

Red Rock Hares (Leporidae, Lagomorpha) past and present in southern Africa, and a new species of *Pronolagus* from the early Pleistocene of Angola

Sevket Sen & Martin Pickford

Sorbonne Université, CR2P-UMR 7202 CNRS-MNHN, 8 rue Buffon, 75005 Paris, France.
(sevket.sen@mnhn.fr) (martin.pickford@mnhn.fr)

Abstract :- Fossil lagomorphs are poorly documented in southern Africa, although the region is inhabited at present by at least seven species of Leporidae : two species of *Lepus*, one species of *Bunolagus* and four species of *Pronolagus*. Astonishingly, the fossil record of Leporidae in southern Africa is only known by brief mentions in faunal lists, nothing being reported with reliable descriptions and illustrations. The new fossil material from Plio-Pleistocene deposits of southwestern Angola is the first contribution to the knowledge of the past history of Leporidae in this region. This material comes from the breccia deposits of the Humpata Plateau in the southwest of Angola and tufa deposits in Kaokoland, Namibia. In order to compare the fossils from Angola, it was necessary, first of all, to review skeletal and dental morphology of the four extant species of this genus. The fossils from Angola and Namibia belong to a small species of *Pronolagus*, with less specialized cranial and dental features, most comparable to the living species *P. rupestris* that inhabits two separate regions, southeastern Africa from southern Kenya to northern Zimbabwe, and northwestern South Africa. It is attributed to a new species of the genus *Pronolagus*. The presence of this new species in SW Angola enlarges the range of the genus beyond its present day distribution.

Key words :- Lagomorpha, Leporidae, *Pronolagus*, Southern Africa, Angola, Plio-Pleistocene

To cite this paper :- Sen, S. & Pickford, M. 2022. Red Rock Hares (Leporidae, Lagomorpha) past and present in southern Africa, and a new species of *Pronolagus* from the early Pleistocene of Angola. *Communications of the Geological Survey of Namibia*, **24**, 67-97.

Introduction

The initial aim of the present study was to describe leporid fossils from two Angolan Plio-Pleistocene localities (Figs. 1, 2). After preliminary investigations, it soon became apparent that these fossils belong to the genus *Pronolagus* Lyon, 1904. According to recent literature (Hoffmann & Smith, 2005; Happold, 2013, 2018; Matthee *et al.* 2016), this genus includes four extant species, all living in southern Africa: *P. crassicaudatus* (I. Geoffroy St Hilaire, 1832), its type species; *P. rupestris* (Smith, 1835); *P. randensis* Jameson, 1907; and *P. saundersiae* Hewitt, 1927. The status of these species as well as over twenty subspecies that have been described is far from reaching consensus.

These species are known colloquially as Red Rock Hares, and they have a patchy distribution in isolated territories of southern and southeastern Africa, within a large region from South Africa to Kenya on the one hand and to south-western Angola on the other (Fig. 3). Matthee *et al.* (2016) explain this patchy distribution as probably due to their restriction

to areas of rocky habitat, and their absence in plains and forests.

These extant species are mainly defined by their external features (fur colour, ears, hindlimb length, tail colour and length...) and by molecular studies. Their skeletal and dental morphology is poorly documented in the available literature, or even totally lacking for some species. The present knowledge on their skeletal anatomy and dentition does not allow comparison of fossil forms with the extant species. Consequently, it was first necessary to locate specimens of extant species in museum collections, to study the skull and dentition of some key specimens (particularly the type material of each species) to throw light on these characters in order to be able to compare the fossil material from Angola with the extant species.

Morphometric and molecular analyses to delimit species characters and to attribute local populations to one or other of the species of *Pronolagus* are often divergent with the systematics based on external features,

indicating local disparity and adaptation under different ecological and climatic conditions (Happold, 2013, 2018). Dental and skeletal characters, at present not documented, could help to define better the extant species and to identify the specimens in zoological collections on a more solid basis. For instance, in the available literature it is hard to find an informative illustration of the skull and dentition of any species of this genus. As was rightly noted by López Martínez (2008), the systematics of fossil lagomorphs are mainly based on the characters of the dentition, and in particular on the third lower premolar (p/3). In such a context it is legitimate to ask what needs to be done to compare the fossils that clearly belong to a genus represented by several extant species that are insufficiently documented in terms of their cranial and postcranial anatomy, even less for their dentitions, all of which are essential for comparisons with fossils? This is the current state of our knowledge about the extant species of *Pronolagus*. Therefore, we first had to look in the collections for osteological remains of the extant species, we illustrate their skulls and dentitions, and provide descriptions of the main characters of each extant species, in order to obtain reliable data about them for comparison with the fossil material.

In the fossil record, the genus *Pronolagus* is mentioned from a dozen localities in southern Africa, without any description or illustration (see below). To express the state of the art, Winkler & Avery (2010, 314) noted that "*None of the fossil Pronolagus material has been described*". In fact, Jameson (1909) erected a new species, *Ronolagus* (sic) *intermedius*, based on a subfossil skull from a cave deposit, probably Holocene, in the lime quarry at Godwan River, on the Delagoa-Pretoria railway line (South Africa). According to Jameson (1909), this specimen is intermediate in size between *P. crassicaudatus* and "*P. ruddi*", which is a junior synonym of *P. crassicaudatus* (see Meester *et al.* 1986; Hoffmann & Smith, 2005; Happold, 2013), it has a broad muzzle, a frontal profile that is more convex than in "*P. ruddi*", the angle between the postorbital wings and the brain case is narrower, the palatal foramina broader in the middle, the bullae large, the main upper incisor deeply grooved, and the upper cheek teeth with crenulated enamel along the hypoflexus. All these characters accord with *P. crassicaudatus*. Jameson (1909) did not

publish any illustration, but a low resolution photograph of this specimen is available on the web page of the Transvaal Museum, Pretoria (<http://sapalaeo.com/dnmnh-archive>), and is labelled as *Pronolagus* sp. Taking into account these observations, and the poor state of preservation of the Godwan River skull (badly damaged and still partly covered in matrix), its systematic status cannot be securely determined. In addition, the above mentioned characters cannot be observed on the available illustration, and thus no reliable comparison can be made with the fossils from Angola.

In subsequent studies on the genus *Pronolagus*, this species has never been mentioned, as though the zoologists and palaeontologists did not want to see this problematic issue and thus avoid having to discuss its status (see in particular Allen, 1939; Robinson & Dippenaar, 1983; Meester *et al.* 1986; Duthie & Robinson, 1990; Collins, 2005; Happold, 2013; Smith *et al.* 2018). More than that, Winkler & Avery (2010, p. 312) point out that "*No extinct species of Pronolagus have been recognized*". According to the International Code of Zoological Nomenclature (1999, Art. 23.9.2), the species *P. intermedius* should be considered a *nomen oblitum*. The following description of the Angolan *Pronolagus* specimens is the first academic report on the fossil occurrence of this genus.

The fossiliferous karst infillings of the Humpata Plateau, southwestern Angola, have been known to science since the surveys of Faber (1926) and Beetz (1933) but the first informative descriptions of the breccia deposits and fossils were published in the 1950's (Dart, 1950; Mouta, 1950, 1954; Arambourg & Mouta, 1952). Most of these early palaeontological studies focussed on the fossil papionine primates, and follow-up studies were undertaken on the same group by Minkoff (1972), Welbourne (1976), Delson & Dean (1992), Jablonski (1994) and Gilbert *et al.* (2009). The presence of other fossil mammals has been summarily mentioned by a number of authors (Antunes, 1965; Amaral, 1973; Pickford *et al.* 1990, 1992, 1994) who inferred a late Pliocene to early Pleistocene age for the indurated cave and fissure infillings. There are also subfossil vertebrate remains associated with lithic instruments in some caves of the region (França, 1964; Matos *et al.* 2021).

The aim of this paper is to describe and interpret the fossil lagomorphs collected by the

Angola Palaeontology Expedition in 1990 from Tchiua (pink breccia) and Cangalongue in

comparison with the extant species of *Pronolagus*.

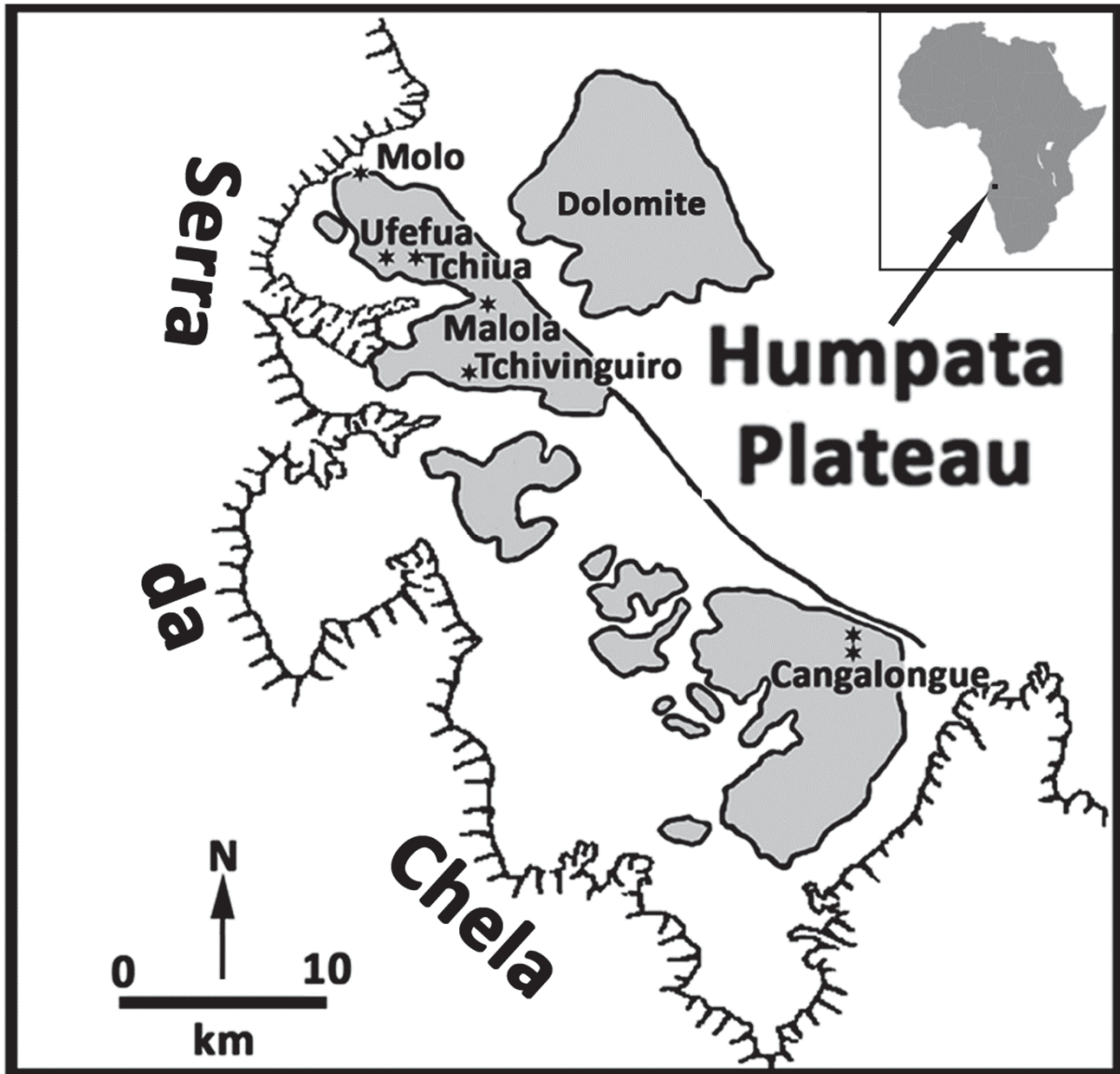


Figure 1. Location of the Humpata Plateau, southwestern Angola. The main map shows the extent of the Chela Dolomite and the positions of the fossiliferous Plio-Pleistocene karst breccias (See Table 1).

Geological and taphonomic contexts of the Humpata breccias

The karstic infillings of the Humpata Plateau are associated with the Cambro-Silurian Chela Dolomites which overlie Pre-Cambrian granites and Cambro-Silurian Sandstones. There is a doleritic sill between the sandstone and the dolomite, and the dolomite is overlain by Pleistocene to Recent deposits associated with the drainage lines and shallow depressions in the surface of the plateau (Faber, 1926; Beetz, 1933; Vale *et al.* 1968; Amaral, 1973; Mason, 1976). The fossils are preserved in sediments

that accumulated in caves and fissures eroded into the dolomite.

Klemme (1955) discussed the speleothem limestones of the region which were mined for preparing quick lime. The infillings of the caves and fissures comprise four main rock types – (A) speleothems, (B) coarse angular dolomite blocks cemented by speleothems (cavern roof and wall collapse breccias), (C) red sandy breccia and (D) grey calcified guano. The bulk of the fossils is

associated with the pink and grey breccias, but some well-preserved specimens were collected from speleothems. The breccia blocks extracted during the mining process were cast aside in dumps, which is where most of the fossils were collected. Fig. 2 indicates that the main fossiliferous breccia occurrences are located close to the steep margins of the presently active hydrographic network that drains the Humpata Plateau. A detailed map of the Tchiua quarries and the breccia dumps left by the miners was published by Pickford *et al.* (1992, fig. 6).

David *et al.* (1999) while analysing fossils from the Humpata Plateau, investigated the geochemical taphonomic processes that

resulted in changes to the mineral phases of bone during fossilisation. The analyses showed the presence of proteins in the fossils despite extensive mineralisation of the organic phases of the bones.

Gilbert *et al.* (2009) postulated that the papionine fossils from the Humpata Plateau were probably the remains of individuals preyed upon by the crowned eagle (*Stephanaoetus coronatus*). This might be so for some of the remains, but the fossils from the grey breccia at Tchiua are unlikely to have been preyed upon by eagles because this deposit is an indurated bat guano that accumulated deep inside a cave (Pickford *et al.* 1994).

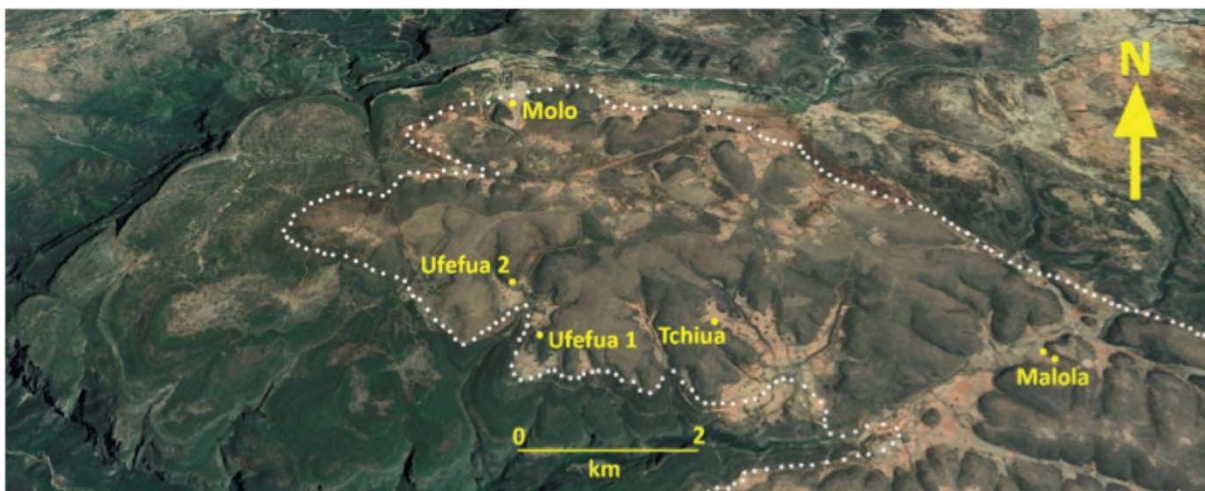


Figure 2. Oblique perspective view of the northwestern extremity of the Humpata Plateau, to show the geomorphological relationship between the fossiliferous karst breccia occurrences (yellow dots), the Chela Dolomite (outlined by the white dotted line) and the hydrographic network that drains the plateau. Image modified from Google Earth.

As concerns the micromammals, the bulk of the fossils appears to represent decomposed owl pellets. The lagomorph fossils from the Tchiua pink breccia, in contrast, are likely to

represent an individual or individuals that lived close to or in the entrance section of the ancient fissures, and died therein.

Table 1. Geographic coordinates of Humpata fossiliferous breccia localities.

Locality	Longitude : Latitude
Leba	13°15'40"E : 15°05'00"S
Tchiua	13°16'10"E : 15°06'40"S
Cangalongue Cave	13°27'45"E : 15°16'45"S
Cangalongue Kiln	13°28'10"E : 15°16'30"S
Cangalongue South	13°27'50"E : 15°17'25"S
Malola	13°18'10"E : 15°07'20"S
Molo	13°15'15"E : 15°04'45"S
Ufefua 1	13°15'15"E : 15°06'50"S
Ufefua 2	13°15'05"E : 15°06'45"S
Tchivinguiro	13°17'50"E : 15°09'50"S

Materials and Methods

The fossils collected by the Angola Palaeontology Expedition during 1989 and 1990 are curated at the Museu Regional da Huila, Lubango. A few breccia blocks were exported on temporary loan for acid preparation treatment and scientific description, and the fossils will be repatriated when the studies are completed. A solution of 7% acetic acid with a calcium triphosphate buffer was used at the palaeontology laboratory at the University of Lyon (P. Mein). Once cleaned and dried the fossils were consolidated with a weak solution

of glyptol, and sorted into taxonomic lots.

