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The microstructure of skeleton elements in some vertebrates from lower Devonian deposits of the USSR

by

A. P. BYSTROW

(Leningrad)

Contents

Fossil vertebrates from Lower Devonian deposits have so far been found on the territory of the USSR comparatively seldom (D. V. Obrutchev, 1938). That is why any new discovery of these fossil vertebrates is of great value.

Some time ago I have received a collection of remains of Lower Devonian vertebrates. These bones of fishes and armour fragments of jawless forms were found on the bank of the creek Krasny, left tributary of the river Nizhni Viluikan (The place of the find: $\varphi = 66° 20' 27''$ N; $\lambda = 107° 01' 15''$ E).

Studying these fragments I discovered two new genera of jawless vertebrates of the order Heterostraci. Small armour elements of a well known Lower Devonian form—*Drepanaspis*—were found in the same pieces of rock. I found a great number of scales of *Porolepsis uralensis* Obrutchev 1938 together with the armour fragments of Lower Devonian Heterostraci as well as a small lower jaw fragment of this Lower Devonian Crossopterygian fish. Two broken teeth were preserved in this fragment.

All this material was so well fossilized that I obtained without difficulty fine transparent sections and could study all the details of microstructure.

I. Sanidaspis sibirica g.n., s.n.

I propose for one of the new genera of Lower Devonian Heterostraci the name *Sanidaspis sibirica* g.n., s.n.

In these collections I found only one small armour fragment of this representa-

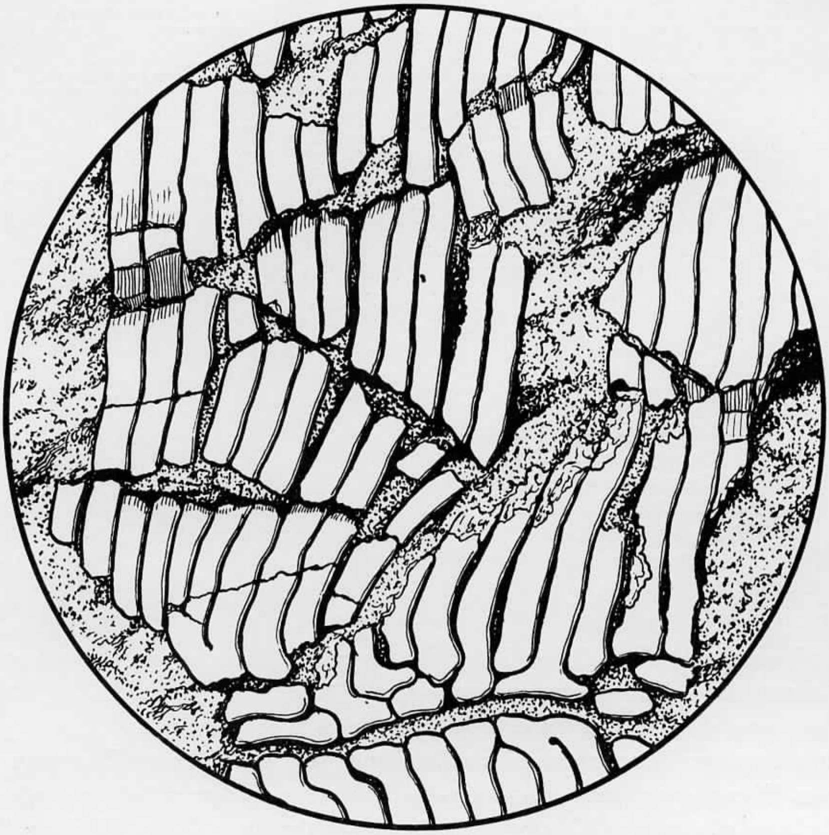

Fig. 1. *Sanidaspis sibirica* g.n., s.n. Fragments of a broken armour in the matrix. × 20.

tive of jawless vertebrates. This fragment was a small part of the shield of the animal and it was impossible to determine its full size. In spite of the insufficient material I have succeeded to prepare both vertical and horizontal transparent sections from small pieces of the armour and to study all the details of the armour microstructure of this new form of Agnatha.

The outer surface of the shield of *Sanidaspis sibirica* g.n., s.n. is covered (at any rate the part which I have at my disposal) with numerous longitudinal glittering plates (fig. 1). These plates have almost the same width throughout and bear a great resemblance to floor boards or deck boards (*σανίς, σανίδος* — a board; I used this word to name the genus *Sanidaspis* g.n.).

The study of the vertical section of the armour of *Sanidaspis sibirica* has shown first of all that the average thickness of its shield is 1,3 mm.

The outer surface of the shield is covered with one layer of dermal teeth (d—fig. 2) Everyone of them is very elongated and has the shape of a plate. Its width varies from 0,30 to 0,35 mm (fig. 1). Everyone of these dental plates

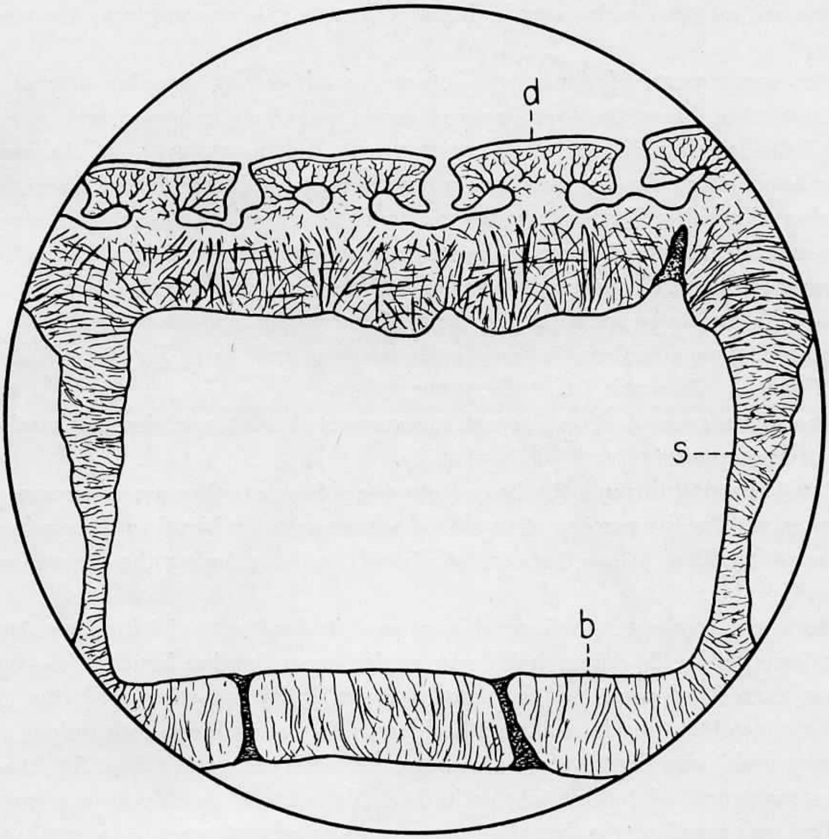

Fig. 2. *Sanidaspis sibirica* g.n., s.n. Vertical section of the armour; b = basal layer; d = cross-section of the tooth lamella; s = vertical septum. × 100.

is connected with the armour by means of a relatively narrow longitudinal trabecula. On both sides of this connecting trabecula two longitudinal pulpar canals pass under every lamellar dermal tooth. Relatively few thin and ramifying dentine tubules branch off from them. These tubules pierce the dentine.

Horizontal canals branch off from the pulpar canals towards the space between neighbouring teeth. These canals are so numerous that vertical sections often cut them longitudinally (fig. 2). In those cases when the section passes between two neighbouring canals one can see the coalescence of the lateral part of lamellar tooth with the armour and the transformation of the pulpar canal into a closed cavity.

The outer surface of lamellar teeth of *Sanidaspis sibirica* is covered with a thick layer of enamel. This layer has a very small longitudinal depression in the middle.

The lateral parts of lamellar teeth were probably covered with a very thin layer of enamel but even under very high magnification it is impossible to discover this layer.

The upper parts of the spaces between neighbouring lamellar dermal teeth are tapered and have the appearance of very narrow longitudinal slits.

All the lamellar dermal teeth coalesce with the upper layer of the armour. This layer in *Sanidaspis* is as strongly developed as in *Pteraspis* and *Poraspis* and consists of aspidin. Sharpey's canals scattered at irregular intervals are very well seen in it. During the lifetime of the animal they contained collagen fibers (fig. 2).

