Investigations of the Lower Ordovician of the Siljan District, Sweden

II.

Lower Ordovician penetrative and enveloping algae from the Siljan District

By

Ivar Hessland

1. Introduction.

Certain microscopic algae and possibly also fungi have the ability of boring in calcareous rocks and in hard organic tissues, such as carapaces and shells of invertebrates, and in bone substances and scales of vertebrates. A few of them are supra-aquatic, but the majority are aquatic. Some occur in freshwater and others in the sea.

In our day, aquatic boring or perforative algae (also called endolithic algae) constitute a large group of species belonging to Cyanophyceae, Chlorophyceae, and Rhodophyceae. They occur in practically all climatic regions, but their frequency is highest in fairly stagnant and shallow bays of the warm seas.

Structures created by boring algae have been recognized in several fossiliferous deposits of various ages. The oldest known are Ordovician. However, they cannot be said to be well-known by geologists. In Swedish and Estonian deposits, for instance, they do not seem to have been recognized at all, in spite of the fact that they are very numerous in certain strata.

The destructive activity of penetrative algae has been noticed by many investigators (destruction of shells and bones, coral and algal reefs; formation of furrows and pits in calcareous rocks; coastal erosion). Their positive activity, on the other hand, has not been sufficiently considered, viz. their activity as a phytal partner of animal societies, i. e. as a producer of oxygen and an absorber of the excretion products of the animals. In fact, the activity of boring algae in combination with that of other groups of algae is certainly one important reason for the luxuriance of certain biotopes, and the reason for the fact that rich faunae can live in such surroundings where they otherwise would have succumbed on account of oxygen deficiency.

Furthermore, they are important as indicators of changes of level: their presence indicates a fairly shallow water during the deposition of the algae-bearing stratum.

Finally, they are certainly of great importance for the precipitation of hydrous iron oxide and for the formation of limonitic ooids.

These questions will be discussed in the present paper in connection with the description of the penetrative and enveloping algae in a part of the Lower Ordovician of the Siljan District.

2. On recent penetrative algae.

Certain tubular structures in shells were observed as early as the fifth decade of the 19th century (cf. CARPENTER 1845, p. 13), but the nature of these structures was not recognized until later.

CARPENTER was first of the opinion that the structures were normal for the shells and of taxonomic importance. QUEKETT (1854) considered at least some of the tubuli of similar appearance in Madreporaria as products of "Confervae, Spongida, or of minute boring animals". ROSE (1855) referred such structures in fish-scales to "infusorial parasites".

WEDL (1859) exposed shells to the action of dilute hydrochloric acid and stated that the boring organisms were plants; he thought they were polycellular filamentous algae. KÖLLIKER (1860) who investigated tubular structures of the present kind in several marine and limnic animals considered them to be bored by monocellular plants, whether by fungi or algae was, according to him, difficult to decide.

CARPENTER later withdrew his former explanation of the structure and referred them to parasitic action of a fungus (cf. STIRRUP 1872).

LAGERHEIM (1886) was the first botanist who investigated these perforating vegetable organisms. He identified two algal species which later appeared to have a very wide distribution, viz. the well-known *Mastigocoleus testarum* LAGERHEIM (Cyanophyceae) and *Gomontia polyrhiza* (LAGERHEIM) BORNET and FLAHAULT (Chlorophyceae).

These finds on the Swedish west coast gave rise to the undertaking of similar investigations by French botanists on their coast. In 1889 a paper appeared on this subject, viz. the fundamental and often quoted investigation by BORNET and FLAHAULT. These authors recognized several penetrative species which are referable to the bluegreen and green algal groups (8 genera), but also 2 genera which are colourless and referred to the algal fungi (Phycomycetes). In 1892 BATTERS reported a find of a perforating red alga from the British Isles.

Later, more and more perforative algae have become known. PIA (1937) made a survey of the boring Thallophytes, which were known at that time. This survey may be fairly complete, but the boring ability does not seem to be completely proved in some cases. To give an idea of the abundance of boring Thallophytes I made a tabular survey of these organisms on the basis of PIA's work:

Group	Marine		Limnic		Terrestic		Σ	
	Genera	Species	Genera	Species	Genera	Species	Genera	Species
Cyanophyceae	11	32	10	25	7	11	25	68
Chlorophyceae	7	13	2	4	—	—	7	17
Rhodophyceae	1	1	—	—	—	—	1	1
Heterocontae	—	—	—	—	2	2	2	2
Fungi	2	2	1?	1?	1	1	4	4
Lichenes	—	—	1	1	18	57	19	58
	21	48	14	31	28	71	58	150

Note. Three Cyanophyceae and two Chlorophyceae genera occur both in the sea and in lakes.

During later times, boring algae have been investigated with new and careful methods. KYLIN (1935) studied their ontogenesis by means of laboratory cultivations, which have also yielded important morphologic and taxonomic results.

LAGERHEIM had already noted that there are generally more than one species boring in the same shell. The sociology of boring algae was studied by BORNET and FLAHAULT, and has been continued by later investigators, for instance ERCEGOVIĆ (1934), who discerned several associations of different rank.

Closely associated with this question is that on the vertical distribution of aquatic perforative algae. Since algae are dependent on the insolation, they live in fairly shallow water; very often the depth is insignificant (many species live in the tidal zone). They are reported as abundant to about 20 m or somewhat deeper. The lower limit is, of course, due to the transparency of the water. BERNER (1931) and ERCEGOVIĆ (1934) have examined the vertical zonation of endo- and epilithic algae in the Mediterranean (French and Dalmatian coasts resp.).

Much weight has been attached to the role which is played by penetrative algae as disintegrators of shell substances, coral and algal reefs, and calcareous rocks. Some authors have also paid attention to the fact that the calcium carbonate dissolved by the action of the algae may be re-precipitated as a calcareous mud (WETZEL 1938).

The chemistry of the penetrative process is but poorly investigated. Most likely the dissolution is caused by an acid. Carbonic acid has been considered, but more probably it is some organic acid. It is not known, to what extent and in which way the dissolved products leave the organism.

It has also been suggested that the penetration is performed to a certain extent in a mechanical way, but this has been considered to play only a subordinate role.

3. The biocoenotic importance of penetrative algae.

When penetrative algae were first described, they were denominated as parasites. Their destructive activity on the shells was easily seen, but only during recent years has one begun to understand that they are also useful to the animal in the hard tissues of which they live. PARKE and MOORE (1935) who investigated the algal infection of the shells of living *Balanus balanoides* pointed to the fact that the algae, in the daytime, contribute oxygen to the animal; the algae, in return, benefit from the excretory products of the barnacle, and thus keep the water around the animal clean. However, the full significance of the symbiosis between animals and penetrative algae does not seem to have been recognized.

A symbiosis between an animal and a plant is a perfect arrangement: the plant produces oxygen, necessary for the animal, and uses, in return, the waste products of the animal. CO_2 is consumed for synthesis of carbohydrates; other excretion products, especially potash salts, sulphur compounds, and compounds of phosphorus and nitrogen are made use of as nutritious substances; phosphorus, nitrogen and sulphur are used for the further transformation of the carbohydrates into protein, which is stored by those lower aquatic plants considered here.

The best result of such a symbiosis is reached when the plant is incorporated in the soft tissues of the animal. This is the case of the so-called zooxanthellae, small yellowish-brown unicellular algae, which occur in many animal groups but which are especially numerous in the reef-building corals.

They may be a most essential reason for the luxuriance of the coral reefs, and they are certainly the factor which determines the position of the lower limit of the reefs (cf. HESSLAND 1946). When the algae, as in this case, are intra-cellular in the soft tissues of the animal, the exchange of gases (O_2 and CO_2) takes place by direct diffusion through the tissues, so that there will be no loss of gas. Furthermore, the vital functions of the animal will be facilitated by the fact that the zooxanthellae serve as excretion organs of the animals.

The effect of the symbiosis is less in those cases where the algae live in the external hard tissues of the animals. The exchange of gases and the transference of animal waste products must take place via the water, and this must mean a certain inefficiency. But in this case also the symbiosis is valuable as stated above as regards *Balanus balanoides*. In the same respects, penetrative algae may be of great importance for such luxurious biocoenoses as reefs. In the coenenchym of reef corals they are very abundant, and there is reason to believe that the results of the vital activity of these algae are added to those of the zooxanthellae.

Penetrative algae must be considered to have a very great importance for animal communities living in shallow stagnant waters. However, recent surroundings of this type do not seem to have been investigated. They may not occur in temperate regions, where, among other things, seasonal convection currents prevent the formation of such waters. In warm regions, on the other hand, they may be easily formed. Seasonal convection currents are not developed there. Furthermore, the fact may be noted that the specific gravity of the water varies by a larger amount for a temperature difference of 1° at a higher temperature than at a lower. Especially in salt waters of warm regions a stratification may be easily developed but difficult to interrupt. Conditions as now described may be found in coastal basins of lower latitudes.

It is evident that a deficiency of oxygen will appear in stagnant waters, supposing that they do not include a producer of oxygen. Plants provided with chlorophyll have this ability. Since such aquatic plants occur only in the upper layers, stagnant waters containing oxygen are shallow. In marine surroundings, algae are the majority of these plants, and among them penetrative species may be of importance in such areas where penetrable substances are present.

The fossil occurrence of penetrative algae described in the present paper is included in a stratum which was formed when the water, on the whole, was fairly stagnant, temporarily very stagnant. At the same time, it was rich in oxygen. These conditions may be necessary for the formation of the limonitic ooids which are abundant in this stratum (cf. p. 421 and part IV of this series of papers). The oxygen, to a great extent, must have been produced by the very numerous penetrative and the partly abundant enveloping algae. Certainly owing to this production of oxygen, a numerous fauna could live in the Siljan District during this period. The flora, in return, profited by the excretion products of the animals. Thus, in this closed water there existed a kind of biocoenosis between the animals and the plants, though the form of the biocoenosis was not the common one, since the plants, as a rule, do not seem to have occurred in the shells of living animals, but lived in dead shells.