The fossils from each locality are kept separate from each other. The lagomorphs, which are the subject of this paper, were collected at Tchiua Pink Breccia and Cangalongue 1 (Table 2). The site abbreviations of these sites are Tch and Can respectively which is followed by a catalogue number and year of collection. Thus Tch 1'89 is specimen 1 collected from Tchiua in 1989. The lagomorphs from the Humpata Plateau are catalogued as follows : Tch 2'90, and Can 2'90.

Table 2. Fauna from the indurated breccias of the Humpata Plateau, southwestern Angola, updated from Pickford *et al.* (1992). **1** - Cangalongue 1, **2** - Cangalongue 2, **3** - Cangalongue 3, **4** - Cangalongue 4, **5** - Malola, **6** - Tchiua (pink breccias), **7** - Tchiua (grey breccias), **8** - Ufefua 2, **9** - Molo.

Taxon /Locality	1	2	3	4	5	6	7	8	9
Amphibia							x		
Chelonia					x				
Lacertidae			x		x				
Ophidea							x		
Macroscelididae	x	x	x	x	x	x			
<i>Crociodura</i>	2	2	x	x	4	x	x	2	x
<i>Uranomys</i>							x		
<i>Acomys</i>							x		
<i>Dasymys</i>	x	x	x	x	x	cf			
<i>Aethomys</i>	x	x		x	x	x	x	x	x
<i>Thallomys</i>				x					
<i>Zelotomys</i>	x	x			x		x		x
<i>Mus</i>	x	2	x	x	2	x	x		x
<i>Pelomys</i>		x			x				
<i>Malacomys</i>							x		
<i>Praomys</i>					x		x		
<i>Grammomys</i>					x				
<i>Dendromus</i>	x	2		x	x	x	x	x	x
<i>Steatomys</i>	x	2		x	x	x	x		
<i>Petromyscus</i>						x			
<i>Tatera</i>		x	x	2		x	x		
<i>Otomys</i>	x		x	x	x	x		x	x
<i>Cryptomys</i>		x		x	x	x			
<i>Graphiurus</i>		x	x		x	x	x		
<i>Hystrix</i>		cf			x				
<i>Rhinolophus</i>			x	x		2	2		
<i>Miniopterus</i>	x				x				
<i>Nycteris</i>							x		
<i>Pronolagus</i>	x					x			
<i>Procavia</i>		x			x				
<i>Gigantohyrax</i>					x				
<i>Theropithecus</i>			x	x		x		x	
Mustelidae		x							
Canidae								x	
<i>Chasmaporthetes</i>					x				
Rhinocerotidae		x							
Equidae									x
<i>Metridiochoerus</i>		x	x						
Hippotragini		x							
<i>Connochaetes</i>		x	x						

Abbreviations

FMNH, Field Museum of Natural History, Chicago, USA
MNHN, Muséum National d'Histoire Naturelle, Paris, France
NHMUK, Natural History Museum, London, United Kingdom
NMB, National Museum of Bloemfontein, South Africa
RMCA, Royal Museum for Central Africa, Tervuren, Belgium

Skulls (or only mandibles if specified) of the extant species that were used in this work to define their main characters and to compare with the *Pronolagus* fossils from Angola are:

- *Pronolagus crassicaudatus* (I. Geoffroy St Hilaire, 1832), Port Natal, South Africa. Type of the species. MNHN, Catalogue number ZM-MO-1992-2005.

- *Pronolagus crassicaudatus ruddi* Thomas & Schwann, 1905, Sibudeni, Zululand, South Africa. Type of the subspecies. NHMUK, London, Catalogue number 1904.5.1.78.

- *Pronolagus crassicaudatus*, mandible, Bushmamla (?), South Africa. Museum of Comparative Zoology - Harvard University, Catalogue number 17915.

- *Pronolagus crassicaudatus* (cranium), South Africa. Ditsong National Museum of Natural History (formerly The Transvaal Museum), Pretoria. Catalogue number AZ/337.

- *Pronolagus rupestris vallicola* Kershaw, 1924, Rift Valley, Kenya. Type of the subspecies. NHMUK, London, Catalogue number 1923.5.1.1.

- *Pronolagus rupestris* (labelled as *P. crassicaudatus*), Mlanje, Malawi. RMCA, Tervuren. Catalogue number R.G. 2624.

- *Pronolagus rupestris*, South Africa. National Museum of Bloemfontein, Catalogue number NMB 4860.

- *Pronolagus randensis*, Johannesburg Observatory, South Africa. Type of the species. NHMUK, London, Catalogue number 1909.3.2.20.

- *Pronolagus randensis*, Kweneng, Botswana. FMNH, Chicago. Catalogue number 38450.

- *Pronolagus randensis*, Transvaal,

Pretoria District, South Africa. Museum of Comparative Zoology - Harvard University, Catalogue number 33983.

- *Pronolagus randensis* (cranium labelled as *P. crassicaudatus*), South Africa. Zoological Institute, Academy of Sciences, Moscow. Catalogue number 289.

The terms anterior and mesial or posterior and distal are used interchangeably. Robinson & Dippenaar (1983) provided skull measurements and Quintana Cardona (2005) measurements of skull and postcranial bones for extant species of *Pronolagus* based on a relatively rich sample. On the fossil material from the Humpata Plateau, we measured bones with digital calipers and teeth with a Mitutoyo measuring equipment on the wear plane of teeth, with a precision of 0.01 mm, and they indicate maximum length and width of the tooth in the sagittal and transverse axes, from the external margin of enamel on the occlusal surface. All measurements are in millimetres (Tables 3-5).

In the illustrations, enamel is represented in black, dentine in white and cement areas in gray. In all illustrations of the dentition, anterior is upward. Dental terminology follows Palacios Arribas & López Martínez (1980) and López Martínez *et al.* (2007), and anatomical terminology is that of Bensley (1948). Upper/lower premolars are abbreviated as P/p, and molars as M/m. The forward slash denotes the occlusal plane, thus « P3/ » with the meristic position above the forward slash represents an upper tooth while « p/3 » represents a lower tooth. All drawings of dentition have been made by the first author with a camera lucida mounted on a Leica M3Z binocular microscope.

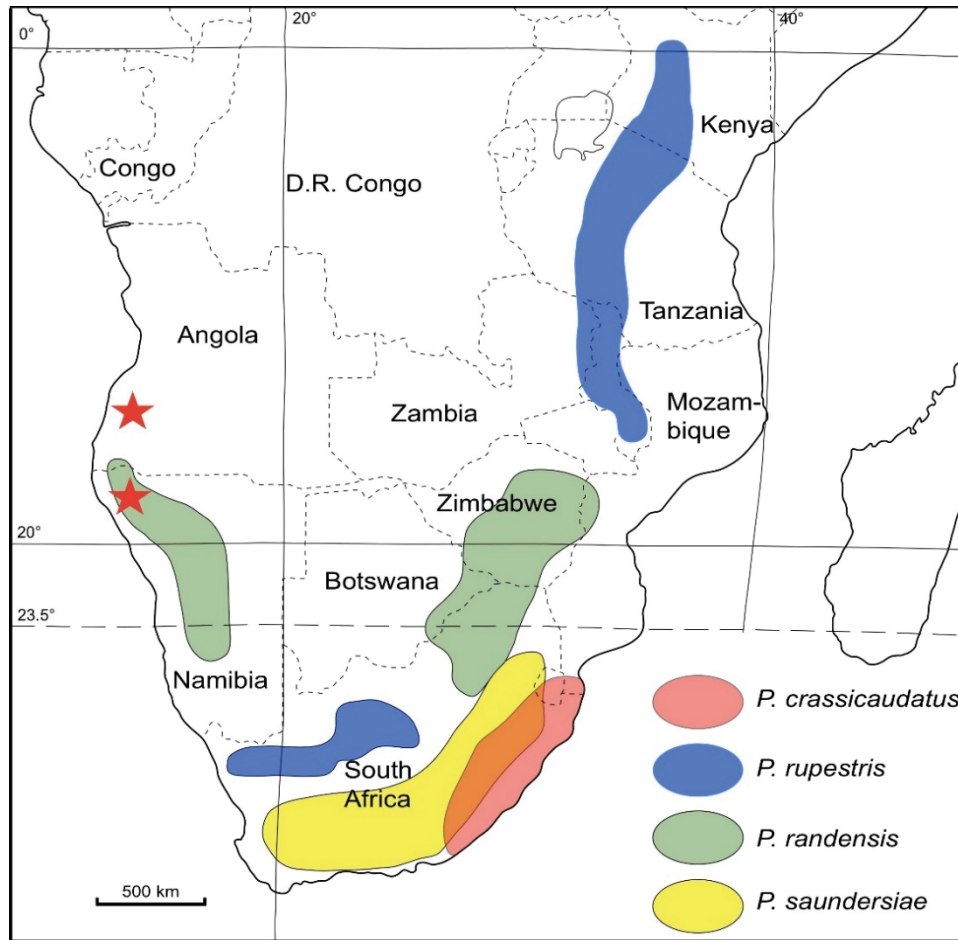


Figure 3. Distribution of the four extant species of the genus *Pronolagus* according to data published by Happold (2013), and the position of the Angolan and Namibian localities, which yielded Plio-Pleistocene fossils of *Pronolagus*, indicated by red stars. Note that the ranges of *P. rupestris* and *P. randensis* are disjunct, separated by several hundred kilometres.

Systematic study

Order Lagomorpha Brandt, 1855

Family Leporidae Fischer, 1817

Subfamily Pentalaginae Gureev, 1948

Genus *Pronolagus* Lyon, 1904

Type species :- *Lepus crassicaudatus* I. Geoffroy St Hilaire, 1832

Other species :- *Pronolagus rupestris* (Smith, 1835); *Pronolagus randensis* Jameson, 1907 and *Pronolagus saundersiae* Hewitt, 1927. For some authors, the latter species is a junior synonym of *P. crassicaudatus* (Roberts, 1951; Robinson, 1982; Robinson & Dippenaar, 1983; Meester *et al.* 1986), and for some others a synonym or subspecies of *P. rupestris* (Meester

et al. 1986; Duthie & Robinson, 1990; Hoffmann & Smith, 2005). Whiteford (1995), Mathee & Robinson (1996) and Robinson & Mathee (2005) recognized it to be a valid species based on molecular studies. In most recent inventories such as that of Happold (2013, 2018), Collins (2005), Mathee *et al.* (2016) and Smith *et al.* (2018) the genus *Pronolagus* includes four species with some twenty subspecies of controversial systematic status.

Emended diagnosis :- Medium- to large-sized leporids, with hindlimbs slightly longer than forelimbs, ears short to medium, fur colour rufous, tail rufous or rufous-black. Lateral profile of cranium well curved with a pronounced dorsal arching; no interparietal bone present in adults; zygomatic arches laterally straight and with antero-external shoulder; breadth of the incisive foramina (palatal vacuity) equivalent or a little less than the length of the hard palate; the width of the mesopterygoid space (choanae) less than the hard palate length, mandibular corpus high,

diastema elongated; the principal upper incisors rather elongate in cross-section, with a single groove not filled with cement; P2/ with two-three flexa, the external one faintly defined when present; upper molariform teeth with deep flexus, tilted at its midway, bordered with thick enamel on its antero-external and postero-internal walls, thin enamel in other parts; M3/ reduced and transversely oval; p/3 with four or five open flexids filled with cement, lower molariform teeth with two lobes connected lingually by a narrow bridge, anterior lobe with an antero-external notch; m/3 bilobed, and its posterior lobe reduced.

Extant species of *Pronolagus* Lyon, 1904

Species *Pronolagus crassicaudatus* (I. Geoffroy St Hilaire, 1832)

Holotype :- Skin and skull of an adult individual, MNHN-CG-1992, preserved in the collections of the Muséum National d’Histoire Naturelle, Paris, France.

Mozambique (Happold 2013, 2018) (Fig. 3).

Type locality :- ‘Port Natal’ (Durban), Cape of Good Hope, South Africa.

Characteristics :- Size generally larger than other species of the genus. The pelage is thick and coarse, the back and sides grayish-rufous with black spots. Ears only as long as the head, rounded at the tip, and lightly furred. Tail short and rounded, entirely covered with long curly hairs varying in colour from brownish red to dark brown (Figs. 4, 5).

Dispersal area :- Southeastern South Africa, Lesotho, Swaziland and extreme south of

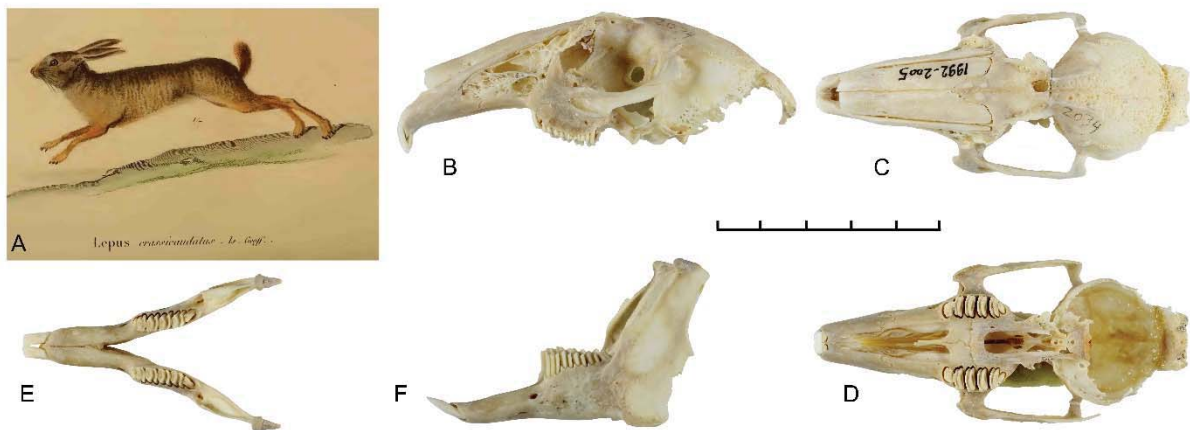


Figure 4. The type specimen of *Pronolagus crassicaudatus* from Port Natal (Durban, South Africa) published by I. Geoffroy St Hilaire (1832) and preserved at the Natural History Museum in Paris, collection code MNHN-ZM-MO-1992. A) illustration of a live specimen in Geoffroy St Hilaire (1832, pl. 9), B) Cranium in left lateral view, C) in dorsal view, D) in ventral view, E) mandible in dorsal view, F) mandible in left lateral view. Scale bar : 5 cm.

On the cranium (length between 85.3-94.8 mm; Happold, 2013), the profile is curved but the frontal part rather flat, the muzzle is narrow and sharp anteriorly, the zygomatic arches are straight and diverge slightly

backwards, the postorbital wings are proportionally smaller than in *P. randensis* and are separated from the brain case by a wide angle. The nasal bone extends backwards beyond the level of the anterior roots of the

zygomatic arches. The suture between the frontal and parietal bones is situated just behind the posterior roots of the zygomatic arches. Ventrally, the incisive foramina are large, evenly broadened to their hinder edge. The hard palate is slightly shorter than the distal breadth of the incisive foramina. The choanae are narrow. The bullae are small, and not surpassed by the paroccipital processes.

Pronolagus crassicaudatus usually has a proportionally longer maxillary premolar tooththrow in relation to frontal length than in *P. randensis* and *P. rupestris* (Robinson & Dippenaar, 1983). Upper principal incisor (I1/) is elongated laterally and flat antero-posteriorly (length between 2.9-3.6 mm; Robinson, 1986), and it has a groove close to its inner margin, not filled with cement. Upper P2/ has three flexa. On the upper molariform teeth the entrance of the hypoflexus is wide and V-shaped, an antero-lingual enamel fold penetrates the anterior loph, hypoflexus is tilted backwards in its narrowing, enamel is thick along its antero-labial and

postero-lingual walls, and thin along other walls, and it is wrinkled along the anterior wall but simply folded along the posterior wall. The degree of plication decreases from P3/ to M2/. The M3/ is reduced and has an ellipsoid occlusal outline (Fig. 5).

In the lower cheek teeth, the enamel is thick on the posterior and labial borders, but thin in other parts. The p/3 has the hypoflexid much less deep than the mesoflexid, which is always open lingually. The proto- and paraflexid are well defined. The anteroflexid is divided into two parts by an enamel fold. All flexids are filled with cement. The p/4-m/2 are bilobed and the two lobes are connected lingually by a thin bar. The anterior lobe is rather diamond shaped and much larger than the posterior one. The anterior lobe has a sharp enamel fold on its antero-labial side filled with cement. The posterior lobe may have a slight depression on its antero-labial side. The m/3 has two rounded lobes, the posterior one being clearly reduced and inclined anteriorly (Fig. 5).

