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THE ORIGIN OF THE P_3 PATTERN OF
SYLVILAGUS, *CAPROLAGUS*, *ORYCTOLAGUS* AND *LEPUS*

By CLAUDE W. HIBBARD

ABSTRACT: An Upper Pliocene population of *Nekrolagus progressus* (Hibbard) represented by 178 P_3 s from the Rexroad fauna has 11.8% of the individuals with a P_3 enamel pattern that is like the P_3 pattern of *Sylvilagus*, *Caprolagus*, *Oryctolagus* and *Lepus*. For the first time in the fossil record there is evidence for the time and place of the variation (mutation) within a population that produced a character of generic grade. It is proposed that this pattern developed in North America and gave rise to that now found in *Sylvilagus*, *Caprolagus*, *Oryctolagus* and *Lepus*. Cenozoic faunas of Eurasia that contain remains of *Oryctolagus* and *Lepus* are younger than the Rexroad fauna. Over 2,000 Recent *Lepus*, *Oryctolagus* and *Sylvilagus* dentitions were examined. Twelve Recent specimens of these three genera were found that contained the *Nekrolagus* pattern. The genera are quite recent in origin. These rabbits provide an excellent group for comparative study with the late Pliocene *Nekrolagus* to establish the rate of generic development. A phylogenetic summary is given to show the relationship of the Leporinae as based upon the development of P^2 and P_3 .

Vertebrate fossils have long been used as evidence of evolution. Seldom in the fossil history of a group is a morphological change noted, in individuals of a population, that is to become a new generic character in the later descendants. Most fossil samples are too small to show the range of individual, age or sexual variation. By the use of the washing technique (Hibbard, 1949) over the past 20 years, at locality 3 of the Upper Pliocene Rexroad local fauna, a good series of upper and lower teeth of *Nekrolagus* has been recovered. In this population of Upper Pliocene rabbits there occurs a variation in the enamel structure of P_3 that becomes the dominant P_3 pattern of four of the living genera of rabbits (*Sylvilagus*, *Caprolagus*, *Oryctolagus* and *Lepus*).

The appearance of this variation within the tooth pattern of the *Nekrolagus* population allows the dating of the appearance of the Recent genera within a rather limited time span.

Because of the large variation observed in the P_3 pattern of *Nekrolagus progressus*, and the fact that I had found a Recent specimen of *Lepus californicus* (Mearns) with a P_3 pattern like that of *Nekrolagus* (Hibbard, 1944), I resumed my study of variation in Recent rabbit teeth. The study of a large series of Recent rabbit P_3 s furnishes data that clearly point to a close relationship of the above four genera to one another and to their origin from *Nekro-*

lagus. Important observed variations are summarized in Tables I and II.

SPECIMENS EXAMINED

The following Recent specimens were examined in the collection of the Museum of Zoology, University of Michigan: *Brachylagus idahoensis* Merriam, 28; *Lepus alleni* Mearns, 13; *L. americanus* Erxleben, 265; *L. arcticus* Ross, 21; *L. californicus* Gray, 346; *L. europaeus* Pallas, 13; *L. nigricollis ruficaudatus* Geoffroy, 18; *L. oistolus hypsibius* Blandford, 9; *L. sinensis* Gray, 6; *L. timidus* Linnaeus, 16; *L. townsendi* Bachman, 98; *Oryctolagus cuniculus* Linnaeus, 17 specimens from wild stock of Europe; *Sylvilagus aquaticus* (Bachman), 28; *S. auduboni* (Baird), 296; *S. bachmani* (Waterhouse), 60; *S. brasiliensis* (Linnaeus), 37; *S. cunicularis* (Waterhouse), 9; *S. floridanus* (Allen), 651; *S. graysoni* (Allen), 7; *S. nuttalli* (Bachman), 78; *S. palustris* (Bachman), 33; *S. transitionalis* (Bangs), 12; *Romerolagus diazi* (Diaz), 3; the one specimen of *Pronolagus crassicaudatus* (Geoffroy) examined is in the U. S. National Museum and the specimen of *Nesolagus netscheri* (Jentink) is in the Rijksmuseum van Natuurlijke Historie Leiden.

The fossil specimens examined included 178 P₃s of *Nekrolagus progressus*, 24 of these came from the Wendell Fox locality and the remaining 154 from Locality 3 of the Rexroad fauna. Seven of these teeth are in the University of Kansas collections. Also examined were 91 P₃s of *Pratilepus kansasensis* Hibbard, from Locality 3, ten of the teeth were from the University of Kansas.

