XXXI.—*On the Teeth of Species of the Genus* Labyrinthodon (Mastodonsaurus *of Jaeger), common to the German Keuper formation and the Lower Sandstone of Warwick and Leamington.*

By RICHARD OWEN, Esq., F.G.S., F.R.S., &c.

[Read January 1841.]

WHETHER the light-coloured sandstone of Warwick be, as Dr. Buckland conceives, the equivalent of the German Keuper, or, as Messrs. Murchison and Strickland contend, of the Bunter-sandstein, was a question which awaited the evidence of organic remains for its decision. For, notwithstanding the nature and number of the lithological characters collated by them, the latter authors do not insist upon this as evidence decisive of the accuracy of their views, but are willing to set the determination of the question upon the issue of organic remains, nay even of a single Saurian.

" If it could be shown," say Messrs. Murchison and Strickland, " that the fossils which we have pointed out as characterizing the upper sandstone, occurred also in the lower,"—" and that the fragments of Saurians found in the sandstones of Guy's Cliff and Warwick really belonged to the species peculiar to the Keuper,—then, indeed, we should willingly allow that the lower sandstone *also* must be grouped with that formation*."

The fossil reptiles which chiefly characterize the German Keuper are of the genera *Dracosaurus* and *Mastodonsaurus*; the former belonging probably to the Saurian order; the latter being undoubtedly a huge Batrachian, hence originally called '*Salamandroïdes*' by its discoverer Professor Jaeger. It is the evidence of the existence of remains of a species of the same peculiar extinct Batrachian genus in the lower sandstones of Leamington and Warwick, that I now propose to lay before the Society.

The genus *Phytosaurus*, also called *Cylindricodon* and *Cubicodon*, is perhaps most familiar, by name, to English geologists†, as a Keuper fossil: it is, however, merely a nominal genus, being founded on the socket of the tooth of some other reptile.

* Geol. Trans., 2nd Series, vol. v. p. 345.

† From the circumstance of its supposed existence in the Wealden formation.

The extremity of the portion of matrix, moulded to the bottom of the socket, having been mistaken for the grinding surface of the tooth, suggested, from its presumed adaptation to crush vegetable substances, the name of *Phytosaurus*. One of the supposed teeth of this reptile has been transmitted to me by Prof. Jaeger, which, upon examination, proves to be a mineral cast.

With respect to the term *Mastodonsaurus*, it has been already objected that it unavoidably recalls the idea of the Mammalian genus *Mastodon*, and not the teat-shaped tooth assumed to be the distinctive character of the genus which the name was invented to express. But there are other and graver objections to the term *Mastodonsaurus*: the rounded and obtuse summit of the crown is an exceptional, not a constant termination of the teeth of this genus, for every tooth in the jaw is originally, and the greater number are permanently, of a cuspidate and not of a mammilloid form. And if the first part of the compound name *Mastodonsaurus* thus conveys a partly erroneous idea of the dental characters of the extinct genus so designated, the second element—*saurus*—is still more objectionable, as being indicative of a wrong affinity; since the genus belongs, not to the *Saurian*, but to the Batrachian order of reptiles. The skull, for example, is joined to the atlas by two condyles developed from the lateral occipitals, and the bony palate is formed chiefly by a divided vomer, supporting teeth.

Conceiving these objections to be valid for the rejection of the name proposed by the respected Palæontologist of Stuttgard, to whose assiduous researches our knowledge of the present most extraordinary Batrachian genus is due*, and believing that I have discovered the true and peculiarly distinctive dental characters of the reptilian genus in question, I propose to designate it by the term *Labyrinthodon*.

With respect to this very characteristic fossil of the German Keuper sandstone, it is to be regretted that, with the exception of *the teeth*, and a fragment of the skull determining its Batrachian character, only a few broken vertebræ have hitherto been found in the Continental formations; certainly nothing approaching to an entire skeleton.

