped, conjoint labially to the parafossette in ~10% of cases.

M1 (Fig. 3.20-24, 30). Mesial hyperloph shorter than distal one; the presence of fossettes is quite variable in number, shape and dimensions (0 fossettes in 3 of 12 specimens, 1 fossette in 5/12 specimens, 2 fossettes in 3/12, and 3 fossettes in 1/12 remarkable specimen persisting also in the "radical" side); the fossettes usually lie distally to the hypoflexus' tip, though in rare cases they lie beside its labial tip; hypoflexus deep to extremely deep; when extremely deep, the hypoflexus curves sharply distally at its labial tip, and appears bottlenecked; it is not clear if the elongated bottlenecked shape in long hypoflexes could be due to the "capture" of a fossette.

M2 (Fig. 3.25-29). As in the other upper molar, the mesial hyperloph quite is short if compared to the distal one, though the difference in size between the two hyperlophs is less evident than in M1 and P4. The hypoflexus is extremely long, almost reaching the labial side of the tooth; it abruptly curves distally at its very end, resulting in a bottlenecked shape; fossettes are absent, except in 1/25

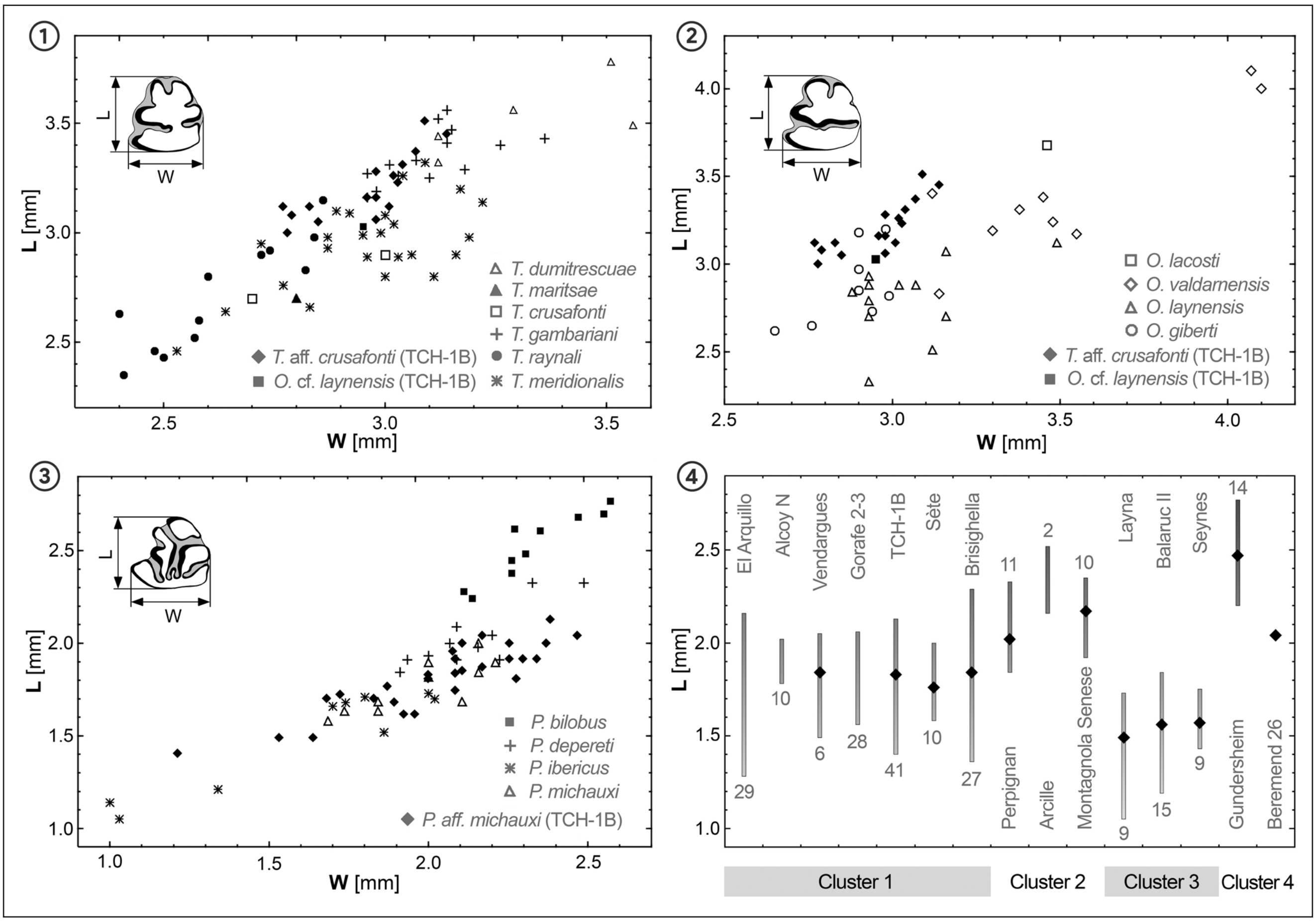

Fig. 4 - Size comparison of p3 of lagomorphs from the Pliocene (MN15b) locality TCH-1B (Guadix Basin, Spain) compared to related species. (1-2) p3 length-to-width measurements of leporids from TCH-1B vs. other species of the genera (1) *Trischizolagus* and (2) *Oryctolagus*; (3) p3 length-to-width of p3 of *Prolagus* aff. *michauxi* from TCH-1B compared to other MN15 congeneric species of western and central Europe; (4) p3 length ranges, average value (indicated by a diamond; unavailable in El Arquillo, Alcoy N, and Gorafe 2-3) of *Prolagus* species from selected Late Miocene-Pleistocene localities of western and central Europe. Metric data taken from Radulesco & Samson (1967), Bruijn et al. (1970), Janvier & Montenat (1971), López Martínez (1974, 1989), Angelone (2007, 2008), Angelone & Rook (2012), Angelone et al. (2018), Čermák et al. (2019), Sen & Geraads (2023), Sen et al. (2024 and references therein). Cluster 1-4: size clusters of MN15 western and central European species of *Prolagus* following repartition indicated in the text. The numbers above/below the range bars represent the number of available specimens.

specimens, which shows a round and small fossette, placed just beside (distally) with respect to the hypoflexus.

Comparisons

Size. When dimensionally compared to coeval congeneric species (MN15) of western Europe, the p3 of the prolagid material from TCH-1B shows a relatively large size with respect to *Prolagus ibericus*; it is smaller than *P. depereti*, and noticeably smaller than *P. bilobus*; its size is instead comparable with the material of *P. michauxi* from the type locality (Sète, MN15), with that of MN15 Spanish populations assigned to *P. michauxi*, and with *P.* cf. *michauxi* from the MN14 French locality Vendargues (see López Martínez 1974, 1989) (Fig. 4.4). A seemingly neat repartition of MN15 western and central European species of *Prolagus* in 4 groups is shown in Fig. 4.4. The four clusters are:

a smaller-sized group including species currently related in literature to *P. ibericus*;

a middle-sized cluster containing the species *P. michauxi*;

a cluster including the larger-sized species *P. depereti* and the Italian MN13-MN17 species (this makes sense if we consider *P. depereti* as a synonym of *P. savagei* as hypothesized in Angelone & Rook 2012);

the very large-sized central European species.

However, it must be taken into account that apart from clusters 3 and 4, the taxonomical attribution of the samples of the first two groups has often been performed simply taking as the main discriminant the dimensional characters, thus biasing and messing up the taxonomy.

Morphology. Under a morphological point of view, the TCH-1B *Prolagus* materials can be easily distinguished from most of the species above mentioned. The main differences with *P. ibericus* are due to the fact that the p3 of the latter species has an anteroconid smaller than the metaconid and a much lesser incidence of the crochet, moreover in P2 the mesial hyperloph is absent. TCH-1B *Prolagus* sample differs from *P. depereti* in having different p3 proportions (L<W), extremely large anteroconid, and simpler entoconid. As for the p3 of *P. bilobus*, with respect those of TCH-1B, we observe in the former much more slender proportions (L>W), constant crochet and complicated enamel.

The materials from TCH-1B do not morphologically match those of *P. michauxi* from the type locality Sète available from different repositories (see list in Materials and Methods). Actually, the p3 from TCH-1B shows very different anteroconid/metaconid proportions and shape (i.e., the anteroconid tends to be hatchet-shaped and larger than the metaconid), the crochet is bulkier, as well as the protoconulid, and the enamel more undulated in the central part of the tooth. Also in the upper dentition, TCH-1B materials show discrepancies with the holotype of *P. michauxi*. The latter sports a P2 with a wide enamel hiatus on the mesial hypercone, J-shaped fossettes on M1, and a round fossette on M2, whereas TCH-1B *Prolagus* has a continuous enamel band on P2 in 70% of specimens, round and small fossettes on M1, and no fossettes on M2.

The p3 of MN15 Spanish populations attributed to *P. michauxi* (namely Gorafe 1+4 and Gorafe 2+3; see López Martínez 1989), show a more satisfactory morphological similarity with TCH-1B specimens than those of the type locality, in general terms. However, the samples which are most similar in terms of p3 morphology to TCH-1B have been retrieved in the MN13 Iberian localities of El Arquillo and Alcoy N (López Martínez 1989: p. 15, fig. 23), and the French locality Vendargues (Fig. 5.6-8). *Prolagus* from TCH-1B appears anyway unique due to the size of its anteroconid and protoconulid, both extremely large. Determining the evolutionary degree of the samples of *P. michauxi* on the basis of the incidence of some features has already been attempted (López Martínez 1989), basing on: (1) the incidence of crochet and the reduction of entoconid on p3, (2) on the variability of enamel hiatus and the development of mesial hyperloph on P2, to which it can be added (3) the development of fossettes on M1-2. Such attempt of biochronological ordering of the Iberian samples of *P. michauxi* did not provide linear results. If we consider the incidence of the above mentioned characteristics (López Martínez 1989), the TCH-1B specimens, with 30% mesial hyperloph enamel hiatus, no entoconid hiatus, and 50% crochet, appear less advanced than the MN15 Iberian Peninsula samples currently attributed to *P. michauxi*.