Nekrolagus progressus (Hibbard), 1939

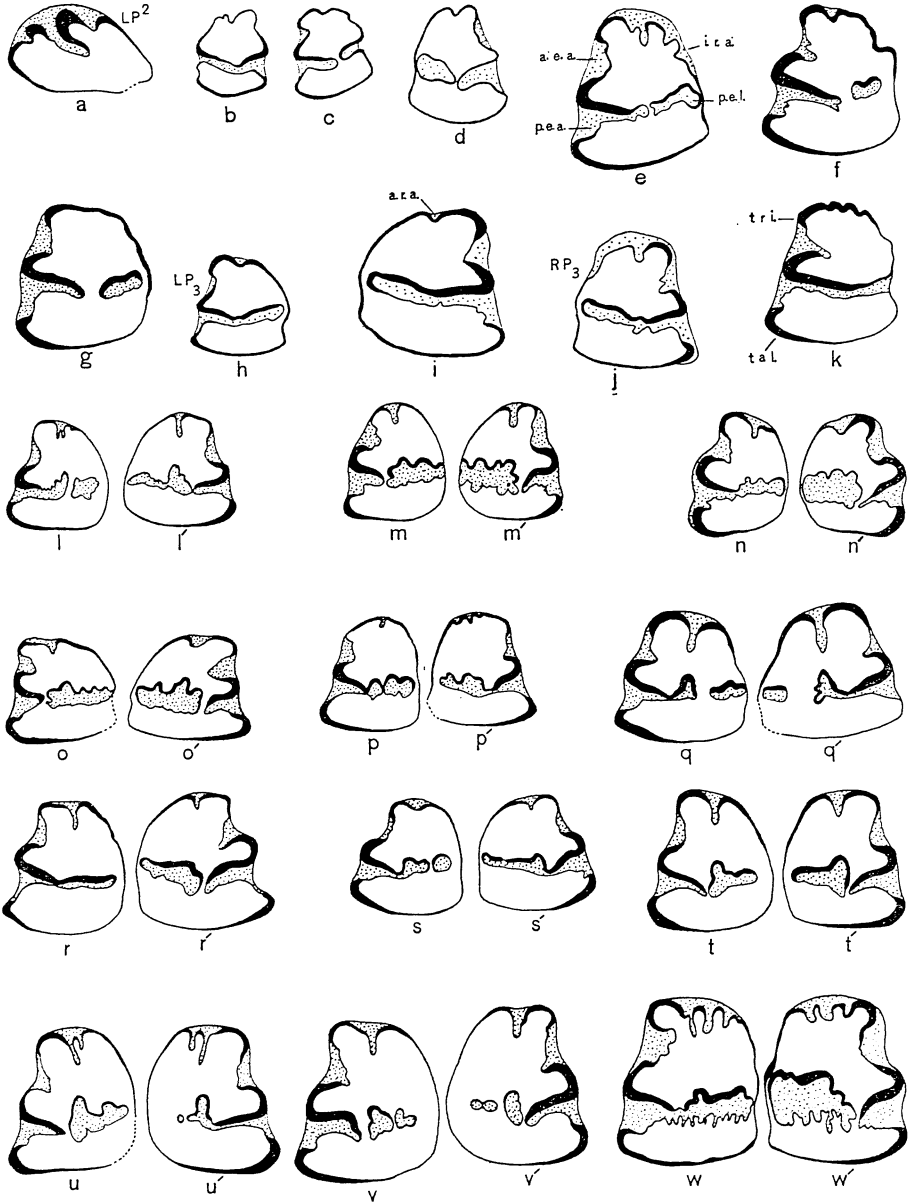
Characters of the genus Nekrolagus.—The P² (Fig. 1a) of *Nekrolagus* has 3 anterior reentrant angles. The figured tooth was recovered from the Wendell Fox locality of the Rexroad fauna (Woodburne, 1961, p. 64) which has produced teeth only of *Hypolagus*, *Notolagus* and *Nekrolagus* during the past 9 years.

P₃ has an anterior reentrant angle (groove), as in *Sylvilagus*, *Caprolagus*, *Oryctolagus*, *Lepus* and other Recent genera, that extends from the triturating surface to the base of the tooth (Fig. 1i; a.r.a.). A posterior external reentrant angle or fold (Fig. 1e; p.e.a.) extends approximately one-half the distance across the tooth. Located opposite the lingual border of this enamel fold and lingual to the enamel wall of the tooth is an enamel lake (Fig. 1e; p.e.l.). The posterior internal enamel lake is derived from an open posterior internal reentrant angle (Fig. 1c). This angle was once present in the ancestral stock and remained open to the base of the tooth but later closed off from the

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FIG. 1.—Occlusal patterns of P² and P₃ of *Nekrolagus*, *Sylvilagus*, *Oryctolagus* and *Lepus*. a–k, *Nekrolagus progressus*; a, LP², No. 44474; b, RP₃, No. 42640; c, LP₃, No. 39782; d, RP₃ base of fig. b, No. 42640; e, LP₃, No. 42639; f, LP₃, No. 44542; g, LP₃, No. 44473; h, LP₃, No. 42604; i, RP₃, No. 44541; j, RP₃, No. 42605; k, LP₃, No. 31080. l–o', *Sylvilagus auduboni*; l–l', L and RP₃, No. 79357; m–m', L and RP₃, No. 56015; n–n', L and RP₃, No. 54526; o–o', L and RP₃, No. 54532. p–p', *S. bachmani*, L and RP₃, No. 55899. q–q', *Oryctolagus cuniculus*, L and RP₃, No. 55721. r–r', *Lepus americanus*, L and RP₃, No. 105447. s–s', *L. californicus*; s–s', L and RP₃, No. 54437; t–t', L and RP₃, No. 55929; u–u', L and RP₃, No. 54473; v–v', L and RP₃, No. 54470. w–w', *Sylvilagus aquaticus*, L and RP₃, No. 65284. All × 6. Specimens in the Univ. Mich. Collections. Abbreviations: a.e.a., anterior external reentrant angle; a.r.a., anterior reentrant angle; i.r.a., anterior internal reentrant angle; p.e.a., posterior external reentrant angle; p.e.l., posterior internal enamel lake; tal., talonid; t.r.i., trigonid or anterior loph.

lingual enamel wall (Fig. 1d-g). In some individuals of *Nekrolagus progressus* the lingual border of the posterior external reentrant angle unites with the labial edges of the enamel lake to form a confluent fold throughout their length (Fig. 1h-j). The union of the posterior external reentrant angle with the enamel lake is complete throughout the length of the tooth. There are no intermediate patterns between the *Nekrolagus* P₃ pattern (Fig. 1e) and the *Lepus* pattern (Fig. 1i).



A shallow anterior external reentrant angle (Fig. 1e; a.e.a.) is present in all these genera. An anterior internal reentrant angle may be present (Fig. 1e and f; i.r.a.) or absent (Fig. 1d).