On the other hand, the reptilian remains in the Warwick sandstone are still more scanty; a few teeth, or fragments of teeth, are the only fossils from which I have as yet been able to decide upon the presence of the existence of reptilian vertebrated animals in that secondary formation. Hitherto no portion of the cranium corresponding with that which yields the Batrachian character of the *Salamandroïdes* of the German Keuper has been found, and the teeth, therefore, are the only fossils on which any comparison likely to solve the question of identity or other-

* Ueber die fossilen Reptilien, welche in Würtemberg aufgefunden worden sind. 4to. 1828, pp. 35, 38, tab. 4 & 5.

wise, between the Warwick sandstone reptiles and those of the German Keuper, can be founded.

It happens, however, that the teeth of the so-called *Mastodonsaurus* or *Salamandroïdes* are of a very common and simple form; they are far from possessing those well-marked external characters that enable the anatomist to distinguish at a glance the teeth of the *Iguanodon* or *Megalosaurus*.

Of the teeth which have been discovered in the Warwick sandstone, the specimen figured in the memoir of Messrs. Murchison and Strickland (Trans. Geol. Soc. vol. v. Pl. XXVIII. fig. 8.), and which has been transmitted to me for examination, together with other fossil teeth, by Dr. Lloyd of Leamington, most nearly resembles the teeth of the *Mastodonsaurus*, in its conical figure and longitudinal striation; but as these are the commonest characters of reptilian teeth, no weight could be attached to them as proving a specific or generic identity, bearing upon a geological problem of so much difficulty as the one which attaches itself to the Warwickshire sandstones.

There only remained, therefore, to resort to the test of the intimate structure of the teeth in question; and by the kindness of Professors Jaeger and Plieninger of Stuttgard, I have been favoured with some portions of the teeth of the *Mastodonsaurus Jægeri*, from which have been prepared the requisite sections for microscopical examination.

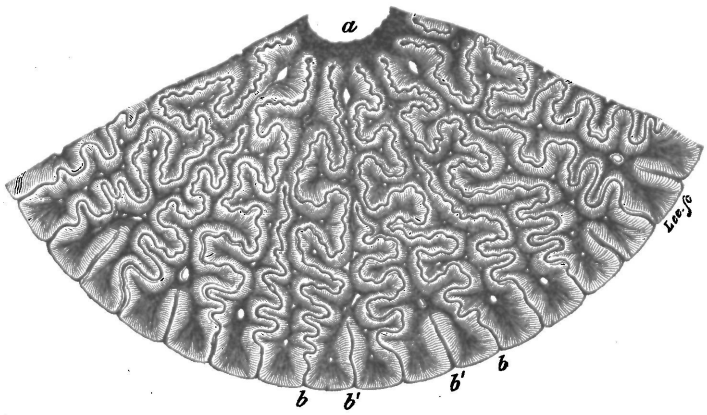
A close similarity prevails in the intimate texture of the teeth of the Crocodile, Plesiosaur, Megalosaur, Monitor, and most recent Lacertians, in which the *dentine*, or body of the tooth, consists entirely of the finest calcigerous tubes, radiating, according to the usual law, from the pulp-cavity at right angles to the external surface of the tooth, which is covered by a simple investment of enamel; and from the prevalence in the Saurian order of this, the ordinary structure of simple conical teeth, I did not build any very strong hopes of detecting such modifications of dental structure in the similarly shaped teeth of the so-called *Mastodonsaurus*, and of the reptile from the Warwick sandstone, as would be sufficiently marked and obvious to convince those who might not be familiar with the value of such characters, of their specific or even generic identity; but from this fear I have been agreeably and unexpectedly relieved.

The first transparent transverse section of the tooth of the *Mastodonsaurus Jægeri* which was placed under the microscope, and viewed by transmitted light with a low magnifying power, presented the singularly complicated structure exhibited in the subjoined woodcut; which structure, the anatomist conversant with the known modifications of dental structure in the animal kingdom, may well conceive not to have been contemplated without much surprise.

It was not, indeed, until I had caused sections of the portions of the tooth of this

species of *Mastodonsaurus* or *Labyrinthodon* to be made in various directions, and had studied them intently at several successive examinations,—comparing the appearances they presented with those of numerous examples of the teeth of true Saurians, Batrachians, and other animals,—that I at length comprehended the nature and principle of the singular cerebriform convolutions or labyrinthic gyrations which pervade every portion of the tooth of this most remarkable reptile of the Keuper formation.

Fig. 1.



