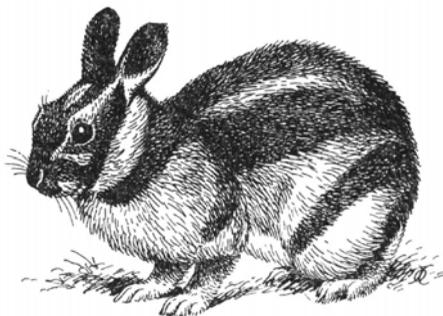


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ALEXANDER O. AVERIANOV, ALEXEI V. ABRAMOV,
ALEXEI N. TIKHONOV

**A NEW SPECIES OF *NESOLAGUS* (LAGOMORPHA,
LEPORIDAE) FROM VIETNAM WITH OSTEOLOGICAL
DESCRIPTION**



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A.O. Averianov, A.V. Abramov, A.N. Tikhonov. A new species of *Nesolagus* (Lagomorpha, Leporidae) from Vietnam with osteological description. Contributions from the Zoological Institute, St. Petersburg, 2000, N 3. 22 p.

Nesolagus timminsi **sp. n.**, based on a partial skeleton from Vietnam, differs from *N. netscheri* (Schlegel, 1880) from Sumatra by skull length larger, foramen lacertum smaller, P2 larger and having two folds on anterior face, m3 with two columns joined by a lingual dentine bridge. Detailed osteological description of *Nesolagus timminsi* **sp. n.** is presented.

А.О. Аверьянов, А.В. Абрамов, А.Н. Тихонов. Новый вид *Nesolagus* (Lagomorpha, Leporidae) из Вьетнама с остеологическим описанием. Известия Зоологического института, 2000, N 3, 22 с.

Nesolagus timminsi **sp. n.**, описан на основе скелета из Вьетнама. Он отличается от *N. netscheri* (Schlegel, 1880) из Суматры большими размерами черепа, меньшим рваным отверстием, более крупным P2, имеющим две складки на передней стороне, m3 с двумя столбиками соединенными лингвальным дентиновым мостиком. Приводится детальное остеологическое описание *Nesolagus timminsi* **sp. n.**

Публикуется по решению Ученого совета Зоологического института

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A NEW SPECIES OF *NESOLAGUS* (LAGOMORPHA, LEPORIDAE) FROM VIETNAM WITH OSTEOLOGICAL DESCRIPTION

© Alexander O. **Averianov**, Alexei V. **Abramov**, Alexei N. **Tikhonov**

INTRODUCTION

The striped, or Sumatran rabbit, *Nesolagus netscheri* (Schlegel, 1880), is without doubts the rarest species of the family Leporidae and one of the rarest species of mammals. It is restricted to montane dense forest, above 600 m, in the Barisan Mountains in Sumatra (Fig. 1). *N. netscheri* is known by fifteen specimens collected or recorded between 1880 and 1916 (Flux, 1989, 1990). After this there was one confirmed sighting in 1972 in north-west Sumatra (Flux, 1990), and one rabbit was photographed by an automatic camera trap in Kerincki Seblat National Park in Sumatra in 1998 (SurrIDGE et al., 1999: fig.2a).

The recent multinational activities of zoologists in Southeast Asia led to some very important theriological discoveries. Among these is the discovery of striped rabbits in Annamite Mountains in Laos and Vietnam. After December 1995 not less than ten specimens were collected and one rabbit was photographed alive in nature (SurrIDGE et al., 1999: fig.2b). Genetic analysis, based on mitochondrial DNA, reveals a considerable genetic distance between the Sumatran and Annamite rabbits, compatible with the distance between leporid genera (SurrIDGE et al., 1999).

Here we present a detailed osteological description of the Annamite rabbit based on a nearly complete skeleton collected in the Annamite Mountains in Vietnam, close to the Laos border, by the expedition of the Zoological Institute, Russian Academy of Sciences in April 2000.

The anatomic nomenclature is generally after Bensley (1948). The method of skull measurements is shown on Fig. 2.

Institutional abbreviations. – BMNH – Natural History Museum, London; MNHN – Muséum National d'Histoire Naturelle, Paris; NRM – Naturhistoriska Riksmuseet, Stockholm; ZIN – Zoological Institute, Russian Academy of Sciences, St. Petersburg.

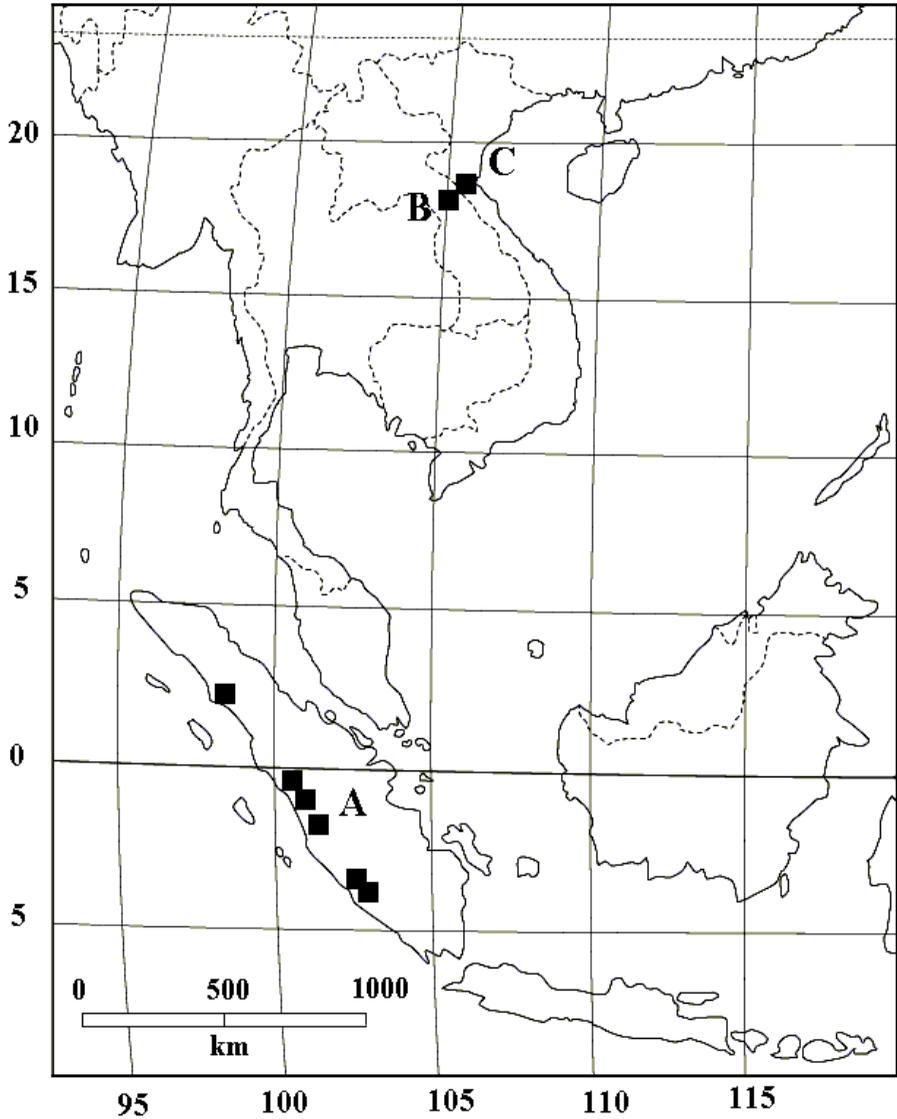


Figure 1. Map showing distribution of the Sumatran rabbit, *Nesolagus netscheri* in Sumatra (A, after Flux, 1990) and the Annamite rabbit, *Nesolagus timminsi* sp. n. in Laos and Vietnam (B – locality reported by Surridge et al., 1999, C – locality of ZIN 84772).

SYSTEMATIC PART

Family Leporidae Fisher, 1817

Nesolagus Forsyth Major, 1899*Nesolagus timminsi* sp. n.

