

A NEW LAGOMORPH FROM THE LATE MIOCENE OF CHAD (CENTRAL AFRICA)

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López-Martínez, N., Likius, A., Mackaye, H. T., Vignaud, P. & Brunet, M. 2007. A new Lagomorph from the Late Miocene of Chad (Central Africa). [Un nuevo Lagomorfo del Mioceno superior de Chad (África central).] *Revista Española de Paleontología*, **22** (1), 1-20. ISSN 0213-6937.

ABSTRACT

A new species of the genus *Serengetilagus* Dietrich 1941, here named *S. tchadensis* n. sp., is described from Toros Menalla deposits, Late Miocene of Djurab Erg (North Chad, central Africa). It shows primitive features, such as a simple archaeolagine-type p3, with only two main external folds, and upper cheek teeth strongly widened with wear. Its size and skeletal features resemble *S. praecapensis* Dietrich 1941 from the Middle Pliocene of Laetoli (Tanzania). They differ in several cranial and dental features (choanae width, zygoma, orbits, basicranial-basifacial angle, lack of hypoflexus in P2, short and asymmetric hypoflexus in P3-M2, lack of lingual folds in p3, etc). Individual variations in *S. tchadensis* n. sp. approach *S. praecapensis*, such as an incipient anteroflexid and a forward-curved hypoflexid in some p3. The genus *Serengetilagus* is here assigned to the subfamily Archaeolaginae Dice 1929 and related to *Hypolagus* Dice 1917, namely to *H. gromovi* Gureev 1964 from the Late Miocene of Southern Russia. Other related species are *Serengetilagus orienteuropaeus* Topachevsky 1987 and primitive species of the genus *Trischizolagus* Radulesco & Samson 1967, such as *T. maritsae* De Bruijn, Dawson & Mein 1970 and *T. crusafonti* (Janvier & Montenat 1971). Pliocene leporids from Spain, Ukraine, Russia, Afghanistan and Mongolia have been questionably attributed to *Serengetilagus* or *Trischizolagus*, which seem synonymous for some authors. Several features are here proposed to distinguish both genera: rounded versus rhombic-shaped p3, weak versus strong lingual anteroconid - anteroflexid, and forward versus backward hypoflexid bend.

Serengetilagus could have a mixed fossorial-cursorial mode of life, as can be inferred by its ecomorphological traits (combining features of hare and rabbit) and taphonomical indications. This new African archaeolagine is contemporaneous of the widespread palaeolagine *Alilepus* Dice 1931, recorded in the Late Miocene of Kenya. The independence of these two lineages is favoured after revision of previous hypotheses on the phylogeny of the highly diverse Mio-Pliocene peri-Tethysian leporid species.

Key words: Late Miocene, Chad, Africa, Mammalia, Leporidae, *Serengetilagus*, phylogeny, mode of life.

RESUMEN

Se describe una nueva especie de Lagomorfo del género *Serengetilagus* Dietrich 1941, llamada *S. tchadensis* n. sp., de los depósitos de Toros Menalla, Mioceno superior del Djurab Erg (norte del Chad, África central). Este leporido muestra rasgos primitivos, como un simple p3 de tipo archaeolagino, con sólo dos surcos externos, y dientes yugales superiores fuertemente ensanchados por el uso. Su tamaño y rasgos esqueléticos son semejantes a *S. praecapensis* Dietrich 1941 del Plioceno medio de Laetoli (Tanzania). Ambas especies difieren en varios rasgos craneales y dentarios (anchura de coanas, zigoma, órbitas, ángulo basicranial-basifacial, falta de hipoflexo en P2, hipoflexo corto y asimétrico en P3-M2, falta de surcos linguales en p3, etc). Las variantes indivi-

duales de *S. tchadensis* n. sp. se acercan a *S. praecapensis*, p.ej. anteroflexido incipiente o hipoflexido curvado hacia adelante en algún p3. El género *Serengetilagus* es aquí asignado a la subfamilia Archaeolaginae Dice 1929 y relacionado con *Hypolagus* Dice 1917, particularmente con *H. gromovi* Gureev 1964 del Mioceno superior del sur de Rusia. Otras especies relacionadas son *Serengetilagus orienteuropaeus* Topachevsky 1987 y especies primitivas del género *Trischizolagus* Radulesco & Samson 1967, como *T. maritsae* De Bruijn, Dawson & Mein 1970 y *T. crusafonti* (Janvier & Montenat 1971). Lepóridos del Plioceno de España, Ucrania, Rusia, Afganistán y Mongolia han sido cuestionados en su asignación a *Serengetilagus* o a *Trischizolagus*, que resultan sinónimos para algunos autores. Proponemos varios caracteres para distinguir ambos géneros: p3 redondeado o rómbico, anterocónido lingual y anteroflexido débiles o fuertes, e hipoflexido doblado hacia delante o hacia atrás.

Serengetilagus pudo haber tenido un modo de vida mixto cavador-corredor, como puede inferirse por sus rasgos ecomorfológicos (que combinan caracteres de liebre y conejo) y por indicaciones tafonómicas. Este nuevo arqueolaguino africano es contemporáneo del ubicuo paleolaguino *Alilepus* Dice 1931, señalado en el Mioceno superior de Kenya. La independencia de estos dos linajes resulta probable tras la revisión de hipótesis previas sobre la filogenia de los muy diversos Lepóridos del Mio-Plioceno *circum-tethysiano*.

Palabras clave: Mioceno superior, Chad, Africa, Mamíferos, Lepóridos, *Serengetilagus*, filogenia, modo de vida.

INTRODUCTION

The Late Miocene sites at Toros Menalla, Northern Chad (Central Africa) have delivered rich fossil vertebrate assemblages, including one of the oldest Hominidae *Sahelanthropus tchadensis* Brunet *et al.* 2002 (see also Brunet *et al.*, 2004, 2005). Besides large mammals, some small mammals have also been recovered by screen-sieving and visual inspection. Here we describe an assemblage of lagomorph remains attributed to a new species of the genus *Serengetilagus* Dietrich 1941, mainly known by its type species *S. praecapensis* Dietrich 1941 from the Middle Pliocene of East Africa.

Some remains attributed to *Serengetilagus* aff. *S. praecapensis* were already signalled in the Lower Pliocene deposits from Chad at Kossom Bougoudi (Brunet *et al.*, 2000). New material from five localities in the Toros Menalla area allows to describe a new species and better precise the biochronological succession and faunal composition of these older assemblages.

GEOLOGICAL SETTING

The material comes from the Toros-Menalla (TM) fossiliferous area, located in the intracratonic Chad Basin at about 500 km north of the present Lake Chad (Fig. 1).

Sedimentological series of TM area comprise aeolian sandstones, perilacustrine sandstones and lacustrine pelites and diatomites. The perilacustrine facies corresponds to a moderately to well cemented sandstone informally named the Anthracotheriid Unit (AU). AU yielded a very rich fauna including fish, reptiles, birds and mammals (among them numerous anthracotheriids remains), which indicate a biochronological age of Late Miocene, around 7 Ma (Vignaud *et al.*, 2002; Brunet *et al.*, 2002, 2004, 2005).

Five localities located in the TM area corresponding to the AU sandstones yielded the material of lagomorph fossil remains described here.

MATERIAL AND METHODS

The material has been collected during the 2001, 2003 and 2004 field missions lead by the Mission Paleoanthropologique Franco Tchadienne (MPFT) and prepared in CNAR N'Djamena (Chad), University of Poitiers (France) and Universidad Complutense de Madrid (UCM, Spain).

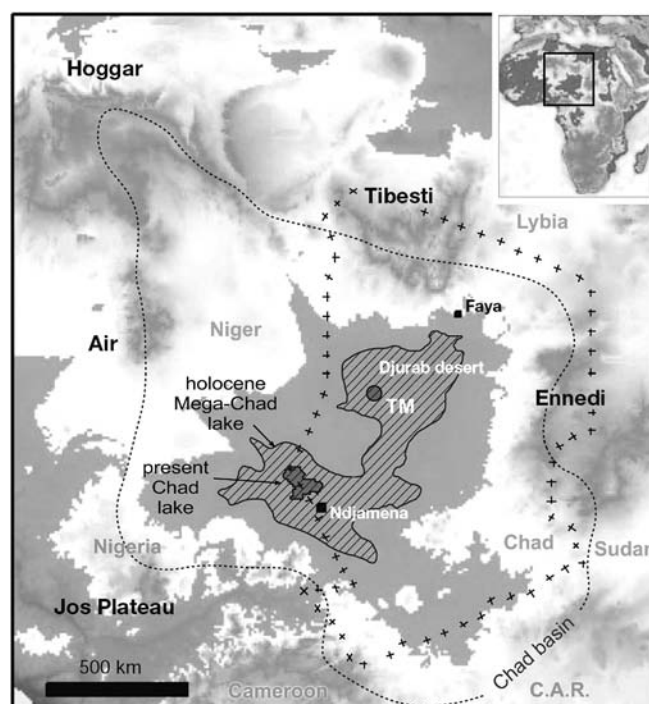


Figure 1. Map showing the situation of Toros Menalla fossil sites. Modified from Vignaud *et al.* (2002).

The anatomical nomenclature is that from López-Martínez (1989; see Fig. 2). Equivalence with other author's terminology is below. The serial order of folds in the list agrees with the order of their appearance in the lagomorph fossil record

for upper cheek teeth (P2 and upper molariforms):

- 1- paraflexus = anterior fold = MAR
- 2- mesoflexus = anteroexternal fold = EAR
- 3- hypoflexus = internal fold = IAR

for lower cheek teeth (p3 and molariforms)

- 1- hypoflexid = posteroexternal fold = PER = *Hauptbuccalfalte* HBF
- 2- mesoflexid = posterointernal fold = PIR = *hintere Innenfalte* = *Hauptlingualfalte*.

mesofosetid = postero-internal enamel island = EL = *Schmelzinsel*

- 3- protoflexid = anteroexternal fold = AER = *vordere Aussenfalte*
- 4- paraflexid = anterointernal fold = AIR = *vordere Innenfalte*
- 5- anteroflexid = anterior fold = AR = *Vorderfalte*

Abbreviators are used for right = dextral (d), left = sinistral (s), million years = Ma.