Taxonomic remarks

A mosaic pattern in the morphological features of occlusal teeth surface is frequent to be observed in the lineages of the genus *Prolagus*. Thus, the above illustrated discrepancy in the evolutionary degree of some selected features of Iberian populations of *P. michauxi* and the sample from TCH-1B would not be surprising nor inconsistent with the attribution of *Prolagus* from TCH-1B to the species *P. michauxi*. However, the characteristics that TCH-1B *Prolagus* shares with Iberian MN15 populations attributed to *P. michauxi* (see Discussion subsection about the taxonomy of MN15 western European *Prolagus*) appear incompatible and incongruent with the iconographic representations of the currently unavailable holotype and of the teeth of the original type series of *P. michauxi* retrieved from the original publication (see Fig. 5.1). As a matter of fact, these characteristics of the holotype of *P. michauxi* clash also with those of the available specimens of *P. michauxi* from the type locality curated at NHM-Basel and UCB-Lyon (CA, pers. obs. 2016) (Fig. 5.16-21). Such discrepancy poses a taxonomic problem whose solution is not obvious and can not be addressed in this paper, being the starting point for a revision of the species *P. michauxi*, since a long time envisaged in literature (Angelone 2007).

For this reason, we propend to provisionally identify *Prolagus* from TCH-1B as *P.* aff. *michauxi*. Insights about the complex status of the taxonomy *P. michauxi* is given in the Discussion.

Family Leporidae Fischer, 1817

Two phenotypic entities can be individuated in the TCH-1B leporid assemblage, based on

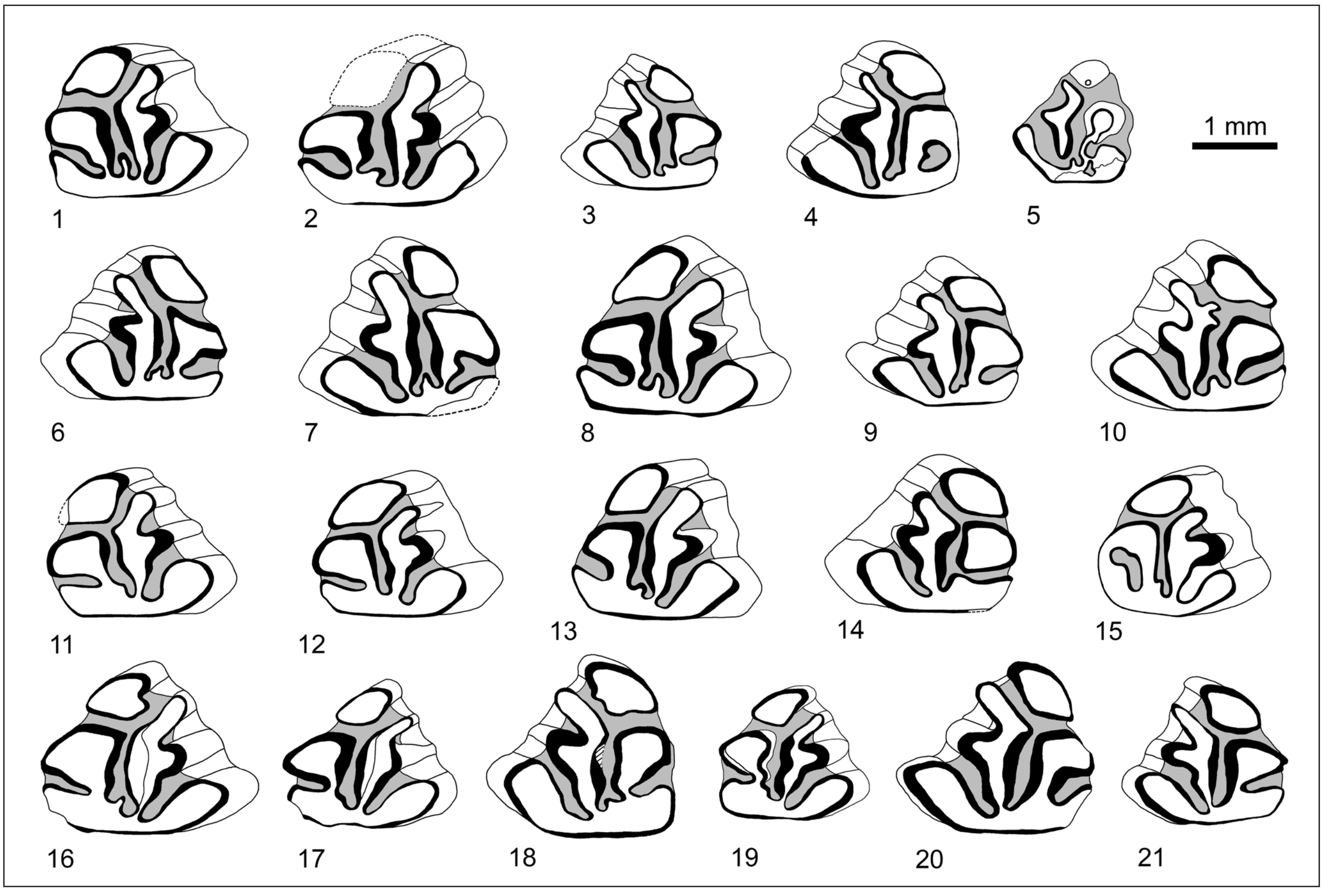

Fig. 5 - Occlusal morphology of p3 of selected *Prolagus* species from the Late Miocene-Pliocene of western Europe. (1-5) *P. michauxi*, Sète (type locality; MN15, France), original type series, redrawn from López Martínez (1974): (1) p3 dx, CB.SL-2005 (López Martínez & Thaler 1975: 856, pl. II, fig. 4; López Martínez 1974: pl. XI, fig. 13); (2) p3 dx (López Martínez 1974: pl. XI, fig. 12); (3) p3 sin (juv.) (ibid.: pl. XI, fig. 11); (4) p3 sin (ibid.: pl. XI, fig. 10); (5) p3 dx (juv.) (ibid.: pl. XI, fig. 9); (6-8) *P. michauxi*, Vendargues (MN14, France), redrawn from López Martínez (1974): (6) p3 sin (López Martínez 1974: pl. IX, fig. 12); (7) p3 sin (ibid.: pl. IX, fig. 13); (8) p3 dx (ibid.: pl. IX, fig. 14); (9-10) *P. michauxi*, Alcoy N (?MN13, Spain), redrawn from López Martínez (1974): (9) p3 sin (juv.) (López Martínez 1974: pl. IX, fig. 9); (10) p3 sin (ibid: pl. IX, fig. 10); (11-12) *P.* aff. *ibericus*, Seynes (MN16, France): (11) p3 dx (López Martínez 1974: pl. XIV, fig. 13); (12) p3 dx (ibid.: pl. XIV, fig. 14); (13-15) *P.* aff. *ibericus*, Balaruc II (MN15/16, France): (13) p3 dx (López Martínez 1974: pl.XIV, fig. 9); (14) p3 sin (ibid.: pl. XIV, fig. 10); (15) p3 dx (ibid.: pl. XIV, fig. 11); (16-21) *P. michauxi*, Sète (MN15, France), collection UCB-Lyon: (16) p3 dx UCB.SE.Pmi.0059; (17) p3 dx (juv.) UCB.SE.Pmi.0061; (18) p3 sin UCB.SE.Pmi.0057; (19) p3 sin (juv.) UCB.SE.Pmi.0058; (20) p3 sin UCB.SE.Pmi.0056; (21) p3 dx (juv.) UCB.SE.Pmi.0054.

p3 and d3. The rest of the tooth positions show no dimensional or morphological differences that allow an unambiguous distinction at the genus level. Nevertheless, we consider appropriate to give a description of the undeterminable material as well. Such specimens are classified here as *Trischizolagus* aff. *crusafonti* seu *Oryctolagus* cf. *laynensis*.

Genus *Trischizolagus* Radulesco & Samson, 1967

Trischizolagus **aff.** ***crusafonti*** Janvier & Montenat, 1971

Fig. 6.1-18

Referred material: 1 d3 sin (TCH-1B 858); 5 d3 dx (TCH-1B 857, TCH-1B 859-861); 24 p3 sin [11 fragmentary] (TCH-1B 808, TCH-1B 811-814, TCH-1B 817-819, TCH-1B 821-824, TCH-1B 826, TCH-1B 881, TCH-1B 883, TCH-1B 889-891, TCH-1B 897-898, TCH-1B 901, TCH-1B 1068, TCH-1B 1070, TCH-1B 1088); 22 p3 dx [16 fragmentary] (TCH-1B 809-810, TCH-1B 816, TCH-1B 820, TCH-1B 825, TCH-1B 827, TCH-1B 884-888, TCH-1B 892-896, TCH-1B 900, TCH-1B 902, TCH-1B 1072, TCH-1B 1089-1091).

Measurements: see Tab. 2.

Age: MN15b, Pliocene.

Occurrence: TCH-1B, Guadix Basin, Granada, Spain.

Description

p3 (Fig. 6.1-14). The occlusal surface of the tooth is elongated anteroposteriorly. The morphology of its individual structures is highly variable. In the available set of adult specimens, the PR0-PR2 morphotypes are present, with PR1 (81%, N = 21) being clearly dominant, followed by PR2 (14%, N