VARIATION IN P₃ PATTERNS

Immature dentitions.—In Fig. 1b (*Nekrolagus progressus*) and Fig. 2l' (*Lepus americanus*) the anterior loph or trigonid is separated from the posterior loph or talonid by a tract of cement varying in depth. The depth across the occlusal surface is controlled by the position of the lingual enamel wall that closes off ventrally the posterior internal reentrant angle. The appearance (in immature specimens) of a trigonid and talonid is an ancestral character found as far back as Oligocene time (*Palaeolagus*). In Fig. 1b-d, one can observe the normal change from an immature tooth pattern to that of an older individual. The posterior internal reentrant angle is open on the side of the tooth in Fig. 1b for a distance of 2.0 mm. In Recent specimens it was observed to remain open down the lingual side of the tooth from 1.0 to 1.5 mm. Dice and Dice (1941) give a good description of age changes observed in *Sylvilagus floridanus*.

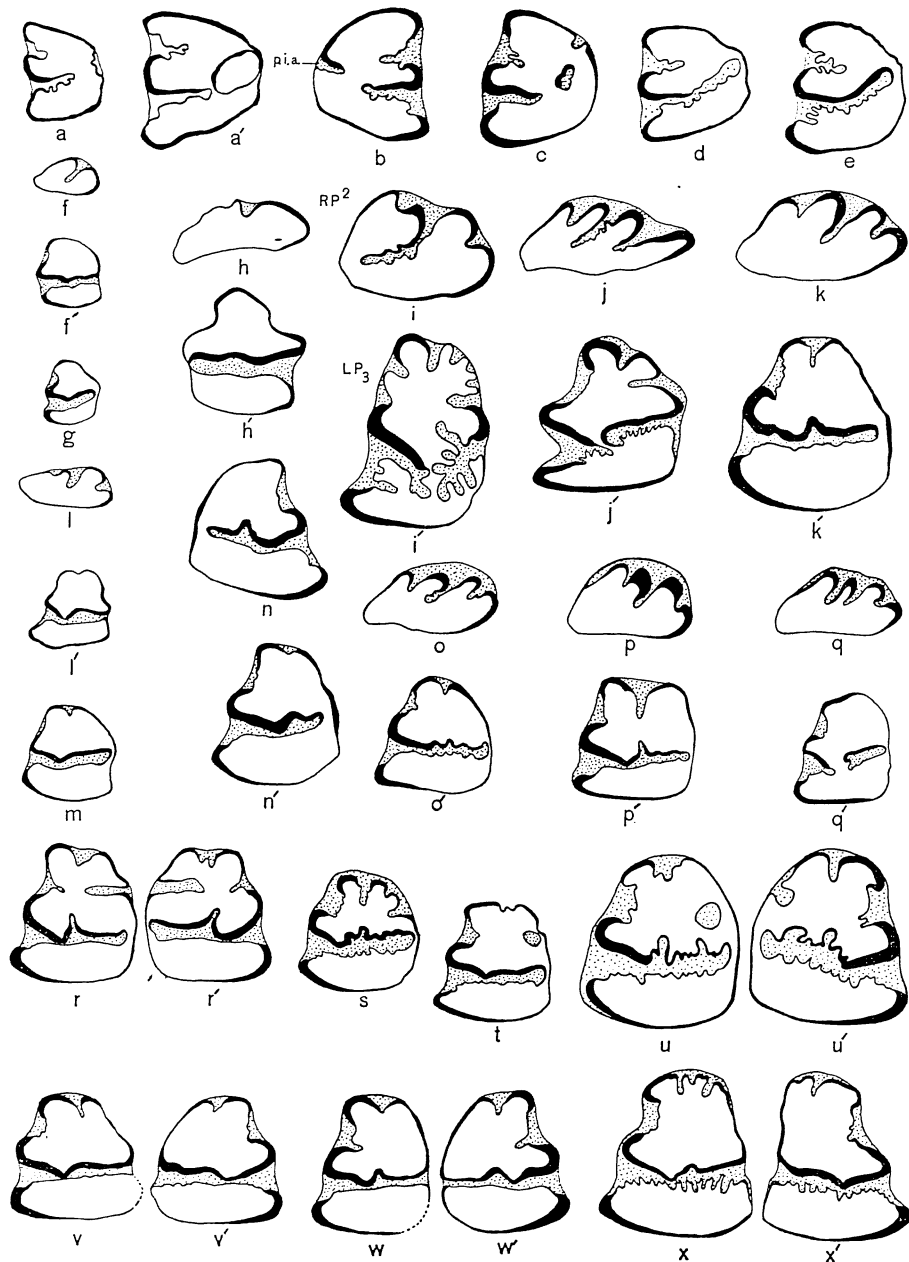
Dawson (1958, p. 45) considers the P₃s that I (Hibbard, 1941, p. 216) assigned to *Hypolagus* as probably young individuals of *Lepus*. After the examination of all the immature and adult teeth of *Lepus* and *Sylvilagus* I was unable to duplicate patterns like those I assigned to *Hypolagus* in 1941.

