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"On the Nature and Limits of Reptilian Character in Mammalian Teeth."

By H. G. SEELEY, F.R.S., Professor of Geography in King's College, London. Received April 4, 1888.

Approximations between reptiles and mammals have been recognised in many parts of the skeleton.* They are most marked between certain genera and orders of the two classes. The oldest known fossil representatives of both groups certainly approximate closer towards each other in all known parts of skeletons than do the orders which survive; so it may be a legitimate induction that, in an earlier period of geological time, the characters of both groups were so blended, that there existed neither the modern reptile, which has specialised by losing mammalian attributes, nor the modern mammal, which has specialised by losing the skeletal characters which have come to be regarded as reptilian. The most ancient mammals exhibit, in the known parts of their skeletons, resemblances to Monotremes, Edentates, Insectivores, and apparently Carnivores; and it is among these orders that the closest correspondence is found, bone for bone, with reptiles. Therefore, if an attempt were made to predict on an inductive basis, the kind of dentition which the earliest mammals which existed would show, it might be expected to be in harmony with the mammalian and reptilian characters of their skeletons. On the same basis it might be suspected that existing mammals, with

* "Resemblances between the Bones of typical living Reptiles and the Bones of other Animals;" "Similitudes of the Bones, &c.," 'Journal of the Linnean Society, Zoology,' vol. 12, 1874, pp. 155, 296.

reptilian elements in the skeleton, would still preserve teeth which might be compared with teeth of reptiles; and as a matter of observation it is found that there are several features in which teeth of reptiles and mammals resemble each other morphologically.

The idea conveyed by the expression "mammalian tooth" is necessarily that specialisation of tooth structure which is limited to the mammalian class. It may be unknown in the dental conditions of entire families and orders of mammals. And there is an absence of pronounced character in the incisor or canine teeth of any mammal order which would distinguish them as mammalian.

Similarly the idea implied in the term "reptilian tooth" is the specialisation of teeth in the reptilian class, which is as far from being universal in the class, as mammalian teeth are universal among mammals. Indeed, the lower mammals emphatically approach towards reptiles in all essential characters of tooth form.

Because the diversities in the teeth of the two classes have been emphasised for purposes of classification, the significance of the resemblances has been less considered.

There are six typical characters of teeth which are regarded as mammalian. They are:—

(1.) The presence of more than one root to a tooth;
(2.) The implantation of teeth by distinct sockets;
(3.) The existence of different kinds of teeth in the same jaw;
(4.) The development of distinct cusps to the teeth;
(5.) The wear of the crown with use;
(6.) Replacement by a successional series;

No one of these characters can be relied on as constant in the class and its loss is in every case an approach towards a reptilian type.

First, the root is not the original or essential part of the tooth. While the sucessional teeth are within the jaw they commonly have the roots undeveloped, and thus up to a certain stage of growth are without this evidence of class character. There is never more than one root to an incisor or canine tooth in any mammal; and never more than one root to any tooth (so far as I can ascertain) in an existing Edentate or Cetacean. Hence if all mammals are supposed to have had a common origin, it is legitimate to conclude that all the teeth originally possessed but one root; and that there is a certain relation subsequently established between the complexity of the crown and the number of the roots.

The situation of a root would imply that its development is due to the same law of growth under intermittent pressure or strain as determines the form or elongation of any other bone.* If more than one root is present they are commonly beneath the several parts of a tooth which have to resist intermittent strain or pressure. If the pressure

* "The Mechanism of Growth," 'Ann. Mag. Nat. Hist.,' April, 1872.

is great and the wear considerable the crown of the tooth grows in length, while the roots are relatively small; but if the intermittent strain on the tooth is great then the crown is relatively short and the roots long. The latter condition is well seen in the molars of Carnivora; the former in the molars of rodents and ungulates. The small roots of ungulates and rodents illustrate a mode of development of roots: for I have seen teeth of an aged fossil horse from the gravel in which the crown was completely worn down, and then the roots appeared to be relatively almost as well developed as in *Rhinoceros*.* Perhaps no order is more instructive in regard to the classificational value of roots of teeth than the Sirenia, because *Manatus* has tuberculate teeth and well-developed roots to the molars, while *Halichore* has but one strong root to these teeth, indistinguishable from the crown, with a hollow conical base, such as is often seen in Reptiles. From these considerations I infer that the type of tooth—at least as regards complexity—is to be correlated with the influences exercised by food, and is not a distinctive inheritance.