Large chambers separated from each other by thin vertical aspidin septa (S—fig. 2) are to be found in the middle layer of the armour of *Sanidaspis*. The volume of these chambers in *Sanisdaspis* was greater than in *Tolypelepis, Anglaspis, Poraspis, Corvaspis* (A. P. Bystrow, 1955).

The lower ends of vertical septa are connected with a horizontal basal layer which also consists of aspidin (b—fig. 2).

Canals passing through the layer from one side to another are often seen in it. They served for the passage of the blood vessels carrying blood to the conjunctive tissue which filled up all the cavities of the chambers during the lifetime of the animal.

Horizontal sections of the layer dermal teeth in *Sanidaspis sibirica* show that two pulp canals (fig. 3—upper half) pass under every dentine lamella (d—fig. 3). These canals are connected by numerous horizontal branches with the spaces between neighbouring lamellar teeth. Somewhat more seldom both pulpar canals passing under one dental plate are connected with each other (fig. 3). Studying the arrangement of dentine tubules in dental lamellae of *Sanidaspis* one is unable to find any proof of the fact that these lamellae were formed as a result of the coalescence of several dermal teeth. The formation of dentine crests owing to the coalescence of long rows of dermal teeth can be readily observed studying the microstructure of *Anglaspis* and *Poraspis* (A. P. Bystrow, 1955).

The horizontal sections of lamellar teeth of *Sanidaspis* do not show any enamel since on their lateral surfaces it was either fully absent or very thin. One can see here only a very narrow slit separating from each other neighbouring dental plates (fig. 3—upper half). In horizontal sections of the middle armour layer of *Sanidaspis* it is possible to study only thin aspidin septa forming relatively large chambers (S—fig. 3—lower half).

II. Gunaspis orientalis g.n., s.n.

I propose for the second new genus of jawless vertebrates which was discovered in Lower Devonian deposits in the basin of the river Nizhni Viluikan the name *Gunaspis orientalis* g.n., s.n.

I found very many armour fragments of this animal in my collections. But all

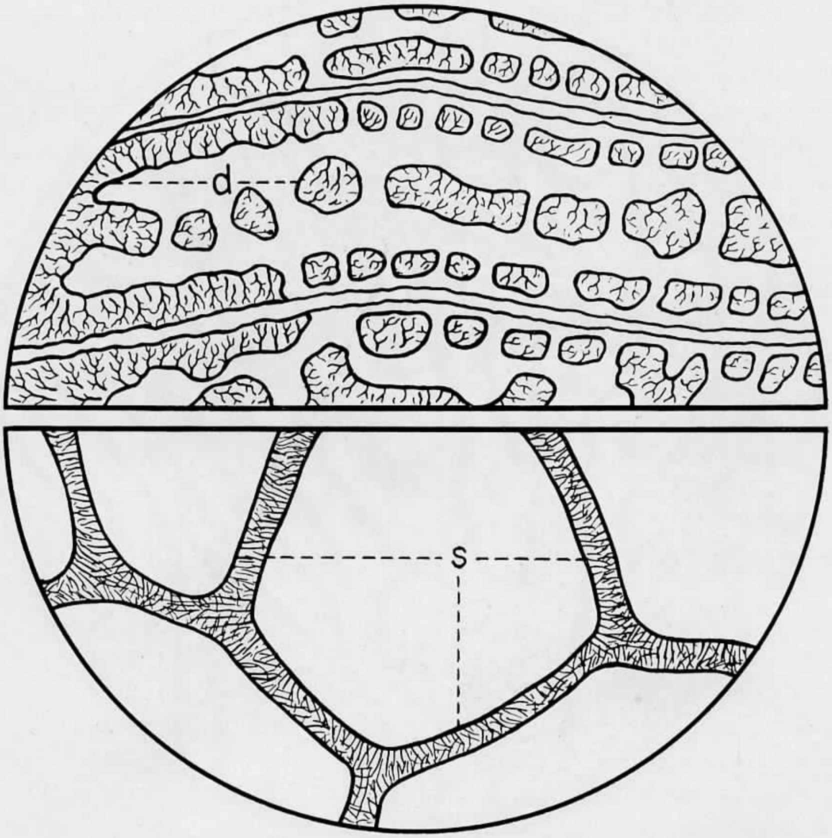

Fig. 3. *Sanidaspis sibirica* g.n., s.n. Upper half—horizontal section of dermal teeth; lower half—horizontal section of the middle layer of the armour; d = dentine; s = aspidin septa. × 100.

of them were fragments firmly connected with the matrix by their external side. Such objects were very convenient for making transparent sections since it was possible to obtain very good preparations in which the external surface of the armour was completely undamaged being protected by the matrix during the making of the sections. All these fragments had one defect: it was impossible to determine the general appearance of relief on the external surface of the armour.

I could study the main details of the appearance of the shield of *Gunaspis orientalis* only because I had at my disposal a small fragment of its armour in which the external surface of the shield was free from the matrix what happens very seldom.

The armour of *Gunaspis orientalis* g.n., s.n. is covered with numerous blunt crests. These crests are arranged in some parts more or less parallel to each other and in others are quite irregularely scattered. They are often curved and ramified.

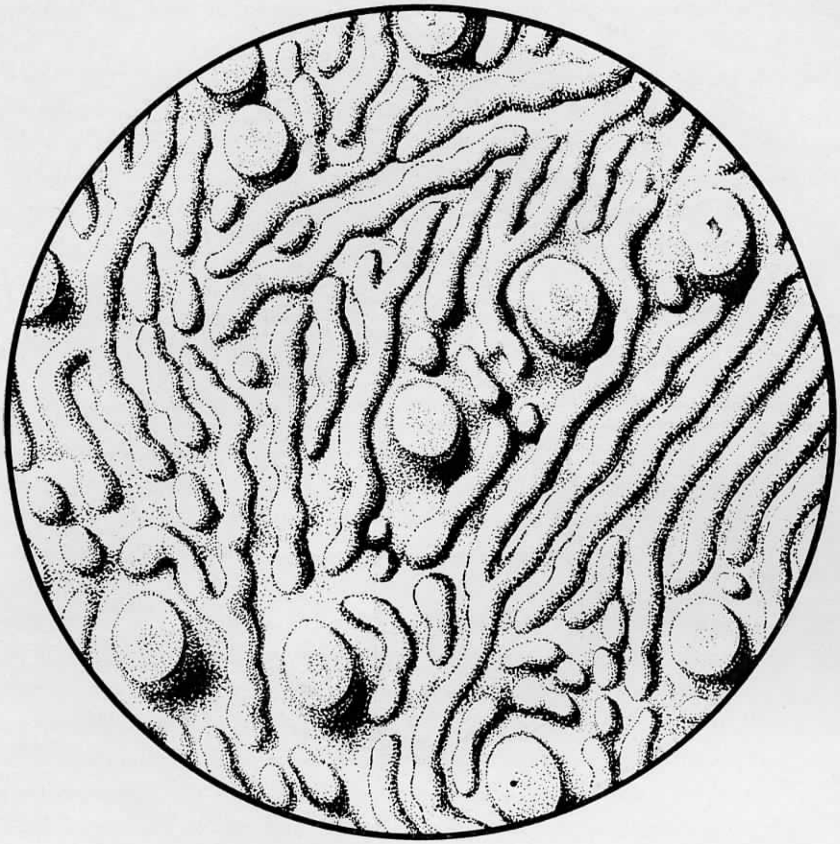

Fig. 4. *Gunaspis orientalis* g.n., s.n. Outer surface of the armour. × 20.

In some cases they are very long and in others—very short and even have the shape of small round tubercles. All these crests are never quite close to each other (fig. 4). They vary in width from 0,3 to 0,4 mm.

On the armour of *Gunaspis orientalis* among the crests one can notice a very interesting detail: the presence of rather numerous and very unusual large round or oval prominences. Their diameter is usually twice as great as the width of the crests and varies from 0,6 to 0,8 mm. All these prominences have flat tops and their height is always greater than that of the neighbouring crests.

The presence of these unusual flat-topped prominences on the armour suggested to me the name *Gunaspis* for this new genus of Agnatha (*γουνὸς* — hill, elevated platform).

