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Yale PEABODY MUSEUM OF NATURAL HISTORY

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On the Biology of Cosmine

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DEDICATION

It is not customary for scientific papers of this nature to bear a dedication. However, while the final version of the manuscript was being prepared Professor Alfred Sherwood Romer (1894–1973), my teacher, advisor, and friend, died. He devoted his whole career to furthering the science of vertebrate zoology and inspired countless individual zoologists and paleontologists with the force of his mind and the charm of his personality. It is a risk to dedicate any work to a man of Romer's stature because it is unlikely to live up to his rigorous and demanding standards. Nevertheless, because any merit in my work derives so greatly from his influence, for whatever value this paper may have as a contribution to the literature in vertebrate zoology and paleozoology, I dedicate it to the memory of A. S. Romer.

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ON THE BIOLOGY OF COSMINE

KEITH STEWART THOMSON

ABSTRACT

Cosmine is a unique combination of dentine, enameloid and, at least in the functional sense, some true bone, with the pore-canal sensory system, and is found only in certain early fishes. The biology of cosmine is explored using the single species of crossopterygian fish *Ectosteorhachis nitidus* (Rhipidistia, Osteolepidae) from the Lower Permian of the United States. The structure of cosmine and various unusual, apparently age-related, manifestations of cosmine are described. The internal architecture of the dentine in this fish is found to be controlled during ontogeny by the arrangement of the pore-canal mosaic and developmental models are proposed to account for different patterns of cosmine formation, including blisters, Westoll-lines, continuous cosmine sheets, reduced cosmine and cosmine tubercles, and total absence of cosmine. Cosmine deposition and resorption are discussed in terms of the general biology of the fish, including physiology, the environment, and growth.

ZUSAMMENFASSUNG

Das Cosmin ist gekennzeichnet durch seine einzigartige Zusammensetzung aus Dentin, aus einem schmelzähnlichen Material und aus wenig echtem (im funktionellen Sinne echtem) Knochen, und dadurch, dass es zugleich ein Sinnes-System in seinen Porenkanälen umschliesst. Cosmin kommt ausschliesslich in einigen urtümlichen Fischen vor. Die biologische Bedeutung des Cosmins wird in einer Reihe von Untersuchungen an einer einzigen Art des crossopterygier ähnlichen Fisches *Ectosteorhachis nitidus* (Rhipidistia, Osteolepidae) aus dem Unteren Perm der Vereinigten Staaten erforscht. Der Aufbau des Cosmins wird dargestellt und eine Anzahl seiner ungewöhnlichen Erscheinungsformen, die offenbar altersbedingt sind, werden beschrieben. Es kann gezeigt werden, dass der innere Feinbau des Dentins in diesem Fisch während seiner Individualentwicklung durch die Anordnung des Porenkanal Mosaikes geregelt ist. Entwicklungsmodelle werden aufgestellt und sind erläutert, die es möglich machen, die verschiedenen Erscheinungsformen des Cosmins, wie zum Beispiel Blasenbildung, Westoll Linien, durchgehende Cosmin Schichten, reduziertes Cosmin, Cosmin Höcker und völliges Fehlen des Cosmins, zu verstehen. Die Ablagerung und die Resorption des Cosmins werden im Zusammenhang mit der gesamten Biologie des Fisches und unter Berücksichtigung seiner Physiologie, seiner Umwelt und seines Wachstums behandelt.

РЕЗЮМЕ

Космин является уникальным соединением дентина, эмалеподобного вещества и, по крайней мере в функциональном смысле, до некоторой степени и настоящей кости, с пористоканальной сенсорной системой, и встречается лишь у некоторых древних рыб. Биология космина изучается на одном виде кистеперной рыбы *Ectosteorhachis nitidus* (Rhipidistia, Osteolepidae) из нижней перми на территории США. Описывается структура космина, а также и различные необычные, очевидно связанные с возрастом, проявления космина. Установлено, что внутренняя архитектура дентина у этой рыбы контролируется во время онтогенеза при посредстве расположения пористо-канальной мозаики и предлагаются модели развития, объясняющие различные образцы формации космина, включая волдыри, линии Уэстолла (Westoll), сплошные листы космина, редуцированный космин и бугорки космина, и абсолютное отсутствие космина. Отложения космина и резорбция дискуссированы с точки зрения всеобщей биологии рыбы, включая физиологию, окружающую среду и рост.

1. INTRODUCTION

Cosmine is the name given to an unusual and rather complex association of "hard" and "soft" tissues at the surface of the dermal skeleton in a variety of early fishes. The details of the structure of cosmine may vary sufficiently between the groups in which it is developed—certain fossil Agnatha, Dipnoi and Rhipidistia—that one may suspect that different names should be given to the cosmine of each, but for the moment the generic term will suffice. It describes the condition in which a layer of dentinous tissue encloses a mosaic pore-canal system consisting of flask-shaped pore-cavities containing sensory organs and a complicated network of interconnecting canals including a vascular system. The whole is covered with an enameloid layer and is situated directly on top of the spongy bone and isopedin layers making up the rest of the dermal skeleton.

A unique feature of all cosmine is that although it is functionally a full constituent of the dermal skeleton, it is topographically and to a great extent also developmentally independent of the underlying constituents. The cosmine often forms in large sheets that extend over a large number of otherwise separate dermal elements, covering the sutures between them. In most osteolepid Rhipidistia, for example, the whole of the skull is covered with a shiny cosmine surface broken only by the tiny openings of the sensory pores, and no sign of the sutures between the dermal bone is visible. This obviously creates problems when it comes to growth in area of the units of the dermal skeleton. Thus, a second unique feature of cosmine in Dipnoi and Rhipidistia is that it is subject to periodic total resorption and redeposition, releasing the sutural regions for growth to occur and then covering them up again. Because cosmine may constitute up to 10% of the calcified tissue in the body, the total resorption and redeposition of the cosmine represents an event of major biological significance to the animal.

Cosmine is presently very poorly understood, particularly with respect to the phylogenetic relationships between all the various cosmine-like tissues and the problem of the first incorporation of laterosensory elements into the dermal skeleton of early vertebrates. While the problems of formal structure and phylogeny are extremely interesting, however, it has always seemed to me that the most exciting questions concern the *biology* of cosmine as a compound tissue. What is the functional significance of the sensory canal system and of its enclosure within hard tissue? What is the full nature and significance of cosmine resorption? What is the manner of growth and regeneration of cosmine? What are the developmental relationships between the cosmine and the rest of the dermal skeleton—these apparently distinct units bound together into a solid dermal unit? What are the physiological consequences and constraints of cosmine resorption and regeneration?

It is with these questions of the biology of cosmine that the present study is concerned. I have tried to tackle them by means of a detailed examination of the various manifestations of cosmine in a single osteolepid rhipidistian fish. The fish

chosen is the Lower Permian osteolepid *Ectosteorhachis nitidus* Cope. The reasons for concentrating on a single species of cosmine-bearing fish rather than a comprehensive survey of a group of fishes are twofold. First there is a problem of availability of material. Excellent material of *Ectosteorhachis* is available and comparable material for a significant number of other fishes would be hard to find. Thus no study could be truly comparative. The second reason stems from the first. I have tried very carefully to avoid the classic problem that confronts a paleontologist faced with insufficient material. In such cases, it is only too easy to take some data from one taxon, some from another, compare this information with previously published descriptions from a distantly related group, repeating this process until what emerges is inevitably a hybrid description or interpretation. In the present study, I have dealt only with data and conclusions drawn from a single taxon. The condition in this fish may not be fully representative of conditions in other fishes, but a point of comparison for any future studies has been established. A particular problem in dealing with osteolepid cosmine is the danger of allowing interpretations based on the Devonian Dipnoi to enter the picture. The two groups have very similar but possibly not identical cosmine. Here I have carefully avoided cross-references to Dipnoi wherever possible and data on dipnoan cosmine does not enter into the development of interpretations of the cosmine of *Ectosteorhachis*.

This is therefore a study of the biology of cosmine in a single fish. It is not intended as a generalization concerning cosmine in other osteolepids, let alone other groups of fishes. It is hoped that the study will be of use to those who work with other cosmine-bearing fishes as a point of comparison, and that eventually it will aid in the reconstruction of the phylogeny of this very interesting compound tissue.

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2. MATERIALS AND METHODS

The fossil materials of *Ectosteorhachis* examined in this study all come from the Early Permian Wichita Formation redbeds of north central Texas, the specific geological provenances being given below. Most of the material is essentially unworn specimens or isolated scales and dermal bones. The principal specimens studied are as follows:

PU 14880. The anterior two thirds of a well-preserved fish, very little distorted. Lower Permian, Belle Plains Formation, Wichita Group; north side of the Little Wichita River, below Fulda, Baylor County, Texas.

AMNH 5724. An almost complete fish, dorsoventrally flattened, the ventral surface exposed naturally, the dorsal surface having been prepared. Lower Permian, Admiral Formation, Wichita Group; 6 miles ESE of Ringgold, Archer County, Texas.

MCZ 8676. A rather poorly-preserved whole fish, partially disarticulated. Lower Permian, Moran Formation, Wichita Group; Cottonwood Creek locality, near Anarene, Archer County, Texas.

MCZ 8641. A collection of isolated scales and dermal bones. Lower Permian, Moran Formation, Wichita Group; Little Bitter Creek locality, near Megargel, Young County, Texas. From MCZ 8641, several specimens have been figured and renumbered as follows: MCZ 13339, isolated scale; MCZ 13342-3, sectioned scales.

MCZ 13350. A small fragment of the dermal bones from the infradentary series of the mandible. This specimen is interesting because it shows exceptionally well the phenomenon referred to here as "mixed" cosmine (now in the form of five thin-sections). Lower Permian, Wichita Group; Godwin Creek, Baylor County, Texas (formerly included in MCZ 8946).

YPM 5000. The anterior two-thirds of a well-preserved fish, crushed dorsoventrally. Unfortunately, the surface details are rather poorly preserved. Lower Permian, Belle Plains or Clyde Formation, Wichita Group; circa 3 miles SE of Electra, Wichita County, Texas.

MCZ 13349. Anterior division of the skull roof, worn dorsally but showing cosmine distribution on the snout. Lower Permian, Belle Plains Formation, Wichita Group; Tit Mountain locality, near Dundee, Archer County, Texas.

MCZ 8930. An excellent head, with some associated fragments. Lower Permian, Putnam Formation, Wichita Group; 0.5 miles west of Anarene, Archer County, Texas.

MCZ 8627. An excellent shoulder girdle. Lower Permian, Moran Formation, Wichita Group; Cottonwood Creek, near Anarene, Archer County, Texas.

MCZ 8630. Disarticulated whole fish. Lower Permian, Moran Formation, Wichita Group; Cottonwood Creek, near Anarene, Archer County, Texas.

MCZ 6499. Anterior division of skull and two posterior divisions, one mandible and a small part of the squamation. Lower Permian, Belle Plains

Formation, Wichita Group; Tit Mountain locality, near Dundee, Archer County, Texas.

MCZ 13340 and MCZ 13341. Two partial cleithra showing cosmine resorption; sectioned. Lower Permian, Wichita Group; Godwin Creek, Baylor County, Texas (formerly included in MCZ 8946).

MCZ 8668. Anterior portion of skull. Lower Permian, Belle Plains Formation, Wichita Group; south side of Little Wichita River, below Fulda, Baylor County, Texas.

MCZ 8660. Small collection of disarticulated remains. Lower Permian, Admiral Formation, Wichita Group; Rattlesnake Canyon, near Dundee, Archer County, Texas. From MCZ 8660, the following specimens have been figured and are now renumbered as follows: MCZ 13344–13348, isolated scales.

MCZ 8632. Disarticulated and incomplete specimen. Lower Permian, Moran Formation, Wichita Group; Cottonwood Creek, near Anarene, Archer County, Texas.

MCZ 8648. Incomplete head of a very large fish. Lower Permian, Moran Formation, Wichita Group; Falls County School land, Section 57, A–130; SW of Anarene, Archer County, Texas.

MCZ 8645. Well-preserved skull and some small fragments. Lower Permian, Wichita Group; Bridwell Ranch, 6 miles SW of Windthorst, Archer County, Texas.

MCZ 8662. Serially sectioned whole skull; see Thomson (1964). Lower Permian, Belle Plains Formation, Wichita Group; Tit Mountain locality, near Dundee, Archer County, Texas.

AMNH 7239. Holotype: little of the cosmine is preserved. Lower Permian, Admiral or Bell Plains Formation, East side of Dundee-Atwood Road, Archer County, Texas.

The preservation of the *Ectosteorhachis* material is worth special mention. The specimens show very little sign of post-mortem biological decay such as fungal borings and the wealth of histological detail preserved is quite outstanding. Many of the "whole" specimens seem to have been partially "mummified" before inclusion in the sediment. They were probably stranded and dried subaerially in a cocoon of mucus before being buried and it may be that this has contributed in some way to the excellence of preservation.

The specimens were examined in the usual macroscopic and microscopic ways. In the examination of microscopic thin-sections, the use of polarized light, as well as colored filters, was found invaluable. In addition to light microscopy, several specimens were examined using the scanning electron microscope. Specimens were prepared using the standard techniques and, in addition, a special technique was used to develop the details of architecture of the hard tissues. Essentially this consisted of extremely delicate etching of dermal bone and scale preparations, using a variety of dilute acids. By this means, for example, it was possible to isolate the entire pore-cavity system, with the interconnecting canals and the entire pulp-cavity system, even down to the finer branches of the dentine tubules. Etching could also be carried out in such a way as to remove progressively deeper layers of a preparation, corresponding in a general way to a horizontal serial sectioning process. These etching techniques, when used carefully, provide valuable details of structure, observable in three dimensions, to be compared with parallel observations of similar structures under normal and polarized light microscopy. They depend on different susceptibility to acid

etching of the material of dentine and enameloid, compared with those materials contained within the pore-cavity and pulp-cavity systems.

Specimen MCZ 8662 is a whole skull that had previously been sectioned serially in the transverse plane using the cellular acetate peel technique. This was especially useful in examining the distribution of certain cosmine phenomena and their relationship to underlying structures.

3. PREVIOUS STUDIES OF COSMINE IN RHIPIDISTIA AND DIPNOI

Although the present work is here strictly concerned with the osteolepid Rhipidistia, it is necessary to trace the history of definition and argumentation with respect to the cosmine of both Rhipidistia and Dipnoi in order to understand current views on the problems of cosmine growth and resorption.

The first really accurate account of the internal structure of rhipidistian cosmine was given by Williamson (1849) whose observations were later discussed to such good effect by Goodrich (1907) in his now classical paper on scale structure and evolution. For an introduction to the terminology of the palaeohistology of early fishes, the reader is referred to the work of Ørvig (1951), where the early literature on general bone and dentine structure is reviewed.

Westoll (1936) began the study of the biological aspects of cosmine resorption and growth with his study of osteolepids; for example, he observes: "It is not at all easy to understand the method of growth of a complex continuously curved sheet of cosmine fixed to a series of separate bony plates, themselves growing, and it seems only possible through some process of resorption and reformation" (1936, p. 166; cf. Gross, 1933). Westoll also made the first observations of evidence of cosmine resorption, in material of Devonian osteolepid Rhipidistia and Dipnoi. He concluded that the processes of resorption and redeposition of cosmine were probably seasonal in occurrence and hormonally mediated. Among the direct evidences of cosmine resorption reported by Westoll was the phenomenon of cosmine "blisters"—a matter that has played a central role in subsequent discussion of cosmine resorption. The cosmine blisters described by Westoll (1936, p. 167) consisted of small patches of cosmine sitting like small islands in a larger sheet of cosmine but set off by a circumferential area of resorption. Westoll interpreted these as representing "small relics of older cosmine surrounded by newly deposited material" (1936, p. 167). Westoll also drew attention to the presence of ringlike narrow zones on the dermal bones of Devonian Dipnoi where the cosmine was absent. These markings (subsequently termed *Westoll-lines*: Bystrov, 1942) were interpreted by him as representing "the stadia of past resorptions" (1936, p. 169).

After Westoll's initial observations, workers such as Bystrov (1942, 1959) and Jarvik (1948, 1950) devoted much work to the interpretation and description of the "blister" and the Westoll-line phenomena, and it has come to be thought commonly that the Westoll-lines are characteristic only of Dipnoi, a point that will be discussed critically here.

Bystrov (1942) thought that his thin-sections of dipnoan dermal bone showed that the Westoll-lines defined areas of cosmine belonging to different "generations." He interpreted them as showing that the innermost zone of each dermal bone was the oldest, and the outermost zone the youngest. Jarvik (1950) on the other hand, concluded that the innermost zone was the youngest.

In consideration of rhipidistian cosmine, Jarvik (1950) gave a detailed description of the blister phenomenon and distinguished between two types—superficial and inserted. The superficial blister is a patch of cosmine (of whatever relative age does not matter here) surrounded by a naked zone where the surface of the underlying spongiosa is exposed. The whole is set within a larger area of cosmine. The inserted blister is an entirely different phenomenon where a patch of cosmine has been laid down directly on top of an intact cosmine surface. This work will devote considerable attention to the discussion of inserted blisters, but the superficial variety were not observed. Jarvik considered that the naked zone around the inserted blister represented an area of active resorption. From his detailed observations Jarvik (1948, 1950) concluded that the processes of resorption and redeposition of cosmine in osteolepid Rhipidistia proceeded in a steady manner. Resorption started at a series of localized points where a tiny naked area appeared. These spread and joined up and then within this rough naked area a blister of new cosmine was formed. It was thought that, as resorption proceeded outwards towards the margin of the dermal elements, the new blister increased in size by apposition of new dentinal units: "it is then easy to imagine that the rough areas have, by succeeding stages of resorption, been enlarged, and have coalesced with adjoining rough areas at the same time as the 'blisters', by addition of new dentine at their margins, have increased in size and fused with adjoining 'blisters', until the old dentine layer has been entirely resorbed and replaced by a new and thicker such layer" (Jarvik, 1948, p. 31).

Bystrov (1942) described resorption cavities excavated in the pulp-cavities of the dentinal units of Devonian *Dipterus* and *Osteolepis*. This was firmly denied by Jarvik (1950) who noted that there was, instead, evidence of enlargement by resorption of the vascular canals of the spongiosa. Bystrov (1959) followed up with descriptions of resorption spaces in the pulp-cavities of *Porolepis* (Rhipidistia, Holoptychoidea) cosmine. Unfortunately, in neither case does Bystrov offer photomicrographs of the critical sections.

Jarvik's interpretation of resorption and redeposition of cosmine was based on detailed examination of thin-sections and whole specimens of osteolepid dermal elements. He observed that phenomena of resorption are far more frequent in material from the Middle Devonian of East Greenland than in Westoll's Old Red Sandstone materials from Scotland.

Next, Professor Walter Gross (1956) brought to the study of cosmine resorption in Dipnoi and Rhipidistia an even wider variety of materials from both Devonian and Carboniferous. He studied a very large number of well preserved thin-sections. Apart from his superb descriptions, Gross's major contribution was to isolate the evidence that the nature of the cosmine margins offered with respect to the processes of growth in the cosmine. Gross (1956) distinguished two types of margin which one may term "finished" and "unfinished" (see Figs. 2 and 14). In the former, the layer of enameloid is folded over onto the vertical surface to complete and seal the cosmine margin. In an unfinished margin, this is lacking and the cosmine is simply cut through vertically. Unfinished margins have been subject to resorption. Further, finished margins cannot grow by apposition, for in that case traces of the old margin with its enclosing enameloid protection would be visible in preparations of the material. Gross, whose knowledge of the histology of hard tissues in vertebrates is quite without equal, is firmly confident that any addition of this sort, which would necessarily involve the prior removal of the finished enameloid-covered edge and apposition of new dentinal units including additional portions of the pore-canal system in new cosmine, would be readily

detected in microscopic examination. Since he has not found such evidence, I am bound to believe that this hypothetical phenomenon has not occurred. Gross established, therefore, that any existing cosmine surface is incapable of growth. For a larger area of cosmine to be produced, the whole of the original cosmine must first be removed and then the new, larger portion deposited. It follows from this that all cosmine surfaces on a given specimen at a given time must be of the same age. That is, even if one such surface was preceded by three previous generations and another surface by only one, the actual surfaces present must have been formed at the same time. This view has been developed by Ørvig (1969) in a discussion of Westoll-lines on dipnoan scales.

An important contribution of both Jarvik and Gross was to point out that growth of the cosmine layer of dermal bones and scales proceeds at different times, from different "centers" and under different developmental influences, independently of growth "centers" of the underlying spongiosa and isopedin (lamellar bone).

According to Gross, a blister is an example of wound healing—a local perturbation of the developmental biology of the cosmine. He shows that blisters have "finished" margins and cannot grow in area. Thus both blister and surrounding cosmine must have been formed at the same time—at least insofar as the immediate cosmine tissue is concerned.

Perhaps a central point in understanding the nature and biology of cosmine is that each finished area of cosmine found in a fossil represents the biological activity of a discrete field within the corium through which all cosmine within that area was laid down at the same time. In addition, it is also thought that all the separate areas must have been laid down at the same time, but this is perhaps not so clearly established. Evidence of resorption is provided primarily by the presence of unfinished margins on the cosmine. Finished edges are not in the process of resorption and cannot be added to incrementally. The influence of the fields in the corium upon the cosmine layer of the dermal skeleton is quite independent of the factors influencing the patterns of growth and structure in the spongiosa and lamellar bone making up the rest of the dermal skeleton.

It is not possible to examine the nature of the fields in the corium directly, but one can make inferences on the basis of observations of the cosmine itself. Nonetheless, it is evident that the whole question of resorption and redeposition of cosmine can only be understood, fundamentally, in terms of the biology of the corium tissue. Modification of certain of the above conclusions will be necessary in the light of the results presented here.

THE SPECIAL PROBLEM OF WESTOLL-LINES

It has frequently been stated that Westoll-lines are a characteristic solely of Dipnoi. However, this requires some investigation for, as will be shown in this study, phenomena remarkably similar to dipnoan Westoll-lines can be observed in certain osteolepid Rhipidistia, as noted, for example, by Denison (1951). Because the biological role and significance of Westoll-lines has not been completely worked out, it is difficult to give a really firm definition of the term. A static, purely morphological definition would be: "A Westoll-line is a narrow band of bone at which the cosmine is lacking, and that separates two discrete and fully formed areas of cosmine." And one could well include under this heading a variety of

different phenomena. It is evident, however, that Westoll-lines reflect some aspect or aspects of the ontogenetic history of cosmine and thus a functionally-based definition is necessary. Ørvig (1969) has given a very interesting and plausible explanation of the formation of Westoll-lines on the scales of dipnoans and from this interpretation it is possible to modify the formal morphological definition as follows: "Westoll-lines represent the boundaries between discrete zones of developmental activity in the corium that are responsible for laying down separate areas of cosmine and are thus reflected as gaps between separate cosmine sheets in the resulting tissues." Central to this definition is that the naked zone actually forming the effect of a line in the cosmine does not technically represent a zone of *resorption* of cosmine. It is, rather, a zone where cosmine has not been laid down. In fact, as is evident from the actual manifestation of Westoll-lines in dipnoans (e. g., Gross, 1956, fig. 60), small discrete islands of dentine may be formed in the naked Westoll-line zone and this presumably reflects some local idiosyncrasy of the marginal regions of the cosmine-forming fields in the corium. A developmental model of the formation of Westoll-lines will be presented below (p. 55).

Ørvig (1969) made a study of Westoll-lines on the scales of certain Devonian dipnoans. According to this view, at a very early stage in the life history of each fish, the scales were naked. Then scales in a shield-shaped area at the anterior ventral region developed an area of cosmine. Later (probably after this has been resorbed), these scales grew and an additional band of cosmine was laid down so that now two zones were present, separated by a Westoll-line. This continued until up to four zones of cosmine were present on these anteroventral scales and at this point the rest of the flank scales (naked up to this point) developed a cosmine covering in a single sheet. This hypothesis thus nicely complements aspects of both Gross's and Jarvik's discussions. The innermost portion of cosmine is historically the oldest. Westoll-lines separate areas of temporally distinct origin, but all cosmine is in fact contemporaneous and not formed progressively by gradual apposition of new dentine to existing cosmine. Ørvig notes that the situation in the dermal bones of the head may reflect a very much more complicated set of processes.

