NORGES SVALBARD- OG ISHAVS-UNDERSØKELSER
LEDER: ADOLF HOEL

SKRIFTER

Nr. 83

THE DOWNTONIAN AND DEVONIAN FLORA OF SPITSBERGEN

BY

OVE ARBO HØEG

WITH 35 FIGURES IN THE TEXT
AND 62 PLATES

OSLO
I KOMMISJON HOS JACOB DYBWAD
1942

RESULTS OF THE NORWEGIAN EXPEDITIONS TO SVALBARD 1906—1926 PUBLISHED IN OTHER SERIES

(See Nr. 1 of this series.)

The results of the Prince of Monaco's expeditions (Mission Isachsen) in 1906 and 1907 were published under the title of 'Exploration du Nord-Ouest du Spitsberg entreprise sous les auspices de S. A. S. le Prince de Monaco par la Mission Isachsen', in Résultats des Campagnes scientifiques, Albert Ier, Prince de Monaco, Fasc. XL—XLIV. Monaco.

Isachsen, Gunnar, Première Partie. Récit de voyage. Fasc. XL. 1912. Fr. 120.00.

With map: Spitsberg (Côte Nord-Ouest). Scale 1 : 100 000. (2 sheets.) Charts: De la Partie Nord du Foreland à la Baie Magdalena, and Mouillages de la Côte Ouest du Spitsberg.

Isachsen, Gunnar et Adolf Hoel, Deuxième Partie. Description du champ d'opération. Fasc. XLI. 1913. Fr. 80.00.

Hoel, Adolf, Troisième Partie. Géologie. Fasc. XLII. 1914. Fr. 100.00.

Schetelig, Jakob, Quatrième Partie. Les formations primitives. Fasc. XLIII. 1912. Fr 16.00.

Resvoll Holmsen, Hanna, Cinquième Partie. Observations botaniques. Fasc. XLIV, 1913. Fr. 40.00.

A considerable part of the results of the Isachsen expeditions in 1909 and 1910 has been published in Videnskapsselskapets Skrifter. I. Mat.-Naturv. Klasse. Kristiania (Oslo).

Isachsen, Gunnar, Rapport sur l'Expédition Isachsen au Spitsberg. 1912, No. 15. Kr. 5,40.

Alexander, Anton, Observations astronomiques. 1911, No. 19. Kr. 0,40.

Graarud, Aage, Observations météorologiques. 1913, No. 1. Kr. 2,40.

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With chart: Waters and anchorages on the west and north coast. Publ. by the Norw Geogr. Survey, No. 198.

Hoel, A. et O. Holtedahl, Les nappes de lave, les volcans et les sources thermales dans les environs de la Baie Wood au Spitsberg. 1911, No. 8. Kr. 4,00.

Goldschmidt, V. M., Petrographische Untersuchung einiger Eruptivgesteine von Nordwestspitzbergen. 1911, No. 9. Kr. 0,80.

Backlund, H., Über einige Olivinknollen aus der Lava von Wood-Bay, Spitzbergen. 1911, No. 16. Kr. 0,60.

Holtedahl, Olaf, Zur Kenntnis der Karbonablagerungen des westlichen Spitzbergens I. Eine Fauna der Moskauer Stufe. 1911, No. 10. Kr. 3,00. II. Allgemeine stratigraphische und tektonische Beobachtungen. 1912, No. 23. Kr. 5,00.

Hoel, Adolf, Observations sur la vitesse d'écoulement et sur l'ablation du Glacier Lilliehöök au Spitsberg 1907—1912. 1916, No. 4. Kr. 2,20.

Vegard, L., L'influence du sol sur la glaciation au Spitsberg. 1912, No. 3. Kr. 0,40.

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With map: Spitsberg (Partie Nord-Ouest). Scale 1 : 200 000 (2 sheets).

Gunnar Isachsen has also published: Green Harbour, in *Norsk Geogr. Selsk. Aarb.*, Kristiania, 1912—13, Green Harbour, Spitsbergen, in *Scot. geogr. Mag.*, Edinburgh, 1915, and, Spitsbergen: Notes to accompany map, in *Geogr. Journ.*, London, 1915.

All the above publications have been collected into two volumes as Expédition Isachsen au Spitsberg 1909—1910. Résultats scientifiques. I, II. Christiania 1916.

As the result of the expeditions of Adolf Hoel and Arve Staxrud 1911—1914 the following memoir has been published in Videnskapsselskapets Skrifter. I. Mat.-Naturv. Klasse.

Hoel, Adolf, Nouvelles observations sur le district volcanique du Spitsberg du Nord 1914, No. 9. Kr. 2,50.

Expeditions of Th. Vogt 1925 and 1928:

Størmer, Leif, Downtonian Merostomata from Spitsbergen. — Skr. Norske Vid.-Akad. I. Mat.-Nat. Kl. 1934. No. 3. Kr. 3,00.

The following topographical maps and charts have been published separately:

Maps:

Bear Island. 1 : 25 000. 1925. Kr. 10,00.

Bear Island. 1 : 10 000. (In six sheets). 1925. Kr. 30,00.

East Greenland. Eirik Raudes Land from Sofiasund to Youngsund. 1 : 200 000. 1932. Kr. 5,00.

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A. W. BRØGGERS BOKTRYKKERI A/S

Preface.

The main scope of the present paper is to describe and discuss collections of Devonian plants brought home from Spitsbergen by Norwegian expeditions, chiefly by the two led by Professor Thorolf Vogt in the years 1925 and 1928. In addition, it has also been found necessary to include most of the specimens collected previously and described by Nathorst, partly for the sake of comparison, partly because a re-examination seemed desirable in view of the very strong increase of our knowledge of Devonian plants generally of late. As the work progressed, it also turned out to be necessary, or at least desirable, to examine personally certain important specimens described in the literature from other Devonian areas. On my application nearly all the specimens in question were most obligingly sent to me on loan from the various museums, a liberality which has greatly facilitated the work.

A number of other undescribed collections of Devonian plants, from Norway and from other countries, were also placed at my disposal, or collected by myself, and for some time, having completed a good deal of the work with them, I hoped to be able to publish the description of all these collections in one volume. Such a paper, however, would have become too bulky, and would have caused an undesirable delay in publication; the plan had therefore to be abandoned, and the various parts will be published independently.

The work has chiefly been carried out at the Museum of Trondheim. But during several visits to the Paleobotanical Department of the *Naturhistoriska Riksmuseet* at Stockholm, of which some have been of rather long duration, I have also had the privilege of benefiting by the facilities of that home of paleobotany. I feel it a pleasing duty to express my deep sense of gratitude to Professor Th. G. Halle and Dr. R. Florin, who have never failed to place all their experience and practical skill at my disposal.

On this occasion, when finishing the present paper on the Devonian flora of Spitsbergen, I also wish to offer my thanks to many other persons and institutions who have rendered help in various ways. I am indebted to Professor Thorolf Vogt, who has entrusted to me the interesting

material collected during his expeditions, and who, during the expedition in which I took part, always encouraged and supported the paleobotanical work. I further wish to return my thanks to *Universitetets Paleontologiske Museum*, Oslo, and particularly to its director, Professor A. Heintz, with whom I have always had the most profitable co-operation; and to Professor A. Hoel, leader of the *Norges Svalbard- og Ishavs-undersøkelser*, and the other members of that institution, by whom I have been given valuable advice and support in all work pertaining to the Arctic.

I have also received information, or loan of specimens, or other help, from the following persons and institutions: *Universitetets Paleontologiska Institution*, Uppsala; *Preussische Geologische Landesanstalt* (now: *Reichsstelle für Bodenforschung*), Berlin, and Professor W. Gothan personally; *Natur-Museum Senckenberg*, Frankfurt a. M., and Professor R. Kräusel; *Musée Royal d'Histoire Naturelle*, Brussels, and Dr. F. Stockmans; *Institut de Paléontologie de l'Université*, Liége, and Dr. Suzanne Leclercq; *British Museum (Natural History)*, London, and Dr. W. N. Edwards; Dr. R. Crookall, of the Geological Survey, London; the *Royal Scottish Museum*, Edinburgh; Dr. F. W. Anderson, of the Geological Survey, Edinburgh; the *Geological Survey Office*, Dublin, and the *National Museum of Ireland*, Dublin; Dr. F. J. Alcock, of the Geological Survey of Canada, Ottawa; Mr. G. E. Mitchell, Librarian, and Miss Taisia Stadnichenko, Associate Geologist, both of the U. S. Geological Survey, Washington; Professor Ch. A. Arnold, University of Michigan, Ann Arbor, Mich.; and the late Professor W. C. Darrah, Harvard University, Cambridge, Mass. To all these institutions and persons I beg to express my sincere thanks.

I am very much indebted to Miss Else Bull for valuable assistance, especially in the photographic part of my work.

The research has been greatly facilitated through grants from the following foundations: *Statens Videnskapelige Forskningsfond av 1919*, and *Den Tekniske Høiskoles Fond.*

Contents.

Introduction.

The Devonian formation in Spitsbergen. — Svalbard has a more varied geological structure than most other areas of the same size, and in Spitsbergen, the mainland of the group, nearly all geological periods are represented by strata which are in part abundantly fossiliferous. The Devonian system here occupies two areas of very different sizes (text-fig. 1):

The smaller one extends on both sides of the inner part of the Hornsund Fjord. It was discovered by G. de Geer in 1899, during the Swedish-Russian expedition for the measurement of an arc of meridian, and some fossil animal remains have since been collected (de Geer 1909 p. 200, Nathorst 1910 p. 315, Hoel 1929 p. 26, Frebold 1935 p. 30, Solle 1935). But no plant fossils having been found there, this area will not be further mentioned in the present paper.

The other and much larger Devonian area (including the uppermost Silurian) occupies the whole central part of Northern Spitsbergen. In the north-south direction it is nearly 150 km long, extending from the north coast as far south as the inner parts of the northern branches of Isfjorden: Ekmanfjorden, Dicksonfjorden, Billefjorden (Klaas Billen Bay). From its eastern boundary, Wijdefjorden, it stretches, with some interruptions, as far west as Raudfjorden (Red Bay) and Kongsfjorden (Kings Bay). This area, consisting of very thick series of sandstone and shale, partly also of conglomerate (p. 161), has afforded an abundance of fossil animals and plants. The former have been treated in a great number of paleozoological works, of which full bibliographical lists will be found in the papers by Nathorst (1910), Heintz, and Solle.

Previous work on the flora; material of present paper. — Fossil plants in the Devonian of Spitsbergen were first discovered in the year 1882 by Nathorst (1884 pp. 43, 45, 58) on the western side of Billefjorden near Skansen, and in Mimerdalen (Mimer Valley). The fossils then collected were described by Nathorst (1894). They belong to the *Riksmuseet*, Stockholm, where I have had the opportunity to examine them or to borrow them for comparative studies. Most of

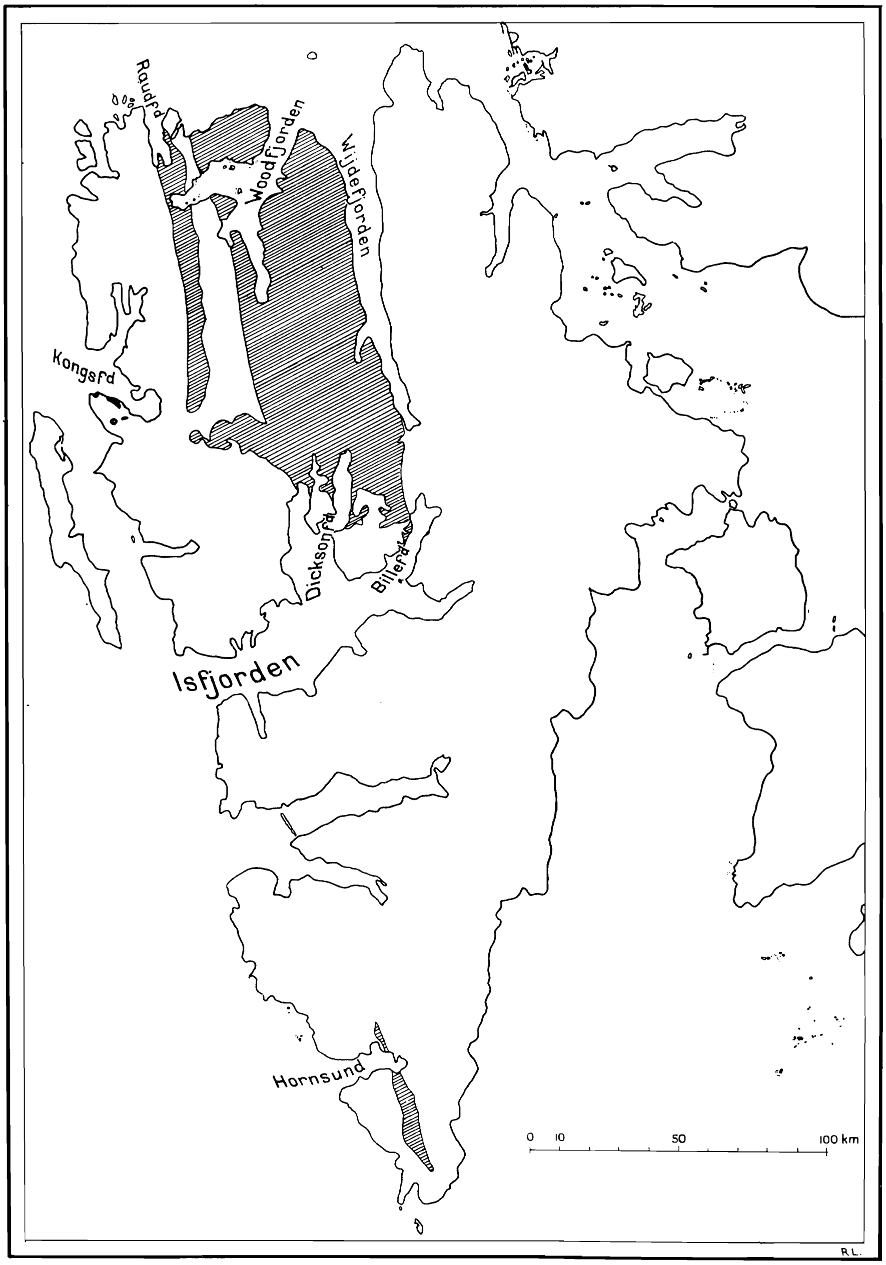

Fig. 1. The Devonian system in Spitsbergen.

Table 1.

Devonian Plants described by Nathorst 1894.

Nathorst 1894			Later literature	Present paper	
Plate, figs.	Locality	Name		pp.	Name
I, 1—3	W. side Billefj	Unbestimmbare *Psilophyton*-ähnliche Reste		31, 58, 88	Uncertain
I, 4—7	—»—	Farnspindel-ähnliche Reste		67	*Hostimella (Aphyllopteris)*
I, 8—11	Mimerdal	Kleinere Trümmer			Indeterminable 'chaff'
I, 12	As I, 1—7	*Cyclopteris* sp.		60, 93, 113	*Platyphyllum* sp.
II, 1—2	Mimerdal	*Psygmophyllum Williamsoni*	Nathorst 1920	93, 113	*Platyphyllum Williamsoni*
II, 3	—»—	Problematische Eindrücke	Nathorst 1920: *Psygmophyllum pusillum*	94, 113	*Platyphyllum pusillum*
II, 4	—»—	Unbest. beblätterter Ast oder Fruchtzapfen			Uncertain
II, 5	—»—	Höckeriger Stielrest			—»—
II, 6	—»—	*Bothrodendron* (?) sp.	Walton 1926 p. 120; Nathorst 1914 p. 68	141	—»—
II, 7	—»—	*Lepidodendron* sp.		127	(?) Same sp. as *B. mimerensis*
II, 8	—»—	*Bergeria*-Form	White 1905 p. 73	127	*Bergeria mimerensis*

them, including an undescribed specimen (p. 67), will be mentioned in the present paper (cf. Table 1).

On the said expedition Nathorst also collected fossils, chiefly fishes, in the gully called 'Fiskekløften' (the Fish Ravine) in the inner part of Mimerdalen. This material largely consisted of nodules, a few of which were later found to contain silicified plant remains. These fossils have never before been described or mentioned in literature, but they are excellently preserved and will be dealt with in the present paper (p. 149).

In 1898 Nathorst, visiting Gråhuken (Grey Hook), collected some fossil mollusks there and searched for plant remains, but did not find any determinable ones (Nathorst 1910 p. 317).

Hoel and Staxrud's expedition in 1912 spent part of the summer working in the Devonian of the north coast (Staxrud & Hoel 1913 p. 106, Hoel 1929 p. 21). On the south side of Vatnedalen (Lake Valley) at Wijdefjorden they discovered fossil plants. The specimens collected were mentioned by Nathorst in a foot-note of his paper from the year 1914 (*l. c.* p. 1), but were characterized as indeterminable. They will be further described below (p. 29).

The next expedition collecting fossil plants in the Devonian of Spitsbergen was the one in 1917, the leader of which was E. A. Stensiö (see Stensiö 1918). During stratigraphical and paleontological work in Mimerdalen, several specimens of plant fossils were collected. After being examined and determined by Nathorst, some of them were mentioned by Stensiö in his report on the geology of Mimerdalen (1918), whereas the broad leaves, referred to *Psygmophyllum Williamsoni* Nath., were treated in a separate paper by Nathorst (1920 *a*); in this paper he also redescribed a specimen collected by himself in the year 1882 (cf. Nathorst 1894 p. 12), giving it the rank of a new species, *P. pusillum* Nath.

The Devonian plants collected after 1917 have not till now been subject to any detailed description. But a very large material has been brought home.

In 1924, as a member of Hoel's expedition, I had the opportunity to search for plant fossils in the Devonian of Dicksonfjorden, also making a journey overland to the inner part of Wijdefjorden (Vestfjorden, Gråkammen). Although a number of fossil fishes were collected, and plant fragments ('chaff', '*Häcksel*') were observed in many places, no plant fossils of any value were found.

In 1925 Professor Th. Vogt led an expedition to Spitsbergen with the special purpose of studying the Devonian system (Vogt 1926). In that expedition Dr. A. Heintz took part as a paleontologist. Among the extensive and valuable collections of fossils brought home were also a considerable number of plants from several localities, old and new, in the outer part of the west side of Wijdefjorden, and from Billefjorden with Mimerdalen; further details as to the localities will be found below. These plants are described in the present paper and, as will be seen, several of them are new to Spitsbergen or even new to science.

In the year 1928 Professor Vogt started a second expedition to Spitsbergen in order to continue and complete the work of 1925 (Vogt 1929 *b*). Among the members were Dr. A. Heintz, Dr. Leif Størmer, Dr. Trygve Strand, and the author. One party, consisting of Heintz, Størmer, and Strand, spent most of the summer in the Raudfjorden area, while the others first worked along the inner part of Wijdefjorden, and then, with Strand, spent two weeks in Mimerdalen (Mimer Valley). The paleobotanical results of this expedition were a fossil flora from the Downtonian of Raudfjorden, discovered in Frænkelryggen (Frænkel Ridge) by Strand and Størmer, plant remains from various localities at Wijdefjorden, and a large material from Mimerdalen. These collections, together with those from 1925, form the main basis of the present paper.

After having finished the study of the collections mentioned above, I wished to visit Mimerdalen again, and did so in the summer of 1939,

Table 2.

Expeditions Collecting Downtonian and Devonian Plants in Spitsbergen.

Year	Leader	Members collecting fossil pl.	Field of work	Collections	
				described by	kept in
1882	Nathorst & de Geer	Nathorst	Billefjorden, Mimerdalen	Nathorst 1894 (partly)	Stockholm
1912	Hoel & Staxrud	Hoel	Wijdefjorden	Nathorst 1914 (partly)	Oslo
1917	Stensiö	Stensiö	Mimerdalen	Stensiö 1918 Nathorst 1920	Uppsala
1925	Vogt	Vogt, Heintz	Wijdefjorden, Billefjorden, Mimerdalen		Oslo
1928	Vogt	Vogt, Heintz, Strand, Størmer, Høeg	Raudfjorden, Wijdefjorden, Mimerdalen		Oslo

bringing home further collections from this interesting area. Only to a limited extent have the results of this expedition been incorporated in the work here issued; it was not found advisable to postpone the publication until the examination of the additional material could be finally completed.

Methods. — The preservation of the Devonian plants from Spitsbergen is, upon the whole, not very satisfactory, and as a rule it has not permitted any study of anatomical structure, either in ground sections or in the other kinds of preparation. Silicified material has been found only in one locality (in Mimerdalen, by Nathorst in 1882), and as to cuticles, a great many attempts at maceration have been made, but only very few have been successful. No specimens have been found suitable for bulk maceration in order to obtain cuticles; but spores are plentiful in some of them.

The preparation had, above all, to be carried out by means of small chisels and needles under the binocular lens. The large-leaved specimens of *Enigmophyton* (*e. g.* PA 356, Pl. XXXVI) had to be uncovered in this mechanical way, originally only very little of the fossil being visible on the surface of the slab.

As is usual when dealing with fossils, it was very often necessary to moisten the specimen or keep it immersed in some liquid for examination or photographing. Xylol was nearly always found to give the best results in the present material. Sometimes, however, I have found it an advantage to use a somewhat different method, that is, to cover the fossil with a cellulose film. At first I tried to pull off the film in the ordinary way, but found that the preservation of the specimens was not such as to give preparations of any value; some of the cell walls and other structural details were apt to follow the film, others to remain on the fossil, the result being quite unsatisfactory. However, sometimes details of interest could be clearly observed through the film, as long as it covered the fossil; examples are given in some of the photographs illustrating the present paper (*e. g.* Pl. II figs. 5—8). This method of film cover has advantages over the immersion in liquid, the optical properties of the cellulose glue being such as to make the details of certain specimens stand out exceptionally well, and the fossil being easy to handle, which is particularly advantageous when dealing with large slabs. A fossil with a film cover is also much easier to photograph in strong magnification than an immersed one, because in a thin layer of liquid the heat from the lamps will often create currents disturbing the photographic picture.

In order to make preparations of spores, I have used two slightly different methods. In both cases the maceration has first to be carried out in the ordinary way, with or without preceding treatment with hydrofluoric acid:

(1). After repeated decanting, the fluid containing the macerated organic remains is examined in a watchglass under the microscope, and the spores and other minute objects of interest are fished out by means of a capillary pipette. I have tried various devices to regulate the pressure on the rubber bulb, but have not found any of them satisfactory; as a matter of fact, after some practice there is no difficulty in moving the tip of the pipette under the microscope and in sucking in just the small quantity of fluid necessary for securing the individual spores. Thus the spores are transferred to a slide, as much as possible of the surplus of fluid is removed by means of the capillary pipette, and some very small drops of glycerine are added. The slide is left for some days until the water has evaporated, and the spores remain in a small quantity of glycerine. The mounting may then simply be carried out by placing some pieces of glycerine jelly in a circle around it and by melting them over a flame. For this purpose I have used a glycerine jelly with somewhat more gelatin in it than usual.

(2). The fluid containing the spores and other organic remains is transferred to the vessel of a hand centrifuge, preferably by means of a pipette, and washed several times with water. After each centrifugation the clear fluid may be removed by means of the pipette. Then some cubic centimeters of glycerine are added. Centrifugation of this mixture will bring the spores to the bottom of the vessel, while much detritus of lesser specific gravity, generally found to be of no value, will still remain dispersed in the glycerine. By means of the pipette the spores may be brought up and transferred to slides. Mounting as above.

When working with fossils, I have always found it a great advantage to have each specimen numbered. It facilitates the reference and particularly the photographing. Every time a specimen has been photographed, the number, and other minutes if necessary, particularly the magnification, are written with an ordinary pencil on the margin of the plate before developing. These notes will be easily legible on the negative permanently. The plates, together with all spare prints, are kept in transparent envelopes, on which the numbers, etc., are written, and which are conveniently filed in numerical order in suitable boxes, one size of box for each size of plate.

The following descriptions of the fossil plants are arranged according to the geographical position of the localities (cf. map, text-fig. 4, p. 25). It is an arrangement which does not fit in with the systematic relationship of the plants, but it is the one which gives the clearest idea of the flora of the various localities. A list of the species, so far as it has been possible to give them definite names, is given on p. 169.

I. Downtonian Flora of Raudfjorden (Red Bay).

As mentioned in the introduction (p. 10), T. Strand and L. Størmer, as members of the expedition in 1928 led by Th. Vogt, discovered a plant-bearing horizon in the Downtonian of Frænkelryggen at Raudfjorden. Dr. Strand has given me the following information as to the stratigraphical conditions (cf. also Kiær & Heintz 1935, particularly p. 12):

> "The plant fossils were collected in a small ravine formed by a brook originating at the end of the glacier north of Frænkelryggen; this ridge is the one north of Andréebreen, extending from Frænkeltoppen westwards and downwards to Klinckowström-fjorden, which is the inner, eastern part of Raudfjorden (cf. map published by Isachsen 1915, and Holtedahl 1926 Pl. VI).
>
> The brook exposes a section at a height of about 60 m above sea level, the beds dipping 20° to 30° in a direction varying from V 10° S to V 40° S, which causes the stratigraphically highest beds to occur lowest down in the ravine. Here red, partly shaly, sandstone is met with in a thickness of about 50 m. The plants were found in two thin beds of green shale in this sandstone, one in the upper and one in the lower part; in the lower bed the plants were found together with small poraspids. Further up, and stratigraphically below this sandstone, comes a thin zone of black shale and further two zones of red beds, each with a thickness of 15—20 m. Between the two latter is a 2 m thick green sandstone in which also badly preserved plant remains were found. Still further up comes greenish sandstone with some layers of red and black shale, and this merges into the yellowish white sandstone, some hundred metres thick, below which comes the probably about 200 m thick basal conglomerate of the Raudfjord Series. It appears from this that the plants were found near the base of the fossiliferous part of the Raudfjord Series."

From the two thin layers of green shale Strand and Størmer brought home a considerable collection of specimens. Many of them, from the lower layer, contained only fish remains, but more than 30 of them contained plant fragments of some interest. They are very incomplete and not well preserved, nevertheless they give at least some information on the flora of the Downtonian age in Spitsbergen, a flora of which we have no other source of knowledge.

In the following description the stratigraphically lower shale has been called No. I, and the other No. II. There is a slight difference between them petrographically, the shale from No. I being lighter and softer, more fine-grained, and less micaceous than the other. The fossil contents are also somewhat different.

Pachytheca cf. *fasciculata* Kidst. & Lang.

Pl. I figs. 14—16.

Locality, material. — Besides some dubious and indeterminable specimens there is a single good one, which has been split, so that about one half of it is left on the slab, the other being lost. — Horizon II.

Description. — The body is nearly globular, measuring about 2.5 × 3 mm across. It is hollow, the diameter of the inner cavity being about one half of that of the whole body. The wall consists of radiating tubes, about 30 μ in diameter, which, to judge by their openings on the inner side of the wall, are about equidistant from one another, but apart from that are arranged with no regularity. On account of the irregular splitting it is difficult to make any exact observations as to their form; probably they branch outwards. As visible on the photographs reproduced they are surrounded by a clear external zone. The latter looks as if it consists of approximately isodiametric cells, but that is probably not the correct interpretation (cf. Kidston & Lang 1924 *b*). — The whole body must have been of a hard or firm texture before imbedding and fossilization.

Affinity. — The generic place of this fossil is undoubted, but our knowledge of its structural details is insufficient for a precise specific determination. It is possible that grinding would have made the structure clearer, but it is also possible that it would have spoiled the specimen without avail, and that could not be risked so long as it is unique. However, all details that have been made out are in agreement with those of *P. fasciculata* Kidst. & Lang (1924*b*) from the Lower Old Red sandstone of Glen Coe, Scotland, and the specimen may provisionally be referred to that species.

The genus *Pachytheca* is known from the Silurian (from the Wenlockian and upwards) and from the Lower Old Red of Great Britain, in at least one case also from the Middle Old Red (see Kidston & Lang 1924 *b* p. 604, and Lang 1937 p. 275); further from the Lower Devonian of Belgium (Stockmans 1940 p. 34). Specimens from the Silurian and Devonian of Bohemia were assumed by Barrande to be the eggs of trilobites, but Raymond (1931) has shown that at least in many cases these bodies are *Pachytheca*. Dawson (1882 p. 108) recorded this type of fossil from Bon

Ami Point on the south side of the Scaumenac Bay (Lower Devonian), under the name of *Aetheotesta*. — From the Lower Devonian of Røragen in Norway, Nathorst (1913 p. 27) mentioned some bodies which he compared with *Pachytheca*, but according to Halle (1916 p. 32) the material is hardly sufficient for a definite determination. Steinmann & Elberskirch (1929 p. 26) described some globular bodies from the Lower Devonian of the Wahnbachtal as *Pachytheca*, but as nothing seems to have been known of the internal structure of these bodies, the reference had better been left out of consideration until corroborated; Kräusel & Weyland (1930 p. 62), however, regard the determination as reliable. A species of the genus has also been described by Cookson (1935 p. 129, Pl. X figs. 1—2) from Silurian beds of Victoria.

The structure of *Pachytheca*, as far as the globular bodies are concerned, is known to an amazing degree of completeness, thanks to the works by Kidston & Lang (1924 *b*) and Lang (1937). But, as emphasized by the latter author, there are still many questions to be solved: Its mode of living, and its position in the plant system, are still very unclear. It is a noteworthy fact that at Raudfjorden, as in so many other localities, *Pachytheca* is associated with *Prototaxites* and with *Zosterophyllum*.

Prototaxites sp.

Pl. IV.

From Horizon II of Frænkelryggen there are several remains which, when examined in reflected light and preferably moistened, seem to possess a structure resembling that of *Prototaxites*. Most of them are flat impressions with scanty remains of organic matter, which in some places may be seen to consist of separate long elements; they must represent tubular cells (or cell rows?), mostly straight and parallel to each other, but sometimes slightly curved and twisted. They are rather different in size in different specimens, being mostly larger than usual in *Prototaxites*; but it has not been possible to bring out further details.

There is, however, also one specimen with somewhat more of the tissue preserved in a carbonized state. It was found on a piece of shale which had been broken just across the bit of tissue (PA 218 and PA 226, Pl. IV fig. 1). The latter was flat on the topside, but as seen in the cross-section on the edge of the slab it was semicircular (Pl. IV fig. 2). If examined directly under the microscope, in reflected light, it was seen to consist of long parallel cells which seemed to be uniform, but no further details could be discerned with certainty in this way.

After being split off from the slab and treated with hydrofluoric acid, the fragment (PA 226) fell into pieces of uniform structure, but quite opaque. They could, however, be imbedded in paraffin and cut transversally and longitudinally on the microtome, thus giving good preparations showing a typical *Prototaxites* structure.

The most conspicuous anatomical elements are tubes, mostly measuring 10 μ in diameter, more rarely as much as 15 μ. Most of them are circular in cross-section, and probably all of them have been so originally. Sometimes they appear to be oval or somewhat angular in cross-section, but this may be due to deformation during the processes of fossilization or preparation, or to the somewhat irregular course of some of them, causing oblique cutting. Making up most of the tissue they sometimes lie close enough to touch each other, but generally they are distinctly apart, and each one always has a definite wall of its own. Apart from their being parallel or nearly so, the tubes do not show any regularity in their arrangement. Where the preservation is good, one may find walls as thin as about 1 μ, but often they are 2—3 μ; whether this is their original thickness or due to secondary changes cannot be made out. The inner side of the tube is smooth. Some of the tubes give the impression of having been quite free, but mostly, and in fact probably always, the outer side of the tube wall is connected with other walls of more or less the same thickness. The cell walls in the interspaces are usually fragmentary and broken in the cross-sections, but they may also, in some places, form a tissue with narrow cell lumina.

In the longitudinal sections the tubes with a diameter of about 10 μ are distinctly seen, some of them being straight, others more or less curved and twisted. Branching has not been observed with certainty. Between them are seen narrower tubes, often measuring about 3 μ in diameter. The latter sometimes quite distinctly seem to be divided by transversal walls into short cells of about the same length as width; fully reliable evidence as to this point could not be obtained, however, and most of the tubes are no doubt simple and undivided.

In some sections there are areas where the tissue is denser than usual. Such areas can be recognized in the longitudinal sections (Pl. IV figs. 5 and 7), but it is difficult to make quite sure whether they have originally had another anatomical composition than the rest of the plant, or whether their particular character is due to the preservation. They contain the usual 'wide' tubes, often twisted to an exceptional extent so as to become cut obliquely; the oval or circular figures thus formed in the preparations look rather strange, but there is scarcely any need to try to explain them in any other way (Pl. IV fig. 7, near the centre). In these dense parts of the sections there are also narrower cells, forming a coherent tissue, but it is difficult to ascertain whether these cells are of the same kind as those found in the other parts of the sections, that is to say thin tubes, transversally cut, or whether they really represent a kind of parenchymatous tissue; the latter possibility seems to be far the more probable.

Along the margin of some of the cross-sections there is a border looking like a cortical tissue (Pl. IV fig. 3). It is dark and dense, the individual cells being scarcely visible. Probably, however, this layer has only been formed secondarily through the collapse of the normal tissue.

Affinity. — The anatomical structure of the specimen shows that it is a typical member of the genus *Prototaxites* Daws., but it is remarkable for the very small dimensions of its tubes. From the enumeration published by Kräusel & Weyland (1934 *a* p. 135), in which they have compiled, in a tabular form, the main characters of all species of the genus, it is evident that no species previously described have such narrow tubes as our plant. Only exceptionally may some of them have diameters below 15 μ, whereas in our plant the wider tubes mostly measure about 10 μ, and the more delicate ones are even much thinner. The *Prototaxites* sp. recently described by Stockmans (1940 p. 37) from the Lower Devonian of Belgium, also has somewhat wider tubes (15—20 μ) than our specimen.

The difference between our specimen and all other species, at least those which have got specific names, is so great that it appears very probable that we are here dealing with a new species, and the peculiar character of the tissue looking like a parenchyma makes this assumption fairly certain. I prefer, however, to desist from introducing a new name for it here, the material being very scanty and limiting our knowledge of the plant to only a very few features of its anatomical structure.

Zosterophyllum sp.

Pl. II figs. 1—10, cf. figs. 11—13.

Locality, material. — Among the indeterminable fragments of axes scattered more or less numerously in the shale, the characteristic branching of *Zosterophyllum* is found in a few cases. All of them are from Horizon I.

Description. — On the slab numbered PA 1542 there are two axes which have happened to lie close to each other (Pl. II fig. 1). They are about 1.2 mm wide. The longer one, which is 5.5 cm long, has three branches, which are as thick as the main axis, but, being pushed out to one side (all of them to the right), have the appearance of being lateral. They leave the main axis at a fairly open angle, and then curve inwards so as to nearly touch it. The lowermost one (Pl. II fig. 3) has a subdivision near its base in the form of a downwardly directed hook, which curves towards the axis. The middle branch is scarcely visible on fig. 1, but is distinct on fig. 2, although it is only partly preserved; it just reaches the base of the uppermost branch, exactly at the place where one might have expected to find a downwardly directed subdivision of the latter, the plant thus looking as if it had formed an anastomosis. This fact might give rise to some speculation, but indeed affords a weak basis for it. Somewhat further up, the uppermost branch gives off a very distinct secondary branch; the latter is incompletely preserved, but there is convincing evidence of a repeated division near its base, after the typical *Zosterophyllum* mode.

The other axis (in the upper left corner of fig. 1, enlarged in fig. 4) is shorter and divided only once. The side-branch has at its base a very distinct, but short, secondary branch, directed downwards.

Both axes give the impression of having been slender and flexible. They have a thin central strand. In one of them (the one seen in Pl. II fig. 4) some details of the cell structure could be made out by covering the fossil with a film of cellulose glue (Pl. II figs. 5—8). As seen on the photograph reproduced here as fig. 5 (which is from the lower part of fig. 4), there are very distinct longitudinal cell walls. They are not found with certainty in the central strand, which is rather poorly preserved in this particular part of the fossil, but on both sides of it; the structure is such that it might easily lead to the conclusion that the plant, or at least this part of its tissues, had been built up by tubular cells of some kind. It would be rash, however, to accept this idea without further and much stronger evidence. Cross-walls are not seen, but there are some fine transversal lines which are visible only at certain places, and which may represent thickenings of the walls; they are rather indistinct, and in order to make it possible to see them in the reproduction some portions of the photograph have been enlarged 3 times, from × 50 to × 150 (Pl. II figs. 6—8).

Another specimen of *Zosterophyllum* is shown in Pl. II figs. 9—10 (PA 223). The main axis first gives off a long side branch, which, at its very base, bears a secondary lateral branch; the latter is divided again, having a short horizontal branch, and a longer one directed downwards, parallel to the main axis. A few centimeters further up, the axis bears two more branches which, however, seem to be simple.

A third specimen which may belong to the same species, Pl. II figs. 11—12 (PA 219), has a similar main axis bearing a side branch. The latter does not seem to have any appendage at the base. It is so erect that it becomes parallel to the main axis.

Film pulls have been attempted from axes of this type. They have not given more information than the photographs taken directly on the fossil, but one is shown on Pl. II fig. 13. It is from an axis (PA 216) which is of the same size and appearance as those just described; but being without any H-shaped branching, it is not characteristic enough for a completely safe identification. In the film pull the central strand is black and intransparent; attempts to clear the preparation did not give any satisfactory results. The tissue on both sides of the strand, however, is seen to consist of cells similar to those described above from PA 1542 (cf. figs. 5—8); there are no traces of transversal walls.

Affinity. — According to their external morphology these axes, in so far as they have the peculiar H-shaped branching, distinctly belong to the genus *Zosterophyllum*. It may be noted, however, that Stockmans (1940 pp. 51, 60) recently has recorded the same mode of branching from *Psilophyton princeps* and *Drepanophycus spinaeformis*. In size and form our specimens agree fairly well with some of those described as *Zosterophyllum myretonianum*, which is known from the Lower Old Red sandstone of Great Britain, and possibly also from the Downtonian (Lang 1937 p. 248); but as we lack a more detailed knowledge of them than this rather scanty material has afforded, it is scarcely possible to make certain of their specific identity.

Z. australianum (Lang & Cookson 1930, Cookson 1935), from the Silurian of Australia, in its vegetative organs is so like *Z. myretonianum* that the determination of a few fragments would probably be impossible. *Z. rhenanum* (Kräusel & Weyland 1935 *b* p. 175, Weyland 1932 p. 4, fig. 4), from the upper part of the Lower Devonian on the Rhine, has proved its relationship to the genus only in its reproductive organs, whereas the characteristic mode of branching has not been found in this species.

Zosterophyllum is a natural genus, and our knowledge of its morphology and anatomy is more exhaustive and complete than one would have expected from a plant found only as incrustations and impressions. The question may be raised whether it is advisable to refer to this genus fossils which in themselves are characteristic enough, particularly with regard to the branching, but which only comprise some fragments of axes: As just mentioned, the same mode of ramification may also occur in genera other than the typical *Zosterophyllum*. In the present case it should further be taken into consideration that in *Z. myretonianum*, Lang (1927 *a*) has demonstrated the presence of epidermal cells, approximately isodiametric, whereas in our specimens it has not been possible to find anything of that kind. From the species of *Zosterophyllum* hitherto described nothing is known like the long, tube-like cells found in our Spitsbergen specimens. Lang (*l. c.* p. 447) certainly mentions that "some preparations suggest a hypodermal layer of elongated thick-walled cells, but the presence or distribution of this has not been definitely established"; it is not probable, however, that it is this hypodermal layer which is observable in the specimen (PA 1542) described above.

In spite of this slight uncertainty we may be justified at present in designating our fossil as *Zosterophyllum* sp., but it is highly desirable to obtain additional material of this interesting and important plant.[1]

Taeniocrada (?) spitsbergensis n. sp.

Pl. I figs. 1—13, Pl. III.

Locality, material. — In both horizons of plant-bearing shale fragments of axes are fairly common, as is the case in all early Devonian and pre-Devonian plant beds, and most of them are indeterminable and

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[1] Since this was written I have been informed that the English-Norwegian-Swedish expedition of 1939, led by Professor Stensiö, visited the locality, but that no further plant material could be found there.

of slight interest. In Horizon II, however, a number of them have certain distinctive peculiarities, making them worth some closer consideration.

Description. — The axes in question are so uniform in appearance that they at once convey the impression of belonging to one species. In one respect there is a certain difference, in so far as some of them are preserved as stone-casts with a rather high relief, while others are flat, with somewhat more of the organic matter left; but they are equal in size and form. They are, or have been, cylindrical, mostly about 2 mm thick. The longest specimen (PA 227 and 228, Pl. III) is about 6 cm long, measured along the curve. Neither top nor base is preserved in any specimen. — They divide rather sparingly in more or less regular dichotomy. The longest specimen, just mentioned, bifurcates three times. In one axis (PA 228, the right-hand corner of Pl. III fig. 1, enlarged in fig. 9) there is a thickening at the base of one of the branches, but it is not a typical 'axillary bud', as the one described below from PA 210 (from Horizon I), nor is any such one found in the other specimens.

The surface of the axes is naked, without spines or similar appendages or scars indicating the position of such organs, except in one case: PA 211, Pl. I figs. 4—6, very distinctly seems to bear a single spine, only 0.7 mm long, standing out at a right angle. It is so distinct and well defined, and so clearly connected with the axis, that there could scarcely be any mistake as to its belonging to the plant. One may ask whether the latter really belongs to the same species as the others; if it does, we shall have to reckon with the possibility that the plant either has been sparingly spinous all over, or at least has borne spines in certain parts.

A central strand is observable in some specimens, best in the flattened ones, but sometimes also in those preserved with a high relief, like PA 211, Pl. I figs. 4—6. But no further details as to their anatomical structure have been made out with certainty.

Some specimens apparently show fairly distinct traces of articulation: either in the form of transversal lines of carbonaceous matter at distances shorter than the diameter of the axis (visible in some parts of Pl. I figs. 2—3, and Pl. III fig. 3), or as a slight nodosity of the stone-casts (barely visible in the middle of Pl. I fig. 8). However, it is not possible to infer from these indications that the plant, when living, has had nodose axes (compare also p. 62).

Associated with these stalks there are a number of small bodies possibly representing some kind of reproductive organs. Most of them are found scattered on the slabs, but there are also some specimens strongly indicating an organic connection with the axes just described:

Pl. III figs. 6—7 show one and the same thing in counterparts (PA 227, 228). It is also seen in natural size in the middle of figs. 2 and 3. There is an egg-shaped body, measuring 4.5 × 3 mm, with its pointed end connected, as it seems, with an axis and nearly at a right angle to it. It is somewhat tuberculate (or, in the counterpart, with corresponding depressions), as if it had been filled with three or possibly four smaller bodies.

Pl. III figs. 4—5 show a similar organ on PA 228, photographed in two different ways, fig. 4 immersed in xylol, fig. 5 dry and in oblique illumination. It is seen in natural size in the lowermost corner of fig. 1. — The body itself resembles the one just described, but is a little more irregular, rather ear-shaped. When the matrix was carefully removed by means of chisels and needles, the body could be traced down to the under side of the axis and most distinctly seemed to be connected with it there. — On the counterpart the same axis is seen, and part of the lateral organ in the shape of a well-defined, brownish tubercle, which may correspond to the cavity in the ear-shaped body, just described; but the connection with the axis is, of course, not directly observable.

A somewhat different type is shown in Pl. I fig. 15 (from the left-hand side of PA 228, Pl. III fig. 1): The axis bears a lateral stalk, which is quite short and ends in a dilatation of some sort, the real nature of which cannot be made out, however. The counterpart is shown in fig. 16, in which also a central strand is well visible. It is possible that this widened lateral stalk or branch is something different from the bodies described, but, at all events, it represents a remarkable sort of branching.

In addition to the specimens described and figured, the same slabs (PA 227 and 228), and also a few others, bear similar bodies, but, as it seems, always detached from the axes. They may be fairly regular and even, like the one shown in Pl. III fig. 8 (PA 227): It is oblong, about 2 × 3 mm, with a little depression in one end (which has been placed downwards on the photograph); it is more smooth and simple in form than the specimens described above, although not lacking a certain nodosity (in reality more distinct than on the photograph, where it is barely indicated on the right-hand side). Others are more lobed or tuberculate, but fairly uniform in size and always with a prominent relief.

Nothing shows that these bodies have been ordinary sporangia containing a powder of minute spores, nor are there any remains of a sporangium wall. On the other hand the tubercles seen on the surface would be most easily explained if it be assumed that the interior has been made up, entirely or partly, of particles of corresponding size.

Affinity. — The axes alone are not without interest, but they are not distinctive enough to make a comparison with other plants profitable (although their resemblance to the contemporaneous *Cooksonia* is very striking). On the other hand, if the ovoid bodies belong to them, which is very probable, they make the fossil particularly interesting, although we know nothing more about their function than that, if they have been formed laterally on the axes, they must be assumed to have represented some kind of reproductive organs.

Among previously described fossils those most resembling the bodies in question are the 'spherical tuberculate bodies' recorded by Cookson (1935 p. 130, Pl. X figs. 3—5) from the Silurian of Australia. They were globular or oval, 3—5 mm in diameter, and had a slightly uneven surface due to small tubercles; so far they resembled our objects from Spitsbergen, but the number of tubercles on the exposed surface of each body might be as great as 18, *i. e.* several times as large as in ours. There is no evidence as to how they have grown; they were found isolated in the rock. — More different is the organism described by Heard (1927 p. 203, text-fig. 2, Pl. XV figs. 5—7), from the Old Red sandstone of Wales, having a still larger number of tubercles; it was about 5 mm in diameter. — A somewhat similar body was described by Halle (1916 p. 32, Pl. III figs. 34—35) from Røragen, but here the numerous tubercles rather had the shape of conical projections.

For the sake of comparison one may also refer to *Spermolithus devonicus* Johnson (1917 p. 248, Pl. XII fig. 2), from the Upper Devonian of Ireland. It was regarded by Johnson as the seed of some pteridosperm, but the proof of this supposition is still lacking. Apart from some difference in size (as 5 : 3), there is a striking resemblance between the one shown in Johnson's illustration, and our Pl. III fig. 8. However, the resemblance may be quite accidental, and it is possible, or even probable, that they are of an entirely different nature. — The interesting bodies described by Carpentier (1931) under the name of *Sporangites? Peneaui*, from Middle Devonian shales in Maine-et-Loire, have probably also been different in structure and function.

The records cited are of interest in so far as, apart from the two last-named ones, which are from the Middle and Upper Devonian, they prove the occurrence of such nodular or tuberculate bodies in several cases in Lower Devonian and pre-Devonian rocks. As they are rather inconspicuous and obscure-looking it is also quite possible that they have been overlooked or put aside in other cases, with the result that they have not been mentioned in the literature. But we cannot yet feel sure that they all represent the same kind of organ of the same plant group.

There are some other fossils consisting of naked stems bearing lateral organs of reproduction: The one most interesting in this connection is the very remarkable *Gosslingia breconensis* Heard (1927), from the Lower Old Red of Wales, with its branches bearing laterally two reniform appendages supposed to be sporangia; they are smaller than those from Spitsbergen, and not tuberculate.

The result of these considerations is that even if the Spitsbergen plant in question is not identical with any one previously described, it is not unparalleled, and we may expect that the fossils mentioned may mutually throw light upon each other when more material has been studied. It is probable that our plant represents a new genus, some of the characteristics of which are indicated in the collection at hand, but it is scarcely advisable to give it any new name at the present stage of our knowledge.

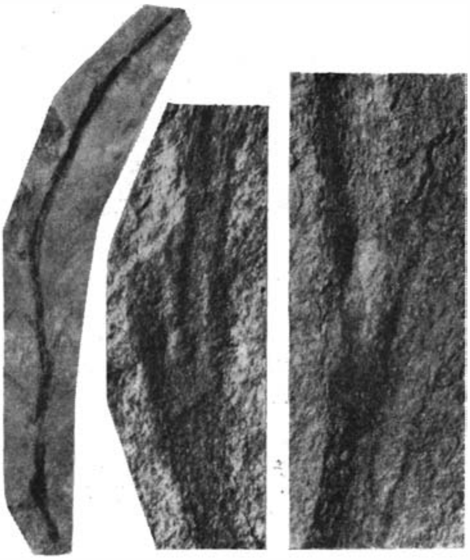

Fig. 2. *Hostimella* sp., from Raudfjorden: Frænkelryggen. *b* shows the lowermost point of division, with a tubercle probably representing an 'axial' branch. *c*. Second branching from below, the depression a little above the point of division probably representing the base of a third branch; hair-bases? in the upper part. — PA 210. Nat. size and × 6. *b* and *c* illuminated from the left.

Addition. — After having completed the preceding review of the possible affinities of the peculiar plant from Frænkelryggen, I received the large work by Stockmans (1940) on the Lower Devonian flora of Belgium, containing a detailed description, with excellent photographs, of *Taeniocrada Langi* Stockm. (diagnosis preliminarily published in 1939). The ovoid bodies attached laterally to the axes of this species bear such a striking resemblance to those from Frænkelryggen that it is difficult to avoid the conclusion that they are of the same nature, and consequently, that the two species are allied. As stated by Stockmans it is doubtful if the Belgian species should be finally included in the genus *Taeniocrada*, although the reasons for preliminarily doing so may suffice at present. In the case of our species from Spitsbergen the same reasons cannot be applied, because in its vegetative characters our plant has no stronger resemblance to the typical species of *Taeniocrada* than to several other genera of naked axes of the early Devonian flora. But it seems very probable that it belongs to the same genus as the Belgian species, and therefore it may be listed preliminarily along with it as a doubtful species of *Taeniocrada*, until it can be decided whether they should both be removed to form a genus of their own.

In the light of *Taeniocrada Langi* our species from Frænkelryggen has got an increased value, and it may deserve a specific epithet. I propose to call it *Taeniocrada (?) spitsbergensis* n. sp. — For diagnosis, see p. 191.

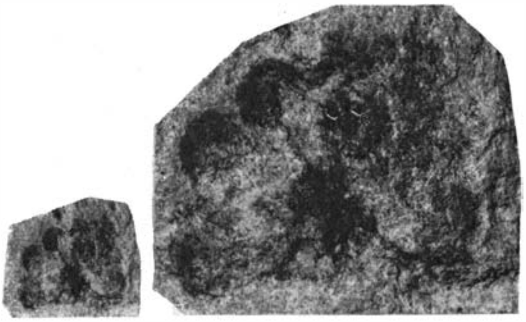

Fig. 3. *Problematicum*, from Raudfjorden: Frænkelryggen. — PA 236. Nat. size and × 3.

Hostimella sp.

Text-fig. 2.

At least one axis found in Frænkelryggen (PA 210) is remarkable in possessing the 'axillary bud' so characteristic of many of the early landplants: As shown in text-fig. 2, the specimen is a slender axis about 7.5 cm long, giving off several branches, all of which, however, have been broken off. At the lowermost point of ramification (text-fig. 2 *b*), there is a projection at the top of the angle formed by the two branches; most probably it marks the base of a third branch put forth in a plane perpendicular to them. At the next branching (text-fig. 2 *c*) there is no projection of this kind, but a little further up along the axis there is a deep, narrow depression which can probably be nothing but the base of a branch hidden in the matrix. It may be noticed that at this place the axis, as is visible on the photograph, also has a number of small tubercles of the form and appearance characteristic of the hair-bases of psilophytes; but as no such tubercles are seen elsewhere, and as there are no hairs or spines visible along the margin of the axis, further evidence is needed before the explanation can be regarded as proved.

The distribution of axillary structures of this type will be discussed below (p. 173). Here it will suffice to mention that, having been recorded from the Walhalla series of Australia (Lang & Cookson 1930 p. 136, Pl. XI), these structures are not previously unknown from pre-Devonian rocks.

Problematicum.

Text-fig. 3.

Among the problematica found on these slabs is the peculiar object shown in text-fig. 3 (PA 236, Horizon I). It forms a little more than half of a circle, about 1.5 cm in diameter. In the middle of it is a deep depression (black in the figure), and along the margin there are a number of other, hemispherical, depressions, which, however, are not nearly so deep; if the circle had been complete there would probably have been about 12 of them. Some of them are connected with the central hollow by a black line. The impression is partly covered with a thin layer of carbonized matter.

This object distinctly gives the impression of being of vegetable origin, but its real nature must remain an open question for the present. Its appearance, however, is so characteristic that it will probably be easily recognisable if more material should be found.

The composition of the flora from Frænkelryggen is in full accordance with its Downtonian age, which is proved by its fossil fauna. — Cf. also p. 162.

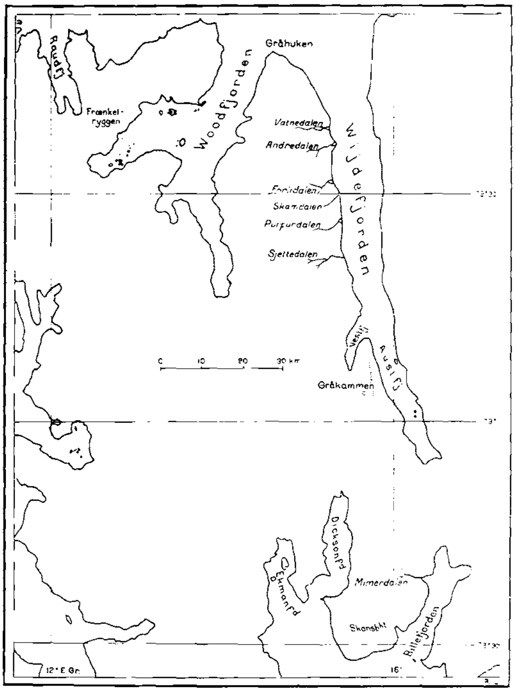

Fig. 4. Central part of northern Spitsbergen, with localities for fossil plants.

II. Devonian Flora of Wijdefjorden (Wijde Bay).

Wijdefjorden forms the eastern boundary of the Devonian of Spitsbergen, and the western coast of this long fjord consists of a complicated system of Devonian sandstone, shale, mudstone, and some conglomerate. Accounts of the stratigraphical conditions have of late been given in various geological and paleontological papers, most of them being based upon Holtedahl's and Hoel's field work in the years 1909—1912 (Holtedahl 1914; for reference to later literature compare Heintz 1937). However, recent expeditions, namely those led by Th. Vogt in the years 1925 and 1928 (see Vogt 1929 *b*) and the English-Norwegian-Swedish one in 1939, have done much to clear up finally the exact age of the various horizons, although the results have only to a limited extent been published so far (cf. p. 161).

For practical purposes the plant localities will be mentioned here according to their position along the fjord, from north to south, and irrespective of their chronological order, which will be discussed on p. 162. The position of the valleys along Wijdefjorden is seen on the map, text-fig. 4.

1. Gråhuken (Grey Hook).

In the beach profile at Gråhuken Nathorst, in the year 1898, collected some fossil mollusks and at the same time observed poorly preserved plant remains. He describes the latter as follows (1910 p. 317):

> "Die Pflanzenreste kommen als vereinzelte, stark mazerierte Reste in einem bituminösen Schiefer vor und sind, wie schon erwähnt, den gabeligen Stengelresten, die im Devon häufig sind, recht ähnlich, obschon sie keine nähere Bestimmung zulassen."

Vogt's expedition in 1925 spent a few days at Gråhuken (Vogt 1926 p. 203), investigating, among other things, the beach profile, and then, on August 11th, discovered a good occurrence of fossil plants, of which a considerable collection was brought home.

The plants are found in a fine-grained shale which is of a dark, somewhat bluish colour, and which contains very small amounts of mica. It splits irregularly, but the preservation of the plant impressions is good. There is but very little left of the organic substance, and no anatomical details could be made out. Owing to a cover of rust a treatment with warm hydrochloric acid often proved advantageous.

Psilodendrion spinulosum n. gen. & sp.

Pl. V figs. 1—2, cf. fig. 3; Pl. VI—VII; text-fig. 5.

Material. — More than half a dozen good specimens and many smaller pieces of the shale described above, contain remains of a very characteristic species of plant. On some of the slabs there are many fragments of it, consisting of stems and branches of various sizes, often in organic connection with each other.

Description. — The largest stems are nearly 1 cm broad, straight, and seem to have been of a firm and solid texture. They are longitudinally striated or groved, with furrows and ridges of varying dimensions; in some cases there are large ridges, about one-third of the breadth of the stem (as seen in the fossil), forming decurrent bases of branches (PA 1140, Pl. VII fig. 2; PA 1109, Pl. VI fig. 2, and others).

The main branches are opposite or nearly so, although branches with larger vertical distances may also be found (PA 294 *a*, Pl. VII fig. 1). Apart from that, the arrangement of the main branches in relation to each other is not clear.

The branches of the first order divide, upon the whole, monopodially in their inner parts, the secondary ramifications being nearly opposite to each other, while the main axis of the branch is straight and gradually tapering from the widened base. There are no axillary tubercles. The body seen in a branch axil of PA 1128 (Pl. VII figs. 3—4) is not such a structure and may possibly not even belong to the same plant. (Another case, PA 1107, is mentioned below, p. 29.)

Fig. 5. *Psilodendrion spinulosum* n. gen. & sp., from beach profile at Gråhuken. Slender branch system with branch tips curved in one direction, as if by running water. — PA 294. Nat. size.

The branches of the higher orders sometimes have the same form as the main branch, but generally they are dichotomous, and that is always the case with the ultimate ramifications. The tips are not recurved. The branch-system as a whole is not expanded in one plane.

All axes may bear thorns, varying in number. They are short, only exceptionally as much as 2 mm long, usually straight and at a right angle to the surface, but sometimes curved upwards. Probably they have been stiff and rigid, but very delicate, to judge from the delicate remains of organic matter still left in some cases; often, however, they appear thick on account of a coat of rust. — On some branches thorns are lacking, either not developed or not preserved; on others they are present in great numbers. In some cases there are thorns, of the same size and shape, on the thick stems (*e.g.* PA 295, Pl. VI fig. 1).

It is a characteristic feature that these axial systems do not always spread only on the bedding-planes of the rock. Thus, the thick stem of PA 294 *a* (Pl. VII fig. 1) follows a plane oblique to that of the branches, and the branches in their turn have divisions deposited in various levels and various directions. In some specimens the finest ramifications were imbedded in the rock, so that during the preparatory work deep holes had to be dug into the matrix.

In several cases the branch-systems look as if they have been deposited in running water, all tips being curved in one direction (*e.g.* PA 294, text-fig. 5; PA 1128, Pl. VII fig. 3; compare also PA 1125, Pl. V fig. 2).

The specimens now described are all very uniform, and it cannot be doubted that they represent parts of one and the same plant species.

There are, however, from the same locality, a few other specimens of a somewhat different appearance:

One of them is PA 296, Pl. V fig. 3. The mode of ramification is distinctly dichotomous; but one of the branches, alternately the one to the left and that to the right, is always stronger than the other, thus forming a pseudomonopodial main axis with zigzag bends. The lateral branch, in each case, has an elongate lower part giving off, in a downwards direction, a secondary branch, which is always fragmentarily preserved. Further on it divides repeatedly, in more or less strict dichotomy and with recoiled tips. Nearly all branch angles are about 90°. There are no axillary tubercles. The surface is almost entirely naked; only in one place there are some indistinct and very delicate short thorns.

A branch-system of the same kind is seen in the lower right-hand corner of Pl. VI fig. 1, PA 295. Here the thorns are numerous and well developed.

As regards the recurved tips these axes differ from the branch-systems which are found in connection with the typical stems, as described above. The regular and characteristic type of branching is also, at first glance, rather different, although there are indications of intermediate forms. The spines, on the other hand, are exactly identical in the two cases. In all probability they belong to the same species, but some reservation may still be in place.

Affinity. — In view of the irregular position of many of these branches in relation to the bedding planes of the rock, the question naturally arises whether they might be interpreted as subterranean organs of some sort; but the type of ramification, the presence of thorns, and other characters make that idea quite improbable. — On the other hand, a specimen like PA 294 (text-fig. 5), and others, with their slender branches all arranged in one direction, might be thought to have been aquatic organs, living submersed in water. It is possible that this is right, but in the case of most of the specimens there is no reason for such an assumption: They have, in all probability, been aerial stems with delicate, slender ramifications, which may partly have been deposited in running water.

As to the systematical position of the plant, we have very few clues, except that its organization, its mode of branching, and its thorns, make it practically certain that we are here dealing with a large psilophyte. It cannot be identified with any species described before, and it is also difficult to find a proper genus in which to place it. In a widened sense *Psilophyton* might be considered, but it would really be quite unnatural to make this genus the home of the new species. Most important of the distinguishing characters of the latter is the differentiation between stem and branches; in this respect our plant is far more developed than *Psilophyton Goldschmidtii* and all other psilophytes. On the other hand the branches are not flattened and expanded in one plane: They are not in any way leaf-like, but have retained and further developed their character as lateral axial organs.

In spite of our defective knowledge of the plant, especially as to its anatomy and its organs of reproduction, I therefore venture to establish a new genus for it. In order to express its resemblance, in some ways, to *Psilophyton*, and at the same time its arborescent habit on a diminutive scale, I propose the name of *Psilodendrion*, with the specific epithet *spinulosum*. — For diagnosis, see p. 192.

Age. — The plant being unknown from other parts of the world, and being of somewhat uncertain relationship, it does not in itself give much information as to the age of the beds in which it occurs. If the assumption is correct that it belongs to the group of spinous psilophytes, its advanced stage of axial differentiation would make it natural to regard it as relatively young, probably belonging to somewhere in the Middle Devonian. However, the discoveries of highly developed plant forms even in pre-Devonian beds of late tend to make one cautious in drawing such conclusions.

On the ground of stratigraphical and paleozoological evidence, however, the Gråhuken beds most probably must be assumed to belong to the upper part of the Lower Devonian (cf. p. 161).

Hostimella sp.

Pl. V fig. 4.

Nearly all fragments of axes in the collection are either referable to *Psilodendrion spinulosum*, or so small or poorly preserved that no determination is possible. Some dubious cases were mentioned above (p. 28). There is only one specimen that is of some interest, and which seems impossible to refer to the said species, *viz.* PA 1107, Pl. V fig. 4. Its general form is seen from the photograph. It is remarkable because there are axillary tubercles at the bases of its two branches (cf. p. 171).

2. Mountain on South Side of Vatnedalen (Lake Valley).

In the year 1912 A. Hoel found the first plant fossils of any value in the Devonian of Wijdefjorden. They were not mentioned in the report of the expedition (Staxrud & Hoel 1913 p. 106), and as it is of some interest to know the exact position of this locality, I have obtained Professor Hoel's permission to quote an extract (translated) from his diary concerning this point:

> [August 18th, 1912] " . . . In an elevation of 300 m above sea level in the mountain south of Lake Valley the dip of the argillaceous shale in the sandstone is 30° towards the ENE.

> I climbed up the ridge S of Lake Valley, to a height of 980 m above sea level, building a cairn here and making observations. Here is a top, so that the ridge is lower both to the W and to the E. The profile was as follows. About 200 m to the W of the cairn there is a black argillaceous shale with typical Grey Hook fossils. This shale continues to about 400 m E of the cairn. Here begins a greyish sandstone, first occurring as thick beds in the Grey Hook shale. These beds become more and more numerous, and finally the sandstone dominates in the rock, with occasional layers of greyish black or brownish argillaceous shale, the thickness of the latter layers being from a couple of meters up to some tens of meters. Within them, particularly in the higher levels, there may be nodules of ferrugineous claystone with fish fossils. Plant fossils occur in the shale. The highest fossil locality was a horizon of ferrugineous claystone, probably with only mollusks: It is possible that this locality still belonged to the Grey Hook Series. Further downwards there were found various remains of plants and fishes, on the labels of which the elevation above sea level is recorded. The higher the elevation, the older the strata, because the latter have a dip of 25—30° towards the ENE. The thickness of the layers exposed above the Grey Hook shale in this ridge, is about 1000 m. Judging from the fish remains, I suppose that they belong to the Upper Devonian."

The plant fossils collected in this locality were sent to Nathorst, who mentioned the collection in the following words in his paper from 1914 (p. 1, foot-note):

> "Allerdings fand Herr Universitätsstipendiat A. Hoel 1912 in den oberdevonischen Schichten an der Westseite der Wijde Bay recht viele Pflanzenreste, und zwar in einem Berge südlich vom Lake Valley etwa 300—400 m ü. d. M. Diese Reste, die er mir bereitwillig zur Untersuchung gesandt hat, sind aber, obschon recht deutlich erhalten, nicht näher bestimmbar. Sie bestehen nämlich aus schmalen Stengel- oder Spindelresten von Farnen oder Pteridospermen, denjenigen recht ähnlich, wenngleich mit ihnen nicht identisch, die ich von der Westseite der Klaas Billen Bay beschrieben habe (Nathorst 1894, Taf. 1). Ich zweifle aber nicht daran, daß man bei fortgesetzten Untersuchungen dieser pflanzenführenden Schicht auch bestimmbare Reste finden wird, weshalb eine solche Untersuchung sehr zu empfehlen wäre."

Unfortunately no further collecting has been done in this locality. I have, however, closely examined the specimens from 1912 in the hope that it might now be possible to identify some of them with one or another of the many Devonian plants described since 1914. These hopes were not realized. But some of the fossils are nevertheless of some interest and deserve to be described and figured, although they are not so completely preserved that they can be given any names.

The plants are preserved as black impressions in a dark grey, nearly black shale, and they are all very fragmentary.

a. Straight stems, less than 1 cm broad, bearing numerous lateral branches in spiral arrangement and with decurrent bases. One of the best specimens, PA 1163, is shown in Pl. VIII fig. 1. Along the margin are seen five lateral branches (two to the left, three to the right), which curve outwards from their thick bases; they are short, less than 1 cm long, evidently broken, but why and how cannot be seen. The surface of the impression is grooved, with rounded ridges and depressions which can be traced only for a short distance, a few centimeters at most, and then disappear, no doubt because they curve out into the bases of branches.

As cited above, Nathorst compared this fossil with those he had described in 1894 (particularly *l. c.* Pl. I fig. 3) from Billefjorden, although he left a specific identity out of the question. It is quite possible, but far from certain, that these plants are truly related to each other. A further discussion of the affinity of a plant so incomplete as this will easily lead to futile speculations and may be desisted from on the present occasion (compare also p. 58). Suffice it to mention that these plant forms, particularly those from Billefjorden, resemble some fossils of uncertain affinity, described from other areas, *e. g.* the so-called *Psilophyton princeps* figured by Dawson 1863 (p. 111, fig. 2). Our specimen (PA 1163) from Wijdefjorden, however, differs in several characters, and with its well-defined leaf bases it may rather be compared with some Middle Devonian forms, among them *Barrandeina* from Bohemia.

b. Striated axes with sporangia. — Among the many fragments of stems and stalks, none of them exceeding 1 cm in breadth, there are several specimens of a fairly characteristic type, probably different from the one described under *a.* They are straight, at least most of them, and longitudinally striated by regular and delicate ridges and furrows. Some of them show details of interest: PA 1159, Pl. VIII figs. 2—4, consists of such an axis, somewhat bent and broken, and bearing some remarkable lateral organs, which may be called leaves, or sporangiophores, formed by repeated bifurcation of a short side branch. The first division takes place at its very base. The lower branch divides again, but has then been broken off. The other half has a straight part of about 1 cm, and then a double or possible triple bifurcation. Owing to an oblique splitting of the rock most of the tips have been lost; there is only one exception, and here (Pl. VIII fig. 4) the branch is seen to end in a small cluster of black bodies, evidently sporangia. They seem to be oval-lanceolate in outline. (I will not omit to mention the possibility that these axes do not form an organic unit, but belong to different plants which have happened to be sedimented together; even if that does not seem to be the case, full certainty as to this point cannot be obtained.)