(Figs 3A, 4B, C)

Holotype. – Zoological Institute, Russian Academy of Sciences, St. Petersburg, ZIN 84772, a partial skeleton with the skull, sex unknown. Vietnam, Ha Tinh Province, Huong Son District, Son Kim Community, about 10 km south from village Nuoc Sot, 18°22' N, 105°13' E, altitude 200 m. Skeleton was found near hunting line by A.V. Abramov 26 April 2000.

Differential diagnosis. – Differs from *N. netscheri* (Schlegel, 1880), the only previously known species of the genus, distributed on Sumatra, by a greatest skull length some 12% larger (78.9 mm, 70.0 mm in *N. netscheri*), foramen lacerum relatively smaller and narrower mediolaterally, P2 relatively longer, being 91% of P3 length (73% in *N. netscheri*), P2 having two folds on its anterior face (one in *N. netscheri*).

Distribution. – Annamite Mountains, Vietnam and Laos.

Etymology. – In honour of Mr. Robert J. Timmins, discoverer of the Annamite rabbit in Laos.

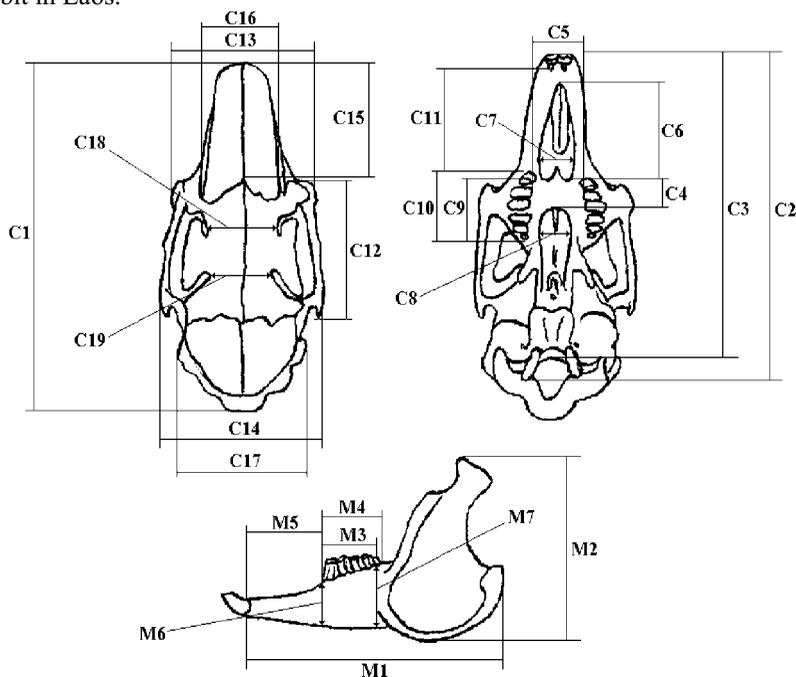


Figure 2. Measurements of the leporid skull.

OSTEOLOGICAL DESCRIPTION

Material. – ZIN 84772 represents a fairly complete skeleton, including skull and dentary with complete dentition, cervicals 2, 3, 5, thoracics 1, 2, 4, 5, 8-10, 12, lumbar 1-7, sacrum, right ribs 1 and 2, left rib 3, three right and two left unidentified sternal ribs, and four unidentified asternal ribs, both scapulae, both humeri, both ulnae, left radius, right II and IV metacarpals, one unidentified second phalanx of manus, both innominate bones, both femora, both tibia-fibulae, left calcaneum, both II and III metatarsals, left IV metatarsal, and right V metatarsal.

Dentition (Figs. 3A, 4B, C). – The dental formula is $dI2, I3 / di2 \quad P2-4 / p3, 4$ $M1-3 / m1-3$. The first upper incisor ($dI2$) is relatively robust, 2.2 mm in length and 3.1 mm in width. The cross section of $dI2$ is sub-rectangular in outline. $dI2$ begins at the premaxilla-maxilla suture. The groove on the anterior surface of $dI2$ is simple, is not filled with cement, and is located near the middle of the crown (Fig. 3A). In the simple incisor groove lacking cement *Nesolagus* is similar with the majority of the Recent leporids (Fig. 3B). Sometimes there is a little cement in a simple incisor groove (Fig. 3C), especially in older animals. In *Caprolagus*, *Poelagus* and *Lepus* (*Tarimolagus*) *yarkandensis* Günther, 1875 the incisor groove is deeper and filled by a cement (Fig. 3D-F). In some species of *Lepus* (subgenera *Sabanolagus*, *Macrotolagus*, and *Indolagus*) this groove is deep and widened distally within the incisor, in *Macrotolagus* and *Indolagus* it is usually divides into two-four branches (Fig. 3H, G, J).

The second upper incisor ($I3$) is simple and peg-like, 1.0 mm in length and 1.1 mm in width (Fig. 3A). A distal portion of $I3$ is bent laterally. Both $I3$ stand rather far from each other and touch the posterior surface of $I2$.

$P2$ is relatively large comparatively to *N. netscheri* (Fig. 4A, B), being almost equal to $P3$ and length and having crown width of 76% from the $P3$ crown width (67% in *N. netscheri*). $P2$ has relatively long buccal crown face and two prominent folds on its anterior surface (one in *N. netscheri*). On the whole the structure of $P2$ in *N. timminsi* **sp. n.** agrees with the morphology of this tooth in derived leporines. This suggests that reduced and simplified $P2$ in *N. netscheri*, recalling $P2$ in primitive extinct leporids like *Archaeolagus*, *Hypolagus*, and *Alilepus*, is in fact secondarily modified. The secondary simplification of $P2$ can be seen also in *Brachylagus*.

$M3$ is a reduced simple peg-like tooth with transversely elongated crown (Fig. 4B), but it is relatively large by leporid standards, with crown width being 44% from the $M2$ crown width (42% in *N. netscheri*). $M3$ is more reduced in *Romerolagus* (Fig. 5), *Brachylagus* (Fig. 6), *Pentalagus* (Fig. 7), *Caprolagus*, *Poelagus*, *Oryctolagus*, and *Lepus*. In *Poelagus* and *Pentalagus* $M3$ may be absent at least in some specimens.

The lower incisor, $di2$, is robust, 2.3 mm in length and 3.3 mm in width, sub-quadrate in cross section. It begins anterior to $p3$, approximately at the middle of the dentary height. Such an anterior position of the place of $di2$ beginning is a derived feature, shared by the majority of the Recent leporids. Only in *Caprolagus hispidus*

(Pearson, 1839) from the southern foothills of Himalayas (India and Nepal) di2 begins at the level of posterior part of p4. This condition in *C. hispidus* is apparently secondarily derived, because its probable ancestor, the Late Pliocene *C. sivalensis* Forsyth Major, 1899 from Hindustan, had lower incisor beginning in a more anterior position, at the level of posterior part of p3. The secondarily posterior shifting of di2 in the evolution of *Caprolagus* is possibly connected with its adaptation to consume rather hard plants. This adaptation has also led to the extreme complication of the enamel folds in cheek teeth in *C. hispidus* (Fig. 8). Similarly, in the Greenland hares, *Lepus arcticus groenlandicus* Rhoads, 1896, living in severe Arctic conditions and fed on harsh plants, the lower incisor is shifted posteriorly up to the level of p3 talonid – p4 trigonid.

