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Lagomorpha (Mammalia) from the Pliocene-Pleistocene locality of Ahl al Oughlam, Morocco

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Abstract

The exceptionally rich vertebrate locality of Ahl al Oughlam near Casablanca (Morocco) yielded abundant remains of Lagomorpha, composed of cranial and postcranial bones and many isolated teeth. They represent a new species of Prolagidae, *Prolagus migrans* n. sp., and two new Leporidae, *Trischizolagus meridionalis* n. sp. and *Afrolagus pomeli* n. g., n. sp. The main characters of the new *Prolagus* species are the large and anteriorly curved mesial hyperloph on P2, the lack of crochet, and the protoconulid isolated in most p3s.

Trischizolagus meridionalis n. sp. is smaller than the common European species *T. dumitrescuae*, and differs in having in most p3 a massive outlined trigonid, mesofossetid and paraflexid. The second leporid *Afrolagus pomeli* n. g., n. sp. displays a unique p3 pattern not seen in the Old World leporids with the hypoflexid penetrating more than two thirds of the total width; it is probably formed by the fusion of hypoflexid and mesofossetid, but leaves a wide lingual connection between the trigonid and talonid. Its upper molariform teeth have strongly wrinkled enamel along the edges of the hypoflexus. Despite these differences, it also shares several dental features with both the African genus *Serengetilagus* and the European genus *Oryctolagus*, to which it is compared. *Prolagus* and *Trichizolagus* are both well-known European genera. Their occurrence in the Plio-Pleistocene of Morocco is certainly due to a dispersal event thanks to terrestrial connection between the Iberian Peninsula and the Moghreb. In the light of recent faunal, biogeographic and chronological data, the beginning of mammalian exchanges in both directions dates from about 6.2 Ma. The locality of Ahl al Oughlam, although much younger, with an age estimated to 3.0-2.5 Ma, retains taxa resulting from this dispersal event, including the lagomorphs described here.

Keywords Lagomorpha, Prolagidae, Leporidae, late Pliocene, Pleistocene, Morocco

Introduction

Ahl al Oughlam in the suburbs of Casablanca, Morocco, is dated by biochronology to the latest Pliocene-earliest Pleistocene (ca. 3.0-2.5 Ma). It is the richest late Cenozoic vertebrate locality of northern Africa, with over 100 species. Remarkably, their biogeographic affinities are generally African for large mammals and some birds, but generally Eurasian for the microfauna and most birds. Most zoological groups have previously been published (reviews in Geraads 2006; Geraads et al. 1998, 2010, 2022) but, in addition, Ahl al Oughlam yielded abundant remains of lagomorphs, consisting of skull and jaw fragments, isolated teeth, and postcranial bones. The aim of the present paper is to provide a detailed description of the three species (one prolagid and two leporids) that we were able to identify, and to enlighten the paleobiogeographic context in which they lived in Morocco, based on their systematic affinities.

It will be an understatement to say that the history of lagomorphs in Africa is poorly documented. For a continent of more than 30 million km², the number of sites with a quantity of fossils sufficient for taxonomic identification and monitoring of their evolution hardly exceeds a dozen (Winkler and Avery 2010). And yet three families of lagomorphs are present in the continent. The Ochotonidae are known by two genera, *Austrolagomys* and *Kenyalagomys* during the early and middle Miocene (Winkler and Avery 2010). The Prolagidae are only known from some sites in the Moghreb, dated from the terminal Upper Miocene and the Pliocene (see below). As for the Leporidae, currently represented in Africa by five genera and at least 13 species (Happold 2013, 2018), they are practically absent from the fossil record. The two extinct genera, *Alilepus* is known from three sites in Kenya and Ethiopia by some scarce remains, and *Serengetilagus* is much better documented in the deposits of Laetoli in Tanzania and at Toros-Menalla in Chad (Winkler and Avery 2010, and references therein). *Alilepus* sp. of the Kenyan localities is apparently one of the first leporid to occur in Africa and survived there between ca. 6.6 and 4.7 Ma. The first occurrence of *Serengetilagus* in East Africa would be slightly earlier than the Mio-Pliocene boundary (Dietrich 1942; Erbajeva and Angermann 1983; Winkler and Avery 2010; Winkler and

Tomida 2011), i.e., about 6.2 Ma, but a little earlier in Chad (López-Martinez et al. 2007; Lebatard et al. 2008). Also, a recent study provided an early Pleistocene record of the southern African genus *Pronolagus* in Angola and Namibia (Sen and Pickford 2022). Other leporids are also known, such as *Trischizolagus raynali* from the middle Pleistocene of Morocco, and *Lepus* and *Oryctolagus* from late Pleistocene cave deposits in Northwest Africa (Geraads 1994; Aouraghe et al. 2012). The last article also synthesized knowledge on the fossil lagomorphs of the Maghreb, showing how incomplete and rare is the documentation. In such a context, the particularly abundant remains from Ahl al Oughlam, composed of cranial, dental and post-cranial elements, that indicate the presence of three species in this site significantly increase our knowledge of African lagomorphs. Moreover, the fact that some of these species certainly are of European affinity brings new light on the faunal exchanges between southwestern Europe and northwestern Africa.

Fig. 1 Approximately HERE.

Material and methods

The material studied in this work was collected by one of the authors (D.G.) and is stored in the Institut National des Sciences de l'Archéologie et du Patrimoine, Rabat, Morocco. It consists of several upper and lower jaw fragments, isolated teeth and postcranial bones. Cranial remains are all fragmentary, mainly preserving palatal parts and maxillaries bearing one or both tooththrows. Nothing was found as articulated. It is easy to distinguish the remains of *Prolagus* from those of Leporidae using size and morphology. On the contrary, the two leporid species present in this locality are fairly similar in size. Consequently, the attribution of the cranial and postcranial remains to one or the other species of leporid is extremely difficult, except for the mandibles bearing the p3, which is the most characteristic tooth of the Leporidae.

To distinguish these two leporids, we used morphological characters of similar leporids already known from other localities and sought for discrete differences in the upper and lower molariform teeth, the bones of the skull, and the mandible. This required a detailed comparison of the discrete characters of all elements, such as the degree of enamel plication in similar age classes, the shape of the flexa and flexids, the morphology of the various

elements of the palate and maxillae. Mandibles are abundant (36 hemimandibles), but about one third lack teeth, and the ramus is only partly preserved. Isolated teeth are the most common elements. Ahl al Oughlam is striking in the abundance of leporid milk teeth, not used for species distinction due to their similar morphology and change in the pattern of occlusal surface by attrition. The abundance of leporid milk cheek-teeth can be explained by the mode of formation of this faunal assemblage (cave and fissure deposits) where the accumulation of small mammalian remains is at least partly due to predators inhabiting this cave (owls and carnivores). It is already well demonstrated (Andrews, 1990) that the young individuals are more easily caught by predators than adults.

The limb bones also are very abundant and many of them complete. Limb bones were compared with those of European rabbit (*Oryctolagus cuniculus*) and hares (*Lepus europaeus* and *L. capensis*), using skeletons preserved in the collections of the Muséum National d'Histoire Naturelle, Paris.

We preferred to illustrate all specimens, except two palates, with drawings rather than with photos, for a better expression of cranial and 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. In the illustrations of teeth, enamel is represented in black, dentine in white and cement with dots. In order not to clutter the figure captions, the catalogue numbers of the illustrated specimens are reported on the images themselves.

The teeth were measured with a Mitutoyo measuring device on the occlusal surface of teeth, and they indicate maximum length and width in the sagittal and transverse axes, from the external margin of enamel. This does not always correspond to the largest diameter of teeth (length or width) since there is as a rule an additional coat of cement. The measuring techniques follow Angelone and Sesé (2009) for *Prolagus* and Erbajeva and Angermann (1983) for the Leporidae. The measuring method elaborated by White (1991: fig. 2) for the Leporidae is not satisfactory for our purpose since his "line of orientation" does not correspond to the longitudinal axis of p3, either in prolagids or leporids. We retained only the three most significant measurements on p3 of leporids: length, width and depth of the hypoflexid. The bones were measured with a digital caliper. All measurements are in millimetres.

The dental terminology follows Angelone and Sesé (2009) for prolagids, Palacios-Arribas

and López-Martínez (1980) and López-Martínez (1989) for leporids (Fig. 1). This terminology utilises the terms of 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.

Fig. 2 Approximately HERE.

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* (Koenig, 1825)

Other species of the genus: According to the NOW Database, consulted in April 2022, at least 27 species from continental Europe and western Mediterranean islands were referred to this genus, which displays a time span from early Miocene to Holocene. We retained here below the most similar species for comparison with the Moroccan species under study.

Species *Prolagus migrans* n. sp.

(Figs 2-4)

Holotype: Right mandible with p3-m2, AaO-666.

Type locality: Ahl al Oughlam (Casablanca, Morocco), close to Plio-Pleistocene boundary.

Etymology: To note that this species arose from populations that dispersed from Europe to North-West Africa.

Other material: Six isolated P2s (AaO-2265–2270), eight isolated P3s (AaO-2271–2277, 2279, 11 isolated P4s (AaO-2289, 2296, 2298–2302, 2308–2309, 2314, 2328), five isolated M1s (AaO-2319, 2323, 2328, 2331, 2341), and seven isolated M2s (AaO-2342–2344, 2346, 2348, 2351, 2356), six hemimandible fragments bearing complete (2) or part of toothrow (AaO-667–672), 19 isolated p3s AaO-673–691), one isolated m2 (AaO-693), four isolated lower molariform teeth (AaO-692–695).

Measurements: See **Table 1**.

Diagnosis: A medium size species. Mandible with moderately deep corpus, curved ventral margin, diastema shorter than alveolar length, distal mental foramen situated below m1, coronoid process absent. Lower p3 with similar length and width, anteroconid as large or often larger than the metaconid and compressed anteroposteriorly, crochet usually absent (20/21), protoconulid often protruding buccally over protoconid and isolated in almost half of the individuals, occasional loss of protoisthmus (4/21) and deep mesoflexid. Lower molariform teeth with a marked notch on the mesiobuccal part of the talonid. P2 with a large mesial hyperloph. P4 with two fossettes of different size. M1 with one small fossette.

