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Evolutionary Trends in the Dentition of *Lagomorpha*

[Pp. 1—12, pls I—III, 1 text-fig.]

Kierunki ewolucji uzębienia zajęczaków (*Lagomorpha*)

Abstract. General developmental tendencies in cheek teeth from the upper Eocene to the Pliocene are briefly reviewed and discussed. An interpretation of changes in morphology of enamel folds, cusps and roots is made in terms of the theory of morphogenetic fields and gradients. The teeth are treated as having their own serial homology and variation. Three basic gradients responsible for the evolution of cheek teeth are distinguished.

INTRODUCTION

The dentition of the fossil *Lagomorpha*, especially those living throughout the Miocene, well exhibits the morphological gradation of the pattern in each particular tooth-row. In evolutionarily younger forms, starting from the Pliocene, the tooth-rows constitute a very uniform, morphologically integrated system, in which one finds it already more difficult to trace this gradation without knowledge of the older forms, while in the permanent dentition of the modern species it is hardly possible to find any characters of the Oligocene ancestors, the oldest ones that are known so far.

Owing to the descriptions of a large number of well-preserved sets of lagomorph dentition presented by many authors (BOHLIN, 1942a, b; BURKE, 1934, 1941; DAWSON, 1958, 1965; FEJFAR, 1961; GUREEV, 1960; HIBBARD, 1939; MAJOR, 1899; SYCH, 1965; TOBIEN, 1974, 1975; WOOD, 1940; and others) it has appeared that there is also a distinct morphological gradation, evolutionary in character, in this dentition. The excellent studies on the morphology of the skull of the Tertiary *Lagomorpha*, mainly those on their dentition, made among other authors by WOOD (1940), DAWSON (1958) and TOBIEN (1974, 1975), explained much as regards both the phylogenetic relations between particular groups of species and their systematics. Treating the characters of dentition as taxonomic criteria, the investigators focused their attention on teeth as individual units and not as systems which, as a whole, are governed by the morphogenetic laws. The results of the studies carried out by BUTLER (1952a, b) and VAN VALEN (1970) on the ontogeny and serial homology of teeth in various groups of mammals seem to be promising in the study of the evolution of dentition in mammalian groups in the terms of the theory of morphogenetic fields (BUTLER, 1939) and gradients.

In this work I have decided to give up the considerations on the systematic significance of the characters of teeth and to treat the dentition of all lagomorphs as a system characterized by serial variation and serial homology and evolving with its morphological gradients changing and interfering with each other. The purpose of such an approach is an attempt to determine these gradients and to explain the origin of some components in the morphological pattern of the dentition of modern species. The changes occurring in its constituent structures over the space of a few successive geological periods make the basis for observation.

OBSERVATIONS

The lagomorph dentition underwent essential changes in the period from the Upper Eocene to the outset of the Pliocene and so I confine this survey virtually to this period.

The evolutionary changes in the morphology of dentition are summarized in Fig. 1. It presents a survey of changes in ten characters of the dentition. In studying the degree of development of a given character in particular species I applied a four-grade scale. E.g., the mean length of the hypostria in a species was compared with its maximum length generally observed in available lagomorphs, conventionally assumed to be grade 4. Thus the number of four lines in the graph represents the maximum occurrence of the given character in a geological period. Crenulation is here an exception. In two genera *(Pliopentalagus* and *Pentalagus)* it reached an unparallel level of development, compared with which the considerably lower level of development in other species would have lain below 1. therefore, indetermining crenulation I omitted these genera and assumed the average number of denticles occurring in most species as maximum.

Upper Eocene

The Upper Eocene Asiatic lagomorphs of the genera *Lushilagus* LI CHUAN KUEI 1965, *Shamolagus* BURKE 1941 and the American genus *Mytonolagus*

Burke 1934, also from the Eocene, have the structure of the premolars and molars of the most primitive type. The remains of the very primitive genus *Mimolagus* Bohlin 1951 from Kansu, regarded as a lagomorph, are not included in this study, because they lack dating and the details on the surface of the teeth are obliterated. The upper teeth of the oldest lagomorphs are divided into distinct crown and root parts and show clear brachydonty on the lateral side

