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longitude according to BROWN, which were also calculated, amounts, however, when we add to it the influence of the adopted corrections of perigee and eccentricity, to $+0''.67$, i. e. $1''.10$ less than the value I derived from the originally adopted formula. The previous investigation of Prof. BAKHUYZEN into the observations of the moon up to 1902 led him to believe that the co-efficient of $\sin g$, which is of special importance here (as we have $g = 278°$) would be in 1912 at least $-0''.6$ greater than its theoretical value, using also the adopted values for the corrections of perigee and eccentricity. From this remark a value of the longitude results, which is $+0''.6$ greater, so that the most probable correction of the longitude I employed would be $-0''.5$. Thus we should have $dl = -0''.5$ and $db = -0''.05$, hence $(d\varphi) = +7''$. In more than one respect, however, some uncertainty remains.

Anatomy. — *"On the structure of the Dental system of Reptiles."* By Prof. Dr. L. BOLK.

(Communicated in the meeting of January 27, 1912).

If we compare the dental system of mammals with that of reptiles two points of difference come especially to the front. One of them bears a more physiological character and regards the fact that with mammals, as a rule, the dental shelf gives off only two series of buds, one for the milk-set and another for the permanent set. With the majority of reptiles on the contrary a shedding of teeth takes place several times during their life-time, though among this group of vertebrates species are known to us, where the shedding of teeth does not take place at all, or is restricted to a special part of the dental system, as may likewise be the case with mammals. These however are exceptions and in general the dental system of mammals as diphyodont (in some cases monophyodont) is placed over against that of reptiles as polyphyodont. It is pretty well the current view that the diphyodontism of mammals must be derived from the polyphyodontism of the lower vertebrates, and it is supposed that the number of renewals of the dental system was gradually reduced from many to a few, whilst the duration of the existence of the teeth was lengthened. Only a few authors take a different stand-point, and are of opinion that the shedding of teeth of mammals should be a property obtained by that group of animals themselves, and the primitive mammals should consequently have been monophyodont (LECHE).

The second point of difference is of a more morphological nature. The dental system of mammals namely is, save a few exceptions, built of more complicated teeth. The crown shows two or more cusps. In the first case both cusps, the lingual and the buccal, can be well developed, and at first view the tooth is to be recognized as a bicuspidal one, or the lingual cusp is so much reduced that the tooth becomes apparently monocuspidal as with caninus and incisivi. By the variation in the number of the cusps the teeth of the dental system of mammals present a great diversity in the shape of the crowns, the set is anisodont, contrary to the more isodont set of reptiles, whose teeth are in general of a more equal and simple conical form.

There are different views of the way in which the anisodont dental system of mammals has developed out of an isodont primitive form.

Two theories on this subject have their supporters and their opponents. The so-called concrescense-theory teaches that the complicated mammal tooth developed itself by fusion of a number of cone-teeth of reptiles, each cusp of such a tooth should represent a primitive cone tooth. The differentiation-theory on the contrary teaches that every mammal-tooth, however complicated it may be, should be homologous with one single cone-shaped reptile-tooth, the crown of which lost its simple form and developed a more complicated relief.

Herewith the two chief points of difference between the dental system of reptiles and the dental system of mammals are indicated as briefly as possible. With the formation of the dental system of mammals from that of reptiles, a polyphyodont isodont dental system was transformed into a diphyodont anisodont one. Is there any relation between these two points of difference? In my opinion too little attention is paid in literature to this question. When animadverting on the formation of the complicated form of the tooth, the question whether there may be some relation between the fact that the tooth becomes complicated, and the diminution of the number of tooth-generations from several to two, is not referred to at all by the differentiation-theory, and hardly ever by the concrescence-theory. It is true that every now and then the supporters of the concrescence-theory express the view that the fusion of several cones to one whole must have diminished the number of tooth-generations. Röse has tried to give a scheme of this phenomenon. I suppose that this essay is to be regarded as incorrect, but I refrain from further criticism. I entirely chime in however with the principle of which this essay is the expression. For I hold that for the derivation of the mammal dental system from the reptilian dental system, one must try, as much as possible, to find a process of transformation, by which the two chief characteristics of the mammal dental system are derived from a single cause. I think I have succeeded in this attempt. I could however only come to the solution I have found of this problem, after I had come to the conviction, especially on account of researches about the development of the dental system of reptiles, that our conception of the structure of this system must be rather importantly modified. It is my intention to restrict myself in this communication to this fundamental point of my theory, in order to explain in a subsequent communication the relation existing, in my opinion, between diphyodontism and polyphyodontism, and how the relation between the diminution of the number of tooth-generations, and the complication of mammal-teeth must be understood.