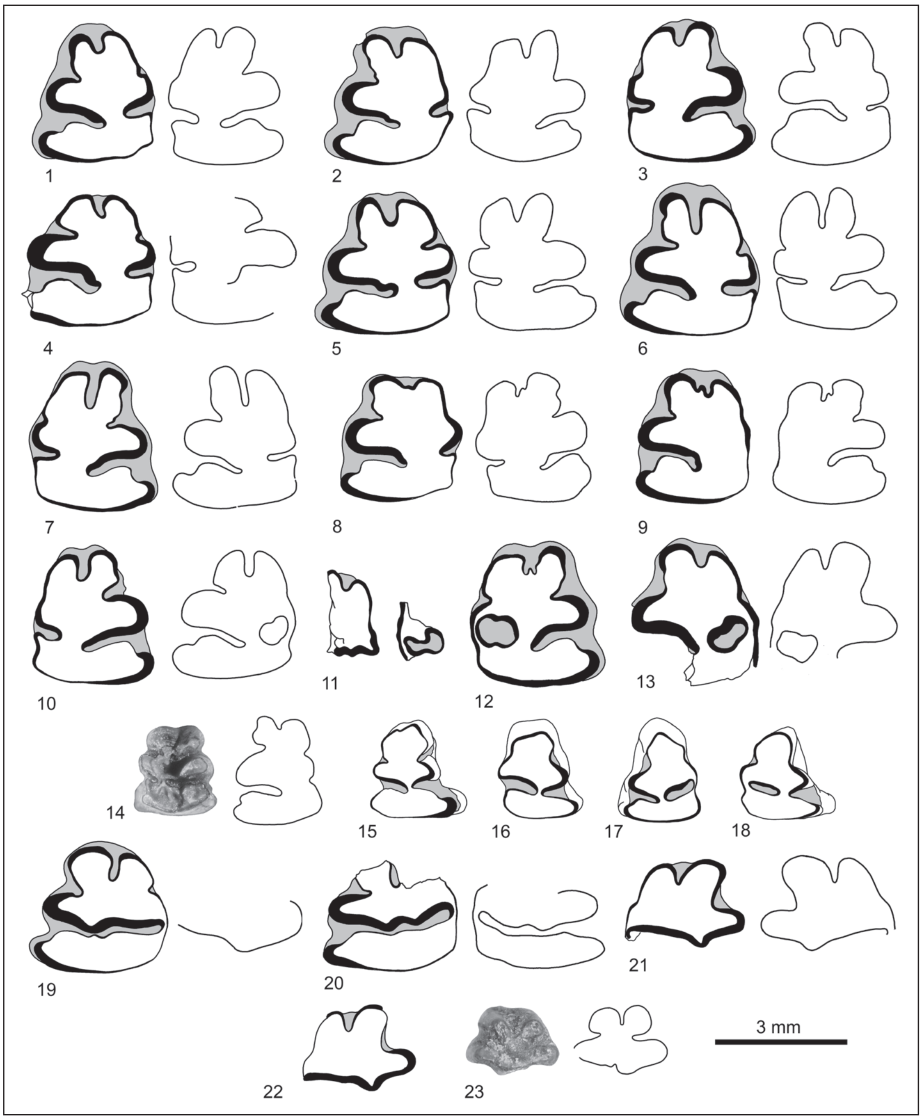

Fig. 6 - Occlusal and root morphology of p3 and d3 of leporids from the Pliocene (MN15b) locality TCH-1B (Guadix Basin, Spain). The root morphology is illustrated by a simple line to the left of the depicted occlusal morphology. (1-18) *Trischizolagus* aff. *crusafonti*: (1) p3 sin TCH-1B 818; (2) p3 sin TCH-1B 814; (3) p3 dx TCH-1B 810; (4) p3 sin TCH-1B 823; (5) p3 sin TCH-1B 811; (6) p3 sin TCH-1B 819; (7) p3 dx TCH-1B 809; (8) p3 sin TCH-1B 824; (9) p3 sin TCH-1B 817; (10) p3 dx TCH-1B 825; (11) p3 sin TCH-1B 901; (12) p3 dx TCH-1B 820; (13) p3 sin TCH-1B 826; (14) p3 dx TCH-1B 827; (15) d3 dx TCH-1B 856; (16) d3 dx TCH-1B 857; (17) d3 sin TCH-1B 858; (18) d3 dx TCH-1B 859; (19-23) *Oryctolagus* cf. *laynensis*: (19) p3 sin TCH-1B 815; (20) p3 sin TCH-1B 882; (21) p3 dx TCH-1B 899; (22) p3 dx TCH-1B 1069; (23) p3 sin TCH-1B 1071.

Tab. 2 - Teeth (p3, d3) measurements (in mm) of *Trischizolagus* aff. *crusafonti* and *Oryctolagus* cf. *laynensis* from the Pliocene (MN15b) locality TCH-1B (Guadix Basin, Spain).

Trischizolagus* aff. *crusafonti						***Oryctolagus* cf. *laynensis***					
		N	**x̄**	**OR**	**CV**			**N**	**x̄**	**OR**	**CV**
p3	L	22	3.16	2.48-3.51	6.68	**p3**	L	1	-	3.03	-
	W	18	2.90	2.15-3.14	7.71		W	2	-	2.95, 3.09	-
d3	L	5	2.01	1.90-2.15	4.78	**d3**	L	-	-	-	-
	W	5	1.70	1.60-1.80	4.68		W	-	-	-	-

= 21) and PR0 (5%, N = 21). In the vast majority of these adult specimens, the pattern remains stable throughout the entire tooth shaft; only in two specimens (Fig. 6.10-11), the morphotype changes from PR2 in the root part to PR1 in the occlusal part. This transition occurs approximately in the lower fifth of the tooth shaft. One specimen represents a juvenile individual with permanent p3 just before the wear of the occlusal surface (Fig. 6.14). This tooth shows a transitional morphotype between PR0/1 in the central part of the tooth shaft and PR1 in the occlusal surface.

The occlusal surfaces of adult teeth show the following combination of features. The length of anteroflexid varies, ranging from 10% to 27% of L (x̄ = 18%; N = 20; CV = 22.3). In 58% of cases (N = 33), the anteroflexid is simple (e.g., Fig. 6.1-7), in the rest (42%) it is doubled (e.g., Fig. 6.9, 6.12). The anteroconid is relatively narrow and elongated anteriorly, its length ranges from 29% to 41% of L (x̄ = 35%; N = 22; CV = 7.4); the labial anteroconid tends to be anteriorly more prominent. The protoflexid is relatively deep, in the vast majority of cases quite wide in the first half of its width, becoming a narrow flexid towards the medial end; its depth varies from 18% to 31% of W (x̄ = 23%; N = 17; CV = 12.6). The paraflexid is frequently present, albeit at different stages of growth. It is well developed in 43% (N = 21) of cases, present in its initial form as a depression in 43% (N = 21) of cases, and missing in 14% (N = 21) of cases. The hypoconid and protoconid are massive. The hypoflexid is not crenulated and its length ranges from 53% to 61% of W (x̄ = 57%; N = 17; CV = 4.1). Morphologically, the medial portion of the hypoflexid varies from morphotype 'a' to 'd'. The labial tip of the hypoconid is simple, usually deformed by a shallow notch in 87% (= morphotype 'c', N = 30); other morphotypes are then represented by 'c' in 3%, 'c/d' in 7% and 'd' in 3% of cases (N = 30). The mesoflexid is shallow with a simple labial end. It is variable in length, ranging from 19% to 34% (N = 15, x̄ = 26, CV = 17.2) of W. In any case, it is much shorter than the hypoflexid. When present (14%, N = 21), the mesofossettid is irregularly oval and large (Fig. 6.13-14). The connection between trigonid and talonid in the case of PR1 is wide to very wide, its width ranges from 11% to 25% (N = 15, x̄ = 17, CV = 26.9) of W.

d3 (Fig. 6.15-18). Six teeth were documented, four of morphotype PR1 (Fig. 6.15-16) and two of morphotype PR2 (Fig. 6.17-18). The teeth exhibit the common three-lobed shape of deciduous teeth with roots. The crown of the tooth is low, occupying about half the length of the tooth. The anteroconid is simple, relatively broad, more or less pointed anteriorly. The anteroflexid is not developed, usually only an anterior flattening of the anteroconid is visible (Fig. 6.16), at most a slight depression (Fig. 6.15). The protoflexid and paraflexid are shallow and of simple morphology. The hypoflexid and mesoflexid (in the case of PR1) are simple, not crenulated, and form a very narrow trigonid-talonid junction. The mesofossettid (if present) is distinctly oval in morphology, elongated buccolingually, the enamel wall is not undulated. The labial tip of the hypoconid is simple; rounded, or with a very shallow notch (= morphotypes 'c' or 'd').

Comparison and remarks

The above leporid material is attributed here to the genus *Trischizolagus* for the following combination of discriminant features:

1. the presence of p3 anteroflexid (= A1 morphotype; in 100%, N = 35);
2. the presence of short hypoflexus associated with mesoflexid/mesofossettid (= PR1/PR2 morphotypes; in 95.5%, N = 22); and
3. the exclusive presence of simple (uncrenulated) flexids in p3 (/lower teeth).

Trischizolagus from TCH-1B differs from the Old World:

1. species of *Hypolagus* Dice, 1917 as they bear A0/PR0 p3;
2. species of *Serengetilagus* Dietrich, 1941 and *Afrolagus* Sen & Geraads, 2023 which show A0-1/PR0 p3;
3. species of *Alilepus* Dice, 1931 bearing A0/PR1-2 p3;
4. monotypic *Nuralagus* Quintana et al., 2011 which is significantly larger in size;
5. monotypic *Sardolagus* Angelone at al., 2018 characterized by A1/PR3 p3;
6. species of *Pliopentalagus* Gureev & Konkova in Gureev, 1964 characterized by crenulated flexids in lower teeth; and
7. species of *Lepus* Linnaeus, 1758 and *Oryctolagus* Lilljeborg, 1874 which bear A1/PR3 p3.

The p3 size comparisons between relevant species of each leporid genus and the p3 morphotype distributions for each *Trischizolagus* species considered here are shown in Fig. 4 and 7. Most species of *Trischizolagus* are documented only from type localities, often with very insufficient material, so their phenotypes are not always well-known or defined. In contrast, *T. dumitrescuae* is well documented by abundant fossil material from different European localities (Čermák & Wagner 2013). In both cases, however, taxonomic co-identifications to particular nominal taxa are often quite uncertain and tentative. It is therefore difficult to make a reliable comparison of p3 sizes between different species. *Trischizolagus* from TCH-1B falls within the p3 size range of most taxa, which appear to have smaller p3 sizes than *T. dumitrescuae*. The differences in length-width proportions are rather a consequence of different methods of width measurement used by different authors. The distribution of individual sizes suggests that older/archaic species such as *T. crusafonti* and *T. maritsae* have the smallest p3, but this observation may be biased since the fossil record is limited and may include sub-adult specimens.