Photographs have been taken in the Departamento de Paleontología of UCM by Carlos Alonso Recio. Drawings have been made by the first author in a camera lucida installed on a Wild Stereoscopic Microscope. Measurements have been done with a

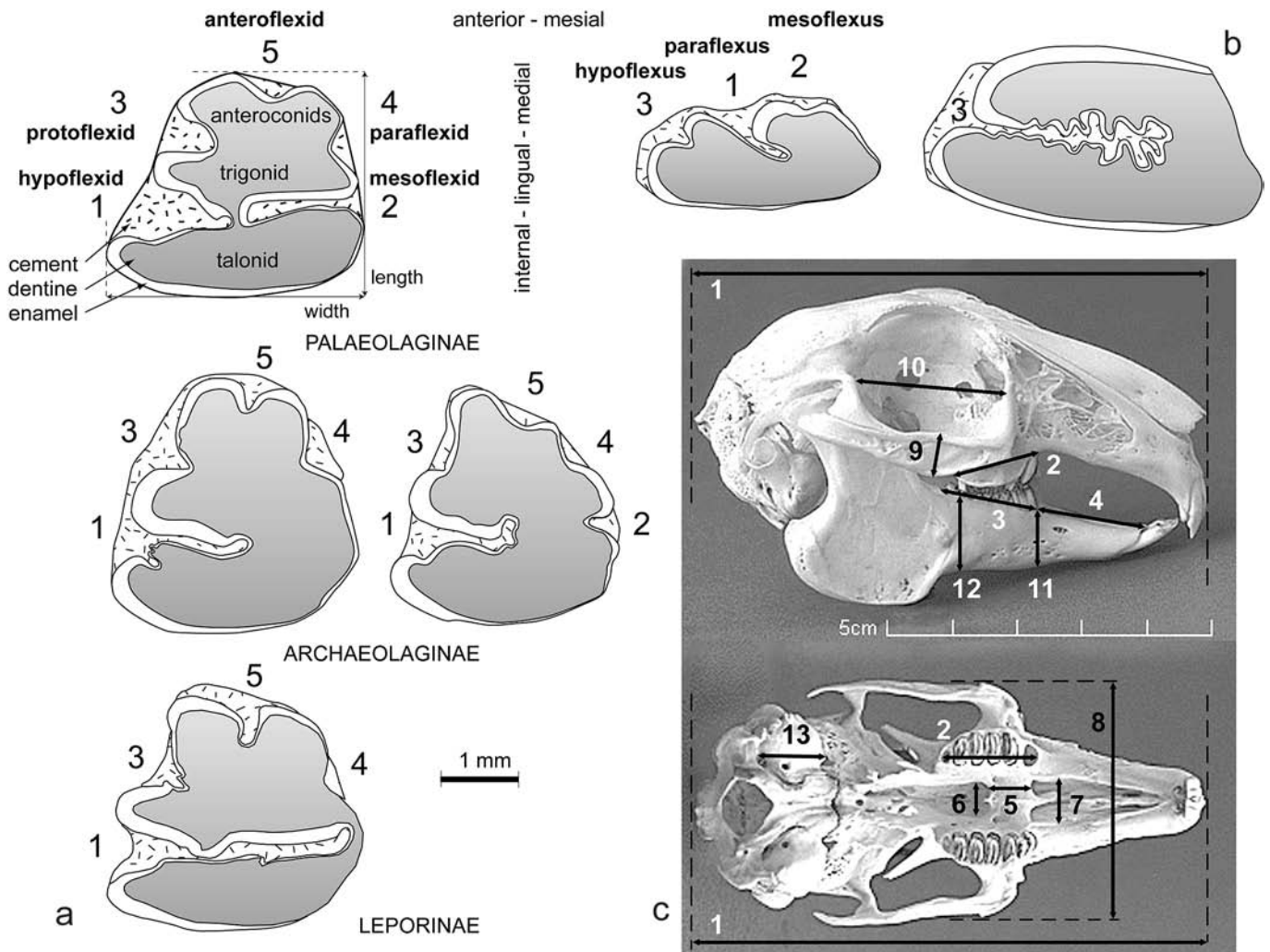


Figure 2. a, dental nomenclature and p3 pattern in the three Leporidae subfamilies: Palaeolaginae are represented by *Pronolagus* Lyon 1904; Archaeolaginae by *Serengetilagus praecapensis* Dietrich 1941 (left an adult, and right, a young individual with an ephemeral mesoflexid) and Leporinae by *Oryctolagus* Lilljeborg 1874. b, upper cheek teeth (P2 and P3) from *Serengetilagus praecapensis*, with nomenclature of P2. The only strongly crenulated fold in P3 is named hypoflexus (occlusal view) or hypostria (in lingual view). c, measurements taken in the cranium and jaw of leporids (*Oryctolagus*): 1-cranial length; 2-upper tooth row length (alveolar); 3-lower tooth row length (alveolar); 4-lower diastema length; 5-palatal length; 6-choanae width; 7-width of incisive foramina; 8-zygomatic breadth; 9-zygomatic height; 10-orbit length; 11-mandible height (at p3); 12-mandible height (at m3); 13-length of tympanic bulla.

calliper and with a micrometer scale under the microscope. Other Lagomorph material has also been studied for comparative purposes. Fossil material of *Serengetilagus praecapensis* from the lower Pliocene of Laetoli (Tanzania) has been borrowed from the Naturalhistorisches Museum collections in Berlin, under the cares of Dr. Hans D. Heinrich. Pictures of *Bunolagus monticularis* Thomas 1929 have been kindly provided by Judith Chupasko, from the Harvard Museum of Comparative Anatomy (USA). Dr. P. Mein, from the Université de Lyon (France) provided access to the rich fossil Lagomorph collection under his care.

SYSTEMATIC PALAEOLOGY

Superorder DUPLICIDENTATA Illiger 1811

Order LAGOMORPHA Brandt 1855

Family **Leporidae** Gray 1821

Subfamily **Archaeolaginae** Dice 1917

Diagnosis: “Cheek teeth hypsodont; only persistent fold on upper molariform cheek-teeth formed by internal hypostria having straight or crenulated walls; upper molariform premolars usually more molariform than in palaeolaginae; two external reentrants on p3, anterior of which is usually shallower than posterior; posteroexternal reentrant on p3 between trigonid and talonid not persistent, usually lost at early stage of wear. Skull seemingly more advanced than in palaeolaginae: angle between basicranial and palatal axes larger; palatine forming proportionally shorter part of bony palatal bridge; anterior zygomatic root situated more anteriorly” (Dawson, 1958: 38).

“Small to large sized leporids with p3 devoid of lingual reentrants (AIR and PIR) in adult specimens; anteroexternal reentrant (AER) slight to deep, cement-filled or not, extending from 1 to 42 percent of occlusal width; posteroexternal reentrant (PER) extending from 36 to 68 percent across occlusal surface, and filled with cement” (from White, 1987: 428).

Genus *Serengetilagus* Dietrich 1941

Type species: *Serengetilagus praecapensis* Dietrich 1941

Diagnosis (previous authors do not provided generic diagnosis):

Archaeolaginae leporids with short snout, large incisive foramen, narrow choanae and relatively developed tympanic bullae; dentary increasing in height backwards; first upper premolar with deep paraflexus, weak mesoflexus and shallow hypoflexus in advanced species; upper molariform teeth with a well crenulated hypostria; p3 crescentic in shape with two main, constant external folds (a hypoflexid entering around half crown width, and a shallow protoflexid) and up to three additional folds variably present (an anteroflexid variably developed, a weak paraflexid and

exceptionally a mesoflexid-mesofossetid, mainly in young individuals); when an anteroflexid is present, the lingual anteroconid is weaker than the labial one.

Other species attributed to genus:

- *Serengetilagus orientieuropaes* Topachevsky 1987 from the Pliocene of Ukraine; synonymized by Averianov & Tesakov (1997) with *Trischizolagus dumitrescuae* Radulesco & Samsón 1967.

- “*Serengetilagus*” *raynali* Geraads 1994 from the Middle Pleistocene of North Africa must be excluded from this genus (see Sen & Erbaeva, 1995, and Averianov & Tesakov, 1997; confirmed by our own data).

- *Serengetilagus* aff. *S. praecapensis* from the Early Pliocene of Chad reported by Brunet *et al.* (2000).

- *Serengetilagus tchadensis*, n. sp., a new species from the Late Miocene of Chad, described below.

- *Serengetilagus* sp. from the Late Miocene of Kenya (Mein & Pickford, 2006).

- Fragmentary material from the Pliocene of Afghanistan, originally described as *Trischizolagus* aff. *T. maritsae* by Sen (1983), has been subsequently assigned to *Serengetilagus* sp. by Sen & Erbaeva (1995), but rejected by Averianov & Tesakov (1997).

Distribution: Late Miocene and Pliocene of Central and East Africa.

Serengetilagus praecapensis Dietrich 1941

Lectotype: MB.Ma 1449/2, fragment of right hemimandible, Naturhistorische Museum Berlin (figured by Erbaeva & Angermann, 1983: 42, Fig. 2).

Type locality: Laetoli (Tanzania).

Type level: middle Pliocene (ca. 3.5 Ma.)

Original diagnosis (extracted and translated from Dietrich, 1942: 58):

“A species belonging to the last Palaeolaginae; it is an advanced species where the lingual posterior fold in p3 is nearly or most often absent; only a single case shows a development as strong as in normal Palaeolaginae (fig. 18). This case can be recognized as an atavism, since it is a recessive trait since the Miocene. Other traits, like the remaining p3 folds, lack of roots, the strong development of the cement, support its character as a progressive Palaeolaginae”.

Extended diagnosis (from Erbaeva & Angermann, 1983: 59): “Most common morphotype of p3 with a short posteroexternal fold that crosses approximately half of the occlusal surface, with an anterior fold, an anteroexternal and an anteroexternal fold. A rudimentary posteroexternal fold is present only in exceptional cases. Length of p3 averages 3,3 mm, width of p3 averages 3,1 mm; occlusal surface of p3 varies in shape, mostly anteroposteriorly elongated.

P2 as a rule with three anterior folds. Hypostriae mostly distinctly crenulated, with a varying degree of crenulation. Base of lower incisor mostly situated below p3. Size of skull and some cranial measurements close to those of recent *Lepus capensis* from East Africa; differs mainly in the short diastema of its lower jaw and the absolutely and relatively narrower foramina incisiva in relation to the foramina mesoptergoidea”.

Systematic and phylogenetic remarks

The genus *Serengetilagus* has not yet found a stable place in the Leporidae taxonomy. Dice (1917, 1929) proposed a systematic subdivision of the family in three subfamilies based on the p3 pattern, which has been widely used since. According to this author, Palaeolaginae are characterized by two symmetric folds between trigonid and talonid; Archaeolaginae, by a short external fold with a broad internal area connecting trigonid and talonid; and Leporinae by trigonid and talonid nearly completely divided by a deep external fold.

The p3 features of *Serengetilagus* agree with the subfamily Archaeolaginae, although Dietrich (1942) assigned it to the subfamily Palaeolaginae, based on the presence of “an atavistic posterointernal fold” in one p3. Kormos (1934) proposed to group both subfamilies because a single tooth can show both patterns at the same time: a palaeolagine pattern in the occlusal face and an archaeolagine one in the root face. In fact, a shallow posterointernal fold (mesoflexid) may be present in the juvenile p3 of almost all lagomorph genera, being an ephemeral feature in most archaeolagine and leporine leporids (Sych, 1965; Fladerer, 1987; Averianov & Tesakov, 1997). Consequently, more recent authors have maintained the three subfamilies (Dawson, 1958; White, 1987). Gureev (1964) considers *Serengetilagus* as an archaeolagine but he transforms this subfamily in a tribe within the Leporinae subfamily. Such conflicts between diagnoses and grouping of taxa frequently arise in studies on phylogeny and systematics, although the Leporidae is a particularly conflictive family (e.g., Halanick & Robinson, 1999; Robinson & Mathee, 2005).

Dawson (1981) and reviewers of Dietrich’s original material (MacInnes, 1953; Erbaeva & Angermann, 1983) have not ascribed *Serengetilagus* to a particular suprageneric taxon, nor concluded about its phylogenetic affinities among Leporidae. Dietrich (1942) suggests a phylogenetic link between *Serengetilagus* and the Eastern African hares attributed to *Lepus capensis* Linnaeus, from he took the specific name *S. praecapensis*. However, he noted several features that related *Serengetilagus* to rabbits instead of hares (presence of interparietal bone; similar shallow basicranial-basifacial angle; long bony palate; shape of the jaw; position of the mental foramen; high length ratio between humerus and radius; size and shape of limb bones, etc). Nevertheless, he favoured two features (width of

choanae larger than half-length of upper tooth row, small size of mental foramen) as indicative of *Serengetilagus* relationships with hares.

