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Pliocene and Pleistocene lagomorphs (Mammalia) from Northwest Africa: new discoveries

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Abstract

This work describes and interprets fossil lagomorphs from seven sites in the Maghreb the ages of which range from the Miocene/Pliocene boundary to the Upper Pleistocene. Some of these sites, such as the Thomas Quarries in Morocco and Tighennif (=Ternifine) in Algeria, are well known for the discovery of fossil humans and their artefacts. The lagomorphs studied herein belong to two families, Prolagidae and Leporidae. The genus *Prolagus* has been recorded in the Maghreb since the latest Miocene, c. 6.2-6.5 Ma, and its last known representatives in Africa occur at Tighennif and Djebel Ressay 5 and 6 (Tunisia) the age of which is estimated to be between 1.2 and 1.4 Ma. In other words, this genus, which is well known in Europe since the Early Miocene, crossed the Rifian Corridor during the Messinian crisis, and became extinct in the Maghreb earlier than in southwestern Europe where it survived until historical times. Its oldest representatives in the Maghreb known from the sites of Afoud and Lissasfa (latest Miocene-Early Pliocene) are related to *P. michauxi*, a species that is well represented in the latest Miocene and Early Pliocene localities in southern Europe. In the Early Pleistocene of Djebel Ressay 1 (Tunisia), it is represented by a new small species, *Prolagus ressayensis* n. sp. *Prolagus* is known in Europe as an inhabitant of wooded and humid environments. But in the terminal Miocene and Plio-Pleistocene this genus was confined more particularly to the Mediterranean rim, probably as an inhabitant of open woodland, temperate regions and certainly more open than the humid and wooded environments of the Early and Middle Miocene of Europe. The Leporidae appear in the Maghreb sites around the same time as *Prolagus*, but in the earlier sites (Afoud and Lissasfa), they are rare and therefore their identification is imprecise (Leporidae indet. at Afoud, *Trischizolagus* sp. at

Lissasfa). In contrast, they are abundant in terminal Pliocene and Pleistocene sites. The genus *Trischizolagus*, that is well documented at Ahl al Oughlam (c. 2.5-3.0 Ma) by *T. meridionalis* Sen and Geraads, 2023, is even more abundant in the deposits of the Casablanca region (Grotte des Rhinocéros, Thomas II, Thomas I-GH) and in Tighennif in Algeria where it is represented by *T. raynali* (Geraads, 1994). The last known representatives of this genus, collected from Grotte des Rhinocéros, occur alongside the first known representatives of the genus *Lepus*, described here as *Lepus berbericus* n. sp. In the Late Pleistocene site of Thomas I, a form of *Lepus* similar to *L. capensis* is represented by numerous mandible fragments. But the systematics of this species are the subject of debate, with no consensus as to whether it is a species occurring over a wide range from South Africa to the Middle East and North Africa or whether it comprises several species of which the morphological and / or genetic features are poorly defined. The genus *Trischizolagus* is well known in Europe and Anatolia with several species described between 6.5 and 3.5 Ma, while it survived in the Maghreb until the Middle Pleistocene, c. 0.5 Ma. It was probably replaced by the first hares of the Maghreb, described here as *L. berbericus* n. sp. The extant species *Lepus capensis* inhabits territories with open grassland and bushland habitats. The introduction of the rabbit *Oryctolagus cuniculus* to the Maghreb occurred later, probably in the Late Pleistocene by prehistoric men for food.

Keywords Lagomorpha, Prolagidae, Leporidae, Pliocene, Pleistocene, Northwest Africa

Introduction

Northwest Africa, or the Maghreb, is at present inhabited by two species of lagomorphs: *Lepus capensis* Linnaeus, 1758 and *Oryctolagus cuniculus* (Linnaeus, 1758). In the fossil record of the region, these species are recorded from the Late Pleistocene onwards (Michel 1992; Aouraghe et al. 2012). The earlier record of lagomorphs is still insufficient, but has gradually improved over the past decades, allowing palaeontologists to trace their evolutionary history in the region and to decipher their relationships to lagomorphs from Eurasia and other regions of Africa

In the present study, we describe abundant lagomorph remains from seven Pliocene to Pleistocene localities in Morocco (Lissasfa, Grotte des Rhinocéros, Level L of Thomas Quarry I and 'Grotte à Hominidés', and Upper Cave of the same quarry), in Algeria (Tighennif) and in Tunisia (Djebel Ressas). These sites have yielded fossils referred to the

genera *Prolagus* (Prolagidae), *Trischizolagus* and *Lepus* (Leporidae). The two first genera are extinct, while *Lepus* is still a common inhabitant of this region.

The presence of Prolagidae and Leporidae in Northwest African deposits has been mentioned in numerous publications, but detailed studies with descriptions, measurements and illustrations of the material are sorely lacking. In most publications they are only mentioned in faunal lists, sometimes with a short description and/or sketchy illustrations. Aouraghe et al. (2012: 165) provided a synthesis of knowledge on the fossil lagomorphs of the Maghreb, and summarised the state of the art as "detailed and published studies devoted to Lagomorpha still remain rare, although several Moroccan sites have yielded remains of lagomorphs, without detailed study". Janvier and de Muizon (1976) were the first to describe in detail and to illustrate an ochotonid from the Maghreb, *Kenyalagomys mellalensis* Janvier and de Muizon, 1976 from Beni Mellal, and Geraads (1994) described the fossils of leporids from Grotte des Rhinocéros, both localities in Morocco. Over the past four decades, many authors have reported the presence of lagomorphs in Pliocene and Pleistocene sites in the Maghreb, but without detailed systematic studies. More recently, two papers (Dupré et al. 2022; Sen and Geraads 2023) described new finds from Morocco that partially fill this gap.

It would be an understatement to say that the history of lagomorphs is poorly documented not only in the Maghreb, but in all of Africa. For a continent of more than 30 million km², the number of reasonably documented sites that have yielded lagomorph fossils barely exceeds two dozen (Winkler and Avery 2010; Avery, 2019). And yet fossils of three families of lagomorphs are known in the continent. The Ochotonidae are represented by two genera, *Austrolagomys* and *Kenyalagomys* during the early and middle Miocene. The Prolagidae are only known by limited material from a few sites in the Maghreb, except at two localities in Morocco where they are well documented (Dupré et al. 2022; Sen and Geraads 2023). As for the Leporidae, they are currently represented in Africa by five extant genera and at least 13 species (Happold, 2013, 2018), but they are rare in the fossil record. *Alilepus* sp. from Lothagam (Kenya, between 7.44-6.54 Ma) and *Serengetilagus tchadensis* López-Martínez et al., 2007 from Toros Menalla (Chad, c. 6.8-7 Ma) may represent the first leporids that entered Africa. The other species *Serengetilagus praecapensis* Dietrich, 1941 is well documented from Laetoli in Tanzania and Lothagam in Kenya c. 2.4 and c. 5 Ma respectively (Winkler and Avery, 2010). Another early leporid was reported from the Mpesida Beds, Kenya, c. 6.3 Ma (Pickford 1975). Recently, Sen and Pickford (2022) described a new species of Red Rock Hare (*Pronolagus humpatensis*) from the Plio-Pleistocene deposits of Angola

and Namibia, but most of the fossil lagomorph remains from Southern Africa, of which there are many (Avery, 2019), have not been studied in detail.

Regarding the Maghreb, four genera of leporids are known there: *Trischizolagus* Radulescu and Samson, 1967 since the ?Early Pliocene, *Afrolagus* Sen and Geraads, 2023, known so far only from Ahl al Oughlam dated to about 2.5-3 Ma, *Lepus* Linnaeus, 1758 since the Middle Pleistocene and *Oryctolagus* Lilljeborg, 1874 since the Late Pleistocene. All are currently documented by material from a limited number of sites.

In such a context, the abundant remains from seven localities of the Maghreb, comprising cranial, dental and post-cranial elements significantly increase our knowledge about North African lagomorphs. Moreover, the fact that some of these species certainly are of European affinities sheds light on faunal exchanges between southwestern Europe and Northwestern Africa.

The localities with lagomorphs under study

The present study focuses on unpublished material from seven localities in the Maghreb, the ages of which range from the Early Pliocene to the Late Pleistocene (Fig. 1). The abundance and state of preservation of the material varies from site to site: for instance, only isolated teeth occur at Tighennif in Algeria and Djebel Ressay in Tunisia, but many mandibles and maxillae have been found at the Grotte des Rhinocéros and Thomas Quarries in Morocco. The localities with lagomorphs are presented below according to their geographical position, from west to east.

Lissasfa, Morocco

The Lissasfa site (LSF) is situated in the southern suburbs of Casablanca, 12 km from the present day seashore. Like many other localities in this region, it is a pocket infilling in a dune sandstone, that was exploited in a quarry, now used as a dump. Large mammals are rare (*Nyctereutes* ? sp., Rhinocerotidae indet., *Sivatherium* sp., *Gazella* sp., cf. *Ugandax* sp.; Geraads et al. 2010), but rodents are extremely abundant (about 2,000 teeth from a few tens of kg of treated sediment). Geraads (1998) described the rodents from Lissasfa and identified 10 species, four of which were new. The fauna indicates an age close to the Miocene/Pliocene boundary, c. 5.5-5 Ma. It is the richest small mammal assemblage known in North Africa for this period. Thanks to its basal position in the local stratigraphy, it provides a minimum age of the base of coastal deposits in the Casablanca region (Raynal et al. 1999). The lagomorph

remains from Lissasfa were collected by D. Geraads and, after study, they will be stored at the Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP), Rabat, Morocco.

Grotte des Rhinocéros (GDR), Morocco

The locality is situated in the Oulad Hamida Quarry 1 (formerly called Thomas Quarry III) in the western outskirts of Casablanca (33.566° N, -7.701° W). It was discovered in 1991 and soon after was explored. It yielded one of the richest faunal assemblages for the early Middle Pleistocene in North Africa associated with abundant lithic artefacts. The cave was used as a food consumption site by both carnivores and hominins (Raynal et al. 1993, 2023a; Daujeard et al. 2012; Campmas and Daujeard 2020; Daujeard et al. 2020). The geological context and stratigraphy of this cave were published in several papers (Raynal et al. 1993, 2023; Daujeard et al. 2020; Geraads et al. 2022), its fauna was studied mainly by Geraads (1993, 1994, 2002, 2010a, 2016a), its lithic industry of the second regional Acheulean by Raynal et al. (2009, 2023a), and the human and carnivoran impact on the accumulation and consumption of faunal remains by Daujeard et al. (2012, 2020). The biochronological age estimation as early Middle Pleistocene was based on the abundant mammalian fossils. In addition, numerical ages were also provided. Rhodes et al. (2006) used the electron spin resonance (ESR) method on mammalian tooth enamel (12 samples) and obtained ages between 435 ± 85 Ka and 737 ± 129 Ka, but Geraads et al. (2022) favoured the earlier part of this age range. Geraads (1994) described some remains of leporids from this site as *Serengetilagus raynali* n. sp. and *Lepus* cf. *capensis*. The lagomorph remains will be stored, after study, at INSAP, Rabat, Morocco.

