Anatomy. — *The Development of the dental system in Trichosurus vulpecula.* By L. BOLK.

(Communicated at the meeting of December 22, 1928).

By courtesy of Dr. HILL from London I obtained a series of marsupial young from Trichosurus vulpecula in various periods of development. This material is very suitable to the study of the development of teeth, since the various stages followed each other closely. This circumstance may be necessary for every research into the development of teeth, it is specially so with marsupials, since phenomena of high importance do change here very rapidly, therefore are only observable during a limited phase of the development. In the literature on the dental system of marsupials statements of great importance are sometimes found, based on insufficient material.

An extensive report on the results of this research will be published elsewhere, in this communication only a few remarkable phenomena in the development of teeth in Trichosurus vulpecula will be set forth, and a brief discussion of the justifiable results will be given.

A summary of the odontological points of view from which I look on the development of teeth in marsupials and of the questions I tried to solve in this research will now be given in order to insure a clear understanding. For in regard to those points I differ from current opinions. As a starting point I mention the fact that the marsupials differ from monodelphous mammals by the absence of a tooth-change : they are monophyodont as contrasted with the diophyodontism of the latter group. This monophyodontism is not absolute ; as a rule a single tooth is changed. This peculiarity in the teeth of marsupials did arise the question which of the two sets of teeth of the monodelphians is homologous with the marsupialian set : the deciduous or the permanent teeth.

Concerning this question the opinion of the authors varies widely, a group regarding the marsupialian teeth as homologous with the deciduous set of the monodelphians, another group to the permanent set of teeth. After both opinions one of the sets should have been lost by a process of reduction ; the monophyodontism should have arisen out of diphyodontism by the loss of one set of teeth. (It must be stated that LECHE regards the diphyodontism of monodelphians as a property acquired by this group.)

It is evident that the opinion regarding monophyodontism as a phenomenon of reduction is the logical application of the hypothesis explaining the diphyodontism in mammals by a gradual decline in the numerous dentitions in lower vertebrates. Therefore, di- and polyphyodontism should be phenomena differing only gradually, and monophyodontism should be the result of a progression of this process.

In former publications [1]) I have opposed myself against this general opinion, since I am convinced by my researches that the changing of teeth in mammals differs qualitatively from that in lower vertebrates — specially in the reptiles — as will become apparent from the following summary.

In mammals the dental lamina gives rise to two rows of dental germs, an outer row or exostichos, an inner row or endostichos, the former developing into the deciduous set of teeth, the latter into the permanent. When the teeth change, the exostichal teeth, which are formed earlier and develop quicker, are pushed out by the endostichal. The tooth changing in monodelphians therefore bears the character of a consecutive appearance of two rows of teeth, and it is clear that in those animals only once a change can take place. The dental system in this group might be characterized by the term "substitutive-dentition".

In reptiles the process of changing has a quite different character. Here also the teeth originate from two rows, but in contrary to the monodelphians the elements of both rows develop simultaneously. During further development each tooth from the inner row moves to an interdental space between two teeth from the exostichos and participates in the composition of the actual functioning set. As contrasted with the dental system of mammalians, that of reptiles can be designated as "intercalated dentition". Whereas the functioning set of teeth in monodelphians is composed either of endostichal or of exostichal teeth only, the dental system of reptiles consists of alternating exo- and endostichal elements.

It is irrelevant that this regularity can be disturbed in the course of life. The phenomenon of intercalation is in itself sufficient proof that the process of changing in reptiles is absolutely different from that in monodelphians. In order to understand the changing process in lower vertebrata it must be born in mind that the teeth in the dental lamina originate from a matrix. In mammals the generating power of the matrix is exhausted after the production of a single tooth ; on the other hand, in lower vertebrata the matrix keeps on forming teeth in intervals. Each matrix in those animals produces, what I have called a family of teeth. The changing process in polyphyodontal vertebrata consists in the periodical elimination of the functioning member of the family by the following younger member. Therefore the changing of teeth can go on unlimited during the life of those animals, in the same way as scales and hairs.

Summarizing : the process of the changing of teeth in mammals is an elimination of the exostichal row and a substitution of this row by the endostichal teeth, in reptiles it consists in an expulsion of the oldest member of a family by the next one. Diphyodontism therefore is not a reduced polyphyodontism ; both processes are fundamentally different.

[1]) Odontological Essays. V. On the Relation between reptilian and mammalian dentition. Journ. of Anat. Vol. 57. 1922.