A similar spore-bearing branch-system is seen on PA 1160, Pl. VIII figs. 5—6, where, however, the sporangia are still more poorly preserved. The branch-system in this case has the same characteristic main features as in the former specimen, with repeated bifurcation, the first of which takes place close by the swollen base. — A third specimen, PA 1157, Pl. VIII figs. 7—8, is still more incomplete, but shows a fairly distinct group of sporangia.

That the three sporangium-bearing specimens described above belong to one species, cannot be doubted, and in all probability this is also the case with the one figured on Pl. VIII figs. 9—10 (PA 1160). The axis to which it belongs, penetrates the matrix nearly at a right angle to the stratification, while the leaf-like portion expands in the bedding-plane, dividing three or possibly four times by very regular bifurcation and at about equal intervals. No sporangia are seen, a fact probably not due alone to defective preservation. The whole organ is decidedly more leaf-like in appearance than the sporangiophorous ones, but no doubt they are homologous.

In all probability this plant represents a new genus, not hitherto described. It is characterized by its striated axes, bearing lateral branch-systems, which divide repeatedly and at short intervals by regular dichotomy, in some cases expanding in one plane, being flat, leaf-like and sterile, in other cases more irregular (?) and terminating in small clusters of simple, narrow sporangia.

The fertile parts might be compared with some forms of *Dawsonites*, such as *D. arcuatus* Halle (*Taeniocrada arcuata* K. & W.) from Røragen, and with some unpublished material from the same locality, and also with the specimen from the Upper Devonian of the Loire Basin, which Bureau (1913 Pl. I *bis* figs. 4—4 *a*) under the name of *Cephalotheca mirabilis*, a determination which is doubtlessly incorrect. These plants, however, are of a much more simple organization than the one from Spitsbergen.

Most probably our fossil represents remains of a plant belonging to the group of primitive fern-like forms, ranging from the Lower Devonian to the Upper and comprising *Protopteridium*, *Aneurophyton*, and others, a group for which the name of *Protopteridiales* will be proposed below (p. 178).

c. Detached group of sporangia. — The object shown on Pl. VIII fig. 11, text-fig. 6, is a small cluster of sporangia, found on the same little piece of rock as the sporangium-bearing axis PA 1159 and in the closest proximity to it; but in all probability it has belonged to another type of plant. On the photograph in natural size, Pl. VIII fig. 2, it is barely visible as a little black spot in the upper left-hand corner. — Most likely it consists of three sporangia or sporangiophores, attached to a short common stalk; the one to the right is incomplete. It would be tempting to interpret the structure in the way illustrated in text-fig. 6, each spore-sac being attached to the lower side of a sporangiophore, which projects above it in a short beak-like prolongation. The restoration is not at all certain, and the relationship of the fructification is

Fig. 6. Sporangium-bearing (?) organ, also shown in Pl. VIII fig. 11. Wijdefjorden: Mountain south of Vatnedalen. — PA 1159. × 9.

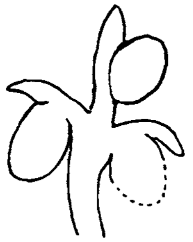

Fig. 6.

unknown; but it is worth keeping in mind for further collecting on the spot, and for comparison with fossils from other localities of the same age.

Age. — Incomplete and indeterminable though these fossils are, they convey the impression of an Upper Devonian age rather than Middle Devonian. That has also been Nathorst's assumption, which is evident not only from the lines quoted above, but also from the labels which he has written (in Swedish): "Indeterminable fragments of stalks and stems. Upper Devonian." — Compare also p. 163.

3. Beach Profile at Andredalen (Second Valley).

In the beach profile at Andredalen at Wijdefjorden, Vogt's expedition in 1925 discovered on August 20th plant fossils in various beds and collected a considerable number of specimens. The collections from two horizons were of great interest. Being entirely different from each other they will have to be described separately. The northernmost locality will be mentioned first.

A. Horizon 6.

The rock is a dark, nearly black shale, splitting up rather irregularly in thin slabs, containing numerous plant fragments. It is fine-grained, and in spite of a considerable amount of minute grains of mica the plant impressions are well preserved and very distinct; but the anatomical structure of the organic remains is completely lost.

Psilophyton arcticum n. sp.

Pls. IX—X, Pl. XI figs. 1—7, Pl. XII figs. 1—5.

Material. — About a dozen slabs, most of them small. They contain a great number of plant fragments, mostly referable to this species, but intermixed with some naked stalks described below.

Description. — The broadest stems, of which there are several specimens, measure 4.5—5 mm across. They are very incomplete, none of them exceeding 7 cm in length. But the fact that even the longest ones taper very slightly, or not at all, indicates that the plant may have been rather tall. Most of the axes are straight.

As a rule the branching is pseudomonopodial, the lateral branch being thinner than the main axis and forming a fairly open angle to it (often about 45° or slightly more). The ultimate ramifications seem to be regularly forking, but over-topping soon takes place; they most distinctly make the impression of being expanded in one plane (see, *e. g.* Pl. X fig. 6). The tips are recurved. Instances of regular dichotomy may occasionally occur in somewhat thicker axes (Pl. XI fig. 5, PA 246; Pl. XII fig. 1, lower right-hand corner, PA 239). Well defined axillary tubercles are never found, but there are perhaps traces of such structures in some cases; thus, the cavity shown in Pl. X figs. 5—6 (PA 241) distinctly seems to represent one.

The surface is smooth and even, but bears hair-like spines, varying in number and length, usually being present in great abundance (see, *e. g.* Pl. IX figs. 1 and 3). They are longest and most numerous on the thicker stems. Here they mostly measure (4—) 5—6 mm in length, but in several cases, which do not seem to have been exceptional, they attain a length of at least 8 mm and probably even more. — They are never adpressed, but as a rule form a right angle to the stem. They are very thin and delicate, very gradually tapering from the base, which is widened to a very low cone (see below); near the base the thickness in several instances has been found to be about 0.3 mm. They are nearly always straight or very slightly curved, the upper side being the convex one. An exceptional case is shown in Pl. XI figs. 3—4 (PA 241), in which they are up to 8 mm long and resemble flexible hairs more than rigid spines.

Long spines as just described may be found on rather thin axes (*e. g.* Pl. IX fig. 3). But the slender ultimate branch-systems, which are also supposed to belong to this species, bear no such spines of that length. Here they are quite short, but, as it seems, they may be rather numerous (cf. Pl. IX fig. 5).

On the thicker stems the scars indicating the bases of the spines are distinctly seen on the surface of the impression. In some cases they are placed in transversal or slightly oblique lines, but upon the whole their arrangement is subject to no such regularity. The scars of the spine-bases are circular (see, *e. g.* Pl. X figs. 2—4), and in some cases they seem to contain a solid central part, looking very much like a nerve in cross-section. But in the many well-preserved spines visible as impressions along the margins of the stems, no such strand is visible.

As mentioned above, the basis of the spine has the form of a low cone; the latter is not at all visible in all cases, a fact most likely due to the state of preservation. The transition from the cone to the spine is abrupt, and it is probably at this point that the spine would be detached if it was broken or fell off for some other reason, leaving the cone as a diminutive leaf-cushion.

There seems to be no cuticle preserved, and various attempts to macerate the lustrous carbonized remains of organic tissue have been in vain. But when examined under high magnification and in incident light, the surface exhibits certain points of interest: On a specimen like PA 253 *b* there are fine striations which must represent longitudinal cell-walls (not very clearly visible on the reproduced photographs, Pl. X figs. 2—3), and a great number of other structures, resembling stomata. These structures (as seen on the figures cited) consist of two lip-shaped elevations separated by a narrow split, which is always orientated in the longitudinal direction of the axis. The length is 0.10—0.18 mm. They are present in very great numbers on the surface, at about equal distances, but without any other regularity in the arrangement. They have a very close resemblance to stomata, and it would be natural to take it for granted that they really are such organs. But they are twice the size of the stomata found in preparations of *Psilophyton* from Gaspé by Edwards (1924) and from Scotland by Lang (1932, compare also 1931). It further seems possible, although not very probable, that they are of the same nature as the markings described from the surface of a good specimen by Lang (1932 p. 503, Pl. II fig. 24) and which this author supposed to be identical with the slightly elevated 'clear areas' found in his cuticle preparations (*l. c.* Pl. IV fig 68); similar structures were noticed by Edwards in the *Psilophyton* from Gaspé. What these 'clear areas' really are, is not known (Edwards tentatively suggested that they might have been hair-bases, but nothing has later been found to support that explanation), but at all events they are different from stomata. In the light of these facts some caution will still be necessary as regards the interpretation of the stomata-like structures of the Spitsbergen plant. Most likely it will be possible to clear up the question if suitable specimens of *Psilophyton* from various localities are examined and compared for this special purpose.

For the sake of completeness reference may also be made to some other cases, of which an illustration is given in Pl. X fig. 4. In the specimen figured (PA 247, which is a negative impression of the plant, and not, as in PA 253 *b*, a carbonized stem) there are numerous small points resembling the bases of spines, but, as it is seen on the photograph, much smaller. If compared with the stomata-like structures described above, it will be found that they are not very different in size (note the different magnification of the photographs), but they are more distant, and they are circular in outline. On the specimen (but not very well when illuminated as on the photograph) it may also be seen that they are surrounded by radiating cells. In this case, more than in the former, it seems probable that we are dealing with structures corresponding to the said 'clear areas'.

A short distance inside the margin of the thickest stems there is often a distinct line. In some cases (*e. g.* PA 251, Pl. IX fig. 3) it forms a border between an external rim, which may be thought to represent some softer cortical tissue, and a broader and more solid central part, which, in the negatives, has left a deeper depression. The border in certain specimens (*e. g.* PA 239, Pl. XII fig. 1) has the appearance of a strand, distinctly different from the tissues both within and without;

these specimens are relatively well preserved, and it is therefore probable that they represent most correctly the conditions in the living plant. In a few specimens (PA 246, Pl. XII fig. 5, right, and PA 252, Pl. X fig. 8) a similar strand is seen more in the middle of the stem. — The idea that there is a solid central core of some sort is corroborated by a specimen like PA 239, Pl. XI figs. 1—2: The stem is preserved in a carbonized state, showing, in some places, the smooth outer surface with spine scars (*e. g.* the lower half of fig. 2); in other places, however, the external layer has fallen off, exposing the striated surface of an internal layer.

Beyond these vague observations, which are partly somewhat difficult to reconcile, no knowledge as to the anatomy could be obtained from the material at hand.

Organs of reproduction are unknown.

Affinity. — It is probable that all spinous axes from this locality represent parts of one species, the only specimen which could be questioned in this respect being PA 241 (Pl. XI figs. 3—4), with its very long hairs. It may also be mentioned that such branch-systems as those shown in Pl. IX figs. 4—5 and Pl. XI fig. 6 have not actually been found in organic connection with the thickest stems; but there are transitional stages making the specific identity present itself as very probable (*e. g.* Pl. IX fig. 3). To be safe, however, the following discussion of the affinity of the plant will chiefly be based upon the thicker axes.

As far as our knowledge of this plant goes, it shows that we are dealing with a typical member of the genus *Psilophyton*. The species interesting us in this connection are the following:

Ps. princeps Daws. em. Halle.
Ps. Goldschmidtii Halle.
Ps. wyomingense Dorf.
Ps. pubescens K. & W.

It is very doubtful whether any of the other species which, particularly in former days, have been referred to this genus, should be recognised. *Ps. grandis* Penh., from the Middle Devonian (Hamilton) of West Hurley, Ulster County, N. Y., has sometimes, by various authors and with varying degree of certainty, been accepted as a true member of the genus. Judging from the photographs published (Penhallow 1894 figs. 12 *a—c*) I do not think that we have a sufficient basis for this supposition. — Lately some authors (Bertrand 1933, Stockmans 1939 *b*) have also referred *Asteroxylon elberfeldense* K. & W. to *Psilophyton*.

As to *Ps. wyomingense* and *Ps. pubescens*, Kräusel & Weyland (1938 p. 187) assume that they may be identical with each other. If this is right, which seems to be quite likely, the species will have to be called *Ps. wyomingense*, as the name '*pubescens*', appearing first as a *nomen nudum* (*? Aneurophyton pubescens* K. & W. 1932 p. 186), was not validly published until 1938, whereas *Ps. wyomingense* Dorf dates from 1933. The very long spines of the species, at least in the American specimens, give it a certain resemblance to the Spitsbergen plant in question, but its external form and mode of growth are quite different.

Ps. princeps is probably the most famous Devonian plant, but, unfortunately, far from being the best known, even as far as the external characters are concerned. This is not the place for a discussion of the difficult question of the characterization and delimitation of *Ps. princeps* and *Ps. Goldschmidtii* and their interrelationship. It may suffice to state that *Ps. princeps*, of which I have seen Gaspé specimens in Stockholm, is doubtlessly different from our plant as regards the form and ramification of the axes, and the length of the spines.

Some of the flattened shoot-systems of the Spitsbergen plant very closely resemble those of *Ps. Goldschmidtii.* But that is not a sufficient basis for an identification, such shoots (*e. g.* Pl. IX figs. 4—5 and Pl. XI fig. 6) really being indeterminable if found alone. On the other hand there are distinct differences between our plant and *Ps. Goldschmidtii*: First, the thorns are longer in the former. In the Røragen material Halle (1916 p. 18 and p. 21) found the length of the thorns of the *Psilophyton* specimens to vary from 1 to 3 mm (in the specimens then determined as *Ps. princeps*) and up to 4 mm (in the typical *Ps. Goldschmidtii*), and even if they may be found somewhat longer in specimens collected later, they are not nearly so long as those of the long-haired specimens from Wijdefjorden. Secondly, the shoots of the latter never seem to be so entirely naked as those of *Ps. Goldschmidtii.* Finally, there is probably some difference in the morphology of the shoots too, but that is difficult to define on the basis of the present material.

Though the points of resemblance indicate that our plant is closely allied to *Ps. Goldschmidtii*, the differences make it necessary to institute a new species; it may be called *Ps. arcticum.* — For diagnosis, see p. 191.

Age. — Being a new species, and so far only known from one locality, *Psilophyton arcticum* cannot of itself be used for any precise determination of the age of the beds in which it occurs. It may, however, be of some interest to summarize what is known as to the age of the other members of the genus.

In Canada the Gaspé sandstone, the *locus classicus* of *Ps. princeps*, is referred to the lower part of the Middle Devonian (Alcock 1935 p. 78). All other occurrences of the various species of *Psilophyton* belong to the Lower Devonian, the age in most cases being determined both on geological and paleozoological evidence: This is the case with the Beartooth Butte formation in Wyoming (*Ps. wyomingense*); the Strathmore beds in Scotland (the specimens regarded by Lang 1932 as representing both *Ps. princeps* and *Goldschmidtii*); the Taunus sandstone of two localities in the department of Pas-de-Calais (*Ps. Goldschmidtii?*, Bertrand 1913, and *Ps. princeps*, Corsin 1933); the Belgian occurrences, recently described by Stockmans (1940, both *P. princeps* and *Goldschmidtii*); and the Klerfer beds at Wilwerath in the Rhineland (*Ps. Goldschmidtii*). In Norway the occurrence at Røragen has also been supposed to be Lower Devonian, but here the fossil flora is the only basis for the determination, and this is also the case with Sørværet, where a species of *Psilophyton* is the only fossil found. — The remains from Siberia, compared by Kryshtofovich (1927) with *Ps. princeps*, seem to be too poorly preserved to be taken into consideration.

In conclusion, we may say that as far as we now know, the genus is confined to the Lower Devonian in Europa, whereas in America there is one occurrence in the Lower Devonian in the United States and one in the Middle Devonian in Canada. — See further p. 162.

Smooth striated axes.

Pl. XI figs. 8—11; Pl. XII figs. 5—10.

On the same slabs as *Psilophyton arcticum* there are a number of striated axes of a characteristic surface structure and mode of branching.

The longest ones (PA 246, Pl. XII fig. 5) are about 7.5 cm long and 5 mm broad. They are straight or nearly so, and sparingly branched, with lateral branches which do not influence the direction of the main axis. Sometimes the branches are relatively thick, about one-third or one-half of the main axis (PA 246, Pl. XII fig. 7; PA 247, Pl. XI figs. 8—9; PA 253 *b*, Pl. XII figs. 9—10); usually they are straight, and standing out at an open angle, but in one case the branch curves up so as to become parallel to the stem. These branches are always broken at a distance of one or a few centimeters from the base. — There are also branches of another kind, in the form of short and thin lateral appendages; they are scarcely 0.5 cm long, probably broken, and always curved, sometimes backwards (PA 246, Pl. XII fig. 8), sometimes in the other direction (PA 246, Pl. XII fig. 6). They are found, in a very small number, not only on the main stems, but also on the thicker branches (PA 253 *b*, Pl. XII figs. 9—10). In one case (PA 247, Pl. XI figs. 8—9) a thick branch gives off abaxially a thin secondary branch, which in turn divides into a straight portion and a recurved one.

These axes are striated longitudinally, with about 10—16 delicate furrows and ridges, which seem to branch and anastomose.

A remarkable specimen, although fragmentary, is PA 1544 (Pl. XI figs. 10—11). It is a portion of a striated axis of the type just described, scarcely 2 cm long; in the upper end it divides simultaneously into four branches of about equal thickness. The connection of these branches with the main axis is clearly seen, the striations of the latter being continuous with those of the branches. As seen on the photographs, one of the branches follows the direction of the stem, another branch is placed to the left of it, and two to the right. The one on the extreme right divides near the base, giving off downwards a little curved secondary branch. On the left-hand side there is also a bifurcate branch which, on the photograph, might seem to belong to the same axial system; but that is not the case.

Affinity. — The association of these axes with a typical *Psilophyton* recalls the many other cases in which the spinous stems and branches of a *Psilophyton* occur together with naked, striated axes (Canada, Scotland, Norway). Here it may suffice to state that in the collection from Wijdefjorden there is no support whatever for assuming a specific identity of the two types. The difference between them is not only due to the presence or absence of spines, which could really be accounted for if the naked axes were supposed to be decorticated, but also to the entirely different mode of branching. But it must be admitted that the systematical position of the naked axes is, at present, unknown.

B. Horizon 4.

The plants here occur in a dark grey shale, splitting irregularly with uneven surface, and containing a considerable amount of mica in minute grains. The fossils are numerous, but in most cases preserved only as impressions with or without structureless remains of the organic tissue. They bear testimony to an abundant vegetation, and although no species can be identified they are of considerable interest as they demonstrate the remarkable size and level of organization of some of the members of this flora, at the same time indicating what may be hoped for when further explorations have been carried out.

a. Sulcate stems. — The flat impression of a large stem, PA 255, is shown in text-fig. 7 *a.* It is not preserved in its entire breadth, but even in its present incomplete state it is no less than 15.5 cm broad; the height of the fragment is about 14 cm. It is longitudinally furrowed, with rounded grooves; along the top of the ridges, which are about 4 mm apart, there is often a depression, the ridge thus appearing double.

A similar stem, although of somewhat smaller size, is preserved as a stone-cast (PA 1177); it has plain, rather broad furrows and ridges. — A flattened impression, PA 1171, illustrated in text-fig. 8, is of interest *i. a.* because the ridges seem to have a tendency to branch and anastomose.

It is not certain that the specimens mentioned here belong to one species, but in no case is the affinity clear. Some of them, particularly PA 1171, text-fig. 8, would no doubt formerly have been determined

Fig. 7. Remains of broad axes, from Wijdefjorden: Beach profile at Andredalen, Hor. 4. — *a.* Flat impression of large sulcate stem. PA 255. Nat. size. — *b.* Probably remains of axis with tape-like bands of fibrous tissue, lying in different levels in the matrix. PA 1178. Nat. size.

as *Bornia transitionis* — compare, for instance, Bureau 1913—14 Pl. I fig. 1, and others, cited below (p. 53) in connection with a similar stem from the profile between Andredalen and Forkdalen (PA 289, text-fig. 13); but both taxonomically and stratigraphically this name is rather ambiguous. There is also an interesting resemblance between these stems and some of the fossils described by Nathorst from Ellesmereland. On the other hand, PA 255 (text-fig. 7), with its grooved ridges, has such a resemblance to the peculiar plant *Pietzschia Schülleri* Gothan & F. Zimmermann (1927), from the Upper Devonian of Saxonia (cf. p. 54), that it suggests a possible affinity, in spite of the difference in size.

Fig. 8. Flat impression of sulcate stem, from Wijdefjorden: Beach profile at Andredalen, Hor. 4. — PA 1171. Nat. size.

Upon the whole, even if they are indeterminable, in so far as they cannot be referred to any natural species or genus, these sulcate stems are important because they distinctly belong to types which only rarely occur in rocks older than the Upper Devonian.

b. — An impression of a stem (?) of another kind is shown in natural size in Pl. XIII fig. 1 (PA 254). It is slightly sulcate, with low and broad ridges, which are somewhat discontinuous. There is practically nothing left of the organic matter. The impression in itself is indeterminable, but of interest chiefly on account of a great number of *Spirorbis* (Pl. XIII fig. 2) developed on its surface and preserved as moulds; mostly they form regular spirals about 1.5 mm wide, all of them wound in the same way (cf. the illustration).

There are more specimens with similar markings, one of them, PA 300, being shown in Pl. XIII figs. 3—4. In some cases *Spirorbis* is here preserved as moulds, in others as elevations. This fact would be difficult to explain except on the assumption that the plant fragment, on which *Spirorbis* has grown, has been rather thin. Some of the markings are nearly circular in outline, semiglobose with a central depression; others, however, are regularly spiral. Those preserved as elevations are wound clockwise, the negative ones in the other direction. The interpretation of these specimens as *Spirorbis* or related animals can scarcely be subject to doubt (cf. also p. 56).

Shells of *Spirorbis* growing on stems or leaves of plants have been reported from many localities and formations. Dawson (1871 *a* p. 43, foot-note) reports that he found them in material from Gaspé but lost the specimens afterwards. Other occurrences of Devonian age do not seem to have been mentioned in literature (compare, however, Steinmann & Elberskirch 1929 p. 25, and Stockmans 1940 p. 43). There is, however, one point which may be worth mentioning in this connection:

Our specimens recall the problematic fossil described by Broili (1928) and by Hirmer (1930) under the name of *Maucheria gemuendensis* Br. from the Lower Devonian of Hunsrück; two specimens of it were found. The nature of this fossil is quite obscure, and both authors emphasize the possibility that it does not belong to the Plant Kingdom at all; the same doubt is expressed by Kräusel & Weyland (1935 *b* p. 187). According to Hirmer there could scarcely be any serious doubt about the identity of the two specimens, in spite of certain points of difference between them: In Broili's specimen (the type) the axis, or what looks like an axis, has small conical elevations of simple form, arranged along regular lines across the surface, like leaf-scars, whereas in the other specimen, described by Hirmer, the corresponding structures are quite irregularly crowded and highly variable in shape, sometimes being distinctly and regularly spiral. I should like to draw attention to the far-going resemblance between the latter and some of the specimens of *Spirorbis* here described from Spitsbergen: It is so striking that a similar origin of the two fossils is strongly suggested. Some of the elevations on the said specimen of *Maucheria* certainly have a different shape, but at least in some of those cases they are exactly as one might expect from a spiral 'shell' of some kind that has been partly worn off. If these markings represent *Spirorbis*, the delicate network found with them (visible in three places of Hirmer's Pl. II) must be something else; if it does not originally belong to the substratum (of whatever kind that may be), one might think of bryozoa. The frequent occurrence in our days of *Spirorbis* together with *Membranipora* or related genera on *Laminaria* and similar objects makes such an idea look very probable, in so far as one can form any opinion on that question without having seen the specimen itself.

It is a serious difficulty, however, that it would be impossible to apply the interpretation here suggested, to the type specimen of *Maucheria* described by Broili. In that specimen the regular arrangement of the small elevations, and also their form, exclude the possibility of regarding them as *Spirorbis* or any other kind of animal that has happened to settle there; like the delicate reticulation they no doubt form a part of the big stem (if it be a stem). If the interpretation as *Spirorbis* in the former case is correct, the consequence must be that the astonishing resemblance between the two specimens will have to be regarded as accidental.

c. — On the slab PA 254 just mentioned there is also another remarkable fossil (Pl. XIII fig. 10). It is about 11 cm long and up to 2 cm broad, irregular in outline and with uneven surface. It has a kind of reticular structure, due to a great number of sharp, but very delicate furrows, irregularly flexuose but, upon the whole, longitudinal. In all probability they could be nothing but the off-print of a fibrous layer of some plant stem.

Fig. 9. Broad bifurcate axis or rachis with sulcate surface. Wijdefjorden: Beach profile at Andredalen, Hor. 4. — PA 1178. Nat. size.

d. — There is also, on the various slabs, a number of axes of varying sizes, most of them of but slight interest. One of them, however, PA 1178, is very large, as seen in text-fig. 9, bifurcate, with coarse longitudinal striations. It may be compared with a fern rachis, but is really indeterminable. Similar longitudinal furrows are indicated on another fragment, PA 1545, Pl. XIV figs. 8—9, which may be mentioned because of its delicate transverse wrinkles; on the photograph it has been illuminated so as to show the latter as distinctly as possible.

e. — A small branched axis shown in Pl. XIV figs. 4—5 (PA 1102) is remarkable on account of the axillary structure clearly visible on the photographs: It is an egg-shaped body, which most decidedly seems to belong to the axis. The fossil is highly suggestive of some forms of *Hostimella.* A specimen of very much the same shape, only somewhat larger, has been figured by Bureau (1913—14 Pl. I *bis* fig. 14) under the name of *Pteridorachis*, from the Upper Devonian of Loire-Inférieure.

f. Bands of fibrous tissue. — Groups of long linear plant organs are found in several specimens. One of the most remarkable is shown in Pl. XIV fig. 1 (PA 242). It looks like a bundle of long and narrow, linear leaves. Although no individual 'leaf' is seen preserved in its whole length, they seem to have been at least 18 cm long, probably more, and about 1—1.5 mm broad. They are nearly straight, with parallel sides, and minutely striated. As is seen on the photograph, there is a great number of them, lying together in a kind of fan-shaped bundle, and diverging, in layers on top of each other, from a point outside the slab. Each of them consists of a considerable amount of carbonized matter, showing that they must have been thick bodies, possibly even terete.

Repeated attemps at maceration only gave very scanty information as to the anatomical structure of these remains. When treated with Schulze's liquid, the 'leaf' would split transversally into small fragments. There seemed to be a central tissue, now completely carbonized, surrounded on all sides by a more light-coloured membrane which resembles a cuticle, but in which no stomata and not even any markings of cell walls could be seen. In some cases the 'leaf' will split up exactly transversally into such short pieces that under the microscope they may be studied (although with no great profit) as if they were ordinary cross-sections; usually they will form a bi-concave figure, because they will split along a median line and the two halves, with the said membrane on the outer side, will curve out from each other so as to touch each other only in the centre. When ammonia is added, all is dissolved; the most resistant parts seem to contain cell walls like those of a thick-walled parenchyma with round cell lumina. No long cells have been observed in the preparations.

The value of these observations is perhaps not great. More reliable is the impression left through the examination of the fossil in oblique light, as is seen in Pl. XIV fig. 2, namely that it consists of very long parallel cells, in which no cross-walls can be observed. A number of delicate transversal lines may represent some kind of wall structure, like annular thickenings, but may also be merely accidental. These long cells form a coherent tissue, in which no other cell types are observable.

These long and narrow bodies look like leaves. If they really should be of foliar nature, there is only one Devonian plant with which they might be compared, *viz. Sigillaria(?) gilboensis* Goldring (1926) from Gilboa in the State of New York, a plant with numerous leaves which are still longer and somewhat broader, but which in their linear form resemble those from Wijdefjorden.

Certainly, however, they are not leaves. At least there are several other specimens in which bands, sometimes indistinguisable from those just described, are found together in such a manner that it is evident they have formed part of some kind of stem. Such a specimen is

PA 244, of which a part is shown in text-fig. 10, the full length being 23 cm. They would be most easily explained as remains of some kind of fibrous tissue forming the mechanical system in the external part of a stem. By way of illustration reference may be made to such specimens as PA 1171 (p. 39, text-fig. 8) and PA 289 (from another locality, p. 53, text-fig. 13): It would be easy to imagine that the sulcate surface of these impressions, as now found, might be due to strands of sclerenchymatic tissue, which a natural maceration would disintegrate. Certainly a specimen like PA 242 (Pl. XIV fig. 1) does not at first glance seem to be in accordance with this idea, but the others are quite compatible with it.

This point of view is strongly supported through the study of other specimens:

PA 1189, Pl. XIV fig. 3, consists of a number of black tape-like bands, lying more or less regularly parallel to each other and at various distances, sometimes covering each other. Some of them have exactly the same breadth and texture as those of PA 242, others differ in being much broader or bifurcate (in the upper right-hand corner of the photograph). On the left-hand side of the specimen is seen a band, about 1 cm broad, which seems to be entirely uniform and coherent, but which in one end splits up into narrower parts. It very much resembles a cortical layer of sclerenchymatic tissue, and suggests a comparison with the broad impressions which Nathorst (1904) described from Ellesmere Land under the name of *Lyginodendron Sverdrupii*. A specific identity, however, is out of the question.

These bands are also, from a histologic point of view, of the same nature as those of the stems of *Arctodendron* Nath. (1919, syn. *Dictyodendron* Nath. 1914) from the Lower Carboniferous of Spitsbergen. Some of the specimens described by Nathorst

Fig. 10. Remains of stem with narrow bands of fibrous tissue, from Wijdefjorden: Beach profile at Andredalen, Hor. 4. Entire length of the fossil 23 cm. — PA 244. Nat. size.

(1914, particularly Pl. VIII) so closely resemble those from Wijdefjorden, described here, that one might feel inclined to refer them to one and the same genus. But our specimens do not show any such regular network of bands as seems to be characteristic of *Arctodendron*, so the reference would not be justified.

PA 1178, text-fig. 7 *b*, probably represents the same kind of structure, but differs in the fact that the bands do not lie in one plane, but in several, separated by layers of matrix. They have the same delicate striation, due to longitudinal cell walls, as PA 242.

It is probable that a number of isolated bands found in various other slabs of shale represent the same kind of fibrous tissue, *e. g.* the one shown in Pl. XIV fig. 6 (PA 1103). In the case of one like Pl. XIV fig. 7 (PA 1175), however, it is difficult to say whether it is of the same nature or perhaps a kind of axial organ.

g. Thick axis with linear leaves (?). — On PA 244 and its counterpart PA 1188 is seen an indistinct impression of a broad axial organ, which at short intervals bends at a right angle alternately to the left and right (Pl. XV). At each bend it gives off either a kind of branch or, in one case, a bundle of linear organs, up to at least 8 cm long, looking like leaves. In reflected light and in strong magnification they are seen to be delicately striated.

Also in this case the long appendages look like leaves, but it is more probable that they are not. Their real nature can scarcely be found out without a more complete material, but it seems quite likely that they are of the same kind as the organs described above under the letter *f*.

The broad axial organ itself may not be an aerial stem. It is equally probable that it is subterranean, as a kind of rhizome.

h. Drepanophycus sp. — The only specimen (PA 254, Pl. XIII figs. 8—9) is a poorly preserved fragment, 5 cm long and 6 mm broad. Some vascular strands are fairly distinctly seen, represented by furrows. The central stele is not quite clear, probably because it has been covered with some of the leaf-traces when the axis was pressed flat. But a number of other leaf-traces are quite distinct; leaving the median line at regular intervals of 2—3 mm they curve towards the margin, which they reach at a right angle. They are placed opposite each other or alternately on either side of the median line. In a few places along the outline there are preserved thorns, 2—3 mm long, curving upwards from a broad base; they are inserted at or just below the points where the strands reach the margin. At least in one case a strand seems to proceed into the thorn. On the surface of the fossil there are indications of thorn-bases, but their form cannot be made out with certainty. There is a fair amount of carbonized matter; attempts at maceration, however, were unsuccessful.

Among the remarkable plant remains of this locality this specimen is the only one that can be determined, in so far as it can safely be referred to the genus *Drepanophycus.* The strong, falcate thorns, probably with nerves, the broad thorn-bases, and the well developed strands, are all characters in which it agrees with that genus. It may be preferable to desist from the application of a specific name in the case of a material so poor and scanty, so it may suffice to state that our fossil has very much in common with *D. spinaeformis* Göpp. It has somewhat smaller dimensions than most of the specimens which have been referred to that species, and the very distinct strands are also rather unusual. But as regards all the characters observable it is really within the range of variations of the said species, which, it may be added, has become rather heterogeneous and will most probably have to be split up.

Drepanophycus spinaeformis has been recorded from the following occurrences:

Canada: Gaspé sandstone (Dawson 1871 *a*). The age of the Gaspé sandstone is Middle Devonian (cf. Alcock 1935 p. 78). — The specimen published by Dawson (1882) from Campbellton as 'fruit of *Arthrostigma gracile*' is a problematicum not belonging to this species, but according to Kräusel & Weyland (1930 p. 25) there are specimens of *Drepanophycus* from Campbellton in Montreal.

Scotland: Strathmore beds (full bibliography is given by Lang 1932, compare also Henderson 1932). Lower Devonian.

Norway: Røragen (Nathorst 1913, Halle 1916). Mostly regarded as Lower Devonian, but only on the basis of the fossil plants.

Germany: Hachenburg in Nassau (Göppert 1852), in *Spirifer* sandstone of Lower Devonian age. Also in the Wahnbachtal and other localities of the Rhenish Lower Devonian, *viz.* Obere Siegener Schichten and Hunsrückschiefer (see Kräusel & Weyland 1930 and 1935 *b*). Two very dubious specimens referred to the genus *Drepanophycus* (*Arthrostigma*), but really of uncertain position, are from the Lower Devonian of the Harz (Mägdefrau 1938) and the old Upper Devonian of Liebichau in Silesia respectively (Gothan & F. Zimmermann 1937).

Belgium: Common in the Lower Devonian (Emsian), together with some other, more dubious species of the genus (Stockmans 1940).

France: Recorded, but not figured, from the Lower Devonian of Pas-de-Calais (Corsin 1933 *a*).

China: Yunnan (Halle 1927 *b*, 1936). Age only determined on the basis of this species.

[Australia: Some specimens, which had been mentioned previously by Chapman and by Vincent, were described and figured by Cookson (1926) with reference to *Arthrostigma gracile* (= *Drepanophycus spinaeformis*). When more material was obtained, however, and *Baragwanathia* became known, one of the specimens turned out to belong to that species (Lang & Cookson 1935 pp. 423, 428), while in the case of another specimen affinity to *Thursophyton* appears more probable (according to Lang & Cookson 1927 p. 44). Australia therefore should disappear from the list of localities of *Drepanophycus*.]

Summing up what is known of the distribution of *Drepanophycus spinaeformis*, we may say that in Scotland, Germany, Belgium, France, and probably in Norway, it is confined to beds of Lower Devonian age, whereas in Canada it is found in the Middle Devonian too.

In view of this fact our plant, if it really belongs to *D. spinaeformis*, and if it alone should be considered as an indicator of the age of the horizon, would suggest the Lower Devonian, although not as an indisputable proof, the lower part of the Middle Devonian also being possible. However, the uncertainty as to the specific identity of the fossil renders the evidence somewhat unreliable.

Of the two other valid species of the genus, *D. Opitzi* K. & W. is from the Lower Devonian of the Hunsrückschiefer, *D. spinosus* (Krejci) K. & W. from the Middle Devonian of Bohemia. *D.* aff. *gaspianus* (Daws.) and *D. (?) Crepini* Stockm. are recorded from the Lower Devonian of Belgium (Stockmans 1940).

i. — A few stems have certain characteristic features in common, the best one being illustrated in Pl. XIII fig. 7 (PA 1322). It has a maximum breadth of 1.5 cm, and a length of 7 cm. There is a broad central part, with delicate and irregular longitudinal striations, and on both sides of it a rim with smoother surface. Other specimens of the same kind are broader, but do not show so well the contrast between the central part and the external ones.

The character mentioned might have been regarded as accidental and of no moment if it had not recalled some specimens from the Upper Devonian of Ellesmere Land, described by Nathorst (1904 Pl. IV figs. 3—4 and Pl. V fig. 1). His specimens are much larger, and they show far more distinctly the feature just indicated in the material from Wijdefjorden. But there is an undeniable resemblance, and an affinity of the plants seems very probable.

j. — The object shown in Pl. XIII figs. 5—6 (PA 1322) is the flat impression of an axis, 1.8 cm broad, with a characteristic structure of the surface: There are irregular longitudinal striations, very delicate, in certain places curving from each other so as to form lenticular figures which no doubt correspond to some kind of scars. The latter are about equidistant from each other, but apart from that there is no regularity in the arrangement. — It may be compared with the fossil figured and described by Dawson (1882 p. 101, Pl. XXIV fig. 19) as *Caulopteris (?)* from the *Archaeopteris* beds of Scaumenac, but the affinity of both fossils is unknown.

Age. — A fossil flora, of which only one specimen, and that one even in doubt, may be given a specific name, should not be thought to afford any reliable basis for stratigraphical conclusions. Nevertheless the fossils described are interesting and important just from that point of view: the large stems of the various types, and the object illustrated in text-fig. 8 (PA 1178), are entirely alien to all Lower and Middle

Devonian floras hitherto known, and, as mentioned repeatedly, comparisons can only be drawn with plants from the uppermost parts of the Upper Devonian.

On the other hand, the flora comprises a representative of the *Psilophyton* flora, a group otherwise not known to pass the boundary between the Middle and Upper Devonian, and this representative is even of a type which preponderatingly belongs to the earlier parts of the Devonian.

If this collection had been brought home from an entirely unknown region, one would have had great difficulty in determining the geological age precisely, but it can scarcely be doubted that most paleobotanists would have been inclined to regard it as Upper Devonian, finding the determination of *Drepanophycus* and its value as an index fossil unreliable. However, as it will be touched upon again later on (p. 163), the paleozoological evidence speaks decidedly against so young an age; the flora cannot be younger than the lower part of the Middle Devonian, at most. This apparent discrepancy can only be regarded as a fresh proof of the formerly unexpected richness of the plant world as far back as early Devonian age (cf. also p. 166).

4. Beach Profile between Andredalen (Second Valley) and Forkdalen (Fork Valley).

During the expedition in 1925, Professor Vogt and his companions collected fossils in a profile along the beach between Andredalen and Forkdalen. In slightly different horizons there were found interesting plants, preserved in a breakable grey shale, splitting up into rather thick slabs, but cleaving somewhat irregularly and containing numerous very fine grains of mica. The preservation of the plants is poor, the impressions indistinct, and nothing is left for maceration. The plants are, however, very remarkable.

Cephalopteris(?) praecox n. sp.

Pls. XVI—XVII, text-figs. 11—12.

The best specimens of this species are found on a single slab, PA 288, the largest and most complete one being that shown in Pl. XVI and Pl. XVII fig. 3 (specimen *a*). It has the form of a bipinnate fern, the main rachis being about 18 cm long, incomplete both at the top and at the base, 5—7 mm broad, delicately, but distinctly striated. It is somewhat curved. It bears straight lateral branches alternately to the two sides, lying in one plane, forming acute angles with the main rachis, and striated in the same way, the striations at least partly proceeding continuously from the main axis to the branch; they are 2—3 mm wide. — The branches bear secondary ramifications, which generally,

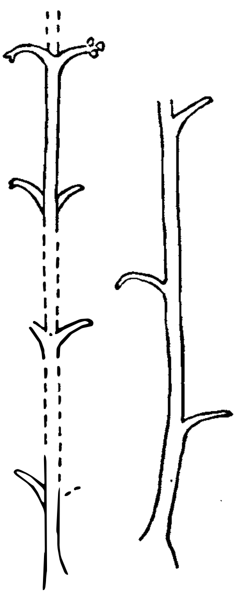

Fig. 11.

Fig. 11. *Cephalopteris(?) praecox* n. sp., from Wijdefjorden: Beach profile between Andredalen and Forkdalen. Two side branches of the holotype, cf. Pl. XVI. — PA 288 *a*. Reduced 3 : 4.

however, are poorly preserved and observable only in some places. They are of two kinds, sterile and sporangiferous, the former being restricted, as it seems, to the upper main branches, while the lower ones are fertile. The sterile secondary branches are alternating, as seen on the middle main branch to the right; they are imperfectly preserved, but their form is seen in another specimen (*b*, on the back side of the same slab), as described below. It may be mentioned that the lowermost 'pinnule' is found on the outer (abaxial) side of the primary branch. — The fertile divisions are opposite, in pairs placed at regular intervals of about 2.5 cm. They are short, less than 1 cm, and rather stout, straight or slightly curved backwards, forming almost right angles to the main branch. Each of them seems to end in a little cluster of a few sporangia, which are sessile or placed on very short pedicels (Pl. XVII fig. 3).

With a view to the comparison with *Cephalopteris* it is of some interest to note a peculiarity only just indicated on the long straight branch to the left near the middle of the specimen, as seen in Pl. XVI (cf. text-fig. 11, which is a tentative reconstruction that should be accepted with every reserve): The uppermost pair of sporangiferous secondary branches (also shown in Pl. XVII fig. 3) are decurrent proximally, while their distal sides distinctly seem to meet on the upper side of the main branch, that is, on the side towards the observer. The second pair is not so well preserved, but it may at least be observed that the main branch continues uncovered through the pair which consequently seems to be placed underneath it. The third pair does not allow of any detailed observations, but there are faint indications of a similarity to number one. The innermost pair is like number two.

On the back side of the slab are found a few small fragments which most probably belong to the same species. One of them (PA 288, specimen *b*), as shown in Pl. XVII figs. 4—5, consists of a part of a striated axis resembling the one just described to such a degree that identity seems to be beyond doubt. In connection with it is seen a leaf-like organ, about 1.5 cm long, without any lamina, but divided three times, dichotomously or pseudomonopodially, evidently in one plane; tips recurved.

Fig. 12. Cluster of sporangia, probably belonging to *Cephalopteris(?) praecox* n. sp. Also shown in Pl. XVII fig. 8. Wijdefjorden: Beach profile between Andredalen and Forkdalen. — PA 288 *c*. × 9.

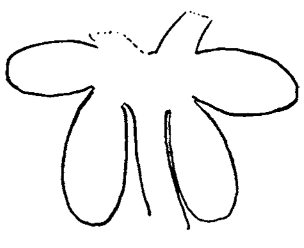

Fig. 12.

Close by is a small group of three sporangiferous branches (PA 288 specimen *c*, Pl. XVII figs. 6—8). They do not show the same regular arrangement in pairs as those of the large specimen (PA 288 *a*). At all events, however, they are of the same size and form, and they terminate in similar clusters of sessile sporangia. The best one is shown in Pl. XVII fig. 8. Its form cannot be made out with full certainty, but seems to be as illustrated in the drawing text-fig. 12: There are four sporangia, arranged symmetrically on both sides of a common pedicel, and attached to the widened end of the latter. Two of them are pendant, two others nearly horizontal. As seen in the illustrations, there is also some kind of structure forming a continuation upwards to the right, whereas the corresponding thing on the left is only indicated on the fossil; the nature of this structure is uncertain, but it may be a sporangium. The individual sporangium, when completely preserved, is oval, about 2×0.8 mm. Some of them are preserved as stone casts with a strong relief. On account of the scarcity of the material maceration could not be attempted. At certain places along the margin there are some indications of the cells of the sporangium wall.

On other slabs there are more specimens of the same kind of striated axes bearing thinner branches at a right angle or somewhat more erect. In one case (PA 293, Pl. XVII figs. 1—2) there are some leaf-like appendages connected with the main axis, in a place which must represent the base of a branch; as seen on the photograph there are four of these radiating linear organs, some of them divided.

Affinity. — As it has not been proved definitely that the various specimens now described belong to one and the same species, the discussion of its systematical position will chiefly be based upon the largest specimen (PA 288 *a*). The connection, however, is very probable, and the other specimens may also be taken into consideration when the necessary reservation is made.

The plant must have had a bipinnate or tripinnate frond of decidedly fern-like habit, recalling some of the primitive filicinean plants of the Upper Devonian, the Middle Devonian forms like *Aneurophyton germanicum* K. & W. being much more remote.

The arrangement of the fertile pinnules or branches has its nearest parallel in *Cephalopteris mirabilis* from the *Archaeopteris* flora of Bear Island (Nathorst 1902 p. 15, 1910 p. 278), with its opposite clusters of sporangia. It was mentioned above that in our new plant there is possibly an alternation of the pairs of fertile branchlets on both sides of the main branch; if verified, this fact would make the resemblance to *Cephalopteris* still more striking, but it should be emphasized that the observation is somewhat weakly founded. The division of the branches into a short fertile part and a long sterile one, which seems to be characteristic of *Cephalopteris*, is not found in our Spitsbergen plant, which, on the other side, is characterized by the differentiation between main branches bearing sporangiferous branchlets, and others bearing sterile ones. There are other differences, too, such as the number of sporangia in the clusters, and probably also the form of the individual sporangium.

Rhacophyton condrusorum Crépin (for full bibliography see Gilkinet 1922), from the upper part of Upper Devonian (Famennian) of Belgium, has a close resemblance to *Cephalopteris*, and several authors have even proclaimed them to be identical. After having been permitted, thanks to the kindness of Dr. F. Stockmans, to borrow and examine the fine material belonging to the *Musée Royal d'Histoire Naturelle* of Brussels, I have become convinced, however, that the two plants not only represent different species, but also belong to different genera. From our new plant the Belgian one differs above all in the arrangement of the sporangia: The latter are gathered in large clusters, the sporangiferous branches being repeatedly divided in a characteristic way; the clusters are not regularly placed opposite each other, and there are also other points of difference, which together are sufficient to make a generic distinction necessary.

Aphyllopteris delawarensis Arnold (1939 p. 292, Pl. X figs. 2—3), from the Upper Devonian of New York, looks very much like parts of the largest specimen (PA 288 *a*) described above. One may also compare the sterile 'pinnules' of our plant with *Hostimella crispa* Arnold (*l. c.* p. 290, Pl. III), like *A. delawarensis* a member of the *Archaeopteris* flora, but found in another locality (Pennsylvania). But, however interesting, both of them are based upon too fragmentary material to throw any light upon the question of the affinity of our plant.

Most probably we are dealing with a new genus, but the material is hardly sufficient to justify a new generic name now. Provisionally the species may be referred to *Cephalopteris*, which among the known genera must be the one to which it is most closely related. It may deserve a specific name, however, in order to make reference convenient, and provisionally I propose to call the plant *Cephalopteris(?) praecox* n. sp. — For diagnosis, see p. 193.

Fig. 13. Sulcate stem from Wijdefjorden: Beach profile between Andredalen and Forkdalen. — PA 289. Nat. size.

Fig. 13.

Independent of the uncertainty as to its systematical position, the plant is of great interest on account of its organization: It represents a type of fern-like plant perhaps even more advanced than any so far known from the Middle Devonian or the lower part of the Upper Devonian, being comparable in the first place with members of the *Archaeopteris* flora. Certainly it is unsafe to base conclusions on the morphology and level of organization of a single and incompletely known species alone, but with reservation as regards the insufficient material, one may state that in this case the paleobotanical evidence would decidedly suggest an Upper Devonian age of the beds. This question will be further discussed below (p. 163).

Sulcate stems.

Text-fig. 13.

From the same locality as the preceding species, but from a slightly different horizon, there are some fragments of fluted stems of considerable size, the best specimen being shown in text-fig. 13 (PA 289). It is 12 cm long, about 5 cm broad, with furrows like those of a calamite pith cast. There are no traces of transversal nodal lines, and it is quite probable that the plant has not been articulate. One may even have to take into account the possibility, however faint, that it belongs to the same plant as the striated rachises of the preceding species. On the other hand it is indistinguishable from PA 1171, text-fig. 8 (p. 41). As in the case of the latter, it is of no use at present applying any specific or even generic name. But it is worth bearing in mind that they belong to a type of fossil which is fairly common in the Upper Devonian, as the following quotations may show:

'*Calamites* (?) sp' Nathorst 1894 Pl. XIV fig. 4, and some other fossils from Bear Island, among them *Anarthrocanna Göppertii* Nathorst 1902 Pl. XIV fig. 4.

'Unbestimmbarer Stengelrest', Nathorst 1904 Pl. IV fig. 1, from Ellesmere Land.

'*Bornia transitionis*' Bureau 1911 Pl. II fig. 11 = 1913—14 Pl. I fig. 1, from Loire-Inférieure.

'Calamariale ou Protocalamariale' Ledoux-Marcelle 1927 Pl. III fig. 2, from the Frasnian of Belgium, and possibly also other Upper Devonian Belgian plants.

Pietzschia Schülleri Gothan 1927 *a* Pl. I fig. 1, from Wildenfels in Saxonia.

'Pseudocalamitoide Stengelreste' Gothan & F. Zimmermann 1932 Pl. XI, from Silesia (in the paper cited also reference to older records by Göppert); lower Upper Devonian.

'*Asterocalamites scrobiculatus*' Zalessky 1937 *a* Pl. I fig. 1, from the Urals, assumed to belong to the lower part of the Upper Devonian.

'*Bornia radiata*' Schmalhausen 1879 Pl. I fig. 1, and possibly '*Asterocalamites scrobiculatus*', Chachloff 1921 figs. 32—34, both of them from Siberia.

Quite possibly these fossils, in spite of habitual resemblance, may represent different plants, and most of them at all events are of unknown affinity. It is possible, although not certain, that some of them may belong to the *Articulatae*, whereas it should also be borne in mind that, among others, also the stem of an *Archaeosigillaria* in a certain state of decortication might form a fossil with a regularly fluted surface (cf. White 1907 and Walkom 1928). In the case of *Pietzschia Schülleri*, the anatomical structure is that of a fern. But at all events it is a fact worth noticing that such fossils have been found in so many cases in the Upper Devonian, even preponderatingly in the uppermost part of it.

From the Middle Devonian we have the 'Corduroy Plant' of the British Isles, found in Shetland, in the Thurso group of Caithness, and at Rhynie in Scotland, and in the Hangman grits of England (Evans & Stubblefield 1929 pp. 135, 149, and Seward 1931 p. 149, both with references to some of the older literature; see also Seward 1923 p. XCVIII). But the other records from the Middle Devonian are both few and dubious: Besides some obscure American specimens mentioned by Dawson (1862 pp. 308, 309, 1863 *a* pp. 108, 111), we have the specimen from Bohemia, referred by Potonié & Bernard (1904 p. 24, fig. 53) to *Asterocalamites scrobiculatus* (with a 'cf.') and revised by Kräusel & Weyland (1933, p. 34); it seems, however, to be very much more irregular in outline and in surface structure than the other specimens in question.

From the Lower Devonian no such specimens have been described at all (unless some of the British occurrences of the 'Corduroy Plant' are reckoned here).

Thus, the presence of these stems, although they must be designated as indeterminable, support from a paleobotanical point of view the idea of a relatively young age of the strata, to which they belong (see further p. 166).

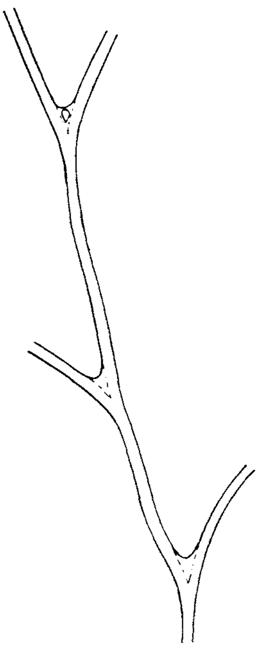

Fig. 14.

Fig. 14. *Hostimella* sp. (*Aphyllopteris*) from Wijdefjorden: South side of the bay at Forkdalen. Cf. Pl. XVIII fig. 4. — PA 286. Half nat. size.

5. South Side of Forkdalen (Fork Valley).

On both sides of Forkdalen plant remains have been met with in several places, both during Vogt's expedition in 1925 and in 1928. Nearly all of them, however, are indeterminable and of slight interest, and only a few of them will be mentioned in any detail here.

A. South Side of the Bay.

Along the beach on the south side of the bay at Forkdalen a dark grey shale crops out in a cliff, and in 1928 I collected several specimens of plant fossils here. The shale is very fine-grained, and the fossils are, as far as impressions go, fairly well preserved, although incomplete. Most of them can be referred to one species:

Hostimella (*Aphyllopteris*) sp. — The largest specimen is PA 286, of which a drawing is shown in text-fig. 14 (compare also Pl. XVIII fig. 4). It is 18 cm long, 3 mm broad, smooth and even, and branching three times at equal distances. The branching is clearly dichotomous, but in each case one of the branches is pushed aside, alternately to the left and to the right, a distinct, but somewhat flexuose main axis thus being formed, with branches in one plane. In the branch angles there is a kind of webbing in the form of a tissue connecting the axes (Pl. XVIII fig. 4); but at least the main axis may be seen with distinct outlines and unaltered breadth from the very point of division, independent of this tissue. In the latter there is a large 'axillary bud', somewhat on the side of the lateral branch and partly covering its inner margin. It has an elongate oval form.

PA 274 (Pl. XVIII fig. 8) is a somewhat thicker axis (4 mm). In its upper end is seen the beginning of a branching, with a well developed axillary bud resembling those of the former specimen. Somewhat further down it has a dilatation with a peculiar scar, which in all probability has been left by a broken branch and its axillary bud; evidently the branch has happened to lie not in the bedding plane, but pressed on top of the axis.

PA 287 (Pl. XVIII fig. 1) probably also belongs to the same species, although the mode of branching is slightly different. It divides three times. The lowermost branching is quite incomplete. The next one is very wide-angled, at more than 90°, and the two parts are equal in size and equally much diverging from the direction of the main axis below. In the uppermost branching the angle is acute and one of the divisions lateral in relation to the other. In the branch angles there are large axillary tubercles like those described above (from PA 286), and there is also a distinct webbing, particularly well developed in the wide-angled branching. The lower part of the axis is 5 mm broad. — The fossil is remarkable for having a number of scars or tubercles, arranged rather regularly along the middle of the impression of the axis and at equal distances (which are about twice the diameter of the axis). Some of them are better seen on the counterpart of the fossil, PA 277 (Pl. XVIII figs. 2—3). Each tubercle is about 1 mm in diameter, and more or less regularly circular; most of them are covered with a well-defined layer of carbonized matter. The nature of these structures could not easily be ascertained by this specimen. The regularity with which they are arranged on the axis might be regarded as something very near a proof of their belonging to the plant as some unknown kind of organ, instead of being foreign organisms which have settled on the surface. Nevertheless the latter explanation is most probably the correct one, as vill be evident from a comparison with another specimen:

PA 274 *b* (Pl. XVIII figs. 5—7) is a small fragment of an axis, 3.7 cm long, 2 mm broad, giving off a lateral branch with an axillary tubercle. Also this axis bears structures resembling those just described, and arranged along the median line of the impression, although at shorter and somewhat irregular distances. In this case they quite distinctly show the form of *Spirorbis* (Pl. XVIII fig. 7). There is scarcely any doubt that this is also the explanation of the similar structures found on the preceding specimen, in spite of the surprising regularity of their arrangement there (as regards *Spirorbis*, cf. p. 41).

Maceration was in vain attempted from PA 287, PA 274 *b*, and from a specimen not described (PA 1191).

It is quite likely that the specimens of *Hostimella* here described belong to one and the same species. They are more or less of the same size, and within a certain range of variation the mode of ramification is the same. They resemble specimens described from other localities, above all one from Cromarty (Lang 1925 Pl. II fig. 37). Our specimens, however, are characterized by their exceptionally large axillary tubercles of an elongate oval shape, and by the 'webbing' in the branch angles, a feature in which they seem to differ from similar shoot-systems known from other localities, and which make them so recognizable that one might be justified in describing them as a new species. As, however, it may be difficult to ascertain from the present material to what degree these structures, as now seen in the fossils, have been influenced by the process of fossilization, it may be better to desist from introducing a new name on this occasion.

B. Southern Branch of Forkdalen.

Some samples were collected in 1928 on the eastern side of the southern branch of the valley, in débris from the lowest part of dark shales above red sandstone. Together with poor fish remains they contained a number of fragments of plants, of which only one type is of some interest:

Striated axes with opposite or verticillate lateral organs (PA 469, Pl. XVIII figs. 9—10). — There are a number of straight stems, up to 5 mm broad (in one case 11 mm), the longest one being 7 cm long. They have a coarse striation, caused by some deep longitudinal furrows separated by rounded ridges. The furrows evidently correspond to strands of some kind. These stems would have been entirely indeterminable if examination and photographing in xylol had not revealed some further details, particularly in one axis, seen on the left-hand side of Pl. XVIII fig. 9, cf. fig. 10. The strands, or furrows, are not so regular in this specimen as in the others, but evidently it is of the same species. It bears lateral branches or foliar organs, of which the bases only are left. They are visible along the margin of the axis as acute triangular projections, somewhat directed upwards. In one case at least they are seen to occur in pairs (or verticils?) nearly, but not entirely, opposite on both sides of the axis. In the case shown in Pl. XVIII fig. 10 there is a strip of tissue going upwards to the left and looking very much as if it belonged there as an organ of the plant. If it really does belong to the plant, however, it is probable that it originally is not a lateral organ, but a part of the axis, with some strands, which has been split off from the rest of the axis through natural maceration. At all events it does not throw any light upon the nature of the lateral organs in question. As regards the latter the specimens really give no clue. — It seems as if the strands, in the places bearing the lateral organs, branch and anastomose so that a node is formed with regular alternation of the strands. This is seen fairly well in the middle of Pl. XVIII fig. 10, but there are also indications of the same arrangement in other cases.

The small axis just below the middle of Pl. XVIII fig. 9 may belong to the same species. It has two subopposite lateral ramifications, which are about as strong as the main axis.

Although indeterminable at present our fossil is of some interest on account of the comparisons which it suggests. If the lateral organs were not known (and as a matter of fact, they easily escape notice), these striated axes would be indistinguishable from those which Gothan & F. Zimmermann (1932 p. 121, Pl. XIII fig. 1) described from the Upper Devonian of Liebichau under the name of '*Pseudocalamitoide Stengelreste*'. The resemblance is particularly striking when they are examined dry, but it is also visible in the photograph reproduced in our Pl. XVII fig. 9, which shows the fossil immersed in xylol.

However, it is the lateral processes which make it somewhat more than a plain striated axis. Our fossil bears considerable resemblance to the specimens which Nathorst (1894 Pl. I, particularly fig. 3) described under cautious reference to *Psilophyton robustius* Daws. (*Loganiella canadensis* Stolley, compare Kräusel & Weyland 1930 p. 43 and 1932 p. 405, and Stockmans 1940 p. 74). It has also some features in common with the sterile parts of *Brøggeria norvegica* Nath. from Nordfjord (*e. g.* Nathorst 1915 Pl. III fig. 6), a species which Nathorst (*l. c.* p. 21) himself also compared with *Ps. robustius.* — In a further discussion of these plants account will have to be taken of some which have been referred to *Rhachiopteris* Dawson (1862 p. 323, non Williamson 1874 p. 677), particularly *R. pinnata* Dawson (*l. c.* Pl. XVI fig. 60), from the Marcellus shale (Middle Devonian) of New York, and var. *angustipinna* White (1905 p. 50, Pl. IV figs. 1—3), from Perry, Maine.

Specimens of a similar type of plant have been found in some of the Norwegian Devonian localities, but they have not yet been described or sufficiently examined. During my expedition to Spitsbergen in 1939 I also found more material on the west side of Billefjorden. It would be of no use to discuss at any length the few specimens described above, before it is possible to take into account also this additional material.

Preliminarily it may be stated that this type of plant particularly seems to belong to the Middle Devonian, but also to the upper parts of the Lower Devonian.

6. Various Localities from Purpurdalen (Purple Valley) Southwards.

In the Devonian on the west side of the inner half of Wijdefjorden, plant remains have been met with in many places (during Vogt's expedition in 1928), but nearly all of them are indeterminable, chiefly consisting of 'chaff', short fragments of thin, naked axes. Axillary tubercles are found in numerous cases, but never of the large, elongate form described above from Forkdalen (p. 55). Some of the specimens may be rather remarkable, particularly those from the beach profile south of Sjettedalen (Sixth Valley), among which there are some long straight stalks of a very characteristic appearance, somewhat resembling *Taeniocrada*.

Along the ridge on the north side of Gråkammen and almost to the summit I found plant remains in many horizons, but all of them of the sort of indeterminable fragments which are so common in the Lower and Middle Devonian. In the uppermost locality there occurred, together with the 'chaff', some broader axes, up to 1 cm broad, some of them preserved as stone casts.

Among the specimens from the vast area of the inner part of Wijdefjorden only the following two deserve a more detailed description and illustration:

Hostimella sp. (PA 256, Pl. XVIII fig. 13), from beach profile (Hor. 8) between Purpurdalen and Sjettedalen. — The specimen is an indistinct impression of an axis, 11 cm long, 3 mm thick, flexuose, a lateral branch, which is nearly as thick as the pseudomonopodial main axis, being given off at each of the four bends. There are well developed axillary tubercles; as seen on Pl. XVIII fig. 13, which shows the upper part of the specimen, at least one of them being very clearly defined and characterized by its circular form. — This *Hostimella* is of the type common in the Lower and Middle Devonian, and although the axillary tubercle is rather remarkable it does not present any distinguishing feature of great value.

Psilophyton sp. (PA 298, Pl. XVIII figs. 11—12), from south of Simledalen at Austfjorden. — The specimen was found through the splitting of a very hard nodule. It is a bit of a straight axis, about 3 mm broad, bearing thorns, one of which is 4 mm long. They have the form characteristic of *Psilophyton*, but a specific determination is impossible.

The Devonian area of the inner part of Wijdefjorden is connected continuously with that on the north side of Isfjorden, particularly from Vestfjorden (Wijdefjorden) to Dicksonfjorden. However, in the green or red shales and sandstones of the Wood Bay series prevailing here, plant fossils are rare, and those which have been found, have been very poorly preserved. In 1924, as a member of Hoel's expedition, I investigated the east side of Dicksonfjorden and, in company with Johannes Lid and Fridtjof Isachsen, made a crossing to Vestfjorden (cf. Lid 1929), but did not find any determinable plant fossils, only 'chaff' in several places. It may be deserving of note that among such indeterminable fragments of naked axes, found in the cliff just north of the hut at Hugindalen (Hugin Valley, Dicksonfjorden), there were examples of branched ones with axillary tubercles (cf. p. 171).

III. Devonian Flora of West Side of Billefjorden (Klaas Billen Bay).

The Devonian is represented along the western shore of Billefjorden, between Skansbukta (Skans Bay) and Mimerbukta (Mimer Bay), by some narrow profiles and outcrops along the sea, at some places also a little further inland in the valleys (cf. Nathorst 1910 p. 312); in the closest proximity to Mimerdalen, however, the Devonian is lacking. It was in the southernmost part of this area, some (3—4) kilometers north of Skansbukta, that Nathorst in the year 1882 discovered the first plant fossils of Devonian age found in Spitsbergen.

Vogt's expedition in 1925 spent three days in examining these strata (Vogt 1926 p. 198), making collections at several places. All plants of any interest were either from a "profile between First Valley and Second Valley", or from one "on the south side of Second Valley", the valleys being reckoned northwards from Skansbukta. The Second Valley is the larger. Between them stands the cairn erected by Nordenskiöld, the astronomical position of which he determined (cf. Nathorst 1910 p. 312, fig. 30).

Some of the specimens collected by Vogt's expedition were of new and remarkable forms. On the other hand, no specimens were found of the species which Nathorst (1894) figured in the description of his material from 1882 (Pl. I figs. 1—3 and 12). The latter specimens, belonging to the *Riksmuseet*, Stockholm, have most kindly been placed at my disposal by Professor Halle for a re-examination. However, the collections brought home by the expedition in 1939 comprised also some more specimens of these species, and although it is not certain that any additional knowledge is to be gained, further remarks on them had better be postponed until the new material has been prepared and examined. With regard to Nathorst's Pl. I fig. 12, *Cyclopteris* sp., see also p. 93 (*Platyphyllum* sp.).

Hostimella strictissima n. sp.

Pl. XIX figs. 1—2; Pl. XX figs. 1—4.

Locality, material. — The species is represented by a considerable number of impressions on at least 4 slabs of a hard grey shale, containing numerous minute grains of mica. It was collected in the profile between First Valley and Second Valley. The application of warm hydrochloric acid cleared the fossils and made them much more distinct.

Description. — The specimen best showing the mode of ramification, is PA 257, Pl. XIX figs. 1—2. It is a branch-system with a zigzag main axis giving off lateral branches at nearly a right angle and at regular intervals of somewhat increasing length. Evidently the ramification has originally been dichotomous; but the lateral branches are thinner than the main axis, which is 2 mm thick in the lower part of the specimen. Although at first glance the whole system gives the impression of having been flat, with all branches lying in one plane, a closer study shows that this is not the case, the arrangement originally having been spiral: The first branch from below lies in the bedding plane of the shale. The next one is put forth from the upper (exposed) side of the main axis. At the third one, the basal part, which is distinctly connected with the main axis, has a downward direction and could be traced down into the matrix for a distance of 6 mm, whereas the branch which on the photograph is seen further out to the right, really has another direction, lying in the bedding plane, and is of doubtful connection with this fossil. — As visible on the figure, all branches are long and slender, and straight nearly to the top; only in the thin ends they may be somewhat curved. They bear small secondary branches, which are only partly preserved, and which are given off at right angles or approximately so; they do not influence the direction of the main branch. There are no traces of thorns, hairs, or other emergences, nor of axillary tubercles; but there is another characteristic feature: The axis, which in this specimen is mostly preserved in the form of a terete cast covered with some coaly matter, is nodose, having constrictions at regular intervals about equal to the diameter of the axis, and mostly made distinct by having a thicker cover of carbonized matter than the convex parts between them.

The counterpart of the lower portion of this axis is preserved (PA 1180, Pl. XX fig. 2). Here the articulation is seen quite exceptionally well.

Some other axes are shown in Pl. XX fig. 1 (PA 1180), all of them very long, slender, and straight. One of them has at least three lateral branches at angles of about 45°, another one, on the right-hand side, gives off a branch at a right angle without any alteration in the direction of the main axis. The same nodosity as in the former specimens is seen distinctly at some places.

Other and more fragmentary specimens exhibit the same characters, the nodular articulation being observable in several cases, but not constantly. Circinate tips do not seem to occur, nor axillary tubercles.

As to the anatomical structure, only very few hints could be obtained. Some of the axes have distinct traces of a central strand, one of the best instances being illustrated in Pl. XX figs. 3—4 (PA 257). The strand consists of very long cells. There is no pith to be seen, nor is it likely, from the form of the strand, that there has been any, or at least not more than a very small one. The strand itself does not show any peculiarities that could be regarded as having any connection with the said nodosity of the fossil, but it may be mentioned that across the space between the strand and the margin there may sometimes be seen transversal black lines at regular distances, which correspond to the length of the nodes; between these lines the margin of the fossil sometimes curves slightly outwards. On the photograph (Pl. XIX, fig. 2) the lines look like diaphragms dividing the axis, but they may just as well be only transversal bands of tissue in the cortical part of the axis. At all events they indicate that the nodular articulation, as now seen on the fossil, may correspond to some anatomical feature in the living plant. As regards this point, cf. p. 20 and below.