Studiyng the armour of *Gunaspis orientalis* under a magnifying glass one can always easily distinguish a dark spot in the centre of the flat top of every round prominence (fig. 4). The presence of these spots is accounted for by the

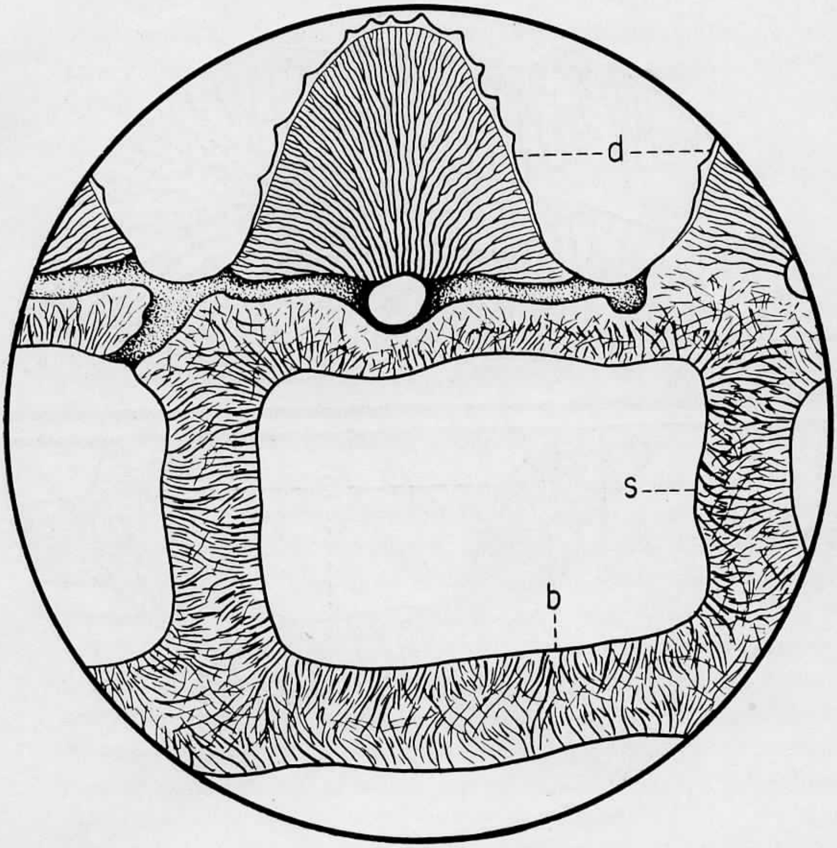

Fig. 5. *Gunaspis orientalis* g.n., s.n. Vertical section of the armour ; b = basal layer ; d = cross-section of crest-like dermal teeth ; s = vertical septum. × 100.

fact that the wall of every prominence is much thinner in the centre portion than on the periphery, being partly ground off. Nevertheless I have never found any holes passing through them from one side to another.

In vertical sections of the armour of *Gunaspis orientated* across the crests it is possible to observe that every crest is a dentine formation (d—fig. 5). Under the crest there is a pulp canal which ramifies into branches opening on the bottom of the depressions between the neighbouring crests. Numerous dentine tubules piercing all the dentine mass of the crest are directed upwards.

All the dentine crests on the armour of *Gunaspis* are covered with a relatively thick enamel layer in which there are 10—13 sharp longitudinal ridges. I have not observed such ridges on the enamel of dermal teeth in any Pteraspidae.

In *Gunaspis* the basis of dentine crests coalesces with the upper lamella of its armour. This lamella consists of aspidin and Sharpey's canals are clearly seen in it.

A series of thick vertical septa forming the walls of spacious chambers (s—

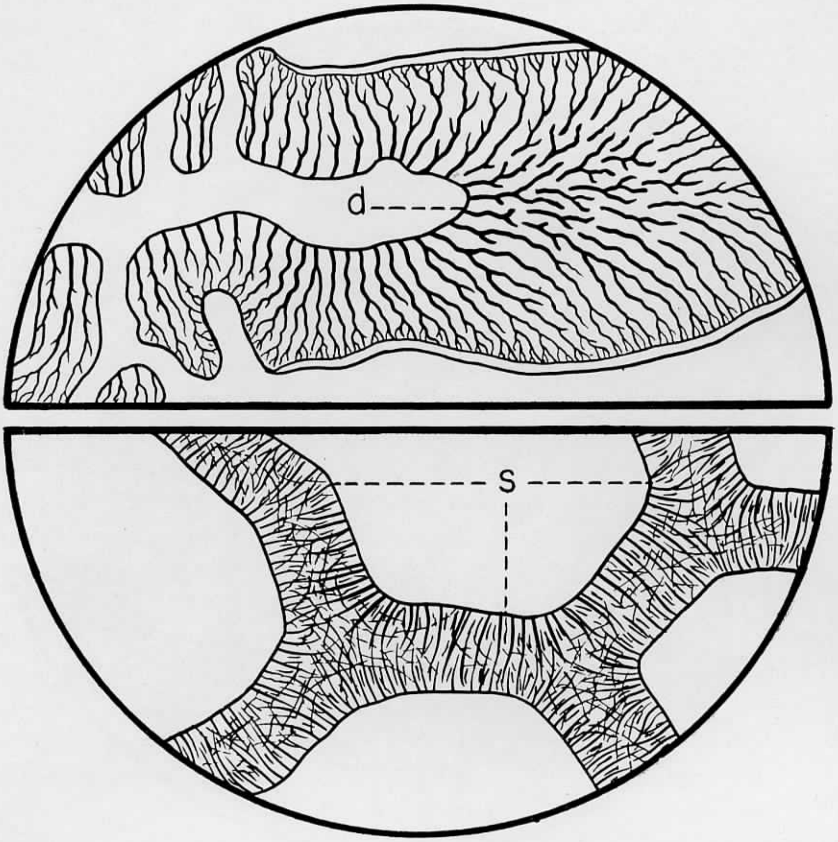

Fig. 6. *Gunaspis orientalis* g.n., s.n. Upper half—horizontal section of the crest-like dermal teeth; lower half—horizontal section of the middle layer of the armour; d = dentine; s = aspidin septa. × 100.

fig. 5) is located in the middle layer of the armour. These septa are connected with basal lamella (b—fig. 5). Both the septa and the basal lamella consist of aspidin. The average thickness of the armour of *Gunaspis orientalis* is 1,5 mm.

The horizontal section passing through the basis of the dentine crest readily shows the pulp canal and its lateral ramifications. In the dentine mass of the crests there are no traces showing that they were formed as a result of the coalescence of a row of dermal teeth (d—fig. 6—upper half) in contrast to that was discovered in the dentine crests on the shields of *Anglaspis* and *Poraspis* (A. P. Bystrow, 1955).

In horizontal sections passing through the middle layer of the armour one can clearly see thick aspidin septa forming the walls of the chambers (s—fig. 6—lower half).

Judging by separate fragments of the armour of *Gunaspis orientalis* the length of its dorsal shield was not less than 15 cm. Consequently this representative of Lower Devonian Heterostraci was of a much greater size than Upper Silurian forms.

III. Drepanaspis sp.

Drepanaspis gemündenensis Schlüter discovered for the first time in Lower Devonian deposits of Germany is known to attract the attention of many paleontologists. R. H. TRAQUAIR (1903—1905) studied it in greatest detail and made the first reconstruction of this interesting animal. In 1943 the reconstruction of *Drepanaspis* was revised, elaborated and corrected by D. V. OBRUTCHEV. Owing to the existence of a great number of well preserved specimens of *Drepanaspis gemündenensis* it was possible to learn its structure in great detail and at present we have quite a good idea about this Lower Devonian jawless vertebrate.

But no information is available in paleontological literature about the microscopic structure of the armour of *Drepanaspis gemündenensis* except a photo of a transparent section and a schematic drawing of J. KIÆR (1915).

J. Kiær wrote in his work that he had succeeded relatively easily in obtaining a good microscopic preparation. But my attempt to repeat Kiær's observations and to prepare a transparent section of a small armour fragment of german *Drepanaspis gemündenensis* did not yield similar results. All the armour of the specimen a small fragment of which was taken by me proved so pyritized that is was quite impossible to investigate its microstructure.

Studying attentively different fragments of scales, bones and the armour of Lower Devonian deposits in the basin of the river Nizhni Viluikan I have found several small hexagonal armour plates. Their maximum width varied from 7 to 10 mm. The external surface of all such plates was covered with tubercles (fig. 7 A). Straight narrow radial grooves and small openings for blood vessels and nerves could be seen on the internal slightly concave side (fig. 7 B). These plates varied in thickness from 0,8 to 1,0 mm.

A great resemblance of the shape of tubercles on the external surface of these polygonal plates with that of the tubercles on the armour elements of *Drepanaspis gemündenensis* Schlüter suggested to me that I had at my disposal the armour plates of just this representative of Agnatha. I think that the small armour plates at my disposal are those numerous polygonal skeleton elements that in *Drepanaspis gemündenensis* are located around its dorsal and ventral shields.