If this be understood the problem of monophyodontism of marsupials obtains a different aspect since several new possibilities arise. One can suppose that the recent marsupials originate from diphyodontal mammalian ancestors, with a milk- and a permanent dentition, one of these rows, exostichos (milkdentition) or endostichos (permanent dentition), being reduced. Reasoning from this hypothesis the question with which of these rows the dental system of recent marsupials is homologous, is justified. But this hypothesis is not very probable. One is inclined to expect that such a primitive group of mammals as the marsupials are, should show the first and still incomplete indication of the new mechanism of teeth changing acquired by mammals, instead of phenomena indicating a complete mechanism markedly reduced. The well-known change of a single tooth in marsupials can be regarded as an indication of the beginning of such a diphyodontism.

The primitive nature of marsupials gives rise to another question, i.e. whether the changing of teeth does not occur because the structure of the dental system is still like that in reptiles, composed of teeth of the endostichal and exostichal row, or using the monodelphian terminology : of deciduous and permanent teeth. If this be true, this primitive group of mammals should possess matrices forming a single tooth, just as in higher mammals, and on the other side they should have the phenomenon of intercalation in common with the reptiles.

In this way the marsupials should represent also in their dental system a link between the reptilian-like ancestors of the mammals and the highly developed class of monodelphians.

A formerly executed research into the dental system of Perameles had made it clear to me that the dental germs are ranged on the dental lamina in two rows, an endostichal and exostichal one, identical with the deciduous and permanent set of monodelphians ; that in both rows several germs reduce ; and that the functioning dentition is formed by the completely developed germs of both rows. The dental system of this marsupial is an intercalation system. By this structure a changing of teeth in this animal is wholly excluded, the matrices forming a single tooth only. In Fig 1 a diagram

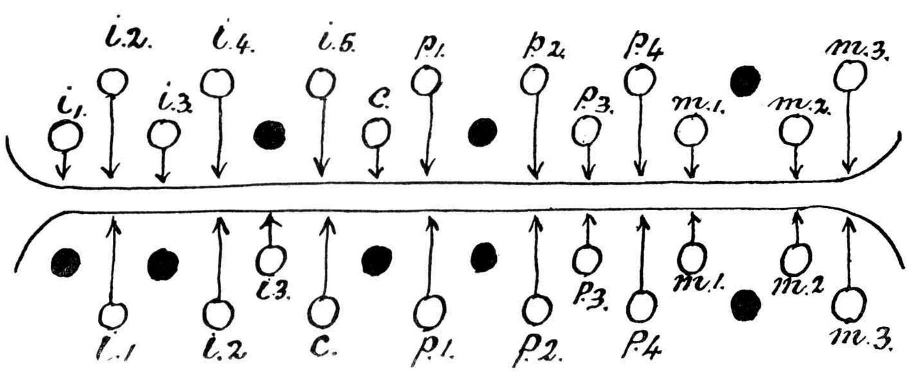

Fig. 1.

is given showing the origin of teeth in this animal in relation to both rows. The black dots indicate germs that do not develop. This figure needs no further explanation ; particulars are found in my paper on this question [1]).

In my research on the ontogenesis of the dental system of Trichosurus special attention was given to this point, but I have not found any indication of intercalation in this very markedly reduced dental system. The explanation is very simple ; the dental lamina is build so irregularly, whereas the dental germs appear in such an irregular manner and such different intervals, that it is impossible to recognize an arrangement in two rows. However, during the development conditions may arise that seem to prove a distichal distribution of the tooth germs and an intercalation of the elements of these two rows, as may be proved by Figure 2. This figure represents a reconstruction of the dental germs in the upper jaw of a pouch young of Trichosurus, measuring in total 58 mm. There exists no regular succession in posterior direction in the enamel organs as is the case with embryos of monodelphians. Four of the germs might be regarded as forming an outer row, and three as forming an inner row. I do not want to exclude the possibility that the arrangement of the dental organs in figure 2 is really caused by a distichal origin of the dental system, and that therefore in Trichosurus also this system is composed of "deciduous" and "permanent" teeth, but I cannot consider this case as conclusive proof, since the arrangement of the dental germs might be caused in other ways. It is evident that the marked reduction of the number of teeth of Trichosurus renders this specimen unsuitable for an inquiry into the phenomenon of intercalation.

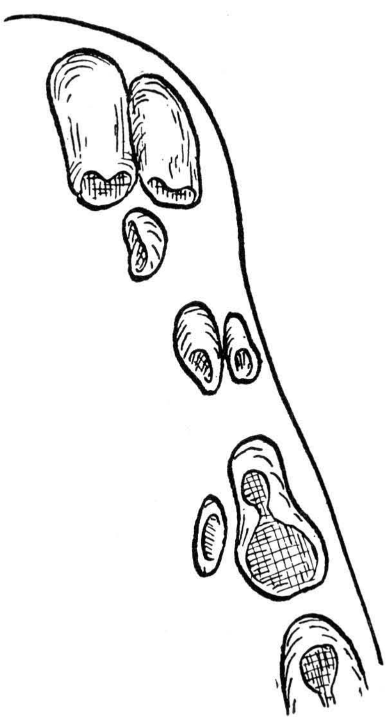

Fig. 2.