Affinity.. — These fossils have certain characteristic features in which they differ from most specimens of *Hostimella* known from other localities: The slender, straight axes, the spiral arrangement of the branches, evidently a firm texture, and the lack of axillary tubercles and of any trace of thorns; one may also mention the open branch angles, which are often 90°. As a negative character of some interest it may be pointed out that these naked axes do not occur in association with any kind of spinous ones.

It is difficult at present to form an opinion of the systematical bearings of the nodular articulation. A similar feature is found in several fossils described by Carpentier (1920 Pl. VII figs. 2 and 4, referred to *Ps. princeps*; 1929 Pl. I fig. 3 and others, compared with *Asteroxylon elberfeldense*; 1931 Pl. I, several figures, ditto). Like our plant some of these specimens seem to have a kind of primary articulation; but they are too fragmentary to make a determination possible.

It is of some interest to recall certain features of *Asteroxylon elberfeldense*, pointed out by Kräusel & Weyland: The *Hostimella*-shoots of this plant may have 'Querriefen', which the authors at first (1923 pp. 159, 161, 163, Pl. VI fig. 2) supposed might possibly correspond to an articulation of the pith of the living plant, but later on (1926 p. 118) found to be cracks which had been formed secondarily and which had become filled with matrix during fossilization. They were only found in a few specimens out of a great number (cf. also Thomson 1940 p. 7 and Arnold 1934).

It is possible that the articulation of our plant should be interpreted in a similar way. Certainly the transversal lines cannot have any connection with cracks in the pith, because the plant probably had no pith; but they might be thought to have been formed secondarily in the outer parts of the plant, after its death. It does not seem probable, however, that the feature is entirely accidental. Even if it is lacking in many specimens, or parts of specimens, it is actually found in a considerable number of the specimens examined, and when present it is always very regular. The 'nodes' are not simply transversal lines of carbonaceous matter, but constrictions separating convex parts of the axis, and they have no resemblance whatever for instance to the cubic cracking of decaying wood; moreover, if they had represented cracks, they should have been filled with matrix. Therefore, although it may be difficult to make use of the articulation for the characterization and recognition of the species, because it is not always visible on the fossil, I do believe that it is really due to a certain anatomical structure in the living plant.

In its general form our fossil bears a certain degree of resemblance to specimens referred to *Psilophyton Goldschmidtii*, both from Røragen (*e.g.* Halle 1916 Pl. II fig. 7) and elsewhere (*e. g.* from Willwerath, Kräusel & Weyland 1930 Pl. XIV fig. 5); but the characters summarized above are no doubt outside the range of variation of that species, points of importance being the length and slenderness of the axes, the straight branches, the spiral arrangement of the latter, the wide branch angles, and the entire lack of thorns. Even if the nodosity is left out of consideration, the plant seems to differ from all branch-systems which have been found in the Røragen flora, whether referable to *Ps. Goldschmidtii* or not.

In consequence of these facts and considerations I find it advisable to describe the plant as a new species of *Hostimella* under the name of *H. strictissima*, n. sp. — For diagnosis see p. 192.

Bucheria longa n. sp.

Pl. XIX figs. 8—9.

Locality, material. — Found only in a few specimens, most of them very incomplete, on a single slab of hard shale (PA 265), labelled: "Profile on the south side of Second Valley. Plant Horizon 2 *a.*" — At first the impressions were hardly visible, but after mechanical preparation and treatment with hydrofluoric acid they could be studied with some profit. Even then, however, the state of preservation must be characterized as very unsatisfactory.

Description. — The best specimen (Pl. XIX figs. 8—9) is an axis, about 10 cm long and only 1 mm wide, nearly straight. It bears, in its entire length, numerous lateral organs in spiral arrangement. They seem to be about 5—6 mm long, which is enough to bring the upper end of each of them up to or slightly above the base of the next one on the same side. The organ has a broad leaf-like part, oval or wedge-formed, widest at a point near the top (at least 3 mm wide); from here it tapers abruptly upwards, but slowly downwards. In several cases the upper margin is seen as a slightly curved line (Pl. XIX fig. 9).

The base seems to be constricted into a short pedicel projecting horizontally or even in a slightly downward direction from the main axis, whereas the upper, and much larger, portion is erect and nearly parallel to it. In its present state the organ does not give the impression of having been thick or cylindrical, but a certain rigidity is probable, to judge by the way in which they spread in various levels and directions within the matrix without having become completely flattened. In a few cases there are seen indications of delicate veins (in the upper part of Pl. XIX fig. 9). Of the organic tissue only traces are left, and nothing that could be interpreted as remains of spore-masses.

A couple of other specimens on the same slab are in a much poorer condition than those shown in the illustrations and do not reveal any further details.

Affinity. — In the Devonian flora of Spitsbergen nothing is found to give any clue to the affinity of this fossil. The axes themselves, in their dimension and in their long, slender, and nearly straight form, bear a certain resemblance to those described above as *Hostimella strictissima*, n. sp., apart from the entire lack of articulation. The plants are from slightly different localities and horizons, but in spite of that a specific identity does not seem to be entirely out of the question. But that is a mere possibility, the resemblance of such axes in a few external characters being of course quite inadequate as a proof of relationship.

In a discussion of the systematical position of the plant, it is a grave difficulty that we have no reliable evidence as to the nature of its lateral organs. At first glance they look like sporangia, or rather like sporangiophores, and the only fossils with which the plant may be compared, have either been proved fertile, or are at least on good grounds supposed to be so. On the other hand, if they were really sterile leaves they would form a new and rather surprising feature in the early Devonian flora. It is therefore by far the more likely that they have something to do with the organs of reproduction. But a certain reservation must still be made as to this point.

Among the fossils described from other parts of the world the following suggest themselves for comparison in this connection:

1. *Bucheria ovata* Dorf (1933), from Beartooth Butte, Wyoming. According to Dorf's description and excellent illustrations (unfortunately none of them are in exactly natural size) the plant has a bilateral symmetry, the sporangia, or rather organs supposed to be sporangia, being arranged in two opposite or subopposite rows. The form of the individual sporangium is also different from the lateral organs of our plant. But apart from these facts, which are important enough, the long dense spikes of the two plants resemble each other a good deal and, provided there is no essential difference in the nature of the lateral

organs in both cases, it would be very probable that they are rather closely related to each other.

2. *Bucheria* sp. from Willwerath, described by Kräusel & Weyland (1930 p. 75) under the name of *? Dawsonites* sp. — Dorf (1933 p. 246) pointed out that it should rather be referred to *Bucheria*, and this view has been adopted by Halle (1936 p. 22) and others. Also here the organs resembling sporangia, are placed in two lateral series, possibly with a third median series between them.

3. *Bucheria (?) pendula* Stockmans (1940 p. 70, Pl. III figs. 9—9 *a*), from the Lower Devonian of Belgium. — As explicitly said by the author, it is doubtful whether this species, which certainly is very interesting, should be referred to the genus *Bucheria*; no doubt it will have to be removed from it when further details about the clusters of sporangia and their mode of attachment have become known. In certain features, despite its smaller size, it recalls *Dawsonites Ellenae*.

4. *Distichophytum mucronatum* Mägdefrau (1938 p. 247, Pl. II fig. 4), from the Lower Devonian of the Harz. — According to the diagnosis, which is based upon a single specimen in a very fragmentary state of preservation, the sporangia also in this species are arranged in two lateral rows. Evidently the author has not been aware of the description of *Bucheria*, which had been published not very long before the description of *Distichophytum*; otherwise the latter genus would probably not have been created, the difference between the two plants chiefly lying in the form of the sporangia, that is, in a character of no more than specific value: They are mucronate in the one case, blunt in the other, as expressed in the respective specific epithets. In both cases, however, they are distichously arranged. — In my opinion, the German plant will have to be named *Bucheria mucronata* (Mägdefrau) n. comb.

5. Halle (1911 p. 22, Pl. I figs. 10—11) described a small fragment of a fertile axis from the Devonian of the Falkland Islands, comparing it with *Zosterophyllum* (which at that time was very incompletely known), although not wanting to refer it to that genus. It is evidently a unilateral organ, with one series of small rounded sporangia on short and thick stalks; if the unilateral arrangement is characteristic of the species, it differs from *Bucheria*, to which genus one would otherwise refer it.

6. *Zosterophyllum*. — The sporangia are spirally arranged, and in *Z. australianum*, as described by Lang & Cookson (1930) and Cookson (1935), as well as in *Z. rhenanum* K. & W. (1935 *b*), they form dense spikes morphologically resembling the one from Billefjorden. The individual sporangium has a very characteristic form, with tangential dehiscence along the upper margin, and it is borne on a little pedicel. The few details discernible in the Spitsbergen plant indicate similar structures here. On the other hand, our plant does not show any traces of the peculiar mode of branching, which is so characteristic of the type species of *Zosterophyllum* (*Z. myretonianum* Penh.), and which

is also represented in *Z. australianum* and in the sterile specimens in the Downtonian flora of Frænkelryggen, as described above (p. 17); but this feature is lacking in *Z. rhenanum.*

Among the genera known, there is none with which our plant has more points in common than with *Zosterophyllum.* But it is difficult to believe that it really belongs to that genus, and objections may be raised against burdening a natural genus so well known, with a dubious and incomplete fragment like the one in question.

On the other hand, *Bucheria* may be used as the name of an organ genus (or perhaps form genus), comprising spike-like fructifications with laterally arranged sporangia (?), sessile or on short stalks. In the species known so far, the arrangement is distichous, in contrast to the spiral arrangement in our plant, which also differs from the others in the form of the lateral organs. It may, however, be justifiable to give the diagnosis of *Bucheria* the necessary extension, comprising not only bilateral organs, and to refer our plant provisionally to it.

In spite of its poor preservation our plant has shown so many details that it can be identified, if more specimens should be found, and for this reason and in order to facilitate reference, it may deserve a specific name of its own. I propose to call it *Bucheria longa* n. sp. — For diagnosis, see p. 192.

Psilophyton sp.

Pl. XIX figs. 4—5.

The only specimen, PA 260 (Pl. XIX figs. 4—5), from the profile between First Valley and Second Valley, is a very poorly preserved impression of a branched axis, 8.5 cm long. The main stem, which has a bend in the middle, is about 3 mm broad, and gives off three lateral branches at angles of about 45°. The branches are a little narrower than the main axis, and at least one of them is divided. An axillary tubercle, although rather small and indistinct, is present at the lowermost branching. The surface is smooth, but along the margin are seen thorns, which are well preserved only in a few cases, both on the main axis and on the branches.

Affinity. — In the case of spinous axial systems like the present one it is difficult to decide whether they belong to the genus *Psilophyton* or have formed parts of plants of the *Thursophyton-Asteroxylon* type. Either is possible, but the fragment described above may safely, at least provisionally, be referred to *Psilophyton.* It does not show any of the characteristic features of *Ps. Goldschmidtii.* On the other hand, the slight difference in thickness between its axis and branches, the spines of the latter, and the acute branch angles, make the plant indistinguishable from Canadian specimens of *Ps. princeps.* A specific determination, however, would be unreliable on so scanty a material.

Hostimella spp.

Pl. XIX figs. 3, 6—7.

Among the various specimens of axes of psilophytes, which Vogt's expedition in 1925 brought home from the western side of Billefjorden, several types are represented. There are thin ones, with circinate tips (PA 264, 299, from Division 3 *c* in the profile on the south side of Second Valley). And there are specimens (from Division 2 *a* in the same profile) which resemble those described by Nathorst (1894 Pl. I fig. 6). The affinity of these specimens cannot be discussed with any profit on the basis of the present material, but will have to be considered in connection with the collections from 1939.

The following two specimens, however, deserve special mention:

PA 1106, Pl. XIX fig. 3, is a naked axis which gives the impression of having been rigid and firm. It has an exceptionally well developed axillary tubercle, which is remarkable for being decurrent in the branch angle. From the profile between First Valley and Second Valley.

PA 1164, Pl. XIX figs. 6—7, is also a naked axis with a large, oval axillary tubercle. From Division 2 of the profile on the south side of Second Valley.

Barinophyton sp.

Pl. XX figs. 5—8.

Locality, material. — In Nathorst's collections from the west side of Billefjorden (1882) there is a remarkable fossil which he has not figured or described, probably because it was found to be too poorly preserved. It deserves, however, to be published as yet another example of the abundance of plant forms in the Devonian flora.

It is found, together with some indeterminable plant fragments of a reddish colour, in a greenish grey shale containing considerable amounts of mica.

Description. — The fossil is a fragment, 3 cm long, consisting of an axis, nearly straight, bearing a great number of lateral organs. The latter are best seen along one side of the axis (the right-hand one), giving the impression of having been arranged in one row. As seen here, they have the form of scales, evidently rather thick, about 2 mm long, which from decurrent bases curve out so that the tips may point slightly downwards. The vertical distance between these scales is less than their length. It cannot be made out whether they have been sterile leaves, or have borne sporangia. — On the other side of the axis, opposite to these distinct scales, there are also, in some places, seen similar organs, although here they generally appear only as thin linear leaves pointing obliquely upwards. It is quite possible that the difference is due only to the different position in the matrix, so that there really have been two lateral rows of equal, scale-like organs; but one should not exclude the possibility of there having been only one such row, and that the opposite side of the axis has borne a somewhat different kind of simple appendages. A spiral arrangement is less probable.

Affinity. — With its strong axis and somewhat recurved scales, probably arranged in one or perhaps two rows, this fossil strongly recalls the two genera *Pectinophyton* and *Barinophyton*, which Arnold (1939) has assumed to be identical. *Pectinophyton* was first described from the Middle Devonian of Nordfjord (Høeg 1935), and has also been recorded from the Middle Devonian of Elberfeld (Kräusel & Weyland 1938); *Barinophyton* was first instituted on the basis of Upper Devonian material from Perry, Maine (White 1905), and has later been studied in detail on specimens from the upper part of the Upper Devonian of New York by Arnold (1939). Probably there are also more occurrences.

Our specimen cannot with certainty be referred to any of the specimens described, but it can scarcely be doubted that it belongs to the same group.

The interest attached to this fossil, in spite of its poor preservation, partly lies also in its resemblance to some objects which Dawson (1871 *a* p. 42, Pl. XIII fig. 154, and 1882 p. 104, Pl. XXIV fig. 22) described from Gaspé and Campbellton. But at present we can do no more than direct attention to this resemblance, the bearing of which cannot be judged of on the basis of the illustrations alone.

IV. Devonian Flora of Mimerdalen (Mimer Valley).

Mimerdalen comprises the youngest parts of the Devonian of the whole of Spitsbergen, although older beds also occur in this valley. The stratigraphy, which is rather complicated, had been studied and described by the various geologists visiting this valley, the first one being Nathorst in the year 1882 (Nathorst, Stensiö, Vogt). The highest horizons are found in the inner part of the valley, in a syncline with its axis approximately transversal to the valley.

As mentioned in the preface (p. 7), plant fossils were first discovered by Nathorst; later both Stensiö's and Vogt's expeditions have made valuable collections. The material brought home by Vogt's two expeditions (1925 and 1928) was particularly comprehensive and interesting; it has not been described before, and forms the main basis of the following descriptions.

During the expedition in 1925, Professor Vogt and his two companions, Anatol Heintz and Fridtjov Isachsen, found plant remains in many places in the valley; even in cases when they were indeterminable, they were often very remarkable forms. The most important localities were the famous Fiskekløfta (Fish Ravine, or Fiskeklyftan, as called by Nathorst), various horizons in a profile from Estheriahaugen (Estheria Hill) to Torfjellet, and at the glacier in Munindalen (Munin Valley). The best specimens were from a locality which will here be called Plantekløfta, which forms a small ravine in the east side of the plateau between Fiskekløfta and Torfjellet. Here, for instance, *Hyenia* was found, and also very good specimens of *Bergeria.*

During the expedition in 1928 Vogt, Strand, and I, with assistants, spent some weeks in September in Mimerdalen. The summer had been extraordinarily hot, at least in the central parts of Spitsbergen, and in the latter part of the summer season the weather was dry and cool; as a consequence, the conditions on our arrival were unusually favourable, the rivers being so small that they scarcely formed any obstacle at all. One of the chief advantages was that the canyons above Fiskekløfta could be investigated easily, even in places which are impassable most years. I spent some days there collecting plant fossils. But soon the rain began, and the streams increased with astonishing rapidity from hour to hour. A pile of plant fossils, which I had been forced to leave behind till later in the western canyon above Fiskekløfta, could no longer be reached along the river, and time did not allow of further attempts to bring it home; this was most unfortunate, for it included some good specimens of *Bergeria.*

Apart from one day on Estheriahaugen, the remaining days were spent on the southeastern side of Torfjellet. As mentioned above, the expedition in 1925 had discovered *Hyenia* in the locality called Plantekløfta; more specimens of the same species were now obtained. Finally I happened to find an occurrence of plants in a horizon of about the same age somewhat further north along the sloping side of the terrace at the foot of Torfjellet. This occurrence, which I have called Planteryggen (Plant Ridge), yielded an abundance of interesting fossils. The flora was not rich in species, but those found were new and remarkable (*Enigmophyton* and *Svalbardia*, for example). After some days of eager collection, however, the snow came for good (on September 8th), making further work in this elevation impossible.

A. Non-petrified Specimens.

Psilophyte (?)

Pl. LVI fig. 12.

In some samples of grey shale, labelled (by Strand): "In the uppermost part of the *e*-layer, east side of river to the east of Estheria Hill", there are remains of thin leafless axes, sometimes bifurcating, but most of them quite short and unbranched ('chaff'). One specimen, however, is somewhat more complete (PA 1101, Pl. LVI fig. 12). It is about 5 cm long, straight, but bifurcating twice, very slender and attenuating upwards, devoid of any kind of appendages. As seen on the photograph, there seems to be a body resembling a sporangium attached to one of the tips; but that is only some little plant fragment which has happened to be deposited there. — The fossil has the appearance of a psilophyte, but nothing more definite can be said at present about its systematical position.

It may be added that these beds in Estheriahaugen represent a stratigraphical horizon somewhat below that of the inner part of Mimerdalen, with Fiskekløfta, Planteryggen, and the other localities, which have yielded all the fossils described below (except the *Platyphyllum*-like fragment PA 1151, p. 116).

Svalbardia polymorpha n. gen. & sp.

Pl. XX fig. 11; Pls. XXI—XXVI; Pl. XXVII figs. 1—3; Pls. XXVIII—XXX; Pl. XXXI figs. 1—9; text-fig. 15.

Locality, material. — Together with *Enigmophyton* and some lepidophytes this plant is the dominant component of the flora of Planteryggen. The various plant organs, stems, foliar parts, and sporangia, which are here regarded as belonging to one and the same species, were found in great abundance on slabs of a yellowish shaly sandstone. The impressions are mostly indistinct when dry, but when moistened, preferably with xylol, they often show up excellently against the matrix, the remains of organic matter making the outlines appear as distinct black lines.

The same species also occurs along the river above Fiskekløfta, particularly in the yellowish white shaly sandstone, but in a more fragmentary state.

The morphology of the plant, and particularly its mode of branching, varies a good deal, if regarded in detail, and the evidence as to the specific identity of the various specimens and the various organs may sometimes seem insufficient. But in spite of all diversity between the various parts, one gets the strong impression of having to deal with one species, and in the following description and discussion I shall attempt to show that this is the case.

Description. — The subterranean and basal parts of the plant are unknown, nor has it been possible to ascertain whether it has had any thick stem; I did not find any kind of fossil trunk which might have been thought to belong to the species. The parts preserved are a great number of branches and branch-systems.

The axes are slender and straight or gently curved. The longest one in the collection is 46 cm long (PA 320, text-fig. 15); it bears many

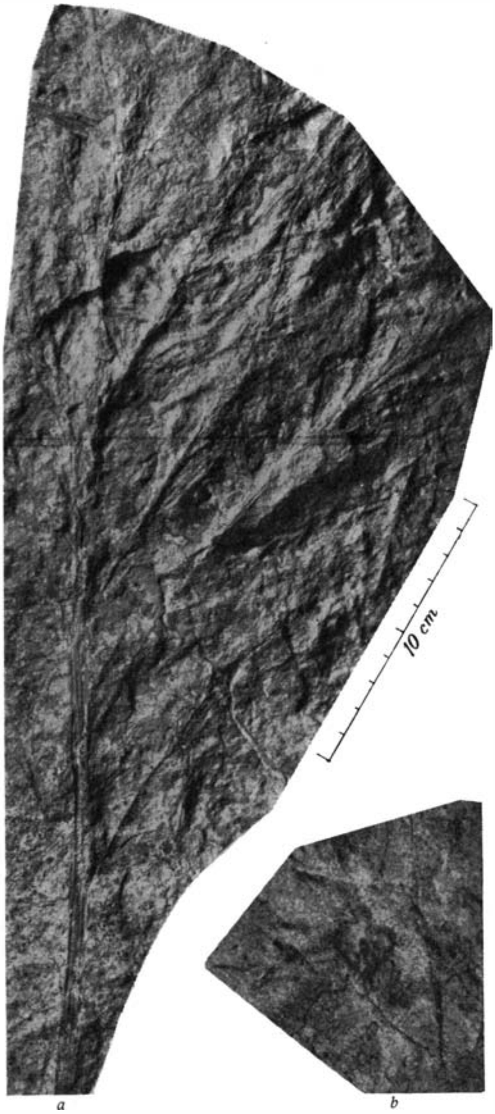

Fig. 15. *Svalbardia polymorpha* n. gen. & sp, from Mimerdalen: Planteryggen. Largest specimen, poorly preserved. Some of the upper branches are fertile, sporangia being shown (indistinctly) in fig. *b*. — PA 320. Reduced and ×2.5.

lateral branches, at acute angles, some of them with filiform 'leaves', others with sporangia (compare also p. 78), but these organs are better seen in other specimens than in this one, which is only a very indistinct impression. — The thickest axis which undoubtedly belongs to the species, is at least 1.5 cm thick (PA 1153, not figured); judging by this fact, and by the very slow tapering of all axes found, the plant may be assumed to have attained a height of a couple of meters, as a minimum.

The axes are smooth, entirely devoid of thorns and other appendages. The thicker ones nearly always have deep longitudinal furrows, or corresponding ridges, which must be assumed to represent strands going out into the branches, one into each; they increase in depth (respectively height) upwards, and then generally disappear suddenly, no doubt because they have left the main axis. Mostly, each internode has only one such furrow, rarely more.

Excepting the foliar organs the branching is, even in the upper parts of the axes, never dichotomous, but strictly lateral. In many cases the branches are approximately opposite (PA 347, Pl. XXI fig. 1; PA 1255, Pl. XXI fig. 4; PA 315, Pl. XXVII fig. 1, the horizontal plant in the middle of the figure). It is somewhat uncertain whether there have been more than two branches at each node; sometimes there are markings indicating that there may have been three or four, but the observations are not reliable. There is often a considerable vertical distance between the branches belonging to one pair, and in several cases they could hardly be considered as being opposite or subopposite. — The lateral branches are not arranged in one plane. Perhaps this may not be immediately evident from the illustrations, but it may be observed in some specimens where an axis lies along the edge of the slab, with branches both in the bedding plane of the slab, and on the sides of it. The arrangement is also indicated by the course of the strands and by the deep depressions which in some specimens mark the bases of branches. One such case is illustrated in Pl. XXI fig. 2 (PA 247), and another may be seen in Pl. XX fig. 11 (PA 314), a little below the middle of the figure. Although it sometimes looks as if such branches had been placed exactly at a right angle to those which are now found in the bedding plane, it is fairly certain that this was not always the case. — It is probably a matter of coincidence that in the specimens where the branches are most distinctly seen in opposite or subopposite pairs, the branch angles are generally widest. That may also be due to the fact that the wide angles make it easier to observe this arrangement than it is when the lateral branches are erect and follow the main axis for a long distance.

The branches may be sterile or sporangiferous.

The sterile branches divide freely. Generally there is a distinct main axis, visible nearly up to the top, and giving off lateral ramifications. The latter may have the appearance of secondary branches of the same type as the primary one, but they may also be different, being transformed into foliar organs, with transitional stages in the ultimate ramifications.

In some cases, which probably represent the end of one line of morphologic development, the foliar organs are decidedly leaf-like, widening from a slender petiole into a pinnule-like frond, wedge-shaped or fan-shaped, about 2.5 cm long, consisting of linear segments, which divide dichotomously two, three, or four times, rarely more, all the tops reaching about the same level (PA 308, Pl. XXVI figs. 1—2; PA 347, Pl. XXI fig. 3; PA 313, Pl. XXV figs. 3—4; PA 302, Pl. XXV fig. 2; PA 348, Pl. XXVIII fig. 1). Such leaves have parallel, bifurcating veins. In the broadest part of the leaf, just below a point of division, there may be as many as 6 veins; a greater number has not been observed with full certainty, but probably it does occur. The ultimate divisions seem to contain only one vein. — These leaves, or leaflets, are borne laterally on the thin branches, as seen in several of the figures just referred to, but they do not seem to be arranged in one plane. Often, but by no means always, they are divergent from the axis, and they have a noticeable tendency towards an arrangement in opposite pairs (PA 308, Pl. XXVI figs. 1—2, and others), although there are also exceptions to this rule (*e. g.* PA 347, Pl. XXI fig. 1).

The dichotomy of the leaf is often very regular, as is evident from the photographs, whereas in other cases it is more unequal (see, for instance, PA 347, Pl. XXI fig. 3, and PA 333, Pl. XXVIII fig. 4), the segments then being of different breadth and the thinner ones pushed aside so as to be lateral in relation to the others. In these cases a flat frond is generally not formed. All fragments are narrow, filiform, or at least appear to be so. In extreme examples of this kind the lateral organs and even the whole top of the axis seem to be transformed into such filaments (see, for instance, PA 311, Pl. XXVIII figs. 2—3, in which the plant has evidently been soft and flexuose). However, the difference from the leaf-like lateral organs is not so profound as it may appear at first sight; it may depend *(1)* upon the position of the organ on the plant, the most decidedly leaf-like ones being evidently found on the sides of proportionally thicker axes, *(2)* upon the age of the shoot when imbedded in the matrix, its state of wilting, decay, and so on, and *(3)* upon the state of preservation. There are fairly continuous series of transition, — compare, for instance, the following specimens:

PA 348, Pl. XXVIII fig. 1, in which the leaves on the left-hand side are cuneate (partly because the tops have been lost) and very distinctly different from the axis; further PA 308, Pl. XXVI figs. 1—2; PA 347, Pl. XXI fig. 1; PA 347, Pl. XXI fig. 3; PA 333, Pl. XXVIII fig. 4; PA 311, Pl. XXVIII figs. 2—3.

It was mentioned above that the lateral organs might be somewhat divergent from the axis. This is not, however, always the case. There is a feature worth mentioning in this connection, although it is of a somewhat uncertain bearing: Where the axis is strong in relation to the lateral organs, the latter may leave it at an open angle, but then rapidly curve towards it again, so as to be erect or appressed; in such cases there are generally no complete 'leaves', but only filaments, simple or sparingly divided. Among the many examples may be mentioned: PA 1255, Pl. XXI fig. 4; PA 347, Pl. XXI fig. 3; PA 315, Pl. XXVII fig. 1; PA 330, Pl. XXIX fig. 2. More rarely a similar feature is found in connection with slender axes: PA 335, Pl. XXIII. Very often one gets the impression that these small appendages represent the remains of 'leaves' which, in some way or other, have been worn off.

An extreme case, and a rather remarkable one, is PA 323, Pl. XXI fig. 6, in which some of the leaves are still fairly long and repeatedly divided, while others, as now preserved, are reduced to simple filaments, standing out at the base and then appressed to the axis. The fossil is rather poorly and incompletely preserved, and if found alone it would have been regarded as indeterminable, or perhaps a comparison with *Haspia devonia* K. & W. would have been suggested (cf. p. 186). But when finding it in this collection, one has no reason to doubt that it belongs to the same species as the other specimens described here.

As to the anatomical structure of the axial and foliar organs the material has little to tell. There is no cuticle left for maceration, nor any internal strands. When examined in incident light, traces of cell structure may be observed in many places. There has evidently been a continuous epidermal tissue. Mostly the longitudinal cell walls are preserved, exclusively or at least predominantly, as black parallel lines (an example is shown in Pl. XXVI fig. 6, PA 328); but it also happens that the transversal walls are visible, forming approximately isodiametrical cells. Stomata have not been observed with full certainty.

The fertile branches form panicles, of which several specimens are present in the collection, together with isolated sporangia.

The panicles are mostly 3—4 cm long, but probably they may attain at least twice that length. The central axis is usually straight or slightly curved (PA 306, Pl. XXVII figs. 2—3; PA 315, Pl. XXVII fig. 1; PA 335, Pl. XXIV). More rarely it is irregularly bent, but that is probably only a secondary change. The axis bears lateral branches, which decrease in length regularly but slowly upwards, those in the lower part usually measuring about 1 cm. Usually these branches, as seen on the fossil, are opposite, with only a slight vertical distance between the branches belonging to one pair. In most of the cases in which there seems to be a single, unpaired branch, the reason is probably that the other one is imbedded in the matrix instead of being exposed on the surface. The axis has a slight widening at the base of each pair. There is no reason whatever to believe that the whole system has been flat and bilateral, but, on the other hand, decisive observations on this point have not been possible. In no case has it been feasible with full certainty to observe more than two branches at a node, but it is very probable that there may have been three or four, not only because that would be in accordance with the conditions in the sterile region, but also because there seem in some cases to be indications of corresponding strands; specimens like those shown in Pl. XXIV (PA 335) would also be most easily understood in that way. As a general rule the branch leaves the axis at a right angle, although occasionally it may be erect or recurved. There is nothing to indicate that the sporangiferous branches have been flattened, like scales; they must have been terete or nearly so.

The sporangia apparently form a cluster on the upper side of the middle portion of each branch; there are none of them on the inner part, near the axis, nor on the distal part, which forms a sterile tip, often curved upwards. Originally the sporangiferous branch must have formed a dichotomous system; but a certain over-topping has taken place, so that there is now a lower part which is generally straight or regularly curved, and which may be traced more or less distinctly out to the sterile tip (see, *e. g.*, PA 322, Pl. XXX figs. 1—2; PA 306, Pl. XXVII figs. 2—3; PA 335, Pl. XXIX fig. 1). In cases when the main branch is seen to divide, there always seems to be a difference between the two parts; the upper one is shorter and repeatedly divided, and all its divisions seem to bear sporangia, while the lower part keeps its direction more or less unaltered. — The sporangia have been directed upwards from the branch bearing them, and when the panicle was pressed together from the sides, the result would be as now seen in most of the fossils, which more or less form longitudinal sections. In specimens so preserved one would not be able to observe if the lower part of the branch (the part which ends in a sterile tip) had been divided into several lying in one horizontal plane. But if that had been the case it would almost certainly have been observable in specimens more irregularly arranged on the shale. In a specimen like PA 329 (Pl. XXXI fig. 4) the sporangiferous branches, especially the one in the middle, is really seen from above, and here it is clear that no such ramification has taken place. Evidently, however, the arrangement is subject to a certain variability; thus, in a few cases there may be more than one sterile tip (PA 324, Pl. XXX fig. 6). At least in some instances this may be due to a pinnate ramification of the distal end of the sporangiferous branch (PA 335, Pl. XXIV).

Each sporangium is borne on a short pedicel. Some of them, probably only those in the most distal position, may be attached directly to the main (lower) part of the branch, the others to its various ramifications. In some cases it simply looks as if the pedicel was bifurcate. — The total number of sporangia on each branch of the panicle varies and can rarely be ascertained with full certainty; it may be as much as a dozen or more, but evidently also sometimes less.

The individual sporangium is pear-shaped or cylindrical, 1.5—2 mm long and 0.5—0.7 mm thick. It is either seen in a flattened condition on the shale, with a more or less complete cover of carbonaceous matter, or preserved as a stone-cast with a high relief elevated above the rock surface; in other cases it has been deposited at a right angle to the bedding of the rock and then split across, so that its circular outline is distinctly visible in a natural transversal section (PA 306, Pl. XXVII fig. 3, and others). The wall of the sporangium is very thin. When examined in a fairly strong magnification (*e. g.* × 12), the surface often appears to be longitudinally striated (PA 304, Pl. XXX fig. 7, and others).

The mode of dehiscence it not quite clear, the observations being somewhat contradictory. There is often a little apical split (as seen in several sporangia on Pl. XXXI fig. 2, PA 326, and in other cases); probably it is not accidental, but shows that the dehiscence starts at the top of the sporangium. The further development, however, is uncertain. In several cases there is a dark line running from the base to the top of the sporangium (*e. g.* PA 335, Pl. XXX fig. 11); if it is not merely accidental, as is quite possible, it must represent some kind of thickened tissue in the wall, probably connected with the opening mechanism. The observation and interpretation are very uncertain, but the idea of a longitudinal dehiscence is supported by the presence of a few sporangia which are split from top to base in equal halves (PA 330, Pl. XXIX fig. 4), and by the fact that the sporangia seen in natural cross-sections remarkably often have an opening on one side of the wall (PA 306, Pl. XXVII fig. 3). — On the other hand, it is far more common to find sporangia which are wide open at the top, as is visible in many of the photographs reproduced, particularly in Pl. XXIX and Pl. XXX.

In the latter cases there is sometimes another structural detail which attracts attention, and that is a kind of double wall. It is visible for instance in Pl. XXX figs. 8—9 (PA 324), and Pl. XXIX fig. 5 (PA 330): Here the wall is simple in the basal and middle part of the sporangium, and it continues with unaltered thickness to the top, where there is an opening; but inside this opening there is a thin inner wall which has retained the shape of the unopened capsule; on the sides it is attached to the outer wall, and at the top it seems to enclose some dark matter. The photographs selected for reproduction may leave the impression that this structure is more common than is actually the case; but in the specimens where this double wall is seen, it is so uniform and distinct that it is inevitable to regard it as a regular and normal development of the sporangium.

The interior of the sporangium does not show any traces of columella, nor of any sterile basal tissue. In the numerous longitudinal sections the wall is of uniform thickness down to the very base, and encloses a space which must have been filled with spores (see, for instance, PA 330, Pl. XXIX fig. 5, and many others).

The spores, or at least sporangium contents which must be supposed to represent the spores, are observable in some cases when the fossil is examined directly in incident light. In a specimen like PA 322, Pl. XXX fig. 4, they seem to be rather large, but their exact form and size cannot be made out in this way; the round clear spaces seen in the sporangia in the figure referred to, are not the spores themselves. Through maceration more reliable results could be obtained, although I have not sacrificed more than a very few specimens for maceration so far, because I wanted to see if more material could be obtained from the same locality. Therefore it is possible that a supplementary note on this point will be necessary on a later occasion.

It is remarkable that maceration from these specimens has resulted in a great variety of spores; a short description of the various forms found will be given below (p. 146). Spores which evidently belong to

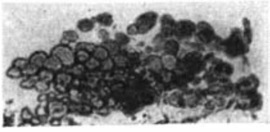

Fig. 16.

Fig. 16. Remains of cell walls, looking like spore masses. From a preparation of *Svalbardia polymorpha*. PA 1251/49 *c*. × 250.

the plant itself were obtained from PA 1251, among other specimens: The maceration of a few typical sporangia also in this case gave various kinds of spores, although I had tried to pick out the sporangia with as little of the matrix as possible; but while the greater number of the different types were represented by only one spore or a few, a certain type was quite preponderating in number: As seen in Pl. XXXI figs. 5—9 these spores are oblong, about 60—70 μ long or a little more, and somewhat narrower; they do not look as if the slight difference between the two diameters is due only to incomplete swelling. The wall is nearly smooth, but has minute tubercles which are only visible under strong magnification; in some spores, which are probably better preserved than the others, each tubercles may end in a little tooth-like projection. There are distinct tetrad marks. These spores are found in great numbers, either isolated, or in tetrads, or in larger aggregates (Pl. XXXI fig. 5), in such a manner that there seems to be no room for doubt as to their having come directly from a sporangium (cf. also p. 119).

In addition to the various types of spores, the preparations also contained some other objects which may be mentioned in this connection (text-fig. 16): There were some very small bodies, brown or yellowish brown, as a rule measuring 3—6 μ in diameter, round or angular, the round ones mostly lying isolated, the angular ones being placed closely together in one layer. At first sight they look like minute spores, and if they had been the only objects obtained through the maceration, and only in small numbers, one would certainly have been tempted to declare them to be the spores of the plant (although they rather look like the spores of a smut or some similar fungus). But they are certainly not spores at all. They are most likely the products of some transformation or disintegration of cell walls (more probable than of cell contents). They are often found in connection with fragments which would be most naturally interpreted as the remains of sporangium walls. — A similar result of the disintegration of tracheid walls has been illustrated by Lang & Cookson (1930 p. 142, Pl. XIII fig. 35).

Before discussing the name and systematical position of this plant, it will be necessary to consider the question whether the specimens described above really belong to one species. At first sight it perhaps does not seem to be so, the specimens being rather different from each other. The most important morphological features causing this diversity, are the following:

(1). Branch angles (*a*) acute, — or (*b*) wide.

(2). Branches (*a*) opposite or nearly so, — or (*b*) more distant from each other.

(3). Small lateral appendages or branchlets (*a*) standing out at the base, then curved upwards and appressed, — or (*b*) lacking.

(4). Branch-systems (*a*) long, divided pinnately or dichotomously into numerous filiform segment, — or (*b*) more frond-like foliar organs of limited length, with narrow, but not filiform segments dividing dichotomously.

(5). Fertile shoots (*a*) present, — or (*b*) absent.

There is no single specimen which shows all these characters combined. The most complete specimen is the large PA 320 (text-fig. 15), which combines the following features: 1 *a*, 2 *a* (?), 4 *b*, 5 *a*, but the value of this specimen is reduced by its very poor state of preservation. However, the other specimens show so many transitions between alternative characters, and so many combinations of others, that a close study leads to the conviction of a specific identity.

Between 1 *a* and *b* there are transitions showing that no systematical importance can be attributed to these characters, and similarly between 4 *a* and *b*, as was pointed out above (p. 73). Also in the position of the branches in relation to each other (2 *a* and *b*) there is a certain irregular variation which certainly does not offer any basis for the distinction between different species.

As to the small appressed lateral appendages (3), they may be found in specimens of the most different appearance, which will be evident from a comparison of the figures referred to above (p. 73). It is also clear that, if they really are the remains of old foliar organs, they have nothing of the systematical importance which their peculiar appearance at first sight might indicate.

Special interest is attached to the organs of reproduction. The constant association of the sterile plant fragments and the fertile ones on the slabs (PA 335, Pl. XXII; PA 347, Pl. XXI figs. 1 and 3; PA 330, Pl. XXIX fig. 2, and several others, also not photographed ones), and the similarity in their mode of preservation, in their texture, dimensions, branching, &c., may convince the person who is working with them that they form parts of one species of plant; but that has but slight value as a proof. However, in PA 315 (Pl. XXVII fig. 1) we have a fertile branch connected with an axis of the typical kind, bearing sterile branches which, however incomplete, are in full accordance with the better preserved sterile specimens. In PA 320 (text-fig. 15) we have a similar case, the specimen being more complete, but also far more indistinct. It is also of some interest to refer to the panicle PA 306 (Pl. XXVII figs. 2—3), which seems to bear sterile 'leaves' below the fertile region. In view of these facts I have no hesitation in considering these organs of reproduction parts of the same plant species as the axes and foliar organs described above.

Affinity. — The plant here described shows resemblance, and no doubt also real affinity, to several plants of Devonian age or slightly younger ones; but it is impossible to identify it with any species or even genus known before.

1. Habitually the shoots, particularly in the sterile, filiform ramifications, bear a striking resemblance to *Pseudosporochnus Krejcii* P. & B., which was first described from the Middle Devonian of Bohemia (redescribed by Kräusel & Weyland 1933), the genus also being known from the Rhine District, Scotland, Belgium, and eastern United States (for references, see Kräusel & Weyland *l. c.* p. 17, and Leclercq 1940 *b* p. 49); it could scarcely be doubted that there is a certain relationship between them, which will be further discussed below (p. 177). But there are also profound differences: In *Pseudosporochnus* no fertile shoots like those described above have been found, and probably they did not exist, the spores having most likely been produced within the swollen tips of filiform ramifications (see, *e. g.* Kräusel & Weyland *l. c.* p. 15). Secondly, *Ps. Krejcii* has no flattened, leaf-like organs like those of the Spitsbergen plant; certainly some of the shoots may have a tendency to expand in one plane (Weyland 1932 p. 7), but still the difference is very considerable.

2. Another plant which has to be taken into consideration is the one which Johnson described in 1914 from the Upper Devonian of Ireland under the name of *Ginkgophyllum kiltorkense* (Johnson 1914 p. 174). Soon afterwards the same author described more specimens which he supposed belonged to the same species, making it the type of a new genus, *Kiltorkensia*, and calling it *K. devonica* (Johnson 1917 p. 250). However, according to the rules of nomenclature the oldest specific epithet must be retained, so that, if the specimens from 1914 and 1917 really belong to one species, the plant will have to be called *Kiltorkensia kiltorkensis*. — The species has also been briefly discussed by Seward (1919 p. 88), as *Psygmophyllum k.*, and by Kräusel & Weyland (1935 *a* p. 7).

Unfortunately, it is somewhat difficult to form a clear idea of the morphology and systematical position of this important plant; the various specimens which the author combined are rather different, and it is not evident to what degree there are convincing reasons for referring all of them to one species. The same doubt has been expressed by Kräusel & Weyland (1935 *a* p. 7).

In the hope that it might be possible to obtain a loan of the type material for a re-examination I have applied to the National Museum of Ireland, in Dublin, but in spite of the kind efforts of Dr. Patr. O'Connor, Keeper of the Natural History Division, it has not been possible so far to locate it either at that museum or at University College, Dublin. I have therefore not been able to compare the Irish plant directly with the new one from Spitsbergen, which would have been very interesting on account of the resemblance evidently existing between them.

The resemblance particularly manifests itself in the specimen shown by Johnson (1917) in his Pl. XII fig. 3 and Pl. XIV fig. 3, in which slender, straight axes bear dimorphic leaves of the same types as the foliar organs of our plant. It would not be surprising if the two plants were found to belong to at least the same genus. So far it might be considered possible to apply the name of *Kiltorkensia* to the Spitsbergen species. However, most of the other organs described as belonging to *Kiltorkensia kiltorkensis* are entirely different from those from Spitsbergen, and for this reason, and on account of the uncertainty attached to the delimitation of the Irish species, it appears most correct, and most practical, at present not to make use of the name of *Kiltorkensia* for our plant. — Cf. also p. 113.

3. As to *Archaeopteris*, there is certainly a very great difference between our plant and most of the species of that genus. But *A. fissilis* (Schmalh.) em. Nath., from the Upper Devonian of Donetz (Schmalhausen 1894) and of Ellesmere Land (Nathorst 1904), forms a connecting link, and in reality some of our specimens bear such a resemblance to this species that they can scarcely be distinguished from it, at least if one has to judge only by the illustrations published. That is not only the case with the large one shown in our text-fig. 15 (PA 320); if this specimen had been found alone, one might indeed have given it the name of cf. *A. fissilis*, with all the reservation necessitated by the poor state of preservation. But the resemblance also goes very far in the matter of the fructifications, which in their general morphology are identical with those of all species of *Archaeopteris*.

An examination of some of Nathorst's specimens from Ellesmere Land, however, has shown that it is out of the question that the two plants should belong to the same species. To mention some of the most conspicuous distinguishing characters, the leaflets of *A. fissilis* are better developed, more fern-like, at least mostly with broader segments, the striations of its axes are far more numerous and delicate, and much longer than those of the other plant, in which they are few in number, coarse, and often discontinuous; further the fertile shoots are much denser in *A. fissilis*. There are also differences which must be of generic importance, the chief one being that in the plant from Spitsbergen there is evidently not formed a composite leaf regularly expanded in one plane, but the branches of higher and lower order, as well as the filiform ramifications at the ends of the branches, may be arranged in all directions.

One cannot deny the possibility that some of the detached fertile shoots in the collection, and perhaps some other, poorly preserved specimens, might belong to some species of *Archaeopteris*, but it is not probable; as stated above they seem to be connected by many transitional forms with the typical and more complete specimens which certainly cannot be referred to that genus.

There are also other fossil plants with which the one here described, might be compared (*Hyenia*, *Haspia*, *Protopteridium*, &c.), but more on account of the light it throws on their morphology than for purely taxonomical reasons; some of them will be dealt with in another connection.

In conclusion it may be stated that although our plant evidently has a central position, with close resemblance, and probably affinity, to various genera, it cannot be included in any of them. I therefore propose to make it the type of a new genus, under the name of *Svalbardia*[1] *polymorpha*. — For diagnosis, see p. 193.

As to the systematical position of the new genus, some of its characters are rather primitive and may be taken as reminiscences of a psilophytalean origin, probably not very remote; but it has clearly developed beyond the limits of that group, if these limits are not drawn excessively wide. Both its vegetative characters and the form of its fructifications show that its place is in the neighbourhood of *Archaeopteris*, as a primitive relative of that genus (cf. pp. 177, 186).

Svalbardia sp., fructification.

Pl. XXVII figs. 4—5.

In the case of some of the fructifications, it is somewhat difficult to ascertain whether they belong to *S. polymorpha* or to a related species. That is particularly the case with the one shown in Pl. XXVII figs. 4—5 (PA 327), from Planteryggen. It differs from all other specimens in its robust and rigid appearance. The axis of the panicle is relatively thick, the branches short and straight, and the cluster of sporangia on the upper side of the middle part of each branch is very dense. But in principle the panicle is like that of *S. polymorpha*, and so is the form of the individual sporangium too. It is therefore quite possible that the specimen belongs to that species, representing perhaps a fructification in a young stage of its development.

Protopteridium (?) sp.

Pl. XXVII figs. 6—7.

Locality, material. — A single specimen (PA 331) of a fructification from Planteryggen (1928).

Description. — The remains of the plant now consist of two parts which are not in organic connection with each other, but that is evidently

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[1] The name *Svalbardia* is preoccupied, in so far as it has been used by the zoologist Sig Thor, in 1930, for a genus of *Acarina*. But this fact does not invalidate it as the name of a plant as well.

because the base of a branch has been lost through the splitting of the rock.

The whole specimen is 2.9 cm long. The lower part is a naked stalk, about 2 cm long. Upwards it divides repeatedly at short intervals. The branch which is best preserved, is stout, nearly horizontal (if the main stalk is vertical), curving up distally, and giving off several secondary branches, all of which are directed upwards and subdivided dichotomously. These branches are short and bear numerous sporangia, thus forming a rather dense cluster with erect sporangia. Each sporangium is elongated, 2.5 mm long and about 0.5 mm wide, thin-walled, ending, as far as it can be seen, in a blunt point.

On account of the extreme scarcity of the material, maceration has not been attempted, being postponed in the hope of obtaining more specimens.

Affinity. — The sporangiferous branch is not without resemblance to *Svalbardia polymorpha*, but differs above all in the much larger number of sporangia. This character, and the curved form of the main branch, strongly recall the Middle Devonian genus *Protopteridium*, known from Bohemia, the Rhineland, Belgium, Scotland, and probably from China (compare Lang 1925, 1926, Kräusel & Weyland 1933, 1938, Halle 1936, and Leclercq 1940). However, although it is very probable that the specimen represents this genus or a closely related one, it is insufficient for a specific determination.

Hyenia (subgen. *Hyeniopsis*) *Vogtii* n. subgen. & sp.

Pls. XXXII—XXXIV; Pl. XXXV figs. 5—8.

Locality, material. — The plant was collected first in 1925, then in 1928, in the localities called Planteklø\u00f8fta and Planteryggen in the the inner part of Mimerdalen, and, like nearly all other fossils found here, it was taken only in loose slabs, not in solid rock. It is present in more than 20 specimens, about 6 of which being very good. In most of the slabs containing *Hyenia* this is the only determinable plant; but there are also cases of association with *Svalbardia polymorpha* (PA 410, cf. also PA 305, p. 88), and with *Bergeria mimerensis* (PA 445, Pl. XXXV fig. 5; PA 394, 407), whereas the association with *Enigmophyton superbum* is uncertain.

Some of the slabs are rather sandy, splitting irregularly, and containing numerous fragments of *Hyenia* in poor preservation, usually without any admixture of other plants. Other specimens, particularly those in which *Hyenia* is associated with *Svalbardia*, are more shaly and fine-grained.

Description. — A very instructive specimen is PA 397 (Pl. XXXIII figs. 1—2), which is the most complete one, although not the best preserved. It consists of a relatively thick axis with branches. The axis cannot be interpreted as a rhizome; it bears leaves just as the ordinary branches do, and it gives off branches in all directions. As is visible from the photograph it is bent in a very regular curve; the length is nearly 20 cm, and the breadth of the impression 5—7 mm. — The branches are evidently placed in a kind of spiral arrangement, although there is no full regularity; but, as their position is intimately connected with that of the leaves, this point will be dealt with in more detail below. The two longest branches preserved are both on the inner side of the curved main axis. They are about 15 cm long, broken below the top, and curved in the same manner as the main axis, both of them bearing one or a few secondary branches. — Both stem and branches bear foliar organs, which are more or less verticillate, causing a corresponding articulation in the axes. In so far as it can be made out from this specimen the verticils are ternate, with a vertical distance between them about two or three times the diameter of the axis, sometimes less. All axes, as now preserved, are longitudinally grooved, this being due, as it seems, to internal strands or vascular bundles; in addition to a central longitudinal impression there are often markings indicating leaf-trace bundles (Pl. XXXIII fig. 3). The leaf bases are somewhat decurrent. In the many instances when a leaf base is found within the impression of the stem, and not at the margin of it (which is regularly the case with at least one leaf of each verticil), it has usually the form of a distinct and well-defined depression. The leaves themselves are small, thin, and divided; but their form is better seen on other specimens described below. An important fact to be noted is that the branches are invariably developed in the place of leaves, and not in the leaf axils.

In other specimens further details are observable:

The stems are always broken in their lower ends, so that it is difficult to form any opinion of the basal or subterranean parts of the plant. The only hint is given by an interesting specimen which may be interpreted as a rhizome (PA 450, Pl. XXXV figs. 7—8): It consists of a thick axis, about 4.5 cm long and 13 mm thick, penetrating through the rock at an angle of 60—70° to the plane of bedding. It has a coarse and uneven surface, with irregular longitudinal grooves. It gives off a great number of lateral organs, which are partly imbedded in the matrix, but which evidently radiate from the main axis, so as to be more or less regularly parallel to the bedding plane of the rock; one of them (to the right in the photograph) is exposed for a length of 6 cm, while another branch in the opposite direction is more incomplete. The former, and possibly others as well, bear leaves which resemble the typical ones on ordinary branches, in so far as their poor state of preservation permits of observation. Some of the other lateral organs are thinner, somewhat irregular, and they do not seem to bear leaves or to be articulate; this may be due to their poor state of preservation, but more likely it shows their original structure.

The interpretation of this specimen is somewhat difficult. The thick axis in many respects has the appearance of a rhizome, and it would be natural to regard the leaf-bearing lateral organs as ascending subaerial stems, whereas the others may rather have been root organs of some kind. The rhizome gives at first sight the impression of still being in the same position in the matrix as when it was growing. But, apart from the fact that, in all probability, the plant remains of this flora have generally been subject to some transportation before imbedding, the position of the lateral organs makes it rather difficult to understand how this could be possible. At all events the axes that are thought to be ascending leaf-bearing stems, have no doubt been brought out of their original position during the imbedding and fossilization.

It must be added that the specific identity of this specimen with the others here described as *H. Vogtii* is not proved.

As to the stems, no specimen has been found with larger dimensions than the one described above (PA 397). The others have more or less the same appearance, but are either curved or straight. There is no specimen showing clearly the top of the plant.

Generally speaking, the leaves are found in pairs, opposite at the margins of the impression of the stem, and a depression on the flattened surface between them indicates the position of a third leaf. In many cases it would be natural to expect that a fourth one would be found imbedded in the counterpart of the fossil, whereas in others it seems to be more likely that the number of leaves at each node has been only three. The verticillation is often quite regular, in other cases not at all so. In PA 393 (Pl. XXXII fig. 2), for instance, there is an equally regular alternation of the leaves along the margin of the stem, and there is no reason to believe that this position is due to deformation during fossilization.

The position of the leaves along the margin of the fossil stem, and the markings of the strands, show that the leaves of adjacent whorls were superposed.

The leaves are short, mostly about 1 cm or less, but sometimes attaining a length of 1.5 cm (Pl. XXXII fig. 4, PA 393). They are filiform without any lamina, although in reality they have certainly been somewhat broader than they seem to be in most of the specimens, which are longitudinal sections (compare, for instance, Pl. XXXIV fig. 2. PA 408). They divide repeatedly and as a rule in strict dichotomy, but overtopping does take place here and there. In some cases (*e. g.* PA 393, Pl. XXXII fig. 4; also visible, less pronounced, in PA 410, Pl. XXXV fig. 6) the leaf bifurcates immediately after leaving the stem;

if this feature is not observable in a greater number of cases the reason probably is that one of the two divisions of the leaf is generally buried in the matrix or has been lost with the counterpart. The number of bifurcations is only rarely ascertainable and is probably somewhat varying; it is certain that the dividing may be repeated as much as five times and probably more (PA 393, Pl. XXXII fig. 4). The angle of the bifurcation is generally acute. The leaf base is widened into a triangular cushion, seen as a projection along the margin of the fossil stem, or as a depression on the surface of it. The leaves are mostly rather erect, at an angle of about 45°.

Thorns are found in considerable numbers on the axes. They are particularly numerous just below the leaves and the branches and on the lower sides of their basal parts, as is observable on many of the photographs if examined by means of a hand lens; but they are also present on other parts of the axes. Small dots or scars, seen here and there on the flattened surfaces of the stems, may be regarded as thorn bases; they are mostly circular, but sometimes elongate (PA 410, Pl. XX figs. 9—10). The thorns are rarely as much as 2 mm long; they are very thin, scarcely widened towards the base, and straight or somewhat curved, sometimes slightly directed downwards.

The branches, as mentioned above, are never developed in the axils of the leaves. On the contrary, the branch takes the place of the leaf itself, and its base differs from that of a leaf only in its greater size. The branches are essentially lateral in relation to the relative main axis, the direction of which being not at all or only very slightly altered at the point of branching; as a rule the branch is thinner than the axis from which it arises. The branch may bear secondary ramifications, a feature, however, which is only rarely observable on the specimens. The direction of the branch, at least at its base, is more or less like that of the leaves.

The arrangement of the branches along the stem is not quite regular. It happens that there are two branches at one node (PA 409, Pl. XXXIV fig. 5, and Pl. XXXII figs. 5—6). But as a rule they are alternating. In some cases there are two nodes without visible branches between one branch given off to the right, and another one to the left; the most distinct examples of this arrangement are seen on PA 393, Pl. XXXII fig. 1. In PA 408, Pl. XXXIV fig. 1, the interval is only one node, that is, two internodes. In PA 397 (Pl. XXXIII) there are often two nodes between two branches given off to the same side. — Some of these cases would be explainable if we presumed that one leaf in each verticil had been transformed into a branch, the branches being arranged spirally along the stem. Then the vertical distance between the branches in the bedding plane of the rock would be determined by the number of leaves in the verticils of that particular plant. But it has to be admitted that there are generally no traces of the branches which, if this were right, must be supposed to be buried in the matrix or to have been removed with the counterpart of the fossil, and at all events the rule does not hold good in all cases. — It may be added that some of the specimens rather look as if the branches had been bilaterally expanded in one plane; but most probably this is only due to the state of preservation.

The transformation of the leaves into branches, or vice versa, denotes an ambiguity which is of considerable interest from a morphological point of view. It will be further touched upon below (p. 185).

The organs of reproduction are unknown.

As to the anatomy there is also very little knowledge to be obtained. The impressions of the axes always have a characteristic deep longitudinal groove, which must correspond to some central strand in the living plant, and in some cases (PA 397, Pl. XXXIII fig. 3) there are markings showing that each leaf was connected with the strand by means of a leaf-trace bundle, which left it at a very acute angle and then, passing through one internode or at least through the larger part of it, curved outwards into the leaf base. But the cells of these bundles are entirely unknown. — There is no cuticle left, but when examined under a strong lens (in a magnification of 10 times or more), remains of the cell structure of the surface are visible (Pl. XXXII fig. 3, PA 393). It consists of parenchymatous cells generally arranged in rows parallel to the longitudinal direction of the organ; stomata have not been observed.

Affinity. — The plant is an entirely new and interesting feature in the fossil flora of Spitsbergen.

As to its generic position, the form of the leaves and their arrangement on the axes are those typical of *Hyenia*, and if the specimen described above as a rhizome (PA 450, Pl. XXXV figs. 7—8) really belongs to the same species as the other specimens (this is not at all certain), it then forms another link with the said genus.

The mode of branching, however, is something quite new. As far as one knows, *Hyenia* is generally found as simple, unbranched stems, arising directly from a horizontal rhizome. Only one specimen has been described as branching, that is the one figured by Kräusel & Weyland (1929 text-fig. 8 = Pl. VI fig. 2). The latter, which is strikingly different from the rest of the material published, is dividing repeatedly, but in strict dichotomy, a mode of branching which also is very different from the characteristic type of the Spitsbergen plant. — The only case of a similar lateral branching seems to be found in some Belgian specimens, figured by Stockmans (1940, Pl. XIV figs. 8—9) under the name of *Hyenia* sp. But they are poorly preserved, and only mentioned preliminarily in an appendix to the text (*l. c.* p. 75) without detailed descriptions, so it is scarcely possible as yet to use them for further comparison.

Another difference which may be of some importance, although seemingly insignificant, is the presence of spines in our species. At least between this species and *H. sphenophylloides* there may also be some difference in the anatomy, concerning the course of the leaf-trace bundles, but the observations on this point are still deficient.

It is quite possible that our plant should most correctly be regarded as the type of a new genus. Provisionally, however, it may be referred to *Hyenia* as a new species. But in order to express the difference between this species and the others I propose to place it in a separate subgenus, *Hyeniopsis*, as distinct from *Eu-Hyenia*. — I feel it an honour to name the new species after Professor Thorolf Vogt, on whose Spitsbergen expedition in 1925 the first specimens were found. — For diagnosis, see p. 194.

For further discussion of the systematical position of the plant, compare also p. 185.

The genus *Hyenia* has previously been known from western Norway (Nathorst 1915, Høeg 1931, 1935), the Rhineland (Kräusel & Weyland 1932, with bibliography), Belgium (Aderca 1932, Kräusel & Weyland 1932, Stockmans 1936, 1939 *b*, 1940, Leclercq 1940 *a*, *b*), and France (Corsin 1933 *b*), in all cases from the Middle Devonian. A single exception is the note by Mägdefrau (1938 p. 248) that *H. sphenophylloides* occurs in the Lower Devonian of the Harz. Fossils referred to the same genus have also been recorded from the eastern slopes of the Urals, by Zalessky (1937 *a*), and from Kasakhstan, by Neiburg (1939).

cf. *Hyenia Vogtii.*

Pl. XXXV figs. 3—4.

Pl. XXXV figs. 3—4 (PA 471) represents the impression of a fragmentary axis, rather poorly preserved. As is visible on the photographs, it is very delicate, 0.5 mm thick, nearly straight, 5.5 cm long (a portion in the middle is lacking). It bears a great number of small leaves, visible only along the margin of the impression, nearly, but not exactly, opposite to each other; in some cases, however, the leaves are nearly alternate (see the lower part of Pl. XXXV fig. 4). The internodes are about 2 mm long. The leaves are filiform and borne on triangular cushions; as now preserved they are simple, but being in their present state only a few millimeters long and probably incomplete, they may very likely have been originally divided by bifurcation.

At first glance this fossil recalls one of the little Sphenophyllums described from the Upper Devonian, but the characteristic arrangement of the leaves and their widened bases show that it must be a relative of *Hyenia*. Its small size and the regular short internodes give it an appearance rather different from even the youngest and thinnest shoots of *H. Vogtii*, preserved in the present collection, but it is uncertain whether or not it belongs to another and new species.

Protoarticulata (?), incertae sedis.

a. — Pl. XXXV fig. 1 (PA 1170) shows part of a fairly strong axis, 10.5 cm long, about 5 mm thick, with irregular verticils of lateral organs to the number of four; each consists of a triangular and somewhat decurrent cushion and a short filiform appendage, looking like the base of a small leaf. Internodes about 3 cm long. — On the same slab is also another axis (Pl. XXXV fig. 2), which is twice as thick, but evidently bearing the same kind of lateral organs (lower left-hand corner), perhaps, however, in somewhat larger number; it seems as if in one place (upper right-hand corner) there is a branch instead of a filiform leaf-base.

The verticillate arrangement is certainly somewhat irregular, but not more so than it may be in *Hyenia*. Although it is uncertain whether the plant belongs to that genus, I have no doubt that it is a relative of it. — Cf. also p. 145.

Plants like this should also be compared with one from Billefjorden which was described by Nathorst (1894, Pl. I fig. 3). However, the latter belongs to a rather dubious group (which will have to be compared to *Loganiella canadensis*), and in spite of the resemblance it is not certain that these plants have anything to do with each other.

b. — Another type of plant with verticillate leaves is illustrated in Pl. XXXV figs. 9—10 (PA 305). It is straight and rather slender, 3 mm thick, with internodes 2.5—3 cm long. At the nodes, on both sides of the stem impression, there are the same sort of triangular cushions as in the specimen just described, but exactly opposite each other, and straight between them there is a narrow and deep impression of a third leaf (Pl. XXXV fig. 10). — From *Hyenia Vogtii* it differs in the length of the internodes, but a relationship is probable.

Enigmophyton superbum n. gen. & sp.

Pl. XXXVI; Pl. XXXVII figs. 1—2; Pls. XXXVIII—XL;
text-figs. 17—18, 25.

Locality, material. — The species is one of the dominant plants of the flora of Planteryggen, and a great number of specimens were collected in 1928.

The leaves were often buried in the matrix, and during the preparatory work in the laboratory they had to be uncovered cautiously by means of needles and small chisels. The incrustations are often very clear and distinct, but, although there is often left a considerable amount of carbonized organic matter, no anatomical details could be made out by means of chemical preparations. Film pulls have not given any satisfactory results, but photographing directly on the fossil, even in relatively strong magnification, has revealed several structural details.

Description. — What is left of the plant are axes and leaves, often in organic connection with each other, so that there is no doubt as to their belonging together; the basal part of the plant, however, is unknown, and likewise the top. As to organs of reproduction possibly belonging to this species, see p. 117.

The stems are very uniform in breadth, mostly measuring about 5 mm. The longest one preserved is 27.5 cm long (PA 1155), and not perceptibly tapering upwards; no doubt they may have been much longer. Thus, the plant may have been of a stately size; on the other hand, if it has been growing free and unsupported up in the air (cf. p. 114), its height must have been limited by the dimensions of the axes, which have evidently had no secondary growth in thickness. — The axes may be nearly straight, but far more frequently they are gently and flexuously curved, the direction of the curves often changing at the points where the leaves are inserted. The surface is smooth and even, without any traces of hairs, spines, or scars, nor are there any markings indicating internal strands or any central cylinder; although giving the impression of having been fairly firm and rigid, they look, in their present state of preservation, as if they have been of a uniform internal structure throughout. Mostly, they are preserved as stone-casts of oval outline with a coat of coaly matter or as corresponding moulds. The appearance is so characteristic that usually even a short fragment of a stem may be recognized.

Branching takes place in two different ways:

Most common is a regular dichotomy, which may occur at rather short intervals; thus, in several specimens the distance between two points of bifurcation is about 6 cm (*e. g.* PA 374, Pl. XXXVII fig. 2), whereas in others it is much more. The branch angle is at first very acute, but then the two branches generally, although not without exceptions, curve out from each other. In most cases the branches are equal in diameter and also equal to the axis below the point of bifurcation. In the few specimens which show more than one bifurcation of an axis, the branches of the successive divisions are certainly not orientated in planes at a right angle to each other; they rather seem to be more or less in the same plane, although wholly reliable observations on this point could not be made.

Beside dichotomy, also a type of lateral ramification is common, side branches often being given off from the stems at a right angle or approximately so (PA 356, Pl. XXXVI; PA 352, Pl. XXXVIII figs. 1—2; PA 387, Pl. XXXVIII figs. 4—5, showing the base of a branch which

Fig. 17.

Fig. 17. *Enigmophyton superbum* n. gen. & sp., from Mimerdalen: Planteryggen. Details of holotype (Pl. XXXVI), showing the venation. — PA 356. × 2.

is buried in the matrix; PA 1114, Pl. XXXVIII fig. 3, upper right-hand corner). These branches are thinner than the main axis, usually being 1—2 mm thick; the base may be slightly widened. Frequently, or perhaps always, they leave the stem at the points of dichotomy and at a right angle to the plane of the two daughter stems. They are straight, and in our specimens always broken, the longest one preserved being slightly more than 2 cm long. Therefore the real nature of these branches is unkown: We do not know whether they have divided further out, or have borne leaves of any kind, or organs of reproduction (cf. also p. 120).

The stems bear large foliar organs in considerable numbers. Such leaves are found isolated on the slabs, as well as in their natural connection with the stems, the latter case being the more frequent. They are fan-shaped, and may attain a length of at least 16 cm (for instance, PA 356, Pl. XXXVI fig. 1), by a breadth between the two upper corners of at least 12 cm, and probably sometimes considerably more (PA 356, Pl. XXXVII fig. 1). There is no petiole, but the leaf is narrow at the base and then widens upwards, at first slowly, the lateral margins forming regular curves with the strongest bend in the upper part. The veins are distinct, parallel to each other, and bifurcating in accordance with the increasing width of the leaf, thus maintaining a fairly constant distance of 1—1.5 mm from each other. In a few cases the vein nearest to the margin seems to be thicker than the others, but there is no full certainty as to this point. — The leaf splits irregularly from the upper margin, thus dividing into lobes of very unequal sizes, and probably becoming more lacerate as it grows older and larger (see, for instance, PA 356, Pl. XXXVII fig. 1); evidently the young leaves have originally been entire. The splitting, which must be a secondary feature, always takes place in the interspaces between the veins. In a few specimens deep incisions of this kind divide the leaf into parts which curve out from each other and sometimes seem to appear as individual leaves (a poor example is seen in Pl. XXXVIII fig. 4, PA 387). The margin is crenulated, with small rounded lobes separated by indentations between the ends of the veins. In some cases it is rolled up so as to form a groove, of which an exceptionally distinct case is illustrated in PA 1255, Pl. XXXIX fig. 2; but it is questionable whether such a marginal groove has always, or often, been formed. — The mode of attachment is not quite clear.

Fig. 18.

Fig. 18. Superficial cell structure of *Enigmophyton superbum* n. gen. & sp., from Mimerdalen: Planteryggen. — PA 374. × 20. Photographed directly on the fossil, through a cover of cellulose glue.

The leaves probably always leave the stem at points of dichotomy, and reversely, there is scarcely any bifurcation without a leaf, but apart from that the specimens at hand do not give sufficient evidence as to how the base of the leaf was actually inserted. In a remarkably great number of instances the leaf gives the impression of being attached laterally to one of the parts of the dividing axis, the veins, one above the other, leaving the edge of the stem, but in all probability this impression is erroneous, the explanation simply being that the leaf is covered by the axis. — It is a characteristic feature that the leaves do not always follow the bedding planes of the rock, but very frequently curve into the matrix, sometimes even so as to become entirely revolute. This fact strongly suggests that the leaves have had a considerable firmness and rigidity.