Pedomorphic pattern.—Over the years more P₃s consisting of an anterior column surrounded by enamel and separated by a cement tract from the posterior column are being found associated with P₃s of normal dental pattern. Such P₃s were reported by Dawson (1958, her Figs. 18 and 38) for specimens of *Palaeolagus* and *Nekrolagus progressus* (Fig. 1k). This was also reported by Fejfar (1961, his Fig. 2a) from specimens of *Alilepus dietrichi* Fejfar. This character was observed in 8 of the 20 species of *Sylvilagus* and *Lepus* examined (Fig. 2v-x). It is the dominant pattern of *Brachylagus* (Fig. 2f'). Of the 28 specimens of *Brachylagus* examined by me only one had both right and left

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 FIG. 2.—Occlusal patterns of P² and P₃ of *Pratilepus*, *Brachylagus*, *Nesolagus*, *Pentalagus*, *Pronolagus*, *Lepus*, *Sylvilagus*, *Oryctolagus* and *Romerolagus*. a-e, *Pratilepus kansanensis*; a-a', LP₃, immature, sectioned in 1943, crown and base views; b, RP₃, No. 29642; c, LP₃, No. 29634; d, LP₃, No. 42603; e, LP₃, No. 44572. f-g, *Brachylagus idahoensis*; f-f', RP² and LP₃, No. 54364; g, LP₃, No. 54366. h-h', *Nesolagus netscheri*, RP² and RP₃, No. 12434, Rijksmuseum Nat. Hist. Leiden. i-i', *Pentalagus furnessi*, RP² and LP₃, No. 75083. j-j', *Pronolagus crassicaudatus*, RP² and LP₃, No. 22972, U. S. Nat. Mus. k-k', *Lepus californicus*, RP² and LP₃, No. 56830. l-n', *L. americanus*; l-l', immature, RP² and LP₃, No. 55173; m, young adult, LP₃, No. 60513; n-n', adult, R and LP₃, No. 84808. o-o', *Sylvilagus floridanus*, RP² and LP₃, No. 54204. p-p', *Oryctolagus cuniculus*, RP² and LP₃, No. 55761. q-q', *Romerolagus diazi*, RP² and LP₃. r-r', *L. o. hypsibius*, L and RP₃, No. 75227. s, *S. auduboni*, LP₃, No. 56062. t, *S. floridanus*, LP₃, No. 103243. u-u', *L. californicus*, L and RP₃, No. 57856. v-v', *S. floridanus*, L and RP₃, No. 105549. w-w', *L. californicus*, L and RP₃, No. 55935. x-x', *S. palustris*, L and RP₃, No. 55785. All × 6. Unless otherwise stated, these specimens are in the Univ. Mich. Collections. Abbreviation: p.i.a., posterior internal reentrant angle.

P₃ with a closed posterior external fold (Fig. 2g). It appears that the gene combination producing this character over a long period of time has been successful only in the genus *Brachylagus*.

Anterior reentrant angle.—This angle (Fig. 1i, a.r.a.) is absent in *Alilepus annectens* Schlosser (1924, his Pl. III, Fig. 37a), and Bohlin (1942, his Fig.



8); *Alilepus laskarewi* Khomenko (1915, his Pl. 1, Fig. 20); *Romerolagus* (Fig. 2q'); *Pratilepus* (Fig. 2a-e); *Nesolagus* (Fig. 2h'); and *Brachylagus* (Fig. 2f and g). The following rabbits possess the anterior reentrant angles: *Alilepus hungaricus* Kormos (1934, his Fig. 1n, p. 74); *Alilepus dietrichi* Fejfar (1961, his Fig. 2); *Serengetilagus* Dietrich (1942, his Pl. III, Figs. 13, 17 & 18); *Pronolagus* (Fig. 2j'); *Pentalagus* (Fig. 2i'); *Nekrolagus* (Fig. 1b-f and h-k); *Sylvilagus* (Fig. 2o'); *Caprolagus* (Major, 1899, his Pl. 37, Fig. 22); *Oryctolagus* (Fig. 2p'); and *Lepus* (Fig. 2k').

Five P₃s of *Nekrolagus* were observed that lack the anterior angle (Fig. 1g). The absence of this angle was observed also in *Sylvilagus* and *Lepus* (Fig. 2n). Six teeth lacking this character were observed in *Lepus californicus*. This condition is an ancestral character.

Anterior internal reentrant angle.—A large number (46%) of the P₃s of *Nekrolagus* had the anterior internal angle or groove (Fig. 1e, i.r.a.). This percentage is much higher than in the Recent specimens examined (see Tables I and II). A number of Recent specimens (Fig. 2r-u') have this angle much better developed than does *Nekrolagus*. In a number of Recent specimens the angle closes off soon after wear and remains as an enamel lake (or tube), extending to the base of the tooth (Fig. 2t and u). This angle is very common on immature teeth of *Sylvilagus floridanus*, but in most individuals it extends but a short distance down the crown of the tooth. Of the 9 specimens of *Lepus oistolus hypsibius* examined, 6 lacked the reentrant angle; 2 possessed enamel lakes; the extreme development of the reentrant angle is shown in the other specimen (Fig. 2r-r'). This gives some idea of the variation observed among the P₃s.

Posterior internal reentrant angle.—This angle (Fig. 2b, p.i.a.) is well developed in two Recent genera (*Pentalagus*, Fig. 2i', and *Pronolagus*, Fig. 2j'). In the late Cenozoic *Alilepus dietrichi* Fejfar (1961, his Fig. 2b-e), the angle extends nearly halfway across the tooth, while in *Pratilepus* (Fig. 2a-b) it may appear as an open angle or as an enamel lake. In *Nekrolagus* (Fig. 1e-g) and *Romerolagus* (Fig. 2q') this angle occurs as an enamel lake.

In *Sylvilagus*, *Caprolagus*, *Oryctolagus* and *Lepus*, this angle has united with the posterior external reentrant angle to form the long enamel fold that extends nearly across the crown of the tooth (Fig. 2k', m, n', o' and p'). It is often possible to see where the two angles have united in the anterior wall of the thickened enamel of the external fold (Fig. 2k'). Vestiges of this angle are sometimes found as distinct enamel lakes in Recent P₃s (Fig. 1l-w').

Anterior external reentrant angle.—This angle (Fig. 1e, a.e.a.) is most constant in the genera examined. It varies in width, depth and degree of crenulation among the different species.