We have checked these two features signalled by Dietrich as linking *Serengetilagus* to hares. The examined samples of *Serengetilagus praecapensis* from the type locality housed in the Berlin Museum show rather narrow choanae and large mental foramen, similar to that of rabbits. The picture of the bony palate figured by Dietrich (1942: Plate III Fig. 12; reproduced in this work, fig. 3), as well as the lectotype specimen figured by Erbaeva & Angermann (1983), show these features more similar to rabbits, supporting our interpretation that *Serengetilagus* would be closer to rabbits than to hares.

Two possible genera, one African and one Eurasian, have been proposed as the *Serengetilagus* closest relative. Dawson (1981) relates it to *Pronolagus* Lyon 1904, a link explicitly rejected by Dietrich (1942: 59). Alternatively, Erbaeva & Angermann (1983) point to dental similarities between *S. praecapensis* and *Trischizolagus maritsae* De Bruijn, Dawson & Mein 1970 from the Lower Pliocene of Rhodes, confirmed by our observations. Averianov & Tesakov (1997) also conceive a phylogenetic link between *Serengetilagus* and *Trischizolagus*, but in a subsequent cla-

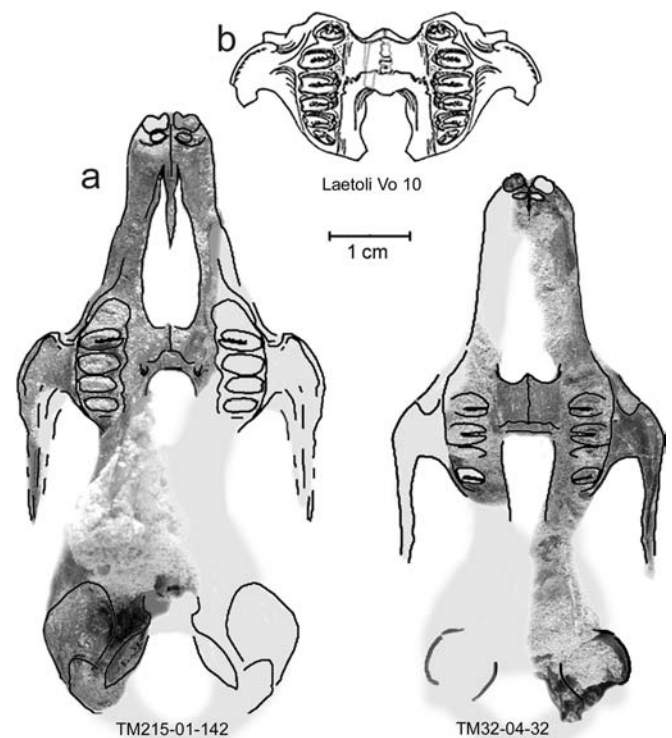


Figure 3. a, Ventral view of two crania from *Serengetilagus tchadensis* nov. sp. (TM-01-142 at the left and TM32-04-32 at the right). b, Reconstruction of maxillae and palatal bridge from *Serengetilagus praecapensis* (modified after Dietrich, 1942: pl. 3 fig. 12).

distic analysis, Averianov (1999) supports instead Dawson's hypothesis, including *Serengetilagus* in a new tribe Bunolagini as the sister-group of living African palaeolagine *Pronolagus* + *Bunolagus*. This African group appears in Averianov's tree within the subfamily Pentalaginae Gureev 1964, although lacking synapomorphies, clustered in a polytomy with Eurasiatic palaeolagine (the living *Pentalagus* and the extinct *Pliopentalagus* Gureev 1964, *Sericolagus* and *Trischizolagus*). Averianov (1999) excludes the Archaeolaginae from the family Leporidae.

An important concern affects the data matrix of this author, where a palaeolagine-type p3 is assigned to *Serengetilagus* although it is extremely rare (less than 4% on a sample up to 143 specimens; see Erbaeva & Angermann, 1983). In fact, almost all Lagomorph genera may bear a weak percent of small mesoflexid (palaeolagine-type p3) mainly in young individuals. For that reason, the diagnosis of Archaeolaginae subfamily applies to the morphology of adult specimens (White, 1987). Consequently, we include *Serengetilagus* in the Archaeolagine subfamily together with *Hypolagus* and other less-well known Leporidae.

Serengetilagus tchadensis n. sp.

Figs. 3, 4, 5.

Holotype: TM266-03-380 (Fig. 4.7-8, 11; Fig. 5.4a-b), articulated lower mandible with rather complete dentition; both mandibular vertical rami are lacking. The left dentary body is complete with p3 broken in its proximal part; the right dentary body is broken and displaced, with eroded teeth.

Paratypes: TM266-03-101 (Fig. 4.1, Fig. 5.5), upper left maxilla with P2-M3, labial part of M2-M3 partially broken; it probably belongs to the same old individual as the holotype. TM266-03-262 (Fig. 4.5, Fig. 5.3), articulated upper maxillae with partially preserved bony palate and lower mandible; nearly complete, heavily eroded dentition, only both P2 are lacking.

Derivatio nominis: From the French spelling name Tchad, honouring the Chad country where these fossils have been found.

Differential diagnosis: A medium-sized leporid with simple archaeolagine p3 and P2 pattern resembling *Hypolagus*, but with significant frequency of a shallow anteroflexid, which correspond with *Serengetilagus*; upper cheek-teeth with primitive wear pattern, becoming strongly enlarged with individual age. It differs from *Serengetilagus prae-capensis* Dietrich 1941 by the lack of lingual folds in p3 (paraflexid and mesoflexid-mesofosetid) and the weakness or absence of anteroflexid. Both species also differ by *S. tchadensis* having longer palate, narrower choanae, more triangular zygomatic tubercle, higher jaw, shorter muzzle, larger and more robust teeth and dentary bones, lack of hypoflexus in P2, shallower hypoflexus in upper molari-form teeth that can be more distally placed, and a simple, inflected backwards hypoflexid in p3.

Assigned material: In addition to the type material, *Serengetilagus tchadensis* n. sp. is well represented by two rather complete skulls and several jaws and postcranial elements from the type locality TM266 and from other TM localities, namely TM32, TM55, TM90 and TM215.

Additional material from the type locality TM266:

- TM266-03-263, articulated mandibles with eroded right p3 and molari-forms.
- TM266-03-379, eroded left maxilla with P2-M1. It could correspond to the same individual as TM266-03-263.
- TM266-03-464, right maxillary fragment with P3-M3, young individual. It could correspond to the same individual as TM266-03-263.
- TM266-03-290, articulated upper maxillae and fragments of lower mandible (hemimandibles fixed with glue, wax and plastic pieces). Both P2 and proximal right p3 are lacking (Fig. 4.2).
- TM266-03-381, fragment of right mandibular diastema and incisor. It could correspond to the same individual as TM266-03-290.
- TM266-03-382, fragment of lower incisor. It could correspond to the same individual as TM266-03-290.

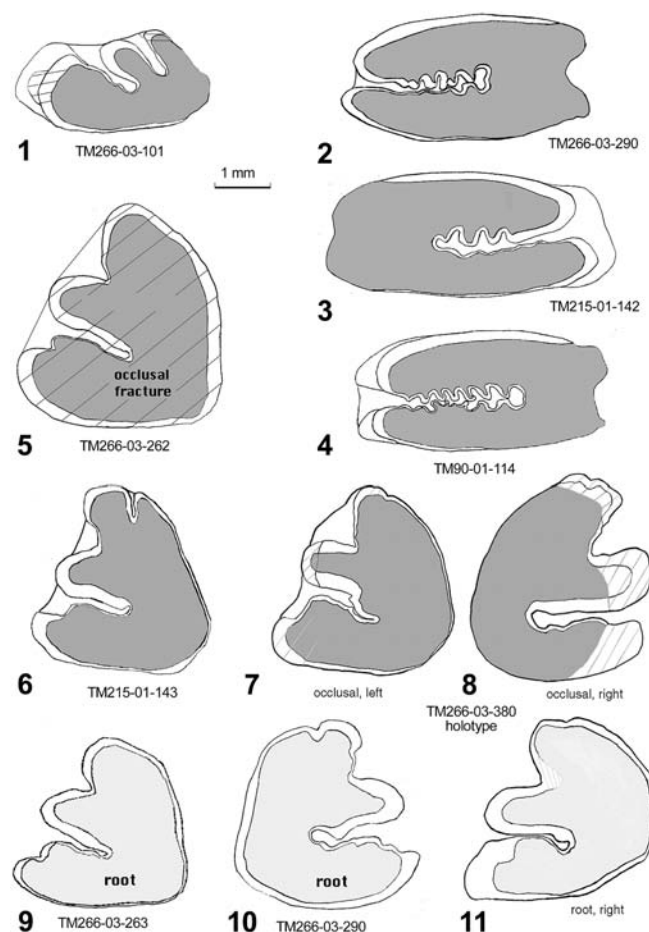


Figure 4. *Serengetilagus tchadensis* n. sp., cheek teeth; camera lucida drawings of the occlusal surface: **1**, P2 s; **2**, P4 s; **3**, P3 d; **4**, M1 s; **5**, p3 s; **6**, p3 s; **7** and **8**, p3 s and d, holotype; root surface: **9**, p3 d; **10**, p3 s, and **11**, p3 d, holotype.

- TM266-03-310, right maxilla with P3-M2.
- TM266-03-378, two left and right fragments of articulated calcanea and astragali, plus six undetermined diaphyseal fragments (Fig. 5.10).

Additional material from other TM localities:

- TM32-04-32 (Fig. 3b, Fig. 5.2), a damaged fragmentary cranium
- TM32-04-33, (Fig. 5.6-7), left and right articulated distal femora and proximal tibiae, plus three articulated lumbar vertebrae.
- TM215-01-142 (Figs. 3a, 5.1), fragment of skull with articulated right mandible and fragmentary dentition.
- TM215-01-143 (Fig. 4.6), fragment of left hemimandible with p3-m3 (probably the same individual as 142).
- TM215-01-144, four articulated lumbar vertebrae (probably the same individual as 142).
- TM90-01-114 (Fig. 4.4), isolated left upper molariform (M1, less probably P4), adult individual.
- TM55-04-017 (Fig. 5.8-9), left distal tibia and calcaneum.

Description

Cranial skeleton

Skull (based on TM266-03-101, -262, -379, -464, -290, -310, TM32-04-32 and TM215-01-142, corresponding to a minimum of six individuals).

The cranium is robust in general, particularly the snout and the zygomatic arches. The specimen TM32-04-32 is less heavily built than that TM215-01-142. The eight maxillae from TM266 indicate they also belong to robust crania. The snout is short and wide, slightly bend downwards like in the rabbit and in *S. praecapensis*. The incisor does not protrude along the wall of the snout. The maxilla is similar in height and thickness as in *S. praecapensis*.

The zygoma is frontally thick, high and powerful, with a concave front profile, a strong anteroventral tubercle and a deep lateral fossa. The tubercle is flanked by a ventral rim that curves abruptly backwards forming a triangular shape, instead of an even, softly curved border as in *S. praecapensis*. The zygomatic arch thins backwards and shows a lateral profile gently curved ventrally. It bends obliquely towards the temporal tubercle and fossa, which are high placed in the braincase. The orbit is relatively long and oriented upwards. The frontal lacks in our specimens, but if normally developed the orbit would be probably reduced in height, comparatively to *S. praecapensis* and modern leporids.

The basicranial-basifacial angle measures about 143° (specimen TM215-01-142) and approximately 155° (TM32-04-32). In this character it is closer to *Lepus* (134°-142°), especially that from East Africa ("*Lepus capensis*"), than to *Oryctolagus* and other rabbits (*Oryctolagus*, 133°; *Pronolagus* 133°; *Pentalagus* young, 119°, adult 131°). In contrast, *Serengetilagus praecapensis* would be similar to rabbits in this character, according to Dietrich (1942: 55). This important character may differ between closely related lagomorph species, for instance *Palaeolagus haydeni* (more flexed basicranium) and *Palaeolagus hyopsodus* (more flattened basicranium) (Dawson, 1958).