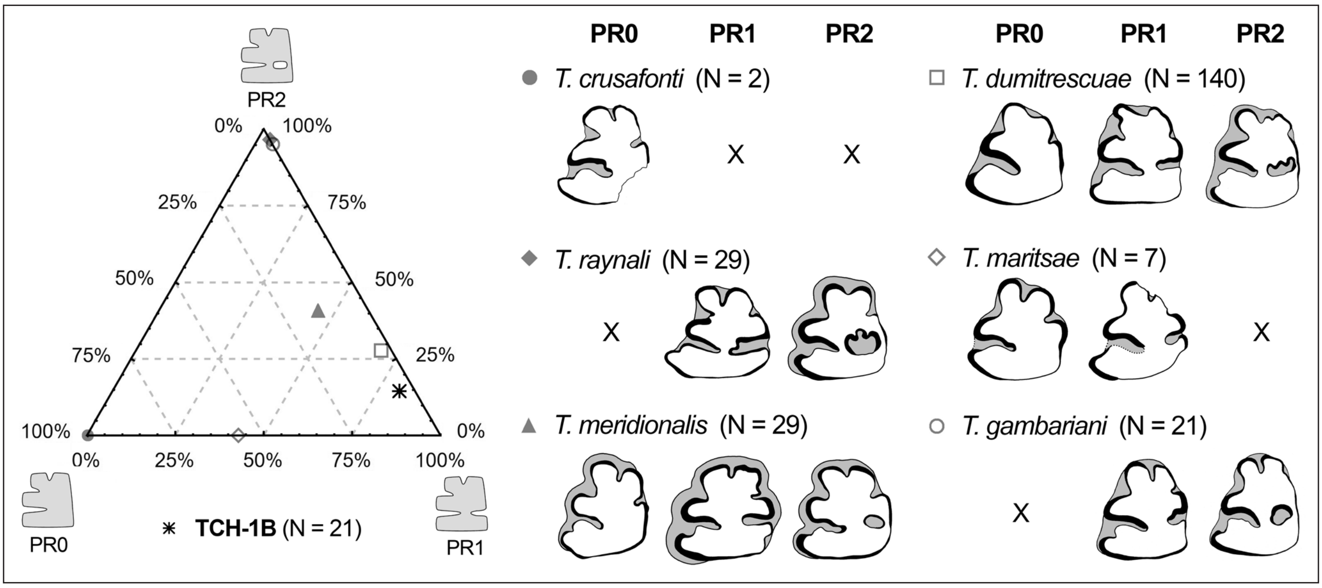

Fig. 7 - Distribution of p3 patterns (PR0-PR2 sensu Čermák et al. 2015) and examples of their occlusal morphologies in Late Miocene to Pleistocene species of *Trischizolagus* from the peri-Mediterranean area. Data from Radulesco & Samson (1967), Bruijn et al. (1970), Janvier & Montenat (1971), Averianov & Tesakov (1997), Čermák & Wagner (2013), Čermák et al. (2019), Sen & Geraads (2023), Sen et al. (2024 and references therein).

The fossil record of the earliest *Trischizolagus* species, *T. crusafonti* (La Alberca, Spain, MN13) and *T. maritsae* (Maritsa, Greece, MN13/14), is unfortunately limited, which considerably hampers reliable assessment of the relative frequencies of the p3 morphotypes within their populations. Additionally, the type material of *T. crusafonti* cannot be revised as it is unavailable from its repository in the ICP-Sabadell, and has been probably lost after a loan to MNHN-Paris at the end of the last century. Indeed, in MNHN-Paris were retrieved other fossil lagomorphs from the type locality La Alberca (S. Sen, in litt. to SČ, March 2023), which were likely loaned together with *T. crusafonti*. At any rate, both the p3 of *T. crusafonti* are commonly associated with the PR0 pattern (cfr. Averianov & Tesakov 1997; López Martínez et al. 2007; Čermák & Wagner 2013; Čermák et al. 2019; Sen & Geraads 2023), and this view is provisionally followed in this paper (Fig. 7). *Trischizolagus gambariani* documented from MN14 localities Nurnus (= type locality; AM) and Tepe Alagöz (TR) differs from *Trischizolagus* from TCH-1B by the almost exclusive presence of the PR2 p3 morphotype (Fig. 7).

In terms of the basic morphotype distribution, *Trischizolagus* from TCH-1B exhibits the highest phenotypic similarity to *T. dumitrescuae* and *T. meridionalis* (Fig. 7). These species have a relatively low proportion of PR0 and over 50% PR1, with the PR1/PR2 ratio differing amongst species. The frequency of PR2 morphotypes increases while PR1 decreases in the sequence TCH-1B → *T dumitrescuae* → *T meridionalis* (Fig. 7). *Trischizolagus* from TCH-1B has the highest PR1 occurrence and along with *T. dumitrescuae*, has similarly low PR0 occurrence. On the contrary, *T. meridionalis* distinguishes itself from the other two species by having a greater proportion of PR2 and PR0 morphotypes. The extreme is then *T. raynali*, which, as *T. gambariani*, has the almost exclusive presence of the PR2 p3 morphotype (Fig. 7).

In addition to the basic differences in morphotype distribution, there are also morphological traits of individual tooth structures that occur across the basic p3 morphotypes. The Iberian-Maghreb *Trischizolagus* species appear to share a broadly similar p3 trigonid arrangement, with a prominent anteroconid that is typically separated by a well-developed paraflexid. In these features, the *Trischizolagus* specimens from TCH-1B more closely resemble *T. crusafonti* and *T. meridionalis* than *T. dumitrescuae*. Comparable traits are also observed in *T. raynali*, although this taxon exhibits a markedly different distribution of p3 morphotypes. *Trischizolagus raynali* also shares general p3 proportions with *T. meridionalis*, which appear to differ from the condition seen in the Iberian species. Although the mesoflexid (morphotype PR1) is the most abundant in TCH-1B, it is generally less developed, shorter, and more stable in length compared to that of *T. dumitrescuae*. As a result, a relatively wide, lingually aligned connection (/isthmus) between the trigonid and the talonid is formed. The tendency for mesoflexid development in *T. meridionalis* is not fully clear. However, based on published data, it seems to be similar to that of *Trischizolagus* from TCH-1B. Although this structure is typically well-developed (when present) in *T. meridionalis*, its frequency is lowest in comparison to *Trischizolagus* from TCH-1B and *T. dumitrescuae* (Fig. 7). In this regard, the situation in *T. crusafonti* is even less clear, as noted above. The tendency for anteroflexid formation appears to be the highest in TCH-1B within these species; actually, in TCH-1B the anteroflexid is well developed, and a very long (Fig. 6.6-7) or double (Fig. 6.9, 12) anteroflexid is frequently present. *Trischizolagus meridionalis* usually has a less developed anteroflexid, as does *T. dumitrescuae*, in which, moreover, specimens with an incipient or even no anteroflexid occur relatively frequently. The two known p3 specimens from the type series of *T. crusafonti* possess weakly and moderately developed anteroflexids, respectively.

According to the current broadly accepted taxonomic model of the genus *Trischizolagus*, the remaining taxonomic identifiable material (see above) from TCH-1B is fully compatible with the current understanding of the phenotypic delimitation of the genus *Trischizolagus*, and is assigned to this genus. Due to the phenotypic specificities of Iberian-Maghreb *Trischizolagus* populations, and due to the paleobiogeographic constraints discussed and considered in this paper, this taxon is pro tempore co-identified with the nominal species *T. crusafonti*, and thus provisionally assigned to *T.* aff. *crusafonti*.

Genus *Oryctolagus* Lilljeborg, 1874

***Oryctolagus* cf. *laynensis* López Martínez, 1977**

Fig. 6.19-23

Referred material: 3 p3 sin [2 fragmentary] (TCH-1B 815, TCH-1B 882, TCH-1B 1071); 2 fragmentary p3 dx (TCH-1B 899, TCH-1B 1069).

Measurements: see Tab. 2.

Age: MN15b, Pliocene.

Occurrence: TCH-1B, Guadix Basin, Granada, Spain.

Description

p3 (Fig. 6.19-23). The taxon is documented by five p3 (four of which are incomplete fragments), representing ~18.5% of the total number (N = 27) of documented leporid p3 from the locality. The occlusal surface of the tooth is widened buccolingually. The morphology of its individual structures is simple and relatively invariable. Only the PR3 morphotype, which remains stable throughout the entire tooth shaft, is present in the available sample. One specimen represents a juvenile p3 not yet exhibiting occlusal surface wear (Fig. 6.23). The anteroconid is relatively short and wide, its length in a single measurable case being 35% of L; the labial anteroconid tends to be more prominent anteriorly. The anteroflexid is simple, its length varies, though in adult specimens is very long (Fig. 6.19-20). The protoflexid is simple and moderately deep; its depth is variable (Fig. 6.19-23). The paraflexid is present, but extremely shallow. The protoconid is relatively thin. The hypoflexid is not crenulated and occupies almost the entire width of the tooth. The medial process of the hypoflexid (doubled in one case; Fig. 6.20) is poorly developed. The labial tip of the hypoconid is simple, usually deformed by a very shallow notch (= morphotype ‘c’/’d’).

Comparison and remarks

At the present state of knowledge, the Iberian Pliocene leporid with p3 morphotype A1/PR3 can only be assigned to the genus *Oryctolagus*. In this context, the species which are both geographically and biochronologically relevant for comparison with the material from TCH-1B are *Oryctolagus laynensis*, *O. lacosti*, *O. valdarnensis*, and *O. giberti*. Unfortunately, the comparison and taxonomic assignment are very limited due to the absence in TCH-1B of cranial remains, which are often used to distinguish individual species.

The p3 dimensions in the type series of the above mentioned *Oryctolagus* species suggest that the p3s from TCH-1B are smaller than those of *O. lacosti* and *O. valdarnensis* and fall within the size range of *O. laynensis* and *O. giberti*. The differences in length-width proportions are, as in the case of *Trischizolagus*, rather a consequence of different methods of width measurement used by different authors. It is difficult to draw more reliable taxonomic conclusions on the morphology of such a small number of isolated and fragmentary p3s. The

Tab. 3 - Teeth measurements (in mm) of *Trischizolagus* aff. *crusafonti* seu *Oryctolagus* cf. *laynensis* from the Pliocene (MN15b) locality TCH-1B (Guadix Basin, Spain).