If one uses the modified definition of a Westoll-line given immediately above, it is possible to regard several observed features in the osteolepid rhipidistian *Megalichthys laticeps* Traquair as being Westoll-lines. As shown in Figures 24 and 25, several dermal bones of the skull show narrow linear zones separating discrete finished areas of cosmine. These even have the additional attributes of being roughly circular and of being approximately concentric with the dermal bone itself. Now it is certainly an implicit, if imperfectly understood, characteristic of the dipnoan Westoll-line, as explored by Jarvik and Ørvig, that the existence of Westoll-lines reflects some kind of sequential phenomenon in the ontogeny and growth of the dermal element concerned. That is, while all the cosmine is laid down at the same time, e.g., is of the same age, the different fields of cosmine belong to progressive developmental stages [reflecting the progressive resorption and redeposition of cosmine in Jarvik's view (1948, 1950) and reflecting the sequence of growth of the scales in Ørvig's view, (1969)]. The Westoll-lines just described for *Megalichthys laticeps* do not immediately suggest to the observer the sequential interpretation that follows so obviously from the condition in the skull of *Dipterus* (see, for example, Gross, 1956), but the definition of Westoll-lines given above does not require such a process to be involved in their formation. Perhaps the failure to recognize Westoll-lines in the cosmine of Rhipidistia has been due in part to an implicit requirement that all such phenomena must show the full and

completely regular "sequential" pattern. However, in the developmental terms, as outlined in the definition given here, both Dipnoi and Rhipidistia may be seen to show Westoll-lines. At an extreme, it is possible to consider the narrow zone setting off certain kinds of blisters as being a Westoll-line in that it meets all the requirements of the second definition. This subject will be taken up again below.

4. THE BASIC COMPOSITION AND DEFINITION OF COSMINE IN *ECTOSTEORHACHIS*

The formal structure of the cosmine in Devonian and Carboniferous members of the rhipidistian family Osteolepidae, and many other early fishes, has been superbly presented by Gross (1956) and no attempt will be made here to add to that account, to which the reader is referred for full details. The following outline description will serve to introduce the terminology used here. Of the fishes that Gross considers, the structure of the cosmine in *Ectosteorhachis* is most nearly similar to that of *Megalichthys* (Gross, 1956, p. 63–66).

In *Ectosteorhachis nitidus*, as in other osteolepids, the cosmine includes two sets of units—the *pore-cavities* and the *dentinal pulp-cavities*—with a complex meshwork of interconnecting canals (Fig. 22). The pore-cavities are vertical cone-shaped cavities, presumably containing seismosensory neuromasts (see p. 39) opening through the enameloid layer at a minute external opening. At their bases the pore-cavities are constricted and connect via a *basal foramen* with a *basal chamber*. At the base of each principal pore-cavity, four simple lateral *mesh-canals* connect with the adjacent pore-cavities. From the sides of the basal chamber four *cross-canals* connect to the bases of the adjacent dentinal pulp-cavities. Both pore-cavities and dentinal pulp-cavities have a vascular supply from below. The whole arrangement may be further complicated by occasional apparently random vertical cross-connection between canals. The mesh-canals and cross-canals thus form two independent but connected mosaics arranged in a horizontal plane.

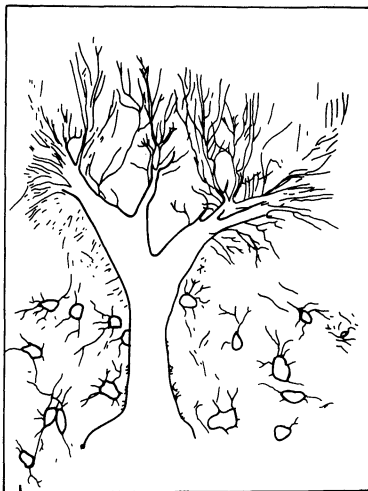


FIG. 1. Detail from vertical thin-section through a scale of *Ectosteorhachis nitidus*, showing a dentinal pulp cavity and dentine tubules. Note that the base of the pulp cavity is surrounded by osteocyte spaces showing typical canaliculi. See also Fig. 22. MCZ 13342. $\times 500$.

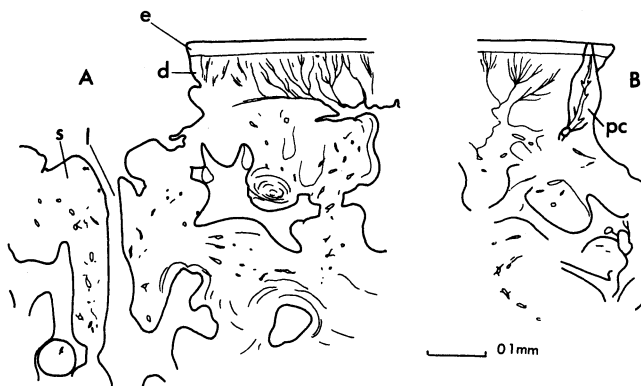


FIG. 2. Detail drawings of two cosmine margins, both from specimen MCZ 13350. Section A on the left shows an "unfinished margin" that is quite natural, with the cosmine and enameloid forming an essentially vertical face close by the opening to a lateral-line organ sunk within the spongiosa. Section B on the right is almost certainly also an "unfinished" margin, but it has also been eroded post-mortem as is shown by the fact that an undamaged pore-cavity, with infilling contents, is preserved just at the edge of the fossil. The later erosion of the margin probably resulted from natural weathering of the fossil. *d* = dentine; *e* = enameloid; *l* = lateral-line canal; *pc* = pore-cavity; *s* = spongiosa.

The pulp-cavity is formed in three parts—a central broad *trunk*, a *crown* of rapidly tapering broad extensions from the trunk, and a branching system of fine tubules that extends through the dentine and into the basal part of the enameloid layer. Virtually all the dentine tubules radiate from the crown region but the walls of the trunk region may occasionally be seen to be perforated by a series of very short tubules that seem to be dentine tubules (Fig. 1). It may be noted that not all the dentinal units contain only a single pulp-cavity. Occasionally there arise from the vascular bed of the spongiosa a series of two or three connected trunks from which dentine tubules radiate. A similar situation has been noted in other osteolepids by Gross (1956: e.g., fig. 31A).

The dentine itself shows signs of internal differentiation (see p. 28) and even under low magnification, thin-sections may show evidence of concentric laminations, particularly at the edge of cosmine sheets. These details will be considered more fully below.

The dimensions of the pore-canal system in *Ectosteorhachis nitidus* fit generally with those given for other cosmine systems (as in the work of Gross, 1956) with the exception that the opening of the pore-cavity at the surface of the enameloid is relatively small. In *Ectosteorhachis* the pore opening has a diameter of only some 6 to 10 μ , and it is roughly this small in most cases in *Megalichthys macropoma* Cope. Gross (1956) gives the range of size in osteolepids as 5–15 μ . The maximum diameter of the pore-cavity base (excluding the entrances to the lateral connecting canals) is in the region of 80–100 μ in all cases, and the whole pore-cavity may be as much as 250 μ high.

Up to this point what has been followed is the simplified definition of cosmine as a compound tissue given in the "Introduction," and one common to modern works in palaeohistology such as those of Ørvig (1951, 1967) and Gross (1956). In fact, however, a qualification needs to be added. In terms of static structures, it is easy to distinguish between the dentine and vascular bone layers of the dermal skeleton. However, the basal chambers of the pore-canal system and lateral connecting canals are not enclosed in dentine as is the rest of the pore-canal

system. Instead, they are enclosed in what appears to be the most superficial part of the spongiosa. Furthermore, it will seem that when cosmine is resorbed, the whole pore-canal system is freed from its connection with hard tissues and this means that not only the dentine and enamel, but also the outermost part of the spongiosa, are resorbed. When new cosmine is redeposited (as Gross, 1956, noted), a new layer of vascular bone is also laid down, forming in a sense a "bone of attachment" for the cosmine layer. From the morphogenetic point of view, therefore, part of the vascular spongiosa acts in concert with the cosmine, and there must be a morphogenetic differentiation between the superficial and deeper parts of the spongiosa that is not demonstrated in formal morphology. The close association of the cosmine with part of the vascular bone of the spongiosa is significant in the developmental biology of the dermal skeleton and its recognition serves to heighten the paradox that the dermal skeleton in these forms is made up of separate types of structure that are nevertheless intimately bound up together.

In Figures 26 to 28, I present the first scanning electron micrographs of cosmine. Figure 26 shows a broken vertical surface with the pore-cavities and pore-canal system of a scale of *E. nitidus* in vertical-section. It will be observed that in simple broken surfaces like this the internal details of the dentinal pulp-cavity system do not show up at all well but nevertheless the trace of a distinct shell of dentinous material is visible around the pore-cavity (see p. 28). figures 27 and 28 show portions of scales of *Ectosteorhachis nitidus* that have been delicately etched so that the whole of the dentine has been removed, leaving the casts of the pore-canal and dentine pulp-cavity and dentine tubules standing free and showing their pattern of interconnections between the two systems.

COMPARISON WITH OTHER EARLY FISHES

Gross (1956) has figured several variations in the structure of the pore-canal system and associated vascular canals between different members of the family Osteolepidae. In his "Osteolepidae gen. et sp. indet., Schliffen Nr 1214u. 1215" from the Baltic Upper Devonian (1956, especially fig. 30) the mesh-canals are double, with a separate *unter Maschenkanal* running under the apparent equivalent of the single mesh-canal in *Ectosteorhachis* and communicating with it by a slit-shaped foramen where the upper mesh-canal opens into the base of the pore-cavity. In this form there is no separate "basal chamber" of the pore-cavity where the four *unter Maschenkanälen* meet. In Gross's "nach unbestimmten Osteolepiden von Estland" from the Middle Old Red Sandstone (1956, fig. 34), the *unter Maschenkanälen* are again present but do not communicate directly with the upper mesh-canals, instead they open into a more well-developed basal chamber which itself opens via a basal foramen into the base of the pore-cavity proper. In Gross's description of the Carboniferous *Megalichthys laticeps* (1956, fig. 51) the *unter Maschenkanälen* are only rarely found, normally only the cross-canals open into the basal chamber which has a quadrilobate opening through the base of the pore-cavity proper, but there may be cross-connections between these cross-canals and the mesh-canals. This description is almost identical to that for *Ectosteorhachis nitidus*, except that in the latter the ramifications of the cross-canal system are somewhat more irregular than appears in Gross's schematic drawings of osteolepids, and no *unter Maschenkanälen* have been found in *Ectosteorhachis nitidus*.

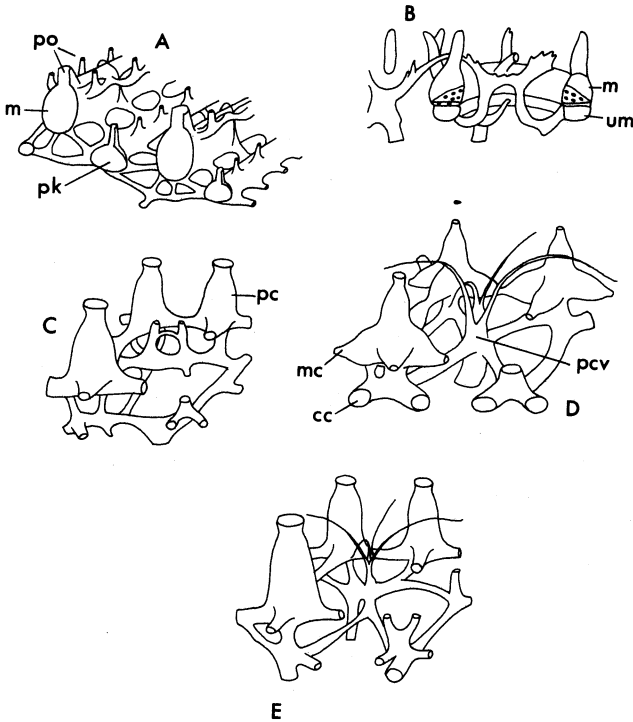


FIG. 3. Restorations of the arrangement of the pore-canal system in five Palaeozoic fishes, after Gross, 1956: A) *Poracanthodes*, B) *Tremataspis*, C) *Dipterus*, D) *Megalichthys*, E) "Devonian osteolepid." *cc* = cross-canals; *dt* = dentine tubules; *m* = Maschenkanal or upper mesh-canal; *mc* = mesh-canal; *pc* = pore-canal; *pcv* = pulp-cavity; *pk* = pulp-canal; *po* = pores; *um* = unter Maschenkanal or lower mesh-canal.

Within the osteolepid rhipidistians one can therefore trace a process of reduction of the mesh-canal system to a single main channel and the formation of a prominent basal chamber in step with the reduction of the *unter Maschenkanälen*. If one then compares the osteolepid fishes with osteostracan Agnatha such as *Tremataspis* (Gross, 1956, fig. 93) this process seems to be part of a consistent scheme of modification of the pore-canal system (see Fig. 3). In *Tremataspis* there is a completely double mesh-canal system with no basal chambers and only very small vertical pore-cavities. The two mesh-canals are separated only by a perforated septum. The arrangement of the pore-canal system in the holoptychoid rhipidistian *Porolepis* and in Devonian dipterid Dipnoi is comparable to that in Osteolepidae. Interestingly, in the earlier forms, there is a tendency for the whole pore-cavity system to be slightly deeper within the dermal skeleton and for a greater part of it to be enclosed within the spongiosa, than in *Ectosteorhachis*.

5. RESORPTION AND DEPOSITION OF COSMINE AS REVEALED IN SUPERFICIAL MORPHOLOGY

One may begin the study with the externally visible manifestations of cosmine in *Ectosteorhachis nitidus*. Unlike most rhipidistian materials, it is rare to encounter a specimen of *Ectosteorhachis* in which the cosmine cover of the skull is complete. The question may immediately be raised whether this reflects something fundamental about the biology of cosmine in this fish, or whether it is an artifact resulting from, for instance, preservation of fishes with a seasonal bias (i.e., from mortality, principally at a stage in the life history when the cosmine is undergoing resorption). This matter will be taken up later. For the moment descriptions of certain different external manifestations of cosmine will be presented, with simple descriptive names where appropriate. The full biological significance of the phenomena described will not be discussed at this point but will be deferred until the final sections of the paper after all the different types of evidence on cosmine structure and development have been described.

Detailed examination shows that the distribution of cosmine over the whole fish is not uniform. There is a distinct pattern of cosmine distribution over the head and trunk. In order to describe this fully it is necessary to deal with the dermal bones of the skull and the scales separately.

DERMAL BONES OF THE HEAD

The cosmine in the head region is of several different types that may be categorized as follows:

1) Major continuous sheets of cosmine. Although one does not find in *Ectosteorhachis* the virtually continuous sheets of cosmine stretching over the whole of the head that are typical of most specimens of Devonian osteolepids, cosmine sheets of significant size are to be found, covering the sutures between adjacent dermal bones in the mandibles. In addition the elements of the gular series always each have a complete and uninterrupted cosmine cover.

2) Discontinuous cosmine. More common than the above are smaller areas of cosmine, often covering part of a suture or set of sutures, but together forming a patchy, and very incomplete cover over the dermal skeleton. Typical examples are seen in Figures 4, 5, 6, 7, 8, 29, 30, and 31. The pattern of the cosmine on the tip of the snout is interesting. Although the surface may not be a single sheet of uninterrupted cosmine, the margins of all the patches and gaps are almost always "finished." Here, very often, a larger patch of cosmine contains several small circular gaps and in these may be located small islands of cosmine resembling either "blisters" or "tubercles." (See categories described below.) The naked

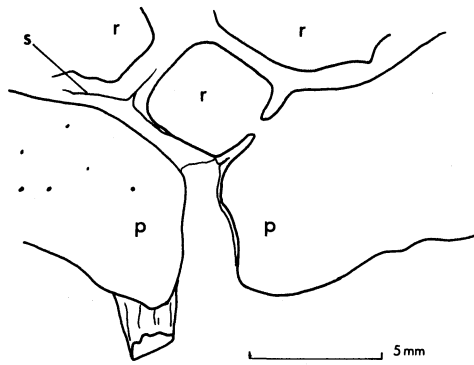


FIG. 4. Sketch of the snout of MCZ 8930 in anterior view showing a bridge developed between two major cosmine areas. *p* = premaxilla; *r* = rostral; *s* = suture.

spaces in the cosmine cover do not usually follow the sutures between the dermal bones exactly, but they do, to a certain extent, reveal the suture pattern. An example of the way in which the cosmine and suture patterns may coincide is shown in Figure 4. This specimen is also most interesting for the way in which two areas of cosmine meet at a delicate bridge over the suture between the premaxilla and a rostral element. This gives the appearance of the fusion of two patches of cosmine. Its development significance will be considered further below (p. 52). It is certainly difficult to categorize the cosmine of the snout region as being either in a stable or unstable condition with respect to cosmine resorption and redeposition.

Only one specimen, MCZ 8630 (Figs. 5A, 29) shows a relatively complete covering of discontinuous cosmine on the upper parts of the head. In all other specimens the upper parts of the head bear only a very incomplete cosmine cover, occurring as small isolated patches with finished margins or as tubercles (see below). Resorption, as indicated by unfinished margins, is observed relatively infrequently. Significantly, where resorption occurs, immediately adjacent margins will be completely finished. This combination of characteristics is discussed separately below, as "mixed" cosmine.

3) Blisters. The inserted blisters that Jarvik described (1950) seem to be of the type where there is a local patch of cosmine surrounded by a larger sheet, all the facing margins of cosmine being finished. This type of blister one may term a *closed blister*. An alternative type is the blister with a finished margin surrounded by cosmine with the enclosing margin unfinished. In the present work it will be termed an *open blister*. The type in which both the blister and the surrounding margin have an unfinished margin has not yet been seen. A closed blister was observed on the mandible of MCZ 8630.

4) Tubercles. This new term describes a phenomenon not hitherto observed in cosmine. The fundamental characteristic of tubercles is that they are formed on a prominent mound or protuberance developed by local growth of vascular bone, on top of which a cap of dentine is formed with a completely finished margin. The typical condition is demonstrated in Figures 32, 33 and 39 which show tubercles from the cheek and postorbital elements of specimens of *Ectosteorhachis* under light and scanning electron microscopy. Typically these tubercles may be found on otherwise completely naked bone, but they are also developed to a lesser extent as small islands in interrupted cosmine areas. It will be seen that the outline of the

cap of dentine and enameloid is always smooth and flowing and that in certain cases there is the appearance of two more or less rounded patches of cosmine having fused together. Each tubercle contains a large number of pore-cavities and dentinal units; even the smallest "seedlike" patches of cosmine contain several units of both systems. The histological structure of these tubercles and their significance are considered further below.

The distribution of the tubercles on the dermal bones of the head is most interesting (Figs. 5, 6, 7, 8, 29, 30, 31 and 34). They are never found on the ventral elements—the mandibles and gular series. They are not found on the very tip of the snout. In these regions, as indicated above, there is normally a more or less complete cover of cosmine. The tubercles are distributed only on the upper parts of the head and are found there on all elements. On the skull table (Fig. 8) they are arranged in two rows on each side of the head. One row passes along the tabular, supratemporal, intertemporal, parietal and rostral bones in a course exactly coincident with that of the principal lateral line of the head. The inner row passes along the postparietal bone to the parietal. In addition, there are usually one large tubercle and also frequently several smaller tubercles on the large medial postrostral bone. On each bone the tubercles are arranged near the center of growth of the bone, the only exception being the very long postparietal element. In most cases the tubercles are found in a radiating pattern roughly following the series of ridges in the spongiosa surface that mark the position of the growth center of the element. Despite the focusing of the tubercle distribution over the growth centers, they nonetheless form distinct rows and one may suggest that the inner row, described above, "joins" the outer row where the latter moves over on to the surface of the parietal bone.

On the cheek series, the tubercles are arranged in radiating patterns on each element, again corresponding to the radiating ridges marking the growth center

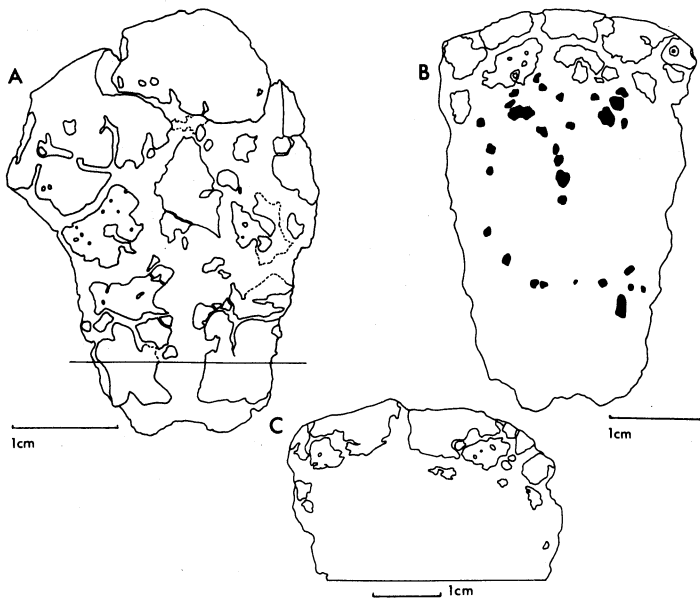


FIG. 5. Drawings of the snout region in three specimens of *Ectosteorhachis nitidus*, showing distribution of interrupted cosmine (unshaded areas), and tubercles (black). A) MCZ 8630, see Fig. 29; B) MCZ 6499, see Fig. 30; C) MCZ 8668, see Fig. 31.

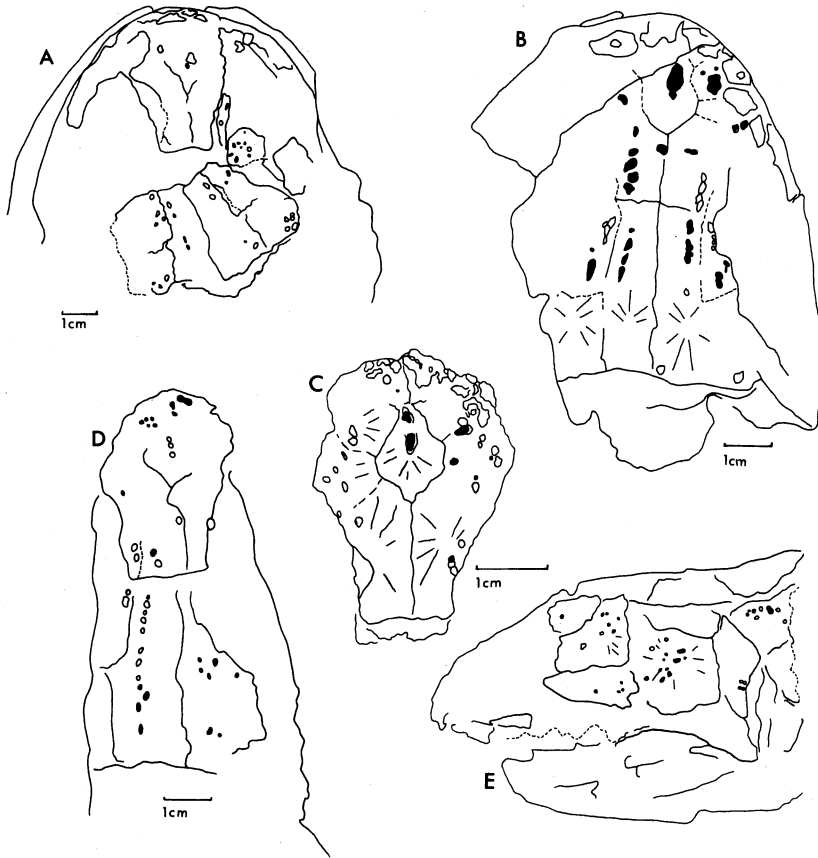


FIG. 6. Drawings showing the distribution of tubercles on the skull of four specimens of *Ectosteorhachis nitidus*. Tubercles are shown in black and the region where a tubercle was present but has been removed (probably in the preparation process) showing as an unshaded area. A) MCZ 8930; B) MCZ 8645; C) MCZ 13349; D) and E) dorsal and lateral views of PU 14480.

of the element. The pattern on the operculum has not been observed completely but was probably the same. There are no tubercles on the dermal shoulder girdle.

Tubercles are also found well developed on the lateral and median extrascapulars. On the former they are again arranged around the growth center of the element, but the situation on the median extrascapular is interesting in that a pair of principal tubercles is developed, either side of the midline, and the pattern seems to be bilaterally symmetrical.

The tubercles developed towards the back of the head and on the extrascapulars may have two shapes. The smaller tubercles are like those on the rest of the head, relatively low and smoothly rounded. However, the bigger tubercles have a tendency to be developed in a hooked shape, with a distinct apex directed backwards. Behind the extrascapulars, the tubercles developed on the dorsomedian scale rows have a similar shape (see below).