Posterior external reentrant angle or fold.—This reentrant angle (Fig. 1e, p.e.a.) when considered as a separate entity is rather uniform in late Cenozoic and Recent rabbits. It reaches its greatest complexity and depth in *Pentalagus* and *Pronolagus* (Fig. 2i' and j'). The posterior external reentrant fold ob-

served in some specimens of *Nekrolagus* (Fig. 1*h* and *j*), *Pratilepus* (Fig. 2*d* and *e*) and those of the Recent rabbits, *Brachylagus*, *Nesolagus*, *Sylvilagus*, *Caprolagus*, *Oryctolagus* and *Lepus* (Fig. 2*g*, *h'*, *o'*, *p'* and *k'*) are the result of the union of the posterior external reentrant angle with a posterior internal enamel lake.

SIGNIFICANCE OF THE UNION OF THE POSTERIOR EXTERNAL
ANGLE AND THE POSTERIOR INTERNAL ENAMEL LAKE

In this paper I have used the term *Lepus* pattern in reference to those that are normal in P₃s of *Oryctolagus*, *Sylvilagus*, *Caprolagus* and *Lepus* (Fig. 2*k'*, *n'-p'*, and to the three teeth of *Nekrolagus*, Fig. 1*h-j*). It is not known whether the first variation (mutation) causing the *Lepus*-like pattern in *Nekrolagus* occurred in both the right and left P₃ of the same rabbit. It is doubtful, however, since the *Nekrolagus* pattern in Recent rabbits will occur in either the right or left P₃, while the opposite tooth will possess a normal pattern (Fig. 1*n-n'*, *p-p'*, *r-r'*, *s-s'* and *w-w'*). In some Recent specimens the *Nekrolagus* pattern does occur in both the right and left P₃ (Fig. 1*l-l'*, *m-m'*, *o-o'*, *q-q'*, *t-t'*, *u-u'* and *v-v'*). Regardless of the magnitude of genetic change in the population, this variation became the later dominant P₃ pattern from which *Sylvilagus*, *Caprolagus*, *Oryctolagus* and *Lepus* were derived.

Of the 178 P₃s of *Nekrolagus* recovered, 21, or 11.8%, possess a *Lepus* pattern. This ratio is a little high since this total does not include the *Nekrolagus* teeth that were sectioned in 1942 and 1943. Twenty-four of the above *Nekrolagus* P₃s were recovered from the Wendell Fox locality 2½ miles from Locality 3. Four of these teeth (16.67%) had a *Lepus* pattern, compared with 11.04% from Locality 3 with the same pattern. At present the sample from the Wendell Fox locality is too small for accurate comparison and should not be taken to indicate a slightly younger age for this locality.

A single P₃ with a *Nekrolagus* pattern was reported by me in 1941 from the Borchers local fauna. This find was made prior to the discovery of the *Nekrolagus* pattern in the P₃ of a Recent *Lepus californicus* (Hibbard, 1944). Dawson (1958) correctly referred this tooth to *Lepus*. I have examined 124 P₃s from the Borchers Quarry and all except the above tooth have a *Lepus* pattern. Over 75% of these teeth were collected after the recovery of the tooth with the *Nekrolagus* pattern.

The geographical distribution of *Nekrolagus* is unknown. The *Lepus* type pattern of P₃ may have originated some distance from the area where the Rexroad specimens were recovered, but the population with this variation toward the *Lepus* pattern was near enough to allow a gene flow that carried the mutation (variation) to individuals in southwestern Kansas.

A study of the frequency of *Nekrolagus* and *Lepus* patterns in rabbit teeth from deposits that are post-Rexroad fauna in age should give an example of the rate of evolution in this group of mammals.

TABLE 1.—Summary of variation in P_3 and P^2 of *Nekrolagus* and *Sylvilagus*

	<i>Nekrolagus progressus</i>		<i>Sylvilagus aquaticus</i>		<i>S. auduboni</i>		<i>S. bachmani</i>		<i>S. floridanus</i>	
	N.	%	N.	%	N.	%	N.	%	N.	%
Number of P_3 and P^2	178*		56		592		120		1,302	
P_3 with anterointernal reentrant angle	82	46.06	0		47	7.93	0		234	17.97
P_3 without anterior reentrant angle	5	2.80	0		0		2	1.67	0	
P_3 with <i>Lepus</i> pattern ..	21	11.80	55	98.22	581	98.14	117	97.50	1,298	99.70
P_3 with <i>Nekrolagus</i> pattern	156	87.64	1	1.78	7	1.18	1	0.83	0	
P_3 with pedomorphic pattern	1	0.56	0		4	0.68	2	1.67	4	0.30
P^2 with two reentrant angles	—	—	3	5.36	8	1.35	2	1.67	6	0.46
P^2 with four reentrant angles	—	—	0		0		0		2	0.15

* Only P_3 .TABLE 2.—Summary of variation in P_3 and P^2 of *Oryctolagus* and *Lepus*

	<i>Oryctolagus cuniculus</i>		<i>Lepus americanus</i>		<i>L. californicus</i>		<i>L. townsendi</i>	
	N.	%	N.	%	N.	%	N.	%
Number of P_3 and P^2	34		530		692		196	
P_3 with anterointernal reentrant angle	0		24	4.53	44	6.35	3	1.53
P_3 without anterior reentrant angle	0		6	1.13	2	0.29	0	
P_3 with <i>Lepus</i> pattern	32	94.12	529	99.81	676	97.70	193	98.47
P_3 with <i>Nekrolagus</i> pattern	2	5.88	1	0.19	8	1.15	0	
P_3 with pedomorphic pattern	0		0		8	1.15	3	1.53
P^2 with two reentrant angles	2	5.88	2	0.38	4	0.58	5	2.55
P^2 with four reentrant angles	0		0		3	0.43	0	

Just how much time elapsed since the Rexroad fauna lived and before the *Lepus* type of pattern became dominant is not known. But the population of rabbits that possessed a dominant *Lepus* pattern or a dominant gene combination that produced this pattern must have developed in North America before spreading to Eurasia. There are no fossil rabbits known from the late Ceno-

zoic of Eurasia with a posterior internal enamel lake which could unite with the posterior external reentrant angle to form the long enamel fold of Recent rabbits, the *Lepus* pattern.