Owing to very good fossilization of armour plates of *Drepanaspis* of Lower Devonian deposits in the basin of the river Nizhni Viluikan I could for the first time obtain fine transparent sections that enable me to get acquainted with the microstructure of this animal's shield using my own preparations.

In vertical sections of the armour plates one can see that every tubercle is a

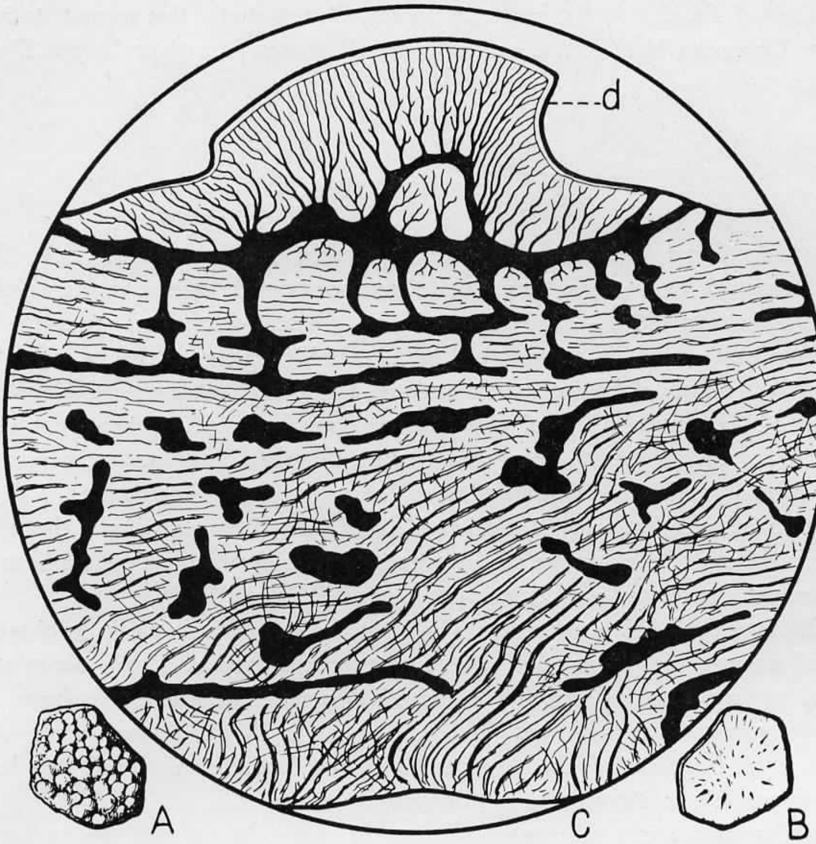

Fig. 7. *Drepanaspis* sp. A = Armour element; view from outside. B = the same armour element: view from inside. C = vertical section of the same armour element; d = dermal tooth. × 100.

small dermal tooth. Usually it has a slightly sharpened inclined top (d—fig. 7 C). All the dentine mass of the tubercle is pierced by numerous ramifying dentine tubules. A system of pulp canals forming extensions in many places is located in the basis of the tubercle.

All dermal teeth of *Drepanaspis* from the basin of the river Nizhni Viluikan are covered with a clearly defined enamel layer. By their general shape they are in no way distinguished from the dermal teeth of *Drepanaspis gemündenensis* Schlüter (J. Kiær, 1915).

The main mass of the armour plates of *Drepanaspis* consists of typical aspidin in which one can well see numerous Scharpey's canals (fig. 7 C).

Irregularly scattered cavities and canals are located in the armour elements of *Drepanaspis*. The middle layer is devoid of those vertical aspidin septa forming chambers in the armour shields of many Silurian and some Devonian Heterostraci (*Sanidaspis* and *Gunaspis*).

IV. The Order Heterostraci

The order Heterostraci was defined in 1868 by R. Lankester. As we know, Heterostraci have the following characteristics: their head and the front part of the body were covered with shields in which bone cells were absent. The external surface of these shields was covered with dermal teeth unless these teeth were reduced. The branchial apparatus as in all Agnatha was represented by gill-sacs but these sacs have one outer opening on each side. The eyes of Heterostraci were located on the sides of the head and olfactory pits were lying on its front part. Nasohypophysal organ was absent; pineal opening could have been absent. Dorsal, pectoral and abdominal fins were absent. Caudal fin had a hypoceral structure.

I think that we have no reasons to reject the customary name "Heterostraci" through it cannot be considered quite apt and I regard as quite groundless the proposal of L. S. Berg (1940, 1955) to substitute the term Pteraspides for the name Heterostraci and to consider this taxonomic rank a ... class and not an order. In this "class" L. S. Berg distinguished six orders, namely: Astraspiformes, Psammosteiformes, Pteraspiformes, Phialaspiformes, Cyathaspiformes, Amphiaspiformes.

In a well known Zittel's Text-book of paleontology (1932) the order Heterostraci is subdivided into three families, namely: Coelolepidae, Pteraspidae and Drepanaspidae.

The representatives of the family Coelolepidae differed from all the other Heterostraci by the absence of solid armour on the front part of their body. Therefore they should be excluded from the order Heterostraci. Coelolepida should form a separate order as it is done, for instance, by A. S. Romer (1945).

D. V. Obrutchev (1945) calls Coelolepida "Thelodonti" and considers them a subclass equivalent to Heterostraci which in his opinion form a second subclass of the class Pteraspidimorphi.

It seems to me that we have quite sufficient reasons to exclude Coelolepidae from the order Heterostraci and to subdivide it in only two families, namely Pteraspidae and Drepanaspidae.

The most ancient representatives of the order Heterostraci *Astraspis desiderata* Walcott, 1892, *Eriptychius americanus*. Walcott, 1892 and *Pycnaspis splendens* Orvig, 1958 found in Ordovician deposits of the USA had aspidin armour shields on which very unusual dermal teeth were located (W. Bryant, 1936, T. Orvig, 1958). These armour elements probably correspond only to the upper layer of the armour of later Heterostraci. Thus *Astraspis, Eriptychius* and *Pycnaspis* are evidently the most primitive representatives of the order Heterostraci and should be placed in the family Pteraspidae and not in the family Drepanaspidae as was Bryant's opinion (1936).

A careful study of the microscopic structure of the armour shields of Silurian and Devonian representatives of Pteraspidae and Drepanaspidae fully confirms the correctness of introducing these two families.

Family Pteraspidae. The representatives of this family had on the head and on the front part of the body the following armour elements: unpaired rostrale, pineale, dorsale, ventrale, paired orbitalia, branchialia, cornualia. Except these elements there were several plates different form and size behind the oral opening. Some Pteraspidae had sharp spines placed on the posterior edge of dorsal armour and along the back.

The coalescence of some armour elements is observed in different representatives of the family Pteraspidae. Thus, in some forms rostrale, pineale and dorsale coalesced (*Tolypelepis, Anglaspis, Poraspis*), in others—branchiale, and cornuale (*Phialaspis*).

A very important detail common to all the representatives of the family Pteraspidae without any exception is the presence of vertical septa in the middle layer of their aspidin armour elements. Owing to their presence this layer has a characteristic cancellous structure (fig. 2, 3, 5, 6 of the present work and A. P. Bystrow, 1955,, fig. 11, 12, 14, 15, 17, 18, 20, 21).

On account of the cancellous structure of the middle layer of its armour Pteraspidae possessed maximum strength with minimum use of "building material". Dermal teeth on the outer surface of Pteraspidae's armour had not only a protective function but also mechanical one.

The best known genera of the Pteraspidae family are: *Tolypelepis, Anglaspis, Poraspis, Pteraspis, Protaspis, Corvaspis, Phialaspis, Cyathaspis, Ctenaspis, Dictyonaspis.* Now one must add to them two new genera: *Sanidaspis* g.n. and *Gunaspis* g.n.

Family Drepanaspidae. Drepanaspidae as well as Pteraspidae had aspidin plates on its very flattened head and on the front part of the body. The outer surface of these plates was covered with dermal teeth or else they were fully reduced as in Upper Devonian *Aspidosteus heckeri* Obrutchev, 1941. Many small polygonal armour elements were located around dorsal and ventral shields of Drepanaspidae so that these shields had no direct contact with large aspidinplates forming the edges of the flattened body of the animal (rostrale, orbitale, praebranchiale, branchiale, cornuale). The fields of small polygonal armour elements of Drepanaspidae were placed directly above and beneath the gill-sacs and were a very useful aequisition since they enabled dorsal and ventral shields to move and facilitated the act of breathing. In Pteraspidae the motion of water in the branchial apparatus was probably due exclusively to the contraction of muscles in the walls of gill-sacs. Drepanaspidae had well developed isolated praebranchiale which in Pteraspidae in all probability very early in life fully coalesced with orbitale or with the front part of the branchiale.