The incisive foramina occupy a single wide and long cavity in the ventral side of the snout. Their maximal width is at

its back, and it equals about the length of the bony palate. The palatal bridge is placed in front of the main premolars P3 and P4. Its length is close to the half of the tooth row length, larger to that of *S. praecapensis* and hares. The palatine part occupies less than one third of the palatal bridge. The choanae are moderately wide, more than one third of the tooth row length. The ratio 'choanae width / palatal length', largely used to differentiate rabbits and hares, is smaller than 1, which differs from hares and approaches most rabbits (except *Bunolagus* and some others). The value of this ratio for *S. praecapensis* has not been indicated by Dietrich, but according to his description it would be larger than 1, a hare ratio (palatal length = tooth row / 2.5 and choanae width > tooth row / 2; thus, choanae width > 1.25 · palatal length, Dietrich, 1942: 55). Erbaeva & Angermann (1983) also report values above 1 in three cases. We infer in this species less high values for choanae width in some cases (Fig. 3).

The tympanic bulla is rather small and well rounded, and is high placed dorsally, with a long and relatively narrow tympanic tube. The occipital condyles are thin and long.

Upper dentition (TM266-03-101, 262, 379, 464, 290, 310, TM215-01-142; TM90-01-114).

The main upper incisor has very thin enamel layer. The external wall is deeply incised by a furrow in a slightly medial position, without cement. The internal side of the teeth is flattened or slightly concave.

Two P2 specimens are available (TM266-01-101, size 1.66 x 3.15 mm and TM266-01-464; Fig. 4). They show two deep anterior folds entering half of the crown and filled with cement. The most lingual one (paraflexus) is shallow and wide, while the most central one (mesoflexus) is deep and curved and has an undulated lingual wall. Both are obliquely directed towards the posterolabial corner. Between them there are a rounded cusp (lagicone) with a thickened enamel wall. The lingual cusp may show a shallow furrow along the lingual shaft but it has not a fold inside the crown (hypoflexus absent). Instead, most specimens of *Serengetilagus praecapensis* have a hypoflexus dividing the lingual cusp, in addition to the two other folds (Fig. 2A; Dietrich, 1942; Erbaeva & Angermann, 1983).

The morphology of upper molariform teeth crowns (P3-M2) show a folded hypoflexus reaching about the half of the crown width, except in the specimen TM90-01-114 that has a deeper hypoflexus, reaching more than half width of the crown (Fig. 4.4; Dh = 2,52). The number and depth of the crenulations decreases from P3 to M2. In the TM266 population there are about five well-marked, closely spaced crenulations on the anterior wall of the hypoflexus, while those in the posterior wall are shallower and more irregular. In the TM215 specimen the hypoflexus is short and poorly folded, with four shallow crenulations in the anterior wall of the P3 and a weak undulation in the posterior one. In TM90 the hypoflexus is complexly folded, with more than seven loops deeply incised in the anterior wall, and eight less marked and more irregular in the posterior wall.

The position of the hypoflexus in the antero-posterior axis of the crown varies in our samples. In TM266 specimens it is well centred, like in most lagomorphs, with the two dental lobes reaching about the same length. In TM215 and TM90 samples instead the anterior lobes are longer and more robust than the posterior ones, which the hypoflexus displaced backwards (Figs. 4.3, 4.4). This unusual feature has not yet been reported in other cases, to our knowledge.

The thickness of the enamel surrounding the crown is clearly differentiated, thicker at the leading edge and thinner at the rear, as in other advanced leporids, but in senile specimens the enamel appears weakly differentiated, as in primitive leporids.

The crown morphology of upper molariform teeth changes with individual age according to the wear stage. Crown length varies (2.10 to 2.44 mm) much less than width (4.13 to 6.45 mm). Relatively young specimens (TM266-03-290, 379, 464) can be distinguished by their smaller wear facets, not affecting the labial part of the occlusal surface of the molariform teeth (Fig. 4.2-4). The senile specimens instead (TM266-03-101) have extremely widened crowns with a strongly curved, concave occlusal surface dorsally bend in the labial part (Fig. 5.5). This strong expansion of the upper molariform teeth along the transversal axis is observed only in primitive lagomorphs, which fail to maintain a continuous growth of the entire crowns during their life span and decrease the growth of the labial cusps in senile states of wear.

Lower jaw (TM266-262, 380, 263, 290 and 381; TM215-142 and 143).

The dentary is a robust bone, with a diastema relatively short and a thick symphyseal area. The root of the lower incisor, weakly protruding in the internal side, starts usually in front of the p3, rarely besides the shaft of this teeth. A single, relatively large mental foramen is placed in the dorso-external side at a short distance (about 3 mm) of the p3. The horizontal ramus is thick, with a marked ventral inflexion in the middle part. Well-marked masseteric crests joint in the middle of the external side laterally between m1 and m2, forming a masseteric tubercle. The vertical ramus is only preserved in one specimen (TM215-142, Fig. 5.1b). It is relatively high and short, and makes a narrow angle with the horizontal ramus, slightly wider than 90°.

Lower dentition (TM266-262 d+s, 380 d+s, 263 d, 290 s, 381 d, 382 s; and TM215-143 s).

The lower p3 is a key structure in Lagomorpha taxonomy and phylogeny. Seven damaged lower p3 from TM sites are available for morphological study, most of them being eroded or broken. In several cases (TM266-262, 290 and 380), morphological features poorly visible at the occlusal surface have been completed with additional observations from the root side of the tooth (Fig. 4.9-11). Both are highly similar in lagomorphs with completely rootless cheek teeth, as Dietrich has also noted for *S. praecapensis* (Dietrich, 1942: 56).

The section of p3 is crescent-shaped, with rounded postero-internal walls and a flattened external wall. The anterior part is pointed-shaped, with an acute anteroconid inclined towards the external side. In these features it resembles *Hypolagus*, while other leporids have a more square-shaped p3 with a flattened anterior face. In three specimens there are a tiny furrow in the anterior face, which forms a narrow anteroflexid fold in two of

them. This feature is similar to that of some advanced *Hypolagus* species, such as *H. gromovi* (see Averianov, 1996: fig. 1, c-f), *H. brachygnathus* (trigonid-type III in Fladerer, 1987) and *H. oregonensis* (White, 1987). Only one specimen (TM215-142) bears a narrow anteroflexid filled by cement that reaches a modest deep, similar to some cases of *H. gromovi* (Averianov, 1996, fig. 1 o). In contrast, 93.7 % of the specimens of *Serengetilagus praecapensis* present a well-developed anteroflexid (Erbaeva & Angermann, 1983).

The external side of the p3 crown in *S. tchadensis* n. sp. has two folds: a shallow anterior protoflexid and a deeper posterior hypoflexid. The protoflexid walls form nearly a straight angle. The hypoflexid enters about half width of the crown. The hypoflexid is simply oriented backwards in some specimens (Fig. 4.9) like in most *Hypolagus* specimens, while in others it slightly bends forwards at its end, after forming a bulge (Fig. 4.10). This latter type also appears in *Hypolagus brachygnathus* (cf. Fladerer, 1987, type C). In *Serengetilagus praecapensis* it is the most frequent one and the bending is more developed (Fig. 2).

The posterior wall of the hypoflexid form a marked step near the external side, similar to that signalled by Fladerer (1987) as 'bilobated talonid' or 'concave talonid' in *Hypolagus brachygnathus*. The enamel is thicker on the anterior wall of the hypoflexid and on the three external cusps, and thin at the rounded postero-internal side of the tooth and at the distal wall of the hypoflexid.

There are not signs of lingual folds in any specimen. The cement is less abundant than in *Serengetilagus praecapensis*, where it covers not only the folds but also the external sides of the cusps.

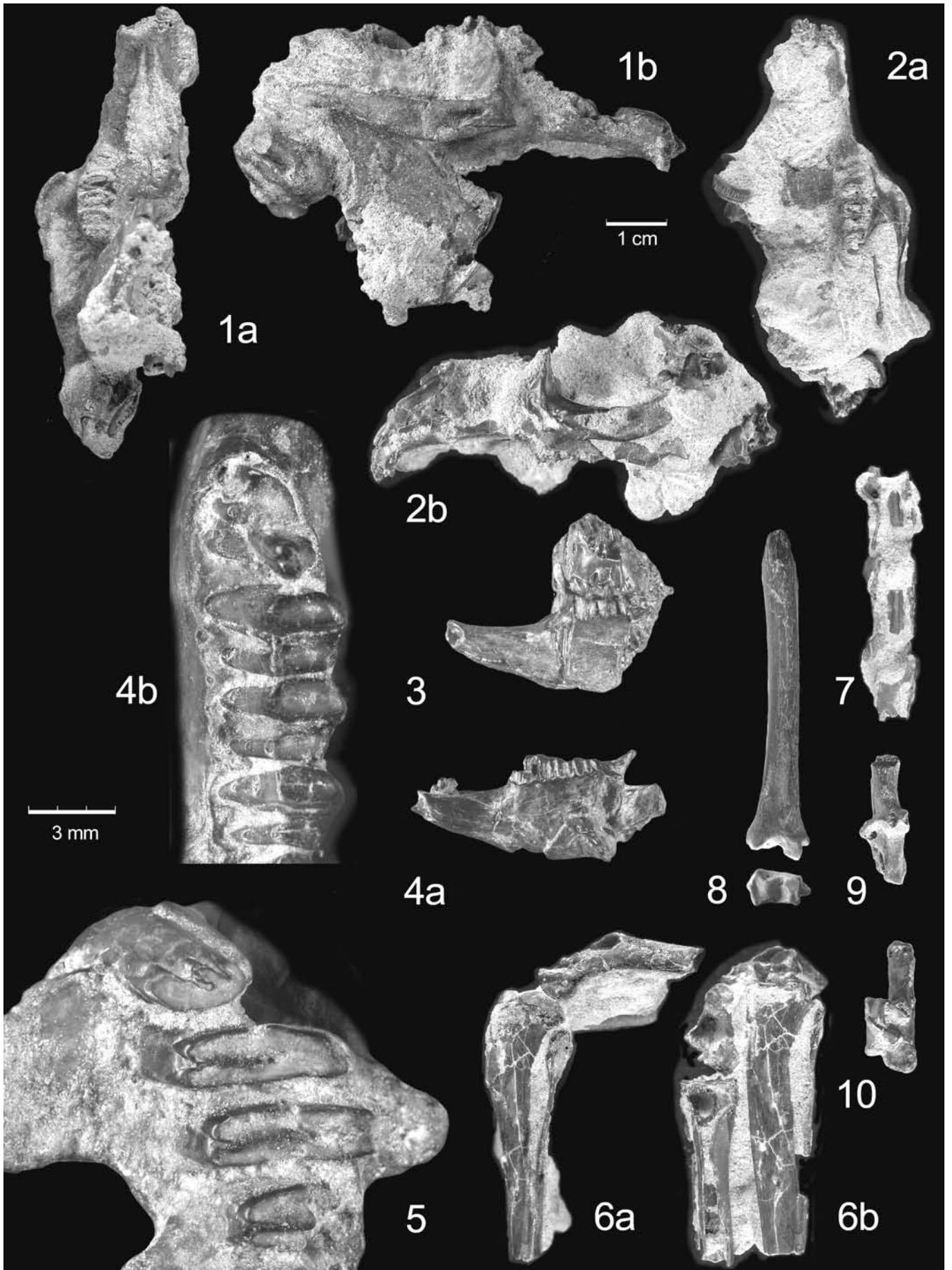
The remaining molariform teeth (p4-m1-m3) show the usual leporid morphology, with two cylindrical columns connected by a narrow bridge at the lingual side. These teeth are rather constant in Lagomorpha, with a comparatively uniform morphology in contrast with the highly variable p3.