Level L of Thomas Quarry (hereafter Th I-L)

Thomas Quarry (33.569° N, -7.697° W) is located close to Oulad Hamida Quarry. It became famous in the late 1960s, due to the discovery of a human mandible in a cave exposed during quarry works that was subsequently attributed to *Homo erectus*. In the same quarry, subaerial deposits consisting of cross-bedded sands and calcareous mudstones, belonging to the first member (OH1) of the Oulad Hamida Formation (OHF), yielded a rich lithic assemblage that is the earliest known well dated Acheulean assemblage in Northwestern Africa, at c.1.3 Ma (Geraads et al. 2022; Gallotti et al. 2023; Raynal et al. 2023b). In a poster presentation at AGU23 in San Francisco, Perini et al. (2023) provided the results of a magnetostratigraphic study in the Thomas Quarry, and confirmed the previous age attribution. The associated fauna is dominated by hippos, in agreement with the fluvio-lacustrine nature of the deposits, along with elephants, a few antelopes, a suid close to *Kolpochoerus majus*, and a few teeth of murid

rodents similar to those found in younger levels of the quarry, but *Paraethomys* and *Gerbillus* look different at the species level. Together with the lagomorphs described below, this material belongs to the INSAP collections.

'Grotte à Hominidés' of Thomas Quarry (hereafter Thomas I-GH)

In Thomas Quarry (there used to be three Thomas quarries but only Thomas Quarry I remains), a thick sequence of intertidal biocalcarenes and aeolianites overlies the OH1 Member, attesting to fluctuating sea levels (OH2 and OH3). A marine cave was excavated into these deposits, and infilled by the OH4 and OH5 members. In the sixties, Philippe Beriro, a local student, discovered a human mandible there, assigned to *Atlanthropus mauritanicus* by Ennouchi (1969), along with rich lithic industries, a mammalian fauna including the lagomorphs described below, and human remains, hence its name of 'Grotte à Hominidés' (GH). Carnivores were certainly more involved in the bone accumulation than at GDR; accordingly, the large mammal fauna is less well preserved. Rodents are also less abundant, and attest to an age slightly different from that of GDR, and also from the assemblage called 'Thomas 1' by Jaeger (1975, 1988), which is certainly from a different, younger, cave filling. The magnetostratigraphic study of the Thomas Quarry (Perini et al. 2023) suggests the correlation of Thomas I-GH to the Brunhes-Matuyama transition at ~0.773 million years ago, an age not very different from that of GDR (Geraads et al. 2022).

Upper Cave of Thomas Quarry (hereafter Thomas I-UC), Morocco

In Thomas Quarry I, the uppermost part of the cave system consists of rubified sands ("RS" in Geraads et al. 2022, fig. 39.2; Raynal et al. 2023b); they were excavated in squares KA23 to KA25. Above a speleothem dated to slightly less than 100 ka, they yielded mostly rodents of modern aspect, together with a good sample of lagomorphs, described below.

Tighennif, Algeria

The site of Tighennif (formerly called Ternifine or Palikao) is situated in the town of the same name, 17 km east of the city of Mascara in northwest Algeria (35.415 N, 0.322 E). It was discovered in 1872 when the site was exploited as a sand pit, and a French settler Mr. Balavoine observed the presence of bones and alerted Dr. G. Tommasini. In turn, Dr Tommasini informed A. Pomel about this discovery and Pomel (1878) published the first report on fossil finds. Arambourg and Hoffstetter (1963) and Geraads (2022) provided a detailed history of excavations carried out at this site since the time of Pomel. Also, two

recent articles (Geraads, 2016b; Pickford, 2020), on carnivores and pigs of this site, respectively, summarised the history of excavations and palaeontological studies on the mammals of Tighennif.

The most extensive excavations were carried out by C. Arambourg and R. Hoffstetter from 1954 to 1956. Several thousand specimens of vertebrates, mainly mammals, including several remains of the Hominidae called *Atlanthropus mauritanicus* Arambourg, 1955, were collected. The remains of small mammals were not neglected, and they were recovered by in situ collecting or by screen-washing of the sediment. Part of the washing residue was transported to the Museum in Paris to be sorted, but it remained stored in the basement of the palaeontology building until 2022. The first author rediscovered this residue and sorted it under a microscope. The lagomorph fossils studied herein include the specimens collected during the excavations of 1954-1956, and those recovered by sorting of this residue. They are preserved in the collections of the Muséum National d'Histoire Naturelle in Paris under the acronym MNHN-F-TER, hereafter TER.

The residue of screen-washing contains a great number of fragments of long bones. All long bones of small mammals are crumbled, fragmentary, with a few exceptions of rather compact elements such as the carpals and tarsals. Their state of preservation suggest that the remains of animals which died in the water or were transported by runoff or rivers were trampled there by the animals frequenting the pond, before their carcasses were buried.

Like most of the fossils collected during the 1954-1956 field campaigns, the micromammals from Tighennif were not studied until J.J. Jaeger included the Muridae in his PhD dissertation on the Neogene and Quaternary rodents of the Maghreb (Jaeger 1975), and Tong (1989) did the same in her PhD dissertation on the Gerbillidae of the Maghreb. The small mammal assemblage is dominated by the Gerbillidae (5 species; Tong 1986, 1989), and the Muridae (3 species; Jaeger, 1975). The arvicolid *Ellobius africanus* Jaeger, 1988 and a large erinaceid are also present. The remains of lagomorphs are rare in comparison to those of rodents and insectivores.

From the beginning of his observations on the fauna and artefacts, Arambourg (1955: 94) correlated the Tighennif fauna to the early Middle Pleistocene based on the presence of “a *Machairodus*, a giant warthog from the *Notochoerus* group and a large *Cynocephalus* close to giant fossil forms from eastern and southern Africa”. In their monograph on this site Arambourg and Hoffstetter (1963: 29) argued that “the presence of genera such as *Machairodus*, *Afrochoerus* and that of a giant baboon, the absence of *Homoioceras* and *Sus* give to this fauna an archaic character which corresponds exactly to what we know about

other African deposits from the beginning of the Middle Pleistocene, such as, in particular, that of level II of Oldoway". In later years, this age attribution was retained by several palaeontologists who studied parts of the Tighennif mammals (e.g. Jaeger 1975; Eisenmann 1981; Geraads 1981, 1987, 2002; Tong 1986, 1989; Geraads et al. 2004).

However, it became increasingly clear in recent years that Tighennif is certainly earlier than the Middle Pleistocene, in part because the other North African sites are older than previously thought. Geraads (2016b, 2022) suggested an age of c. 1.0 Ma for the Tighennif fauna, and correlated it to the late Calabrian. In their analysis of Late Pliocene and Pleistocene mammalian faunas from the Maghreb, van der Made et al. (2021) correlated the Tighennif fauna to the Jaramillo normal polarity event, i.e. c. 1.1 Ma. Pickford (2020) studied the abundant suid fossils from Tighennif, and concluded that "The fossil suids from Tighennif (Algeria) comprise a taxonomically homogeneous sample which is close in morphological variability and range of metric variation to the collection of *Metridiochoerus andrewsi* from Bed II, Olduvai Gorge (Tanzania), Homa Mountain (Kanjera, Kagua, Rawi) and parts of the Koobi Fora Formation (Kenya) and the Shungura Formation (Ethiopia). ... It is therefore concluded that the Tighennif suids indicate an age for the faunal assemblage of c. 1.4 ± 0.3 Ma". In summary, the Tighennif fauna is better correlated with late Early Pleistocene, rather than the Middle Pleistocene.

Indeed, many radiometric analyses of tuff horizons included in Olduvai Bed II yielded ages between 1.68-1.34 Ma (see for instance McHenry and Stanistreet 2018), and the most fossiliferous horizon was dated as 1.338 ± 0.024 Ma by Dominguez-Rodrigo et al. (2013). If the fauna of Tighennif is correctly correlated to that of Olduvai Bed II as some palaeontologists have suggested, its age would be close to c. 1.4 Ma. However, such a direct correlation to Olduvai Bed II needs a careful comparison of faunas and evolutionary stage of the common taxa, which is out of the scope of the present study. We will see here below that the lagomorphs are in agreement with an Early Pleistocene age of the Tighennif fauna.

Djebel Ressas, Tunisia

The quarries of Djebel Ressas (Lead Mountain) are situated about 25 km south of Tunis, on the northern end of the mountain of the same name. In the late 1980s, they were visited by MP who discovered abundant remains of small vertebrates in blocks collected from the fissures in the Jurassic limestone exploited for their content of galena (Mein and Pickford, 1992: 247). These authors noted that "At the northeast end of "Petit Ressas" ($10^{\circ} 20' 58''$ E: $36^{\circ} 37' 15''$ N), blocks of indurated marl occur as float in the scree and as fissure fillings in

the cliffs above. These fissure fillings consist of well-indurated fine pink silts and microbreccia, containing rich concentrations of well-preserved micromammals and gastropods". The faunal content of eight blocks collected from different fissures and infills were analysed by Mein and Pickford (1992). They provided a commented preliminary list of small mammals, and noted that faunal composition differs from one block to another. The oldest assemblage is from the block of breccia Djebel Ressas 1, that these authors correlated with Djebel Irhoud Ocre, previously studied by Jaeger (1975), who considered it to be Early Pleistocene. The other blocks yielded slightly younger assemblages. In addition to faunal lists, they analysed the size and pattern of the murid teeth referred to various species of *Paraethomys*, in comparison with those from other North African localities. This genus is common in North African Pliocene and Pleistocene localities and is represented by at least seven species that display size increase over time, in addition to some changes in dental morphology and hypsodonty. Mein and Pickford (1992) measured the occlusal surface of the main molar M1 (mean length x width), and they used the enlargement of the occlusal surface as a chronological criterion. They thus showed that the masticatory surface of M1 increases from 3.14 mm² in the oldest species *Paraethomys anomalus* of Amama 3 (ca. 3.6 Ma) to 10.51 mm² in *P. darelbeidae* of Aïn Mefta (ca. 0.3 Ma). The value increases as the masticatory surface of M1 enlarges. This method allowed Mein and Pickford (1992) to estimate the age of the oldest assemblage Djebel Ressas 1 as 1.6 Ma, and the three other assemblages with lagomorphs (Djebel Ressas 5, 6 and 8) as between 1.4-1.2 Ma. The name of this locality has often been mentioned in publications on North African micromammals, but the material has remained undescribed until now. The Djebel Ressas fossils are preserved in the collections of the University Claude Bernard-Lyon 1 under the acronym UCBL-FSL-DJR.

Material and methods

In the introduction to her doctoral thesis López-Martínez (1974: 8) noted that "The palaeontological study of lagomorphs is essentially based, like that of other groups of micromammals, on the morphology and variability of dental parts. They contain much more information than any other bony part of the body". This is even more true for the study of fossil lagomorphs, the systematics of which are essentially based on the size and morphology of P2s and p3s, and incidentally complemented by the characteristics of the other teeth, cranium and mandible.

The lagomorph fossils in the present study came from seven localities where they were collected at various times by different researchers, using diverse methods. Their state of preservation therefore varies from one site to another, for instance comprising only isolated teeth from Tighennif and Djebel Ressas, but essentially fragments of jaws from Thomas I-GH and Thomas I-UC.

We prefer to illustrate all teeth with drawings, rather than with photos, for a better expression of dental features. All drawings have been made by the first author with a camera lucida mounted on a Leica M3Z binocular microscope. In all illustrations of cheek teeth, the mesial side is towards the top, enamel is represented in black, dentine in white and cement with dots.