THE ORIGIN OF *ALILEPUS DIETRICH* AND *NEKROLAGUS*

Dawson (1958) presented an excellent contribution on the late Tertiary Leporidae of North America. This work points clearly to the scarcity of fossil rabbits in North America and Eurasia from the Miocene and early Pliocene.

The genus *Alilepus* is the first known rabbit whose characters are such that it can be considered as the stem stock from which the later genera of the Leporinae are derived. *Alilepus* is known chiefly from the lower dentitions. P² is not known in association with P₃ from the early finds. Fossil evidence indicates that one line of the *Alilepus* stock which possessed an open posterior internal angle developed a P² in the early Pliocene with 3 anterior reentrant angles (Fig. 1a). This stock also possessed a P₃ without an anterior reentrant angle. The fossil record further indicates that soon after the development of the P² with three reentrant angles, this stock either spread from Asia to North America, or originated in North America and later gave rise to *Romerolagus* and *Pratilepus*. This will be discussed in more detail under *Pratilepus*.

A second stock of *Alilepus* in Eurasia or North America with an open posterior-internal reentrant angle and a P² with 3 anterior reentrant angles developed a line with an anterior reentrant angle on the face of P₃ (Fig. 1i). Part of this stock gave rise to *Nekrolagus* in North America and another part in Eurasia gave rise to "*Alilepus*" *dietrichi* Fejfar, which I consider more closely related to *Pronolagus* Lyon and *Serengetilagus* Dietrich than to *Alilepus laskarewi* (Khomenko). "*Alilepus*" *dietrichi* is very close to if not the ancestral stock from which *Pronolagus*, *Serengetilagus* and *Pentalagus* are derived.

After the *Nekrolagus* population in North America developed a dominant *Lepus* pattern it spread into Eurasia. This early rabbit stock in North America is the forerunner of *Sylvilagus*. From this pro-*Sylvilagus* stock were derived *Sylvilagus*, *Caprolagus* in Asia, and *Oryctolagus* in Europe; the latter subsequently spread into North Africa. *Lepus*, the hare, could be derived from either of these stocks. The hares are adapted to both desert and arctic habitats. The genus *Lepus* may be a composite group that may have arisen from both pro-*Sylvilagus* and *Oryctolagus* instead of from just one of the stocks.

The gene combination that resulted in the appearance of the *Lepus* pattern in *Nekrolagus* occurred in a most vigorous stock that had a wide range of tolerance and potentialities for considerable adaptive radiation.

In North America *Hypolagus*, an old genus, was associated with *Nekrolagus*, *Notolagus* and *Pratilepus* in the late Hemphillian (Upper Pliocene). In Eurasia during this time interval *Hypolagus* lived with the *Alilepus dietrichi* stock. Soon after the development of the *Lepus* pattern as a dominant char-

acter in *Nekrolagus*, this line of rabbits displaced *Pratilepus* and *Hypolagus* in the early Pleistocene of North America and *Hypolagus* and probably *Alilepus dietrichi* in Eurasia. *Hypolagus* withstood the first glaciation but disappeared as the *Lepus* type pattern became common in early faunas. The climatic change at the beginning of the Pleistocene and during the first glaciation may have had much to do with the extinction of *Notolagus*, *Pratilepus* and *Hypolagus*. Whatever detrimental effect the changing climate of the Pleistocene may have had on *Notolagus*, *Pratilepus*, *Hypolagus* and other genera, its action upon the pro-*Sylvilagus* stock must have served as a stimulus, since this line gave rise to four genera, *Sylvilagus*, *Caprolagus*, *Oryctolagus* and *Lepus* in the early Pleistocene. The rigorous climate of the Pleistocene has left the genera *Sylvilagus* and *Lepus* with many and varied species.

Pronolagus, *Pentalagus*, *Nesolagus*, *Brachylagus* and *Romerolagus* are genera of rabbits representing early stocks that now exist in relic populations. The ranges of these genera appear to have been restricted in the Pleistocene by the more vigorous and closely related genera, *Sylvilagus*, *Caprolagus*, *Oryctolagus* and *Lepus*.

More data are needed concerning the *Lepus* pattern in fossil and Recent rabbits throughout North America and Eurasia. The 12 individual rabbits from the United States that possess the *Nekrolagus* P₃ pattern have the following distribution: the 5 specimens of *Lepus californicus* are from west of the Rocky Mountains: Idaho, 1 (Hibbard, 1944); Oregon, 1 and California, 3. *Sylvilagus bachmani*: Oregon, 1. *Sylvilagus auduboni*: California, 3 and Texas, 1. The one specimen of *Lepus americanus* is from North Dakota and *Sylvilagus aquaticus* is from Indiana. Seventy-five per cent of the *Nekrolagus* patterns in Recent specimens occur west of the Rocky Mountains, 83.33% in western species. The pattern occurs in P₃ of both sexes.

I consider the sample of *Sylvilagus floridanus* (651 specimens or 1,302 P₃s) to be large enough to be of significance in the study of the occurrence of the *Nekrolagus* pattern in Recent rabbits. *Sylvilagus floridanus* appears to be a homogeneous species which either has lost the gene combination producing the *Nekrolagus* pattern or the pattern is most rare. Also, the low frequency of the pedomorphic pattern of P₃ appears significant. There are many species of Recent rabbits to be studied, but from the material at hand the findings indicate that *S. floridanus* may be closely related to and derived from the stock of *Nekrolagus* at or near the center of population where the *Lepus* pattern was most dominant. Some of the western forms could have developed from a fringe population of *Nekrolagus* that was developing the *Lepus* pattern but split off before the pattern was as firmly fixed as in that part of the population that gave rise to *S. floridanus*. A study of large series of *Caprolagus*, *Oryctolagus* and *Lepus* from Eurasia should give considerable information. The single specimen of *Oryctolagus* from Kinlock Rannoch, Scotland, with the *Nekrolagus* pattern was taken from too small a sample to be compared with

our Western species, but it does indicate that the frequency of occurrence of the *Nekrolagus* pattern in *Oryctolagus* is probably as high or possibly even higher than in *Sylvilagus auduboni* or *S. bachmani*.