The dental system of most of the now living reptiles consists of a sometimes great number of little teeth, placed in a single straight line in the upper- and underjaw. Besides these teeth we find with several species, especially with those having lived in former periods, other teeth in different skeleton parts of the roof of the mouth (Palatinum and Vomer), but as these have not been inherited by mammals, we can leave them out of discussion, and restrict ourselves to the rows of teeth united with the jaws.

I should like to indicate a dental-system, the teeth of which are placed in a single row as a monostichical one. And if we regard the grouping of the teeth in the skull of a reptile, this term might justly be applied to such a system. But if we carefully examine the development of the dental system of reptiles, we discover symptoms that seem to place that system in a somewhat different light, and that awake the supposition that the simplicity of the rows of teeth of reptiles is only a semblance, or to express it more correctly forms a secondary situation which renders the real character of this dental system irrecognizable. As it is, my researches with regard to the teeth of the vertebrates convinced me that this dental system is not a monostichical system, but what I wish to call a "distichical" one. Though the teeth stand in a single row, they must after all be regarded as belonging to two rows, the elements of which have secondarily been placed in one single row, because they have interposed themselves between each other. This fact has as yet not been recognized because teeth that in reality were not replacing-teeth, have been considered as such. If once the attention has been fixed on this primary distichism, the development of the dental system of reptiles teaches still more: namely that originally the dental system of reptiles was not a distichical one, but even a "tristichical" i. e.

that this dental system is to be deducted from a form in which the teeth stood in three parallel rows, an outer, a middle, and an inner one, consequently a circumstance as is known to us with anamniotes. Of these rows the outer one however has become rudimentary and is still found with several of the now living reptiles in the form of abortive teeth, which offer a much more primitive mode of development, never function, and are very soon removed or resorbed. Consequently only two rows remain, an outer one and an inner one, which I shall distinguish as the *"exostichos"* and the *"endostichos"* whilst I shall distinguish the just mentioned row that has become rudimentary as the *"parastichos"*. I shall now briefly demonstrate my views.

There exist about the development of the dental system of reptiles already several researches. For instance of ROSE (Crocodile, Chamaelaeon) LECHE (Iguana) HARRISON (Hatteria) LEVY (Anguis, Lacerta). In how far my views deviate from those of these authors will soon be apparent.

In my elucidation I shall proceed from the dental system of a Crocodillus porosus having sixteen teeth in the upper-jaw. I can directly corroborate for this form an observation of Röse that with this group of reptiles directly from the mouth-epithelium, consequently not from the dental shelf a number of rudimentary teeth is formed on the spot where the dental shelf is connected with the mouth-epithelium. LECHE found these teeth likewise with Iguana, and HARRISON with Hatteria, and myself observed them with Lygosoma. I differ in my view of the value of these teeth in so far, that they form for me a rudimentary row — the above-mentioned "parastichos", whilst RÖSE and LECHE conceive them as a rudimentary first generation of teeth. It must be well understood that to both authors the notion of rows of teeth is unknown. I shall not expiate further upon this difference of view.

When comparing the sixteen enamel buds in the teeth-shelf I was struck by the fact that they behaved differently with regard to that lamina. Some were placed at the buccal side of the peripheric half, whilst the tooth-papilla formed by the - mesenchym grows from aside in the enamel-organ. A second group of lamina buds was formed at the free border of the lamina and the tooth-papilla grows in the thickened rim of the shelf. Fig. 1 shows the diagram of a section of the dental lamina with the two types of dental-organs. Further I give in Fig. 2, as