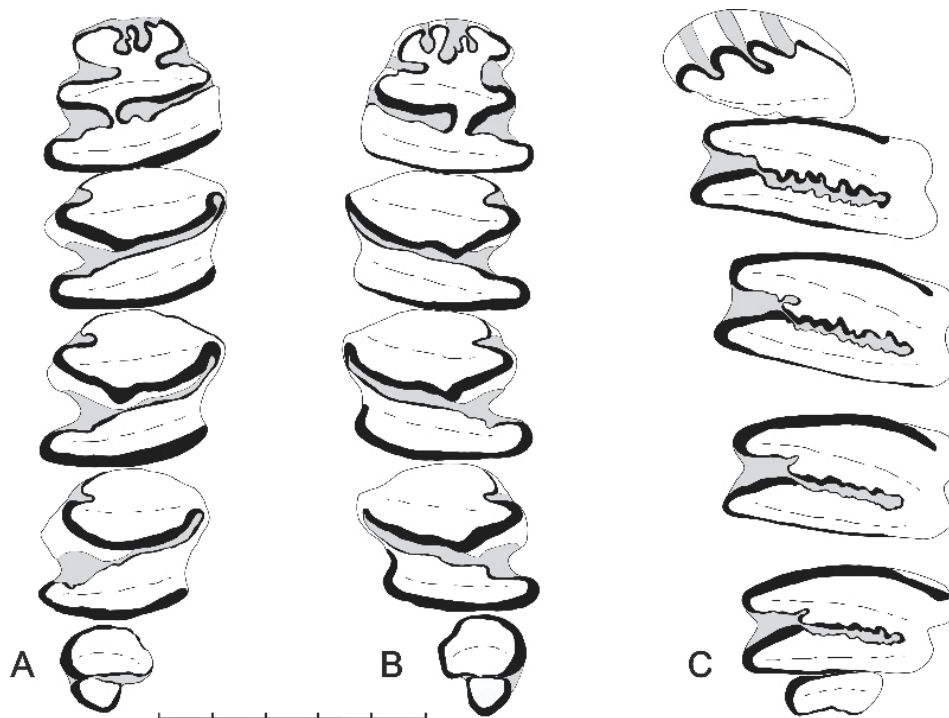


Figure 5. Lower and upper dentition of the type specimen of *Pronolagus crassicaudatus* from Port Natal (Durban, South Africa). Natural History Museum in Paris, collection code MNHN-ZM-MO-1992. A) left p/3-m/3, B) right p/3-m/3, C) left P2/-M3/. Anterior is upward. Scale bar : 5 mm.

Duthie & Robinson (1990) recognized five subspecies of which *P. crassicaudatus ruddi* Thomas & Schwann, 1905, is the best known. It was initially described as a distinct

species and later recognized as a subspecies (see details in Robinson & Dippenaar, 1983; Meester *et al.* 1986; Duthie & Robinson, 1990).

Species *Pronolagus rupestris* (Smith, 1835)

Holotype :- Smith (1835: 174-175) provided a general description without indication of a particular specimen.

Type locality :- Smith (1835) did not indicate the origin of the specimen he studied other than "South Africa". According to Shortridge (1942: 49) Smith's specimen comes from Swartkop, near Upington, middle Orange River (south bank), above the Augrabies Falls. According to Roberts (1951) the specimen described by Smith (1835) comes from north of the Olifants River, in the Vanrhynsdorp District, Western Cape Province, South Africa.

Dispersal area :- *Pronolagus rupestris* populations inhabit two disjunct regions, i.e. the ones in northwestern South Africa, and the other in eastern Africa in territories extending from Kenya to Malawi. The two populations are separated by 1,200 km and thus their belonging to the same species is questioned (Happold, 2013; Matthee *et al.* 2016) (Fig. 3).

Characteristics :- Smith (1835) gave only a description of the pelage. This species is generally smaller than the other *Pronolagus* species. Dorsal pelage is rufous-brown with black grizzling, rufous on the rump. The colour of sides lighter than dorsal pelage. Ventral pelage whitish rufous. Muzzle, forehead and top of head rufous brown. The limbs are bright rufous. The forelimbs and hindlimbs are rufous,

the tail always dark rufous and the tip of the tail is black or brown-black (Smith, 1835; Happold, 2013, 2018) (Figs 6, 7, 8).

The cranium has a well-arched profile, but less so than in *P. randensis*. The top of the curvature is situated just above the distal margin of the orbits. This makes the facial part of the cranium longer than the braincase. The muzzle is short and robust. The suture between the nasals and the frontal is V-shaped and sharp anteriorly. The nasal bones do not extend backward beyond the level of the anterior limit of the zygomatic arches. Postorbital wings are small, remarkably smaller than those of *P. randensis*, with anterior and posterior notches as in the latter. The suture between the frontal and parietal bones is just at the level of the posterior roots of the zygomatic arches. Zygomatic arches widen backwards, have a weak anterior projection, short anterior root and wider posterior root. In lateral view, the orbital fossa is proportionally wider and higher than in *P. crassicaudatus* and *P. randensis*. In ventral view, the incisive foramina are not flared in their central part as much as they are in *P. crassicaudatus* and *P. randensis*, but their distal ends are wider than in *P. crassicaudatus*, and as wide as in *P. randensis*. The hard palate is longer than the distal breadth of the incisive foramina. The choanae are moderately large, but notably narrower than the length of the hard palate. The bullae are large and are not covered by the paroccipital processes (Fig. 6).

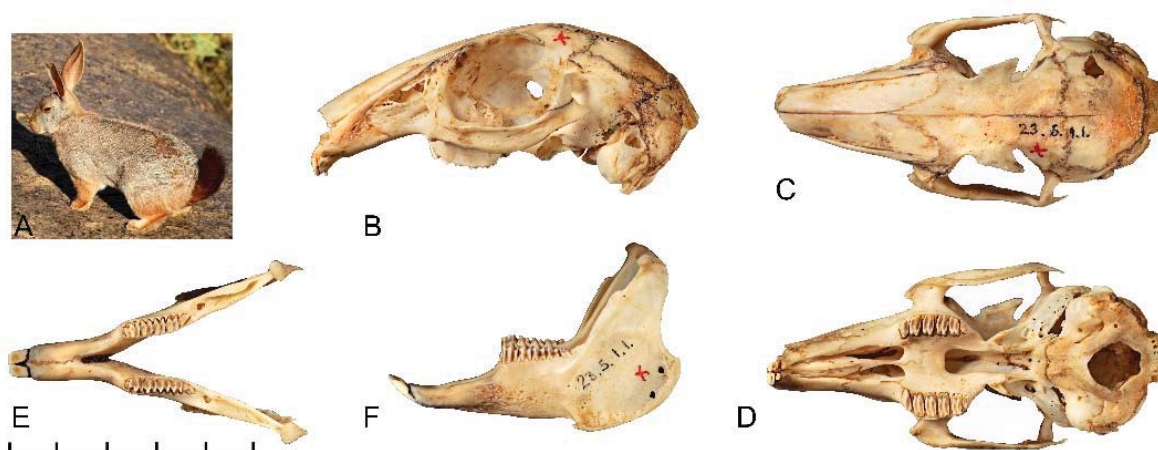


Figure 6. The type skull of *Pronolagus rupestris vallicola* Kershaw, 1924, from the Rift Valley in Kenya. It belongs to a female individual and is preserved at the Natural History Museum, London, catalogue no 1923.5.1.1. A) picture of a living individual (Wikipedia commons), B) Cranium in left lateral view, C) in dorsal view, D) in ventral view, E) mandible in dorsal view, F) mandible in left lateral view. Scale bar : 5 cm. Photos courtesy of the Natural History Museum, London.

In the upper dentition, the main incisor has a faint groove without cement close to its inner margin. It differs from that of *P. crassicaudatus* and *P. randensis* in being smaller and more square in outline (length between 2.3-2.8 mm; Robinson, 1986). The P2/ is short and bears two or three flexa of which the central and lingual ones are almost equally deep but the labial one is often barely developed or even lacking. The upper molariform teeth have a hypoflexus with a narrow entrance, tilted trajectory at the midway; the enamel is thick on the antero-labial and postero-lingual walls of the hypoflexus, but thin in its other walls. Enamel is gently folded on P3/ and P4/ along the anterior wall of the hypoflexus. The M3/ is transversely elongated and bordered by a thick enamel band (Figs 7, 8).

The p/3 has a wide hypoflexid and narrow mesoflexid, which is deeper than the previous one. The trigonid and talonid are connected by a narrow bridge. The protoflexid is wide but the paraflexid is narrow. The anteroconid does not bear a well-defined anteroflexid but there is a faint depression in its place. The lower molariform teeth are double-lobed as in all leporids, which are connected lingually by a thin dentine bridge. The anterior lophid has a well-marked antero-labial depression filled with cement, but different from the protoflexid of *P. crassicaudatus*. Enamel is thick along the posterior margins of the lophids, and thin or absent on their anterior margins. The m/3 is bilobed, its lophids have rounded occlusal outlines, the distal one being particularly reduced (Figs 7, 8).

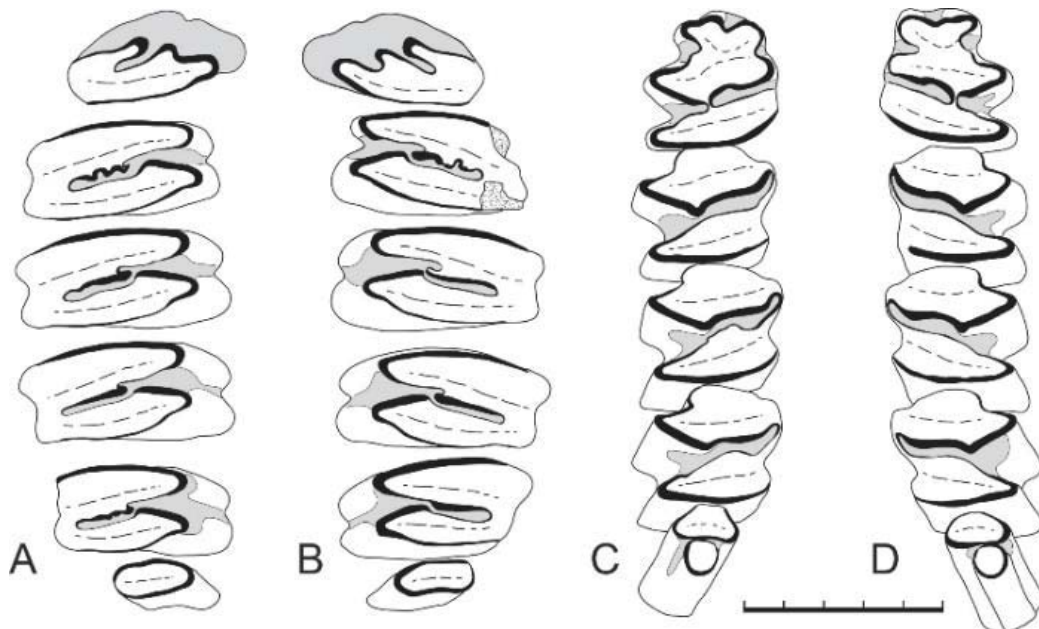


Figure 7. Cheek teeth series of the type skull of *Pronolagus rupestris vallicola* Kershaw, 1924 from the Rift Valley in Kenya. Natural History Museum, London, catalogue no 1923.5.1.1. A) right P2/-M3/, B) left P2/-M3/, C) left p/3-m/3, D) right p/3-m/3. Anterior is upwards. Scale bar : 5 mm.

The skull and dentition illustrated by Daxner & Fejfar (1967: fig. 6 and pl. 3) as *P. crassicaudatus* (Museum für Naturkunde Berlin, catalogue number 47527) apparently belong to *P. rupestris* as suggested by Ruf (2014), an attribution with which we agree. In addition this specimen was collected in northwestern Mozambique which is within the dispersal area of the latter species. Also, the skull from Malawi, no RG 2624 at the Royal Museum for Central Africa in Tervuren, labelled as *P. crassicaudatus*, fits in all

characters with *P. rupestris* (see Fig. 8). However, we observed that, although similar in size, the dentition of the Malawian specimen is different from that of the Kenyan and South African ones, in particular in the occlusal pattern of P2/ and p/3. As noted above, the systematic status of *P. rupestris* populations disjointly distributed in vast territories between southern Kenya to South Africa needs to be better clarified by additional morphological and molecular studies.

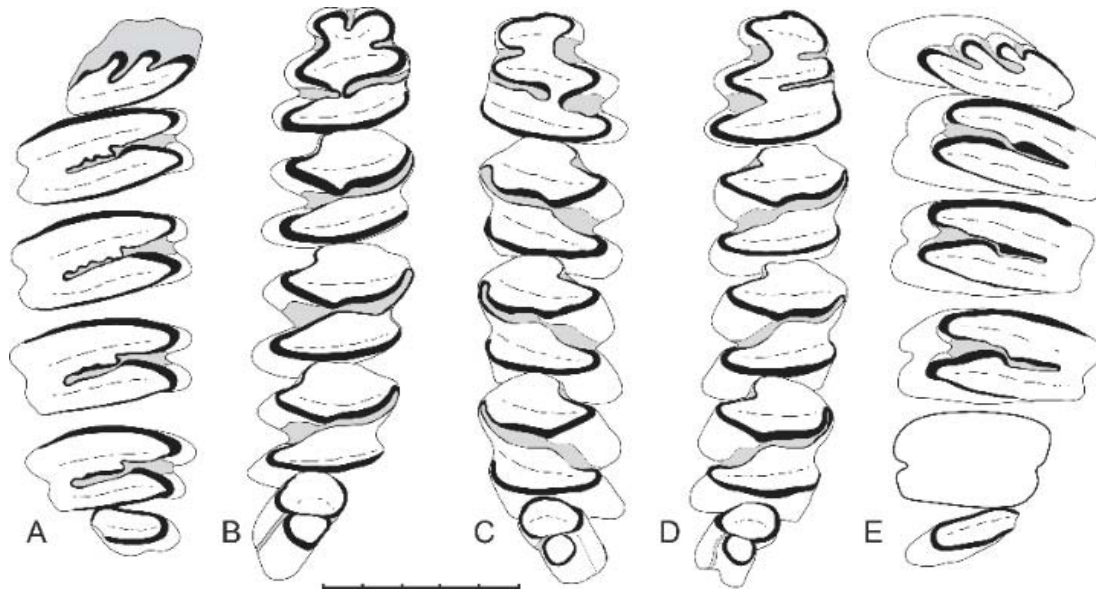


Figure 8. Cheek teeth series of *Pronolagus rupestris* from South Africa (A, B: National Museum, Bloemfontein, catalogue no NMB 4860) and Malawi (C-E: Royal Museum for Central Africa, Tervuren, catalogue no RG 2624). A) right P2/-M3/, B) left p/3-m/3, C) right p/3-m/3, D) left p/3-m/3, E) left P2/-M3/. Anterior is upwards. Scale bar : 5 mm.

Species *Pronolagus randensis* Jameson, 1907

Holotype :- A female individual preserved at the Natural History Museum, London; Catalogue number 1909.3.2.20 (Fig. 9).

Type locality :- Observatory Kopje, Johannesburg, Gauteng Province, South Africa.

Dispersal area :- *Pronolagus randensis* (Jameson's Red Rock Hare) occurs in northeastern South Africa, Botswana, Zimbabwe, western Mozambique, and an isolated population inhabits central Namibia to southwestern Angola (Happold, 2013, 2018; Mathee *et al.* 2016). It is thought that there is no gene flow between these two isolated populations, which are some 900 km apart, and thus they might represent different species (Fig. 3).

Characteristics :- This is a medium-sized species. Its dorsal pelage is brown, grizzled, grayish rufous on rump and flanks, the tip of the muzzle is light rufous, ears are brownish-gray with rounded tips, forelimbs and hindlimbs are pale rufous, tail black (Jameson, 1907; Meester *et al.* 1986; Happold, 2013; Mathee *et al.* 2016) (Figs. 9, 10).

The type skull of this species has a very curved lateral profile, much more than in other species of the genus. The top of the curvature is

situated just above the orbit, i.e. much more anteriorly than in *P. rupestris*. In *P. crassicaudatus* the tip of the curvature is also situated above the orbit, but the curvature itself is much less pronounced than in *P. randensis*. The muzzle is short and wide. Nasal bones end backwards at the level of the anterior root of zygomatic arches. The suture between the nasal and frontal bones forms a forward pointing V which extends slightly beyond the zygomatic shoulders and reaches the anterior limit of the dental row. Zygomatic arches diverge backwards much less than in *P. rupestris*. The postorbital wings are stronger than in any other species of *Pronolagus*, well delimited by an anterior and a posterior notch, and their tip is sharp and almost touches the distal roots of the zygomatic arches; the angle between this process and the brain case is narrower than in other species. The brain case is voluminous. The suture between the frontal and parietal is situated behind the posterior roots of the zygomatic arches, clearly on the brain case, while in *P. crassicaudatus* and *P. rupestris* this suture is situated between the distal roots of the zygomatic arches; as such the frontal bone occupies a much larger surface on the roof of the cranium than in the latter two species.

In ventral view, the incisive foramina are flared in their distal half, as in *P. crassicaudatus*

(narrow in *P. rupestris*) and its distal end reaches the level of P2/s. The hard palate is much longer than the breadth of the mesopyterygoid fossa. The zygomatic arches are slightly undulating (rather straight in other species except *P. crassicaudatus ruddi*) and

diverge backwards. The anterior root of the zygomatic arch reaches the level of the P2/-P3/ limit (it is at the level of the middle of P3/ in *P. crassicaudatus* or even a little further behind in *P. rupestris*). The bullae are moderately large.



Figure 9. The type skull of *Pronolagus randensis* Jameson, 1907, from Johannesburg Observatory, South Africa. Skull of a female individual preserved at the Natural History Museum, London, catalogue no 1909.3.2.20. A) picture of a living individual from the Johannesburg region, B) Cranium in left lateral view, C) in dorsal view, D) in ventral view, E) mandible in dorsal view, F) mandible in left lateral view. Scale bar : 5 cm. Photos courtesy of the Natural History Museum, London.

