The Structure of the Teeth of some Mammal-like Reptiles

By D. F. G. POOLE

(From the Department of Zoology, University of Bristol, and latterly the Department of Biology, University College of East Africa, Kampala, Uganda)

With two plates (figs. 1 and 2)

SUMMARY

The principal changes in calcified tissues which have fossilized are the loss of organic material and the conversion of hydroxyapatite into fluorapatite. Since these two minerals are very similar and because, initially, mammalian enamel has a low organic content, its optical properties are hardly affected by fossilization. On the other hand, the loss of optically active collagen results in a modification of the characters of dentine.

The teeth of synapsid reptiles possess dentine similar to that of recent reptiles. Occasionally the dentine contained globuli, but unlike mammalian dentine, there appeared to be no 'spheritic' orientation of crystallites within the globuli. Certain dicynodont tusks consisted of dentine only and it is possible that enamel was missing even in the original condition. Other synapsid teeth possessed a thin, well-defined enamel layer made up of incremental lamellae but lacking true prisms. Nevertheless, cylindrical groups of crystallites exist throughout this enamel within which the orientation of the crystallite axes varies regularly. Between crossed nicols of a polarizing microscope this crystallite arrangement gives the enamel a prismatic appearance. However, the enamel is quite homogeneous, for these pseudo-prisms are not physically separated from each other. Furthermore, this regular prismatic appearance and an irregular Säulengliederung, such as occurs in crocodile enamel, may exist in the same tooth. There is, therefore, no evidence that the prismatic enamel characteristic of mammals existed in the pre-mammalian reptiles.

INTRODUCTION

CONSIDERABLE evidence has accumulated recently showing that the enamel-like tissue covering the teeth and scales of fish, as well as that covering the teeth of amphibians, is fundamentally different from mammalian tooth enamel (Levi, 1939, 1940; Kvam, 1946, 1950; Kerr, 1955; Poole, 1955). In these lower vertebrates the enamel-like material is of mesodermal origin, lacks prisms, and differs in other minor respects from the ectodermal, prismatic enamel of mammals. Reptilian enamel is more similar to that of mammals because it is ectodermal and its organic matrix is of a keratinous nature (Kvam, 1950). Moreover, hydroxyapatite crystallites are oriented in the same general direction in relation to the enamel surface, but as yet no prisms have been found in reptile enamel (Erler, 1935; Schmidt, 1948a, 1948b). In view of this, the problem of the origin of ectodermal prismatic enamel is of considerable interest and, for this reason, an examination of the teeth of pre-mammalian reptiles has been made.

The submicroscopic structure of mammalian teeth is now well known (Harders-Steinhauser, 1938; Thewlis, 1940) and the determination of the corresponding features of synapsid teeth has been a valuable way of comparing...
them with mammals. However, since all the teeth to be described are fossils of considerable age it was felt that before any structural interpretations were made, careful consideration must be given to the possible effects of fossilization upon calcified tissues. To this end, a brief account of certain fossil mammalian teeth has also been included.

It has long been known that fossilizing bone accumulates fluorine, a fact which is of use in the estimation of the ages of fossil bone samples (Carnot, 1893; Oakley and Hoskins, 1950). It has been suggested that the accumulation is due to the replacement of (OH)\(^{-}\) ions by F\(^{-}\) ions in the apatite lattice, converting hydroxyapatite into fluorapatite (Oakley, 1948), and the results of X-ray analyses of fossil specimens are in agreement with this (Poole, unpublished results). Both are negative, uniaxial minerals with very similar optical properties and, therefore, it would seem that the principal changes occurring in a calcified tissue undergoing fossilization are due to the loss of organic material. Since enamel has a low organic content, few changes may be expected in it, whereas the properties of dentine, which initially contains a considerable amount of optically active collagen, are likely to be modified. That the latter is so was shown by an observation of Schaffer (1891) that sections of fossil dentine reverse their sign of birefringence when transferred from xylene to Canada balsam. In doing so such sections behave in precisely the same way as sections of recent dentine from which the collagen has been removed by chemical means. Nevertheless, it is of interest in this connexion that it has been possible to identify collagen in the tusks of the late Siberian mammoth (*Elephas primigenius*) after a period of 10,000–15,000 years (Randall and co-workers, 1952). However, as pointed out by the same authors, the collagen structure would eventually break down at all temperatures above zero over a sufficient length of time.

It is hoped that the account of fossil mammalian teeth given below will help to amplify some of these points, and also serve to illustrate the fine structure of mammalian enamel and dentine generally.