All measurements are in millimetres. They were taken with a Mitutoyo measuring equipment on the occlusal surface of teeth, and they indicate maximum length and width of teeth in the sagittal and transverse axes, from the external margin of enamel. This does not always correspond to the greatest diameter of teeth (length or width) since in many lagomorphs there is, as a rule, an additional coat of cement of variable thickness. For the Leporidae, the measuring techniques follow the method of Erbajeva and Angermann (1983). We retained the most significant measurements: two dimensions for incisors and P2, four for upper molariforms, three for p3 and lower molariforms. The dental terminology follows López-Martínez (1974, 1989) for Prolagidae and Palacios et al. (1980) for Leporidae (Fig. 2). This terminology uses the terms flexus (id) and loph (id) for respectively folds and crests, and the names of cusps as in many other mammalian groups. Upper/lower premolars are abbreviated as P/p, and molars as M/m. The general name of “upper/lower molariforms” is used for P3-M2 and p4-m2, respectively.

As noted above, after study the materials from the Moroccan localities will be stored in the Institut National des Sciences de l'Archéologie et du Patrimoine, Rabat, Morocco. The Tighennif material is preserved at the Muséum national d'Histoire naturelle in Paris, and that from Djebel Ressas in the collections of the Université Claude Bernard-Lyon 1 in Villeurbanne.

Systematic study

Order Lagomorpha Brandt, 1855

Family Prolagidae Gureev, 1960

Remark: For the family status of *Prolagus*, see discussion in Sen 2020.

Genus *Prolagus* Pomel, 1853

Type-species: *Prolagus oeningensis* (König, 1825)

Other species of the genus: According to the NOW Database, consulted in April 2023, at least 27 species from continental Europe, Turkey and western Mediterranean islands are referred to this genus. In addition to this, Sen and Geraads (2023) described a new species from Morocco. Altogether, their time span extends from the Early Miocene to the Holocene. The Northwest African species under study are compared with the most similar to them.

Species *Prolagus michauxi* López-Martínez, 1975

(Figs 3, 4)

Type locality: Sète (Hérault, France, MN15)

Material from Lissasfa: Fragment of right maxilla bearing P3, P4 and M2 (LIS-7); fragment of right maxilla bearing P4 and M1 (LIS-9); left p3 (LIS-8); right M2 (LIS-10); right hemimandible bearing incisor and p3-m2 (LIS-11); fragment of left hemimandible bearing p4-m1 (LIS-16); four isolated p3s (LIS-12-15).

Measurements: Table 1.

Description

On the palate, the premolar foramen is oval in outline (1.72 x 0.98 mm) and extends from the P3/P4 limit to the mid-level of M1. López-Martínez (1974: 64) noted that in *P. michauxi* from Sète this foramen “is situated between P4 and M1, and is as long as one tooth”. The infraorbital foramen (1.66 x 0.67 mm) is located at the front of the orbit five millimetres above the anterior margin of the P2 alveolus. The P2 is lacking; but its alveolus is preserved on the right maxilla LSF-5, and its outline clearly indicates a tooth with a large mesial hyperloph. On the P3, the buccal margin is straight, the buccal end of the precone lacks enamel, the lagiloph reaches the buccal surface, and the hypoflexus is present but shallow. The P4 has the usual pattern of *Prolagus* having a hypoflexus, parafofsette and mesofossette. The M1 and M2 lack fossettes, and the hypoflexus almost reaches the buccal margin.

The mandible has a diastema (5.9 mm) that is shorter than the p3-m2 alveoli length (6.9 mm). A large foramen is situated 0.7 mm behind the m2, and it communicates with the mental foramen. The ventral margin of the body is strongly convex below the tooth row. On the buccal surface, the mesial mental foramen is small and situated just anterior to the p3,

while the distal mental foramen is larger, located beneath the m1 and close to the ventral margin. In lingual view, the distal end of the incisor makes a protuberance below the p3. The mylohyoid line extends from beneath the anterior margin of p3 to the middle of m2.

All five p3s have the occlusal surface longer than wide. The anteroconid is larger than (3/5) or similar in volume (2/5) to the metaconid and has a distobuccal depression. One p3 has the anteroconid connected to the protoconulid. The protoconulid is moderately thick in all specimens and is oriented mesiobuccally. The crochet is absent on four p3s, but one p3 has a weak oblique crochet at the base of the metaisthmus. The m1 and m2 have a deep notch on the mesial face of the talonid.

Comparison and remarks

The Prolagidae are mainly known in Europe and Anatolia since the Early Miocene and are thus considered to be a European group of lagomorphs. In North Africa, Jaeger (1971) was the first to report on the occurrence of *Prolagus* in a Tunisian locality, Lac Ichkeul. Since that time, *Prolagus* remains have been recorded in many other North African localities for the time interval spanning the latest Miocene to Early Pleistocene (c. 6 to 1 Ma). Most of the fossils have been referred to as *P. michauxi* or *P. cf. michauxi* (see Dupré et al. 2022, and references therein). Sen and Geraads (2023) identified a new species of *Prolagus*, *P. migrans*, from the richest Moroccan locality (Ahl al Oughlam; (#2 on Fig. 1)) the age of which is close to the Plio-Pleistocene boundary.

The specimens from Lissasfa compare well with *Prolagus migrans* Sen and Geraads, 2023 in having similar dimensions, a large mesial hyperloph on the P2, a large and trapezoidal anteroconid and an occasional crochet on the p3, and a buccal notch on the lower molariforms. Despite these resemblances, *P. migrans* differs in having p3 with the anteroconid always larger than the metaconid, a rounded metaconid (not pear-shaped as at Lissasfa), isolated protoconulid in almost half of the p3s, and lacking the crochet in most specimens.

Several species of *Prolagus* are known from the Late Miocene and Pliocene of Western Europe, in particular from Spain and southern France. Species that are of comparable size and shape are *P. crusafonti* López-Martínez, 1975, *P. michauxi* López-Martínez, 1975, and *P. ibericus* López-Martínez, 1975. Among these taxa, *P. crusafonti* has a mandible with a very short diastema, P2 without mesial hyperloph and straight lagiloph, P4 with a short parafossette, M1 and M2 with fossettes, p3 short and wide the anteroconid often rounded and

a strong central crochet in most individuals, and lower molariforms without talonid notch (López-Martínez, 1989).

Prolagus ibericus, the type locality of which is Layna in Central Spain (MN15 according to López-Martínez and Thaler 1975) has cheek teeth that on average are a bit smaller than those from Lissasfa (Fig. 5). As rightly noted by Angelone (2008: 447-448) the main characteristics concern the combination of ancestral and evolved features: “*P. ibericus* López-Martínez, 1975 ... is a quite remarkable species as it retains pre-Messinian features, such as small size, P2 without mesial hyperloph, p3 with anteroconid often smaller than metaconid, together with more advanced characters such as, for example, the loss of the fossettes on M1–2 and a modified, lingually elongated anteroconid on p3”. In all these characters, *P. ibericus* differs from the Lissasfa prolagid.

The prolagid from Lissasfa accords better with *P. michauxi* in the characters and proportions of the maxilla and mandible, and the dimensions and morphology of the teeth. The type locality of *P. michauxi* is Sète (Hérault) in southern France (Fig. 5). The type material is housed at the Muséum National d’Histoire Naturelle in Paris, and we had the opportunity to compare directly the material from Lissasfa with it. Regarding the size of the teeth, the material from Lissasfa plots within the range of variation of that from Sète (Fig. 5). In morphology, the rare differences that we noted concern variable characters such as the presence and position of a crochet and the size of the anteroconid relative to the metaconid on the p3. For instance, in the Sète sample, one p3 has a well-developed crochet, it is weak on seven others and located behind the metaisthmus, while two others are devoid of it. In the Lissasfa sample, one p3 has a clearly visible crochet, on three others it is barely visible, and one is devoid of it. The volume of the anteroconid relative to the metaconid is considered to be an important criterion for distinguishing species. Three p3s from Sète have an anteroconid that is larger than the metaconid, on five others they are of equal volume or the anteroconid is slightly smaller. Of five p3s from Lissasfa, three have an anteroconid larger than the metaconid, while on two others these two cusps are of equal volume. The only difference is the slightly deeper hypoflexus on M1s and M2s from Lissasfa. The other characters of the cheek teeth are identical, hence the attribution of the Lissasfa prolagid to *P. michauxi*.

Mahboubi et al. (2022) and Dupré et al. (2022) reported a large collection of *Prolagus michauxi* from the localities of Afoud (Fig. 1, # 4), dated between 5.9 and 6.2 Ma, in the Aït Kandoula Basin in Morocco. As Dupré et al. (2022: 870) noted " The measures performed on the p3, P2 and P4 from AF12-1 and AF12-2 ... encompass the measures of both African and European *P. michauxi* and *P. cf. michauxi* from the literature (the African specimens often

being smaller than their European counterparts), which is a further argument concerning the assignment of the previous Moroccan specimens (from Aghouri, Afoud 2 and 8) to the species *P. michauxi* or *P. cf. michauxi*". This remark by Dupré et al. (2022) implies that the remains from numerous sites in Western Europe and the Maghreb, referred to *P. michauxi* or *P. cf. michauxi* show a very wide variation in size and morphology, well beyond what is observed in material from the type locality. Such an observation leads to the question of whether it is a species with high variability due to adaptations to local environments, or whether several species having similar dental morphologies are grouped under this species name. The available material from Lissasfa does not resolve this enigma.

Species *Prolagus ressasensis* n. sp.

(Figs 6)

Holotype: right p3 (DJR1-2; Fig. 6L).

Type locality: Djebel Ressay 1, situated in the northern part of Djebel Ressay quarry (36.6217 N; 10.3472 E). Early Pleistocene.

Etymology: Ressay means lead in Arabic. Djebel Ressay = Mountain of Lead, where there is a former Roman mine for galena.

Material: 16 isolated teeth: left D3, left P2, right P3 juvenile, three right P3s, two left P3s, right M1, right M2, two left M2s, right p3, two left p3s, one lower molariform, and fragment of left hemimandible bearing m2 (DJR1-1 to 17).

Measurements: Table 2.

Diagnosis: A small species of *Prolagus*; p3 with an outline longer than wide, a short crochet, and flattened and oblique anteroconid; P2 with a strong mesial hyperloph which reaches the buccal margin; P3 with an arc-shaped mesial hyperloph and short lagiloph, M1 and M2 with a deep hypoflexus, and M1 preserving enamel islands in place of the mesoflexus.

Differential diagnosis: It differs from most species of *Prolagus* by its smaller dimensions and the elongated outline of its p3; it differs from *P. ibericus*, which is of similar size, in having a strong mesial hyperloph on P2, and the presence of fossettes on M1. It differs from the other *Prolagus* species known in the Maghreb in being smaller, having p3 elongated, P3 with a short lagiloph and M1 with enamel islands.

Description and comparison

The bulk of the lagomorph material from Djebel Ressas came from the fissure DJR 1, whereas other spots yielded a few teeth of *Prolagus* and of an indeterminate leporid. As shown in the diagrams of Fig. 5, this is a small species, smaller than *P. michauxi* and *P. migrans* already known in the Maghreb, and is also smaller than the species known in the Plio-Pleistocene localities of Western Europe, such as *P. depereti* López-Martínez, 1975 and *P. calpensis* Major, 1905. Only *P. ibericus* López-Martínez, 1975 is closer in size to the material from Djebel Ressas 1. This species is known only from a few localities in Spain and displays a combination of ancestral and derived characters as mentioned above. Its P2 without mesial hyperloph and its p3 with a small anteroconid are sufficient to prevent attribution of the Djebel Ressas 1 fossils to this species.

Concerning the tooth pattern, *P. michauxi* differs in having p3 rather massive and much less elongated than the p3s from Djebel Ressas 1, anteroconid well separated from the protoconulid and of similar volume to the metaconid, while on the p3s from Djebel Ressas 1 the metaconid is smaller, and the mesoflexid deeper.