Trischizolagus* aff. *crusafonti* seu *Oryctolagus* cf. *laynensis											
Lower teeth						**Upper teeth**					
		N	**x̄**	**OR**	**CV**			**N**	**x̄**	**OR**	**CV**
i1	L	14	2.05	1.54-2.36	11.23	**I1**	L	7	1.94	1.75-2.04	6.19
	W	14	2.90	2.56-3.10	4.61		W	7	2.85	2.60-2.98	4.23
p4	L	12	2.73	2.29-2.93	6.23		Wg	7	0.77	0.66-0.88	10.44
	Wtrig	13	2.95	2.63-3.16	4.48	**P2**	L	33	1.82	1.19-2.11	12.04
	Wtal	12	2.68	2.01-2.89	8.97		W	33	3.01	2.70-3.28	5.28
m1	L	14	2.76	2.69-2.92	2.90	**P3**	L	13	2.33	1.88-2.63	9.03
	Wtrig	14	2.95	2.86-3.07	2.05		Want	13	3.18	2.85-3.54	7.04
	Wtal	16	2.66	2.40-2.85	4.96		Wpost	13	3.67	3.28-4.23	7.97
m2	L	9	2.77	2.69-2.84	2.02	**P4/M1**	L	46	2.32	1.79-2.63	9.12
	Wtrig	9	2.97	2.90-3.04	1.59		Want	43	3.30	2.68-3.85	7.99
	Wtal	9	2.64	2.43-2.75	4.08		Wpost	43	3.46	2.62-3.93	8.31
m3	L	20	2.20	1.81-2.26	7.98	**M2**	L	18	2.19	1.89-2.54	7.65
	Wtrig	26	2.06	1.68-2.26	7.17		Want	15	3.31	3.07-3.64	4.79
	Wtal	19	0.89	0.59-1.16	17.66		Wpost	16	3.10	2.56-3.38	6.26

p3 in all the aforementioned species exhibit the morphological features typical of *Oryctolagus*, i.e., a relatively shortened occlusal surface in the antero-posterior direction with a more or less oval outline, lingually prominent in the hypoflexid region; and mostly with a relatively wide and short anteroconid, which, however, is still relatively narrow compared to the rest of the occlusal surface of the tooth. In its morphological simplicity of particular structures, the p3 of TCH-1B is comparable to those of *O. laynensis*, *O. lacosti*, and *O. giberti*. The anteroflexid of TCH-1B p3 seems to be more developed, as in *O. valdarnensis*. However, the latter exhibits a noticeably more undulated hypoflexid with a pronounced protuberance in its anterior enamel wall.

Thus, based on the limited evidence available, it can be stated that phenotypically and biochronologically the p3 A1/PR3 finds from TCH-1B are closest to *O. laynensis*. We therefore provisionally assign these records to *O.* cf. *laynensis*.

Trischizolagus aff. ***crusafonti*** Janvier & Montenat, 1971 seu ***Oryctolagus*** cf. ***laynensis*** López Martínez, 1977

Fig. 8

Referred material: 1 fragmentary I1 sin (TCH-1B 874); 5 fragmentary I1 dx (TCH-1B 876, TCH-1B 879-880, TCH-1B 1075-1076); 10 fragmentary I1 of indeterminable laterality (TCH-1B 875, TCH-1B 877-878, TCH-1B 1092-1098); 3 I2 (TCH-1B 1080, TCH-1B 1083-1084); 28 P2 sin [12 fragmentary] (TCH-1B 830, TCH-1B 834, TCH-1B 838-841, TCH-1B 844, TCH-1B 847-848, TCH-1B 852-855, TCH-1B 865-869, TCH-1B 872-873, TCH-1B 1061-1964, TCH-1B 1066, TCH-1B 1085-1087); 20 P2 dx [6 fragmentary] (TCH-1B 828-829, TCH-1B 831-833, TCH-1B 835-837, TCH-1B 842-843, TCH-1B 845-846, TCH-1B 849-851, TCH-1B 864, TCH-1B 870-871, TCH-1B 1065, TCH-1B 1067); 82 upper molariforms: 5 P3 sin (TCH-1B 1003, TCH-1B 1007, TCH-1B 1009-1010, TCH-1B 1014); 8 P3 dx (TCH-1B 1002, TCH-1B 1004-1006, TCH-1B 1008, TCH-1B 1011-1013); 19 P4/M1 sin (TCH-1B 1011, TCH-1B 1019-1022, TCH-1B 1030, TCH-1B 1034-1037, TCH-1B 1041-1044, TCH-1B 1048, TCH-1B 1051-1052, TCH-1B 1055, TCH-1B 1060); 27 P4/M1 dx (TCH-1B 1015-1016, TCH-1B 1018, TCH-1B 1023-1029, TCH-1B 1031-1033, TCH-1B 1038-1040, TCH-1B 1045-1047, TCH-1B 1049-1050, TCH-1B 1053-1054, TCH-1B 1056-1059); 6 M2 sin (TCH-1B 986, TCH-1B 991, TCH-1B 993, TCH-1B 996-998); 12 M2 dx (TCH-1B 984-985, TCH-1B 987-990, TCH-1B 992, TCH-1B 994-995, TCH-1B 999-1001); 4 M3 (TCH-1B 1078-1079, TCH-1B 1081-1082); 1 fragment of upper molariform P/Mx dx (TCH-1B 1073). 8 fragmentary i1 sin (TCH-1B 903-906, TCH-1B 910-911, TCH-1B 915, TCH-1B 1077); 6 fragmentary i1 dx (TCH-1B 907-909, TCH-1B 912-914); 1 fragmentary i1 of indeterminable laterality (TCH-1B 916); 70 lower molariforms: 2 d4 dx (TCH-1B 862-863); 9 p4 sin (TCH-1B 955, TCH-1B 957, TCH-1B 960-963, TCH-1B 965-967), 4 p4 dx (TCH-1B 956, TCH-1B 958-959, TCH--1B 964); 8 m1 sin (TCH-1B 969-970, TCH-1B 974-976, TCH-1B 978, TCH-1B 981-982), 8 m1 dx (TCH-1B 968, TCH-1B 971-973, TCH-1B 977, TCH-1B 979-980, TCH-1B 983); 3 m2 sin (TCH-1B 950-951, TCH-1B 953), 6 m2 dx (TCH-1B 947-949, TCH-1B 952, TCH-1B 954, TCH-1B 1074); 30 m3 (TCH-1B 917-946).

Measurements: see Tab. 3.

Age: MN15b, Pliocene.

Occurrence: TCH-1B, Guadix Basin, Granada, Spain.

Description

I1 (Fig. 8.1-3). The upper incisor is antero-posteriorly flattened (L/W index: x̄ = 68%, OR = 62-73%, N = 7), roughly rectangular in shape, the tooth length-width ratio is quite stable (L/W index: CV = 5.2). The anterior enamel is of moderate thickness with no substantial variation. The anterior notch is shallow, V-shaped with quite widely opened enamel walls, not filled with cement, dividing the tooth in two parts at approximately one-third (from the medial wall) of the tooth width (x̄ = 27%, OR = 25-31%, CV = 8.8, N = 7).

P2 (Fig. 8.7-17). The occlusal surfaces of the tooth are highly variable, both in length-to-width ratios and in the morphology (degree of development) of individual structures. However, the set in question is morphologically and metrically continuous with no obvious signs of the presence of two

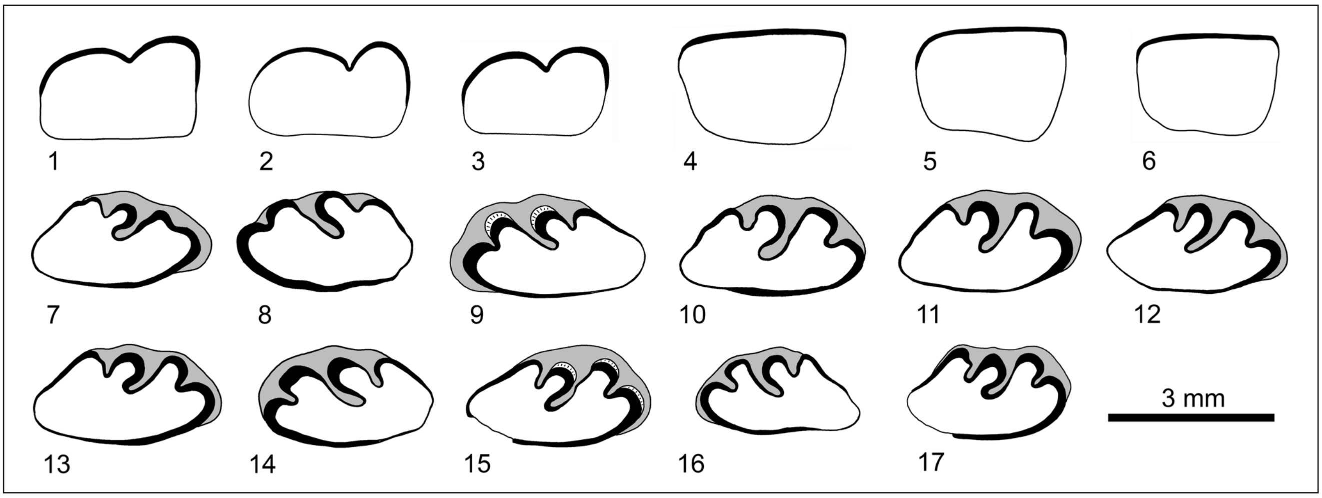

Fig. 8 - Morphology of incisors (I1/i1) and P2 *Trischizolagus* aff. *crusafonti* seu *Oryctolagus* cf. *laynensis* from the Pliocene (MN15b) locality TCH-1B (Guadix Basin, Spain). All incisors are shown as left teeth in their perpendicular cross-section from the occlusal view. All P2 in occlusal views. (1) I1 sin TCH-1B 874; (2) I1 side indet. TCH-1B 875; (3) I1 dx TCH-1B 876; (4) i1 sin TCH-1B 903; (5) i1 sin TCH-1B 904; (6) i1 sin TCH-1B 905; (7) P2 dx TCH-1B 836; (8) P2 sin TCH-1B 834; (9) P2 sin TCH-1B 847; (10) P2 dx TCH-1B 832; (11) P2 dx TCH-1B 833; (12) P2 dx TCH-1B 835; (13) P2 dx TCH-1B 829; (14) P2 sin TCH-1B 838; (15) P2 dx TCH-1B 843; (16) P2 sin TCH-1B 830; (17) P2 dx TCH-1B 846.

distinct phenotypic entities. In general, the morphology of the individual tooth structures is quite derived with relatively well-developed flexids. The hypercone is morphologically quite derived, always consisting of two lobes (distal and mesial) divided by a hypoflexus, dominated by LL-morphotypes VI (39%, N = 31) and V (35.5%, N = 31), then minority by IV (19%, N = 31) and III (6.5%, N = 31). The lagicone is similarly developed, with a predominance of BMR-morphotypes B (55%, N = 31) and C (42%, N = 31), morphotype A occurs only marginally (3%, N = 31). The paraflexus is moderately developed, reaching about half the tooth length ($\bar{x}$ = 56% of L; N = 34, OR = 44-60%), and its length is fairly constant (CV = 8.4). The cementum in the anterior and anterolingual part of the tooth shaft is quite well developed.