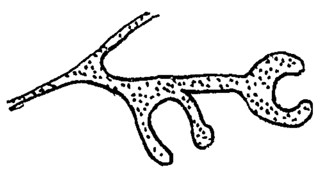
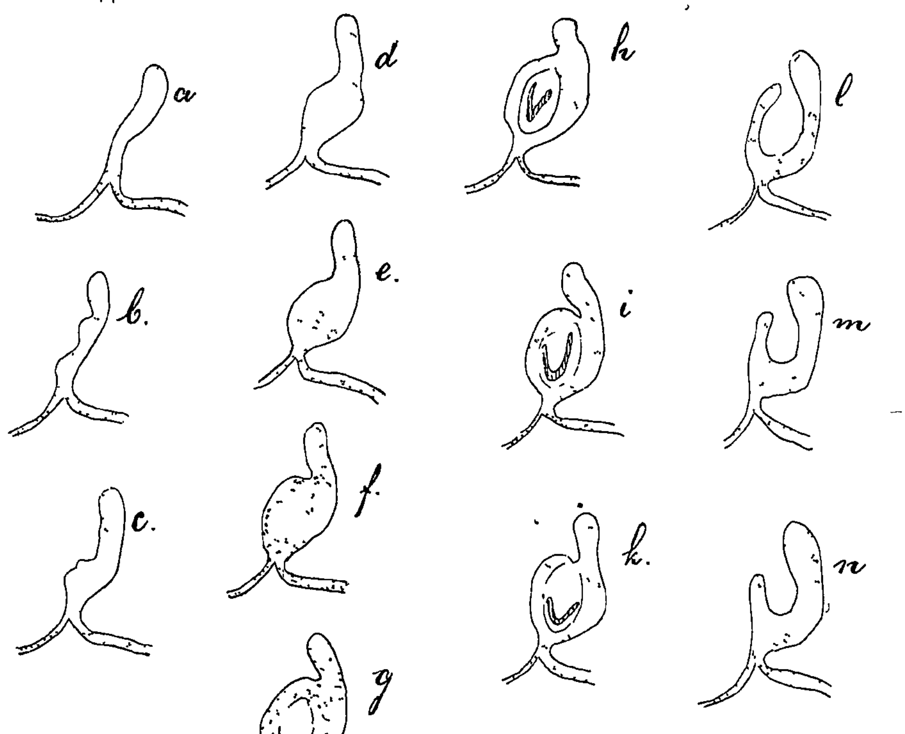


Fig. 1.



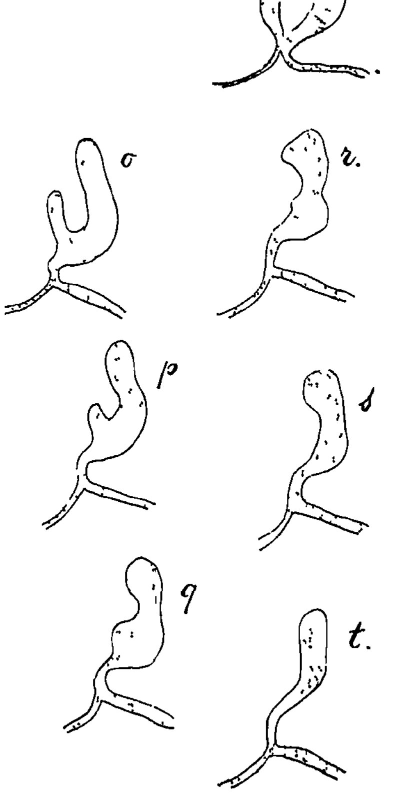


Fig. 2.

an elucidation, a series of sections of a dental organ developed from aside of Crocodilus porosus, and in Fig. 3 another of an organ originating in the border. In this series also an abortive tooth was found. If now we carefully observe the formation of all 16 teeth, it appears that there is an undisturbed regularity in the suces-sion of the two groups, for, without exception, they alternate. A lateral bud is succeeded by a terminal one, which is again succeeded by a lateral one and so on. Seen from the buccal plane a part of the teeth-shelf would have, with regard to the arrangement of the buds, an appearance as it is sketched in Fig. 4. This alternation of the dental organs with reptiles was already known in literature. In his extensive and exact description of the dental system of Hatteria