P. migrans from Ahl al Oughlam is a bit larger than the specimens from Djebel Ressas 1, its p3 has a larger and more rounded metaconid (pear-shaped in the Djebel Ressas 1 specimen), its protoconulid is isolated in about half of the specimens and most individuals lack the crochet. Its P3 has a lagiloph reaching the buccal edge whereas it is short on all P3s from Djebel Ressas 1 (n = 5).

Taking into account these differences, the prolagid from Djebel Ressas 1 merits a new species name, *Prolagus ressasensis* n. sp.

Species *Prolagus* sp. 1

(Fig. 7a-i)

Material: Djebel Ressas 5: Three isolated teeth: two fragments of right upper incisors (1.35 x 1.07; 1.37 x 0.88) and one right P2 (1.27 x 2.01) (DJR5-1 to 3).

Djebel Ressas 6: Four isolated teeth: left P3 (1.31 x 2.18), left P4 (0.96 x 1.83), left M1 (1.33 x 2.23), left p3 juvenile (1.33 x 1.17) (DJR6-1 to 4).

Djebel Ressas 8: Three isolated teeth: right P4 (1.26 x 2.55), right M1 (1.18 x 2.11), left M1 (1.09 x 1.86) (DJR8-1 to 3).

Description and remarks

The material from these three spots is not homogenous. For instance, some teeth indicate a small form such as a juvenile P2, a P4 and a juvenile p3 from Djebel Ressay 6, whereas a P2 from DJR 5, a P4 from DJR 8 and an M1 from DJR 5 clearly represent a large form with derived features such as deep flexa and folded enamel on the P2, lack of fossette on the M1 in place of mesoflexus. As noted above, all M1s from DJR 1 have this fossette. The heterogeneity of the material in size and morphology as well as the limited number of specimens do not allow the comparison to be broadened, hence their attribution as *Prolagus* sp.

Species *Prolagus* sp. 2

(Fig. 7j)

Locality: Tighennif, Department of Oran, Algeria

Material: Right P4 (TER- 5154), length x width = 1.39 x 2.46 mm.

Description and remarks

This isolated P4 from Tighennif has a large U-shaped parafossette and a smaller comma-shaped mesofossette. The hypoflexus does not reach the half width of the occlusal surface.

The length of this tooth is slightly greater than in *Prolagus michauxi* López-Martínez, 1975 and *P. migrans* Sen and Geraads, 2023, the two species known in Northwest African localities, but its width plots within the size range of these species. Also, its occlusal pattern does not display any differences. Unfortunately, this tooth is not characteristic enough for species identification.

The genus *Prolagus* is known in the Maghreb since the latest Miocene with *P. michauxi* from Afoud 12-1, dated c. 6.2 Ma (Dupré et al. 2022) and from Lissasfa. The P4 from Tighennif (c. 1.4 Ma) and the poor remains from Djebel Ressay 5, 6 and 8 are apparently the latest records of this genus in the region.

Family Leporidae Gray, 1821

Genus *Trischizolagus* Radulesco and Samson, 1967

Type species: *T. dumitrescuae* Radulesco and Samson, 1967

Other species referred to this genus: *T. maritsae* De Bruijn et al., 1970; *T. crusafonti* (Janvier and Montenat, 1971), *T. gambariani* (Melik-Adamyam, 1986); *T. raynali* (Geraads, 1994); *T. meridionalis* Sen and Geraads, 2023; *T. mirificus* Qiu and Storch, 2000.

Species *Trischizolagus raynali* (Geraads, 1994)

(Figs 8-14)

Holotype: Left hemimandible bearing p3-m3, GDR, Square EIO, fig. 16A in Geraads 1994, Fig. 10a.

Type locality: Grotte des Rhinocéros, Casablanca, Morocco.

Material from Grotte des Rhinocéros: Four P2, two P3, two P4, three M1, three M2, eight more or less complete hemimandibles bearing various cheek teeth, one isolated p3, six lower molariforms, two m3, two d3 and one distal extremity of humerus (DT x DAP = 8.64 x 6.24).

Material from Thomas I-L: Right P2 (1.42 x 3.27), right M2 (1.90 x 3.13), two isolated p3s (2.93 x 2.82).

Material from Thomas I (GH): a left p3 (Thomas I-GH-95; 2.94 x 2.75) and right hemimandible (Thomas I-GH) bearing p3 (2.97 x 2.81), p4 (2.33 x 2.38 x 2.44), m1 (2.59 x 2.58 x 2.63) and m2 (2.66 x 2.35 x 2.33). This hemimandible could have been collected either at Thomas I-GH or GDR, as the indications on its label are confusing.

Material from Tighennif: Isolated teeth and postcranial bones: 24 upper incisors, 10 P2s, 11 P3s, 13 P4s, 19 M1s, 13 M2s, three M3s, 24 lower incisors, 18 p3s, 13 lower molariform teeth, seven m3s (number TER 5001 to 5153); two distal parts of humerus, two distal parts of tibia, one astragalus, one calcaneum, and several metapodials and phalanges; postcranials unnumbered, except a tibia 1955-13-1041).

Measurements: See Tables 3 and 4.

Original diagnosis: *Serengetilagus* of size intermediate between *T. maritsae* and *S. praecapensis*. Postero-internal sinus always transformed into a large island of enamel, over the entire height of the crown (translated from Geraads 1994: 165).

Emended diagnosis: A species of rather smaller size compared to other species of the genus. p3-m3 alveolar length a little shorter than diastema; foramen mentale situated far mesial to p3 and high on the corpus; its p3 with a V-shaped anteroflexid, paraflexid variable in depth, hypoflexid short, extending over less than half the width of the crown, all individuals bearing an oval mesofossettid, wide isthmus between trigonid and talonid, talonid with a mesiobuccal depression; upper incisor without cement in the anterior groove and medial part with rounded

anterior outline; P2 with a deep and oblique paraflexus, shallow mesoflexus and hypoflexus, lagicone and mesial hypercone at the same level anteriorly; upper molariforms have enamel folding along the mesial wall of hypoflexus, but rather flat along the distal wall; enamel folding decreasing from P3 to M2.

Description and remarks

Trischizolagus raynali was initially described from Grotte des Rhinocéros in Morocco (Geraads 1994). We report here its occurrence in two other localities, Thomas IL in Morocco and Tighenif in Algeria. As shown in figures 8 to 14, the specimens from these four localities do not display size or morphological differences to prevent their attribution to *T. raynali*. Consequently, we will provide a short description for all of them, and mention any variations where necessary.

The type material of *T. raynali* consists of “une trentaine de dents molariformes isolées, quelques P2/, et quelques fragments de mandibules. La P/3 est représentée par 4 spécimens en tout” (Geraads 1994: 165). The author illustrated a lower toothrow (holotype) and three p3s. Much later more material was collected from GDR, including a complete right hemimandible GDR-5768 (Fig. 9; Table 3).

The upper incisor has a sharp anterior groove (1/3 medial) devoid of cement. Both parts have the anterior surface well rounded. In section, it is longer medio-laterally but short antero-posteriorly. The lingual surface is depressed in all specimens. The shaft length of a complete right upper incisor (TER-5003) measures 15.1 mm.

The P2 has three flexa, although mesoflexus and hypoflexus are shallower, and poorly defined in juvenile specimens. The lagicone and mesial hypercone are in line anteriorly. The enamel is smooth, thicker along the lingual margin of cusps, and interrupted at the buccal tip of the tooth.

The upper molariform teeth have mesial and distal lobes of similar length, except M2 which has a longer mesial lobe than a distal one. The depth of the hypoflexus decreases from P3 to M2, as does the degree of enamel folding along its mesial edge. In contrast, the enamel is barely folded or often smooth and thin along its distal edge.

The mandible is only known from GDR (Fig. 9). The most complete specimen GDR-5768 has a length of 58.8 mm, its ramus depth is 34.7 mm, the depth of the body below m2 is 11.7 mm on the buccal side, the diastema length 16.3 mm, and the tooth row length 15.1 mm. The depth of the body increases regularly from the symphysis to the level of m3. On the

buccal surface, the foramen mentale is situated 3 mm mesial to p3 in the upper part of the body as in *Oryctolagus* and *Trischizolagus*; in *Lepus* it is smaller and is situated more mesially. The body is perforated by several nutritive foramina under this foramen and below the p3. In *L. capensis* the mental foramen is more mesial and the nutritive foramina extend much further under p4. The masseteric crest reaches anteriorly beneath the level of m2-m3 as in *Lepus capensis*. The angular process is strong, the angle of the ramus is about 140°. In these features, this hemimandible is similar to that of *L. capensis*. However, its dentition is like that of a species of *Trischizolagus* in having a p3 with *Nekrolagus* pattern. The mandible of *Trischizolagus* is known from Moscovci in Moldova for *T. dumitrescuae* and from Ahl al Oughlam in Morocco for *T. meridionalis* (Averianov 1995; Sen and Geraads 2023). In both of these cases, it is characterised by the distally increasing body depth, diastema a little longer than the tooth row alveoli, mental foramen located near the p3, strong angular process and angle between tooth row and ramus less open than in *Lepus*, but more than in *Serengetilagus*. In all these characters, the hemimandible from Grotte des Rhinocéros fits that of *Trischizolagus*.

The lower incisor has a trapezoidal section, the medial part being wider and squarer than the lateral part. The mesial surface is flat and without any ornamentation. The shaft length of a complete left lower incisor (TER-5081) is 18.1 mm and the length of its cutting edge is 3.3 mm.

The p3 has the shaft curved lingually, and its distal surface is smoothly curved. The trigonid is twice as long as the talonid in adult individuals but much less in juvenile ones. The bridge between the trigonid and talonid is variable in width between 0.19-0.71 mm (average = 0.37 mm). The anteroflexid and paraflexid are always present but variably deep. The buccal and lingual anteroconids are almost equal in volume, and the buccal one protrudes mesially on 15/18 p3s from Tighennif and 5/8 p3s from GDR. The protoflexid is wide, with an angle of about 80-90°. The hypoflexus does not extend beyond the mid width. Only one juvenile p3 from Tighennif has the mesoflexid open lingually, while on all others p3s from GDR, Tighennif and Thomas IL, there is a mesofossettid more or less stretched transversely. Two of the three p3s from Thomas IL and one p3 from GDR have enamel folded along the mesial margin of hypoflexid (Figs 10 and 14). The mesial edge of the hypoconid is grooved or depressed on 3/8 p3s of GDR, 11/18 p3s of Tighennif and 2/3 p3s from Thomas IL; other p3s have this edge rounded. Enamel is thick along the buccal margins of cusps and along the mesial margin of the hypoflexid and mesofossettid, but thin along the lingual margin of the tooth and the distal walls of the hypoflexid and mesofossettid.

The lower molariform teeth have the trigonid longer and broader than the talonid. In some specimens the talonid is slightly depressed on its mesiobuccal part, while in the others this surface is flat. The m3 is bilobed as usual in leporids. The trigonid and talonid have no enamel connection, but are fused with cement, except one specimen from GDR (Fig. 9c) where they are joined lingually. One m3 from Tighennif (TER-5151) has the talonid bilobed in both occlusal and root views (Fig. 13y).