As to the anatomy of the plant our knowledge is deplorably defective. In some places there are some remains of coaly matter, but attempts to bring out cuticle or tracheids have proved abortive, owing to imperfect preservation, or to the fact that such structures have not been developed in the living plant. As mentioned above, there are no traces of strands of any kind in the axes. But through direct examination of the fossil under a strong binocular lens, and by means of photographing in magnifications up to 20 times, certain details may be made out, particularly as regards the stems: In strong incident light there are often seen longitudinal ridges and furrows, straight or slightly flexuose, no doubt representing traces of the original cellular tissue. The breadth of the ridges appears to be about 0.05 mm (rarely upwards to 0.1 mm). In some places the furrows anastomose so as to form a network with long and narrow meshes which, though certainly erroneously, might be thought to represent epidermal cells a few times as long as broad; but more often the meshes are much longer and may be traced for relatively considerable distances, at least some millimetres (cf. PA 454, Pl. XXXIX figs. 5—7; PA 374, Pl. XL fig. 3). Upon the whole, when examined in that way the surface structure often looks as if the plant had been built up by cell-tubes, which, at least on the surface of the plant, might form a coherent tissue. — However, further observations on certain well-preserved parts of the stems made it necessary to reject entirely the possibility of such a *Prototaxites* structure. In the said parts the walls of the superficial cells are represented by furrows filled with carbonized matter; they are particularly well seen when the fossil is immersed in alcohol, or, still better, if the spot is covered with a cellulose film. Film pulls have not given such good results. As seen on the photographs (PA 374, Pl. XL fig. 1 and text-fig. 18; PA 1259, Pl. XL fig. 5) the longitudinal walls in such places may be very distinct and may be traced for very long distances; but an important point is that there are also transversal walls at regular distances, all the cells being rectangular and nearly equal in size, measuring about $50 \times 100\,\mu$. Where observable at all, this structure is very regular and uniform; there are no traces of other kinds of cells, or of such organs as stomata, hair-bases, or the like.

The tube-like structures which were mentioned above, and which are observable on the dry fossil under incident light, doubtlessly correspond, at least in most cases, to these rows of rectangular cells (cf. Pl. XL figs. 2—3, which partly cover the same area). The distinctly flexuose ridges may perhaps be thought to represent somewhat deeper parts of the stems than the straight ones.

On the incrustations of the leaves there are often considerable remains of organic matter, but generally the anatomical structure has been completely destroyed, and attempts to macerate or to make film pulls have been unsuccessful. In a few places, however, traces of cell walls are observable, and although the first impression, just as in the case of the stems, is that of tubes, cross-walls are certainly present also here (cf. Pl. XL figs. 4 and 6). Stomata have not been observed, but this negative evidence is not very reliable, because in the leaves the areas where any structure is seen at all, are quite small and imperfectly preserved.

Affinity. — In order to facilitate references it may be stated at once that the plant just described represents a new species and a new genus, for which the name of *Enigmophyton superbum* will be proposed. — For diagnosis, see p. 195.

As its morphology is very remarkable and fairly well known owing to the very considerable number of specimens on which the description could be based, it is natural here to make a detailed comparison with previously described plants with large, fan-shaped leaves, particularly those of Devonian age, in the hope that the new species may help in some measure to clear up the nomenclature, the interrelationship, and the systematic position of the whole group. Nearly all these plants have been described on the basis of a very scanty material, consisting often only of a single specimen, and almost only of detached leaves.

I. Comparison with plants previously described from Spitsbergen. — Leaves similar to those described above have been found before in the same part of Spitsbergen, and described by Nathorst:

1. *Cyclopteris* sp. Nath. (1894 p. 13, Pl. I fig. 12). — The specimen is the fragment of a large leaf, found in the year 1882 by Nathorst on the west side of Billefjorden, in a dark grey shale which he regarded as Lower Devonian. In addition to his first description of the specimen (1894), under the name of *Cyclopteris* sp., Nathorst also mentioned it in his *Psygmophyllum*-paper (1920 *a* p. 4), emphasizing its resemblance to *Cyclopteris Brownii* Daws. The plant seems to have a considerable resemblance to the one described above, from the Mimerdalen, but it is too imperfect for a complete determination, as was also held by Arber (1912 p. 399). It may be named *Platyphyllum* sp.

2. *Psygmophyllum Williamsoni* Nath. (1894 p. 15, Pl. II figs. 1—2). — The species was described on the basis of some specimens from the green sandy shale immediately above the horizon of Fiskekløfta. In the same stratigraphical level Stensiö found in 1917 more and better specimens of the same species; also these specimens were described and discussed by Nathorst (1920 *a*), and regarded as being of Upper Devonian age (as to the age, cf. p. 165). Both petrographically and stratigraphically the occurrence is somewhat different from that of Planteryggen, where *Enigmophyton* was found; the latter is younger, but the difference is not great. — Arber (1912 p. 399), refiguring the type specimen, agreed with Nathorst in regarding the species as belonging to the genus *Psygmophyllum*.

The specimens belong to the museums of Stockholm and Uppsala, and thanks to the kindness of Professor Halle and Professor Stensiö I have had the opportunity to examine them under comparison with the new material described above. Some details, enlarged 2 times, are shown in our text-fig. 19.

The slabs, on which these leaves are preserved, do not contain any other remains of plants; it is particularly noteworthy that there are no traces of the characteristic smooth stems which are nearly always associated with the leaves from the Planteryggen locality. As is apparent from the illustrations in the paper by Nathorst, the leaves of the two plants resemble each other a good deal. But *Ps. Williamsoni* is smaller, more regular in form (far more like a *Ginkgo*), and its venation is denser and more delicate. In the latter character there is a certain variation: In some parts the veins are distinct and very thin, with a distance between them of about 0.5 mm or slightly less; such veins are best seen in the lower part of the largest leaf figured by Nathorst 1920 (see our text-fig. 19 *a*). These veins multiply upwards by bifurcation, and about in the middle of the leaf fragment they become much denser; at the same time they become indistinct, but evidently they correspond to the striations which are seen in the upper part of the leaf, with distances of about 0.2—0.3 mm (text-fig. 19 *b*). However, in the upper

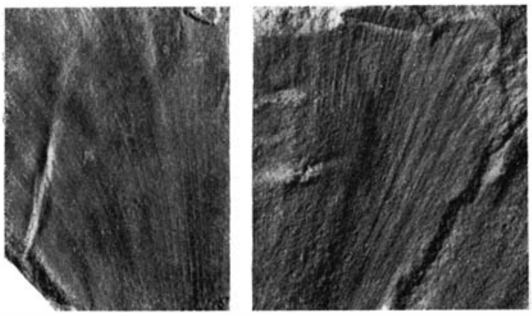

Fig. 19.

Fig. 19. *Platyphyllum Williamsoni* (Nath.) n. comb., from Mimerdalen. Details of the holotype (Nathorst 1920 *a* Pl. I fig. 1). — Geol. Inst. Uppsala No. 232. × 2. Fig. *a* photographed in xylol, *b* dry.

part of the leaf there are also some coarser lines, or ridges, about 0.7—1 mm apart; they are fairly distinctly seen in Nathorst's Pl. I fig. 1, and also in some places in our text-fig. 19*b*, but their real nature is doubtful.

The differences between *Ps. Williamsoni* and our new plant may to some extent be due to difference in the age of the leaves when imbedded in the sediment, and to the state of preservation. But even if this fact is taken into account it is not possible to regard them as one species.

It is quite possible, and even probable, that they belong to one and the same natural group, but at present the relationship between them is really quite uncertain. While our new plant, with its characteristic stems, is relatively well known, at least in so many morphological and structural details that it will have to be referred to a natural genus, *Ps. Williamsoni* should rather remain in an artificial genus together with other detached leaves of that general form. Accordingly it may be called *Platyphyllum Williamsoni* (Nath.) n. comb. (see p. 111).

3. *Psygmophyllum? pusillum* Nath. (1920 *a* p. 5). — A small piece of greenish sandstone, probably from the same horizon as *Ps. Williamsoni*, and like the first specimen of this species collected by Nathorst 1882, contained some fossils which Nathorst (1894 p. 12, Pl. II fig. 3) called '*Unbestimmbarer Abdruck*'. In his paper of 1920, however, Nathorst (*l. c.* p. 5) re-figured these rather problematical remains, and founded a new species on them, *Psygmophyllum? pusillum*, expressing as his conviction that they had some connection with the said genus. — The nature of this fossil will probably not become clearer until more material has been found. Provisionally it may be called *Platyphyllum pusillum* (Nath.) n. comb., although I do not feel at all convinced that it has anything to do with the other leaves referred to that form genus.

From this review it will be clear that our plant has probably not been found before in Spitsbergen: Among Nathorst's plants, the one listed here as No. 3 may be left out of consideration. No. 2 may belong to the same genus, but it is another species. No. 1, from the west side of Billefjorden, is too incomplete for a safe determination, but it has some points in common with our plant, and an identity is not entirely out of the question; if it really should belong to the same species it would be of some interest from a stratigraphical point of view, the rest of the flora being quite different in the two localities.

Although the remains previously found do not help much to clear up the systematical position of our plant, it is a fact of considerable interest that these large, fan-shaped leaves with bifurcating veins occur in several horizons of the Devonian of Spitsbergen. (Compare also the fragment from Estheriahaugen, PA 1151, described below, p. 116).

II. Comparison with other Devonian plants. — Habitually, as regards the form and venation of the leaves, our plant has a marked resemblance to several others previously described from Devonian rocks in other parts of the world, mostly under the name of *Psygmophyllum*, but also under other generic names: *Cyclopteris*, *Platyphyllum, Ginkgophyllum*, *Prototaxites*. The most important of these fossils will be treated of separately:

1. *Prototaxites psygmophylloides* K. & W., from the Lower Devonian of Germany, may be dealt with first, because it stands in an isolated position, and because Kräusel & Weyland, when describing it (1930), stressed the resemblance which seemed to exist between this plant and *Psygmophyllum Williamsoni* Nath. from Spitsbergen. As reconstructed by the said authors (*l. c.* p. 11, fig. 5) the German plant also seemed to show a certain resemblance to the new plant from Spitsbergen described above.

In addition to the type locality at Kirchhundem in Westphalia, the species has been recorded from the Harz by Mägdefrau (1938 p. 249, Pl. II fig. 5), on the basis of a single fragmentary leaf.

Thanks to the kind permission of the *Preussische Geologische Landesanstalt* (now: *Reichsstelle für Bodenforschung*), Berlin, and of Professor Kräusel, I have been allowed to borrow and examine the three specimens figured by Kräusel & Weyland, and to give some more illustrations of them for the sake of comparison with the other plants under discussion here.

As to the external morphology a direct comparison showed that there is really a profound difference between *Enigmophyton*, with its very regular and characteristic mode of ramification, and the axis of the German plant. Even though the specimens of the latter are very poorly preserved, they show at least that the plant has had an irregular branching of quite another type. The difference is great enough not only to make it impossible to refer these plants to one genus, but also to create doubts as to the existence of any particularly close relationship between them at all (cf. p. 188).

As to the anatomy of the German species, it has been described by Kräusel & Weyland (1930) as a typical *Prototaxites* structure, that is, as consisting of long cell-tubes without pores or wall thickenings or cross-partitions, of slightly flexuose form, sometimes bifurcating, but not connected with each other, and visible in cross-sections as irregularly scattered roundish figures. Unfortunately no photographs of this important discovery have been published.

The best specimen is the one figured by Kräusel & Weyland (1930) in their Pl. I figs. 2*a*—*b* (our Pl. XLI fig. 1). In a few places on this specimen there are traces of a structure which is in accordance with the description just quoted. But these remains are limited in extension and rather poorly preserved, and it is difficult to obtain any satisfactory photographs. Our Pl. XLII figs. 8—9 are from the lower left-hand corner of the specimen, where a few tubes are exposed as short longitudinal sections, and where also cross-sections are seen; they are about 0.1 mm wide. Pl. XLII fig. 7 represents a somewhat oblique cross-section found on Pl. XLII, fig. 6, a little to the left of the middle; there are small oval figures which may be interpreted as sections of tubes. Pl. XLI fig. 2 is from a spot a little below that cross-section, and gives the best idea of the course of the tubes in the longitudinal section.

In the specimen figured by Kräusel & Weyland (1930) in their Pl. I fig. 3 (our Pl. XLII fig. 5), the *Prototaxites* structure is very poorly preserved. Our Pl. XLI fig. 9 shows a long, flexuose tube, or perhaps two, and other traces are found in a few more places. Mostly, they are rather irregular and give the impression of having been wider than in the other specimen. On the basis of this specimen alone it would not have been possible to advocate the idea of a *Prototaxites* structure.

In addition to these remains of the anatomical structure which seem to be in agreement with the interpretation as *Prototaxites*, I should like to mention some other observations, although they are of a somewhat uncertain bearing:

Pl. XLI fig. 3, which illustrates the same part of the fossil as fig. 2, but photographed in a different way, on close examination shows that the ‘tubes’ really look like strings of pearls, being divided by black lines at distances about equal to the diameter; this is shown in stronger magnification in Pl. XLI fig. 4. — Further examination has revealed that a similar structure, looking like a tissue of small isodiametric cells, may be found in more places on the two smaller specimens of the three which have been figured by Kräusel & Weyland (1930 Pl. I figs. 2—3; on the largest specimen, *l. c.* Pl. II fig. 1, of which a part is shown in our text-fig. 20, I have not found any structural details whatever).

Fig. 20. *Germanophyton psygmophylloides* (K. & W.) n. comb. Part of large leaf (Kräusel & Weyland 1930 Pl. II fig. 1). — *Reichsst. f. Bodenf.*, Berlin. Nat. size. Light from the right.

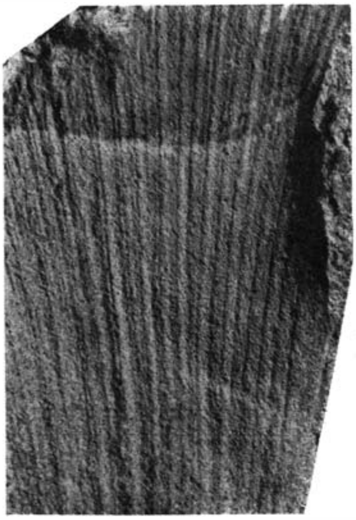

Fig. 20.

The cells, however, are scarcely observable at all by visual examination, even under a good binocular lens. They were only found with certainty in the photographs; but good photographs have been difficult to obtain on account of the roughness of the uneven surface of the fossil. In view of the scarceness of the material no attempts at maceration could be made, nor is it likely that they would have lead to any success. In some cases it was an advantage to make enlarged prints from the negatives; therefore some of the photographs reproduced may look as if they had not been quite in focus.

In some of these photographs (see Pl. XLI) there is a structure looking like an ordinary parenchyma, with cells mostly of rectangular or quadratic form and closely connected with each other. They have a tendency to arrange themselves in longitudinal rows. No pores or similar structures are observable. In some cases it looks as if the *Prototaxites* tubes were surrounded by, or imbedded in, a ground tissue of such cells.

I am rather at a loss as to the interpretation of these observations. As will probably be found evident from the photographs reproduced, the structures just described have such a resemblance to a cellular tissue that any other explanation may seem impossible. But one should nevertheless bear in mind the possibility of their being inorganic: If the mineral grains of the matrix of a fossil are small and of more or less uniform size, a photograph in high magnification will show the individual grains as clear spots surrounded by dark lines in such a way that they may resemble cells, and if the fossil, of which a mould or a cast is studied, has been built of anatomical elements of a pronounced longitudinal course, the grains, accordingly, will probably arrange themselves in rows, thus appearing, if studied in high magnification, like strings of isodiametric cells. Therefore such photographs are not so reliable as, for instance, sections which can be studied under the microscope. If the cell-like structures described in the present case, however, had been of an entirely inorganic origin, they should have been expected to occur everywhere, whereas, in fact, regular patterns like those seen in the photographs reproduced have only been detected in a few places. Personally I feel convinced that they represent the remains of a cellular tissue which the plant has possessed in addition to the tubes, but I am aware of the lack of objective proof.

With regard to the external morphology of the plant it may be added that from the three specimens that I have seen, I would not feel justified to combine the large leaf (Kräusel & Weyland *l. c.* Pl. II fig. 1) with the stems; but no doubt the whole original material has been large enough to show that they belong together.

As to the nomenclature and systematical position of the plant, the presence of a parenchymatous ground tissue, if proved, would be of great importance, making it necessary to give the plant another generic name than that of *Prototaxites*. But in my opinion that will be necessary in any case: *Prototaxites* is essentially an organ genus, characterized as stems with a certain type of anatomical structure, and it does not seem advisable to apply the same name to impressions of 'leaf'-bearing shoots, even if they should be proved to have the same type of internal structure. It is not at all certain that all species of *Prototaxites* have been so similar in external morphology and in other characters that they could be referred to one and the same natural genus.

As a new generic name for *P. psygmophylloides* K. & W. I propose *Germanophyton*. — For diagnosis, see p. 196.

That *Germanophyton psygmophylloides* is generically different from our new plant from Spitsbergen is beyond doubt. As regards the possible relationship between them, see also p. 188.

2. *Platyphyllum Brownianum (Cyclopteris B.)*, from the Perry Basin in Maine, was described by Dawson in 1861 or, probably more correctly, 1862.

As to the specific name of this plant some words will be necessary. — It was described by Dawson in two papers which appeared almost simultaneously. In one of them, *viz.* in a chapter on plant fossils in "General Report upon the Geology of Maine. Sixth Annual Report of the Secretary of the Maine Board of Agriculture", by C. H. Hitchcock (p. 250; text-fig. 5) he used the name of *Cyclopteris Browniana*. This report bears the date of 1861 on the title-page. — In a paper in the Quart. Journ. Geol. Soc. Vol. XVIII (p. 320; Pl. XII fig. 9), read on May 7th, 1862, he also described some plants from the Devonian of North America, among them the same specimen from Perry; also here he called it a n. sp., but used the epithet of *Brownii*. As this part (Vol. XVIII Part 4) of the Quart. Journ. was published on November 1st, 1862, it would appear that '*Browniana*' was the older name and consequently the valid one, but for two circumstances that complicate matters:

In a foot-note of the paper in the Quart. Journ (p. 298) Dawson referred to the Report from Maine as being still in press. This statement might seem to indicate that, after all, '*Brownii*' must have appeared first. A probable explanation is, however, that it was in press when he prepared his manuscript for the paper to the Quart. Journ., and that he did not alter the note even if the Report was published at the time when the said paper was printed.

In the bibliography compiled by Ami (1901) the year of publication of the Report is given as 1861. In order to make quite sure I have applied to Mr. G. E. Mit-

Fig. 21. First illustration of *Platyphyllum Brownianum* Dawson (1861).

Fig. 21.

chell, Librarian of the U. S. Geological Survey, who has most kindly directed my attention to facts proving that the Report must at least have been printed after December 31st, 1861. Accordingly it will be very difficult, or perhaps impossible, to ascertain whether the form '*Brownii*' or '*Browniana*' is the one that was published first. The weight of the evidence seems to be rather in favour of '*Browniana*', and this form of the name was also used by Dawson in some other publications from the years 1862 and 1863, whereas he later always wrote '*Brownii*'. It is not unlikely that the name has at first been altered by the editor of the Quart. Journ., the change having then been accepted by Dawson.

As the adjectival form may be the older one, it will be used here.

The specimen on which the species was founded in 1861, was a poor fragment (text-fig. 21) which I have not been able to locate.

The species was mentioned in several papers after 1861 by Dawson (for bibliography, see White 1905 p. 37, where, however, there is a misprint, as the quotation from the Quart. Journ. 1862 should be read '*Brownii*' instead of '*Browniana*'); the best description and illustration is the one from 1863 (Dawson 1863 *b* p. 463, Pl. XVII fig. 6), which was founded on new material from the Perry Basin, comprising at least one good specimen. The same specimen was also figured by White (*l. c.* Pl. II fig. 1), who at the same time published a drawing of another specimen and gave a full redescription and discussion of the plant. — In 1882 Dawson described some specimens of a plant from Scaumenac Bay, Canada, referring them (no doubt erroneously) to the same species; on that occasion he proposed *Platyphyllum* as a new genus name for it, in case it should be "considered desirable to remove it from *Cyclopteris*".

Lesquereux (1879—1884 p. 312) regarded the species as probably identical with the plant which he described (*l. c.*) under the name of *Rhacophyllum truncatum;* but that cannot be so. — Arber (1912 p. 398) transferred it to the genus *Psygmophyllum*.

All figures of this plant published so far have been drawings; this fact alone made it desirable to examine some specimens, the more so because among all fossils described it seemed to be the one best comparable to those from Spitsbergen. Thanks to the great kindness of the late Professor W. C. Darrah I have obtained a photograph of a specimen which belongs to the Boston Society of Natural History and which he was permitted to borrow in order to have it photographed. It is reproduced here as Pl. XLIII. This specimen must be the one figured by Dawson 1863 and by White 1905, as referred to above, and it ought to be regarded as the type specimen (neotype), as also proposed by Arber. — For comparison I have further, through the kindness of Dr. W. N. Edwards, obtained the loan of some excellent speci-

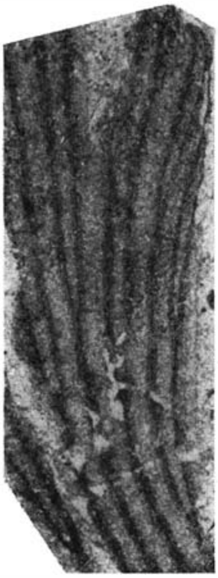

Fig. 22.

Fig. 22. *Platyphyllum Brownianum* Daws., from Perry, Maine. Details, showing the venation. — Brit. Mus. V. 19358. × 2.

mens belonging to the British Museum (Pl. XLIII figs. 1—2); for this permission I beg to express my respectful thanks.

These leaves from Maine are fairly distinct, but not really well preserved. In the general form and in the venation they have a marked resemblance to our Spitsbergen plant, and the points of difference, as far as the morphology is concerned, are rather unimportant: The veins are slightly coarser and somewhat less well-defined. At the base the leaves are somewhat more attenuating into a distinct petiole. Further, to judge by the descriptions and by the specimens examined, they are always found isolated, in contrast to the new species from Spitsbergen, which, in the collection at hand, are practically always attached to axes of a very characteristic type. A specific identity is out of the question, but, from the evidence of the external characters mentioned, it might seem quite likely that they belonged to one and the same natural genus.

However, it has also been possible to obtain at least some knowledge of the anatomical structure, although the state of preservation is far from promising, giving no opportunity to make preparations of any kind (attemtps in that line also had to be desisted from on account of the scarcity of the material). The only structural details found are of the kind shown on Pl. XLIV figs. 3—8, which have been photographed directly on the fossil. All of them are from the veins of V. 699 (Pl. XLIV fig. 2).

What is seen are tracheid-like cells. In some cases they seem to be rather short, perhaps only as the result of defective preservation. In other cases (as in Pl. XLIV fig. 3) they are considerably longer; exact measurements have not been possible, but they may perhaps attain a length of at least 1 mm. The breadth may be about 50—60 μ. Mostly they are strictly longitudinal and quite straight, but it also happens that they are somewhat more irregular and slightly flexuose. They are closely in contact with each other, leaving no intercellular spaces between them. The walls give the impression of having been thin; but there are annular thickenings, which are delicate and dense, the distance between the thin transversal bands being much less than the diameter of the cell. In neighbouring cells the transversal bands are generally on the same level; alternation does occur, but has been observed much less frequently. — Between these cells there are sometimes

Fig. 23. *Platyphyllum Peachii* n. sp., part of holotype, from John o'Groats. — Brit. Mus. V. 9412. × 2.

Fig. 23.

narrower ones, which may be more curved and flexuose, and in which the annular thickenings are either lacking or difficult to observe; in the case illustrated in Pl. XLIV fig. 8 there even seems to be tube-like cells curved in an almost horizontal direction. Observations as regards these narrower cells are very incomplete, but at all events they do not give the impression of representing a histological element much different from the wider tracheid-like cells. Other cell types have not been found.

The anatomical details here described differ from what little is found in the new plant from Spitsbergen, but the bearing of this difference is difficult to judge of at present.

It is preferable to retain these isolated leaves provisionally in an organ genus, for which *Platyphyllum* will be the proper name. The reasons for choosing this genus name from among those which might come into consideration will be given below (p. 110).

3. In connection with *Platyphyllum Brownianum* it will be necessary to consider some British specimens, which have been mentioned in the literature with reference to that species.

3 *a*. Most important of them is the V. 9412 of the British Museum, a specimen which has been referred to by several authors, but which has never been figured in literature. Thanks to the kindness of Dr. W. N. Edwards I have obtained a loan of this specimen, with permission to publish the necessary description of it here (cf. Pl. XLV, Pl. XLVI figs. 1—9, and text-fig. 23).

The specimen bears several labels. One of them, and probably the oldest one, has the following text: "Beautiful. John o'Groats. Caithness. C. W. Peach. Coll. April 1869", another label, of the same kind of blue paper: "*Cyclopteris* allied to *C. Brownii*".

According to information from Dr. Edwards, there is no doubt that this is the specimen referred to by Dawson (1871 *a* p. 77) in the following words: "Mr Peach's collections also include a *Cyclopteris* of the type of *C. Brownii*." This remark is later quoted by Peach (1880 p. 151), who adds some details about the place where the specimen had been found. — Seward (1923 p. XCIX) also referred to the specimen, in the following words: "A specimen in the British Museum (Natural History) from the Middle Devonian of Caithness bears a close resemblance to an Upper Devonian species named by Dawson *Platy-*

phyllum brownianum, and in shape agrees with the genus *Psygmophyllum* as represented in the Upper Devonian flora of Spitsbergen and in the Carboniferous floras of different regions. Dr. David White considers that Dawson's *Platyphyllum* is probably algal, and not a true leaf. The Caithness fossil, although it may be a leaf, shares with the Canadian specimens the possession of delicate vein-like markings which do not suggest true vascular strands." (Compare also Seward 1931 p. 139, where the specimen is briefly mentioned.) It has also been referred to by Lang (1927 *b* p. 6—7): "One of the few peculiar plants known from John o'Groats has the appearance of a fan-shaped leaf and is called *Platyphyllum Brownii.*"

The specimen is preserved in a dark, somewhat olive-coloured shale of fine grain, and forms a very thin film with small amounts of organic matter. As visible from the photograph (Pl. XLV fig. 1) it is fan-shaped, in the form of a sector of a circle, the sides being slightly curved inwards. It is about 3.4 cm long and equally broad at the top; the base is incomplete. There are numerous veins, radiating from the base, where they seem to be quite few in number, and bifurcating somewhat irregularly upwards, so that they are denser at the periphery than at the base. The veins are somewhat curved and flexuose, perhaps partly due to distortion during fossilization. Beside the main ones, which are rather uniform in breadth (mostly 1.5—2 mm), there are others, much thinner, leaving the main veins at acute angles, and forming an irregular network between them. (Some further details are given below.)

The leaf is split from the periphery and inwards between the veins. It looks as if the margin had originally been regularly dentate, each tooth corresponding to the end of one vein, or to a couple of them. Perhaps there have also been some slightly deeper incisions, but the large fissures reaching far into the leaf seem to have arisen through secondary splitting. It is not certain whether the lateral borders, as seen on the fossil, represent the original sides of the leaf, or are the result of the splitting of a broader lamina; to judge from the appearance of the outline the latter alternative is quite probable.

With regard to the internal structure, only rather incomplete, but quite remarkable results could be gained. Some details are seen when the fossil is examined, or better photographed, in a dry state, under fairly strong magnification (× 50 and more) and under various kinds of illumination (Pl. XLV figs. 4—5). But far more becomes visible if the specimen is moistened with xylol (Pl. XLV fig. 6, Pl. XLVI fig. 1—5). It has not been possible to make preparations and to deal with this unique and very valuable specimen as can be done when the material is more ample; but I covered a very small area (on the left-hand side of the fossil) with cellulose glue, in the hope of obtaining such results as in the case of the Spitsbergen material. This attempt failed, no additional structure becoming visible; but when the cellulose film was removed, some very small fragments of carbonized tissue followed, so that two small film pulls were thus obtained. They might have been macerated, but in a cautious attempt to clear one of them, the fragments of tissue began to loosen from the cellulose film, and I therefore preferred to keep them unchanged. Even in this state, however, they showed a few details of interest.

When examined dry on the fossil the veins are seen to consist of straight parallel cell tubes (or cell rows?) of uniform breadth, only about 15—20 μ. Ends not being observable, the length cannot be measured, but it must certainly be very considerable. They have not the properties of tracheids, but in some cases there are indications of transversal lines which must be either cross-walls or annular thickenings (Pl. XLV figs. 4—5). Similar lines are faintly seen in the film pulls (Pl. XLVI), and quite distinctly in a few instances when the specimen is photographed in xylol (Pl. XLVI figs. 2 and 4). The distance between the transversal lines is about equal to the diameter or somewhat less.

In photographs like Pl. XLV fig. 6 and Pl. XLVI figs. 1 and 5 some other remarkable features are seen: The veins, when examined in this magnification (× 50), are by no means so uniform and well defined as they might seem to be to the naked eye or when the fossil is examined dry. They are really disintegrated, split up into bundles of very unequal size, some of which consist of only a few tubes, or even of one. Sometimes these bundles are twisted around each other (Pl. XLV fig. 6). They may reunite with the main strand, but it also happens that they diverge, either disappearing into the matrix, or uniting with a neighbouring strand. Cross-sections, or oblique sections, of bundles running through the matrix at an angle to the splitting plane, are found in considerable numbers; some of these sections, when somewhat oblique, strengthen the impression that the tubes are septate (Pl. XLVI figs. 3—4). — The most natural explanation of this distintegration is that the fossil has undergone some maceration before becoming imbedded. It shows that the tubes, whether septate or not, have a certain strength and a certain independency in relation to each other.

In the preparations there are also some very poorly preserved remains which could scarcely be interpreted as being anything but a cortical tissue. It is best, but not exclusively, seen between the veins. It appears to consist of isodiametric cells of somewhat unequal sizes, arranged without any strict order and mostly incompletely preserved. A conspicuous feature are some holes, measuring only about 3—4 μ, irregularly scattered, but quite numerous. They are distinctly bordered by a wall, from which, in some cases, other lines (cell-walls?) are radiating. In a very few cases a structure, looking like a regular ring of cells, completely surrounds the hole (upper left corner of Pl. XLVI fig. 9). Under the holes one might expect to find remains of stomata, but there are no traces of such structures. — It should be emphasized that the lines looking like cell-walls, as well as the holes, may merely be the results of shrinkage, unequal dissolution, or other physical and chemical processes. But at all events these preparations prove that the plant has consisted of something more than the tubes referred to above.

As to the systematic position of this fossil, it doubtless represents an undescribed species, but the question is to what genus it may be referred. The only species previously described with which it may be compared, seems to be *Psygmophyllum fissipartitum* K. & W. There are some points of undeniable resemblance in the general morphology of these leaves, although there is evidently a rather profound difference in the internal structure (cf. p. 105), a fact, the significance of which it is difficult to judge of at present. However, even if there should be a natural relationship between the two species, it will be of but little help in the choice of a generic name for the plant from Caithness, because it is equally uncertain to what genus the German species may belong; in my opinion it should not be referred to *Psygmophyllum* (p. 105).

Personally I am convinced that the leaf from Caithness represents a new genus. But as it is not yet so completely known for a diagnosis of sufficient value to be given, it is preferable to keep it provisionally in an artificial genus together with several other broad, fan-shaped leaves, and the name for such a genus used here is *Platyphyllum* (p. 110).

The new species may be called *Platyphyllum Peachii.* — For diagnosis, see p. 196.

3 *b*. After having mentioned the specimen just described, Peach (1880 p. 151) also refers to another specimen in the following words: „At Turin Bay, near Forfar, the same kind of *Cyclopteris* occurs, also well marked and in a beautiful state of preservation. It occurred in the calmstone there, with *Psilophyton* stems in abundance; these as opaque objects show the structure well."

Thanks to the kind assistance of Mr. F. W. Anderson, Paleontologist of the Geological Survey at Edinburgh, I have obtained the loan of the specimen, which belongs to the Royal Scottish Museum, Edinburgh (as Number PB—D 53), and have most obligingly been permitted to include a description and illustration of it here; to my knowledge the fossil has never been figured before in literature.

It is preserved in a greenish grey shale of very fine grain and irregular splitting. According to a label fixed to it it was collected on October 10th, 1871, by W. Peach. The only fossil on the slab is the impression of a leaflet (Pl. XLVI figs. 10—11). It is approximately triangular, unsymmetrical, somewhat cordate at the base and rounded along the two other sides. Petiole thick, but very incompletely preserved. Margin entire or very slightly undulating. Veins fairly thick and distinct, starting in a small number in the petiole (so far as this is preserved) and dividing upwards in a somewhat irregular dichotomy. Anastomoses distinctly observable, but not very frequent. The vein ends reach the leaf margin.

In spite of its characteristic form and venation (as to which it might be compared with a small *Linopteris* pinnule) this fossil is too imperfect for a full determination. It seems to occupy a very isolated position among Devonian plants, being different from all other broad leaves here under consideration. Certainly it is probable that the plant belongs to the same main group as some of the species here referred to *Platyphyllum*; but presumably it will be most correct at present to list it as an indeterminable leaf of uncertain position.

4. *Psygmophyllum fissipartitum* K. & W. was recently described by Kräusel & Weyland (1935 *a*) on the basis of a specimen from the Lower Devonian of the Rhine Area, and the authors succeeded in demonstrating, in admirable preparations, that it possessed two slightly different types of parenchymatous tissue, surrounding strands of cells which looked very much like tracheides; they were described as having reticular or scalariform thickenings.

As to the external form, this species (which I have not seen personally) seems to have a marked resemblance to *Platyphyllum Peachii* (described above, p. 101), but in the anatomical structure, as far as is known, they are rather different.

As to the generic name of this species, it is impossible to refer it to *Psygmophyllum* if this genus is accepted in the delimitation given to it by Saporta (cf. p. 108) and afterwards by Zeiller, Zalessky, and Gothan & Kukuk. Kräusel & Weyland (1935 *a* p. 6; 1934 p. 173) declared that they agreed with the two last-mentioned authors in their conception of the genus, but to refer the species *fissipartitum* to the genus *Psygmophyllum* is not in keeping with this view: Gothan & Kukuk reserved the name of *Psygmophyllum* for the species with pinnatisect leaves of the *cuneatum*-type (from which *fissipartitum*, in spite of its divided lamina, is very different), and it is not correct to say: "Als *Psygmophyllum* möchten Gothan & Kukuk dagegen die Formen mit 'deutlicherer lockerer Aderung' zusammenfassen", *viz.* "*Ps. majus*, *haydeni*, *williamsoni* etc.". The confusion is increased by the fact that Gothan & Kukuk, in the place referred to, put *Williamsoni* in the group of species with 'lockerer Aderung', whereas it really has a dense and delicate venation.

It will be necessary to remove this species (*fissipartitum*) from *Psygmophyllum*, and until more is known of the entire plant it will have to be left in some artificial genus. In spite of the very remarkable and characteristic details which have been made known, and which are somewhat different from what little is known from the other species here referred to *Platyphyllum* (cf. p. 110), it seems justifiable to give it, provisionally, the name of that genus.

5. *Ginkgophyllum Buddei* K. & W. (1934), from the Middle Devonian of Elberfeld, is very interesting in this connection, and I am very much obliged to Professor Kräusel for kind permission to borrow the specimen and to publish some more photographs, in addition to those published by Kräusel & Weyland (1934).

As to the macroscopical characters this leaf is peculiar, above all on account of its very broad and dense veins, which are about 0.7—1 mm broad, the distance between them often being less (Pl. XLII fig. 1). In this respect it differs from all other leaves here described; the one most resembling it so far is the large leaf of '*Prototaxites*' *psygmophylloides*, but that leaf is so poorly preserved that the structure is not clearly seen (text-fig. 20). The resemblance has also been mentioned explicity by Kräusel & Weyland (1934 *b* p. 174), who, however, rejected the possibility of a relationship on account of the anatomical structure.

To a large extent the systematic position of *Ginkgophyllum Buddei* depends upon the nature of the cells of its veins, described by Kräusel & Weyland as tracheids with 'Tüpfelstrukturen'. These cells are very long, and may be traced continuously for a distance of at least upwards to 1 mm; branching has not been observed with full certainty. They are about 50 μ wide and less. It was rather difficult to observe and to photograph the pits of the walls, which were preserved only in a few places; but our Pl. XLII figs. 3—4 may show them fairly well: The pits are small, of uniform size, placed densely all over the wall and often, but not always, in transversal rows; one such row may contain 5 or perhaps more pits. Other cell types have not been observed.

This fossil no doubt represents a distinct species, differing both in its external and internal characters from the other broad leaves of Devonian age here described; but it may well belong to the same main group as some of them. As a provisional name for it I would prefer to use the new combination *Platyphyllum Buddei*, for reason given on p. 110.

6. *Psygmophyllum Gilkineti* Leclercq, from the Middle Devonian of Belgium (Malonne, Prov. de Namur) is so far unique in the Devonian flora; the external morphology of its vegetative organs is fairly well known and different from that of the contemporaneous plants, the axis being stout and branched, the leaves very large, fan-shaped, and borne on very long, not decurrent petioles. The venation is dense, and of the same type in the leaf blade and in the petiole, the latter containing a great number of parallel or rarely bifurcating veins. Thanks to the

Fig. 24. *Ginkgophyton Gilkineti* (Leclercq) n. comb. ad int., from Belgium. Details of holotype, compare Leclercq (1928). *a.* Part of long petiole (*l. c.* Pl. III fig. 6, 13 *b*₁); entire length of the petiole about 30 cm, part of it being found on a fragment not visible on the figured cited. *b.* Part of leaf (*l. c.* Pl. III fig. 5, right-hand side). — Univ. Liége. Nat. size.

Fig. 24.

kindness of Mlle Leclercq, I have had the opportunity to see two specimens from the *Musée Royal d'Histoire Naturelle de l'Université de Liége*, among them the one shown in Pl. III figs. 5—6 of Leclercq 1928; photographs of some parts of it are also shown here in text-fig. 24. To judge by the specimens seen and by the original description and figures, the species in my opinion deserves to be placed in a separate genus, which, in spite of the lack of knowledge as to the reproductive organs, will have the character of a natural genus. However, as it is the intention of Mlle Leclercq to re-examine the plant it will not be discussed further here; but as it is impossible to retain the species in the genus *Psygmophyllum*, in the delimitation accepted here, I propose to refer it provisionally to the genus *Ginkgophyton* (p. 110).

Apart from the double size of its leaves it has a very marked resemblance to *Ps. Williamsoni*, but as in *Ps. Williamsoni* the mode of attachment of the leaves is entirely unknown, it is impossible at present to judge of their systematic relationship.

7. From the lower Upper Devonian of Liebichau and other places in the neighbourhood of Waldenburg (Silesia), Gothan & F. Zimmermann (1932, 1937) have described some large, *Cyclopteris*-like leaves, of which one (1937 p. 500, Pl. XXIV fig. 7) is fairly complete and evidently attached to a slender axis, whereas the others, which possibly represent the same species, are much more fragmentary (1937 p. 499, Pl. XXIII fig. 11, and p. 502, Pl. XXV fig. 4; 1932 p. 118 Pl. XIV fig. 4, and p. 120, Pl. XVII fig. 5). They certainly do not represent the same species as our *Enigmophyton* from Spitsbergen. But it is scarcely possible to say anything definite about their relationship to that plant, or to any of the other Devonian plants with a similar type of leaf.

The species cannot remain in the genus *Psygmophyllum*. In spite of its axis, but on account of its uncertain characters, it may rather be transferred to *Platyphyllum*, although that is particularly a genus of detached leaves.

III. Nomenclature of *Psygmophyllum*. — Many of the species mentioned in the preceding pages have been referred, by one author or another, to the genus *Psygmophyllum*, and for the sake of nomenclature it will be necessary in this place to go into details concerning this genus.

For many years *Psygmophyllum* has been the centre of great confusion, not only because of our total ignorance of the reproductive organs of nearly all the plants in question, and of their true systematic position, but also, and chiefly, because so many widely different plants have from the very beginning been brought together under this generic designation. The question has attracted considerable interest of late, and several recent contributions, notably by Zalessky, Gothan & Kukuk, and Halle, have done much to clear up the question. At the same time the opinion of the right use of the name of *Psygmophyllum* has changed among most authors; but still, even within the last ten years, new species of the most different organization have been added to those already bearing this misused name.

Schimper, when instituting the genus (1870—1872 p. 192) let it comprise four species. One of them, *P. ctenoides* (Goepp.) Sch., from the Permian of Silesia, stands in an isolated position and may be excluded from further consideration. — Among the other species, the two from the Permian of Russia, *Ps. expansum* (Brogn.) Sch. and *Ps. cuneifolium* (Kutorga) Sch., both of them previously included in *Noeggerathia* Sternb., have pinnate leaves with large, cuneate, dissected leaflets, with midribs (according to Halle 1927 *a* p. 215), whereas the fourth species, *Ps. flabellatum* (L. & H.) Sch., from the British Upper Carboniferous, has simple, fan-shaped leaves borne on decurrent petioles in spiral arrangement on an axis.

Already Saporta called attention to the fact that these plants were generically different, and (1878) proposed to refer *Ps. flabellatum* to the genus *Ginkgophyllum* which he had instituted a few years before for the species *G. Grasseti* Sap. from the Permian of Lodève. Renault (1881 p. 65) and Schimper & Schenk (1890 p. 260, cf. p. 252) agreed with him.

Arber (1912), however, adopted the opposite course, regarding *flabellatum* as the type of the genus *Psygmophyllum*, and excluding the other species. Seward (1919), in a detailed review of the genus, used the name in a similar sense and with a very wide circumscription, and that has also been done by Nathorst, Leclercq, and others.

Zalessky also recognized the generic difference between the *expansum-cuneifolium*-group and the *flabellatum*-group, and in 1912 removed the former to a new genus *Palamophyllum* (in which he also included *Ps. mongolicum* Zal.), thus (at this time) using *Psygmophyllum* in the same sense as Arber. Zeiller, in some letters which Zalessky afterwards published in part, brought to light again what Saporta had written in 1878, and agreed with Saporta that the *expansum-cuneifolium*-group should be regarded as the typical *Psygmophyllum*, in accordance with the diagnosis given by Schimper. Agreeing to this view Zalessky abandoned the genus *Palamophyllum*, as a synonym for *Psygmophyllum*, using the latter name and that of *Ginkgophyllum* in the same meaning as Saporta. — In 1918 (p. 47) Zalessky proposed a new name, *Gingkgophyton*, to replace *Ginkgophyllum* for the plants of the *flabellatum*-group, because he arrived at the conviction (as did Arber in 1912) that it was not correct, or at least not practical, to keep these large, fan-shaped leaves in the same genus as *G. Grasseti* Sap. with its

Table 3.

Some main points in the synonymy of Psygmophyllum.

	expansum —cuneifolium	*flabellatum*	*Grasseti*
Schimper 1870—72	*Psygmophyllum* Sch.	*Psygmophyllum* Sch.	
Saporta 1878	*Psygmophyllum*	*Ginkgophyllum* Sap.	*Ginkgophyllum* Sap.
Arber 1912		*Psygmophyllum*	*Ginkgophyllum*
Zalessky 1912	*Palamophyllum* Zal.	*Psygmophyllum*	
Zalessky 1918	*Psygmophyllum*	*Ginkgophyton* Zal.	*Ginkgophyllum*
Gothan-Kukuk 1933	*Psygmophyllum*	*Ginkgophyllum*	*Ginkgophyllum*
Present paper	*Psygmophyllum*	*Ginkgophyton*	*Ginkgophyllum*

smaller leaves, deeply divided into narrow segments; the new genus (as to the history of its name, *Ginkgophyton*, see also Halle 1927 *a* p. 215) was consequently a substitute for Arber's *Psygmophyllum*. Gothan & Kukuk (1933) adopted this view, so far as the definition of *Psygmophyllum* was concerned, but did not regard the differences between *Ginkgophyllum* and *Ginkgophyton* as sufficient for the separation of genera. The same course was followed by Halle (1927 *a* p. 214) and by Kräusel & Weyland (1934 *b*, but not 1935 *a*, compare above, p. 105).

The *flabellatum*-group is the one that particularly interests us on this occasion. There are three possibilities as to the choice of a genus name: (1) *Psygmophyllum*, (2) *Ginkgophyllum*, (3) *Ginkgophyton*.

The name of *Psygmophyllum* may be left out of further account. The diagnosis given by Schimper, and his comparison with *Sphenopteris*, evidently make it necessary to follow Saporta and the other authors mentioned, and to reserve the name for the group of *expansum-cuneifolium*, although it is regrettable on account of the many names which will then have to be changed.

The choice between *Ginkgophyllum* and *Ginkgophyton* is more difficult; it depends upon the relation of *G. Grasseti* to the other species. If we had to deal only with the two species *Grasseti* and *flabellatum* no uncertainty would arise at all: They are so different that no one would think of uniting them into one genus. In the former the leaf lamina is divided by regular dichotomy whenever the breadth has passed a certain maximum, the leaf thus having a striking resemblance to some species of *Baiera* (from which it differs in having a long sheathing leaf-base), in contrast to the other species, *flabellatum*, with its simple, broad, fan-shaped leaves, in which, at most, the upper margin may be sinuous or secondarily split. There are also other species grouping naturally around these two: The type of *flabellatum* is joined by *Ps. Delvali* and probably others (cf. *Ps. Gilkineti*, *majus*, and *Williamsoni*, p. 110, 111). To the group of *Grasseti* belong *G. Vselovodi* and *simile*. — But there are forms which may be said to be intermediate: In *Ps. Kidstoni* some of the leaves seem to be divided nearly to the base by a median fissure; however, its leaf-form in general is that of *flabellatum*, and if there really is any true relationship between these two species (which may be very doubtful) *Ps. Kidstoni* does not in the least bridge the gap between the *flabellatum* group and *G. Grasseti*. — There may be some more uncertainty in the case of *Ps. scoticum* Wilson, which was described in 1934, on the basis of four detached and probably incomplete leaves from the Upper Carboniferous of Scotland. As regards the breadth and form of the leaves, which are constantly bifid, and obtusely pointed, the species may be said to be fairly intermediate between the two groups. But it seems somewhat doubtful whether it belongs to any of them at all, the anastomoses of the veins being an important character, evidently not found in any of the other species. At all events it is impossible to include it in the *flabellatum*-group.

Thus, there are no real difficulties in drawing a boundary line between the two groups, and on account of the very considerable difference between them (a difference far more marked than that between *Ginkgoites* and *Baiera*, for instance), it seems preferable to keep them apart as different genera, respectively *Ginkgophyllum* Sap., with the type species *G. Grasseti*, and *Ginkgophyton* Zal.; the latter genus corresponds to the emended diagnosis given by Leclercq (1928 p. 10) for *Psygmophyllum*, being characterized by broad cuneate or flabellate leaves, borne spirally on herbaceous or woody axes, usually with sheathing leaf-bases, and with a dense venation of delicate, bifurcating veins. The type species is *G. flabellatum* (Lindl. & Hutt.) Sap., to which *G. Delvali* (Camb. & Ren.) n. comb. is closely related.

The genus *Ginkgophyton*, which interests us particularly here, is still very incompletely known, all information as to its anatomical structure being lacking, and the only hint as to its reproductive organs being the discovery, by Gothan & Kukuk, of *Telangium*-like organs in association with the leaves of *G. Delvali* (but not in organic connection with them).

In addition to those mentioned, there are not many post-Devonian plants, if any, to be included in the genus *Ginkgophyton*. Some authors have put the South African species *Psygmophyllum Kidstoni* Sew., which was mentioned above, into the same group as *G. flabellatum;* a true relationship between them does not seem probable, but temporarily it may be referred to *Ginkgophyton*. This course is scarcely possible in the cases of *Ps. Haydeni* Sew., from the Permian of Kashmir (supposed by Seward to be closely allied to *G. Kidstoni*); in all probability these two species belong to other genera than *Ginkgophyton*.

Among the Devonian species of plants with cuneate or flabellate leaves, *Ps. Gilkineti* is the only one (apart from our new *Enigmophyton superbum*) in which the leaves have been found in connection with the axis. It differs from *G. flabellatum* and *Delvali* in the form of the petiole, which is long and slender in relation to the size of the leaf, and not decurrent, and it is also remarkable for its stout woody axis; as mentioned above, it probably belongs to another natural genus, but provisionally it may be referred to *Ginkgophyton*.

As to the other Devonian plants in question, most of them are strikingly different from the true Ginkgophytons, and, although the difference may be difficult to define in a precise diagnosis, they should rather be kept apart in order not to burden the genus *Ginkgophyton* more than necessary. Only one of them has already got a valid generic name, *viz. Platyphyllum Brownianum* Daws.; the fact that this genus name was proposed by Dawson (1882 p. 101) in connection with the description of some additional material which he erroneously referred to the type species (and which does not even belong to the genus at all), has no influence upon its validity, and it may be taken as the name for most of the species in question, *viz. Brownianum*, *Peachii*, *fissipartitum*, *Buddei*. The characters which they have in common are mentioned in the diagnosis p. 196.

Platyphyllum is an artificial genus, and rather heterogeneous. No doubt, it will one day become possible to unburden it of such a species as *P. Buddei*, and it is also quite possible that *P. fissipartitum* and *P. Peachii* will be found to be more closely related to each other than to the rest; but provisionally they may be kept together. The delimitation against *Ginkgophyton* may be difficult, however; this is particularly due to the uncertain position of *P. Williamsoni* Nath.

The structure of the leaves of *P. Williamsoni*, particularly their dense and delicate venation, gives it a strong resemblance to the typical Ginkgophytons, and is in contrast to that of the other species referable to *Platyphyllum*. However, the appearance of its venation may to a certain extent be due to the mode of preservation, and the external form of the leaf differs from that of *G. flabellatum*; further (and what is perhaps the most important point), the leaves of *Williamsoni*, in contrast to those of the true Ginkgophytons, are only known in a detached state. It therefore seems more practical to refer the species, at least temporarily, to the genus *Platyphyllum*.

The same will probably also hold good of the plant which Arber in 1912 described under the name of *Ps. majus*, from the Lower Carboniferous of Newfoundland. It has more distant and well-defined veins than the preceding species; in fact, as far as this character, and the size and form of its leaves are concerned, it resembles our new *Enigmophyton superbum* more than any other species. On account of our incomplete knowledge of these detached leaves, however, it is perhaps best at present not to refer it to any of the two relatively well-known genera *Ginkgophyton* and *Enigmophyton*, but to list it provisionally together with the preceding species as *Platyphyllum*. It may be added that, according to the explicit statements of Arber (*l. c.*), only detached leaves have been found of this species; it must therefore be a lapse when Gothan & Kukuk 1933 p. 72 mention it as one of the more completely known species with leaves spirally attached to shoots.

These two species, *Williamsoni* and *majus*, show that doubt may arise as to the circumscription of the genus *Platyphyllum* in relation to other genera, particularly *Ginkgophyton;* this fact is regrettable, but it is compensated for by the advantage of having a practical name for these remarkable leaves, most of which doubtless bear no close relationship to the typical species of *Ginkgophyton*.

As to the new plant from Spitsbergen, which has made the preceding review necessary, the comparison with specimens and descriptions now referred has shown that it is specifically different from all Devonian plants previously described. It has a good deal in common with *Platyphyllum*, and if its leaves had been found detached, they might have been referred to that genus. But with our knowledge of their mode of attachment and of the axes, with their very characteristic mode of branching, it will be possible and necessary to put it into a genus of its own (*Enigmophyton*), the latter being a natural genus, not an artificial form genus like *Platyphyllum*.

Prototaxites psygmophylloides, however poorly known, is also sufficiently well characterized for being removed from the genus *Platyphyllum*, to which it otherwise might belong, in order to form the type of a separate genus (*Germanophyton*).

A number of other species, including some from the Devonian, have been referred to *Psygmophyllum* at various times, but should be excluded from this genus and transferred to others; among them are *Ps. kiltorkense* (Johnson) Seward (p. 79), *Ps. pusillum* Nath. (p. 94), *Ps. Kolderupi* Nath., and *Ps. obtusum* (Lesq.) Arber.

The last-mentioned species was founded, in 1858, by Lesquereux under the name of *Noeggerathia obtusa*, on the basis of some leaves from the Carboniferous of Pennsylvania, and to the same species, which he transferred in 1880 to *Archaeopteris*, Lesquereux himself, as well as other authors, afterwards referred various plants from other localities and horizons; among them were the fine leaves from the Devonian of Scaumenac Bay, described by Dawson (1882 p. 100, Pl. XXII, as *Cyclopteris obtusa*). A good specimen from the Devonian of Sullivan County, N. Y., was figured by Prosser (1894 p. 49, Pl. II). On the basis of the figures published by Lesquereux and Dawson, Arber (1912 p. 398) wrote a new diagnosis of the species and most unfortunately included it in *Psygmophyllum*. — The plant from Scaumenac Bay has recently been fully treated, partly on new material, by Arnold (1936 *a*), who has shown that it is right to regard it as an *Archaeopteris* or at least as a relative of that genus. A discussion of the intricate nomenclature of the species is given by Stopes (1914 p. 56), with particular reference to a plant from St. John, New Brunswick, included in it by Dawson (1862 p. 319, Pl. XV fig. 33, and 1871 *a* p. 46, Pl. XVI fig. 188).

To conclude this discussion of the nomenclature of the genus *Psygmophyllum*, in its widest sense, we may give the following recapitulation of the genera and most important species:

I. *Psygmophyllum* Schimp. emend. Sap., syn. *Palamophyllum* Zal.
   1. *Ps. expansum* (Brogn.) Schimp. — Permian, Ural, Asiatic Russia. Type species.
   2. *Ps. cuneifolium* (Kut.) Schimp. — Ditto.
   3. *Ps. santagouroulense* Sap. — Ditto.
   4. *Ps. multipartitum* Halle. — Permian, China.

   Excludenda: *Ps. mongolicum* Zal. and *Ps. Potaninii* (Schmalh.) Zal. have been transferred to the genus *Angaridium* by Zalessky. — *Ps. ctenoides* (Goepp.) Schimp., from the Permian of Silesia, and probably *Ps. angustilobium* Schenk, from the Permo-Carboniferous of China, should also be excluded.

II. *Ginkgophyllum* Sap.
   1. *G. Grasseti* Sap. — Permian, France. Type species.
   2. *G. Vsevolodi* Zal. — Permian, Petchora.
   3. *G. simile* Zal. — Permian, Kousnetzk.
   4. *G. (?) scoticum* n. comb. (syn. *Psygmophyllum scoticum* Wilson). — Upper Carboniferous, Scotland.

   According to Zalessky (1937 *c* p. 66), *G. kamenskianum* Sap. from the Permian of the Ural Mountains, is identical with *Ps. cuneifolium*. — *G. kiltorkense* Johnson, see p. 113.

III. *Ginkgophyton* Zal., syn. *Psygmophyllum* sensu Arber.
   1. *G. flabellatum* (Lindl. & Hutt.) Zal. — Upper Carboniferous, Great Britain. Type species.
   2. *G. Delvali* n. comb. (syn. *Psygmophyllum Delvali* Camb. & Ren., *Ps. Purkynei* Šusta). — Upper Carboniferous. Central Europe.

   3. *G. (?) Kidstoni* n. comb. (syn. *Psygmophyllum Kidstoni* Seward). — Ecca Beds, Natal.
   4. *G. (?) Gilkineti* n. comb. ad int. (syn. *Psygmophyllum Gilkineti* Leclercq). — Middle Devonian, Belgium.

IV. *Platyphyllum* Daws.

   1. *P. Brownianum* Daws. — Upper Devonian. Maine.
   2. *P. Peachii* n. sp. — Middle Devonian, Scotland.
   3. *P. fissipartitum* n. comb. (syn. *Psygmophyllum fissipartitum* K. & W.). — Lower Devonian, Rhineland.
   4. *P. Buddei* n. comb. (syn. *Ginkgophyllum Buddei* K. & W.). — Middle Devonian, Elberfeld.
   5. *P. Williamsoni* n. comb. (syn. *Psygmophyllum Williamsoni* Nath.). — Middle Devonian, Spitsbergen.
   6. *P. majus* n. comb. (syn. *Psygmophyllum majus* Arber). — Lower Carboniferous, New Brunswick.
   7. *P. pusillum* n. comb. (syn. *Psygmophyllum (?) pusillum* Nath.). — Middle Devonian, Spitsbergen.
   8. *P.* sp. (syn. *Cyclopteris* sp. Nath.) — Middle (?) Devonian, Spitsbergen (West side, Billefjorden).
   9. *P.* sp. (syn. *Psygmophyllum* sp. Gothan & F. Zimmermann). — Upper Devonian, Waldenburg.
   10, 11. *P.* spp., cf. below, p. 116.

V. *Enigmophyton* n. gen.

   1. *E. superbum* n. sp. — Middle (or lower Upper) Devonian, Spitsbergen. Type species.

VI. *Germanophyton* n. gen.

   1. *G. psygmophylloides* n. comb. (syn. *Prototaxites psygmophylloides* K. & W.). — Lower Devonian, Germany. Type species.

VII. Some synonyms:

Ginkgophyllum kiltorkense Johnson, *Kiltorkensia devonica* Johnson, *Psygmophyllum kiltorkense* Seward = *Kiltorkensia kiltorkensis* n. comb.
Psygmophyllum Kolderupi Nath. = *Barrandeina Kolderupi* K. & W.
Psygmophyllum obtusum (Lesq.) Arber = *Archaeopteris obtusa* Lesq.

IV. — Conclusions as regards the biology of *Enigmophyton* and its position in the plant system depend very largely on the nature of its organs of reproduction. If the fructifications described below (p. 117) really belong to this plant, we know much more about it, and have a far safer basis for conclusions than otherwise. But as this connection cannot at present be demonstrated with full reliability, it is more correct first to consider the question in the light of our knowledge of the leaves and stems alone.

There is no reason to believe that the plant has been of a subaquatic habit. Particularly the form of the large solid leaves, which must have had a considerable firmness, is by no means what one would expect in a submersed plant, nor is their strong venation. If it had been possible to demonstrate the presence of cuticle and stomata, the case would not have been subject to any doubt; but the fact that it has not been possible to do so, may just as well be due to the preservation of the fossil as to its original structure.

Fig. 25. *Enigmophyton superbum* n. gen. & sp. Restoration. About 1/2 nat. size.

The long flexuose axes have probably also been rather stiff and firm; in so far they, no more than the leaves, bear any resemblance to the algae or other subaquatic plants. On the other hand, it must be admitted that if the plant has been terrestrial, as there is good reason to believe, the form of the axes does not make it easy to reconstruct the life-form of the plant: So far as one can judge from specimens, of which none is longer than 27.5 cm, the axes give the impression of having been of a very considerable length, and they are of a uniform thickness throughout, thus being relatively thin at the base. The position of the leaves shows that the plant must have been growing erect, not decumbent, but it is then difficult to understand that the axes have been strong enough for the large foliage. If one could assume that it had found support in climbing on other plants the difficulty would have been solved; but there is nothing to prove this supposition, nor to disprove it. To interpret the small lateral branches as hooks, like those found in some other climbing plants, recent or extinct, would be far-fetched; their shape is not what would have been expected if that had been their function.

At any rate, the plant is probably the finest member of the Devonian flora known so far. It has a regular and simple build, but within the limits of the strict regularity there is a great variation in the length of the internodes, in the gentle curves of the axes, and in the size of the leaves, some of which may have been more or less rolled up. The slender axes have a graceful flexuosity, and the form of the large leaves is beautiful.

Tracheids or similar cell forms have not been found in the fossil. This fact does not preclude the possibility of its having been a vascular plant, but the entire lack of strands, or impressions of strands, in the remains of the axes is rather remarkable. The only thing we know with certainty about the anatomical structure of the plant is that it had a superficial tissue looking like a parenchyma. But this fact is of no great help, because parenchymatous tissues are not characteristic of the cormophyta only.

On account of the resemblance of *Enigmophyton superbum* to the reconstruction of *Germanophyton psygmophylloides (Prototaxites p.)* published by Kräusel & Weyland (1930 p. 11), it may be emphasized that *Enigmophyton* certainly does not consist entirely of tubular cells like those of a *Prototaxites*, and that it does not even seem probable that any of its cells had that form. But from this fact we should not be justified in inferring, for example, that the plant has belonged to the pteridophyta, even in the widest sense of the word: it is possible that this was the case, but it is not yet proved.

The result of these considerations is rather poor: *Enigmophyton superbum* has probably been a terrestrial plant, but it is uncertain that it has been vascular.

If the fructifications described below (p. 117) belong to *Enigmophyton superbum*, it has had resistant, and probably cuticularized, spores, formed in tetrads. Although that would not prove that the species has belonged to the vascular plants, it would at least either show beyond doubt that it has been terrestrial, or that it has descended from terrestrial ancestors.

The position of the plant in the Devonian flora and in the plant system will be further discussed below (p. 187).

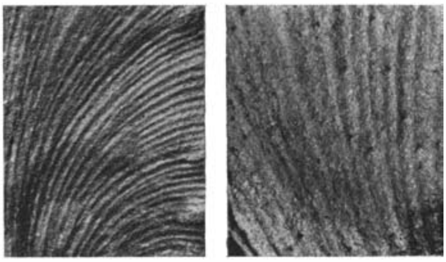

Fig. 26.

Fig. 26. *Platyphyllum* sp., from Mimerdalen: Planteryggen, compare Pl. XXXVII fig. 3. — PA 1256. *a* photographed dry, × 2, *b* in xylol, × 4.

Platyphyllum sp.

Pl. XXXVII fig. 3; text-fig. 26.

In the Planteryggen, and in the same beds as *Enigmophyton superbum*, there was found in 1928 a single fragment of a leaf, preserved as an impression without there being any organic matter left (PA 1256). The fragment is nearly circular, about 3 cm in diameter, incomplete both at the base and along the margin. The form must have been broadly fan-shaped. The veins are numerous, bifurcating, radiating from the basal part and curving towards the margin. They give the surface a very distinct relief, with ridges of a very uniform breadth of about 0.5 mm. — Scattered over the surface there is a great number of small conical depressions, filled with carbonaceus matter, which makes them appear as little dots, particularly when the specimen is moistened (text-fig. 26 *b*). They evidently belong to the fossil in some way or other, and they would be most easily explained as hair-bases; but one cannot entirely preclude the possibility of their being due to a parasite in the leaf. Other explanations do not seem likely.

This fossil might be supposed to represent a juvenile leaf of *Enigmophyton superbum*, but that is scarcely possible. The venation is much denser, and the specimen is therefore very distinctly different from that species, of which even the smallest leaf fragment seems to be characteristic enough to be easily recognized.

It is also different from *Platyphyllum Williamsoni* as regards the venation, but it is difficult to ascertain to what degree that is due to the mode of preservation. Identity is not entirely excluded.

On the other hand, the leaves of *Barrandeina Dusliana* and allied plants in a defective state of preservation may well be thought to have an appearance not unlike this fossil.

The specimen may be named *Platyphyllum* sp.

cf. *Platyphyllum* sp.

Pl. LVI fig. 13.

On a slab labelled (by Heintz, 1925): "Yellow sandstone above purple sandstone with plant fossils. Estheria Hill", is the plant fragment shown in Pl. LVI fig. 13 (PA 1151). It is leaf-like, about 2 cm long, 1.5 cm broad, with numerous parallel veins radiating from the base. It is split into several linear segments, which subdivide so as to end in filiform points.

The fossil is comparable to some of those which are above referred to the artificial genus *Platyphyllum*. It is, however, indeterminable, and it is mentioned here chiefly in order to show that in Mimerdalen also the parts older than Fiskekløfta have comprised rather remarkable forms.

Enigmophyton (?), fructification.

Pls. XLVII—XLVIII; Pl. XLIX figs. 1—12.

Locality, material. — The collection comprises four slabs containing good remains of this type of fructification (PA 390, 391, 469, 470), and a few more of minor value, all of them from Planteryggen in Mimerdalen (1928). Only parts of the fossils were originally exposed on the surface of the slabs, in which they were irregularly imbedded; most of them had to be uncovered cautiously by means of chisels and needles. As is the case with most of the fossils from this locality, a good deal of information could be gained through direct examination and photographing, whereas attempts to make film pulls were unsuccessful, and also had to be restricted on account of the scarcity of the material. But, by means of ordinary maceration, preparations of spores were obtained.

Description. — The fructifications have the form of elongate spikes, borne on smooth axes which bifurcate just below the spore-bearing region. Repeated bifurcation is seen in at least one case (Pl. XLVIII figs. 1—2, PA 470); here the second bifurcation takes place within the fertile part. The axis below the sporophylls does not bear any hairs or leaves or leaf-scars; as now preserved it is entirely naked and smooth, and it gives the impression of having been so also in the living plant.

The spike itself is generally 2—3 cm long and consists of an axis, bearing a great number of close-set sporophylls.

It is somewhat uncertain how the sporophylls have actually been arranged on the axis. As is evident from several of the photographs reproduced, there are facts strongly suggesting that the whole organ was bilaterally flattened, with sporophylls only along two opposite sides of the axis. But a closer study of the specimens, and particularly of the few cases where there is a kind of natural cross-section, makes it probable that the arrangement was not strictly bilateral, but spiral, or perhaps approximately verticillate, the sporophylls seen on the two sides of the axis often being nearly opposite (*e.g.* Pl. XLVII fig. 4); but it cannot be made out with full certainty whether this arrangement corresponds to any general rule. At all events the axis is not articulate.

Each sporophyll leaves the axis at about a right angle; very often it has a slightly downward direction, or more rarely it makes a double curve, first downwards, then upwards. The base of the sporophyll seems to be thick, while the distal part is quite thin; most probably it forms a flat, thin lamina, expanded transversally (cf. PA 469, Pl. XLVIII figs. 3—4). The length of the sporophyll is 2 (—2.5) mm. All observations make it probable that there is only one sporangium on each sporophyll. It is placed on the upper side of the latter, near the axis, and looks like a bladder of somewhat variable shape. The whole under-side of the sporangium is connected with the sporophyll. Usually it is somewhat irregularly semicircular in longitudinal section, with its greatest height near the central axis, and attenuating distally, running out into a beak-like prolongation. On the best preserved specimens this form is most frequently seen (Pl. XLVII figs. 3—4, PA 390). The slightly different forms sometimes found, may chiefly be due to changes during the process of fossilization; an exceptional case, although no doubt representing the same species, is seen in Pl. XLIX fig. 1 (PA 390), with its very high and narrow sporangium. The mode of dehiscence is unknown. Quite frequently there are found specimens without any sporangia observable, but consisting only of central axis and sporophylls, or remains of sporophylls (Pl. XLVIII figs. 7—9); it is natural to regard them as old fructifications which have lost their sporangia.