Secondly, the implantation of teeth in bony sockets is a mammalian character which is not less well marked in the Crocodilia and some extinct orders of Reptiles. The implantation in mammals with single roots to the molars differs in no way from the conditions which I have observed in Theriodont Reptilia. There are some exceptions among mammals to the location of teeth in sockets, since in certain Cetacea the teeth are in a groove at the posterior end of the series. And the Ornithorhynchus may be regarded as another exception, since it has three teeth on each side closely united together into one long ovate mass which is contained in a groove. The teeth are closer together than those of *Ichthyosaurus*, and there is no more definition of the groove into separate sockets than in that genus; but there is nothing else in common, since the base of the dental plate of *Ornithorhynchus* can scarcely be said to have roots. Frederick Cuvier described these teeth as horny,† and many writers have been disposed to regard them as horny plates rather than true teeth. Sir R. Owen quotes a French analysis of the tooth substance as yielding 99·5 horny matter and 0·3 calcareous matter.‡ This may be true of the long anterior horny plates on the jaws, but it can hardly apply to the posterior teeth which are in a socket-groove. If the dental plate is extracted from the jaw and examined against transmitted light, each of the three teeth which form it will be seen to consist of a large opaque subquadrate central portion, and an external translucent border of a horny appearance. I regard the latter as representing the uncalcified enamel of the tooth, while the central portion corresponds to the

* The specimen was obtained by the Rev. N. Brady from near Cambridge.

† 'Des Dents des Mammifères,' 1825, p. 203.

‡ 'Odontography,' p. 311.

remainder of the tooth. I have had an opportunity, by the kindness of Dr. Garson, of examining the microscopic sections of these teeth prepared by the late Professor Quekett, and preserved in the Museum of the Royal College of Surgeons, and they confirm my previous impression that the central portion of the tooth is bony (at least in some specimens), and in microscopic structure it shows large haversian canals surrounded by spaces and canaliculi. I therefore regard these teeth of *Ornithorhynchus* as true teeth. But they seem to me to be teeth in course of degeneration, and in process of losing their calcareous matter. They have already lost their root or roots, and have partially lost their individuality. The long anterior dental ridges appear to have carried this change one step further and have become dental layers formed of vertical parallel plates of horn in which there is no division into separate teeth, which are not imbedded in the jaw, but are a horny superficial substance. It is not without interest to remark that some other animals which have lost their teeth, like birds, and presumably Chelonians, which use the jaws for biting, also have them sheathed in horn; for the condition in *Ornithorhynchus* suggests that the horny substance may represent the lost substance of teeth.

Thirdly, mammalian teeth are commonly distinguishable into different kinds, which when fully developed vary in the forms of their crowns, and are thus recognised as incisors, canines, premolars, and molars. This differentiation is almost entirely absent from the dentition of Cetacea and Edentata; and it is well known that in different orders, canine teeth, or incisor teeth, or both, may be absent. These conditions can be frequently correlated with food. But just as the grouping of the teeth in mammals may approach in simplicity the condition in reptiles, so the teeth of some reptiles in different parts of the jaws may parallel the divisions found in the jaws of mammals which show considerable differentiation.

