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Unworn teeth of *Hypolagus brachygnathus* KORMOS *(Leporidae, Mammalia)*

[Pp. 19—26, pl. VIII and 1 text-fig.]

Uzębienie guzkowe *Hypolagus brachygnatus* KORMOS *(Leporidae, Mammalia)*

Ранные стадиа роста постоянных зубов у *Hypolagus brachygnatus* KORMOS *(Leporidae, Mammalia)*

Abstract. The author gives detailed description and morphological analysis of the early growth stages of permanent cheek teeth of the fossil leporid *Hypolagus brachygnathus* KORMOS. Unworn cuspid teeth are compared with those in some recent leporids and ungulates. It was possible to establish the probable homology only of the central and two lateral cusps in upper cheek teeth of *Hypolagus brychygnathus* and recent leporids. Some facts against the hypothesis of the relationship between lagomorphs and ungulates are discussed and emphasized.

INTRODUCTION

Three basic types of structure may be distinguished in the cheek teeth of lagomorphs: brachyodonty, hypsodonty and hypso-brachyodonty. The teeth of the third type are partly rooted and partly rootless, that is, they are furnished with roots on the buccal side and lacking in them on the lingual side, e. g., teeth of *Amphilagus* POMEL (TOBIEN, 1963). In addition, in numerous fossil species hypsodont and hypso-brachyodont teeth occur side by side. Hypsodonty is a secondary development in the *Lagomorpha*. In the recent species some vestiges of brachyodonty will be found only in the deciduous dentition, subsisting for a very short time. The typical characteristics of hypso-

dont teeth, continuous wear and growth, ousted the original cuspidate structure of the crown. The presence of cusps may be observed, as in many other mammals, only in very early stages of eruption of deciduous and permanent teeth. Soon after the teeth have broken through the gum they are subject to wear and successively show different forms of enamel pattern. Single deciduous and permanent teeth were described in fossil species many a time. Observation of the early developmental stages of these teeth may be of some importance for the attempts of homologization of different tooth structures in the *Lagomorpha* with the corresponding structures in other mammalian orders and for the inquiries into the phylogenetic relationships within the group under study.

For this reason it seems to be purposeful to present a description of some early developmental stages of permanent cheek teeth in *Hypolagus brachygnathus* KORMOS, 1934 in this paper. The find of unworn teeth of this species has already been signalled (SYCH, 1965).

MATERIAL AND METHOD

Observations were made on young permanent teeth of *Hypolagus brachygnathus* KORMOS, 1934 from the Pliocene breccia at Rębielice Królewskie in the Kłobuck District (34 specimens) and from the early Pleistocene locality at Kadzielnia in Kielce (8 specimens). In some specimens inner structures were partly uncovered, by means ot an eccentric high-speed drill with a diameter of about 20μ so as to make their investigation possible.

DESCRIPTION OF MATERIAL

All the specimens of teeth under study exhibit hypsodonty and their walls taper towards the occlusal surface. The parallelism of walls becomes evident no earlier than in the teeth of adults. The alveolar end of each specimen is similar in general outlines to the final pattern of enamel, which does not appear till a fairly long time after the original sculpture of the occlusal surface has been worn away completely.

On the occlusal surface there are numerous eminences and depressions, which sometimes contain small amounts of cement. Somewhat larger amounts of cement cover the medial wall in most of the specimens examined. No correlation was found between the shape of the surface in the teeth being described and the sculpture of the alveolar surface of the corresponding milk teeth. Their detailed description was given in my previous paper (SYCH, 1965).

The age of the specimens represented by the teeth with completely unworn crowns is fairly difficult to determine. In some recent species, e. g., *Sylvilagus floridanus mearnsi* ALLEN 1894 (L. R. DICE and D. S. DICE, 1941) and *Oryctolagus cuniculus* LINNAEUS 1785 (STACH, 1911; and author's own observations)

the period of eruption of the permanent dentition, though varying from tooth to tooth for the most part terminates by the end of the first month of life.

The anterior wall of the upper cheek teeth, except P^2 and M^3, is built of a thicker layer of enamel than the posterior wall. On P^3 the medio-lateral width of the anterior part of the tooth, usually called the „anteroloph" is smaller than that of the posterior part, called the „posteroloph". On M^2 this relation is reversed. As in the case of adults, it is difficult to tell P^4 and M^1 apart, and the crowns of these teeth are sculptured identically before their cusps are worn away.