Geraads (1994: 166) initially referred this species to the genus *Serengetilagus*, with the proviso that “Being in doubt, I include the species of OH 1 to *Serengetilagus*, because this genus is African, and in case of synonymy [with *Trischizolagus*], this name has priority”. Indeed, Flynn and Bernor (1987) noted the resemblances between these two genera when describing a lower jaw fragment of a leporid from Kholobolchi Nor in Mongolia that they identified as *Trischizolagus* sp. Topachevsky (1987) preferred to name his discovery of a new species from the Odessa region as *Serengetilagus orientieuropaeus* n. sp., thus increasing the apparent complexity of the dispersal pattern of these genera (see discussion in Sen and Geraads 2023, p. 646 on the systematic status of these records). However, from the 1980s, Erbajeva and Angermann (1983) and López-Martínez (1989), and subsequent studies on new discoveries of leporids in Eurasia and Africa (Winkler 2003; López-Martínez et al. 2007; Winkler and Tomida 2011) have clearly established the distinction between these two genera.

Serengetilagus is well documented in East African latest Miocene and Pliocene localities (Dietrich 1942; MacInnes 1953; Erbajeva and Angermann 1983; Winkler and Avery 2010; Winkler and Tomida 2011) and it shares many features with the mainly Eurasian genus *Trischizolagus*: similar size, on the p3 presence of anteroflexid, protoflexid and hypoflexid, and the occasional presence of paraflexid and mesoflexid, in juvenile individuals, P2 with a deep paraflexus and shallow hypoflexus and mesoflexus, and the lagicone and hypercone in line mesially, upper molariforms with a moderately deep hypoflexus along with wrinkled enamel, particularly on the mesial wall. However, in both species of this genus (*S. praecapensis* Dietrich, 1941 and *S. tchadensis* López-Martínez et al., 2007) p3 has a straight lingual edge, the anteroflexid is often weak or even lacking, when existing often double or with folded enamel, paraflexid and mesoflexid absent in adult individuals or exceptionally present in juveniles, lingual anteroconid weaker than the buccal one. In addition, on the upper molariform teeth of *S. praecapensis* enamel is often well crenulated along the distal wall of the hypoflexus, in particular on P3-M1, while it is generally flat in *Trischizolagus* (Erbajeva and Angermann 1983; Winkler 2003; López-Martínez et al. 2007; Winkler and Tomida 2011). In addition, the anteroflexid is missing in most p3s of *S. tchadensis*. Both species of

Serengetilagus are much older than *T. raynali*. *S. praecapensis* is found in East African localities dated between 6.2-2.5 Ma, while *S. tchadensis* is known only from Toros Menalla in Chad, dated to about 7 Ma (Lebatard et al. 2008) although there has been debate about the precise ages of the Chadian sites (Pickford, 2009) with some of the deposits at Toros Menalla being interpreted to be as young as 6 Ma and some as old as 10 Ma.

The leporid from GDR, Tighennif, Thomas I-L and Thomas I-GH is better compared to *Trischizolagus*, which is known by seven species. Its type species *T. dumitrescuae* is well documented in eastern European localities (Radulesco and Samson, 1967; Koufos and Koliadimou 1993; Averianov 1995; Averianov and Tesakov 1997; Terzea 1997; Popov 2004; Čermák and Wagner, 2013; Vasileiadou and Sylvestrou 2022). It is a medium-sized to large leporid (Fig. 11). On its p3s the *Alilepus* pattern dominates (65% up to 100% of p3s depending on the locality; see Table 5), the anteroflexid is in most cases a wide depression, and consequently, the anteroconid is barely divided. On the type material from Mălușteni in Romania the bridge between the trigonid and talonid is narrow, but exceptionally it may be lacking in some specimens from other localities, such as at Muselievo in Bulgaria (Popov 2004: fig. 23C) or very broad as in one p3 from Ciuperceni-2 in Romania (Terzea 1997: fig. 4d). Ünay and de Bruijn (1998) referred to this species a few teeth from the Early Pliocene locality of Tozaklar in Turkey. As noted by Čermák et al. (2019), the *Nekrolagus* pattern of p3, the development of lagicone and paraflexus on the P2 and the degree of enamel wrinkling along the hypoflexus of upper molariform teeth recall those of *T. gambariani* (see below). Some leporid remains from latest Miocene/earliest Pliocene localities in Spain (Gorafe 1, La Gloria 4, Orrios 7, Peralejos E, Salobreña, Villalba Alta) were tentatively referred to *T. dumitrescuae* (Aguilar et al. 1984; López-Martínez 1989; Mein et al. 1990; Ünay and de Bruijn 1998; Piñero et al. 2017, 2023), but their record is either limited to a few specimens or they are simply mentioned in faunal lists. On the p3s of *T. raynali* the *Nekrolagus* pattern dominates, the anteroflexid is a deep groove in most specimens and the anteroconid is well divided, thus displaying a radically different configuration compared to that of *T. dumitrescuae*.

Piñero et al. (2017) considered *Trischizolagus crusafonti* (Janvier and Montenat, 1971) to be a junior synonym of *Trischizolagus maritsae* de Bruijn et al. 1970. However, in a more recent paper (Piñero et al. 2023) they accepted that the two species should be retained until their characteristics are better defined by more abundant and more informative records. The type material of *T. maritsae* from Maritsa (Greece, latest MN13 or early MN14) and that of *T. crusafonti* from La Alberca (Spain, latest MN13) are too poor to be securely compared

to the other species of the genus. They are the smallest species referred to this genus (Fig. 11). On their p3s an incipient mesoflexid or mesofossettid may be present, but it is apparently lacking on adult specimens. The specimens here referred to *T. raynali* are considerably larger than those of *T. maritsae* and *T. crusafonti*, and their p3 pattern is different in having a mesofossettid in almost all specimens.

This North African leporid recalls *Trischizolagus gambariani* (Melik-Adamyanyan, 1986) from Nurnus, Armenia, in having a dominant *Nekrolagus* pattern on its p3s. This species was initially named '*Alilepus*' *gambariani*. Later on, Čermák et al. (2019) transferred it to *Trischizolagus* and referred to this species abundant material from Tepe Alagöz in Turkey. Both of these localities are correlated to the Early Pliocene, MN14. The p3s of this species are characterised by their *Nekrolagus* pattern (96%, n=16) contra 6% with the *Alilepus* pattern (Table 5). However, this species is close in dimensions to *T. dumitrescuae* and larger than *T. raynali* from all the Maghreb sites, its P2 has a very small lagicone, its upper molariforms have enamel well folded along the distal edge of the hypoflexus, most of its p3s are devoid of the paraflexid and the hypoflexid is strongly oriented backwards.

Trischizolagus meridionalis Sen and Geraads, 2023 was defined on the basis of fossils from Ahl al Oughlam, Morocco. It differs from *T. raynali* in having almost half of its p3s with the *Alilepus* pattern (45%), whereas all p3s from GDR, Thomas I-L and Thomas I-GH, and 73% of those from Tighennif display the *Nekrolagus* pattern i.e. with a mesofossettid instead of a mesoflexid (Table 5). In addition, the p3s of *T. meridionalis* have a short and often wide anteroflexid, while it is deep and narrow in *T. raynali*, and the hypoconid bears an anterior fold, which is absent or weakly expressed in *T. raynali*.

Species *Trischizolagus* sp.

(Fig. 15)

Material from Lissasfa: Isolated D2, D3, D4 and P2, a right maxilla bearing P3-M3, isolated M2, m3 and a trigonid of a lower molariform. Specimens numbered as LIS 17 to 24.

Measurements: See Table 6.

Description and remarks

The D2 lacks a hypoflexus, while the mesoflexus is poorly defined. The D3 is not worn enough to expose any occlusal pattern. The D4 has a hypoflexus that reaches half the width

without any enamel crenulation. P2 has a moderately deep paraflexus, weak mesoflexus and barely outlined hypoflexus. Its distal edge is rounded. On P3-M2 the hypoflexus penetrates about 2/3 of the occlusal width; enamel is moderately undulated along its mesial wall, slightly wavy on the distal wall on P3, P4, but flat on M1 and M2. The M3 has an ellipsoid occlusal outline. The single m3 is bilobed as usual in Leporidae.

The general pattern of these teeth accords with that of *Trischizolagus*. They are different from *Lepus* (in this context *L. capensis* sensu lato) which has larger teeth, P2 with stronger flexa, the upper molariforms with clearly more folded enamel on the anterior and posterior edges of the hypoflexus (MacInnes 1953; Vismara 2012; Pelletier et al. 2015; Pelletier 2018). The African genus *Serengetilagus* (both *S. praecapensis* and *S. tchadensis*) has upper teeth with even more wrinkled enamel on both edges of the hypoflexus. Likewise, *Afrolagus pomeli* from Ahl al Oughlam has even deeper flexa on the P2 and more wrinkled enamel along the hypoflexus walls on the upper molariform teeth than in the genera and species cited above. In summary, the Lissasfa leporid cannot be assigned to *Lepus*, *Serengetilagus* or *Afrolagus*, but the characters of its upper teeth compare best with those of *Trischizolagus*.

The P2 from Lissasfa is smaller than specimens from Grotte des Rhinocéros (*T. raynali*) and Ahl al Oughlam (*T. meridionalis*), in particular concerning its width. This could be explained by the fact that it probably belongs to a sub-adult individual. In contrast, the P4-M3 from Lissasfa have dimensions greater than those of *T. raynali*, but well within the limits of variation of *T. meridionalis*. However, most of the P3s and P4s from Ahl al Oughlam have slightly wavy enamel on the distal margin of the hypoflexus. Despite this resemblance, the scarcity of the material and the absence of p3 prevent us from securely identifying the species, hence the attribution of the Lissasfa leporid to *Trischizolagus* sp.

Dupré et al. (2022) reported three upper molariform teeth from Afoud 12-2 in Morocco, dated to 5.9 Ma. Their size is within the range of metric variation of *T. raynali*, but their morphology is different in having a deep hypoflexus with crenulated enamel on both margins, as in *Serengetilagus tchadensis* (see López-Martínez et al. 2007, fig 4). Together with that of Lissasfa, this is the oldest leporid found in the Maghreb.

Genus *Lepus* Linnaeus, 1758

Type species: *Lepus capensis* Linnaeus, 1758

Species *Lepus berbericus* n. sp.

Figs 16 and 19

Holotype: right hemimandible bearing p3-m1 (GDR-G10, Fig. 16c).

Type locality: Grotte des Rhinocéros, Casablanca, Morocco.

Etymology: The adjective *berbericus* is derived from Berberia, the name of the lands inhabited by the Berbers, which covers large parts of North Africa, including the Casablanca region.

Material from Grotte des Rhinocéros: In addition to the holotype, the material includes a right lower incisor (GDR-C14-24), a left hemimandible with the alveoli of p3 and m3 and the series p4-m2 (GDR X00-30), a right p3 (GDR-C14-25), a left p3 (GDR-C14-26), two right lower molariforms (GDR-C14-27 and 28) and a left M2 (GDR-C14-23).

Measurements: Table 7.

Diagnosis: *Lepus* similar in size to the extant “*Lepus capensis*” (see below for a discussion of this name) from the Maghreb, p3 with convex buccal edge, deep anteroflexid dividing anteroconid into two unequal parts, lingual anteroconid tapering mesially, paraflexid absent, enamel wrinkled along the mesial wall, and slightly undulated along the distal wall of hypoflexid. Presence of a central mesial loop of hypoflexid and a centrally positioned constriction. Enamel depressed or grooved on the anterior edge of hypoconid on p3 as well on most of the lower molariform teeth.