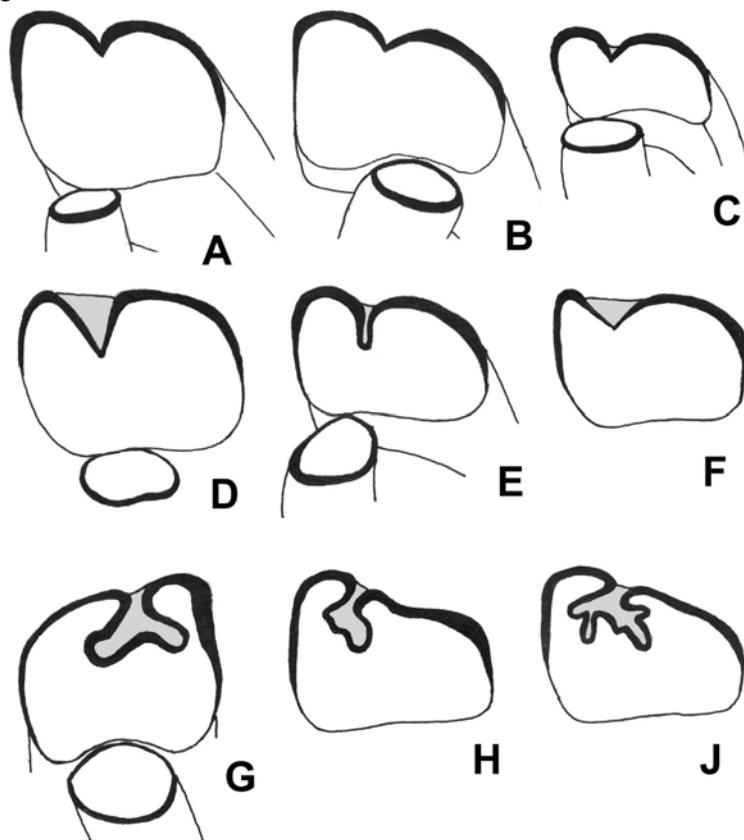


Figure 3. Upper incisors in selected leporids. A – *Nesolagus timminsi* sp. n., ZIN 84772, Vietnam; B – *Pentalagus furnessi*, ZIN 15887a, Japan; C – *Romerolagus diazi*, MNHN 1960-3808, Mexico; D – *Caprolagus hispidus*, NRM A585848, India; E – *Poelagus marjorita*, MNHN 1971-99, Central African Republic; F – *Lepus (Tarimolagus) yarkandensis*, MNHN 1911-759, China; G – *Lepus (Macrotolagus) callotis*, MNHN 1962-2542, Mexico; H – *Lepus*

(*Sabanolagus*) *crawshayi*, MNHN 1973-297, Malawi; J – *Lepus* (*Indolagus*) *peguensis*, MNHN 1862-1249, Thailand. Not to scale.

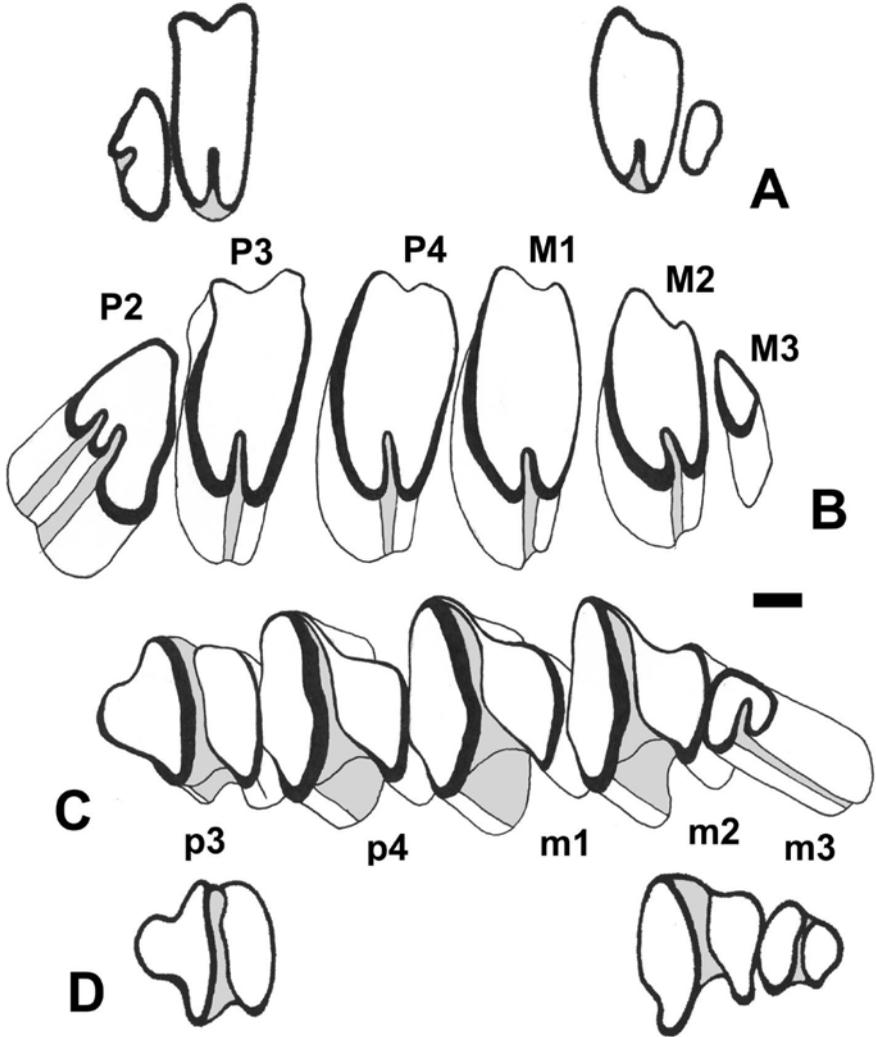


Figure 4. Cheek dentition of *Nesolagus netscheri* (A, D, after Schreuder, 1936; D reversed) and *Nesolagus timminsi* sp. n. (B, C; B reversed; based on ZIN 84772, Vietnam). Scale bar is 1 mm for B and C, the scale for *N. netscheri* is unknown.

P3 is simplified and of “paedomorphic” pattern (Averianov & Tesakov, 1997: fig.2), with trigonid and talonid completely separated by a cement (Fig. 4C). There are a very shallow antero-external reentrant and a deeper antero-internal reentrant, both lacking cement. In *N. netscheri* the structure of p3 is almost identical to that of

ZIN 84772 (Schreuder, 1936: fig.5; Fig. 4D), except the antero-external reentrant is deeper and filled by a small amount of cement. In older specimens of *N. netscheri* the antero-internal fold of p3 disappear (Schreuder, 1936: 232, fig. 5a). In ZIN 84772 the trigonid and talonid of p3 have become joined by a lingual dentine bridge about 2 mm below the occlusal surface. This means that at a slightly later ontogenetic stage this tooth will get the typical leporine morphology (“*Lepus*” morphotype of Averianov & Tesakov, 1997: fig.2). As it is known, all the specimens of *N. netscheri* have p3 of “paedomorphic” morphotype. Probably the “*Lepus*” pattern of p3 is completely absent from the ontogenesis in the latter species, or it appears at a very late ontogenetic stage.

The lower molariform teeth (p4 m1, 2) are uniform in morphology, as in other leporids (Fig. 4C), and do not bear any specific features. A narrow lingual dentine bridge joins the trigonid and talonid early in the ontogenesis.

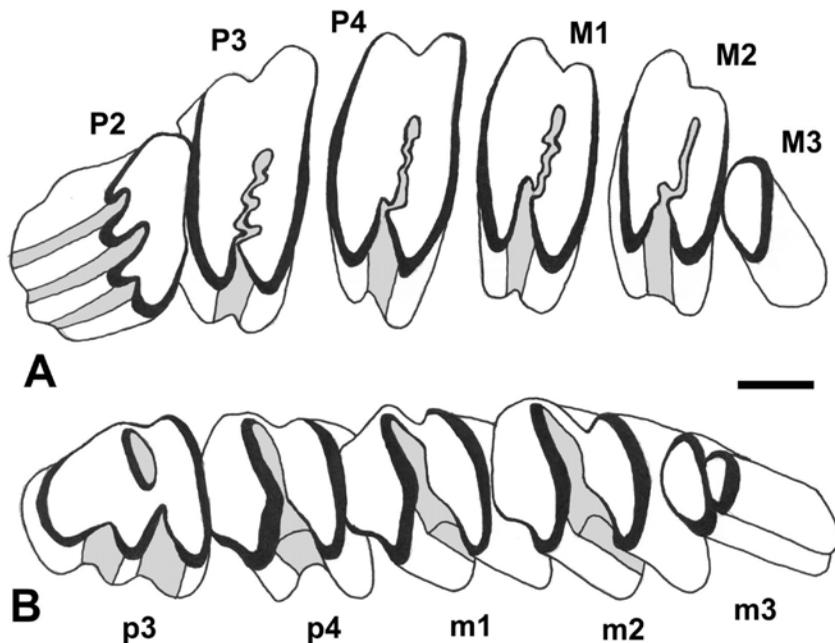


Figure 5. Upper (A) and lower (B) dentition of *Romerolagus diazi*, ZIN 38940, Mexico. Scale bar is 1 mm.