The consistency of the pattern of distribution of the tubercles is apparently a matter of great developmental and phylogenetic significance, as will be discussed in a following section (p. 54).

5) Naked areas. These might seem scarcely worth mentioning, but in fact the evidence discussed below (p. 43) suggests that some areas of the dermal skeleton in adult specimens of *Ectosteorhachis* permanently lack a complete cosmine

cover and are internally constructed in a special way. This pertains particularly to the anterior portion of the compound cleithrum.

6) "Mixed" cosmine. An indication of the difficulty that sometimes applies in describing the nature of the cosmine covering in *Ectosteorhachis* can be seen in a detailed examination of the specimen (MCZ 13350) shown in Figures 9, 15, 37, and 38. This specimen also is interesting in that it demonstrates several of the phenomena described above. It is a small fragment from the lower part of the external wall of the mandible and includes portions of two infradentary elements. On the surface of this specimen may be seen both finished and unfinished cosmine patches and small beadlike patches of cosmine that have the appearance of being open blisters, filling exactly the description of the hypothetical stage of Jarvik and Westoll in which a patch of "new" (i.e., finished) cosmine is surrounded by an area of resorption. However, the situation is not so simple, for the other margins on the complicated surface show a mixture of unfinished and finished margins. And it is interesting that of the five large pitlike openings in the cosmine (Fig. 9) two have unfinished and three have finished margins. It will be noted also, especially in examination of the thin-sections (Fig. 15), that the central triangular patch of finished cosmine on this specimen is slightly elevated above the other surfaces. This fragment will be discussed again below. For the purpose of categorization of cosmine phenomena one may term the condition of this fragment "mixed" discontinuous and interrupted cosmine. Such "mixed" cosmine may be found on the mandible, the snout, and the anterior skull table.

These different phenomena having been defined, their relative distribution over the head may now be summarized. In virtually all specimens the anterior part of the snout and the gular elements retain a cosmine cover. The mandibles have either a continuous, discontinuous or very occasionally a "mixed" discontinuous-interrupted cosmine cover. The central and posterior portions of the skull roof, the cheek and the opercular elements have either an interrupted cosmine cover or are naked except for tubercles.

SHOULDER GIRDLE

The complicated nature of the patterns of cosmine resorption and regeneration in *Ectosteorhachis* is pointed up further by consideration of the shoulder girdle. Here, in all specimens seen, the cosmine is restricted to a thin strip along the posterior border of the double cleithrum (for description of the shoulder girdle of *Ectosteorhachis*, see Thomson and Rackoff, 1974). In certain cases it is clear that the anterior edge of this narrow strip of cosmine is unfinished (e.g., Fig. 16) and the remaining cosmine is in fact a remnant of a more extensive sheet. In other cases, however, microscopic examination of the anterior margin of the cosmine shows that it is finished (Fig. 17). Here the thin posterior strip of cosmine is not an eroded remnant of an earlier sheet, but has been laid down in exactly that pattern on an otherwise completely naked cleithrum. In Figure 17, a section is shown through the area of the suture between the two cleithra, and it will be seen that the edges facing each other at the suture are also finished and in this case the topography of the cosmine coincides partially with that of the underlying dermal bones. The permanence of the naked area on the dermal bone of the cleithra is probably indicated by the patterning of the externally exposed surface of the spongiosa. Not only is there a constant and characteristic pattern of ridges; the pattern

includes a single ridge running parallel to the edge of the remnant of cosmine and roughly perpendicular to the main ornament (Thomson and Rackoff, 1974).

SCALES

The scales of *Ectosteorhachis* have not been fully described anywhere. Yet they are most interesting and differ significantly in general shape from those of other osteolepids including *Megalichthys* (with which *Ectosteorhachis* has often, quite erroneously, been taxonomically linked or even synonymized). In the scales of *Ectosteorhachis* (e.g., Fig. 40) the anterior border (the position of insertion in the flank) is developed into a series of pronounced toothlike projections. The inner surface of the scale is relatively smooth, with the prominent diagonal ridge and peg-and-socket articulation seen in Devonian osteolepids (for description see



FIG. 7. Skull and anterior portion of the trunk of specimen AMNH 5724 in dorsal view, with cosmine areas and tubercles indicated in solid black; see also Fig. 34.

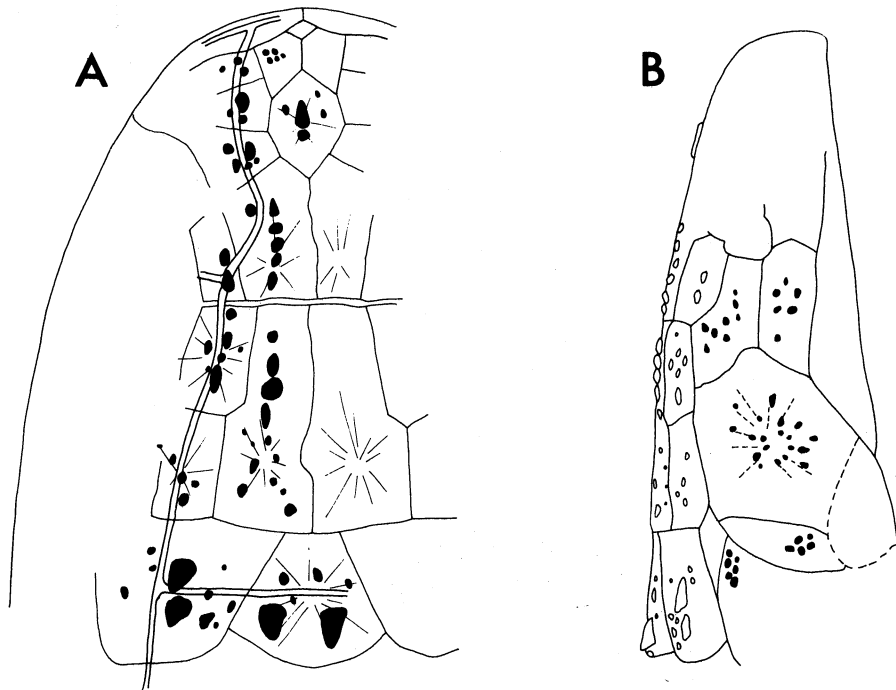


FIG. 8. Diagrammatic representation of the distribution of tubercles on the head (A) and cheek (B) of a "mature" *Ectosteorhachis nitidus*, i.e., of more than 50 cm overall length.

Jarvik, 1948) rather poorly developed. No doubt these differences are associated with the fact that the scale also is relatively thinner than in the Devonian forms and has a less rhomboidal shape. Another interesting feature is that in most specimens the cosmine layer overlaps the rest of the bone at the posterior border of the scale so that its rim is clearly visible from the underside. A variety of different isolated scales from *Ectosteorhachis nitidus* are illustrated in Figures 10 and 40 to 46.

The external appearance of the cosmine on the scales of *Ectosteorhachis nitidus* shows a variety of patterns, suggesting different developmental phenomena. The principal manifestations are as follows.

1) Complete continuous cosmine. This is overwhelmingly the most common condition, in which the scales have a complete cosmine cover over the total exposed surface area.

2) Incomplete continuous cosmine. Certain scales, particularly the very large ones, have a single cosmine sheet on their external surface, but this does not extend to give a complete coverage. A small band of naked spongiosa is seen on the anterior margin of the scale immediately in front of the beginning of the (finished) anterior margin of the cosmine. This is demonstrated in Figure 41. It is noteworthy that in both types of scale—with complete or incomplete continuous covering—the cosmine reaches right to the posterior—dorsal margin of the scale and may even overlap, forming the tiny overhanging shelf previously mentioned.

3) Interrupted cosmine sheet. A very few examples are available of scales in which the cosmine sheet is in the process of resorption and only isolated patches with unfinished margins remain (Fig. 42).

4) Tubercles. These seem to be comparable in general aspect with the similar phenomena observed on the dermal bones of *Ectosteorhachis nitidus*. A small area of

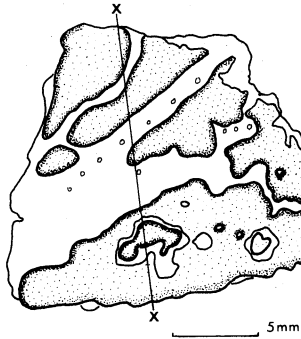


FIG. 9. External surface of specimen MCZ 13350, the specimen is referred to in the text as demonstrating the "mixed" cosmine condition. The line X-X marks the plane of the vertical thin-section shown in Figs. 15 and 37; see also Fig. 38.

the basal vascular bone layer is thickened and capped with a finished layer of dentine and enameloid. Such tubercles are usually found on scales that are otherwise naked, although in a very few cases there may be more than one hillock in each scale, sometimes crowded close together. The principal, or sole, tubercle is always approximately triangular in shape and is always found in the same position—near the posterior part of the exposed portion of the scale, with the apex of the triangle pointing backwards and forming a somewhat hooked shape. Some examples of the shapes of these principal and accessory tubercles are shown in Figures 10, 42 and 43.

Two scale types are worth special mention. The first, shown best in MCZ 13344, seems to show two tubercles in the position where most scales have but one (Figs. 45 and 46). The two tubercles crowd into each other and seem to reflect an aberration in the developmental biology. The second scale type is typified by MCZ 13345. The external surface of this scale shows three separate patches of cosmine separated by Westoll-lines (Figs. 11 and 44). The outer two look almost as if they

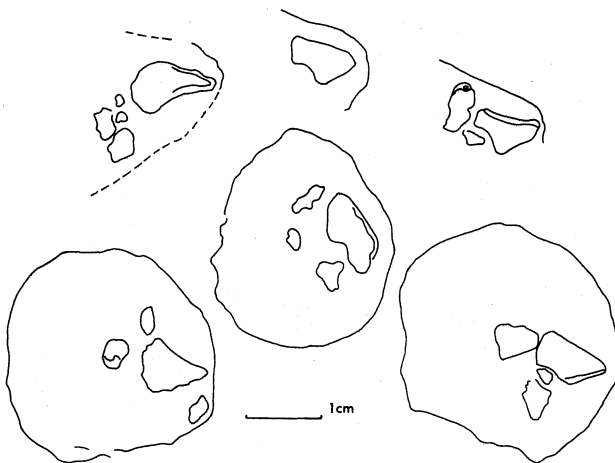


FIG. 10. Outline drawings of a series of scales from near the dorsal midline of specimen MCZ 8676, showing the shape and position of tubercles and cosmine remnants; see also Figs. 42 and 43.

form a ring around the inner part, but in fact do not quite do so. The surface of the inner part is developed at a much lower level than that of the two outer parts. Similar scales were seen in place on specimen PU 14880 and on a fragment showing scales in natural association (MCZ 8630). This type of scale is rare in the material at hand.

PATTERN OF DISTRIBUTION OF COSMINE

Specimens of *Ectosteorhachis nitidus* are available in the size range 45 to 77 cm. Unfortunately, however, except for the very smallest of these specimens, all show approximately the same patterns of cosmine formation and distribution. MCZ 8630 (estimated length 45 cm) is the smallest of the specimens for which can be seen details both of the head and the trunk. It shows a complete cosmine cover on all scales and the most complete cover on the head of any specimen seen. However, even so, the cosmine on the head is discontinuous (Figs. 5A and 29) and does not form the sort of continuous coating seen in other osteolepid fishes. It is probably highly significant that on this specimen no tubercles were observed, either on the head or trunk. Interestingly, specimen AMNH 5724 (estimated length, 47 cm) is not much bigger, but it shows a totally different condition. On the head there is relatively little cosmine—merely some small rounded patches near the sides of the head, together with a large number of well-developed tubercles. On the trunk, the ventral and lateral scale rows have the full cover of cosmine, but the four scale rows immediately lateral to the dorsal midline are made up solely of scales with tubercles, at least as far back as the insertion of the second dorsal fin (Figs. 12 and 35). The rows of tubercles are a pronounced feature of the dorsal surface of the fish and must have been most striking in life. (In the photograph shown here (Fig. 35), the tubercles are more prominent than they were in life because the scales bearing them are displaced so as to elevate the posterior borders where the tubercles are developed). It will be noted that the rows of tubercles lead directly to the less well-defined rows of tubercles on the postparietal bones of the skull roof. All the other specimens show a similar pattern, with the exception that on the roof of the skull only tubercles are found, and no small flattened cosmine patches. The tip of the snout, the mandibles and gular series retain a full cosmine cover throughout the size range. In no specimen was a full cosmine cover seen on the cleithra nor was the posterior marginal strip of cosmine ever lacking.

The limited evidence available seems to indicate reduction in the cosmine cover and an increase in the occurrence of tubercles with growth, but the early stages are, unfortunately, not well represented in our samples. Insofar as a

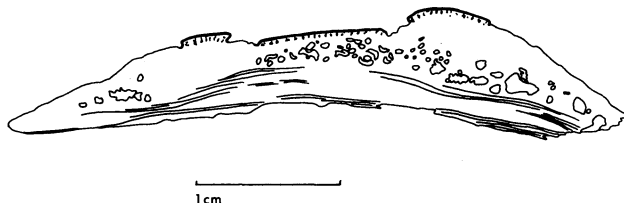


FIG. 11. Vertical transverse section through scale, MCZ 13345; see also Fig. 44.

pattern may be distinguished in the reduction of the cosmine covering, the distribution of the different manifestations of cosmine appears to follow a double gradient—from anterior to posterior and from dorsal to ventral—and this may possibly be taken as confirmation that these processes are hormonally mediated. One might suppose then that the physiological processes of cosmine resorption did not occur all at once over the whole body, but began anterodorsally and proceeded in a wave passing backwards and ventrally along the body. In view of the “mixed” nature of the cosmine on parts of the head, one must conclude that a complicated set of phenomena involving resorption and redeposition of cosmine, with or without growth of the dermal skeleton, may have been in progress at certain times.

At this point it is necessary to leave descriptions of the superficial manifestation of cosmine in *Ectosteorhachis nitidus* and enter into a description of the microscopic structure. When this is completed it will be possible to return to a discussion of the possible significance of the features described.

6. ASPECTS OF THE FINE STRUCTURE OF COSMINE AND THE ASSOCIATED SPONGIOSA

The external appearance of cosmine in its various manifestations in *Ectosteorhachis nitidus* has been described; it is now appropriate to examine the fine structure of the system as revealed by light and scanning electron microscopy. No attempt will be made, however, to repeat the descriptions of the general aspects of cosmine structure that are already available (see "Introduction").

The superficial covering of the cosmine is an enameloid layer that is partially penetrated by the tips of the dentine tubules and, of course, is also perforated by the pore-cavity openings. The enameloid is of varying thickness and, although no systematic pattern of differences in thickness according to position on the body could be found in the material to hand, it is not impossible that such might occur. I have been able to distinguish no consistent differences between the enameloid coverings of the scales and dermal bones.

Considerable differences in the shapes of the pore-cavities of the pore-canal system were noticed in the thin-sections. Again, the material is not complete enough to determine whether the differences occur in a systematic pattern over the whole body. The differences observed involve both the shape of the pore-cavities and their relative size. A good example is seen in sections from the tip of the left mandible of specimen MCZ 8630. At the anterodorsal rim of the dentary the pore-cavities are in the shape of flasks, slightly taller than broad (Fig. 13A). In the more ventral (medial) parts of the same region the pore-cavities have the shape of low pyramidal cones, almost broader than they are tall (Fig. 13C) and the total height is less. This second type of pore-cavity is also found most frequently on the scales. Perhaps the most interesting divergences in pore-cavity shape are seen in the cosmine covering the "tubercles." Here, as shown in Figures 13B and 47, the pore-cavities are relatively very tall and narrow, almost cylindrical. This shape of pore-cavity has only been seen in the tubercles. The differences in the height of the pore-cavities necessarily reflect (or cause) differences in the relative thickness of the whole cosmine layer here.

The internal arrangement of the dentine in the cosmine system is not easy to see in the light microscope, even with the use of polarizing filters. The most readily observable feature in light microscopy is that the dentine is layered in a concentric lamellar fashion at the margins of the cosmine. This presumably indicates a periodicity in its deposition. This feature is not readily observed in the main body of the cosmine but is seen in thin-sections of the tubercles on specimen MCZ 8676 (Fig. 50), where the lamellar arrangement can be seen around the pore-cavities also. An interesting observation, however, is that the main body of the dentine is not laid down directly in concentric zones around the dentinal pulp-cavities but is organized in sheaths around the pore-cavities. This can be seen readily in sections viewed with polarized light (Fig. 49). This is perhaps a little surprising, for one might expect that the bulk of the dentine would be laid down around the

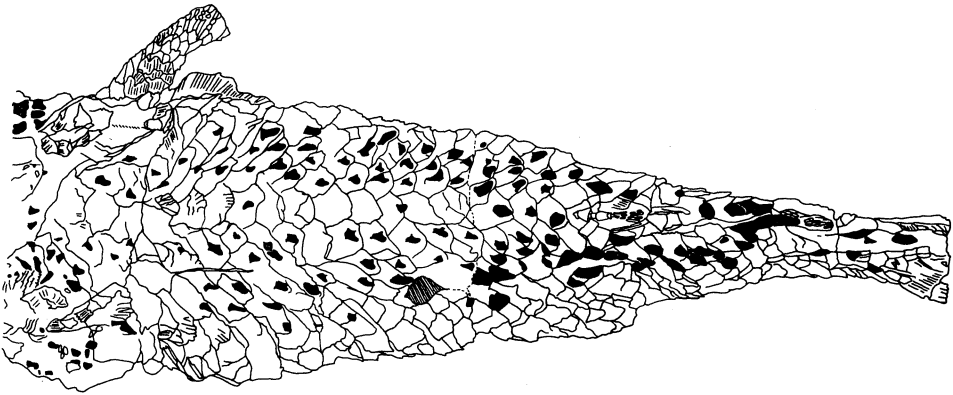


FIG. 12. Trunk of specimen AMNH 5724 in dorsal view, showing the distribution of tubercles; see also Fig. 35.

pulp-cavity (forming some sort of odontode) and that the pore-cavities would lie in the spaces between these units.

Gross (1956, e.g., fig. 46) has already shown the interesting relationship between the direction of the dentinal tubules and the pore-canal system in the cosmine of an osteolepid. It will be seen that although the dentinal tubules all radiate from the dentinal pulp-cavity, at their extremities they converge upon the pore-cavity of the pore-canal system. It was decided to investigate this relationship in more detail using the scanning electron microscope.

By using the slow acid etching method, a series of scales were prepared so as to reveal the internal architecture of the dentine as if a series of progressively deeper sections had been "cut" in the horizontal plane. The most superficial cosmine surface so exposed, immediately beneath the enameloid layer, has the appearance seen in Figure 57. The openings of the pore-cavities are seen as a series of minute foramina and immediately surrounding them is a radially arranged structure obviously representing the top of a shell or cylinder laid down around the pore-cavity. Not far below the surface these cylinders are quite thick and come to occupy a major portion of the hard tissue. As one traces progressively deeper layers of the cosmine, one sees (Figs. 53-58) that the cylinders of hard tissue around the pore-cavities extend down the sides of the pore-cavities,

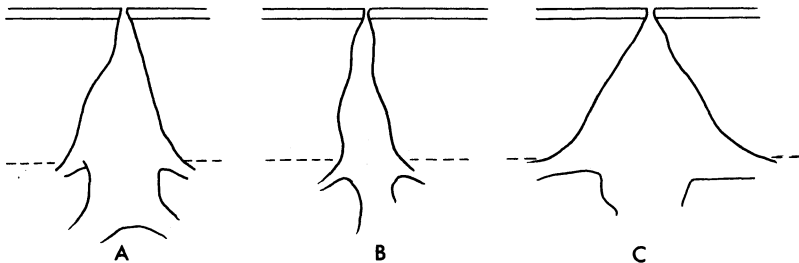


FIG. 13. Diagrammatic representation of the shapes of pore-cavities from three regions of the body of *Ectosteorhachis nitidus*. A) Typical pore-cavity from the dorsal surface. B) Elongate and narrow pore-cavity from a tubercle. C) Low and broad pore-cavity from the ventral surface. Not to scale.

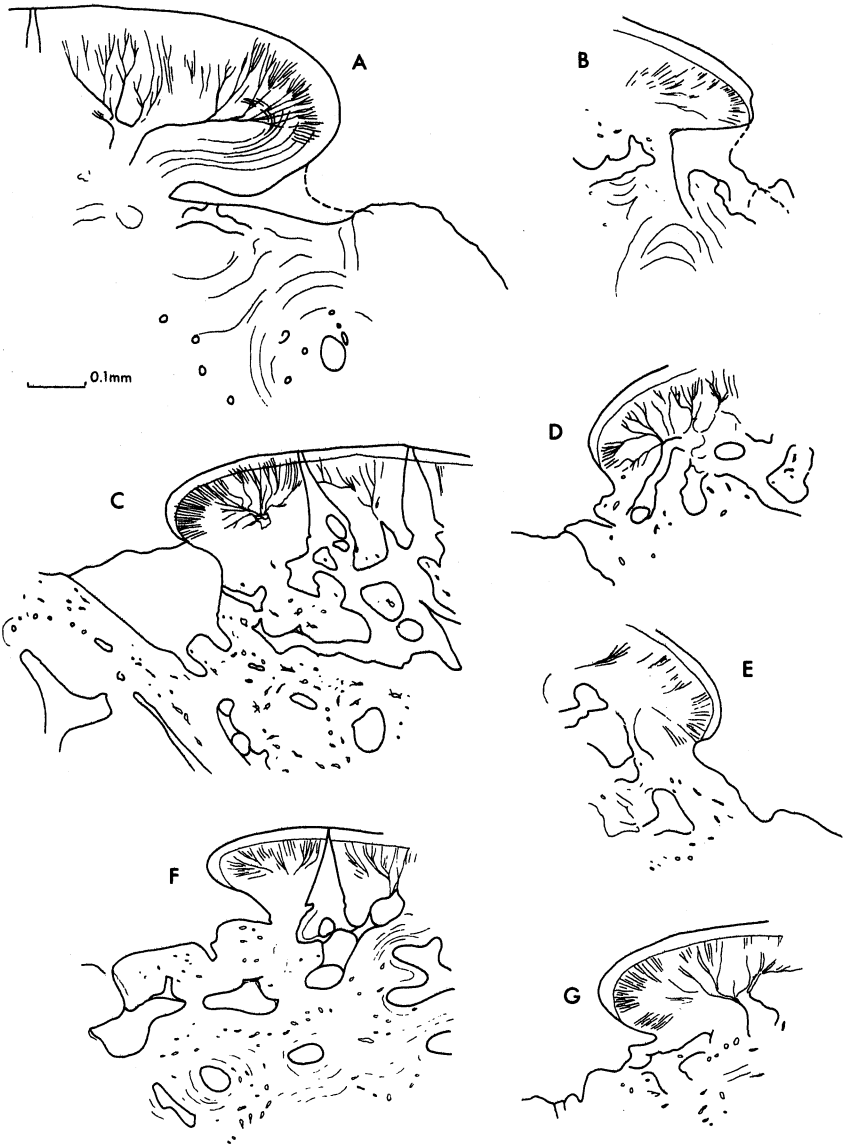


FIG. 14. Seven finished margins, taken from photographs of vertical thin-sections of specimens MCZ 13345 and MCZ 13350.

eventually petering out in the thin walls of the lateral mesh-canals. An interstitial type of tissue is seen between the cylinders around the pore-cavities and within this the dentine tubules are more clearly visible. This interstitial tissue is rather open in texture and loosely organized. At yet deeper levels this interstitial tissue becomes a smaller and smaller part of the cosmine as the cylinders around the pore-cavities become larger. Finally, at the lowest levels between the bases of the pore-cavities, there is a columnar set of structures which are the bony tissues laid down around the vertical vascular canals supplying the base of the dentinal pulp cavity.

Figures 1 and 2 show the region of contact between the base of the dentine and the upper surfaces of the spongiosa. It will be seen that a boundary is demarcated by the limits of the dentine tubules and of the canaliculi from the osteocyte spaces in the vascular bone layer. Osteocyte spaces are never found in a more superficial level than the base of the pore-cavity. Occasionally, osteocyte spaces are seen that give the appearance of two cells having been fused or at the very least having been in contact with each other, but of course one cannot tell whether they might actively have been fused. No physical connection was ever seen between the osteocyte space canaliculi and the dentine tubules. The branching dentine canals from adjacent dentine units frequently fuse.