Differential diagnosis: This species differs from *Lepus capensis* sensu lato in having a p3 with a strongly convex lingual edge, a well-defined central loop on the anterior wall of the hypoflexid, enamel thinner and much more folded on this wall than in *L. capensis* and wavy along the distal wall. The constriction of the hypoflexid is rather central, whereas it is more buccal in *L. capensis*. It differs from *Lepus veter* MacInnes, 1953 from Kenya, in having larger buccal anteroconid, non-wrinkled enamel around the anteroflexid and protoflexid, presence of enamel loops on the anterior wall of the hypoflexid and the constriction of the hypoflexid rather centrally positioned.

Description and remarks

The dimensions of the teeth fall within the size range of the extant species *Lepus capensis* sensu lato as reported from different parts of Africa by Pelletier (2018) (Fig. 19). *L. capensis* was initially defined on the basis of a specimen from South Africa near Piketburg, in the Western Cape Region. Its species concept and geographic distribution vary greatly among students depending on external morphological criteria and genetic distinctiveness between the populations (see below). Palacios et al. (2008) provided a detailed description of tooth

characters of South African *L. capensis*, including specimens from its type area: upper incisor rectangular in outline, with a deep anterior groove and slightly concave posterior face; paraflexus shallow to medium depth on P2; on the P3 the mesial loph thicker than distal loph, and the number of crenulations is usually 7 or more; on the p3 the outline of lingual anteroconid is wavy, paraflexid deep, enamel along the distal edge of hypoflexid is slightly undulated and lingual contour rounded.

The pattern of p3s from GDR does not fit this description in its sharp lingual anteroconid, lacking the paraflexid, and on the p3s from GDR, the enamel is folded along the mesial wall of the hypoflexid and forms one or several loops; the constriction of its hypoflexid is rather central, while it is clearly buccal in *L. capensis* (see arrows on Fig. 16a).

Vismara (2012) described dental features of *L. capensis* from Sardinia and North Africa. According to this author (p. 22), “the Sardinian hare appears to have been introduced on the Italian island most probably by the Catalan community living in Sardinia from North Africa”. Also, Vigne (1992) noted that, based on the results of excavations, the presence of *Lepus* in both Corsica and Sardinia is due to human introduction, and is not older than 2,000 years. Vismara (2012) highlighted the salient features of *L. capensis* of Italian and North African populations: smaller size of teeth compared to those of *L. timidus* and *L. europaeus*, on the p3s very convex lingual wall, narrow hypoflexid with more crenulated mesial and distal walls than in the two European hares, without terminal loop as *L. europaeus* has, but with a central enamel loop on the mesial wall (more or less well formed), protoconid better defined by the constriction of protoflexid and the mesial loop of hypoflexid, lack of paraflexid; on the P2, mesoflexus generally present and better defined than in *L. timidus* and *L. europaeus*, lagicone distant from the lingual margin, distal edge rounded.

On the p3 from Grotte des Rhinocéros the lingual anteroconid has a sharp outline, the paraflexid is absent, enamel is thinner than in *L. capensis* (*s.l.*) and clearly much more undulated in having at least one large or several enamel loops on the mesial wall of the hypoflexid; its lingual edge is strongly convex. On the p3s of *L. capensis* from Italy and North Africa the mesial enamel of the hypoflexid is thick, often flat or slightly wavy, and has only one poorly defined loop. On the p3s from GDR, the hypoflexid is constricted in its central part by a distal hook of the trigonid. Similar narrowing also exists on the p3s of *L. capensis* (*s.l.*), but is located more buccally. The enamel is very thin and slightly wavy on the distal edge of the hypoflexid on most p3s from GDR. On the p3s as well as on lower molariforms the mesial edge of the hypoconid is depressed (generally round in *L. capensis*).

The only previously described fossil species of *Lepus* from Africa is *L. veter* MacInnes, 1953 from the Middle Pleistocene localities of Chianda-Uyoma and Kanjera in Kenya. The author noted that it was comparable in size to a large *L. capensis*, but was more robust, with teeth having a more complex enamel pattern, and with the anterior flange of the angular process of the mandible more pronounced and displaced laterally. This species is larger than the ones we report from Grotte des Rhinocéros and Thomas I-UC (Fig. 18). In addition, enamel is strongly folded along the mesial margin of the talonid in p3-m2, as well as in the anteroflexid and protoflexid of p3. Also, in its upper molariform teeth, enamel is strongly wrinkled along both margins of the hypoflexus, in particular on the P3 and P4, significantly more so than in the other African species of *Lepus*. These differences indicate that the second leporid from Grotte des Rhinocéros belongs to a hitherto undescribed species, herein named *Lepus berbericus* n. sp.

Species *Lepus* cf. *capensis* Linnaeus, 1758

Figs 17-18

Material from Thomas I-UC: Eight hemimandibles, three of which belong to juvenile individuals, all devoid of the ascending ramus and m3 (right hemimandible with diastema and p3-m2; right hemimandible with p3-m2 and alveolus of m3; right hemimandible with broken incisor, diastema, p3-m2 and alveolus of m3; right hemimandible with p3-m1; juvenile right hemimandible with alveolus of p3 and p4-m1; left hemimandible with incisor, diastema and p3; left hemimandible with diastema and p3-m1; left hemimandible with p4-m2). They are numbered as ThI-KA23/25-1 to 8.

Measurements: See Table 8.

Description and remarks

On the mandible the diastema is longer than the p3-m3 alveoli (on average alveolar length 86% of the diastema length). The mental foramen is located more than 3 mm anterior to the p3 and close to the dorsal margin of the body. The buccal surface of the body is riddled with nutrient foramina of various sizes, under the diastema and p3. The masseteric crest makes a continuous arc between the anterior border of the ascending ramus and the angular process; its anterior margin does not extend beyond the level of the distal edge of the m3 alveolus. The depth of the mandibular body increases slightly from beneath the p3 to the m3 (Fig. 17).

The p3 has a stocky outline, the convexity of the lingual margin increases from juvenile to adult individuals, the anteroflexid is simple and moderately deep, except in one specimen that has wavy enamel in its place (TH1-KA23/25-5; Fig. 18d), the paraflexid is lacking, the protoflexid is wide and its thin enamel is undulated in three of five p3s. The protoconid is delimited by the folds of the protoflexid and hypoflexid. The hypoflexid is transverse, bounded by a thick and moderately wavy mesial and thin and flat distal enamel band; its mesial wall has a central loop, better expressed in young individuals, rather wide in adults. Next to the central loop, a distal extension of the trigonid narrows the hypoflexid buccally. The presence of a central loop and buccal hook of the hypoflexid are the typical characters of *L. capensis* from North Africa and Italy, as shown by Vismara (2012). The lower molariform teeth have the trigonid larger than the talonid. The enamel is thick along the mesial wall of the hypoflexid, but extremely thin along the distal wall, in both cases slightly wavy.

The leporid from Thomas I-UC differs from that of Grotte des Rhinocéros in having a shallower anteroflexid on the p3s, thick enamel along the anterior wall of the hypoflexid, poorly defined mesial loop, and hypoflexid constriction buccally situated in both the p3s and the lower molariform teeth.

The leporid from Thomas I-UC is significantly smaller than the extant European hares *L. europaeus* Pallas, 1778 and *L. timidus* Linnaeus, 1758, and plots into the lower part of the size range of *L. capensis* (Fig. 19). Vismara (2012) provided a detailed comparison of dental features between the three main Old World species, *L. capensis* (Sardinia and North Africa), *L. europaeus* and *L. timidus*. In *L. europaeus*, the outline of p3 is elongated, the lingual edge is almost straight, the paraflexid is present in most individuals, the protoflexid more open than in *L. capensis* and consequently the protoconid is not defined as in the latter species, the hypoflexid is transverse and lacks the mesial loop, but has a lingual loop in its extremity. On the P2 of *L. europaeus*, the mesoflexus is not as deep as in *L. capensis*, and the distal edge of this tooth is less rounded than in *L. capensis*. *L. timidus* shows major differences from the Thomas I leporid, in having p3 with an elongated outline, an almost straight lingual margin on the p3, a triangular protoconid, and the hypoflexid without mesial loop. Its P2 has an obtuse buccal margin and its distal edge is rectilinear.

The characters of the mandible and teeth from Thomas I-UC are similar to those of *Lepus capensis* (*s.l.*) (see below). Although we tentatively attribute the leporid from Thomas I-UC to *Lepus cf. capensis*, we are aware of the problems concerning the systematics of this species. For most authors its dispersal area covers most regions of Africa and the Middle East (see for instance, Hoffmann and Smith 2005; Happold 2013, 2018). In molecular studies

carried out over the last two decades, particularly focused on *L. capensis* (*s.l.*), the authors recognised large genetic variability without a clearcut distinction between several cryptic species that it may include (Suchentrunk et al. 2009; Ben Slimen et al. 2017; Lado et al. 2019, and references therein). At present, consensus is far from being reached concerning the number and names of African hares, and in particular on the systematics of extant populations grouped collectively under the species name *L. capensis*. Whatever the outcome, the specimens from Thomas I-UC are similar in size to the populations from North Africa for which Vismara (2012) and Pelletier (2018) provided measurements and descriptions of dental morphology. This species is often mentioned as present in Late Pleistocene sites of Morocco (Amani et al. 2012a, b; Aouraghe et al. 2012; Stoetzel et al. 2012). Pending clarification of the systematic status of North African hares, we tentatively identify these fossils as *Lepus* cf. *capensis*.

Species Leporidae genus and species indet.

Material from Djebel Ressay 1: Right upper incisor (2.13 x 1.62), right P2 juvenile and right d3.

Remarks: These specimens indicate the presence of a leporid similar in size to extant *Lepus capensis*. The upper incisor has an elongated outline with a deep anterior groove without cement, and a sharp medial lobe. The P2 has a deep paraflexus and shallower hypoflexus and mesoflexus. The d3 is unworn and displays a trilophid occlusal surface. These teeth are not characteristic enough for further comparison, so cannot be securely referred to any genus and species of Leporidae.

Discussion and conclusions

The Late Miocene, Pliocene and Pleistocene deposits of Northwest Africa have yielded the remains of five lagomorph genera: *Prolagus*, *Trischizolagus*, *Afrolagus*, *Lepus* and *Oryctolagus*. *Prolagus* first appears in the Maghreb a little before the Mio-Pliocene boundary as an immigrant from Europe, where it is known from the Early Miocene onwards. It apparently took advantage of the continental connection between the Iberian Peninsula and the Maghreb (Rifian Corridor) to pass into North Africa shortly before the Messinian Salinity Crisis, c. 6.5-6.2 Ma (Capella et al. 2018; Mahboubi et al. 2022; Dupré et al. 2022). Many other groups of mammals (camels, hippopotamus, rodents...) took part in this event. The

modalities and timing of Iberian-Northwest African mammalian exchanges have been documented and discussed for several decades (Jaeger et al. 1977, 1987; Brandy and Jaeger 1980; Aguilar et al. 1984; Coiffait-Martin 1991; Benammi et al. 1996; Garcés et al. 1998; Geraads 1998; Raynal et al. 1999; Agustí et al. 2006; Minwer-Barakat et al. 2009, 2018; Gibert et al. 2013; García-Alix et al. 2016; Mahboubi et al. 2022; Dupré et al. 2022). The present study of lagomorphs once again confirms how much these latest Miocene intercontinental interchanges contributed to the mammalian fauna of the Maghreb. The last reported occurrences of *Prolagus* in the Maghreb are at Tighennif and Djebel Ressay 5, 6 and 8, c. 1.4-1.2 Ma, whereas it survived in Corsica and Sardinia until historical times (Angelone et al. 2008).