4. On previous observations of fossil penetrative algae.

Structures in hard tissues of fossils caused by penetrative algae have been known practically as long as corresponding structures in recent material.

ROSE (1855) reported such structures from fossil fish-scales. WEDL (1859) found them in fossil gastropods, bivalves and brachiopods. KÖLLICKER (1860) examined other groups as well, and DUNCAN (1876) made a special investigation of penetrative algae in fossil corals.

PIA, in his survey of penetrative organisms, 1937, also gave a list of fossil penetrative algae. He points out that fossil boring Thallophytes were earlier usually considered to be fungi, but that they in fact for the greater part were algae belonging to a few recent genera, or to genera closely related to them.

PIA says, in this connection (1937, p. 341), that canals of similar appearance can be bored by different species. Furthermore, he points out that the same alga can make canals of dissimilar appearance in different parts of a shell. Nowadays, there are a lot of penetrative algae, and during the past geological periods there certainly existed a great many genera which are now extinct. For this reason I agree with PIA that fossil algal structures should not be confined to recent genera. I also agree with him when he says that it is not possible to establish certain species within the genera. PIA proposed the algal structures to be classified from other points of view, viz. according to the age of the formation and to the substance which is penetrated.

WETZEL (1938), referring to the papers of PIA (1937) and KYLIN (1935), rightly rejected such generic names of fossil penetrative algae as *Chaetophorites* PRATJE and *Gomontia* BORNET and FLAHAULT. Instead, he proposed a morphological grouping of the canals bored by microscopical plants. He grouped the canals of a few such recent organisms mainly according to their diameter and intended to class fossil canals in this system. Other distinctive features were the course of the canals, their ramification, and the appearance of certain bladders. He discerned 6 groups divisible into 2 divisions, viz. one with proportionally wide canals and another with narrow. The former should consist of green algae, the latter of phycomycetes or blue-green algae. However, his system is seriously impaired by the fact that he did not know the recent organisms which had created the canals which he proposed as standard types of the system.

Rather many structures bored by penetrative algae are known from the Palæozoicum. A few of them are referable to the Ordovician. STØRMER (1931) described such structures in trilobite carapaces (Middle and Upper Ordovician of Norway). HØEG, in reporting *Girvanella problematica* NICHOLSON and ETHERIDGE from the Lower and Middle Ordovician of the Trondheim Area in Norway, pointed to the fact that f. *lumbricalis* of this species "is not unlike a perforating specimen. It should be compared with *Palaeachlya perforans* DUNCAN" (1932, p. 65). ROHON and ZITTEL (1887) described canals bored by algae in Ordovician conodonts.

So-called *Girvanellae* credited with the ability of boring in iron compounds are reported by CAYEUX (1909) and HAYES (1915). According to CAYEUX they occur abundantly in ooids of hematite, less abundantly in ooids of siderite, and occasionally in chamosite; they were also observed in opal. According to HAYES, they are best developed in spherules of hematite and chamosite but they also occur in siderite. Like PIA (1937, p. 362), I am inclined to consider these structures as non-organic.

5. The present algae-bearing deposits.

The present deposits including perforative and enveloping algae belong to the Ordovician section of the Siljan District in the province of Dalarna, Sweden.

Rock samples including penetrative and enveloping algae from other parts of the Palæozoic Scandoestonian Region have also been examined, viz. from the Island of Öland (stratum corresponding about to the stratum *G* of Dalarna investigated here), the province of Uppland (drift boulders from the *Schroeteri* Limestone of the submarine region of the Bothnian Gulf, Lower Ordovician), and from Estonia (Obere Linsenschicht, Aseri stage, Lower Ordovician).

In the paper of ORVIKU (1940) on the iron oolite of the Aseri stage, canals bored by penetrative algae have been reproduced (Pl. XXII, Fig. 6); they were interpreted by ORVIKU as inorganic structures.

Only a short section of the Lower Ordovician of Dalarna was examined, viz. the layer which in earlier literature was called the Lower Grey *Ortho-*

ceras Limestone (for instance TÖRNQUIST 1883), plus the uppermost part of the subjacent stratum (the Lower Red *Orthoceras* Limestone), and the lowermost part of the superjacent one (the Upper Red *Orthoceras* Limestone). Later, these strata have been given other names, but they are partly unsuitable and are therefore not used in this paper. It is also scarcely possible to make complete correlations to the better investigated Estonian Region. Certain strata seem to be correlatable, however, such as the *Limbata* Limestone (the Lower Red) = $BII\alpha$. Furthermore, the Ingermanland *Asaphus expansus* Zone ($BIII\alpha$) is represented in the middle part and somewhat below the midheight of the Lower Grey: fauna with *Asaphus expansus* (L) WAHLENBERG, *Illaenus centrotus* DALMAN, *Ptychopyge angustifrons* (DALMAN), *Ampyx nasutus* DALMAN, and *Orthis callactis* DALMAN. In the upper part of the Lower Grey, the Estonian *Asaphus raniceps* Zone ($BIII\beta$) seems to be represented: fauna with *Megalaspis heros* (DALMAN), *Megalaspis rudis* ANGELIN, and *Clitambonites* (?) *zonata* (DALMAN).

Whether the Estonian zones $BII\beta$, $BII\gamma$, and $BIII\gamma$ are represented in the Siljan District is not ascertained. What the Upper Red corresponds to is not known: its lower part may not be called *Gigas* Limestone as is now done, since this fossil appears first about 5 m above the lower limit of the Upper Red.

In order not to confine the results obtained to the prevailing but, in several respects, inappropriate or erroneous stratigraphic names, provisional denominations for the strata investigated have been used. In the solution of these stratigraphic problems the whole necrocoenoses (not least the semimicro- and microorganisms, especially the ostracods) and the inorganic sedimentary phase must be examined, but such investigations have only begun.

In this paper, the mainly grey stratum (the Lower Grey), including the *Expansus* and *Raniceps* Zones, is given as stratum *G*. The former zone is abundantly oolitic (limonitic ooids), the latter is somewhat oolitic (parts of the ooids chamositic). The subjacent reddish maroon stratum is called *RI* and the maroon superjacent is named *RII*. The boundaries *RI*/*G* and *G*/*RII* may be mainly synchronous in the whole Siljan District (cf. parts I and IV of the present series). Moreover, the Siljan District was in close connection with the ocean during the *RI* and *RII* stages, but the communication was restricted during the *G* stage.

The positions of the localities investigated appear from the map, p. 114, in part I of the present series.

6. Description of the present penetrative and enveloping algae.

Penetrative and enveloping algae are abundant in stratum *G*, especially just below the midheight of the stratum. They occur occasionally in the uppermost part of stratum *RI* and the lowermost part of stratum *RII* (Fig. 1).

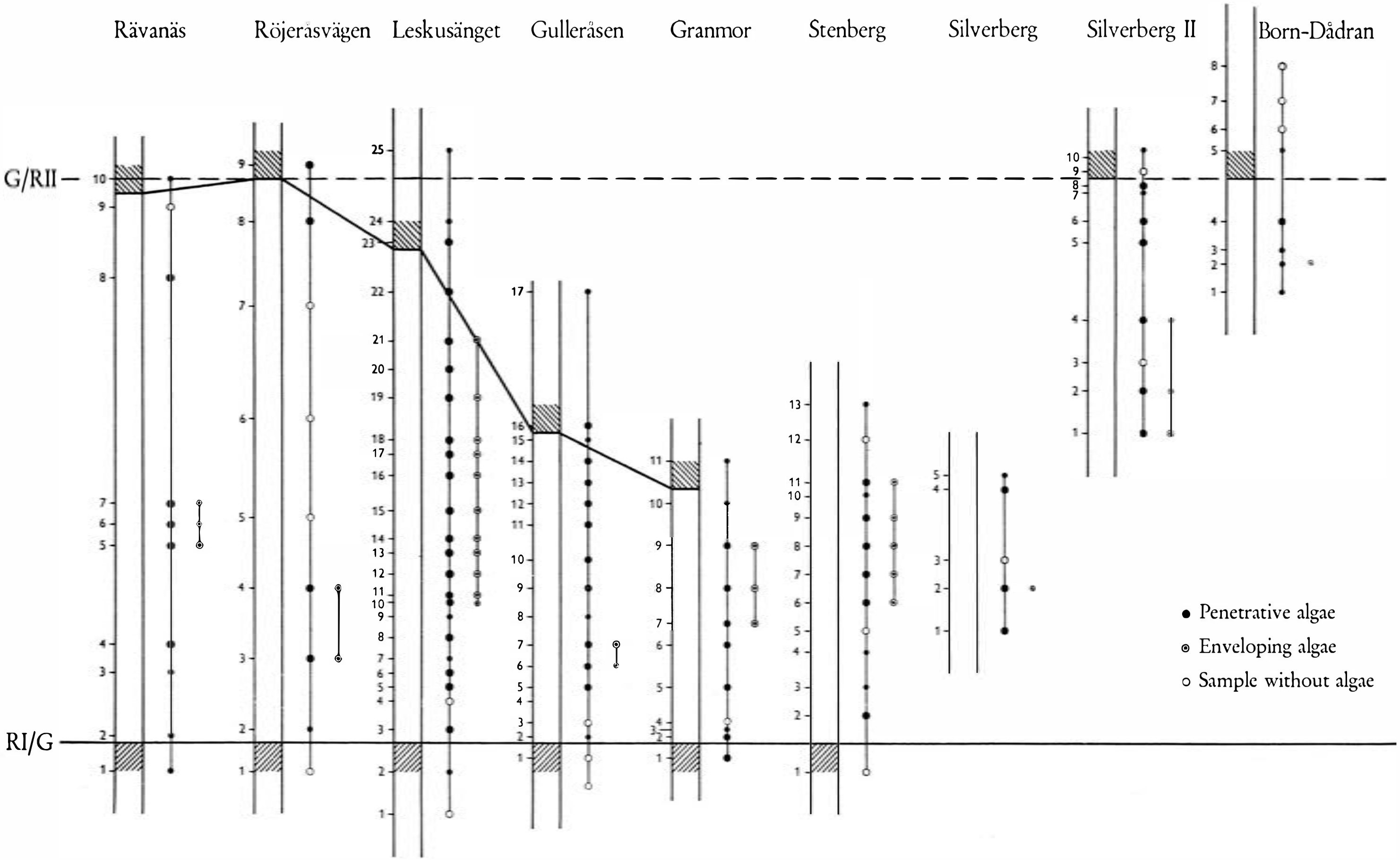


Fig. 1. Vertical distribution of penetrative and enveloping algae (small-sized types of markings indicate an inferior frequency). Greatest distance between *R I/G* and *G/R II* 4 m. Figures indicate number of samples.