Spores may sometimes be seen in the sporangia, when the fossil is examined under a sufficiently strong magnification and moistened with a suitable liquid. The most conspicuous ones are seen in Pl. XLIX fig. 2 (PA 390, from the lower left-hand part of Pl. XLVII fig. 2); they are circular in their present flattened state, and very large, measuring up to 250 μ; such large ones are seen in the lower sporangium on the figure cited, whereas the very distinct ones in the upper sporangium measure about 140 μ. When examined in this way they are always isolated, not united in tetrads or in any other way, and triradiate scars could not be observed with certainty (cf. below). — Other sporangia in the same spike (PA 390) contain smaller bodies, visible as dark dots or as circles; they measure about 50—75 μ in diameter (Pl. XLVII fig. 3); from direct observation it is difficult to ascertain that they are spores, but the assumption could be confirmed in preparations.

Through maceration spores were obtained from a couple of specimens, although the material, on account of its scarcity, had to be spared as much as possible.

The best preparations were made from a fragmentary but typical spike on PA 470. Some macrospores could even be picked out separately, while the microspores were obtained from other sporangia evidently belonging to the same spike (Pl. XLIX figs. 6—11, cf. also figs. 12—13 from PA 470 and PA 386). Apart from the difference in size the macro- and microspores resemble each other. When completely swollen the microspores are circular in outline or nearly so, while the macrospores usually retain a somewhat elongate form. The wall is thin, apparently consisting of one layer only, and smooth; a certain granulation, sometimes seen on the surface, probly does not represent any original structure, but is the result of an incipient disintegration of the wall. Triradiate tetrad markings have been observed in the microspores (Pl. XLIX fig. 8), but not with full certainty in the macrospores. In the preparations, the diameter of the microspore is mostly from 60 to 85 μ, while the macrospores measure about 270×200 μ.

It is a remarkable fact that the microspores resembles the spores found in the sporangia of *Svalbardia* (p. 77); but there seems to be some difference in the size and in the structure of the wall. At all events, there is scarcely any doubt as to the two types of spores just described: A photograph like the one reproduced in Pl. XLIX fig. 2 shows the macrospores in their original place in the sporangium, and from similar sporangia spores could be picked out, cleared, and mounted (Pl. XLIX figs. 9—11). The microspores were obtained in hundreds and hundreds through the maceration of similar sporangia, and all of them were of the same size and form, lying together in loose aggregates or detached; it is impossible that groups like those shown in Pl. XLIX figs. 6 and 12 should have been transported and deposited any distance whatever from their mother sporangium. We therefore necessarily have to reckon with heterospory in this fructification.

In some of the preparations, particularly in those of the microspores of PA 470 (Pl. XLIX figs. 6 and 12) there was no admixture of other spore forms; but in some of the cases when small pieces of the matrix with sporangia were splitt off and macerated, also foreign types of spores were obtained (Pl. XLIX figs. 13—16), just as in the case of *Svalbardia* (for description, see p. 146).

As to the anatomy of the axis, only a very fragmentary knowledge could be gained, and exclusively in the same way as in the case of the stems of *Enigmophyton*. When examined dry in incident light, the surface may show delicate longitudinal ridges and furrows, which must correspond to the cell structure (Pl. XLVIII fig. 5, PA 469). When examined or photographed immersed in alcohol or xylol, or preferably under a hyaline cover of cellulose glue, the cell walls are clearly seen in several parts of the fossils (several figures on Pls. XLVII and XLIX). The longitudinal walls are particularly distinct, and may at first convey the impression, no doubt erroneous, that the cells are tubular. Transversal walls are far more rarely preserved, and often incomplete, but they are certain enough: The longitudinal elements are rows of cells, not tubes, and in a few cases one can find a regular pattern of rectangular or quadratic cells. — Mostly, the cell-rows are very regular, but at certain places, distributed, as it seems, without any order, they converge as if there were holes, or hair-bases, or stomata, surrounded by radiating cells; some instances are seen in Pl. XLIX fig. 4 (PA 390), near the upper and lower ends. But there are found no remains that can actually prove the presence of stomata.

If examined, or preferably photographed, in stronger magnification the fossils also show some other structures which may be rather remarkable: The carbonized remains of the plant mostly form a thin black cover without any indication of the original cell structure; but in several places there are small figures, looking like circular, wheel-like groups of cells. These figures may be very regular and characteristic, and it is tempting to interpret them as remains of plant tissue. They have a close resemblance to structures found in *Enigmophyton superbum* and, perhaps still more pronounced, in *Germanophyton psygmophylloides*. But evidently structures very much like these may come into existence through purely physical forces during the process of fossilization, and a broader comparative study than is possible on this occasion would be necessary if one should try to base any conclusions upon them.

Affinity. — As far as I know there is no previously described type of fructification to which the present one could be referred, the resemblance to *Barinophyton* (Arnold 1939 p. 285, Pl. IV) at least certainly not amounting to generic identity, whatever significance may otherwise be placed upon it (compare further p. 191). Therefore it will be necessary to give our fossil a new generic name, if it cannot be proved to belong to any of the other plants known from this locality.

The flora of Plantekløfta, and of the corresponding strata in Planteryggen, comprises only the following plants: *Svalbardia* (p. 70), *Hyenia* (p. 82), *Enigmophyton* (p. 88), and lepidophytes (pp. 121, 131). Of *Svalbardia* the organs of reproduction are known, and *Hyenia*, with its articulate axis, cannot come into consideration as the mother plant of the fructification just described.

The position of solitary sporangia on the upper sides of scale-like sporangiophores, is a feature in which the fructification in question very much resembles the lepidophytes (and, it may be added, *Drepanophycus*). The dichotomy of the axis also finds its parallel in that plant group. However, it does not seem at all probable that any lepidophyte should have fertile shoots with entirely smooth and naked axes, without the slightest traces of leaves or leaf-scars below the sporangiferous region. As a point of minor importance it may also be noted that the lepidophytes are not associated with these fructifications on the same slabs, and not even in exactly the same strata, in contrast to *Enigmophyton*.

Much may be said in favour of regarding these fructifications as belonging to *Enigmophyton*: Just as the latter represents a new and peculiar type of leaf-bearing axes, so is the fructification also new and different from everything that is known so far from other localities. *Enigmophyton*, together with *Svalbardia*, is the most common species in the beds where the fructification is found, and out of four good specimens containing the fructification, three also contain remains of *Enigmophyton*, while *Svalbardia* is present on two of them, and lepidophytes on none. As regards the morphology, the axes of the fertile shoots are regularly bifurcating, like those of *Enigmophyton*, and the smooth surface is the same in both. The cell structure is incompletely known, and no very characteristic features have been pointed out in either of them; but in this respect there is at least no tangible difference between them. The stalks of the fructifications correspond in thickness to the broken lateral branches of *Enigmophyton* (cf. text-fig. 25, p. 114).

Personally I feel convinced that we here have the reproductive organs of *Enigmophyton.* But a conclusive proof has not been given; what is mentioned are only indications. It might therefore be most correct to refer the fructification provisionally to an organ genus, from which it would be transferred to the combination genus *Enigmophyton* if its identity with the species *E. superbum* should be proved. However, in the hope that new material from the same locality may before long possibly throw some more light upon these questions, I prefer to desist from introducing any new names at present. Cf. also pp. 115, 189.

Bergeria mimerensis n. sp.

Pl. L figs. 1—3; Pl. LI figs. 1—2; Pl. LII figs. 1—7; cf. Pl. LIII figs. 1—6; text-figs. 27—30.

Locality, material. — The specimens to be described under this heading have been found in the inner part of Mimerdalen. The best ones are from a brown, fine-grained sandstone of Planteryggen (and Plantekløfta); most of them are moulds of thick stems (5—10 cm), but a few thinner axes may also belong to the same species. It also occurs at Fiskekløfta and further up along the river, above all in the whitish, very hard sandstone, from which several stone-casts have been brought home.

Some morphological details may be clearly visible on the specimens, but no cell-structure is preserved (compare, however, PA 425, Pl. LII figs. 5—6).

Description. — Most of the impressions have a characteristic pattern, the surface being divided into quadrangular or rhombic areas. They are about 1 cm high or somewhat less (8 mm, or sometimes even only 6 mm); usually the breadth is about the same as the height, but in some cases it is considerably more. — The sides of the areas form conspicuous lines, running across the surface of the fossil stem at angles of about 45° to the vertical, thus cutting each other at right angles or approximately so. Mostly these lines are somewhat zigzag, because the sides of the individual areas may have a somewhat steeper course than the main direction of the lines of which they form part (see, for instance, Pl. L fig. 2, PA 1169). More rarely the two upper (?) sides of each area are curved upwards, so as to make the area rounded above; correspondingly, the lower half of it is then limited by lines curved inwards and running out into an acute point, the area thus becoming somewhat fan-shaped (text-fig. 27, PA 1168). It may be added that this orientation of the axes in question is not necessarily correct; possibly the pointed corners of the areas have really been directed upwards.

Fig. 27.

Fig. 27. *Bergeria mimerensis* n. sp., from Mimerdalen: Plantekløfta. Specimen with fan-shaped areas. PA 1168. Nat. size.

The areas have rather a different appearance in the various specimens and in the various parts of the specimens: (*a*). In most of them there is a vertically elongated scar, which is sometimes small and situated near the upper corner, but more often larger so as to form, more or less completely, a vertical diagonal. Usually no structural details are discernible in the scar, which is in most cases simply formed as a convex ridge. In a few cases there is a certain lack of symmetry (PA 443, Pl. LII fig. 7) which, however, is better understood if compared with one of the thinner axes found (see below, p. 125). — (*b*). In some other instances the rhombic area is equally well marked, but without any such scar or ridge whatever. In cases of good preservation there may be a system of minute ridges, slightly elevated, radiating in a fan-like arrangement from the lower corner and with a slight curve to either side. Particularly in these cases (although also, in a varying degree, when the scar is visible) the two upper sides of each area, as seen in the negative impression, are in a slightly higher level than the areas next above, so that they appear to be imbricate, like fish-scales. — (*c*). In still other specimens the rhombic areas disappear, while the scars become particularly well visible. In extreme cases (like PA 1262, text-fig. 28) the fossil resembles an indeterminable *Knorria*, but intermediate stages form connecting links with the other specimens and make the determination safe: A stone-cast like PA 1246 (Pl. LI fig. 2) has, on one side, very distinct oval scars without any rhombic pattern whatever, whereas on other sides the latter is well developed, each of the diamond-shaped areas containing an elongate-oval marking, distinctly outlined and corresponding to the diagonal scars mentioned above (under *a*). There are several other specimens, in the form of stone-casts or as flattened impressions, in which such scars are well developed, often elevated, and markedly knorrioid. Some of these specimens, particularly from the canyon above Fiskekløfta, are of considerable dimensions, one of the largest being PA 1262 (text-fig. 28), which is at least 13 cm broad. Another one, PA 1184 (text-fig. 29), of which both a slightly flattened stone-cast and a corresponding mould is preserved, is 40 cm long by a breadth of 10 cm. The specific identity of the latter two specimens is not beyond doubt, but it is very probable that they belong to the same species as the other specimens just mentioned, the more so because PA 1184 shows very distinct traces of rhombic pattern.

Fig. 28. Large stem of same species as *Bergeria mimerensis* n. sp., but in knorrioid preservation. Mimerdalen: Western canyon above Fiskekløfta. — PA 1262. Nat. size.

Fig. 28.

Fig. 29. Large stem of *Bergeria mimerensis* n. sp., from Mimerdalen: Eastern canyon above Fiskekløfta. — PA 1184. Reduced.

A specimen in an unusual state of preservation is PA 428 (Pl. LI fig. 1). In each of its rhombic areas, which are formed by very regular diagonal lines, there is an oval pit with well-defined outline; the height of the pit is about one third or one half of the height of the area.

Another specimen which differs from the others, is PA 407 (text-fig. 30). Its rhombic areas are separated by elevated bands, mostly 2—4 mm broad and sharply defined.

As to thinner axes, it is remarkable that all the typical specimens, as now described, are rather uniform in size and always represent fairly large stems, mostly measuring 5—10 cm across. The fact that they are present in a considerable number, and that they occur in association with many other plant remains of variable size, some of them quite delicate and small, makes it reasonable to expect that also more slender ramifications of the same plant should be found, provided that the plant really has been ramified at all. However, of the thinner twigs of lepidophytic plants, occurring in the same beds and partly even on the same slabs, the greater number have probably belonged to other species (compare, however, p. 127), and only a few may be mentioned here:

Fig. 29.

PA 425 (Pl. LII figs. 1—6) is the impression of an axis, about 1 cm wide, partly bare, partly covered with some brittle coaly matter. The surface bears numerous concave markings, some of which have the form of well preserved leaf-cushions (Pl. LII figs. 5—6). The latter more or less resemble those of *Protolepidodendropsis pulchra* described below (compare particularly PA 414, Pl. LV fig. 8), but they are somewhat shorter and broader, being oval in outline and never attenuated in the lower end. In a few of them there is a flat, nearly circular disc in the upper end; it may be supposed to represent the leaf-scar (Pl. LII fig. 6, right-hand side). The surface between the leaf-cushions has sometimes preserved the outlines of the cell-structure, but further details are

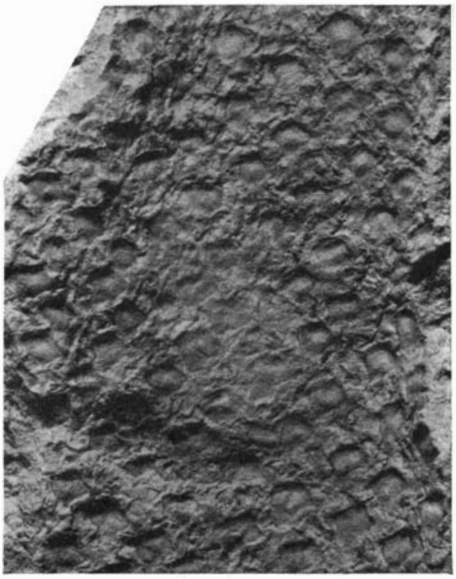

Fig. 30.

Fig. 30. Probably same species as *Bergeria mimerensis*, from Mimerdalen: Plantekløfta. Part of specimen in unusual state of preservation with elevated bands between the rhombic areas. — PA 407. Nat. size.

not visible. There are no flexuose bands forming a reticule as in *Protolepidodendropsis pulchra,* but the leaf-cushions themselves sometimes form a remarkable pattern: The upper end of each of them may be prolonged upwards into a long tail-like point, which is curved to the left (as seen on the negative impression) and reaches nearly up to the next leaf-cushion in the same parastich, thus forming conspicuous diagonal lines (Pl. LII figs. 2 and 4). Usually these lines have the form of furrows, the areas between them being convex. This feature is particularly distinct in the upper part of the fossil, but in the enlarged photograph reproduced it is not well seen, because the specimen had to be photographed immersed in xylol. Diagonal lines in the other direction (upwards to the right) are less clear, but are indicated in some places, thus producing a pattern of quadrangular or rhombic areas. In some places, as shown in the photographs, the remains of organic matter form the same kind of areas, either in connection with furrows, or on a flat surface (as shown in the upper part of Pl. LII figs. 4—5). — This pattern resembles that of the thicker stems described above, the resemblance being particularly strong in that part of the specimen (PA 425) which is shown in Pl. LII fig. 3 (and in the upper end of Pl. LII fig. 2): Here are rhombic areas of which the lower left and upper right sides are formed by the usual furrows with some carbonaceous matter in them. The other sides are not furrows, but are formed by irregular bands of carbonaceous matter, except in one case (as shown in Pl. LII fig. 3), where there is a delicate, slightly elevated ridge forming the straight upper left side of the area, very much resembling those of the larger specimens described above (cf. Pl. L). In the same area there is also a line forming, but not quite exactly, a vertical diagonal. When examined closely this line is seen to correspond to the left-hand side of the impression of a prolonged leaf-cushion. This is a fact of considerable interest, and it does not only represent a single case, which might be thought to be due to secondary distortion: In other parts of the same specimen the markings sometimes suggest the same feature, and in the impressions of other, larger stems there may also, although rarely, be indications of a similar unsymmetrical structure: In PA 445 (Pl. L fig. 3), and in PA 443, of which a detail is shown in Pl. LII fig. 7, most of the areas have the usual longitudinal ridge along the diagonal line, and there is then no difference between the halves of the area on both sides of it; but in a few of the rhombic areas, as shown on the photograph, the ridge is less prominent, or nearly lacking, and the left half-area is smooth and slightly convex, separated by a furrow from the other (the right-hand part), which is more or less crescent-shaped, at a somewhat deeper level, and of a form strongly resembling the scar just described from PA 425. If one compares Pl. LII fig. 3 with fig. 7, there is scarcely any doubt that they represent the same morphological feature. — These facts are of some interest, first because they make it very probable that the specimen PA 425 is of the same species as PA 445 (Pl. LII fig. 7) and the other large axes, and, secondly, because they give some hints about the existing intimate connection between the leaf-cushions and the rhombic areas and the vertical diagonal ridges, although the material at hand does not supply facts enough for a complete understanding of the anatomy. When this specimen (PA 425) has been described in such detail, it is also on account of the connection which it suggests to *Protolepidodendropsis pulchra* (cf. pp. 127, 131).

There are no other specimens of thin axes which with full certainty can be referred to the same species. But there is at least one which deserves to be mentioned in this connection:

PA 418 is a piece of yellowish sandstone, partly with some mica in it, bearing on its surface impressions of several (at least 7) axes which, in spite of some difference in structural details, resemble each other so much that they must belong to one and the same species. They are about 1.5 cm broad, straight, not tapering, and unbranched except in one case, which is shown in Pl. LIII fig. 1: Here the stem divides into two equal branches, one of which continues in the bedding plane of the rock, while the other goes down at an angle of about 30° and is visible on the side of the slab. On its surface the latter branch has a distinct rhombic pattern formed by lines of black organic matter, or in some cases by small fissures; how it really comes into existence cannot be clearly seen, the leaf cushions not being visible, but there is certainly some connection with the bases of the leaves, which are observable in some cases along the margin of the specimen. This pattern makes it probable that the specimen belongs to the same species as those described above (*Bergeria mimerensis*), or at least that it is related to it, and so far justifies the description of the specimen here.

Some of the other axes on the same slab (PA 418) have well preserved leaf-cushions, as shown on Pl. LIII figs. 5—6. They have a strong resemblance to those of the specimen on PA 445, described below under the heading of *Protolepidodendropsis pulchra* (Pl. L fig. 4), but there are no ridges forming any reticule between them.

Leaves are still attached to some of the axes on PA 418. The bifurcate axis just described bears some leaves (Pl. LIII fig. 2), and another case is shown in Pl. LIII fig. 4. In this figure there are two axes crossing each other in different levels, the upper one bearing numerous leaves along the side; to judge by their direction the stem fragment is seen top down on the photograph. The leaves are simple and undivided, and may probably attain a length of about 1 cm.

Affinity. — Where no reservation has been made in the preceding description, it is probable that all the specimens belong to one and the same species, which, if that is correct, is represented both in Plantekløfta (and Planteryggen), and in the canyon above Fiskekløfta.

This type of stem, with a fairly large diameter and a characteristic rhombic pattern, has before been recorded from the same part of Spitsbergen, *viz.* by Nathorst who, in 1894 (p. 14, Pl. II fig. 8), described a *Bergeria* from a green shaly sandstone found in one of the canyons of Mimerdalen. This sandstone belonged to a somewhat higher horizon than that of Fiskekløfta. There is no reason to doubt the specific identity of Nathorst's specimen with our new material. It is also possible that Nathorst's *Lepidodendron* sp. (*l. c.* p. 13, Pl. II fig. 7) belongs to the same species, although the dimensions of the scars and the distance between them is considerably larger than usual; but in other respects it is indistinguishable from our PA 1184 (p. 122). However, being rather poorly preserved, these specimens do not help us to elucidate the questions of relationship and nomenclature.

It may be pointed out that it is somewhat difficult to draw a line of distinction between the plant described above, and the following species, *Protolepidodendropsis pulchra.* If PA 425 (p. 124, Pl. LII figs. 1—6) does belong to the same species as the larger stems with rhombic pattern (as is very probable), and if, on the other hand, PA 445 (p. 134, Pl. L figs. 4—5) and similar specimens belong to *P. pulchra*, they show that the leaf-cushions, or leaf-scars, may attain more or less the same form under certain conditions of preservation. Therefore the relation of the two forms to each other is not quite clear; but it is impossible at present to refer them to one and the same species.

There is a number of other Devonian plants which offer themselves for comparison in this connection:

1. The genus that is of prime interest is *Leptophloeum* Daws.; the resemblance of that genus to Nathorst's specimens from Spitsbergen has already been pointed out by White (1905 p. 73): In connection with a redescription of *L. rhombicum* from Perry Basin, he expressed as his opinion that Nathorst's specimen from Spitsbergen almost certainly belonged to the same species.

Of the genus *Leptophloeum*, three species have so far been described:

L. rhombicum, the type species, was instituted by Dawson 1861 on material from the (?) Upper Devonian of the Perry Basin, Maine, and redescribed and refigured repeatedly by Dawson himself, further by White (1905 p. 69, with full bibliography), and, on the basis of White's illustrations, by Walton (1926). Walton gave an emended interpretation of its structure in the light of the closely related Australian species. As yet, *L. rhombicum* has not, with certainty, been found outside the type locality.

The second species, *L. australe* (McCoy) White, was described by McCoy (in 1861, according to David & Pittman 1893 p. 195) under the name of *Lepidodendron australe* on the basis of specimens from Victoria. Fossils more or less resembling these specimens were subsequently described from various other parts of Australia, partly under other names (especially *L. nothum* Carruthers non Unger), but later, by most authors, combined with McCoy's species. A review of the literature up to the year 1893 was given by David & Pittman (1893), and up to 1907 by Seward (1907). A new description was published by Walton (1926), corroborating and extending Carruther's interpretation of the peltate leaves. — In connection with the Australian species we may also mention the South African *Lepidodendron albanense* Schwarz (1906 p 355, Pl. VI fig. A), from the Witteberg Series. Its resemblance to some of the Australian specimens has been pointed out by several authors, but it is really too poorly preserved to allow of a reliable determination (compare also Seward 1909). *L. albanense* has a strong resemblance to some of our specimens from Spitsbergen, to which it corresponds in size and in the rhombic pattern of the surface. It is of some interest to note that also *L. albanense* occurs in association with smaller specimens without any rhombic pattern, but with various kinds of leaf scars or cushions; Schwarz described these specimens as distinct species, but Seward was inclined to regard all of them "as possibly referable to a single type". However this may be, a specific identity with the plant from Spitsbergen is not possible. — Another and somewhat younger South African plant, from the Dwyka Series, was described by Seward (1907 p. 484, Pl. XXI figs. 6—8) and identified with *L. australe*. However, in the light of our present knowledge of the Australian species also this identification may now stand in need of a revision.

The third species, *L. sibiricum* Krystofovitch (1927), was described some years ago from the (probably) Middle Devonian of the Minusinsk Region of Central Siberia. It seems to differ considerably from the other two species, and was transferred to a new genus, *Blasaria*, by Zalessky (1934). The species is also mentioned by Neiburg (1939), according to whom the age of the type locality is Lower Devonian.

At first sight the most conspicuous feature of the genus *Leptophloeum* is its rhombic pattern, which is also so distinct in our plant from Spitsbergen; this feature alone, however, is not at all sufficient to refer it to the said genus, because a similar pattern may be found equally marked in other lepidophytes of Carboniferous age. Thus, to mention one example, some of the large stems from Spitsbergen can hardly be distinguished from specimens of *Lepidophloios laricinus* Sternb., figured in the literature.

The same is the case with another structure, the vertical keel of the rhombic areas (as mentioned already by Nathorst 1894 p. 14), a feature which is so distinct in many of our specimens, and also in *L. australe*, but which, rather remarkably, has not been observed in the American species (according to White 1905 p. 73).

However, the most important characteristic of the genus *Leptophloeum* is the form of the peltate leaves, which, as demonstrated by Walton, is the cause of the transverse wrinkling seen in parts both of the Australian species and of the American one. Of these wrinkles, or the corresponding type of leaf, there is not the faintest trace in any of the many Spitsbergen specimens. Now, according to Carruthers, Chapman, and Walton, it is quite probable that these peltate leaves have been sporangiferous, and Walton mentions the possibility of their having been confined to certain parts of the stems, while the regularly rhombic areas in other parts may have borne a different type of leaf. If so, one might assume that the only specimens preserved to us were from such parts of the plants as had only borne simple leaves, or that the peltate leaves had fallen off from all these stems before they were fossilized. It is very unlikely, however, that the large collection from Spitsbergen should by mere chance happen to comprise only specimens not showing a structure which in other floras seems to be quite conspicuous. It is far more probable that our species has never possessed that structure.

If the specimen PA 425, which was described above (p. 124), is really of the same species as the larger stems (as is very probable), we also have more positive evidence of the difference between our plant and *Leptophloeum*; thus, the latter genus has nothing like the leaf-cushions of the said specimen (shown in Pl. LII figs. 5—6).

In conclusion, it may be said that *Leptophloeum* is now a well defined genus with a very characteristic morphology known in considerable detail, and that it would be wrong to include our plant from Spitsbergen in this genus. The resemblance which seems to exist between them, chiefly concerns characters of slight systematic value, and not, as far as is known, such essentials as the leaf-form and the leaf scars. Our species is also much larger.

2. Some specimens from the Upper Devonian of the Ogur River near Yennisey were described by Schmalhausen in the year 1876 under the names of *Bergeria regularis* and *B. alternans*. In a paper printed in the year 1879 he united them with other specimens from Trifonova, another tributary to the Yennisey, under the name of *Lepidodendron Veltheimianum*. To judge by the drawings, some of these specimens have a strong resemblance to our stems from Spitsbergen, but it is

scarcely possible to form an opinion of their real nature without examining the specimens themselves. When discussing the systematic position of *Leptophloeum sibiricum*, Krystofovitch (1927), although pointing out its resemblance to *Bergeria regularis* and *B. alternans*, excludes the possibility of a specific identity, certainly with good reason.

3. *Lepeocaulus aphyllus* Zalessky (1933), from Devonian limestone of Novaya Zemlya, has axes up to 22 mm in diameter; they are covered with rhombic areas, or scales, each of which having a vertical diagonal keel. In spite of the difference in size, the plant must bear a strong resemblance to some of the stems from Spitsbergen; but, however that may be, it is certainly not advisable to refer our species to the same genus. — Zalessky regards *Lepeocaulus* as a primitive psilophytalean plant, even suggesting a resemblance to *Rhynia*. That is a view to which it is difficult to subscribe.

4. *Protostigma sigillarioides* was described by Lesquereux (1877) and, to judge by the illustrations (*l. c.* Pl. IV fig. 7), it may be comparable with a stone-cast of *Leptophloeum* or with one of our Spitsbergen specimens. But the fact that it is said to have come from the Cincinnati Group of Ohio, now regarded as Ordovician, makes it necessary to regard it with particular suspicion, the more so because the organic origin of the specimen was subject to doubt already very soon after the publication (Foerste 1893).

5. Further, it may be mentioned that a large *Knorria* has been described by Arber & Goode (1915 p. 100), from the uppermost part of the Devonian System of North Devon. Seen alone it is indeterminable, but it is of some interest to note the resemblance of this plant to some of our specimens, for instance, to PA 1262 (p. 122, text-fig. 28).

6. Finally, still another Devonian plant may be taken into consideration, *viz. Lepidodendron burnotense* Gilkinet (1875 *b*), from the Lower Devonian of Belgium. To judge from the illustration published by Gilkinet (*l. c.* fig. 5), it might be supposed to have some resemblance to our plant, particularly if compared with our PA 418 (Pl. LIII). However, the plant is widely different from the one from Spitsbergen, its leaf-bases and leaf-scars being of a much simpler organization, as one might also expect from its Lower Devonian age. Stockmans (1940 p. 63) has recently identified it with the species which he has named *Drepanophycus* aff. *gaspianus* (Dawson). Before I learned that Dr. Stockmans would be working at the early Devonian flora of Belgium, I had been permitted to borrow the type-specimen from the University of Liége, thanks to the courtesy of Dr. Suzanne Leclercq, and after examining it I arrived at the conclusion that its nearest relative is *Gilboaphyton Goldringiae* Arnold, from the Middle Devonian of New York, although there is certainly no complete identity. In so far as one can judge from the vegetative characters only, these plants are closely related to *Drepanophycus*, but I concurred in the reasons put forward by Arnold (1937) for keeping them apart. Perhaps the excellent new material from Belgium, now described by Stockmans, may help to unite them (compare, among others, also Crépin 1875 Plates IV—V; Halle 1916 Pl. I fig. 8; Seward 1932; Zalessky 1937 *a* Pl. V fig. 7; ? Gothan & F. Zimmermann 1937 Pl. XXV fig. 3).

The conclusion of the preceding pages is that, in spite of its resemblance to various specimens previously described in literature there is no Devonian species with which our plant may be identified, and no Devonian genus into which it fits. However, there are also some younger fossils with which it may be compared:

Thus, it is instructive to draw a comparison with Nathorst's *Sublepidodendron* (from the Lower Carboniferous of Spitsbergen, Nathorst 1920 *b*), of which some species may have regular leaf-cushions, whereas in other species, represented by specimens which have probably come from older parts of the plant and are somewhat differently preserved, there are surface structures resembling those of our stems with their rhombic areas and vertical keels. It is out of the question to include our plant in *Sublepidodendron*; but the resemblance is of some interest on account of the position of *Protolepidodendropsis pulchra* (compare further p. 136).

At first sight our plant has a striking resemblance to *Phialophloios quadratus* Hörich (1915), from the Upper Carboniferous of the Saar Basin. However, one of the most characteristic features of that genus is the insertion of the leaf in the lower corner of the quadrangular area, where it leaves a distinct leaf-scar, whereas in our plant the leaf is evidently inserted in the upper corner. The morphological and systematical bearing of this detail is difficult to judge of at present, but at all events it is important enough to make it impossible to refer our plant to the genus *Phialophloios*.

In consequence of this uncertain position of our plant, particularly with regard to its relation to *Protolepidodendropsis pulchra*, it may be advisable at present to apply a non-committal name to our plant and to avoid the introduction of a new genus name; most of the specimens may simply be called *Bergeria*. In order to facilitate reference, it would, however, be convenient if it had a specific name, and as such I propose *B. mimerensis* (derived from the name of the locality). — For diagnosis, see p. 194.

Comparison with more material from the same locality and from others will no doubt some day make it possible to elucidate the true nature of these specimens and to refer them to a natural genus.

Protolepidodendropsis pulchra n. sp.

Pl. LIV figs. 1—8; Pl. LV figs. 1—8; text-fig. 32; probably also Pl. L figs. 4—7.

Locality, material. — From the inner part of Mimerdalen, and at least mostly from the same beds as the specimens of *Bergeria* described above, there are about a dozen samples of thinner axes of lepidophytic plants, varying in diameter from about 1 cm to a few millimetres. The state of preservation is rather unequal, and the different aspect of the various specimens may partly be due to this fact; therefore it has been difficult to draw the lines of distinction between various forms, which may be present; some of the specimens will be described separately below as lepidophytic axes of uncertain position (p. 138).

Description. — The best specimen, which is regarded as the holotype of the new species, is PA 419*a*, Pl. LIV figs. 1—5. It is about 7 cm long and 1 cm broad, slightly curved. It is a negative, in which the leaf-cushions are represented by depressions. The surface is reticulate, because the interspaces between the leaf-cushions have the form of furrows of uniform breadth; on the negative these furrows stand out as longitudinal flexuose ridges, about 0.5 mm broad, with distinct, but rounded relief. Each ridge runs for a short distance alongside of its neighbour on one side, touching it, but not uniting with it, then turns gently to the other side and meets the other neighbouring ridge. The meshes of the network thus formed correspond to the leaf-cushions, which are arranged in regular vertical and spiral lines. Each leaf-cushion is about 0.6 mm broad and about 3 mm long, fusiform, with a rounded upper end, which is more elevated (in the negative forming a deeper depression) than the lower end, which gradually attenuates into a thin tail reaching nearly to the next cushion below (in the negative forming the narrow cleft separating two ridges). The leaf-cushion sometimes has a longitudinal median keel, which is best seen when examined in a dry state and very obliquely illuminated. On the fossil, where the original relation between elevations and depressions is reversed, there may be, in the lower part of the leaf-cushion, a slightly prominent ridge which bifurcates upwards (visible in the upper right-hand part of Pl. LIV fig. 2, with a detail more magnified in Pl. LV fig. 1). This bifurcated ridge must originally correspond to a groove, and in the upper part of the leaf-cushion there must have been a median keel in the living plant.

When immersed in a suitable liquid (xylol has mostly been used) the fossil shows several details which are quite invisible on the dry specimen; they are illustrated in Pl. LIV figs. 3—5. In the cases of best preservation the leaf-cushion is then seen to consist of two parts, which may be separated from each other by a black line and a slight constriction. The upper part, which is much smaller than the lower one, has a broad oval form with a rather blunt top; this area could scarcely be interpreted as anything but a leaf-scar. In the centre of it there are seen the remains of what must be supposed to be the leaf-trace bundle, mostly represented by a number of small dots, forming an irregular star-shaped figure, or in one case (perhaps quite accidentally) a little circle. There are no parichnos. — In other and more frequent cases the limit between the leaf-scar and the area below is less distinct or not noticeable at all; then the upper end is prolonged and acute, and the leaf-trace bundle may be visible in an oblique longitudinal section (*e. g.* Pl. LIV fig. 3). If the interpretation of the said black dots as the remains of the leaf-trace bundle is correct, there is nothing whatever to prove the existence of a ligule; this fact is most likely not due solely to the state of preservation, leaf-cushions like those photographed showing clearly so many details in their structure that the lack of any indication of a ligular pit makes it probable that the plant has not possessed any ligule at all, or that it has been situated in such a place that it could not leave any mark on the fossil. — There are no lateral pits (infrafoliar parichnos marks) on the lower part of the leaf-cushion.

On this specimen (PA 419 *a*) no leaves are preserved. However, leaves, or at least leaf-bases, are visible on the fragment of another axis, found on the other side of the same slab (PA 419 *b*, Pl. LIV figs. 6—8). This axis is narrower, about 4 mm broad, and differs slightly in the number and arrangement of the leaf-cushions, but the specific identity with the first specimen could scarcely be doubted. There is the same net-work of flexuose ridges, and the outline of the leaf-cushions is the same. The details of the leaf-scar are not clearly visible, but the keel, or black line, in the lower part of the cushion is very distinct (Pl. LIV fig. 8). Along the margin of this axis there are seen remains of leaves. They are only a fraction of a millimeter long (scarcely more than 0.3 mm), either straight and projecting at right angles, or somewhat erect with recurved tip. The leaf-cushion is fairly well visible in profile. In all probability the leaf has been longer than it now appears to be on this fossil, only the basal parts being left (a long-leaved specimen, PA 412, which may belong to the same species, or at least the same genus, is described below, p. 139).

Among the other specimens showing similar structure and believed to belong to the same species, the following are worth mentioning:

PA 424 (Pl. LV figs. 2—5). Like the other specimens it is a negative impression; reticular ridges (in reality grooves) are very distinct. Leaf-cushions slender, sometimes with keel clearly visible. Leaf-scar (Pl. LV fig. 5) nearly circular.

PA 414 (Pl. LV figs. 6—8). A very small fragment, scarcely 4 mm broad, but interesting on account of its relatively good preservation. The flexuose ridges of the surface are less prominent than in the specimens described above, but they are not entirely lacking, and the leaf-cushions are so like those of the other specimens as to arrangement and form that the fragment may safely be regarded as belonging to the same species. Some of the leaf-cushions, however, are somewhat broader than usual. The most remarkable feature of this specimen is the distinctness with which the cell structure is seen in the space between the leaf-cushions, appearing as a delicate reticulation (Pl. LV fig. 8). The cells form longitudinal rows, sometimes straight and regular, sometimes curved and traceable only for a short distance. The length of the cells, in the vertical direction, cannot be measured; the breadth is about 40—50 μ.

PA 445. On a large slab, chiefly remarkable for a large and good specimen of *Bergeria* (p. 126, Pl. L fig. 3) and a good *Hyenia* (p. 82, Pl. XXXV fig. 5), there is also a fragment of a smaller lepidophytic axis in a poor state of preservation (Pl. L fig. 3, lower end, and figs. 4—5). In the upper part of it there are rather distinct ridges forming a reticule (Pl. L fig. 5), and fairly well preserved leaf-cushions; the leaf-scar is just visible, as is also the median bifurcated keel, whereas other details are not observable. The reticule and the leaf-cushions in this part of the fragment resemble those of the specimens described above (PA 419) so much that it may be referred to the same species. In the larger part of the fragment, however, the flexuose ridges are not preserved. Here the most conspicuous feature is the impression in the upper end of each leaf-cushion, and, while some of the leaf-cushions are still quite distinct, with regular oval outline, this depression is in other cases nearly all that is left. — The specimen is of considerable interest, not only because it occurs in association with the other plants mentioned (*Bergeria* and *Hyenia*), but also because it shows what axes of this species may look like when preserved in such a state that the reticule of flexuose ridges disappears. (For the same reason there are also given some illustrations of another poorly preserved fragment, PA 439, Pl. L figs. 6—7, which may well belong to the same species.)

Affinity. — No fossil plants previously recorded from Spitsbergen are clearly identical with the one now described, and it is even doubtful whether the species can be included in any genus known before.

1. In a certain state of preservation it seems to have some resemblance to certain species referred to *Cyclostigma* (cf., *e. g.*, Nathorst 1902 Pl. XII fig. 15). But, among other points of difference, *Cyclostigma* has never anything like the flexuose ridges forming such a conspicuous and characteristic feature of the best specimens of our plant, nor has it such well developed leaf-cushions.

2. The genus most naturally offering itself for comparison is *Heleniella*, recently created by Zalessky (1931) on the basis of *H. Theodori* from the Upper Devonian of the Donetz Basin (later, in 1937, also recorded from the Ural Mountains); to the same genus Zalessky also refers some species of *Sigillaria* with flexuose ribs, described from the Carboniferous of Great Britain (*S. Youngiana* Kidst., *S. canobiana* Kidst., and *S. strivelensis* Kidst.), and one from the Lower Carboniferous of the Donetz Basin (*S. Tchirkoveana* Zalessky 1930). Some additional material from Germany has been referred to the genus by Mägdefrau (see next page).

Our plant, with the decidedly lepidodendroid aspect of its leaf-cushions, is at first glance seen to be entirely different from any species of *Sigillaria.* But *Heleniella Theodori* seems to possess leaf-cushions which, in some specimens, may be well developed and of such a form that they are comparable to those of our plant, and, to judge from some of the photographs published by Zalessky, they may be arranged in the same way, with a similar system of flexuose furrows (in the negative: ridges), — compare, for instance, Pl. V figs. 2—3 of Zalessky 1931 with our Pl. LV figs. 1—2. It is, however, difficult to carry out a detailed comparison as regards the leaf-scar without illustrations on a larger scale of magnification or a personal examination of the specimens; unfortunately it has not been possible to arrange a loan. — On the other hand, some of the leaf-scars of *Heleniella Theodori* are said to have parichnoi, organs which are certainly lacking in our plant from Spitsbergen (while ligule is not observable in either of them). Very important is also the fact that Zalessky emphasizes the relationship of *H. Theodori* to *Sigillaria*, combining it with species which in most respects are typical members of that genus. If our plant should be included in *Heleniella*, these species of *Sigillaria* would, no doubt, have to be removed from it, and to such a radical change we are not at all entitled at present. I therefore prefer not to use the genus name of *Heleniella* for our species, although a relationship is probable. —

There is a number of other Devonian plants which it is of some interest to mention for comparison on this occasion:

3. *Heleniella Theodori* Mägdefrau 1936 p. 216, Pl. IX fig. 6 (and cf. 7—8), from the Upper Devonian of Thuringia. — It seems to have a strong resemblance to our plant, as well as to the original *H. Theodori*, but the structural details of the leaf-scars being lost, it can scarcely be determined with full certainty. The identification with *Heleniella* is strongly criticized by Gothan (1939*b* p. 765).

4. The 'Naples Tree' of New York, identified by Dawson with *Lepidodendron primaevum* Rogers from Pennsylvania and fully described by White (1907) under the name of *Archaeosigillaria primaeva* (Rog.) Wh. (compare also Walkom 1928, Berry 1933). — With the varying preservation of its leaf-scars, in some parts being sigillarioid, in others lepidodendroid, this remarkable fossil, as emphasized by Zalessky, is of great interest also for the understanding of *Heleniella* and related forms. But, in addition to the difference in the size of the leaf-scars, which are much larger than those of the Spitsbergen plant in question, there are a distinct ligular pit and well developed parichnos scars, which exclude a close relationship to our plant. — On account of its age, being Middle Devonian, this large arborescent lepidophyte is of particular interest in this connection (cf. p. 165).

5. *Lepidodendron gaspianum* Dawson 1859, from Gaspé; compare particularly the specimen figured by Dawson 1862 Pl. XIV fig. 26. (Several other fossils later referred to this species by Dawson and by other authors, *e. g.* Gilkinet, are entirely different from it.)

6. *L. Veltheimianum* Heer 1872 Pl. IV fig. 1 (non Sternb.), from the Upper Devonian, Ireland.

7. *L. Veltheimianum* Schmalhausen 1879 Pl. I fig. 7 (non Sternb.), from the Upper Devonian, Siberia.

8. *L. karakubense* Schmalhausen 1894 Pl. II figs. 13—14, from the Upper Devonian, Donetz. Referred by Mägdefrau (1936 p. 216) to *Heleniella Theodori.*

9. *L. nothum* Gilkinet 1922 Pl. XIII fig. 76, from the Upper Devonian, Belgium. Referred by Mägdefrau (*l. c.*) to *Heleniella Theodori.*

It is possible that a re-examination of the specimens might clear up the relationship of the five last-mentioned species; but on the basis of the descriptions and illustrations alone it cannot be done. At present it must be sufficient to state that the Upper Devonian flora in various parts of the world comprises forms which may be closely related to the Spitsbergen plant in question; some of them are perhaps even identical with it, but the name of none of them can at present be applied to our plant.

10. A comparison with *Protolepidodendron* also suggests itself. There is an undeniable resemblance between, for instance, our PA 419 *b* (Pl. LIV figs. 6—8) and some of the specimens figured by Potonié & Bernard (1904 fig. 98 &c.) or by Dawson (1881 Pl. XIII figs. 15—16, as *Dicranophyllum australe*), but it does not seem probable that this resemblance is more than a correspondence in habit. Our plant does not show any trace of the bifurcate tips which characterize some of the leaves of *Protolepidodendron*, and on the other hand the latter has no leaf-cushions and leaf-scars like the very characteristic ones of the Spitsbergen plant (cf. Halle 1936 p. 13 & 15). *Protolepidodendron* is one of the best known Devonian genera, with several interesting and important features, and if our species should be included in it, we should have to revise and extend the diagnosis of the genus in a way which would not be at all fortunate. A different thing is that the genus is rather heterogeneous, and among the species to be excluded there may be some which are more closely related to the one described above; but to make sure of that would require a material better preserved than generally seems to be the case (in addition to the quotations above, concerning this genus, compare also Kräusel & Weyland 1929, 1932, and 1933, Lang 1926, Walkom 1928, Sze 1936, Stockmans 1940, and Leclercq 1940 *b*).

11. Finally it will be necessary to draw a comparison in another direction: The plants which Nathorst (1920 *b*) described from the Lower Carboniferous of Spitsbergen under the name of *Sublepidodendron* (as a section of the genus *Lepidodendron*) have a strong resemblance to our plant from Mimerdalen, a fact which is the more striking because it may also, with some reserve, be said of some of the *Bergeria* specimens described above (p. 131). *Lepidodendron (Sublepidodendron) Norden-*

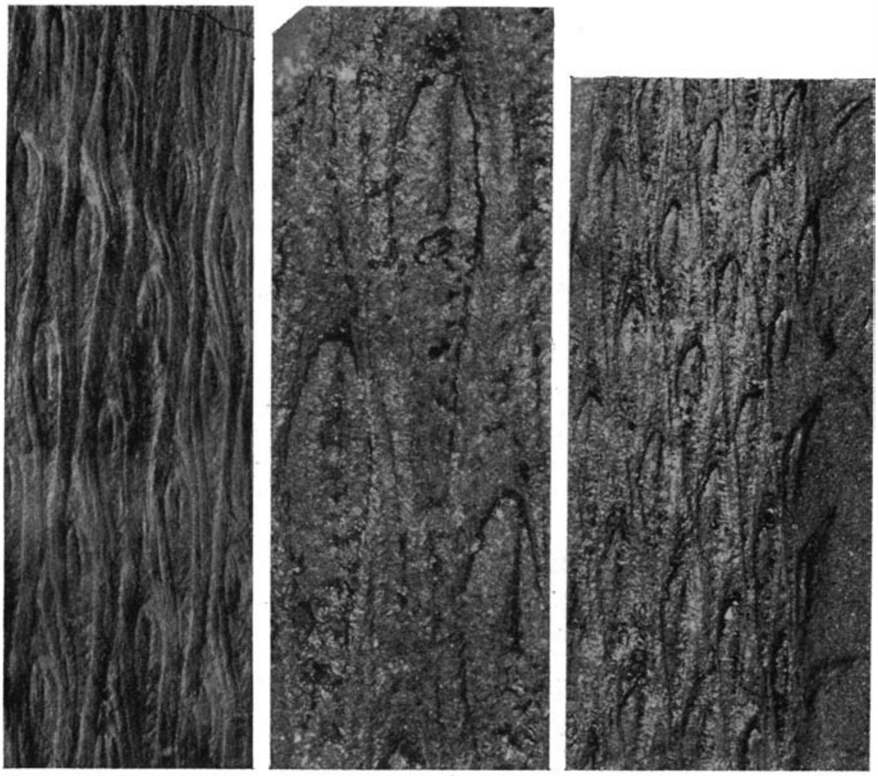

Fig. 31. Details of Nathorst's type specimens of *Lepidodendron* Sect. *Sublepidodendron* from the Lower Carboniferous of Spitsbergen. *Riksmuseet*, Stockholm. — *a*. *L. subfallax* Nathorst 1920 *b* Pl. III fig. 11 *b*. × 4. — *b* & *c*. *L. Nordenskiöldii* Nath. *l. c.* Pl. VI figs. 8—9. × 12 and × 4.

skiöldii, as illustrated by Nathorst (*l. c.*) in his Pl. VI figs. 6, 8, and 9 (cf. our text-fig. 31), does not seem to differ very much from our plant. It is a feature common to all species of *Sublepidodendron* that there is no leaf-scar like that of the typical *Lepidodendron*, a fact which Nathorst explained by assuming that the leaf had been attached to the top of the leaf-cushion in such an erect position that the scar would be invisible in lateral view. The cushion itself was divided into two parts, of which the lower was by far the larger one. One might assume that something similar had been the case in our Devonian species, *viz.* that the leaf-scar was not visible, and that the part which in the description above was interpreted as the leaf-scar, in reality corresponded only to the upper portion of the cushion. This is, however, impossible: Leaf-cushions like those shown in Pl. LIV fig. 3 (PA 419*a*) are so distinct and clear that one has no right to assume that there has been a leaf-scar in such a position that it is now invisible. Consequently, there is probably a deeper difference between our plant and *Sublepido-*

dendron than is apparent at first sight. (It may be added that in later years the conception of *Sublepidodendron* has been changed considerably through the works by Gothan & Sze 1933 and by Gothan & F. Zimmermann 1937.)

After having written down the preceding comparisons and considerations, with the conclusion that the plant described represented a new genus, I received the work by Gothan & F. Zimmermann on the flora of the lower Upper Devonian of Waldenburg (1937). Among the lepidophytic plants described here, *Protolepidodendropsis Frickei* G. & Z. (*l. c.* p. 497, Pl. 24 fig. 6), seems to have a very strong resemblance to our plant from Spitsbergen. The size of the cushions and their arrangement are more or less the same, apart from a much more regular verticillation, and they are separated from each other by similar flexuose ridges. Certainly the leaf-cushions themselves appear to be of a somewhat simpler structure, being described as follows: "Die Polster sind länglich rhombisch und sehr klein und zeigen im oberen Teil eine kleine Längsrille. Außerdem tritt im Mittelpunkt des Rhombus öfter ein kleiner Punkt hervor." The importance of that central point is difficult to judge of; it has no parallel in our specimens. But the rest of the description applies well to them. Certainly it does not mention any bipartition of the cushion; but it should be remembered that also in the Spitsbergen specimens the smaller upper portion, here interpreted as the leaf-scar, is only observable in places where the fossils are well preserved and when they are very carefully examined and photographed in suitable liquids. We may therefore at present be justified in applying the same generic name, calling our plant *Protolepidodendropsis pulchra* n. sp. — For diagnosis, see p. 195.

It was mentioned above (p. 127) that there are specimens which seem to connect this species with the larger stems chiefly preserved in a bergerioid state, for which the name *Bergeria mimerensis* was proposed. If these specimens should be proved to belong to *P. pulchra* they would widen our knowledge of that species very considerably.

Various lepidophytic axes.

In the collection from Mimerdalen there is a number of lepidophytic axes, some of which may belong to the species just discussed. However, they are not sufficiently well preserved for a safe determination, but being of considerable interest, they may be described here.

a. Specimens with transversally undulate surface, cf. *Protolepidodendropsis pulchra.* — One such specimen, PA 416, is shown here in Pl. LI fig. 8; when photographed it was immersed in xylol and illuminated in such a way that the undulation, which is very distinct on the specimen, does not show up conspicuously. Another specimen is PA 423, Pl. LIV figs. 9—11. In both specimens the leaf-cushions are arranged alternately in almost transversal rows, which are somewhat elevated, thus giving rise to the undulation of the surface. The details of the leaf-cushions and of the scars are not well preserved, but, as shown in Pl. LIV fig. 11, they correspond in size to those of *P. pulchra*, and also in form and structure, as far as it can be seen on these specimens. Their arrangement is also the same, apart from the fact that the rows are more distinctly transversal. There is no reticule due to flexuose ridges; but the surface between the leaf-cushions in some places (Pl. LIV fig. 11) bears traces of the cell-structure, similar to that described above (PA 414, Pl. LV fig. 8). — A fully reliable determination of these specimens is not possible at present. While on one side they are connected with *Protolepidodendropsis*, they are on the other side hardly distinguishable from the specimens described below (p. 141) under comparison with *Cyclostigma.*

It is worth noticing that a tendency to arrange the leaf-cushions in transversal rows is frequently met with in *Cyclostigma*. Among others, Gothan has pointed out and discussed this fact (Gothan 1927 p. 323, Gothan & F. Zimmermann 1936 p. 209).

b. Leaf-bearing axes, cf. *Protolepidodendropsis pulchra.* — In addition to one described above (PA 418, p. 126, Pl. LIII), there are only a few specimens of lepidophytes showing leaves in their original position, and most unfortunately these specimens are but poorly preserved in other respects. In the best preserved one, PA 412 (Pl. LV figs. 9—12), the axis is 3—4 mm broad, with no flexuose ridges. The leaf-cushions are visible in a few places as knorrioid elevations; they are of the same form as those of the specimens just described, but somewhat smaller, and no structural details are preserved. Leaves are still attached to the sides of the axis, forming very wide angles to it. They are straight, about 1 cm long, and seem to have been very thin; their breadth, in the horizontal plane, is not observable, but the form of the leaf-scar indicates that they have been quite narrow. The leaf-cushions, to which the leaves are attached, are seen, more or less distinctly, in profile along the margin of the axis (Pl. LV figs. 11—12); they seem to be of the same form as those of the well-preserved specimen of *Protolepidodendropsis pulchra*, PA 419 *b*, described above (p. 133, Pl. LIV fig. 8), a fact which strengthens the probability of their specific identity.

Another leaf-bearing specimen is PA 411 (Pl. LII figs. 8—10), consisting of a thin (2.5 mm wide) axis, which seems to branch. The leaf-cushions are poorly preserved, but have certain points in common with those of the previously described specimens. A median black line is often conspicuous in them. — This specimen is more dubious than the one mentioned above (PA 412), but it seems possible that they belong to the same species.

A fragment resembling those just described, but rather incomplete, is PA 455, Pl. LVI figs. 5—6. It is remarkable on account of some black bodies found in connection with the leaves, on the upper sides of them, near the axis. The best ones are seen a little below the middle of Pl. LVI fig. 6. They are of such a form, and are placed in such a position, that they strongly recall sporangia, but as it is impossible to attempt maceration, we have no proof whatever that they really are such organs, and it would indeed also be surprising if they were. They may be foreign plant fragments accidentally deposited there (that is certainly the case with the black bodies seen higher up on the same side of the axis).

c. Indeterminable leaf-bearing shoots. — On a piece of yellow, somewhat micaceous sandstone from Plantekløfta, PA 472, there are remains of two very small shoots, which may belong to one species. They bear numerous leaves. One of them, shown in Pl. LVI figs. 3—4, is straight, 2.5 cm long. The leaves are about 3 mm long, or perhaps somewhat more, some of them at about right angles to the axis, others more erect. They are rather thick in their inner parts, probably scale-like, while their distal parts seem to be thin. There is no indication of verticillation. The leaves are not sporangiferous. — The other shoot, Pl. LVI figs. 1—2, is curved in a semi-circle, and the leaves are even more numerous than in the other specimen, which it resembles in other respects.

The species must be a lepidophyte. It has some resemblance to PA 411, which was described above (p. 139), and which possibly belongs to *Protolepidodendropsis pulchra*. But the fact that the leaves, at least partly, are broad and probably scale-like, puts it in a position of its own. Although it is a very characteristic form, its real affinity could scarcely be ascertained at present.

d. Bifurcating thin axes, partly preserved as *Knorria*. — On a large slab, PA 407, which also bears impressions of *Bergeria* and *Hyenia* (p. 82 and p. 124), there are some axes, three of which are shown on Pl. LI figs. 3—7. The thickness is 2.5—6 mm. They all branch in the same way, and, upon the whole, it is not possible to doubt that they belong to one and the same species, although their surface structure, when examined more closely, is rather varying. In the largest axis (Pl. LI figs. 4, 6) the leaf-cushions (or leaf-scars) are represented by narrow elongate markings, rather blunt in the lower end and slowly attenuating upwards; they are arranged in a regular manner, as is visible on the photograph. In another axis (Pl. LI figs. 5, 7) there are indications of similar leaf-cushions near the lower end; but the greater part of the specimen is less decorticated, and here they are substituted by small, more or less irregular areas, filled with black carbonaceous matter. Along the margin of the impression the corresponding leaf-cushions, or rather leaf-bases, are seen in profile.

They are broadly triangular, the lower side of the triangle being somewhat longer than the upper, and each of them ends in a little point, which may represent only the base of the leaf, although it looks as if there had never been any longer lamina.

This plant is of some interest on account of its very close resemblance to various fossils which have been described previously from other localities under the name of *Cyclostigma* — compare, for instance, those from Bjørnøya, published by Nathorst 1902 Pl. XI figs. 10—11 (*C. kiltorkense*). If our specimens had been found alone, one would not probably have hesitated very much to regard them as *Cyclostigma*, but the association with *Protolepidodendropsis* and with indeterminable intermediate forms shows that it is necessary to be more cautious.

e. Decorticated stem fragments. — Among the specimens of lepidophytes of unknown affinity, preserved as impressions or casts of more or less decorticated stems, the two following may further be mentioned:

PA 417 (Pl. LIII fig. 7), from Planteryggen, is the impression of a stem, 12 mm broad; the greater part of it is still covered with a thin layer of carbonized matter. The stem shows distinct leaf-trace bundles, with accompanying tissues; they are preserved as elongate elevations rarely exceeding 2 mm in length. They are disposed in regular vertical and transversal rows, but no structural details are discernible in them. Between the elevations the surface, when not covered with the carbonized tissue, has a delicate structure of longitudinal furrows, forming a network with minute ridges in the meshes, doubtless representing the original cell structure.

It is quite probable that the specimen is of the same species as the one figured by Nathorst (1894 Pl. II fig. 6) from a nodule of ferrugineous clay-stone from Fiskekløfta. On account of the delicate striation of the surface Nathorst was inclined to refer it to a species of *Bothrodendron* (*Cyclostigma*), comparing it with a plant which, in the same paper (p. 45), he described from the Lower Carboniferous of the Pyramide Mountain and which he identified with *B. tenerrimum* (Auerb. & Trautsch.) Nath. This identification has been rejected by later authors (cf. Walton 1926 p. 120, and also Nathorst 1914 p. 68); on the whole, the specimen from Fiskekløfta does not help to throw much light upon the new one described here. — The size and position of the markings representing the leaf-trace bundles, make it possible that our specimen belongs to *Protolepidodendropsis pulchra*, but other species might also receive consideration. It bears a good deal of resemblance to the one from the Upper Devonian of Thuringia that Mägdefrau (1936 p. 214, Pl. X fig. 2) has referred to *Cyclostigma kiltorkense*. —

Another remarkable decorticated fragment in a knorrioid state is PA 394, Pl. LIII figs. 8—9. It is of somewhat larger dimensions. The surface is delicately wrinkled transversally in a very characteristic way. But the specimen cannot at present be referred to any definite species, the characters which it shows not being of sufficient systematic value. Apart from some difference in size, our specimen, with its fusiform elevations, has very much the same surface as a petrified branch of *Lepidophloios Wünschianus* from the Lower Carboniferous of the Island of Arran, described by Walton (1935 p. 326, Pl. II fig. 5). This strong resemblance may not be taken as a sign of any particularly close relationship, but shows only the identity in the state of preservation, as far as certain characters are concerned. It also throws an interesting light upon the organization of our plant, which belongs to the oldest lepidophytes known.

Caulopteris sp.

Text-fig. 32.

On a slab (PA 1146) of the hard, yellowish white sandstone from the canyon above Fiskekløfta there is a poorly preserved cast of a stem, slightly convex, about 8 cm broad (the original breadth may have been somewhat more), with irregular and coarse longitudinal furrows. The most conspicuous feature is a number of oval tubercles or scars, 1.5—2 cm high and half as broad, in regular arrangement along steep spiral lines, the vertical distance from one scar to the one next above being about 6—7 cm. Evidently the arrangement has originally been quincuncial, but during fossilization they have been slightly displaced. The scars are distinctly outlined and more or less elevated, but they do not, with certainty, show any traces of vascular bundles or similar details. A slowly attenuating ridge, a couple of centimetres long, forms a tail-like prolongation of the scar, from that end of it which is here supposed to be the lower one.

The scars give the fossil a superficial resemblance to some specimens of *Halonia*, described in the literature from various Carboniferous floras (compare, for instance, Zeiller 1886—1888 Pl. LXXII fig. 5), and it might appear possible that it represented a halonial axis of the same species as *Bergeria mimerensis*, of which a large ordinary stem is preserved in the form of a concave impression on the reverse side of the slab. One may also compare our specimen with the very large one which Bureau (1911—1913 p. 184, Pl. LII fig. 1) described from the Lower Carboniferous of the Basse Loire under the name of *Knorria*, but which is very different from the smaller ones which he described under the same designation. However, our specimen has certainly nothing to do with lepidophytes. It must be the stem of a fern-like plant, and may be included in the genus *Caulopteris* Lindl. & Hutt.

The many species of *Caulopteris* of the Carboniferous have mostly far larger scars, and differ in other characters as well. There is also a number of species from the Devonian (*C. antiqua* Newberry 1889, cf. Arber 1921 p. 37, Kräusel & Weyland 1933 p. 24; *C. Lockwoodi*

Dawson 1871 *a* p. 59, 1871 *b* p. 270, cf. Goldring 1924 p. 57, Kräusel & Weyland 1926 p. 131, 1935 *a* p. 15; *C. Peachii* Salter, in Murchison 1859 p. 408, cf. Seward 1923 p. XCV, Lang 1926 p. 789, 1927 *b* p. 7; *C. peregrina* Newberry 1889; *C.*? sp. Dawson 1881 *b* p. 11, 1882 p. 101). Only one of them, *C. antiqua* Newb., may be compared with the one described above; it is from the Middle Devonian of Ohio. Certainly, as is evident from the original drawing, it has much larger scars; but they are of the same form as those of our specimen, and there is scarcely any room for doubt as to the affinity of the two plants. They represent the same kind of plant organ, but probably the one from Spitsbergen is a new species; although very characteristic, it is so incomplete, however, that it is better not to introduce any new name for it at present.

Fig. 32. *Caulopteris* sp., from Mimerdalen: Eastern canyon above Fiskekløfta. — PA 1146. Nat. size.

The discovery of this kind of stem in the flora of the inner part of Mimerdalen is of considerable interest. It cannot be combined with any of the other plant organs found there so far; probably it has borne foliar organs of a more or less fern-like habit, of which no remains are represented in the collections. There is no reason to assume that they have been of the type of *Archaeopteris*: *Caulopteris* stems and *Archaeopteris* foliage have never been known to have anything to do with each other.

Dictyoxylon sp.

Pl. LVI fig. 11.

From the yellow sandstone of Planteryggen there are a few specimens showing impressions of cortical structures different from the usual lepidophytic ones. By far the best one is illustrated in Pl. LVI fig. 11 (PA 435). It is 5.5 cm broad and 7 cm long, consisting of parallel bands, mostly 2—3 mm broad, about 3—4 mm apart, transversally wrinkled, connected with each other by interlacing thin fibres, forming acute angles (of about 20°) to the broader vertical bands. A network is thus formed, in which the meshes are mostly irregular, but sometimes have a fairly constant size and a uniform lenticular shape, best visible in the lower part of the specimen.

This fossil has doubtless come from a stem with cortex of the *Dictyoxylon* type, that is, with a fibrous layer perforated by spindle-shaped groups of parenchyma. The broad vertical bands, being very regular and well defined, and the course of the thin strands connecting them, give our specimen a very remarkable and characteristic appearance, but it is scarcely possible at present to refer it to any natural species or genus, or even to any definite group of higher taxonomical order. It has a strong resemblance to many specimens described under the name of the form-genus *Lyginodendron* (compare particularly a cast of *Lyginopteris Oldhamia* figured by Williamson 1872 Pl. XXVII fig. 28), but it is scarcely a real *Lyginodendron*. — At all events, the specimen is of some interest as showing the high degree of development of the flora in this locality.

Another specimen of *Dictyoxylon*, quite different from ours, but of about the same age, has been described from Waldenburg by Gothan & F. Zimmermann (1937 p. 503, Pl. XXIII fig. 8).

Various axes, *incertae sedis*.

a. Long axis with subverticillate branches. — PA 1141 (Pl. LVII) is an axis about 40 cm long, straight, broken in both ends, and of a uniform breadth of about 7—9 mm throughout. The surface at certain places has delicate striations, and if examined in the magnification of a strong lens it shows very small longitudinal ridges and furrows, doubtless due to the cell structure; in several places there are also distinct transversal walls, forming cells of about quadratic form, 40—80 μ long, in a uniform tissue. There are lateral branches at fairly regular intervals of 5—6 cm. At most of the nodes there is one branch to the left, one to the right, and between them, in the median line of the stem impression, there is a distinct marking of a third branch given off at right angles to the bedding plane of the rock. Possibly a fourth one has had a similar position on the counterpart of the fossil, but that is not certain, the position of the branch bases in some cases being such as to indicate a ternate arrangement. The branches are approximately verticillate, but with no complete regularity, the vertical distance between branches belonging to the same node being in some cases quite considerable, as is visible on the photograph. The branches, leaving the stem at right angles, are always incomplete, the longest one being 2.5 cm long. They are rather thin, only about 2 mm thick, except at the bases, which are widened and somewhat decurrent, evidently having contained some very solid tissue.

There are also some other specimens of this remarkable type of stem, but of smaller size and poorer preservation. All of them have the same thick branch bases, and a subverticillate arrangement.

Our specimen (PA 1141) seems to be very nearly identical in size and form, and in the arrangement of the branches, with one from the Middle Devonian of Bohemia, figured by Stur (1881 Pl. IV fig. 1, p. 27) under the name of *Hostinella hostinensis*. In the work by Potonié & Bernard (1904 fig. 21) there is a drawing said to represent the same specimen in natural size; but it is reverse in relation to Stur's photograph, and only half its size. The specimen is referred to by Kräusel & Weyland (1937 p. 5) as one of the sterile branches assumed to belong to *Protopteridium hostimense*.

The Bohemian specimen and ours resemble each other to such a degree that the only inference possible seems to be that our plant at least belongs to the same genus. But a determination on this basis alone would not be very trustworthy. There are in fact, also other possibilities to be considered.

In their form and mode of attachment, the branches of the specimen figured (PA 1141) recall certain specimens which have been referred to *Caulopteris*, *e. g. C. (?) Peachii* Salter (in Murchison 1859 p. 408, fig. 14). But in the absence of the characteristic large scars, and without any further knowledge of the plants in question (cf. Lang 1926 p. 789), it is difficult to judge of the bearing of this fact.

It is uncertain how much importance should be attributed to the approximate verticillation of the branches. It may be of no higher systematic value at all, and that is the case if the plant really belongs to, or is related to, *Protopteridium*. But it is tempting to regard it as a character of systematic importance, the more so, because it is a parallel to the arrangement of the leaf-cushions in the specimen (PA 1170) which was described above (p. 88), and which in all probability belongs to the *Protoarticulatae*. However, there is a profound difference between all known members of the *Articulatae* (even in the widest sense of the word), with their numerous small leaves, and our plant with its fairly strong branches and no foliar organs.

b. Problematic leaf-bearing axis. — PA 452 (Pl. LVI figs. 7—8) is a piece of the ordinary yellowish sandstone of Planteryggen. On one side of it is the impression of a fragment of *Svalbardia*, on the other the fossil shown in Pl. LVI figs. 7—8. It is a fragment of an axis, a few centimetres long and about 2 mm thick, apparently firm and rigid, bearing a great number of linear leaves, which seem to have been at least 4.5 cm long, but less than 1 mm broad; in a few places they have traces of veins, at least as many as three parallel ones being observable in one leaf. The lamina is straight or nearly so, but the base has a very characteristic form: It is somewhat thicker than the lamina itself, and leaves the axis at a right angle or even, for a very short distance (1 mm or so), in a slightly downward direction, then turning upwards, the long distal part of the leaf forming an angle of about 45° to the axis. — Although this fossil has a very characteristic and easily recognizable form, its real nature cannot be determined at present. It can scarcely be doubted that it represents a new genus, but the material is too scanty to deserve a new name.

A somewhat similar fossil is found, in several specimens, in the hard whitish sandstone along the river above Fiskekløfta. The best one (PA 493, Pl. LVI fig. 9, upper part, and fig. 10) is about 3 mm thick and bears a great number of lateral organs, probably leaf-bases. They are curved twice, first downwards, then upwards (if the axis is correctly orientated). As now preserved, they are only a couple of millimetres long, but it cannot be ascertained by this material whether they have been longer. A few other remains, in a poor state of preservation, seem to have been up to 2 cm broad; also these specimens bear only short, nearly thorn-like appendages. — Some of these axes (*e. g.* the one in the upper corner of Pl. LVI fig. 9) have a striking resemblance to some specimens of *Lycopodites* which have been figured previously (Kidston 1885 Pl. XVIII fig. 6, cf. Kräusel & Weyland 1937). But in all probability the resemblance is only accidental, the 'leaves' in our specimens only representing the bases of long foliar organs, like those seen in the specimen described above (PA 452, Pl. LVI fig. 7).

Spores of unknown affinity.

Pl. XXXI figs. 5—19; Pl. XLIX figs. 14—16.