In regard to another question I obtained a more positive result. The ontogenesis of the dental system of Trichosurus does not procure any indication in favour of the hypothesis that ancestors of this animal should have been diphyodontal in the sense of the monodelphians. If one assumes the occurrence of a regular diphyodontismus in the ancestors of marsupials, it is possible to interprate certain abortive germs as belonging to the first, others to the second dentition. But this point of view is purely aprioristic. An objective research into the correctness of this hypothesis fails to yield

[1]) Die Beziehungen zwischen Reptilien- Beutler- und Plazentaliergebisz. Zeitschr. f. Morphologie und Anthropologie. Bnd. **20**. 1917.

proof in favour of it. The changing of the so-called fourth praemolar of the marsupials is the indication of a beginning diphyodontism.

In regard to structure and morphological significance of the dental system of Trichosurus, my research of its development did not yield the results I expected, the intercalation of both rows, so evident in Perameles, not being observable in Trichosurus, by cause of the considerable reduction of the number of teeth.

On the other hand, in regard to another fundamental odontological problem, viz. the morphological structure of the tooth, this development yields very important data. In order to make their significance clear I must summarise shortly the quintessence of my theory on the dimery of the mammalian tooth. After this theory each mammalian tooth corresponds with two consecutive members of a tooth-family of the reptiles.

The matrices in the dental lamina of these vertebrates, produce — as pointed out already — teeth during the entire life, two products are separated by a longer or shorter period of rest, each tooth therefore is anatomically independent. In mammals this process has been changed in two senses. In the first place the function of the matrix is limited to the production of a single tooth, but also — and this is the second change — this process includes the formation of two tooth-germs. The activity of the matrix therefore is not only very much decreased, also concentration has taken place ; the period of rest between two activities is eliminated, and the product therefore is a double-tooth ; the relief of the crown still showing the limit between the two components. For the buccal row of tubercles represents the older generation — the protomer —, the lingual the younger — the deuteromer. The polyphyodontism of reptiles finds therefore still its expression in the relief of the crown of mammalian teeth. Such a tooth represents two generations of a tooth-family of reptiles.

Now, in the ontogenesis of mammalian teeth two phenomena occur that are connected with the origin of teeth as set forth here, i.e. the double connection of the enamel organ with the dental lamina and the originating of the pulpa on two centers of the organ : one in the buccal and one in the lingual half. Temporarely those centra of pulpa formation are separated by a layer of indifferent cells : the enamel septum. Those phenomena can be observed very clearly in the course of development of teeth of Trichosurus, but I do not enter further into this question since I am unable to communicate anything new. On the other hand I have observed some peculiarities in the ontogenesis of those teeth that I have not seen in any other mammal and that yield new support to the correctness of the dimer theory of the mammalian tooth. The description of the following facts may make this clear.

The dental system of Trichosurus is markedly reduced, and certainly not a few teeth, present in its ancestors, are lost. This is sufficiently proved by the fact that during the development several dental germs originate that do not further develop. Some of those exist for a short period only and are quickly resorbed, others remain for a longer time. Fifteen developmental stages of the dental system have been investigated by me and a compilation of all dental germs observed in upper and lower jaw is given in Fig. 3.

Those that develop regularly have been striped ; all other germs disappear sooner or later even if dentine substance has been formed already. The

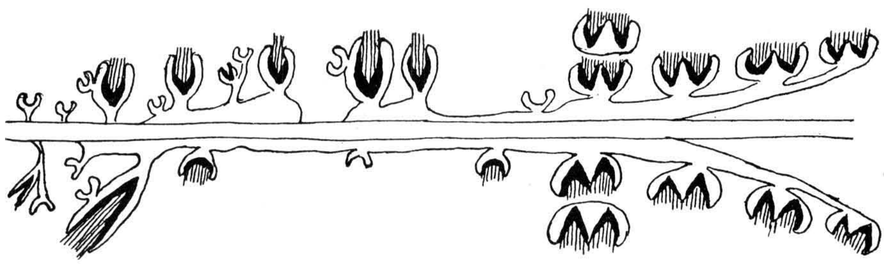

Fig. 3.

abortive germs ask our special attention. The diagram in which their topographical relations are given as accurately as possible, shows that they may arise : *a*, directly from the epithelium of the jaw ; *b*, from the dental lamina ; and *c*, from a dental germ that develops itself into a complete tooth. Those from the last group are the most important from an ontogenetic point of view. The occurrence of such a rudimental germ arising from another has been observed by me in the upper jaw in the germs of the medial incisors and canines, in the lower jaw in the germ of the incisor. They appear without exception in an early stage of development before the germ from which they arise has been invaginated. During my odontological researches this is the first time I found such conditions and their great rarity certainly is a sign of their uncommon significance. It is not difficult to understand their meaning if we consider the facts from the point of view of the dimer theory.