It appears from Fig. 2 that the majority of the canals have a diameter of 1—5 μ, most of them 1—3 μ (317 measurements in 35 penetrated shell fragments). Rather many have a somewhat larger diameter (5—20 μ); a few isolated higher values were noted. Thinner canals branch off successively from the thick canals: the finest ramifications are those which constitute the majority of the canals, i. e. those which have a diameter of 1—3 μ. In Pl. VI, Fig. 3 a fragment is shown in which such a diminishing of the diameter can be followed from about 100 μ to about 1 μ. However, whether the thickest canals contained more than one algal thread cannot be definitely stated, but this appears to have been the case.

The thickest branches are most often gently tortuous. Branches of median thickness are not seldom rather straight. The most minute canals are fairly straight or gently curved; their course is extremely minutely and somewhat irregularly zigzag.

The fine canals are abundantly ramose with acute or right angles. At the points of ramification they sometimes form a triangular or rounded swelling. The ends of the algal threads are sometimes swollen. There are also larger irregular swellings.

The algologist, Prof. H. SKUJA, had the courtesy to examine some preparations which I had made by dissolving the calcareous carbonate substance around the algae in acetic acid so that the algal threads were set free.[1] He stated, mainly on account of the type of ramification and the thickness of the threads, that there are two or possibly three types of algae present:

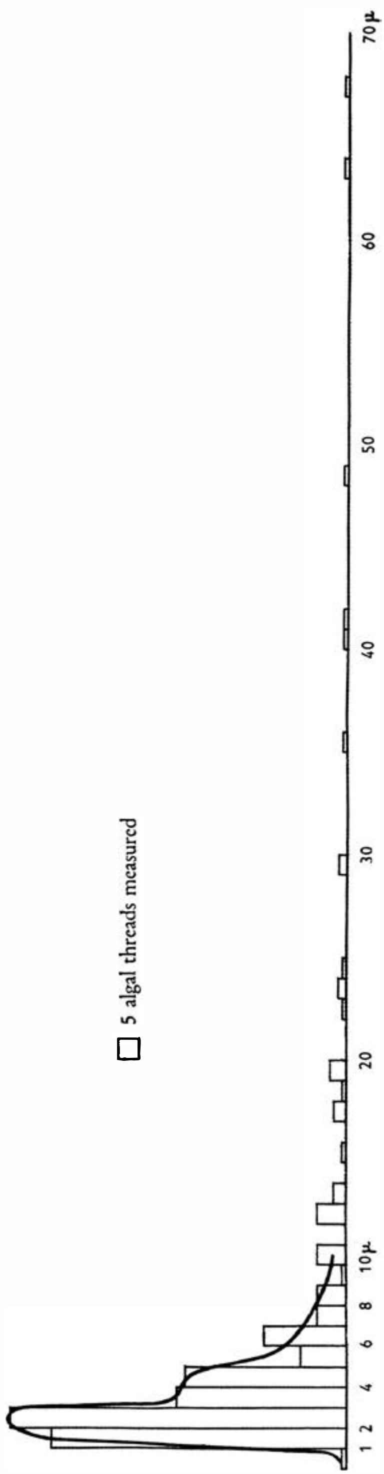


Fig. 2. Thickness of the algal threads.

[1] I wish to express my gratitude to Prof. SKUJA for his kindness to perform this examination and for valuable discussions on algae of the present type.

I. Bluegreen algae of *Plectonema* type, reminiscent of *P. terebrans* BORNET and FLAHAULT (thin threads with a false, acute ramification).

II. Possibly green algae (thicker threads with a real, right ramification).

III. Possible fungal hyfes (thin threads with a real, right ramification).

The present material helps to find the way in which shell fragments are infected by algae and thus disintegrated.

First may be mentioned that especially shells of trilobites and orthoids are infected. Shells of these groups are very numerous. Also a few fragments of strophomenoids and inarticulate brachiopods occur, and they were observed to be bored to some extent. Algal threads are often found in the cavities of crinoids, but the crinoid skeleton was not observed to be bored. Shells of cephalopods, conulariae, and gastropods, as well as the skeletons of bryozoans and calcareous algae, were not seen to be infected; ostracods may occasionally be slightly infected, but, as a rule, they are not bored.

Sometimes, the algal canals follow the structures of the shell, such as the laminae of orthids, but this seems only to be occasional; in most cases, the canals run quite irregularly. The algae attacked the shells from any part. In some cases one may observe, however, that the infection took place most easily from broken ends of lamellar shells and that the algae followed already existing pores and canals.

In newly infected shells the canals are most abundant just below the surface, and only isolated canals traverse the inner parts of the shell. As the infection proceeded, the shells became more and more filled with canals. Thick stems were developed, and these could traverse the whole shell. In this way, the shell became parted. In fact, this was in the present case an important phase in the process of disintegration of shells.

During the course of infiltration, angular parts of the shells had been more or less completely consumed, so that the fragments had grown more and more rounded.

By the partition and consumption of shell substance by the algae the shell fragments had diminished in size. When this process had proceeded so far that only a small part of the shell was left, it happened very often that the fragment was covered with layers of enveloping algae. If these algae became filled with hydrous iron oxide a limonitic ooid with concentric structures was formed. On the other hand, if a fragment had become encrusted with limonite at an earlier stage, viz. when a shell fragment had been parted into a suitable size, and the angles had become rounded so that an ovoid form had been created, a so-called false (i. e. a non-stratified) ooid would have appeared. As a matter of fact, in the present material one finds all stages of this process: non-infected shells; slightly infected, angular fragments; rounded fragments in different stages of partition; fairly small fragments, abundantly bored, and covered with a thin layer of enveloping algae; and finally very small and abundantly bored fragments surrounded by a thick layer of regularly stratified enveloping algae.

Considering enveloping algae, such occur also around non-bored fragments. Sometimes crinoids are enveloped by a fairly thin layer of algae.

Whether the enveloping algae are specifically different from the penetrative is not known. Judging from the thickness of the threads, they possibly belong to the above-mentioned group II (green algae).

7. Penetrative and enveloping algae as indicators of changes of level in the stratal sequence investigated.

As mentioned (p. 416), penetrative algae are most abundant in the middle part and somewhat below the midheight of stratum *G*. Enveloping algae are restricted to this horizon. Penetrative algae also occur in other parts of stratum *G*. Furthermore, they generally occur just below *R I/G* and just above *G/R II*. They were not observed in somewhat deeper parts of stratum *R I*, and they generally soon disappear somewhat above *G/R II*.

Considering the fact that shell fragments occur abundantly in those parts of *R I* and *R II* where penetrative algae are absent, one may conclude that the water was too deep for these organisms during those times.

On the other hand, the water must have been more shallow during the *G* stage, judging by the fact that penetrative algae were abundant during this stage and that the enveloping are confined to this stratum. Since the algal frequency culminates in the middle part and just below the midheight, the depth of water may have been least just during the sedimentation of this horizon. This is emphasized by the fact that the transparency of the water contemporarily seems to have been decreased owing to the circumstance that large quantities of minerogene fine-particles were settled in many cases. The sedimentation of minerogene fine-particles was less comprehensive during the next proceeding and following periods (cf. part IV of this series of papers).

From the appearance of the algae, the conclusion may be drawn that, in the Siljan District, a regression took place during the last part of the *R I* stage and the first part of the *G* stage, and that a transgression followed during the later part of the *G* stage and continued during the *R II* stage.

The fact that the Siljan District during the *R I* and *R II* stages was in closer communication with the ocean than during the *G* stage may not have influenced the frequency of penetrative algae; such organisms are common both in the open sea and in more or less closed oceanic areas.

8. The importance of penetrative and enveloping algae for the precipitation of hydrous iron oxide and for the formation of limonitic ooids.

The precipitation of the hydrous iron oxide which fills up penetrative algal canals and enveloping algae is here considered to have been caused by the activity of the algae themselves.

In discussing this question, one has first to consider the following suppositions as regards the hydrology in the Siljan District during the *G* stage, i. e. when algae of the present types constituted a quantitatively important part of the organisms in this district (the suppositions are accounted for and discussed in parts I and IV of the present series).

The communication with the ocean was restricted, judging by the development of the ostracodal fauna and the appearance of the sediment. From the composition and structures of the sediment it appears, furthermore, that the water was stagnant to a rather high degree. The water's content o strong electrolytes was fairly low; but its CO_2-pressure may have been high, as is the case in corresponding recent surroundings. The pH may have been high (presumably around 8), at least in the bottom layer of the water, where a buffer solution was probably formed of calcium carbonate (shells and other calcareous substances) and of carbonic acid, mainly formed at the decomposition. Finally, the water's content of O_2 may have been rather considerable; the oxygen was produced by algae.