Part of a transverse slice of the tooth of *Labyrinthodon Jægeri*, as seen by transmitted light; magnified 10 diameters.

A transverse section from the base of the tooth of the *Ichthyosaurus* gave the first clue to the structure of that of the *Labyrinthodon*. Before investigating the latter, I had been accustomed to regard the tooth of the *Ichthyosaurus* as presenting at its base the most complicated condition of dental structure in the class of Reptiles; but it is simple as compared with the structure which pervades nearly the entire tooth of the *Labyrinthodon*.

It is scarcely necessary to observe, that teeth vary in structure according to the number and disposition of the substances which enter into their composition.

In the herbivorous Mammalia, as the elephant, rhinoceros, horse, &c., where the crown of the tooth consists of dentine or tooth-bone, enamel, and cement, vertical folds of the enamel and cement penetrate the body of the tooth, and receive in their interspaces corresponding vertical processes of the dentine: the consequence of this disposition in maintaining a grinding surface of the tooth, by the unequal attrition of the edges of the interblended laminæ of the three different substances, is well known.

The pattern, however, in which the folds of enamel and cement are arranged in the substance of the tooth in these and other herbivorous Mammalia, although

constant in and characteristic of each genus or species, is always more or less irregular and unsymmetrical in itself.

There is no instance in the Mammalian class of these folds converging at regular intervals from the whole of the circumference of the tooth towards its centre; such a disposition of the external substance of the tooth may be traced at the base of the tooth in a few fishes, but in reptiles has hitherto been met with in the fang of the *Ichthyosaurus* alone.

In this extinct Saurian the external layer of cement (for the enamel ceases at the base of the crown) is inflected at pretty regular distances around the circumference of the tooth towards its centre, the vertical folds being straight and plane, and extending into the substance of the tooth to a distance about equal to the breadth of their interspaces. These interspaces are occupied by corresponding processes of the dentine, which radiate or diverge from the central mass of that substance.

If we could suppose the tooth of the *Ichthyosaurus* to be worn down in the living animal as far as its complicated basis, then an eighth part of the diameter of the tooth around its circumference would present a series of ridges of the denser substance converging in straight lines from that circumference towards the central pulp-cavity.

The plan and principle of the structure of the tooth of the *Labyrinthodon* are the same as those of the tooth of the *Ichthyosaurus*, but it is carried out to the highest degree of complication. The converging folds of the external cement, (Cut 1, *b*, *b*.) instead of being arrested at one-fourth of the distance from the circumference to the centre of the tooth, are continued close to that centre; and instead of consisting of simple, straight, and plane lamellæ, they are bent upon themselves in a series of irregular folds resembling the labyrinthine convolutions of the surface of the brain.

The ordinary laws of the complication of dental structure are here, however, strictly adhered to, and every space intercepted by a convolution of the converging folds of the cement is occupied by a corresponding process of the diverging layers of the dentine, and thus is produced the singularly complicated appearance which a transverse section of the tooth of the *Labyrinthodon* exhibits.

The external longitudinal flutings of the base of the tooth of the *Ichthyosaurus* are much coarser, and more indicative of the converging vertical folds of the cement than are the corresponding longitudinal lines on the exterior of the tooth of the *Labyrinthodon*,—a difference which is owing to the layer of the inflected cement being much thicker in the *Ichthyosaurus*.

The external striæ of the *Labyrinthodon's* tooth are thus of a nature to attract but little attention, and could not have been suspected to be the lines of inflection

of a series of vertical folds of the external substance, so extensive and so complicated as they actually are.

Accordingly, Professor Jaeger has described the tooth of his *Mastodonsaurus* as being simply longitudinally striated on the superficies, noting where the striæ terminate, their relative distances, and where they are most marked: the texture of the tooth where it was exposed by fracture, he states, as indeed it appears to the naked eye, to be an uniform or homogeneous compact mass (gleichformig derbe masse), and he concludes his description by stating that the tooth resembles most closely that of the *Lacerta Nilotica* and of some species of *Monitor**.