TUBERCLES

Study of thin-sections (Figs. 47–52, 57–60) shows that the tubercles consist of two main portions—a bony base that is continuous with the spongiosa and a relatively normal cosmine cap. Tubercles are smoothly rounded in cross section and the enameloid outer coating curves down over the margins to finish them. From under the edges of this seal the cross-canals of the pore-canal system pass out presumably to connect with those of the adjacent neuromasts enclosed solely in soft tissues. The internal structure of the tubercles is not modified significantly by the presence or absence of lateral-line canals in the underlying spongiosa, always being far more superficial in position. It therefore seems safe to conclude that there is no direct mechanical association between tubercles and the lateral-line canals or their branches. Pleromic dentine is found in the pore-cavities of the tubercles. Its significance will be discussed in a future paper.

Where the diffuse bone layer in the base of the cosmine is locally thickened to form a tubercle it usually has a characteristic pattern, consisting of a series of more or less vertical vascular channels that stand out in comparison with the more random arrangement of the bone of the spongiosa (Fig. 52). This arrangement is somewhat variable but there is no doubt that the vascular base of many tubercles stands out, in thin-section, as being quite differently arranged from that of the mass of the spongiosa.

RESORPTION

Examination of microscopic thin-sections readily confirms that the structure of unfinished cosmine margins is quite different from that of finished margins and

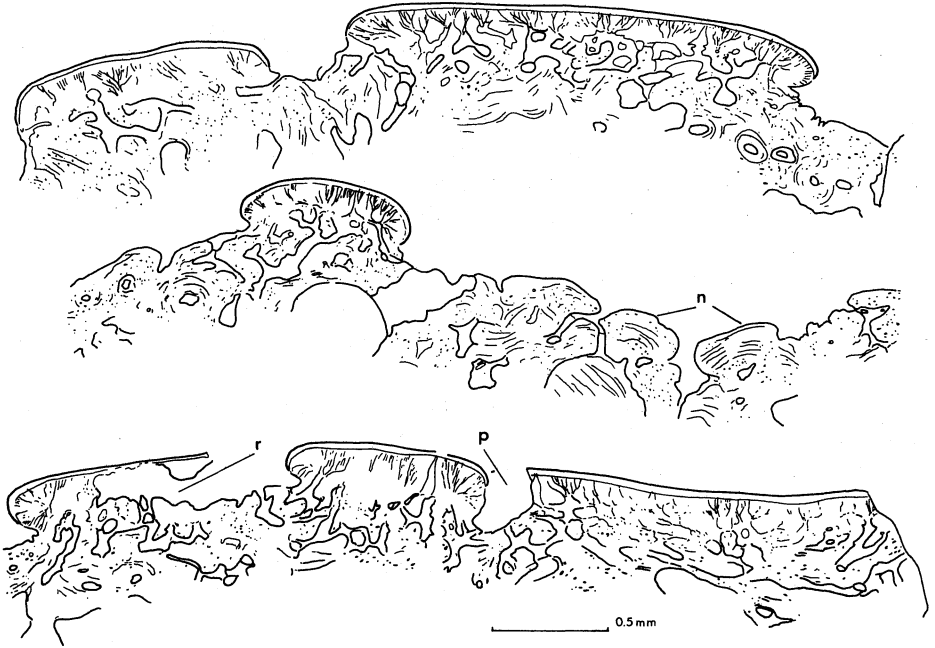


FIG. 15. Drawings of vertical thin-section across specimen MCZ 13350, showing the general structure of the cosmine areas, and the sites of resorption. The section is continuous from the top left to bottom right. *n* = naked spongiosa; *p* = pit; probably under resorption; *r* = area of active resorption; see also Fig. 37.

there can be no doubting Gross's (1956) identification of unfinished margins as having been produced by resorption. Typical examples of these are shown in Figure 2. It will be seen that the margins are more or less vertical, especially the edge of the enameloid layer. The margin is formed without respect to the internal structure of the cosmine.

In a few cases, and one in particular (MCZ 13350), thin-sections give us more complete evidence of resorption in process. As shown in Figure 23 (cf. Figs. 9, 15, 37 and 38) the cosmine margin is unfinished and in addition there is evidence of considerable excavation of the dentine. It will be seen that excavation has proceeded laterally underneath the enameloid and into the cosmine forming a space bordered below by the spongiosa and above by a thin roof of enameloid and traces of dentine. This space has numerous connections with the network of vascular spaces in the spongiosa, some of which may be enlarged. The small number of specimens show clearly that the edges of the eroded space simply cut through the cosmine structure—pore-cavities or dentine—indiscriminately. The "bone of attachment" is simultaneously removed to the extent that the basal chambers of the pore-cavities are completely freed from the spongy bone, as are the cross-canals to the dentinal system. There is no evidence of a selective enlargement or excavation of the dentinal pulp-cavity or tubules, nor are the spaces of the pore-canal system individually modified. It is more difficult to be sure about modification of the underlying spongiosa in connection with the resorption process because the cavities of the spongiosa are normally so variable in size, but the bulk of the spongy bone is not affected.

To the above observations two important qualifications must be added.

1) Not all unfinished edges show evidence of *fresh* resorption. In many cases (Fig. 2A, for example) there is no evidence of excavation of the cosmine. Instead, although unfinished, the cosmine margin has a remarkably stable appearance. This seems to be evidence for the view that a complete uninterrupted cover of cosmine is not always the normal condition for the dermal bones and that where the cosmine is incomplete a stable configuration may have also occurred, perhaps for some time before resorption is continued.

2) Not all finished margins are free from suspicion of resorption. In some cases (Figs. 14B, 14C and 14E, for example) there seems to be the beginning of an excavation starting underneath the overhanging lip of dentine and enamel. Again, it is not always easy to be sure about this because the cross-sectional shape of the finished margin is quite variable.

The question must also be examined, of course, whether the phenomena described here truly represent *in vivo* resorption or merely some type of

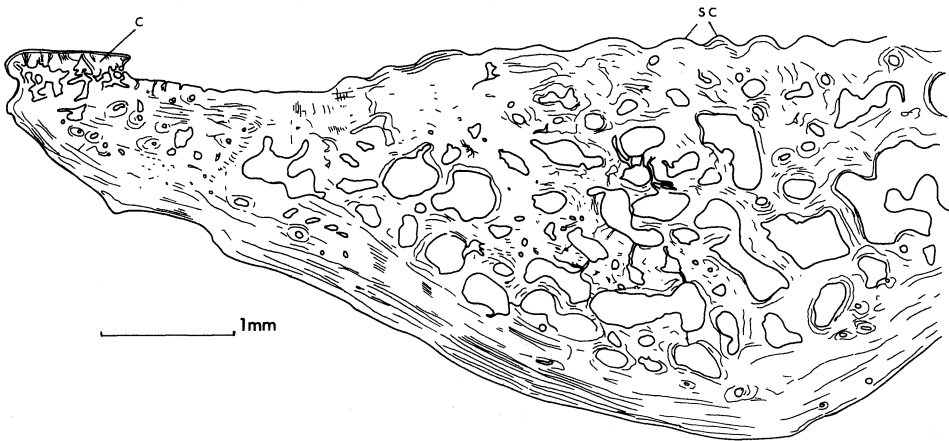


FIG. 16. Vertical-section through the cleithrum of specimen MCZ 13340. The posterior margin is to the left and bears a very narrow band of cosmine with an unfinished margin. *b* = relic of primary osteonal bone; *c* = cosmine; *sc* = sculptured surface of naked spongiosa.

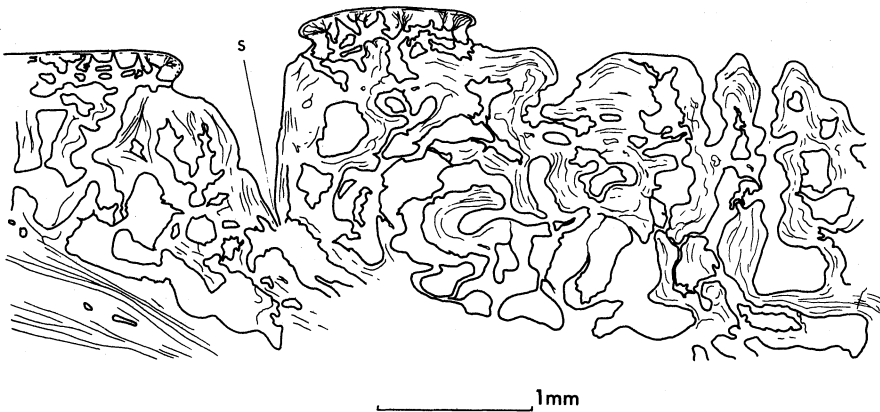


FIG. 17. Vertical-section through the cleithrum of specimen MCZ 13341, at the region of the suture between the two cleithra components, showing the narrow band of cosmine with finished margins either side of the suture. *s* = suture.

post-mortem erosion of the surface tissues. While the evidence can never be completely conclusive, I believe that the following features indicate *in vivo* resorption. First the excavated areas are always localized only within the dentine and the basal bone layer despite the fact that the spongiosa must surely have been less resistant to post-mortem chemical or biological action, once the cosmine had been pierced. This is particularly striking in those cases where the excavated area proceeds laterally to remove the dentine for a considerable area. No removal of the spongiosa was observed in these cases, no evidence of fungal or other borings was seen in the margins of the excavated area, and the excavation did not extend into obvious cavities available within the bone such as lateral-line canals. A possible example of post-mortem erosion is shown in Figure 26.

In the light of these new observations, one may re-examine Bystrov's claim (1942, 1959) to have observed resorption cavities in the cosmine of *Osteolepis* and *Porolepis*. Bystrov himself thought that his material showed selective resorption in the pulp-cavities. However, his figure of *Osteolepis* (1942, fig. 18) could be interpreted as the same sort of resorption as is seen in *Ectosteorhachis*, with a major excavation of the cosmine and the top of the underlying spongiosa, extending laterally a small way under the original cosmine layer. It is not really confined to the pulp-cavity. Bystrov's description of *Porolepis* resorption (1959) is so localized and does not correspond to anything seen in the *Ectosteorhachis* material.

THE SPONGIOSA

Perhaps a more intricate set of structures to understand than the cosmine itself is the underlying spongiosa. Although strictly quite separate from the cosmine in histological terms, this system is sufficiently bound up with the cosmine in terms of developmental phenomena that some observations on its organization are necessary.

The spongiosa is formed as a ramifying set of bony channels (primary and secondary osteons). The system seems generally to be without a unifying pattern (i.e., of random orientation) but in certain cases this is not so. If the spongiosa underlying the cosmine are examined in a typical scale or dermal bone that is covered with cosmine, the random pattern appears. When the spongiosa of a dermal bone that is naked is examined, a different picture appears. For example, in the case of the cleithra, the anterior portions of which are naked, the spongiosa bears a characteristic and constant pattern of superficial ridges and internally is much more dense. Furthermore, the vascular channels in the spongiosa may have a more or less distinct orientation, with vertical main channels dominating the pattern. These local differences in the architecture of the spongiosa may be seen in the cross-sections of specimens MCZ 13340 and 13341 (Figs. 16 and 17). Where the spongiosa is naked it has an entirely different histological appearance from that which underlies cosmine. The former has few vascular channels and shows many secondary osteons whereas the latter is more open and vascularized, with primary osteons having thin walls. This pattern seems to be quite consistent—naked spongiosa always having a more dense and less vascularized structure. It suggests that the naked zones are more permanent than transitory and probably are not destined to regain a cosmine cover.

It has already been noted that the cosmine may functionally interact with a basal layer of true bone, developmentally distinct from the spongiosa, and that

during resorption both the dentinal and bone material is excavated. This set of observations of a functional incorporation of bone into the cosmine is extended by an additional set of data. In examining the sectioned material it is observed that in cases where the spongiosa itself is composed of a dense mass of secondary osteons, the thin layer of diffuse primary osteonal bone is always present immediately underneath the dentine. If the cosmine is absent, the exposed surface of the spongiosa rarely shows a fully diffuse type of primary osteonal tissue at the surface (although relics of it may be seen; see MCZ 13340, Fig. 16).

7. GROWTH OF THE PORE-CANAL MOSAIC

With respect to the all-important question of the manner of growth of the cosmine, it is necessary to examine the dimensions of the pore-canal mosaic during growth. Specifically, one needs to know whether the dimensions of the whole pore-canal/pulp-cavity mosaic in the cosmine increased in size at each growth increment, or whether the dimensions of the lattice work remained constant while more units were added as the surface area increased. In order to check this it is necessary to have a series of specimens encompassing a wide size range, and to measure the dimensions of the mosaic directly. In the case of *Ectosteorhachis*, there were seven specimens for which an accurate estimate of overall length could be gained and on which the details of the pore-spacing on the trunk scales were freely visible. The size range was from 47 cm to 77 cm and the relationship between average pore-spacing and overall length is shown in Figure 18. It will be seen that the mean distance between pore openings increases with length in a straight line relationship. This result comes as somewhat of a surprise since it had been expected, intuitively, that pore-spacing would remain more or less constant during growth because the spacing would directly affect the functioning of the pore-canal system. [The intercept of this straight line gives a minimum pore-spacing of $90\ \mu$ for the youngest (smallest) fishes. However, it does not seem reasonable to extrapolate the nature of the relationships in the 40 to 80 cm range back to cover the 1 to 40 cm range.] With these problems in mind it was decided to investigate this relationship in another osteolepid rhipidistian fish. Again there were problems in obtaining a large enough size range, but for the species *Osteolepis macrolepidotus*, pore-spacing was measured on seven specimens of 15 cm to 32 cm overall length. The results are shown in Figure 18. In this case the pore-spacing remains constant with respect to a twofold increase in size and is in the same range as the minimum spacing recorded in *Ectosteorhachis nitidus*. This strongly suggests that the increase in pore-spacing in the *Ectosteorhachis* specimens measured is a function of their absolute size but the matter is currently under further investigation. At the present one can say definitely that within the observed size range, in *Ectosteorhachis nitidus*, increase in length of the fish is accompanied by an increase in the mean distance between pores. To put it another way, between an overall length of 50 cm and 80 cm, the number of pores per mm^2 on the surface of the trunk scales decreases from approximately 24 to 16. This can only mean that increase in the surface area of the fish is not accompanied by an equivalent production of new neuromast sense organs.

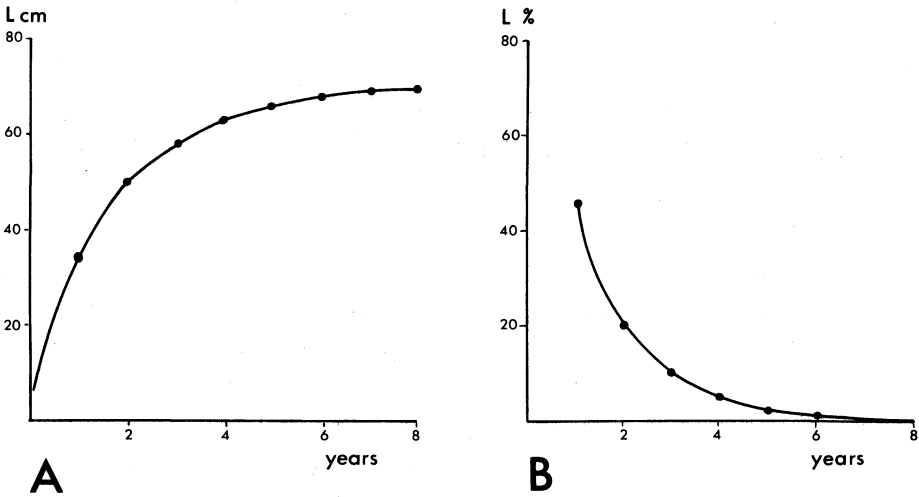


FIG. 18. Graphs showing a reconstruction of the probable course of growth in *Ectosteorhachis nitidus*. A) shows increase of estimated length (*L cm*) with age in years and B) shows percentage increase in length (*L %*) per year.

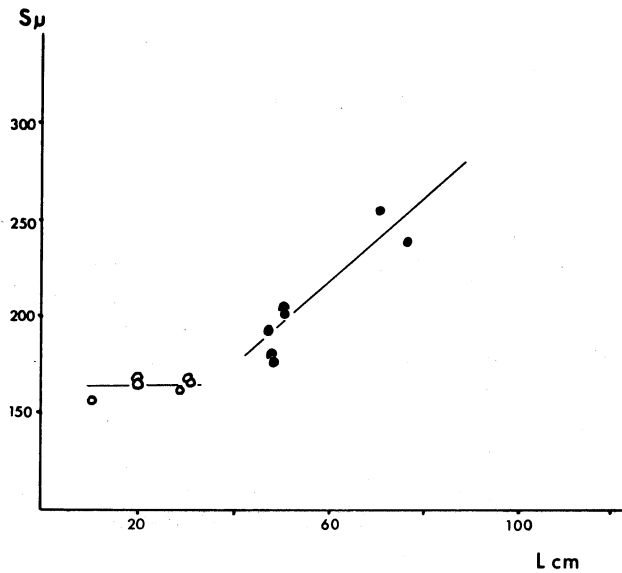


FIG. 19. Graph showing the change in pore-cavity spacing (*S*) with increase in estimated length (*L*), in two species of osteolepid rhipidistians. The open circles represent five specimens of *Osteolepis macrolepidotus* from the Middle Devonian of Scotland. The black circles represent specimens of *Ectosteorhachis nitidus* from the Lower Permian of Texas. The slope of the line drawn through the *Osteolepis* specimens is zero. The slope of the line through the *Ectosteorhachis* specimens fits the equation $y = 91.4 + (2.1) x$.

8. DISCUSSION: THE BIOLOGY OF COSMINE IN *ECTOSTEORHACHIS*

It is easy to concentrate attention upon the essential role of cosmine resorption simply with respect to the growth of fishes such as *Ectosteorhachis nitidus*, because growth would be impossible without such resorption. However, in order to understand the general biology of cosmine it is necessary to investigate its significance in the whole life of the fish. Cosmine and cosmine physiology must have many different roles in the life of the organism. There is considerable evidence to suggest that cosmine has a major mechanical (protective and strengthening) function and it is significant that when it is absent the underlying spongiosa is always greatly reorganized and reinforced. The inclusion of the sensory pore-canal system in a rigid matrix may be critical to its normal operation. Evidently there are complicated morphogenetic interrelationships between the cosmine and the other dermal-bone components. The processes of cosmine resorption and regeneration represent major physiological upheavals that may be significantly correlated with environmental and metabolic factors. The evidence of the physical manifestations of cosmine in fossils of *Ectosteorhachis nitidus* allows us to make some speculations about these factors and then to draw some general conclusions about the biology of cosmine in this fish.

THE PATTERN OF GROWTH OF *ECTOSTEORHACHIS NITIDUS*

It is extremely difficult to discuss the growth of *Ectosteorhachis nitidus* because there is no way of estimating the time factor. In contrast to some other Rhipidistia (see Jarvik, 1948; Thomson and Hahn, 1968) there are no growth rings on the underside of the scales, and it is difficult to be confident about the temporal interpretation of lamellae in the isopedin, although they must surely be laid down in a periodic manner.

Fishes of the size range seen in *Ectosteorhachis nitidus* probably reached maturity in one or two years. It is doubtful that they would have lived much longer than six years, and most probably did not survive more than four. Based on this simple estimate, a hypothetical growth curve for the species may be constructed, as in Figure 18.

It will be seen that growth must have been most rapid in the earliest stages of life and then slowed drastically, but probably did not end completely at the fourth year although it was probably very slow indeed after that point. Growth in the first and second years probably amounted to some 60% of the total growth and for this

reason it seems unlikely that at these stages the fish would have been encumbered with a complete cover of cosmine. Thereafter growth would have been considerably less each year and rather more likely to be restricted to a particular phase of the year when food was most plentiful—alternating, furthermore, with the period of reproductive activity. Therefore, I believe it is most unlikely that a full cover of cosmine, extending over all sutures and preventing continuous growth, would have been developed in any cosmine-bearing fish until the first phase of rapid growth had ended and reproductive maturity had set in. In *Ectosteorhachis nitidus*, that was probably no earlier than the second year of life. Before this time, cosmine was probably present in small patches in connection with the pore-canal sensory system—the enclosure of which in hard tissues seems likely to have been a functional requirement. The possible nature of the early cosmine cover is discussed further below (p. 46). After this, growth of less than 10% per year could easily be accommodated in a period when the otherwise continuous cosmine cover had been resorbed. However, as discussed below, there are strong reasons to suppose that only a very incomplete cosmine cover is present towards the end of the life of the fish.

THE FUNCTION OF THE PORE-CANAL SYSTEM

Extremely little is known of the functional significance of the pore-canal system in early fishes. Denison (1966) has produced the most recent summary of evidence and from this it appears that the pore-canal system is probably the most ancient of the superficial sensory receptor systems in fishes. In certain Agnatha the lateral-line system shows evidence of having evolved from parts of the pore-canal system and in later forms, such as the Osteolepidae and Dipnoi, a direct connection between the pore-canal system and pit-line system can be seen (see Gross, 1956, fig. 40). Still later, the pore-canal system is completely abandoned, leaving the lateral-line canal system, the pit-lines and a variety of discrete cutaneous receptor organs, all of neuromast origin. In the Agnatha, the pore-canal system probably consisted of a large number of neuromast sensors situated in the lower mesh-canals (*unter Maschenkanälen*) with sensory kinocilia projecting through the perforations in the septum separating these from the (upper) mesh-canals proper. The (upper) mesh-canal was filled either with water or mucus that communicated with the exterior at the numerous small pores at the end of small vertical pore-canals. This system gave a generalized system for the detection of localized nonacoustic water disturbances. The lateral-line system developed as a set of structures allowing stricter localization of pressure disturbances in the water, and the neuromasts of the lateral lines were probably derived from the original pore-canal organs by the sinking in of the neuromasts and their special enclosure in large spaces. The pore-canal system persisted, as a more generalized system for the detection of water disturbances. In the Osteolepidae and Dipnoi, it seems clear that the sensory neuromasts were no longer widely distributed in the mesh-canal system but became localized in the new specialized pore-cavities. At first, the neuromast cells were still located in the lower mesh-canals, but only where they met the pore-cavities. The sensory kinocilia passed through the slit-shaped openings from the lower mesh-canals into the enlarged tips of the upper mesh-canals. Thus the sensory hairs were arranged in a series of four strips at right angles to each other around the base of each

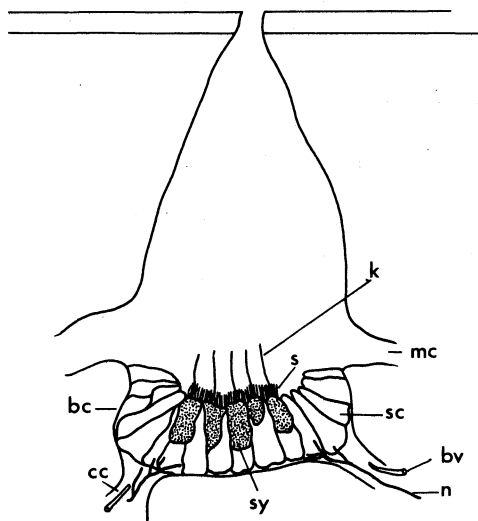


FIG. 20. Reconstruction of the possible contents of a single pore-cavity in *Ectosteorhachis nitidus*, showing a sensory neuromast consisting of sense cells and supporting cells. *bc* = basal chamber; *bv* = blood vessel; *cc* = cross-canals; *k* = kinocilium; *mc* = mesh-canal; *n* = nerve; *s* = stereocilia; *sc* = supporting cell; *sy* = sensory cell.

pore-cavity. Next the mesh-canal system was reduced to a single canal (apparently the upper canal) and a large basal chamber formed where the former lower mesh-canals met under the base of the pore-cavity. The sensory neuromasts were now presumably restricted to this basal chamber and their kinocilia extended upwards into the base of the pore-cavity through the foramen between the two spaces (Fig. 20). The occasional cross-connections between the cross-canal system and the mesh-canal system (like the remnants of the lower mesh-canals sometimes found in *Megalichthys* specimens) presumably existed for the passage of vascular elements to the mesh-canals, these vascular elements having previously been carried in the lower mesh-canals. In all the latter forms the (upper) mesh-canal presumably continued to contain either water or mucus.