The mandible of *P. randensis* has a deep corpus and a stout ascending ramus, almost as in *P. rupestris*, in contrast to *P. crassicaudatus* which has a less high corpus and ascending ramus high and gracile. The mental foramen is close to and beneath the p/3, while it is situated far anterior on the mandibles of *Pronolagus crassicaudatus* and *P. rupestris*.

The main upper incisor has an anterior groove on its medial third, without cement. In size it is quite similar to that of *P. crassicaudatus*, but is much less enlarged laterally (length between 2.8-3.4 mm; Robinson, 1986). The P2/ has a short and wide occlusal outline, and it bears two flexa, lingual and central ones. The upper molariform teeth are all aligned lingually. The lingual hypoflexus opening gradually widens from P3/ to M2/, and the anterior enamel fold, observed in *P. crassicaudatus*, is barely developed on the type skull of *P. randensis*. The backward tilting of the hypoflexus is much less than in *P. rupestris*. Along the hypoflexus, enamel is thick on the postero-lingual and antero-labial walls, and thin elsewhere; it is folded along the anterior wall of the hypoflexus, the degree of wrinkling decreasing from P3/ to M2/. The M3/ is reduced

and its occlusal outline is oval (Fig. 10).

The p/3 has an hourglass occlusal outline in having hypoflexid and mesoflexid almost equally deep. The protoflexid is deep and wide, while the paraflexid is rather deep and narrow. The anteroflexid is variable in shape, well-defined or barely sketched in the form of an enamel fold. In the lower molariform teeth, the anterior loph is higher, larger and wider than the posterior loph. They are lingually connected by a thin dentine band. The antero-labial notch of the anterior loph, well-defined in *P. crassicaudatus* and moderately in *P. rupestris*, is represented with a wide depression on the type mandible of *P. randensis*. The m/3 is bilobed, and its distal lobe is reduced and button shaped (Fig. 10).

All these characters are also observed on a skull of *P. randensis* from Botswana, which is preserved at the Field Museum of Natural History in Chicago, catalogue No FMNH 38450.

According to Petter (1971), *P. randensis* is diverse with ten subspecies, nine according to Meester *et al.* (1986) and Duthie & Robinson (1990).

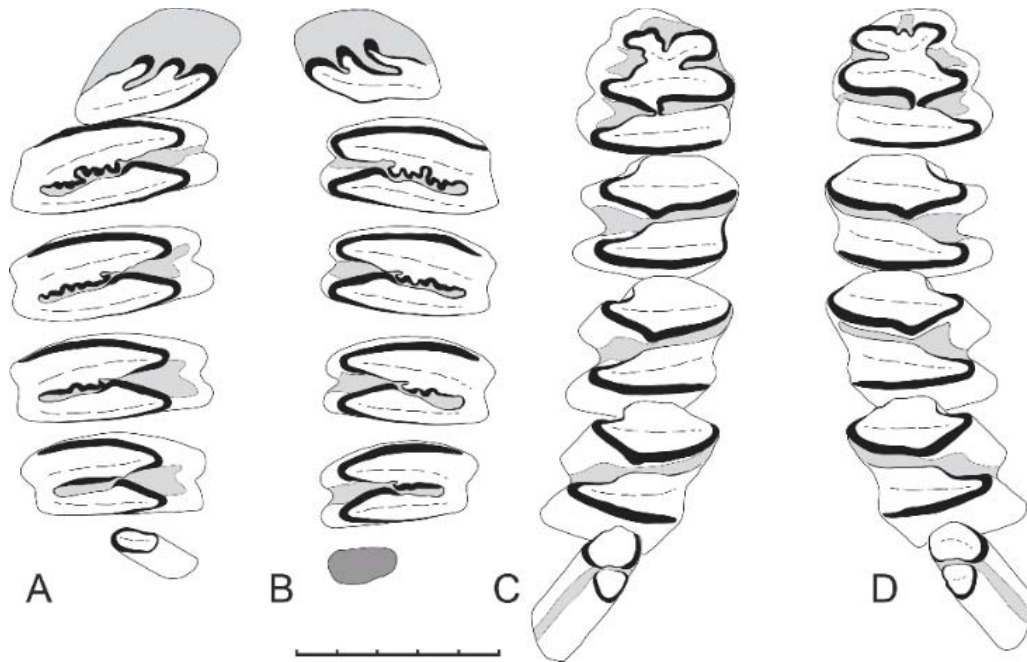


Figure 10. Cheek teeth series of the type skull of *Pronolagus randensis* from Johannesburg Observatory, South Africa. Natural History Museum, London; Catalogue number 1909.3.2.20. A) right P2/-M3/, B) left P2/-M2/ and the alveolus of M3/, C) left p3-m/3, D) right p3-m/3. Anterior is upwards. Scale bar : 5 mm.

Species *Pronolagus saundersiae* Hewitt, 1927

Holotype :- Skin and skull from "Hounslow" Farm preserved at the Albany Museum, Grahamstown, South Africa.

Type locality :- "Hounslow" Farm, Albany District, Eastern Cape Province, South Africa.

Dispersal area :- Southern provinces of South Africa (Happold, 2013) (Fig. 3).

Characteristics :- This species was initially described as a subspecies of *P. crassicaudatus*. It was considered by some authors to be a subspecies of *P. rupestris* (Meester *et al.* 1986; Duthie & Robinson, 1990; Hoffmann & Smith, 2005), but by some others it was elevated to species status following molecular studies (Whiteford, 1995; Mathee & Robinson, 1996; Mathee *et al.* 2004; Robinson & Mathee, 2005). Indeed, Mitochondrial DNA analyses done by Mathee & Robinson (1996) evidenced the presence of two major genetically and geographically distinct maternal lineages within *P. rupestris*: one located in the south-eastern portion of South Africa, and the other in the

north and northeast. In later studies, the southeastern clade was referred to *P. saundersiae*, and the second, which extends from the Northern Cape eastwards towards the Free State, has been accepted as *P. rupestris* (Bronner *et al.* 2003; Friedmann & Daly, 2004; Robinson & Mathee, 2005).

This is a médium-sized hare with thick woolly pelage. Dorsal pelage grizzled, rufous posteriorly, flanks paler, ventral pelage pale rufous to whitish, head grayish-brown, feet light rufous, tail red or pale sandy (Hewitt, 1927).

Only Hewitt (1927: pl. 26, fig. 2) illustrated a skull in dorsal view. Most characters of this skull recall *P. rupestris*. According to some details given by Happold (2013, 2018) and Mathee *et al.* (2016) the main upper incisor is grooved close to the inner margin, without cement; the length of the frontal bone is shorter than the length of muzzle as in *P. rupestris*. We have not found any specimen or illustration to better describe and illustrate the skeletal and dental features of this species, and to compare it with the others.

Table 3. Measurements (in mm) of some cranial and mandibular distances on some extant species of *Pronolagus* and the fossil material from the Humpata Plateau. 1 - *P. crassicaudatus* Type; 2 - *P. crassicaudatus*; 3- *P. randensis* Type, South Africa; 4 - *P. randensis* (MCZ33983); 5 - *P. rupestris* Malawi; 6 - *P. rupestris* Kenya; 7 - *P. rupestris* - Bloemfontein; 8 - *P. humpatensis*, Tchiua pink breccia.

<i>Pronolagus</i> measures / specimen	1	2	3	4	5	6	7	8
Skull total length	87.5	90.5	101.9		94.6	83.2	77.2	
Skull breadth at anterior zygoma	36.0	41.2	42.1		40.2	36.5	34.1	36.9
Nasal length	35.9	44.4	38.6			27.5	?	38.1
Upper diastema length	26.9	32.6	31.3		30.2	28.5	24.5	24.4
Width upper incisor	2.56		4.5					2.6
Length P2/-M3/	14.4	16.3	17.9		14.6	13.8	13.4	15.7
Palatal breadth between P2/-P3/	13.0	14.3	13.5		14.8	14.1	11.0	12.5
Minimum length hard palate	8.4	8.8	11.7		9.6	9.8	6.8	6.6
Breadth of choanae	4.9	6.2	5.8		6.5	6.2	4.8	6.1
Mandible diastema length	20.8		25.0	25.8	19.3	18.1	24.2	17.9
Mandible corpus height below m/1	12.3		13.8	14.2	12.4	12.1	13.5	13.1

Pronolagus is extremely rare in the fossil record of Africa. As noted above, the presence of this genus was mentioned in several localities in South Africa, Namibia and Angola. Apparently their remains are scarce, and they have never been described and illustrated to be useful for future systematic studies. Their presence is merely mentioned, sometimes with the number of specimens recorded, in the lists of taxa found, mainly from prehistoric sites. Thus Cooke (1963) listed *P. randensis* in the fauna of Makapansgat Limeworks, Brain (1981) cautiously mentioned the same species at Sterkfontein Member 5, Swartkrans Member 2 and channel fill, and Kromdraai A and B. Concerning *P. intermedius* that Jameson (1909) described as a new species based on a fragmentary skull from Holocene lime deposits of Godwan River near Pretoria, we already noted its doubtful identification (see above). This specimen needs further study to be correctly identified. To summarize the present state of the knowledge, we here list the localities that yielded fossil *Pronolagus* remains, with reference to the related papers.

- Amis, Inner Brandberg, Namibia: Late Pleistocene, *Pronolagus randensis* (Van Neer & Breunig, 1999).
- Apollo 11 Cave, Karas Region, southern Namibia: Middle and Later Stone Age, *Pronolagus* (Avery, 2019).
- Cave of Hearths, Makapansgat, Northern Transvaal, South Africa: Late Pleistocene, *Pronolagus randensis* (Avery, 2019).

- Gondolin, Bloubaan River Valley, Pretoria, South Africa: Plio-Pleistocene, cf. *Pronolagus rupestris* (Adams, 2018).
- Haasgat, Pretoria, South Africa: Early Pleistocene, *Pronolagus rupestris* (Adams, 2012).
- Leba Cave, Humpata Plateau, southern Angola: Holocene, *Pronolagus* sp. (Gautier, 1995).
- Lower Kemp's Cave, Gauteng, South Africa: Pleistocene, *Pronolagus* (Avery, 2019).
- Makapansgat Limeworks, Northern Province, South Africa: Early Pleistocene, *P. randensis* (Cooke, 1963; Pocock, 1987).
- Okongwe 2017, Kaokoland, Namibia: Late Pliocene; Leporidae indet. (Pickford 2019).
- Sibudu Cave, Kwazulu-Natal, South Africa: Late Pleistocene, *Pronolagus crassicaudatus*, *Pronolagus rupestris* (Wells, 2006).
- Sterkfontein, Pretoria, South Africa: Early Pleistocene, *Pronolagus* sp. (Brain, 1981; Avery, 2019).
- Swart Duinen, Namaqualand, Southwest Namibia: Late Pleistocene, *Pronolagus* sp. (Pickford & Senut, 1997).
- Swartlintjies 1, Namaqualand, Southwest Namibia: Acheulean, *Pronolagus* sp. (Pickford & Senut, 1997).
- Wonderwerk Cave 11 & 12, Northern Cape Province, South Africa: Oldowan and early Acheulean, *Pronolagus* sp. (Brink *et al.* 2016).

Fossil remains of *Pronolagus* from Angola

Species *Pronolagus humpatensis* nov. sp.

Holotype :- Right hemimandible bearing the symphysis, diastema and corpus with p/3-m/3 (Tch 2'90), curated at the Museu Regional da Huila, Lubango, Angola.

Other specimens :- Right hemimandible corpus bearing p/3-m/3 (Tch 3'90); right hemimandible with damaged corpus bearing p/3-m/3 (Tch 4'90); left hemimandible corpus bearing p/3-m/3 partly damaged (Tch 5'90); cranium bearing muzzle, palate, alveoli of cheek teeth, and anterior parts of zygomatic arches (Tch 6'90); palate with choanae and bearing left P3/-M2/ and right M1/-M2/ (Tch 7'90); left maxilla bearing P3/-M2/ (Tch 8'90); left maxilla bearing damaged P4/-M2/ (Tch 9'90); left principal upper incisor (Tch 10'90); right P2/ (Tch 11'90); right P4/ or M1/ (Tch 12'90); right M2/ (Tch 13'90); right hemimandible bearing the root of incisor, diastema and p/3-m/2 (Can 2'90); 15 vertebrae more or less complete (unnumbered); three ribs including one complete (unnumbered); distal half of right humerus (Tch 14'90); proximal part of right ulna (Tch 15'90); proximal parts of three femora including two juveniles (Tch 16'90-Tch 18'90); distal parts of two femora including one juvenile (Tch 19'90, Tch 20'90); proximal part of left tibia, juvenile (Tch 21'90); distal parts of two left tibiae (Tch 22'90, Tch 23'90); right astragalus (Tch 24'90); left calcaneum (Tch 25'90); proximal part of a metacarpal (Tch 26'90); first phalanx (Tch 27'90) (Tables 3-5).

Type locality :- Tchiua Pink Breccia, Humpata Plateau, Southwest Angola.

Etymology :- From its home country Humpata Plateau.

Diagnosis :- Small sized species. Muzzle short and robust. Incisor foramina widest in their distal end, not flared in their middle portion, and distally reaching the level of P3/s. Hard palate short and wide, and mainly composed of the palatal plates of maxillae. Choanae large, their anterior brim at the level of the junction between P4/-M1/. Anterior root of the zygomatic arch at the level of P2/-P3/ limit. Mandibular body high, symphysis much longer

than cheek teeth alveoli. P2/ with two flexa and an antero-labial depression, all filled with cement. Upper molariform teeth with a deep flexus tilted backwards halfway, with an enamel loop that penetrates the anterior loph, enamel of the hypoflexus walls smooth or slightly folded, shearing blade along the hypoflexus comprises the thick enamel on the inner side of the posterior loph and outer side of the anterior loph. According to its alveolus, M3/ is small and round in outline. p/3 well divided into anterior (trigonid) and posterior (talonid) parts, with a narrow bridge in between; mesoflexid deeper than hypoflexid, protoflexid and paraflexid well defined and filled with cement, anteroconid narrow and anteroflexid absent or incipient. Lower molariform teeth with a lingual dentine connection between trigonid and talonid, trigonid without protoflexid but a depression in its place; m/3 bilobed, its posterior lobe reduced and with a round occlusal outline.

Differential diagnosis :- The cranial, dental and poscranial elements of the Angolan form are smaller than those of *P. crassicaudatus* and *P. randensis*. The latter species have a more elongated muzzle and narrower interorbital breadth than in the Angolan form. The flaring of the incisor foramen in its middle part is barely marked, in any case much less than in all extant *Pronolagus* species. The hard palate is shorter than in the extant species in comparison to the width of choanae. *P. crassicaudatus* has three flexa on the anterior face of P2/, while two and eventually an antero-lingual depression in *P. rupestris*, *P. randensis* and *P. humpatensis* nov. sp. The upper molariform teeth of *P. crassicaudatus* and *P. randensis* have enamel well wrinkled in particular along the anterior wall of the hypoflexus, much less in *P. rupestris*, and almost flat on the Angolan specimens. The anteroconid of p/3 narrower than in all extant species of *Pronolagus*.

Description :- On the specimen Tch 6'90 (Fig. 11), the dorsal part of the cranium is very damaged and therefore does not allow observation of its degree of curvature. On the roof of the skull, the distal part of the right nasal bone is preserved, and it ends distally far behind

the anterior root of the zygomatic arch. The other sutures and the extent of other bones of the cranial roof cannot be observed. In ventral view, the anterior part of the skull is relatively well preserved and therefore informative. The muzzle is moderately long (about 25 mm), the incisor foramen measures 24 mm in length, the flaring in its middle part is barely marked, in any case much less than in all extant *Pronolagus* species, and its posterior rim forms two perfect semicircles (total width 10 mm) separated by the strong anterior spine of the hard palate. The incisor foramen extends posteriorly to the level of P2/-P3/ limit. The hard palate is surprisingly short for a

Pronolagus (length 6.6 mm; largest breadth at the level P2/-P3/, 12.5 mm); its anterior and lateral parts are formed by the maxillae and its posterior part, less extended, by the horizontal plate of the palatine. The distal spine of the hard palate is barely visible. The alveoli of the cheek teeth are well arched laterally, but almost linear lingually. The choanae are wide and extend anteriorly to the level of the anterior lophs of M1/s. The anterior root of the zygomatic arch is 6 mm in length and extends from mid P3/ to mid M1/. The zygomatic arch is well detached from the cranium by a shoulder 3 mm wide. Its anterior spine is short and sturdy.