Differential diagnosis: This species is different from *Prolagus apricenicus*, *P. calpensis*, *P. bilobus*, *P. depereti*, *P. figaro*, *P. imperialis*, *P. italicus*, *P. major* and *P. sardus* in its smaller size, from *P. crusafonti*, *P. ibericus*, *P. major*, *P. oeningensis*, *P. pannonicus* and *P. tobieni* in having a P2 with large and anteriorly curved mesial hyperloph, from *P. bilobus*, *P. caucasicus*, *P. crusafonti*, *P. latiuncinatus*, *P. michauxi*, *P. oeningensis*, *P. pannonicus* and *P. sorbinii* in the lack of crochet in almost all p3s. In addition, *P. bilobus*, *P. caucasicus*, *P. depereti* and *P. figaro* have elongated p3 (much longer than wide). The species is different from all known *Prolagus* species in having the protoconulid isolated in about half of the p3s, and protoisthmus lacking in some specimens.

Table 1. Approximately HERE.

Description

No skull remains are preserved, but upper teeth are very abundant. The P2 displays occlusal pattern variable. In five specimens out of six, the mesial hyperloph is strong and covers either the lagicone (3) or even reaches the level of the postcone (2), while in another P2 the mesial hyperloph is rather straight and directed mesially. Such a variation in the occlusal pattern was previously observed in *Prolagus* cf. *michauxi* from Alcoy in Spain (latest Miocene; López-Martínez 1974: pl. 3). The lagicone is always smaller than the postcone, and mesially it is less developed than the latter cusp. It is oriented lingually (5/6) or straight (1/6). The postcone may be ellipsoid in outline (4/6), rounded (1/6) or triangular (1/6). One specimen displays a

distinct postlobule marked by an incipient hypoflexus depression. The mesoflexus penetrates a little more than paraflexus. Three P2s have an enamel hiatus on the precone (Fig. 2b, d, e). The P3 is characterized by its trapezoidal occlusal outline. The mesial hyperloph is very long its tip reaches the level of the lagiloph in half of P3 (Fig. 2g, h), or it ends slightly lingual to it. The lagicone is distinguished from the lagiloph by a slight mesial depression. The lagiloph reaches (7/9) or does not reach (2/9) the buccal margin. The hypoflexus is short, and in most specimens (6/9) it is hardly marked (Fig. 2g, i).

The P4 has a large parafossette and smaller mesofossette, both U-shaped with unequal branches. The hypoflexus does not reach the half width of the occlusal surface. The M1 has lophs almost equal in length, deep hypoflexus and a remnant of mesoflexus. On the M2 the hypoflexus divides the occlusal surface in two unequal lophs (the mesial one shorter but wider), devoid of fossette (Fig. 2p).

Seven more or less complete hemimandibles are preserved. The missing parts are the articular and angular processes. On the buccal side, its depth below p4 varies between 6.1 and 7.5 mm (average 6.8 mm, n=4). The alveolar length, measured on two specimens (7.8 and 8.1 mm) is greater than the diastema length (between 6.1 and 7.1 mm). The angle between the occlusal surface of cheek teeth and the ramus is 110° as measured on one specimen that preserves the ramus. The body is slender. In buccal view, the ventral margin of the body is moderately curved, regularly convex between the incisor and m1, and then concave between the m1 and the angular process. The mesial mental foramen is situated below or slightly in front of p3, while the posterior mental foramen is situated below the m1 and very close to the ventral margin. The mesial border of the masseteric fossa is far from reaching the m2 level. In lingual view, the distal end of the incisor forms a strong bulge at the mid depth below p3-p4. The symphyseal surface is short. The mylohyoid line extends from the level of anterior border of p3 to the level of the m1 trigonid, and it is rather straight. The mandibular foramen is a large hole at the bottom of a large pterygoid fossa. The coronoid process is not preserved.

Fig. 3 Approximately HERE.

Twenty-three p3s are preserved either on the hemimandibles (4) or as isolated teeth (19). Its average length and width are almost identical (Table 1). The anteroconid is isolated (15/16), except in one specimen where it is connected to the protoconulid. Its shape is an ellipsoid

obliquely situated rather lingually in front of the centroflexid. Its lingual edge is sharp, while its buccal and mesial edges may be sharp or rounded, and its distal edge undulated (13/16) or delicately folded (3/16). The metaconid is smaller than (11/15) or roughly identical (4/15) in size to the anteroconid. Its outline is rather rounded without distal widening toward the metaisthmus as usually observed in many *Prolagus* species (see below). The metaconid is always connected to the entoconid by a very narrow metaisthmus. Consequently, the mesoflexid is deep and slightly oblique backwards. The centroflexid is rather straight, and distally ends with a round fossette. In one specimen (probably belonging to a young individual) out of 21, this fossette is divided by a central and rather strong crochet (Fig. 4d). The crochet is absent in other specimens. The protoisthmus is very narrow. It is lacking in 4/21 specimens. An unusual character of p3 from Ahl al Oughlam is the isolated protoconulid as observed on 9/21 specimens. When isolated, it forms an ellipsoid island. Otherwise, it is rather thick and connected distally to the protoconid. The protoconulid protrudes buccally much more than the protoconid. The enamel is thick all around the anteroconid and metaconid, on the buccal edges of the protoconid and protoconulid, and on the distal edge of the hypoconid. In other parts, it is thinner, but there is no enamel break, even on the entoconid which usually lacks enamel in its buccal and distal margins in many European species of *Prolagus*.

The lower molariform teeth are bilobed, except the m2 which is trilobed, and the mesial lobe is strongest. An unusual character of these teeth is the presence of a strong notch on the mesiobuccal edge of the hyperconid (talonid).

Fig. 4 Approximately HERE.

Comparisons

In her extended study on the Western European Neogene and Quaternary lagomorphs, López-Martínez (1989) retained 12 species in the genus *Prolagus*. Later on, new species were reported from several parts of Europe, and at present 27 species are included in this genus (Angelone 2008a; Angelone and Sesé 2009; Hordijk 2010; Angelone and Čermák 2015). In Europe and Anatolia, this genus lived from the early Miocene until the Holocene. Its occurrence in North Africa is known since Jaeger (1971) first mentioned its discovery in the Pliocene locality of Lac Ichkeul in Tunisia. Later on, *Prolagus* remains were found in several

other localities in Morocco, Algeria and Tunisia. These North African findings were either referred to or compared with the western European species (*P. sardus* and *P. michauxi*) or left in open nomenclature, i.e., *Prolagus* sp.

The specimens from Ahl al Oughlam are different from the “primitive” early-middle Miocene species in having many derived features such as a strong mesial hyperloph on P2, the loss of the fossette on the M2, a large and compressed anteroconid, the loss of the crochet, a large protoconulid and the metaconid only connected to the talonid on p3. Therefore, the comparison will be limited to the latest Miocene and Plio-Pleistocene species of this genus. Among them, several species are large sized, such as *Prolagus apricenicus* Mazza, 1987, *P. depereti* López-Martínez, 1975 (in López-Martínez and Thaler 1975), *P. figaro* López-Martínez, 1975 (in López-Martínez and Thaler 1975), *P. imperialis* Mazza, 1987, *P. italicus* Angelone, 2008b, *P. major* López-Martínez, 1977, *P. osmolskae* Fostowicz-Frelik, 2010 and *P. sardus* (Wagner, 1832). Measurements taken on mandibles and lower and upper cheek teeth from Ahl al Oughlam are all lower than the values published for the mentioned species (see in particular López-Martínez 1977, 1989; Mazza 1987; Angelone 2008; Fostowicz-Frelik 2010). On the other hand, the Moroccan species shares several features with some species largely distributed in Europe. Among them *P. michauxi* López-Martínez, 1975 (type loc. Sète, France, MN15, in López-Martínez and Thaler 1975) is a common species in the latest Miocene and early Pliocene of Western Europe, and several records from North African localities are either referred or compared to this species (see below). Compared with the type material from Sète, the specimens from Ahl al Oughlam share many features with this species, such as the size, large mesial hyperloph on the P2, large anteroconid and metaconid, protoconulid protruding. Despite these resemblances, *P. michauxi* is different from the Moroccan form in having on the p3 the anteroconid always smaller than the metaconid, and a strong and centrally placed crochet in most specimens. In this species, the protoconulid of p3 is never isolated, the protoisthmus is always present and the P3 has a buccal edge more oblique than in the Moroccan form (López-Martínez 1974, 1977, 1989; López-Martínez and Thaler 1975).

Prolagus sorbinii Masini, 1989 was initially described from the latest Miocene locality of Monte Castellaro, Central Italy. Later on, Angelone (2007), Angelone and Cavallo (2010) and Angelone et al. (2021) referred to this species several other findings from Mio-Pliocene localities of Italy, Greece and Turkey, which were initially referred to *P. michauxi* or *P. cf.*

michauxi. This is a middle-sized species like *P. michauxi*, but it differs from the latter in having p3 with anteroconid as large as the metaconid, V-shaped mesoflexid, thick entoconid with continuous enamel, crochet absent or reduced and shifted towards the metaisthmus, rather than being central as it is in *P. michauxi*, a rather straight mesoflexid; P2 with mesial hyperloph and continuous enamel on the precone; upper molars with very deep hypoflexus (see details in Angelone 2007, 2008; Angelone et al. 2021).

P. sorbinii is different from the Ahl al Oughlam species in having a p3 with an anteroconid smaller or as large as the metaconid, a metaconid pear shaped and connected to the entoconid by a large metaisthmus, a crochet, although reduced, in about half of individuals, a V-shaped and transverse mesoflexid, an entoconid lacking enamel lingually in most individuals. On the p3 of *P. sorbinii*, the protoisthmus may be lacking mainly in young individuals (Masini 1989), but Angelone (2007, 411) notes that the absence of the protoisthmus is a rare but recurrent feature observed in many species, especially in juvenile specimens; it seems to have a higher incidence in *P. sorbinii*, but this character cannot be considered as distinctive as to be put in the diagnosis". *Prolagus sorbinii* may have an isolated metaconid in up to 15% of individuals (Angelone and Veitschegger 2015), which is never the case in the Ahl al Oughlam specimens. On the P3 of this species, the buccal edge is very sharp and the lagiloph does not reach the buccal edge (Masini 1989; Tesakov and Averianov 2002; Angelone 2007; Angelone and Cavallo 2010).

Prolagus ibericus López-Martínez, 1975 (type locality Layna; MN15) is only known in Spain. This is a small sized species, smaller than the specimens from Ahl al Oughlam, with a mix of primitive and derived dental features (López-Martínez 1989). In this species the P2 is short and lacks the mesial hyperloph and its hypercone is triangular in outline. On the p3, the anteroconid is wide and compressed mesiodistally, in that different from Ahl al Oughlam where the anteroconid is obliquely oriented, but not larger than the metaconid. The protoconulid is thin and never isolated, and the complex protoconulid-entoconid-entoisthmus is rather sagittal, while it is bent buccally on the p3 from Ahl al Oughlam.