I may observe, however, that the teeth of those species of *Lacerta*, *Monitor*, and other Lacertian genera which I have submitted to microscopic investigation, have all presented the general structure of simple saurian teeth; and that, since ascertaining the structure of the *Labyrinthodon's* tooth, I have minutely inspected the outer surface of the teeth of numerous species of Saurians, but have not detected striæ penetrating the substance of the tooth, like those which indicate the complicated structure of the tooth of the Keuper Batrachian.

The portion of the tusk of the *Labyrinthodon Jægeri*, from which the microscopic sections now described were prepared, included about the middle third part of a tooth, nearly as large as the one figured by Professor Jaeger†. That tooth is three and a half inches in length, one and a half inch in breadth at the basis, whence it gradually converges with a slight bend towards the apex, which is obtuse, with a slightly depressed summit three lines in diameter, and having a small rising in the centre of the terminal depression.

The external longitudinal striæ are regularly arranged, with intervals of about one line at the base of the tooth, and they maintain nearly the same position throughout the lower three-fourths of the tooth, by decreasing in number as the tooth diminishes in thickness; they finally altogether disappear about half an inch from the summit of the tooth. Here therefore, I presume, the structure of the tooth may be more simple; but whether there be any inflected folds, or to what extent they are continued into the summit of the tooth; and whether, beside a layer of cement, the tooth be at this part invested likewise by a coating of enamel, can only be determined by the examination of sections similar to those which I have had prepared from the middle part of the crown in the tooth of the *Labyrinthodon Jægeri*.

At this part the dentine or body of the tooth is invested by only a very thin sheath of cement, and it is a vertical fold or duplicature of this cement which penetrates into the substance of the tooth at each of the striæ, which, as before

* *loc. cit.* p. 36.

† *loc. cit.* tab. 4, fig. 4.

observed, are arranged at intervals of about one line around the whole circumference of the tooth. The inflected fold runs straight towards the centre of the tooth for about half a line, and then becomes wavy, the undulations rapidly increasing in breadth; the first two, three, or four undulations are simple, then their contour itself becomes broken by smaller or secondary undulations, and these become more numerous as the fold approaches the centre of the tooth, near which it slightly increases in thickness, and finally terminates by a dilated loop or extremity (as seen in the transverse section) close to the pulp-cavity, from which the free margin of the inflected fold of cement is separated by an extremely thin layer of dentine. The number of the inflected converging folds of dentine is about fifty at the middle of the crown of the tooth, but it must be greater at the base.

All the inflected folds of cement at the base of the tooth have probably the disposition and extent above described, but as they approach their termination towards the upper part of the tooth (and we have seen that they progressively decrease in number as the tooth diminishes in size) they also gradually diminish in breadth, and consequently penetrate a less distance into the substance of the tooth.

Hence, in such a section as I have delineated, we observe that some of the convoluted folds, or those marked *b*, *b* (fig. 1, p. 506.), extend to near the centre of the tooth. Others reach only about half-way to the centre; and those folds (*b'*, *b'*), which, to use a geological expression, are "thinning out," penetrate to a very short distance into the dentine, and resemble in their extent and simplicity the converging folds of cement in the fang of the tooth of the *Ichthyosaurus*.

The disposition of the dentine in the tooth of the *Labyrinthodon* is still more complicated than that of the cæmentum. The dentine, or the main constituent of the tooth, consists of a slender central conical column, or 'modiolus,' hollow for a certain distance from its base, and radiating outwards from its circumference a series of vertical plates, which divide into two, or dichotomize once or twice before they terminate at the periphery of the tooth.

Each of these diverging and dichotomizing vertical plates gives off throughout its course narrower vertical plates, which stand at right angles or nearly so to the main plate; they are generally opposite, but sometimes alternate. Many of the secondary plates which are given off near the centre of the tooth also divide into two before they terminate: their contour is seen in the transverse section to partake of all the undulations which have been described as characterizing the inflected folds of cement which invest the dentinal lamellæ and separate them from each other.