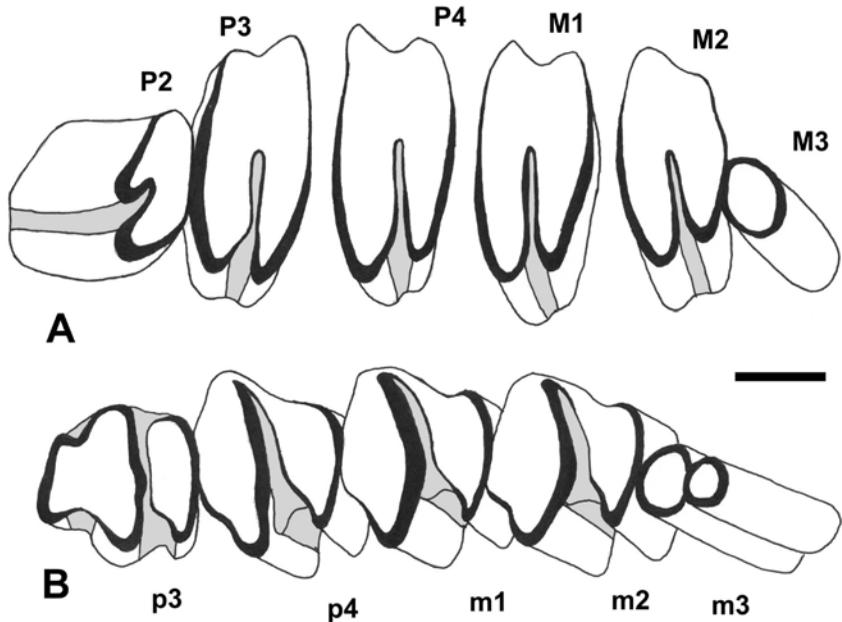


Figure 6. Upper (A) and lower (B) dentition of *Brachylagus idahoensis*, ZIN 39403, USA. Scale bar is 1 mm.

M3 consists of two columns, joined by a relatively wide lingual dentine bridge on the left m3 in ZIN 84772 (Fig. 4C), but separated by cement on the right m3 of the same specimen. The posterior columns are about twice transversely narrower than the anterior one. M3 in *N. netscheri* (Schreuder, 1936: fig. 5b) looks relatively larger, with two columns of similar width and completely separated by cement. The presence of m3 with joined columns on one side of ZIN 84772 should be considered as primitive, atavistic character. Such connection of two m3 columns by a dentine bridge is characteristic for some Paleogene lagomorphs (“Palaeolagidae”, *Litolagus*). In all Neogene-Recent “archaeolagines” and leporines both columns of m3 are separated by cement.

The dentition of *Nesolagus* is highly paedomorphic. The common paedomorphic characters for two *Nesolagus* species include short hypostralia with smooth margins and p3 with separated trigonid and talonid and lacking an anterior reentrant. *N. netscheri*, being somewhat smaller, living further south, and probably maturing earlier, has a dentition further derived towards this trend, i.e. more paedomorphic: P2 become more reduced and have only one anterior fold, p3 trigonid and talonid possibly remain separated during the whole of ontogenesis (should be joined by a lingual dentine bridge in *N. timminsi* sp. n. in late ontogenesis), two columns of m3 remains

separated probably during the whole of ontogenesis (joined in *N. timminsi* **sp. n.** relatively earlier in the ontogenesis).

There is only one Recent leporid species compatible with *Nesolagus* in the degree of paedomorphosis in the dentition. This is the North American *Brachylagus idahoensis* (Merriam, 1891), the smallest Recent leporid. In the population of *B. idahoensis* the paedomorphic morphotype of p3, with the trigonid and talonid separated, is most common (88%, n=219, after White, 1991; Fig. 6). Similarly to *Nesolagus*, *Brachylagus* has reduced P2 with one anterior fold, hypostria on P3-M2 with not crenulated margins, and p3 without an anterior reentrant (Fig. 6). However, *Brachylagus*, like other leporids, still have a quite long hypostria on P3-M2, exceeding half of the crown width (Fig. 6), which mean that this taxon is less derived towards paedomorphosis in the dentition comparatively to *Nesolagus*.

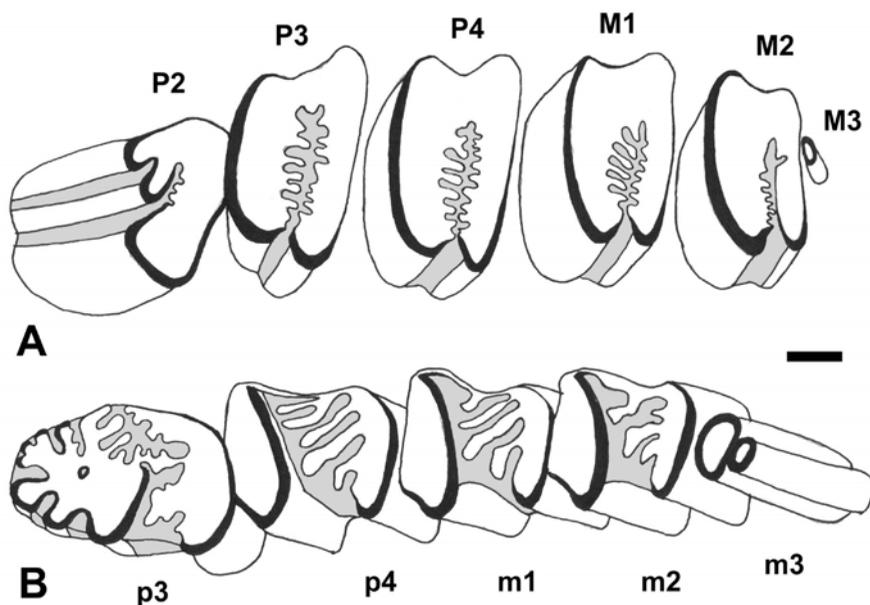


Figure 7. Upper (A) and lower (B) dentition of *Pentalagus furnessi*, ZIN 15887a, Japan. Scale bar is 1 mm.

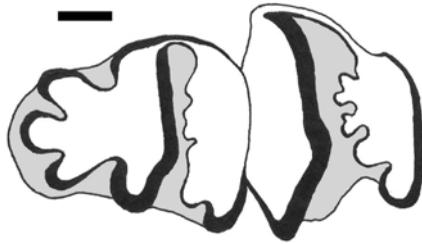


Figure 8. p3 and p4 of *Caprolagus hispidus*, NRM A585848, India. Scale bar is 1 mm.

Skull. – The skull is almost identical with that of *N. netscheri* (Forsyth Major, 1899: pl.39, fig.38; Bemmelen, 1910: figs.2, 14, 26, 65, 80, 81, 99, 101-106; Schreuder, 1936: pl.2, fig.3), except somewhat larger size (Table 1) and relatively smaller and narrower foramen lacerum. The skull morphology in the Recent Leporidae is essentially uniform and this very successful morphotype was established as early as the Late Oligocene - Early Miocene. Therefore it is not surprising that the skull in both *Nesolagus* species has generally the same morphology. However, *Nesolagus* possess some distinctive characters, mostly primitive, which are described below.

The supraorbital process of the frontal is relatively small, with a short posterior projection and without an anterior projection. Such structure of the supraorbital process was characteristic for the Oligocene and Early Miocene lagomorphs, like *Palaeolagus* and *Archaeolagus*. Among the Recent leporids this primitive condition is retained, except *Nesolagus*, also in *Romerolagus*, *Pentalagus*, *Caprolagus*, and *Poelagus*. In the remaining Recent leporids the supraorbital process is better developed, with a variably developed anterior projection. Juvenile hares (*Lepus*), however, have a primitive structure of the supraorbital process. The postorbital process is completely lacking in Prolagidae and Ochotonidae.