Postcranial skeleton:

Lumbar vertebrae (TM215-01-144, TM32-04-34). Two specimens from different TM localities show a similar preservation, with three articulated elements curved in a ventral (natural) direction. Each of them is associated to rather complete skulls, which presumably correspond to the same individual.

The morphology of the vertebrae is hardly visible because of the cover by strongly silicified matrix. Both specimens correspond to three vertebra, TM215-01-144 probably to L3-L5, and TM32-04-34 to L1-L3 (Fig. 5.7). The TM215 specimen is more robust while TM32 is more delicate, which coincides with the same architectural differences of the skulls. The size corresponds to that a small European rabbit (see measurements in Table 1). The bases of some postzygapophyses and transverse processes

Figure 5. *Serengetilagus tchadensis* n. sp. **1**, TM215-01-142, cranium, **a** – ventral view; **b** - lateral view. **2**, TM32-04-32, cranium, **a** – ventral view; **b** - lateral view. **3**, TM266-03-262, articulated maxillae and mandibles, lateral view; Paratype. **4**, TM266-03-380, left dentary, **a**- lateral view; **b**- detail of anterior lower cheek teeth (p3-p4-m1-m2); Holotype. **5**, TM266-03-101, left maxilla, detail of anterior upper cheek teeth (P2-P3-P4- broken M1); Paratype. **6**, TM32-04-33, knee; **a**- lateral view of left distal femur and proximal tibia; **b**- anterior view. **7**, TM32-04-33, three lumbar vertebrae, ventral view. **8**, TM55-04-17. left tibia, anterior and distal views. **9**, TM55-04-17, left calcaneum, dorsal view. **10**, TM266-03-378, left articulated calcaneum and astragalus, dorsal view.



TM215-01-142	Fragment of skull with articulated mandibles.						
	Total length	74.8					
	Right maxilla			16.25	20.01	2.22	4.82
	zygomatic height		7.15				
	palatal length	7.55					
	choanae width		5.6				
	tympanic bulla	11.2	7.8				
TM215-01-143	Fragment of left dentary with p3-m3 Probably the same individual as 142			15.95	-		3.39 3.21
TM215-01-144	Four articulated lumbar vertebrae. Probably the same individual as 142	14.0*	9.50*				
TM90-01-114	left M1	2.20	4.27				
TM55-04-017	Left distal tibia; epiphysis		10.45 6.23				
	Left distal tibia; diaphysis		5.21 4.39				
	Left calcaneum	21.2*	- 7.52				

Table 1. *Serengetilagus tchadensis* n. sp., skeletal measurements in mm. Asterisks indicate approximated values.

are preserved in some cases, as well as the ventral keel of vertebral centra. Unfortunately, the possible presence of an hypophysis cannot be observed.

Femur (TM32-04-33). Two distal epiphyses with a part of the distal diaphyses of a same individual have been preserved articulated with the tibiae (Fig. 5.6), presumably from the same slender individual which produced the skull (TM32-04-32) and lumbar vertebrae (TM32-04-34). The general size corresponds to a small *Oryctolagus cuniculus*, just as Dietrich (1942) noted it for *S. praecapensis*. However the ratio between epiphysis width and diaphysis width is different, being larger in *S. tchadensis* n. sp. (ratio dw/ew = 0.54) than in *Oryctolagus* (dw/ew = 0.48). This is probably another primitive feature of *S. tchadensis* n. sp.

Tibia (TM55-04-17; TM32-04-33). The material corresponds to a left distal epiphysis and part of the diaphysis (Fig. 5.8) in relation with one anklebone (see below) and two proximal epiphyses of the same individual from TM32 (Fig. 5.6). The former specimen seems even more delicate than the later one, which is one of the most slender individuals of the TM assemblages. Size and architecture of TM55-04-17 distal tibia agrees with that of European rabbit, but the tendinous grooves of the distal end are less deep than in *Oryctolagus*. TM32-04-33 tibia is somewhat more robust than that of rabbit, like *S. praecapensis* (Dietrich, 1942: fig. 25; Leakey, 1965: fig. 3). The reconstructed total length and the relative position of the fibular synostosis would agree with those of *Oryctolagus*.

Calcaneum (TM266-03-378 s+d, TM55-04-17). The first specimen corresponds to left and right articulated upper anklebones; the second is an isolated left calcaneum related to the distal tibia described above (Fig. 5.9-10). As it was already stated, this latter specimen is the most delicate individual of the TM *Serengetilagus* collection, and has the size of a small *Oryctolagus cuniculus*. The TM266 specimen is somewhat more robust than TM55, both less heavily built than the rabbit. The length of calcaneum has been shown to be the osteological measurement that better correlate with body size (Sych, 1965).

The calcaneum body of these specimens is slender, its distal part is about as long as the proximal part (tuber calcanei) and only slightly wider. There is a calcaneum-navicular joint as in most leporids. There is not a sulcus between the medial and lateral facets for the astragalus, which are evenly connected (only observed in TM55-04-17). The *sustentaculum talii* is small and protrudes very weakly from the calcaneum body. The trochlea for the fibular joint is also remarkably small, in contrast with that is has been reported for *S. praecapensis* (see McInnes, 1953). The calcaneum features of *S. tchadensis* n. sp. correspond thus to a weak upper ankle joint, as it has been observed in other archaevolagine like *Hypolagus vetus* (Dawson, 1958).

Astragalus (TM266-03-378 s+d). The only two astragali available correspond to the same individual. They can be observed only partially, because both are articulated with the corresponding calcaneum. The size corresponds to a small *Oryctolagus cuniculus*; its distal facet for the navicular is comparatively shorter and the trochlear groove is shallower than of the rabbit.

Discussion

A number of distinctive features of *Serengetilagus tchadensis* n. sp. will be discussed in relation to its nearest taxon *S. praecapensis* Dietrich 1941 from Laetoli (Early Pliocene, Tanzania) and to other less-well known fossil leporids also close to it, such as *Hypolagus gromovi* (Late Miocene, Eastern Europe) and *Trischizolagus* (Late Miocene-Pliocene of Southern Europe).

Comparison with *Serengetilagus praecapensis* Dietrich 1941

Serengetilagus tchadensis n. sp. from TM is close in size to the type population of *S. praecapensis*. They share similar length of the tooth rows, and dental portion of maxillae and jaws. The muzzle is somewhat shorter and the

isolated teeth are slightly larger in average in the Chad species, which indicates a short-nosed and macrodont taxon in relation to the Tanzanian one (Table 2, Fig. 6).

The cranium of the Chadian leporid differs from the Tanzanian one by a more wide basicranial-basifacial angle, longer palatal bridge, less open choanae and a different shape of the zygomatic arch and orbits (Fig. 3, Fig. 5.1-2).

The jaw of *Serengetilagus tchadensis* n. sp. is thicker and higher relative to *S. praecapensis* (Fig. 6), and the lower incisor have a less protruding root in relation with *S. praecapensis* and modern leporids. The lower incisor root in *S. tchadensis* n. sp. starts in front of the p3, while in *S. praecapensis* starts besides it.

Both *Serengetilagus* species have a short diastema comparatively with other leporids (Fig. 6), except *Hypolagus brachygnathus* that (as indicated by its name) is one of the shortest-nosed leporid known up to now. The ratio between tooth row length and diastema length is characteristic of different leporid groups. That from both *Serengetilagus* species fits well with Palaeolaginae (*Alilepus*) and Archaeolaginae (most *Hypolagus* species). These ratios are thus probably primitive in relation to rabbits (*Oryctolagus*, *Sylvilagus*, *Bunolagus*, etc), which have a larger diastema comparatively to dental row. A more derived state is

present in hares (*Lepus*) and rockrabbits (*Pronolagus*) with still longer snouts. The largest absolute and relative value of diastema length is reported in the extinct Archaeolaginae '*Hypolagus schreuderae*' (Fostowicz-Frelik, 2003).

The mentonian foramen in *S. tchadensis* n. sp. is variably large and is placed rather close to the p3, similarly to *S. praecapensis*. Also they share a similar shape of the mandible, with an increasing height of the dentary from p3 to m2 (Fig. 6). In contrast, modern leporids such as *Oryctolagus*, *Lepus* and *Pronolagus* have a dentary equal or decreasing in height backwards.

The dental pattern of *S. tchadensis* n. sp. is diagnostic for the species. Particularly, its P2, upper molariforms and p3 are distinct from that of *S. praecapensis* and other leporids.

The upper P2 of *S. tchadensis* n. sp. has only two anterior flexa (a rather deep paraflexus and a shallow mesoflexus); the lingual hypoflexus is not developed, as far as we can see in the few preserved specimens. Instead, the P2 of *S. praecapensis* presents three flexa, with a well-developed lingual hypoflexus in addition to the two anterior flexa. Erbaeva & Angermann (1983) report in *S. praecapensis* a single case of P2 without hypoflexus, attributed to a young individual. This difference between both species is probably significant, as the number of flexa

variable	<i>S. tchadensis</i> n. sp.		<i>S. praecapensis</i>		<i>Hypolagus gromovi</i>		<i>Trischizolagus dumitrescuae</i>		<i>Oryctolagus cuniculus</i>	<i>Lepus europaeus</i>
	mm	s.d.	mm	s.d.	mm	s.e.	mm	s.d.	mm	mm
cranial length	74.8	-	80	-	-	-	-	-	75.65	89.6
palatal length	7.05	0.757	6.33	0.416	6.4	-	-	-	6.33	5.93
upper tooth row length	16.55	0.563	15.91	0.777	-	-	-	-	13.81	17.73
upper diastema length	19.81	0.283	22.0	-	-	-	-	-	22.34	29.54
length P3	2.35	0.120	2.34	0.401	2.77	-	2.5	-	1.7	2.4
width P3	4.69	0.647	4.53	0.616	5.22	-	4.8	-	4.2	4.85
length p3	3.41	0.205	3.27	0.424	3.80	0.17	3.57	0.324	2.7	3.25
width p3	3.28	0.131	3.08	0.454	3.6	-	3.48	0.452	2.6	3.17
lower tooth row length	16.20	0.937	16.20	1.002	19.6	0.21	-	-	14.38	19.96
lower diastema length	15.45	0.656	15.33	1.093	19.58	0.21	15.4	-	17.38	24.26
dentary thickness	5.83	0.871	5.40	0.495	-	-	-	-	4.65	5.89
dentary height at p3	12.55	-	11.11	0.924	13.59	0.44	11.8	-	10.35	12.45
dentary height at m2	14.6	-	12.97	0.844	18.23	0.68	17.3	-	11.5	13
distal tibia width	10.45	-	9.05	-	12.54	0.17	-	-	12.3	16.3
calcaneum length	21.68	0.672	19	-	29.05	-	28	-	23.5	35.5

Table 2. Average values of selected variables of *Serengetilagus tchadensis* n. sp. compared with *S. praecapensis* Dietrich 1941, *Hypolagus igromovi* Gureev 1964, *Trischizolagus dumitrescuae* Radulesco & Samson 1967, and European rabbit and hare. Measurements originals and/or taken from Dietrich, 1942; Sych, 1965; Erbaeva & Angermann, 1983; Koufos & Koliadimou, 1993; Averianov, 1995; Averianov & Tesakov, 1998; Fostowicz-Frelik, 2003; s.d. = standard deviation. s.e. standard error.

in P2 is a relatively conservative feature. The absence of hypoflexus in P2 is correlated with the absence of anteroflexid in lower p3 (Fladerer, 1987). Both flexa are absent in *S. tchadensis* n. sp. as well as in primitive leporids (such as *Hypolagus* and *Alilepus*), while both are present in *S. praecapensis* and modern leporids. Actually, some rare modern leporids lacking anteroflexid in p3 (such as *Nesolagus* and *Lepus castroviejoi*) show indeed the correlative absence or weak development of hypoflexus in P2 (Schreuder, 1936; Palacios & Lopez-Martinez, 1980). Exceptionally, this correlation does not hold for *Pentalagus* that practically lacks hypoflexus in P2 but has an anteroflexid (even multiple) in p3.