The fourth mammalian character is the cuspidate condition of the crown of the tooth. This results from a folding of the substance out of which the tooth is formed, and among the molar teeth of many mammals shows a specialisation which is unparalleled among reptiles. But on the other hand the complexity of some hinder-molars becomes simplified in the premolar region, and among Edentates and Cetaceans the tooth crowns are simpler than among some reptiles. In several orders of mammals it is obvious that the direction in which the folds of tooth substance are disposed is at right angles to the direction of movement of the lower jaw; and therefore it may be a fair inference that the transverse widening of molar teeth, no less than their diverse cuspidate character, is to be attributed to the increased work which food has given them to do in the molar region; and that development or suppression of a cusp in allied genera of mammals depends upon this

cause. With simplicity of function there is simplicity of detail in the crown of the tooth. Some of the simplest teeth are found among the Edentata, where the tooth is often sub-cylindrical, but as the crown is worn down, its original form is not seen. *Tatusia*, however, is an Edentate with successional teeth, and while the crown is still within the jaw it has a form which is as reptilian in aspect as the molar tooth of a *Teius*. The crown of the tooth of a Cachalot is a short curved cone. Hence it is manifest that the molar teeth of mammals are not necessarily cuspidate, and that in simplicity of crown there may be no character to distinguish a mammal from a reptile. From which it is probable that some primitive fossil mammals may also have a reptilian type of dentition. The recent discovery of a set of teeth in the jaws of *Ornithorhynchus*, hitherto unknown, raises the question whether those teeth are mammalian. Mr. Poulton has only contributed a vertical transverse section of one of these teeth,* which shows elevated external and internal cusps. I have no other knowledge of those teeth, but the condition figured is suggestively similar to a corresponding section of a molar tooth of the lizard genus *Teius*.† Professor Mivart quotes‡ from Mr. Poulton a passage, which I do not find in that gentleman's paper, describing the tooth, and from that description it would appear to correspond generally with the tooth of the adult *Ornithorhynchus*. I have already considered some characters of those teeth, and allowing for their degeneration, they seem to me to approach as close perhaps to the form of crown in lizards like *Teius* as to any of the larger bats.

Fifthly, mammalian teeth are often remarkable for the wear of the crown. This attrition appears to depend upon the form of the crown, the apposition of crowns, the development of enamel, and the nature of food. It is exceptionally well seen among Elephants, Ungulates, and Edentates; but almost all mammalian teeth show some change of aspect with wear. This condition is much less general among reptiles; but in the extinct Ornithischia the serrated crowns of the teeth are as well worn as in any mammal. The long teeth of *Hyperodapedon*§ appear to be well worn down to the palate. Exceptionally teeth of *Ichthyosaurus* and *Polyptychodon* show both vertical wear and lateral wear, and there are specimens in the Woodwardian Museum from the Cambridge Greensand in which teeth of these genera have the crown worn away transversely almost down to the root; so that neither wear nor its absence has any importance as a class character,

* 'Roy. Soc. Proc.,' vol. 43, p. 355.

† Sir R. Owen compares the teeth of *Ornithorhynchus* to those of the reptilian fossil *Placodus* ('Geol. Soc. Quart. Journ.,' vol. 36, p. 423), but the details of structure of the crown are not the same.

‡ 'Roy. Soc. Proc.,' vol. 43, p. 373.

§ Lydekker, 'India Geol. Surv. Mem.,' ser. iv, vol. 1, part 5, pl. 2.

but this condition of teeth varies in every order with the habitual food.