Upper molariforms (P3-M2). The given teeth are morphologically and metrically fully compatible with the common phenotype and its variability known in leporines. The ratio of antero- to posteroloph length varies, but typically the anteroflexus is shorter in P3 and longer in M2. The hypoflexus is relatively short, occupying approximately 60% of the tooth width. Its waveness varies greatly, from negligible to substantial. In general, the anterior enamel wall of the hypoflexus is more undulated. Within the tooth row, the anterior tooth positions are more undulated and the undulation decreases caudally. No taxonomically significant trends can be identified within this set to clearly indicate the existence of two distinct phenotypic entities. The occurrence of cement at the lingual end of the hypoflexus is quite variable. The enamel shows moderate development, with thicker enamel typically present on the anterior portion of the anteroloph and the lingual tip of the posteroloph. The thickness of the enamel in the anterior part of the hypoflexus varies. Enamel thickness is not dependent on tooth position.

i1 (Fig. 8.4-6). The lower incisor is roughly trapezoidal in shape, approximately as anteroposteriorly flattened as the upper incisor (L/W index: $\bar{x}$ = 70, OR = 60-79%, N = 14), with a similarly stable tooth length-width ratio (L/W index: CV = 7.8). The anterior enamel is thin, with constant thickness.

Lower molariforms (p4-m2). The teeth are morphologically and metrically compatible with the known phenotype and variability of leporines. The trigonid is considerably larger than the talonid. The anterobuccal corner of the talonid is smooth without flexids. The labial part of the talonid is frequently deformed by a shallow depression. The connection between the trigonid and talonid is narrow and elongated. The flexid between trigonid and talonid is not undulated, perpendicular to the anteroposterior axis of the tooth, its lingual end is curved anteriorly. On the labial part of the tooth and on the posterior trigonid, the enamel is relatively well developed.

m3. The trigonid is bean-shaped and larger and wider than the oval-shaped talonid. Both exhibit thicker enamel labially.

d4. The sole available specimen has the common two-lobed shape of leporid deciduous teeth. The crown of the tooth is relatively high, corresponding approximately to the length of the occlusal surface. The trigonid is larger than the talonid, and both lack flexids or depressions in the enamel. The anterobuccal corner of the talonid is smooth (without flexids). The enamel connection between the trigonid and talonid is missing, and the structures are separated by cement.

Discussion

Taxonomy of MN15 western European *Prolagus* species: at present, an inextricable riddle

Three species of *Prolagus* have been officially recognized in the MN15 of western Europe: *P. depereti*, *P. ibericus*, and *P. michauxi*. It may seem a fairly clear framework, however there are several problematic aspects:

1. the materials assigned to these species are not always morphologically congruent with the holotype,
2. unsatisfactory diagnostic characterization,
3. intraspecific morphology ranges overlap excessively, whereas interspecific variation is sometimes too wide.

All those are alarming features in the perspective of a correct identification and characterization of such species.

Prolagus depereti. Originally considered a subspecies of *P. figaro*, it has an extremely concise diagnosis: "p3 smaller than *P. sardus*, anteroconid more robust. P2 without enamel hiatus. As large as the Capo Figari form" (= *P. figaro*) (López Martínez & Thaler 1975: p. 859). The author mentioned that in this species she included different materials (retrieved from two localities in Roussillon), and though the collective sample presented a bimodal size distribution, the totality of the specimens was grouped in *P. depereti*. The specimens pertaining to the larger-sized cluster are morphologically similar to *P. savagei* (CA, pers. obs. MDC-Lyon 2023). The other cluster falls in the problematic cloud of the *P.* aff. *michauxi*/*P.* aff. *ibericus* group (see below).

P. ibericus. Unlike *P. depereti,* the characterization of *P. ibericus* seems not to suffer big problems. Actually, the diagnosis of *P. ibericus*, "small size, p3 with small anteroconid, long and thin protoconulid, no crochet; P2 without mesial hyperloph; upper molars without fossettes" (López Martínez & Thaler 1975: p. 858) fits relatively well the variability of the species, except for the observations about the crochet (which is relatively frequent in specimens from Layna not included in the type series figured in López Martínez & Thaler 1975: pl. II, figs. 1-4, but illustrated in López Martínez 1974: pl. XI, figs. 9-12), and for some additional minor features (i.e., the anteroconid/metaconid proportions).

P. michauxi. It is the most problematic taxon of the three. The materials on which the species was later erected were described in detail in an unpublished Ph.D. Thesis by López Martínez (1974: p. 73). However, the diagnosis of the species is quite telegraphic as far as dental materials are concerned: "P2 developed as in *P. sardus* […], upper molars with fossettes as in *P. oeningensis*, […] p3 large, with crochet frequent and large protoconulid are new characters" (López Martínez & Thaler 1975: p. 856).

In western European populations assigned to *P. michauxi* by the author of the species, it is possible to observe a scenario which is not compatible with the diagnosis. The development of the P2 (intended as the development of the mesial hyperloph) is highly variable, the fossettes in M1-2 tend to be reduced or lost, the crochet (typical of several other species) is never constant and tends to be lost, and the large protoconulid is not so frequent. The variability of those characters is such, that they have been used to attempt a relative biochronological ordering of such samples (López Martínez 1989).

To worsen the situation, the diagnosis of *P. michauxi* clashes with the morphology of the specimens from the type locality Sète. This happens not only with those stored at UCB-Lyon and NHM-Basel (CA, pers. obs. 2016; see Fig. 5.16-21), but also with the sample used to erect the species, figured for the first time in López Martínez (1974: pl. XI, figs.9-13) (see Fig. 5.1-5), which according to the original publication (López Martínez & Thaler 1975: p. 856) is curated at the ISE-Montpellier. In particular, the p3 of the UCB-Lyon series shows a wider range of morphological variability (three main p3 morphotypes recognizable in juveniles and adults can be individuated basing on the tooth overall shape, the anteroconid/metaconid relative proportions, and the characteristics of the crochet; see Fig. 5.16-21), and some traits incompatible with the diagnosis (as the P2 acquiring the mesial hyperloph with wear). Paradoxically, the specimens of *P.* cf. *michauxi* from the slightly older locality Vendargues (MN14, Fig. 5.6-8) fit the diagnosis better than the specimens from the type locality, due to the constantly large protoconulid and the constant crochet.

Judging from iconographic documentation (Dupré et al. 2022; Sen et al. 2024), North African samples attributed to *P. michauxi* have a quite heterogeneous morphology. The p3 specimens from Afoud 12-2 and Lissasfa seem to have an extremely slender p3 (= have a significantly higher L/W ratio), though the materials from Afoud 12-2 figured in Mahboubi et al. (2022) seem to show the opposite. In Afoud 12-2, the metaconid is often larger than the anteroconid (according to the figures in Dupré et al 2022, but see again contradictory evidence in those in Mahboubi et al. 2022), whereas the specimens from Lissasfa show an extremely reduced metaconid. In both cases, this clashes with the morphology of p3 from the type locality, and in general with Iberian samples referred to this species (contra Mahboubi et al. 2022: p. 60). Moreover, in African samples, there are some contradictions with the diagnosis of *P. michauxi*: the protoconulid is not so enlarged, and the crochet ranges from variable (Afoud 12-2) to extremely reduced/absent (Lissasfa). As for Afoud 12-1, its description is neither addressed in Mahboubi et al. (2022), nor supported by iconographic documentation.

Prolagus aff. *michauxi* and *P.* aff. *ibericus*. In the MN15 and MN16 of western Europe, several populations, part of populations, and even single specimens inside a population have been left in open nomenclature as *P.* aff. *michauxi*/*P.* aff. i*bericus.* For example, in the very abundant sample from Layna, the type locality of *P. ibericus*, three sole specimens (a skull, a jaw and a P2) showing non-*P. ibericus* features were retrieved. They were classified first as *P.* cf. *michauxi* (López Martínez 1974: pl. XII, figs. 1-5 and 7-8), and later as *P.* aff. *michauxi* (López Martínez 1989: p. 142, fig. 26). According to the provided comparisons (ibid.: p. 141), the resemblance of the Layna "alien" specimens with *P. michauxi* from Sète is null, except for the large size and the P2 with mesial hyperloph. Additional reports of *Prolagus* aff. *michauxi* are recorded in Iberian localities, i.e., Sarrión (MN16) and Cova Bonica (MN17). As for the former locality, the reason of the open attribution is due to the evolutionary degree of the sample, which is lower than expected (López Martínez 1989: p. 141-142); as for Cova Bonica, there was a sole available p3 which showed intermediate features between *P. michauxi* and *P. calpensis* (López Martínez 1989: p. 142).

The taxonomic mayhem is maximal in the MN15/16 of southern France. In Balaruc II and I (MN15/16), the *Prolagus* sample was classified as *P.* aff. *ibericus*, for having intermediate characters between *P. michauxi* and *P. ibericus* (López Martínez 1974: p. 86). However, López Martínez & Thaler (1975: p. 858) suggest that two specimens are possibly similar to *P. ibericus* (namely a P3 and a p3 figured in López Martínez 1974: pl. XIII, fig. 9 and pl. XIV, fig. 12), while the other could be hypothetically related to *P. calpensis*.

In Seynes (MN16), one specimen (a P2) is attributed to *P.* aff. *michauxi* due to its large size (López Martínez 1974: p. 72; pl. III, fig. 21), whereas the other three specimens (two complete maxillaries and one isolated P2) were recognized as *P.* aff. *ibericus* (López Martínez 1974: p. 87, fig. 16b and pl. III, fig. 20). Shortly after (López Martínez & Thaler 1975: p. 858), in Seynes was hypothesized the presence of three species: two small species, one assimilated to *P. calpensis* (referring to the specimen figured in López Martínez 1974: pl. III, fig. 20), and one not defined (ibid: p. 87, fig. 16B), while the other specimens were attributed to *P. michauxi*.