On the surface of P^2 there are 3 cusps, of which the lateral one, sometimes bifid, is the highest. The prominent middle cusp, neighbouring directly upon it, is separated from it by a shallow and narrow groove with traces of cement. This groove is not a continuation of the shallower lateral fold of enamel commonly described on the anterior wall of this tooth in the genus *Hypolagus* DICE (pl.VIII, 1). A wide depression, which is the extension of the deeper medial fold of enamel on the anterior wall, separates the lateral cusp from the medial. A thin layer of cement lies on the bottom of the depression. The lateral cusp, as well as the medial one, is crescentic in shape.

A conspicuous cusp (No. I) with a shape approximating to a crescent whose horns point somewhat laterad has a central position on the occlusal surface of P^3, P^4, M^1 and M^2; this becomes particularly evident with wear. On the unworn crown this cusp occurs in two cases as a prominent straight ridge (pl.VIII, 2).

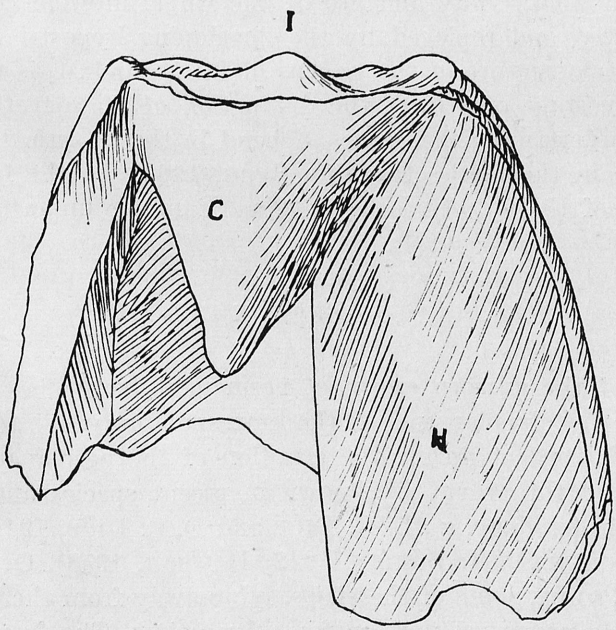

Fig. 1. The view of the young P^4 of *Hypolagus brachygnathus*. The anterior wall of the tooth is lacking. I — central cusp; C — conical structure; H — internal hypostria.

Laterally the crowns of P^4 and M^1 are occupied by two cusps: an antero-lateral (No. II) and a postero-lateral (No. III). In some specimens the ridges of these cusps are slightly wavy. On M^2 the antero-lateral cusp (No. II) is inconspicuous and the postero-lateral (No. III) prominent (pl.VIII, 2).

An oblong eminence of enamel (No. IV) runs along the anterior margin of the crown of the teeth (exept P^2 and M^3). Two cusps are present in the medial part of the crown: an antero-medial (No. V) and a postero-medial (No. VI) (pl.VIII, 2). They form a part of the anterior and the posterior wall, respectively. A fold cuts in between them from the medial side. It crosses one-third of the occlusal surface and constitutes the internal hypostria, typical of lagomorphs. In some specimens the alveolar part of the hypostria is crenulated.

A careful removal of the anterior or posterior wall of a tooth (except P^2 and M^3) uncovers a structure, which usually escapes an observer's attention. It is an elongated cone of enamel and dentine, turned with its rounded apex towards the alveolus. The base of the cone, facing the occlusal surface, constitutes the central part of the crown, including its central cusp (No. I) and depressions surrounding it. The cone reaches with its apex beyond the mid-height of the whole tooth.

Another structure detected is the anterior or posterior wall of the hypostria. Close to the cuspidate surface of the tooth the hypostria is very shallow, the bulk of the internal mass of the tooth being formed by the conical structure described above.

As the tooth wears away and grows, the whole internal conical structure becomes destroyed and replaced by the developing hypostria.

The cuspidate structure of the crowns of P_4, M_1 and M_2 is uniform so that at such an early stage of growth the distinction of these teeth is impossible. It is difficult to determine the planes of bend in these teeth, though they are very distinctive in the teeth of adults (Sych, 1965). In the face of this fact the description of these teeth is left out as of minor importance.