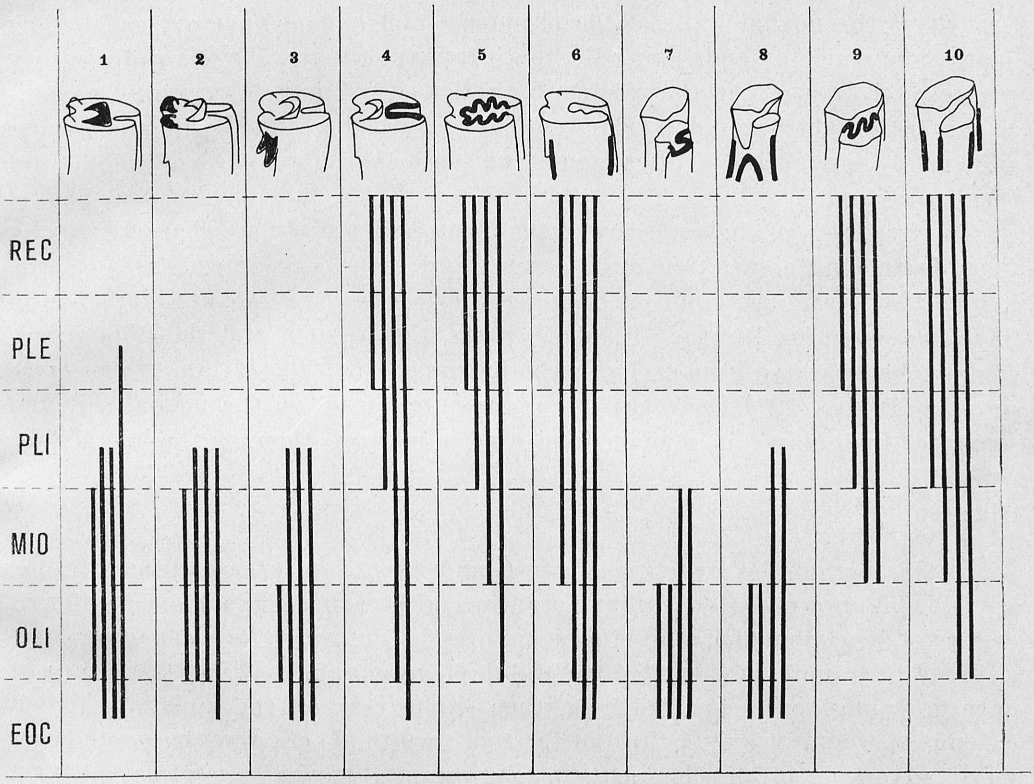

Fig. 1. Diagram of the occurrence of particular tooth characters of lagomorphs in time. The lines (1—4) mean the general intensity of the occurrence. The characters: 1. crescent, 2. lateral cusps, 3. two lateral brachydontic roots 4. hypostria, 5. upper teeth crenulation, 6. hypsodontic upper root, 7. additional talonid, 8. antero-posterior lower roots, 9. lower teeth crenulation, 10. lower hypsodontic root

and partial hypsodonty on the medial. Brachydonty is manifested by the presence of usually two short lateral rootlets (in *Lushilagus* and *Mytonolagus* grown together into one root divided by a groove, Li-Chuan-Kuei, 1965, page 30). Two cusps on the wear surface, an anterior and a posterior, heavily worn in asiatic specimens, correspond with these roots. The partial hypsodonty of a single tooth, termed "unilateral hypsodonty" by various investigators, is represented by a big medial root, which passes into the crown on the lingual side. The crowns of the premolars and molars are not differentiated into an anterior and a posterior lobe. The central part in P^4-M^2 is occupied by a structure named the „crescent" for its shape (Wood, 1940), also termed the mesoflexus (Lopez Martinez, 1974) the horns of which are pointed to the buccal side, and which is a portion of dentine surrounded by an enamel layer. The crescent is best developed on P^4, while on the molars, notably on M^2, it is hardly a rounded islet. The first premolars have two folds pressed in on the anterior side, the medial one of them being a serial homologue of the crescent. In *Mytonolagus* and *Gobiolagus* the medial walls of the premolars and molars have a very shallow depression, which extends along the tooth towards the root. It is a rudimentary enamel fold known as the hypostria (hypoflexus in Lopez Martinez's nomenclature 1974), which would develop towards the buccal side and divide the molars, and, partly, premolars of later lagomorphs into two lobes, the anteroloph and the posteroloph.

The five teeth of the lower row of the forms under study are characterized by their distinct differentiation into a crown and roots. The crown has as a rule a bipartite structure, and in *Lushilagus lohoensis* Li-huan-kuei, 1965 and *Shamolagus medius* Burke, 1941 both parts, the trigonid and the talonid, are completely separated from each other in its upper part (Pl. II). In *Mytonolagus petersoni* Burke 1934 these two structures are joined on the medial side and separated by a deep fold of enamel squeezed in between them on the buccal side.