Dissociable Fe-salts of volcanic and terrigenous origin, as well as those released from decaying organisms were, in this water with high CO_2-pressure, and in presence of oxygen, transformed into iron bicarbonate:

$$Fe^{\cdot\cdot} + 2CO_2 + H_2O + \frac{1}{2} O_2 \rightarrow Fe(HCO_3)_2$$

Iron bicarbonate was probably also supplied by streams.

The content of iron bicarbonate in the water could be high as long as the CO_2-pressure was high. But, if the CO_2-pressure was lowered (by the carbon dioxide assimilation of the algae) the instable iron bicarbonate was transformed into ferrous oxide:

$$Fe(HCO_3)_2 \rightarrow FeO + H_2O + 2CO_2$$

The ferrous oxide, in turn, was oxidized into ferric oxide (oxygen produced during the carbon dioxide assimilation of the algae):

$$2FeO + \frac{1}{2} O_2 \rightarrow Fe_2O_3.$$

The iron oxide was hydrolysed into a hydrous iron oxide:

$$Fe_2O_3 + nH_2O \rightarrow Fe_2O_3 \cdot nH_2O$$

Under these conditions with a high pH, the hydrous iron oxide was precipitated, since its solubility product at such a pH is extremely low. As the content of strong electrolytes was fairly low, the hydrous oxide can be expected to have been precipitated in a weak concentration.

The circumstance that this colloidal substance was precipitated in such a high degree as was the case just around shell fragments bored or surrounded by algae is explained by the fact that, in the stagnant water, spheres around these fragments were formed where the deciding conditions in the process related above could appear, i. e. the CO_2-pressure was lowered and the O_2-pressure was high. Whether the weakly concentrated colloid was incorporated intramembranously during the life-time of the algae or post-mortally is difficult to decide. I think that it took place during the life-time. SJÖSTEDT (1921), and NAUMANN and SJÖSTEDT (1923) found that an intramembranously enrichment of iron is common in algae, especially in Cyanophyceae.

The limonitic ooids with a concentric structure were thus created by the fact that enveloping algal threads were fixed by hydrous iron oxide. If, on the other hand, the surface of a shell fragment, rounded and penetrated by algae, was encrusted before having been enveloped, a false ooid without concentric structures was formed.

9. On the formation of limonitic and hematitic oolite according to some other authors.

Oolitic iron ores of great economic importance occur in several countries. The genesis of iron ooids has been discussed mainly in connection with mining investigations. Among the more prominent investigators on this subject are CAYEUX and HAYES.

The descriptions of French oolitic iron ores by CAYEUX, and his reproductions of microscopic sections of thin slides are well-known (1909 and 1922). He had studied several types of iron oolite (siderite, chamosite, magnetite, pyrite, hematite, and limonite.)

In the earlier paper, CAYEUX considered limonite to be final product in a sequence of changes. The original substance in the ooids was thought to be calcium carbonate which via siderite, chamosite, and hematite had been transformed into limonite. *Girvanella* was considered to have taken a great part in the formation of the calcareous ooids, but such algae were not thought of as precipitators of iron substances. (CAYEUX interpreted some structures in iron ooids as bored by algae — thus the borings should have been made in iron compounds — but, as pointed out by PIA 1937, p. 361, this interpretation is certainly not tenable.)

The opinion of CAYEUX on the replacement of calcareous ooids by iron ooids is not chemically established, and there is reason not to attach too great importance to these ideas.

In his later work, CAYEUX holds that hematite (which according to French usage of this term also includes limonite — *hématite brune*) is additionally precipitated directly. Bacterial activity is considered as most important for this type of iron ooid formation.

False ooids should, according to CAYEUX, be formed by wave action. As a matter of fact, false ooids consisting of shell fragments can be formed in this way, as is seen on certain beaches of lower parallels (Pl. X, Fig. 2), but these ooids are not encrusted with limonite. For the precipitation of limonite in the form of false ooids the water must be assumed to be stagnant, as shown in the previous chapter. The false limonitic ooids in CAYEUX's material are of the same type as the present ones and have certainly been formed in the same way.

The monograph by HAYES (1915) on the Lower Ordovician oolitic Wabana ores in Newfoundland contains much of interest. In this investigation, HAYES has noticed the production of oxygen by algae. However, he does not attach the same importance to this production as is made in the present paper. Like other authors (for instance HARDER 1919) which have also recognized oxygen as the most important waste product of plants, HAYES has not observed the important rôle of the algal-produced oxygen for the very precipitation of hydrous iron oxide as discussed in this paper. This process must be considered much more essential for the genesis of iron oolite than the oxidation of for instance chamosite into hematite which these investigators consider as the essential rôle of the algae in this case.

Furthermore, as a matter of fact, it is very doubtful whether some structures, as interpreted by CAYEUX and HAYES, are bored by algae (cf. p. 415). On the other hand, the canals in shells of inarticulate brachiopods in ferrugineous sandstones (as illustrated by HAYES) and in false ooids of different types (as illustrated by CAYEUX) are certainly of algal origin.

An additional interpretation of general interest in HAYES' paper will be shortly considered, viz. that the climate should have been temperate during the deposition of the Wabana formation (Arenig and Llandeilian). HAYES based this assumption on the fact that the content of calcium carbonate in the stratal sequence is low and that there are traces of algae (as mentioned above, definite traces have not been found in the iron oolite but in intercalating ferrugineous sandstones). He suggested, in warm seas, calcium carbonate is precipitated by denitrifying bacteria (DREW's important discovery of *Pseudomonas calcis* had recently become known), and for this reason the water in warm seas is considered poor in nitrogen substances, so that the algal vegatation is very scanty (DREW's explanation). On the contrary, in a temperate climate, the algal vegatation is rich, but calcium carbonate precipitation induced by bacteria is of no importance. Also if HAYES' idea should be correct that bacteria are the only or the most important inducers of calcium carbonate precipitation in warm seas, his argument is not tenable. It is true that non-calcareous algae are scarce in warm seas, but calcareous algae generally form a greater part of the coral reefs than the corals do themselves; moreover, in calcareous skeletons of different organisms, boring algae are very numerous, not least in the reef-forming corals and calcareous algae. Thus, HAYES' idea that the climate during the Lower Ordovician should have been temperate has to be rejected. On the contrary, exactly the iron precipitation by means of penetrative and enveloping algae indicates that the climate was warm: the required stagnation in a shallow water can scarcely have been formed elsewere than in a warm climate, as indicated above (p. 423).

Bibliography.

BATTERS, A. L. 1892. On Conchocelis, a new genus of perforating algae. Phycological Memoirs. I. London.

BERNER, L. 1931. Contribution à l'étude sociologique des algues marines dans le golfe de Marseille. Ann. Mus. Hist. Natur. Marseille. 24. Mém. 1. Marseille.

BONAR, L. 1936. An unusual Ascomycete in the shells of marine animals. Univ. California Publ. Botany. Vol. 19. No. 5. Berkeley, California.

BORNET, Ed. and FLAHAULT, Ch. 1889. Sur quelques plantes vivant dans le test calcaire des mollusques. Bull. Soc. Bot. France. XXXVI. Paris.

CARPENTER, W. 1845. On the microscopic structure of shells. Rep. British Ass. Advancement Sci. 1844. London.

CAYEUX, L. 1909. Les minerais de fer oolithique de France. Fasc. I. Minerais de fer primaires. Études Gîtes Min. France. Paris.

—— 1910. Les algues calcaires du groupe des Girvanella et la formation des oolithes. C. R. Sci. l'Acad. Paris.

—— 1914. Existence de nombreuses traces d'algues perforantes dans les minerais de fer oolithique de France. C. R. Sci. l'Acad. Tome 158. Paris.

—— 1916. Introduction à l'étude pétrographique des roches sédimentaires. Paris.

—— 1922. Les minerais de fer oolithique de France. Fasc. II. Minerais de fer secondaires. Études Gîtes Min. France. Paris.

DANGEARD, L. 1935. Les Pisolithes à Girvanelles dans le Jurassique de Normandie. Bull. Soc. Geol. France. Ser. 5. Tome 5. Paris.

DUNCAN, M. 1876. On some Thallophytes parasitic within recent Madreporaria. Proc. Roy. Soc. London. Vol. XXV. London.

—— 1876. On some unicellular algae parasitic within Silurian and Tertiary Corals, with a notice of their presence in Calceola sandalina and other fossils. Quart. Journ. Geol. Soc. London. Vol. 32. London.

ERCEGOVIĆ, A. 1934. Wellengang und Lithophytenzone an der ostadriatischen Küste. Acta Adriatica. Inst. Biol.-Ocean. Split. No. 3. Split.

ETHERIDGE, R. 1890. On the occurrence of microscopic fungi, allied to the genus Palaeachlya DUNCAN, in the Permo-Carboniferous rocks of N. S. Wales and Queensland. Rec. Geol. Survey New South Wales. Vol. I. Sidney.

—— 1899. On two additional perforating bodies, believed to be Thallophytic cryptogams, from the Lower Paleozoic rocks of N. S. Wales. Rec. Austr. Mus. Vol. III. Sidney.

FEARNSIDES, W. G. 1910. The Tremadoc slates and associated rocks of South East Carnarvonshire. Quart. Journ. Geol. Soc. London. Vol. 66. London.

HARDER, E. C. 1919. Iron depositing bacteria and their geologic relations. U. S. Geol. Survey. Prof. Paper 113. Washington.

HAYES, A. O. 1915. Wabana iron ore of Newfoundland. Canada Department of Mines. Geol. Survey Canada. Mem. 78. No. 66. Ottawa.

HENSMAN, R. 1895. Some causes of the disintegration of shells. Irish Naturalist. Vol. IV. No. 6. Dublin.