DISCUSSION

The shape of the unworn crown of permanent teeth does not depend on the pattern of the alveolar end of the corresponding milk teeth in spite of their fairly close contact during the eruption of the permanent teeth. Cuspidate structures of the crown are known in recent species and were sporadically described in fossils (e. g., L. R. Dice and D. C. Dice, 1941; Major, 1899; Wood, 1941; Burke, 1934; Bohlin, 1942; Dawson, 1958). Occasionally, e. g. in *Amphilagus* Pomel, some of the cusps, lying away from the occlusal surface of the crown, are preserved unworn for a long time. The foregoing fact suggests that the crowns of hypsodont teeth of lagomorphs with their cusps preserved may provide information on the genesis of the dentition in this group

of animals. A comparison of the young upper dentition of *Sylvilagus* GRAY (DICE, 1941) and *Lepus americanus* ERXLEBEN with that of fossil *Hypolagus brachygnathus* shows the completely unquestionable homology of only three cusps: the central (No. I) and the two lateral ones (Nos II and III). The lower dentition is admittedly of little importance for the homologization of cusps. As many authors differ considerably in opinions on the homologies of cusps not only in various groups of mammals but even within the fossil *Lagomorpha*, the determination of the cusps in *Hypolagus brachygnathus* has been carried out not by using the terminology, sometimes controversial, of different authors but by marking the basic cusps of the upper dentition with Roman numerals.

Without entering into the rightness of different opinions on the homologization of cusps, it is worth while to give special attention to the central cusp (No. I). In different species of fossil lagomorphs the so-called crescent borders directly upon this cusp or lies on it. At its base, inside the tooth, is the cone of dentine described above, with its apex pointing towards the alveolus. An analogous structure has also been found in the erupting permanent upper cheek teeth of recent *Lepus americanus* and *Oryctolagus cuniculus*. Investigating the ontogenesis of incisors of the rabbit *Oryctolagus cuniculus*, STACH made horizontal sections through the jaws of embryos, among others, in the region of the roots of the cheek teeth. As will be seen from his diagrammatic drawing of horizontal sections of the buds of the upper cheek teeth (STACH, 1910, fig. 7) there is an unidentified structure, sectioned horizontally, in the middle of the developing tooth. A comparison of this structure with the conical structure discussed in the present paper indicates their identity. In the course of growth the direct connection of the middle portion of the crown with the deepest part of the tooth becomes interrupted and thus the transient conical structure comes into being. Its presence has also been found in *Palaeolagus haydeni* LEIDY 1856 and in correspondingly early stages of teeth in various species of the *Bovidae* and *Cervidae*. In view of the similarity of the mechanism of development of the upper cheek teeth ascertained in the *Lagomorpha* and *Ungulata* I decided to find out whether this is also true of primitive ungulates of the group *Protoungulata*. A close examination of 3 specimens of young upper cheek teeth belonging to *Protungulatum donnae* VAN VALEN et SLOAN, 1965 showed the lack of the structure under discussion in this species. This would indicate that the mechanisms of growth of the upper cheek teeth in the *Protungulatum* and *Lagomorpha* differ from each other. We are thus in possession of another argument against the hypothesis, set forth by some authors, on the close relationship of the primitive *Lagomorpha* and the primitive *Ungulata*.

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STRESZCZENIE

Autor podaje szczegółowy opis i analizę morfologiczną wczesnych stadiów rozwojowych stałych zębów kopalnego zającowatego *Hypolagus brachygnathus* Kormos z górnego pliocenu w miejscowości Rębielice Królewskie k. Kłobucka i z wczesnego plejstocenu w Kadzielni w Kielcach. Na podstawie analizy kilkudziesięciu okazów tych zębów posiadających dobrze zachowaną, niestartą strukturę guzkową koron i porównania ich z materiałem współczesnym (*Lepus americanus* Erxleben, *Sylvilagus floridanus mearnsii* Allen) uznano, że całkowicie pewną homologię guzków można ustalić tylko dla trzech: centralnego i dwóch bocznych. Nie wdając się w słuszność poglądów różnych autorów na nazwy homologizowanych guzków zwrócono szczególną uwagę na guzek centralny (nr I). U różnych gatunków kopalnych *Lagomorpha* sąsiaduje z nim lub bezpośrednio na nim spoczywa tzw. „crescent". U jego podstawy znaleziono po rozpreparowaniu korony zęba stożek zębiny zwrócony wierzchołkiem w kierunku zębodołu. Taką budowę korony znaleziono również u gatunków współczesnych. Opisany stożek zębiny jest pozostałością po dużej strukturze zębinowej łączącej koronę z korzeniem w najwcześniejszych stadiach wzrostu zęba. Istnienie stożkowatej struktury wewnątrz zębów policzkowych znaleziono u różnych gatunków ssaków kopytnych. Wobec znalezionego podobieństwa mechaniki rozwoju górnych zębów policzkowych *Lagomorpha* i *Ungulata* próbowano sprawdzić, czy istnieje ono również pomiędzy prymitywnymi

kopytnymi z grupy *Protungulatum*. Szczegółowe zbadanie zębów policzkowych u *Protungulatum donnae* VAN VALEN et SLOAN wykazało brak istnienia omawianej struktury u tego gatunku. Jest to więc jeszcze jeden argument przemawiający przeciwko hipotezie o bliskim pokrewieństwie prymitywnych *Lagomorpha* i prymitywnych *Ungulata*, wysuwanej przez niektórych autorów.