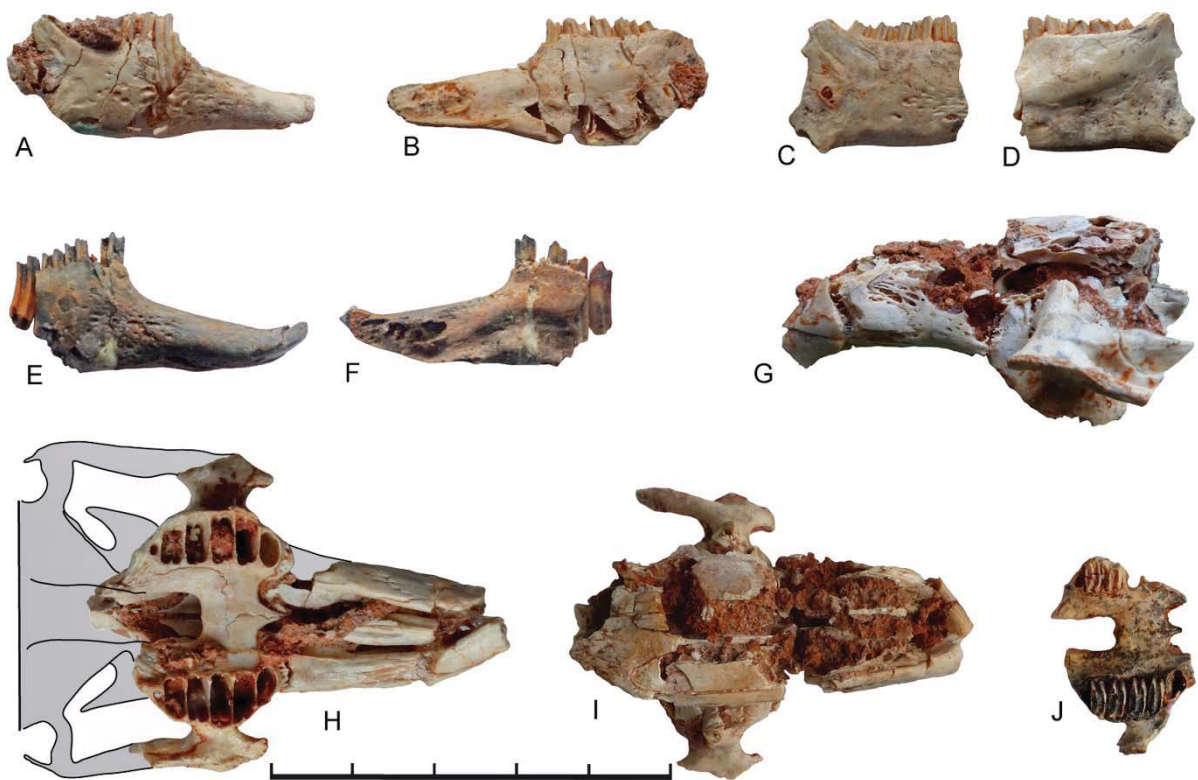


Figure 11. Cranial remains of *Pronolagus humpatensis* nov. sp. from Angolan localities of Tchiua Pink Breccia and Cangalongue 1. A) right hemimandible (holotype) from Tchiua (Tch 2'90) in lateral view, B) the same specimen in medial view, C) right hemimandible corpus from Tchiua (Tch 3'90) in lateral view, D) the same specimen in medial view, E) right hemimandible from Cangalongue 1 (Can 2'90) in lateral view, F) the same specimen in medial view, G) fragment of cranium from Tchiua (Tch 6'90) in left lateral view, H) the same specimen in ventral view with some missing parts completed, I) the same specimen in dorsal view, J) palate with partial cheek teeth from Tchiua (Tch 7'90) in ventral view. Scale bar : 5 cm.

The principal upper incisor is wide laterally and narrow antero-posteriorly. Its anterior margin has a thin enamel band and bears a rather medially situated groove without

cement (Fig. 12C).

The P2/ has two flexa filled with cement. Its antero-labial face has a wide depression. All the anterior face is covered of cement (Fig. 12D).

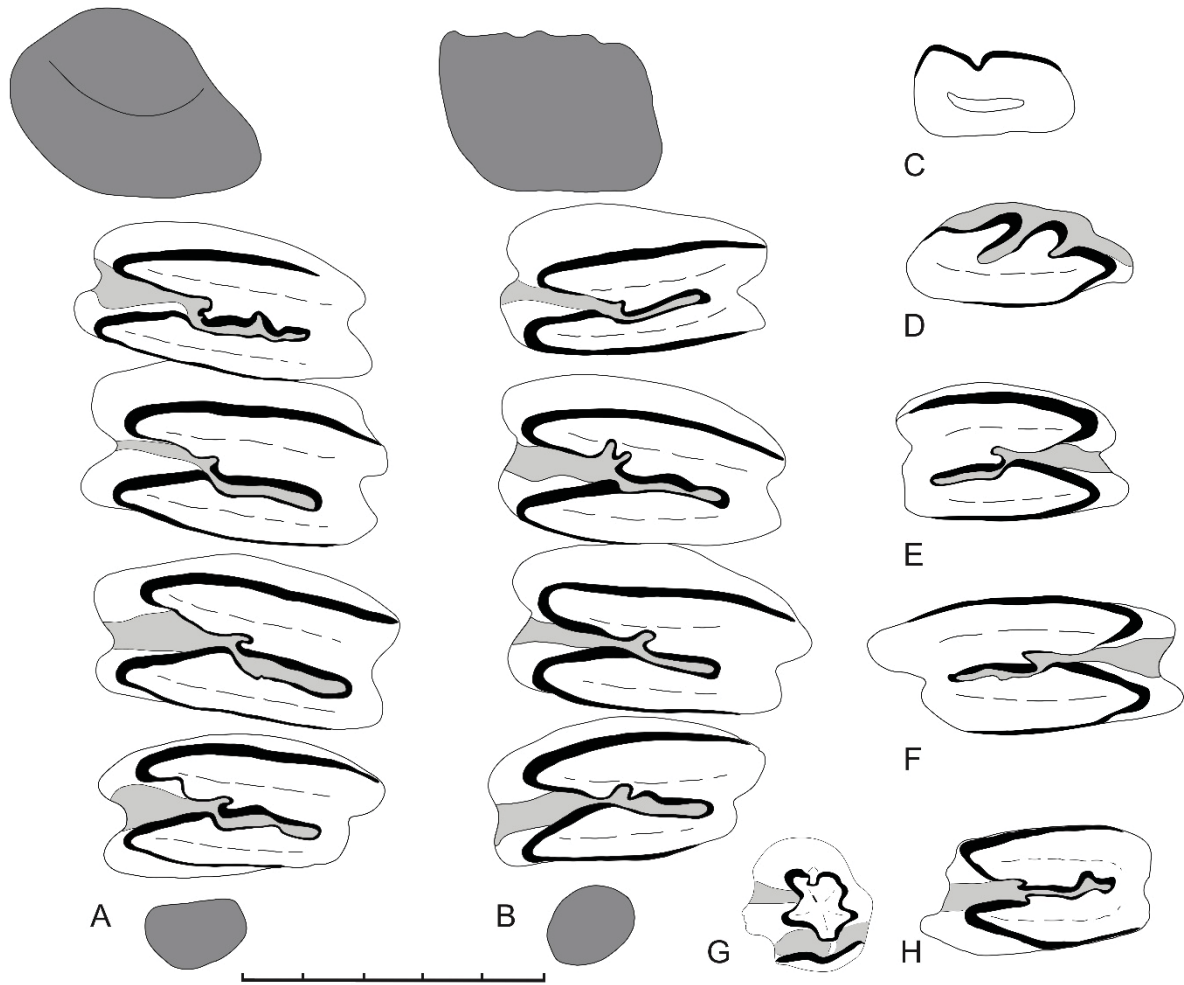


Figure 12. *Pronolagus humpatensis* nov. sp. from the Angolan locality of Tchiva Pink Breccia. A) left P3/-M2/ and the alveoli of P2/ and M3/ (Tch 7'90), B) left P3/-M2/ and the alveoli of P2/ and M3/ (Tch 8'90), C) left principal upper incisor (Tch 10'90, D) right P2/ (Tch 11'90), E) right P4/ or M1/ (Tch 12'90), F) right M2/ (Tch 13'90). *Pronolagus* sp. from Okongwe 2017, Kaokoland, Namibia. G) anterior part of a juvenile left p/3, H) left P4/ or M1/. Anterior is upwards. Scale bar : 5 mm.

The upper molariform teeth have almost the same size. The anterior loph is longer than the posterior one. The posterior loph is wider than the anterior one on P3/ and P4/, but narrower on M1/ and M2/. The pattern of the hypoflexus is typical of *Pronolagus*, and different from that of all other leporid genera, except the extant Mexican species *Romerolagus diazi* (Ferrari-Perez, in Diaz, 1893). It is slightly oblique backwards compared to the longitudinal axis, and almost reaches the labial margin. It is differentiated into a wide V-shaped inner part and a narrow outer part. Its inner part has a marked enamel fold on P3/-M2/ that penetrates the anterior loph, which is also frequently present on P3/ and P4/, not on M1/ and M2/, in the extant species of *Pronolagus* and in *R. diazi*.

The hypoflexus is tilted slightly backwards at halfway. Along its walls, the enamel band of the anterior side is thin in the lingual part and thick in the inner part. Along its posterior wall, in contrast, the enamel is thick in the lingual part, but extremely thin in the inner part. Both thickened sections are situated in such a way that together they form one continuous shearing blade. Along the walls of the hypoflexus, enamel is smooth or gently folded, not crenulated as in *P. crassicaudatus* and *P. randensis*.

The M3/ is missing in all the upper jaws but its alveolus, which is preserved in several specimens (average length and width 1.08 x 1.57 mm) indicates a small tooth with irregular ellipsoid outline.

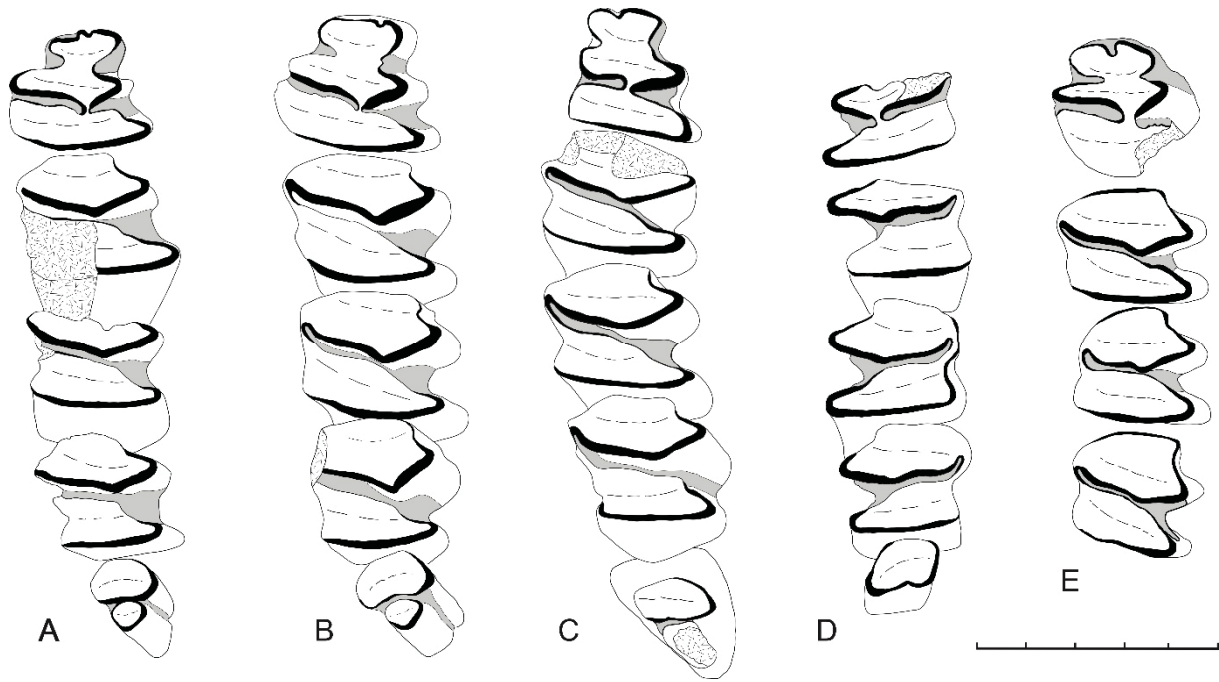


Figure 13. Lower cheek teeth of *Pronolagus humpatensis* nov. sp. from Angolan localities of Tchiua Pink Breccia and Cangalongue 1. A) right p/3-m/3, Holotype (Tch 2'90), B) right p/3-m/3 (Tch 3'90), C) right p/3-m/3 (Tch 4'90), D) left p/3-m/3 partly damaged (Tch 5'90), E) right p/3-m/2 from Cangalongue 1 (Can 2'90). Anterior is upwards. Scale bar : 5 mm.

Four series of lower cheek teeth from Tchiua and another one from Cangalongue 1 are preserved. The p/3 has an occlusal pattern bearing a trifold trigonid which is connected to the short and wide talonid by a narrow bridge. This bridge is situated labially to the longitudinal axis. The trigonid is narrower than the talonid. The trigonid has a wide protoflexid and narrow paraflexid. The anteroconid is narrow. The shape of its anterior edge is variable, bearing either an incipient anteroflexid (2/4) or a weak enamel fold (2/4). The mesoflexid is much elongated and narrower than the hypoflexid. Enamel is thick on the distal margins of the trigonid and talonid, and around the external angles of the main cusps. On one specimen, the talonid is depressed on its antero-external part.

The lower molariform teeth are bilophodont with a narrow lingual connection between the trigonid and talonid. The talonid is shorter and a little bit wider than the trigonid. Enamel is thick along the distal margins of the lophs, but thin along their mesial margins.

The m/3 is also bilobed, but its two parts are not connected. The trigonid has an ellipsoid outline with an incipient depression on its distal part. The talonid is reduced and it has a round occlusal outline. In all lower cheek teeth, the

flexids are filled with cement and the enamel is smooth.

The main postcranial bones from Tchiua Pink Breccia are enumerated above in the list of material and their dimensions are given in Table 5. We did not find any postcranial bone of *Pronolagus* in the collections of the Paris Museum. In the literature only Lyon (1903) provided a reliable comparative account on the postcranials of many extant lagomorphs known in his time, with illustrations except for humerus and femur. In his PhD thesis Quintana Cardona (2005) compared the postcranials of an endemic Pliocene leporid from Minorca Island, *Nuralagus rex* Quintana *et al.* 2011, with that of some extant leporids, including *Pronolagus*, and he also provided drawings and measurements of some of these bones. Consequently the comparison of the postcranials from Humpata Plateau with other leporids is limited to what is available in the literature.

The size of postcranial bones indicate a small species comparable with wild individuals of the European rabbit *Oryctolagus cuniculus*, and also Smith's Red Rock Hare *Pronolagus rupestris* (Table 5, Fig. 15).

Table 4. Measurements (in mm) of cheek teeth of *Pronolagus humpatensis* nov. sp from Angola. N = Number of measured specimens; Want = Width of the anterior loph(id); Wpost = Width of the posterior loph(id); Lantd = Length of the anteroconid of p/3; Whypofl = Width of the hypoflexus on the upper molariform teeth; alv. = alveolus.

Tooth	Length		N	Want		Wpost		Lantd	
	range	mean		range	mean	range	mean	range	mean
p/3	2.62-2.87	2.75	3/4			2.85-3.34	3.03	1.69-1.92	1.78
p/4	2.36-2.81	2.63	4	2.89-3.32	3.14	3.09-3.50	3.21		
m/1	2.39-2.76	2.57	4	2.83-3.15	2.98	2.98-3.10	3.03		
m/2	2.33-2.97	2.66	4/3	2.91-3.18	3.04	2.72-2.81	2.77		
m/3	1.54-1.64	1.59	3	1.48-1.86	1.56	1.56-1.70	1.64		
Upper I	2.64		1	1.49					
P2/		1.54	1		3.40				
P3/	1.84-1.99	1.90	3	3.80-4.18	3.92	4.05-4.19	4.14	2.75-3.19	3.04
P4/	2.01-2.19	2.10	4	3.98-4.33	4.21	3.85-4.47	4.20	3.25-3.56	3.41
M1/	1.96-2.25	2.07	5	3.62-4.31	3.91	3.19-4.20	3.13	2.75-3.69	3.24
M2/	1.80-2.07	1.95	4	3.66-4.00	3.87	3.30-3.65	3.46	2.84-3.10	2.95
M3/ (alv.)	0.86-1.21	1.08	4	1.31-1.83	1.57				

Only a lower portion of the humerus is preserved (Fig. 14 I, J). It indicates a small sized individual. The distal end is flared, much more laterally than medially, more so than in *Lepus*. The olecranon fossa is perforated by a small supratrochlear foramen. As already noted by Lyon (1903: 375) "*The humeri of the Leporidae are all much alike in form and proportions,....The variations in this bone in the different genera are few, hard to define, and apparently of little significance*". Quintana Cardona (2005) provided simple illustrations and measurements of the humerus for several Leporidae, including three extant species of *Pronolagus*. In size the humerus from the Humpata Plateau compares to the European rabbit *Oryctolagus cuniculus*, it is smaller than the extant species *Pronolagus crassicaudatus* and *P. randensis*, and larger than the south African riverine rabbit *Bunolagus monticularis* (Quintana Cardona 2005). Concerning the morphology, we did not observed any significant difference.

Of the ulna, only a part of the proximal end is preserved. The apex of the olecranon process is missing. The anconeal process is incipient. The articular facet with the humerus and radius is flared more medially than laterally. At this part, dorsally, the external face of the bone is slightly convex but the internal face bears a wide proximo-distal groove. The facet for the radius is arc-shaped. All these characters are quite common in all Leporidae, but the Humpata bone is small in comparison with that of the extant species of *Pronolagus*, using the measurements in Quintana Cardona (2005).