HESSLAND, I. 1946. Om uppkomsten av korallrev. Naturen. No. 6. 1946. Bergen.

HØEG, O. A. 1932. Ordovician algae from the Trondheim area. Skr. Norske Vid. Akad. I. Mat.-Nat. Kl. No. 4. Oslo.

KYLIN, H. 1935. Über einige kalkbohrende Chlorophyceen. Fysiogr. Sällsk. Lund. Förh. Bd. 5. No. 19. Lund.

KÖLLIKER, A. 1860. Ueber das ausgebreitete Vorkommen von pflanzlichen Parasiten in den Hartgebilden niederer Thiere. Zeitschr. Wiss. Zoologie. Bd. 10. Leipzig.

LAGERHEIM, G. 1886. Codiolum polyrhizum n. sp. Ett bidrag till kännedomen om slägtet Codiolum A. Br. Öfvers. K. Vet. Akad. Förh. No. 8. Stockholm.

LAPPARENT, J. de. 1923. Leçons de pétrographie. Paris.

LINDGREN, W. 1933. Mineral deposits. New York.

NADSON, G. 1901. Die perforierenden (kalkbohrenden) Algen und ihre Bedeutung in der Natur. Scriptae Bot. Univ. Imp. Petropolitanae. Fasc. XVII. St. Petersburg.

—— 1927. Les algues perforantes, leur distribution et leur rôle dans la nature. C. R. Sci. l'Acad. Paris. Tome 184. Paris.

—— 1932. Contribution à l'étude des algues perforantes. Bull. l'Acad. Sci. U. R. S. S. No. 6. Leningrad.

NAUMANN, E. and SJÖSTEDT, G. 1923. Über eine Lagynion-Siderocapsaartige Struktur in marinem Aufwuchs vom Öresund. Undersökningar över Öresund X. Lunds Univ. Årsskr. N. F. Avd. 2. Bd. 19. No. 5. Lund.

ORVIKU, K. 1940. Lithologie der Tallinna-Serie (Ordovizium, Estland) I. Publ. Geol. Inst. Univ. Tartu. No. 58. Tartu.

PARKE, M. W. and MOORE, H. B. 1935. The biology of Balanus balanoides. II. Algal infection of the shell. Journ. Marine Biol. Ass. Vol. XX (N. S.). No. 1. Plymouth.

PIA, J. von. 1937. Die kalklösenden Thallophyten. Archiv Hydrobiol. Bd. XXXI. Stuttgart. (*Comprehensive bibliography on boring organisms.*)

PRATJE, O. 1922. Fossile kalkbohrende Algen (Chaetophorites gomontoides) in Liaskalken. Centralblatt Min. etc. Jahrg. 1922. No. 10. Stuttgart.

QUEKETT, J. 1854. Lectures on histology. London.

ROHON, W. and ZITTEL, K. v. 1887. Über Conodonten. S. B. Bayr. Akad. Wiss. Math.-Phys. Kl. 16. München.

ROSE, C. B. 1855. On the discovery of parasitic borings in fossil fish-scales. Transact. Microscop. Soc. London. N. S. 3. S. 7. London.

SJÖSTEDT, G. 1921. Om järnutfällning hos havsalger vid Sveriges kuster. Botaniska Notiser. Lund.

SPRING, W. 1899. Ueber die eisenhaltigen Farbstoffe sedimentärer Erdböden und über den wahrscheinlichen Ursprung der rothen Felsen. N. Jahrb. Min., Geol. und Paläont. Jahrg. 1899. Bd. 1. Stuttgart.

STENSIÖ, E. 1936. On the placodermi of the Upper Devonian of East Greenland. Medd. Grönland. Bd. 97. No. 2. København. (Excellent figures of boring Thallophytes in dermal bones of fishes.)

STIRRUP, M. 1872. On shells of mollusca showing so-called fungoid growths. Proc. Lit. Phil. Soc. Manchester. Vol. XI. session 1871—1872. Manchester.

STØRMER, L. 1931. Boring organisms in trilobite shells. Norsk Geol. Tidskr. Bd. 12. Oslo.

TÖRNQUIST, S. L. 1883. Öfversigt öfver bergbyggnaden inom Siljansområdet i Dalarne. Sv. Geol. Unders. Ser. C. No. 57. Stockholm.

WEDL, C. 1859. Über die Bedeutung der in den Schalen von manchen Acephalen und Gastropoden vorkommenden Canäle. S. B. Ak. Wiss. Wien. Math.-Nat. Kl. 33. Wien.

WETHERED, E. B. 1895. The formation of oolite. Quart. Journ. Geol. Soc. London. Vol. 51. London.

WETZEL, W. 1938. Die Schalenzerstörung durch Microorganismen. Erscheinungsform, Verbreitung und geologische Bedeutung in Gegenwart und Vergangenheit. Kieler Meeresforsch. Bd. II. H. 2. Kiel.

Explanation of plates.

Photographs taken by the author, no retouch.

PANPHOT photographic equipment, filter light green (γ), GEVAERT Replica orthochromatic plates.

Plate I.

265 ×

Shell fragments of orthoidean brachiopods penetrated and enveloped by algae. The enveloping algae form a thick felt-like structure which appears black in the photograph. The canals of the penetrative algae should be distinguished from the laminated structures of the shell (Leskusänget 15).

Plate II.

265 ×

Shell fragments of orthoidean brachiopods penetrated by algae.

Fig. 1 shows a thick stem branching off fine threads.

Fig. 2 shows, inter alia, a rounded excavation in the shell, certainly formed by algae; extremely fine canals radiating from the excavation.

(Fig. 1: Leskusänget 13; Fig. 2: Leskusänget 10.)

Plate III.

130 ×

Slightly infected shell fragments.

Fig. 1: Trilobite fragment with perforating pores (the shell's own structure) and a few canals bored by algae (Born-Dådran 4).

Fig. 2: Another trilobite shell fragment with pores (broad perpendicular and straight canals) and algal canals which have partly attacked the shell from the pores (Gulleråsen 9).

Fig. 3: Trilobite shell fragments in the process of rounding by algal activity (Gulleråsen 10).

Plate IV.

130 ×

Orthoidean shell fragments, partly filled with limonite in fissures along the shell's own structures and partly penetrated by algae which, to some extent, have attacked from these fissures.

(Fig. 1: Stenberg 4; Fig. 2: Leskusänget 13; Fig. 3: Leskusänget 14.)

Plate V.

130 ×

Fig. 1: Trilobite shell fragment pierced by fairly thick algal threads without ramifications (Röjeråsvägen 4).

Fig. 2: Orthoidean shell fragments; the larger penetrated by a thick algal stem branching off thin threads, and excavated by algae; the smaller not penetrated but filled with limonite along structural fissures (Röjeråsvägen 4).

Fig. 3: Orthoidean shell fragment, pierced by broad, irregularly swollen algal threads (most likely green algae) and thin threads (most likely bluegreen algae) (Granmor 7).

Plate VI.

Figs. 1, 2, and 4: 130 ×; Fig. 3: 19 ×

Figs. 1—3 (trilobite shells) illustrate different stages of partition of shells by means of algae.

Fig. 1: Beginning wedge-like attacks from the upper side (Born-Dådran 2).

Fig. 2: Shell fragment almost completely partitioned in two separate fragments (Rävanäs 6).

Fig. 3: Shell fragment practically completely divided into two parts (attack from the upper part of the shell); a second splitting attack also took place from the under side but had not extended so far (Gulleråsen 9).

Fig. 4: Orthoidean shell fragment excavated and penetrated by algae, and also partly filled with limonite along structural fissures of the shell (Leskusänget 17).

Plate VII.

130 ×

Fig. 1: Trilobite shell rich in algal canals and cavities, and fairly well rounded, but not enveloped by algae (Gulleråsen 13).

Fig. 2: Well rounded orthoidean shell, penetrated and somewhat enveloped by algae (Röjeråsvägen around samble 4, sample taken by Prof. G. SÄVE-SÖDERBERGH).

Fig. 3: Limonitic ooid, consisting of a shell fragment, penetrated and enveloped by algae (Stenberg 11).

Plate VIII.

Fig. 1: 40 ×; Fig. 2: 265 ×

Fig. 1: Limonitic ooidic shell fragments and limonitic ooids with a concentric structure formed because enveloping algae have been filled with hydrous iron oxide (Leskusänget 12).

Fig. 2: Detail of the concentric structure showing separate algal threads (Stenberg 6).

Plate IX.

Fig. 1: 40 ×; Fig. 2: 40 ×; Fig. 3: 130 ×

Fig. 1: The specimen in centrum is a crinoid enveloped by algal threads, the ellipsoidic specimens are ooids with a concentric structure formed by enveloping algae (Röjeråsvägen around sample 4, sample taken by Prof. G. SÄVE-SÖDERBERGH).

Fig. 2: Ooids with concentric algal structures (Röjeråsvägen 4).

Fig. 3: Crinoid fragment with algal threads in the skeleton interspaces, and covered with a chamositic layer (Stenberg 11).