It was mentioned above that, through the maceration of the sporangia of *Svalbardia*, there were obtained numerous small, smooth spores which were assumed to belong to that plant (p. 77, Pl. XXXI figs. 5—9), and from the fructification which perhaps belongs to *Enigmophyton*, there was isolated a still greater number of spores of a similar type, which there was good reason to regard as microspores, while much larger spores (macrospores) of the same form were observable directly in the sporangia and also could be picked out from them (p. 118, Pl. XLIX figs. 6—13). In the same preparations, and in others, there was also found a considerable number of other types of spores, of very different forms, all of them represented only by one or a very few spores each; there were no clues of their mother plants.

The attribution of the said spores to *Svalbardia* and *Enigmophyton* needs confirmation, and the spore contents of the plant-bearing rocks of Mimerdalen deserve a much more thorough investigation than has been carried out so far; I have, however, postponed it in the hope that more material might be obtained. In a future study of the spores it will also be desirable to try photographing with infra-red light, for which I have not at present had any facilities.

It will further be necessary to take into consideration the spore contents of the Devonian cannel coal which was discovered by Vogt in 1928 (Vogt 1929 *b*, Horn 1929), and of which a detailed account by Horn and Vogt is now in preparation.

Spores of pre-Carboniferous age have been mentioned several times in literature, in increasing number of late. In the year 1902 (p. 43, Pl. XI), Nathorst described macrospores from the *Archaeopteris* flora of Bjørnøya (Heer had previously mentioned their occurrence). A few other remarks on Devonian spores, and figures of them, are also found in the earlier literature; but the fundamental work, so far, is the one by Lang, from 1925, in which 9 different types of spores were described from the Middle Old Red of Cromarty (spore-types A—I).

Descriptions and figures of Devonian and older spores have further been published by: Kidston & Lang 1917, 1921 *b*, 1924 *a*; Lang 1926, 1931, 1932, 1937; Kräusel & Weyland 1929, 1937; Arnold 1933 *a*, 1936 *a*, 1939; Nikitin 1934; Halle 1936; Darrah 1937; Leclercq 1940 *a*, *b*.

In a recent paper Thomson (1940) has proved the existence in the Middle Devonian of Esthonia of several (about 17) different types of spores, many of which had not been found before in the Devonian. I agree with Thomson that it would be desirable to have a system, with appropriate names, for the various spore forms of the Devonian, and welcome the start he has made in that direction. To me it appears probable that it will become possible, and necessary, to split up Thomson's group VII, *Apiculati*, according to the different types of spines, but I have no material at present to suggest any alterations or to express any opinion of the other groups.

The indeterminable spores found in the material from Mimerdalen (Planteryggen) are as follows, all of them belonging to Thomson's groups *Granulati* and *Apiculati*:

a. (*Granulati*). Pl. XXXI fig. 12 (PA 1251/49 *c*). Spore large, oval, about 330 μ long, wall covered with conical projections, ending in a delicate short tooth.

b. (*Granulati*). Pl. XXXI fig. 16 (PA 1251/49 *c*). Spore medium-sized, oval, 160 μ long, wall delicately granular.

c. (*Apiculati*). Pl. XXXI figs. 10—11 (PA 322/45); Pl. XLIX fig. 16 (PA 386/41 *a*). Spore large, about 300 μ in diameter, with thick spines, which may be up to 100 μ long, ending in a small tooth or hook. Owing to its size this type of spore easily breaks into pieces, and it has not been possible to clear any of the few specimens found. One of them (Pl. XLIX fig. 16), which does not give the impression of being much changed in form, is quadrangular, somewhat elongate, with three wide angles and the fourth angle acute. — This type of spore seems to be identical with the one described by Arnold (1936 *a* p. 45, Pl. IV fig. 5), from the *Archaeopteris* beds of Scaumenac Bay, but it is not known from what mother plant it has come.

d. (*Apiculati*). Pl. XXXI figs. 14—15 (PA 1251/49 *c*). Spore small or medium-sized, globular, about 100 μ in diameter, with numerous long, thin, simple spines, which are often curved or flexuose, and which hold the spores of this type together in groups. Two such groups are illustrated; they are somewhat different from each other, and may have come from different plant species. — These spores have some resemblance to one figured by Lang (1925 Pl. I figs. 18—20), but the latter is more than twice as big.

The single spore shown in Pl. XLIX fig. 14 (PA 386/41 *c*) may be identical with Pl. XXXI fig. 14 or fig. 15. Certainly most of its spines are shorter and thicker, probably because they represent only the basal parts; also in some of the other spores referred to, some of the spines are seen to be fairly wide and conical at the bases.

e. (*Apiculati*). Pl. XXXI fig. 13. Spore rather large, oval-elongate, about 250 μ long not including the spines, which are about 50—60 μ long, each of them rising from a conical base and ending in grapnel-like hooks (which are not very well preserved or developed). — This spore recalls Lang's G1 (*l. c.* fig. 13), but as our spore is somewhat incomplete, and only known in a single specimen, an identification is impossible.

f. (*Apiculati*). Pl. XXXI figs. 17—19 (PA 1251/49 *b*); Pl. XLIX fig. 15 (PA 386/41 *a*). Spore medium-sized, nearly globular, longest diameter 120—150 μ, spines about 20 μ long, not very numerous, ending in grapnel-like bifurcations. The thickness of the spines in the two spores found of this type is somewhat different. — Spores indistinguishable from these have been described from the Middle Old Red of Cromarty by Lang as type G2 (*l. c.* fig. 17), and from the *Archaeopteris* beds of Scaumenac Bay by Arnold (1936 *a*, particularly Pl. III fig. 5), and very similar ones were also found by Kräusel & Weyland (1929 p. 346) in association with *Aneurophyton germanicum* in the Middle Devonian of Elberfeld. It may be added that spores of the same size and, as it seems, with similarly bifurcating spines have been described by Arnold (1933 *a*) as the macrospores of a lycopodiaceous strobilus from the uppermost Devonian of Pennsylvania.

B. Petrifications.

The most interesting and richest locality for fossil fishes in the Devonian of the Mimerdalen Area has been Fiskekløfta. The south-western side of this gully is a good exposure of a black, crumbling shale with nodules of ferrugineous claystone, the latter often containing fish fragments. Plant remains are not rare, but in almost every instance they have only the character of very fragmentary impressions of no value, neither the external form nor the internal structure being usually preserved.

As far as is known, specimens in a better preservation have been found only once; they were petrified, with the cell structure very well preserved. Taking into consideration the very great number of nodules which have been examined in order to find fossils, it must be supposed that such plant fossils are extremely rare, although, on the other hand, it should be remembered that, when not examined in slides under the microscope, they are far more easily overlooked than the fishes.

The specimens mentioned belong to the collection brought home by Nathorst from the Swedish expedition in the year 1882. Probably Nathorst has not been aware that the nodules contained these plant fossils. They were discovered in the slides in the Paleozoological Department of the *Riksmuseum* at Stockholm by Professor E. A. Stensiö, and then handed over to the Paleobotanical Department. Professor Halle has now kindly passed them on to me for examination and description.

There are 20 slides which contain plant fossils of any interest. I have numbered them from *a* to *t*. The slides *f*, *k*, *m*, *n*, and *p* must have been prepared from one and the same nodule, at short distances and parallel to each other. The others seem to have been picked out among slides prepared for other purposes.

The preservation of the plant remains is good. But a certain decay has taken place before fossilization was completed, and some of the tissues have been destroyed.

Prototaxites sp.

Pl. LXII fig. 1.

In one of the slides (No. *i*) there is, along the edge of the preparation, a tiny fragment of *Prototaxites* tissue, measuring about 1.5 mm × 0.35 mm. Its most conspicuous feature are wide tubes, which must have been nearly parallel, all of them being seen in transverse or oblique section; the diameter ist mostly about 30 μ (20—40). The wall is thick, about 6 μ, and black. Some of them seem to have been cut at a point of bifurcation. As seen in the photograph, they are irregularly dispersed, the distances between them being less than their own diameter. The space between them mostly shows no structure, but there are also organic remains strongly indicating the existence of thinner tubes, about 4 μ in diameter.

The fragment is too small to render a specific determination possible. The genus is known from the Silurian and Devonian periods, the Devonian species being confined to the lower and middle parts of the period (cf. also p. 15).

Actinopodium Nathorstii n. gen. & sp.

Pl. LVIII figs. 1—5; Pl. LIX; Pl. LX figs. 6—7; text-figs. 33—35.

Material. — The specimen chosen as the holotype, is represented in five sections (slides *f*, *k*, *m*, *n*, *p*), evidently cut from one nodule at short distances from each other. Each of them contains a good cross-section of one and the same stem. In addition, the other slides contain sections probably belonging to other specimens of the same species.

Description. — To judge from the sections, which are exactly transversal, the axis of the holotype has been somewhat flat, the diameters measuring about 2.0 mm and 1.3 mm respectively. It consists of a stele surrounded by cortical tissues, the latter, however, only partly preserved.

The cortex is of variable thickness, but approximately its inner boundary may be said to be somewhere near the middle of the distance between the centre and the surface. It consists of thin-walled cells which, as may be seen in the places where they have been cut obliquely, have been somewhat elongate, with rounded corners so that there are intercellular spaces between them. The existence of different zones within the cortex cannot be ascertained, but the cells distinctly seem to become smaller and more thick-walled towards the surface (Pl. LIX fig. 2). The epidermis is not preserved in any of the thicker axes.

The inner cells of the cortex and those belonging to the zone which probably represents the phloem, are not sufficiently different from each other in the cross-sections to allow of the boundary being drawn with certainty in all cases. But, as is seen in the photographs reproduced here, the tissues often split along a line which mostly may be supposed to correspond to that boundary. The cells of the phloem have the same diameter as the cortical cells or somewhat less, but, that apart, it has not been possible in the cross-sections to make any reliable observations as to their form (compare the description of longitudinal sections below, p. 158). A number of the cells in the phloem are more or less completely filled with some dark lumps, which could scarcely be but the fossilized cell contents. As is shown in text-fig. 33, these cells are generally somewhat smaller than the others, and frequently they are surrounded by a regular ring of empty cells. On account of their smaller diameter and dense cell contents they have a

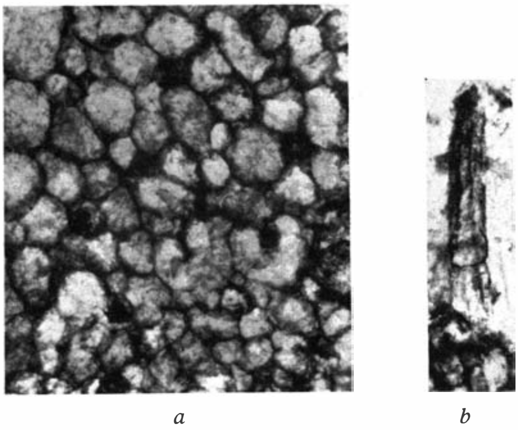

Fig. 33. *Actinopodium Nathorstii* n. gen. & sp., from Mimerdalen: Fiskekløfta. *a*. Holotype. Cross-section of phloem. × 110. — *b*. Single phloem cell, unusually thin, in longitudinal section, probably same species (p. 159). — × 200. *Riksmuseet*, Stockh. Slides *n* and *d*.

striking resemblance to companion cells, although the position is somewhat unusual.

The stele is elongate in cross-section, its longest diameter being at least twice as long as the shortest one. It is uncertain whether this feature is characteristic of the species or only of the specimen available. The outline of the stele in cross-section is determined by its xylem, which forms a star-shaped figure with about 7 rays. Both the ends of the rays and the sinuses between them are gently curved. The sinuses are broader than the rays; mostly, the latter are about as long as they are broad, sometimes longer.

The stele, apart from the phloem, consists of the following tissues: Outer wood, forming a layer all around the xylem strand; protoxylem; and pith, mixed with inner wood.

The position of the protoxylem is not very marked in the cross-sections, but it is found in small groups in the centres of the rays of the star-shaped figure, and also scattered here and there along the inner side of the outer xylem (the sinuses not excepted). The tissue is interpreted as protoxylem on account of the slightly smaller diameter of its tracheids, and especially on account of their scalariform walls, which are in contrast to the multiseriately pitted walls of the metaxylem. The structure of the walls has only been observable at certain places where the tracheids have been cut somewhat obliquely (Pl. LVIII fig. 5). It seems as if the protoxylem has had a mesarch position.

The inner parts of the stele consists partly of tracheids, forming an irregular metaxylem corresponding to the one which Harris (1929), when describing *Schizopodium Davidi*, called *X 1*. The tracheids of this tissue vary in diameter to some extent; they have multiseriate pits on all walls. — But there is also some parenchyma, which, at least partly, consists of large thin-walled cells (Pl. LIX). In most cases these cells have been destroyed before fossilization.

The outer parts of the xylem strand are built of tracheids arranged in radial rows, thus forming a tissue looking very much like secondary wood, varying somewhat in thickness, but mostly about 0.4—0.5 mm thick, being formed of about 7—9 layers of tracheids. The ends of the rays of the star-like figure are entirely made up of such rows, radiating from the primary xylem in the centres of the rays. The protoxylem is distinctly observable in several cases, and must be assumed to be surrounded by some ordinary metaxylem, which, however, cannot generally be distinguished from the inner tracheids of the radial rows; irregular xylem is found further in. The rows multiply in number outwards, as if branching; some rows divide only once, if at all, others do so repeatedly, so as to form, in the cross-section, a broom-like figure (cf. Pl. LVIII fig. 3 and Pl. LIX). Rather frequently a number of rows may be seen to start from one common point (evidently near a strand of protoxylem) and curve outwards, becoming straight and parallel further out and more or less transversal to the outer border of the wood. The tangential walls in neighbouring cells are often, but not always, on the same level, particularly in the outer layers.

Usually the tracheids of the secondary wood are rectangular in cross-section, more rarely irregular, the diameter very often 30—40 (—60) μ. The outermost ones in each row are smaller than those further in. They are not very thickwalled, but the dark colour of their walls, as now preserved, distinguishes them fairly clearly from the non-lignified cells with their more brownish walls. Sometimes they may be studied in oblique sections, which show that they were multiseriately pitted. On the radial walls the pits are seen to be numerous and probably always present, mostly in 3 (2—4) vertical rows. On the tangential walls they may also be found, sometimes just as numerous as on the radial walls; but that does not constantly seem to be the case: There are oblique sections showing tangential walls without any pits, a feature which does not seem to depend upon the preservation. — In the cases when the cell wall is more or less in the plane of the section, no borders are visible around the pits; but in a few cross-sections there are structures looking very much like bordered pits: The walls seen in Pl. LX fig. 7 strongly recall those of the tracheids of a conifer.

As now seen in the fossil, this secondary wood has very often split up, the individual cell rows, or groups of them, being separated from each other radially, but never breaking up tangentially. At least in many cases these splits must have been formed through shrinkage and decay; generally, the separation seems to have taken place along the middle lamella, the cells on both sides of the split usually being entire.

In a number of cases, however, narrow splits between the tracheid rows seem to represent medullary rays. If that is correct, they have been uniseriate, probably also biseriate (and multiseriate?), consisting of parenchymatous cells which have either been completely

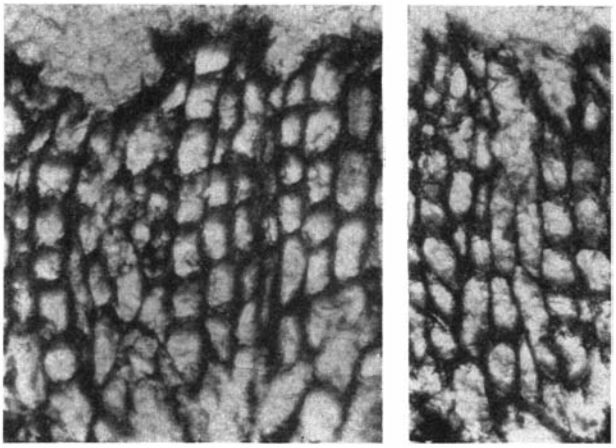

Fig. 34. *Actinopodium Nathorstii* n. gen. & sp., holotype, from Mimerdalen: Fiskekløfta. Cross-sections of secondary wood, probably with medullary rays. — *Riksmuseet,* Stockh. Slides *f* and *m*. × 125.

destroyed before and during the fossilization, or have left some brownish substance, in a few cases also remains of walls, or even fairly complete cells (text-fig. 34). Horizontal ray tracheids (as in some species of *Callixylon*) are not found.

At first sight the outer xylem, now described, gives the impression of being ordinary secondary wood; there is, however, also a possibility that it is of the same nature as that of the Australian *Schizopodium Davidi* which Harris (1929) described as a remarkable type of primary wood. Some of the arguments which Harris (*l. c.* p. 404) brought forward in the case of that plant, may also be used here. The most difficult question, however, and an important one in this connection, is that of the existence or non-existence of a cambium between the xylem and the tissue regarded as phloem. It is a remarkable fact that in our preparations the tissues, in contrast to what is the case in *S. Davidi*, evidently have a tendency to split along this line, just as one would expect if there were a zone of thin meristematic cells; in the cases when the layers are still in contact, there is very often a dark line of crushed cells, as is visible in the illustrations. Only in a few places is the preservation of these parts fairly good. No regular cambium is then seen, but it is clearly observable that the rows of tracheids usually end in some smaller cells (text-fig. 35), and, if *S. Davidi* had not been known, one would certainly have declared without hesitation that these cells mark the position of a cambium. It is scarcely possible, from the material available, to arrive at full certainty on this point, but, everything considered, we may probably be quite justified in assuming that the formation of tracheids has continued through cell-

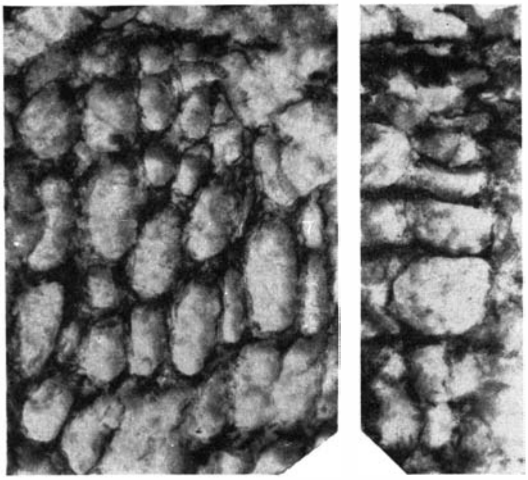

Fig. 35. *Actinopodium Nathorstii* n. gen. & sp., holotype, from Mimerdalen: Fiskekløfta. Cross-sections of secondary wood, probably with remains of cambium above, *i. e.* on the border towards the phlcem. The walls of the tracheids in fig. *a* have bordered pits, better seen on Pl. LX fig. 7, which is from a place to left of this figure. — *Riksmuseet,* Stockh. Slide *n.* × 250.

division in a layer on the border between xylem and phloem, in other words, that the wood is truly secondary.

It should be borne in mind that radial rows of cells like the tracheids in question can come into existence only through repeated division, by means of tangential walls, from one cell, which in that way pushes itself outwards. The process may take place in the apical meristem; then the tissue is 'primary'. But it is also possible, and in this case probable, that such a formation of new cells has continued without interruption, long after the growth in length of that part of the axis, and the maturation of most of the cells, had ceased. In that case the tracheids will form a 'secondary' wood. The difference will not always be very profound, and there may really be cases when it is impossible to draw a sharp line of distinction between the two kinds of wood. Harris is of opinion that in *Schizopodium* the meristematic activity of the procambium, if present at all, would stop early, and that after the maturation of the cells thus formed, there would be no meristematic tissue left. In the Spitsbergen plant, on the other hand, there is good reason to believe that the meristem, which was probably of exactly the same origin as the transitory one in *Schizopodium,* preserved its faculty of forming new cells indefinitely, as long as the axis was alive.

The stele gives off small bundles, which start from the ends of the rays of the star-like xylem; one example is seen on the right-hand side of Pl. LVIII fig. 2, and another somewhat below the centre of Pl. LVIII fig. 1. In the latter case the bundle has left the wood, but is still within the cortex. In one preparation (slide *m*) two rays on opposite sides of the xylem strand, are seen in the state of emitting small bundles. — A bundle of this type consists of a protostele; at least in some cases it has been possible to ascertain that it has scalariform tracheids (protoxylem) in the centre and pitted ones further out.

The real nature of these small bundles is somewhat uncertain. At first sight one would not hesitate to regard them as simple leaf-traces, and the comparison with *Caracuboxylon* makes this interpretation very probable. However, it is remarkable that in the matrix, outside the axes, there are several cross-sections of thin cylindrical organs, consisting of similar bundles surrounded by parenchymatous tissues, as will be described more in detail below. It is probable that the bundles within the cortex are going out to form these particular organs; but it is difficult to believe that the latter are parts of leaves. Could they be roots? Their distribution in the matrix makes this idea probable, and the bundles still within the cortex might be compared with those forming the adventitious roots of some *Coenopteridae*; but the bundle invariably seems to be a simple protostele with a concentric arrangement, and not diarch as the roots of those ferns with which the comparison might be made; upon the whole; there is nothing root-like in the anatomy of these organs. Most of all they resemble thin axes, or branches; thus, it is a striking fact that in anatomical structure they can scarcely be distinguished from the thin axes of *Botryopteris cylindrica* (see, for instance, Bancroft 1915). In a primitive plant, where the leaves are not much differentiated from the axis, and where real roots are not developed at all, the question would scarcely have any purpose; but in the case of the present plant, which is highly advanced in anatomical organization, one cannot say that. If in the following these bundles are simply spoken of as leaf-traces, it is done with a certain reservation.

No doubt these bundles originate in the circum-medullary primary strands and then work their way out through the secondary wood. The material available does not make any observations on that point possible. But at all events it is certain that no leaf gap is formed in the wood.

As just mentioned, some such bundles are found in the type specimen, within the axis, either still in connection with the wood of the main stele from which they are emitted, or further out in the cortex. However, both the same slides and others also contain a considerable number of circular cross-sections of similar organs which lie isolated in the matrix. Some of them are seen, somewhat indistinctly, on the left-hand sides of the photographs Pl. LVII figs. 1—2. Those which are found in the slides containing the type specimens, are fairly uniform. Among those found in other slides, there is a certain variation; but it seems quite probable that most of them, at any rate, are of the same kind of organ and belong to the same species. A section of a fairly complete specimen, which may be regarded as typical of this kind, is shown in Pl. LX fig. 10 (slide *o*). It is about 0.6 mm thick. The outer cell layer, probably epidermis, is rather thick-walled; as in the other specimens (cf. Pl. LX fig. 8), the radial walls in these cells have a tendency to break, so that the outer wall, more or less entire and complete, may become detached from the inner tissues; it looks as if it has been particularly strong. The outer layer of cells is always uniform, without any kind of appendages or intercellular openings. The stele in Pl. LX fig. 10 has split up on the border between xylem and phloem. That is also usually the case in the other sections, although there is a certain variation; it even happens that the splitting up takes place within the outer part of the xylem strand.

A somewhat remarkable strand is shown in Pl. LX fig. 11 (slide *m*). It belongs to the cross-section of an organ situated close to the star-shaped strand of the holotype described above; it cannot, however, be proved that they belong to each other. It has been badly damaged before fossilization, and the only part of the stele that has been well preserved is the centre; but that is of some interest because it consists exclusively of exceptionally distinct scalariform tracheids.

Branching of these thin bundles has been observed only in one case, shown in Pl. LVIII fig. 6. It is found in a slide (No. *b*) which, in addition, also contains some other cross-sections of the same kind of organs, and some longitudinal sections, probably of stems. The branching one has been cut exactly transversally just beyond a point of bifurcation, the two parts being equal in size. As now preserved, they are very thin; but the outer tissues having been lost, it is difficult to judge of their original diameter. What is left of the steles, consists only of scalariform tracheids; but it is quite possible that there has been some surrounding metaxylem.

As a summary with regard to these thin cylindrical organs it may be said that they often contain a considerable number of fairly wide tracheids, but that there is nothing to indicate any secondary growth, the tracheids never being arranged in radial rows.

Description of further specimens of axes, which probably, but not with full certainty, belong to the same species, will be found below (p. 158).

Affinity. — In order to facilitate reference, it may at once be stated that the plant described must be regarded as the representative of a new genus, for which the name of *Actinopodium* will be proposed, retaining the same ending as in *Schizopodium*, and at the same time expressing the radiate form of the xylem strand. As the specimens were brought home by Nathorst's expedition (in the year 1882), the name of this great pioneer will be commemorated in the specific name. — For diagnosis, see p. 194.

Actinopodium may be compared to the following genera previously described from the Devonian of other areas:

1. *Caracuboxylon*. The genus was created by Zalessky & Tchirkova (1930) on the basis of two beautifully preserved fragments of axes, which were referred to different species, resembling each other very much; they came from the Upper Devonian of the Donetz basin. — The genus resembles our plant in the following characters: In the general arrangement of the tissues, in the wide pith, mesarch protoxylem, position of primary strands in relation to the secondary wood, and in the mode of emitting small bundles from the projections of the secondary wood (if these bundles are of the same nature). They differ chiefly in the following characters: The pith in *Actinopodium* consists of parenchyma mixed with some tracheids, whereas in *Caracuboxylon* it has entirely disappeared, probably already in the living plant (a difference of slight systematic importance). Secondly, the stele of *Actinopodium* is star-shaped, in contrast to that of *Caracuboxylon*, of which the outline is only slightly and irregularly undulating. Finally, the small

bundles in *Caracuboxylon*, which are doubtless leaf-traces, divide regularly within the cortex. — These differences are at least of generic importance, but the relationship between the two genera is indubitable.

2. *Schizopodium*. The type species, *S. Davidi*, described by Harris (1929) from Queensland, in all probability came from the Middle Devonian. Lately a second species, *S. Mummii* Read (1938), has been added to the genus; it was found in the Middle Devonian (Hamilton) of New York. While evidently corresponding in the main features with *S. Davidi*, it is unfortunately represented by a very scanty material in defective preservation.

Schizopodium differs from *Actinopodium* above all in the lack of pith. Further its stele has a much more irregularly dissected outline in cross-section, with a tendency to disintegrate into separate strands. (Such a disintegration of the stele with increasing size may simply be an adaptation in order to maintain a high proportion of surface to bulk, as has been shown in the case of several plants, among others by Wardlaw 1924; but if one may judge by the material available, *Actinopodium* evidently maintains the proportion by other means than *Schizopodium*). Evidently also the primary bundles of the two plants have been entirely different. As points of minor importance we have the character of the outer wood, which probably was 'primary' in the one plant, and 'secondary' in the other, and the small bundles emitted from the stele of *Actinopodium*, but lacking in *Schizopodium*. The sum of these differences is so great that it is out of the question to refer the two plants to one genus, and it may be doubted whether they are very closely related to each other at all (compare also p. 180).

3. *Asteroxylon, Palaeopitys*, *Aneurophyton*, and *Cladoxylon* were discussed by Harris (1929), who pointed out what differences they showed from *Schizopodium Davidi*. With the exception of *Palaeopitys* (compare below, p. 160) they are still more remote from the new plant from Spitsbergen. Later literature (*e. g.*, in the case of *Aneurophyton*, Kräusel & Weyland 1929) has only intensified the difference. — *Asteropteris noveboracensis* Dawson (1881 *a*), from the Upper Devonian of New York, with its radial plates of xylem and its petiolar bundles resembling those of *Clepsydropsis*, is far more complicated than our plant, being a typical member of the *Filicales*. The other species once referred to the same genus, *A. Kopfi* Arnold (1935 *a*), from the basal beds of the Upper Devonian of New York, has been shown by Read (1938) to represent a separate genus, *Arachnoxylon*; its stelar structure does not suggest any affinity to our plant.

Thus, among Devonian genera hitherto described there is none with which our plant may be combined, and the same is still more distinctly the case if it is compared with younger fossils. As stated above, it will therefore be necessary to institute a new genus for it. Its systematic position will be further discussed below (p. 180).

Other sections.

a. Cross-section of axis, cf. *Actinopodium Nathorstii* (Pl. LX figs. 1—5). — In slide *l* there is a small stem which has been cut exactly transversally. It is nearly circular in outline; its diameter is 0.95 mm. The cortex is only partly, and not well, preserved. The stele occupies a smaller proportion of the axis than it does in that of the type specimen described above, the two most distant points of the xylem being about 0.5 mm apart. It is star-shaped, the rays narrower, longer, and more acute than in the type specimen; they are somewhat different from each other in shape and size, but correspond symmetrically to one another on both sides of a median plane, the stele thus becoming bilateral. There are 8 rays in all. They are fairly well preserved, and usually contain some narrow tracheids in the middle; at least in some cases these tracheids are scalariform, and no doubt they represent the protoxylem. They are surrounded by wider tracheids with multiseriate pits; in some places these wider tracheids are arranged in rows, making the impression of being truly secondary. The tissue in the sinuses is poorly preserved, and at first sight the rays therefore appear isolated from each other; but in some places (particularly on the right-hand side of Pl. LX fig. 2) there is, in the sinus, some irregular wood with some secondary wood outside it. — Of the tissue in the interior of the stele not much is left, but it seems to have been a large-celled parenchyma.

In the cortex are found several separate bundles. The large one, of which a part is indistinctly seen in the upper left-hand corner of Pl. LX fig. 2, is a somewhat dubious thing of uncertain relation to the rest of the plant. But further out in the cortex there are at least 3 very small strands, indubitably belonging there (Pl. LX fig. 5). They are very thin, circular, as it seems, in cross-section, and hollow, consisting of a ring of narrow tracheids, which at least in some cases have scalariform walls, some others seem to be pitted.

The resemblance of this axis to the type specimen described above, preponderates the differences, but whether they belong to the same species or not, it is difficult to decide without further material.

b. Longitudinal sections. — There are several longitudinal sections of axes, most of them, like the one shown in Pl. LVIII fig. 7 (slide *d*), with a thicker or thinner stele, surrounded by a parenchymatous cortex. Others consist only of fragments of wood; a specimen of that kind is shown in Pl. LXI fig. 3 (slide *e*). The size, and the histological details observable, make it probable that they represent remains of *Actinopodium Nathorstii.*

In some of these longitudinal sections there are cells which must represent the phloem (text-fig. 33), according to their position between the wood and the large-celled parenchyma of the cortex. They are rather thin-walled, somewhat wider than the tracheids, of varying length (some of them about 10 times as long as wide, others more or less), the end-walls at least mostly horizontal or slightly oblique; there is often a slight constriction at the partition, the corners of the cells being rounded. No pores are visible.

The xylem is often very well preserved. It consists of both scalariform tracheids and pitted ones (cf. Pl. LXI). In the scalariform tracheids the bars are sometimes very thin, so that the tracheids may look like annular ones. The pitted tracheids are connected with the scalariform ones by intermediate stages with transversally elongate pores. There are only exceptionally so many series of pits as in the cell seen in the upper right-hand corner of Pl. LXI fig. 2. Bordered pits have not been observed, but that may be due to defective preservation. —

An interesting longitudinal section is found in slide *s*. Only parts of it are preserved, comprising some parenchyma and some of the tissue interpreted as phloem. The remarkable thing about them, however, is the xylem. In some portions it has the same appearance as, for instance, that of slide *e*, shown in Pl. LXI figs. 4—5. The character changes, however, in other parts, where the tissue is as illustrated in Pl. LXI fig. 6: Here the tracheids are very loosely connected with each other and often become detached (secondarily, through natural maceration), so that they are found single or in small groups separated by interspaces often broader than the groups themselves. The course of the cells is irregular, sometimes even slightly flexuose. The sculpture of the walls is poorly preserved, but is certainly in some cases multiseriately pitted, in other places possibly scalariform. Medullary rays are not seen with certainty. It is possible that some of the gaps between the tracheids (as seen, for instance, in the lower right-hand part of Pl. LXI fig. 6) correspond to rays; if so, they have been uniseriate and not very high. But precise observations are not possible, nothing of the ray cells being left.

The appearance of this section is about as one might expect from a longitudinal tangential section of the secondary wood and some of the outer tissues of *Actinopodium Nathorstii*, and quite possibly it belongs to that species. It should also be compared with the transversal sections of wood described below, and with *Callixylon.* As regards its resemblance to Stigmaria, see next page:

c. Transversal sections of wood. — In some of the slides there are fragments of wood, cut transversally, the largest one measuring nearly 8×8 mm (slide *j*, Pl. LXII figs. 2—4). It consists only of tracheids, arranged in radial rows and showing no traces of growth zones. They are rectangular in cross-section, or rarely polygonal, and have multiseriate pits. On the radial walls the pits seem to be constantly present, frequently in three vertical rows, whereas on the tangential walls they are much less constant, if occurring at all. In some places (*e. g.* in the lower right-hand corner of Pl. LXII fig. 4) the tracheids seem to be tangentially elongated, but that may be due only to oblique cutting of tracheids of irregular course. — The fact that the rows of tracheids very rarely double, but mostly run parallel and undivided, shows that the piece of wood must have come from a stem of considerable size. There are no indications of growth zones. — It would be very surprising if a piece of wood of this structure and this dimension had no medullary rays (in fact, they should be thought necessary for physiological reasons), but they are at all events not well preserved, in spite of the comparatively good preservation of the wood in other respects. There are numerous long, radial splits between the rows of tracheids. No doubt they have mostly been formed, or at least widened, post mortem (as is evidently also often the case in *Callixylon*, for instance); but it is quite probable that many of them correspond to rays. There is not much, if anything, left of the ray cells, which may have been less resistant than the lignified tracheids; but in a number of cases there are narrow splits which run with unaltered breadth for long distances, and which contain some brown matter, which may be the remains of parenchymatous ray cells, the walls having been destroyed. Therefore, although the observations are not very positive, it is not possible with certainty to regard the wood as destitute of rays.

A fragment found in slide *r* (Pl. LXII fig. 5), has smaller cells than the one just described, but is built in the same way.

It would be natural to regard these fragments as the secondary wood of old stems of *Actinopodium*, the structure being as one might expect to find it in that plant, if the secondary growth had gone on for some time. On the other hand, it has to be compared with *Callixylon* and *Palaeopitys*; in fact, there is no difficulty in assuming that the secondary wood of *Actinopodium* has been of the same general type as in one of these genera, although differing, as far as we know, from *Callixylon* in not having the tracheid pits grouped between pitless areas, and from *Palaeopitys* in the scarcity or lack of pits on the tangential walls. However, as long as nothing more is known about the rays, to mention the most important feature, a decision with regard to the relationship or identity is impossible. — Compare also p. 182.

It may be added that this wood, just as the tangential section described on the preceding page (slide s, Pl. LXI fig. 6), to a certain extent recalls that of *Stigmaria*; but the character of the tracheids, and the entire absence of root-trace bundles, show that they are of a different nature.

V. Stratigraphical Discussion.

The sedimentary rocks of Devonian and Upper Silurian ages in Spitsbergen, the total thickness of which was estimated by Hoel (Staxrud & Hoel 1913) at about 10 000 m (compare also Orvin 1940 p. 15), are generally divided into four series.

Unfortunately the geological and paleozoological results of the latest expeditions have not been published in full, and the last word has not yet been said about the regional extension of these series and about their ages and subdivisions. A review of the fossil faunas, particularly with regard to the fishes, as far as known up to the year 1937, was published a few years ago by Heintz (1937), together with a stratigraphical discussion and accompanied by a correlation table; but that is now partly out of date, a fact above all due to Heintz's own work. — Thanks to the kindness of the respective authors, however, I have been permitted to read and use the manuscripts of a paper which will soon be published by Vogt on the stratigraphy of Mimerdalen, and of one by Føyn & Heintz on the stratigraphical results of the English-Norwegian-Swedish expedition in 1939 (see bibliography). Through these papers, with their abundance of new observations and their correlation between the various areas, many problems are solved, and we are getting a new and solid basis for further work.

According to Føyn & Heintz the ages of the four series are as follows, if determined by the fish faunas:

Wijdefjord Series	Fiskekløfta	Upper Middle Devonian
	Wijdefj. Series s. str. .	Middle Devonian
Gråhuk Series	....	?
Woodfjord Series	Stjørdalen Division ..	?
	Lyktan Division.....	?
	Kapp Kjeldsen Division	Lower Lower Devonian
Raudfjord Series	Ben Nevis Division .	Dittonian
	Frænkelryggen	Downtonian

While it is fairly certain that the base of the Woodfjord Series, resting conformably and without hiatus upon the Ben Nevis Division, represents the oldest Lower Devonian, the paleozoological evidence as regards the two upper divisions of the Woodfjord Series, and the Gråhuk Series, is not clear. But being older than the Middle Devonian Wijdefjord Series, they must range somewhere between the lower or middle Lower Devonian, and lower Middle Devonian.

This is not the place to discuss the stratigraphical problems at any length. But it is of considerable interest to inquire whether the fossil plants can be of any help in the determination of the ages of these beds, and particularly to compare their evidence with that of the fossil animals. We may therefore take up separately for consideration the various fossil floras, remains of which have been described in the preceding chapters, and see how they may fit into the stratigraphical system as exposed in the papers just quoted. As in the preceding descriptive part, it may be practical to mention the floras of the various localities in geographical order, and not according to their position in the stratigraphical sequence, because the regional extension of the series and the boundaries between them may still, in some cases, be subject to doubt or discussion. — A summary in tabular form is given below (pp. 169—170).

At Raudfjorden the only plant-bearing horizon is the one in Frænkelryggen (p. 13), belonging to the older part of the Raudfjord Series. As determined by means of its very rich fossil fauna, this series is assumed to correspond to the upper part of the Downtonian and to the Dittonian. The flora alone would not be sufficient for any very precise determination of the age of the locality, but it is entirely consistent with the paleozoological evidence.

From Woodfjorden no plant fossils have been brought home. This is much to be regretted, because the Woodfjord Series is the thickest division of the Devonian and has at the same time a wider regional extension than any of the others. Føyn & Heintz have shown that it comprises three subdivisions, which petrographically are clearly defined. The Woodfjord Series, particularly its middle division, extends eastwards to Wijdefjorden and southwards to Isfjorden, and some of the plant localities in these districts belong stratigraphically to it; although mostly of slight paleobotanical interest, some of them will be mentioned below.

Among the plant fossils found in the various localities along the west side of the Wijdefjorden the best preserved belong to new species, one of them also to a new genus, and, although being of considerable interest, also from a stratigraphical point of view, they cannot be used as guide fossils. That is the case with *Psilodendrion spinulosum* n. gen. & sp. (p. 26), from near Gråhuken itself, and with *Psilophyton arcticum* n. sp. (p. 33), from the beach at Andredalen, the former from typical Gråhuk beds, the latter from the Wijdefjord Series: To judge from their affinities and from their morphological development, it is very probable that both of them are of Lower Devonian age, or possibly Middle Devonian, whereas they should certainly not be expected to be younger. Thus they are in agreement with the paleozoological determination of the age.

In some other localities of the Wijdefjord Series, however, we have the remains of a vegetation comprising plants of such a high organization and large size that it is quite alien to early Devonian floras. One striking case is that of Horizon 4 in the beach profile at Andredalen, where the fossils occur in a dark grey shale belonging to the Wijdefjord Series: As was mentioned in connection with the description of these remains (p. 39), we have certainly not a single species here which may be definitely determined as Upper Devonian; but when looking for forms with which to compare most of these fossils, we have to turn to the Upper Devonian floras, or to even still younger ones, of other countries, nothing similar having ever been found in the Middle Devonian or older floras. There is only one exception: the poor fragment determined as *Drepanophycus* sp. (p. 46). That genus belongs to the Lower Devonian, or more rarely to the Middle Devonian (the specimen recorded by Gothan & F. Zimmermann 1937 from the lower Upper Devonian of Liebichau is of uncertain affinity). Thus, if we accept the determination of the Wijdefjord Series as based upon the fossil fishes, the testimony of this somewhat problematic *Drepanophycus* fragment will be correct, and all the other plants, which alone would have made a younger age probable, will have to be regarded as additional proofs of the remarkably early appearance of highly developed forms in the Devonian of Spitsbergen (cf. p. 166).

We have a similar case in another plant locality a little farther south, at the beach between Andredalen and Forkdalen (p. 49), except that there is nothing at all here to indicate that the flora may be as old as the Middle Devonian. Certainly, it is not definitely settled to what genus one should refer the only form which it has been possible to give any specific name, *Cephalopteris(?) praecox* n. sp., but there can be no doubt that both this remarkable plant and the large sulcate stems, with which it is associated, very strongly indicate an Upper Devonian age; they should even be expected to date from a rather young stage of that period. The locality belongs to the typical Wijdefjord Series, and should consequently be Middle Devonian, a fact rather contradictory to all that is known before about these types of fossils.

The collections made by Hoel (in 1912) in the mountain south of Vatnedalen, in beds of the Wijdefjord Series (p. 29), comprise forms which, although indeterminable, were assumed by Nathorst (according to an unprinted label) to represent the Upper Devonian; the same impression of a relatively young age of these fossils is strengthened through further study of them, even if they are not entirely unparalleled in the older parts of the Devonian. — The *Hostimella (Aphyllopteris)* from the Wijdefjord beds on the south side of the bay at Forkdalen (p. 55) is a Lower or Middle Devonian form.

The striated axes with opposite lateral organs, from the southern branch of Forkdalen (p. 57), cannot at present be determined with such accuracy that they can give any information about their age; it is not quite certain whether they are from the Gråhuk Series or Wijdefjord Series. The plant remains from the other parts of the Wijdefjord area are also too uncertain for a precise determination of the ages of the beds. According to Professor Heintz some of them belong to the Gråhuk Series, others to the middle division of the Woodfjord Series.

The Devonian on the west side of Billefjorden (p. 60) was regarded as Lower Devonian by Nathorst (1894, 1910, compare also Stensiö 1917 p. 71); other authors have recorded Lower Devonian (Woodfjord Series) from here, too. However, the conditions are somewhat complicated, several horizons being represented. The plants brought home by Vogt's expedition in 1925, and which are described above (p. 60), are consistent with a Lower Devonian age of the beds in question, although their value as index fossils is not very great and a precise chronological determination is not possible. Among the specimens which Nathorst, in 1882, brought home from the west side of Billefjorden, the fragment of *Barinophyton* sp., described above (p. 67), is very remarkable; certainly, it is too incomplete for a specific determination, at least at present, but it decidedly belongs to a group of plants which, so far, are known only from the Middle and Upper Devonian. Another specimen worth consideration is the one which Nathorst (1894) described under the name of *Cyclopteris* sp. (*Platyphyllum* sp., p. 93), and which strongly resembles those from the inner parts of Mimerdalen, from strata which are certainly younger than the Lower Devonian; but, as was mentioned above (p. 93), it is not preserved well enough to allow of a reliable determination. During the expedition in 1939 I found further material of such broad leaves (but, it may be added, no specimens of the characteristic axes of *Enigmophyton*); as these additional collections, however, need preparation and closer study before any conclusions may be drawn, a further discussion of the chronological position of the flora of the west side of Billefjorden had better be postponed.

From Mimerdalen no plant fossils of any value have been found in the lower beds in the eastern (outer) part of the valley. The oldest plant mentioned in the description above (p. 69) is from the eastern side of the river east of Estheriahaugen. In all probability it is a psilophyte, and if so, the only member of that group from Mimerdalen. But chronologically it does not tell us more than that the bed in question is not younger than the Middle Devonian, at most.

The youngest strata of the Devonian in Mimerdalen (and, in fact, in the whole of Spitsbergen, compare above, p. 161) are in the inner part of the valley: Those in Estheriahaugen are partly contemporaneous with the horizon of Fiskekløfta, above which follow the shales and sandstones further up along the canyon, and the beds of the south-eastern corner of Torfjellet, including Plantekløfta and Planteryggen. To judge from the plant fossils, there does not seem to be any great difference in age within this succession.

The flora of Fiskekløfta was previously known to consist of a few plants described by Nathorst (1894) under the names of *Bothrodendron (?)* sp. and *Lepidodendron* sp. Both of them probably belong to species also represented in the horizons above. They strongly indicate an Upper Devonian age (compare below, p. 167). In the present paper two more plants are added to the flora of Fiskekløfta: *Actinopodium Nathorstii* n. gen. & sp., and *Prototaxites* sp. — *Actinopodium* (p. 150) may be compared with the (probably) Middle Devonian *Schizopodium* from Australia, but there is certainly no very close relationship between them, at all events not close enough to make possible any conclusions as to their age. Its nearest relative is evidently *Caracuboxylon* from the young Upper Devonian of the Donetz Basin. — The discovery of *Prototaxites* (p. 149) is rather surprising, the genus chiefly being known from older strata. But it has also been recorded from the Middle Devonian, in Scotland, Canada, and Ohio.

The assemblage of plants found as impressions in the youngest Devonian beds of Mimerdalen (p. 70 et seq.) from the strata immediately above those of Fiskekløfta, is rather puzzling from a stratigraphical point of view:

(1). *Enigmophyton superbum* n. gen. & sp. (p. 88) and the other fan-shaped leaves are of no great use for a detailed determination of the age.

(2). *Svalbardia polymorpha* n. gen. & sp. (p. 70) is one of the interesting plant forms which mark the transition from the *Psilophyton* flora to the *Archaeopteris* flora, and its natural place would seem to be somewhere near the boundary between the Middle and Upper Devonian; from our present knowledge of the plant we should certainly be inclined to refer it to the Upper Devonian.

(3). The lepidophytes (p. 121 et seq.) are of an Upper Devonian aspect and contrast distinctly with practically all Middle Devonian floras. Although they cannot be identified with any species from other localities, some of them are comparable with some from the lowermost Upper Devonian (Gothan & F. Zimmermann 1937), but they might as well belong to a somewhat higher horizon. The large specimens of *Bergeria mimerensis* are of a greater size than any lepidophytes known previously from typical Middle Devonian floras, and they are probably the oldest arborescent lepidophytes known in the world; those which come nearest to them in age and size, are some specimens of '*Protolepidodendron*' *primaevum* (or related species) from Pennsylvania and Virginia (see

Berry 1933), probably from the uppermost Middle Devonian, the 'Naples Tree' from the Middle Devonian of New York (cf. p. 135), and *Protolepidodendron(?) arborescens* Sze (1936) from Hunan, which is said to come from the Middle Devonian. Particularly the former seem to equal our *Bergeria* in size. But, in spite of these cases, one would not hesitate for a moment to determine the age as Upper Devonian, if one were to judge from the lepidophytes alone. (As regards the relation to *Leptophloeum*, cf. p. 128).

(4). On the other hand we have *Hyenia* (p. 82), a genus which, as far as is known, is confined entirely to the Middle Devonian, being in fact one of the most characteristic genera of that age. In the present case we are confronted with a new species and a new subgenus of *Hyenia*, differing from those previously known in some characters, of which one, at least, denotes a certain primitiveness: Its spines, or hairs, could scarcely be anything but a reminiscence from a psilophytalean origin (cf. p. 185).

Thus, as in so many cases in the Devonian of Spitsbergen, the plant fossils of Mimerdalen do not give any unequivocal answer to the question of the age of the beds, owing to the peculiar mixed composition of the flora. With regard to the highest horizons in the valley, the natural conclusion to be drawn from the floristic facts, everything considered, would be that the beds are from somewhere near the transition from the Middle to the Upper Devonian, rather above than below that boundary. This conclusion is in fairly close agreement with the results obtained from the study of the fossil fishes: The fauna of Fiskekløfta has previously been regarded as Upper Devonian, but most authors (Vogt, Heintz, Stensiö, and Säve-Söderbergh) now find it more correct to refer it to the uppermost Middle Devonian. As was mentioned above, there does not seem to be any great difference in age between Fiskekløfta and the superposed layers, so that, if the modern view of the age of Fiskekløfta is the right one, it would be natural to regard the whole succession as Middle Devonian; but for the youngest beds, in which no animal remains have been found, an early Upper Devonian age would not be excluded.

The conclusions which it has been possible to draw from the fossil plants as regards the chronology of the Devonian of Spitsbergen, are somewhat unsatisfactory, as will be evident from the preceding pages. This is not, principally, due to any general unreliability of the paleobotanical evidence in such questions, but to certain special features. Above all, most of the recognized species are new, and not being known from other localities, they cannot be used with any great profit for the determination of the age of the beds, except within rather wide limits. But there is also another remarkable feature, the importance of which it is difficult to appraise at present: In several cases relatively young plant forms occur in beds which, according to the paleozoological and geological determination, are older than would be expected for such plants; sometimes we find a mixture of younger and older plant forms. With regard to the arborescent lepidophytes, their early appearance has been pointed out by Vogt in the unpublished paper mentioned above (p. 161; cf. also pp. 33, 49, 53, 165). Our knowledge of the flora of Spitsbergen, and of the Devonian plant world generally, is not detailed enough to enable us to understand this fact, or even to discuss its possible causes, a certain degree of caution also being necessary until the chronological determination of the divisions of the Devonian formation in Spitsbergen has been unanimously agreed upon. But, at all events, the fact is of considerable interest, the more so because it has parallels in the fish fauna.

It is a noteworthy fact that *Archaeopteris*, which is so abundant in Bjørnøya, is entirely lacking in Spitsbergen proper. Certainly some of the fructifications found in the Planteryggen of Mimerdalen are hardly distinguishable from those of *Archaeopteris*, but there can scarcely be any doubt about their belonging to *Svalbardia*; of the characteristic foliage of *Archaeopteris* no traces have been found with certainty. The absence of this index fossil, so dominating in the upper part of the Upper Devonian, must be due to the age of the flora. Certainly one might also try other explanations, but they are not necessary, and there are scarcely sufficient reasons for them.

The missing of *Archaeopteris* in Spitsbergen might be thought to be a question of preservation: In Bjørnøya, it chiefly occurs in fine-grained dark shales, that is, in rocks in which the delicate foliage will have the best chances of preservation, and the plant remains have probably not been subject to any long transport. In Mimerdalen, the plants are found in shales of a much coarser grain, and in sandstones, and some transportation has taken place before the embedding. Thus, they have certainly been exposed to forces which may have destroyed particularly much of such organs as leaves. But in view of the comparatively good preservation of the many sporangiferous shoots of *Svalbardia* and of the leaves of *Enigmophyton*, this explanation does not suffice.

Paleogeographically there is no reason why *Archaeopteris* should not occur in Spitsbergen. The distribution of the various species of the genus is shown in Table 4. It illustrates clearly the well-known fact that the genus is almost exclusively confined to Europe and the eastern part of the North American Continent, the only exception being an Australian species, which, to judge from the original figures (Dun 1898), may be somewhat dubious. But it also shows that the distribution of the genus does in no way support the idea that Europe and eastern North America at the time of the youngest Devonian should have been divided into phytogeographical provinces. The countries on the west, north, and east sides of the North Atlantic Ocean are the home of the genus, and we have no reason, paleobotanically or otherwise, to assume that Spitsbergen at that time, or immediately before or after it, has belonged to a separate biogeographical province.

It is also impossible to point out any ecological reasons for the lacking of *Archaeopteris* in Spitsbergen; but in that respect we really have but weak basis for conclusions: Only very little can be said about the conditions under which the Devonian vegetation of Mimerdalen has grown, the deposits being allochtonous. The red colour of some of the beds bear witness of arid conditions, but that does not

Table 4.

Geographical distribution of the species of Archaeopteris.

S (in Canada): Scaumenac; NY, P, and M (in U. S. A.): New York, Pennsylvania, and Maine; A and S (in Germany): Vicinity of Aachen (Aix-la-Chapelle), and Silesia.

	Bear Isl.	Ellesmere L.	Canada	Eastern U.S.A.	Ireland	Great Britain	Belgium	Germany	Donetz	Esthonia	Australia
A. Archaetypus		×							×		
A. Berderkei								S			
A. fimbriata	×									?	
A. fissilis		×							×		
A. Halliana				NY, P							
A. hibernica				P	×	×					
A. Howitti											×
A. Jacksoni (incl. *gaspiensis*)			S	M							
A. intermedia	×										
A. latifolia				P							
A. macilenta				P							
A. obtusa			S	NY, P							
A. Roemeriana	×						×	A, S			
A. Rogersi				M, P							
A. sphenophyllifolia				NY, P							

apply to all of the strata, and especially not to those which contain the most abundant flora; they are differently coloured shales and sandstones. The open sea has probably not been very far off. In Bjørnøya, where the Devonian formation is more of the continental type, the growing-place of *Archaeopteris* has probably rather had the character of a swamp. It is probable that the flora here has grown under somewhat different climatic conditions from those of the *Svalbardia* flora of Mimerdalen; one should expect that the temperature had been higher (an assumption of which we have no proof, however), and the air more humid. Most likely, such conditions have been favorable to *Archaeopteris*. But it is much more probable that the floristic difference between the Devonian of these two places is due to changes during the time rather than to physical differences between two adjacent regions at a certain moment in the history of the earth.

Evidently *Archaeopteris*, in contrast to the arborescent lepidophytes, does not appear earlier in Spitsbergen than usually.

Table 5.

Downtonian and Devonian flora of Spitsbergen.

LD, MD, and UD = Lower, Middle, and Upper Devonian respectively. *G* = Genus.

	Locality	Horizon	Plant fossils	Otherwise known from	Probable age
Raudfjorden	Frænkel-ryggen	Raudfj. Ser.	*Pachytheca* cf. *fasciculata* K. & L. *Prototaxites* sp. *Zosterophyllum* sp. *Taeniocrada* (?) *spitsbergensis* n. sp. *Hostimella* with axillary tubercles	*G*: Silurian and LD *G*: Silurian to MD *G*: Silurian and LD *G*: LD—UD Cf. p. 171	Downtonian
Wijdefjorden	Gråhuken, beach	Gråhuk Ser.	*Psilodendrion spinulosum* n. g. & sp.		Upper LD or lower MD
	Mountain S. of Vatne-dalen, 400 m	Wijde-fjord Ser.	Indeterminable, but highly organized forms	Comparable to UD plants	Middle MD
	Andredalen, Beach prof., Hor. 6	Wijde-fjord Ser.	*Psilophyton arcticum* n. sp.	*G*: LD—MD	Middle MD
	Andredalen, beach prof., Hor. 4	Wijde-fjord Ser.	*Drepanophycus* sp. Many indeterminable, but highly organized plants	*G*: LD—MD Partly of UD character	Middle MD
	Beach between Andredalen & Forkdalen	Wijde-fjord Ser.	*Cephalopteris* (?) *praecox* n. sp. Sulcate stems	Related to UD forms Mostly found in UD	Middle MD
	S. side of bay at Forkdalen	Wijdefj. Ser.	*Hostimella* (*Aphyllopteris*) with axillary tubercles	Cf. p. 171	Middle MD
	S. branch of Forkdalen	?	Striated axes with opposite lateral organs		
	Beach between Purpurdalen & Sjettedalen	Gråhuk Ser.	*Hostimella* with axillary tubercles	Cf. p. 171	Upper LD or lower MD
	Austfj., S. of Simle-dalen	Wood-fjord Ser.	*Psilophyton* sp.	*G*: LD—MD	LD
Dixonfj.	East side, beach	Wood-fjord Ser.	*Hostimella* with axillary tubercles	Cf. p. 171	Lower LD

Table 5 (continued).

Locality		Horizon	Plant fossils	Otherwise known from	Probable age
Billefjorden	West side, 3—4 km N. of Skansbukta		*Hostimella strictissima* n. sp.	*G*: LD—MD	
			Hostimella with axillary tubercles	Cf. p. 171	
			Bucheria longa n. sp.	*G*: LD	
			Psilophyton sp.	*G*: LD—MD	
			Platyphyllum sp.	Cf. p. 93	
			Barinophyton sp.	*G*: MD—UD	
Mimerdalen	Inner part of the valley, beds younger than Fiskekløfta	Uppermost Wijdefjorden Ser.	*Svalbardia polymorpha* n. g. & sp.		Probably uppermost MD
			Hyenia (subg. *Hyeniopsis*) *Vogtii* n. subg. & sp.	*G*: MD	
			Enigmophyton superbum n. g. & sp.		
			Platyphyllum Williamsoni (Nath.) n. comb.		
			Bergeria mimerensis n. sp.	Chiefly comparable to UD forms	
			Protolepidodendropsis pulchra n. sp.		
			Caulopteris sp.		
			Dictyoxylon sp.		
	Fiskekløfta		*Actinopodium Nathorstii* n. g. & sp.		
			Prototaxites sp.	*G*: Silurian to MD	

VI. Botanical Discussion.

The flora described in this work does not distinguish itself among Devonian floras for its good preservation; indeed, in that respect it is partly rather unsatisfactory. But it ranges over a very long space of time, from the Downtonian up to or perhaps above the boundary between the Middle and Upper Devonian, with many horizons entirely different from one another in the composition of the flora and in the life-conditions they represent; correspondingly, the number of species is considerable, greater than is generally found to be the case when dealing with the Devonian flora of a limited area, and although it has been necessary to leave many of the species out of consideration on account of defective preservation, the material has given us at least some knowledge of several remarkable plant forms, new to science. — It may be added that there is not the slightest trace of any influence of a depauperating Arctic climate, corresponding to modern Polar conditions; on the contrary, and in accordance with the general rule for the pre-Tertiary floras, the Devonian vegetation in Spitsbergen has been at least as rich in species and in vigorous and well developed individuals as any contemporaneous flora in lower latitudes.

It is natural to inquire to what extent these plants may help to throw light on any of the unsolved problems, of which there are so many connected with the oldest known terrestrial vegetation of the earth. Unfortunately, the most important of these problems will still remain as obscure as before: The plant forms found in Spitsbergen do not give any information about the origin of the psilophytes, about their gametophytic generations, or about their possible connection with the algae, to mention some of the crucial points. But the material does invite to some discussion of certain other questions, most of which I have also treated of, although without reference to the Spitsbergen material, in an article in the Botanical Review (1937); in the following pages parts of that article will be repeated without any further indication of source.

1. Classification of the Psilophytes.

The classification of the *Psilophytales* is still very difficult, because the number of genera and of different morphological and ecological plant forms has increased a great deal, while at the same time it has become more and more clear that our knowledge of the group is very incomplete. The latest discoveries, which have made known the most unexpected forms, partly in surprisingly old strata, show that the class has developed into an abundance of forms of which we are now catching only occasional glimpses, and which must have been the result of a very long evolutionary history. Any attempt to classify the forms known at present, must therefore necessarily lead to unsatisfactory results.

This is not the place to discuss the various attempts which have been made (among which the one proposed by Hirmer, in Wettstein's Text-book 1935, seems to me to be the best, until a further subdivision of the very heterogeneous family *Rhyniaceae* has been made possible). Only a few points of special interest may be briefly considered.

a. 'Axillary tubercles'. — As is well known, the so-called Hostimellas are often characterized by the presence of an oval tubercle at the base of each branch or, in the case of dichotomy, in the axis just below the point of bifurcation. The real nature of this structure is a question still unsolved: Potonié & Bernard (1904 p. 18) called them '*bourgeons*', while Zimmermann (1930 p. 111) suggested the possibility that they might be water-absorbing organs comparable with the ligule of the *Lycopsida.* Lang & Cookson (1930 p. 137), describing a specimen with the base of a branch in the position of the tubercle, and referring to the occurrence in *Gosslingia breconensis* of a sporangiferous branch in the same position, supported the idea that the tubercle, at least in some species might develop into, or be replaced by, a branch. But Lang (1932 p. 515) explicitly states that the nature of the axillary structure is still problematic.

Our material comprises several specimens with well developed organs of this kind. They do not contribute to the elucidation of the question of the physiological and morphological nature of this structure. But as the specimens are from several horizons and evidently belong to different plant specimens, it may be of some interest to inquire to what extent the axillary tubercles, as they may most properly be termed, have any systematic value, and if such axes may be used as index fossils. On this point opinions have been somewhat divergent.

Table 6 is an attempt to sum up what is known about the occurrence of axillary tubercles in the world, chiefly based upon literature, but to some extent also upon material hitherto unpublished. In this table '*Hostimella*' is used in the customary way as a name for naked axes branching in more or less strict dichotomy, while '*Aphyllopteris*' denotes similar axial systems of a more sympodial form.

From this table the following facts are evident:

(1). Axillary tubercles range in age from the Silurian to the Middle Devonian, and consequently the presence of them in indeterminable fragments of axes gives no information as to the exact ages of the fossils.

(2). Axillary tubercles have been found with certainty in *Protopteridium*, *Asteroxylon*, *Psilophyton*, and *Gosslingia*. In several cases, particularly in Spitsbergen and in Australia, they have also been found in naked axes which probably belong to other genera, but it may be regarded as questionable that they occur in any typical spineless psilophytes. It is true that *Gosslingia*, at first sight, is spineless; but the small protuberances on the surface of its axes may perhaps be regarded as initial spines (cf. p. 176). In those spineless psilophytes which are best known no axillary tubercles have been found, and this fact does not seem to be due merely to defective knowledge, because, as a rule, great numbers of specimens have been found in the respective localities; that is the case with *Horneophyton*, *Rhynia*, *Taeniocrada*, *Hicklingia*, *Pseudosporochnus*, and *Zosterophyllum*. On the other hand it is true that in the flora of Frænkelrygggen, which among other fossils also comprises a fragment of a naked axis with axillary tubercle, no traces of spinous psilophytes are found, and there is good reason to believe that such plants have not occurred in this flora; but this negative evidence is not sufficient to prove that the axillary tubercle in this case has belonged to a psilophytalean plant devoid of spines.

It cannot be said for certain whether the fact that axillary tubercles have not indubitably been found in the spineless psilophytes, is a sign of any deeper difference in systematic respect between this group and the other psilophytes (compare below, p. 176). But it is an indication worth keeping in mind during future research. On the other hand,

Table 6.

Occurrence of 'axillary tubercles'.

Locality	Age	Plant	Authors
Spitsbergen			
a. Raudfjorden: Frænkelryggen. .	Downtonian	*Hostimella*	p. 24.
b. Wijdefjorden: Bay at Forkdalen	Middle Devonian	*Hostimella (Aphyllopteris)*	p. 55.
c. W. B.: Between Purpurdalen & Sjettedalen	Upper Lower Dev.	*Hostimella*	p. 59.
d. Dicksonfjorden .	Lower Lower Dev.	*Hostimella*	p. 59.
e. Billefjorden	? Lower Devonian	*Hostimella*	p. 59.
Norway			
a. Nordfjord	Middle Devonian	*Hostimella* (cf. *Asteroxylon*)	Høeg 1931 p. 7.
b. Tristein.	Middle Devonian	*Asteroxylon* sp.	Unpublished (leg. Høeg)
Germany			
Elberfeld etc.	Middle Devonian	*Asteroxylon elberfeldense*	Kräusel & Weyland 1923 p. 159.
Bohemia	Middle Devonian	*Protopteridium hostimense*	Potonié & Bernard 1904 p. 18. Kräusel & Weyland 1933 p. 6.
France			
Belgian frontier. . . .	Middle Devonian	*Hostimella*	Carpentier 1930 p. 654.
Wales			
Brecon	Lower Old Red	*Gosslingia breconensis*	Heard 1927 p. 199.
Scotland			
a. Cromarty etc. . . .	Middle Old Red	*Hostimella (Aphyllopteris)*	Lang 1925 p. 262.
b. Strathmore Beds	Lower Old Red	*Psilophyton* & *Hostimella*	Henderson 1932. Lang 1932 p 501.
Canada: Gaspé			
E. of Douglastown .	Middle Devonian	*Hostimella (Aphyllopteris)*	Unpublished (leg. R. Florin).
Australia			
Victoria.	Silurian	*Hostimella*	Lang & Cookson 1927 p. 45, and 1930 p. 136; Cookson 1935 p. 133.

one may certainly attribute some systematic importance to this organ where its existence is really ascertained. That such a characteristic feature should have been developed in several plant groups independent of each other, does not seem probable, and it may therefore be taken as an indication of the phylogenetic relationship between the above-mentioned genera in which it has been found. As to *Protopteridium*, compare also p. 178.

Kräusel & Weyland (1933 p. 6) have stated that the axillary tubercles have no systematic value as regards a distinction between different types of *Hostimella*. This is an experience to which most paleobotanists may subscribe: Possibly with the exception of *Gosslingia* the axillary tubercles, when developed at all, seem to be so uniform that they cannot serve to distinguish between naked branches from different plant species. — On the other hand, they are not so constant in their occurrence that the fact that they are lacking in a single specimen or a few specimens of *Hostimella* proves that the plant, of which that particular *Hostimella* formed part, may not have developed such organs in other branches.

It is a question whether the name of '*Hostimella*' should be reserved only for naked axes possessing axillary tubercles. Theoretically, such a course would give the name a clear circumscription; but it would be difficult to follow in practice, and it would leave us without any term for the innumerable psilophytalean remains, for which *Hostimella* is now a handy name, irrespective of the occurrence of these tubercles.

The table only mentions plants from the age of the psilophytes, that is, from up to the Middle Devonian. In the Upper Devonian, and also in younger floras, there are fern-like plants in which side-branches may have a thickening at the base. This feature is found very distinctly developed in specimens of *Sphenopteris Keilhaui* from Bjørnøya, of *Rhacophyton condrusorum* from Belgium, and in other species. Even if it can scarcely be doubted that these plants are descendants of the psilophytes, one cannot feel sure that the said thickenings are homologous with the axillary tubercles of Hostimellas; at least they often differ quite considerably from them in form and position.

b. Spinous and naked psilophytes. — The psilophytes may be divided into two groups, which, at least at first sight, differ very considerably from each other: those possessing spines or hairs, and those lacking such appendages. The typical members of the former group are *Psilophyton*, *Asteroxylon*, and *Psilodendrion* (p. 26), to which may be added *Dutoitia* and possibly *Gosslingia* (see below, p. 176); one might also mention *Drepanophycus*, although that genus cannot be regarded as belonging to the psilophytes. Spineless psilophytes are *Rhynia*, *Horneophyton*, *Taeniocrada*, *Zosterophyllum*, *Hicklingia*, *Scia-*

dophyton, and *Pseudosporochnus*, to mention those which are fairly completely known.

The systematic value of these appendages is a question of considerable interest, not only for the classification of the various genera of psilophytes in relation to one another, but also as regards the starting points of the different lines of development which have led to the groups of higher vascular cryptogams. It would therefore be important to know: (1) whether the spines, &c., in all cases are of the same nature and origin; (2) whether there are any transitions between spinous and spineless psilophytes; and (3) whether the spinous ones otherwise possess any character in common in which they contrast with the spineless ones, and vice versa.

As to the homology of the spines, there may be some reason for doubt in the case of *Drepanophycus* (cf. p. 183); but in the other genera they certainly represent what Bower (1935) called enations: They do not, like axial organs, or telomes, originate at the apical growing point, but superficially and secondarily on the side of the axis and generally without any regularity in their arrangement. This evidently holds good also in the case of the *Thursophyton*-leaves of *Asteroxylon*; as demonstrated by Lang (1925 p. 261, 1931 p. 439) both in *Thursophyton* and in *Psilophyton princeps* small and large 'leaves' may be inserted close together on the shoot, in a manner which could scarcely be explicable if they were not developed as enations.