Lagomorphs have very hypsodont crowns that enlarge with wear. The wear pattern of the upper cheek teeth in *S. tchadensis* n. sp. is very primitive in showing an important transversal expansion with advanced wear stage, from young individuals to adults. Old individuals of *S. tchadensis* n. sp. with highly wearing teeth show broadened and deformed upper crowns, strongly concave and displaced out of the maxillae at a more dorsal level than the occlusal surface. A similar dental wear pattern is found in primitive Oligocene lagomorphs (*Palaeolagus*, *Chadrolagus*, *Piezodus*, *Amphilagus*, etc). In such cases, the lingual part of the crown grows more rapidly than the labial part, which produces a curved shaft of the tooth and an increasingly oblique occlusion (Lopez-Martinez & Thaler, 1975). It also occurs in primitive hypsodont mammals when root loss is not fully acquired, but is not observed in *S. praecapensis* or modern leporids, where upper dental crowns are more evenly wear and change little with age. The upper molariform teeth from *Serengetilagus praecapensis* from Laetoli have a much deeper and centred hypoflexus, not displaced backward as in some TM samples of *S. tchadensis* n. sp. Both, *S. praecapensis* and *S. tchadensis* n. sp. share a weak differentiation of hypoflexus enamel and a complex folding, with symmetrical and irregularly crenulated walls. As is usual in leporids, crenulations become weaker from P3 to M2.

The lower p3 in *S. tchadensis* n. sp. is a rather simple, crescent-shaped tooth with only two external flexids (hypoflexid and protoflexid), plus a shallow groove in the anterior wall in some cases (28 %), or a narrow anteroflexid filled with cement in a single case (14 %). This simple p3 pattern contrasts with the more complex p3 of *S. praecapensis*, where four or five flexids are common. In addition to hypoflexid and protoflexid, the anteroflexid is generally present (94 %) and can reach an important development (deep, wide and double). Lingual folds are also present in *S. praecapensis*, mainly an anterolingual paraflexid (75 %) and in some rare cases a posterolingual mesoflexid or an isolated mesofossetid (3 %), mostly in young individuals. These folds are absent in the *S. tchadensis* n. sp. sample, which includes two young specimens. A simple p3 pattern similar to that of *S. tchadensis* n. sp., is only present

in less than 3.5 % (5 up to 143 cases) in the abundant *S. praecapensis* sample studied by Erbaeva & Angermann (1983). A simple p3 pattern close to *S. tchadensis* n. sp. is also present in the *Serengetilagus* material reported from the Late Miocene and Early Pliocene of Kenya (Lukeino Fm, 6.1-5.8 Ma, *Serengetilagus* sp. according to Mein & Pickford, 2006; Lothagam Apak Mb, older than 4.2 Ma, attributed to *S. praecapensis* by Winkler, 2003). Thus, *Serengetilagus* species seems to increased their p3 complexity from Late Miocene to middle Pliocene.

The simple archaeolagine p3 pattern of *Serengetilagus tchadensis* n. sp. confirms the ascription of the genus *Serengetilagus* to the Archaeolaginae subfamily. Also in the case of *S. praecapensis*, an archaeolagine p3 pattern is dominant, on the evidence of the morphology of its abundant population. The osteological features of *Serengetilagus tchadensis* n. sp. also confirm its affinities with Archaeolaginae (Fig. 6). The short muzzle, the lower tooth row much shorter than the upper one, the shape of the dentary that increases in high backwards, the narrow and weak ankle joint, all are remarkable similarities between both *Serengetilagus* species shared with several archaeolagine *Hypolagus* species, which differentiate them from other leporids (Fig. 6).

Inferences about *Serengetilagus* mode of life

The weight of *Serengetilagus tchadensis* n. sp. can be estimated at around 1 kg, by using a regression analysis between body weight and skeletal measurement of recent leporids (cranium, tooth row and diastema length). This estimation takes into account that the ratio between head length and body length was larger in primitive Leporidae than in modern ones.

The overall similarity in size and morphology between *Serengetilagus praecapensis* and *Serengetilagus tchadensis* n. sp., according to the observed skull and postcranial skeletal remains, allows to include both species in a same genus and infer its mode of life based in their combined evidences. These extinct leporids were small animals with short muzzle, robust masticatory apparatus and relatively weak legs. Their common features can be compared with the two major ecomorphs of modern leporids: rabbits and hares. The first ones tend to have fossorial habits, although they can also have climber and aquatic habits). The latter are specialized, cursorial animals.

Rabbits differ from hares by:

- 1- narrower basicranial-basifacial angle at the cranium base
- 2- slender crescent-shaped postorbital processes, posteriorly free (not fused to cranium)

- 3- relatively longer palatal bridge and narrower choanae
- 4- relatively longer palatine lamina in the palatal bridge
- 5- interparietal present in adults
- 6- incisor roots invisible from the outside of the premaxillary bone
- 7- zygomatic arch slender with straight, narrow upper edge (in *Lepus* is usually flattened and everted outwards)
- 8- large zeugopodial segments in relation with stylopods in limbs
- 9- shorter forelimbs in relation with hind limbs

Serengetilagus shares with rabbits the characters 5, 6 and 7, and with hares the character 4. Both *Serengetilagus* species differ in characters 1 (*S. tchadensis* has a large basicranial-basifacial angle, similar to hares, while *S. praecapensis* is more similar to rabbits) and 3 (the opposite occurs with the palate). *S. praecapensis* shares with rabbits characters 2 and 8, not observed in *S. tchadensis* n. sp. Data on character 9 are not available for *Serengetilagus*. This mosaic distribution of characters suggests that *Serengetilagus* was more similar to rabbits in general, with some hare features. Therefore, a mixed, partly fossorial and partly cursorial mode of life can be hypothesized.

In order to approach the reconstruction of *Serengetilagus* mode of life, other lines of evidence can be obtained

from taphonomical data. The type of fossilisation observed in TM leporid, where articulated skeletal elements or associated parts of a single individual are preserved in massive sandstones, is rarely observed in micromammals. It suggests a rapid burial in a natural position of either, a fresh corpse or a living animal, probably within a burrow. Otherwise the process of drying and meteoric alteration of carcasses would have disconnected the anatomical parts and destroy the natural arched shape kept by the articulated lumbar vertebrae.

Usually the fossilisation process for micromammals goes through a previous process of carcass production by carnivores, assembled in dens and traps, or by floods. This process of accumulation produces the breakage of bones and a preservation bias towards the most resistant skeletal parts. Thus, isolated teeth, jaws and rare ankle-bones mainly compose the fossil record of lagomorphs, a mammal group heavily consumed by predators. Instead the mammals with a fossorial mode of life can eventually fossilize inside the burrows, keeping articulated bones in a natural position. That is also possible in open air, when animals are killed by a rapid volcanic eruption. Fossils from both *Serengetilagus* species show rather complete and articulated skeletal material, that can be attributed to volcanic processes in the case of *S. praecapensis*. In the case of *S. tchadensis* n. sp. there are not evidences of associated volcanism till now, although the neighbour Tibesti

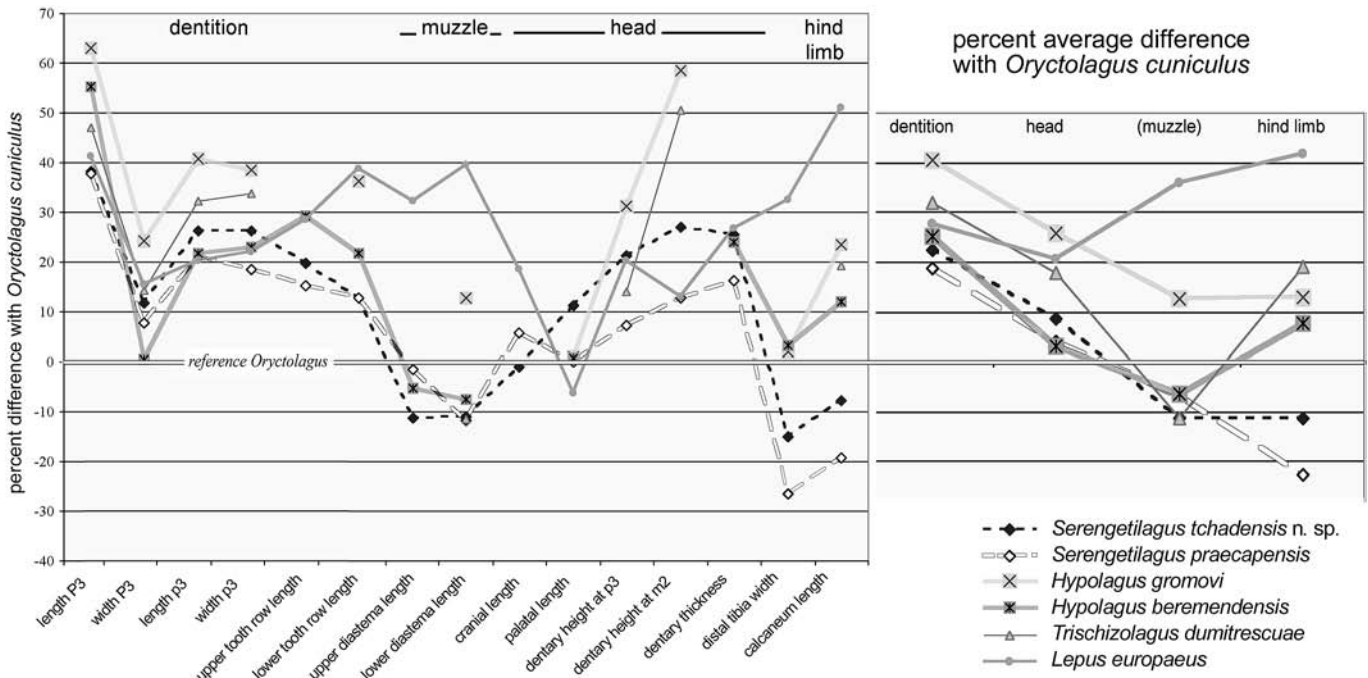


Figure 6. Comparison of dental and osteological biometric features between *Serengetilagus tchadensis* n. sp. and five other leporid species, expressed as percent of the differences referred to *Oryctolagus cuniculus*. Left, detail of individual variables. Right, summary of averaged differences by skeletal system: dentition, head (of which the muzzle) and hind limb. *Serengetilagus* species show parallel paths, indicating their similarity to each other. Both differ from *Oryctolagus* in the same way: larger teeth, similar cranium length, shorter muzzle, more robust dentary and weaker hind limb.

volcanic area was active by these times. Possibly the Chad hares were buried inside burrows by floods, like other fossorial mammals with articulated skeletons, such as Xerini squirrels and armadillos (Denys *et al.*, 2003; Lehmann *et al.*, 2005a, b, in press).