The microstructure of the armour elements of Drepanaspidae is characterized by the absence of cancellous structure of their middle layer. Aspidin septa are disposed in this layer quite irregularly and form a spongy mass not distinguished in any way from the ordinary substantia spongiosa. The armour shields of Drepanaspidae were already sufficiently thick and strong. Probably this accounts for the absence of the regular cancellous structure of their middle layer. Dermal teeth of Drepanaspidae also lost their mechanical function.

Several representatives of the family Drepanaspidae have been found in Devonian deposits. They are the genera *Drepanaspis, Schizosteus, Ganosteus, Pycnosteus, Psammolepis, Psammosteus, Aspidosteus.*

Kallostracon padura LANKESTER (L. Old Red Sandstone, Herefordshire) has the spongy structure of the middle layer of the armour (A. P. BYSTROW, 1955, fig. 22, 23, 24). Therefore this form should also be placed in the family Drepanaspidae and not in the family Pteraspidae as it is done in K. ZITTEL's Text-book of paleontology (1932).

The mysterious form *Cardiopeltis wallacii* BRANSON and MEHL, 1931 from Lower Devonian deposits of North America was at one time considered similar to *Poraspis* and *Pteraspis* on account of the general structure of its armour. This suggested that *Cardiopeltis* should be placed in the family Pteraspidae. But taking into consideration the fact that the middle layer of the armour of *Cardiopeltis* consists of irregularly disposed trabeculae and has no cancellae characteristic for Pteraspidae R. H. DENISON (1953) comes to conclusion that *Cardiopeltis* is much nearer to the family of Drepanaspidae. I think that on account of this detail *Cardiopeltis* should be considered a representative of the family Drepanaspidae.

V. Porolepis uralensis Obrutchev 1938

I have found among the armour fragments of *Sanidaspis sibirica* g.n., s.n. and *Gunaspis orientalis* g.n., s.n. a small fragment of the lower jaw of *Porolepis* which had two broken teeth.

So far as I know, the microscopic structure of the teeth of *Porolepis* has never been studied. Therefore I tried to prepare transparent sections of these teeth.

The long axis of the cross-section of the tooth basis of *Porolepis* in my preparations was 4,0 mm (fig. 8).

The dentine wall of the tooth of *Porolepis* has slight folds resembling the folds in the teeth of *Osteolepis* (A. P. BYSTROW, 1942). The enamel covering the teeth has numerous longitudinal sharp ridges.

In 1935 W. GROSS published the first detailed description of the microscopic structure of the dermal bones of *Porolepis posnaniensis* (KADE). It was found that all the bones of this Crossopterygian fish are covered on the outside with a layer of unusual coalescent dermal teeth very similar in their shape to the teeth

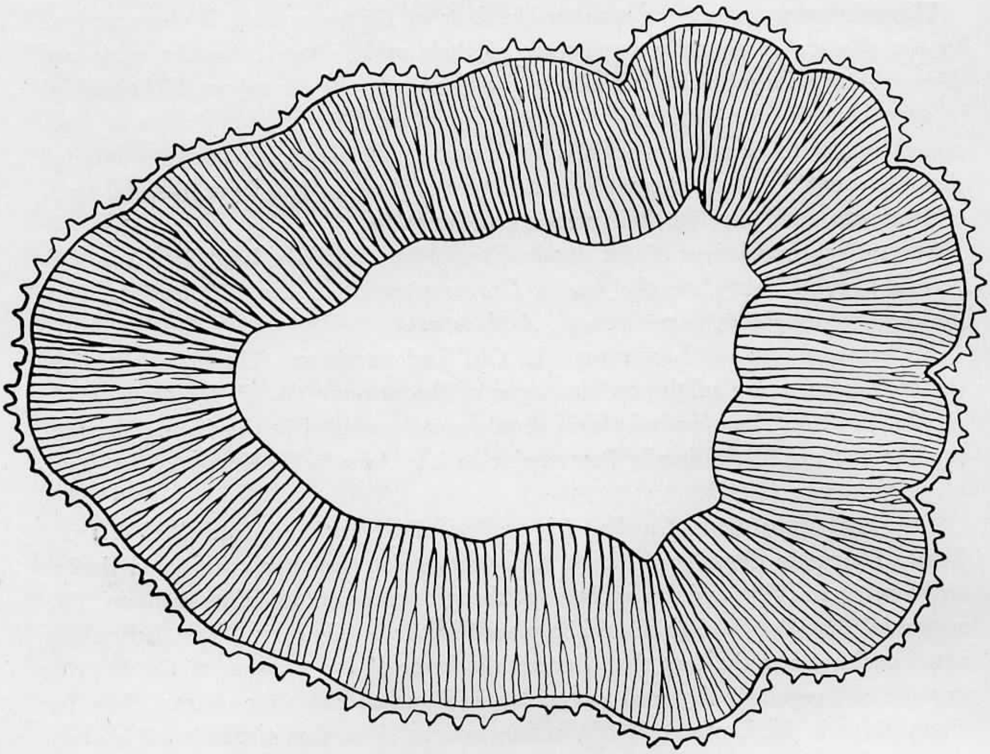

Fig. 8. *Porolepis uralensis* Obr. Cross-section of the tooth. Long axis is 4,0 mm long.

on the bones of *Osteolepis* and *Megalichthys*. I shall call these teeth "parquet dermal teeth" ("Hautzahnparkett", W. Gross, 1930).

A surprising detail of the structure of *Porolepis* discovered for the first time by W. Gross is the presence of a second layer of teeth under the layer of ordinary coalescent dermal teeth. The teeth in this layer have a conical form and are fully immured in the bone tissue. According to W. Gross (1935) they bear a great resemblance to the dermal teeth of *Glyptolepis*.

W. Gross drew from this the conclusion that the scales of young specimen of *Porolepis* at first had been covered with isolated conical dermal teeth which later during the growth of the scale in thickness were immured in the bone. Only after this a layer of coalescent "parquett" dermal teeth appeared on the surface of the scale and these teeth were not replaced during the whole life of the fish.

In his work of 1956 W. Gross again publishes a drawing of the second layer of teeth in *Porolepis posnaniensis* (Kade) and calls them "dermal teeth of the former bone surface" ("Hautzähne der ehemaligen Knochenoberfläche", W. Gross, 1956, p. 68).

During 20 years I could obtain neither the dermal bones nor scales of *Porolepis*

Fig. 9. *Porolepis uralensis* Obr. Vertical section of the scale. × 200.

for microscopic investigations. At present I have at my disposal such material from Siberia and this gives me the possibillity to repeat all W. Gross's observations.

Studying vertical microscopial sections of the scales of *Porolepis* one can see on their surface a well defined layer of coalescent dermal teeth (fig. 9). The height of the teeth in this layer varies with the individual age of the fish but usually is 0,2 mm. Every tooth representing a part of the tooth "parquet" has a flat top and a slightly tapered base coalescent with the bone. The dentine wall of the tooth is very thick and is pierced by a great number of dentine tubules. The pulp cavity is represented by one or several relatively wide canals. The enamel layer on the upper surface of these teeth is very thick and on their lateral parts it is much thinner.