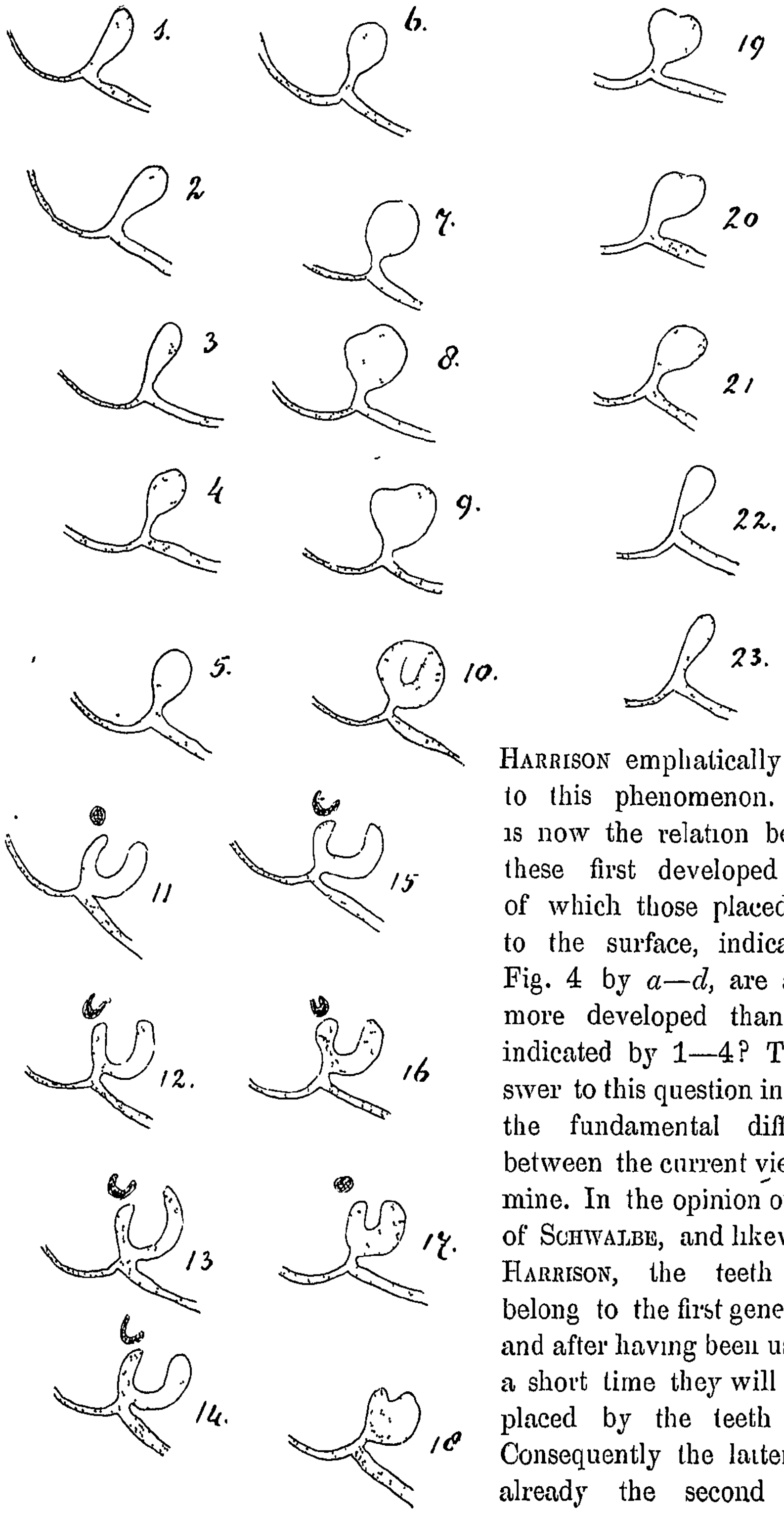


Fig. 3.

HARRISON emphatically points to this phenomenon. What is now the relation between these first developed teeth, of which those placed more to the surface, indicated in Fig. 4 by *a—d*, are a little more developed than those indicated by 1—4? The answer to this question indicates the fundamental difference between the current view and mine. In the opinion of ROSE, of SCHWALBE, and likewise of HARRISON, the teeth *a—d* belong to the first generation, and after having been used for a short time they will be displaced by the teeth 1—4. Consequently the latter form already the second teeth-generation.

In this process tooth *a* would be replaced by tooth 1, tooth *b* by tooth 2 and so successively. I shall immediately prove that this conception cannot be correct. The mutual relation between the eight teeth sketched in Fig. 4 is of a wholly different nature. We have to do here with two rows of four teeth, which are not to be regarded as first and second generations, for the teeth 1 to 4 will not displace the teeth *a*—*d*. In their further development every time a tooth of the row 1—4 penetrates between two teeth of the row *a*—*d*. Consequently instead of there being question of a first and a second generation, we have here two primary rows, the teeth *a*—*d* and the teeth 1—4 are entirely equivalent. In its first development the dental system of the Crocodillus is consequently distichic, the teeth *a*—*d* represent the first generation of the exostichos, the teeth 1—4 the first generation of the endostichos.