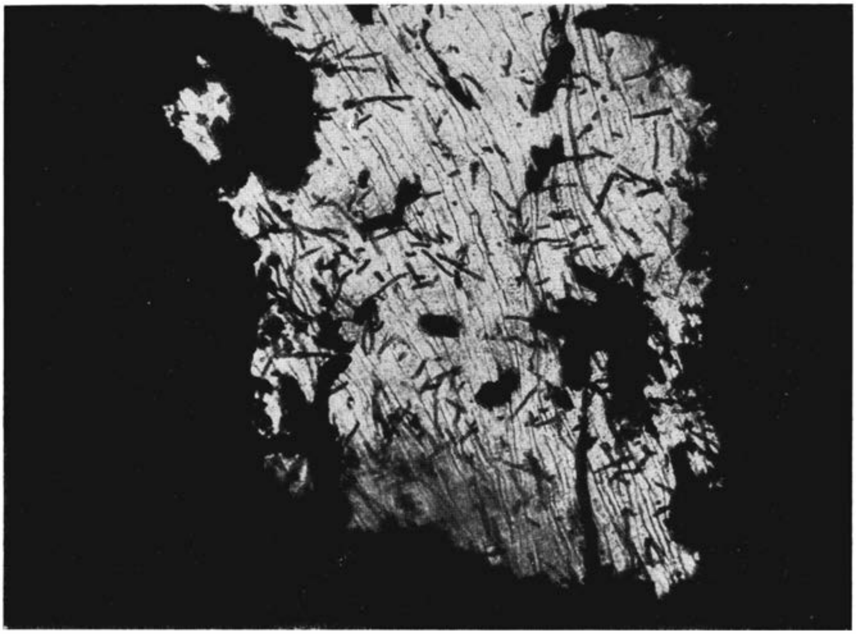
Plate X.

Fig. 1: 130 ×; Fig. 2: 30 ×; Fig. 3: 27 ½ ×

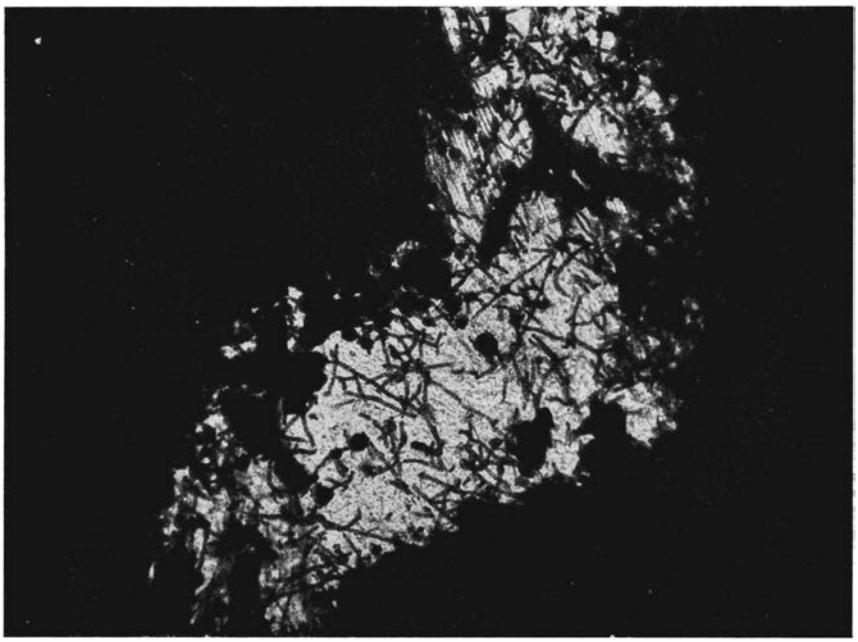
Fig. 1: Fragment of a strophomenoidean shell fragment (Plectambonitidae) showing pseudo-punctae and lamination which should not be taken for algal canals (a few traversing algal canals discernible) (Leskusänget 14).

Fig. 2: Recent false ooids consisting of fragments of Lithothamniaceæ, and rounded by wave action. Tropical beach sand.

Fig. 3: Recent molluscan shell fragment crowded with canals bored by algae. Canals filled with methylene blue. Tropical coral sand.