In Fig. 3 I have summarized my present concept of the relationships of the known Leporinae genera.

DISCUSSION

Relationships of Pratilepus kansasensis Hibbard.—Dawson (1958) considered *Nekrolagus* as a synonym of *Pratilepus* because certain specimens of *Pratilepus* possessed an isolated lake in some P₃s (Fig. 2a and c), a character

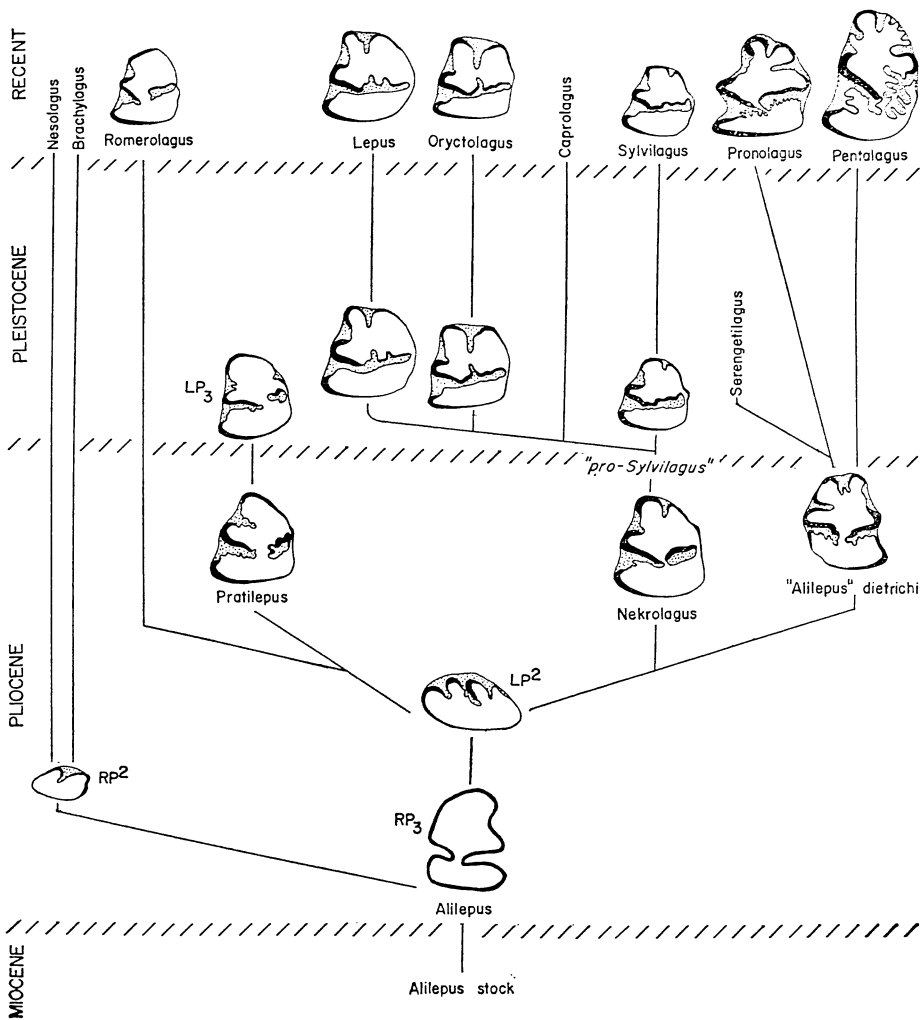


FIG. 3.—Suggested phylogeny of the Leporinae as based on the development of P² and P₃.

in common with *Nekrolagus*. It should be noted that this, as well as the lack of the anterior reentrant angle (Fig. 1i, a.r.a.), are also characters of *Romerolagus* (Fig. 2q'). The anterior reentrant angle on the anterior face of P₃ in *Nekrolagus*, is a most distinctive character. Fossil evidence indicates that this variation has been developed but once in the history of the Leporinae.

Of the 91 P₃s of *Pratilepus* examined, 13 of the teeth have the posterior internal reentrant angle open to the base (Fig. 2b). A posterior internal enamel lake was present in 69 (75%) of the P₃s (Fig. 2c). Fourteen of the premolars possessed an anterior internal angle (Fig. 2c). Nine (9.9%) of the 91 teeth had the posterior external reentrant angle united with the posterior internal enamel lake to give a posterior external fold that extends nearly to the lingual enamel border of P₃ (Fig. 2d and e). This fold is directed more anteriorly than in *Nekrolagus* and other Recent genera possessing the deep enamel fold.

The posterior and anterior external reentrant angles, as well as the posterior and anterior internal reentrant angles, or the enamel lake, can be considered as ancestral characters in common with "*Alilepus*" *dietrichi*, *Pentalagus* and *Pronolagus*.

Nekrolagus (Fig. 1a), *Pratilepus* (see Hibbard, 1939, Fig. 1b), *Romerolagus* (Fig. 2q) and *Alilepus dietrichi* Fejfar (1961, Fig. 2h) have a P² with 3 reentrant angles. I consider that these rabbits had a common ancestor in the *Alilepus* stock, an ancestor that had a P² with 3 reentrant angles.