РЕЗЮМЕ

Автор даёт подробное морфологическое описание и анализ ранних стадий развития постоянных зубов ископаемого представителя зайцеватых *Hypolagus brachygnathus* KORMOS, найденного в отложениях верхнего плиоцена в местности Рэмбелицэ Крулевске, близ Клобуцка (Польша) и Кадзельни в Киельцах (Польша). На основании анализа нескольких десятков экземпляров этих зубов, на которых хорошо сохранилась не стёртая бугорчатая структура корон, и на основании сравнения их с современным материалом *(Lepus americanus* ERXLEBEN, *Sylvilagus floridanus mearnsi* ALLEN*)* признано, что совершенно точную гомологию бугорков можно установить только для трёх: центрального и двух боковых. Не вдаваясь в вопрос правильности различных взглядов многих авторов по поводу названия гомологических бугорков, автор обратил особое внимание на центральный бугорок (№ I). У различных ископаемых видов *Lagomorpha* находится по соседству с ним, либо покоится непосредственно на нём, так наз. „crescent". У его основания, (после того, как был сделан препарат короны зуба), найден конус дентина, повёрнутный в направлении зубных ячеек. Такое же строение корон найдено также у современных видов. Описанный конус дентина является остатком мощной зубной структуры, соединяющей корону с корнем в ранних стадиях роста зуба. Существование конусообразной структуры внутри боковых зубов найдено у различных видов копытных млекопитающих. Ввиду обнаруженного сходства механизма развития верхних боковых зубов *Lagomorpha* и *Ungulata* автор решил проверить, существует ли сходство также между примитивными *Ungulata* из группы *Protungulatum*. Подробное исследование боковых зубов у вида *Protungulatum donnae* VAN VALEN et SLOAN показало отсутствие обсуждаемой выше структуры у этого вида. Таким образом существует ещё один аргумент против гипотезы о близком родстве примитивных *Lagomorpha* и примитивных *Ungulata*, выдвигаемой некоторыми авторами.

Plate VIII

1. Young permanent P^2 of *Hypolagus brachygnathus* — trituration surface.
2. Young permanent P^4 of *Hypolagus brachygnathus*. I — central cusp; II — anterolateral cusp; III — posterolateral cusp; IV — oblong eminence of the enamel; V — antero-medial cusp; VI — postero-medial cusp.
3. The generalized shape of the young permanent P_4, M_1 and M_2 of *Hypolagus brachygnathus*.

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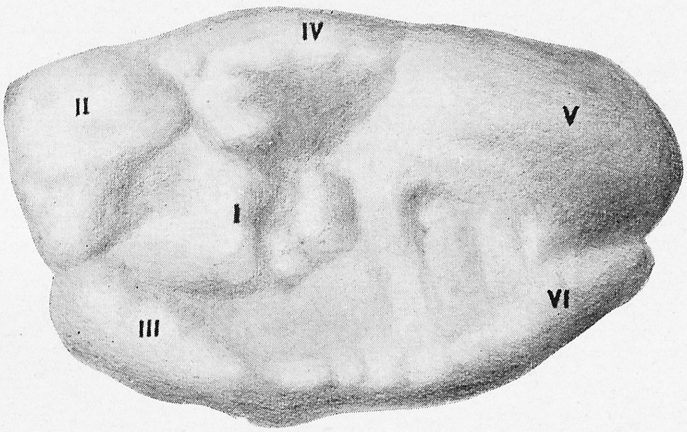

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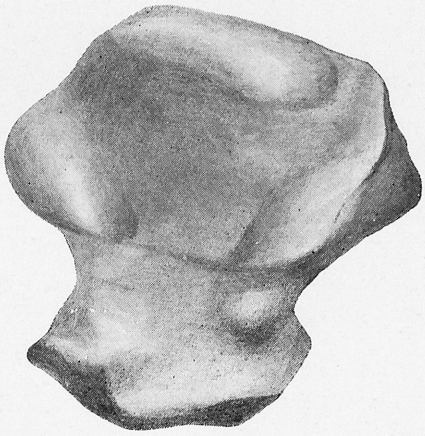

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L. Sych

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