Little is known, however, of the function of these appendages, and it is probably not the same in all cases: In *Psilophyton princeps*, Lang (1931) has proved that they were capitate, each of them ending in a glandular sac; but nothing similar is known from any other species, this being in some cases perhaps because the material has not been sufficiently well preserved, or simply because the necessary preparation has not been carried out. In the petrified material of *Asteroxylon Mackiei* nothing was found to indicate that they were of a glandular nature (Kidston & Lang 1920 *b*; Lang 1931 p. 438). In a plant like *Thursophyton* the best developed 'leaves' must have acted as photosyntetic organs. But in the many cases when they only had the form of small cylindrical or conical hairs, it is very difficult to see what purpose, if any, they have served. So far they resemble most other plant hairs: One can understand that if well developed, hairs may act, for instance, as a protection against animals or as a cover to hinder a too strong evaporation; but their initial stages in their evolutionary history cannot have been of any use in these respects, and their development appears to be enigmatic. —

The cases of transition between the spineless psilophytes and the spinous ones are few and uncertain (cf. Høeg 1937 p. 569):

The spines might be compared with the hemispherical protuberances of *Rhynia*, which often developed beneath a stoma. One might regard them as homologous with, or, morphogenetically, as initial stages of the spines of other psilophytes; but undoubtedly they are of a different nature. It was from them that the deciduous adventitious branches were formed in *R. Gwynne-Vaughanii*. We have an interesting parallel in *Lycopodium Selago*; Williams, in a work on the experimental morphology of that plant (1933), has shown that it develops similar protuberances which give rise to adventitious branches. — It may, however, be noted that Browne (1935 p. 388) regards the protuberances of *Rhynia* as homologous with, or at any rate forerunners of, the spines of *Psilophyton*.

Greater interest in regard to the present problem attaches to *Gosslingia*. As described by Heard, this remarkable plant had small, irregularly placed projections, consisting of a more or less hemispherical cell mass and terminating in a delicate hair, apparently consisting entirely of cuticle. They certainly differed a good deal from the appendages of other psilophytes, but the similarity prevails. If not so well preserved as in the type material, *Gosslingia* would probably have been referred unhesitatingly to the spineless group.

If we search for other characters which the spinous psilophytes have in common, and in which they differ from the naked ones, we shall find that at the present state of our knowledge there is only one feature that may come into consideration, that is, the axillary tubercle. As was mentioned above (p. 172), all specimens of psilophytes possessing this structure, if determinable at all, have been found to belong to genera of the spinous group, and, on the other hand, all the best known genera of spineless psilophytes are devoid of it. However, it is not certain that this is a general rule: In some of the cases referred to above, when indeterminable *Hostimella* fragments with axillary tubercles were found together with other plant remains, there was some reason to believe that spinous species had not been represented in the flora; but, of course, such negative evidence is far from conclusive. It may also be added that in *Dutoitia* we have no axillary structures; but this genus, in spite of its spines, occupies in several respects an isolated position in relation to the other psilophytes (for instance, in the form and structure of its sporangia).

Even if we cannot feel sure that our knowledge is sufficient for any generalization, we may at least say that among the psilophytes axillary tubercles are known with certainty at present only from spinous genera, and conversely, that most of the members of that group have been found to possess such structures. This fact makes it more probable that all spinous psilophytes constitute a natural systematic unit. But there is no reason to doubt its close affinity to the spineless ones.

2. Psilophytes and Pteropsida.

a. Pseudosporochnus, Svalbardia, and *Archaeopteris.* — The systematic position of *Svalbardia* (p. 70) is somewhat intermediate. On one side it is connected morphologically with the psilophytes through one of the most highly developed members among them, *i. e. Pseudosporochnus.* Certainly, the stem of *Svalbardia* is unknown, so that we do not know whether it has possessed the characteristic habit of *Pseudosporochnus.* But the branches and leaf-like divisions are very much alike. However, the foliar organs of *Svalbardia* are morphologically more specialized, and both these parts, and still more the fructifications, are developed beyond the primitive psilophytalean stage. The genus cannot be included in the *Psilophytales*, in contrast to *Pseudosporochnus*, which may still be retained within that group.

On the other side, *Svalbardia* points towards *Archaeopteris.* The fertile shoots which for very good reasons are assumed to belong to *Svalbardia*, resemble those of *Archaeopteris* so much that they are scarcely distinguishable. The pinnule-like lateral ramifications, when best developed, are also very similar to the pinnules of *Archaeopteris*, and the tendency of the sterile branches of *Svalbardia* to form flattened, plane foliar shoots must have given the plant a certain fern-like aspect, although this tendency was not visible in all parts of the plant. In fact, *A. fissilis* is less different from *Svalbardia* than from the species with large, entire pinnules; it is quite possible that the generic limits will have to be drawn otherwise than at present, when a more thorough comparative study, preferably based on a re-examination of the specimens themselves, has been carried out.

Archaeopteris has been believed by some authors to be a seedfern. If that were correct, it would mean a very profound difference from *Svalbardia*, of which we may feel sure that it has not borne seeds. But also in the case of *Archaeopteris* the idea is very weakly founded (unless the genus comprises two groups of species with entirely different modes of reproduction); in view of the exceedingly great number of specimens of leaves and sporangia found in a locality like Bjørnøya, without the slightest traces of seeds or of cupules or other plant organs which might be thought to have borne seeds (the object reported by Nathorst 1902 p. 43, Pl. XIV fig. 6 as sporangium or seed, probably the former, may safely be ignored), it is incredible that the *Archaeopteris* species of that flora (*A. fimbriata*, *intermedia*, and *Roemeriana*) should have possessed any other organs of reproduction than the sporangia (compare also Arnold 1935 *b*, 1938 *b*, Gothan 1936 p. 379, and Kräusel 1937 p. 532).

b. Protopteridiales n. ordo. — *Svalbardia* is more closely connected with *Archaeopteris fissilis* than with *Protopteridium*, *Eospermatopteris*, *Rhacophyton*, *Aneurophyton*, or any other genus of the Middle or Upper Devonian. Yet it would be practical to group it together with these genera in one systematic unit, placed between the psilophytes and the true ferns, to which they form a transition, just as *Hyenia* and its allies do to the *Arcticulatae.* The group will be somewhat heterogeneous, but the plants in question have enough in common to justify the institution of it. As an appropriate name we may suggest *Protopteridiales.* (It is somewhat unfortunate that the name, at first sight, may suggest not only the Devonian *Protopteridium*, but also the much younger *Protopteris* Presl, with which it has nothing to do; but this fact should scarcely cause any confusion.)

The *Protopteridiales* may be subordinated under a larger unit, for which the name *Primofilices* may be used, certainly in a somewhat wider sense than given to it when instituted by Arber (1906 p. 222). The nomenclature in this part of the Vegetable Kingdom has been more confused than perhaps in any other part, but the course suggested by W. Zimmermann (1930 p. 185) seems a practical one: to use the name *Primofilices* as a designation for the different groups of most primitive ferns or fern-like plants. The number of orders to be included in it may be discussed, but it will at any rate have to comprise the *Coenopteridiales* and the *Protopteridiales.*

The *Protopteridiales* may be defined as follows:

Plants of a more or less fern-like habit, the foliar shoots having a tendency to flatten in one plane, but with slight differentiation between axes and leaves. The ramifications of the foliar shoots may resemble pinnules, but no broad laminae are found. Sporangia borne terminally on pedicels, forming panicles or clusters. Sporangium, as far as is known, with apical dehiscence. Homospory, or in some species probably heterospory.

Genera referable to this group are *Svalbardia*, *Protopteridium*, *Aneurophyton*, *Eospermatopteris*, *Rhacophyton*, probably also *Dimeripteris* Schmalhausen (1894).

It is very noteworthy that *Protopteridium*, in its thinner ramifications, has axillary tubercles of the type otherwise chiefly found in the group of spinous psilophytes (cf. p. 172). That this is a structure of systematic importance is beyond doubt, and if its occurrence among the psilophytes is really restricted to the spinous ones, it suggests a close affinity between this group and *Protopteridium.* On the other hand *Svalbardia* and some related genera rather seem to have developed from a form like *Pseudosporochnus*; if it is correct to regard the latter genus as a highly developed member of the group of spineless psilophytes, the consequence will be a polyphyletic origin of the *Protopteridiales.*

c. *Dawsonites Ellenae.* — Among the plants which might be thought to belong to the *Protopteridiales*, is *Dawsonites Ellenae*, which I described in 1935 from the Middle Devonian of Western Norway (compare also Høeg 1937 p. 579). The fructification has the form of a panicle with branches arranged spirally and bearing clusters of broad, nearly reniform sporangia; this fertile shoot is not flattened. Sterile shoots evidently belonging to the same species, are flattened into one plane and pseudomonopodial. Both the fertile shoots and the sterile ones are sparingly spinous.

When describing this type of fructification I called it *Dawsonites*, in order to avoid the introduction of a new generic name, and in order to express its probable psilophytalean affinity. At about the same time, Halle (1936 p. 22) has advocated a rather restricted use of the name, so that it should be applied only to dichotomously or sympodially divided branch-systems bearing sporangia in terminal position. No doubt it is an advantage to exclude such forms as the spike-like *Bucheria* from *Dawsonites*, but, even so, it seems entirely justifiable to make it comprise a form like *D. Ellenae.* Otherwise we shall have to institute a new organ genus.

Kräusel & Weyland (1938 p. 186) have expressed as their opinion, "daß es sich bei *Dawsonites Ellenae* um eine Pflanze von Psilophyten-Verwandtschaft handelt, auch an etwa mögliche Beziehung zu der norwegischen *Thursophyton*-Art wäre zu denken". The various parts of the *Thursophyton* species are the most common component of the fossil flora of Nordfjord, also in the place where this fructification was found, and it is really quite likely that it belongs to that species. The sterile shoots seem to be indistinguishable. For some reason or other the idea had not occurred to me, although I have regarded it as very probable that we were dealing with a psilophyte (cf. Høeg 1937 p. 579). Until the connection is proved, however, *D. Ellenae* will have to be kept under a name of its own.

However this may be, *D. Ellenae* in its morphology foreshadows the simplest *Primofilices.* As has just been said, it most probably does not belong to that group, but it forms a very strong connecting link between the spinous psilophytes and the *Protopteridiales.*

Schizopodium and Actinopodium, Cladoxylales and Pteridosperms.

Judged only by its external morphology, the only Devonian species referred to the genus *Cladoxylon*, *C. scoparium*, from the Rhenish Middle Devonian, might be placed among the *Primofilices*, as a member of the *Protopteridiales* or in a parallel group. Its anatomical structure, however, shows that it is closely connected with the younger species for which the genus was originally created, although some authors, among them

Sahni (1930 p. 466) and Halle (1938 p. 578), do not consider it a true member of that genus. If it is correct, as held by Hirmer, Harris, and others, to found a systematic unit of higher rank on this little group, the Middle Devonian species must be included in it, and thus, in the plant system, be removed from the contemporaneous plants with which one might otherwise be inclined to group it together

Harris (1929), when discussing the systematic position of *Schizopodium*, emphasized its affinity to *Cladoxylon*, regarding it as a connecting link between that genus, on one side, and the psilophytes, represented by *Asteroxylon*, on the other. In all probability that view is correct.

With the star-shaped outlines of their pithless steles, in which the wood often disintegrates into separate bundles, *Arachnoxylon* and *Asteropsis* seem to belong to branches of the same line of evolution as the *Cladoxylales*. But it should be noted that Read (1938), discussing the affinity of *Arachnoxylon*, attributed a considerable systematic value to the 'peripheral loops' of the stele, concluding that they indicate affinity to primitive ferns. The same view is held by Arnold (1940 p. 12), who includes *Arachnoxylon, Reimannia*, and *Iridopteris* (of which I have not had access to the detailed description) in a new suborder, *Iridopteridineae*, intermediate between psilophytes and true ferns.

Our new *Actinopodium* (p. 150) has probably not so much affinity to these plants as one might think at first sight, on comparing it with *Schizopodium*. Certainly there are some points of resemblance between these two genera, particularly in the structure and arrangement of certain parts of the wood, and it is quite possible that this is a sign of their descent from a common ancestral root. But the weight of the resemblance may easily be overestimated, because there are so few Devonian plants to compare them with. At all events, the characters in which they differ, are all of such a nature as to make it clear that *Actinopodium* has nothing whatever to do with the *Cladoxylales*.

It may, however, be of some interest to see what comparisons may be drawn between *Actinopodium* and the other groups of pteridophytes:

In its anatomy, *Actinopodium* has certain primitive characters, such as: mixed pith, mesarch protoxylem, protostelic leaf-traces (if the thin bundles emitted from the main stele be leaf-traces). The pitted tracheids of the secondary wood cannot in themselves be called primitive, but it is in any case worth noticing that they have not developed the grouped arrangement of the pits, so characteristic of *Callixylon*. — These features are by no means enough to link it with the psilophytes, *Actinopodium* being much farther removed from that group than *Schizopodium*, but they decidedly give our plant a primitive position in relation to the other groups to which it shows any resemblance.

In a few characters *Actinopodium* may be compared to some primitive ferns, *e. g.* the *Coenopteridae* of the Carboniferous period. At first sight the difference is indeed more striking than the resemblance: *Actinopodium* has nothing similar to the large, complicated petiolar bundles so characteristic of these early ferns; even if the small bundles of *Actinopodium* really are a kind of leaf-traces, they bear no resemblance whatever to the large ones found, for instance, in the zygopterid ferns, and leave no leaf-gaps in the stele; on the other hand, *Actinopodium* has a secondary wood not frequently matched in the *Coenopteridae*, its very large pith, the arrangement of its protoxylem, and the form of its stele also being important points of distinction. But *Botrychioxylon* (which, according to Sahni 1932, represents the anatomy of the stem of *Zygopteris*) has *(1)* a pith, although a much narrower one than that of *Actinopodium*, *(2)* a zone of secondary wood, in which, it may be noted, the presence of true medullary rays has not been demonstrated (Scott 1920 p. 321); it may also be worth mentioning *(3)* that roots are emitted from the main stele of *Botrychioxylon* in much the same way as the thin bundles of *Actinopodium*, but as their anatomical structure is quite different (being diarch in the one case, 'centrarch' in the other), the resemblance may be rather accidental. — However, the value of these characters, which they have in common, may be slight, and it does not appear probable that they denote any systematic affinity. *Actinopodium* does not serve to connect the true ferns with the psilophytes or with any other groups.

Actinopodium most strongly points towards the pteridosperms. It is true that it has not borne any large leaves like those of *Lyginopteris* and similar genera, but the anatomy of the axis decidedly has its nearest parallel in the seed plants. As points of resemblance may be mentioned: (*1*) the large pith (the tracheids in the pith may be rudiments of a central wood like that of certain primitive pteridosperms, cf. *Heterangium*), (*2*) the mesarch primary strands (although they are perhaps not so well defined in *Actinopodium* and particularly not so well marked off from the secondary wood as they are in many pteridosperms and allies); (*3*) the mode of development and growth of the secondary wood, with (*4*) multiseriate pits chiefly on the radial walls; and other characters. There are certainly also points of difference; besides the stellate outline of the stele of *Actinopodium* (a character which is probably only of generic value), one may mention the lack of leaf-gaps, a natural consequence of the lack of large leaves, and, further, the medullary rays, which are very numerous and mostly broad in the pteridosperms, evidently rather different from those of *Actinopodium*, which, it may be admitted, are incompletely known.

With its lack of large leaves *Actinopodium* cannot belong to that group of seed-ferns of which *Lyginopteris* is the best known member.

But there are other seed-plants that in the main features are built like them: *Poroxylon*, *Calamopitys*, &c., and it would be quite natural, and justifiable, to regard *Actinopodium* as a relative of them all, but representing certain primitive features. If correct, that would be of considerable interest, because what Scott laid down in 1924: "At present, in fact, we know of no really simple pteridosperm" (Scott 1924 p. 170) really still holds good.

Zalessky & Tchirkova (1930) arrived at the conclusion that the dividing of the leaf-traces in *Caracuboxylon* suggested flat leaves with parallel veins, and therefore, and on account of its general anatomical structure, assumed that their plant was related to the *Cordaitales*. Our plant has no such division of the leaf-traces within the cortex, but *Caracuboxylon* is, nevertheless, clearly its nearest relative among the fossils known so far.

The relation of *Actinopodium* to *Callixylon* is rather obscure, but, particularly if the small pieces of secondary wood described separately above (p. 159) really belong to the same species as the young axes, we clearly have to do with plants of the same general structure, and very likely phyletically related to each other.

Thus, while *Schizopodium* points backwards to *Asteroxylon* and forwards to *Cladoxylon,* consequently linking the latter with the psilophytes, *Actinopodium*, which is much more advanced, and specialized in another direction, combines a certain primitiveness with several structural features occurring in the seed-plants.

It is somewhat difficult, however, to place it in any well-defined systematic group. Perhaps we may bring into use the name proposed by Arnold (1930 p. 46) for *Callixylon* and its allies: *Archaeopteridopsida.* The name is so long that it takes a good deal of practising to manage it, and it is ill-chosen, as suggesting an affinity, certainly not existing, with *Archaeopteris.* The group for which it is intended, has not been clearly defined, and most of the genera which might come into consideration are incompletely known, particularly with regard to their external morphology and their organs of reproduction; but there really seems to be a certain need for such a systematic unit, which would combine a number of primitive characters and at the same time point towards both the pteridosperms and the *Cordaitales*; as a name for that group, *Archeopteridopsida* would evidently have priority. Beside *Callioxylon*, the group might comprise both *Caracuboxylon* and our *Actinopodium.*

4. Psilophytes and Lycopsida.

a. Microphylly. — In a paper published in 1937 I quoted the ideas of Lignier without feeling any hesitation in regarding as probably correct the homologizing of the leaves of the *Lycopsida* with the emergences of *Psilophyton.* At the same time Halle (1936) published the Chinese specimens of *Drepanophycus*, demonstrating their very strong leaf-trace bundles, sometimes even bifurcating, which would be far better understood if these leaves were reduced 'cauloïds' (in the sense of Lignier) than if they were 'phylloïds'. The consequence would be that the leaves of *Drepanophycus*, and consequently also those of the *Lycopsida*, were homologous with the leaves of the other microphyllous plants, which no doubt have developed from telomes. It is a strong argument, but the question is not yet settled, and the collections described in the present paper do not contribute to its solution.

On this occasion I should like to draw attention to the use of the term 'microphyll', which is somewhat ambiguous. In Lignier's morphological system the leaves of the *Lycopsida* were 'phylloïds', developed from enations (spines, hairs, or other emergences distributed more or less irregularly on the axes, and developed secondarily and superficially, independently of the apical growing points). All other leaves were 'cauloïds', developed from branches of the axis (telomes of Zimmermann) through flattening into one plane, through lateral fusion ('webbing' of Bower), and through limitation of the growth. In some plant groups the leaves developed at the expense of the stems; these were the macrophyllous plants, comprising ferns and cycadophytes. Along another line of development, according to Lignier's view, the leaf became reduced in size; these were the plants which Lignier termed microphyllous: conifers, *Cordaites*, *Gingko*, and others. A third group would be the mesophyllous plants, in particular the angiosperms, and finally, along a separate line which left the macrophyllous one at an early point, the *Articulatae* would be derived; in the latter the characteristic features are, chiefly, reduction in the size of leaves, their verticillate arrangement, and their lateral union so far as to form broad laminae or sheaths (cf. Høeg 1937 p. 571).

From this quotation it is evident that Lignier used the term 'microphyllous' in an entirely different meaning from that of modern usage, which applies the word particularly to the *Lycopsida* and often to the *Articulatae*. Nothing would be gained by trying to restore Lignier's terminology on this point, but the change should be noted. Generally it has not been made clear by those who have discussed the origin of the leaf.

b. Drepanophycus, *Baragwanathia*, and allies. — At present, *Drepanophycus* is one of the most interesting and important plants of the Devonian flora. In the abundant collections of it from a locality like Røragen, it is striking on account of the very wide limits within which the species seems to vary. As has been pointed out by Halle and by Kräusel & Weyland, some of the specimens may be indistinguishable from *Psilophyton*, while others are very distinctly different, and the reproductive organs, as made known by Kräusel & Weyland, are such that it is scarcely possible to retain the genus within the *Psilophytales* (although the annular thickenings of their tracheids are of the type characteristic of that group).

Some authors have been disposed to combine *Drepanophycus* and *Baragwanathia* in one genus. However, with the great difference in the vegetative characters it is difficult to accept such a view.

The position of the sporangium on the upper side of a leaf, near the axis, makes it very difficult to connect, systematically and morphogenetically, these two genera with the psilophytes. Among the possible ways of development, the following two may be mentioned:

(1). The ancestral form of *Drepanophycus* might have a sporangiferous branch in the axil of a leaf (phylloïd or cauloïd). Through the reduction of the branch the sporangium would be left sessile in its present position. But no such ancestor is known, and as long as nothing resembling it has been found, there would be a very weak basis for postulating its existence, particularly because the axial position of a branch is entirely alien to the morphology of all spinous psilophytes. (The word 'axial' is then used with referenee to the leaf axil. That the 'axial tubercle' in the branch angles of Hostimellas should have any bearing upon the question is rather a remote possibility). It is possible that the study of the vascular bundles on suitable specimens may give some information on this point. Is there perhaps an indication in Halle's discovery of the occasional bifurcation of the leaf-trace bundles?

(2). The 'sporophyll' might be a sporangiferous telome, the sporangium of which has been displaced from its original terminal position towards the axis, as a kind of initial serial splitting. This explanation would be incompatible with the interpretation of the leaves of *Drepanophycus* as enations.

The second alternative is the simplest one, implying hypothetical ancestors less different from known forms than the first alternative. But it is not possible at present to decide what has happened; there are, indeed, also other possibilities. At all events the distance between *Drepanophycus* and *Psilophyton* is, as far as we now know, so great that even the shortest bridge imaginable will be too long; we shall have to wait for the discovery of intermediate forms before any phylogenetic transition between them can be reconstructed.

As has been pointed out by Lang, Kräusel & Weyland, and others, *Drepanophycus* and *Baragwanathia* together form a group which it would be natural to place at the base of the *Lycopsida*; the reasons for doing so are as good as those for regarding *Hyenia* as a 'protoarticulate'. It seems desirable to institute a new class for these genera, corresponding to the *Protopteridiales* (p. 178) and the *Protoarticulatae*. But as the material described in the present paper does not comprise any species belonging to that class, in so good a state of preservation that it could add anything to our knowledge of its morphology, it is preferable not to propose any name for it at present.

It is a question of very great interest whether the group of *Drepanophycus* and *Baragwanathia* has formed the starting point of two very different lines of development, one leading towards the true *Lycopsida*, the other to such large-leaved forms as *Barrandeina* and *Duisbergia*. Much may be said in favour of this view, which has already been done by the best authorities. It is of no use to repeat or to try to add anything here. But the question has also some connection with another which will be mentioned below; it will therefore be necessary to return briefly to it again there (p. 190).

5. Psilophytes and Articulatae.

When Nathorst (1915) described the type species of *Hyenia*, *H. sphenophylloides*, he pointed out the characters in which it resembled the *Articulatae*; and the subsequent discovery of the fructifications of the genus, first made by Kräusel & Weyland (see also Leclercq 1940), has strengthened the impression that it may be regarded as a primitive precursor of the typical representatives of that phylum. In fact, in spite of a certain inconstancy in the verticillation of the leaves, it is much more closely connected with the *Articulatae* than with the psilophytes, from which it should be expected to have developed. Certainly, there is no difficulty in deducing the sporangiophores of *Hyenia* from fertile telomes of psilophytes. But the verticillate arrangement, however variable and unsettled, and the pronounced contrast between the well developed foliar organs and the stems, are characters not found within the latter group. Intermediate stages might easily be imagined, but they have not as yet been found or recognized; the origin of the *Articulatae* has therefore been rather uncertain.

Hyenia (Hyeniopsis) Vogtii has lent a few new features to the picture of the genus, and of the group *Protoarticulatae*.

One of these features is the mode of ramification. Previously, *Hyenia* has been known chiefly as undivided axes, rising from a thick, horizontal rhizome. One exceptional case of a repeatedly bifurcating axis has been figured by Kräusel & Weyland (1929 p. 326); it was referred to *H. elegans*, although it was strikingly different from all other specimens of that species (as regards Belgian specimens with branched axes, cf. p. 86). — In our new species, branching is frequent and regular; it is of considerable interest to note that the branches are strictly lateral, and that they take the places of leaves, thus showing that they are homologous with those organs. We have a parallel case of development within another group of primitive plants, still living, the bulbils of *Lycopodium Selago* and other bulbilliferous species of *Lycopodium* being inserted in the places of leaves (as regards the discussion of this fact, see Bower 1935 p. 207, with references).

Another new feature is the presence of hairs, or spines, which, if any systematic value may be attributed to them, connect *Hyenia* more directly with the psilophytes than might otherwise seem to be the case. Certainly, hairs are generally found in innumerable plant species, and as a rule it is only in cases when they are of a really characteristic type that they have any systematic value. The hairs of the psilophytes, however, form an isolated feature in the Devonian flora; probably, as was pointed out above, they are all of the same origin, although in some cases they seem to have been adapted to special purposes, as glands or as organs for photosynthesis. They may be regarded as a character of systematic value, and when similar appendages are now found in a species of *Hyenia* they may be taken as an indication, if not as a proof, of a direct phylogenetic connection between that genus and the group of spinous psilophytes.

If this assumption is correct, it also leads to some further consequences of interest: There were reasons to believe that *Hyenia* and *Archaeopteris* might have risen from a common stock developed from the psilophytes. This possibility was pointed out already by Lignier (1908 p. 283), in as far as he assumed that, among the plants known at that time, the Sphenophyllums were those to which *Archaeopteris* presented the closest affinity. However, it is probable that *Archaeopteris* has developed from forms more like *Svalbardia* and *Pseudosporochnus*, that is, from naked psilophytes; consequently, if we have to search for the ancestors of *Hyenia* among the spinous ones, the history of *Hyenia* and *Archaeopteris* must really be assumed to have parted long before the two lines of development had left the psilophytalean stage.

In a discussion of the origin of the *Articulatae* it might be natural to include *Sphondylophyton hyenioides* Schultes & Dorf (1938), from the Lower Devonian of Wyoming. As stated by the authors in the original description, however, the plant is rather like an alga, and personally I do not feel at all convinced that it is a vascular plant; until that has been proved, or at least made probable, it is scarcely possible to make this plant the basis of any conclusions as regards the origin of *Hyenia* and allies. That *Sphondylophyton* should be a link in a direct evolutionary line from algae to *Hyenia* is imaginable, but quite improbable.

The verticillation of the leaves, both in *Hyenia* and in *Calamophyton*, may be regular in some parts of the plants, but at least in some species the verticillation gives place to a spiral or irregular arrangement in some parts of the stems. I therefore find no difficulty in regarding *Haspia devonica* K. & W. (1929) as a relative of *Hyenia*. *Haspia* may have been a plant which had not acquired the character of verticillation, and yet was a relative of *Hyenia*. But, as all that is known of the species is a fragment only about 10 cm long, we may also take into account the possibility that in other parts of the plant the leaves were more approximately, or regularly, verticillate; in an extensive material of *Hyenia* from Spitsbergen or from Western Norway it would certainly not be difficult to pick out a stem fragment in which the leaves above all made the impression of being spirally arranged. The course of the conductive strands of *Haspia* recalls *Hyenia*, and the leaves are identical in external form, apart from the fact that those of *Haspia* are probably terete, those of *Hyenia* flat.

6. Enigmophyton and the Origin of Cormophytic Plants.

There has been good reason to regard the vascular cryptogams as a monophyletic group, because all their main divisions: *Filices*, *Articulatae*, *Psilotales*, and *Lycopsida*, seem to have developed from one common root, the psilophytes, the origin of which is shrouded in darkness, but which must be assumed to have risen from some algal ancestors.

A plant like our *Enigmophyton*, however, raises the question whether there are not also other lines of evolution which have led to terrestrial plants that in size, external morphology, and habit of living, form a parallel to the vascular cryptogams and the other cormophytes, but phyletically are entirely independent of them.

In itself, the idea is not impossible. The tendency to develop forms which are independent of the medium of fluid water, has manifested itself in numerous ways and within several divisions of the Plant Kingdom: Even among the unicellular plants this tendency is met with, at least in some stages of the ontogenetic cycles of certain species. Among the higher plants, recent or extinct, the *Rhodophyceae*, as far as we know, are entirely subaquatic, and this is the case with the *Phaeophyceae*, if *Prototaxites* does not belong to that group (the faculty of some litoral species of *Fucaceae* to grow at the highwater-mark, some of them even so high up that they may remain dry for 24 hours, may scarcely be mentioned as instances of plants in the process of transmigration, because in their anatomical structure, in their metabolism, and particularly in their mode of reproduction, these plants are not much different from their relatives which pass all their lives in the water; but they show that also within this class the tendency is noticeable). The *Chlorophyceae* comprise primitive subaërial forms to-day (*Trentepohliaceae*, *Pleurococcus*, &c.), and within this large phylum has even probably, in a remote past, been the starting point of the line leading to the *Cormophyta*. The fungi, with the lichens, have made themselves independent of fluid water, some of them even in a higher degree than almost any other plants.

But it is worth noticing that, while the subaërial mode of living has been acquired by members of entirely different plant groups, the various evolutionary lines have led to the most widely differing results, and parallel forms have practically never been developed within the different phyla: Apart from the faculty of living with at least parts of their bodies in the air, and not in fluid water, these plants do not possess much in common; the transmigration, however important, has not in itself been a factor sufficient to stamp them uniformly. For instance, all subaërial algae known to us resemble their subaquatic relatives infinitely more than they do any phanerogam. There are a few exceptions, *e. g. Usnea* and *Tillandsia*; such cases, however, are not only very rare, but they are always due to adaptation to extreme conditions, and they concern at most only the external form, whereas the anatomical structure remains fundamentally different. — This fact, which is of course well enough known, is worth keeping in mind, because below we have to consider the possibility of the development of analogous forms within widely different plant groups.

The question of the early existence of terrestrial plant groups entirely different from those known to us from later periods, has been discussed on several occasions in the paleobotanical literature. A new light was thrown upon it by the discovery of certain plant fossils:

Nematothallus and similar plants, described from the British Downtonian by Lang (1937), proved some years ago that cells, very much like tracheids, have once been developed in plant bodies of such anatomical type that it would be impossible to include them in any group of terrestrial plants previously recognized. Tracheidal cells can be developed only in response to a demand for transport of water, that is, in plants growing either on dry land, or at least with a greater part of their bodies above water. *Nematothallus* and its allies may therefore be regarded as representatives of a group of terrestrial plants (the Class *Nematophytales* Lang) independent of those with which we are otherwise acquainted. But as regards external morphology and organs of reproduction, little or nothing has become known about them.

Germanophyton psygmophylloides (= *Prototaxites psygmophylloides* K. & W.), which, with *Prototaxites*, was included in the *Nematophytales* by Lang (1937 p. 287), gives a hint in the same direction. In my opinion it is far more probable that this plant, and also the true species of *Prototaxites*, have been terrestrial or at least partly subaërial, than that they have lived immersed like sea-weeds; as arguments for this view, which is also held by several leading authorities (including Lang), but opposed by others (Kräusel & Weyland), may be mentioned the form and particularly the venation of the leaves, the well developed conducting tissue of the stems (although without any cells with tracheidal thickenings), and the fact that these plants almost always occur in association with plants which have no doubt been terrestrial, and at least often in continental deposits (compare, however, the detailed discussion of the problem by Kräusel 1936 *b*). But, whether that is correct or not: These plants are not so completely known that they can give us more than exceedingly vague impressions of what they may have looked like when living. What they, or at least *Nematothallus*, do prove, is that "the algae of the period were doing a little transmigration on their own account" (Scott 1922 p. 607).

At least externally, our *Enigmophyton* has some features in common with *Germanophyton* (as regards the connection of the large leaves of the latter with the stems referred to the same species, cf. p. 98). Does this resemblance denote a real relationship? Or has *Enigmophyton* its natural place in an entirely different part of the plant system?

Let us first summarize some main points concerning *Enigmophyton*: We have a fairly complete knowledge of its vegetative morphology, which gives us good reason to believe that the plant has not been subaquatic (p. 115). But, unfortunately, we do not know much about its anatomical structure: It is certain that it had a continuous tissue of isodiametric cells on the surface, whereas there are no traces left of the long conducting cells which it may be supposed to have possessed, and which, indeed, this large-leaved plant *must* have possessed if it has been growing on dry land; it is a fact of considerable interest, but of unknown importance, that the impressions and casts of the axes never show any traces of strands. As regards the reproductive organs, there is very good reason to assume that they have had the form of cuticularized spores, developed in tetrads in the sporangia of the spike-like shoots described in detail above (p. 117). But most unfortunately, these shoots have not been found in organic connection with the rest of the plant; if they had been, they would have proved beyond dispute that the plant itself, or its ancestors, had either been living on dry land or at any rate with parts of their bodies emerged from the water, because cuticularized spores, no more than tracheids, can be developed in a plant group living entirely under water; if found in such plants they must be inherited from subaërial ancestors.

With regard to the systematic position of *Enigmophyton*, and to the phylogeny of the group to which it may belong, there are two possibilities to be considered here:

(1). If the resemblance which seems to exist in leaf-form between *Enigmophyton* and *Germanophyton*, is a sign of real relationship, then these two genera, and at least several species of *Platyphyllum*, may constitute a group which, probably with *Prototaxites*, *Nematothallus*, and others, represent an attempt to take possession of the dry land along a road other than the one followed by the psilophytes and their descendants, that is, *Enigmophyton* would either belong to the *Nematophytales* or at least to the same phylum as that class. The surface tissue of *Enigmophyton,* consisting of parenchymatous cells without intercellular gaps, could scarcely be used as an argument against such an idea, a cortical pseudoparenchymatous tissue not being unknown in *Prototaxites*, although in a somewhat different form; there is at all events no difficulty in assuming that a tissue like the one of *Enigmophyton* has been developed in other plant groups than the cormophytes.

But *Germanophyton* and *Enigmophyton* have not been proved to be of the same internal structure and of real affinity to each other; all we know is that they have possessed large foliar organs of the same general type, and that it would be most surprising if such a characteristic form had come into existence in two contemporaneous plant groups entirely independent of each other.

The idea, however, is weakly founded, and is mentioned here merely as a possibility. It should certainly be dropped if a more likely systematic position of *Enigmophyton* could be pointed out. But in that case, the parallelity in leaf-form between *Germanophyton* and the other Devonian plants with large fan-shaped leaves has to be accounted for: Is this a real case of analogy between plants belonging to different phyla? And if so, does the artificial genus *Platyphyllum* comprise natural species belonging to either of them? Or is perhaps *Germanophyton* no true member of the *Nematophytales*? — At our present stage of knowledge we may ask such questions, but it is better not to discuss them at any length until more facts have afforded a more solid basis.

(2). Notwithstanding the gaps in our knowledge of *Enigmophyton*, we do know its very characteristic vegetative morphology well enough to see that it is entirely different from that of all psilophytes: Any relationship to that group seems at first sight to be out of the question, just as it is impossible to include *Enigmophyton* in any of the other known groups of vascular cryptogams. There is only one hypothetical line of development within the pteridophytes which deserves some closer consideration: Is it possible that *Enigmophyton* may be connected with plants like *Barrandeina* and through them with the psilophytes?

The systematic position of *Barrandeina* is still rather uncertain, but at all events the genus and its relatives belong to the vascular cryptogams in the customary sense of the word, and it is quite possible that they have developed from forms belonging to the same group as *Baragwanathia*; in that case they would probably be remotely connected with the psilophytes (p. 183).

The idea that *Barrandeina* is also related to *Enigmophyton* is conjectural, but cannot be rejected a priori; in fact, a good deal may be said in favour of it: *Barrandeina* has bifurcating axes of considerable, but rather uniform, thickness (not altogether unlike those of *Baragwanathia* and certain forms of *Drepanophycus*), bearing lateral foliar organs widened into wedge-shaped laminae with parallel, bifurcating veins. Apart from the phyllotaxy, which is very different, this organization has an undeniable resemblance to that of *Enigmophyton*; particularly the leaves of *B. Dusliana* are very similar to some of the broad leaves from Spitsbergen, although of a smaller size. If the fertile shoots referred to above really belong to *Enigmophyton*, they also, with their sporangia placed solitarily on the upper sides of sporophylls, would add considerably to the resemblance; but no great importance should be attributed to that character until the question of the mother plant of these fructifications has been indisputably settled. On the other side the leaves of *Barrandeina*, being arranged spirally in great numbers on the whole surface of the axis, have a position very different from those of *Enigmophyton*, where they may certainly also be spirally arranged, but where they are very limited in number (as is natural on account of their great size) and evidently always attached to the points of bifurcation. The small lateral branches of *Enigmophyton* also form a very peculiar character, to which it is difficult to find a parallel in any plant known before. If *Enigmophyton* has developed from anything like *Barrandeina*, the development has really gone very far along a line of specialization; but although not proved at present, such a development may be imagined.

To me the idea seems to be much more probable than the former alternative mentioned above. If correct, it will no doubt mean that it will become necessary to institute among the vascular cryptogams a new class, or whatever rank may be given to such a systematic unit. But it would be premature to introduce a new name for that hypothetical class at present, the more so, because it will perhaps not be necessary for the name to be a new one: We should have to consider whether the name *Palaeophyllales* Arber (1912 p. 405) might not be used as a designation, although with some change in circumscription.

Besides comprising *Enigmophyton*, some species now referred to *Platyphyllum*, and *Barrandeina*, such a group would probably offer a natural place for some other plants which are now rather homeless. Thus, it is tempting to mention *Duisbergia*, although the reserve expressed by Kräusel & Weyland (1934 p. 168) concerning speculations as regards its affinities is a recommendable example, particularly to one who has not personally studied any specimens of that peculiar genus.

There is a considerable resemblance between the fructifications described above (p. 117) and *Barinophyton* (together with *Pectinophyton* Høeg), of which the latest description by Arnold (1939 p. 285, Pl. IV) has considerably enlarged our knowledge. But in view of the uncertainty attached to the said fructification, and the almost complete lack of information regarding the vegetative organs of *Barinophyton*, the mere suggestion of a possible relationship may suffice at present.

Highly interesting comparisons may be drawn with *Noeggerathiales*, but the mere suggestion may suffice here.

VII. Diagnoses of New Genera and Species, with List of Other New Names and Combinations.

Taeniocrada (?) spitsbergensis n. sp. (p. 19).

Axes cylindrical, mostly about 2 mm thick, scarcely tapering upwards (neither base nor top preserved), sparingly bifurcating, generally (or always?) without spines or other appendages, but bearing laterally ovoid bodies about 3—4.5 mm long, with tuberculate surfaces.

Holotype: Paleontological Museum, Oslo, PA 228.

Locality: Spitsbergen: Raudfjord District: Frænkelryggen.

Age: Downtonian.

Psilophyton arcticum n. sp. (p. 33).

Main axis mostly straight, up to 8 mm broad, dividing dichotomously or more frequently with lateral branching. Tips recurved. Axillary tubercles probably present. Spines standing out at about right angles, very numerous and long, up to 8 (—10?) mm, thin, measuring about 0.3 mm in diameter, mostly straight or more rarely slightly flexuose, with a slightly swollen conical base, leaving circular, somewhat elevated scars. — Ultimate branch systems (supposed to belong to this species) slender, repeatedly bifurcating or pseudomonopodial, expanded in one plane, with short thorns and recurved tips.

Holotype: Paleontological Museum, Oslo, PA 250.

Locality: Spitsbergen: Wijdefjorden: Beach profile at Andredalen.

Age: Middle Devonian.

Psilodendrion n. gen. (p. 26).

Spinous psilophyte. Stems at least partly erect, strong, bearing lateral branch systems, which are pseudomonopodially divided and not flattened in one plane. Ramifications of first, second or higher order often subopposite, ultimate divisions dichotomous.

Psilodendrion spinulosum n. sp. (p. 26).

Characters of the genus. Stems attaining a breadth of at least 1 cm. Lateral branches opposite or nearly so, gradually tapering from thick and somewhat decurrent bases, which make the stems longitudinally ridged and grooved. Branch angles usually very wide in the dichotomously divided parts. Thorns short, sparse on the stems, more numerous on the branches, standing out at nearly right angles.

Holotype: Paleontological Museum, Oslo, PA 1108.

Locality: Spitsbergen: Gråhuken.

Age: Probably upper Lower Devonian (or lower Middle Devonian).

Hostimella strictissima n. sp. (p. 60).

Pseudomonopodial axial systems, the branches arranged spirally, with wide branch angles, no axillary tubercles, all axes slender, terete, mostly long and straight, without thorns, possessing a central strand of long cells. Axes (often) articulate, constricted at the nodes, which have a mutual distance about equal to the diameter.

Holotype: Paleontological Museum, Oslo, PA 257.

Locality: Spitsbergen: West side of Billefjorden.

Age: Lower (?) Devonian.

Bucheria longa n. sp. (p. 63),

Unbranched axes, straight and slender (about 1 mm wide), spikelike, bearing radially arranged lateral organs which are slightly overlapping, each consisting of a very short horizontal pedicel and an erect, dilated upper part (about 5—6 mm long, 3 mm wide), delicately veined, widest near the rounded upper end.

Holotype: Paleontological Museum, Oslo, PA 265.

Locality: Spitsbergen: West side of Billefjorden.

Age: Lower (?) Devonian.

Svalbardia n. gen. (p. 70).

Slender axes with lateral branch-systems which divide into filiform ramifications, and which partly bear lateral, pinnule-like foliar organs, fan-shaped in outline but split up dichotomously into narrow segments; leafy shoot not flattened in one plane. Fertile shoots paniculate, each primary branch of the panicle bearing several sporangia. Sporangia thin-walled, blunt, without columella or other sterile tissue. Spores developed in tetrads, with tri-radiate markings, delicately tuberculate.

Svalbardia polymorpha n. sp. (p. 70).

Plant probably at least 1 (—2) m high. Axes long, slender, straight or slightly curved, branches (probably) spiral, with a tendency to arrangement in opposite pairs. Pinnule-like organs about 2.5 cm long, with up to four bifurcations, rarely more; each segment with one vein. Panicles mostly 3—4 cm long, sometimes longer, terminal on branches. Sporangiferous branches at about right angles to the axis of the panicle, divided, but bearing sporangia (up to at least 12) only in the middle part, and ending in sterile tips which are usually curved slightly upwards. Sporangia on short, simple or divided pedicels, generally erect, pear-shaped or cylindrical with rounded tops, about 1.5—2 mm long and 0.5—0.7 mm in diameter. Spores oblong, mostly 60—70 μ long, nearly smooth, but with minute tubercles.

Holotype: Paleontological Museum, Oslo, PA 347. — Syntype: PA 306.

Locality: Spitsbergen: Mimerdalen.

Age: Upper Middle Devonian (or lowermost Upper Devonian?).

Cephalopteris (?) praecox n. sp. (p. 49).

Delicately striated branch-system or leaf, consisting of main axis, about 5—7 mm broad, with alternating lateral branches in one plane. Upper main branches sterile, bearing alternating small ramifications. Lower primary branches fertile, bearing pairs of opposite sporangiferous branchlets, each pair probably connected distally across the primary branch, alternately on its upper and lower side. Fertile branchlet nearly 1 cm long, with a terminal small cluster of sporangia.

[On the assumption that the various specimens described in the text belong to the same species, the diagnosis may be extended thus]: Ramifications (leaflets) of the sterile branches divided pseudomonopodially in one plane, linear, without lamina. Clusters of sporangia consisting of a few sessile sporangia, some of them being pendant. Sporangium about 2 mm long, nearly 1 mm broad, oval, with rounded top.

Holotype: Paleontological Museum, Oslo, PA 288.

Locality: Spitsbergen: Wijdefjorden: Beach profile between Andredalen and Forkdalen.

Age: Middle Devonian.

Actinopodium n. gen. (p. 150).

Leafless axis consisting of a broad parenchymatous cortex and a star-shaped stele, composed of a mixed pith with irregular metaxylem, probably mesarch protoxylem, and an outer zone of secondary xylem, surrounded by phloem. Protoxylem tracheids scalariform, the other tracheids multiseriately pitted on all walls. Small protostelic bundles, leaf-traces or roots, given off from the rays of the star-shaped stele. The axis probably attaining a considerable size due to secondary growth of xylem, without annual rings.

Actinopodium Nathorstii n. sp. (p. 150).

Characters of genus. — Young axis (as far as is known) somewhat flattened, about 2 mm broad. Star-shaped stele with about 7 rays.

Holotype: Slide in the *Riksmuseum*, Stockholm.

Locality: Spitsbergen: Mimerdalen: Fiskekløfta. Collected by Nathorst 1882.

Age: Middle Devonian.

Hyenia Nath., n. subgen. *Hyeniopsis* (p. 82).

Axes laterally branched, with branches developed in the position of leaves; bearing hairs or thorns.

Hyenia (subgen. *Hyeniopsis*) *Vogtii* n. sp. (p. 82).

Axis at least up to 9 mm thick. Leaf 1—1.5 cm long, abruptly constricted from a broad base, filiform, divided in more or less regular dichotomy up to five times, arranged in superposed verticils of four (or probably sometimes three or five) leaves, more rarely spirally. Lateral branches resembling the main axis, but somewhat thinner, arising from some of the nodes, rarely more than one branch from any node. Thorns thin, patent, about 2 mm long, scattered, particularly found on the lower sides of leaf and branch bases.

Holotype: Paleontological Museum, Oslo, PA 393.

Locality: Spitsbergen: Mimerdalen.

Age: Upper Middle Devonian (or lowermost Upper Devonian?).

Bergeria mimerensis n. sp. (p. 121).

Lepidophytic axes in bergerioid state, at least up to 8 cm broad, surface covered with areas generally of rhombic outline, sometimes quadratic or fan-shaped, (6—) 10 mm high, usually in immediate contact with each other, rarely separated by bands some millimetres broad. Appearance of areas varying according to mode of preservation. Each generally with a vertical diagonal keel, slightly unsymmetrical, or with an oval scar which in some specimens is more clearly visible than the outline of the area (transition to a knorrioid preservation). Leaf inserted at the upper end of the area.

Holotype: Paleontological Museum, Oslo, PA 1169.
Locality: Spitsbergen: Mimerdalen.
Age: Upper Middle Devonian (or lowermost Upper Devonian?).

Protolepidodendropsis pulchra n. sp. (p. 131).

Axes slender, known upwards to 1 cm in thickness, with well defined leaf-cushions surrounded by a system of flexuose furrows (in the negative impressions preserved as ridges) forming a network with the leaf-cushions in the meshes. Leaf-scar occupying the upper part of the cushion, varying in appearance according to the preservation, either circular with a central group of small dots representing the leaf-trace bundle, or elongated with bundle in oblique or longitudinal view; in the former cases the leaf-scar separated from the lower and larger part of the cushion by a constriction. Lower part of leaf-cushion attenuating downwards, with a weak median furrow (in the negative: keel) which bifurcates upwards. Entire leaf-cushion about 3 mm long and 0.6 mm broad. No ligular pit, parichnos marks, or infrafoliar pits. Leaf probably simple and short.

Holotype: Paleontological Museum, Oslo, PA 419.
Locality: Spitsbergen: Mimerdalen.
Age: Upper Middle Devonian (or lowermost Upper Devonian?).

Enigmophyton n. gen. (p. 88).

Plants of considerable size. Stems of uniform breadth, dividing dichotomously and bearing lateral branches (of unknown function). Leaves large, flabellate, inserted at the points of bifurcation; veins parallel, bifurcating, not anastomosing.

Enigmophyton superbum n. sp. (p. 88).

Plant probably more than 1 m high. Stems of uniform breadth, about 5 mm thick, smooth, bifurcating at acute angles and without any alternation in the thickness of the axis. Lateral branches about 1—2 mm thick, one at each point of bifurcation, standing out at nearly right angles (always broken at a length of a few centimeters). Leaf from a narrow base widening with curved sides into a broad fan-shape, at least up to 16 cm long and 12 cm broad, often split from the upper margin and in between the veins. Veins rather thin, but distinct, about 1—1.5 mm apart. Superficial tissue of the axis uniform, consisting only of rectangular cells, about 100×50 μ, arranged in longitudinal rows, without intercellular spaces.

Holotype: Paleontological Museum, Oslo, PA 356.
Locality: Spitsbergen: Mimerdalen.
Age: Upper Middle Devonian (or lowermost Upper Devonian?).

Germanophyton n. gen. (p. 95).

Plants of considerable size, consisting of irregularly branched axes bearing large fan-shaped leaves with bifurcating veins. Axis containing tubes of *Prototaxites* type, and (probably) parenchymatous tissues.

Type species: *G. psygmophylloides* (K. & W.) n. comb. (syn. *Prototaxites psygmophylloides* K. & W.), from the Lower Devonian of Germany.

Platyphyllum (Daws.) emend. (p. 110).

Old-Paleozoic form genus, comprising detached fan-shaped leaves with parallel bifurcating veins.

Platyphyllum Peachii n. sp. (p. 101).

Leaf in the form of a wide-angled sector of a circle, dentate along the upper margin and splitting secondarily between the veins from the margin inwards. Veins consisting of cell tubes which are either parallel or twisted around each other, frequently giving off small bundles of one or a few tubes, which run irregularly through the matrix and often unite with other bundles or veins. Tubes with annular thickenings or divided by cross-partitions. Other tissue than the tubes probably also present. Length of type specimen about 3.5 cm.

Holotype: British Museum, London, V 9412.
Locality: John o'Groats, Caithness.
Age: Middle Devonian.

Other New Names and Combinations.

Bucheria mucronata (Mägdefrau) n. comb. (p. 65).
Ginkgophyllum (?) scoticum (Wilson) n. comb. (p. 109).
Ginkgophyton Delvali (Camb. & Ren.) n. comb. (p. 110).
— *Gilkineti* (Lecl.) n. comb. ad int. (p. 106).
— *(?) Kidstoni* (Sew.) n. comb. (pp. 109, 110).
Kiltorkensia kiltorkensis (Johns.) n. comb. (p. 79).
Platyphyllum Buddei (K. & W.) n. comb. (p. 106).
— *fissipartitum* (K. & W.) n. comb. (p. 105).
— *majus* (Arber) n. comb. (p. 111).
— *pusillum* (Nath.) n. comb. (p. 94).
— *Williamsoni* (Nath.) n. comb. (pp. 93, 111).
Protopteridiales n. ordo (p. 178).

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Names of fossils described or redescribed in the text, and new names and combinations, are printed with thicker italics.

EXPLANATION OF PLATES

The specimens, when nothing else is stated, belong to the Paleontological Museum of the University, Oslo.

Plate I.

Raudfjorden: Frænkelryggen, Horizon II. Vogt's expedition 1928.

Fig. 1. Taeniocrada (?) spitsbergensis n. sp. (p. 19). Two branched axes with indications of transversal lines of carbonized matter. PA 225. Nat. size. — *Figs. 2—3.* Details from fig. 1. × 4. — *Fig. 4.* Same species. Bifurcating axis. PA 211. Nat. size. — *Fig. 5.* The same, enlarged. The branch to the left is subdividing. The upper part of the branch to the right has a distinct central strand and bears a spine. × 4. — *Fig. 6.* Part of same photo enlarged. × 12. — *Fig. 7.* Same species. Bifurcating axis, preserved as a cast with high relief. The branch to the left is constricted at regular short distances, a feature not visible on this photograph (which was taken with the fossil immersed in xylol). PA 230. Nat. size. — *Fig. 8.* Detail of the same, photographed dry. × 4. — *Fig. 9.* Same species. Bifurcating axis. PA 217. Nat. size. — *Fig. 10.* Same species. Bifurcating axis. Specimen treated with hydrofluoric acid. PA 220. Nat. size. — *Fig. 11.* Detail of same, showing the central strand. × 4. — *Fig. 12.* Same species. Straight axis with a lateral branch ending in a dilatation. The same specimen is seen in natural size on the left-hand side of Pl. III fig. 1. PA 228. × 6. — *Fig. 13.* Counterpart of same. PA 227. × 6. — *Fig. 14. Pachytheca* cf. *fasciculata* (p. 14). PA 236. Nat. size. — *Fig. 15.* Same. Illuminated from the left. The central part is hollow (except on the left-hand side). The external hyaline layer and the cortex, consisting of radiating tubes, are visible. × 15. — *Fig. 16.* Detail of same. × 50.

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Raudfjorden: Frænkelryggen, Horizon I. Vogt's expedition 1928.

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Plate III.

Raudfjorden: Frænkelryggen, Horizon II. Vogt's expedition 1928.

Fig. 1. Taeniocrada(?) spitsbergensis n. sp. (p. 19), holotype. Piece of shale with branched, naked axes associated with globular or pear-shaped bodies. PA 228. Nat. size. — *Fig. 2.* Counterpart of fig. 1. PA 227. Nat. size. — *Fig. 3.* Detail from the centre of fig. 1: Axis with transversal stripes of carbonized matter. × 4. — *Fig. 4.* From the lower end of fig. 1: Axis with a laterally attached body. Photographed in xylol. × 6. — *Fig. 5.* The same, photographed dry. × 6. — *Fig. 6.* Detail from a little above the centre of fig. 2: Axis with a laterally attached body. × 6. — *Fig. 7.* Counterpart of the same, from fig. 1. × 6. — *Fig. 8.* An oval body, from the lower part of fig. 2. × 6. — *Fig. 9.* Detail from the right-hand corner of fig. 1: Bifurcate axis. × 2

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Raudfjorden: Frænkelryggen, Horizon II. Vogt's expedition 1928.
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Wijdefjorden: Beach profile at Gråhuken. Vogt's expedition 1925.

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Plate VI.

Wijdefjorden: Beach profile at Gråhuken. Vogt's expedition 1925.
Psilodendrion spinulosum n. gen. & sp. (p. 26).

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Plate VII.

Wijdefjorden: Beach profile at Gråhuken. Vogt's expedition 1925.
Psilodendrion spinulosum n. gen. & sp. (p. 26).

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Wijdefjorden: Mountain south of Vatnedalen, 300—400 m above sea-level.
A. Hoel, 1912

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Wijdefjorden: Beach profile at Andredalen, Horizon 6. Vogt's expedition 1925.
Psilophyton arcticum n. sp. (p. 33).

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Plate X.

Wijdefjorden: Beach profile at Andredalen, Horizon 6. Vogt's expedition 1925.
Psilophyton arcticum n. sp. (p. 33).

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Wijdefjorden: Beach profile at Andredalen, Horizon 6. Vogt's expedition 1925.

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Plate XII.

Wijdefjorden: Beach profile at Andredalen, Horizon 6. Vogt's expedition 1925.

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Plate XIII.

Wijdefjorden: Beach profile at Andredalen, Horizon 4. Vogt's expedition 1925.

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Plate XIV.

Wijdefjorden: Beach profile at Andredalen, Horizon 4. Vogt's expedition 1925.

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Plate XV.

Wijdefjorden: Beach profile at Andredalen, Horizon 4.
Vogt's expedition 1925.

Branched axis, possibly rhizome, bearing a tuft of linear leaf-like bands. The connection of the latter with the axis is better seen on the counterpiece (p. 46). PA 244. Nat. size.

Plate XVI.

Wijdefjorden: Beach profile between Andredalen and Forkdalen.
Vogt's expedition 1925.

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Plate XVII.

Wijdefjorden: Beach profile between Andredalen and Forkdalen.
Vogt's expedition 1925. *Cephalopteris (?) praecox* n. sp. (p. 49).

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Wijdefjorden. Vogt's expedition 1928.

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Plate XIX.

West side of Billefjorden. Vogt's expedition 1925.

Fig. 1. Hostimella strictissima n. sp. (p. 60), holotype. As described in the text, all side-branches are not in one plane. PA 257. Nat. size. — *Fig. 2.* Part of main axis of fig. 1. × 4. — *Fig. 3. Hostimella* sp. (p. 67). PA 1106. Nat. size. — *Fig. 4. Psilophyton* sp. (p. 66). Thorns visible on the main axis and on the lowermost branch. PA 260. Nat. size. — *Fig. 5.* Detail of the same, showing thorns on main axis. × 4. — *Figs. 6—7. Hostimella* sp., with axillary tubercle (p. 67). PA 1164. Nat. size and × 3. — *Fig. 8. Bucheria longa* n. sp. (p. 63), holotype. PA 265. Nat. size. — *Fig. 9.* Detail of the same, showing upper parts, but not ends, of the two stalks with lateral appendages. × 3.

Plate XX.

Fig. 1. Hostimella strictissima n. sp. (p. 60), from west side of Billefjorden' collected by Vogt's expedition 1925. PA 257. Nat. size. — *Fig. 2.* Same species, counterpart of the holotype, lowermost internode (cf. Pl. XIX fig. 1), showing the articulation. PA 1180. × 3. — *Figs. 3—4.* Axis of same species, on the same slab as the holotype, but on the reverse side, showing unarticulate central axis and indications of transverse lines (on right-hand side of figure). PA 257. × 4 and × 15. — *Figs. 5—6. Barinophyton* sp. (p. 67). In fig. 5 the light comes from above, in fig. 6 from below. From the west side of Billefjorden, collected by Nathorst 1882. Belonging to the *Riksmuseum*, Stockholm. Nat. size. — *Fig. 7.* Top of same specimen, showing that the lateral organs are not unilateral. Lighted from the base. × 3. — *Fig. 8.* Lower part of same specimen, lighted from the top. × 4. — *Figs. 9—10. Hyenia Vogtii* n. sp. (p. 82), from Plantekløfta, Mimerdalen, Vogt's expedition 1928. Note hair bases, some of them circular, others elongate. PA 410. Nat. size and × 3. — *Fig. 11. Svalbardia polymorpha* n. gen. & sp. (p. 70), from Planteryggen, Mimerdalen, Vogt's expedition 1928. PA 314. Nat. size.

Plate XXI.

Mimerdalen: Planteryggen. Vogt's expedition 1928.

Fig. 1. Svalbardia polymorpha n. gen. & sp. (p. 70), holotype. Sterile branch with opposite secondary branches bearing pinnule-like lateral organs. PA 347. Nat. size. — *Fig. 2.* Detail of same specimen with a strand ending upwards in a deep depression probably representing the base of a branch going down into the matrix. On fig. 1 (which has been placed in inverted position in order to save space) it is found at the white spot about 2 cm above (on the plate: below) the first branching. × 3. — *Fig. 3.* Another branch of same species, on same slab. On lower part of axis the lateral leaves, or remains of leaves, are erect, higher up they are more spreading. Note the several detached groups of sporangia. PA 347. Nat. size. — *Fig. 4.* Same species. PA 1255. Nat. size. — *Figs. 5—6.* Probably same species. Relatively thick axes, partly with appressed 'leaf-bases', partly with more complete foliar organs. Fertile shoots in lower right-hand side of fig. 5. PA 323. Nat. size.

Plate XXII.

Mimerdalen: Planteryggen. Vogt's expedition 1928.

Svalbardia polymorpha n. gen. & sp. (p. 70), fertile and sterile. PA 335. Reduced.

Plate XXIII.

Mimerdalen: Planteryggen. Vogt's expedition 1928.

Svalbardia polymorpha n. gen. & sp. (p. 70). Same specimen as Pl. XXII. Sterile axes. × 1.5.

Plate XXIV.

Mimerdalen: Planteryggen. Vogt's expedition 1928.

Svalbardia polymorpha n. gen. & sp. (p. 70). Same specimen as Pl. XXII. Paniculate sporangiferous axes. Cf. also Pl. XXIX fig. 1 and Pl. XXX fig. 11. × 1.5.

Plate XXV.

Mimerdalen: Planteryggen. Vogt's expedition 1928.

Svalbardia polymorpha n. gen. & sp. (p. 70).

Fig. 1. Sterile axes, with foliar organs of various forms. PA 1142. Nat. size. — *Fig. 2.* Similar specimen. PA 302. Nat. size. — *Fig. 3.* Similar specimen, but foliar organs more like well-defined pinnules. PA 313. Nat. size. — *Fig. 4.* Detail of the same. × 2.

Plate XXVI.

Mimerdalen: Planteryggen. Vogt's expedition 1928.

Svalbardia polymorpha n. gen. & sp. (p. 70).

Figs. 1—2. Fragment of axis with two opposite pinnule-like organs. PA 308. Nat. size and × 3. — *Fig. 3.* Relatively thick axis, with branches in different planes. PA 328. Nat. size. — *Fig. 4.* Sterile axes, with different types of foliar organs. PA 344. Nat. size. — *Fig. 5.* Detail of the foliar organ in middle of same specimen. × 12.5. — *Fig. 6.* Surface structure of same specimen, from the spot marked with an arrow. Longitudinal cell walls distinct, the transversal ones visible only in a few places. × 12.

Plate XXVII.

Mimerdalen: Planteryggen. Vogt's expedition 1928.

Fig. 1. Svalbardia polymorpha n. gen. & sp. (p. 70). Branched axis, one branch bearing sporangia. PA 315. Nat. size. — *Figs. 2—3.* Same species, syntype. Paniculate sporangiferous branch. PA 306. Nat. size and × 3. — *Figs. 4—5. Svalbardia* sp. (p. 81). Paniculate sporangiferous branch. PA 327. Nat. size and × 4. — *Figs. 6—7. Protopteridium (?)* sp. (p. 81). Sporangiferous branches. PA 331. Very slightly reduced (93: 100), and × 4.

Plate XXVIII.

Mimerdalen: Planteryggen. Vogt's expedition 1928.

Svalbardia polymorpha n. gen. & sp. (p. 70).

Fig. 1. Poorly preserved specimen. The foliar organs on the left-hand side have cuneate and rather broad bases, while others, on the right-hand side, are narrower. PA 348. Nat. size. — *Figs. 2—3.* Ends of a group of sterile, curved branches, the numerous lateral organs mostly divided into filiform segments and appressed. PA 311. Nat. size and × 2.5. — *Fig. 4.* Several axes with different forms of foliar organs, more

or less pinnule-like, divided dichotomously or pinnately into segments which are mostly filiform. On the right-hand side a fertile shoot. PA 333. Nat. size. — *Fig. 5.* Detail of the same, showing the sporangiferous shoot. The sterile tips of the sporangiferous branches of the panicle seem unusually long. × 4.

Plate XXIX.

Mimerdalen: Planteryggen. Vogt's expedition 1928.

Svalbardia polymorpha n. gen. & sp. (p. 70).

Fig. 1. Detail from Pl. XXII, showing a fertile shoot. PA 335. × 3. — *Fig. 2.* Axes, with remains of foliar organs, and sporangia. PA 330. Nat. size. — *Fig 3.* Detail of same specimen, showing group of sporangia. × 4. — *Figs. 4—6.* Details of same specimen, showing sporangia more highly magnified. × 12. — *Figs. 7—8.* Two axes. The longest branch of the axis on the right-hand side bears sporangia (near the upper margin of fig. 7), as is shown in magnification in fig. 8. PA 340. Nat. size and × 3.

Plate XXX.

Mimerdalen: Planteryggen. Vogt's expedition 1928.

Svalbardia polymorpha n. gen. & sp. (p. 70).

Fig. 1. Two sporangiferous shoots. PA 322. Nat. size. — *Fig. 2.* Detail from lower end of fig. 1. × 3. — *Fig. 3.* Sporangia from near the top of the panicle in upper right-hand corner of fig. 1. × 12. — *Fig. 4.* Ditto, from middle of fig. 2. × 12. — *Figs. 5—8.* Fragment of sporangiferous shoot. PA 324. Nat. size, × 4, and × 12. — *Fig. 9.* Fragment of sporangiferous shoot. PA 304. × 12. — *Fig. 10.* Portions of sporangiferous shoots. PA 325 *b.* × 4. — *Fig. 11.* Sporangiferous branch from upper right-hand part of Pl. XXIV. PA 335. × 12.

Plate XXXI.

Mimerdalen: Planteryggen. Vogt's expedition 1928.

Fig. 1. Svalbardia polymorpha n. gen. & sp. (p. 70). Sporangiferous shoot. PA 326. Nat. size. — *Fig. 2.* Upper part of the same. × 5. — *Fig. 3.* Another fertile shoot of same species. PA 329. Nat. size. — *Fig. 4.* Part of the same. × 4.8. — *Figs. 5—8.* Spores probably belonging to same species. PA 1251/49 *c*, *c*, *a*, and *a*, × 100. — *Fig. 9.* Fig. 8 in higher magnification. × 500. — *Figs. 10—19.* Indeterminable spores (p. 146). Type numbers refer to descriptions in text. Figs. 10—11: Type *c*, PA 322/45. — Fig. 12: Type *a*, PA 1251/49 *c*. — Fig. 13: Type *e*, PA 1251/49 *c*. — Figs. 14—15: Type *d*, PA 1251/49 *c*. — Fig. 16: Type *b*, PA 1251/49 *c*. — Figs. 17—19: Type *f*, PA 1251 49 *b*. × 100 (figs. 10—17) and × 500 (figs. 18—19).

Plate XXXII.

Mimerdalen: Plantekløfta. Vogt's expedition 1925.

Hyenia Vogtii n. sp. (p. 82).

Fig. 1. Holotype. Thorns are found in several places, but they are not distinctly seen on the figure. PA 393. Nat. size. — *Fig. 2.* Detail from long branch of the axis on left-hand side of fig. 1, showing alternating leaves. × 3. — *Fig. 3.* Cell structure of surface of axis in upper right-hand corner of fig. 1. × 12.5. — *Fig. 4.* Broken axis, with much-divided leaves. PA 393 (but not on same side as fig. 1). × 2. — *Figs. 5—6.* Axis with two opposite branches and with exceptionally well-developed thorns. PA 409. Nat. size and × 4.

Plate XXXIII.

Mimerdalen: Plantekløfta. Vogt's expedition 1925.

Hyenia Vogtii n. sp. (p. 82).

Figs. 1—2. Largest determinable specimen of the species. Fig. 2 forms the continuation of the left-hand side of fig. 1. There are thorns on the lower sides of the leaf bases in some places, but not clearly visible on the figure. PA 397. Nat. size. — *Fig. 3.* Detail of branch in middle of fig. 1, showing leaf-traces. × 2.

Plate XXXIV.

Mimerdalen: Plantekløfta. Vogt's expedition 1925.

Hyenia Vogtii n. sp. (p. 82).

Fig. 1. Several sterile axes. PA 408. Nat. size. — *Fig. 2.* Detail from centre of fig. 1, showing connection of the uppermost leaf with the strand in the axis. × 3. *Fig. 3.* Ditto, showing short branch bearing thorns and leaf with relatively broad segments. × 3. — *Fig. 4.* Ditto, from upper left-hand corner. Note the vertical distance between the leaves. × 3. — *Fig. 5.* Axis with opposite branches. PA 409. Nat. size.

Plate XXXV.

Mimerdalen: Plantekløfta (figs. 1, 2, 5, and 6) and Planteryggen (figs. 3, 4, 7—10). Vogt's expedition 1928.

Figs. 1—2. Stems, probably of protoarticulate plants (p. 87). PA 1170. Nat size. — *Figs. 3—4.* Cf. *Hyenia Vogtii* (p. 87). PA 471. Nat. size and × 3. — *Fig. 5. Hyenia Vogtii* n. sp. (p. 82), associated with *Bergeria mimerensis* n. sp. Cf. also Pl. L fig. 3. PA 445. Nat. size. — *Fig. 6.* Same species. Branched axis, with thorns. PA 410. Nat. size. — *Fig. 7.* Probably part of a basal or subterranean stem of same species, with root organs. The slab is photographed in a slanting position. Upper half of figure shows side of slab, with the thick axis, while the lower half represents bedding plane, with organs supposed to be 'roots'. Long branch to the right may be an ordinary leaf-bearing shoot (cf. fig. 8). PA 450. Nat. size. — *Fig. 8.* Detail from fig. 7, showing end of long branch to the right. × 2. — *Figs. 9—10.* Axis, probably of protoarticulate plant (p. 88). PA 305. Nat. size and × 3.