The interparietal is distinct. In *N. netscheri* the interparietal is distinct in subadult and adult animals (Schreuder, 1936: fig.6a, b) and becomes fused with the supraoccipital in aged animals (Schreuder, 1936: fig.6c). The retention of the separated interparietal during most of ontogenesis is related to the paedomorphosis of *Nesolagus*. The similar paedomorphic retention of the separate interparietal in adults is characteristic also for *Romerolagus*, *Bunolagus*, *Brachylagus*, *Sylvilagus*, and *Oryctolagus*.

The posterior zygomatic process of the maxilla (processus temporalis ossis maxillaris, =processus zygomaticus posterior) is quite long, extending posteriorly far beyond the zygomatic process of the squamosal. The polarity of this character is not certain, it is probably a plesiomorphic state, characteristic also in *Archaeolagus*, *Romerolagus*, *Pentalagus*, and *Caprolagus*. The posterior zygomatic process is

relatively short with rounded end in *Bunolagus*, *Pronolagus*, *Sylvilagus*, *Oryctolagus*, and *Lepus*. In the Oligocene "Palaeolagidae" this process was short, and it is secondarily considerably elongated in *Prolagus* and Ochotonidae. The lengthening of the posterior zygomatic process was apparently connected with the strengthening of the m. masseter profundus, increasing its attachment surface.

The incisive foramina are completely divided longitudinally by a septum formed by the palatine process of premaxilla and an anterior process of maxilla. Moreover, on this septum at the premaxilla-maxilla suture there are remnants of the transverse processes, separating earlier in ontogenesis the incisive foramina transversely. In *N. netscheri* the incisive foramina are separated in subadults (and, surely, juveniles) by a transverse bone bridge, which is resorbed in older animals (Schreuder, 1936: 234, pl.2, fig.3a), an unique character among the Leporidae. There is no other modern leporid which shows transverse separation of the incisive foramina at least for the part of the ontogenesis. Only in *Romerolagus diazi* (Ferrari-Perez in Diaz, 1893) (ZIN 38940; Cervantes et al., 1990: fig.2) and *Caprolagus hispidus* (NRM A585848; Angermann, 1966: fig.8) the incisive foramina are subdivided longitudinally by a long anterior process of maxilla, joining the palatine process of premaxilla, as in *Nesolagus*. This condition could be considered as plesiomorphic and *Nesolagus* is the most primitive leporid in this respect. An intermediate stage can be seen in the African *Pronolagus rupestris* (A.Smith, 1834) (ZIN 289) and *P. crassicaudatus* (I.Geoffroy, 1832) (Lyon, 1904: pl.78, fig.2b), where the anterior process of the maxilla is relatively long, but connected with the premaxillary palatine process only by a connective tissue tendon. The remaining Recent Leporidae have a much shorter anterior process of maxilla, not contacting the palatine process of premaxilla.

The bone palate is relatively long, being 11.7% of the condylobasal skull length. Among the Recent leporids only *Pentalagus* and *Caprolagus* have a similarly long bone palate, 12.8 and 12.0% of the condylobasal skull length respectively (ZIN 15887a and NRM A585848). In other Recent leporids this ratio is less than 10%. The relatively long bone palate is a plesiomorphic character. In many derived leporids reduction of the bone palate is connected with the enlargement of choanal chamber, reflecting improved running ability. The relatively shortest bone palate is characteristic for species of the genus *Lepus*, the most efficient runners. However, the neonate hares still possess a primitively long palate (e.g. Bemmelen, 1910: fig.25).

The foramen lacerum is relatively large. Except *Nesolagus*, the relatively large foramen lacerum is present in *Pentalagus* and *Caprolagus*. The polarity of this character is uncertain. It is usually characteristic for juvenile leporids. The foramen lacerum is relatively larger in *N. netscheri* comparative to *N. timminsi* sp. n., which may reflect more profound skull phoetalisation in the former species.

The auditory bullae are relatively very small, being in length only 9.8% from the condylobasal skull length. The size of the auditory bulla in Lagomorpha is allometrically connected with the size of the skull in general. There are few genera which do not follow this regularity. The non-proportionally increased bulla is present in *Pewelagus*, *Hypsopalaeolagus*, and *Brachylagus*. The non-proportionally small bulla, smaller than the occipital condyle, is characteristic for *Palaeolagus*, *Alilepus*,

Pentalagus, *Caprolagus*, and *Nesolagus*. The small bulla is a primitive character retained in these taxa.

Dentary. – The dentary is of typical leporid morphology and bears only two distinctive characters listed below.

The angle between the horizontal and vertical mandible portions (corpus mandibulae versus ramus mandibulae) is relatively low. For the sake of simplicity this angle is measured as between the occlusal plane of lower cheek teeth and the coronoid process. In ZIN 84772 it is 125° , in *N. netscheri* – $125\text{--}130^{\circ}$ (measured after Forsyth-Major, 1899: pl.39, fig.28; Bemmelen, 1910: fig.106). The similarly low angle there is in *Pentalagus* ($115\text{--}120^{\circ}$), *Romerolagus* (121°), and *Caprolagus* (122°). The remaining Recent leporids have a greater angle between the cheek teeth occlusal plane and the coronoid process, lying between $130\text{--}140^{\circ}$. The more upright position of the coronoid process evidently is a primitive character, inferred from the Oligocene lagomorphs.

The coronoid process is relatively small, in form of a short ridge-like thin plate at the middle of the anterior margin of ramus mandibulae. This is a derived feature characteristic for the majority of Recent leporids, except *Pentalagus*, *Caprolagus*, and *Poelagus*. In the latter genera the coronoid process is relatively longer. The reduction of the coronoid process in the evolution of Lagomorpha is connected with the decreasing importance of m. temporalis for mastication. *Pentalagus*, *Caprolagus*, and *Poelagus* are apparently adapted to consume more harsh vegetation comparatively to other leporids, as can be deduced from their highly specialised dentition, and this may explain the relatively larger size of the coronoid process in these taxa.

Skull measurements (Fig. 2, in mm). – M1 - 55.0; M2 - 35.6; M3 - 16.1; M5 - 17.5; M6 - 8.7; M7 - 13.1; C1 - 78.5; C2 - 71.3; C3 - 64.1; C4 - 8.4; C5 - 13.3; C6 - 18.6; C7 - 6.7; C8 - 7.8; C9 - 16.1; C11 - 21.7; C12 - 33.3; C13 - 37.2; C14 - 36.4; C15 - 22.2; C16 - 15.5; C18 - 14.0; C19 - 13.5 (ZIN 84772).

Postcranial skeleton. – We give a more detailed description of the known postcranial elements of ZIN 84772, because the postcranial anatomy is not adequately known for the Leporidae as a whole and specifically for *Nesolagus*.

Vertebral column. – The vertebral column is incompletely preserved in ZIN 84772. The presacral vertebral formula is generally uniform within Leporidae: C7 T12 (rarely T13) L7 (rarely L6). In ZIN 84772 there are seven preserved lumbar, and thus the presacral vertebral count for *Nesolagus* should be C7 T12 L7. There are four coossified vertebrae in the sacrum. The number of caudals is not known.

Cervical vertebrae. – As in other leporids, the cervicals decrease in length caudally (centrum length at midline, in mm: C2 (without the odontoid process) – 10.3; C3 – 9.4; C5 – 8.1; neural arch length at midline, in mm: C2 – 9.7; C3 – 7.7; C5 – 4.3).

The atlas is not preserved.

The axis (epistropheus) has a well-developed cylindrical odontoid process (dens epistrophei), projecting dorsocranially at the angle of 31° from the centrum ventral surface plane (15° in *Pentalagus*, 30° in *Lepus*). The neural spine is relatively short; its length does not exceed the length of the centrum (distinctly longer than centrum in

other leporids). Caudally the neural arch is considerably lowered, so its dorsal margin is almost rounded in the lateral view (it is straighter in other leporids). In articulation neural spine of the axis contacts neural spine of C3 (does not contact in *Lepus*). In *Lepus* the axis neural spine divides caudally into two spin-like projections directed caudolaterally. This structure comes to an extreme in *Pentalagus*, where the axis neural spine is divided into two thin plates between which there is a depression with a narrow vertical hole for placement of the C3 neural spine during vertebra articulation. This structure in *Pentalagus* possibly limits the neck movements at this joint. The condition of *Nesolagus*, having the most simply constructed axis neural arch, is apparently the primitive state for Leporidae. The transverse processes are in the form of short spines caudally projecting. The transversarium canal is relatively shorter than in other leporids.