Prolagus calpensis Major, 1905 was initially defined based on a mandible from the brecciated early Pleistocene deposits of Gibraltar. López-Martínez (1989) and Montoya et al. (1999) added new records from Spain and southern France. It is similar in size to *P. michauxi* and *P. sorbinii*, and to the Ahl al Oughlam specimens. The shape of the mandible, the large and compressed anteroconid, the simple metaconid, and the lack of crochet on the p3 are all

characters shared with the specimens from Ahl al Oughlam. Also, the upper cheek teeth from Moreda (Granada), Castelldefels (Barcelona) and Cueva de Gracia (Barcelona) that López-Martínez (1989) identified as *P. cf. calpensis* are similar in size and tooth pattern to the specimens of Ahl al Oughlam. However, the p3 of this species, from all localities, never displays an isolated protoconulid, in contrast to Ahl al Oughlam, the hypoflexid is short, and on the lower molariform teeth of *P. calpensis* and *P. cf. calpensis*, the mesiobuccal notch of the talonid is absent.

All these distinctive characters of the Ahl al Oughlam prolagid justify its attribution as a new species, named here *Prolagus migrans* n. sp.

Fig. 5 Approximately HERE.

***Prolagus* in North Africa**

The oldest occurrence of *Prolagus* in Africa is documented in several latest Miocene localities in the Moghreb: Voie Ferrée in Tunisia (Robinson et al. 1982), Argoub Kemellal 1 in Algeria (Coiffait-Martin 1991) and Afoud 1, 2, 12-1 and 12-2 in Morocco (Benammi et al. 1995, 1996; Mahboubi 2014; Mahboubi et al. 2022; Dupré et al. 2022) (Fig. 5). The main Pliocene and Early Pleistocene localities with *Prolagus* are Aghouri and Aïn Guettara in Morocco (Jaeger et al. 1977; Brandy 1979; Brandy and Jaeger 1980; Benammi et al. 1995), Argoub Kemellal 2 and Bel Hacel in Algeria (Coiffait et al. 1985; Ameer-Chebbeur 1988; Coiffait-Martin 1991), and Lac Ichkeul in Tunisia (Jaeger 1971) (Fig. 5). Only a few cheek teeth from Afoud 1, Afoud 12-2, Aghouri, Aïn Guettara and Lac Ichkeul were briefly described and illustrated (Jaeger 1971; Brandy 1979; Benammi et al. 1995; Mahboubi 2014; Mahboubi et al. 2022), and they were referred to *Prolagus michauxi* or *P. cf. michauxi*. Lastly, Dupré et al. (2022) described the rich material from Afoud 12-1 and 12-2 and showed that it is similar to *P. michauxi* in size and its general features of the dentition. The single p3 (1,72 x 1.70) from Lac Ichkeul is similar in size and morphology to those from Ahl al Oughlam. This is also the case of the specimens from Aïn Guettara that Brandy (1979) referred to as *P. cf. michauxi*. All these fossils might be included in the new species after a detailed review. Contrary to these, the specimens from Afoud localities (Mahboubi 2014; Mahboubi et al. 2022; Dupré et al. 2022) are larger in size, the p3 is elongated, its anteroconid

is smaller than the metaconid, and a strong crochet is present. The specimens from Afoud 1, 2, 12-1 and 12-2 seem indeed very similar in the size and morphology of all cheek teeth to *P. michauxi* from the western European localities as showed by Dupré et al. (2022).

The presence of the genus *Prolagus* in the Mio-Pliocene deposits of the Moghreb is due to the desiccation of the Mediterranean during the Messinian crisis, tectonics along the Betic-Rifain corridor and the land connection between the Iberian Peninsula and Africa (López-Martínez 2001; Gibert et al. 2013).

Family Leporidae Gray, 1821

Systematic remarks: The number of subfamilies and genera included in the family Leporidae has been debated by lagomorph specialists for over a century. Based on the characters of the third lower premolar, Dice (1929) distinguished three subfamilies: Palaeolaginae (p3 with both hypoflexid and mesoflexid), Archaeolaginae (p3 without mesoflexid, with hypoflexid crossing no more than half of the p3 occlusal surface), and Leporinae (p3 with only deep hypoflexid). This subdivision was followed by several fossil lagomorph specialists, such as Dawson (1958, 1967), White (1991) and López-Martínez (1989, 2008). On the other hand, Gureev (1964) followed by Erbajeva (1988), considered these subfamilies as the tribes of the subfamily Leporinae, to which they also added two other subfamilies, the Mytonolaginae and Agispelaginae. Based on a cladistic analysis of the morphological characters of fossil and extant Leporidae, Averianov (1999) retained only two subfamilies, Pentalaginae and Leporinae (plus some genera incertae sedis), each containing several tribes. However, other morphological and molecular studies (Wible 2007; Ge et al. 2013, 2015; Kraatz et al. 2015; Kraatz and Sherratt 2016) were not conclusive to define subfamilies among the Leporidae. Lastly, facing the lack of consensus in the morphologic and molecular studies, Flynn et al. (2013, 3) resolved to retain the subfamily of Leporinae “for the crown group (living hares and rabbits; i.e. *Lepus* and *Oryctolagus*); close fossil genera are stem Leporidae”, but did not retain other subfamilies waiting for future studies to decipher phylogenetic relationships among the Leporidae sensu lato. Pending consensus on the subfamilial division, we describe the material from Ahl al Oughlam as Family Leporidae.

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-Adamyanyan, 1986); *T. raynali* (Geraads, 1994); *T. mirificus* Qiu and Storch, 2000.

Species *Trischizolagus meridionalis* n. sp.

(Figs 6a, 7, 8a, 9, 10)

Holotype: Left hemimandible with p3-m3 and broken incisor, AaO-2650 (Fig. 8a, 10a)

Type locality: Ahl al Oughlam (Casablanca, Morocco), Plio-Pleistocene.

Ethymology: In relation to the country of discovery Morocco on the southern shores of the Mediterranean.

Other material from Ahl al Oughlam: One palate preserving part of cheek teeth (AaO-4901), five fragments of maxilla bearing part of cheek teeth (AaO-4902–4906), eight fragments of edentulous maxillae (AaO-4907–4914), four isolated upper incisors (AaO-4915–4918), 24 isolated P2s (AaO-4919–4942), 36 isolated upper molariform teeth (AaO-5001–5036), 21 hemimandibles preserving some cheek teeth (AaO-4785–4786, AaO-4944–4963), nine edentulous hemimandible fragments (AaO-4785, 4964–4971), six isolated lower incisors (AaO-4992–4997), 20 isolated p3s (AaO-4972–4991), 28 complete or partial isolated lower molariform teeth (grouped as AaO-4998), six isolated m3s (AaO-4999–5004).

Measurements: See Tables 2 and 3.

Diagnosis: Medium sized leporid with incisor foramen and choanae moderately large, hard palate shorter than the choanae breadth. Lower p3 with three flexids on the trigonid and with mesoflexid or mesofossetid in most specimens; anteroconid divided in two equal parts by a moderately deep anteroflexid, and with mesial margins at the same level. Upper incisor short laterally and wide anteroposteriorly. P2 with a moderately deep paraflexus, and marked hypoflexus and mesoflexus. Upper molariforms have hypoflexus extending for two thirds of the breadth, with enamel moderately crenulated along the mesial wall, but flat or barely undulated along the posterior wall.

Differential diagnosis: This species is different from *T. maritsae* and *T. raynali* in its larger size and presence of mesoflexid or mesofossetid in most specimens. The type species *T. dumitrescuae* is different in having p3 with anteroposteriorly elongated trigonid, mesoflexid

on most p3, but rarely mesofossetid; its anteroflexid is variable in shape and depth and barely divides anteroconid in two often unequal parts, and the buccal anteroconid clearly protrudes anterobuccally; the paraflexid is incipient, never well marked as in *T. meridionalis* n. sp. *T. crusafonti* is different in lacking mesoflexid and mesofossetid of p3 in most specimens. *T. gambariani* is characterized in having p3 with a thinner protoconid, paraflexid lacking or barely developed, and in particular in having p3s with “*Nekrolagus* morphotype” (p3 with mesofossetid) in most individuals. *T. mirificus* from Chinese localities lacks in most individuals mesoflexid or mesofossetid and paraflexid (76% of p3s), and the anteroflexid is occasionally present, shallow and wide. In addition, its P2 is devoid of mesoflexus, hypoflexus barely developed or absent.

Fig. 6 Approximately HERE.

Description:

Cranium (Fig. 6a): Only the palatal parts of the cranium are preserved. The posterior end of the incisive foramen forms two rounded notches separated by a sharp mesial palatal spine, and they extend posteriorly to the mid-level of P2s. The choanae are a little wider than the incisive foramen. In *Oryctolagus cuniculus* the choanae are narrower, but much wider in *Lepus europaeus*. The hard palate is surprisingly short, and it is composed mesially by the palatine processes of maxillae, and posteriorly by the palatine. The palate has no posterior spine, which is present in most leporids, but absent in *Serengetilagus tchadensis* López-Martínez et al., 2007 from Chad. On one specimen (AaO-4901) the mesial parts of the zygomatic arches are preserved (Fig. 6a). The width between their anteroexternal borders is 34.7 mm. This part is well detached from the maxilla with mesial and distal semicircular notches. The mesial root of zygomatic arch has a vertical slit-like aperture perforated by a deep infraorbital foramen which is divided in three foramina. The zygomatic arches diverge slightly backwards. On the ventral side, there is a small protuberance for the attachment of masseter muscles.

Fig. 7. Diagram - Approximately HERE.

Table 2 Approximately HERE.

Lower jaw (Fig. 8a): The size of the lower jaw is similar to that of the extant rabbit *Oryctolagus cuniculus* but smaller than that of *Lepus europaeus* and *L. timidus* (Table 2). The p3-m3 alveolar length is almost equal to the diastema length. The average ratio of alveolar length/diastema length is 0.99 in this Moroccan species, 0.88 in *Oryctolagus* and 0.85 in *L. europaeus* and *L. timidus*. The high alveoli/diastema ratio of the Moroccan species indicates a shorter muzzle compared to the above-mentioned species.