Finally, the succession of the teeth has been regarded as a mammalian class character. It is exceptional, and an individual peculiarity, for more than two sets of teeth to be cut in a mammal, though evidence has been brought forward that this reptilian condition is occasionally present in man. But even in those mammals which cut a second set of teeth there are commonly some molars which have no predecessors, and are a single series throughout life. So far as is known, most Edentata and Cetacea have but one set of teeth, which is never renewed; and according to Professor Flower, *Tatusia* is the only Edentate in which successional teeth are known to be developed. I have seen no evidence of a successional tooth in any Dicynodont reptile. Sir R. Owen has found no evidence that the Theriodontia possessed "a milk series of teeth."* When a successional tooth is present in mammals it usually originates below the tooth in wear, or behind it as in the elephant. This condition is seen in some reptiles as in the Ornithischia. But the typical condition of reptilian succession is for the germ of the new tooth to be on the inner side of the tooth in wear. This is the condition in Ichthyosaurs and most of the extinct Reptilia, and is often though not invariably seen in Crocodiles. It is, therefore, interesting that Mr. Poulton describes the new-found teeth in *Ornithorhynchus* as possibly on the inner side of the so-called horny plates, though in the lower jaw they are certainly below those plates. Hence, if those germs are successional teeth their relative position would not be inconsistent with reptilian or mammalian type.

From this discussion I conclude that in all morphological relations the teeth of mammals may be so simplified as to approach closely to conditions which would be regarded as typically reptilian.

I have next to show that the prevalent conception of the reptilian type of tooth is equally indefinite. The differentiation is less striking than among mammals, but in almost all morphological characters reptiles suggestively approach mammals, though these characters seem to me most remarkable in the grouping of the teeth into analogues of molars, premolars, canines and incisors, and in the characters of the crown in molar and other teeth. It is rather among the oldest extinct Reptilia that we should expect to find the nearest approach to mammalian dentition, and so it is; but evidences of a similar differentiation may be detected among Crocodiles and Lizards.

The form of the crown varies very little from front to back among Crocodiles, though some teeth are relatively large, and the smaller posterior teeth are a little compressed transversely; but when the teeth are drawn from the jaw the alveoli show modifications which

* 'Geol. Soc. Quart. Journ.,' vol. 37, p. 261.

might be regarded as mammalian. This character has been figured from the lower jaw, and in 1878 it was remarked* "among Crocodiles, I recognise in the well-known wavy outline of the jaws a demarcation of teeth into regions which have a fair right to be named incisors, canines, premolars, and molars, and constitute a dentition as Theriodont in principle, but not so specialised, as is seen in the South African fossil group. In the Crocodile the regions are easily recognised by the form, size, and characters of the tooth sockets when all the teeth are drawn, especially in the lower jaw. The incisors occupy a flat or slightly concave region below the premaxillary bone. Then at the head of the crest is the large canine placed between the premaxillary and maxillary bones. Next succeeds a portion of jaw with concave outline occupied by small teeth, which sometimes become larger from before backward; these are the premolars. And, lastly, there are teeth in another concave region which have the position of molars; these may, in the young animal, all be contained in a groove, with sockets scarcely better indicated than among Ichthyosaurs or some Cetaceans. In many Teleosaurs and Plesiosaurs the incisor teeth are relatively large, and the succeeding molars are smaller; and in the Ornithosaur *Dimorphodon* the incisor teeth are exceptionally large, as compared with the molars. The teeth of South African reptiles termed Theriodontia differ from such types chiefly in the development of large canines. The incisors remain large, the canines are larger, and the molars relatively small, as may be seen in such genera as *Cynodraco* and *Lycosaurus*. In this group the incisors have both crown and root compressed from side to side. The crown often has a prominent sharp chisel-like external cusp, and a small internal cusp which gives the tooth a mammalian aspect. This character is well seen in the Russian genus *Deuterosaurus* as figured by Eichwald and by Mr. Twelvetrees, the latter specimen being in the National Collection. A similar condition, but with the inner cusp less conspicuous, is seen in a new genus from South Africa allied to *Deuterosaurus*, here figured, which may be named *Glaridodon*. In this tooth, besides the elevated outer and inner cusps, there are on both sides elevated lateral borders to the crown, so that it includes a concave area, which in mode of formation of the concavity may be compared to the concave crown of the molar tooth of *Ornithorhynchus*, though the proportions of the tooth are dissimilar. Yet if a tooth of this type is supposed to lose its root by degeneration, it might show a close approximation to the tooth of such a mammal as *Ornithorhynchus*. The canine teeth in Theriodonts, like those of some of the lower mammalian orders, appear to be placed in the maxillary bone, and not in the suture between that bone and the premaxillary, as in the higher mammals.