Cervicals 3 and 5, apart from the above-mentioned shortening in the caudal direction, show also slight increasing of the neural spine height in the same direction. It is 3.0 mm in C3 and 3.3 mm in C5 (measured from the dorsal margin of the foramen vertebrae). The cervical neural spines in ZIN 84772 are relatively longer than in corresponding cervicals in *Lepus*, and approximately the same as in *Pentalagus*. The neural spine is oriented dorsally in C3 and dorsocranially in C5. In C3 and 5 the anterior (ventral) radix of transverse process is a thin plate-like structure, directed ventrolaterally, and relatively short craniocaudally. The posterior (dorsal) radix of transverse process in these cervicals is spine-like and directed caudally (C3), or dorsocaudally (C5). In *Pentalagus* both anterior and posterior radices of the transverse process in C3 are plate-like and noticeably longer, separated by a marked depression. In *Pentalagus* the transverse process in C5 is similar to that in ZIN 84772, except the posterior radix is directed more dorsally. In *Lepus* both radices of the transverse process become confluent in C3 to form a common plate, remain separated in C5, but relatively much longer than in ZIN 84772. Concluding, *Nesolagus* has a relatively simple (primitive?) structure of cervical neural spines and transverse processes compared with other Leporidae. The similarly simple cervical transverse processes, with craniocaudally shortened anterior radix (=‘costal process’) is apparently present also in *Pronolagus* (Lyon, 1904: 357).

Thoracic vertebrae. – The centrum length of thoracics increases caudally (measured at midline from ventral side, in mm): T1 – 6.3; T2 – 6.7; T4 – 8.1; T5 – 8.0; T8 – 9.4; T9 – 10.4; T10 – 11.4; T12 – 13.1. The neural arches are highest at T4-5, vertically oriented in T1-2 and T10, posteriorly deflected in T4-8, and craniodorsally projecting in T12. T10 apparently is the anticlinal vertebra, thoracics before it have caudally deflected neural spine, and after it spines in T11-12 and lumbar are cranially inclined. In other leporids the anticlinal vertebra is T10 (*Brachylagus*, *Romerolagus*) or usually T11 (*Pronolagus*, *Sylvilagus*, *Oryctolagus*, *Lepus*) (Lyon, 1904: 358, 359). The neural spine is spine-like in T1-2, more transversely flattened but craniocaudally short in T4-5, somewhat longer in T8-10, and longest and lowermost in T12. The height of the neural arch is following (measured from the dorsal margin of the foramen vertebrae, in mm): T1 – 7.7; T2 – 12.1; T4 – 9.9; T5 – 11.0; T8 – 10.3; T9 – 9.7; T10 – 9.0; T12 – 7.4. The centrum

height is slightly increasing caudally (measured on posterior side, in mm): T1 – 3.0; T2 – 2.9; T4 – 3.7; T5 – 3.7; T8 – 4.0; T9 – 3.9; T10 – 3.9; T12 – 4.3. The centrum articulation facets in T1, like in cervicals, remain obliquely oriented. Starting with T2 the centrum articulation facets become more vertically oriented, and they are almost vertical in T4-9. In T4-5 the posterior centrum articulation facet is distinctly incised from the ventral side, a feature not known for other leporids. The ventral median ridge on the thoracic centra is better developed on more posterior thoracics, but do not become so prominent as in *Lepus*, more recalling the condition of *Pentalagus*. The transverse process in T1-2 is stout and spine-like, projecting laterally, and shorter in T2. The costal facet of transverse process in T1-2 faces almost laterally. In T4-5, 8 the transverse process become more plate-like, dorsolaterally projecting, with costal facet facing ventrolaterally. In T8 the transverse process become incipiently subdivided into two processes, a ventral true transverse process (=anapophysis of Lyon, 1904: 358) and a dorsal mamillary process (=metapophysis). Both processes bear a joint costal facet. Already in T9 both these processes become completely separated. The mamillary process has thin plate-like projections directed craniolaterally, and considerably increasing in height and craniocaudal length at the base from T9 to T12. The transverse process in T9-10 is shorter than the mamillary process, plate-like, and projecting laterally. In T 12 the transverse process almost disappears, although a well-marked superior costal demifacet is still present here. This pattern of appearance and subsequent development of the mamillary process in T8-12 and lumbar is generally uniform in all leporids (Lyon, 1904: 358). The centrum of T1 has complete facet for the rib head. In T2, 4, 5, 8 there are superior (anterior) and inferior (posterior) costal demifacets on the centrum. T9 centrum has only a superior costal demifacet. In T10 and 12 there is only one rib head facet, close to the anterior side of the centrum. Other leporids have the same pattern of costal head articulation (Lyon, 1904: 358).

There is a little variation in thoracics in leporids. *Nesolagus* is closer to *Romerolagus* in having the relatively low neural spines of anterior thoracics, which are about or less than two times the centrum length. In *Sylvilagus*, *Brachylagus*, and *Pronolagus* this ratio is about 2.5, in *Oryctolagus* and *Lepus* it is equal to 3.0 or evens more (Lyon, 1904: 359). Another variable character is the appearance of a well-developed mamillary process (metapophysis). In *Pronolagus*, *Lepus*, and in some *Sylvilagus* it occurs first in T9, in the remaining genera only in T10 (Lyon, 1904: 359). If thoracics in ZIN 84772 were correctly identified, *Nesolagus* would apparently possess a derived state of this character.

Lumbar vertebrae. – All seven lumbar are preserved in ZIN 84772. The centrum length of lumbar is slightly increasing caudally towards L5 and then somewhat decreasing (measured at midline from ventral side, in mm): L1 – 14.1; L2 – 14.6; L3 – 15.5; L4 – 16.1; L5 – 16.6; L6 – 15.8; L7 – 13.4. The centrum articulation surfaces in lumbar are obliquely oriented, like in cervicals and T1. All lumbar centra bear a prominent median ridge on the ventral surface (worst developed in L7). In L1 this ridge forms a slight elevation closer to the anterior end, an incipient hypophysis (=processus spinosus ventralis, or anterior spinous process). In L2 and 3 the hypophysis is well developed, a thin projection directed cranioventrally, 2.9 mm long

in L2 and 5.1 mm long in L3. In L4-7 there is no a hypophysis. In *Pentalagus* a well-developed hypophysis is present in L1-3 (longest in L2). In *Lepus* the hypophysis is a ridge-like plate in T11-12 and L1, and a very long spine in L2 and 3 (in L2 is compatible in length with the centrum). In Leporidae the longest hypophysis is usually placed at L2, but at L3 in some *Lepus* (Lyon, 1904: 362). The hypophyses serve for insertion of *m. psoas major* and *m. quadratus lumborum*, and work as levers, facilitating the bent of vertebral column, which increase the speed of the animal when running (Gambaryan, 1974).

The most striking feature of the leporid lumbar is the transverse processes, which are extraordinary long, craniolaterally projecting, and craniocaudally widened at the distal end. In ZIN 84772 these transverse processes are relatively modestly developed by leporid standards. Their length considerably increases caudally (in mm): L1 – 5.7; L2 – 8.9; L3 – 12.0; L4 – 14.0; L5 – 16.5; L6 – 19.5; L7 – 19.0. In L1 the transverse process is short and laterally projecting, with a separated cranially oriented spine-like projection. In L2 the transverse process is longer and widened distally, with an anterior spine-like projection. In L3-6 the transverse process is relatively wide craniocaudally and only slightly widened distally (except L6). In L7 the transverse process is relatively narrower craniocaudally. In *Pentalagus* the lumbar transverse processes are relatively longer and much wider craniocaudally, in L4-5 this width is compatible with the centrum length. A similar condition is characteristic for *Romerolagus*, where lumbar transverse processes are even shorter (Lyon, 1904: 361). In *Lepus* the lumbar transverse processes are extremely developed, their length exceeds the centrum length, even in anterior lumbar, they are quite slender and shifted cranially on the centrum, and they are considerably craniocaudally widened at the distal end. The transverse processes in leporids serve for insertion of *m. psoas major* and *m. quadratus lumborum* ventrally, *m. iliocostalis*, *m. semispinalis* and *m. longissimus dorsi* dorsally. The lengthening of these processes is connected with the strengthening of the vertebral column flexors and extensors, which provide speed increase during the propulsive phase of locomotion (Gambaryan, 1974).