In lateral view the body is rather high; its depth slightly increases backward below the toothrow. The foramen mentale is situated 3-4 mm mesial to p3 in the upper part of the body as in *Oryctolagus*; in *Lepus* it is smaller and situated more mesially. The buccal face of the body is pierced by numerous nutritive foramina, some of them as large as the foramen mentale. These foramina are mainly grouped under p3 and along the ventral side of the corpus below the diastema, and their density shows great variations in the specimens of Ahl al Oughlam as in many extant leporid species. The ridge of the angular process, which delimits mesially the masseteric fossa is a little stronger than in *Oryctolagus*, but clearly weaker than in *Lepus*.

In lingual view, the posterior end of the incisor forms a distinct swelling on the body in front of p3 or partly below it. The same pattern is also observed in *Oryctolagus*, while in *L. europaeus* and *L. timidus* the incisor ends far in front of the p3, and its swelling is tenuous. In *S. praecapensis* the incisor swelling is located below p3 according to Erbajeva and Angermann (1983).

Fig. 8. Mandibles-Approximately HERE.

Upper dentition (Fig. 9): Four upper incisors similar in size and morphology are referred to this species because of their smaller size and morphological similarities with those of other species of the genus. Their outline is squarish with a narrow mesial groove, which divides the buccal face into a narrow medial (about 1/3 of the width) and a broader (2/3 of the width) lateral parts. The buccal face on both sides of the groove is rounded and covered by a thin enamel band, while the lingual face is flat or slightly convex, and lacks enamel. There is no cement on the buccal face nor in the groove.

The P2 is represented by 17 adult and four juvenile specimens. The latter ones are smaller and have hypoflexus and in particular mesoflexus barely sketched Fig. 9f, g). In adult specimens the occlusal outline is more or less compressed anteroposteriorly, and the depth of both hypoflexus and mesoflexus may be shallow or well-marked. In other terms, the size and pattern of this tooth are quite variable.

Fig. 9. Upper teeth-Approximately HERE.

The upper molariform teeth have a short and wide occlusal outline. The hypoflexus penetrates about 2/3 of the occlusal surface in the P3 and its width progressively decreases from P4 to M2 (Table 3); the enamel is wrinkled on its mesial wall, but barely wavy or flat on its posterior wall. The depth of the hypoflexus and the degree of enamel plication decrease on M1 and M2. The lingual entrance to the hypoflexus may be narrow or slightly widened and rather transverse (20/33) or slightly oblique forwards (13/33).

No M3 has been recovered.

Table 3 Approximately HERE.

Lower dentition (Fig. 10): The lower incisor is preserved on several hemimandibles and in addition six isolated incisors can be referred to this species. Its section is rectangular, a little less wide than that of the other leporid of Ahl al Oughlam, and clearly smaller. The enamel of the anterior face is smooth.

The shaft of p3 is curved lingually, but its posterior face is straight. The shape of the occlusal outline is rather trapezoidal; it may have four to five flexids. The trigonid complex is separated from the talonid by the hypoflexid and mesoflexid or mesofossetid, although the bridge in between is quite broad. The enamel is thick around the tips of conids but weak or extremely thin on the tip of flexids, along the distal margin of the hypoflexid and around the posterolingual margin of the talonid.

On the trigonid complex, the anteroflexid is either deep (16/28), shallow (11/28) or absent (1/28). It divides the anteroconid in two almost equal parts, except in five p3s which have a slightly larger buccal anteroconid. The buccal anteroconid slightly protrudes on 7/28 specimens, while it is at the same level in the others (21/28). The trigonid is penetrated

buccally by an open angle (nearly 90°) protoflexid in 18/29 specimens, or a rather acute-angled protoflexid in the other 11 specimens. Lingually the paraflexid is rather variable in shape and size; it may be virtually absent (7/28), deeper (6/28) or well-marked (15/28). When present, it is rather transverse (12/21) or slightly directed backwards (9/21). The metaconid protrudes lingually in 22/28 p3s. The bridge between the trigonid and talonid is wide. The hypoflexid does not reach the half-width of the tooth surface (Table 3), and it is rather transverse (20/29) or slightly directed backwards (9/29). The mesoflexid may be absent (4/26 = *Hypolagus* pattern), present as an enamel island (12/29 = *Necrolagus* pattern) or as a complete flexid opposite to the hypoflexid (13/29 = *Alilepus* pattern). It is generally transverse or slightly oblique in two specimens. The hypoconid has a well-marked anterior groove on 22/29 specimens, or the anterior margin of the hypoconid is round on the others. On the lower molariform teeth, the trigonid is higher, longer and broader than the talonid, and they are connected by a narrow lingual bridge. The distal margin of the trigonid is angular posterobuccally, which narrows the hypoflexid, while this margin is rather straight in the new genus described here below. The mesiobuccal margin of the talonid bears a depression more or less well marked, but present in all lower molariforms. The enamel is smooth along the walls of the hypoflexid.

The m3 is reduced in size. The trigonid and talonid lack enamel connection, but are joined by cement.

Fig. 11. Lower teeth-Approximately HERE.

Comparisons:

This leporid of Ahl al Oughlam displays similarities with the genera *Trischizolagus* Radulesco and Samson, 1967 and *Serengetilagus* Dietrich, 1942 in size and characters of its dentition, in particular the p3: short hypoflexid, trigonid with two or three flexids, anteroconid divided by an anteroflexid and presence of mesoflexid or mesofossetid, present only occasionally and in juvenile individuals in *Serengetilagus*. However, *Serengetilagus* Dietrich, 1942 is different in having narrow choanae, dentary increasing in depth backwards, P2 with deep paraflexus and shallow mesoflexus and hypoflexus, p3 with a straight lingual profile, anteroflexid variably developed, paraflexid and mesoflexid absent in adult individuals or exceptionally present in juveniles, lingual anteroconid weaker than the buccal one. The

type species, *Serengetilagus praecapensis* Dietrich, 1942, was initially described from Laetoli in South Serengeti region, Tanzania. MacInnes (1953) reported on new specimens collected by Louis Leakey. Later on, Erbajeva and Angermann (1983) and Winkler and Tomida (2011) redescribed the type material and new finds from several localities in the Laetoli area (age between 4.4 and 2.66 Ma) and added some other records from the Pliocene deposits of Kanam West, Kenya. The above-mentioned characters and in particular those of the p3 (straight lingual outline, narrower trigonid, lack of mesoflexid or mesofossetid in adult individuals and paraflexid in most specimens) imply that *T. meridionalis* n. sp. cannot be referred to this species. The same differences are also observed with *S. tchadensis* López-Martínez et al., 2007 from the late Miocene of Chad.

Serengetilagus orientieuropaeus Topachevski, 1987 from Trudomirovka (Odessa region, Ukraine, late Pliocene) is known from a hemimandible fragment bearing p3-m1 and three isolated p3s. It is different from *T. meridionalis* n. sp in having p3 with a rounded lingual edge, hypoflexid directed backward (transverse in *T. meridionalis* n. sp.), mesoflexid absent on p3, anteroflexid and paraflexid either absent or just incipient, and consequently the anteroconid is not well defined. Averianov and Tesakov (1997) referred this species to as *Trischizolagus* cf. *maritsae*. However, *S. orientieuropaeus* displays a p3 occlusal pattern similar to that of *Hypolagus igromovi* Gureev, 1964, which is a common species of latest Miocene and Pliocene localities of western Russian and Ukrainian territories. In both species the p3 may occasionally has short anteroflexid and paraflexid, and fully lacks the mesoflexid. In addition, an oblique hypoflexid is a typical feature of *Hypolagus*. In summary, *S. orientieuropaeus* most closely resembles *Hypolagus* species, and perhaps even synonymized with *H. igromovi*.

The material from Ahl al Oughlam is better assigned to *Trischizolagus* than to any other leporid because of its similarities in size, morphology of the cranium and mandible, and the pattern of teeth with the species referred to this genus. However, as rightly noted by Angelone et al. (2021) the systematic status of the species included in this genus is rather problematic. The type species *T. dimitrescuae* is from Mălușteni (Romania, early Pliocene). Averianov (1995), Averianov and Tesakov (1997) and Čermák and Wagner (2013) included in *T. dimitrescuae* leporid remains from several localities all over Europe (Moldova, Bulgaria, Greece, Hungary, Italy and Spain: see map in Čermák & Wagner 2013, and Fig. 5). Čermák and Wagner (2013) referred to this species materials from 14 localities in Central and

Southeastern Europe. As seen in Fig. 11, the specimens from these localities display a large variation in size that exceeds reasonable limits for a species of Leporidae. Note in particular four largest p3s from Tatareshty (Moldova) which are significantly greater than those of Malusteni, type locality of the species. Furthermore, the number of specimens from each of these localities, and in particular the number of p3s, is insufficient to appreciate individual morphological variation and to indicate the dominant morphotype.

As for the species *T. maritsae* (Maritsa, Island of Rhodes, Greece) and *T. crusafonti* (La Alberca, Spain), they are established based on a limited number of specimens, fragmentary and poorly preserved. Consequently, adequate morphological comparison of new findings with either of these species is difficult.

Trischizolagus dumitrescuae from Mălușteni is different in having p3 with a shallow and wide anteroflexid which divides the anteroconid into two parts, but the buccal anteroconid tapers anterobuccally and protrudes forwards, the mesoflexid is present in most individuals, and the mesofossetid is rare (less than 30% of p3s). This is also the case in the specimens of Moscovei (early Pliocene, Moldova), Beremend 39 (early Pliocene, Hungary), Ciuperceni (early Pliocene, Romania) and Muselievo (early Pliocene, Bulgaria) (Averianov 1995; Terzea 1997; Popov 2004; Čermák and Wagner 2013), which are indicated on Fig. 10 as the Central and Southeastern European findings. On the specimens from Ahl al Oughlam the anteroconid of p3 is divided in two parts, almost equal in volume, by a deep and narrow anteroflexid. The buccal anteroconid does not protrude, and almost half of p3s have mesofossetid or lack mesoflexid, contrary to those of *T. dumitrescuae*. Materials from several latest Miocene and early Pliocene localities in China were also referred or compared to this species, but their systematic status needs to be reconsidered.

Fig. 11. Diagram p3-Approximately HERE.