Thus, the fossil preservation of articulated *Serengetilagus* skeletons for Tanzanian assemblages is related to volcanic eruption in open-air habitat, while for the Chad assemblages is probably related also to the flood of subterranean shelters where they lived. Therefore the taphonomical data, like the skeletal features, points to a mixed fossorial-cursorial mode of life for these leporids.

COMPARISON WITH OTHER CLOSE TAXA

The closest archaeolagine taxon with the p3 pattern most similar to *Serengetilagus tchadensis* n. sp. is *Hypolagus gromovi* Gureev 1964, from the Late Miocene of southern Russia, although it has a much larger size (Table 2). *Hypolagus gromovi* shares with *Serengetilagus tchadensis* n. sp. the absence of lingual folds in p3 and the variable presence of an anteroflexid. They differ in *H. gromovi* having a deeper anteroflexid, even crenulated, and more frequent than in *S. tchadensis* n. sp. (60 %, n=10 versus 14 %, n=7) (Averianov, 1996; Fostowicz-Frelik, 2003).

The genus *Hypolagus* Dice 1917 was the most widespread Archaeolaginae during Pliocene times, known from North America (Middle Miocene to Late Pliocene), Asia (Pliocene) and Europe (Late Miocene to Early Pleistocene; last record in the Middle Pleistocene of Sicily; Fladerer & Fiore, 2003). *Hypolagus* has not yet been recorded from Africa.

Hypolagus gromovi is one of the earliest Old World Archaeolaginae, known from the Late Miocene-Earliest Pliocene of the Don valley (Russia). The original name *Hypolagus I. gromovi* coined by Gureev (1964: 119) has subsequently been corrected as *H. gromovi* by Sych (1965) and as *H. igromovi* by Averianov (1996). Since the name was honouring Dr. Gromov, the correct spelling must be *H. gromovi*. This European species seems to be geologically older than any other *Hypolagus* from Asia. Since the genus *Hypolagus* is much older in North America (known from 11 Ma ago) than in the Old World, it supposedly crossed Asia before spreading in Europe. Up to now, the older Asiatic *Hypolagus* comes from younger Pliocene deposits (Harr Obo) and only *Alilepus* is recorded before (Qiu, 1987). However, large Asiatic areas from low palaeolatitudes lack of the pertinent fossil record, and the hypothesis of a North American - Asian origin for *H. gromovi* can be validated in the future.

In the Late Miocene of East Africa, *Serengetilagus* has been recorded in the Lukeino Fm of Kenya (Mein & Pickford, 2006). These authors reject the report by Winkler (2003) of a palaeolagine being also present in Kenya

in these times (*Alilepus* sp. at Lothagam - Lower Nawata - and Lukeino), disappearing later on in Pliocene times when *Serengetilagus* swarmed in East Africa. In any case, a phylogenetic link between these taxa is not straightforward. Until a more abundant material could be available, we consider provisionally *Alilepus* and the new Chadian leporid as representing two separated lineages, because of their p3 morphology strikingly different (De Bruijn *et al.*, 1970; see below).

Other Pliocene and younger assemblages attributed to *Serengetilagus* from Africa are less well represented. Brunet *et al.* (2000) reported a small lower jaw identified as *S. aff. praecapensis* from the Early Pliocene of Kossom Bougoudi (Chad). Moreover, Winkler (2003) attributed to *Serengetilagus praecapensis* two specimens from Kenya (a jaw from the Early Pliocene of Lothagam Apak Member and a p3 from the Pliocene of Kanam West reported by Flynn & Bernor, 1987). These specimens are smaller than the type species of the genus.

The Pleistocene species "*Serengetilagus*" *raynali* Geraads 1994 from the Plio-Pleistocene of Morocco (Geraads, 1994, 1995) shows distinctive p3 features (large lingual anteroconid, constant mesofosetid) which put it apart from the genus *Serengetilagus* (see also Sen & Erbaeva, 1995).

Out of Africa, a leporid from the Lower Pliocene of Ukraine named *Serengetilagus orientieuropeus* by Topachevsky (1987) show striking similarities with the African genus, such as the crescent-shaped p3, small lingual anteroconid, incipient anteroflexid in all p3 and shallow paraflexid in one out of four specimens. The jaw figured by Topachevsky (1987, fig. 1) also fits well with that from *S. praecapensis*, although no measurements were provided. Moreover, a possible *Serengetilagus* is signalled at Pul-e-Charkhi (Early Pliocene of Afghanistan) by Sen & Erbaeva (1995), originally attributed to the genus *Trischizolagus* Radulesco & Samson 1967. Finally, Flynn & Bernor (1987) also referred to the genus *Trischizolagus* a specimen from Mongolia dated Late Miocene-Pliocene, considering a possible synonymy between *Trischizolagus* and *Serengetilagus*. Averianov & Tesakov (1997) distinguish both genera by the persistence of archaic features (archaeolagine-like p3) in the African taxon and transfer the Ukrainian, Moroccan and Afghan leporids to the genus *Trischizolagus*.

Trischizolagus dimitrescuae Radulesco & Samson 1967, the type species of the genus from the Late Pliocene of Romania, correspond to a large Palaeolaginae that can be phylogenetically related to *Alilepus*. However, as noted by Erbaeva & Angermann (1983), primitive species attributed to *Trischizolagus* have an archaeolagine p3 pattern rather similar to *Serengetilagus*. This is the case of *T. maritsae* De Bruijn, Dawson & Mein 1970, from the Early Pliocene of the island of Rhodes (Greece), and *Hispanolagus crusafonti* Janvier & Monténat 1971 from the Late

Miocene of Spain, transferred to the genus *Trischizolagus* by López-Martínez (1989). This species was originally described as having a short mesoflexid in anterior position, but it corresponds in fact to a paraflexid (López-Martínez, 1989: 202). The fragmentary material from *Trischizolagus crusafonti* (Janvier & Montenat 1971) does not allow to observe if a mesoflexid was present or not.

The primitive *Trischizolagus* species differ from the advanced one in features shared with *Serengetilagus*, such as the lack of lingual folds in P2 and p3. However, these are primitive features that cannot be an evidence for closer phylogenetic relationships.

In our view, some features support the distinction between these two vicariant genera:

- 1- The rounded p3 in *Serengetilagus* (crescent-shaped in *S. tchadensis* n. sp.) contrasts with an angular, rhombic-shaped p3 in *Trischizolagus*.
- 2- The relatively weak lingual anteroconid and anteroflexid in *Serengetilagus* differs from the notably developed lingual anteroconid and the very deep anteroflexid in *Trischizolagus*.
- 3- The hypoflexid variably bend forwards (type C-D in Fladerer, 1987) is present in *Serengetilagus* (predominant in *S. praecapensis*, less frequent in *S. tchadensis* n. sp.). Instead, it bends backwards in *Trischizolagus* (type A-B in Fladerer, 1987).

The high similarity between primitive *Trischizolagus* species (*T. maritsae*) and advanced *Serengetilagus* species (*S. praecapensis*) suggests some relationships between them (cf. Erbaeva & Angermann, 1983). However, very strong similarity also exists between *Alilepus* and *Trischizolagus dumitrescuae*, whereas many specialists have mistaken them (Daxner & Fejfar, 1967; Gureev, 1964). If primitive *Trischizolagus maritsae* actually belong to the *Trischizolagus dumitrescuae* lineage, which has not yet been fully documented, homoplastic evolution need to be hypothesised to explain the convergent features of Miocene *Alilepus* and advanced Pliocene *Trischizolagus*.

AN OVERVIEW OF MIO-PLIOCENE PERI-TETHYSIAN LEPORIDS

The widespread archaeolagine p3 pattern (Fig. 2a, middle), present in leporids during Late Miocene-Pliocene times, contrasts with the pattern in recent leporids where the archaeolagine p3 pattern is entirely absent. The most frequent p3 types in modern leporid genera are the palaeolagine (*Pronolagus*, *Bunolagus*, *Pentalagus*; Fig. 2a top) and leporine types (*Lepus*, *Oryctolagus*, *Sylvilagus*, *Caprolagus*; Fig. 2a bottom). The history of this replacement can be documented in the fossil record.

In Late Miocene times around the Tethys basin three different leporids were present, characterized by their p3's patterns (Fig. 7):

- type-1. archaeolagine-type; p3 with two folds (proto- and hypoflexid) and sometimes an incipient anteroflexid; e.g. *Hypolagus gromovi* in Ukraine; *Serengetilagus tchadensis* n. sp. in Chad.
- type-2. palaeolagine-type; p3 with three folds (proto-, hypo and mesoflexid); e.g. *Alilepus turoliensis* from the Late Miocene of Spain and Greece; *Alilepus laskarewi* from Moldavia (Khomeenko, 1914; López-Martínez, 1989; De Bruijn, 1995) and *Alilepus* sp. from Kenya (Winkler, 2003).
- type-3. archaeolagine-type; p3 with four folds (proto-, hypo, antero- and paraflexid); e.g. *Trischizolagus crusafonti* (Janvier & Montenat 1971) from Late Miocene (Messinian) of Spain (López-Martínez, 1989).

Subsequently during Early Pliocene times, these three leporid types were widespread in the Old World: type-1 leporids are recorded in Mongolia, type-2 in Asia and Eastern Europe, and type 3 in Greece, Ukraine, Afghanistan, Mongolia, Spain, Chad, Kenya and Tanzania.

Later on, three new types of leporids appeared according to their p3's pattern:

- type-4. palaeolagine-type; p3 with five folds or more (proto-, hypo-, meso-, para- and anteroflexid that can be multiple); e.g. *Pliopentalagus* and *Trischizolagus dumitrescuae* in Eastern Europe and Asia. Recent African leporids such as *Pronolagus* and *Bunolagus* belong to this type (Fig. 2a).
- type-5. palaeolagine "Nekrolagus"-type; p3 with three folds and a fosset (proto, antero- and hypoflexid and mesofossetid): e.g. "*Serengetilagus*" *raynali* from the Quaternary of North Africa. The recent North American *Romerolagus* belong to this type, which is usually observed as a rare variant in populations of types 3, 4 and 6.
- type-6. leporine-type; p3 with three or four folds (proto-, anteroflexid, a deep hypoflexid, and eventually a paraflexid); e.g. *Oryctolagus*, *Sylvilagus*, *Caprolagus/Pliosivalagus* and *Lepus* from Middle Pliocene to Pleistocene and recent. The first appearance of type 6, the most widespread type in modern leporids, occurs around mid-Pliocene. The first *Oryctolagus* is dated 3.5 Ma in Spain (Lopez-Martinez, 1989). The first record of *Sylvilagus* would be somewhat younger (around 3 Ma in USA; White, 1991). *Lepus* is not well documented until 2.5 My ago (but see Haile-Selassie *et al.*, 2004).

The evolutionary radiation of Old World leporids in the Pliocene is parallel and simultaneous to that occurred in the New World, amounting about 16 new genera in total. The decision of what type is primitive or derived lies mainly in four criteria, which do not always coincide:

- embryological criterion (ontogenetically younger would be primitive),
- palaeontological criterion (chronologically older would be primitive),
- widespread criterion (most common would be primitive) and
- outgroup criterion (the character state present in the outgroup would be primitive). The outgroup of Leporidae would be the primitive stem lagomorphs (*Megalagus*, *Desmatolagus*, etc).