All five fragments of femora belonged to

juvenile individuals since the head and great trochanter are missing, and the bone is porous (Fig. 14 A, B). In its proximal part, the neck is short as in the European rabbit, as well as in *P. crassicaudatus* and *P. randensis* (Quintana Cardona, 2005, fig. 127), and in contrast to *Lepus* in which it is rather elongated. The lesser trochanter is strong, it starts upward below the neck and extends on the distal face of the shaft. It is stronger and more distally extended than in *Oryctolagus* and *Trischizolagus* (Averianov, 1995; De Marfà, 2009). The intertrochanteric fossa is V-shaped, and its lateral border is sharp but medial border flat. The shape of this fossa is similar to that of *Trischizolagus dimitrescuae* from the locality of Moscovei in Moldova (Averianov, 1995), while in extant rabbits it is rather rounded and narrow. The third trochanter protrudes laterally and it is much less developed than the lesser trochanter. The shaft is relatively thin. On the dorsal face the patellar groove narrows slightly upward. On the plantar face the intercondylar groove is a little wider than each of the condyles, which are almost equal in size but the medial one descends a little more downward than the lateral condyle. Quintana Cardona (2005, fig. 127) illustrated the femora of *Pronolagus randensis* and *P. crassicaudatus*. The only apparent difference is that *P. crassicaudatus* has a narrow patellar groove while it is wide on the femora of *P. randensis* and *P. humpatensis* nov. sp.

The proximal end of the tibia is damaged and has lost its epiphysis, hence preventing any reliable character to be noted, except that the tibial tuberosity is thin and sharp, and laterally inclined. In *Oryctolagus* and *Lepus* this crest is

stronger and more inclined laterally to form a true groove on the upper lateral surface of the tibia. In its distal epiphysis (Fig. 14E), the medial part is larger (8.0 mm) antero-posteriorly than the lateral part (6.4 mm). In *Oryctolagus* these two parts are roughly equal, in *Lepus*, slightly differentiated, but much less than on the tibia from Tchiua Pink Breccia. Contrary to *Oryctolagus* and *Lepus*, the medial extremity projects downwards more than the lateral extremity. The central articular groove for the talus appears well notched on the anterior and posterior faces of the bone, as in *Lepus*, while in *Oryctolagus*, the anterior notch is poorly defined.

The talus has head and trochlea dorsoventrally aligned (Fig. 14 F, G). In dorsal view, the trochlea has a rather quadrangular outline as in *Lepus*. The neck, which joins the head to the trochlea, is flat and rather long, and its lateral margin is convex. The ventral edge of the head bears a large rounded articular facet that covers both its dorsal and plantar faces. The medial part of the trochlea is higher, larger and antero-posteriorly twice as long as the lateral part. In plantar view, the ectal facet extends from the lateral trochlea to the articular surface of the head, and its central part is widened to make the plantar medial groove oblique. The sustentacular facet is triangular in outline.

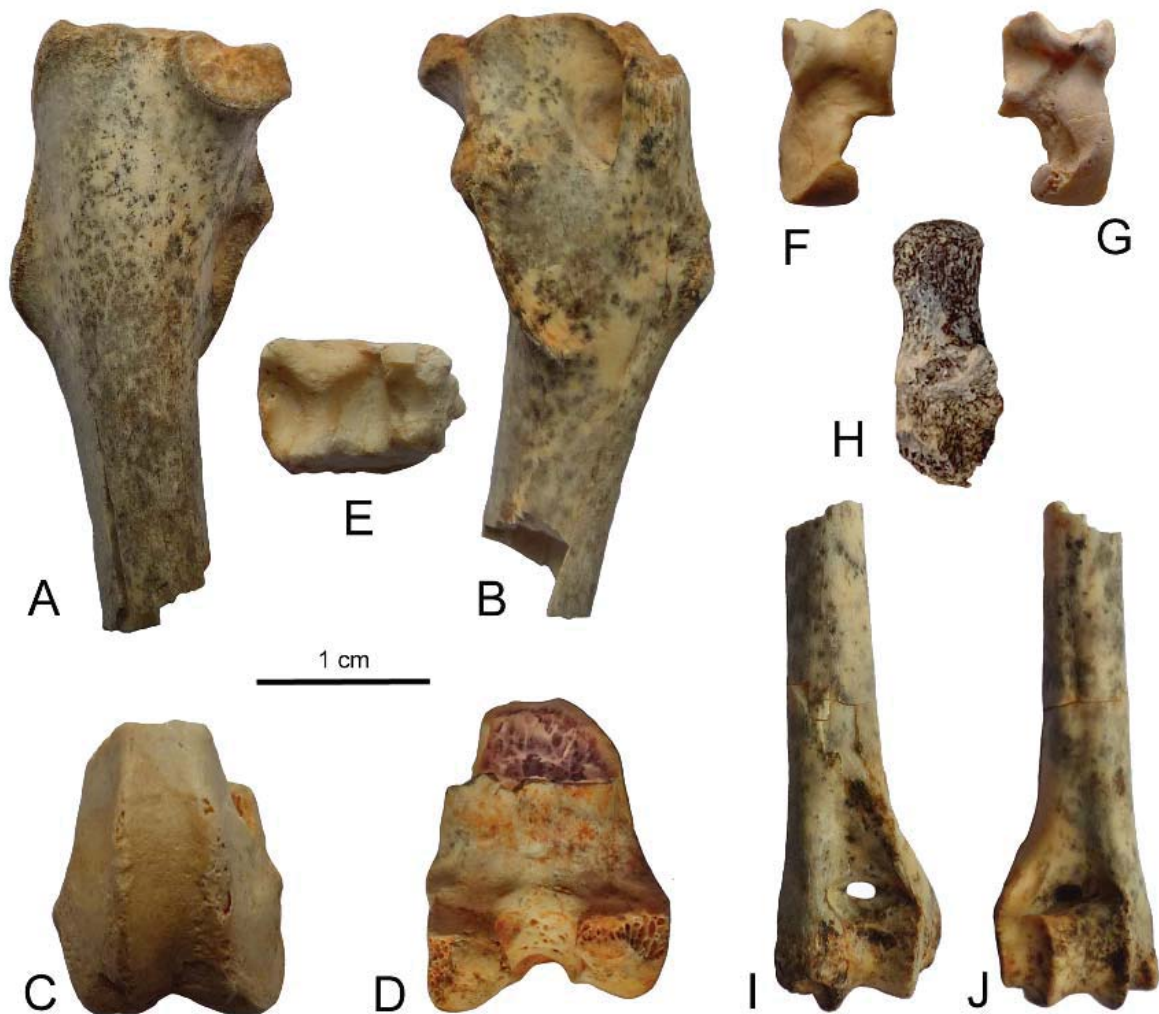


Figure 14. Postcranial bones of *Pronolagus humpatensis* nov. sp. from Tchiua Pink Breccia in Angola. A & B) proximal part of right femur (Tch 16'90) in anterior and posterior views, C & D) distal part of a left femur (Tch 19'90) in anterior and posterior views, E) distal articular face of a left tibia (Tch 22'90), F & G) right astragalus (Tch 24'90) in anterior and posterior views, H) left calcaneum (Tch 25'90) in anterior view, I & J) distal half of right humerus (Tch 14'90) in posterior and anterior views.

Table 5. Measurements (in mm) of postcranial bones of *Pronolagus humpatensis* sp. nov. from Tchiua, Angola. DAP = Antero-posterior diameter, DT = Transverse diameter, prox = proximal, juv = juvenile.

Catalogue N°	Bone	Length	Proximal		Distal	
			DT	DAP	DT	DAP
Tch 14'90	Humerus distal				9.3	7.1
Tch 15'90	Ulna prox		5.3	4.5		
Tch 16'90	Femur prox		14.9	8.2		
Tch 17'90	Femur prox juv		9.1	6.9		
Tch 18'90	Femur prox juv		10.4	7.1		
Tch 19'90	Femur distal				14.0	11.6
Tch 22'90	Tibia distal				12.2	7.9
Tch 23'90	Tibia distal				12.3	6.6
Tch 24'90	Astragalus	11.6	7.5	5.1		
Tch 25'90	Calcaneum	15.9	6.9	7.1		
Tch 26'90	Metacarpal prox		5.4	3.9		
Tch 27'90	First phalanx	9.5	3.7	3.8	2.7	2.4

A right calcaneum preserves the tuber calcanei, articular facet with talus and fibula, but its distal extremity is damaged (Fig. 14 H). The greatest length of the calcaneum is estimated to be 17 mm, which is almost half the value of that of *Lepus europaeus* and *L. capensis*. According to measurements

published by Quintana Cardona (2005), the size and proportions of this calcaneum approach that of *Pronolagus rupestris*, but are smaller than those of *P. randensis* and *O. cuniculus*. In *Lepus*, the tuber calcanei is particularly elongated compared to that of *Pronolagus* and *O. cuniculus*.

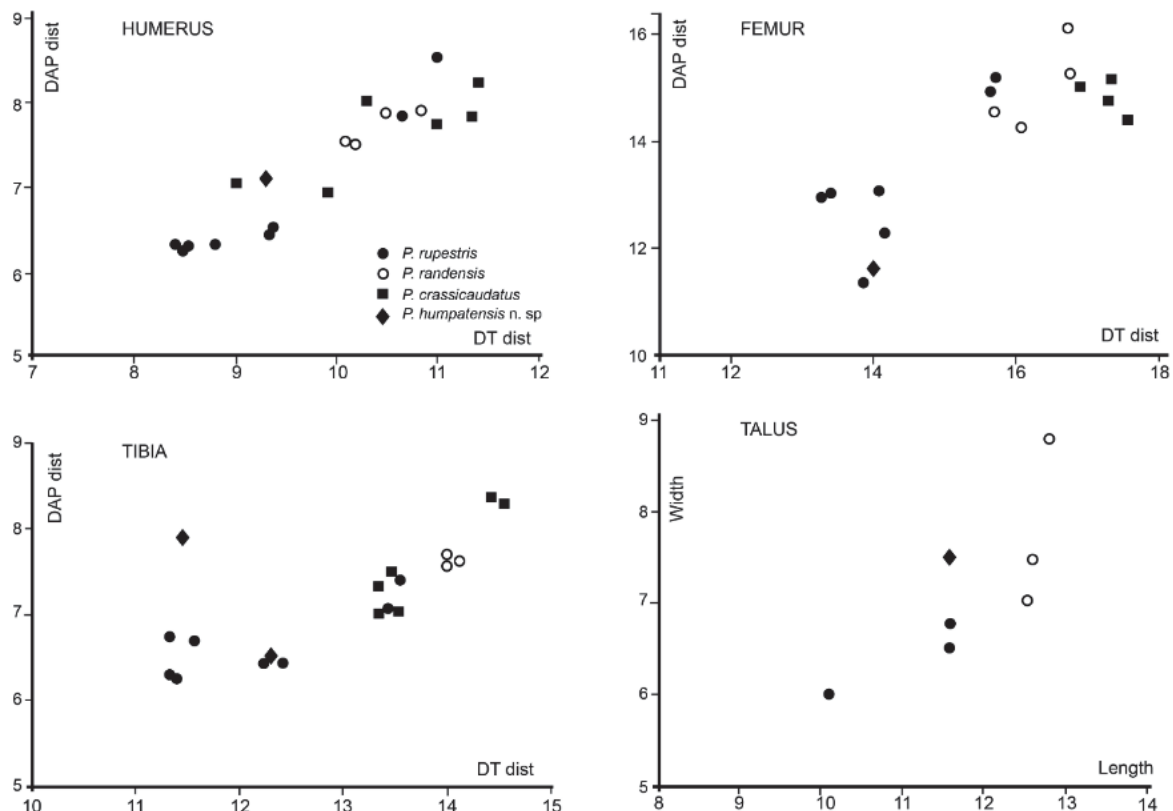


Figure 15. Diagrams for comparison of dimensions of some postcranial bones from Tchiua Pink Breccia with those of three extant species of the genus *Pronolagus*. Data for the extant species are extracted from the PhD thesis of Quintana Cardona (2005) (DAP dist – distal antero-posterior diameter; DT dist - distal transverse diameter).

Material from Okongwe 2017, Kaokoland, Namibia

Pickford (2019) described and illustrated a left P4/ or M1/ and a fragmentary left p/3 of a lagomorph, which is almost unworn (Fig. 12 G and H). The upper molariform measures 1.58 mm in length, 2.50 mm in anterior width, and 2.31 mm in posterior width. The lingual opening of the hypoflexus is wide and V-shaped. Before narrowing labially, hypoflexus has an enamel fold which penetrates the anterior loph, a typical feature observed in all species of *Pronolagus*. The hypoflexus is slightly tilted backward in its labial 1/3 depth. The enamel is thick along its antero-labial and postero-lingual walls, and thin in its other parts. The enamel of the anterior wall is slightly tilted, similar in that to the specimen Tch 7'90 of *Pronolagus humpatensis* nov. sp.

On the p/3, the talonid is badly damaged, and consequently the dimensions of the tooth cannot be measured. The trigonid and talonid are connected by a narrow enamel bridge rather labially situated. The mesoflexid is oblique and deeper than the hypoflexid. The paraflexid is a little distal to the protoflexid, and both are wide open. The anteroconid is narrow and bears a shallow anteroflexid that would disappear with attrition. All these features are identical to that of *P. humpatensis* nov. sp., and recall in particular the p/3 of the hemimandible Tch 4'90.

Because of their great similarities, these two teeth might be referred to *P. humpatensis* nov. sp., but the limited material prompts a cautious identification as *Pronolagus* sp.

Discussion

At present, southern Africa is inhabited by seven species of Leporidae : *Lepus capensis* Linnaeus, 1758 (Cape hare), *Lepus saxatilis* F. Cuvier, 1823 (Scrub hare), *Bunolagus monticularis* (Thomas, 1903) (Riverine rabbit) and four species of *Pronolagus* (Red rock rabbits) as shown above (see detailed discussion on the systematics of southern African leporids in Bronner *et al.* 2003; Collins, 2005; Happold, 2013, 2018). Palacios *et al.* (2008) recognized the presence of *Lepus victoriae* in central and western Cape Province. However, according to Happold (2013: 706) this species is "widespread in savanna and semi-desert regions of Africa south of the Sahara, but is not present in southern Africa where it is replaced by an allopatric species *L. saxatilis*".

The southern African species of *Lepus* are easily distinguished from *Pronolagus* in many characters of their skeletal anatomy and dentition. In particular, the skull has a robust face and shorter braincase compared to *Pronolagus*, very wide incisor foramina and choanae, shorter hard palate, less deep mandibular corpus, upper and lower dentition totally different in occlusal pattern: the upper principal incisor has a deep anterior groove filled with cement, P2/ has three deep flexa, upper molariforms have straight hypoflexus and crenulated enamel all along its walls, on the p/3 hypoflexid and mesoflexid are connected, and thus the bridge between the trigonid and talonid is not central as in *Pronolagus* but is lingual.

Bunolagus monticularis (Thomas, 1903) is the only species of its genus and inhabits a restricted area in Northern and Western Cape Provinces in South Africa. It is smaller than *Pronolagus*, except *P. rupestris*. Its fossil representatives are unknown. Its skull is well arched, has moderate restriction between the orbits, prominent supraorbital processes, thick zygomatic arches, maxilla with numerous foramina, hard palate shorter than the width of mesopterygoid space, it lacks the antero-external shoulder on the zygoma, the frontal/temporal suture is far behind the posterior roots of the zygoma as in *P. rupestris*, mesopterygoid space very wide, the principal upper incisor is short, rounded in outline and has a single groove not filled with cement, and the corpus of the lower jaw is slender (Happold, 2013). It differs from the Humpata species in having a shorter muzzle, wider incisor foramen, shorter hard palate, and wider and anteriorly bilobed choanae, low mandibular body, shorter and wider upper incisor with a rounded outline and incipient anterior groove.

The fossil record of red rock hares is documented since the early Pliocene at Langebaanweg (Pocock, 1976; Hendey, 1981). However, the most recently published faunal list by Avery (2019: 69) and the review of African fossil lagomorphs by Winkler & Avery (2010) do not include any leporid at Langebaanweg. Another Pliocene site is Limeworks Makapansgat. For later

occurrences, see the list of localities provided above.

The extant species of *Pronolagus*, except *P. rupestris*, are all larger than the species from Humpata in the dimensions of skull portions, dentition and postcranial bones. On the skull from Tchiua, the distal end of the nasal bone is far behind the anterior root of the zygomatic arch. In *P. crassicaudatus* the same bone ends at the level of the anterior root of the zygomatic arch, in *P. rupestris* and *P. randensis* even further forwards. The hard palate is shorter than in any species of *Pronolagus*, but longer than that of *Bunolagus*.

In *P. crassicaudatus* the muzzle is longer, the anterior rim of the choanae reaches the level of the posterior loph of M1/, while in the Angolan specimens it is at the P4/-M1/ limit. Its first upper incisor is wide mediolaterally and has the anterior groove closer to the medial border while the upper incisor from Tchiua is short and its groove is rather central.

P. humpatensis nov. sp. is similar in size to *P. rupestris* and also in having P2/ with two flexa, and a small M3/ with rounded outline. However, *P. humpatensis* nov. sp. differs from the *P. rupestris* in having an elongated muzzle, much distal nasal bones, wider incisor foramina in their distal part which end backwards at the level of P2/s while it does not exceed the anterior limit of P2/ in *P. rupestris*. In addition, in *P. rupestris* the P2/ is short, upper molariform teeth lack the labial enamel fold on the anteroloph, enamel is wrinkled along the anterior wall of the hypoflexus (gently folded in *P. humpatensis*). The p/3 of *P. rupestris* has a larger trigonid and larger anteroconid, p/4-m/2 have an anteroflexid which labially notches the anterolophid. Its m/3 is smaller than that of *P. humpatensis* nov. sp.