Our personal observations suggest that *P.* aff. *ibericus* from Seynes and Balaruc II have no other resemblance with *P. ibericus* from the type locality except for their small size, smaller than *P. michauxi*. Under a morphological point of view, the samples of *P.* aff. *ibericus* from Seynes and Balaruc II appear instead quite advanced, cfr. for example the anteroconid as large as metaconid vs. the small anteroconid of *P. ibericus* from Layna.

Finally, if we notice that elements of the type series of *P. michauxi* resemble morphologically and dimensionally *P.* aff. *ibericus* from the above mentioned French localities (Fig. 5.4), the doubts about the fact that those which should be the "essential characters" of *P. michauxi* under a linnaean point of view (Linnaeus 1758: p. 143) are indeed expressed in the diagnosis become very actual.

Thus, *P. michauxi* at present shows a too wide spectrum of mosaic combinations and too many intraspecific morphological incongruencies that cast an ominous light to the currently accepted taxonomic scenario. Such "worrying" elements induce to re-formulate Wood's (1957) famous question, though several taxonomic categories below: "What, if anything, is *P. michauxi*?".

Notes on the dentition of Pliocene leporids and the difficulties of their taxonomic determination

Phenotype. In the studied sample the whole spectrum of morphotypes from PR0 to PR3 is represented, though PR1 and PR2 are entirely dominant. In the Early Pliocene (ca. MN14-15) of Europe, the morphotypes PR0-2/A1 are, within the current state of knowledge, associated with the genus *Trischizolagus* (the exception is *Pliopentalagus* from MN15b, clearly distinguished by other characters). The PR3 morphotype is reliably documented in the Early Pliocene only from southwestern Europe, namely in the Iberian Peninsula, and is associated exclusively with the genus *Oryctolagus*. The leporid material from TCH-1B studied here fits into this framework, as it highlights that the PR3 p3 morphotype was present in the Iberian Peninsula much earlier than in the rest of Europe, which at that time was populated by leporids with PR0-PR2 p3 as *Hypolagus* and *Trischizolagus*.

The ontogenetic morphocline PR1 → PR2 indicated by Averianov & Tesakov (1997: fig. 7.4), which is undoubtedly typical of the genus *Trischizolagus*, was documented in the studied *Trischizolagus* from TCH-1B. The transition in question was localized very close to the occlusion in the TCH-1B sample; the position (distance from the occlusion) of the transition in other species of *Trischizolagus* has been specified and documented neither in the literature, nor in the well-documented and relatively common *T. dumitrescuae*.

Within the phenotypically similar taxa with a low percentage of PR0, there is an increase in representation from PR1 to PR2 in the direction TCH-1B (MN15) → *T dumitrescuae* (MN14-MN15) → *T meridionalis* (Pliocene/Pleistocene boundary), with the extreme cases of *T. gambariani* (MN14) and *T. raynali* (Early/Middle Pleistocene) (Fig. 7). This does not fit the hypothesis of a presumptive morphocline, which assumes a continuously increasing proportion of PR2 over time (this was not confirmed even in the abundant MN14-15 material of *T. dumitrescuae*; see Čermák & Wagner 2013). Moreover, *T. meridionalis* differs in having the highest abundance of PR0. Thus, the simple correlation between time and the increase in PR2 abundance within the genus *Trischizolagus* does not hold. These facts support the hypothesis of the presence of more evolutionary lineages (clades) of the genus *Trischizolagus*. This is fully consistent with the aforementioned finding that the Iberian-Maghreb *Trischizolagus* species appear to share certain morphological traits of individual tooth structures that occur across the basic p3 morphotypes and together form a phenotypically cohesive and internally compatible group, distinct from the eastern taxa such as *T. dumitrescuae* or *T. gambariani*. However, it should be noted that these findings are based on the currently limited fossil record from western Europe, and the observed traits may be biased by this constraint.

Taxonomic considerations and assignment. The presence of PR3 in populations of *Trischizolagus* has not been documented so far in the very rich material at present available, and certainly no ontogenetic transition to another morphotype has been up to now recorded as in the case of *Trischizolagus*, for which is documented the transition PR1 → PR2. For the sake of completeness, we cite a possible indication of PR2 → PR3 transition within *Oryctolagus* figured in López Martínez (1989: figs. 56.3, 6); however, the root part of the specimen, necessary to visualize the transition, is not shown. Without any evidence of a transitional state documenting the ontogenetic transition PR2 → PR3 within *Trischizolagus* p3 (which should reflect the phylogenetic trend), it cannot be confirmed or refuted whether the two sets of p3 distinguished in TCH-1B belong to one or two leporid taxa. Based on the updated paleobiogeographic distribution of the Iberian taxa (see paleobiogeographical discussion), the most parsimonious solution, under the Occam's razor principle, appears to be separating the leporid sample from TCH-1B in two species: *Oryctolagus* cf. *laynensis* and *Trischizolagus* aff. *crusafonti*, based on their phenotypes. Such attribution also is in accordance with the up-to-date accepted biochronological distribution of European late Neogene leporids.

Phylogenetic position of TCH-1B lagomorphs

Prolagus. Indeed, the taxonomic mayhem highlighted in MN15 western European species, especially regarding *P. michauxi*, which became a waste basket for any MN13-MN15 sample (with the further complication to be a chimeric taxonomic entity, as highlighted above), did not help a precise taxonomic assignment of TCH-1B *Prolagus*. In fact, we preferred for the moment to leave its specific assignment in open nomenclature not to complicate the current taxonomic scenario, though *Prolagus* from TCH-1B shows several peculiarities and it may represent the progressive form of a local lineage (and possibly a new taxon). Thus, for the moment its phylogenetic affinities cannot be stated with certainty and it is possible to state only that *P.* aff. *michauxi* from TCH-1B is neither related to the mysterious *P. ibericus*, nor to the French Pliocene *Prolagus* "world", but to a putative Iberian Pliocene stock waiting to be revised and properly defined.

Trischizolagus. Neither the phylogenetic or paleobiogeographic origin of the western Mediterranean occurrences of *Trischizolagus* cannot yet be traced, however, the oldest documented occurrences in this region so far are the Iberian records assigned to *T. crusafonti* (López Martínez 1989). Although this taxon is very poorly documented and poorly known, the phenotype of *Trischizolagus* from TCH-1B documented and discussed here supports the tentative hypothesis that the probable ancestor of *Trischizolagus* from TCH-1B was derived more or less directly from *T. crusafonti* or from a taxon from its phylogenetic vicinity.

Considering that the phenotype of *T. meridionalis* is also very close to *Trischizolagus* from TCH-1B, a European origin of *T. meridionalis* is very likely. It can therefore be tentatively assumed that *T. crusafonti* and the TCH-1B materials studied here, together with the African *T. meridionalis* and probably also *T. raynali*, belong to one evolutionary clade (see section below for details).

Oryctolagus. The currently available fossil record of the western Mediterranean supports the hypothesis of an Iberian origin of the genus *Oryctolagus* (López Martínez 2008). However, though most of the early history of the clade very likely took place autochthonously on the European continent, in a broader phylogenetic context, a more distant ancestry of this clade is likely to be tracked back in Africa (ibid).

Paleobiogeographical context

The lagomorphs of TCH-1B represent an important tile for the discussion about Euro-African dispersals.

Prolagidae. Recent papers revise northwestern African lagomorphs (Dupré et al. 2022; Mahboubi et al. 2022; Sen & Geraads 2023; Sen et al. 2024), and discuss the temporal and geographical distribution of Prolagidae and Leporidae in northwestern Africa. Indeed, an Iberian origin is the most parsimonious hypothesis to explain the presence of *Prolagus* in the latest Miocene of the southwestern Mediterranean rim, due to the geographical vicinity, the evidence of an emerged land connection, and the evidence of other mammalian dispersals.

The continental mammal exchanges between Iberia and northern Africa were several during the latest Miocene. The dating of the Afoud locality oldest level bearing small mammals of European origin at 6.21 Ma (Gibert et al. 2013), corrects the datum of 6.1 Ma in Benammi et al. (1995, 1996; though Sen et al. 2024 keep a wider window for the Ibero-African earliest dispersal, i.e., between 6.5-6.2 Ma). In this framework, a phylogenetic link between MN13 south-western European *Prolagus* and African ones may appear almost automatic, and the attribution of the Afoud 12-1 prolagid to *P. michauxi* may seem reasonable (Sen et al. 2024 with references). However, as highlighted above, the Iberian MN13-15 populations attributed to *P. michauxi* have little to share with the specimens of the type locality described in the original publication. At present it is not likely to invoke a lacune in the dense Late Miocene fossil record of the Iberian Peninsula to justify the absence of the morphotype(s) found in Sète in this geographic area. This means that the species described in the MN15 of the type locality Sète as *P. michauxi* probably never reached the Iberian Peninsula. In our opinion, neither the north African samples attributed to *P. michauxi* show noteworthy resemblance with the type series (see above). Thus, the Maghreb latest Miocene-Early Pleistocene *Prolagus* lineage(s) originated from a basal form of the MN13-15 Iberian morphological cluster of prolagids now lumped in *P. michauxi*.

This last observation solves a quite peculiar consequence of assuming instead a specific identity between African Pliocene *Prolagus* and the type population of *P. michauxi*. Natural world is complex and its responses are not linear and obvious, however it would have been indeed surprising if a hypothetical MN13 basal populations of *P. michauxi* maintained at least for ca 1 Myr (i.e., till MN13/14), and after the dispersal in a new territory, a perfect similarity with the sample from the type locality Sète, which is dated to 3 Myr later and lived in a completely different environment and ecological context.

Leporidae. In the case of leporids, the situation is somewhat more intricate. Any consideration of paleobiogeographic scenarios is significantly constrained by the fact that the majority of potential dispersal pathways fall within the Miocene/Pliocene transition, a time window in which the leporid fossil record is severely scanty, thereby precluding invariant taxonomic delimitation, often even at the genus level. The phenotype of the genus *Trischizolagus* in this period of time is only presumptive, and indirectly postulated mainly based on the numerous fossil records of the genus from the Pliocene of eastern Europe. The known phenotype of this early *Trischizolagus*, represented by only a few records, then overlaps in many respects with the phenotype generally attributed to the genus *Serengetilagus*. Most taxonomic or paleobiogeographic conclusions on the subject are more in the realm of speculation than plausibly verifiable invariant models based on fossil material.