**Material and Methods**

The mammalian teeth examined were from two Oligocene ruminants, *Oreodon* and *Leptomeryx*. All the other teeth belonged to a range of mammal-like reptiles collected in southern Africa and North America. Some of the specimens were not completely identified, but the following synapsid groups were represented: Pelycosauria (*Dimetrodon*); Dicynodontia (*Lystrosaurus* and an unidentified genus); Gorgonopsia (unidentified); and Cynodonta (*Thrinaxodon* and an unidentified genus).

Thin sections, both longitudinal and transverse, of all these teeth were prepared and mounted in Canada balsam. Examination was made with normal and phase-contrast microscopes, and the optical properties of the various tissues were determined by examination between the crossed nicols of a polarizing microscope.
Fossil Mammalian Teeth

Ordinary microscopical examination revealed that the teeth of both *Oreodon* and *Leptomeryx* possessed a typical orthodentine (see Orvig, 1951) similar in all respects to the dentine of recent mammals. In polarized light the dentine of *Leptomeryx* had a uniform birefringence throughout, which was negative with respect to the tooth surface and indicated that the negatively birefringent crystallites of apatite are arranged with their optic axes parallel with the surface of the tooth. A similar crystallite arrangement existed in *Oreodon* dentine, but in addition a well-marked ‘spheritic’ orientation was superimposed upon it. This is suggested by the occurrence of whole, partial, or distorted circles, as seen in fig. 1, A, each of which is marked by a polarization cross. Both types of orientation are to be found in recent mammalian dentine (Keil, 1939).

In both specimens the sign of birefringence reversed on transferring a section from xylene to a medium of higher refractive index. In recent dentine the positive birefringence of the collagen overcompensates that of the negative mineral; if these fibres are removed (e.g. by boiling in glycerol-potash solution), spaces are left which, when penetrated by a liquid of quite different refractive index from that of the mineral, set up a positive ‘form’ birefringence, again overcompensating the mineral. However, when a liquid with a refractive index nearer to that of the mineral is used, the ‘form’ birefringence is removed and only that of the mineral remains. This accounts for the reversal of birefringence when fossil dentine, or recent dentine from which the collagen has been removed, is transferred from xylene to Canada balsam.

As was anticipated, the properties of fossilized enamel proved to be very similar to those of recent enamel. The prisms were perhaps a little less obvious, possibly because the loss of organic material from the interprismatic substance decreased the relief between it and the actual prism substance. Nevertheless, the characteristic cross-striation of the prisms was still apparent under all conditions and this is also seen very clearly in the enamel of certain fossil rodents (Korvenkontio, 1934).

Between crossed nicols each prism exhibits a negative birefringence with respect to its length, so that the crystallites within must lie with their optic axes approximately parallel with the prism axis. By rotating a section it is found that the extinction position of the prisms is different from that of the interprismatic substance. Fig. 1, A shows an enamel layer close to an extinction position and producing, as a result, anomalous polarization effects. In many places the prisms are extinct and appear dark, whilst the thinner interprismatic zones separating them are still light. Since the prism direction varies somewhat, certain prisms which have passed the extinction position may also be seen; these are light whereas the interprismatic substance is now dark. The same effect is true of human enamel, as illustrated in fig. 2, D and E. Thus, as in recent enamel (Thewlis, 1940), the crystallites in the interprismatic substance of fossil enamel are not parallel with those within the prisms. Gustafson (1945) distinguishes carefully between prism sheath and the very
thin interprismatic cementing material, concluding that it is the former, a largely organic region, which is responsible for the different properties of the prisms and the material which separates them. Yet this difference persists even in fossilized enamel, so that if all organic material is presumed lost, the difference must be due to mineral whatever its exact location may be. In this account, the term 'interprismatic substance' will be used loosely to describe all the material occurring between the prisms.

The zonation of the enamel seen in fig. 1, A is due to striae of Retzius running out gradually from the amelodentinal junction across the prisms and eventually reaching the enamel surface. The effect is caused by slight displacement of the prisms during formation (Gustafson, 1945) and is well known in human enamel. As with recent enamel (fig. 2, D), the cross-striation of the prisms is seen clearly in polarized light. In addition the activity of the innermost enamel is considerably greater than elsewhere, for in this region the prisms are comparatively straight and parallel throughout the section; on moving outwards, considerable bending and twisting occurs and the effects of surface prisms are partially compensated by those of more deeply lying prisms running in a slightly different direction. As a result of this there is a reduction in the overall activity of the outer enamel.