In this evolutionary sequence (which is, no doubt, only the most crude approximation of the actual situation) the striking features are: the concentration and reduction of the neuromast organs; the enlargement of the pore-cavity; the migration of sensory elements to a position immediately underneath the pore opening; and a change of the potentiality for directional response, as the neuromasts move from a linear to a point configuration. At the same time, the essential features of the pore-canal system—namely the functional integration via the mechanism of the mesh-canals and the enclosure of the system in hard tissue—are preserved.

All this suggests that the pore-canal system in *Ectosteorhachis* represents the last stage in the evolution of a general system for detection of water pressure disturbances that was being progressively overtaken by the more sophisticated lateral-line and pit-line systems. It may be significant that the young stages of teleost fishes usually show large numbers of free epidermal neuromast organs in the skin and it has recently been shown that in the amphibian *Siren intermedia*, at metamorphosis, the lateral lines break down to form a series of "pit fields" made up of discrete neuromast receptors (Reno and Middleton, 1973). No direct homology can be drawn between these free neuromast receptors and the

pore-canal organs of cosmine-bearing fishes, but it is evident that there is at least a functional similarity in that a diffuse field of neuromasts is a basic form of superficial sensory receptor system.

There are no neuromast structures in living fishes that directly resemble the pore-cavity organ system in cosmine-bearing fishes. No living fish has a system in which the individual neuromast sensors are physically integrated into a meshwork over the whole body, although of course the lateral-line canals and the ampullae of Lorenzini do show a certain interconnection of mucus canals and may be thought to be derived from part of some early pore-canal system. If one leaves aside the question of the interconnection between units via the mesh-canal system, the most obvious parallels to the individual pore-canal organs are probably the simple pit-organs found in Elasmobranchii (see, for example, Tester and Nelson, 1967) in which the sensor is partially enclosed by the hard material of the dermal denticles, and the individual pit-organs of the pit fields in postmetamorphosis *Siren intermedia* mentioned above. A larger discussion of the function of the pore-canal system will be given elsewhere (Thomson, MS).

THE PHYSIOLOGICAL AND ECOLOGICAL CONTEXT

So far I have been concerned with developmental aspects of cosmine and, as with most other workers who have been interested in the problem, I have concentrated upon a connection between cosmine resorption and growth of the fish. That growth is dependent upon cosmine resorption seems indisputable, but is necessary to examine what other physiological and also ecological factors may also play a part in the process. This is particularly important since some of the evidence examined (specifically the appearance of the "mixed" cosmine and patchy local resorption) indicates a pattern of cosmine resorption that is not necessarily linked to overall areal growth of the dermal skeleton.

There may be a change in the mechanical characteristics of the dermal skeleton, according to whether it bears the full cosmine, is naked, or bears only tubercles. It is surely significant that the ventral regions of the dermal skeleton that interpose between the body and the substrate show a complete cosmine cover most frequently. Furthermore, resorption of the cosmine and its regeneration, without doubt, represent a considerable physiological upheaval in the life history of the fish.

The thickness of dermal bones and scales is highly variable, but it is possible to make measurements of a number of cross sections in order to estimate the proportion of the dermal skeleton that is made up of cosmine. In both the dermal bones and scales of *Ectosteorhachis nitidus* the cosmine constituted on average 14% of the total thickness, with a maximum of some 20%. In the scales of *Megalichthys macropomus* cosmine made up on average some 14% of the total thickness. Judged from the drawings in Gross's (1956) study, in scales of Devonian osteolepids the cosmine was of essentially similar proportion: roughly 11% to 25%. It is probably safe to take 15% as an average figure for the relative thickness of the cosmine in the whole of the dermal skeleton of *Ectosteorhachis*, if one assumes a complete cosmine cover. In view of the relative proportions of the dermal and endochondral parts of the rhipidistian skeleton, and the great density of mineralization in cosmine, it is probably a safe guess that the cosmine in such fishes constitutes no less than 5% and perhaps as much as 10% of the total mineralization in the body. Thus,

whatever the primary functional significance of cosmine resorption and regeneration may be, they represent highly significant aspects of the metabolism of calcium, phosphate, and other bone minerals. One may add to this a simple calculation about growth. If the linear dimensions of the fish increase by 5% at each growth phase, then the surface area will increase by roughly 10%. If cosmine constitutes 15% of this new dermal skeleton, then at each growth phase 15% of the original dermal skeleton has to be removed and an amount equivalent to 16.5% has to be laid down anew. It might seem that such major physiological upheavals would be kept to a minimum by a very strong selection, but this is probably too anthropomorphic a view and indeed there are very many Paleozoic fishes that lived quite happily with the constraints that possession of cosmine imposed on their growth and physiology.

From what is known of cosmine it seems that at least once a year a great volume of mineral is metabolized and it is tempting to try to associate this with changing environmental parameters. The most obvious environmental factor that could be linked with calcium and phosphate metabolism is the nature of the medium itself (fresh or salt water)—including seasonal changes in its mineral content, and the degree of food abundance. Another major factor could be the demand for the mobilization of metabolic resources for reproduction, especially in a freshwater environment where phosphate might be in short supply. Certainly, by the very nature of the resorption and regeneration processes, cosmine acts as a *store* for calcium and phosphate and other bone salts. It is important to notice that the physiology of the dentine is quite different from that of the vascular bone, for the dentine mineral is not metabolically active—lacking the constant cycling of the constituents seen in the rest of the skeleton. One is tempted to imagine that cosmine resorption is linked to conditions in which the minerals locked up in the cosmine are in short supply environmentally, or needed metabolically in especially large quantities, or both. Similarly, cosmine regeneration is likely to be limited to periods when abundant food is available, which means conditions of high productivity in the environment. It might be significant that evidence of cosmine resorption is most pronounced in fish from the red beds of Texas, less common but still insignificant in Rhipidistia from East Greenland (Jarvik, 1950) and least common in the Scottish Old Red Sandstone specimens. Geological age does not seem to be a major factor in this, for many specimens of Carboniferous *Megalichthys* show little more evidence of major cosmine resorption than their Devonian relatives.

It is not a reasonable hypothesis that cosmine resorption would take place in order to provide large volumes of metabolically available calcium and phosphate when the fish is living *normally* in fresh water. However, for a fish living in fresh water and needing phosphate for a major seasonal physiological event such as the production of vast numbers of sperm or ova, cosmine resorption might be useful. Similarly, the regeneration of cosmine is presumably possible for fishes living in fresh water, as long as enough food is available. But food of such quantity and quality is most likely to be available during the season of high aquatic productivity (based on plankton) or in the sea, or both. The most extreme pattern of biology that one could associate with these factors would be met in a fish that was anadromous. The fish would have lived and grown in the seas, entered fresh water to breed, lost its cosmine as the reproductive products are formed and through direct osmotic stress, then passed back to the seas where growth and cosmine regeneration are possible at the next season of high productivity. Alternative versions of this sort of pattern will be presented in the following discussion.

The geological evidence concerning the environment in which *Ectosteorhachis nitidus* lived is sketchy. The specimens all come from the redbed deposits of the Wichita Group in the Texas Lower Permian. The deposits have been described by Romer (1958) and are all deltaic in general nature. The landscape in which the fish died was a very low-lying country with practically no elevation. The sea was nearby to the west and while conditions were generally extremely dry, occasional pockets have been preserved in which there was a rich swamplike environment. The specimens are found either as isolated (but not at all eroded or worn) scales or as more or less complete specimens. These latter all give the impression of having been stranded and mummified subaerially before being included in the sediment. Perhaps one could construct that *Ectosteorhachis nitidus* and also many lungfish of the genus *Sagenodus* (actinopterygians are found much less commonly) were living in a deltaic area with productive swamps and barren open sand flats and pools. The whole was probably subject to seasonal flooding and drying. The fish, when caught in shallow pools that dried up, probably died as much through heat and dessication as through an inability to escape—for studies have recently established that *Ectosteorhachis* probably had a fair ability to move amphibiously by means of paired limbs (Thomson and Rackoff, 1974). There the carcasses remained until buried in sediment with the next floods. The richness of the vertebrate faunas is liable to be overestimated from the collections from these localities, according to Romer (1958), and one does not have the impression that there was abundant food for fishes to eat. (The relative scarcity of actinopterygians is probably due to problems of respiratory physiology rather than food availability.)

There is no direct evidence that *Ectosteorhachis* ever occurred in the nearby marine environments. Rhipidistia are usually taken to be basically freshwater fishes, but it has been shown (Thomson, 1969) that probably a large number of genera were capable of surviving in salt water, and the possibility that *Ectosteorhachis nitidus* itself could live in the sea cannot be excluded.

THE DIFFERENT MANIFESTATIONS OF COSMINE IN *ECTOSTEORHACHIS*

The commonly held hypothesis, that cosmine resorption and regeneration is a complete cyclic process occurring once each year in order to allow growth, would lead one to expect to find in the fossils a large proportion of specimens with a complete cosmine cover and only a few with incomplete or totally absent cosmine. Indeed, this is the usual case with most osteolepids. But, the available date for *Ectosteorhachis nitidus* shows us that the most common situation in this species is a type of incomplete cosmine cover, often showing both resorption and regeneration together, and only very rarely indeed is there a complete cosmine cover. This then leads one to ask whether *Ectosteorhachis nitidus* is different from the other osteolepids, whether the available specimens of *Ectosteorhachis nitidus* represent the preservation of some special physiological condition (including extreme age) or whether the material preserved reflects some particular stage in the life cycle not usually "caught" in other species, and possibly also some particularly specialized environmental influences.

I may express the problem in the question: do dermal bones of the head in *Ectosteorhachis* have a complete covering of cosmine similar to that of *Osteolepis* at

any stage of the life history? There is, in fact, only one specimen that suggests the presence of a complete cosmine cover at any stage in the life history. That specimen is MCZ 8630, the skull of which is shown in Figures 5 and 29. The skull of this specimen shows a relatively complete cosmine cover, composed largely of what appears to be interrupted cosmine, in the process of resorption. All the observable scales, dorsal and ventral, on the trunk of this specimen show a complete cover. The estimated length of the specimen is 45 cm. For the scales at least, and probably the skull roof, one can be reasonably sure that a complete covering was present, at an early stage in the life history. *However*, in later stages, either permanently or for a short term, a more complicated situation prevailed.

Some of the different manifestations of the cosmine of *Ectosteorhachis nitidus* may be discussed separately.

1) Discontinuous cosmine. These areas of cosmine have finished margins but may be surrounded by extensive naked areas. The best explanation of this phenomenon is that these discontinuous patches represent areas where a complete cosmine cover had formerly been present, laid down by a single cosmine field, but this field became fragmented at a later stage in the life history. They might also appear in an early stage, as the antecedents of a full cosmine cover. The case of the cleithrum may be significant here. The cosmine on the (double) cleithrum is always either a narrow band of finished cosmine, or a similar band of unfinished cosmine, occupying a greater or lesser area of the posterior margin of the double cleithrum (see Thomson and Rackoff, 1974). The unfinished margin of specimen MCZ 13340 (Fig. 16) seen in cross section, has the appearance of being stable and inactive, rather than the site of active resorption. One may therefore guess that the unfinished cosmine represents the reduction of a once larger cosmine surface that at the next generation was destined to be replaced only by a partial cover.

2) "Mixed" cosmine. More common and more complicated than the discontinuous cosmine cover (but probably very closely related), is the association of patches of cosmine with finished margins, some with unfinished margins and even, apparently, blisters, that has been termed "mixed" cosmine. The first thing that can be said about this phenomenon is that in developmental terms it must reflect the breakdown of a once large cosmine field in the corium. This breakdown affects both the *topography* of the cosmine produced and, more interestingly, the *temporal sequence*, for the different regions of the cosmine are clearly in different developmental stages. The situation can only be explained if it is assumed that the genetic constraints (presumably associated with areal growth of the whole fish) that normally dictate synchronous resorption and regeneration of the cosmine, have been modified. The evidence is not conclusive, but it seems most probable that the appearance of "mixed" cosmine is an age-related phenomenon. The hypothesis may therefore be put forward that "mixed" cosmine is formed in the following sequence. First a complete cosmine cover is resorbed, but at the next regeneration only a discontinuous type of cosmine is laid down. This means that the cosmine field has become disrupted, with only certain areas showing regenerative activity. The production of cosmine by the rest of the original cosmine field may come much later, perhaps not until the immediately preceding discontinuous cosmine is starting to be resorbed. Or, in some areas, cosmine may never be produced again. After this, resorption and regeneration within the "mixed" cosmine proceeds in an unsynchronized manner.

3) Blisters. Blisters may be found in otherwise complete cosmine sheets (for example, on the mandibles) but are most commonly found in "mixed" cosmine in

Ectosteorhachis. Open blisters, consisting of a patch of finished cosmine in a sheet of cosmine with an unfinished surrounding margin, must represent a rather unstable configuration in the cosmine. They are "new" cosmine formed while resorption of the original cosmine sheet is proceeding. That is they belong neither to the original generation nor, strictly, to the next cosmine generation.

The most obvious explanation of isolated blisters is that they represent wound healing, and it is possible to link together explanations of open blisters and closed blisters, as follows. If the surface of the dermal skeleton were injured by abrasion or some similar trauma, the cosmine might be resorbed over a local area. As an interim measure, a patch of new cosmine with finished margins would be formed in the center of the wound, thus giving the open blister. The process of resorption would not necessarily extend over the whole cosmine sheet but could be confined to the immediately affected area, leaving unfinished (but "inactive") margins around the open blister. Then, the whole cosmine is normally resorbed and at the next generation several possibilities are available for the future development of the situation. Cosmine formation may remain out of step so that the next generation a new sheet of cosmine is formed around the existing blister, separated from it by a Westoll-line. This would then leave a closed blister where the two cosmine surfaces are of different "generations." Secondly, the blister of cosmine might be resorbed before the new generation appears. At the next generation the whole area might then be covered with a single sheet of cosmine, leaving no trace of the original blister, or the distinction between the blister and the surrounding cosmine might have become fixed in the cosmine field, so that a new, closed blister would be of the same generation. Finally, it is possible that the blister area would be replaced by a tubercle, without any cosmine being laid down in the surrounding region.

The blisterlike structures found in mixed cosmine (e.g., Specimen MCZ 13350, Figs. 9, 37 and 38) or in a discontinuous cosmine cover (on the rostral region of many specimens, e.g., MCZ 8668, Figs. 5C and 31), are probably not formed through wound healing but represent stages of discontinuity and breakdown of the cosmine cover. Developmentally they are similar: that is, they are formed through the isolation of small units within the original cosmine field that either temporarily or permanently act out of step with the rest of the field. But their origin may be in natural processes rather than trauma. Whether it is strictly correct to call all these phenomena blisters may be doubted, but a better classification cannot be devised without having sure knowledge of the sequence of events leading to their formation. All that can be said at the moment is that the inserted blisters, whether open or closed, all reflect a similar morphogenetic situation, namely, temporal and topographic subdivision of the cosmine field, but their causal origins are obscure.

4) Tubercles on the dermal bones and scales. Tubercles are not found in direct conjunction with other types of cosmine. Two interpretations of their presence are readily available. They represent either a) a final stage in a progressive breakdown of the pattern of cosmine production and are a more or less permanent feature of the mature fish, or b) they are a specialized intermediate stage of short duration in the life history. The first explanation would be strengthened if one could show conclusively that tubercles are a feature only of very mature specimens (see below). In fact, one small specimen (MCZ 8630) has been found in where they are absent. The second alternative explanation of the tubercles is that they represent special adaptations concerned with a particular portion of the life cycle, perhaps with a strong physiological basis. They might

then be some kind of interim specialization between the phases when otherwise complete cosmine sheets cover the dermal skeleton. Perhaps, in later stages of life, the formation of a new cosmine cover first takes several generations and involves a considerable thickening of the spongiosa layer which must be remodeled as adjacent tubercles come to merge with each other. If this second explanation is correct, then the absence of large numbers of specimens of *Ectosteorhachis nitidus* showing a complete cosmine cover must be explained, presumably, as reflecting a bias in the fossilization process that leads to the preservation of large numbers of specimens caught at the same particular phase of the life history.

Specimen AMNH 5724 (Figs. 7, 12, 34–36) gives some assistance in this problem. It is among the smaller fishes in the available size range and shows a large number of smallish round patches of regular flat cosmine where larger specimens show either tubercles or (towards the margins of the head) naked bone. This tends to support the view that there is an age-related breakdown of the cosmine of which the production solely of tubercles is a final stage. No direct evidence can be seen to link tubercles with the sites of former blisters, but it seems quite likely that such a relationship might pertain in certain cases, particularly the blisterlike phenomena seen in “mixed” cosmine.

5) Complete coverings of cosmine. These are either maintained by a process of total removal and total regeneration of the cosmine, or by a patchy “mixed” process. On the whole the former explanation seems far more likely. And it is improbable that a cosmine field that has become disjunct to produce patches of “mixed” cosmine would secondarily become reformed into a single unit. The fact that the gulars of *Ectosteorhachis* specimens always show a full cosmine cover suggests that maintenance of the complete cosmine cover on these elements has a functional significance. Thus any naked stage here is likely to be extremely transient and rarely preserved in the fossil record.

RECONSTRUCTIONS OF THE LIFE HISTORY OF COSMINE IN *ECTOSTEORHACHIS NITIDUS*

The preceding discussion suggests two possible interpretations of the life history and biology of cosmine in this fish. It is not possible to distinguish between them because of the absence of crucial data concerning the mode of life of the fish. Both are constructed in accord with the hypothetical growth curve given in Figure 19. Both include the assumption that during the first and most of the second year of life the young fish bore only small patches of cosmine that were not completed across any sutures and thus did not interfere with growth. Such patches are likely to have been most complete on the ventral parts of the head and trunk, and on the tip of the snout, where they served for protection against abrasion. During this period, growth was rapid and more or less continuous. Following this period of rapid growth, growth slowed down and probably a complete covering of cosmine was present at the end of the second year or early in the third year. After this, growth was more periodic, being restricted to certain times of the year during which the entire cosmine cover was resorbed and then regenerated according to a double topographic gradient: anteroposterior and dorsoventral. This may have continued for two or more further seasons. At present no specimens have been collected representing this phase in the life history.

First alternative: after this stage, growth in surface area fell to a rate of 5% per year, or less, and essentially a new pattern of cosmine appears. Resorption and

regeneration of the cosmine still occurs and in general it still follows the original double gradient. But now the cosmine is resorbed and replaced only in localized patches, resulting in the phenomena first of discontinuous cosmine and subsequently of "mixed" cosmine formed by the subdivision of the original cosmine fields and loss of synchrony in cosmine regeneration. In accordance with the gradients and a functional necessity for keeping a protective cover on the tip of the snout, the snout, the ventral parts of the head, and the ventral scales maintain a complete cosmine cover throughout life. Eventually, however, the rest of the head and the dorsal scales are further modified so that they become largely naked and develop only a series of very localized patches of cosmine in the form of special tubercles. This hypothesis presents a sleek young fish maturing into a grizzled and tuberculated grandfather and has a certain aesthetic appeal. It fits with the observation that larger specimens never have a complete cosmine cover dorsally. The continuance of cosmine resorption in a localized and unsynchronized fashion, not connected with a real growth phenomena, can only be explained in physiological terms. It is necessary to suppose that the release of calcium and phosphates at resorption continues to be physiologically and metabolically necessary, i.e., linked with some other biological process, after growth stops. Most likely this process is reproduction. It is unlikely to have reflected any simple, direct, environmental problem such as a general shortage of these minerals, because if the fish was feeding well enough to maintain healthy metabolism, maintenance levels of such salts would be available. However, the explanation is reinforced if a further factor is added, namely a migration between fresh and salt water during the life cycle of the fish. The correlates of such a migration are discussed below.

For the second alternative explanation, there is no direct evidence, and it is probably less plausible. According to this scheme, the possession of a complete cosmine cover is the normal situation throughout life and it happens that the part of the life cycle "sampled" via the fossil record is biased. The fish normally lose their cosmine in preparation for some major physiological event, probably reproduction and then, once the loss has occurred, there follows a long stage during which it is regenerated. The "mixed" cosmine must then represent a temporary intermediate stage, developed in order to continue protection. On the head and body tubercles are formed as a seasonal specialization, perhaps partly as a protective device and partly perhaps in connection with the reproductive process—for sexual recognition, for example. This second interpretation is rendered more plausible if a further, perhaps extravagant, reconstruction of the environmental conditions is added: it is reinforced if the fish is normally living in the sea where plenty of food is available and is stored for the journey into fresh water to breed. In the passage upstream when the reproductive products are being grown, most all the cosmine is resorbed and the breeding tubercles produced. After reproduction the fish begins its journey downstream, mostly in its "naked" and physiologically exhausted state. It retains cosmine ventrally because it is essential for protection and a bare minimum of "mixed" cosmine is developed that represents local repair of the remnants of the cosmine sheet left over from the passage from the sea. The fish preserved as fossils represent these "spent" fishes passing downstream to the sea. (Note that a marine-freshwater migration for reproduction is also a useful addition to the first alternative hypothesis.) One drawback in such a scheme is that it supposes a very long time in fresh water without full cosmine and a relatively shorter period in the sea before resorption starts again. On the whole, the first explanation is to be preferred.

9. THE DEVELOPMENTAL RELATIONSHIPS OF THE COSMINE

In a wholly fossil group of fishes there seems little hope of discovering anything about the developmental relationships of systems such as the cosmine of the dermal skeleton. Yet it is important to attempt a reconstruction of developmental relationships because in so doing we can test our understanding of the structures involved. There is, of course, a danger of circular reasoning in such attempts, but the effort is probably justified. The following conjectures on the possible developmental relationships between the various components of the cosmine and between the cosmine and the rest of the dermal skeleton in *Ectosteorhachis nitidus* are offered with the hope of illuminating the general subject of cosmine biology in early fishes.

It has generally been accepted (for example, Jarvik, 1950; Gross, 1956; Ørvig, 1951, 1969): that cosmine is developmentally independent of the rest of the dermal skeleton. Its growth proceeds separately, at different times, and with a different topography, from the rest of the dermal skeleton. This view accords with the commonly held developmental interpretation "that the dentine in the exoskeleton... developed in the superficial part of the corium" (Ørvig, 1951, p. 361) while the spongiosa developed in the middle part and the isopedin in the basal part of the corium (see also, for example, Ørvig, 1968, fig. 3). From this it follows that what might loosely be thought of as "fields of influence" in the superficial part of the corium may be supposed to be responsible for cosmine morphogenesis and that separate morphogenetic fields in the middle and basal layers control the formation of spongiosa and isopedin, forming the discrete dermal element—bone or scale. Because the "cosmine fields" may be of large area, and nearly always of a different area from the other fields, cosmine is formed covering the sutures and its formation in no way matches the shape of the dermal elements proper. This lack of topographic matching applies even with respect to the scales, where the cosmine area is always smaller than the total dermal element, being formed only over the exposed surface. Such a view of the morphogenetic relationships is slightly complicated by some of the new evidence presented here because in the functional and developmental sense, cosmine formation includes not only the superficial dentine (traditionally believed to be the sole production of the superficial layer of the corium) but also involves diffuse true bone, merging with the spongiosa proper (traditionally believed to be produced solely by the middle layer of the corium).

In attempting to reconstruct the morphogenetic history of cosmine in *Ectosteorhachis* the interrelationships between at least the following elements must be considered: the pore-canal system (including the mesh-canals); the dentinal formations (plus enameloid layer); the vascular system (particularly the cross-canals); the diffuse vascular bone at the base of the cosmine, and the spongiosa proper. The basal chambers are here considered as part of the

pore-cavities, although they are actually located in the vascular bone layer. In developmental terms this concerns the competency of the epidermis and dermis and various inductive relationships involving the presumptive sensory and hard tissue precursors.

A simple but obviously by no means complete reconstruction of the sequence of developmental events in the formation of cosmine may be drawn up as follows [the whole interpretation depending on current understanding of the role of the neural crest in vertebrate morphogenesis (see, for example, Hörstadius, 1950; Weston, 1970), and the developmental sequences involved in the formation of dentine in teeth (see, for example, Osborn, 1971)].