The central pulp-cavity (Cut 1, *a*, p. 506.) is reduced to a mere line about the upper third of the tooth, but fissures radiate from it corresponding in number with the radiating plates of the dentine. One of these fissures is continued along the middle of each plate, dividing where this divides, and extending along the middle of each

bifurcation and process. The main radiating fissures extend to within a line or half a line of the periphery of the tooth, and suddenly dilate at their terminations into canals, the areas of which in transverse section are subcircular, oval, or pyriform; the branches of the radiating fissures, which are continued into the lateral secondary plates or processes of the dentinal lamellæ, likewise dilate into similar and generally smaller spaces. All these spaces or canals in the living tooth, must have been occupied by corresponding processes of the vascular pulp; they constitute as many centres of radiation of the fine calcigerous tubes, which, with their uniting clear substance, constitute the dentine.

If the dilated spaces of the complicated and ramified pulp-cavity of the *Labyrinthodon's* tooth were isolated, and their respective systems of calcigerous tubes circumscribed by a coat of cæmentum, then the tooth of the *Labyrinthodon* would present the type of that of the *Orycteropus*, and of the *Myliobates*, *Pristis*, and many other cartilaginous fishes: or on the other hand, if the pulp-cavities of the component cylindrical denticles of the tooth of the *Orycteropus* were connected together by lines converging to and uniting in a common centre, then it would somewhat resemble the peculiar type of dental structure presented by the *Labyrinthodon*.

It would be foreign to my present purpose to pursue the description of the tooth of the *Labyrinthodon* into the modifications of the dentinal tissue, as displayed by the higher powers of the microscope; suffice it to say, that the dentine everywhere presents the structure of fine calcigerous tubes, obeying in their course the usual law, *i.e.* radiating or converging, with primary curvatures and secondary undulations at right angles, or nearly so, to the surface of the dentine which the cement invests.

The number of these calcigerous tubes, which are themselves the centres of minor ramifications, defies all calculation; their diameter is $\frac{1}{7000}$th of a line, with interspaces equal to seven diameters of their cavities*.

It has already been stated, that among the few teeth presumed to be reptilian from the Warwick sandstone, the small, conical, externally striated one, figured in the memoir of Messrs. Murchison and Strickland (Geol. Trans. vol. v. Pl. XXVIII. fig. 8.), bears the nearest resemblance to the teeth of the German *Labyrinthodon* or *Mastodonsaurus*; it is however much smaller, and the cone is broader and shorter.

I have subsequently received a larger tooth from my friend Dr. Lloyd, which was discovered in the Warwick sandstone at the Coton-end Quarry. This tooth still more closely resembles in size and form the teeth of the *Labyrinthodon* figured by Professor Jaeger, especially the smaller specimens (figs. 5. and 6. Pl. IV. of his above-cited work); it differs only in being somewhat more compressed at the

* Their general disposition is shown in a section of one of the simple lateral processes of the radiating plates of dentine, in Plate LXIV. A. fig. 2. of my 'Odontography.' The undulation and ramification of the terminations of two of the calcigerous tubes, magnified 650 diameters, are figured at Plate LXIV. A. fig. 3.

base and less obtuse at the apex, resembling more the ordinary simple form of a laniary tooth. The external surface of the Warwick sandstone tooth is similarly impressed with fine longitudinal striæ, continued with a very slight degree of convergence towards the apex of the tooth, where the longest striæ terminate.

The interspaces of the striæ are more prominent and convex than in the *Labyrinthodon Jægeri*. The apex of the tooth, though rather obtuse, and worn by attrition obliquely down one side, does not present the depression and central eminence which Professor Jaeger describes as the chief characteristic of the larger tooth of his salamandroid *Labyrinthodon*. This appearance in the tooth of that species may, however, be due to the mode in which it has been worn down; and we have just seen that the tooth of the *Labyrinthodon* possesses a distinctive character of a very different and much more important kind.

It was in relation to this structural modification that I felt most anxious to examine the teeth from the Warwick sandstone. I could perceive indications at the fractured basis of the larger tooth of fissures leading from the external striæ into the substance of the tooth, and the question was, were these fissures continued to the same extent, and in the same convoluted course which they had presented in the tooth of the *Labyrinthodon* of the German Keuper? This I was unable to determine by inspection of the fractured surfaces of the dense and opake tooth from the Warwick sandstone, either by unaided vision or the use of the microscope with reflected light.

I solicited, therefore, and obtained permission from Dr. Lloyd, to have the requisite sections made, selecting such a portion of the larger tooth as least interfered with the exposition of its external form and characters.