This brief account is sufficient to demonstrate that all the important features of mammalian enamel are retained after fossilization. The only important change in fossil dentine is the loss of collagen, and the properties of the dentine are still very much the same as those of recent dentine from which collagen has been removed artificially. Therefore, the methods of examination outlined above should be a valuable guide to the presence or absence of prismatic enamel in fossil material of even greater antiquity than that already dealt with.

**Teeth of Mammal-like Reptiles**

Some of the material examined was very well preserved; the cynodont teeth were still socketed in jaws with the result that sections of the whole specimen yielded information concerning all of the tooth tissues, including cementum, and the bone of the jaws. The insertion of the teeth resembled that of mammals, both primary and secondary cement layers being distinguished.

The orthodentine showed very constant properties throughout the range of teeth studied. Dentinal tubules ran out from the pulp cavity towards the amelodentinal junction, and a thin, structureless layer occurred between the ends of the tubules and the beginning of the enamel. Longitudinal sections had a negative birefringence with respect to the tooth surface, whereas transverse sections showed little or no activity between crossed nicols. In

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**Fig. 1 (plate).** A, longitudinal section of a tooth of *Leptomeryx* arranged close to an extinction position between crossed nicols. The enamel prisms are crossed by striae of Retzius whilst illuminated arcs and circles occur throughout the dentine.

B, longitudinal section of a cynodont tooth under the same conditions. The presence of alternating light and dark zones in the enamel produces a superficial resemblance to mammalian enamel. This pattern is somewhat obscured in certain parts of the enamel.
FIG. 2

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general, therefore, apatite crystallites are arranged with their optic axes parallel with the surface and the long axis of the tooth. Occasionally, patterns of arcades or circles were seen between crossed nicols, particularly in the dentine of *Dimetrodon*, but these differed from those of a similar shape and size in mammalian dentine in that polarization crosses were either weak or absent. Very small globuli, again lacking polarization crosses, may be seen in crocodile dentine where all the crystallites lie with their optic axes parallel with the direction of the collagen fibres. This suggests that the presence of globuli does not necessarily imply a 'spheritic' orientation of crystallites such as occurs in mammals, and that it is possible for crystallites within the spheres to be orientated in the same general direction as the collagen. This view is shared by Schmidt (1955).

The dicynodont tusks possessed no enamel; one of these was weathered on one side but the other side seemed to be quite intact, and, furthermore, the tusk of *Lystrosaurus* was still completely embedded in rock. The general characters strongly suggested that, had it ever existed, an enamel layer ought still to be present. Enamel may have been lacking even in the original condition, for the tusks of *Lystrosaurus* grew continuously from persistent pulps (Broom, 1932) and a parallel could exist with certain mammals where this is also true; e.g. elephant and *Babirusa*. In such cases the production of dentine is continuous, but the enamel organ ceases to function after eruption and only the original tip is covered by enamel.

The enamel covering the cynodont and gorgonopsid teeth was well defined but very thin, being no more than 0.1 mm in thickness on a tooth with a long diameter of 15 mm. With ordinary microscopic examination gorgonopsid enamel appeared almost structureless except for thin, faint lines parallel with the enamel surface breaking it up into lamellae. The same was true of cynodont enamel, but in this case many tubule-like spaces, lying at right angles to the amelodentinal junction, were present in the innermost region. Between crossed nicols this enamel again appears almost structureless when it is arranged in the position of maximum illumination and it has a positive birefringence with respect to its surface, indicating that the negative mineral crystallites lie, in general, with their optic axes perpendicular to the surface. However, if the gorgonopsid or cynodont enamel is now rotated towards

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**Fig. 2 (plate).** The enamel of various teeth as seen in polarized light; in each case the enamel is arranged near to an extinction position.

A, transverse section of gorgonopsid enamel with a well-marked 'prismatic' appearance and with very thin layer lines running parallel with the surface.

B, enlargement of a fragmented portion of the same gorgonopsid enamel showing that the characteristic pattern is still visible even in very thin sections.

C, transverse section of the enamel of *Dimetrodon*, again with layer lines and a simulated 'prismatic' appearance.

D, human enamel possessing illuminated prisms separated by thinner, dark, interprismatic regions.

E, the same human enamel rotated so that the prisms are extinguished. Since the crystallites within the prisms have a different orientation from those in the interprismatic substance, the latter now lights up.
extinction position a new pattern is produced, which is illustrated in figs. 1, B and 2, A and B. Here are seen alternating black and white lines perpendicular to the enamel surface, crossed by the lamellae, and bearing a superficial resemblance to mammalian prisms examined under the same conditions. The effect is clearer in gorgonopsid enamel than in cynodont, where it is obscured by the tubule-like spaces (fig. 1, B).