The first stage is the establishment within the superficial tissue of the rudiments of the neuromasts that will form the pore-cavity sense organs. Presumably these arise either directly from migrating cranial neural-crest cells or from the lateral head placodes that give rise to the lateral-line organs (see Denison, 1966). As the migrating neuromast precursors settle in their final position they establish in the tissues around them a zone in which development of another neuromast is inhibited. This phenomenon of inhibition will determine the spacing between pore-cavity organs and the migrating precursor cells will settle within a relatively constant distance of each other, forming a regular mosaic in the skin. Eventually neuromast rudiments are distributed uniformly over the whole surface of the fish. The next stage is the migration of the neural-crest cells that are destined to become the odontoblasts of the dentine layer. These migrate to the most superficial layer of the dermis, immediately under the epidermis, and here form an essentially continuous layer (Fig. 21). These preodontoblasts induce the overlying epidermal layer to form a dental epithelium that is continuous over the surface of the body, except for the fact that it is interrupted by the neuromast organs. Next, after this dental epithelium has become more differentiated, it reinduces the underlying neural-crest cells so that they differentiate into odontoblasts. In the final cosmine, the dental epithelium and the odontoblasts will participate together in amelogenesis, and the odontoblasts will form the dentine.

The architecture of the hard tissues is determined in large part by the spatial relationships between the two tissue layers—the dental epithelium and the odontoblast layer (superficial dermis)—and the developing neuromast organs. As the odontoblasts are differentiating, the neuromasts are also developing and sinking in slightly to form shallow open pits. The bases of these pits reach down to the top of the vascularized middle layer of the dermis and the neuromasts therefore punctuate the superficial layer. But this layer and the apposed dental epithelium remain essentially undivided.

Because the dental epithelium remains unfolded, the surface of the cosmine is flat (for the formation of raised tubercles, see below). But internally, by the growth and insinking of the neuromast organs, the arrangement of the odontoblasts is modified from the original single layer to include a series of cylinders around the forming pore-cavities (Fig. 21). When the dentine is laid down, its architecture reflects this condition. The dentine is apparently laid down slowly, with a periodicity that is reflected in concentric markings in the fully formed tissue. Basically, the odontoblasts all act in the same way; dentine is laid down as they withdraw to a central point—the site of the future dentinal pulp-cavity formed initially as a knot of blood capillaries and nerve endings. The position of each future pulp-cavity is presumably dictated again by the mosaic distribution of the pore-cavity neuromasts, such that the pulp-cavity rudiments are regularly interspersed between them. One can imagine the neuromasts as

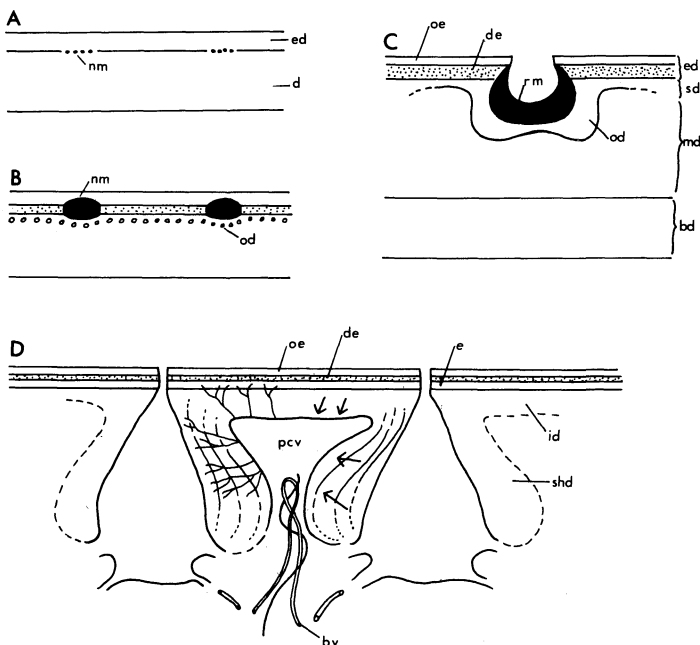


FIG. 21. Diagrams showing the possible sequence of cell migrations and inductions in the formation of cosmine. A) Migrating neural-crest cells arrive at the dermis-epidermis interface and become arranged in discrete groups to form, eventually, the neuromast organs. B) A second wave of neural-crest cells arrives and become distributed evenly in the uppermost part of the dermis. These induce the overlying epidermal layer to form a dental epithelium, except where interrupted by the neuromast precursors. C) The dental epithelium is formed and reinduces the underlying neural-crest cells to form a layer of odontoblasts that is continuous except where interrupted by the neuromasts that are beginning to develop and sink into the uppermost part of the dermis. D) The dental epithelium in an inductive interaction with the odontoblast layer is laying down the enameloid while the odontoblasts are laying down dentine around the pore-cavities and withdrawing towards the pulp-cavities (arrows show direction of odontoblast movement), leaving dentine tubules. *bd* = basal layer of dermis; *bv* = blood vessel; *d* = dermis; *de* = dental epithelium; *e* = enameloid; *ed* = epidermis; *id* = interstitial dentine; *md* = middle layer of dermis; *nm* = neuromast cells; *od* = odontoblast cells; *oe* = overlying epidermal layer; *pcv* = pulp-cavity; *sd* = superficial layer of dermis; *shd* = sheathing dentine.

each being the focus of a gradient and the pulp-cavities being formed at the positions where the lowest points of the adjacent gradients intersect. Because of their position relative to the pore-cavities and the future enameloid layer, the odontoblasts migrate differently. Those around the pore-cavities tend to move principally in a lateral or even superficial direction, and those under the enameloid layer principally move inwards, in order to reach the pulp-cavity. This difference in position is also reflected in a difference in the nature of the dentine produced. That produced by the odontoblasts around the pore-cavity is formed as a broad cylinder of dentine with a radiating "parallel-fibred" appearance. In between these cylinders, the remainder of the dentine is formed as a loose pallial dentine. These differences show up very well in the preparations made for the electron microscope (Fig. 57-62). The topographic distinction between the two sorts of dentine produced resulting from the direction of migration of the odontoblasts seems also to dictate, at least in a general sense, the shape of the resulting "crown" of dentine tubules in each dentinal "unit." The wide tubules that make up the principal branches of the crown seem to be arranged more or less along the line of separation between those odontoblasts that migrate principally

laterally and those migrating principally inwards (Fig. 1). These wide branches obviously represent the course of more than one odontoblast, while the finer dentine tubules may be taken to indicate the direction of migration of single cells.

At some stage before the differentiation of the neural-crest cells into odontoblasts is complete, the neural-crest preodontoblasts induce in the underlying mesenchyme a series of osteoblasts. These form the thin layer of diffuse true bone that encloses the base of the pore-cavities and the lateral connecting-canals, and cements the whole set of cosmine structures to the spongiosa.

[It is interesting that in none of the material of *Ectosteorhachis nitidus* were intermediate stages in the formation of the dentine preserved. However, such stages have been observed by Williamson (1849) in *Megalichthys* and by Gross (1956) in *Latvius*.]

An important feature of this interpretation, which is based on the architecture of the dentine, the orientation of the dentine tubules, and the fact that the dentine tubules of adjacent pulp-cavities may join, is that the odontoblasts must be organized originally beneath the ectoderm in an undivided layer only partially modified by the presence of pore-cavity neuromasts, rather than as discrete groups of cells each originally arranged around a pulp-cavity. That is, there is no indication of the presence of "odontodes." Cosmine is not formed by the fusion of a myriad tiny dentinal units each with its own pulp-cavity with the pore-cavity organs interspersed in the spaces between them. The reverse seems to be true, that the position of the pore-cavities is fundamental to the whole system. These results then provide corroboration for two important points developed by Ørvig (1969, 1972; cf. Gross, 1956) in his consideration of cosmine and the relationship of hard tissues to neuromast organs. First, it is direct evidence that although in cosmine "the individual units structurally speaking are very like small odontodes... all of them must have arisen simultaneously, or very nearly so, in one single common dental papilla..." (Ørvig, 1969, p. 242). Ørvig, whose references are to the cosmine of dipnoans, continues the sentence to the effect that this papilla must be... "of the same size as the cosmine sheets of which they [i.e., the units, KST] are component parts" (1969, p. 242). This point, which is not fundamental to the point in question, will be taken up later when we turn to consider the natural units within cosmine (p. 52). Second, in his paper on the relationship of hard tissue structures to lateral-line organs in early vertebrates Ørvig (1972) notes that "there is no unequivocal evidence to the effect that the initially existing, primitive pit-lines or their primordia, the free neuromast cell groups, ever exerted any special influence on mineralization in their immediate surroundings..." (Ørvig, 1972, p. 152). To the extent that the pore-canal system can be considered a direct precursor of the pit-lines, and to the extent that the pore-canal neuromasts are equivalent to the type of free neuromast receptors hypothesized by Ørvig, the result presented here does form direct evidence of the influence of this type of sensory system on hard tissue architecture. The cylinders of dentine formed around the pore-cavities and containing neuromast receptors are morphogenetically analogous to the ossifications formed around lateral-line canals in the dermal-bone rudiments of higher fishes.

The formation of new cosmine after resorption of the old must follow essentially the pattern given above. The neuromast organs are already present in the superficial tissues and new presumptive odontoblasts are probably formed from undifferentiated cells in the dermis. The formation of tubercles is worth special mention. Here the pattern of events is slightly different. The dental

epithelium is thrown into a domelike fold and the cosmine is laid down in a curved layer over a central core of vascular bone. In this case there is an obvious parallel with the formation of a specially shaped "tooth." The principal role in determination of the shape of the tubercle must lie in the dental epithelium and particularly its interface with the dermis. But it may very well be the case that when a tubercle is resorbed, at least some of the bony base remains, projecting slightly from the surface of the spongiosa. This then forms a foundation upon which a new tubercle is formed.

The remarkable sculpturing of the surface of the spongiosa that is seen in the cleithrum of *Ectosteorhachis* (see Thomson and Rackoff, 1974), occurs only when the cosmine is absent. When cosmine is present the interface between cosmine and spongiosa is irregular and undifferentiated. This suggests that when cosmine formation has ceased permanently in these regions, the epidermis comes to exert a direct influence on the surface of the spongiosa, in the form of a complex folding that is reflected in the outer surface of the dermis. The functional significance of the sculpturing is unclear; it was apparently all overlaid by soft tissues and did not appear on the surface of the animal.

The preceding discussions raise further interesting points concerning the biology of cosmine and the dermal bones in general. However, these points are ones for which concrete evidence is likely never to be found, for they concern the immediate nature of developmental processes rather than their anatomical results. Without wishing to build conjecture upon conjecture, the following observations may be made.

If, as has always been thought, there is no correlation (topographic or temporal) between the centers of ossification of the dermal bone (i.e., the spongiosa and isopedin of each element) and their cosmine cover, then the question of the control of the shape of the cosmine fields—their subdivision and fusion—is completely a mystery. In examining this problem, the question of the organization of the cosmine itself becomes important. It has just been noted that the cosmine probably does not consist of a series of fused odontodes, phylogenetically and ontogenetically discrete, but rather the cosmine is laid down in sheets upon which the pore-cavity organs confer an internal architectural mosaic pattern. However, there is direct evidence that cosmine in *Ectosteorhachis* may be produced in large sheets, in small discrete patches, or in specialized tubercles. In certain cases blisters are formed in which the continuity of a cosmine sheet is interrupted. It is known (e.g., Fig. 4) that closely adjacent patches may "fuse" at a succeeding generation—that is, merge together without trace of a joint, presumably as a direct result of their proximity to each other and of the linking factor of the pore-canal mosaic around which the hard tissue is laid down. All this indicates that any given cosmine sheet is capable of subdivision, and it must signify also at least the possibility that any cosmine sheet may develop in ontogeny through the union of several subunits.

It has been noted that the pattern of rapid growth in the early stages of the individual life history of the fishes is such that it is unlikely that a complete cover of cosmine, continuous over the sutures, was present. It is quite possible that the young fish were completely naked and that when cosmine first appeared it was developed as a full continuous cover over the whole outer surface of the dermal skeleton only at a late stage. However, I believe that a more complicated explanation is more probable, namely that the development of the first generation cosmine cover is directly connected with the ontogeny of the pore-canal mosaic. Possibly, in the larval stages of the life history, the pore-canal system consisted only

of a series of discrete individual neuromast receptors—free pit organs. At a relatively early stage, however, groups of these neuromast receptors lying in the skin grew in size, with the addition of supporting cells, sank deeper into the superficial tissues, and began to acquire the principal set of interconnecting canals—the mesh-canals. This probably occurred in scattered groups of neuromasts located over or near the centers of the forming dermal bones (that is, the vascular bone and isopedin portions of the dermal skeleton). Most probably there is a direct inductive relationship here (see below, p. 55). In any case, there certainly would be a direct functional reason for the formation of these separate patches of the future pore-canal mosaic over the dermal-bone sites, for here there will be maximum stability (freedom from distortion) of the supporting tissues and clearly the whole pore-canal system relies for its function on a great degree of mechanical stability. As each primordial patch of the pore-canal system is forming, a patch of cosmine is laid down around it. Again, there is a direct morphogenetic relationship between the two events: formation of the sensory organs and formation of the supporting hard tissues. The result is the development, in the early stages of the life history, of dermal bone rudiments consisting of vascular spongiosa and isopedin, bearing small patches of cosmine complete with the pore-canal system, dentine and enameloid, and connected with the deeper bony portion of the skeleton at least through the vascular network and perhaps already by a layer of true bone surrounding the pore-cavity bases. Subsequently, growth of the dermal skeleton may occur in several ways (not necessarily mutually exclusive). First the spongiosa and isopedin portion may grow in area and thickness, and more patches of cosmine may be added to the surface, or alternatively, the original patch of cosmine may be resorbed and a new larger patch formed as the pore-canal mosaic is added to peripherally by the addition of new neuromast organs and connecting canals and a corresponding set of hard tissues is laid down around them. Soon the pore-canal mosaic is complete over the whole body surface. At this point, sometime after the second year of life and corresponding with the onset of sexual maturity, the next period of resorption of the cosmine patches is followed by a shift in morphogenesis such that the succeeding cosmine cover is produced in one or more continuous sheets.

This hypothetical account of cosmine ontogeny is supported by a certain amount of direct evidence. First, it seems to be the case that in the earliest stages a complete cosmine cover was not present in *Ectosteorhachis*. It seems reasonable to assume that when the full cosmine cover is again reduced in the later stages of the life history, the resultant discrete patches of cosmine might reflect both the functional requirements of the cosmine system (because it is not totally reduced) and the developmental history of the cosmine. Because function and morphogenesis are bound to be linked, one may be justified in interpreting the distribution of the separate patches of cosmine (mostly tubercles) in “mature” fishes, as an indicator of the position of the primordial patches of cosmine formed in ontogeny and thus of a series of natural subunits of cosmine fields. In fact, as has been seen, they are found on or around the centers of ossification of the dermal bones.

A second piece of evidence concerning the possible ontogenetic units within large cosmine sheets comes from the work of Jarvik on the Devonian genus *Osteolepis*, and is thus not necessarily applicable to *Ectosteorhachis*. In *Osteolepis* Jarvik (1948, figs. 10 and 11, plates 9 and 22; cf. Säve-Söderbergh, 1941; Gross, 1956; Ørvig, 1969) observed that in certain conditions (including the immersion of the specimens in liquids) a series of concentric markings could be seen in the

cosmine. There were often several of these on each bony element and they seemed to bear little relationship to the dermal bone pattern. These markings have not been observed in *Ectosteorhachis*, but they are in more or less the positions that one would predict for our hypothetical primordial patches of pore-canal system cosmine in individual ontogeny. The "centers" of these annular markings are distributed over the surface of the bones in patterns *generally* but not totally, similar to the distribution of tubercles in specimens of *Ectosteorhachis*. A particular point of similarity is that in the median extrascapular of a specimen of *Osteolepis macrolepidotus* (Jarvik, 1948, fig. 11F) there is a pair of such markings in exactly the same position as the a pair of major hook-shaped tubercles in *Ectosteorhachis nitidus* (Figs. 7 and 34). Obviously not all the elements in *Osteolepis* show such a striking resemblance. Jarvik interpreted these concentric markings as a feature of the latest stages of cosmine formation—the "successive growth of blisters" (1948, p. 33), in his hypothesis. The only difference between the explanations is that I consider these markings to indicate patterns set up in the very earliest developmental stages both of the hard tissue patterns and the mosaic of the pore-canal system. In the case of the squamation, the same general hypothetical framework would apply except that, judging from the evidence of scales like MCZ 13345 (Fig. 44) the number of primordial patches of cosmine per scale may be low; in fact, usually they are single and the explanation of cosmine ontogeny of the scales of Devonian dipnoans given by Ørving (1969) may be generally applicable.

These two pieces of evidence therefore suggest that there *are* definite subunits in the cosmine fields and that there is a strong possibility that the first subunits to appear in ontogeny bear a direct topographic (and therefore possibly morphogenetic) relationship to the centers of dermal-bone formation.

Finally, it may be noted that these hypothetical considerations yield possible explanations of the developmental basis for a cosmine "field" and for the disruption of the cosmine cover into separate smaller "fields." In a topographic sense, the cosmine field is the observable single area of cosmine produced—whether a large continuous sheet or a small localized patch. In developmental terms, the cosmine field that produces such an area may have one of two bases. 1) The cosmine field could be a predetermined area of competency fixed as a target for cell migration (neuromasts and preodontoblasts), or 2) the field could be produced as a result of the specific actions of the active neuromast or odontoblast cells, or both, once they are *in situ*. In either case, a mechanism can be added to the explanation whereby the primordial fields can "fuse"—that is, come to act as a single larger unit—and whereby larger units can subdivide. Although it is normally stated that all the hard tissue within a single cosmine sheet is laid down simultaneously, this cannot be precisely so. In fact, although the hard tissue *is* laid down in a single uninterrupted developmental event, it is a lengthy process with a certain periodicity as shown by the internal arrangement of the dentine (e.g., Fig. 50; see p. 28) and probably proceeds sequentially from the center to the periphery. If any sheet has more than one primordial region (see above) then there may be a series of growth centers within the cosmine, all acting together and from each center there will be a "developmental gradient" that will be the basis of sequential deposition of hard tissue. Further, it can be assumed that the activity of each primordial center in the cosmine is under a genetically determined control, such that it may be programmed to produce hard tissue, or not produce hard tissue, at given stages in the life history. Hard tissue will only be produced at a certain level within the overall field of developmental gradients produced by the separate centers. If a large number of centers are activated at a given stage of

cosmine regeneration, they will be sufficiently close together that their developmental gradients will overlap and there will be no "gaps"—that is, no zones where the gradient is too weak for hard tissue formation to be induced. If the activated centers are more distant from each other or the gradient weak, then cosmine will be produced in a discontinuous fashion, with naked areas in between. This explanation can also be modified readily to account for the zonal arrangement of cosmine sheets and Westoll-lines. The "Westoll-lines" formed around blisters are obviously formed in a very similar way—except that the interruptions are caused by the fact that the different cosmine areas are produced out-of-phase and thus the developmental gradients, to whatever extent they might be close enough potentially to overlap, are disjunct.

SYNTHESIS OF DEVELOPMENTAL HYPOTHESES

The two hypotheses given above, of the ontogenetic relationship between the hard tissues and soft tissues in cosmine, and of the ontogenetic history of the cosmine sheets, may be brought together into a simple hypothetical scheme of the developmental biology of cosmine and the dermal skeleton as a whole.

There is ample evidence in the literature on the dermal skeleton of fishes (e.g., Pehrson, 1922; Moy-Thomas, 1938, 1941; Devillers, 1947) of a morphogenetic relationship between the centers of dermal-bone formation and the developing neuromasts of the lateral-line system. A similar situation must have occurred in *Ectosteorhachis* also, and the doubts that exist about the nature and direction of the causal interactions concerned must be included in the present considerations. In the development of the dermal skeleton as a whole there are three main sets of migrating cells, whose activities will determine the nature of hard tissue formation. The lateral-line (and pit-line) neuromasts will be concerned in some way with the centers of formation of isopedin and spongiosa. The preodontoblasts will be responsible for the formation of dentine and enameloid. The neuromasts of the pore-canal system will determine the gross architecture of the dentine and enameloid, and in all probability the sequence of deposition (see above). It is significant that all three types of cell are ultimately of neural-crest origin.

It may be suspected that there was a definite sequence in the migration of the three types of cells. The various possibilities are as follows.

- 1) The first cells to arrive in the superficial tissues are the migrating precursors of the lateral-line neuromasts. They migrate to previously determined target sites in the dermis and there begin to induce the formation of osteoblasts in two main generations—forming the isopedin and spongiosa respectively. (I am not including here any possible contribution, by delamination, to deeper-lying skeletal elements.) Next the pore-canal neuromasts begin their migrations and become distributed evenly all over the body. Finally the preodontoblasts migrate to a superficial position in the dermis, and are formed in an even layer all over the body surface. There soon begins induction of the dental epithelium and reinduction of the odontoblasts. Then, groups of hitherto isolated pore-canal neuromasts begin to develop connections with each other and with the incipient pulp-cavities of the dentinal layer. Because this is a double process involving the interaction of the neuromasts both with adjacent neuromasts and with adjacent

pulp-cavities, it is likely that the two processes are exactly contemporaneous. If this is the case, and given the high probability that these primordial patches are formed at or near the centers of formation of dermal bone (isopedin and spongiosa), it is most probable that there is a direct (inductive?) relationship between the events occurring in the dermal bone and in the cosmine. The final stage is the induction by the odontoblasts of mesenchyme cells that will form the "bone of attachment" linking the cosmine and spongiosa.

2) An alternative hypothesis could be developed according to which the pore-cavity neuromasts and preodontoblasts arrive first at the target sites and the developing primordial patches of cosmine induce the formation of dermal bone in the deeper parts of the dermis. These centers of dermal-bone formation then form the target sites attracting the migrating lateral-line neuromasts to the same sites. This is a far less likely hypothesis. A variant of this second hypothesis is that the lateral-line neuromasts and pore-canal neuromasts are actually differentiated *in situ* from a single migration of neuromast precursors. This also seems unlikely.

In any such discussion as this the key questions always become: what is the nature and origin of the target site? How is it determined? The target site is a region that has somehow acquired "competency." A region of the dermis is "competent" such that mesenchyme cells react inductively with the lateral-line neuromasts to produce osteoblasts. A region of the epidermis is competent to react inductively with a neural-crest cell and produce dental epithelium. The same neural-crest cells may be competent to react inductively with the dental epithelium to produce odontoblasts. Some osteoblasts and odontoblasts are produced immediately; others are produced (develop or manifest their competency) later when growth occurs and new cosmine is laid down. This competency is the result of a whole set of developmental processes occurring at a level that cannot be explored with fossil material. The phylogenetic significance of these discussions of cosmine morphogenesis will be discussed in a separate work (Thomson, MS).

SUMMARY

In summary of the lengthy descriptions and discussions of cosmine in *Ectosteorhachis nitidus* given above, the following points are of importance.

1) Cosmine, at least in *Ectosteorhachis* and probably in other osteolepid fishes also, is functionally associated in resorption and regeneration with a basal layer of diffuse true bony tissue in addition to the dentine and enameloid that enclose the pore-canal and pulp-cavity systems. New terminology is introduced for the component structures of cosmine.

2) Westoll-lines occur in Rhipidistia (family Osteolepidae) as well as Dipnoi and may be defined best in developmental terms as reflecting the boundaries between zones in the corium that are responsible for laying down separate areas of cosmine.

3) The scales of *Ectosteorhachis nitidus* have a characteristic shape with a "toothed" anterior margin.

4) A variety of different manifestations of the cosmine may be seen in *Ectosteorhachis nitidus*, from complete sheets of cosmine to isolated patches of cosmine, special tubercles with a thickened bony base, and a peculiar "mixed" cosmine where the processes of resorption and redeposition of cosmine seem to be

occurring simultaneously. Many areas of the surface of the dermal skeleton seem permanently to lack cosmine in older fishes.

5) Plotting the pattern of these cosmine phenomena, it is seen that a complete cosmine cover is always maintained at the tip of the snout and on the ventral side of the fish, but usually very incomplete cover is found in older (larger) specimens. In all except the smallest specimens, the dorsal and dorsolateral surfaces of head and trunk bear only tubercles on naked dermal bone.

6) The tubercles have a consistent distribution. They occur on the dorsal and lateral parts of the head, including the opercular series, but not on the lower jaws or ventral dermal elements, and not on the cleithrum or clavicle. On the trunk, tubercles have been found on the four longitudinal scales rows either side of the dorsomedian scale row, and on that median row itself as far back as the insertion of the first dorsal fin.

7) Microscopic examination of the cosmine shows that there are local differences in the shapes of the pore cavities, especially those in the tubercles.

8) The internal architecture of the dentine is revealed by the use of etching preparations for the scanning electron microscope. The dentine is of two types—a cylinder or sheath of radially arranged dentine around the pore-cavities and a looser textured dentine in the interstices between the cylinders.