Oligocene

In this period the structure of teeth underwent an intense differentiation (Pl. I, II). Various species, contemporaneous with each other, achieved different degrees of development of individual structures. In Mongolian *Desmatolagus gobiensis* Matthew and Granger, 1923 of Middle Oligocene age the hypostria is present only in young specimens and even then exclusively on the molars, where it extends at the most over a third of the tooth-width. The hypostria is somewhat more advanced in development in European *Piezodus brassatensis* Viret, 1929 from the late Oligocene of France, in this species it occurs, in addition to the molars also on P^4, not excluding adult specimens. In comparison with these forms the American genera *Palaeolagus* Leidy 1856, *Litolagus* Dawson 1958 and *Megalagus* Walker 1931 (species *Megalagus turgidus* Cope, 1873) are marked by a small increase in depth of the hypostria and its presence on P^4 and M^1 irrespective of the time of their occurrence in the Oligocene. The incision of this fold reaches a maximum in Asiatic *Sinolagomys* Bohlin 1937, whose molars are in consequence distinctly bilobular. An intermediate stage of the development of the hypostria deep into the tooth is observed in a number of species of the American genus *Palaeolagus*, in which this structure is present, in addition to the molars, also on the premolars except P^2, having an extreme position in the row (Pl. III).

In all the species of the genera *Desmatolagus*, *Palaeolagus* and in *Piezodus brassatensis* the crescent attains the highest known level of development in the Oligocene. The gradation of its shape is visible in all successive teeth of the upper row, starting from P^2, where it occurs only in the form of an anterior fold, which gradually sinks to the rear and loses its contact with the anterior wall (Pl. I, C). In most Oligocene species, only one, the deeper, out of the two anterior folds on P^2, becomes transformed into the crescent. In Upper Oligocene *Piezodus brassatensis*, however, both anterior folds of P^2 are changed into two independent crescents (LOPEZ MARTINEZ, 1974). On the other hand, American *Litolagus* has its crescent poorly developed and only in juveniles (DAWSON, 1958). The crescent is missing on the molars of the Asiatic forms of the genus *Sinolagomys*.

Desmatolagus, *Palaeolagus* and *Megalagus turgidus* have the best-preserved lateral cusps, which are always low and partly worn by the transverse movements of the mandible. Brachydonty still persists to a considerable degree both in premolars and in molars in *Desmatolagus*, the non-growing lateral parts of these teeth having small short lateral roots, two on P^4 and M^1 each and one on M^2. In American *Megalagus brachyodon* (MATTHEW, 1903) and *Megalagus turgidus* the lateral roots are preserved to a similar degree (DAWSON, 1958). I found only slight traces of these roots on M^1 of adult *Palaeolagus haydeni* LEIDY, 1856, whereas *Piezodus brassatensis* still has their distinct remnants on the molars (LOPEZ MARTINEZ, 1974). In *Sinolagomys* the lateral roots are completely missing (BOHLIN, 1942a). The reduction of these roots in the Oligocene species is accompanied by the expansion and elongation of the medial root with hypsodont properties. The division into a crown part and a bipartite root part is very conspicuous in the lower dentition of the genera *Megalagus* and *Desmatolagus*. As the tooth grows old, the anterior and posterior roots above the margin of the alveoli. This character, together with some other ones, was used as the basis for the division of the specimens of *Desmatolagus gobiensis* into age groups (SYCH, 1975). The place in which the trigonid and talonid join generally constitutes the boundary between the crown and the root in this type of teeth. This is morphologically important, especially on the lateral side, where this junction is gradually shifted downwards towards the root, which is connected with the union of the anterior and posterior parts of each root into a hypsodont unit. Thus the boundary between the crowns and the roots generally lies above the alveoli in all P_3—M_3 of *Desmatolagus*. Although these teeth have relatively high crowns, it is hardly possible to speak about hypsodonty here. In *Palaeolagus*, *Megalagus*, *Litolagus* and *Sinolagomys* the lateral coalescence of the talonid and trigonid descends, on the average, to or even below the margin of the alveoli. Out of the Oligocene forms, *Palaeolagus*, especially *Palaeolagus haydeni*, and *Sinolagomys* undoubtedly show the most advanced hypsodonty of the lower cheek-teeth.