Despite the superficial resemblance, the effect described above differs in several important respects from mammalian enamel. For example, it only manifests itself under certain circumstances, whereas mammalian prisms are visible under all conditions. Fig. 2, D is a photograph of mammalian enamel arranged close to an extinction position between crossed nicols; the illuminated prisms are cross-striated and separated from each other by the much thinner interprismatic regions. The latter are never cross-striated and here they appear dark because the crystallites within them are extinguished. The same enamel, rotated so that the prisms have become extinguished, is shown in fig. 2, E; because of their different orientation the crystallites of the interprismatic material have now passed the extinction position and begin to light up. The important point is that the pattern of broader prisms separated by thinner zones of interprismatic substance is always the same. In contrast to this, the apparent prismatic appearance of synapsid enamel is more precise when the enamel is parallel with an extinction position than when the enamel is in any other position, although there is always a tendency for the black and white zones to grade into each other through shades of grey. On rotating a section from the extinction position, the black lines, which are in general thinner than the white for any position of the enamel, move gradually across areas originally illuminated. As the rotation is continued, all zones become less and less distinct until at 45° from extinction, the position of maximum illumination, little trace of the prismatic pattern remains. If the enamel is now returned to the extinction position and a sensitive tint (first order red) quartz plate is inserted at 45°, a very interesting colour pattern is produced. In very thin enamel there is a regular repetition of a blue-red-orange colour sequence, so that the prism appearance is produced by groups of crystallites whose orientation varies regularly about a normal to the enamel surface. All these points indicate that synapsid enamel is not broken up into units separated from each other by material with rather different properties, but is a continuous homogeneous layer of crystallites the orientation of which varies slightly but regularly. In other words, these are not true prisms.

Although true prisms may not exist in synapsid enamel, by focusing at different depths of a thick section it may be observed that individual groups of crystallites exist throughout the enamel. Furthermore, when a section parallel with the surface is viewed between crossed nicols, a mosaic of small circles, each with a diameter equal to the width of a ‘prism’, is observed. This means that each group of crystallites is in fact cylindrical in shape and runs from the amelodentinal junction to the enamel surface. As shown above, these cylinders are not physically separated from each other. The ‘prisms’
could not be seen by ordinary phase-contrast microscopy, but when a source of plane-polarized light is substituted the effect is again noticeable as a series of alternating lighter and darker zones, that is to say, alternating areas of positive and negative phase.

To explain these various properties of synapsid enamel, the following structure is proposed. Fig. 3, A represents a section of enamel built up of a series of lamellae which undulate regularly. These undulations can actually be observed in a specimen, but since the groups of crystallites are cylindrical, any one lamella does not consist of elongated corrugations but of hemispherical elevations and depressions. Crystallites tend to lie with their optic axes at right angles to the lamellae, but, as shown in fig. 3, A, because of the

![Diagram of a suggested structure of gorgonopsid enamel. A, the enamel is made up of lamellae containing crystallites. The crystallite and optic axes, which are coincident, are at right angles to the undulating lamellae so that there is a regular variation in crystallite direction, e.g. a, b, and c. The two vibration directions of the crystallites, with differing refractive indices \( n_e \) and \( n_o \), are indicated by mutually perpendicular axes. B, the appearance produced in polarized light by such a crystallite arrangement when the enamel as a whole is parallel with an extinction position. Crystallites along direction a will appear dark, those along b and c will be illuminated. Light and dark zones tend to grade into each other.](image)

undulations there will be a variation in the crystallite direction about the surface normal \( a \). If the enamel as a whole is arranged parallel with an extinction position the condition shown in fig. 3, B is produced; all the crystallites with their optic axes parallel with direction \( a \) will be extinct and the area around them dark. On the other hand, crystallites parallel with directions \( b \) and \( c \) will be illuminated, but since the orientation changes only gradually, the light and dark zones tend to grade into each other. Should a quartz sensitive plate be placed with its positive axis parallel with direction \( c \), the crystallites here will become orange-yellow because the mineral is negatively birefringent; crystallites along direction \( a \) are inactive and will appear red, whilst those parallel with \( b \) will become blue-green. Furthermore, if the enamel in fig. 3, A is rotated, the orientation of the different groups relative to the
extinction position becomes less regular and the prism-like pattern less and less distinct as the $45^\circ$ position is approached.