9) Evidence of the process of resorption is found in thin-sections of the cosmine. Resorption starts at the edges of a sheet of cosmine or at positions within the cosmine sheet, or both. In both cases the first part attacked is the base of the cosmine and then a large resorption space is formed by the simultaneous erosion of dentine and bone. Resorption does not follow the internal architecture of the cosmine and the cells involved do not seem to be derived from existing odontoblasts or osteoblasts.

10) Resorption of the cosmine seems to be associated with remodeling of the whole spongiosa, with many secondary osteons being formed. This is particularly marked in those portions of the dermal bones that seem to lack a permanent cosmine cover and the surfaces of such elements may be highly sculptured.

11) Any single sheet of cosmine is laid down by an essentially undivided cosmine field in the corium and not as fused odontodes, but this field may show traces of earlier ontogenetic stages when the pore-canal system was becoming organized. The formation of the cosmine field is directly linked morphogenetically with the ontogeny of the pore-canal system. The cosmine field is capable of subdivision, possibly returning to a pattern reflecting the original sites of organization of the cosmine and pore-canal system.

12) Blisters represent either wound healing or, in the case of “mixed” cosmine, a special case of subdivision of the cosmine field as part of a diffuse process of cosmine resorption and regeneration.

13) Cosmine represents up to 10% of the total calcification in the body and thus cosmine resorption and regeneration are major physiological events in the life history.

14) An hypothesis is put forward to explain the seasonal nature of cosmine resorption in connection with a need to make large volumes of phosphates available for reproduction as well as in connection with growth of the dermal skeleton. The ecological correlatives of cosmine resorption suggest that *Ectosteorhachis* may have migrated between sea and fresh water to breed.

15) During the first and probably at least part of the second year of life, *Ectosteorhachis* lacked a complete cosmine cover, although a partial cover may have been growing from a very early stage. During this time the fish was growing

rapidly in size, probably continuously rather than episodically. After this initial rapid growth phase, a complete cosmine cover was formed and growth become periodic. Later, growth was reduced to 5% or less per year. A complete cosmine cover was present probably only in the early years after maturity, but the evidence concerning patterns of activity in the cosmine after this is open to various interpretations, of which two have been given. Either 1) in later years growth has largely ceased and cosmine resorption and regeneration broke down to a diffuse rather than coordinated process, giving rise to "mixed" cosmine and eventually naked dermal bone with tubercles. Or 2) it is possible that the breakdown of the complete cosmine cover was associated only with the reproductive period each year and the common appearance of incomplete cosmine in the fossils is an artifact of the fossil record.

16) During growth of the fish, the spacing between pore-cavities increased owing to a shortfall in the production of new neuromast organs while the surface area increased.

17) A series of hypotheses are put forward to explain the developmental biology of cosmine in *Ectosteorhachis*. The most probable sequence of events is as follows: the lateral-line neuromasts migrate to target positions in the dermis and become associated in some way with the centers of growth of the isopodin and spongiosa portions of the individual dermal bones. Neuromasts of the pore-canal system migrate and become regularly spaced in the superficial tissues by a phenomenon of local inhibition. Neural-crest cells migrate and induce the epidermis to form a dental epithelium which later reinduces the same neural-crest cells to form odontoblasts. These lay down two sorts of dentine around the pore-cavity neuromasts, according to their position in the superficial portion of the dermis and their spatial relationship to the neuromasts. In the early ontogenetic stages there is a direct morphogenetic relationship between the incorporation of originally isolated neuromasts into a network including the pulp-cavities of the dentine and the formation of the dentine itself. The result is the formation of a series of primordial patches of cosmine (dentine plus enameloid plus pore-canal system). Between these lie free neuromasts. During growth, further cosmine patches are added and at some time in the second or third year there is a shift in development such that, at the next regenerative phase, a series of large sheets of cosmine is laid down around a complete pore-canal mosaic. Later in life this may break down again resulting in the "mixed" cosmine and tubercle phenomena. But the sensory mosaic persists. A developmental explanation of Westoll-lines and blisters is presented in terms of the differential combination of developmentally separate zones of cosmine formation.

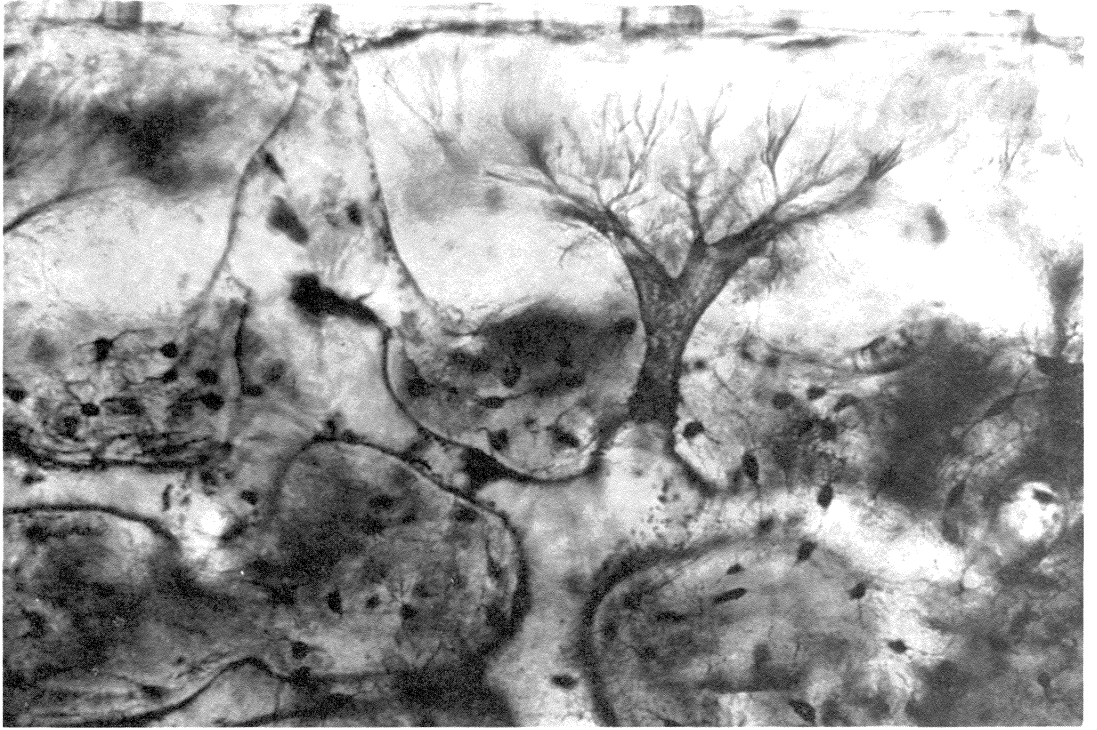
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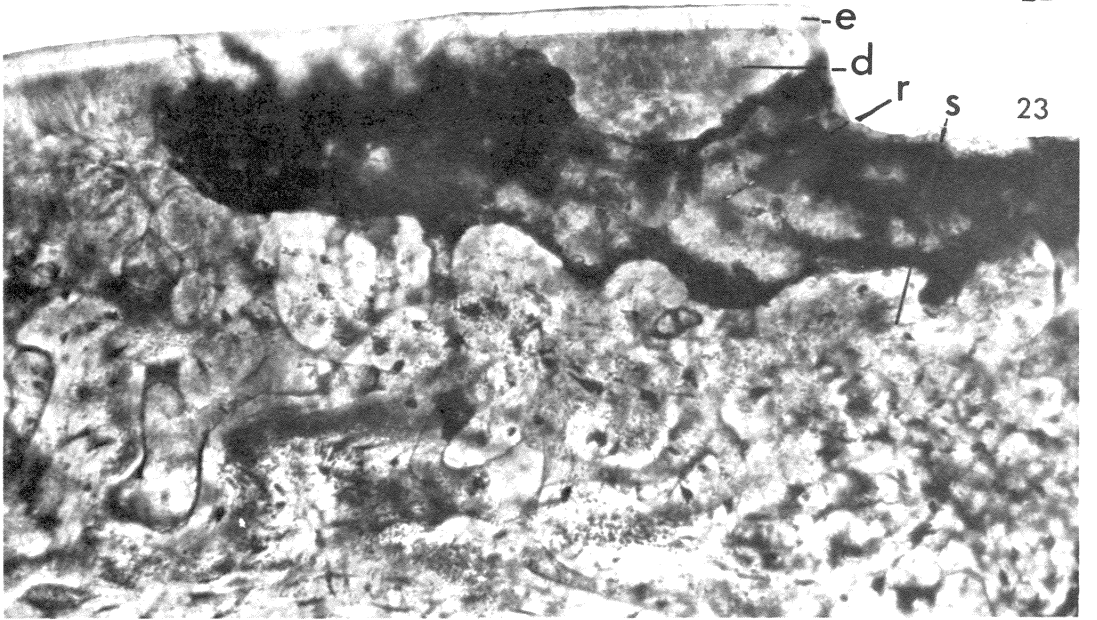
FIGURES 22-62

FIG. 22. Vertical section through the cosmine of a scale of *Ectosteorhachis nitidus* (MCZ 13342) showing one pore-cavity and one pulp-cavity. The cross-canal is well shown but the mesh-canals are out of the plane of the section. $\times 250$.

FIG. 23. Vertical section through a portion of the mandible of *Ectosteorhachis nitidus* (MCZ 13350) showing an area of active resorption; see also Figs. 9, 15, 37 and 38. *d* = dentine; *e* = enameloid; *r* = resorption; *s* = spongiosa. $\times 170$.



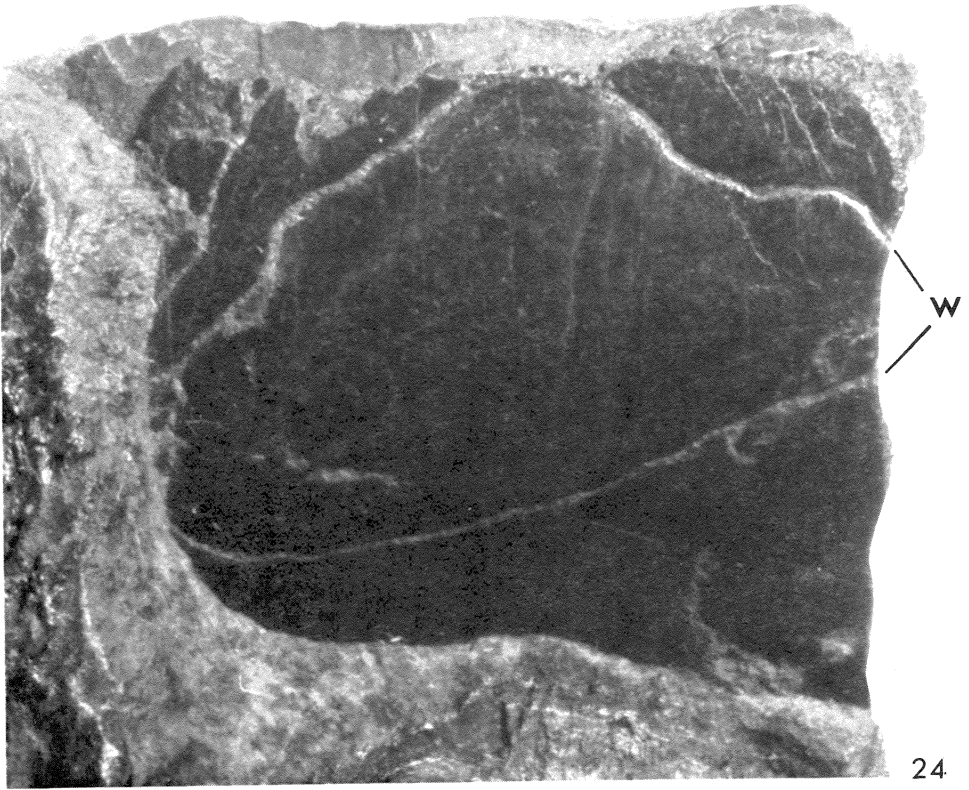
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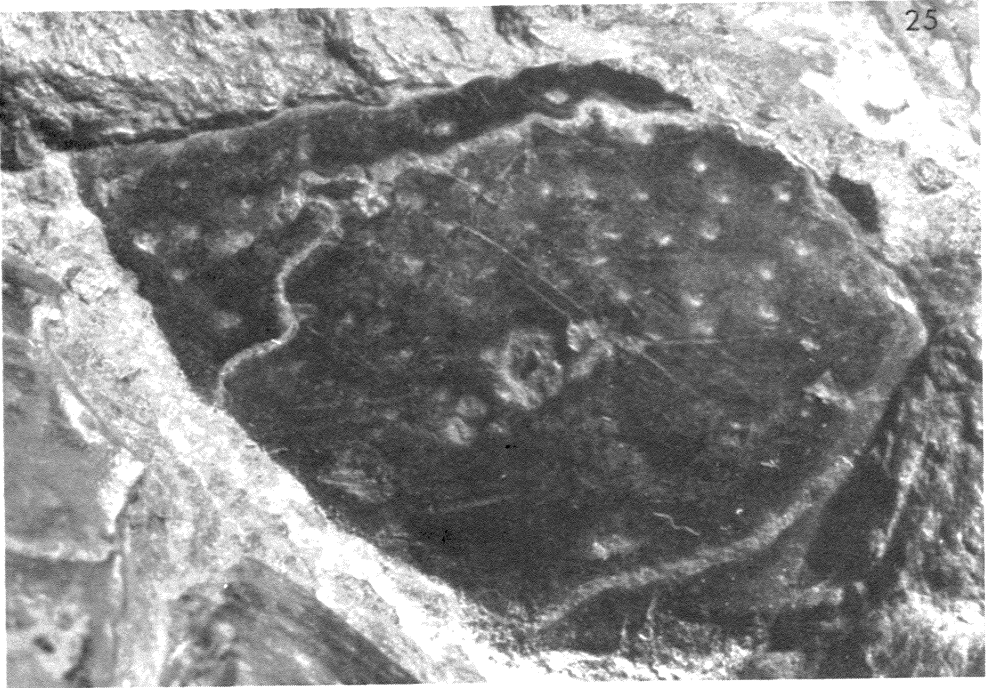
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FIG. 24. *Megalichthys laticeps* Traquair, Lower Carboniferous, Burdiehouse Limestone, Scotland, view of right extrascapular, showing Westoll-lines. MCZ 8941. w = Westoll-line. $\times 5$.

FIG. 25. *Megalichthys laticeps*, same specimen as Fig. 24, showing Westoll-line on left jugal; note also central blister. $\times 5.4$.



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FIG. 26. Scanning electron micrograph of a pore-cavity exposed on a broken surface of a scale of *Ectosteorhachis nitidus*, showing the cross-canals and also the sheathing dentine. *s* = sheathing dentine. × 300.

FIG. 27. Scanning electron micrograph of pore-cavity and associated cross-canals and dentinal system prepared by acid etching of a portion of a scale of *Ectosteorhachis nitidus*. × 225.

FIG. 28. Another preparation similar to Fig. 27.

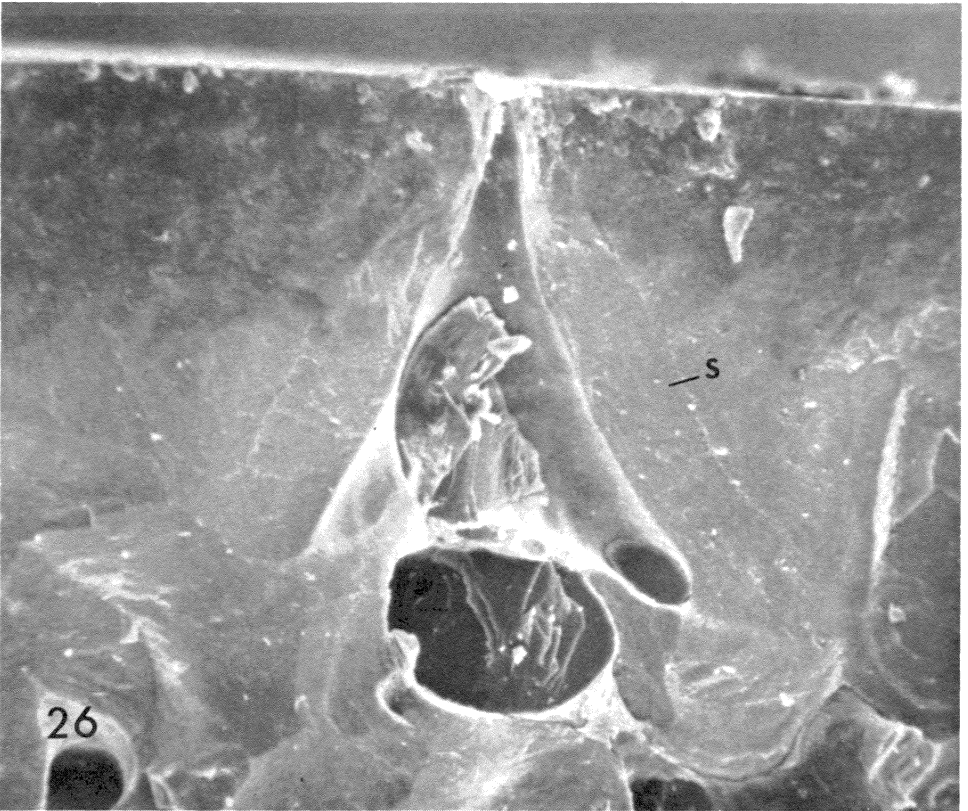
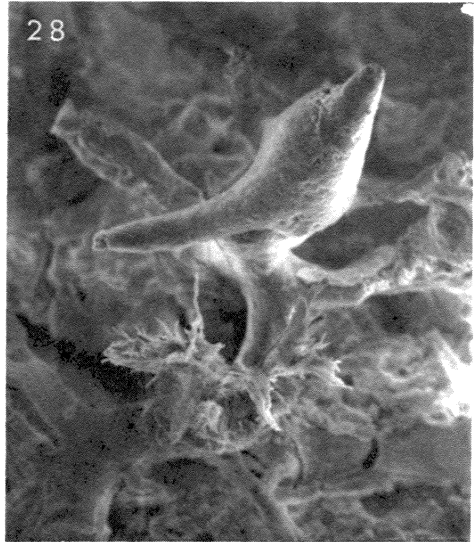


FIG. 29. *Ectosteorhachis nitidus*, anterior skull roof of very small specimen showing incomplete cosmine but no tubercles; see also Fig. 5A. MCZ 8630. $\times 1.5$.

FIG. 30. *Ectosteorhachis nitidus*, anterior portion of skull roof showing distribution of cosmine and some tubercles; see also Fig. 5B. MCZ 6499. $\times 1.3$.

FIG. 31. *Ectosteorhachis nitidus*. Close-up of snout showing cosmine distribution; see also Fig. 5C. MCZ 8668. $\times 1.5$.

FIG. 32. *Ectosteorhachis nitidus*. Scanning electron micrograph showing portion of a tubercle from the postorbital of MCZ 8676. $\times 60$.

FIG. 33. *Ectosteorhachis nitidus*. A second tubercle similar to that shown in Fig. 32. $\times 60$.



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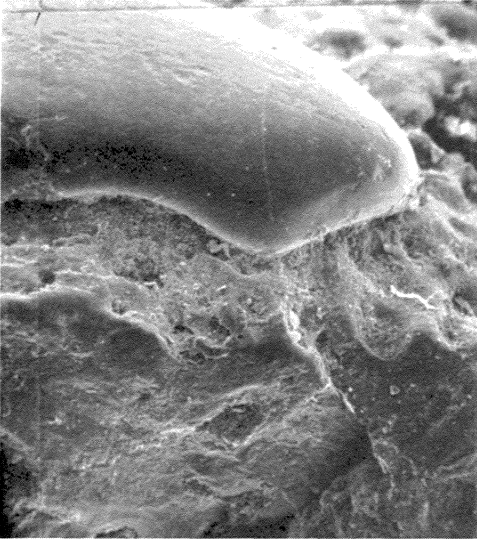


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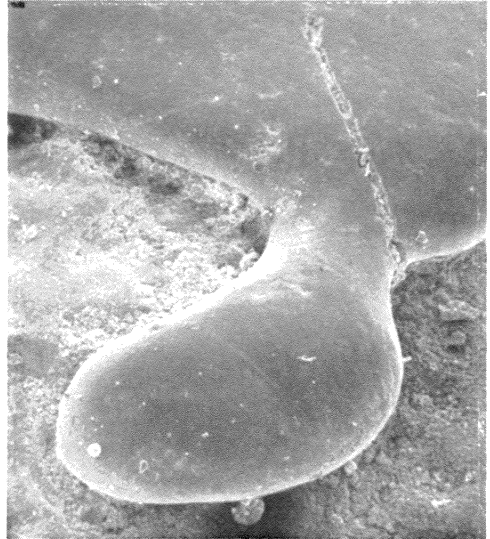


FIG. 34. *Ectosteorhachis nitidus*. Skull of AMNH 5724 in dorsal view showing cosmine distribution; see also Fig. 7. $\times 1.2$.