The subjoined cut (fig. 2.) faithfully exhibits the appearance which a portion of one of the transverse sections presented, as seen by transmitted light; the complication of the structure of the tooth is as great and its plan is the same as in the *Labyrinthodon Jægeri*; all the peculiarities indeed of this most extraordinary type of tooth are so clearly preserved in the specimens from the Warwick sandstone, that I conclude it to have belonged to a reptile of the same genus as that which characterises the Keuper of Wirtemberg.

Fig. 2.

The differences which remain to be noticed in the tooth of the Warwick *Labyrinthodon* are of a comparatively slight and probably only of a specific nature.

At the upper part of the tooth a thin layer of enamel*, besides a coating of cement, is inflected at

* I have subsequently ascertained that this is not true enamel.

each groove towards the centre of the dentine, but about the middle of the tooth the enamel disappears, and the convolutions consist of interblended layers of cement and dentine. Thus, on the supposition that the tooth of the *Labyrinthodon* of the German Keuper be capped with enamel, this constituent of the tooth must have a less extent than in the congeneric tooth from the Warwick sandstone.

The inflected folds in the Warwick tooth are continued for a greater relative extent before the lateral inflections commence, than in the German species, and the inflections or anfractuosities are rather fewer in number; some of the inflected converging folds in the Warwick tooth, having nearly reached the central pulp-cavity, are reflected backwards for a short distance before they terminate.

The modifications of the complex diverging plates of the dentine correspond with those of the tooth of the *Labyrinthodon Jægeri*, the observable differences hardly amounting to anything beyond those of a specific character. Thus the peripheral or terminal quadrilateral lobes, as seen in the transverse section, are relatively longer in the *Labyrinthodon laniarius*, as the Warwickshire species may be provisionally termed.

The number of the inflected folds of enamel at the upper third of the tooth is about forty-five; such of the folds as nearly reach in the vertical direction to the apex of the tooth extend inwards transversely almost to its centre, and the shorter folds are inflected to an extent proportionate to their length.

The dentine is composed of calcigerous tubes of the same relative size and disposition as the *Labyrinthodon Jægeri*. The base of the tooth is similarly anchylosed to the osseous substance of the jaw.

In the transverse section of the smaller and relatively broader and shorter conical tooth from the Warwick sandstone already mentioned, I found, as I had anticipated, that the superficial longitudinal striæ indicated inflections of converging folds of the external cement as extensive as those in the *Labyrinthodon Jægeri* and *Labyrinthodon laniarius*. They present the same peculiar pattern, being bent from side to side in lateral undulations; but these are more complicated with numerous secondary and tertiary foldings; I find also that the second and third lateral folds, counting inwards, are the broadest, and that the rest decrease as they approach the centre of the tooth.

The section was taken from the middle of the portion of the tooth preserved; this part is not covered by enamel but by cement only, which is relatively thicker than in the *Labyrinthodon Salamandroïdes*. These differences are sufficiently characteristic of the tooth itself, but whether they indicate a difference of species or of age, or of situation in the jaws of one and the same individual, I cannot at present determine. It may be convenient, however, provisionally to indicate this tooth as belonging to the *Labyrinthodon ventricosus*.

It is my intention to prosecute further inquiries into the structure of other teeth

from the Warwick sandstones; but so far as I have hitherto had opportunities of carrying on this investigation, the results, I trust, will be allowed to be decisive as to the existence of reptiles in that formation which belong to the same natural genus, as does one of the most peculiar and characteristic reptiles of the German Keuper.

So far, therefore, as the geological problem to which reference was made at the beginning of the present paper, depends upon the determination of the correspondence, in a peculiarly characteristic dental character, of the reptilian fossils of the formations in question, the present researches must be regarded as decisive in favour of the view entertained by Dr. Buckland of the identity of the Warwick and Bromsgrove sandstones with the German Keuper. And if, on the one hand, geology has thus really derived any essential aid from minute anatomy, on the other hand I may venture to affirm, that in no instance has the comparative anatomist been more indebted to geology than for the fossils which have revealed the most singular and complicated modification of dental structure hitherto known; and of which not the slightest conception had been gained from investigation of the teeth of existing animals.