The presence of an additional small lobe on the posterior side of the talonid of P_4-M_2 in some species of the genera *Desmatolagus*, *Palaeolagus* and *Megalagus* is a very ancient character, found in Eocene *Shamolagus* and *Mytonolagus*, which became extinct probably at the boundary between the Oligocene and

Miocene. Presumably it is a vestige of the heritage of the trilobular structure characteristic of the lower teeth in the pre-Eocene ancestors of the lagomorphs. A fairly peculiar character, which would play an essential part in the structure of the lower and upper dentition of lagomorphs in the next periods appeared, probably for the first time in their history, in the Middle and Late Oligocene. This character is the presence of a very subtle folding of the thin layer of enamel which forms the anterior wall of the talonid on the lower molar (M_1 and M_2) and the posterior wall of the fold of the hypostria on the upper molars. This folding, referred to an crenulation, was described by WOOD (1940) from the lower molars, especially M_1, in young specimens of *Megalagus turgidus* and by DAWSON (1958) from P^3-M^2 in *Palaeolagus burkei* WOOD, 1940.

Miocene

In the Miocene the lagomorphs display the greatest wealth of morphology. At the decline of this period full hypsodonty becomes definitively established in the upper and lower teeth. The bilobularity of P^4-M^2 increases in thoroughness, in which it is accompanied by the gradual decline of their lateral roots. These roots, distinctly separated from the main hypsodont root in older forms, grow in length and are pressed to it. This phenomenon is well exemplified by *Piezodus brassatensis*, a near ancestor of *Prolagus vasconiensis* VIRET 1930, found in numerous localities in Western Europe. This last species is already fully hypsodont. Full hypsodonty occurs, among other species, in Mongolian *Bellatona forsythmajori* DAWSON 1961, and *Alloptox gobiensis* YOUNG 1932. European *Titanomys visenoviensis* H. v. MEYER 1843, still has vestigial lateral roots (TOBIEN, 1974).

The evolution of the crescent reaches its maximum. Being a structure the depth of which was previously limited in general to about half the height of respective teeth, the crescent grows in more and more towards the root in the successive teeth. In the members of the genus *Prolagus* POMEL, 1855, it even extends as far as the very end of the root. N. b. the developmental possibilities of *Prolagus* are not restricted to one crescent only; not one but both anterior folds of P^2 undergo a transformation into crescents, which reach the „bottom" of the tooth, as I found while grinding the root parts of M^2 in *Prolagus vasconiensis*. The crescent of some Miocene species is atypical as regards its shape, especially when one of its arms has disappeared and there remains only a tubular structure seen on the occlusal surface as an elongate islet of enamel. The same is also true of American *Archaeolagus ennisianus* COPE, 1873, common in the Middle Miocene, which has only darkenings in the dentine in place of the crescent (DAWSON, 1958).

The hypostria expands towards the buccal side, deepening particularly distinctly on the molars. In the genus *Archaeolagus* it extends over about a third of the tooth-width, in some species, however, e.g. in African *Kenyalagomys* MAC INNES 1953, it reaches two-thirds of the width (MAC INNES, 1953).

Pliocene to Holocene

Once attained full hypsodonty tends towards forming a striking likeness between the occlusal and the root part of every lower and upper tooth. Palaeontologists use that resemblance for reconstructing the shape of those tooth partly which have not been preserved.

The crenulation expands gradually along the hypostria, but the stage of the advancement of this character varies distinctively from species to species. In ochotonids the crenulation has not appeared, their hypostria remains smooth. The changes in the lagomorph dentition during the pliocen to holocen time are of quantitative nature. In some species such as *Pliopentalagus*, *Alilepus ditrichi* or recent *Pentalagus* the development of hypostria and its crenulation have reached unusual stage. Most of the inner space in every upper and lower molariform tooth of those species is occupied by very complicated enamel folds of hypostria.

DISCUSSION

The understanding of the evolutionary changes in the dentition treated as a system of dental units, which are subject to the laws of serial variation and serial homology in the light of BUTLER'S (1939, 1952) theory of morphogenetic fields and gradients is facilitated by the assumption that the action of these gradients was changing in the course of evolution. Thus the gradient responsible for the development and expansion of the crescent to the rear of the upper tooth-row gradually changed its range of action and eventually retained its influence only in P^2 and P^3, in which up to the present time it has been causing the process of deepening of the anterior fold backwards in the ontogeny of these teeth, but without its being detached from the anterior wall in the form of a typical crescent. In the modern rabbit the crescent occurs in the early development stages of the permanent teeth up to M^2 inclusive and was identified in the period of about 12 days following birth (SYCH and SYCH, 1976). The time of its existence has thus been shortened enormously. In addition, it does not attain its typical shape in the rabbit, because it soon becomes dominated over by the hypostria, which develops and undergoes crenulation. The third and fourth upper deciduous premolars of the rabbit retain the crescent, which can be seen soon after the eruption of these teeth. The same can be observed in the Pliocene and Pleistocene species *Hypolagus brachygnathus* KORMOS 1934, whose deciduous teeth have the crescent typically situated. As the dentition of the *Lagomorpha* has been characterized by a great uniformity since as early as the Pliocene, there is no reason to suppose that the situation in the rabbit and *Hypolagus brachygnathus* is not representative of the remaining leporids. Then the reduction of this gradient proceeded not only as the limitation of the number of the teeth in which the crescent was present, but also as the shortening of the time of functioning of this gradient. This makes it possible for other structures, e.g. the hypostria, to dominate over the crescent.