The upper principal incisor of leporids is characteristic enough to be used in genus and species identification. The shape of its cross-section, the form and place of its anterior groove, and the presence or absence of cement in this groove or on the whole anterior face are characters varying from one species to another. Apparently Petter (1959) initiated the interest in this tooth for systematic purposes, which was later on successfully used by Robinson (1986), Collins (2005), Palacios *et al.* (2008), and others. In *Lepus capensis*, the upper incisor has a squarish cross-section and the anterior face is covered with cement (Robinson, 1986). In *L. saxatilis* this incisor is trapezoidal in outline

with a deep anterior groove filled with cement (Robinson, 1986; Collins, 2005). In *Bunolagus monticularis* the cross-section recalls that of *L. capensis* with, however, more rounded angles, and the anterior groove lacks cement. In *Pronolagus* species, the principal upper incisor is wide and short, its anterior groove is situated more labially than in the species mentioned above, and it lacks cement. The unique upper incisor from Tchiua (Fig. 12C) recalls in all characters that of *P. rupestris* (small size, moderate breadth, groove rather central). In *P. crassicaudatus* and *P. randensis*, this incisor is larger, widened medio-laterally and the anterior groove is closer to the medial face.

The cheek teeth of *P. humpatensis* nov. sp. are also somewhat similar to that of *P. rupestris* in some characters, and to *P. randensis* in some others, but different from those of *P. crassicaudatus*. The latter has a large P2/ with three flexa, upper molariform teeth with deep flexa and crenulated enamel along the walls of the hypoflexus. Its p/3 has the trigonid deeply notched by three or even four flexids, and the posterior wall of its hypo- and paraflexid are often crenulated, and the lower molariform teeth have a well-defined protoflexid.

In summary, while the Humpata Plateau fossils recall in size and some dental features *P. rupestris*, they bear many other distinctive characters that deserve a new species status.

Phylogenetic relationships of *Pronolagus* are debated on morphologic, morphometric and molecular grounds. According to Hibbard (1963: 9), who studied in detail the origin and diversification of the leporid p/3 pattern, the European species "*Alilepus dietrichi* Fejfar is very close if not the ancestral stock from which *Pronolagus*, *Serengetilagus* and *Pentalagus* are derived". This opinion is well supported in phylogenetic analysis conducted by Averianov (1999) based on 30 multistate morphological characters and on 28 Neogene to Recent leporid genera. It appears that *Pronolagus* is the sister group of *Bunolagus*, derived from an old stock of *Alilepus*, together with several other genera that Averianov (1999) included in the subfamily Pentalaginae Gureev, 1948. Among studies during the past decade, Ge *et al.* (2015) provided a geometric morphometric analysis of the skull morphology in 12 extant genera of Leporidae. Their results indicate a sister taxon relationship of *Pronolagus* with *Poelagus* from East Africa and *Nesolagus* from South Asia.

Based on molecular data (mitochondrial, nuclear and nuclear β mt data), *Pronolagus* occupies the basal position in the phylogeny of extant leporids, together with *Romerolagus* and *Pentalagus* and it appears as the sister group of all other genera (Sparwel *et al.* 2019, and references therein).

Winkler & Avery (2010) gave an account on the fossil occurrences of Leporidae in Africa and noted (p. 314) that "*Some of the Alilepus specimens from Kenya show similarities in p/3 morphology with extant Pronolagus and Bunolagus, suggesting that these may be sister taxa*". Indeed, the extinct genus *Alilepus* first appears in North America ca 12 Ma (White, 1991; Voorhies & Timperley, 1997), and it entered Eurasia ca. 9-10 Ma through Beringia

(Cermak *et al.* 2015) or a little later during the MN 11 Mammalian zone (Flynn *et al.* 2013). *Alilepus* is a common element of Late Miocene and Early Pliocene faunas all over Eurasia. In Africa, Winkler (2003) reported its occurrence with relatively abundant remains from the Nawata Formation at Lothagam in Kenya, dated to ca. 6.5 Ma. Wesselman *et al.* (2009) described some remains of *Alilepus* sp. from the Sagantole Formation (4.85 Ma), Middle Awash, Ethiopia). Darwent (2007) described a fragmentary maxilla from Lemudong'o (ca. 6 Ma) in Kenya as ?*Alilepus* sp. This account shows the poor state of knowledge on the fossil occurrences of African leporids, which does not allow the development of discussion on their systematic relationships.

Discussion and Conclusions

This study initially aimed to describe fossil remains of Leporidae from the Plio-Pleistocene sites in the Humpata Plateau in southwestern Angola. It soon became apparent that fossil lagomorphs of southern Africa are poorly studied, and the extant leporids are known mainly by their external features (size, fur, length of ears and hindlimbs, colour of tail...), while their skeletal and dental characters are poorly understood. To fill this gap, this study first focussed on the definition of the cranial and dental characters of the extant species of the genus *Pronolagus*, to which the Angolan fossil material is attributed. For doing this we illustrate and describe the osteology and dentition of the type specimens of *P. crassicaudatus*, *P. randensis* and *P. rupestris vallicola*, and comment on their differences in skull and tooth morphology. Comparison of the fossils from the Humpata Plateau with these extant species shows that they display many characters different from those of the extant species, and thus they are identified as a new species, *Pronolagus humpatensis* nov. sp. This is the first fossil species of *Pronolagus* to be described from southern Africa, except for *P. intermedius* Jameson, 1909, which is a *nomen oblitum* (see above).

For the extant species of *Pronolagus*, we mainly noted that the curvature of the cranium in lateral view is stronger in *P. randensis* than in the other species and the tip of the skull is situated above the orbits, while in *P. rupestris* it is more backwards above its distal limit. *P. crassicaudatus* also has the tip of the curvature

above the orbit, but the curvature is much less and the anterior portion of the cranium is almost flat in lateral view. *P. rupestris*, and to a lesser degree *P. randensis* have short and robust muzzles while it is elongated in *P. crassicaudatus*. Also, *P. randensis* is distinguished by its strong supraorbital wings, which are rather gracile in the other extant species of the genus, and the frontal/parietal suture is much more distal. The width of the choanae and incisor foramina are important characters for distinguishing leporid species. Among the extant species of *Pronolagus*, *P. rupestris* has these apertures somewhat larger than the others. In this respect, a special mention is needed for *Pronolagus ruddi* Thomas and Schwann, 1905, from Zululand, which is considered to be a subspecies of *P. crassicaudatus* (Collins, 2005; Happold, 2013; Matthee *et al.* 2016). In this form, the choanae and incisor foramina are even larger than in *P. rupestris*, and in these characters it clearly differs from the type skull of *P. crassicaudatus*. Leporids having strong saltatorial and cursorial capacities have large palatal openings such as incisor foramina and choanae. In South African hares *L. capensis* and *L. saxatilis*, as well as in the riverine rabbit *Bunolagus monticularis*, these palatal openings are very wide, indicating for these species high speed running (*Lepus*) or jumping (*Bunolagus*) that the zoologists describe as characteristic of their behavior (Kraatz *et al.* 2015; Kraatz & Sherrat, 2016). From this observation, we can deduce a more cursorial capacity for *P. rupestris*, "*P. ruddi*"

and *P. humpatensis* nov. sp. than the other representatives of the genus. In some characters, the cranial remains from the Humpata Plateau recall *P. crassicaudatus* and *P. randensis* in having an elongated muzzle and distally elongated nasal bones, but its size is rather closer to that of *P. rupestris*. Also, the width of the choanae and the shape of the upper incisor recall the latter species, although many differences exist between the proportions of cranial and postcranial bones, and in particular in their dentition. As shown above, the description of *Pronolagus* from the Humpata Plateau represents the first detailed report of this genus in the fossil record, although its occurrence has been mentioned in faunal lists from a dozen localities in southern Africa.

The fossil lagomorphs of the Humpata Plateau do not allow us to deduce any age for this species, neither for their sites due to the fact that the evolutionary history of the genus *Pronolagus* and morphological changes in its skeletal and dental characters are totally unknown. In the southern African fossil record the genus *Pronolagus* is mentioned from the Lower Pliocene upward. Unfortunately none of these occurrences has been described and/or illustrated to be useful for further analyses. Winkler (2004) noted that even when present, the remains of this rock rabbit are rare in fossil records. This is probably due to their habitat characteristics. The extant pronolagids are dependant on the availability of rocky habitats and remain closely confined to krantzes and rocky hillsides where they graze on grass (Watson, 1993).

However, the mammalian fauna of the Humpata Plateau deposits contains elements of high chronological significance. The majority of the fossils from the Humpata breccias consists of micromammals, especially rodents,

with macroscelideans, soricids and bats being common and lagomorphs rarer. The faunal list includes a few larger mammals such as *Theropithecus baringensis*, *Metridiochoerus andrewsi*, large bovids, *Chasmaporthetes* sp. (hyaenid) and hyracoids (*Gigantohyrax*, *Procavia*). The faunas from the diverse localities are listed in Table 2.

The suid *Metridiochoerus andrewsi* from Cangalongue 2 and 3 is represented by specimens that are compatible with stage II of the evolutionary series of the species as determined by Harris & White (1979) which suggests an age of 1.8-1.3 Ma for these deposits. In contrast the presence of *Gigantohyrax* at Malola indicates an age closer to 3.3 Ma (Pickford *et al.* 1992).

Jablonski (1994) revised the fossil baboons from the Humpata Plateau and attributed them to a single species *Theropithecus baringensis*, the type locality of which is the Chemeron Formation, Kenya, dated between 3 and 2 Ma (Jablonski & Frost, 2010). The youngest record of the hyaenid *Chasmaporthetes* is ca 1 Ma (Werdelin & Peigné, 2010). From this it is inferred that, as an ensemble, the Humpata breccias span the period ca 3 Ma to ca 1 Ma.

The Tchiua Pink Breccia which yielded the best preserved lagomorph specimens probably dates from the Pleistocene (1.8-1.3 Ma). At Tchiua, the pink breccia is younger than the primate-rich grey breccia (Pickford *et al.* 1992) which is estimated to be late Pliocene to basal Pleistocene in age (ca 3-2 Ma). The breccias from Cangalongue which also yielded lagomorphs, are possibly coeval with the Tchiua Pink Breccia occurrence (ca 1.8-1.3 Ma).

Acknowledgements

The fossils described herein were collected during the Angola Palaeontology Expedition, funded by the Collège de France and supported administratively by the Muséum National d'Histoire Naturelle, Paris. Dr. Samel Aço (Luanda) directed the Angolan contingent of the expedition. The assistance of the Museu Regional da Huíla, Lubango (Dr. José Ferreira) is greatly appreciated. Pierre Mein treated the breccia blocks, sorted and identified the fossils and prepared the micromammalian faunal lists.

We are indebted to the curators of museums and colleagues who allowed us to study specimens under their care and/or provided photographs: Cécile Callou and Violaine Colin (MNHN, Paris), Emmanuel Gelissen (Royal Museum for Central Africa, Tervuren), Roberto Portela Miguez (Natural History Museum, London), Josep Quintana Cardona (Institut Català de Paleontologia, Sabadell), Nico L. Avenant (National Museum, Bloemfontein), Ge Deyan and Zhang Zhaqun

(IVPP, Beijing). Other colleagues provided advice and/or documents on the southern African Leporidae: Chiara Angelone (Università Roma Tre, Roma), Renata Angermann (Museum für Naturkunde, Berlin), Margarita Erbjajeva (Geological Institute, Ulan Ude), Fernando Palacios (Museo Nacional de Ciencias Naturales, Madrid), Josep Quintana Cardona (Universitat Autònoma de Barcelona),

Florah Ratema (Ditsong National Museum of Natural History, Pretoria), Terry Robinson (McGregor Museum, Kimberley), Alisa Winkler (Southern Methodist University, Dallas), which were very helpful for studying the Angolan fossils. Martine Faure (Université Lyon 2) helped with pictures and documents, and encouraged the progress of this study at every step. We are grateful to all.

References

- Adams, J.W. 2012. A revised listing of fossil mammals from the Haasgat cave system ex situ deposits (HGD), South Africa. *Palaeontologia Electronica*, 15.3.29A, 88 pp. palaeo-electronica.org/content/2012-issue-3-articles/323-haasgat-hgd-assemblage
- Adams, J.W. 2018. Fossil mammals from the Gondolin Dump A ex situ hominin deposits, South Africa. *PeerJ* 6, e5393. doi: 10.7717/peerj.5393.
- Allen, G.M. 1939. A Checklist of African Mammals. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 83, 1-763.
- Amaral, L. 1973. Nota sobre o « karst » ou carso do Planalto da Humpata (Huila), no Sudoeste de Angola. *Garcia de Orta*, Lisboa, 1 (2), 29-36.
- Antunes, M.T. 1965. Sur la faune de vertébrés du Pléistocène de Leba, Humpata (Angola). Actas del Vº Congreso Panafricano de Prehistoria y de Estudio del Cuaternario, Museo Arqueológico, Santa Cruz de Tenerife, 1 (5), 127-128.
- Arambourg, C. & Mouta, F. 1955. Les grottes et fentes à ossements du sud de l'Angola. *Actes du Congrès Panafricain de Préhistoire*, Alger 1952, 2è Session, Communications, 12, 301-304.
- Averianov, A. 1995. Osteology and adaptations of the Early Pliocene rabbit *Trischizolagus dumitrescuae* (Lagomorpha: Leporidae). *Journal of Vertebrate Paleontology*, 15, 375-386. <https://doi.org/10.1080/02724634.1995.10011236>
- Averianov, A.O. 1999. Phylogeny and classification of Leporidae (Mammalia, Lagomorpha). *Vestnik zoologii*, 33 (1-2), 41-48.
- Avery, D.M. 2019. *A Fossil History of Southern African Land Mammals*. Cambridge University Press, 315 pp. doi: 10.1017/9781108647243
- Beetz, P.F.W. 1933. Geology of South West Angola, between Cunene and Lunda axis. *Transactions of the Geological Society of South Africa, Johannesburg*, 36, 137-176.
- Bensley, B.A. 1948. *Practical Anatomy of the Rabbit*, 8th Edition, Toronto, University of Toronto Press, 391 pp.
- Brain, C.K. 1981. *The Hunters or the Hunted? An Introduction to African Cave Taphonomy*. The University of Chicago Press. x+365 pp.
- Brandt, J.F. 1855. Beiträge zur nähern Kenntniss der Säugethiere Russland's. *Mémoires de l'Académie impériale des Sciences de St. Pétersbourg*, 6è série, *Sciences naturelles*, 7, 1-336.
- Brink, J., Holt, S. & Horwitz, L.K. 2016. The Oldowan and early Acheulean mammalian fauna of Wonderwerk Cave (Northern Cape Province, South Africa). *African Archaeology Review*, 33, 223-250.
- Bronner, G.N., Hoffmann, M., Taylor, P.J., Chimimba, C.T., Best, P.B., Matthee, C.A. & Robinson, T.J. 2003. A revised systematic checklist of the extant mammals of the southern African subregion. *Durban Museum Novitates*, 28, 56-96.
- Čermák, S., Angelone, C. & Sinitza, M.V. 2015. New Late Miocene *Alilepus* (Lagomorpha, Mammalia) from Eastern Europe casts a new light on the evolution of the earliest Old World Leporinae. *Bulletin of Geosciences*, 90, 431-451. <https://doi.org/10.3140/bull.geosci.1523>
- Collins, K. 2005. Order Lagomorpha. In: Skinner, J.D. & Chimimba, C.T. (Eds) *The Mammals of the Southern African Subregion* (3rd Edition). Cambridge University Press. pp. 63-76. doi:10.1017/CBO9781107340992.013.
- Cooke, H.B.S. 1963. Pleistocene mammal faunas of Africa with particular reference to southern Africa. In: Howell, F.C. &