In many places it is possible to find in the bone tissue of the scale under the

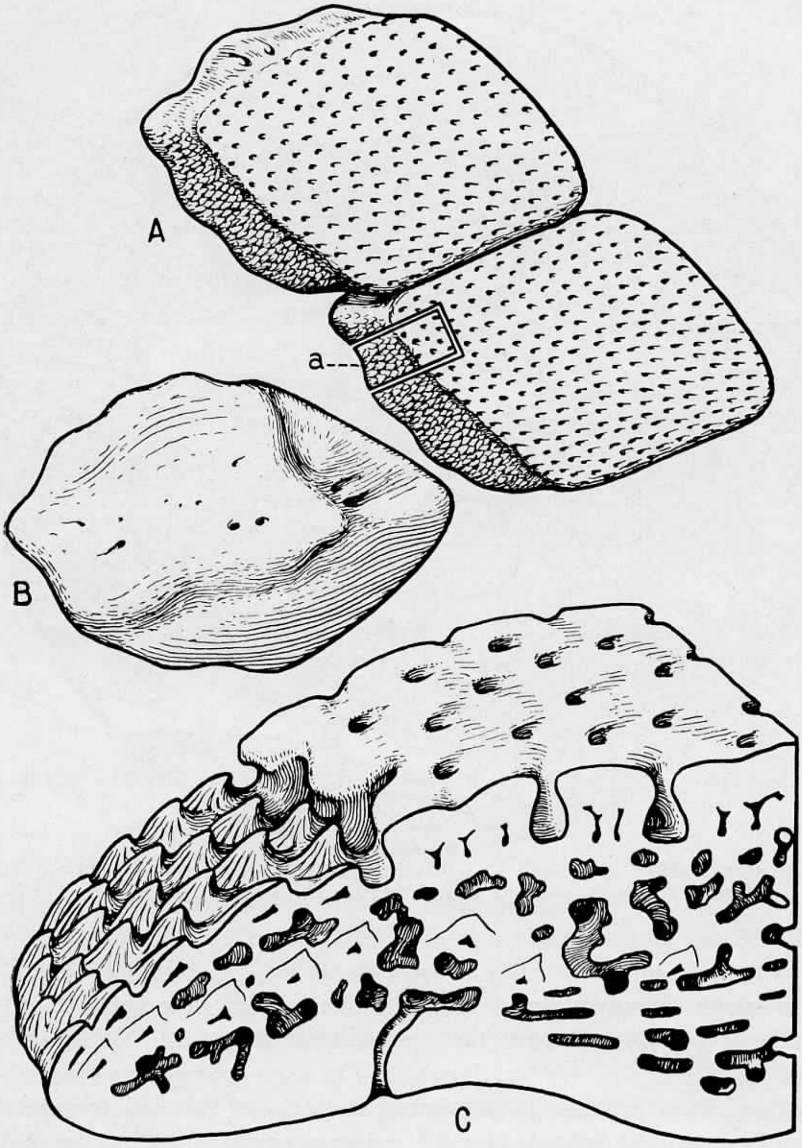

Fig. 10. *Porolepis uralensis* Obr. A = Two scales; view from outside. B = a scale; view from inside. The length of the scales is 10 mm. C = small portion cut out of the front edge of the scale (see a).

layer of "parquet" dermal teeth one or two generations of conical dermal teeth (fig. 9). The shape of these teeth differs greatly from that of the teeth of the "parquet" layer and they never coalesce. Their dentine wall is relatively thick and is pierced by radiating dentine tubules. The pulp cavity usually has the shaps of

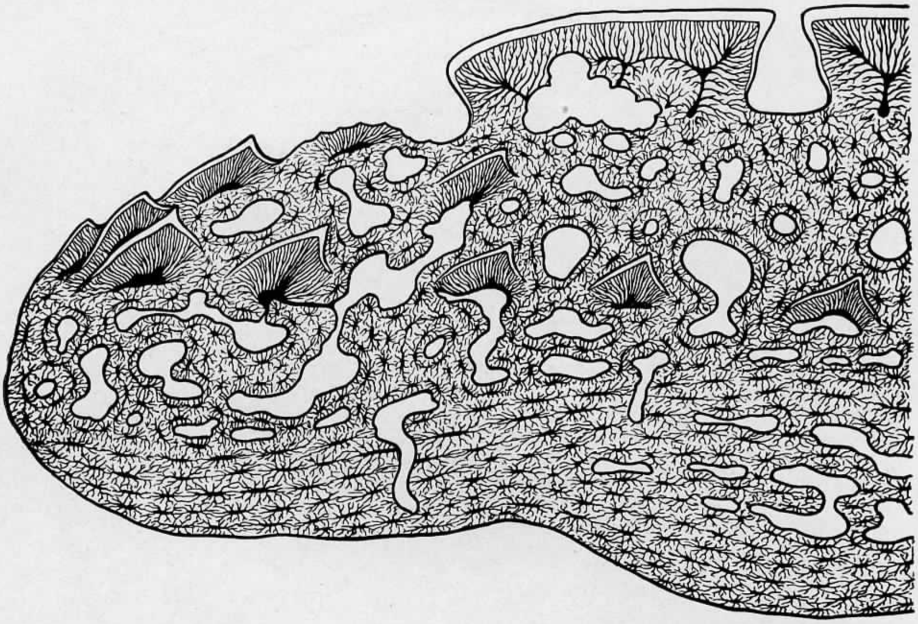

Fig. 11. *Porolepis uralensis* Obr. Vertical section of the front edge of the scale. × 100.

a horizontal slit. The enamel layer usually covers all such tooth and forms a sharp point on its top.

The supposition of W. Gross (1935) that these generations of conical teeth immured in the bone formerly covered all the outer surface of the scale seemed to me both interesting and quite probable. But at present studying the well preserved scales of *Porolepis* I could find some important details that induce me to alter my opinion. The fact is that numerous conical dermal teeth were found on the front parts of the scales of *Porolepis* covered with sharpened back parts of the scales of the preceding row. They are present in greatest number on the frontal-lower slanting edge of the rhomboid scale (fig 10 A). All the surface of this part of the scale is covered with teeth and their sharp tops are always inclined caudalwards. Sharp ridges stretching from the top to the base can be clearly seen on the enamel of these teeth (fig. 10 C).

Studying under the microscope the edges of the scale (a—fig. 10 A; fig. 10 C; fig. 11) one can readily distinguish different generations of conical dermal teeth immured in the bone tissue of the scale. The teeth not yet immured in the bone are located on the slope of this edge. Here they are sometimes literally placed over each other (fig. 11). The sections orientated across the edge of the scale (perpendicularly to the plane of the section represented on fig. 11) and passing through

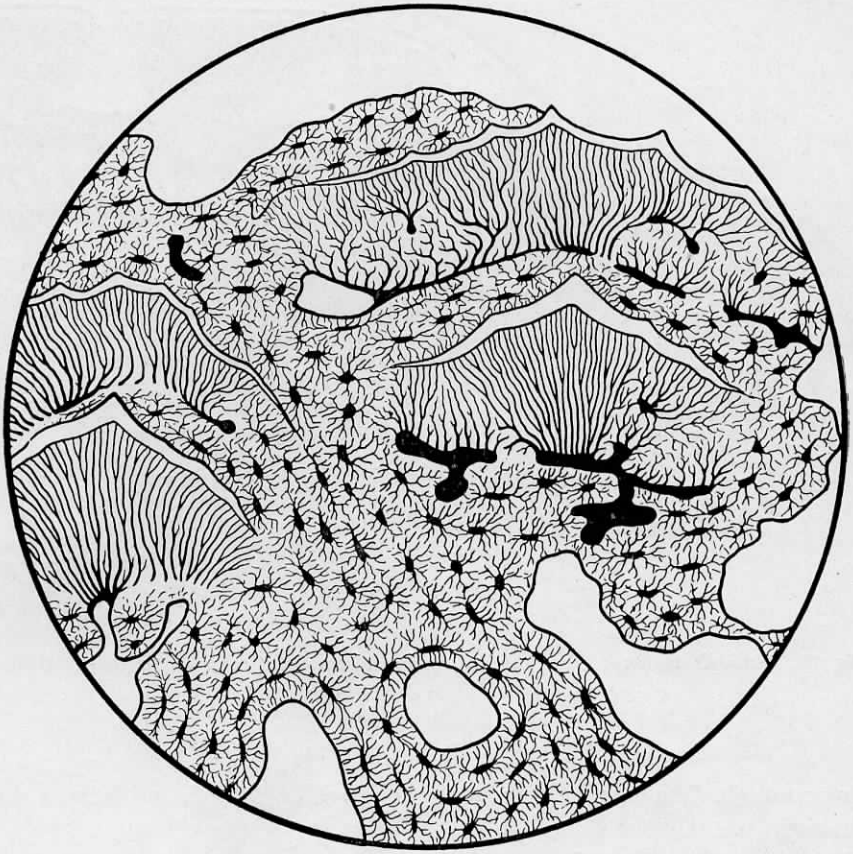

Fig. 12. *Porolepis uralensis* Obr. Vertical section of the front edge of the scale (perpendicular to the surface of the section on fig. 11). × 300.

the zone of conical teeth show the ridge-bearing enamel layer on the surface of those dermal teeth (fig. 12).

The growth of the scales of *Porolepis* evidently took place in the following way: the continuous deposition of new generations of bone tissue on the front edges of the scale caused their gradual extention in the cranial direction. During this process the surface of the slopes of the scale was being covered with conical dermal teeth which were immured in the bone when the edges of the scale thickened. The displacement of the front par of "parquet" teeth in the cranial direction occured simultaneously and this layer gradually covered the immured conical teeth. As a result of all this process different generations of the conical edge teeth were placed in the bone tissue of the scale far from its front edge and sometimes were located deeply under its "parquet" teeth (fig. 9; fig. 11; fig. 13).