The gradient to which the development of the hypostria is attributed virtually forms a continuity with the gradient of the large external fold at the bottom. Ontogenetically, this continuity would be represented by the greatest density of the evocator or inductor along the morphogenetic field which includes both tooth-rows in the position of circumnatal development. The power of the evocator decreases gradually on the buccal and medial sides, correspondingly stimulating the development of the large lateral fold and hypostria. In the Eocene forms the action of the medial portion of the gradient was limited very much and gave hardly a trace of the hypostria on molars with the simultaneous development of the large external fold at the bottom. In course of time the action of the evocator spread over the upper row, bringing about the development of the hypostria, the fold serially homologous with the large external fold.

The gradient responsible for the development of the hypsodont roots of the lower and upper teeth may be assumed to be the third one. Its action would be directed upwards for the upper row and downwards for the lower. As a result it would cause the lowering of the place where the two roots part, till the tooth becomes prismatic in shape, in the lower row, and the extension of the root upwards, especially the extension of its lateral part, in the upper teeth.

The assumption that there three gradients of the main structures does not explain all the changes in the dentition. VAN VALEN'S (1970) study demonstrates that interferences may occur between the gradients in the morphogenetic field of dentition. The origin of crenulation might be regarded as the result of the joint action of the three gradients: 1. the gradient of crescent with its capacity to induce the formation of folds of enamel and dentine on successive teeth, 2. the gradient of hypostria and large fold and, in this connection, of the capacity to induce the formation of crenulation in the buccal direction on successive teeth and 3. the gradient of hypsodonty of the roots and, as a result, possibility for crenulation to arise not only in the occlusal regions but also in those of roots.

The decline of brachydonty was probably connected with the displacing action of the hypostria and the simultaneous decline of the gradient of crescent, which constituted the basis for brachydonty. The moments of the dominance of the hypostria over the crescent are perceptible not only in the ontogeny of the cheek-teeth of the rabbit.The union of the hypostria and crescent can be seen on the surface of DP^3 of as old a species as Miocene *Oreolagus nebrascensis* (DAWSON, 1965). This is the outset of the dominance of the gradient of hypostria over the gradient of crescent, which is receding from the morphogenetic field.

The presence of two different zones in each permanent tooth (except the incisor) was a striking character of the dentition of the *Lagomorpha* up to the end of the Miocene. They are 1. the medial zone, including the ever-growing part of the tooth, with an open hypsodont root and 2. the lateral zone, the growth of which must have been arrested early, along with the closing of the two lateral roots. The lateral most two-cuspid parts of the molars and two premolars kept up unworn for a fairly long time, whereas the evergrowing medial part was worn quickly, more quickly even than it was growing, so that, e.g. in old specimens of *Desmatolagus gobiensis* and *Desmatolagus robustus* it became much lower (Sych, 1975) and deprived of details. Besides, rapid wear of the buccal side of the upper teeth was not permitted by the lateral movements of the jaw, the amplitude of which was smaller in the phylogenetically old forms than it is in the modern species, as I found in various species of the genus *Desmatolagus*, while the occlusion in the *Lagomorpha* is most effective between the medial side of the upper teeth and the latero-middle part of the lower teeth. The developing hypostria, present only in young specimens of the Oligocene forms (Sych, 1975), was subject to the most intense wear. I observed the gradual prolongation of the time of existence of the hypostria by its expansion towards the root and to the lateral side of the tooth. This is one of the symptoms of the phenomenon defined as molarization. The rudiments of the hypostria are, however, first observed on the molars in the oldest lagomorphs. In course of time the hypostria underwent crenulation, which in some species assumed quite a singular size. In this way the medial part of the teeth became still more hardened by the numerous folds of enamel. Nevertheless, it should not be thought that the development of crenulation as a protective measure against excessively rapid wear was an indispensable condition of the survival of lagomorphs. Actually, the *Ochotonidae*, which persist up to now, have not developed in the *Leporidae*. Both groups have ever-growing cheek-teeth with a hypostria and large external fold. In the *Lagomorpha* the development of this crenulation and the rate of growth and wear of the lateral cheek-teeth seem to be specifically balanced, that is to say, the lack of the crenulation is compensated by the faster growth of the teeth that lack it. This will, however, be the subject of another study.