Soon after the development of this type of P², which was prior to the development of the anterior reentrant angle on P₃, the stock divided and that group that did not develop an anterior reentrant angle on P₃ gave rise to *Romerolagus* and *Pratilepus* (see Fig. 3). It is possible that the stock that gave rise to *Romerolagus* and *Pratilepus* was in North America as early as late Miocene or early Pliocene. I have not been able to examine the teeth reported as *Hypolagus apachensis* Gazin, but some of the teeth found associated with typical *Hypolagus* patterns are not typical of that genus in the shape of the crown or the presence of a deep posterior internal reentrant angle that extends to the base of the tooth (see Dawson, 1958, Fig. 25b and c). Wood (1937) considered one of these teeth as that of a Palaeolagine. The tooth is similar to teeth assigned to *Alilepus* (see Bohlin, 1942, Fig. 8).

In *Pratilepus* it has been observed that the long posterior reentrant enamel fold has developed independently from that of *Nekrolagus*. It clearly shows how this structure is developed in the P₃ of rabbits.

Only time and further collecting will furnish data that will show if this character became dominant in *Pratilepus* for a short time in the history of the group and was later replaced by the more progressive *Sylvilagus* and *Lepus*.

After observation of the development of the long posterior external reentrant enamel fold of P₃ in *Nekrolagus* and *Pratilepus* it is logical to consider the development of *Nesolagus* Major and *Brachylagus* Miller from an ancestral stock that had an open posterior internal reentrant angle that later closed to

form an enamel lake which in turn united with the posterior external reentrant angle to give the long reentrant enamel fold of P₃. Furthermore, the ancestral stock must have had a P² with only a single reentrant angle.

I consider *Nesolagus* and *Brachylagus*, on the basis of their dentition, to be more closely related to each other than either is to the other living genera of Leporinae. It is incorrect and most misleading to consider *Brachylagus* as a subgenus of *Sylvilagus*.

Age of the Rexroad fauna.—The appearance of the *Lepus* pattern of P₃ in the *Nekrolagus* population living at the time of the Rexroad fauna provides evidence for the correlation of vertebrate faunas between Eurasia and North America. It would take some time after the appearance of the *Lepus* pattern in the Rexroad population for this pattern to become a persistent character in later generations. However short, this interval is the amount of time needed to give the rate of generic differentiation in this group of rabbits. The time required to develop the dominant *Lepus* pattern, plus the time it took this population to spread from northeastern Asia to Europe, is the amount of time that the Rexford fauna and the deposits in which it is contained precedes the arrival of the *Lepus* P₃ pattern in Europe.

Faunas in Europe that contain *Oryctolagus* and *Lepus*, or faunas of their equivalent, are younger than the Rexroad fauna. *Oryctolagus* appears in the earliest Villafranchian fauna, the Perrier (*vide* Viret, 1958), in Europe.

Thenius (1959, p. 178) considered all Blancan faunas of North America to be equivalent to the Villafranchian faunas of Europe, and to be of Pleistocene age. Thenius (p. 178) states, "Auch die Saw-Rock-Canyon (Seward Co.), die Rexroadfauna (Meade Co.) und deren Äquivalente sind bereits als Pleistozän zu betrachten. Sie entsprechen dem Villafranchium in Europa, das ebenfalls noch, 'Warmfaunen' enthält." Previously, on the same page, Thenius assigns *Pliomastodon* (= *Mammut*) and *Osteoborus progressus*, members of the Sawrock Canyon fauna, to the Hemphillian. This assignment is correct, but it must include the entire Sawrock Canyon fauna. The gophers (*Pliogeomys*) of the Sawrock Canyon fauna have rooted teeth (Hibbard, 1954, p. 356). The Sawrock Canyon fauna is more closely related to the Rexroad fauna than to the earlier Hemphillian faunas. The slightly younger Rexroad fauna is distinct from the other known Blancan mammalian faunas. This is evident by the morphological development of the insectivores, some of the carnivores, mastodons, and most of the rodents. The microtine rodents morphologically follow the same pattern of progressive development as shown in the rabbits. *Ogmodontomys* of the Rexroad fauna has shorter crowned teeth and better developed roots than *Cosomys* from the Hagerman fauna of Idaho. There is a root reduction in M³ between the time of the Rexroad fauna and the appearance of *Cosomys* (Hibbard, 1956, Fig. 8c and e). *Cosomys* is distinct from the genotype of *Mimomys pliocaenicus* Major from the Villafranchian of Europe; the latter possesses cement in the reentrant angles of the teeth (*vide* Hinton, 1926, p. 359). I examined all specimens possible of *Mimomys pliocaenicus* in

Europe in the summer of 1960. All of the specimens had higher crowned teeth, with cement, and later development of roots than found in *Cosomys*, which has no cement. To consider the dentition of *Ogmodontomys* as that of a *Miomys* is like assigning a *Pliohippus* tooth to *Equus*.

I am most grateful to Oldrich Fejfar for allowing me to study the Ivanovce rabbits and rodents (Fejfar, 1961, 1961a and 1961b), and to Kazimierz Kowalski for permission to study the Węże fauna (Kowalski, 1960) before publication. These are pre-Perrier and pre-Valdarno faunas. The microtines in the Ivanovce and Węże faunas are more primitive than those of the Villafranchian faunas of Europe. The Ivanovce and Węże faunas contain slightly more advanced microtines than are found in the Rexroad fauna. These faunas are considered by Fejfar and Kowalski to be Late Pliocene. The Rexroad fauna of North America shows a closer relationship to the Astian faunas of Europe than to the Villafranchian faunas.

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The drawings of the RP₃ of *Alilepus* in Fig. 3 is after Khomenko (1915, Pl. I, Fig. 20) and that of the RP₃ of *Alilepus dietrichi* is after Fejfar (1961, Fig. 2d).

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