- Bourlière, F. (Eds) *African Ecology and Human Evolution*. Chicago, Aldine Press, Illinois. pp. 65-116.
- Cuvier, F. 1823. Lièvre des rochers, *Lepus saxatilis*. *Dictionnaire des Sciences Naturelles*, **26**, 309-310.
- Dart, R. 1950. A note on the limestone caverns of Leba, near Humpata (Angola). *The South African Archaeological Bulletin*, **5** (20), 149-151.
- Darwent, C.M. 2007. Lagomorphs (Mammalia) from late Miocene deposits at Lemudong'o, southern Kenya. *Kirtlandia*, **56**, 112-120.
- David, H., Dauphin, Y., Gautret, P., Pickford, M. & Senut, B. 1999. Composition en acides aminés d'os de mammifères fossiles de deux sites du Plio-Pleistocène d'Angola. Comparaison avec la conservation de la phase minérale. *Geodiversitas*, **21**, 215-228.
- Daxner, G. & Fejfar, O. 1967. Über die Gattungen *Alilepus* Dice, 1931 und *Pliopentalagus* Gureev, 1964 (Lagomorpha, Mammalia). *Annalen des Naturhistorischen Museums in Wien*, **71**, 37-55.
- De Marfà i Taillefer, R. 2009. *Els lagomorfs (O. Lagomorpha, Cl. Mammalia) del Pliocè i Pleistocè europeus*. Tesis Doctorals, Universitat de Barcelona - Departament Estratigrafia i Paleontologia, 205 pp.
- Delson, E. & Dean, D. 1992. Are *Papio baringensis* R. Leakey, 1969, and *P. quadratiostris* Iwamoto, 1982, species of *Papio* or *Theropithecus*? In: Jablonski, N. (Ed) *Theropithecus, The Rise and Fall of a Primate Genus*. Cambridge University Press, pp. 125-156.
- Díaz, A. 1893. *Catálogo de los objetos que componen el contingente de la Comisión, precedido de algunas notas sobre su organización y trabajos*. Exposición Internacional Columbina de Chicago. Comisión Geográfica-Exploradora de la República Mexicana, Tipografía de la Comisión Geografico-Exploradora, Xalapa-Enriquez, 24 pp.
- Duthie, A.G. & Robinson, T.J. 1990. Chapter 8: The African Rabbits. In: Chapman, J.A. & Flux, J.E.C. (Eds) *Rabbits, Hares and Pikas: Status Survey and Conservation Action Plan*. IUCN, Gland, Switzerland, pp. 121-127.
- Faber, F.J. 1926. *Bijdrage tot de Geologie van Zuid-Angola (Afrika)*. Proefschrift. Delft, Gedrukt bij de Technische Boekhandel en Drukkerij, J. Waltman Jr, 104 pp.
- Fischer, G. 1817. *Adversaria zoologica. Fasciculus primus. Mémoires de la Société impériale des Naturalistes de Moscou*, **5**, 357-428.
- Flynn, L.J., Winkler, A.J., Erbajeva, M., Alexeeva, N., Anders, U., Angelone, C., Čermák, S., Fladerer, F.A., Kraatz, B., Ruedas, L.A., Ruf, I., Tomida, Y., Veitschegger, K. & Zhang, Z. 2013. The Leporid datum: a late Miocene biotic marker. *Mammal Review*, **44** (3-4), 164-176.
- França, J. 1964. Nota preliminar sobre uma gruta pré-histórico do Planalto da Humpata (Angola). *Memórias da Junta da Investigações do Ultramar*, **2** (50), 59-67.
- Friedmann, Y. & Daly, B. 2004. Lagomorpha: taxon data-sheets and distribution maps. Section 9. In: *Red Data Book of the Mammals of South Africa: A Conservation Assessment, CBSG Southern Africa*. Conservation Breeding Specialist Group (SSC/IUCN), Endangered Wildlife Trust, South Africa, pp. 418-426.
- Gautier, A. 1995. Restes animaux holocènes et du paléolithique moyen (MSA) de la grotte de Leba sur le plateau de Humpata (Angola). *Archaeofauna*, **4**, 131-141.
- Ge, D., Yao, L., Xia, L., Zhang, Z. & Yang, Q. 2015. Geometric morphometric analysis of skull morphology reveals loss of phylogenetic signal at the generic level in extant lagomorphs (Mammalia: Lagomorpha). *Contribution to Zoology*, **84**, 267-284.
- Geoffroy Saint-Hilaire, I. 1832. Remarques sur les principaux caractères des espèces du genre Lièvre, considérés dans leurs rapports avec les circonstances locales; suivies de la Description de trois nouvelles espèces. *Magasin de Zoologie*, **2^e année**, Cl. I, pls. 9, 10.
- Gilbert, C.C., McGraw, W.S. & Delson, E. 2009. Brief communication: Plio-Pleistocene eagle predation on fossil cercopithecids from the Humpata Plateau, southern Angola. *American Journal of Physical Anthropology*, **139** (3), 421-429.
- Happold, D.C.D. 2013. Genus *Pronolagus*. In: Happold D.C.D. (Ed.) *Mammals of Africa. Volume III: Rodents, Hares and Rabbits*. London, UK, Bloomsbury Publishing, pp. 713-717.
- Happold, D.C.D. 2018. Family Leporidae. In: Smith, A.T., Johnston, C.H., Alves, P.C. & Hackländer, K. (Eds) *Lagomorphs. Pikas, Rabbits and Hares of the World*. Baltimore,

- Johns Hopkins University Press, pp. 87-224.
- Harris, J.M. & White, T.D. 1979. Evolution of the Plio-Pleistocene African Suidae. *Transactions of the American Philosophical Society*, **69**, 1-126.
- Hendey, Q.B. 1981. Palaeoecology of the late Tertiary fossil occurrences in 'E' Quarry, Langebaanweg, South Africa and a reinterpretation of their geological context. *Annals of the South African Museum*, **84**, 1-104.
- Hewitt, J. 1927. On several new rodents in the Albany Museum. *Records of the Albany Museum*, **3**, 430-440, plates 26-27.
- Hibbard, C.W. 1963. The origin of the p/3 pattern of *Sylvilagus*, *Caprolagus*, *Oryctolagus* and *Lepus*. *Journal of Mammalogy*, **44** (1), 1-15.
- Hoffmann, R.S. & Smith, A.T. 2005. Order Lagomorpha. In: Wilson, D.E. & Reeder D.M. (Eds) *Mammal Species of the World. A Taxonomic and Geographic Reference*, Third edition, Volume 1. Baltimore, The Johns Hopkins University Press, pp. 185-211.
- International Code of Zoological Nomenclature 1999. *International Trust for Zoological Nomenclature*, 106 pp.
- Jablonski, N. 1994. New fossil cercopithecoid remains from the Humpata Plateau, southern Angola. *American Journal of Physical Anthropology*, **94** (4), 435-464.
- Jablonski, N. & Frost, S. 2010. Cercopithecoidea. In: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*. Berkeley, Los Angeles, London, University of California Press, pp. 193-428.
- Jameson, H.L. 1907. On a new hare from the Transvaal. *Annals and Magazine of Natural History*, **7** (20), 404-406.
- Jameson, L. 1909. On a sub-fossil hare from a cave deposit at Godwan River. *Annals of the Transvaal Museum* **1** (3), 195-196.
- Kershaw, P.S. 1924. Two new mammals from East Africa. *Annals and Magazine of Natural History*, **13**, 79-81.
doi: 10.1080/00222932408633008
- Klemme, M. 1955. Southern Angola and the limestone industry. *Relatorio Copia Serviços de Geologia e Minas de Angola*, pp. 5-44.
- Kraatz, B. & Sherratt, E. 2016. Evolutionary morphology of the rabbit skull. *PeerJ*, 4:e2453; doi:10.7717/peerj.2453.
- Kraatz, B.P., Sherratt, E., Bumacod, N. & Wedel, M.J. 2015. Ecological correlates to cranial morphology in leporids (Mammalia, Lagomorpha). *PeerJ*, 3:e844; doi 10.7717/peerj.844.
- Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species cum Characteribus, Differentiis, Synonymis, Locis, Editio Decima, Reformata*. Vol. I. Laurentii Salvii, Olmia. <https://doi.org/10.5962/bhl.title.542>
- López-Martínez, N. 2008. The lagomorph fossil record and the origin of the European rabbit. In: Alves, P.C., Ferrand, N. & Hackländer, K. (Eds) *Lagomorph Biology: Evolution, Ecology, and Conservation*. Berlin, Heidelberg, Springer-Verlag, pp. 27-46.
- López-Martínez, N., Likius, A., Mackaye, H.T., Vignaud, P. & Brunet, M. 2007. A new lagomorph from the late Miocene of Chad (Central Africa). *Revista Española de Paleontología*, **22**, 1-20.
- Lyon, M.W. 1903. Classification of the hares and their allies. *Smithsonian Miscellaneous Collections*, **45**, 321-447.
- Mason, R. 1976. Exploration archaeology of the Kaokoveld and Southern Angola and the potential australopithecine sites in the Serra da Chela massif, southern Angola. *Annals of the South African Museum*, **71**, 215-223.
- Matos, D. de, Francisco, R., Fernandes, J., Robakiewicz, E. & Barros, B. 2021. A paisagem cársica do Sudoeste de Angola. Primeira abordagem ao património subterrâneo da Formação Leba. *Revista Angolana Geociências*, **2** (1), 127-143.
- Matthee, C.A. & Robinson, T.J. 1996. Mitochondrial DNA differentiation among geographical populations of *Pronolagus rupestris*, Smith's red rock rabbit (Mammalia: Lagomorpha). *Heredity*, **76**, 514-523.
- Matthee, C.A., Jansen van Vuuren, B., Bell, D. & Robinson, T.J. 2004. A molecular supermatrix of the rabbits and hares (Leporidae) allows for the identification of five intercontinental exchanges during the Miocene. *Systematic Biology*, **53**, 433-447.
- Matthee, C., Wilson, B., Robinson, T.J. & Child, M.F. 2016. A conservation assessment of *Pronolagus* spp. In: Child, M.F., Roxburgh, L., Do Linh San, E., Raimondo, D. & Davies-Mostert, H.T. (Eds) *The Red List of Mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa, pp. 1-8.
- Meester, J.A., Rautenbach, I.L., Dippenaar, N.J.

- & Baker, C.M. 1986. Classification of southern African mammals. *Transvaal Museum Monographs*, **5**, 1-359.
- Minkoff, E. 1972. A fossil baboon from Angola, with a note on *Australopithecus*. *Journal of Palaeontology*, **46**, 836-844.
- Mouta, F. 1950. Sur la présence de Quaternaire ancien dans les hauts plateaux du sud de l'Angola (Humpata-Leba). *Comptes rendus des Séances de la Société géologique de France*, **14**, 261-262.
- Mouta, F. 1954. Notícia explicativa do esboço geológica de Angola 1 : 2 000 000. *Junta da Investigações do Ultramar*, pp. 1-148, pls 1-13, geological map.
- Palacios Arribas, F. & López Martínez, N. 1980. Morfología dentaria de las liebres europeas (*Lagomorpha*, *Leporidae*). *Doñana Acta Vertebrata*, **7**, 61-81.
- Palacios Arribas, F., Angelone, C., Germán, A. & Reig, S. 2008. Morphological evidence of species differentiation within *Lepus capensis* Linnaeus, 1758 (*Leporidae*, *Lagomorpha*) in Cape Province, South Africa. *Mammalian Biology*, **73**, 358-370.
- Petter, F. 1959. Eléments d'une révision des lièvres africains du sous-genre *Lepus*. *Mammalia*, **23**, 41-67.
- Petter, F. 1971. Order Lagomorpha, Part 5. In: Meester, J. & Setzer, H.W (Eds) *The Mammals of South Africa: an Identification Manual*. Smithsonian Institution Press, Washington D.C., pp. 1-7.
- Pickford, M. 2019. Kaokoland Cascade Tufa Survey: Interim Report. *Communications of the Geological Survey of Namibia*, **21**, 82-93.
- Pickford, M. & Senut, B. 1997. Cainozoic mammals from coastal Namaqualand, South Africa. *Palaeontologia africana*, **34**, 199-217.
- Pickford, M., Fernandes, T. & Aço, S. 1990. Nouvelles découvertes de remplissages de fissures à primates dans le "Planalto da Humpata", Huíla, Sud de l'Angola. *Comptes rendus de l'Académie des Sciences*, **II-310**, 843-848.
- Pickford, M., Mein, P. & Senut, B. 1992. Primate bearing Plio-Pleistocene cave deposits of Humpata, Southern Angola. *Human Evolution*, **7**, 17-33.
- Pickford, M., Mein, P. & Senut, B. 1994. Fossiliferous Neogene karst fillings in Angola, Botswana and Namibia. *South African Journal of Science*, **90**, 227-230.
- Pocock, T.N. 1976. Pliocene mammalian microfauna from Langebaanweg: A new fossil genus linking the Otomyinae with the Murinae. *South African Journal of Science*, **72**, 58-60.
- Pocock, T.N. 1987. Plio-Pleistocene fossil mammalian microfauna of southern Africa - A preliminary report including description of two new fossil muroid genera (Mammalia : Rodentia). *Palaeontologia africana*, **26** (7), 69-91.
- Quintana Cardona, J. 2005. *Estudio morfológico y funcional de Nuralagus rex (Mammalia, Lagomorpha, Leporidae)*. PhD Thesis, Universitat Autònoma de Barcelona, 359+142 pp.
- Quintana, J., Köhler, M. & Moyà-Solà, S. 2011. *Nuralagus rex*, gen. et sp. nov., an endemic insular giant rabbit from the Neogene of Minorca (Balearic Islands, Spain). *Journal of Vertebrate Paleontology*, **31**, 231-240.
- Roberts, A. 1951. *The Mammals of South Africa*. Johannesburg. Trustees of 'The Mammals of South Africa' Book Fund., viii + 701 pp.
- Robinson, T.J. 1982. Key to the South African Leporidae (Mammalia: Lagomorpha). *South African Journal of Zoology*, **17**, 220-222.
- Robinson, T.J. 1986. Incisor morphology as an aid in the systematics of the South African Leporidae (Mammalia: Lagomorpha). *South African Journal of Zoology*, **21** (4), 297-302, doi: 10.1080/02541858.1986.11448002
- Robinson, T.J. & Dippenaar, N.J. 1983. Morphometrics of the South African Leporidae. I. Genus *Pronolagus* Lyon, 1904. *Annalen - Koninklijk Museum voor Midden-Africa : Zoologische Wetenschappen*, **237**, 43-61.
- Robinson, T.J. & Mathee, C.A. 2005. Phylogeny and evolutionary origins of the Leporidae: a review of cytogenetics, molecular analyses and a supermatrix analysis. *Mammal Review*, **35** (3-4), 231-247.
- Ruf, I. 2014. Comparative anatomy and systematic implications of the turbinal skeleton in Lagomorpha (Mammalia). *The Anatomical Record*, **297**, 2031-2046.
- Shortridge, G.C. 1942. Field notes on the first and second expeditions of the Cape Museum's mammal survey of the Cape Province: descriptions of some new subgenera and subspecies. *Annals of the South African Museum*, **36**, 27-100.
- Smith, A. 1835. African Zoology, continued. *South African Quarterly Journal*, **2**, 169-192.

- Smith, A.T., Johnston, C.H., Alves, P.C. & Hackländer, K. 2018. *Lagomorphs: Pikas, Rabbits and Hares of the World*. Baltimore, Johns Hopkins University Press, 280 pp.
- Sparwel, M., Doronina, L., Churakov, G., Stegemann, A., Brosius, J., Robinson, T.J. & Schmitz, J. 2019. The Volcano Rabbit in the phylogenetic network of lagomorphs. *Genome Biology and Evolution*, **11** (1), 11-16. doi:10.1093/gbe/evy257
- Thomas, O. 1903. On a remarkable new hare from Cape Colony. *The Annals and Magazine of Natural History*, **11**, 78-79.
- Thomas, F.R.S. & Schwann, H. 1905. The Rudd exploration of South Africa. III. List of the mammals obtained by Mr. Grant in Zululand. *Proceedings of the General Meetings for Scientific Business of the Zoological Society of London*, **1**, 254-276.
- Vale, F., Gonçalves, F. & Simões, M. 1968. *Carta geológica de Angola, escala 1:100 000. Notícia explicativa da folha N° 355 (Humpata-Cainde)*. Serviços de Geologia e Minas de Angola. 38 pp.
- Van Neer, W. & Breunig, P. 1999. Contribution to the archaeozoology of the Brandberg, Namibia. *Cimbebasia*, **15**, 127-140.
- Voorhies, M.R. & Timperley, C.L. 1997. A new *Pronotolagus* (Lagomorpha: Leporidae) and other leporids from the Valentine Railway Quarries (Barstovian, Nebraska), and the archaeolagine-leporine transition. *Journal of Vertebrate Paleontology*, **17**, 725-737.
- Watson, V. 1993. Glimpses from Gondolin: A faunal analysis of a fossil site near Broederstroom, Transvaal, South Africa. *Palaeontologia africana*, **30**, 35-42.
- Welbourne, R. 1976. Remarks on the fossil fauna of the Serra da Chela massif, Southern Angola. *Annals of the South African Museum*, **71**, 223-224.
- Wells, C.R. 2006. A sample integrity analysis of faunal remains from the RSp layer at Sibudu Cave. *Southern African Humanities*, **18**, 261-277.
- Werdelin, L. & Peigné, S. 2010. Carnivora. In: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*. Berkeley, Los Angeles, London, University of California Press, pp. 603-637.
- Wesselman, H.B., Black, M.T. & Asnake, M. 2009. Small mammals. In: Haile-Selassie, Y. & WoldeGabriel, G. (Eds) *Ardipithecus kadabba, Late Miocene Evidence from the Middle Awash, Ethiopia*. University of California Press, pp. 105-134.
- White, J.A. 1991. North American Leporinae (Mammalia: Lagomorpha) from late Miocene (Clarendonian) to latest Pliocene (Blancan). *Journal of Vertebrate Paleontology*, **11**, 67-89. doi:10.1080/02724634.1991.10011376
- Whiteford, C.E.M. 1995. *Molecular Phylogeny of the Genus Pronotolagus (Mammalia: Lagomorpha) and the Use of Morphological and Molecular Characters in the Delineation of P. rupestris*. Doctoral dissertation, Universiteit van Pretoria.
- Winkler, A.J. 2003. Rodents and lagomorphs from the Miocene and Pliocene of Lothagam, Northern Kenya. In: Leakey, M.G. & Harris, J.M. (Eds) *Lothagam. The Dawn of Humanity in Eastern Africa*. New York, Columbia University Press, pp. 169-190.
- Winkler, A.J. 2004. Fossil history of African lagomorphs. *Proceedings of the XIXth International Congress of Zoology, Beijing*, pp. 23-27.
- Winkler, A.J. & Avery, D.M. 2010. Lagomorpha. In: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*. Berkeley, California, University of California Press, pp. 305-317.