Janvier and Montenat (1971) described *Hispanolagus crusafonti* from the latest Miocene locality of La Alberca (Spain), and López-Martínez (1989) included it in the genus *Trischizolagus*. The material from the type locality is poor and fragmentary. It was redescribed and re-illustrated in Sen (2020) who referred the material from Dorkovo (earliest Pliocene, Bulgaria) to this species. The size is similar to that of *T. meridionalis* n. sp., but the pattern of P2 and p3 is different. The P2s have shallow hypoflexus and mesoflexus, and the

first one may even be lacking. All known p3s from La Alberca lack the mesoflexid or mesofossetid. At Dorkovo, one juvenile p3 displays a tiny mesofossetid, while the three adult ones are devoid. In addition, all p3s from Dorkovo have a protruding buccal anteroconid, although this character is not obvious in the scarce material of La Alberca.

“*Alilepus*” *gambariani* from the early Pliocene of Armenia (MN14; Melik-Adamyanyan 1986) was reassigned to *T. dimitrescuae* by Averianov and Tesakov (1997), but Čermák and Wagner (2013) held it as a separate species of *Trischizolagus* based on the predominance of the ‘*Nekrolagus*’ morphotype of p3. Indeed, the p3 of this species is characterized by the dominance of a mesofossetid and rare occurrence of individuals with a mesoflexid. In addition, on the p3s of this species the anteroflexid is absent in most cases or badly defined. Lastly, abundant remains of this species were recorded in Turkey (Čermák et al. 2019). The measurements given in the latter study indicate a species slightly larger than *T. meridionalis* n. sp. (Fig. 11).

Trischizolagus maritsae De Bruijn et al., 1970 from Maritsa (earliest Pliocene, Rhodos Island, Greece) is the smallest species referred to this genus (for instance length x width of p3 average 2.0 x 2.6 mm, n=3). Based on the limited number of specimens, it appears that the mesoflexid may exist or not on p3, its trigonid has three flexids as in other species of the genus, but its lower molariform teeth are considerably longer compared their width. Mazo et al. (1985), López-Martínez (1989) and Pinero et al. (2017) have tentatively attributed to this species some scarce remains from several Spanish localities (Alcoy N, Salobreña, Caravaca, Gorafe 1, Puerto de la Cadena, Huéscar 3), all close to the Mio-Pliocene boundary, based on the smaller dimensions of teeth and, for p3, deeply penetrating hypoflexid and the lack of mesoflexid.

Trischizolagus raynali (Geraads, 1994) from the Grotte des Rhinocéros (middle Pleistocene, Casablanca, Morocco) was initially included in the genus *Serengetilagus* due to its discovery in Africa, its similarities with *S. praecapensis* and also with the suspicion of synonymy of *Trischizolagus* with *Serengetilagus*. In later studies, these two genera are recognized distinct. López-Martínez et al. (2007) included this species in the genus *Trischizolagus*. It is different from *T. meridionalis* n. sp. in having p3 elongated compared to the massive appearance of p3 in *T. meridionalis* n. sp., the buccal anteroconid is stronger than the lingual one and protrudes anteriorly, and all five p3s known from Grotte des Rhinocéros have mesofossetid. Other differences of p3 are the much more open protoflexid and incipient presence of paraflexid,

which is generally well defined in *T. meridionalis* n. sp. On the lower molariform teeth of *T. raynali* the talonid is much less depressed in its anterobuccal edge. Finally, the dimensions of the p3 given by Geraads (1994) indicate a species of size clearly smaller than that of Ahl al Oughlam (Fig. 11).

Trischizolagus mirificus Qiu and Storch, 2000 was initially reported from the early Pliocene of Bilike, Inner Mongolia. The p3 of this species has a *Serengetilagus* pattern in having a straight or slightly rounded lingual outline, and lacking mesoflexid or mesofossetid and paraflexid in most specimens. One can wonder whether this species and other discoveries in China tentatively referred to this species and to *T. dumitrescuae* do not represent a separate genus, but this question is outside the scope of the present work.

Scarce remains reported to *Trischizolagus* sp. were also found in Italy, France and Spain.

Angelone and Rook (2012) described as *Trischizolagus* sp. a few teeth from the Messinian locality of Borro Strolla (Tuscany, Italy), and Angelone et al. (2021) referred to as cf.

Trischizolagus sp. the material from the latest Messinian locality of Cava Monticino (Romagna, Italy) and noted the similarities of this form with *T. maritsae* and *T. crusafonti*. De Marfà (2009) tentatively ascribed to *Trischizolagus* sp. a damaged hemimandible and a few limb bones from an early Pliocene site near Perpignan in southern France, and based on morphometric analysis of p3, he concluded the similarities of these fossils with *T. maritsae*. In summary, this leporid from Ahl al Oughlam displays all main characters of the species referred to the genus *Trischizolagus*, but differs from all known species in many details of the dentition and also in its larger size compared to those of *T. maritsae* from southern Europe and *T. raynali* from Morocco.

Genus *Afrolagus* n. g.

Type species: *Afrolagus pomeli* n. sp.

Derivatio nominis: Derived from Africa.

Diagnosis: Large size; cranium with wide choanae, large incisor foramen, but short hard palate. Mandible with high horizontal branch slightly increasing backwards in depth, diastema and alveoli of cheek teeth of equal length, lower incisor end below the front of p3. P2 with three anterior folds. Upper molariform teeth short and wide, with a deep hypoflexus bordered by strongly wrinkled enamel, especially anteriorly. The p3 has a deep hypoflexid

and a broad connection between trigonid and talonid, but lacks paraflexid and mesoflexid; lower molariform teeth with a protoflexid, in particular on m1 and m2.

Species *Afrolagus pomeli* n. sp.

(Figs 6b, 8b, 12, 13)

Holotype: Left lower jaw with broken incisor and the tooth-row p3-m3 (AaO-5052) (Figs 7b, 11a).

Other material: Two palates with part of cheek teeth (AaO-5040–5041), one upper incisor (AaO-5042), three isolated P2 (AaO-5043–5045), five isolated upper molariforms (AaO-5046–5051) one lower incisor (AaO-5056), one right and two left hemimandibles with part of cheek teeth (AaO-5053–5055), one isolated lower incisor (AaO-5056), 16 isolated p3 (AaO-5057–5072), one isolated m3 (AaO-5073).

Measurements: See Tables 2 and 4.

Type locality: Ahl al Oughlam (Casablanca, Morocco), late Pliocene-early Pleistocene.

Ethymology: Dedicated to Auguste Pomel (1821-1898), famous French geologist, paleontologist, botanist and politician, for his contribution to the knowledge of North African fossil mammals, including lagomorphs.

Diagnosis: As for the genus.

Fig. 12. Upper teeth-Approximately HERE.

Description:

Upper jaw (Fig. 6b): Only the palatal part and maxillary bones are preserved. The incisor foramen is wide, distally well divided in two parts by a strong anterior spine of the palate. The hard palate is shorter than the choanae breadth, and it does not bear distal spine but a barely visible swelling.

Lower jaw (Fig. 8b): On the mandible, the diastema is as long as the p3-m3 alveoli. In lateral view the mental foramen is situated about three millimeters in front of p3, and high in the body. Lower down, the body is riddled with many nutritive foramina. The depth of the body slightly increases backwards (Table 2). The masseteric fossa is anteriorly delimited by an arc-

shaped ridge which extends beyond the m2-m3 limit. In lingual view the distal end of the lower incisor forms a strong bone swelling beneath the rear of the diastema.

Upper teeth (Fig. 12): One upper incisor is tentatively attributed to this species. Its size is larger and its occlusal surface is elongated and anteroposteriorly flattened, while the upper incisors of *Trischizolagus meridionalis* n. sp. are smaller and have more square outline. The anterior groove divides the buccal face in two unequal parts as in *T. meridionalis* n. sp., but it is wider. Cement is absent.

The P2 has a short and wide outline. The hypoflexus and mesoflexus are equally deep, but the paraflexus is deeper and its enamel is undulated in some specimens. The upper molariform teeth are also short and wide. The hypoflexus penetrates about 2/3 of occlusal width (Table 4). Along its walls, the enamel is equally folded anteriorly and posteriorly. Its lingual aperture is strait and V-shaped. The degree of enamel plication decreases somewhat on M1 and M2, in particular in old individuals.

Table 4. Approximately HERE.

Lower teeth (Fig. 13): One broken lower incisor on the type mandible and an isolated one are larger than those of *T. meridionalis* n. sp. The section is almost rectangular, and the anterior face smooth.

The shaft of the p3 is curved posteriorly and lingually. The occlusal face is divided in trigonid and talonid by a deep hypoflexid, but these two parts are connected by a wide lingual dentine bridge. The mode of formation of this type of hypoflexid, never observed in the Leporidae of the Old World, will be discussed below in the discussion. The anteroflexid, which divides the anteroconid in two almost equal parts, is deep and rather narrow on eight specimens but shallow in one. It is generally simple (7/9), but may also be double (2/9). The buccal anteroconid is oblique, rounded on its anterior margin and protrudes anteriorly on 7/9 p3s. The lingual anteroconid is straight, short, wide and its tip rounded. The protoflexid is well marked, rather narrow on six, but wider with an angle about 60-70° in three p3s. The paraflexid is absent in all specimens. The hypoflexid penetrates over 2/3 of the tooth width (Table 4). It is constricted in its middle part by a distal extension of the trigonid, which divides it in large external and short internal parts. Enamel is thick on its anterior wall but

extremely thin along its posterior wall, which is slightly undulated in 3/9. Enamel is thin along the posterior wall, and may be slightly undulated. The length of the talonid is about 1/3 of the total length, and its anterobuccal margin bears a groove or depression on 4/9 p3s. The talonid protrudes buccally more than the metaconid on five p3s, while it is at the same level on four others.

The lower molariform teeth have a trigonid higher, longer and wider than the talonid. Their anterobuccal margin bears a depression on p4, which becomes a marked groove on m1 and m2. This groove is absent on the molariform teeth of *T. meridionalis* n. sp.

The m3 is preserved on the type hemimandible. It has an ellipsoid trigonid and a rounded and much smaller talonid. An isolated m3, a little larger than those attributed to *T. meridionalis* n. sp., does not present any reliable difference with the m3s referred to this species.

Fig. 13. Lower teeth-Approximately HERE.