Both fossil and modern lagomorphs show a distinct heterochrony of characters in species living at the same time, viz. in different species the degree of advancement in the development of the dental structures was different in the same period of life. This is true of both the number of the teeth in which the crescent, hypostria or cusps were present and the degree of development of these characters in corresponding teeth in different species of the genus *Desmatolagus* (Sych, 1975). Another feature, occurring parallel to the previous one in the Oligocene species, was the remarkable variation of the pattern of the grinding surface according to the individual age of specimens. It is just on the basis of this variation that four age groups have been distinguished in *Desmatolagus gobiensis* (Sych, 1975). The fact that the occlusal surface assumed different shapes in course of life was due to the various depths of the structures in the undoubtedly connected with the gradient action of the biochemical evocators of the corresponding structures in the morphogenetic field.

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STRESZCZENIE

Podstawowe dotychczas znane zmiany w uzębieniu policzkowym (wszystkie zęby z wyjątkiem siecznych) zajęczaków dokonały się w okresie od górnego eocenu do dolnego pliocenu. Dotyczą one korzeni (stopniowe przejście uzębienia korzeniowego, brachydontycznego, w typ bezkorzeniowy, hypsodontyczny), fałdów szkliwa (tzw. „crescentu" czyli mesoflexus, który w toku ewolucji zanikł), hypostrii rozwijającej się i uzyskującej stopniowo obficie sfałdowaną strukturę zw. krenulacją, wielkiego fałdu zewnętrznego między trigonidem a talonidem, także nabywającego owej krenulacji, resztek guzków bocznych nie istniejących już w końcu pliocenu. Zmiany mają charakter kompleksowy tj. pojawienie się pełnej hypsodoncji spowodowało zanik mesoflexus, stworzyło warunki dla pogłębienia się fałdu hypostrii i dalszego jej sfałdowania, poszerzenie poprzecznych ruchów trących żuchwy spowodowało zanik guzków bocznych. Autor nie tylko zbadał cechy poszczególnych zębów w szeregach zębowych, lecz analizował zmienność ich cech w świetle homologii serialnej, znajdując stopniowanie patternu morfologicznego na kolejnych zębach badanego szeregu. Ten sposób traktowania poszczególnych struktur skłonił autora do próby objaśnienia zmian ewolucyjnych za pomocą teorii gradientów i pól morfogenetycznych. Wyróżnione zostały trzy podstawowe gradienty, których stopniowe zmiany w czasie doprowadziły do istotnych przekształceń uzębienia: 1. griadient, któremu przyporządkowany jest rozwój hypostrii w zębach górnych i wielkiego fałdu zewnętrznego w zębach dolnych, 2. gradient recesywny, odpowiedzialny za rozwój i ekspansję ku tyłowi górnego szeregu zębowego fałdu zwanego „crescentem" (mesoflexus), którego zakres działania został stopniowo ograniczony wskutek zdominowania go przez gradient pierwszy, 3. gradient hypsodontycznego rozwoju korzeni dolnych i górnych zębów policzkowych. Wśród zajęczaków zarówno u współczesnych, jak i kopalnych zaobserwowano wyraźną heterochronię cech, tj. występowanie u równoczesnych względem siebie gatunków cech uzębienia o różnym stopniu ewolucyjnego zaawansowania.

Plate I

A. A simplified scheme presenting in ascending order basic changes in upper molariform teeth from the Oligocene to the Holocene. Two upper drawings show upper molariform teeth of the modern leporids (left) and the ochotonids (right)

B. A simplified scheme presenting in ascending order basic changes in lower molariform teeth from the Oligocene to the Holocene. Two upper drawings show lower molariform teeth of the modern leporids (left) and the ochotonids (right)

C. Schematic view of the occlusal surface of upper tooth row (from P^2 at the top, to M^3 at the bottom of the drawing). The gradation of the morphological pattern is shown along the tooth row and the serial homology of structures is marked with the same numbers as in A and B

Explanation of numbers is the same as in Fig. 1, p. 3: 1. crescent, 2. lateral cusps, 3. two lateral brachydontic roots, 4. hypostria, 5. upper teeth crenulation, 6. upper hypsodontic root, 7. additional talonid, 8. antero-posterior lower roots, 9. lower teeth crenulation, 10. lower hypsodontic root