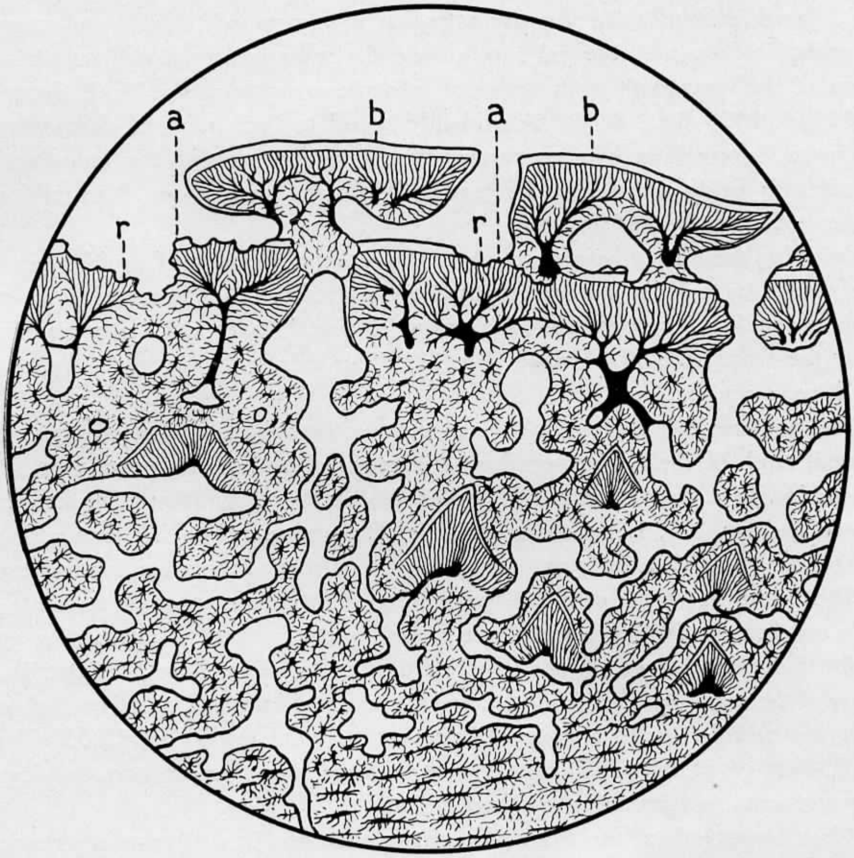

Fig. 13. *Porolepis uralensis* Obr. Vertical section of the scale. a = "parquet" dermal teeth of an earlier generation; b = teeth of the same kind of a later generation; r = resorbed portion. × 100.

Then during the process of the bone rebuilding many conical teeth were destroyded and vanished completely.

In 1942 I published the results of my study of the replacement of consecutive generations of "the parquet of coalescent dermal teeth" ("Hautzahnparquett") in Middle Devonian *Dipterus* and *Osteolepis* (A. P. Bystrow, 1942). I described in this work the destruction of dentine in dermal teeth of consecutive generations. In 1950 E. Jarvik studying the bones of *Dipterus* did not confirm my observations and did not find a single case of destruction of dermal teeth forming a part of the so called teeth "parquet".

E. Jarvik writes that "No spaces of resorption in the pulp cavities of the individual dermal teeth of the dentine layer of the type described by Bystrow (1942) have been observed either along the Westoll-lines or elsewhere" (E. Jarvik, 1950, p.

45). Jarvik evidently did not pay attention to my remark that the phenomena described by me are observed rarely since the replacement of different generations of the "parquet" teeth does not take place continuously (A. P. Bystrow, 1942, pp. 286—287). E. Jarvik evidently hoped to find traces of destruction of "parquet" dermal teeth in every transparent section crossing the boundary between two fields formed by the teeth of different generations. Naturally such hopes could not be justified.

Studying the microscopic structure of the scales of *Porolepis* I could again find the resorption cavities in the "parquet" dermal teeth. The traces of destruction usually could be observed in those elements of dental "parquet" that were located near the front part of the scale (fig. 11). This means that here the "parquet" teeth were replaced first.

I have at my disposal several transparent sections showing that the "parquet" dermal teeth of the first generation semidestroyed by the resorption process are covered with a row of similar teeth of the second generation deposited from above (b—fig. 13). Later the rebuilding of the bone led to full destruction of "parquet" teeth of an early generation. They vanished without leaving any traces.

The "parquet" teeth of a later generation on the front part of the scale not only covered the semidestroyed layer of "parquet" teeth of the preceding generation but also were partly deposited on the conical dermal teeth located in the slope of the scale. As a result of this several layers of immured small conical teeth were covered here with a layer of "parquet" dermal teeth (fig. 13). Evidently R. H. Denison (1951, p. 250, fig. 48) met with the same phenomenon studying the bones of some representative of Osteolepidae.

Thus the growth of the front part of the scale of *Porolepis* was accompanied by a continuous process of immurement of consecutive generations of sharp conical teeth into the bone and of covering them with a layer of "parquet" teeth. During this process the "parquet" of a former generation was substituted by the "parquet" of a new generation. Such substitution of layers of the "parquet" dermal teeth led to the thickening of the scale. Besides, the growth of the scale in thickness also took place on account of the deposition of new bone lamellae on its lower surface. The traces of such deposition can readly be seen on every vertical cross-section of the scale of *Porolepis* (fig. 11).

D. V. Obrutchev in his work "Discovery of Lower Devonian Ichthyofauna in the USSR" writes that "*Porolepis* from the Taimyr peninsula is distinguished from all known species by the presence on the outer surface of the joints of flat tubercles similar to the tubercles on the scales of *Glyptolepis*" (D. V. Obrutchev, 1939, p. 292).

I had at my disposal the scales of *Porolepis uralensis* Obrutchev 1938 from the Taimyr peninsula and from the banks of the river Kureika.

The "tubercles" (= dermal teeth) mentioned by D. V. Obrutchev are present also on the scales *Porolepis* from Lower Devonian deposits in the basin of the river Nizhni Viluikan but they cannot be called "flat" (fig. 9, 10, 11, 12, 13). The presence of similar dermal teeth in *Porolepis posnaniensis* (KADE) was discovered by W. GROSS (1935, 1956). I means that these dermal teeth are typical not only for the scales of *Porolepis uralensis* Obr. from the Taimyr peninsula. It is quite possible that the conical dermal teeth on the front part of the scales will be discovered in all species of *Porolepis*. On the scales of the Taimyr specimen of *Porolepis uralensis* Obr. these teeth were "flat" (D. V. OBRUTCHEV, 1939) in all probability only because their sharp tops were broken off. On the preparation of W. GROSS (1935) the tops of the two conical dermal teeth immured in the scale were doubtless destroyed during the rebuilding of the bone.

I have at my disposal no proof of the fact that the outer surface of the scales in young specimens of *Porolepis* and *Osteolepis* was covered with a layer of conical dermal teeth (W. GROSS, 1935). W. GROSS supposes that these teeth were covered with a "parquet" of coalescent dermal teeth only in grown-up fishes. According to W. GROSS the destruction of the teeth and their replacement never took place in this "parquet" of teeth.

My investigations of the microscopic structure of the scales of *Porolepis* have shown that the destruction and formation of new "parquet" dermal teeth can be observed rather often in this Crossapterygian.

As to the conical dermal teeth, they are always present on the front edge of the scale and become surrounded with its bone tissue owing to the intensive growth of its front part. During this process the layer of "parquet" dermal teeth gradually enlarges its area and inevitably covers all the conical dermal teeth immured in bone.

It seems to me that the presence of conical dermal teeth even on the narrow strip of the front edge of the scale of *Porolepis* proves that the scales of the ancestors of Lower Devonian *Porolepis* were covered not with a "parquet" of coalescent specialized dermal teeth but with numerous conical shagreen teeth the sharp tops of which were inclined caudalwards. Nevertheless these teeth did not cover all the outer surface of the scales in young specimens of *Porolepis* or *Osteolepis* as W. GROSS (1935) supposes.

VI. Archaeomycelites odontophagus g.n., s.n.

In 1956 in my work on the destruction of the skeleton elements of fossil animals by fungi I publisher drawings of several preparations in which one could clearly see canals or borings made by hyphae of a saprophyte fungus for which W. Roux had proposed the name *Mycelites ossifragus* (W. ROUX, 1887).

The most ancient form destroyed by the hyphae that I found up to 1956 was a Middle Devonian *Psammolepis paradoxa* Agassiz.