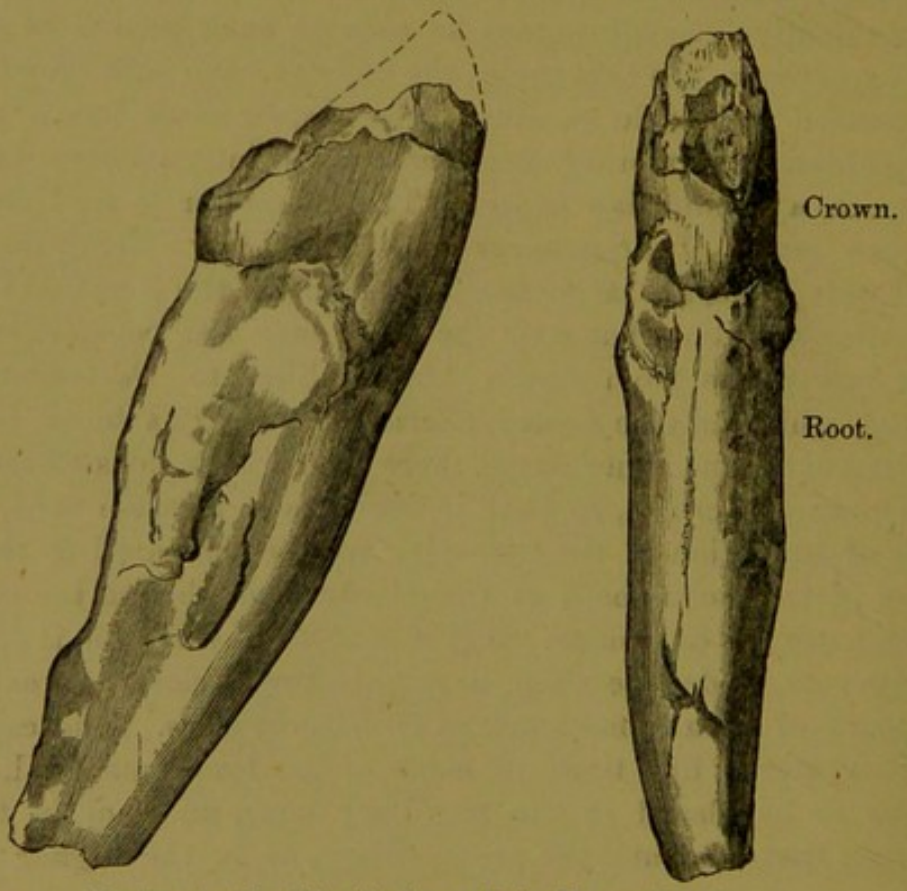
* "On Procolophon," 'Geol. Soc. Quart. Journ.,' vol. 34, 1878, pp. 804–5.

Fig. 1.

Lateral aspect of an incisor tooth, *Deuterosaurus*, Brit. Mus., R. 303.

Fig. 2.

Lateral aspect. Posterior aspect.



Incisor tooth, *Glaridodon*.—Brit. Mus., 49425.

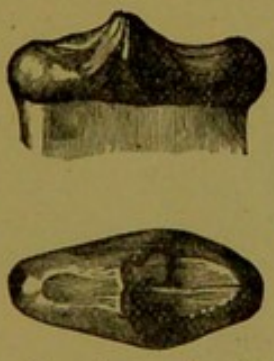
As Sir Richard Owen has shown, these teeth in size, form, and serration are altogether like canines of carnivorous mammals. The molar teeth of Theriodonts are usually but little specialised, and are small and often simple cones. Even in *Galesaurus* the crowns of the molars are compressed from side to side, and they have a central cusp no more developed than in a lizard, with a smaller cusp on each side, much as in some seals and porpoises, and as among porpoises there is a long single root.