Comparisons

This species is different from *Trischizolagus meridionalis* n. sp. in its slightly larger size (cranium, mandible, dentition), but above all in its wider choanae and many features of its dentition (hypoflexus of the upper molariform teeth deeper and with strongly wrinkled enamel on its edges, p3 with a deep hypoflexid, without mesoflexid and paraflexid, lower molariform teeth with a protoflexid). There is no genus of Leporidae in the Old World combining all these features, hence the assignment of this leporid to a new genus and new species. Tooth patterns somewhat reminiscent of those of this Ahl al Oughlam species are known from only a few North American leporids, such as the genus *Aluralagus* Downey, 1968, or the species *Pratilepus kansasensis* Hibbard, 1939 and *Sylvilagus hibbardi* White, 1984. All these species are of Blancan and/or Irvingtonian age (late Pliocene-early Pleistocene). Given the absence of any direct phylogenetic relationship with these North American taxa, these resemblances can only be explained as the convergence of characters. Among the Old World leporids, the most similar genera are *Serengetilagus* Dietrich, 1942, *Lepus* Linnaeus, 1758 and *Oryctolagus* Lilljeborg, 1874. As noted above, the first genus is only African and known with two species *S. praecapensis* Dietrich, 1942 and *S. tchadensis* López-Martínez et al., 2007. The first species is recorded in East Africa, in the localities of the Lower (>4.4–3.85 Ma) and Upper (3.85–3.63 Ma) Laetolil Beds, in the Upper Ndolanya

Beds (2.66 Ma) in Tanzania and Kanam West in Kenya (Winkler and Tomida 2011), while *S. tchadensis* is only known from Toros Menalla in Chad, dated to about 7 Ma (Lebatard et al. 2008).

S. praecapensis is reminiscent to *Afrolagus pomeli* n.g. n. sp. by its similar size and many features of its dentition. Erbajeva and Angermann (1983) and Winkler and Tomida (2011) analyzed in detail the occlusal morphology of p3 and the latter authors distinguished five morphotypes (A, B, B-, B+ and C). The most common morphotypes are B, B- and B+, which represent more than 90% of specimens in all sites of Laetolil and Upper Ndolanya beds. These three morphotypes are characterized in having simple or double anteroflexid, L-shaped protoflexid, short hypoflexid (less than half of the total width) and lack of mesoflexid and mesofossetid. In the Moroccan species, the anteroflexid is simple in most specimens, the protoflexid is narrower and the hypoflexid is always transverse and deep, reaching more than 2/3 of the total width. In addition, the p3 of *S. praecapensis* has in most specimens a rather straight lingual margin, while it is rounded on the specimens of Ahl al Oughlam. The upper dentition of this species was described by MacInnes (1953) and Erbajeva and Angermann (1983). The pattern of P2 is similar to that of the Moroccan species in having a deep paraflexus and preserving hypoflexus and mesoflexus. On the contrary, its upper molariform teeth are different in being less compressed anteroposteriorly, and the shorter hypoflexus (not reaching the half width), with much less folded enamel, in particular along the posterior wall. The other species *S. tchadensis* is also similar to *Afrolagus pomeli* n.g. n. sp. in the size of its teeth and in the proportions of diastema versus alveolar length. However, this species has a narrower incisor foramen, narrower choanae, much less wrinkled enamel along the hypoflexus of upper molariform teeth, short hypoflexid (about 1/2 of the total width), open protoflexid, occasionally present anteroflexid and straight lingual edge on the p3.

Concerning *Lepus*, according to López-Martínez (2008) and Ge et al. (2013) it is most likely emerged in North America around 2.5 Ma, while for Averianov and Tesakov (1997) it is derived from *Trischizolagus* sometime during the late Pliocene-early Pleistocene. In any case, this genus is absent from the European and North African record before the end of early Pleistocene, ca. 1.2 Ma (Aouraghe et al. 2012; Pelletier et al. 2015; Pelletier 2018).

Oryctolagus is well known in southwestern Europe since the early-late Pliocene transition, ca. 3.6 Ma (López-Martínez 1989, 2008; De Marfà and Mein 2007; De Marfà 2009; Flynn et al. 2013; Pelletier et al. 2015; Pelletier 2018). This genus is apparently originated in the Iberian

Peninsula and extended to Northwest Africa during the Pleistocene (López-Martínez 2008; De Marfà 2009; Aouraghe et al. 2012), hence the comparisons developed here.

The genus *Oryctolagus* is represented by one extant species, *O. cuniculus* (Linnaeus, 1758), and five recognized fossil species: *O. laynensis* López-Martínez, 1977, *O. giberti* De Marfà, 2008, *O. lacosti* (Pomel, 1853), *O. burgi* Nocchi and Sala, 1998 and *O. valdarnensis* (Weithofer, 1889). Recently, Pelletier (2021) provided a complete overview of tooth morphology, and spatial and temporal extent of all species included in this genus.

The pattern of the p3 of *Afrolagus pomeli* n.g., n.sp. is different from those of all the species mentioned above, i.e, in having a hypoflexid which does not reach the lingual edge as in all species of *Oryctolagus* and *Lepus*, but only 2/3 of its width, thus leaving a wide band of connection between the trigonid and the talonid. Likewise, in all extant and fossil species of *Oryctolagus*, the upper molariform teeth have a hypoflexus whose width hardly exceeds half the width of the tooth, and only the anterior edge of the hypoflexus has folded enamel, while the enamel on the posterior edge is smooth or sometimes barely wavy. In all extant and fossil species of *Oryctolagus*, the length of the alveoli p3-m3 is always shorter than the mandibular diastema, while in this species of Ahl al Oughlam, the length of the alveoli is equivalent or even sometimes a little longer than the diastema. Despite these main morphological differences, in the hypothesis that this new genus could have phylogenetic relations with *Oryctolagus*, to be supported in the light of new discoveries, we would like to indicate its resemblances with some species of the last genus.

O. laynensis is the oldest species and is known only in central and southern Spain between 3.5 and 2.5 Ma (López-Martínez 2008). It is smaller than *Afrolagus pomeli* n.g., n. sp. and has the typical p3 pattern of *Oryctolagus* species. In addition, it has shorter hypoflexus in all upper molariforms with lightly folded enamel along the mesial and flat along the distal edges.

O. lacosti is the most common fossil species of the genus known in many late Pliocene and early Pleistocene localities of Iberian Peninsula, southern France and northern Italy. The material of its type locality (Perrier, Auvergne region, France; latest Pliocene, MN 16b) was redescribed by De Marfà and Mein (2007). This species has a hard palate longer than the width of choanae, the mandibular diastema longer than the alveoli of cheek teeth, and the pattern of its cheek teeth displays many differences, such as shallower flexa on P2, shorter hypoflexus and much less folded enamel along its anterior and in particular posterior walls on

P3-M2, p3 with a deep hypoflexid that reaches the lingual border. Despite some characters shared, this species is different from *Afrolagus pomeli* n.g., n. sp.

O. giberti from Cueva Victoria (Murcia, Spain; early Pleistocene) is different in having a deep hypoflexid, wider anteroflexid and protoflexid, and occasional presence of the paraflexid on p3, and short hypoflexus and protoflexus on P2. In this species the upper molariform teeth have hypoflexus shorter and with enamel folding only on their anterior wall.

O. burgi was described from Valdemino Cave (Savona, Italy). On its p3 the anteroflexid is deep and narrow, the buccal anteroconid protrudes anteriorly and the lingual anteroconid is triangular in shape, the protoflexid has a L-shaped open angle, often over 90°, the hypoflexid is very deep and consequently the trigonid-talonid connection is narrow. This species is known from a few middle Pleistocene localities in Italy, and is considered endemic to the Ligur region (Nocchi and Sala 1997; Angelone et al. 2020).

O. valdarnensis is a common species of late Villanyian and early Biharian (early Pleistocene) localities in central and southeastern Italy (Angelone and Rook 2012; Angelone et al. 2020). It was synonymized by Viret (1954) with *O. lacosti*, but Angelone and Rook (2012) showed that it is considerably larger than any other species of the genus and its p3 has a straight anteroflexid, and a paraflexid filled with cement.

Discussion

As shown above, the faunal assemblage of Ahl alOughlam includes two species of leporids, slightly different in size, but clearly differentiated by several cranial and dental features.

Although *Trischizolagus meridionalis* n. sp. displays dental features already known in many other species of Palaeolaginae (sensu Dice 1929), the characters of the p3 of *Afrolagus pomeli* n.g., n. sp., in particular the shape of its hypoflexid, are unusual for the leporids of the Old World. The origin and the shape of the hypoflexid in *Lepus-Oryctolagus*-type of leporids is one of the key criteria for the suprageneric subdivision of the family Leporidae. Remember that fossil leporid systematics are based mainly on the pattern of p3, and in particular on the form of the hypoflexid and presence or absence of the mesoflexid/mesofossetid.

Dice (1929: 340) wrote: “On the basis of the character of the enamel folding of p3, I propose to divide the family Leporidae into three subfamilies, each of which is presumed to indicate an independent phylogenetic series”. He distinguished three subfamilies: the Palaeolaginae

with the type genus *Palaeolagus* Leidy, 1856; Archaeolaginae with the type genus *Archaeolagus* Dice, 1917; Leporinae with the type genus *Lepus* Linnaeus, 1768. Hibbard (1963: 6-7) explained the origin of the p3 hypoflexid in the *Lepus-Oryctolagus* type of leporids that Dice classified in the subfamily Leporinae as follows: “The posterior external reentrant fold observed in some specimens of *Nekrolagus*, *Pratilepus* and those of the Recent rabbits, *Brachylagus*, *Nesolagus*, *Sylvilagus*, *Caprolagus*, *Oryctolagus* and *Lepus* is the result of the union of the posterior external reentrant angle with a posterior internal enamel lake”. In other terms, according to this hypothesis, the deep hypoflexid of many leporids mentioned here above is formed by the fusion of the hypoflexid and the mesofossetid, and consequently the loss of the dentine bridge connecting the trigonid to the talonid. The distal hook of the trigonid, which narrows the hypoflexid of p3 in both *Lepus* and *Oryctolagus* species would be the remainder of this bridge and of its location. The p3 pattern of *Afrolagus pomeli* n.g. n.sp., reinforces the Hibbard’s hypothesis in having a “posterior external reentrant fold” composed of the connection of the hypoflexid and mesofossetid, and a strong distal hook of the trigonid in the place of the dentine bridge. However, this new taxon has a p3 pattern different from that of *Lepus*, *Oryctolagus* and many other leporids included in the subfamily Leporinae in having a wide lingual connection between the trigonid and talonid. Given the diversity of leporids having p3 with “posterior external reentrant fold” as in *Lepus* and *Oryctolagus*, and their past and present spatial distribution in Eurasia, Africa and North America, the fusion of hypoflexid and mesofossetid could occur multiple times, independently in the history of Leporidae, and would in fact be a trait of convergence. In this debate, *Afrolagus* of Ahl al Oughlam seems to confirm the hypothesis of Hibbard (1963), but does not allow us to affirm that it could be an intermediate step between the *Alilepus* and *Lepus-Oryctolagus* p3 patterns. The increase of the number of re-entrant folds (flexa and flexids) and their crenulation favorize the grinding function and increase the capacity of teeth to degrade more abrasive and fibrous plants (von Koenigswald et al. 2010). In this aspect, *Afrolagus* should have, with the numerous flexids of the lower cheek teeth and hypoflexus with strongly wrinkled enamel of the upper cheek teeth, a somewhat more efficient mastication than *Trischizolagus*.