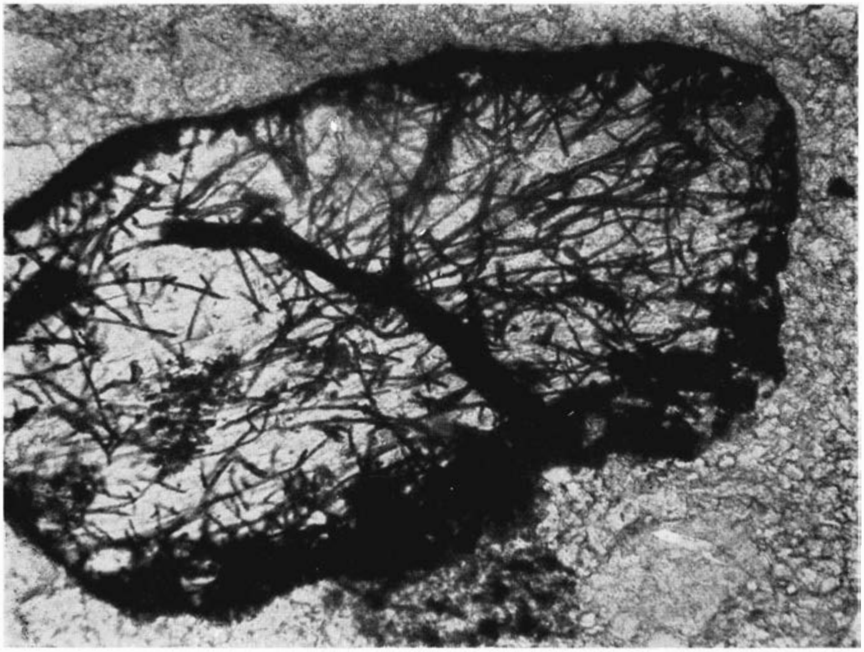


1

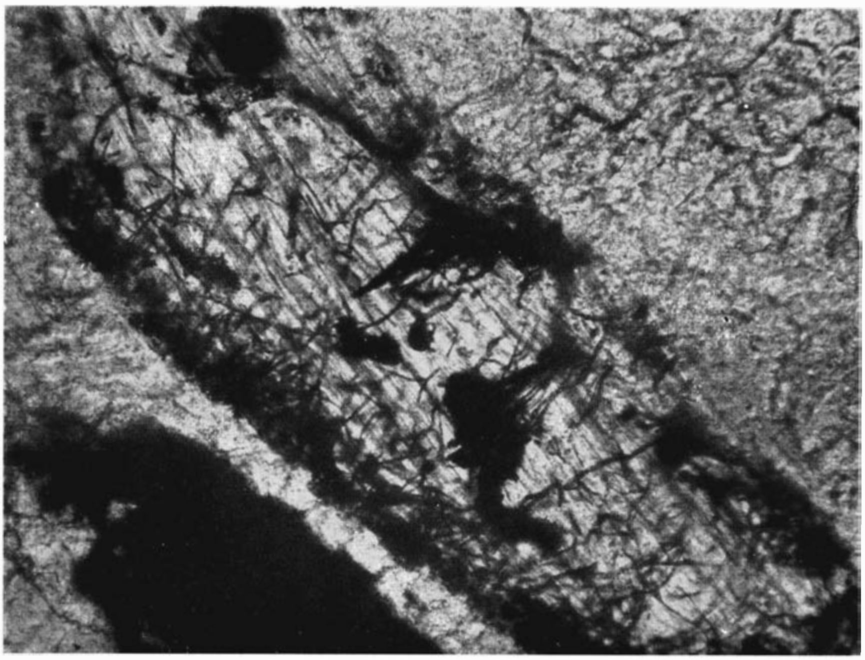


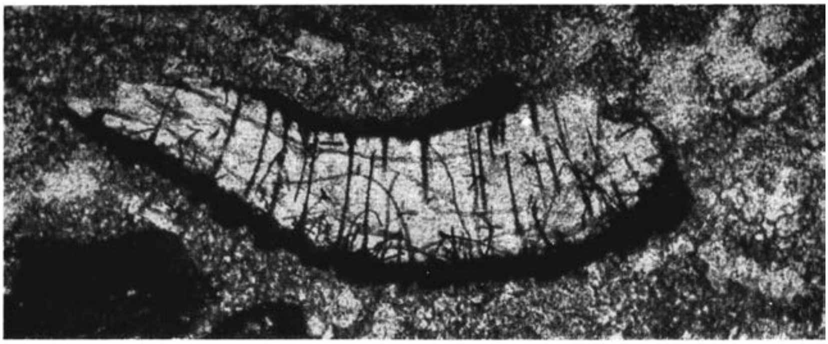
2

1

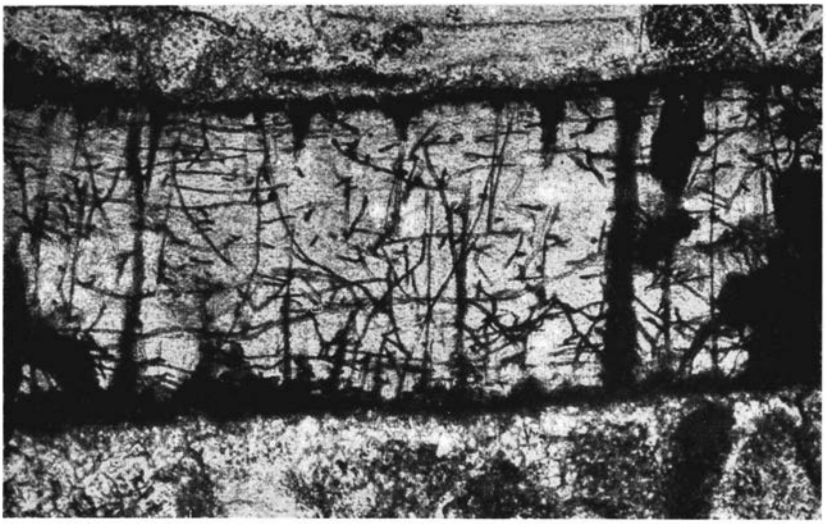


2

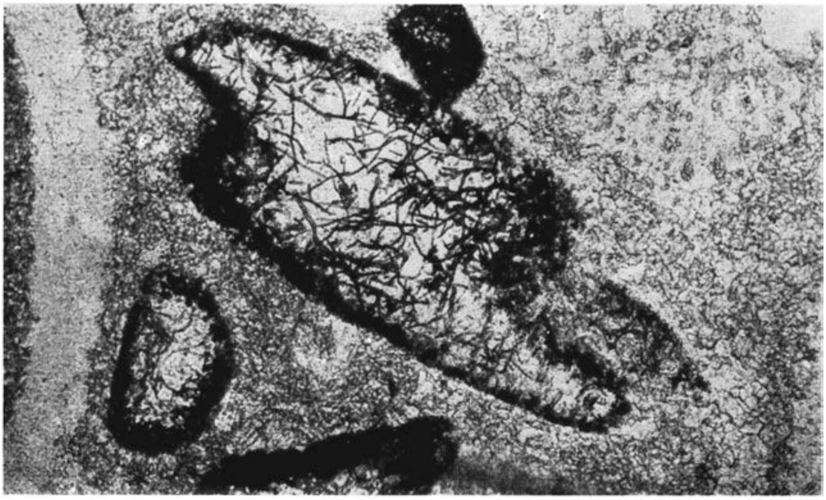




1

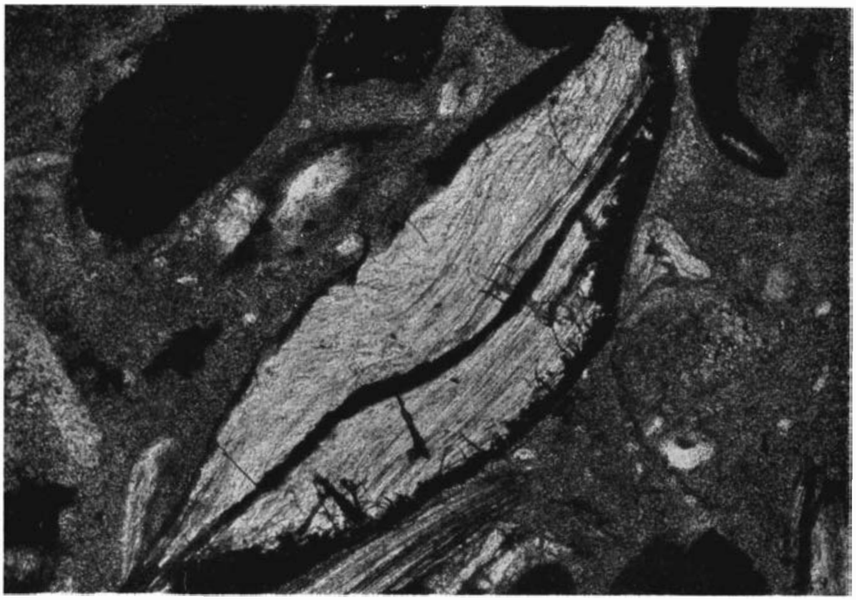


2

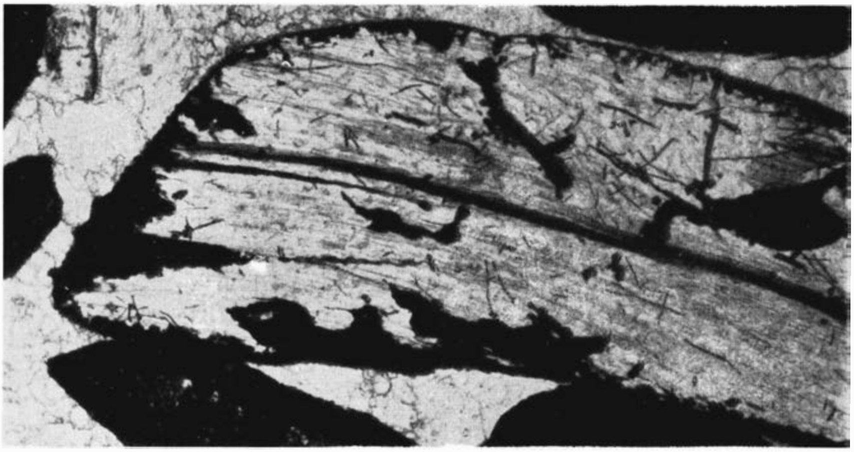


3

1



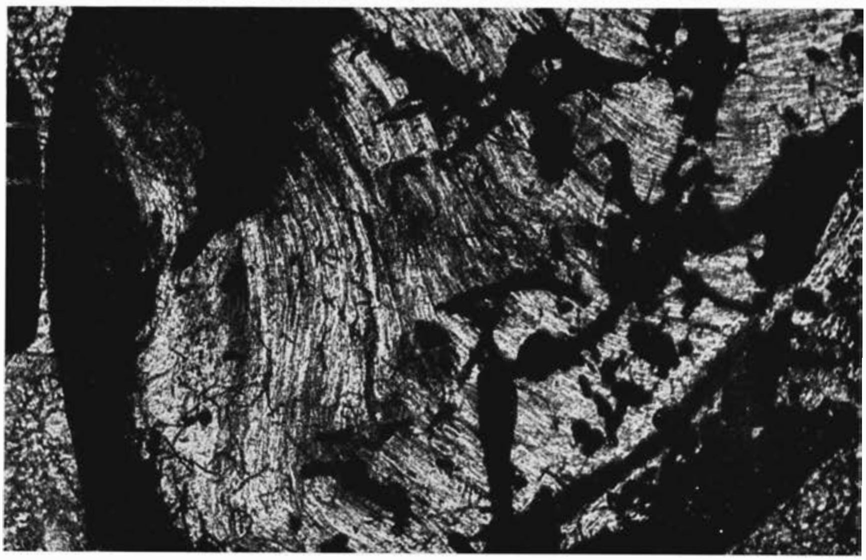
2



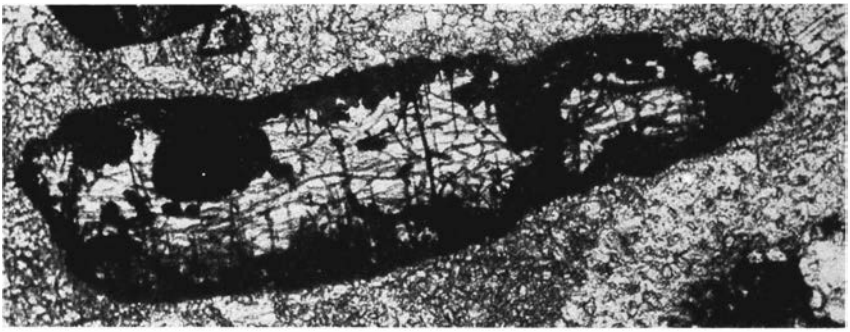
3

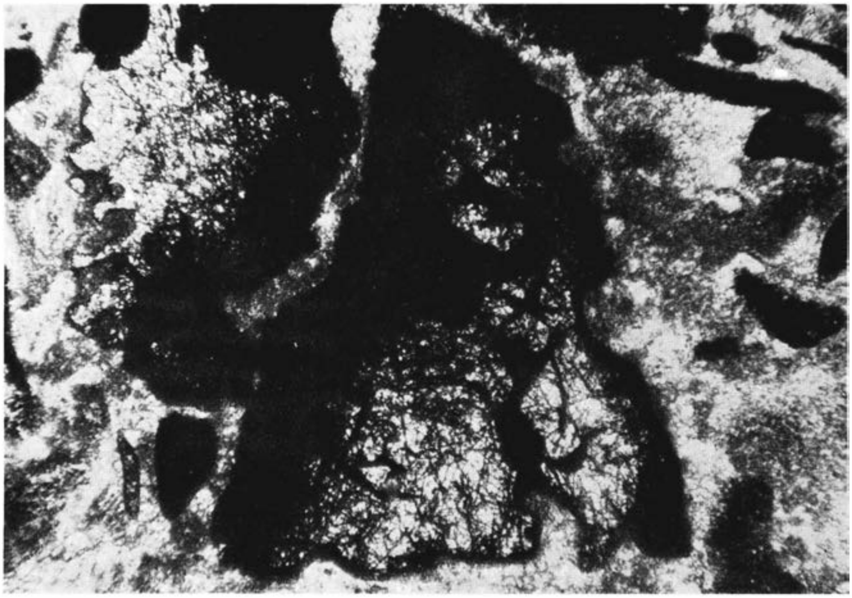