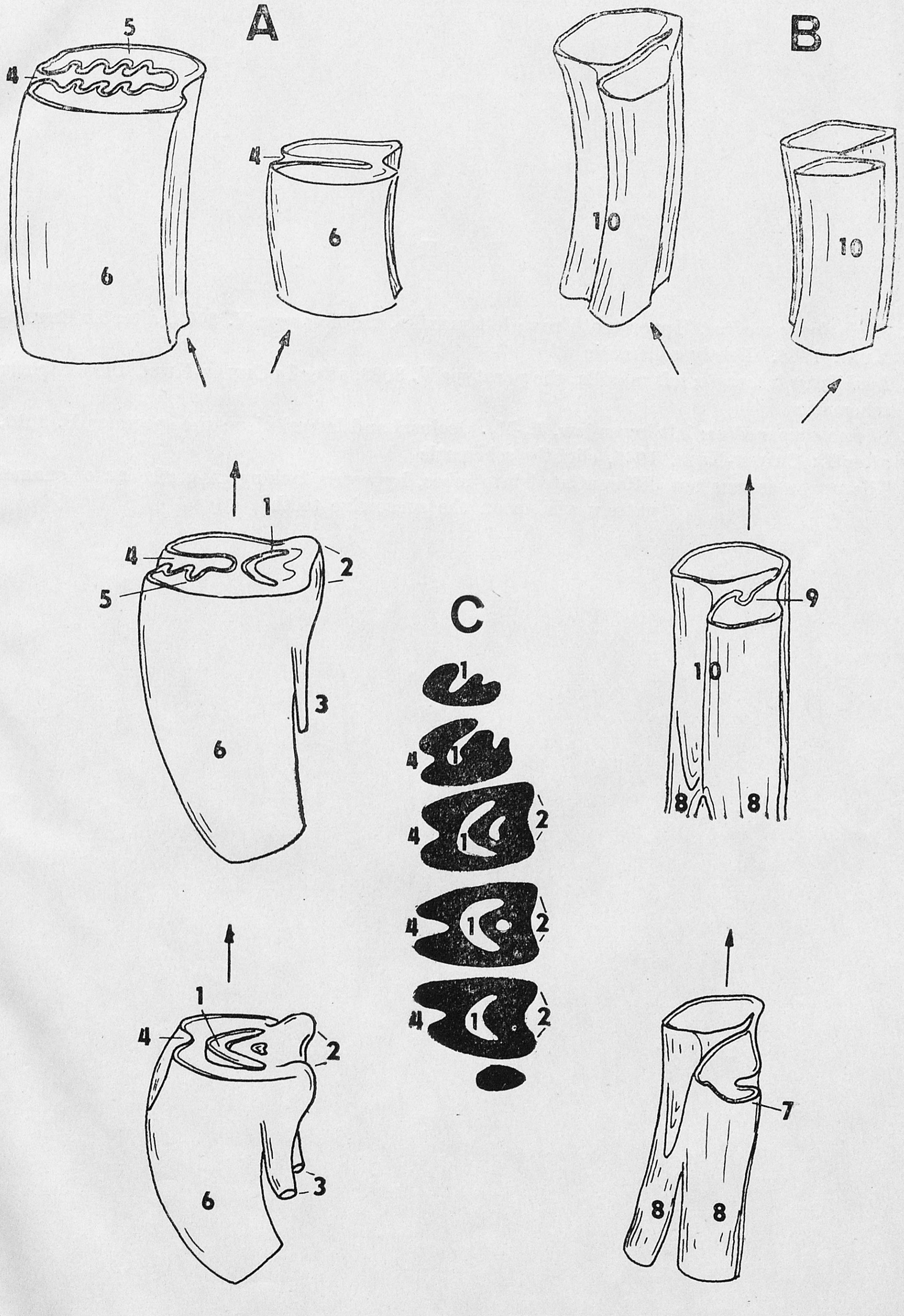
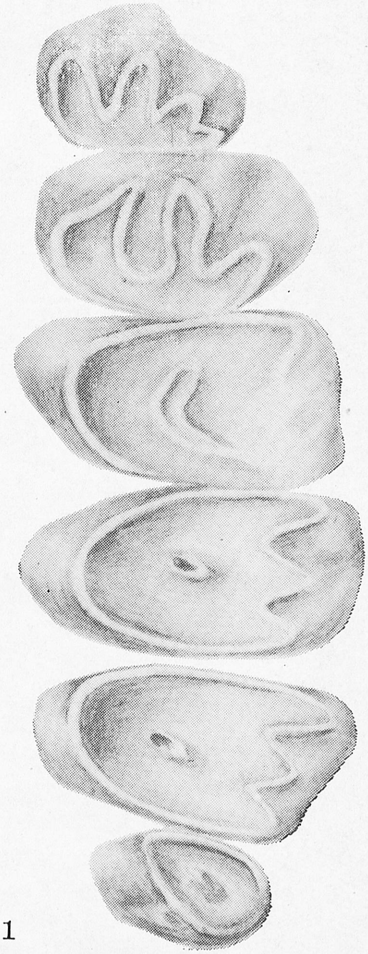