Fig. 3.

Molar and canine teeth of *Galesaurus*.—Brit. Mus., R. 845. The posterior teeth are fractured, showing that the pulp cavity is closed at the base.

An American genus, *Empedias*, from Permian or Triassic rocks, referred by Professor Cope to a distinct order, the Pelycosauria, shows an unusual specialisation of the molar teeth. They are compressed from front to back, so as to have a great transverse extension on the palate, which is absent from the premolars. There is a contraction below the crown which is quite mammalian, and the root is single. The crown may be described as having three cusps. The median

Fig. 4.

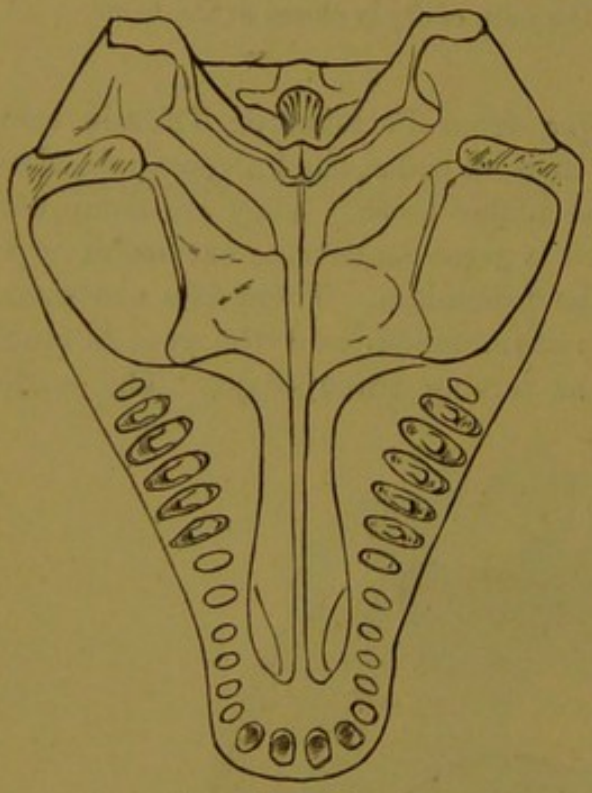


Transverse and superior views of molar tooth of *Empedias*.—Brit. Mus., R. 613.

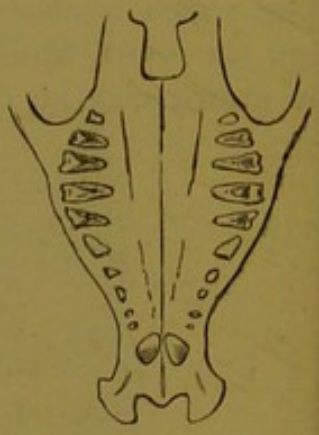
central cusp is the most elevated, and is the only one which shows evidence of wear, but the external and internal limits of the crown are both elevated above the level of the concave spaces which divide them from the middle cusp. Hence the tooth offers some evidence of three cusps in parallel series as a reptilian character, and so far helps to approximate reptilian and mammalian types. This dental condition in *Empedias* has its chief interest in an approximation which

it makes to the Golden Cape Mole, *Chrysochloris aurea*. Its teeth are rather more numerous in the premolar region, but otherwise the molars in the mammal similarly have one root; they have the same transverse extension with three cusps, of which the middle one is similarly well-developed, so that the chief differences are that in *Chrysochloris* the crown is wide on the outer margin and narrows internally as a wedge, while the external cusp is subdivided into two. The lower jaw teeth of *Empedias* resemble those in the skull, but in *Chrysochloris* the mandibular teeth are bicuspid, except that the first two molars have the inner cusp divided longitudinally. In the accompanying figures these genera are contrasted; and if *Galesaurus* suggests a primitive mammalian type allied in dentition to seals, *Empedias* as strikingly resembles an insectivorous mammal.