Fig. 14. Postcranials-Approximately HERE.

Postcranial bones of Leporidae from Ahl al Oughlam

Lagomorph postcranials are abundant at Ahl al Oughlam, and all main bones are represented by several specimens (measurements: **Table 5**/suppl.data). Prolagids were certainly present among them, but were left with limb bones of micromammals, and not systematically sorted. All other lagomorph limb bones indicate animals of similar size but proved impossible to sort into two distinct morphs. Whether this means that the two large species were similar in postcranial morphology, or that one species is too poorly represented by postcranials to be identified among them is unknown. The latter alternative might look less likely, but it should be remembered that differential representation of cranial or dental vs. postcranial material is common at Ahl al Oughlam, and can be explained by taphonomic reasons. For instance, there is abundant postcranial material of the giraffid *Sivatherium*, but few dental remains, whereas there are many equid, primate and suid teeth, but very few long bones of these groups (Geraads 2006); so, it is conceivable that one of the leporids, perhaps because of a different mode of life, is represented by too few specimens to be identified. Because the site is no longer accessible to further research, it is highly unlikely that new material will ever come to light to solve this issue. Thus, we provisionally describe the Ahl al Oughlam postcranials as a whole.

Comparisons were made with modern skeletons of *Oryctolagus cuniculus* (N=4), *Lepus capensis* (N=4) and *L. europaeus* (N=3). In addition to new features, we tried to use the characters described by Callou (1997) on modern *Lepus* and *Oryctolagus*, by Averianov (1995) on *Trischizolagus dumitrescuae*, by Fostowicz-Frelik 2007) on *Hypolagus beremendensis*, and by Winkler et al. (2016) on *Serengetilagus praecapensis* (but the size range at Laetolil is too large for a single species). Still, the total of clear morphological differences between the various genera remains low.

Table 5. Approximately HERE.

Scapula (**Fig. 14a**): There are eight incomplete specimens, none of which preserves the acromion. The glenoid cavity has a distinctly trefoil outline, even better indicated than in *Oryctolagus*, and well distinct from the more oval outline of *Lepus*. The coracoid process is rather short, located much farther from the glenoid cavity than in *Lepus* and *T. dumitrescuae*, and even more than in *Oryctolagus* and, presumably, *Serengetilagus* (Winkler et al. 2016

write that it resembles *Oryctolagus*). The area for the gleno-humeral ligament does not form a flat platform, unlike in *Lepus* (Callou 1997).

Humerus (Fig. 14b): Eight of 33 specimens are relatively complete. The bone is less slender than in *Lepus*, but larger than in *Oryctolagus*. The bicipital groove has converging, indistinct borders, unlike *Lepus*, but as in *Oryctolagus*, and presumably also as in *Serengetilagus* (Winkler et al. 2016) and *T. dumitreascuae* (Averianov 1995, fig. 5E). The deltoid crest is much longer than in *Lepus*; it resembles instead those of *Oryctolagus* and *Trischizolagus* (Averianov 1995, fig.5C-D). Differences at the distal epiphysis are not obvious. The epicondylus medialis is never as short as it may be in *Lepus*.

Radius: We could find no clear difference on this rarely complete bone, except regarding its size. We found that the shape of the distal articulation (square vs. rectangular) strongly varies within *Lepus*; however, the Ahl al Oughlam radii are certainly unlike *L. capensis*, which has a rectangular distal articulation in distal view.

Ulna (Fig. 14c): Of 22 specimens, three complete ones show that the diameters of the diaphysis decrease only slightly towards the distal end, as in *Oryctolagus*, but in sharp contrast to *Lepus*. Complete bones have not been described in the other genera. The two crests at the top of the olecranon process are of unequal size, as in *Oryctolagus* (Callou 1997).

Pelvis (Fig. 14d): Although none of the 5 specimens preserves it in its entirety, it is clear that the foramen obturatum is smaller than in *Oryctolagus*; only the partial pelvis of *Trischizolagus*, if correctly reconstructed by Averianov (1995) is similar in this regard. There is no evidence that its outline differed from those of *Oryctolagus* and *Lepus* but that of *Trischizolagus* is unique in being rather rectangular instead of oval, with straight cranial and medial borders (Averianov 1995, fig. 6A). AaO-2494 differs from the other specimens in that the cranial branch of the pubis is more transversely directed and the acetabular notch closed.

Femur (Fig. 14e-g): Six of 19 specimens are almost complete. In proximal (upper) view, the head of *Lepus* is directed medially, so that it usually hides part of the trochanter minor; it is slightly more cranially directed in *Oryctolagus*, so that the trochanter minor is fully visible; in all eight specimens from Ahl al Oughlam in which this character can be observed, the head is directed cranio-medially rather than medially, and its orientation is thus sharply different.

Unfortunately, this important feature has not been described or illustrated in other genera. The notch between the head and greater trochanter is latero-medially short, as in *Oryctolagus*. On the caudal face, the wide, flat area between the trochanter minor and trochanter tertius, distal

to the trochanterin fossa, usually extends farther distally than in either *Lepus*, *Oryctolagus* or *Hypolagus*. It is limited distally by a rough area that provides insertion for the m. quadratus femoris.

Tibia: there are few clear discriminant features on this bone (34 specimens, 12 of which are virtually complete). All bones resemble *Oryctolagus* more than *Lepus* in their anteroposteriorly compressed distal diaphysis with at least a hint of anterior distal depression, but the fusion with the fibula occurs more proximally than in *Oryctolagus*. The largest bone lacks the proximal epiphysis but was about 12% longer than the shortest ones, a difference that might reflect (but does not imply) species distinction.

Astragalus (Fig. 14h): There are 15 specimens, many of them well-preserved; strangely, the variation in size is greater than in the long bones (medial length 11 to 14 mm). In proximal view, the trochlea is broader relative to its anteroposterior diameter and the lips are less unequal than in *Lepus*. The medial side of the trochlea is somewhat concave, whereas it is flat in *Lepus*. In these two characters, they resemble *Oryctolagus*. In addition, and although there is some variation in this regard, the Ahl al Oughlam bones differ from both these genera, from *Hypolagus*, and from *T. dumitrescuae* in that, in front view, the lateral outline of the column gradually passes to the lateral border of the trochlea, instead of being distinctly L-shaped.

Calcaneus: this bone is also rather variable in size (length 22.5 to 27.2 mm) but no significant differences can be observed.

Metapodials: The metacarpals are less straight than in *Lepus*, and more like *Oryctolagus*; relative to the metatarsals, they are not as short as in *Lepus*.

In the proportions of its limb bones, *Lepus* mainly differs from *Oryctolagus* in that its radius is longer than the humerus, and its posterior limb much longer than the anterior one, including MtIII much longer than McIII. Figure 15 clearly shows that the Ahl al Oughlam form, although larger, is similar to *Oryctolagus* in these proportions, with a radius distinctly shorter than the humerus, and a much less lengthened tibia. The few complete bones of *Oryctolagus giberti* De Marfà, 2008, from the late early Pleistocene of Cueva Victoria in Spain, are very similar in size and proportions to those from Ahl al Oughlam.

The Ahl al Oughlam postcranials sharply differ from those of *Lepus*, less so than those of *Oryctolagus cuniculus*, but are certainly distinct from both. Unfortunately, very few comparisons with other taxa can be made.

Conclusions

The occurrence of European rodents and lagomorphs in latest Miocene and Pliocene deposits in North Africa is used as a key argument to evidence faunal exchanges between SW Europe and NW Africa during the Messinian (Jaeger et al. 1977; Geraads 1998; Agusti et al. 2006; Gibert et al. 2013; Garcia-Alix et al. 2016). The available record suggests that the oldest *Prolagus* occurs in north-western Africa during the Late Miocene (Dupré et al. 2022). In space, its North African dispersal remains limited to the Maghreb, i.e., from Morocco to Tunisia. The *Prolagus* remains were found at Afoud 1, 2, 12-1, 12-2 and Aghouri in Morocco (Brandy and Jaeger 1980; Benammi et al. 1995; Dupré et al. 2022), Argoub Kemellal 1 and 2 in Algeria (Coiffait et al. 1985; Coiffait-Martin 1991), and La Voie Ferrée in Tunisia (Robinson et al. 1982) (Fig. 5). Among these localities Afoud localities and Argoub Kemellal 1 are apparently the oldest, dating the arrival of this genus in the Maghreb to 6.2 Ma. This date implies that mammalian exchanges occurred between the Iberian Peninsula and North Africa before the Messinian Salinity Crisis (5.59-5.96 Ma; Krijgsman et al., 1999). Aghouri and Argoub Kemellal 2 are the youngest localities with an age of about 3 Ma, as calibrated by magnetostratigraphy (Benammi et al. 1996; Gibert et al. 2013). In all these localities, the record is limited to a few dental specimens, and these were referred to as *Prolagus* cf. *michauxi* or simply *Prolagus* sp. The occurrence of *Prolagus* at Ahl al Oughlam is not therefore unexpected, but this locality is apparently the youngest to yield the remains of this genus, and confirms its survival in late Pliocene-early Pleistocene. Jaeger (1975) mentions, without description, *Prolagus* from two sites of similar age (Geraads 1995), Bulla Regia in Tunisia and Irhoud Ocre in Morocco, but not in younger sites. We may therefore suspect that the genus went extinct in north-western Africa by the earliest Pleistocene.