1

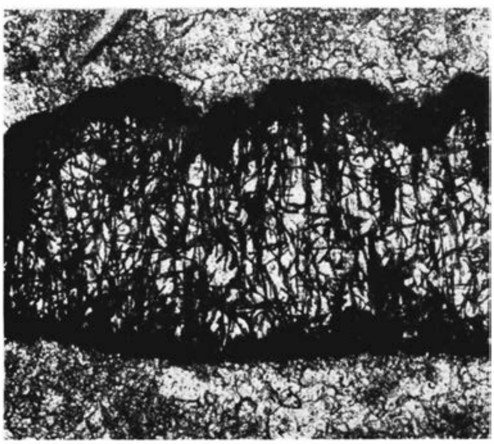
2



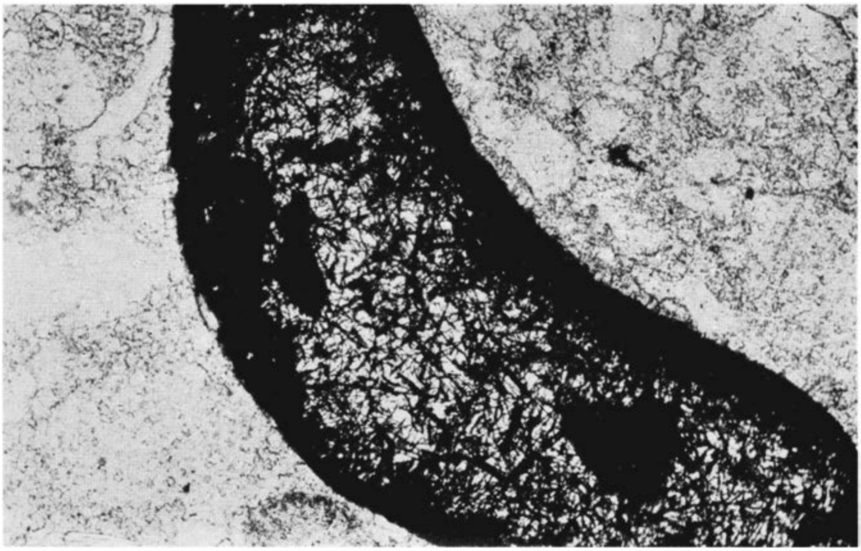
3

2


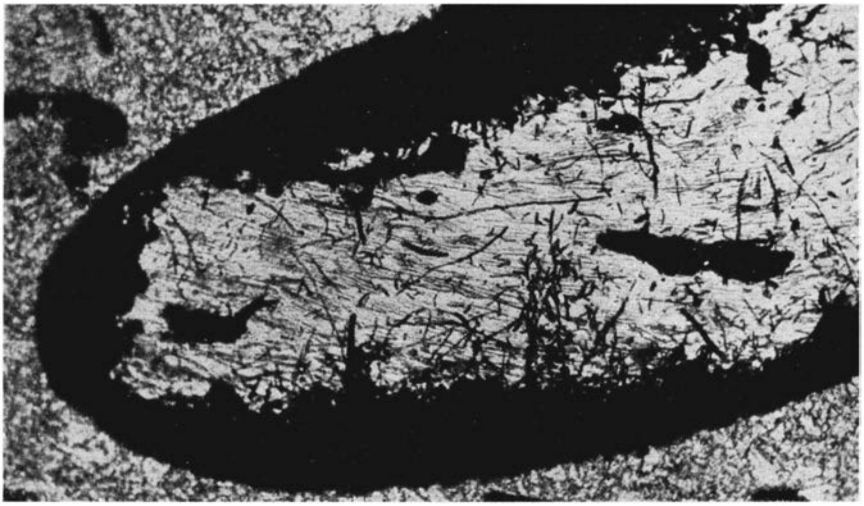
3


1


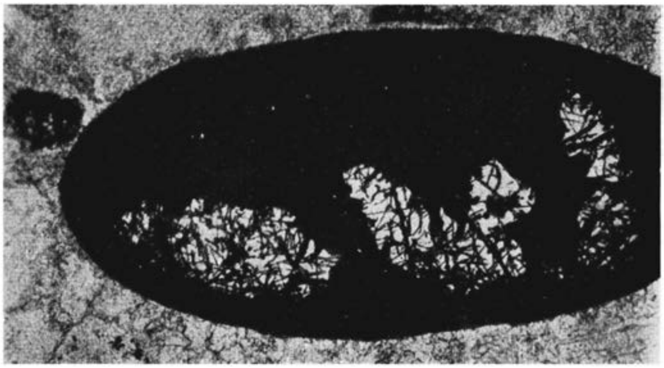

4



1

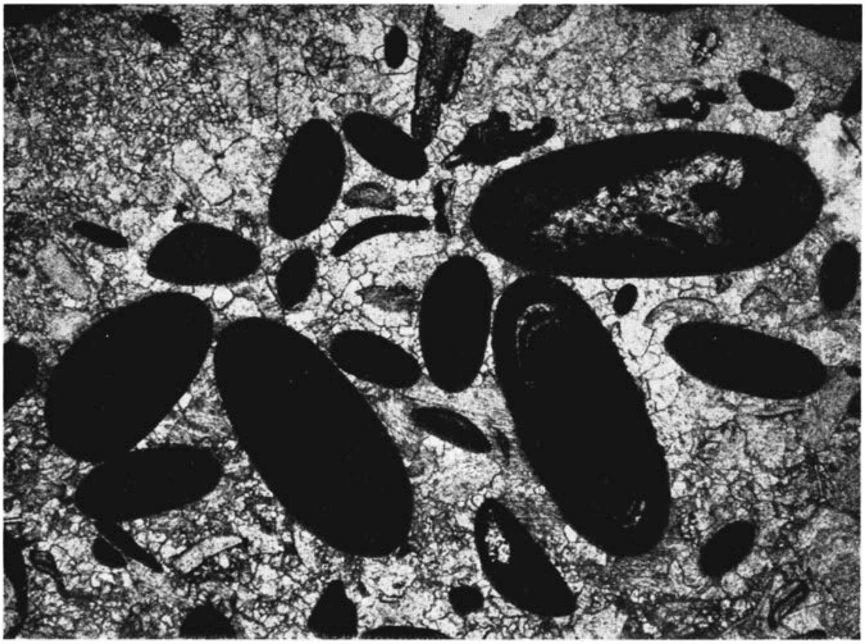


2

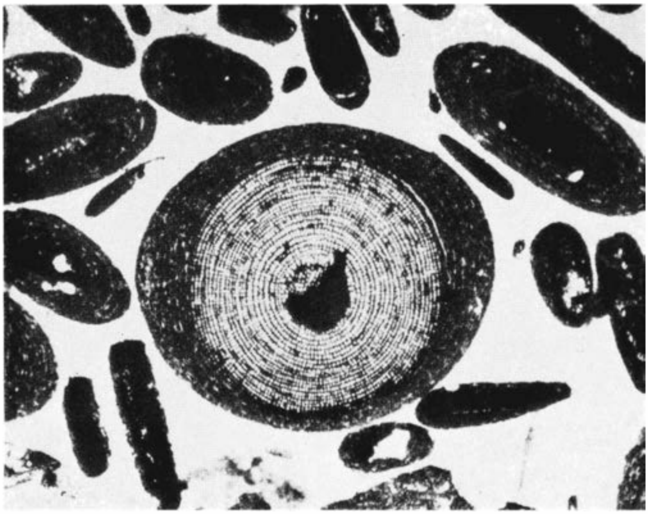


3

1

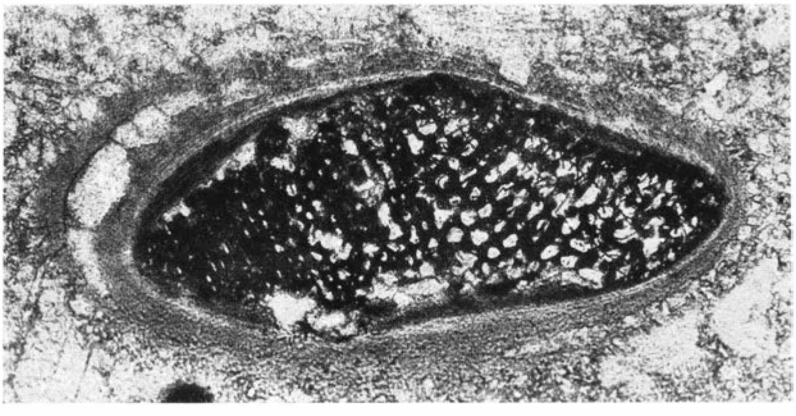


2



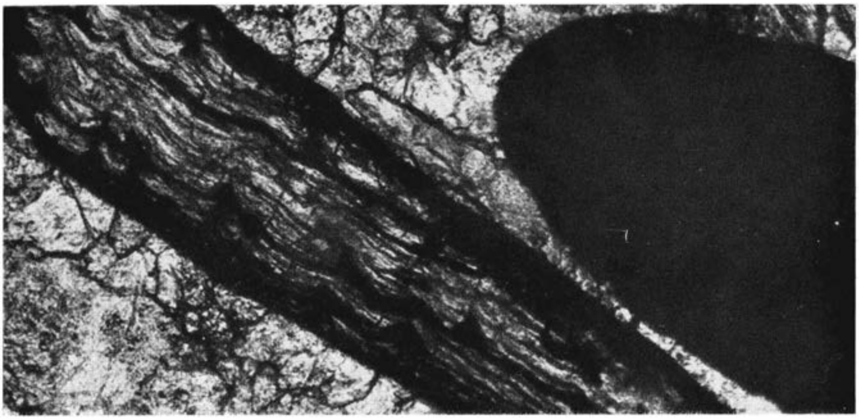
1

2

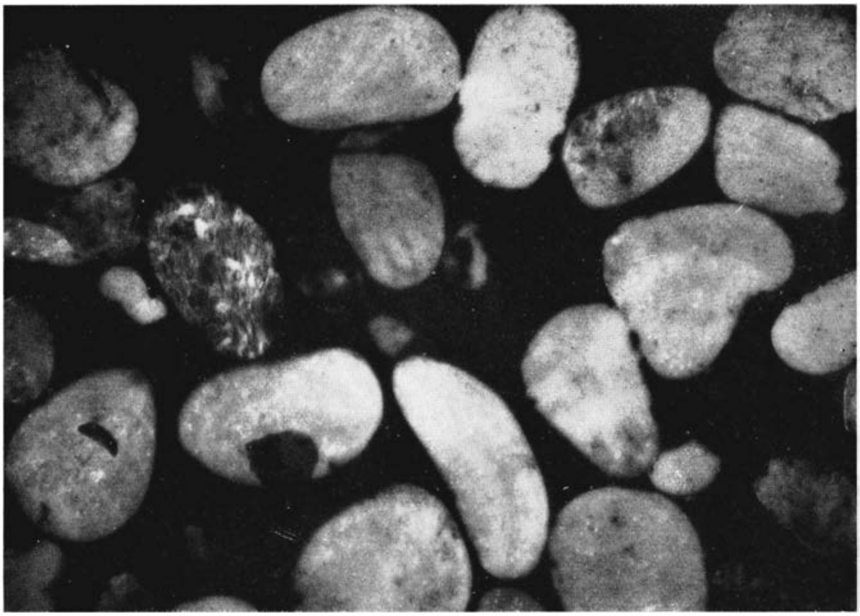


3

1



2



3