The mamillary processes gradually decrease in height from L1 towards L7. They are plate-like projections directed craniodorsally. In *Pentalagus* and *Lepus* the lumbar mamillary processes are more dorsally oriented, sometimes with the distal ends curved caudally. The neural spines from L1 to L7 become higher and more dorsally oriented, in L1 the neural spine is inclined cranially at an angle of about 45° , in L7 this angle is about 65° . The accessory process (anapophysis of Lyon, 1904), well developed in *Pentalagus*, *Oryctolagus* (being much better developed in domesticated rabbits: Lyon, 1904: 362), and some other leporids, in ZIN 84772 is present as a very faint horizontal ridge, sometimes slightly projecting caudally into the intervertebral foramen. Among the Leporidae, the accessory processes are also very weak in *Pronolagus* (Lyon, 1904: 362). As in other leporids (Lyon, 1904: 360), the articular surfaces of the zygapophyses in lumbar are obliquely oriented, in contrast to their horizontal orientation in cervicals and thoracics.

Sacrum. – In ZIN 84772 there are four coossified vertebrae, as usually in leporids. This count is ontogenetically variable, being three in immature animals, and

five in aged animals (Lyon, 1904: 363). The fifth vertebra is added from the caudal region. The sacrum curvature in the sagittal plane in ZIN 84772 is intermediate between the more flat sacrum of *Pentalagus* and the more curved sacrum of *Lepus*. The length of sacrals is roughly constant (measured from the ventral surface, in mm): S1 – 10.7; S2 – 11.1; S3 – 10.4; S4 – 9.7. The sacrals are decreasing caudally in the width (measured from the anterior surface, in mm): S1 – 12.8; S2 – 7.0; S3 – 6.2; S4 – 4.9, and especially in the height (measured from the ventral surface to top of neural spine, in mm): S1 – 15.5; S2 – 10.5; S3 – 7.1; S4 – 5.7. The sacral neural spines are vertically oriented, with craniocaudally expanded distal ends (partly ossified interspinous tendons). The first sacral has widely expanded (both transversely and craniocaudally) transverse processes, serving for articulation with the ilium. This articulation surface (facies auricularis) consists of two portions (wings), rounded dorsal and craniocaudally elongated ventral. The ventral wing is relatively shorter than in *Pentalagus*, *Lepus*, and other leporids. In S2 the anterior part of the transverse process is laterally widened and fused with the transverse process of S1 and takes part in articulation with the ilium by forming the most posterior part of the ventral wing of facies auricularis. The posterior part of the transverse process in S2 and the transverse processes in S3-4 are longitudinal ridges, joined to transverse processes of the preceding and following vertebrae. The transverse process is separated from the centrum by a posterior sacral foramen dorsally and an anterior sacral foramen ventrally. Longitudinally elongated metapophyses and anapophyses, coalescing between vertebra form a second, more dorsal, system of longitudinal ridges. As in *Pentalagus*, the medial sacral foramina are totally lacking (well developed in *Oryctolagus* and *Lepus*). In *Pentalagus* reduction of the medial sacral foramina come to an extreme: the neural spines expands cranially along the neural arch dorsal surface to join the neural spine of the preceding vertebra, completely closing the space of the median sacral foramen. In ZIN 84772 there are similar anterior projections of neural spines, but they are much lower.

Caudal vertebrae. – Unfortunately, the caudal region, the most variable part of leporid vertebral column, is completely lacking in ZIN 84772. In *N. netscheri* there are 8 caudals (Lyon, 1904: 363; Corbet, 1983: 12). In other leporids this number may be 9 (*Romerolagus*, *Brachylagus*), 10 (*Pentalagus*), 11-14 (*Sylvilagus*), 12-15 (*Lepus*), 16-17 (*Oryctolagus*) (Lyon, 1904; Corbet, 1983). Thus *Nesolagus* apparently has the shortest tail among the Leporidae.

Ribs. – The first rib is short, some 53% of the second rib length (53% in *Lepus*, 66% in *Pentalagus*, about 70% in *Caprolagus*). The supratubercular apophysis (spine of Lyon, 1904: 372; apophyse supra-tuberculaire of Lessertisseur, Saban, 1967: fig.440) is absent on rib 1 (the same in *Pentalagus*, *Lepus*, and other leporids, Lyon, 1904: 372), very short on ribs 2 and 3 (somewhat longer in *Pentalagus* and *Lepus*), short, but separated from the tuberculum by a notch in subsequent sternal (true) ribs (short in *Romerolagus* and *Pronolagus*, longer in *Pentalagus*, quite a long in *Lepus*, Lyon, 1904: 372, 373). The neck of the rib (collum costae) bears a longitudinal groove from the capitulum towards the tuberculum in ribs 1 and 2, like in other leporids. In the subsequent sternal ribs this groove disappears. The body of the rib

(corpus costae) is slightly widened mediolaterally in sternal ribs (not widened also in *Caprolagus*, somewhat widened in ribs 2-8 in *Pentalagus*, considerably widened and flattened in ribs 1-5 in *Lepus*). The asternal (false) ribs, as in other leporids, do not have a tuberculum.

Scapula. – The scapular blade has the superior and axillary borders of almost equal size, and a relatively short, quite straight vertebral border. There are similar proportions of the scapular blade in *Romerolagus*, *Brachylagus*, *Pronolagus* (Lyon, 1904: pl.97, figs.4, 8, 9), and *Poelagus* (St.Leger, 1932: fig.2B), but in these taxa, except *Poelagus*, the blade is relatively longer. *Pentalagus* and *Caprolagus* also have superior and axillary borders of equal size, but the vertebral border is longer and more convex. In *Lepus* the superior border is noticeably shorter than the axillary border and the vertebral border is much more convex. The inferior angle is not so protruding caudally, as in *Sylvilagus* and *Lepus*. The supraspinous fossa is relatively narrow, as in *Romerolagus* and *Brachylagus* (Lyon, 1904: pl.97, figs.8, 9); in other leporids it is distinctly wider. The distal projection of the acromion (beyond the level of the metacromion) is short, but distinct (longer in *Oryctolagus* and *Sylvilagus*, almost lacking in *Lepus*). The metacromion is relatively longer than in *Pentalagus*, but not as long as in *Pronolagus*, *Oryctolagus*, and *Lepus*. The coracoid process and glenoid cavity are of the same morphology as in other leporids. The greatest scapula length (from coracoid process to vertebral border) is 61.0 mm. The length of vertebral border is 34.4 mm. The minimum width of scapular neck is 5.8 mm. The craniocaudal diameter of glenoid cavity and coracoid process is 11.0 mm.

Humerus. – The morphology of the humerus is very uniform among leporids (Lyon, 1904: 375), the differences between genera relate to the relative length of the humerus and other limb bones. The head is globular, compressed mediolaterally, and slightly overhanging the shaft of the bone. The latter indicate rather limited anterior-posterior movements of the femur, which is connected with a low running ability of *Nesolagus* (the head of the humerus which most overhangs the shaft is in *Lepus*). The greater trochanter is almost in level with the head of humerus, a primitive picture (distinctly higher in *Lepus*). The lesser trochanter is about half as large as the greater trochanter. The intertubercular groove, positioned to hold the m. biceps brachii, is relatively shallow (the same in *Pentalagus* and *Caprolagus*, noticeably deeper in *Lepus*). The shaft of the humerus is slightly tapers towards the distal end. The deltoid crest (tuberositas deltoidea) is quite long, 43% of the greatest humerus length (over 50% in Miocene *Archaeolagus*, 42% in *Caprolagus*, 35% in *Pentalagus*, 36-37% in *Lepus*; quite long also in *Romerolagus*, Lyon, 1904: 376). It is a primitive character, the concentration of m. spinodeltoideus at the proximal part of the humerus provides more rapid flexion of this bone. The distal end, as in other leporids, is relatively narrow mediolaterally, with medial and lateral epicondyles much reduced. The supinator crest (above the lateral epicondyle) is distinct, as in *Pentalagus* (less developed in *Lepus*). The trochlea humeri is well developed. The supratrochlear (radial) fossa (fossa supratrochleare) is perforated, as in other Recent leporids, except *Brachylagus*. The olecranon fossa is relatively deep, as in *Lepus* (more shallow in *Pentalagus*). The greatest humerus length is 65.6 mm. The length from humerus head

to distal end is 65.4 mm. The maximum width of proximal end is 12.0 mm. The minimum width of humerus shaft is 4.7 mm. The maximum width of distal end is 9.0 mm.