Type-1 p3 (Fig. 7) would be primitive according to the palaeontological and outgroup criterion. In contrast, type-2 would be primitive according to the embryological criterion. Following one or another criterion, authors have proposed different evolutionary polarities linking these different morphotypes, which results in three phylogenetic hypotheses:

- 1) *Alilepus* (Leporinae) and primitive *Trischizolagus* (Archaeolaginae) form two independent lineages in European Mio-Pliocene: one originally with mesoflexid in adults, the other, originally without it, converge with the first one by finally developing a mesoflexid in adults (De Bruijn *et al.*, 1970); *Ser-*

engetilagus is not taken into account by these authors.

Dawson (in De Bruijn *et al.*, 1970) proposes a *Trischizolagus* lineage (types 3 and 4) derived from a type-1 (archaeolagine) leporid, indicating that the strong mesoflexid present in adult stages of advanced *Trischizolagus* species is a derived feature. It implies that *Trischizolagus* was not a descent of *Alilepus* (type 2). The author did not comment the similarities between primitive *Trischizolagus* and *Serengetilagus*.

- 2) *Alilepus* and *Trischizolagus dumitrescuae* (Leporinae) form a single lineage characterized by a developed mesoflexid (Averianov, 1995, and Averianov & Tesakov, 1997).

These authors suppose that type-4 derives from type-2, tracing a phylogenetic link between *Alilepus* and *Trischizolagus*, which implies a single lineage between these European Mio-Pliocene leporids. They propose the synonymy of *Trischizolagus maritsae* and *Serengetilagus orientieuropaes* (type-3) with *T. dumitrescuae* (type-4). They do not explain why these species lack a mesoflexid in adults that was present before (*Alilepus*) and after them (*T. dumitrescuae*).

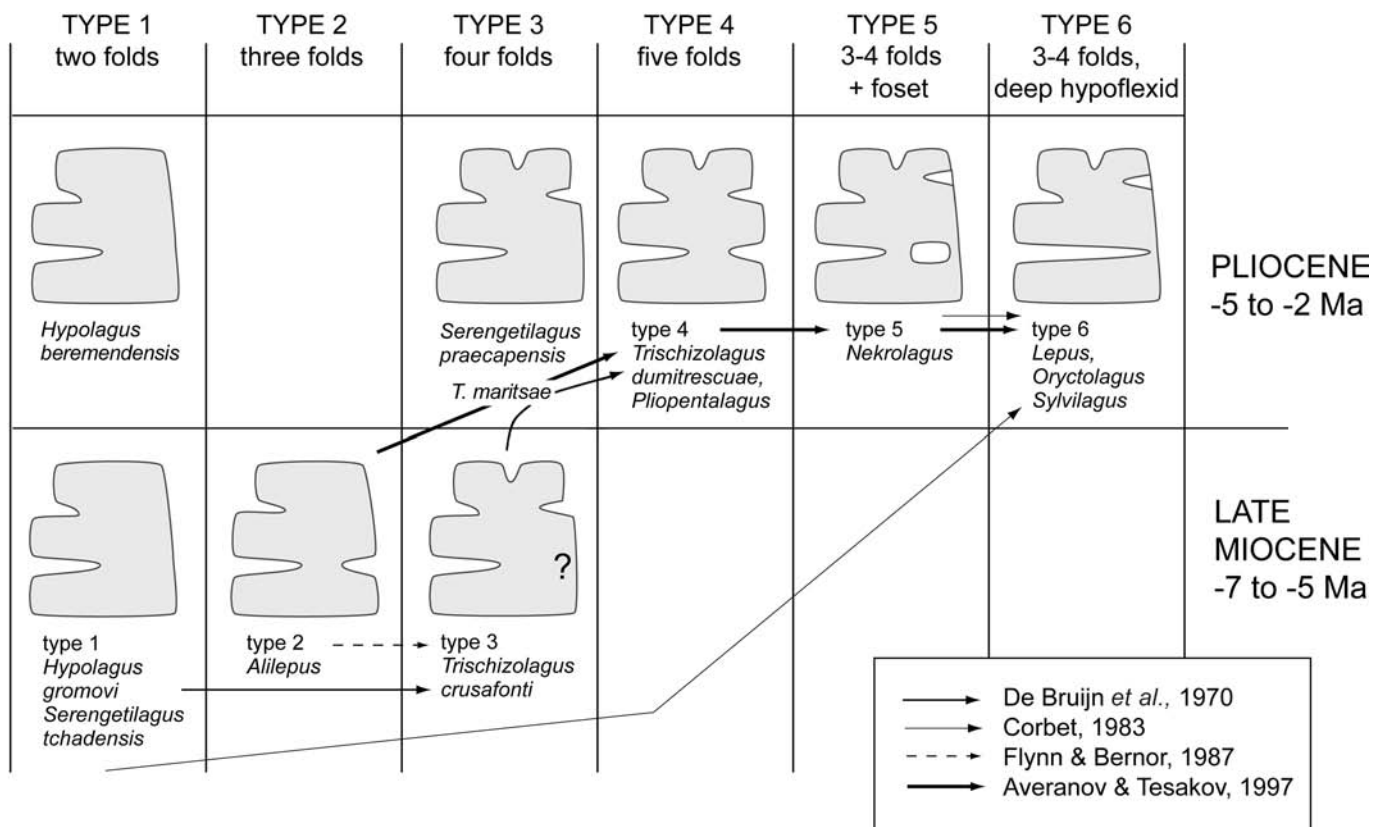


Figure 7. Chart showing schematic p3 patterns of some peri-Tethysian leporid species, recorded across the Miocene-Pliocene transition. Arrows connecting taxa indicate phylogenetic links proposed by different authors.

- 3) *Alilepus* and *Trischizolagus* (proposed synonym of *Serengetilagus*) form a lineage characterized by the loss of the mesoflexid (Flynn & Bernor, 1987). Flynn & Bernor (1987) suppose that type-3 derived from type-2, which implies that the mesoflexid would be a primitive feature for leporids and suffered a secondary loss in *Serengetilagus* and *Trischizolagus maritsae*. This reversion is based in the observed ontogenetic sequences starting with a weak juvenile mesoflexid that disappear subsequently with wear. The ontogenetic transition from type-2 to type-1 during individual tooth growth has been already signalled in archaeolagine leporids (Fladerer, 1987; Averianov & Tesakov, 1997). As it has been reported before, almost all lagomorphs have a juvenile ephemeral mesoflexid, which is a different feature that the deep adult mesoflexid of Palaeolaginae. Transitional populations between *Alilepus* and archaeolagine leporid species have not been documented yet. Therefore, the fossil record does not support a phylogenetic hypothesis deriving primitive *Trischizolagus* and *Serengetilagus* from *Alilepus*.

The last p3 type in order of appearance is type-6 (true leporine leporids). Corbet (1983) proposed an origin from type-1, either directly or indirectly through types-2 and 5 (Hibbard's classic hypothesis). Therefore, American authors consider Late Miocene type-2 *Alilepus* (with palaeolagine p3) as the first Leporinae, source of typical type-6 Leporinae (Dawson, 1958; White, 1991; Voohries & Timperley, 1997). Although types-5 and 6 coexists in modern leporine species (Averianov & Tesakov, 1997), individuals showing type 5 in the crown and type 6 in the root have never been observed, thus the origin of the typical leporine type-6 p3 is not yet fully documented.

In summary, the fossil record shows a high leporid diversity surrounding the Tethys in Late Miocene times, with a widespread palaeolagine-like genus (*Alilepus*), and two peculiar archaeolagine genera (primitive *Trischizolagus* and *Serengetilagus*). *Serengetilagus* was present in Eastern and Central Africa in Late Miocene, and may be *Alilepus* also in Eastern Africa. Because of its wear-broadened upper cheek teeth and its simple P2 and p3 pattern, *Serengetilagus tchadensis* n. sp. from the Late Miocene of Chad is up to now the most primitive species of its lineage. The different phylogenetic hypotheses proposed by previous authors do not agree towards a simple evolutionary scenario. Our best guess suggests the Late Miocene Archaeolaginae *Serengetilagus* could be a lineage derived from a *Hypolagus* stock (like the East European *Hypolagus gromovi*), itself probably immigrant from North America through Central Asia to the peri-Tethys area.

CONCLUSIONS

The Late Miocene deposits of Toros Menalla, Djurab Erg (North Chad) have delivered several, partly articulated skeletal pieces of a leporid mammal, here ascribed to a new species of the genus *Serengetilagus* Dietrich 1941 named *S. tchadensis* n. sp. It shows primitive features, such as a simple, archaeolagine-type p3 with only two main external folds and a strong transversal expansion with wear in the upper cheek teeth, which is related to an incomplete hypsodonty. Its size and general shape resembles *S. praecipensis* Dietrich 1941 from the Middle Pliocene of Laetoli (Tanzania). It differs from the Pliocene leporid in several cranial and dental features (choanae width, zygoma, orbits, basicranial-basifacial angle, lack of hypoflexus in P2, short and asymmetric hypoflexus in P3-M2, weak anteroflexid, lack of lingual folds in p3, etc). The variability of rare individuals of *Serengetilagus tchadensis* n. sp. shows some features closer to *S. praecipensis*, such as an incipient anteroflexid and a forward-curved hypoflexid in some p3. The similarities between both species allow to ascribe them to a single genus *Serengetilagus*.

The mode of life of the leporid *Serengetilagus* can be inferred by its ecomorphological traits and by taphonomical indications. Preliminary morphological observations show a mosaic character distribution combining both, hare and rabbit features. These features and some taphonomical indications point to a mixed fossorial-cursorial mode of life for *Serengetilagus*.

The genus *Serengetilagus* has been previously considered either as a Palaeolaginae or a Leporinae. It is here assigned instead to the subfamily Archaeolaginae Dice 1929 and related to *Hypolagus* Dice 1917, namely to *H. gromovi* Gureev 1964 from the Late Miocene of Southern Russia. Other related species are *S. orientieuropeaeus* Topachevsky 1987 and primitive species of the genus *Trischizolagus* Radulesco & Samson 1967, such as *T. crusafonti* (Janvier & Montenat 1971) and *T. maritsae* De Bruijn, Dawson & Mein 1970. Fossil findings variably ascribed either to the genus *Serengetilagus* or to primitive species of the genus *Trischizolagus* extend from Spain, Russia, Afghanistan to Mongolia during Miocene and Pliocene. Authors have discussed the possible synonymy of both genera. Here, we propose some features allowing to distinguish them (rounded versus rhombic-shaped p3, weak versus strong lingual anteroconid and anteroflexid, and forward versus backward hypoflexid bend).

The new African archaeolagine leporid is contemporaneous with the widespread palaeolagine *Alilepus* Dice 1931, recorded in Late Miocene of Kenya. Previous studies of the high diversity of leporids surrounding the Tethyan area in Mio-Pliocene times give way to several phylogenetic proposals. Here we favoured the hypothesis of an independent evolution of *Alilepus* and *Serengetilagus* lineages during Mio-Pliocene times.

ACKNOWLEDGEMENTS

We thank the Chadian authorities, Ministère de l'Éducation Nationale, de l'Enseignement supérieur et de la Recherche (Université de N'Djamena; CNAR and its Head Dr. Baba) and French ones, Ministère de l'Enseignement Supérieur et de la Recherche (Université de Poitiers; CNRS: SDV & ECLIPSE); Ministère des Affaires Étrangères (DGCID Paris and SCAC N'Djamena); the Région Poitou-Charentes; the French Army (MAM and Epervier); the NSF/RHOI, all the MPFT members, G. Florent and C. Noel for administrative guidance of the MPFT; C. Alonso Recio, photographer of the UCM; P. Mein and P. Peláez-Campomanes for comments of the manuscript; and Ministerio de Educacion y Ciencia, Spain (funding projects BTE2002-1430 and CGL2006-04646).

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