A
B
C
1
2
3
4
5
6
7
8
9
10

Plate II

1. *Shamolagus medius,* Upper tooth row; left maxilla, the holotype V. 3008, after Li Chuan-Kuei, 1965, slightly schematic
2. *Lushilagus lohoensis*; left maxilla, the paratype V. 3009, after Li Chuan-Kuei, 1965, slightly schematic
3. *Shamolagus medius*; left lower jaw, P_3-M_3. Occlusal and lateral view; the specimen V. 3010, after Li Chuan-Kuei, 1965, slightly schematic

   The upper crowns not differentiated into lobes, hypostria lacking. A gradation of enamel pattern visible on the successive teeth



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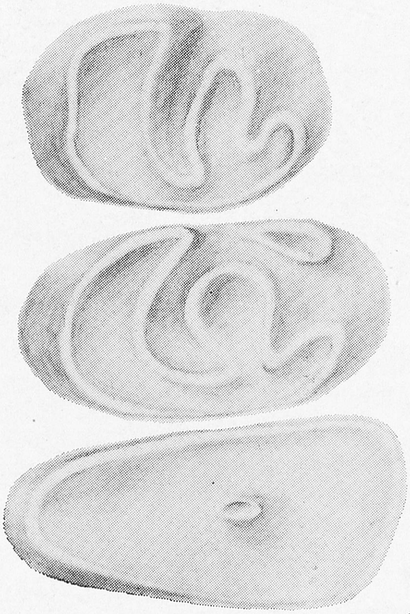

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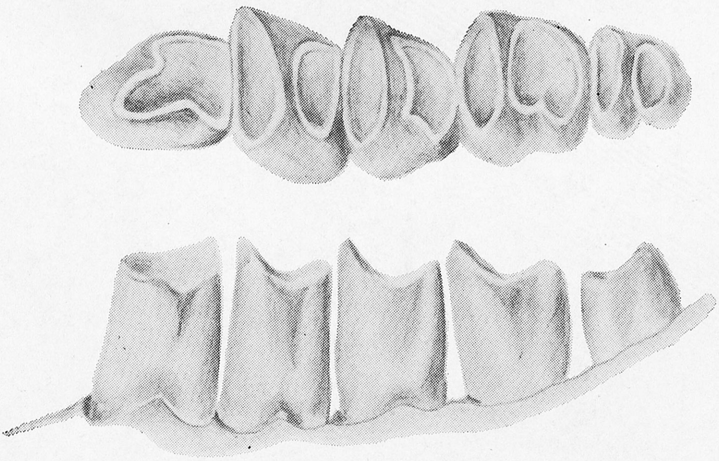

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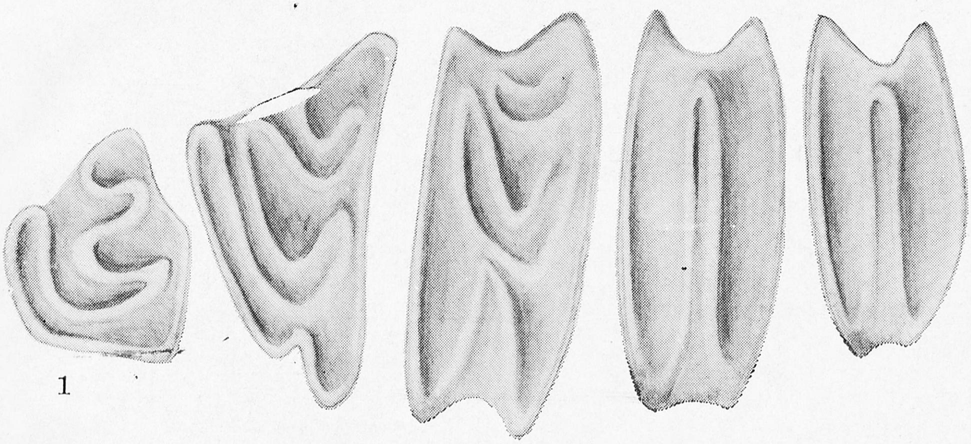
L. Sych

Plate III

1. *Prolagus sardus,* Pleistocen, M. San Giovani. Coll. Forsyth. Major. Brit. Mus. M. 3460
Various stages of development of crescent and hypostria on successive teeth in every tooth row
2. *Piezodus brassatensis* Viret, from Lopez Martinez, 1975
3. *Palaeolagus haydeni,* left upper tooth row



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Sych

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