One of the two leporids of Ahl al Oughlam, namely *Trischizolagus meridionalis* n. sp., is certainly of Eurasian origin. This genus is known in Europe since the late Miocene, it shows a spatial extension in most parts of Europe and western Asia (Fig. 5), perhaps in China, and it became extinct in early late Pliocene at about 3.5 Ma (Čermák et al. 2019; Angelone et al. 2021). The only species previously known from North Africa was *T. raynali* from Grotte des Rhinoceros in Morocco dated between 0.7–0.4 Ma (Raynal et al. 2004). *T. meridionalis* n. sp. demonstrates that this genus probably appeared in North Africa before the Plio-Pleistocene

boundary. However, to confirm the date of entry of this genus into this region, new records are needed.

The evolutionary trend of dental characters in the genus *Trischizolagus* are identified as the progressive loss of mesoflexid and paraflexid, the lengthening of the labial anteroconid, the larger opening of the protoflexid on the p3, the development of the flexa on P2, and the more stretched hypoflexus on the upper molariform teeth (Averianov 1995, 1999; Čermák and Wagner 2013; Čermák et al. 2019). Taking into account these criteria, it is not conceivable that *T. raynali* is derived from *T. meridionalis* n. sp. because the latter has some more derived characters than *T. raynali*. This could mean that there would be a second arrival of *Trischizolagus* in the Maghreb. But remember that this genus disappears in the European register much earlier, shortly after the early/late Pliocene boundary.

A few paleoecological conclusions can also be drawn. A well-known character that is traditionally regarded as related to the cursorial and jumping abilities of rabbits and hares is the width of choanae and incisor foramina. In the extant species *Oryctolagus cuniculus* these apertures are narrow while in the species of *Lepus* they are rather wide. However, some species referred to *Oryctolagus* have larger apertures, such as *O. lacosti* and in some extent *O. laynensis* (De Marfà 2009). Long ago, Pomel (1853) and later Viret (1954) noted that *O. lacosti* from late Pliocene localities of France has larger choanae compared to *O. cuniculus*, and consequently they considered *O. lacosti* an intermediate form between the rabbits and hares. In a more detailed morphological and biometrical analysis of the palate, diastema and dentition, De Marfà (2009) confirmed the similarities of *O. lacosti* from Perrier and Saint-Vallier with *Lepus*, despite its great resemblance of dentition and many other characters with *O. cuniculus*, hence its attribution to this genus. Both leporids from Ahl al Oughlam have large incisor foramina and choanae, *Afrolagus pomeli* n. g., n. sp. having the larger apertures. These characters suggest improved breathing capacities, usually regarded as correlated with fast-running, for both leporids of Ahl al Oughlam, especially *Afrolagus*. However, the proportions of the postcranials of the Ahl al Oughlam leporids are definitely closer to those of *Oryctolagus* than to those of *Lepus*, thus contradicting the cranial adaptations, and one might wonder whether the breadth of the choanae is as a good proxy for running abilities as is usually assumed.

Regarding their diets, because the increase of enamel surface is indicative of a change in dietary habits towards food that includes more abrasive and fibrous plants, we can tentatively

surmise that *Afrolagus pomeli* n.g., n.sp., which has a highly folded enamel along the walls of hypoflexus on the upper molariform teeth, fed upon tougher plants than *Trischizolagus*. In any case, as shown by their abundance at Ahl al Oughlam, the lagomorphs were well adapted to the open-country environment that prevailed there.

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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.** Tooth terminology used in the present study to describe 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 parts covered with cement are dotted. Not to scale.
- Fig. 2.** Upper cheek teeth of *Prolagus migrans* n. sp. from Ahl al Oughlam, Morocco. **a** left P2 (AaO-2267). **b** left P2 (AaO-2265). **c** left P2 (AaO-2266). **d** right P2 (AaO-2268). **e** right P2 (AaO-2270). **f** right P2 (AaO-2269). **g** left P3 (AaO-2271). **h** left P3 (AaO-2272). **i** right P3 (AaO-2274). **j** right P3 (AaO-2279). **k** left P4 (AaO-2298). **l** left P4 (AaO-2299). **m** left P4 (AaO-2318). **n** left P4 (AaO-2296). **o** left M1 (AaO-2328). **p** left M2 (AaO-2346). All figures are in occlusal view. Blackened lines represent enamel; white, dentine; dotted areas, cement infill. Scale bar 1 mm.
- Fig. 3.** Mandible fragments of *Prolagus migrans* n. sp. from Ahl al Oughlam, Morocco. **a-a'** left hemimandible with p3-m3 (AaO-666, Holotype) in buccal and lingual views. **b** left hemimandible with p3-m1 (AaO-668) in buccal view. **c** right hemimandible with p3-m3 (AaO-667) in buccal view. Scale bar 5 mm.
- Fig. 4.** Lower cheek teeth of *Prolagus migrans* n. sp. from Ahl al Oughlam, Morocco. **a** right p3-m2 (AaO-666). **b** left p3-m2 (AaO-667, Holotype). **c** left p3-p4 (AaO-669). **d** left p3-m1 (AaO-668). **e** left p3 (AaO-686). **f** left p3 (AaO-683). **g** right p3 (AaO-675). All figures are in occlusal view. Scale bar 1 mm.
- Fig. 5.** European, North African and western Asian Pliocene localities with *Prolagus* and *Trischizolagus*. Localities mentioned in the text (solid symbols) are the following: 1, Ahl al Oughlam, MN 16; 2, Aghouri, MN 16; 3, Aïn Guettara, MN 14; 4, Lac Ichkeul, MN 14; 5, Gorafe 1, MN 14; MN 15; 6, Moreda, MN 16; 7, Caravaca, MN 13/14; 8, Puerto de la Cadena, MN 14; 9, Alcoy, MN 14; 10, Layna, MN 15; 11, Perpignan, MN 15; 12, Sète, MN 15; 13, Borro Strolla, MN 14; 14, Valdarno, MN 17; 15, Beremend 26 and 39, MN 15; 16, Muselievo, MN 15; 17, Dorkovo, MN 14; 18, Ciuperceni, MN 15; 19, Mălușteni, MN 15; 20, Moscovei, MN 15; 21, Tatareshty,

MN 15; 22, Trudomirovka, MN 14; 23, Maritsa, MN 15; 24, Nurnus, MN 14. MN ages are only indicative. Other localities are represented by open symbols.

Fig. 6. Palatal view of cranium remains from Ahl al Oughlam, Morocco. **a** *Trischizolagus meridionalis* n. sp. (AaO-4901). **b** *Afrolagus pomeli* n. g. n. sp. (AaO-5040). Scale bar 10 mm.

Fig. 7. Scatterplot diagrams showing the size relationship of the Ahl al Oughlam leporids with other related genera and species. **a** length of the hard palate (PL) versus the width of choanae (CW) in several species of *Oryctolagus*, *Trischizolagus*, *Serengetilagus* and *Afrolagus* n. g. **b** length of alveoli p3-m3 (AL) versus the length of the diastema (DL) of mandible in several species of the same genera. Data for *Oryctolagus* species from De Marfà (2009), De Marfà and Mein (2007) and our own measurements, for *Serengetilagus* from Erbajeva and Angermann (1983) and López-Martínez et al. (2007), for *Trischizolagus dumitrescuae* from Averianov (1995) and Čermák and Wagner (2013).

Fig. 8. Hemimandibles of Leporidae from Ahl al Oughlam, Morocco. **a-a'** left hemimandible of *Trischizolagus meridionalis* n. sp. in lateral and medial views (holotype). **b-b'** left hemimandible of *Afrolagus pomeli* n. g. n. sp. in lateral and medial views (holotype). Scale bar 10 mm.

Fig. 9. *Trischizolagus meridionalis* n. sp. from Ahl al Oughlam, Morocco. Upper teeth in occlusal view. **a** left upper incisor. **b** right upper incisor. **c** right upper incisor. **d** left upper incisor. **e** right P2. **f** right P2. **g** right P2. **h** right P2. **i** right P2. **j** right P2. **k** right P2. **l** right P2. **m** right P4. **n** right P4. **o** left P2-P4. **p** right M1. **q** right M2. **r** left P4-M2. Catalogue numbers are indicated on the illustrations. Scale bar 1 mm.

Fig. 10. *Trischizolagus meridionalis* n. sp. from Ahl al Oughlam, Morocco. Lower teeth in occlusal view. **a** left p3-m2 and alveolous of m3 (holotype). **b** left p3-m2. **c** right p3-m3. **d** right p3-m2. **e** left p3-m2. **f** left p3 with *Alilepus* pattern. **g-h** left p3s with *Necrolagus* pattern. **i** left p3 with *Hypolagus* pattern. Catalogue numbers are indicated on the illustrations.

Fig. 11. Scatter diagram comparing the length and width of p3s *Trischizolagus meridionalis* n. sp. from Ahl al Oughlam 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. raynali* from Geraads (1994), for *T. crusafonti* our own measurements.

Fig. 12. *Afrolagus pomeli* n. g. n. sp. from Ahl al Oughlam, Morocco. Upper teeth in occlusal view. **a** left P2-M2 and alveolus of M3. **b** right P2-P4. **c** right P2-P4. **d** right P2. **e** left P2. **f** left P2. **g** right ?M1. **h** right ?M1. **i** right upper incisor. Catalogue numbers are indicated on the illustrations. Scale bar 2 mm.

Fig. 13. *Afrolagus pomeli* n. g. n. sp. from Ahl al Oughlam, Morocco. Lower teeth in occlusal view. **a** left p3-m3 (holotype). **b** left p3-m1. **c** left p3-m2. **d** left p3. **e** right p3. **f** left p3. **g** right p3. **h** right p3. **i** right p3. Catalogue numbers are indicated on the illustrations. Scale bar 2 mm.

Fig. 14. Lagomorph postcranials from Ahl al Oughlam, Morocco. **a** scapula AaO-2488, proximal view. **b** humerus AaO-1930, anterior view. **c** ulna AaO-1898, anterior view. **d** pelvis AaO-2492, ventral view. **e** femur AaO-1957, anterior view. **f** same specimen, posterior view. **g** same specimen, proximal view (the arrow points to the fully visible trochanter minor). **h** astragalus AaO-2726, anterior view (the arrow points to the rounded lateral outline). Scale bar 25 mm for Figs g-h, 50 mm for all others.

Fig. 15. Length of the main long bones in some lagomorphs: Ahl al Oughlam (mean values), *Oryctolagus giberti* (mean values), *Trischizolagus dumitrescuae* (individual specimens), *Oryctolagus cuniculus* (mean values from Holocene sites [Callou 2003] and individual specimens), *Lepus capensis* and *L. europaeus* (individual specimens).