Ulna. – The ulna, as well as the radius, is relatively short in ZIN 84772 (see description of radius). The olecranon is short craniocaudally, as in all leporids except *Lepus*. The shaft of the ulna is of almost equal width along its length (a primitive character, characteristic for rabbits with short fore legs; in *Lepus* the shaft of ulna is tapers considerably towards the distal end). The crest of the interosseus ligament occupies distal half of the shaft and rather weak. It is much more prominent and longer in *Pentalagus*, very long but weak in *Lepus*. The styloid process is completely fused with the shaft of ulna. The greatest length of the ulna is 68.0 mm. The length of the olecranon is 8.3 mm. The maximum width of the proximal end of the radius is 5.8 mm.

Radius. – In ZIN 84772 the radius is relatively short, 86% of the humerus length (81% in *Caprolagus*, 89% in *Pentalagus*, 93% in *Lepus* (*Poecilolagus*) *americanus*, 103% in *Lepus* (*Eurolagos*) *europaicus*; in *Romerolagus* and *Brachylagus* the radius is shorter than the humerus, *Pronolagus*, *Oryctolagus* and *Sylvilagus* the radius equals the humerus in length, Lyon, 1904: 377, 378). The tuberosity of the interosseus ligament is well defined on the ventral surface and widens distally, as in *Pentalagus* (much weaker but longer in *Lepus*). On the dorsal surface of the shaft of radius there is a distinct longitudinal groove for the m. flexoris digitorum profundus (less pronounced in *Pentalagus* and *Lepus*, not depicted in *N. netscheri*, Forsyth-Major, 1899: pl.38, fig.28). The carpal articular surface is relatively narrow mediolaterally and shallowly concaves. The greatest length of the radius is 56.2 mm. The maximum width of the proximal end of the radius is 6.3 mm, of the distal end is 6.0 mm.

Manus. – There are no carpal bones preserved. The metacarpals are remarkably short but slender, similar in proportions to metacarpals in *Caprolagus* (Forsyth-Major, 1899: fig.36-40) and *Lepus* (quite stout in *Pentalagus*). The length of metacarpals (II and IV, in mm) is: 17.4 and 14.7; width of proximal ends 2.7 and 2.4; width of distal ends 3.1 and 2.9. There is one unidentified second phalanx of manus.

Pelvis. – The innominate, or coxal bone (os coxae) does not vary much in the Leporidae. The iliac wing in ZIN 84772 is expands less distally than in other leporids. The superior anterior and the inferior posterior spines of ilium are quite distinct, the latter is a real spine-like short projections. In this respect ZIN 84772 is similar to *Pentalagus*, in *Lepus* these structures are less prominent. The anterior margin of the iliac wing is almost straight in *Pentalagus* and *Caprolagus*, in ZIN 84772 and *Lepus* it is more convex. The acetabular notch is less developed and shorter than in other leporids. The ischial spine is distinct. On the ventral surface of the superior ramus of the ischium there is a distinct convex tuberosity of triangular shape for the m. gemellus inferior pars posterior. In *Pentalagus* this tuberosity is of similar shape but flat, in *Lepus* it is not distinct and this area is slightly concave. The ischial tuberosity is relatively less developed than in other leporids. The angle between the bodies of the ischium and the pubis is about 60° (55° in *Pentalagus*, 65° in *Lepus*). The obturator foramen is almost round (longitudinally elongated in other leporids), and relatively

small, 16% of the length of the innominate (19% in *Pentalagus*, 21% in *Caprolagus*, 22-23% in *Lepus*). The inferior ramus of pubis is wider mediolaterally than in other leporids. The pubic symphysis is relatively short, 20% of the length of innominate (23% in *Pentalagus*, 25% in *Caprolagus*, 24-29% in *Lepus*). The greatest length of the innominate is 77.6 mm. The length of the acetabulum is 11.8 mm. The length of the pubic symphysis is 15.7 mm. The maximum diameter of the obturator foramen is 12.6 mm. The height of the body of the ilium is 7.8 mm.

Femur. – The femora in all the Leporidae resemble one another very closely (Lyon, 1904: 382). The femur is slender, compatible with that of *Lepus* (more stout in *Pentalagus* and *Oryctolagus*). The femoral head is globular, with an almost indistinct fovea capitis. The femoral neck is very short. The greater trochanter is directed dorsally and protrudes beyond the level of femoral head. The third trochanter is located somewhat more distally than the lesser trochanter (a primitive character found in the Oligocene lagomorphs, in other Recent leporids both trochanters are almost at the same level). The intertrochanteric (“digital”) fossa is deep. The shaft is of almost equal width through its length (widens distally in *Caprolagus*). The patellar groove is deep and long, with sharp margins. The medial and lateral condyles are nearly of equal size. The epicondyles are not distinct. The greatest length of the femur (the first figure is for ZIN 84772, the second for BMNH 1921.1.18.1 of *N. netscheri*): 85.7 and 76.2 mm. The length from the femoral head to the distal end: 82.8 and 72.6 mm. The width of the proximal end of the greater trochanter margin to femoral head: 15.8 and 13.3 mm. The width of the proximal end between the lesser and third trochanters: 15.4 and 14.0 mm. The craniocaudal diameter of the femoral head: 7.3 and 5.9 mm. The minimum width of the femoral shaft: 7.0 and 6.0 mm. The width of the distal end: 14.0 and 11.8 mm.

Tibia and Fibula. – In ZIN 84772, as in other lagomorphs, the tibia and fibula are fused along the distal 57% of the bone length (46% in *Pentalagus*, 52% in *Caprolagus* and *Romerolagus*, 53% in *Brachylagus*, 55% in *Pronolagus*, 55-58% in *Sylvilagus*, 61% in *Oryctolagus*, 60-62% in *Lepus*). The proximal portion of the tibia is noticeably bent caudally in *Pentalagus* and *Romerolagus*, straighter in ZIN 84772 and in *Lepus*. The lateral condyle expands more caudally than the medial condyle. The distal end of the tibia is relatively narrow mediolaterally. The free part of the fibula is a very thin spine-like bone, with some widening at the proximal end, bearing the articular surface with the medial condyle of the tibia. The greatest length of the tibia is 84.7 mm. The width of the proximal end is 15.3 mm. The width of the distal end is 9.4 mm. The craniocaudal diameter of the distal end is 6.7 mm.

Pes. – From the tarsal bones only the calcaneus is present. The tuber calcanei is about half of the calcaneus length. The proximal calcaneostragalar facet (CaAp facet of Szalay, 1985) is divided by a horizontal ridge into two portions. The caudal portion is large, as in *Lepus* (small in *Pentalagus*). The sustentacular facet (Su) is almost round (more elongated transversely in *Pentalagus* and *Lepus*). The distal calcaneostragalar facet (CaAd) is well developed, rounded, and distinct from the calcaneonavicular facet. The length of calcaneum is 20.3 mm.

The metatarsals are slender bones (more stout bones in *Pentalagus*, Otsuka et al., 1981: fig.15). The middle metatarsals (II-IV) are of similar length (mt III is somewhat longer in *Lepus*). The length of the metatarsals II, III, IV, and V is 27.1, 26.1, 24.4, and 20.5. The proximal width of the metatarsals II, III, IV, and V is 4.4, 3.6, 3.9, and 3.4, at the distal end is 4.5, 3.9, 3.9, and 3.4.

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