Fig. 5.



Empedias molaris.
Reptilian dentition.



Chrysochloris aurea.
Mammalian dentition.

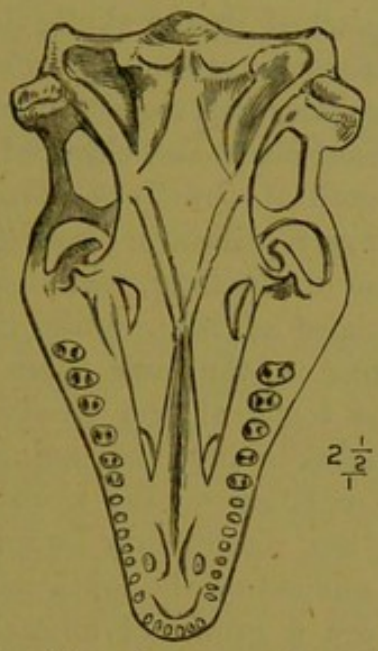
The Lacertilia include many types of dentition, among which are genera with characters suggestively mammalian both in the grouping of the teeth and forms of the crowns.

In the Frilled Lizard, *Chlamydosaurus*, there is one canine tooth at each anterior angle of the lower jaw, and these teeth are separated from each other by small incisors. In the skull there are on each side in corresponding positions two canine teeth placed side by side laterally in succession to each other.

In most lizards, as in many mammals, canine teeth are absent; and sometimes there is a more or less marked gap in the positions in which they might occur.

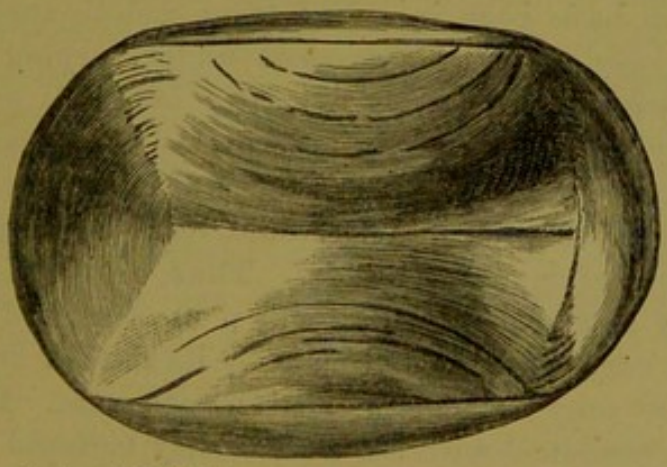
The teeth which are in the position of molars may exhibit modifications in the forms of the crown which correspond to premolars and molars. Thus, in species of *Teius*, there are five or six bicuspid teeth which have the cusps one internal to the other,* while in front of them

Fig. 6.



Palate of *Teius*, showing bicuspid molars, premolars with one cusp, and incisors.—After a photograph by Herbert Jackson, Esq.

Fig. 7.



A molar tooth of *Teius*, seen from above, much enlarged.

* I have on more than one occasion inadvertently attributed this character to the genus *Cnemidophorus*, as my specimen was so labelled when it came into my possession. I am indebted to Mr. Boulenger for the rectification, and whenever I have referred to the character it should be associated with the genus *Teius*.