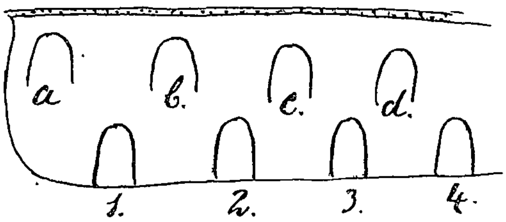


Fig. 4.

This structure-principle of the dental system of the Crocodillus can however not be observed in a more advanced stage of development, because the teeth of the two rows unite in a single line with the border of the jaws.

In order to confirm my view that in the first stage of development the dental system of reptiles consists of two rows of teeth running parallel and not of two generations, I refer in the first place to Fig. 5 in which a horizontal section through the upper jaws and the teeth in a young stage of development of Lacerta is represented. In the section both the premaxillary and the maxillary ones have been struck. We shall restrict ourselves to the origin of the maxillar teeth. Touching the maxillary bone we find three teeth, *a*, *b* and *c*. As the direction of the section is somewhat slanting, the teeth have been struck in a different level. These three teeth belong to the exostichos. Alternating with these there are three teeth, indicated by 1, 2, 3. According to the views of Röse and other authors these teeth, belonging to the inner row or endostichos, should form the second generation of the teeth *a*, *b*, and *c*, they should displace the latter. But from the figure it is, without more, clear that this view cannot be correct, that 1, 2, and 3 cannot become the substituting teeth of *a*, *b*, and *c*, but will, between the latter, grow together with the maxilla.

It is true, that here likewise the teeth *a*, *b*, and *c* are a little more developed than 1, 2, and 3, but the difference is so slight, that on this ground already it might be doubted if in reality there exist here two generations. Consequently Lacerta appears to have likewise a distichical dental system, and both the teeth *a*, *b*, and *c* and the group 1, 2, and 3 represent a first generation, the former of the exostichos, the latter of the endostichos. In Fig. 5 the origin of a second generation is perceptible indeed, though in a young stage of development. In the section of the dental lamina we see namely the origin of three teeths.

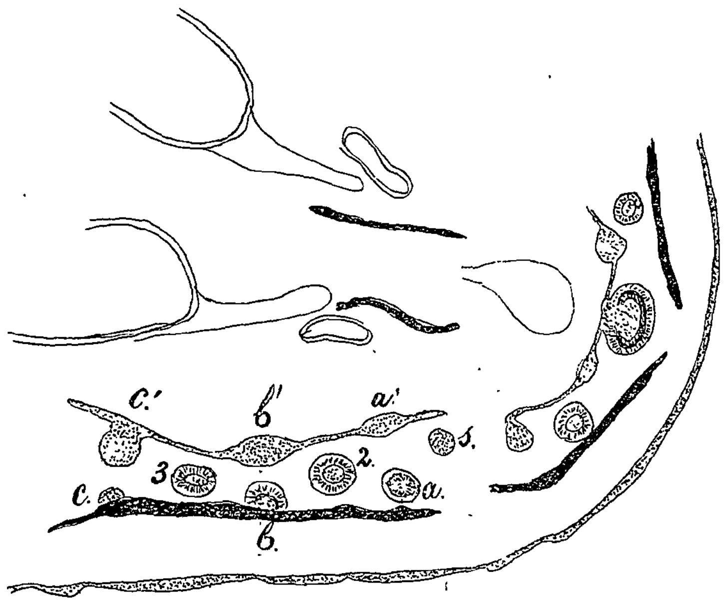


Fig. 5.

It is these teeth that at their further development, whilst moving towards the maxilla, will displace and substitute the teeth *a*, *b*, and *c*. These three teeth indicated as *a'*, *b'*, and *c'* form the second generation of the exostichos. In this preparation a second generation for the endostichos had not yet originated. In several reptile-embryos I found similar phenomena as in Lacerta. It is self-evident that for such like observations horizontal sections through the origin of the dental system are preferable. In Fig. 6 we find such a section through the premaxillar dental system of Lygosoma olivaceum.