The leporids appear in the Maghreb simultaneously with *Prolagus*, since they have been found associated at Afoud 12-2 and Lissasfa, both in Morocco (Dupré et al. 2022; this study). The family Leporidae originated in North America and penetrated the Old World during the Late Miocene (Flynn et al. 2013). They are known in East Africa with *Alilepus* (c. 6.6-4.7 Ma) and *Serengetilagus* (c. 6.2 Ma) since the late Miocene (Darwent 2007; Winkler and Avery 2010; Winkler and Tomida 2011), perhaps a little earlier in Chad with *S. tchadensis* (López-Martinez et al. 2007; Lebatard et al. 2008). In the Maghreb, the earliest recorded leporids are from Afoud 12-2 (5.9 Ma) and Lissasfa (c. 5.5 Ma), both in Morocco. The material is not rich enough for clear identification, hence their attribution to Leporidae indet. for Afoud 12-2 (Dupré et al. 2022) and tentatively to *Trischizolagus* sp. for Lissasfa (this study). There is a sampling gap between these localities and those dated to the latest Pliocene-earliest Pleistocene such as Aghouri and Ahl al Oughlam in Morocco and Ain Boucherit in northeastern Algeria (Fig. 20). Ahl al Oughlam yielded a rich collection of lagomorphs including two leporids, *Trischizolagus meridionalis* Sen and Geraads, 2023 and *Afrolagus pomeli* Sen and Geraads, 2023. The age of this locality was initially estimated to be about 2.5 Ma (Geraads 2010b). However, according to van der Made et al. (2021) the oldest African *Equus* is known in North Africa at Ain Boucherit at 2.44 Ma; if this age is correct, this genus would thus appear a little earlier than in East Africa where it occurs first in the Member G of the Shungura Fm dated to 2.32 Ma (Bernor et al. 2010). The abundance of *Hipparion* and the absence of *Equus* suggest that the age of Ahl al Oughlam should be older than 2.5 Ma. For the Algerian locality Ain Boucherit, Sahnouni et al. (2013) and van der Made et al. (2021) mentioned the presence of “Lagomorpha indet.” without further detail.

Pickford et al. (2022) reported on a left hemimandible of a leporid from Wadi Natrun (Egypt) and illustrated it on three faces. Unfortunately it is covered by a thick layer of

varnish, which obscures most of the morphological details, in particular that of the cheek teeth. It recalls *Trischizolagus* in size and in some characters of its body: diastema shorter than the tooth row, foramen mentale close to the p3 and higher up on the body, in buccal view the mesial edge of the masseteric crest is beneath the distal limit of m2, in lingual view similar profile of teeth, and the end tuberosity of incisor mesial to p3. However, its ventral margin is unusually curved, a morphology that has never been observed in *Trischizolagus* and *Lepus*. The increase in body height from p3 to m3 level is negligible. Nothing can be said concerning the pattern of the teeth because they are coated by a sediment crust.

Trischizolagus went extinct in Europe at the transition of Middle-Late Pliocene, c. 3.5 Ma (Čermák and Wagner 2013), while it survived in the Maghreb until the Middle Pleistocene as shown in the present study. *Prolagus* and *Trischizolagus* remained confined to the Maghreb, unlike *Lepus*, which spread over almost the entire continent of Africa.

One of the oldest records of a *Trischizolagus*-like leporid was reported from the Messinian locality of Cava Monticino in northern Italy. Angelone et al. (2021) illustrated five p3s from this site as cf. *Trischizolagus* sp. The pattern of these specimens fit better with the genus *Serengetilagus* rather than *Trischizolagus* or any other leporid: sharp lingual edge, lingual anteroconid poorly defined and with a sharp anterior edge compared to the buccal one, lack of mesoflexid/mesofossettid, lack of paraflexid, slight depression on the anterior edge of hypoconid, similar size to *S. praecapensis* and *S. tchadensis*. In all these features, it recalls *S. praecapensis* from East Africa. We suggest that the Cava Monticino leporid is better referred to *Serengetilagus*, and it appears in Italy as an African immigrant, with many other mammals that took advantage of the Messinian sea level drop to reach Italy via the Tunisian-Sicilian corridor, as did the aardvarks and macaques, and probably camels from the same site (Rook and Masini 1994; Alba et al. 2014; Colombero et al. 2017) giraffids, an anthracotheriid, an African rhinocerotid *Ceratotherium advenientis* and the proboscidean *Stegotetrabelodon* in the Messinian Cessaniti fauna (Marra et al. 2011, 2017; Marra 2019).

The earliest *Trischizolagus* in Europe is documented in the latest Miocene of Spain (*T. crusafonti* from La Alberca and Alcoy) and perhaps in Greece with *T. maritsae* from Rhodes Island. However, the poor record from the latest Miocene-earliest Pliocene localities is insufficient to throw light on the origin of this genus in Europe. It went extinct there at the transition of Early/Late Pliocene, c. 3.5 Ma (Čermák et al. 2019; Sen 2020; Angelone et al. 2021), whereas it survived in the Maghreb up to the Middle Pleistocene as shown by the present study (Fig. 20).

Concerning *Lepus*, according to López-Martínez (2008) and Ge et al. (2013), it most likely emerged in North America around 2.5 Ma, while for Averianov and Tesakov (1997), it was derived from *Trischizolagus* sometime during the Late Pliocene-Early Pleistocene. The latter hypothesis is unrealistic because there is no species of *Trischizolagus* showing a tendency of morphological transformation, in particular for the p3, towards a *Lepus* pattern. Lopez-Martinez (2008: 39) also noted that “No transitional populations are known whose p3 transformed from palaeolagine to leporine type”. This implies that we are unable to determine when and where the genera with the *Lepus* pattern on p3 (*Oryctolagus* and *Lepus*) appeared, or derived from which ancestral group. In summary, there is no data available to link this genus to any other earlier leporid. What is certain is that, throughout the Old World there is no clear documentation prior to the Early Pleistocene to judge its origin (see below).

Among the Old World Leporidae, the leporine type dentition is the main characteristic of the genera *Lepus* and *Oryctolagus*. The latter genus exists in southwestern Europe since the Early/Late Pliocene transition c. 3.5 Ma with *O. laynensis* or cf. *laynensis* in the localities such as Layna (type locality of the species), El Rincón 1, Maluenda 3 and Gorafe 2 in Spain and Perpignan in southern France (López-Martínez 1977, 1989; Alberdi et al. 1997; van Dam and Sanz Rubio 2003). In the latest Pliocene or the basal Pleistocene, it was replaced by *O. lacosti* (Pomel, 1853) in Spain and France and *O. valdarnensis* (Weithofer, 1889) in Italy, which are more frequent in Early Pleistocene faunas and widespread. These are large-sized species having cranial and dental affinities with *Lepus* which have attracted the attention of several authors, starting with Weithofer (1889), Viret (1954), López-Martínez (1989) and Angelone and Rook (2012). Pelletier (2018, 2021) provided a detailed analysis of morphological and biometric characters in all *Oryctolagus* species, as well as evolutionary trends in various lineages and the chronology of the dispersal of the genus in Western Europe. Instead of looking for the origin of the genus *Lepus* in North America, we are tempted to hypothesize that this genus could derive from a species of *Oryctolagus* at the time when Europe began to experience the effect of the Quaternary glaciation, favorable for speciation. However, this hypothesis does not answer the origin of the *Lepus* pattern dentition, but only adjust the time to the Early/Late Pliocene transition. This does not rule out spread of *Lepus* to North America.

The earliest *Lepus* in the Maghreb is from Grotte des Rhinocéros, dated to about 600 or 700 kyr. In older faunas such as those of Ahl al Oughlam, Tighennif and Djebel Ressay 1 this genus is absent. In their synthesis of African lagomorphs, Winkler and Avery (2010: 314) noted that “Leporids with a p3 pattern similar to that of *Lepus*... are first reported ... in the

Early Pliocene of eastern Africa. None of this material has been described formally and it remains to be determined if this early material actually pertains to *Lepus*?. Since 2010, nothing new clarifies the issue. In the fossil record, the earliest mentions of ?*Lepus* sp. are from the Adu-Asa Formation in Middle Awash (Ethiopia; 5.8-5.2 Ma; Haile-Selasie et al. 2004) and *Lepus* sp. from the Kanapoi Formation (Kenya, 4.17-4.07 Ma; Manthi 2006). However, the material from these sites, and that from many other younger sites of East Africa has not been studied sufficiently well to confidently demonstrate the early presence of *Lepus* in Africa. The only named African fossil species *Lepus veter* MacInnes, 1953 from the Middle Pleistocene localities of Chianda-Uyoma and Kanjera in Kenya was comparable in size to a large *L. capensis*, but was more robust, with teeth having a more complex enamel pattern. Above, we have presented a detailed assessment of this species with those from the Maghreb. It probably represents a specialised and local form which developed teeth with more pleated enamel than in other species, and a larger size. In summary, the genus *Lepus* is very poorly documented in fossil form, not only in the Maghreb, but throughout Africa.

Pertinent to the overall understanding of the palaeontology of African lagomorphs, is the recent study of the genus *Pronolagus* by Sen and Pickford (2022). As for the rest of the continent, most of the prior reports concerning this hare were simple mentions in faunal lists (Avery, 2019). Sen and Pickford (2022) attributed the Plio-Pleistocene Red Rock Hare fossils from Angola and Namibia to a new species *Pronolagus humpatensis*. Study of the other material from neighbouring countries (South Africa, Botswana, Zimbabwe) would be well worth undertaking.

In the Middle East, *Lepus capensis* was reported from Gesher Benot Ya'akov (Israel) dated to the Early-Middle Pleistocene boundary, c. 780 Ka (Goren-Inbar et al. 2000; Rabinovich and Biton 2011), and several other Late Pleistocene localities (Bar-El and Tchernov 2000). All these occurrences are simply mentioned in faunal lists without any description and illustration to support taxonomic identifications.

In Europe, the first fossil *Lepus* was named from Pirro Nord in Italy, *Lepus valdarnensis* Weithofer, 1889. However, Viret (1954) referred the material to *Oryctolagus lacosti* (Pomel, 1853), and later on Angelone and Rook (2012) retained it as a distinct species of *Oryctolagus*, restricted to Italy and abundantly documented from several Early Pleistocene localities dated between 2.1-1.2 Ma (Angelone 2013; Angelone et al. 2020; Pelletier 2021).

Kretzoi (1956) named *Lepus terraerubrae* from Beremend 9 (Hungary, late Biharian) without any description and illustration. Van der Meulen (1973) recognised this species in the Monte Peglia fauna (Italy, late Early Pleistocene), the earliest occurrence of the genus in Italy.

In later periods, the presence of *Lepus* is mentioned in Middle and Late Pleistocene faunal lists, without, however, detailed study (Angelone et al. 2020). Elsewhere in Europe, fossil remains referred to *L. terraerubrae* are rare and poorly studied. Fladerer (1987) described some remains from the Early Pleistocene of Deutsch-Altenburg (Austria, age estimated between 1.3-1.8 Ma) as *L. cf. terraerubrae*, and noted that the Early Pleistocene hares from Europe are smaller than their extant equivalents *L. europaeus* and *L. timidus* (see also Pelletier et al. 2015; Pelletier 2018). Shuspanov (1983) illustrated three p3 from Early Pleistocene localities of Chishmikioi (Moldova), Nogaisk, Cherevychnoe (Ukraine) as *Lepus* sp. Averianov (2001) noted that it is impossible to determine what species they belong to. Early Pleistocene *Lepus* also exists in Greece. It was found in two localities, Tourkobounia 2 and 3, both correlated to MNQ19 (latest Early Pleistocene; Vasileiadou and Sylvestrou 2022). In addition, these authors (2022: fig. 7) referred to *Oryctolagus lacosti* several cheek teeth from Alikes in central Greece (Early Pleistocene, MNQ19). The characters of the illustrated p3s suggest *Lepus* sp. The dimensions of the teeth are greater than those of *O. lacosti*, and on the p3, the buccal anteroconid is inclined, the lingual anteroconid is triangular, and the hypoflexid has a central extension, these characters agreeing with *Lepus* sp.