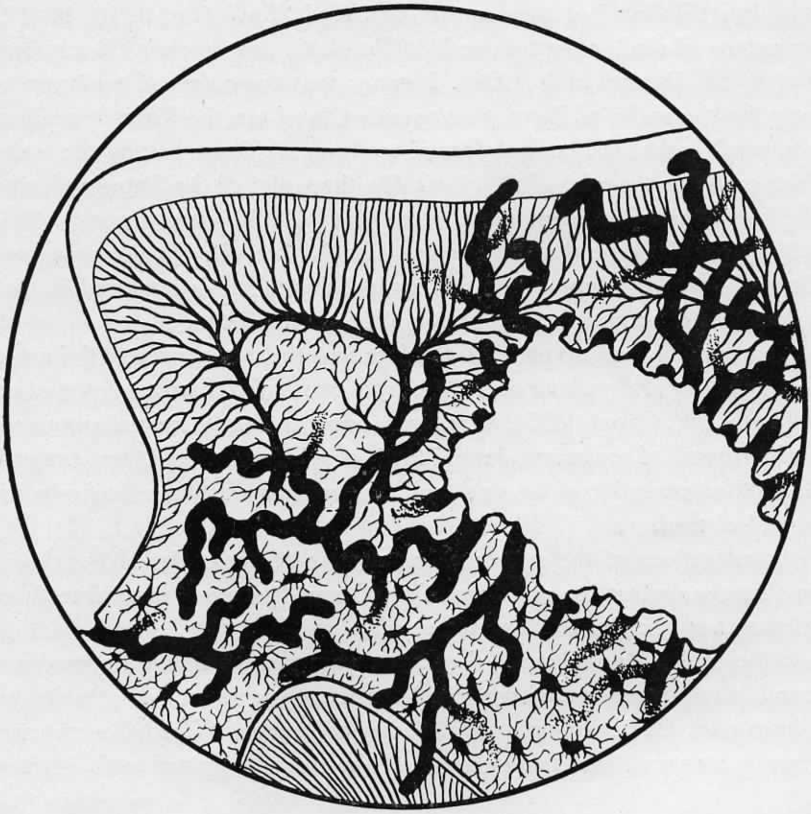

Fig. 14. *Porolepis uralensis* Obr. Vertical section of the scale. One can see the borings made by the hyphae *Archaeomycelites odontophagus* g.n., s.n. × 400.

At present I have also found borings formed by the hyphae of saprophyte fungi in the bones of a Lower Devonian Crossopterygian fish *Porolepis uralensis,* and in the armour elements of a Lower Devonian representative of the family Pteraspidae—*Gunaspis orientalis* g.n., s.n.

The destruction of the bones of *Porolepis uralensis* by the hyphae of a fungus usually started from the space between the two neighbouring "parquet" teeth. During this process the hyphae of a fungus penetrated first through the thin layer of enamel covering the lateral surface of the tooth and then developed in its dentine. Growing through the dentine they in many cases approached from beneath the thick enamel layer lying on the flat upper surface of a "parquet" tooth. I could observe several times the penetration of the ends of the hypha into this layer (fig. 14). Sometime they bored it through and evidently passed outside.

Those hyphae which were directed from the space between the neighbouring "parquet" teeth downwards often penetrated very deeply the bone mass of the

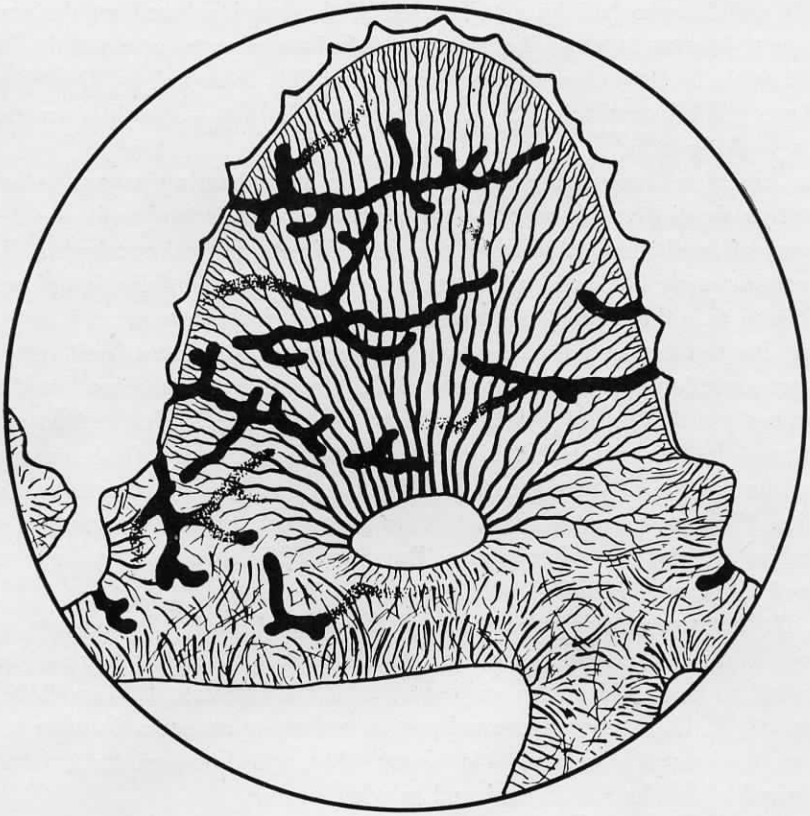

Fig. 15. *Gunaspis orientalis* g.n., s.n. Vertical section of the armour. One can see the borings made by the hyphae of *Archaeomycelites odontophagus* g.n., s.n. × 400.

scale and not only destroyed the bone but also the conical dermal teeth immured in it. Approaching them from above or laterally hyphae usually at first dissolved the thin enamel layer and then penetrated dentine (fig. 14).

Studying a great number of transparent sections of the armour elements of *Gunaspis orientalis* g.n., s.n. I could often find in its crestlike dermal teeth borings made by the hyphae of saprophyte fungi.

They usually penetrated the tooth crest from the outside, evidently easily destroyed the enamel layer and then were introduced into the dentine mass (fig. 15). Those hyphae that penetrated the armour between the tooth crests at once reached aspidin and grew through it (fig. 15).

In *Gunaspis orientalis* the borings made by the hyphae of a fungus can be seen not only in the upper layer of its armour but also in the basal lamella.

The diameter of the borings made by the hyphae of fungi in the bones of *Porolepis* and in the armour shields of *Gunaspis* varies from 5 to 7 μ.

It is well known that the classification of the fungi is based on the study of their spore-bearing organs. Therefore the definition of systematic position of any fungus solely by its hyphae is considered impossible in mycology. Owing to this W. Roux (1887) considered the name proposed by him—*Mycelites ossifragus*—only a working term.

The complete impossibility to discover the spore-bearing organs in ancient saprophyte fungi that left only the borings made by their hyphae in the skeleton elements of fossil animals presents a great difficulty for paleontologists. Taking into consideration all these circumstances we should base our definition of systematic differences in these fungi chiefly on their *physiological* characteristics.

Studying the destruction of the skeleton elements of different fossil vertebrates by saprophyte fungi I (A. P. Bystrow, 1956) found that in marine forms of the cretaceous period the fungi destroyed bone and dentine. I observed no cases of the destruction of enamel. In Upper and Middle Devonian fresh-water vertebrates the hyphae of fungi penetrated bone and aspidin but did not penetrate dentine. This physiological characteristics permitted me to distinguish a saprophyte fungus *Palaeomycelites lacustris* Bystrow 1956 that inhabited the lakes and rivers of Upper and Middle Devonian periods.

R. H. Denison studying the scales of Devonian Osteolepidae complains that "many details of the structure are obscure because of the abundance of borings attributed to fungi (*Mycelites ossifragus*)". (R. H. Denison, 1951, p. 248). Unfortunately R. H. Denison presented neither a description nor a drawing of these borings. Therefore it is impossible to say what was destroyed in the scales of Osteolepidae that he has studied and in what degree.

The investigation of the microstructure of the skeleton elements of Lower Devonian vertebrates (*Porolepis* and *Gunaspis*) has provided me with material proving the presence in fresh-water basins in the beginning of Devon of a saprophyte fungus capable to destroy not only bone and apsidin but also dentine and enamel (fig. 14, 15). Though I have nothing at my disposal except the preparations in which only the borings made by the hyphae can be seen, taking into consideration such important physiological detail of the hyphae as their ability to destroy all hard tissues of Lower Devonian vertebrates (bone, aspidin, dentine and enamel) I think that it is possible to distinguish a new genus of saprophyte fungi. I propose for it the name *Archaeomycelites odontophagus* g.n., s.n. Its genetic name shows the great age of the fungus and the specific name—its ability to destroy teeth.

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