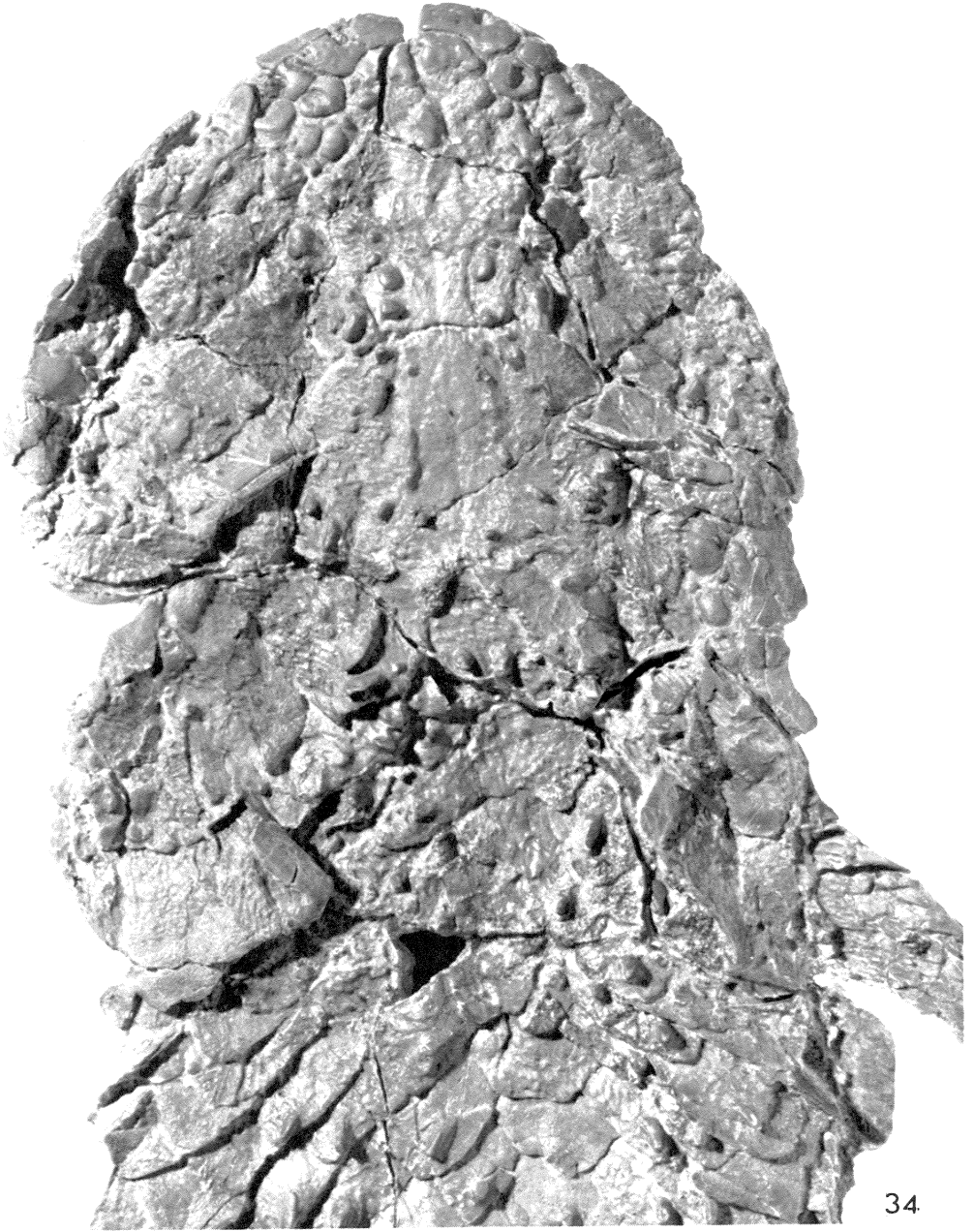
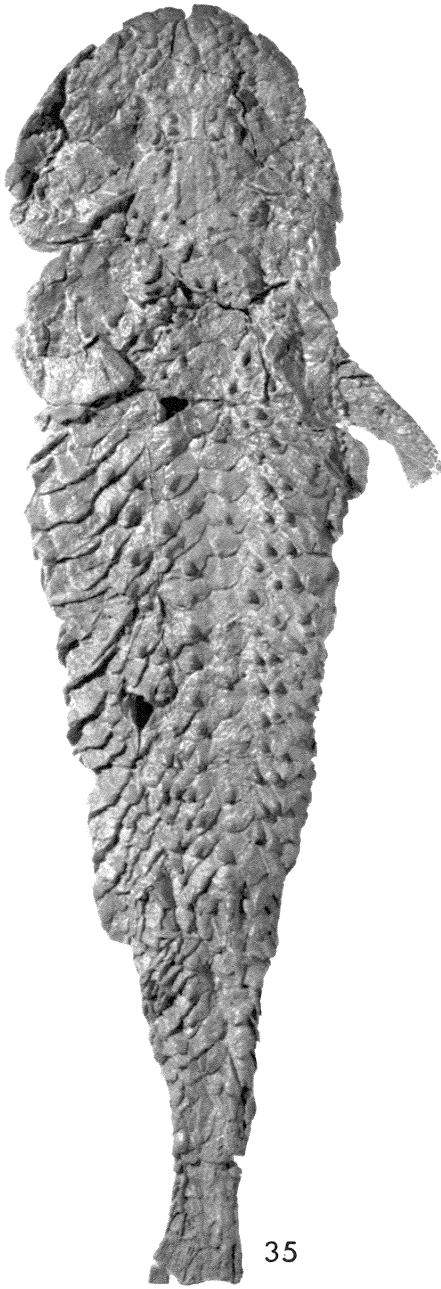
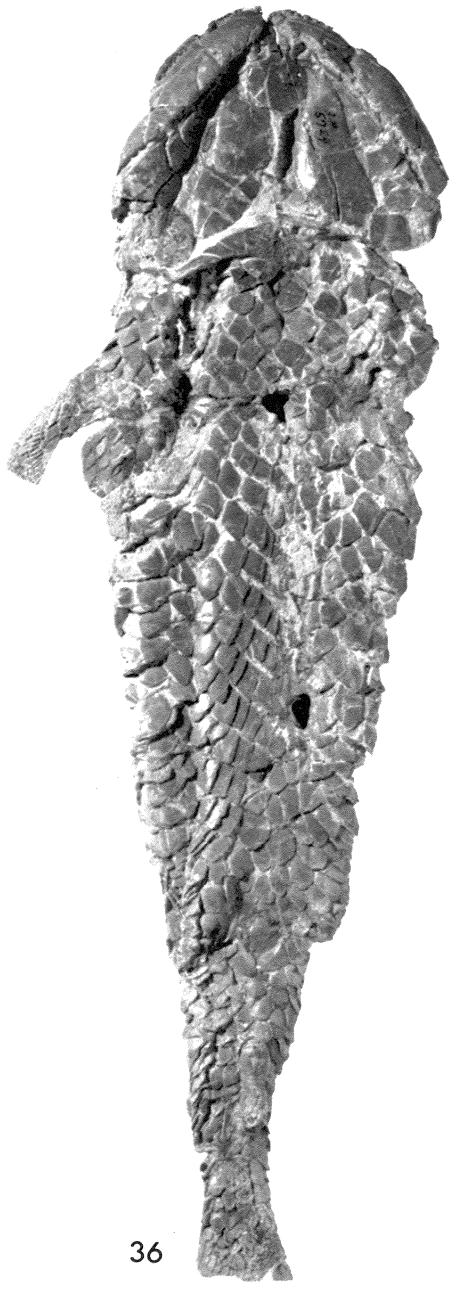


FIG. 35 and 36. *Ectosteorhachis nitidus*. AMNH 5724, whole specimen lacking tail in dorsal (Fig. 35) and ventral (Fig. 36) view; see also Fig. 12. $\times 0.45$.



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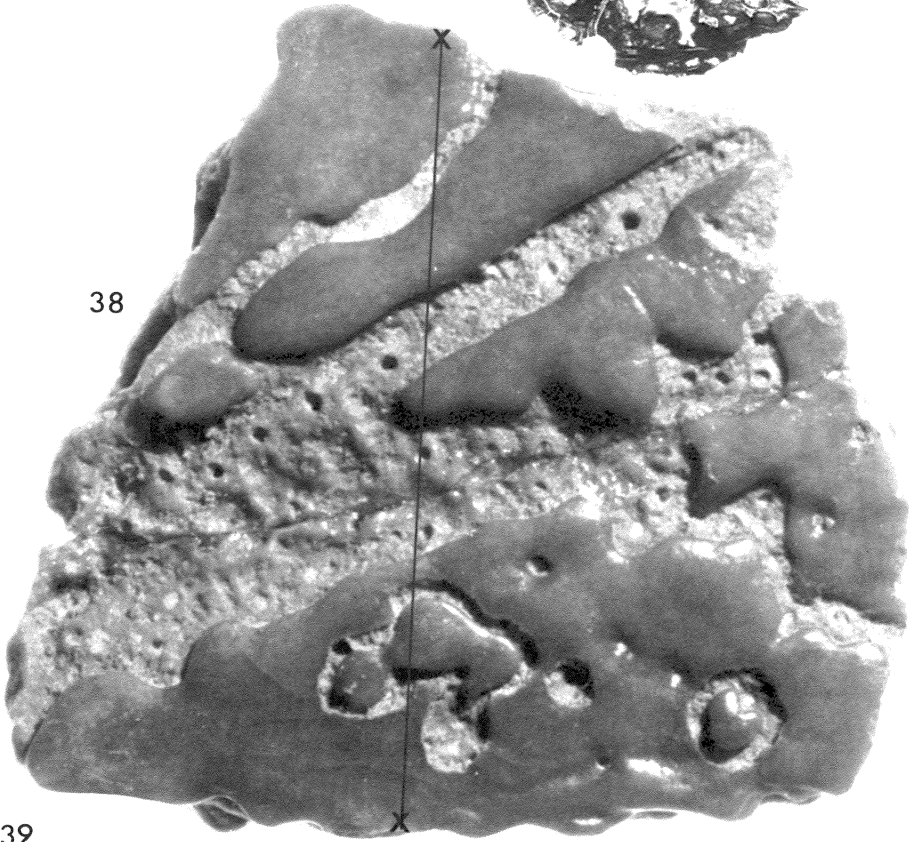
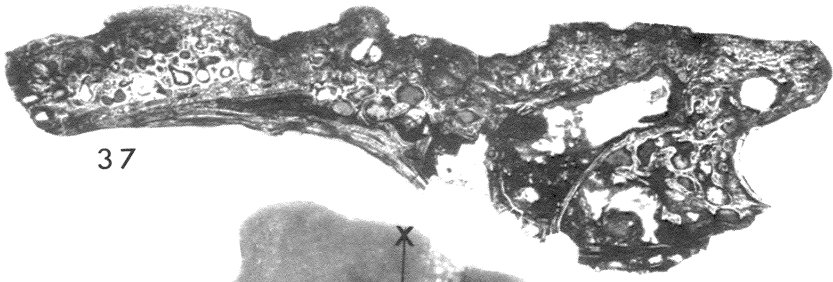


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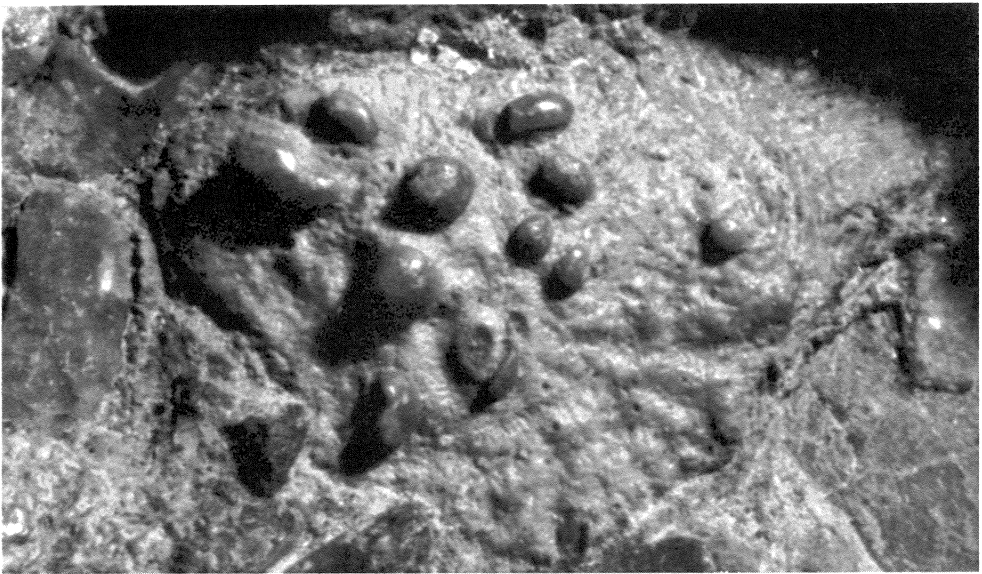
FIG. 37. *Ectosteorhachis nitidus*. Vertical thin-section through specimen MCZ 13350; see Figs. 9 and 38. \times 7.8.

FIG. 38. *Ectosteorhachis nitidus*. Specimen MCZ 13350, showing "mixed" cosmine. Line X-X shows the plane of the thin-section shown in Figs. 15 and 37. See also Fig. 9.

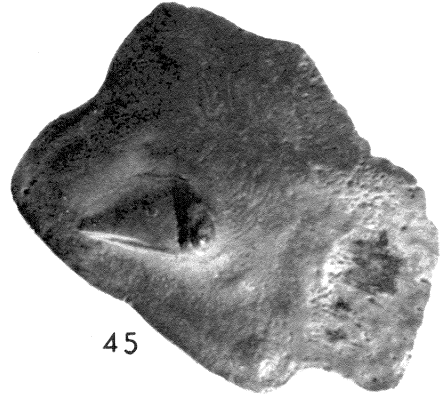
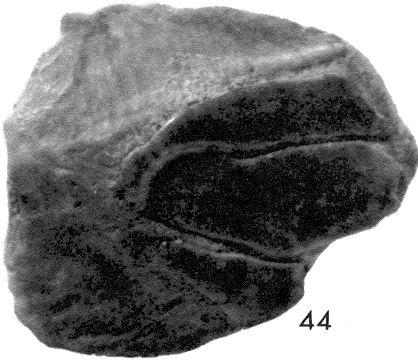
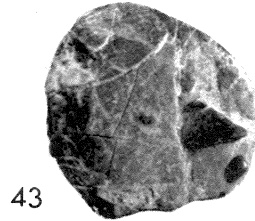
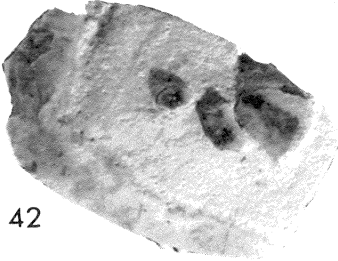
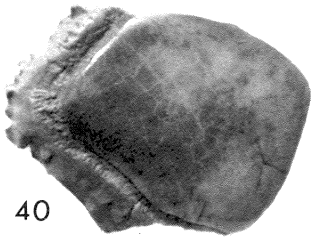
FIG. 39. *Ectosteorhachis nitidus*. Right postorbital of specimen MCZ 8930, showing tubercles. \times 5.



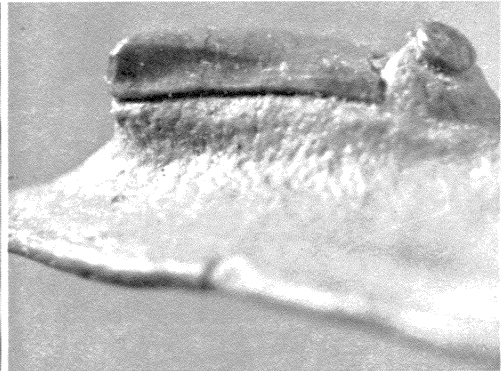
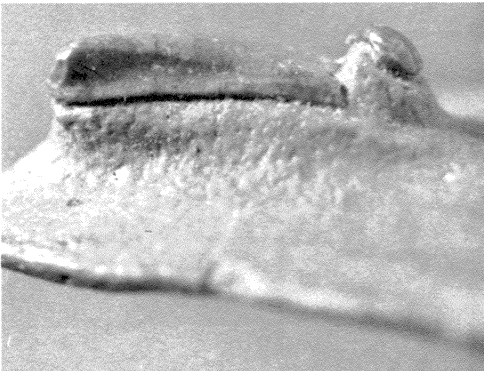
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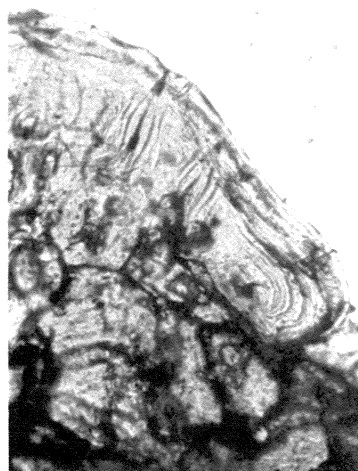
FIGS. 40-46. Scales of *Ectosteorhachis nitidus*. Fig. 40, whole scale in external view, MCZ 13339. $\times 2$. Fig. 41, incomplete scale showing resorption of the anterior margin of the cosmine (finished margin), MCZ 13346. $\times 4$. Fig. 42, scale showing scattered trace of cosmine with unfinished margins, MCZ 13347. $\times 3$. Fig. 43, scale showing single tubercle near posterior margin, MCZ 8676. $\times 2$. Fig. 44, unusual scale showing "concentric" zones of cosmine, MCZ 13345. $\times 4$. Fig. 45, unusual scale showing a "double" tubercle, MCZ 13344. $\times 4$. Fig. 46, same specimen as Fig. 45 in side view; stereo pair.



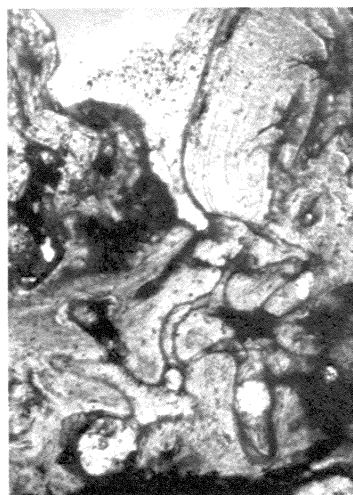
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FIGS. 47-52. *Ectosteorhachis nitidus*. Thin-sections of cosmine. Fig. 47, part of a tubercle from MCZ 8676, showing concentric markings in the cosmine and elongated pore-cavities. $\times 260$. Fig. 48, another part of the same specimen as Fig. 47. Fig. 49, cosmine in diagonal section and polarized light showing the sheathing cosmine around the pore-cavities, MCZ 8676. $\times 260$. Fig. 50, finished margin from MCZ 13345, showing concentric markings. $\times 260$. Fig. 51, general view of two tubercles, MCZ 8676. $\times 260$. Fig. 52, tubercle from the postparietal of MCZ 8676. $\times 260$.

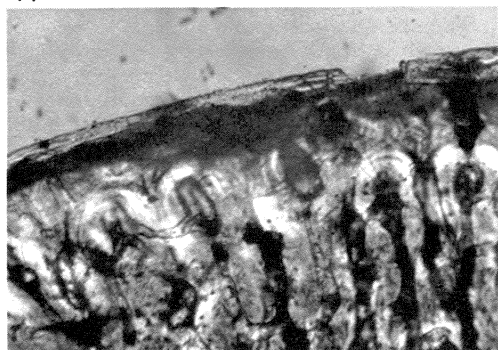


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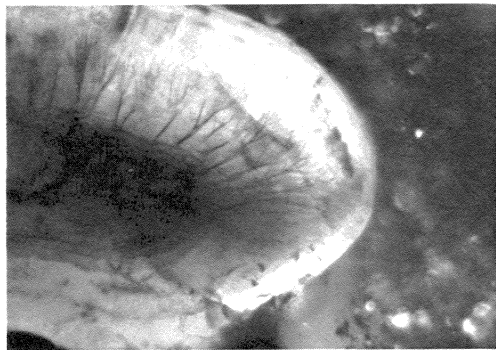
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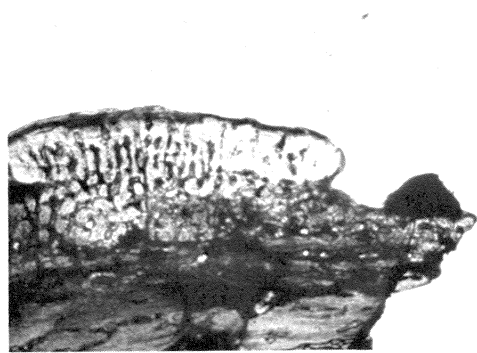
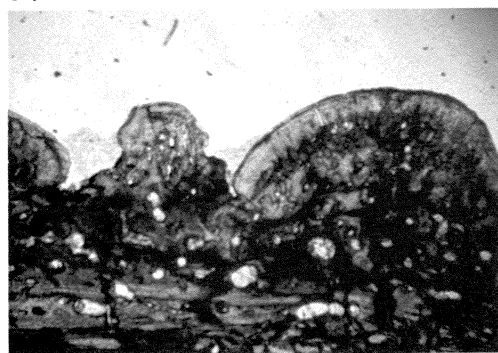


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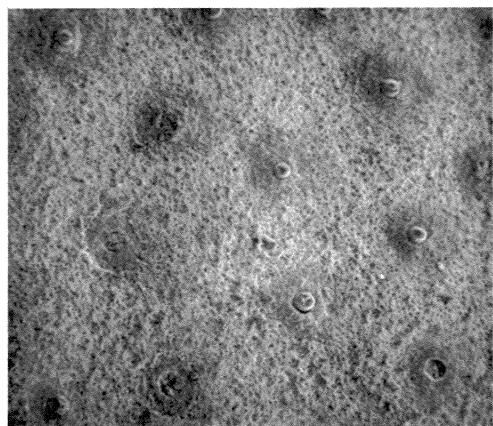
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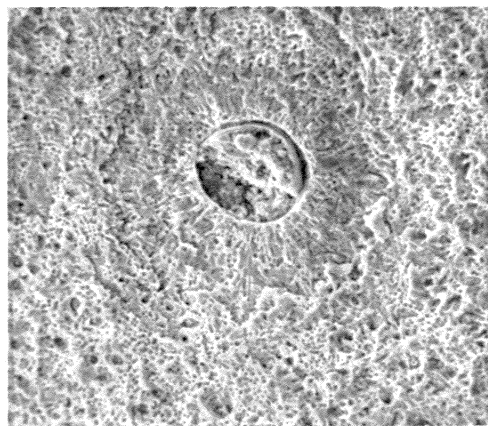
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FIGS. 53-58. *Ectosteorhachis nitidus*, scanning electromicrographs of acid-etched preparations of the surface of a scale. Fig. 53, surface of dentine layer, enameloid having been removed; $\times 62.5$. Fig. 54, close-up of a single pore at a level slightly deeper in the dentine than Fig. 53; note the beginnings of a development of a sheath of radially arranged dentine around the pore-cavity; $\times 280$. Fig. 55, deeper level showing the pore-cavities and surrounding sheaths clearly separated from the interstitial dentine, $\times 100$. Fig. 56, close-up of the interstitial dentine between the sheathing dentine; note the radiating dentine tubules; $\times 188$. FIG. 57. View of the bases of the pore-cavities, the whole of the dentine having been etched away; the anastomosing canals are the mesh-canals and between them may be seen the transected pulp-cavities with enclosing cylinders of true bone; $\times 62.5$. Fig. 58, close-up of a single pore-cavity base showing the mesh-canals and the pulp-cavities; $\times 188$.



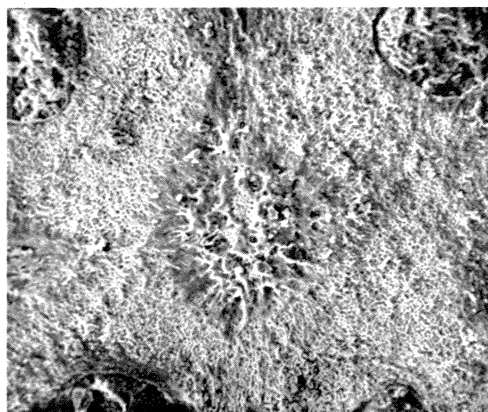
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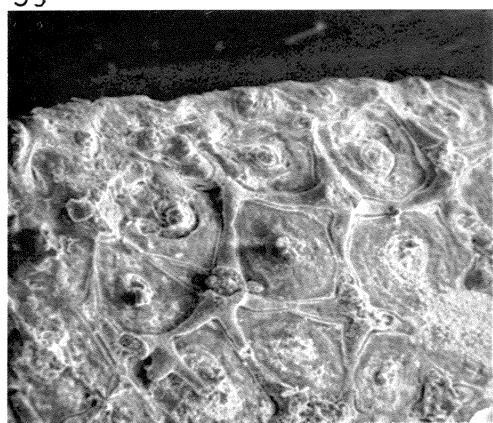
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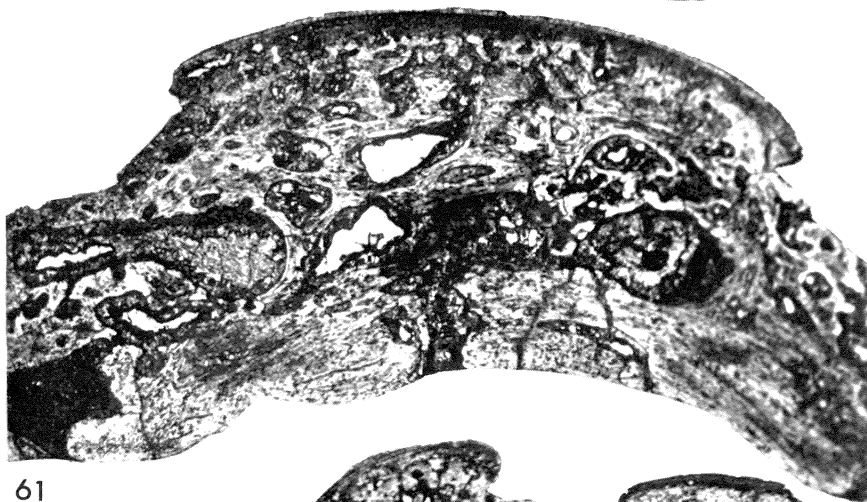
FIGS. 59-62. *Ectosteorhachis nitidus*, vertical-sections through four tubercles, all from the head of a serially sectioned specimen (MCZ 8662) using the cellulose acetate peels of the sections (Thomson, 1964) as a photographic negatives. Note lateral-line canal in Fig. 59. $\times 26$.



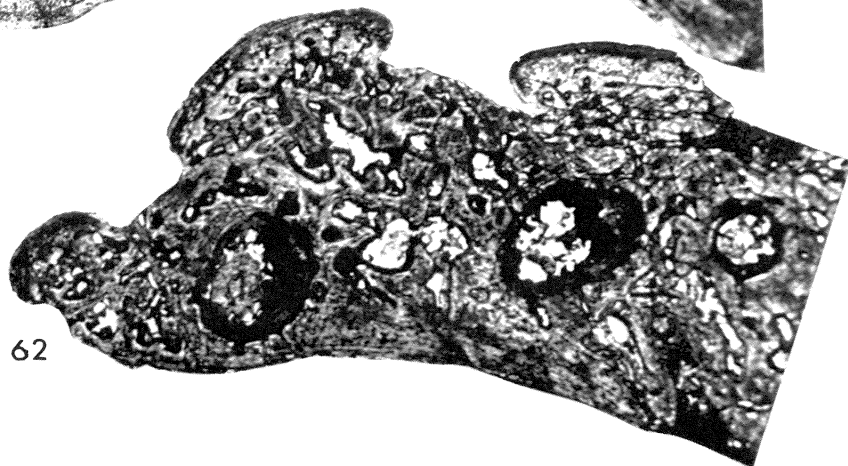
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