In summary, our knowledge of fossil *Lepus* is fragmentary, insufficiently documented and very incomplete not only for Europe and the Middle East but also for Africa, at least up to the Middle/Late Pleistocene boundary. The data provided by the present work on lagomorphs from seven sites in North Africa and that on Ahl al Oughlam (Sen and Geraads 2023), indicate that the Maghreb is the region where the knowledge of fossil lagomorphs is the most comprehensive for the whole of Africa. This group should be better known in order to make it even more useful not only for dating sites but also for defining palaeoenvironments. It is time that fossil lagomorphs attracted a bit more attention from palaeontologists in order to decipher their evolutionary history and their geographic dispersal through time.

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Declarations

Conflict of interest. The authors declare that they have no conflict of interest.

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Figure captions

- Fig. 1.** North African localities that have yielded *Prolagus* and *Trischizolagus*, showing all sites mentioned in the text. 1 Grotte des Rhinocéros and Thomas Quarries; 2 Ahl al Oughlam and Lissasfa; 3 Aghouri; 4 Afoud 1, 2, 12-1 and 12-2; 5 Aïn Guettara (Morocco); 6 Bel Hacer; 7 Tighennif; 8 Argoub Kemellal 1 (Algeria); 9 Lac Ichkeul; 10 Oued Mellègue, Bulla Regia and Voie Ferrée; 11 Testour; 12 Djebel Ressay (Tunisia).
- Fig. 2.** Dental terminology used in the present study to describe teeth of Prolagidae (modified after López-Martínez and Thaler 1975; López-Martínez 1989) and Leporidae (modified after Palacios et al. 1980; Angelone and Sesé 2009). (a) right p3 of *Prolagus*. (b) left P3 of *Prolagus*. (c) left p3 of *Trischizolagus*. (d) right P2 of *Trischizolagus*. Enamel is represented in black, dentine in white, and the cement covered parts are dotted. Not to scale.
- Fig. 3.** *Prolagus michauxi* from Lissasfa, Casablanca, Morocco. Upper and lower teeth in occlusal view. (a) right upper jaw with P3, P4, M2 and the alveoli of P2 and M1. (b) left P3. (c) left P4-M1. (d) left p3. (e) left p3. (f) left p3. (g) right p3 with unusual connection between anteroconid and protoconulid. (h) right p3-m3 of the hemimandible of Fig. 4. Anterior is upward. Scale bar = 1 mm.
- Fig. 4.** *Prolagus michauxi* from Lissasfa (Morocco). Right hemimandible (LSF-8) in occlusal (a), lateral (b) and medial (c) views. Scale bar = 10 mm.
- Fig. 5.** Scatterplot diagram comparing the lengths and widths of p3s and P3s of *Prolagus* from different localities. Data for *P. michauxi* of Sète, *P. migrans* and *P. ressasensis* n. sp. are our own measurements; data for *P. michauxi* of Vandargues and for *P. ibericus* of Layna are from López-Martínez (1974), for *P. michauxi* of Afoud 12-1 and 12-2 are from Dupré et al. (2022).
- Fig. 6.** *Prolagus ressasensis* n. sp. from Djebel Ressay 1, Tunisia. Upper and lower teeth in occlusal view. (a) left P2. (b-c) left P3s. (d-f) right P3s. (g) juvenile left M1. (h-i) right M1. (j) left M1. (k-l) left p3s. (m) right p3 (holotype). (n) left lower molariform. Anterior is upward. Scale bar = 1 mm.
- Fig. 7.** *Prolagus* sp. 1 from Djebel Ressay 5 and 6, Tunisia. Upper and lower teeth in occlusal view. (a) right upper incisor. (b) left upper incisor. (c) left juvenile P2. (d) right P2. (e) left P3. (f) left P4. (g) right P4. (h) right M1. (i) right juvenile p3. *Prolagus* sp. 2 from Tighennif, Algeria. (j) right P4. Anterior is upward. Scale bar = 1 mm.

- Fig. 8.** Upper teeth of *Trischizolagus raynali* from Grotte des Rhinocéros, Casablanca, Morocco. (a) left juvenile P2. (b) Right juvenile P2. (c) left P2. (d) right P2. (e) left P4. (f-g) right P3s. (h) left M1. (i) right M2. (j) right M1. Anterior is upward. Scale bar = 1 mm.
- Fig. 9.** Right hemimandible (GDR-5768) of *Trischizolagus raynali* from Grotte des Rhinocéros, Casablanca, Morocco. (a) buccal view, (b) lingual view, (c) occlusal view of its cheek teeth p3-m3. Scale bars are 20 mm for the hemimandible and 1 mm for the dentition.
- Fig. 10.** *Trischizolagus raynali* from Grotte des Rhinocéros, Casablanca, Morocco. Lower teeth in occlusal view and a fragment of right hemimandible. (a) left lower cheek teeth p3-m3 of the holotype specimen. (b) left lower cheek teeth p3-m3. (c) left p3-m1 of a juvenile individual. (d) right p3-p4. (e) left p3-p4. (f-g) right p3-p4 and its hemimandible fragment in buccal view. For tooth rows anterior is upward. Scale bar = 1 mm for teeth, 5 mm for mandible fragment.
- Fig. 11.** Scatterplot comparing the lengths and widths of p3s of *Trischizolagus raynali* from Grotte des Rhinocéros and Tighennif with the other species referred to this genus. Data for *T. dumitrescuae* are from Čermák and Wagner (2013), for *T. maritsae* from de Bruijn et al. (1970), for *T. gambariani* from Čermák et al. (2019), for *T. meridionalis* from Sen and Geraads (2023), for *T. raynali* of Grotte des Rhinocéros, Thomas IL Quarry and Tighennif, and for *T. crusafonti* our own measurements.
- Fig. 12.** Upper teeth of *Trischizolagus raynali* from Tighennif, Algeria. (a-f) section of left upper incisors. (g-h) section of right upper incisors. (i-k) left P2s. (l-o) left P2s. (p) left P2. (q-r) right P3s. (s) left P4. (t) right P4. (u-v) right M1s. (w) left M1. (x-y) right M2s. (z1) left M2. (z2) left M3. (z3) right M3. Anterior is upward. Scale bar = 1 mm.
- Fig. 13.** Lower teeth of *Trischizolagus raynali* from Tighennif, Algeria. (a-b) section of left lower incisors. (c-e) section of right lower incisors. (f-g) left p3s. (h-o) right p3s. (p-r) left lower molariform teeth. (s-t) right lower molariform teeth. (u-y) right m3s. Anterior is upward. Scale bar = 1 mm.
- Fig. 14.** *Trischizolagus raynali* from Thomas 1L Quarry, Casablanca, Morocco. (a) right P2. (b) right M2. (c) left p3. *T. raynali* from 'Grotte à Hominidés' of Thomas Quarry: (d) left p3. (e) right hemimandible fragment in buccal (e1), lingual (e2) views, and its cheek teeth p3-m2 in occlusal view (e3). For teeth, anterior is upward. Scale bar = 5 mm for hemimandible and 1 mm for teeth.

- Fig. 15.** *Trischizolagus* sp. from Lissasfa, Casablanca, Morocco, in occlusal view. (a) right upper jaw teeth P3-M3. (b) left D2. (c) left D3. (d) left D4. (e) right P2. (f) left M1 or M2. (g) right m3. Anterior is upward. Scale bar = 1 mm.
- Fig. 16.** Upper and lower teeth of *Lepus berbericus* n. sp. from Grotte des Rhinocéros, Casablanca, Morocco. (a) right p3. (b) left p3. (c) right p3-m1. (d) left p4-m2 and the alveolus of m3. (e) section of right lower incisor. (f-g) right lower molariform teeth. (h) left M1 or M2 tentatively referred to *Lepus*. Anterior is upward. Scale bar = 1 mm.
- Fig. 17.** *Lepus* cf. *capensis* from Thomas I-UC, Casablanca, Morocco. Right hemimandible (ThI-1) with broken incisor and p3-m2 in occlusal (a1), buccal (a2) and lingual (a3) views. Scale bar = 10 mm.
- Fig. 18.** Lower cheek teeth of *Lepus* cf. *capensis* from Thomas I-UC Quarry, Casablanca, Morocco. (a) right p3-m2 and alveolus of m3. (b) right p3-m2 and alveolus of m3. (c) right p3-m2. (d) left p3. (e) juvenile right p3-m1, all in occlusal view. Scale bar = 1 mm.
- Fig. 19.** Scatterplot diagram comparing the lengths and widths of p3s of two extant species of *Lepus* (data from Pelletier 2018) with p3s of *Lepus berbericus* n. sp. from Grotte des Rhinocéros and *L. cf. capensis* from Thomas I-UC Quarry, Casablanca, Morocco.
- Fig. 20.** The time ranges for lagomorph genera from the Maghreb with tentative chronology of localities which have yielded lagomorphs. Localities yielding material studied in this work are indicated in bold letters.

Legends of tables

Table 1 Measurements of upper and lower teeth of *Prolagus michauxi* from Lissasfa, Casablanca Department, Morocco. N=number of specimens, ant=anterior, post=posterior. All measurements are in millimetres.

Table 2. Measurements of upper and lower teeth of *Prolagus ressasensis* n. sp. from Djebel Ressay 1, Tunisia. N=number of specimens, ant=anterior, post=posterior. All measurements are in millimetres.

Table 3 Measurements of upper and lower teeth of *Trischizolagus raynali* from Grotte des Rhinocéros, Casablanca, Morocco. N=number of specimens, ant=anterior, post=posterior, hypfls=hypoflexus, hypfld=hypoflexid. All measurements are in millimetres.

Table 4 Measurements of upper and lower teeth of *Trischizolagus raynali* from Tighennif, Oran Department, Algeria. N=number of specimens, ant=anterior, post=posterior, hypfls=hypoflexus, hypfld=hypoflexid. All measurements are in millimetres.

Table 5 Frequency of the p3 morphotypes in several species referred to the genera *Serengetilagus* (*S.*) and *Trischizolagus* (*T.*). *Alilepus* pattern with hypoflexid and mesoflexid ; *Nekrolagus* pattern with hypoflexid and mesofossetid, *Hypolagus* pattern with hypoflexid only. N=Number of specimens.

Table 6 Measurements of upper and lower teeth of Leporidae g. and sp. indet. from Lissasfa, Casablanca, Morocco. N=number of specimens, ant=anterior, post=posterior, hypfls=hypoflexus, hypfld=hypoflexid. All measurements are in millimetres.

Table 7 Measurements of lower teeth of *Lepus* n. sp. from Grotte des Rhinocéros (Casablanca, Morocco), Middle Pleistocene. N=number of specimens, tld=talonid, All measurements are in millimetres.

Table 8 Measurements of lower teeth and mandible of *Lepus capensis* from Thomas 1 (Casablanca, Morocco), Late Pleistocene. H= height, N=number of specimens, tld=talonid, All measurements are in millimetres.