The section is in a transversal direction somewhat slanting, so that on the right half of the figure the origin of more teeth is struck than on the left side. In the median line lies the unpaired tooth. The exostichos consists on both sides of two teeth *a b* and *c d*, and the endostichos of an equal number 1 2 and 3 4. It is likewise clear in this section that 1 2 3 and 4 are not the substituting teeth of a b c and d, not a second generation, but a first generation of an independent row. They will soon have shoved between the elements of

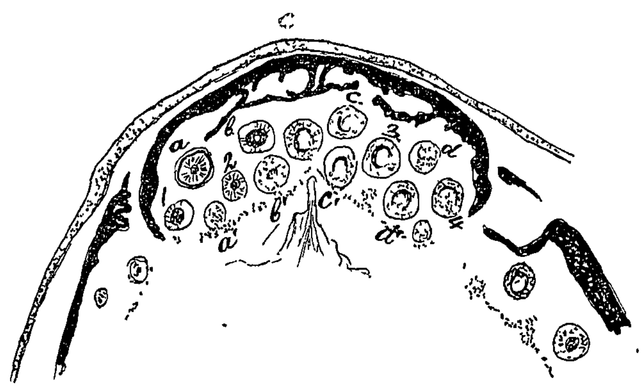


Fig 6

the exostichos. In this preparation the second generation both of the exostichos and of the endostichos had originated already. The teeth a' b' c' and d' form the second generation of the exostichos. Exactly as with Lacerta also with Lygosoma a tooth is not displaced by another lying askance before or behind it, consequently not by an alternating tooth, but by a tooth originating directly behind the tooth that must be substituted. In our subsequent communication we shall revert to this point, as, with regard to the shedding of the teeth of mammals, it is not devoid of interest. Of the endostichos the second generation has likewise originated; on account of the slanting direction of the section its elements are only visible in the right half of the figure. It is the two teeth which, still connected with the dental lamina, are situated to the right behind the teeth 3 and 4.

Consequently it is very evident that Lygosoma possesses a distichical

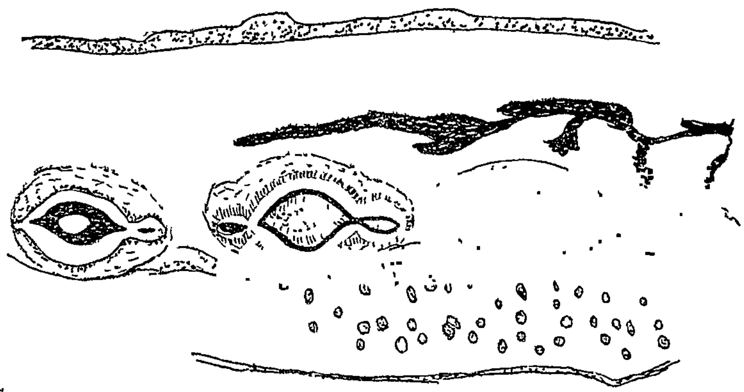


Fig. 7.

dental system. Whether this property of structure is still peculiar to the dental system of all reptiles, must be proved by subsequent investigations. Perhaps these will show that it is not the case. In my opinion e. g. it is doubtful whether the dental system of Calotes, of which I give a horizontal section in Fig. 7, is of a distichical nature.

I do not find an indication of it in the stage represented here. Neither was there any vestige of substituting teeth. It may certainly be imagined that, with some groups of reptiles, one of the two rows is checked in its origin and development, which would render the dental system monostichical. That this circumstance does not occasion a suppression of the shedding of the teeth requires no further argument.

We fixed already the attention to the fact that in its origin and development the exostichos is somewhat in advance of the endostichos. If this relation is not disturbed by later influences, the renewal of the teeth in the exostichos will also every time take place a little earlier than in the endostichos. A beautiful example of this fact is

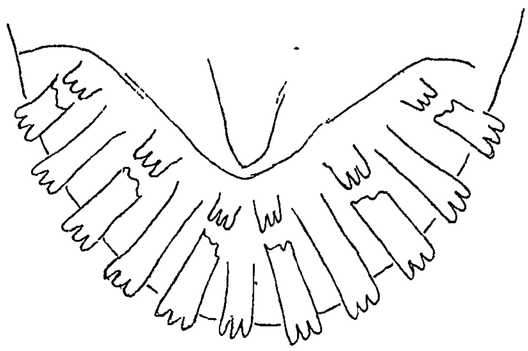


Fig. 8.