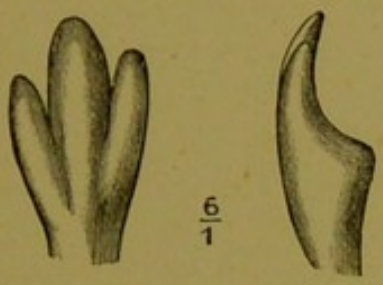
are about seven teeth with single cusps which correspond to the outer cusps of the posterior part of the series. In this genus there is a longitudinal channel between the cusps of the molar teeth. Seen from the palatal aspect the crown of a tooth is sub-quadrate, and the external cusp is the more elevated, so that the tooth has an aspect which is insectivorous rather than edentate. Both cusps are compressed so as to form sharp longitudinal cutting edges. At their bases they are connected on both the anterior and posterior borders of the tooth by low transverse concave ridges. In my specimen these transverse ridges are sufficiently marked in the skull; but are stronger in the lower jaw, where their surfaces are not quite smooth. If the anterior and posterior ridges were stronger, the crown of this tooth in quadrate form, external and internal cusps and elevated border, would be sufficiently similar to the tooth of *Ornithorhynchus* to give some ground for regarding that tooth as reptilian in plan. And it has already been seen that in degeneration of the fang, which induced Sir R. Owen to compare the teeth to those of the reptile genus *Placodus*, and in implantation in a groove in the jaws there is no departure from reptilian types. If the tooth of the *Ornithorhynchus* as a whole cannot be exactly paralleled in any other animal, it is at least evident that the teeth are as reptilian as the skeleton; and if the correspondence is not closer, the reason may be found in the degeneration which has replaced the enamel of the tooth with horny matter.

Modern lizards are not a group of animals in which theoretical considerations would suggest a search for mammalian characters in the teeth, but they happen to be the only group of Reptilia which is at all well known in which the teeth show a diversity which is in any degree comparable with the diversity of mammalian teeth. Whether those characters have been inherited from remote ancestry, or spontaneously developed in their possessors under varying conditions of existence, as seems probable, is a matter of small moment, for in either case they throw illustrative light on the classificational value of teeth of mammalia. If the different forms of cusp development found in lizards could be combined, teeth would result with crowns like the cuspidate crowns of many mammals. Thus, in *Cnemidophorus* there are two cusps arranged longitudinally; in *Ameiva* the tooth may have one large cusp with a small cusp by its side, or in the fore-part of the jaw there may be a small cusp on each side. If this kind of serration were combined with the transversely bicuspid teeth of *Teiu* or of *Empedias* crowns would result which would have mammalian patterns. In *Amblyrhynchus cristatus* the external part of the crown is deeply cleft so as to be divided much as in some seals into a median denticle, flanked by a lateral denticle on each side; but on the internal side the base of the crown thickens, forming a large flattened oblique area, which is evidently an undivided internal cusp, like the internal

incisor cusp of *Deuterosaurus*, for it is equally developed in successional teeth which have not come into use. Thus, *Amblyrhynchus* makes a partial combination of the characters of *Ameiva* and *Teius*, and shows what may be termed a sub-mammalian type.

FIG. 8.

Anterior aspect. Lateral aspect.



Teeth of *Amblyrhynchus*.

External aspect.

Two molar teeth of *Ameiva*.

The teeth of *Iguana* are serrate and acuminate, but if they were supposed to lose the acuminate character by all the denticles growing to the same height from a depressed base, then the parallel vertical serrations would reproduce the incisors of *Galeopithecus;* and that the incisors have originated in some such way is suggested by the premolars in that genus being acuminate and serrated. The grooved tooth of *Plagiaulax* and *Hypsiprymnus* is equally suggestive of the origin of complicated molars from a simpler form such as may be found in reptiles. It is well to remember, as showing how difficult it is to recognise class characters in the form of a tooth crown, that a naturalist so familiar with mammals as de Blainville was of opinion that the small mammalian jaws from Stonesfield, known as *Amphitherium*, were the jaws of reptiles before Sir R. Owen demonstrated that the molar teeth possessed two roots. But whether the molar teeth of mammals were evolved out of simple reptilian types of teeth such as have been discussed as consequences of other changes in the skull, or are due to the influence of habitual food on inherited structure, it is to be anticipated that the primitive mammals possessed teeth of reptilian type, less differentiated than the molar teeth of some existing lizards.

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