The oldest documented leporid taxa of the Iberian Peninsula are *Alilepus turolensis* and *Trischizolagus crusafonti*. The origin of these taxa remains uncertain and the available knowledge of their phenotype is constrained by the aforementioned facts. For paleobiogeographic considerations and to understand the context from a European perspective, the records of *Nuralagus rex* and *Hypolagus balearicus* from Mallorca (MN14) are then relevant. The most parsimonious explanation for the presence of these leporids in the Balearic Islands is to assume their dispersal from the Iberian Peninsula during the Messinian salinity crisis s.l. It can be further postulated that also the presence of at least some of the leporid taxa reported from northwestern Africa are the consequence of dispersals from the Iberian Peninsula during this period. The earliest leporid representatives in northwestern Africa are documented in sediments slightly younger than those yielding *Prolagus*, i.e., in Afoud 12-2 (undetermined leporid; Sen et al. 2024), and Lissasfa (attributed to *Trischizolagus*; ibid.), dated at 5.9 Ma and 5.5 Ma, respectively, i.e., a lag of 0.4 Myr. This discrepancy may reflect a bias in the fossil record (as leporids are in general much less common than *Prolagus* in the assemblages of the Late Miocene-Pliocene) or to an actual delayed dispersal of leporids in the Maghreb with respect to *Prolagus*. At any rate, in our opinion, the phylogenetic and paleobiogeographic framework of the earliest leporids in the Iberian-Maghreb area, especially in the African part, is less simple, clear, and certain than suggested by Sen et al. (2024). For example, the findings from Lissasfa do not allow an unequivocal classification to the genus *Trischizolagus*. Possible candidates are also *Alilepus* and *Hypolagus*, since both are present in the Iberian Peninsula and/or Balearic Islands with endemic modified descendants during the Pliocene. Interestingly, *Hypolagus* from the Balearic Islands (~MN13-14) represents one of the earliest records of the genus in Europe, together with *H. igromovi* from the Don Valley. As for *Alilepus*, it is recorded in Africa since ~7.44 Ma (Winkler et al. 2003), and it is present in the Iberian Peninsula in the latest Miocene (López Martínez 1989). *Alilepus* is also the first leporid to reach the Italian Peninsula after its connection to continental Europe at ~6.5 Ma, in this case apparently together with prolagids, and preceding of ~1 Myr another leporid recorded from central Italy (Cava Monticino, 5.4 Ma; Rook et al. 2015), provisionally classified as cf. *Trischizolagus* sp. waiting for a revision of non-*Hypolagus* and non-*Alilepus* leporids of the latest Miocene-Pliocene of Europe, to evaluate the possibility that they could be phylogenetically related to the genus *Serengetilagus* and not to later Pliocene eastern Europe *Trischizolagus dumitrescuae* (Angelone et al. 2021: p. 112). Sen et al. (2024), though without further analysis of the materials, use Angelone et al.'s (2021) to-be-verified hypothesis, and assign the leporid from Cava Monticino to the genus *Serengetilagus*, further arguing about its African origin and dispersal through a Tunisian-Sicilian corridor. Leaving aside the fact that the latest Miocene Afro-Arabian faunal complex of the Italian Peninsula did not penetrate the Italian territory north of Calabria, recent studies confirm that the assemblage of Cava Monticino has affinities mostly with western European fossil mammal assemblages (and among them other Italian fossil assemblages) dated between 7 and 5 Ma, though some common component with southern Balkans (namely Greek assemblages related to the so called Pikermian Fauna, dated to ~7 Ma) are undoubtedly evident (Bartolini-Lucenti et al. 2021). Nevertheless, leporids with *Serengetilagus* p3 pattern were reported in central Africa since ~7 Ma (*S. tchadensis* López Martínez, 2007; TM266, Toros Menalla, Chad; age from Lebatard et al. 2010). Other scattered records of *Serengetilagus* followed in the latest Miocene and the Pliocene of eastern and central Africa, since the 6.1-5.8 Ma *Serengetilagus* sp. from the Lukeino Fm (Tugen Hills, Kenya; Mein & Pickford 2006; however see Winkler & Avery 2010), until possibly the Pleistocene (~1.8 Ma) of Olduvai Bed I (Winkler & Tomida 2011 and references therein; age in Deino 2012). Thus, *Serengetilagus* cannot be excluded from being the leporid recorded in the latest Miocene Maghreb localities Afoud and Lissasfa.

To further complicate the above illustrated complex taxonomic framework, it cannot be excluded that the records of leporids in the late Cenozoic of the Maghreb may be rather the result of multiple dispersal events, not only from Europe. In the case of the genus *Trischizolagus* in Maghreb, the interruption of the Gibraltar corridor after 5.3 Ma and the phenotypic similarity of *T. meridionalis* to *T.* aff. *crusafonti* from TCH-1B (evidenced in the systematic discussion) support its dispersal from the Iberian Peninsula. The alternative scenario of a dispersal from territories situated eastwards from the Maghreb is an unlikely option in the given context. Subsequent to the closure of the Gibraltar corridor, a period of isolation and independent evolution in the Maghreb of *Trischizolagus* resulted into the appearance of *T. meridionalis*. This process may have persisted for more than 2.5 Myr. For the sake of completeness, it is worth mentioning that the occurrence of *Trischizolagus* from TCH-1B may be almost synchronous with the extinction of the genus *Trischizolagus* in eastern and central Europe (Čermák & Wagner 2013). On the other hand, the occurrence of *T. meridionalis* in the Maghreb is still about 1 Myr younger.

In the paleobiogeographic context provided above, and within the commonly accepted taxonomic-phylogenetic model of the genus *Trischizolagus*, the presence of the phenotypic entity "*raynali*" in the Maghreb at the Early/Middle Pleistocene transition is a phenomenon that remains quite obscure. In the view of Sen et al. (2024), it is not conceivable that *T. raynali* is derived from *T. meridionalis* because the latter exhibits some more derived characters than *T. raynali*. They further infer that its occurrence should be a consequence of a second dispersal of *Trischizolagus* in the Maghreb. We disagree with these interpretations. In our opinion, the species in question fully fit into the presumptive evolutionary morphocline PR0 → PR1 → PR2. Although as shown above (see also Čermák et al. 2015), this trend cannot be generalized to the genus *Trischizolagus* as a whole, it is evident in the sequence *Trischizolagus* from TCH-1B → *T. meridionalis* → *T. raynali* (see Fig. 7). Moreover, the paraflexid of p3 is more developed in these Iberian-Maghreb taxa than in the eastern ones (e.g., *T. dumitrescuae*, *T. gambariani*). Concurrently, the lengthening of the labial anteroconid and opening of the protofexid on p3 cannot be universally applied to all species of the genus *Trischizolagus*. The affinity of *T. raynali* to *T. gambariani* seems very unlikely, although at first glance both taxa share a near identical proportion of the PR2 morphotype (Fig. 7). Anyway, it would be indeed strange and unusual that the ratio of basic morphotypes in relatively distant species would remain unchanged for such a long time. The basic morphology of *T. raynali*, especially the trigonid structure with the characteristic anteroconid and the development of paraflexids, is fully compatible with *T. meridionalis*. Similar traits, albeit in a lesser and rather initial extent, can be discerned in *T. crusafonti* (based on the two known p3 of the type series) and *Trischizolagus* from TCH-1B. A hypothetical dispersal of the genus out of Europe, where no dispersal corridors were available since the Messinian crisis, and where the last eastern and central European populations became extinct more than 2 myr before the appearance of *T. raynali*, can be clearly ruled out. Other possible alternative scenarios can be postulated to explain the presence of the phenotypic entity "*raynali*", however these cannot be verified due to the lack of fossil record and are not mentioned here. In any case, the taxon is fully compatible with the current understanding of the phenotypic delimitation of the genus *Trischizolagus*, and this generic assignment is accepted here for the time being. In light of the current phenotypic evidence for the "*raynali*" entity, the provisional hypothesis that *T. meridionalis* and *T. raynali* belong to a single autochthonous evolving clade appears to be the most plausible and parsimonious explanation.

Finally, it is worth adding to the paleobiogeographic considerations that *T.* aff. *crusafonti* from TCH-1B and *T. meridionalis* both coexisted with other leporid taxa. In TCH-1B, the earliest clearly proven coexistence of the genera *Trischizolagus* and *Oryctolagus* is recorded, while in Ahl al Oughlam, *T. meridionalis* coexisted with a probable ecological equivalent of *Oryctolagus* (absent in northern Africa until historical times), namely the genus *Afrolagus*, whose phylogenetic origin is currently unknown (Sen & Geraads 2023).

Concluding remarks

The taxonomic revision of Lower Pliocene lagomorphs from Tollo de Chiclana-1B (Guadix Basin, southern Spain) highlights the necessity to reassess, in the Iberian region, the "traditionally" accepted framework relative to lagomorph taxonomy.

In fact, the presence in TCH-1B of *Prolagus* aff. *michauxi*, a phenotypic entity significantly different from the holotype and type series of *Prolagus michauxi*, supports the long-known hypothesis of a substantial intraspecific variability of the species, and the importance of a revision of a taxon that has become a waste basket for MN13-15 Euro-Anatolian *Prolagus* (Angelone 2007).

The leporid assemblage of TCH-1B consists of two phenotypic entities, attributed to *Trischizolagus* aff. *crusafonti* and *Oryctolagus* cf. *laynensis*. The former is one of the latest European reports of the genus, whereas the latter *represents* one of the earliest records of *Oryctolagus*. Moreover, TCH-1B probably provides the earliest well-proven evidence of the co-occurrence of the two genera.

Given the key geographical position of the Guadix Basin in the framework of the latest Miocene faunal interchanges between Africa and Europe, the lagomorphs of TCH-1B represent an important basis for further paleobiogeographical studies. If, as we postulate here, *P. michauxi* s.s. is absent in the Iberian Peninsula, the presence of the species in northern Africa reported at ~6.2 Ma should be definitively excluded, with an obvious cascade effect on the taxonomy, phylogeny, and paleobiogeography of northern African prolagids. It is not clear if leporids reached northern Africa along with prolagids (actually in the north African fossil record leporids appear slightly later). However, the phenotype of *Trischizolagus* from TCH-1B seems to show a close phylogenetic relationship with *T. meridionalis*, which is reported from northern Africa ~1 Myr later.

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