sketched in Fig. 8. It regards the premaxillary dental system, as I found it in a skull of Tupinambus nigropunctatus. The teeth of this part of the dental system are regularly provided at their rims with two notches. Besides the unpaired tooth standing in the median line, one finds on either side five premaxillary teeth. And now it is very interesting to see, that, regularly alternating, a still intact tooth and an already partly resorbed tooth with an underlying substituting tooth succeed each other. Here has evidently the chronological difference in origin and substitution of the elements of the two rows been preserved in such a degree that in this part of the full-grown dental system the composition from two rows can still be demonstrated.

This latter fact seems finally to be especially distinctly the case with Hatteria, as here according to HARRISON's [1]) representations and description the teeth differ in size, so that regularly a large and a little tooth alternately succeed each other. HARRISON's very accurate description of the development of the dental system removes every doubt that the two sorts of teeth belong to a different row. Yet this naturalist has neither been able to free himself from the notion of two generations, and consequently describes as a peculiarity of the dental system of Hatteria that, what he calls the teeth of the second generation do not seem to displace those of the first generation, but the latter give way and receive the elements of the second generation among them. The dental system consists consequently, as the author expresses himself, of two dentitions: "The teeth which are developed on the dental lamina during the incubation period and which function during the early life of the living animal, are almost certainly the members of two distinct dentitions, the later teeth instead of displacing the earlier coming to alternate with them". (l.c. p. 202). The distichous character of the dental system of Hatteria appears likewise from the further details in the development which HARRISON informs us of, but into which I do not enter here.

As I hope the given examples are indeed sufficient to show that our conception of the dental system of reptiles needs modification. It will be necessary to distinguish in it a functionary and a genetic structure. According to the former the dental system consists of a single row of teeth, but the history of the development teaches that this condition is not a primitive one, and that this simple row is in reality a compound one built of two primary series to which, with different species (Crocodillus, Iguana, Lygosoma, Hatteria) at the lateral side another rudimentary row is joined, the elements of which develop themselves in the same way as with amphibia. This new aspect on the one hand connects the dental system of reptiles more closely with that of the Anamnia, and forms, on the other hand, a point of issue for a modified conception of the relation between the dental system of reptiles and that of mammals.

With regard to the first part I remind of the fact that especially with the tailed amphibia "Polystichism" of the dental system is by no means rare. Now we can imagine that, with regard to the maxillar dental system, this Polystichism, through diminution of the rows, has become a Tristichism, respectively a Distichism. The way in which this diminution was accomplished is closely connected with

[1]) Quarterly. Journal of micr. sc. Vol XLIV.

the way in which, with reptiles, a dental lamina has been developed. As a rule it is represented, as if a fold of the epithelium had penetrated into the jawmesenchym. I do not think that this view is entirely correct, but I suppose that the dental lamina has been developed because both in the upper-jaw and in the lower-jaw in mediolateral direction, a fold of the mucous membrane has overgrown the area in which the teeth were developing. This area was, as it were, operculated. In order to prove this view I could add several observations, but I restrict myself to simply mentioning it in order to revert to this point at length elsewhere. We only call the attention to the fact, that by this conception of the origin of the dental-lamina it is clear, why teeth never originate from the medial surface of this lamina. By this operculation the formation of enamel-organs became possible. Now I imagine that with reptiles two primary rows of teeth came to development in this operculated area whilst a third outside row was not overgrown and remained at the surface. The elements of this series — indicated above as "parastichos" — preserved the primitive character of their origin and developed themselves like the teeth of amphibia. These simple teeth however gradually lost their function on account of the greater strength of the elements of the two operculated rows. This short indication of the relation between the dental system of reptiles and that of lower vertebrates, may suffice here. I intend to develop my views about the relation between that of mammals in a next communication. Only for completeness' sake be communicated here as the essential part of my views that, in my opinion, mammals have inherited the distichism of the dental system of reptiles, and that this distichism comes to the front here in a much more distinct form namely as the lactal teeth and the permanent teeth. In my opinion the lactal dentition represents the exostichos of reptiles, the permanent dentition the endostichos whilst the so-called prelactal dentition must be derived from the parastychos. Consequently there would not exist the least relation between the diphyodontism of mammals and the polyphyodontism of reptiles.