An arrangement of mineral such as this also accounts for the prism-like effect produced with a phase-contrast microscope and plane-polarized light. In fig. 3, A the vibration directions of crystallites are represented by two mutually perpendicular axes and, since fluorapatite is a negatively bi-refringent, uniaxial mineral, the refractive index along the optic axis ($n_e$) is smaller than that at right angles to it ($n_o$). When plane-polarized light vibrates through the enamel parallel with the direction $c$, it will be subjected to the lesser refractive index ($n_e$) of crystallites lying in this direction but to the greater refractive index ($n_o$) of those with their optic axes parallel with direction $b$. With the phase-contrast microscope these areas of alternating refractive index will appear as zones of positive and negative phase. If the section is rotated so that the plane-polarized light is now vibrating parallel with direction $b$, a change of phase in each zone will result. The crystallite arrangement suggested in fig. 3, A does, therefore, account for all the observed properties of this enamel.

Finally, brief mention of pelycosaur enamel must be made. The teeth of Dimetrodon are compressed laterally, sections parallel with the long, transverse axis again showing a simulated prismatic appearance (fig. 2, c). However, sections along the shorter axis presented no distinct pattern, resembling the irregular Säulengliederung typical of crocodile enamel (Schmidt, 1948a). It is possible, therefore, for a variation of pattern to occur in the same tooth.

**Discussion**

As a result of the investigations carried out it seems that enamel consisting of individual, separate prisms did not occur on the teeth of mammal-like reptiles. Although, in some cases, the enamel is composed throughout of regular, cylindrical groups of crystallites, in others variation occurred from this condition to that of the more irregular Säulengliederung first described in crocodile enamel. In the enamel of certain placodonts the two conditions may also be found, and the Säulengliederung is to be seen in the enamel of certain other fossil parapsids (Schmidt, 1948a, 1948b). Recent investigations show that the same general properties are possessed by the enamel of pterosaurs (Schmidt, 1955), cotylosaurs, and recent Squamata (Poole, unpublished results), so that if the ‘prismatic’ effect is simply a more regular form of the Säulengliederung, there is a very constant enamel structure throughout a wide range of reptiles.

Unless true prismatic enamel is found in some other more direct, and possibly unknown, reptilian ancestor, it must be presumed that it originated with the early mammals. At this stage a number of specializations of mammalian teeth and feeding habits took place; for instance, there was the development of the habit of mastication, causing greater wear on the teeth and subjecting them to increased mechanical stresses and strains as well as to the actions of saliva and mouth-acids. In addition, there was a reduction in the total number
of teeth during the life of an animal, only a limited number of sets being formed. Even the advanced cynodonts differed from the mammals in that many of the teeth were replaced several times and the replacement of the incisors was alternate or 'ditischic' (Crompton, 1955). Thus the increased thickness of mammalian enamel might well be a response to new functions of the teeth, and it is worth noting that the massive teeth of placodonts, used for crushing, had an enamel layer much thicker than that covering the teeth of other reptiles. It is also possible that the prismatic properties of mammalian enamel confer greater mechanical advantages in localizing the effects of crushing forces which would be spread over a much larger area in a thin shell of material.

Nevertheless, there are many points of similarity between reptilian and mammalian enamels. The histological appearance of the developing teeth of a crocodile embryo is very similar to that of mammals, and in each case the orientation of mineral crystallites in relation to the enamel surface is the same. Each cylindrical group of crystallites in gorgonopsid enamel may well be the product of one ameloblast, since it is of the correct dimensions; if so, mammalian enamel could have arisen by the extended growth of the ameloblasts, each one eventually acting independently in forming a separate calcified rod surrounded by an organic sheath representing the remains of the original matrix.

Perhaps the whole problem has been oversimplified here, and, indeed, no consideration has been given to the 'tubular' enamel of marsupials and certain other mammals in the proposed evolutionary story. Since no recent accounts of this type of enamel seem to exist and earlier ones (e.g. Tomes, 1897; Mummery, 1914) resulted in differing views, the true affinities with the more usual type of mammalian enamel cannot be assessed. Nevertheless, evidence is in favour of the view that the reptilian enamel described above may be some sort of direct precursor of mammalian enamel. For this reason, an investigation is at present being made into the formation of crocodile enamel, which, since it is comparatively simple in structure, may possibly yield information on some of the fundamental properties of all ectodermal enamels.

I should like to express my gratitude to Mr. F. R. Parrington, of the Cambridge Zoology Museum, and Professor A. S. Romer, of the Harvard Museum of Comparative Zoology, for supplying the reptilian material used in this work. My sincere thanks are also offered to Professor J. E. Harris for all his help during the early part of the work, to the technical staff of the Geology Department, University of Bristol, for preparing many of the sections, and to Professor L. C. Beadle for reading and criticizing the manuscript.

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