We must start from the fact that we meet here single tooth-germs showing tendency to develop two teeth, one of which develops regularly, the other being resorbed. It is clear that they do not represent a deciduous tooth and its substitute, for in mammals those two arise never from a single germ and simultaneously. The only acceptable explanation is that in those cases the dimer origin of the mammalian tooth is demonstrated, each germ corresponding with an odontomer, of which only one develops completely. The historical course of development of the mammalian tooth in those cases takes a more or less reversed direction : two independent tooth-germs which once merge into a single formation now are separated again. If both separated products should develop completely, two teeth should appear, placed side by side as a buccal and lingual one. But one of those germs atrophying very soon, a single tooth develops completely, which however is not a dimer element, not aequivalent to a mammalian tooth, because it is monomer like a reptilian tooth.

With this last conclusion the importance of the phenomenon described in favour of the theory of dimery is expressed. And the correctness of this conclusion is proved by the following facts.

Whereas the presence of the ontogenetic symptoms of dimery — enamel septum and double connection with dental lamina — could be ascertained in the development of all teeth of Trichosurus, they are absent in the three teeth with abortive adhaerent germ. This fact proves that it was correct to diagnose this germ as one of the odontomers, probably the deuteromer. The medial incisor and canine in the upper jaw as well as the incisor in the lower jaw are therefore monomer teeth. This peculiarity in the ontogenesis of the indicated teeth probably explains the following fact. The medial incisor of the upper jaw has a crown with a perfectly smooth lingual surface, whereas this surface in the second and third incisor shows a tubercle, oblong in shape and bordered by a deep groove that reaches the edge. Therefore in the latter teeth the dimery is witnessed by the relief of the crown, bearing a lingual and buccal tubercle, in the medial incisor on the contrary no such indication can be found.

In regard to the historical development of the mammalian tooth the investigation of Trichosurus has yielded more important data than in regard to the structure of the dental system ; they support the hypothesis of dimery.

During the development of the teeth of Trichosurus still another phenomenon occurs, that yields an argument for this theory in no less convincing manner. As Fig. 3 shows, a number of rudimentary germs appear, arising either directly from the epithelium of the mouth or from the dental lamina.

We will not enter here into a discussion upon all these germs, but the attention may been drawn to two of those germs, i.e. the most medial in the lower jaw and that between third and fourth incisor in the upper jaw. Those show an extremely peculiar development from which Fig. 4 offers a diagram.

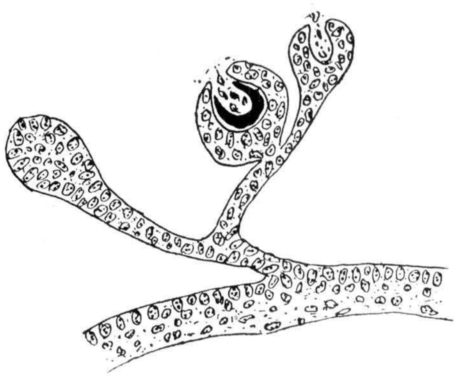

Fig. 4.

From the dental lamina, a string arises bearing a rudimental tooth germ, the papilla of which is covered by a thin layer of dentine. Probably this germ represents a tooth reduced relatively not long ago, an incisor functioning yet in a rather recent ancestor of Trichosurus. The peculiarity is that after forming the first rudimental germ the stem that connects the germ with the dental lamina proceeds and ends in a second tooth-germ. This germ also is invaginated but there is no dentine substance. An absolutely aequal development is shown by the most medial rudimental tooth germ in the lower jaw as is shown in Fig. 3. A situation as represented in Fig. 4 was never seen by me in any mammalian, but the conditions of development in reptilian teeth are immediately called to mind. The diagram might have been taken from a section through the embryonic dental lamina of a reptile, the dental matrix having produced the first member of the tooth-family and now starting to form the consecutive member.

This comparison with the manner in which the dental system of reptiles develops is made on purpose, since I am convinced that in Fig. 4 an aequivalent and not an analogous process is represented. For what is the case? We are concerned with reduced mammalian teeth of which the phylogenetic development is followed in reversed direction; the dimer organ, once formed by the concentration of two dental germs, is again divided into its components. Both germs from Fig. 4 therefore represent the odontomers of a normal tooth and in the first of the two even dentine has been formed. Fig. 4 therefore represents a historical stage in the development of the mammalian tooth; if both germs are conceived to be in anatomical connection we have a representation of the dental germ of a mammalian tooth.

The circumstance that it was possible to demonstrate the anatomical evidence of a double generating power in mammalian teeth in two reduced teeth of Trichosurus vulpecula, is of no little importance, since it excludes the possibility of accidental variation.