Plate XXXVI.

Mimerdalen: Plantekløfta. Vogt's expedition 1928.

Enigmophyton superbum n. gen. & sp. (p. 88).

Fig. 1. Holotype. In lower right-hand corner a fertile branch of *Svalbardia polymorpha*; the larger axis just above it probably also belongs to that species. Some details from the leaf in the centre are shown in text-fig. 17. PA 356. Nat. size. — *Fig. 2.* Detail from upper part of fig. 1, showing beginning of a bifurcation, and a thin lateral branch at nearly right angles to the plane of bifurcation. × 2.

Plate XXXVII.

Mimerdalen: Planteryggen. Vogt's expedition 1928.

Fig. 1. Enigmophyton superbum n. gen. & sp. (p. 88). The upper parts of these leaves are seen on the left-hand side of Pl. XXXVI fig. 1. PA 356. Nat. size. — *Fig. 2.* Same species. Axis with double bifurcation and bearing leaves. The continuation

of the branch to the left is seen in Pl. XL fig. 1. The superficial cell structure of the axis is shown in Pl. XL fig. 2. PA 374. Nat. size. — *Fig. 3. Platyphyllum* sp. (p. 116). Cf. text-fig. 26. PA 1256. Nat. size.

Plate XXXVIII.

Mimerdalen: Planteryggen.

Enigmophyton superbum n. gen. & sp. (p. 88).

Fig. 1. Axis with double bifurcation. PA 352. Nat. size. — *Fig. 2.* Detail from fig. 1, from the branch to the left, showing the beginning of a bifurcation and a thinner lateral branch in a plane at right angles to that of the bifurcation. × 1.5. — *Fig. 3.* Bifurcate axis. In upper right-hand corner is seen a lateral branch. PA 1114. Nat. size. — *Fig. 4.* Axis with double bifurcation and a large leaf, deeply split. PA 387. Nat. size. — *Fig. 5.* Detail from somewhat below the middle of fig. 4, showing axis and base of a lateral branch which is given off from under side of axis. × 3.

Plate XXXIX.

Mimerdalen: Planteryggen. Vogt's expedition 1928.

Enigmophyton superbum n. gen. & sp. (p. 88).

Fig. 1. Long axis with bases of large leaves. PA 354. Nat. size. — *Fig. 2.* Upper part of leaf, involute along the margin. Photographed with light from below. PA 1255. × 2. — *Fig. 3.* Branched axis. PA 454. Nat. size. — *Fig. 4.* Part of the same. × 4. — *Fig. 5.* Detail from fig. 3, from left-hand side of axis a little above the middle. × 12. — *Fig. 6.* Detail from upper half of fig. 3. × 12. — *Fig. 7.* Part of the same, upper half. × 30.

Plate XL.

Mimerdalen: Planteryggen. Vogt's expedition 1928.

Enigmophyton superbum n. gen. & sp. (p. 88).

Fig. 1. Bifurcating axis, forming continuation of branch to the left in Pl. XXXVII fig. 2, but appearing on reverse side of slab. PA 374. Nat. size. — *Fig. 2.* Detail from fig. 1, showing cell structure of surface of left-hand axis. Photographed under a cover of cellulose glue. × 12. — *Fig. 3.* Detail of same specimen, photographed dry. × (about) 12. — *Fig. 4.* Part of a leaf. PA 1155. × 20. — *Fig. 5.* Detail of axis. PA 1259. × 20. — *Fig. 6.* Part of leaf, photographed dry. PA 354. × 20.

Plate XLI.

Germanophyton psygmophylloides (K. & W.) n. comb. (syn. *Prototaxites psygmophylloides* K. & W.) (p. 95), type specimens, from the Lower Devonian, Westphalia: Kirchhundem b. Olpe. Belonging to the *Reichsstelle für Bodenforschung,* Berlin.

Fig. 1. Same specimen as Kräusel & Weyland 1930 Pl. I fig. 2. Compare also our Pl. XLII fig. 6. Nat. size. — *Fig. 2.* Detail from left-hand side of fig. 1, showing tubes exposed as longitudinal sections on the surface. × 12. — *Fig. 3.* Same, differently photographed. × 12. — *Fig. 4.* Central part of fig. 3, enlarged. × 55. — *Fig. 5.* Detail from centre of Pl. XLII fig. 5. To secure some details it had to be photographed with light from the right, and is therefore reproduced upside-down. × 12. — *Fig. 6.* Lower right-hand part of fig. 5, enlarged. × 36. — *Fig. 7.* Left-hand side of fig. 5. × 48. — *Fig. 8.* Upper part of fig. 7, photographed somewhat differently. × 72. — *Fig. 9.* Another detail from same specimen. × 12.

Plate XLII.

Fig. 1. Platyphyllum Buddei (K. & W.) n. comb. (syn. *Ginkgophyllum Buddei* K. & W.) (p. 106), holotype, from the Middle Devonian, Elberfeld. Belonging to the *Natur-Museum Senckenberg*, Frankfurt a. M. No. 2104. Detail, showing the veins. × 3. — *Fig. 2.* Same specimen. Part of a vein, photographed dry. × 50. — *Figs. 3—4.* Details of veins of counterpart of same specimen, showing tracheids with pitted walls. × 100. — *Fig. 5. Germanophyton psygmophylloides* (K. & W.) n. comb. (syn. *Prototaxites psygmophylloides* K. & W.) (p. 95), from the Lower Devonian, Kirchhundem b. Olpe. Belonging to the *Reichsstelle für Bodenforschung*, Berlin. Specimen also figured by Kräusel & Weyland 1930 Pl. I fig. 3. Nat. size. — *Fig. 6.* Same species. Detail from centre of Pl. XLI fig. 1, photographed so as to show the relief. Nat. size. — *Fig. 7.* Detail from same specimen, a little to left of centre of fig. 6. The upper part of the figure is a natural cross-section, with several oval figures probably representing tubes, while in the lower part, which is in another plane, at least one tube is seen in longitudinal section. The edge between the two planes is a little below the middle of figure, in a somewhat oblique direction (upwards to the right). × 15. — *Fig. 8.* Detail from same specimen, from lower left-hand corner of Pl. XLI fig. 1. Particularly in lower part of figure a few tubes are seen as longitudinal sections. × 10. — *Fig. 9.* Part of fig. 8, photographed with light more from below so as to show better the relief and the openings of some tubes seen in transversal sections. × 10.

Plate XLIII.

Platyphyllum Brownianum Daws. (p. 98), neotype, from Perry, Maine. Belonging to the Boston Society of Natural History. Photograph obtained by courtesy of the late Professor W. C. Darrah. Nat. size.

Plate XLIV.

Platyphyllum Brownianum Daws. (p. 98), from Perry, Maine. Specimens belonging to the British Museum.

Fig. 1. Brit. Mus. V. 19358. Nat. size. — *Fig. 2.* Brit. Mus. V. 699. Nat. size. — *Fig. 3—4.* Details from the veins of fig. 2. × 50. — *Figs. 5—8.* As figs. 3—4. × 100.

Plate XLV.

Platyphyllum Peachii n. sp. (p. 101), holotype, from the Middle Devonian, John o'Groats, Caithness, collected by C. W. Peach 1869. Belonging to the British Museum, V. 9412.

Fig. 1. Nat. size. — *Figs. 2—3.* × 9. — *Fig. 4.* A vein, photographed dry. × 50. — *Fig. 5.* Same photograph as fig. 4, enlarged. × 150. — *Fig. 6.* Detail from lower part of fig. 2, photographed in xylol. × 50.

Plate XLVI.

Figs. 1—5. Platyphyllum Peachii n. sp. (p. 101), holotype, as Pl. XLIV. Details of veins. Photographed in xylol. Fig. 2 is from upper part of fig. 1, and fig. 4 is from upper part of fig. 3. × 50 (figs. 1, 3, and 5) and × 200 (figs. 2—4). — *Figs. 6—9.* Same specimen. Cellulose film pulls. × 250 (figs. 6—7) and × 750 (figs. 8—9). — *Figs. 10—11.* Indeterminable leaf (p. 104), from Turin Bay, near Forfar, collected by C. W. Peach. Royal Scottish Museum, Edinburgh, PB-D 53. Nat. size and × 3.

Plate XLVII.

Mimerdalen: Planteryggen. Vogt's expedition 1928.
Enigmophyton?, fructification (p. 117).

Fig. 1. Best specimen, with several fertile shoots in lower part, axis and leaves of *Enigmophyton superbum* in upper part, and axes of *Svalbardia polymorpha* to the right. PA 390. Nat. size. — *Fig. 2.* Detail from centre of fig. 1. × 4. — *Figs. 3—5.* Details from right-hand branch of fig. 2. Compare also Pl. XL fig. 2. × (about) 12.5. *Fig. 6.* Remains of rectangular cells. From near the centre of fig. 4. × (about) 50.

Plate XLVIII.

Mimerdalen: Planteryggen. Vogt's expedition 1928.
Enigmophyton?, fructification (p. 117).

Fig. 1. Two fertile shoots. PA 470. Nat. size. — *Fig. 2.* The uppermost specimen on fig. 1. × 4. — *Fig. 3.* Fertile shoots, some of them probably belonging together. PA 469. Nat. size. — *Fig. 4.* The lowermost specimen on fig. 3. × 4. — *Fig. 5.* Surface structure of same specimen, at point of bifurcation, photographed dry. × 12.5. — *Fig. 6.* The specimen on the right-hand side of fig. 3; only partly preserved. × 4. — *Figs. 7—9.* Fertile shoots. The sporangia have disappeared from most of the sporophylls. PA 470, PA 391, and PA 390. × 4.

Plate XLIX.

Mimerdalen: Planteryggen. Vogt's expedition 1928.

Fig. 1. *Enigmophyton?*, fructification (p. 117). Part of specimen with very high and narrow sporangium. PA 390. × 12.5. — *Fig. 2.* Same species. Detail from lower left-hand corner of Pl. XLVII fig. 2. Sporangia with macrospores. PA 390. × 18. — *Figs. 3—5.* Same species. Details from lowermost specimen on Pl. XLVII fig. 1. PA 390. × 12.5, × 31, and × 40. — *Figs. 6—8.* Same species. Microspores. PA 470/50 *a.* × 100 (figs. 6—7) and × 500 (fig. 8). — *Figs. 9—11.* Macrospores from same specimen. PA 470/50 *a.* × 100. — *Fig. 12.* Microspores from another spike on same slab. PA 470/13. × 100. — *Fig. 13.* Spore isolated from a similar fructification on another slab. Probably a macrospore. PA 386/41 *b.* × 100. — *Figs. 14—16.* Foreign spore forms obtained in the same preparation as fig. 13. They are described in the text (p. 146) under the type numbers, respectively, of *d*, *f*, and *c*. PA 386/41 *c*, *a*, and *a*. × 100.

Plate L.

Mimerdalen: Plantekløfta. Vogt's expedition 1925 (figs. 1—2) and 1928 (figs. 3—7).

Figs. 1—2. *Bergeria mimerensis* n. sp. (p. 121), holotype. PA 1169. Nat. size and × 5. — *Fig. 3.* Same species. In lower end a poorly preserved fragment of *Protolepidodendropsis pulchra* (cf. figs. 4—5). On same slab also specimen of *Hyenia Vogtii* (Pl. XXXV fig. 5). PA 445. Nat. size. — *Fig. 4.* *Protolepidodendropsis pulchra* n. sp. (p. 113). Part of the poorly preserved fragment in lower end of fig. 3. × 3. — *Fig. 5.* Detail from upper part of fig. 4, showing reticular ridges and leaf-cushions with bifurcating keel. × 12. — *Figs. 6—7.* Cf. *Protolepidodendropsis pulchra* (p. 113). Poorly preserved fragment in which the leaf-cushions have nearly disappeared. PA 439. Nat. size and × 3.

Plate LI.

Mimerdalen: Planteklø̸fta (figs. 1—7) and Planteryggen (fig. 8).
Vogt's expedition 1928.

Fig. 1. Bergeria mimerensis n. sp. (p. 121). PA 428. Nat. size. — *Fig. 2.* Stone-cast of same species. The rhombic areas are distinct on one side, whereas only the oval scars are visible in other parts. PA 1246. Nat. size. — *Figs. 3—5.* Bifurcating lepidophytic axes, partly preserved as *Knorria* (p. 140). PA 407. Nat. size. — *Figs. 6—7.* Details from fig. 4 and fig. 5, respectively. × 4. — *Fig. 8.* Lepidophytic axis with undulate surface (p. 138). Being photographed in xylol, it does not show the relief of the surface well. PA 416. Nat. size.

Plate LII.

Mimerdalen: Plantekløfta (figs. 1—7) and Planteryggen (figs. 8—10).
Vogt's expedition 1928.

Fig. 1. Cf. *Bergeria mimerensis* (p. 124). PA 425. Nat. size. — *Fig. 2.* Upper end of fig. 1. × 4. — *Fig. 3.* Part of the same. Note rhombic area, somewhat unsymmetrically divided by vertical line. Cf. fig. 7 (which, however, is only magnified × 2). × 12. — *Fig. 4.* Detail from lower half of fig. 1, photographed in xylol. × 4. — *Figs. 5—6.* Parts of the same, photographed dry, showing leaf-cushions and outlines of cells. × 12. — *Fig. 7. Bergeria mimerensis* n. sp. (p. 121). The specimen, which in all essentials is identical with PA 445 (Pl. L fig. 3), is not illustrated in natural size. PA 443. × 2. — *Fig. 8.* Cf. *Protolepidodendropsis pulchra* (p. 139), with leaves still attached, poorly preserved. PA 411. Nat. size. — *Figs. 9—10.* Details of same specimen. × 3.

Plate LIII.

Mimerdalen: Plantekløfta (figs. 1—6 and figs. 8—9) and Planteryggen (fig. 7).
Vogt's expedition 1928.

Fig. 1. Lepidophyte, probably belonging to the same species as *Bergeria mimerensis* (p. 126). Bifurcating axis, the branch to the right lying in the bedding plane of the rock, while the left-hand branch forms an angle of about 30° to it. Some leaves still attached. PA 418. Nat. size. — *Fig. 2.* Detail of same specimen, showing leaf-bearing portion of left-hand branch. × 3. — *Fig. 3.* The same, photographed in a different way, and showing the rhombic areas. × 4. — *Fig. 4.* Same species. Two axes crossing each other in different levels. The higher one, to the right, is probably seen in inverted position, judging from the direction of the leaves. PA 418. Nat. size. — *Figs. 5—6.* From an axis not photographed in natural size, but belonging to same species as those shown in fig. 1 and fig. 4, and found on same slab. Leaf-cushions. In fig. 6 there are traces of the cell-structure. PA 418. × 6. — *Fig. 7.* Decorticated lepidophytic axis (p. 141). PA 417. Nat. size. — *Figs. 8—9.* Decorticated lepidophytic axis, with wrinkled surface (p. 142). PA 394. Nat. size and × 3.

Plate LIV.

Mimerdalen: Plantekløfta (figs. 1—8) and Planteryggen (figs. 9—11).
Vogt's expedition 1928.

Fig. 1. Protolepidodendropsis pulchra n. sp. (p. 131), holotype. PA 419 *a.* Nat. size. — *Fig. 2.* Detail of same specimen. × 4. — *Figs. 3—5.* Details of same specimen, showing leaf-cushions photographed in xylol. × 12. — *Fig. 6.* Another axis

of same species, found on same slab. PA 419 *b*. Nat. size. — *Figs. 7—8*. Details of same specimen. × 4 and × 10. — *Fig. 9*. Cf. *Protolepidodendropsis pulchra* (p. 138). Axis with undulate surface. PA 423. Nat. size. — *Figs. 10—11*. Details of the same. × 3 and × 12.

Plate LV.

Mimerdalen: Plantekløfta (figs. 1—5 and 9—12) and Planteryggen (figs. 6—8). Vogt's expedition 1928.

Fig. 1. *Protolepidodendropsis pulchra* n. sp. (p. 131). Detail of the holotype, Pl. LIV fig. 1, showing impression of a leaf-cushion with bifurcate keel (originally a furrow). Photographed dry. PA 419 *a*. × 12. — *Fig. 2*. *Protolepidodendropsis pulchra* n. sp. PA 424. Nat. size. — *Figs. 3—4*. Details of the same. × 4.5. — *Fig. 5*. Single leaf-cushion from left-hand side of fig. 3. × 10. — *Figs. 6—7*. Same species. A small well-preserved fragment. PA 414. Nat. size and × 3. — *Fig. 8*. Details of same specimen. × (nearly) 12. — *Fig. 9*. Leaf-bearing axis, cf. *Protolepidodendropsis pulchra* (p. 139). PA 412. Nat. size. — *Fig. 10*. Detail of the same. × 4. — *Figs. 11—12*. Details of the same. × 12.

Plate LVI.

Mimerdalen: Vogt's expeditions 1925 and 1928.

Figs. 1—2 Indeterminable leaf-bearing shoot of lepidophyte (p. 140), Plantekløfta, 1928. PA 472. Nat. size and × 3. — *Figs. 3—4*. Another shoot, probably of same species, found on same slab. PA 472. Nat. size and × 3. — *Figs. 5—6*. Leaf-bearing shoot, cf. *Protolepidodendropsis pulchra* (p. 140). Note black bodies on upper sides of leaves near the middle of fig. 6 Planteryggen, 1928. PA 455. Nat. size and × 4. — *Figs. 7—8*. *Problematicum* (p. 145): Axis of unknown affinity, bearing long linear leaves with curved bases. Planteryggen, 1928. PA 452. Nat. size and × 3. — *Figs. 9—10*. Same species? (p. 146). Greyish white hard sandstone along the river above Fiskekløfta, 1928. PA 493. Nat. size and × 3. — *Fig. 11*. *Dictyoxylon* sp. (p. 143). Planteryggen, 1928. PA 435. Nat. size. — *Fig. 12*. Psilophyte? (p. 69). East side of the river east of Estheriahaugen, 1928. PA 1101. Nat. size. — *Fig. 13*. Leaf-like fragment, cf. *Platyphyllum* sp. (p. 116). Estheriahaugen, 1925. PA 1151. Nat. size.

Plate LVII.

Mimerdalen: Plantekløfta. Vogt's expedition 1928.

Long axis with bases of branches in approximately verticillate arrangement (p. 144). PA 1141. Nat. size.

Plate LVIII.

Mimerdalen: Fiskekløfta. Petrifications in nodules collected by A. G. Nathorst in 1882. Belonging to *Riksmuseet*, Stockholm.

Fig. 1. *Actinopodium Nathorstii* n. gen. & sp. (p. 150), holotype. Slide *k*. Cross-section, showing star-shaped stele surrounded by cortex. A small bundle is seen within the cortex, right below the stele. Cross-sections of small axes, which may or may not belong to the same plant, are seen in the matrix in lower left-hand corner of photograph. — Slide *k*. × 5. — *Fig. 2*. The same, in another slide. To the right, a ray of the star-shaped stele emitting a small bundle. A similar bundle is seen

in lower left corner. Slide *f.* × 5. — *Fig. 3.* Detail from fig. 2. × 25. — *Fig. 4.* As fig. 3. Rows of tracheids of the outer wood, cut obliquely and showing multiseriate pitting. There is a split between the outer wood (in the cambium?) and the phloem, the latter not being visible on the photograph. × 100. — *Fig 5.* The same plant, holotype, in another section. From the centre of a ray of the star-shaped xylem, cut slightly obliquely and showing scalariform tracheids of protoxylem. Slide *m.* × 100. — *Fig. 6.* Small axis, probably belonging to *Actinopodium Nathorstii*, cut at a point of bifurcation. Only inner parts are preserved. Small cells in centre are scalariform tracheids. The nature of the cells surrounding them at some distance cannot be made out with full certainty, but probably they are pitted tracheids. Slide *b.* × 100. — *Fig. 7.* Part of longitudinal section of an axis (p. 158), probably belonging to *Actinopodium Nathorstii*, with stele and cortex. Details of the wood are shown in Pl. LXI fig. 1. Slide *d.* × 5.

Plate LIX.

Mimerdalen: Fiskekløfta. Petrifications in nodules collected by A. G. Nathorst in 1882. Belonging to *Riksmuseet*, Stockholm.
Actinopodium Nathorstii n. gen. & sp. (d. 150), holotype.

Fig. 1. End of ray of the star-shaped xylem. Slide *f.* × 25. — *Fig. 2.* Similar section, chiefly showing the cortex. Slide *n.* × 15. — *Fig. 3.* From a sinus of the star-shaped xylem. There are splits in the tissues: (1) along radial lines within the outer wood; (2) between outer wood and phloem; (3) between cortex and tissue interpreted as phloem. Slide *m.* × 25. — *Fig. 4.* Similar section. Slide *k.* × 25.

Plate LX.

Mimerdalen: Plantekløfta. Petrifications in nodules collected by A. G. Nathorst in 1882. Belonging to *Riksmuseet*, Stockholm.

Fig. 1. Cross-section of an axis (p. 158), possibly belonging to *Actinopodium Nathorstii*, showing star-shaped stele in excentric position, surrounded by parts of the cortex. Some small bundles found in cortex (cf. fig. 5) are not visible in this magnification. Slide *l.* × 5. — *Fig. 2.* Part of the same, showing the stele. × 15. — *Fig. 3.* Part of the same, from lower median group of xylem, showing protoxylem and metaxylem, some of the outer wood being arranged in radial rows and possibly of secondary origin. × 50. — *Fig. 4.* A similar photograph. The section being slightly oblique, several tracheids show the multiseriate pitting of their walls, but that is not distinctly visible in this magnification. × 50. — *Fig. 5.* Small bundle from cortex in upper side of fig. 1. × 50. — *Fig. 6.* *Actinopodium Nathorstii* n. gen. & sp. (p. 150), holotype. A slightly oblique section, showing outer wood, phloem, and between them dark zone of small cells perhaps representing the cambium. Slide *n.* × 50. — *Fig. 7.* Another part of same slide. Tracheids of outer wood in cross-section with bordered pits. Very near the part shown in text-fig. 35. × 500. — *Fig. 8.* Cross-section of a thin axis, found in a slide containing the holotype of *Actinopodium Nathorstii*, and possibly belonging to that species. Slide *n.* × 50. — *Fig. 9.* Another section of a similar organ. Slide *b.* × 100. — *Fig. 10.* The same. Slide *o.* × 50. — *Fig. 11.* Central part of a (?) root, with scalariform tracheids. Slide *m.* × 250.

Plate LXI.

Mimerdalen: Fiskekløfta. Petrifications in nodules collected by A. G. Nathorst in 1882. Belonging to *Riksmuseet*, Stockholm.

Longitudinal sections of wood, cf. *Actinopodium Nathorstii* (p. 158).

Fig. 1. Detail of axis, part of which is shown in Pl. LVIII fig. 7. Slide *d.* × 250. — *Fig. 2.* Tracheids, scalariform or multiseriately pitted, from a small fragment of tissue, cut longitudinally and showing well preserved tracheids, but giving no information as to the external form of the axis to which it belonged. Slide *b.* × 250. — *Fig. 3.* Fragment of wood. Slide *e.* × 6. — *Figs. 4—5.* Details of fragment of wood similar to that shown in fig. 3. Slide *e.* × 250. — *Fig. 6.* Probably a longitudinal tangential section of secondary wood (p. 159). Slide *s.* × 50.

Plate LXII.

Mimerdalen: Fiskekløfta. Petrifications in nodules collected by A. G. Nathorst in 1882. Belonging to *Riksmuseet*, Stockholm.

Fig. 1. Prototaxites sp. (p. 149). Slide *i.* × 100. — *Fig. 2.* Cross-section of fragment of wood (p. 159), probably belonging to *Actinopodium Nathorstii* or a related plant. Slide *j.* × 5. — *Figs. 3—4.* Details of the same. × 50. — *Fig. 5.* Fragment of similar wood, consisting of smaller cells. Slide *r.* × 50.

Plate I


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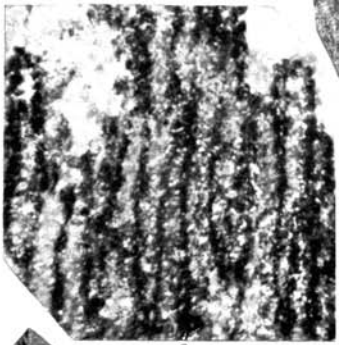
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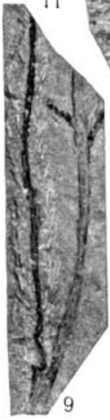
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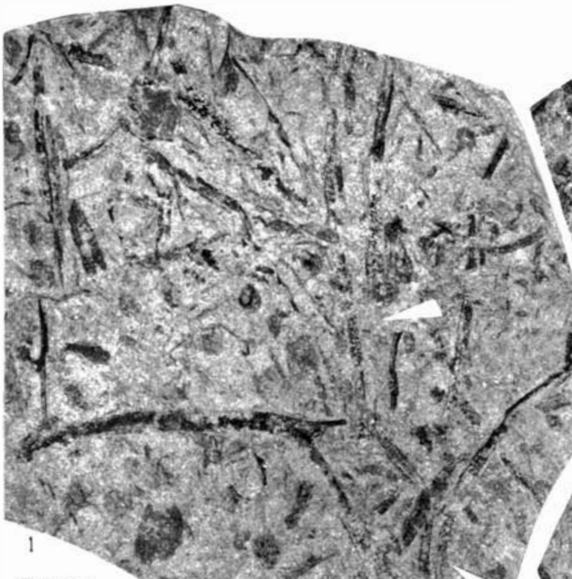
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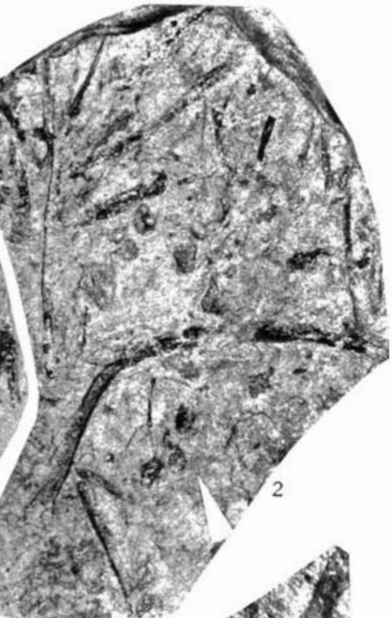
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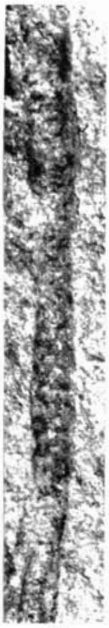
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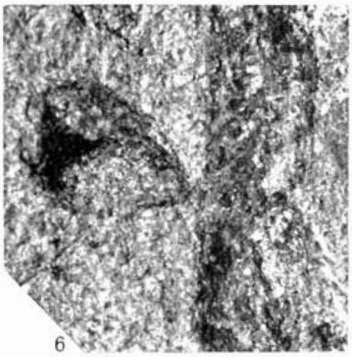
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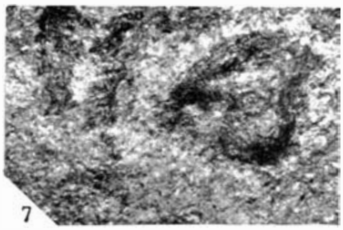
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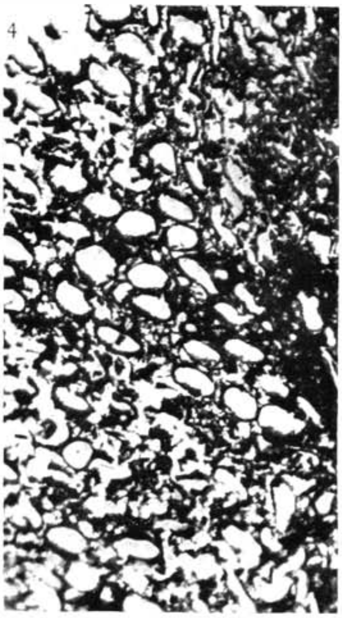
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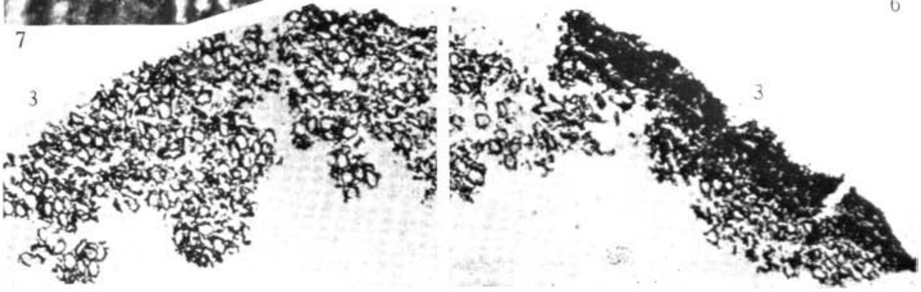
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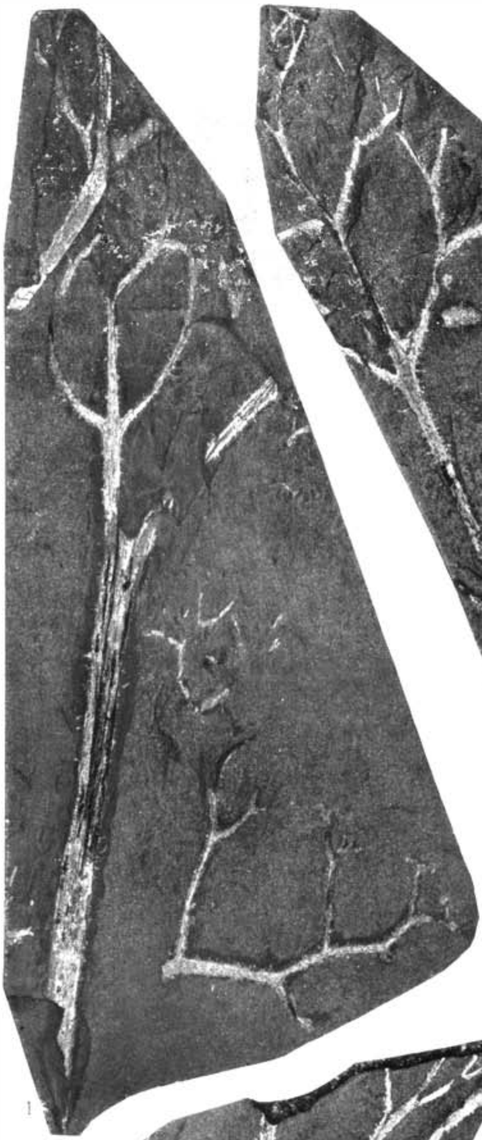

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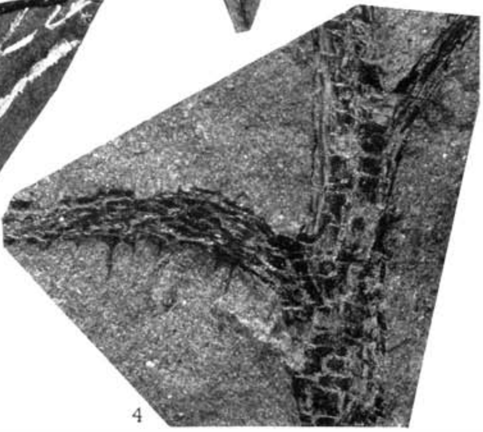

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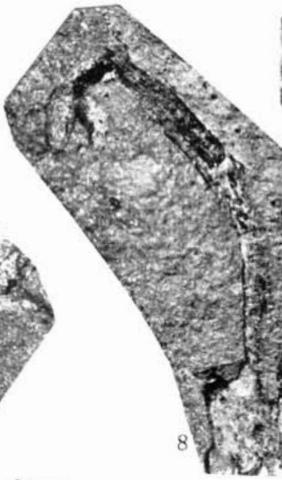
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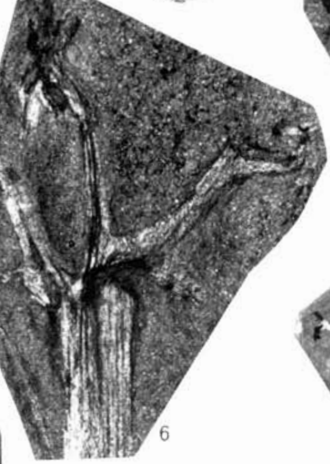
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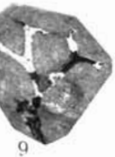
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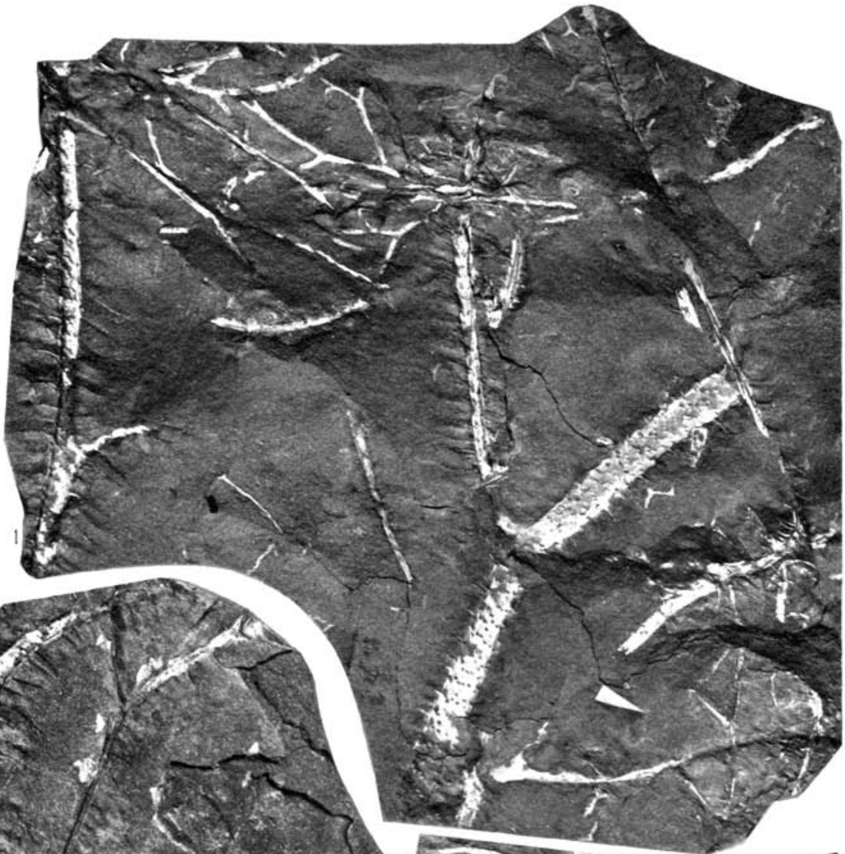
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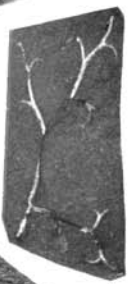
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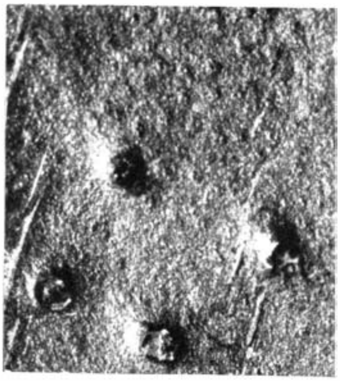


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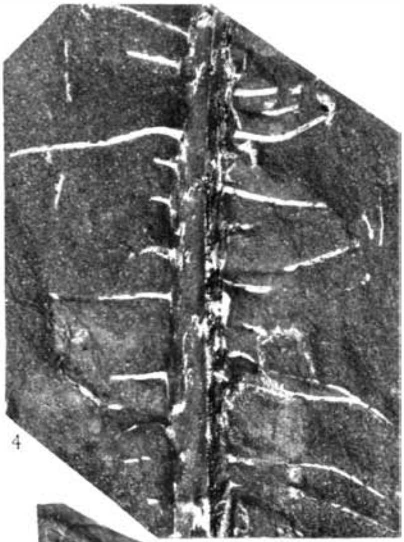
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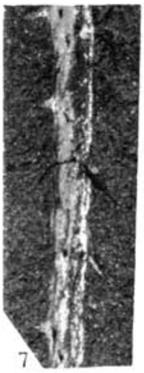
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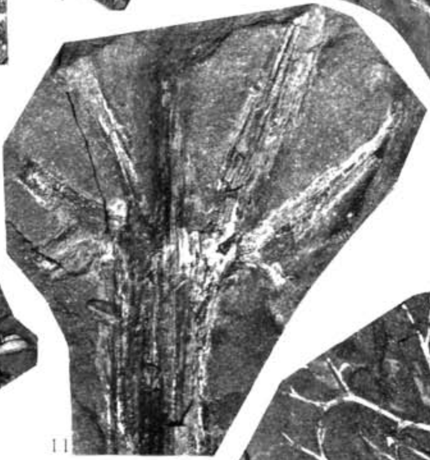
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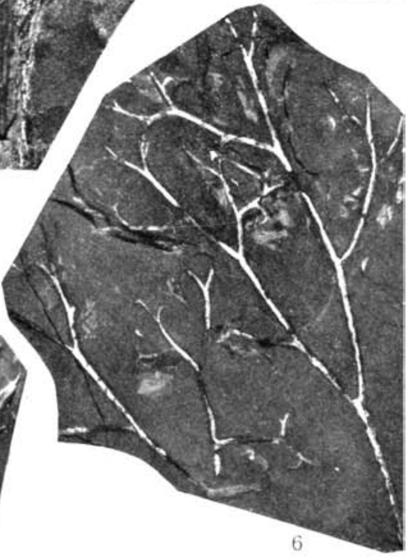
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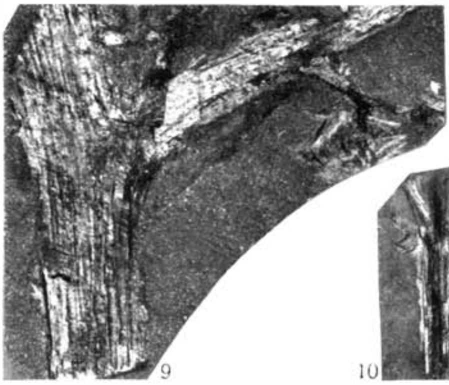
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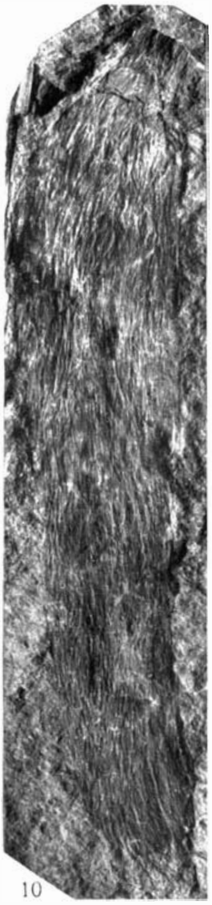
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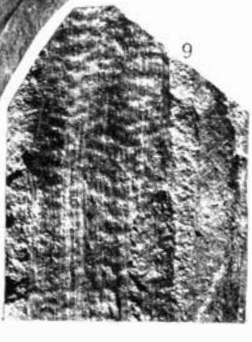
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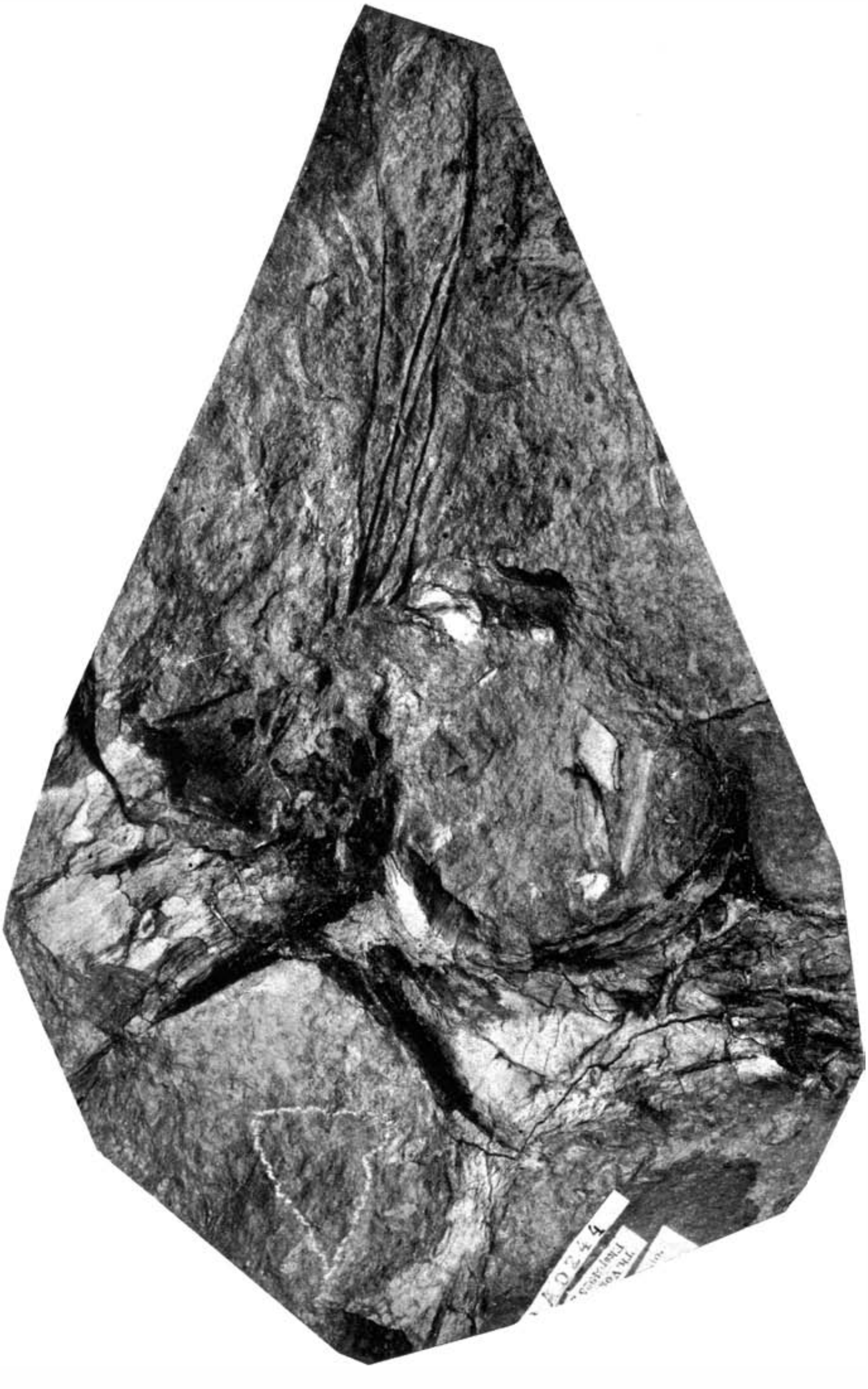
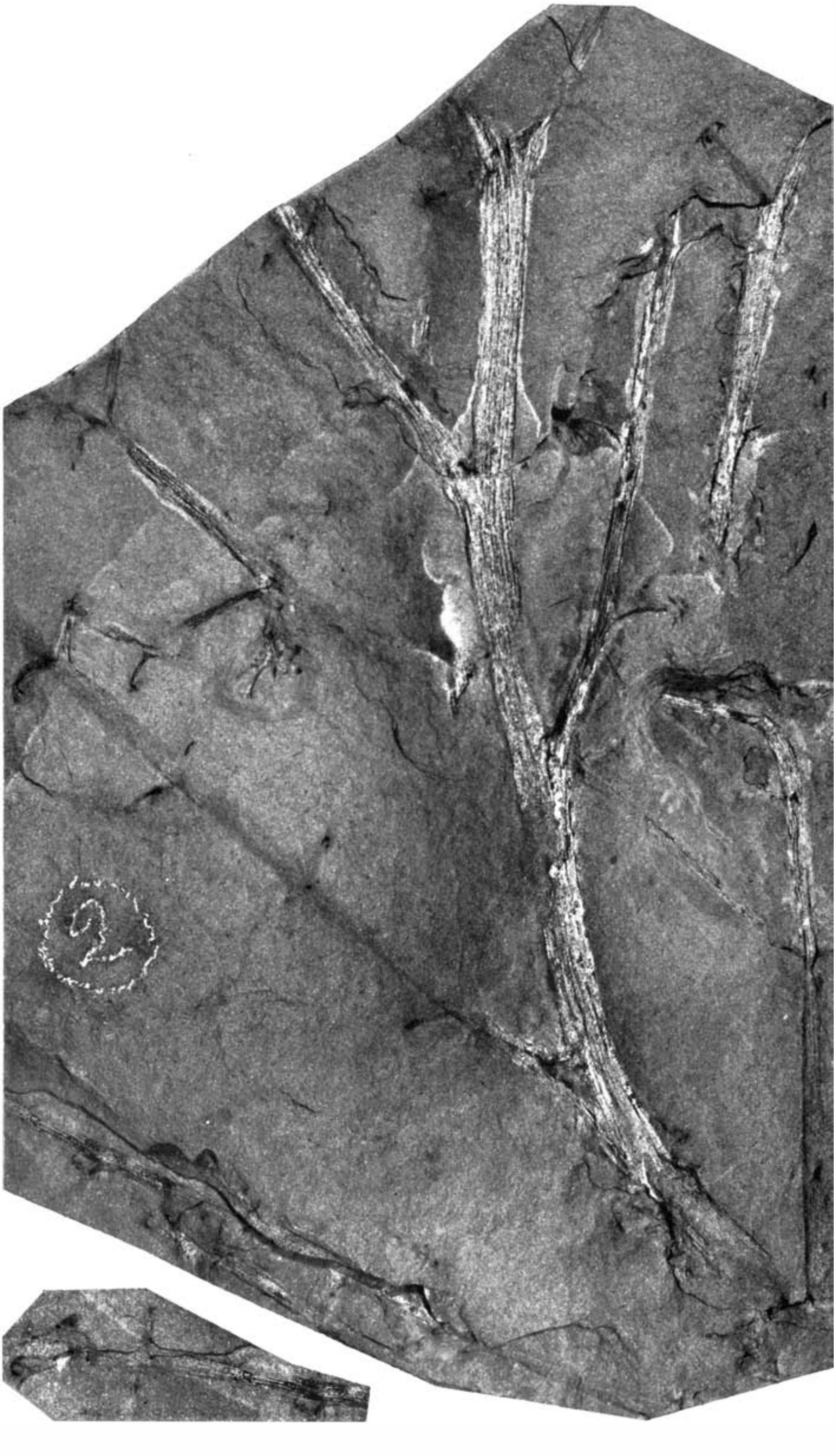
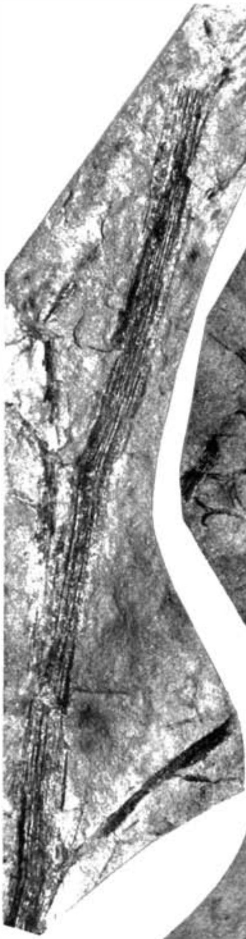


Plate XVI

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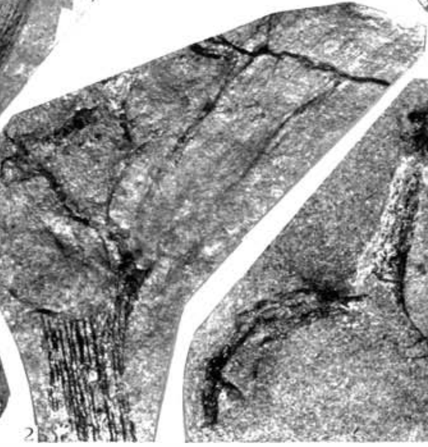
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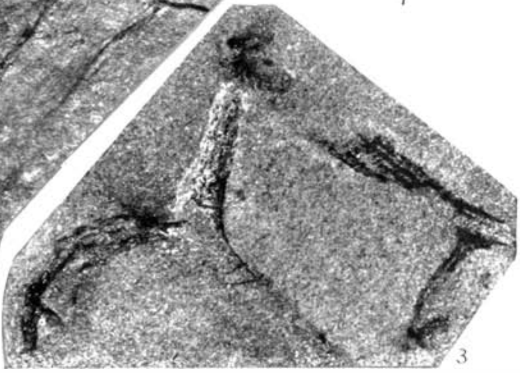
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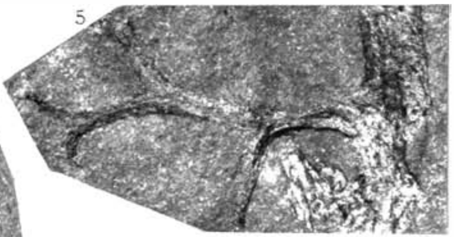
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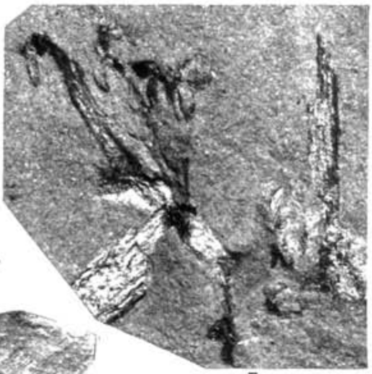
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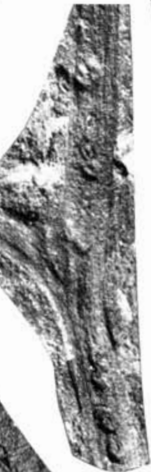
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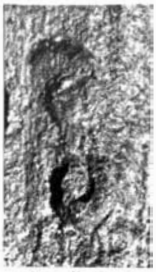
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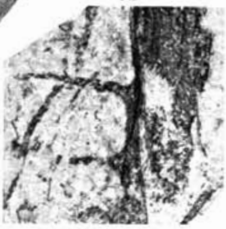
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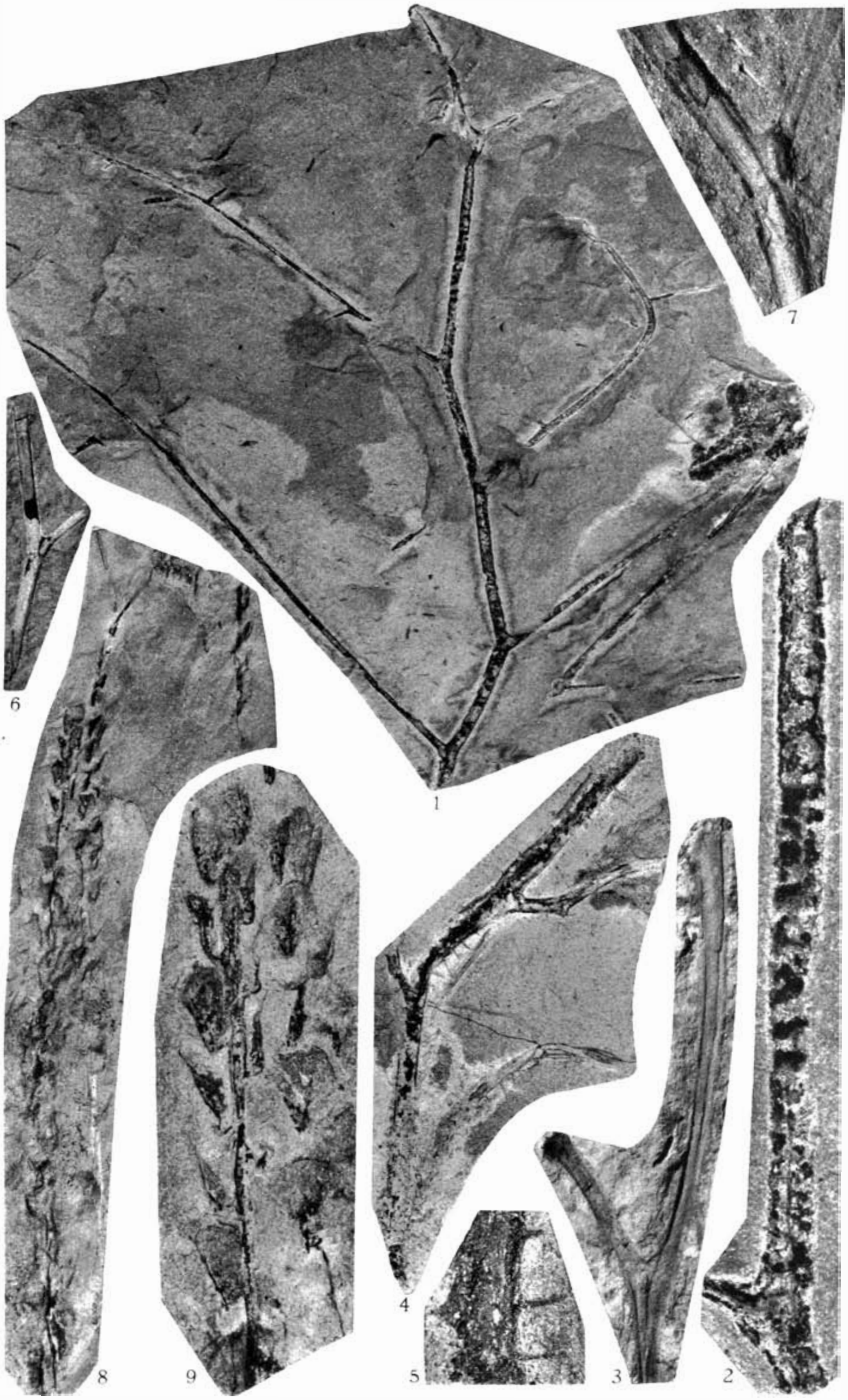
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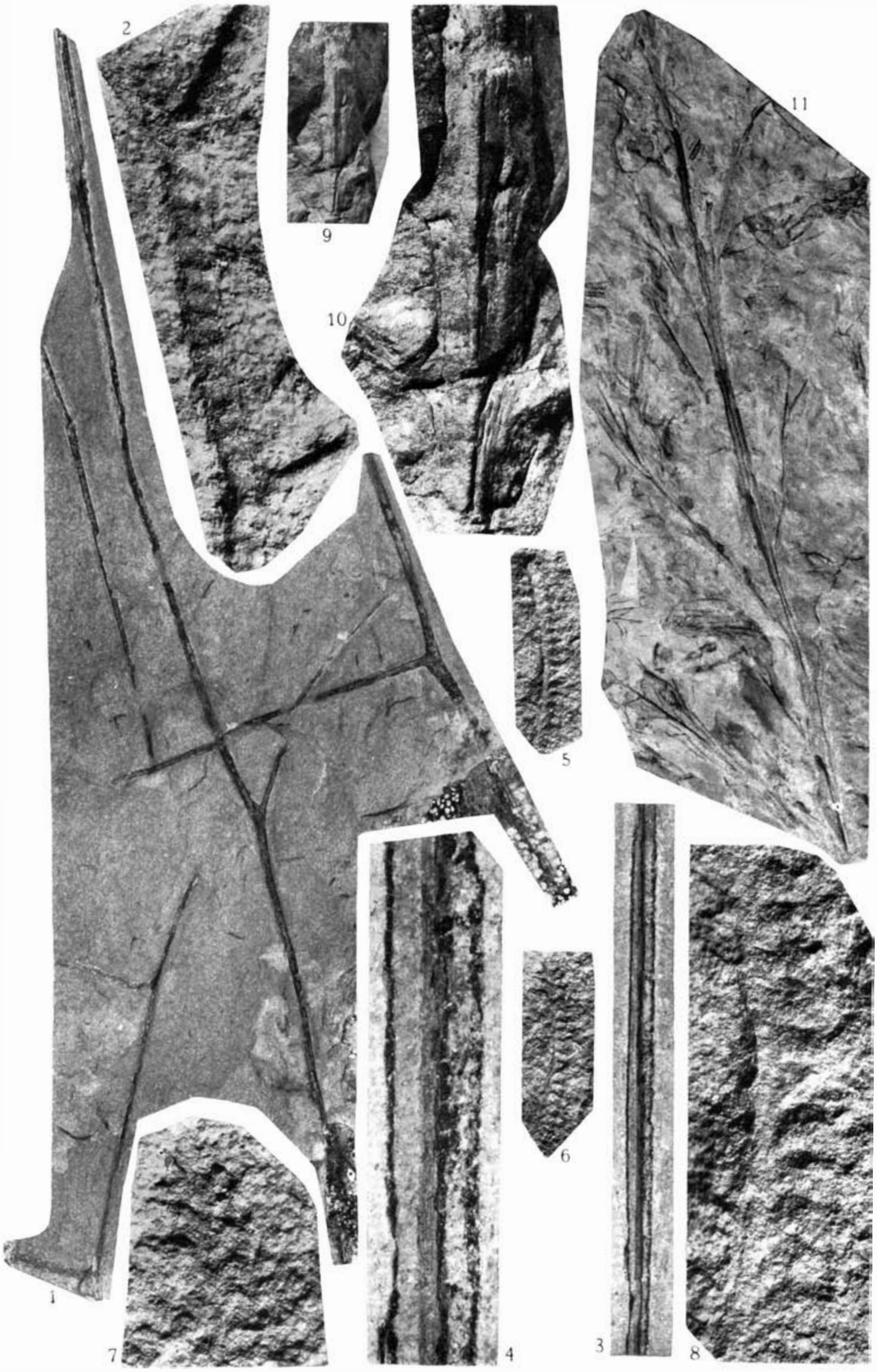
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Plate XXI

Plate XXII

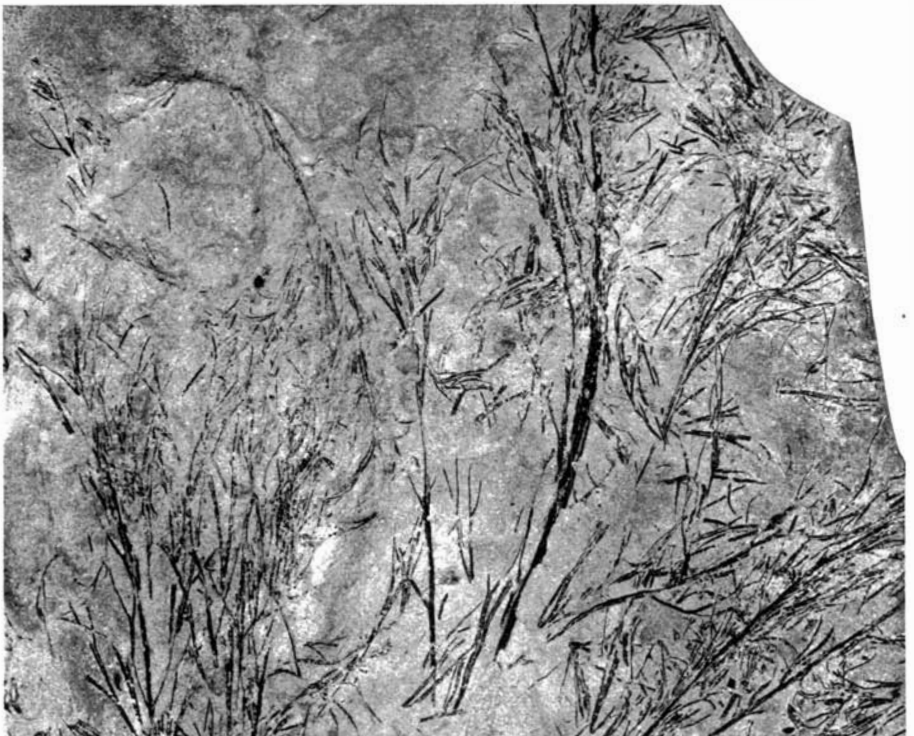


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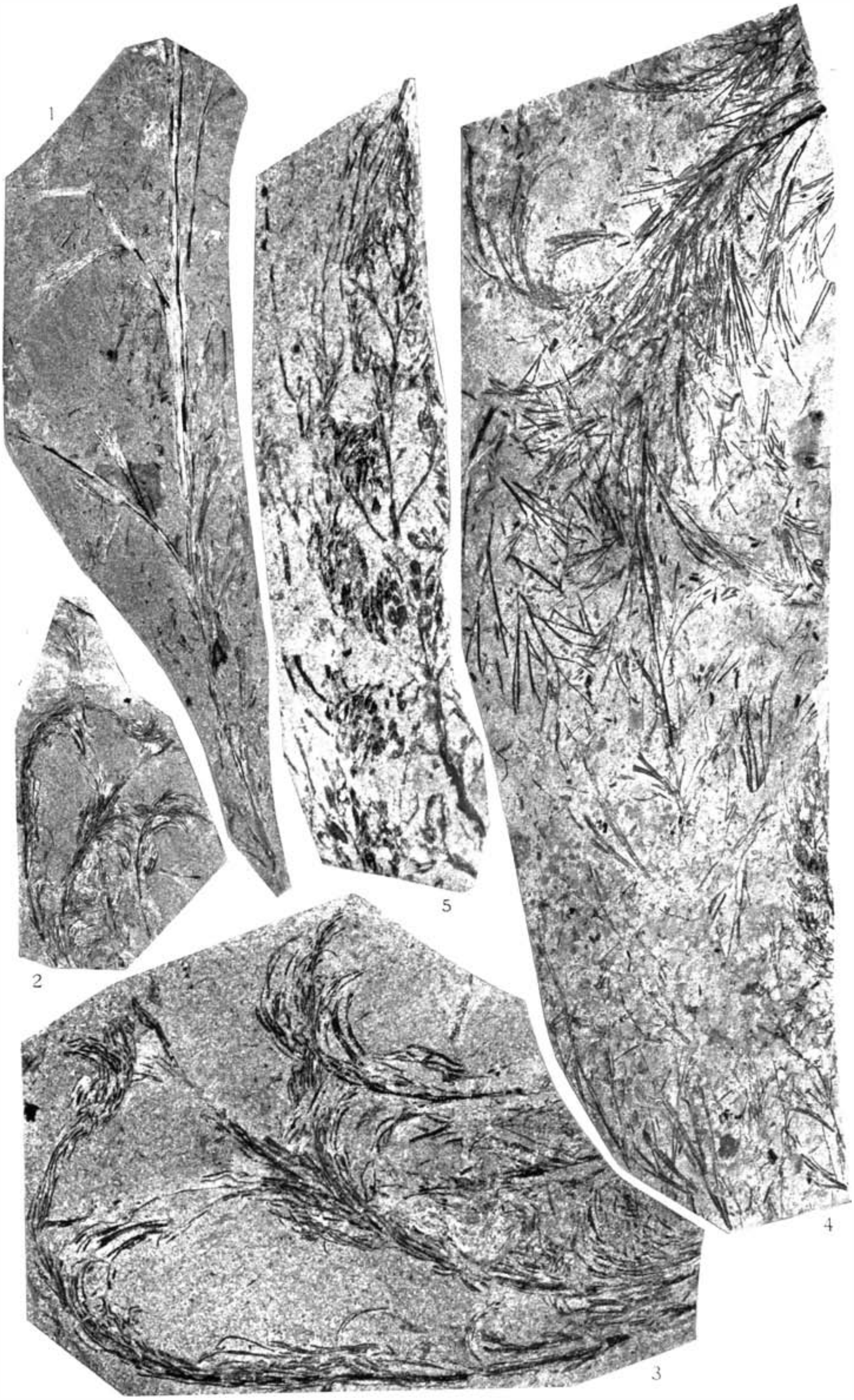
Plate XXVII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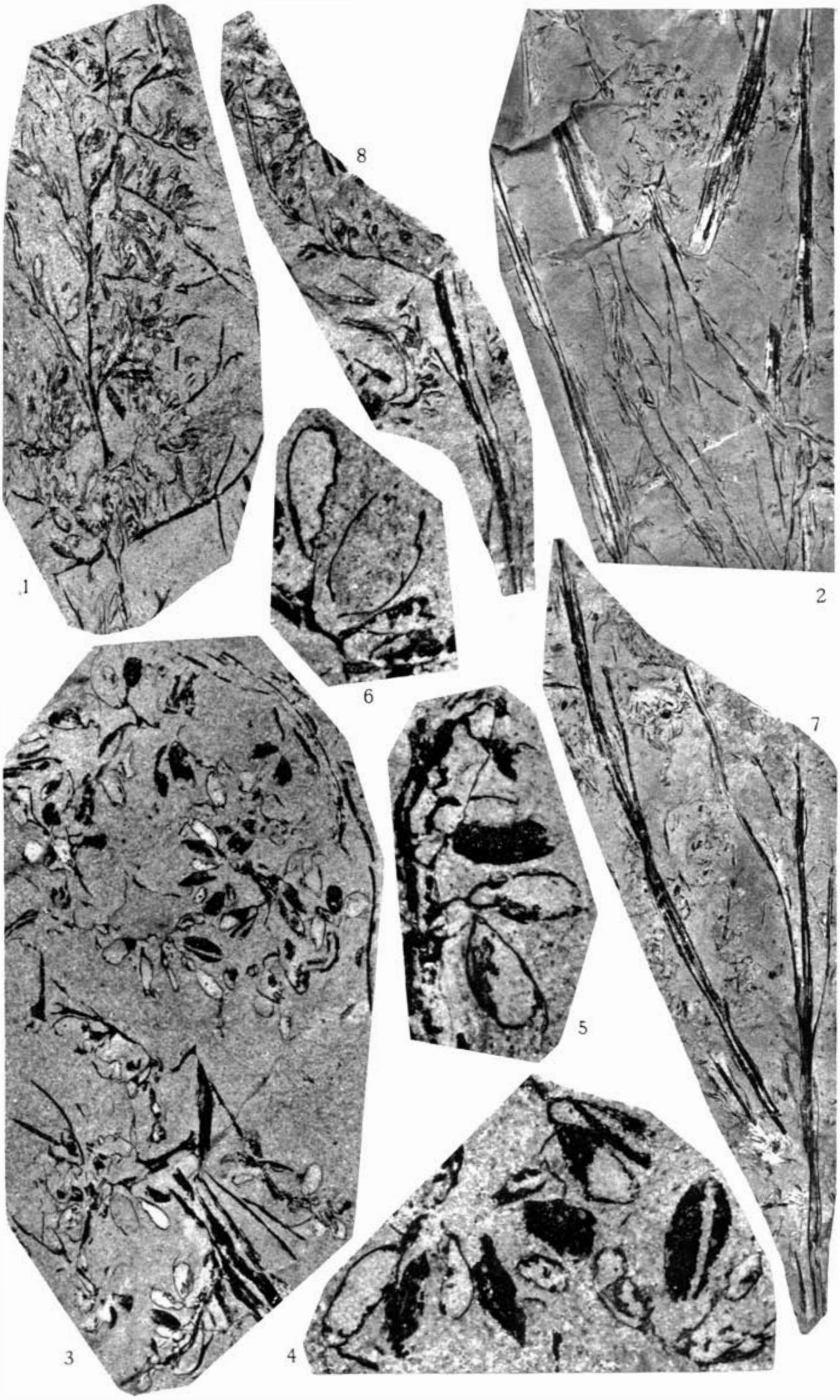
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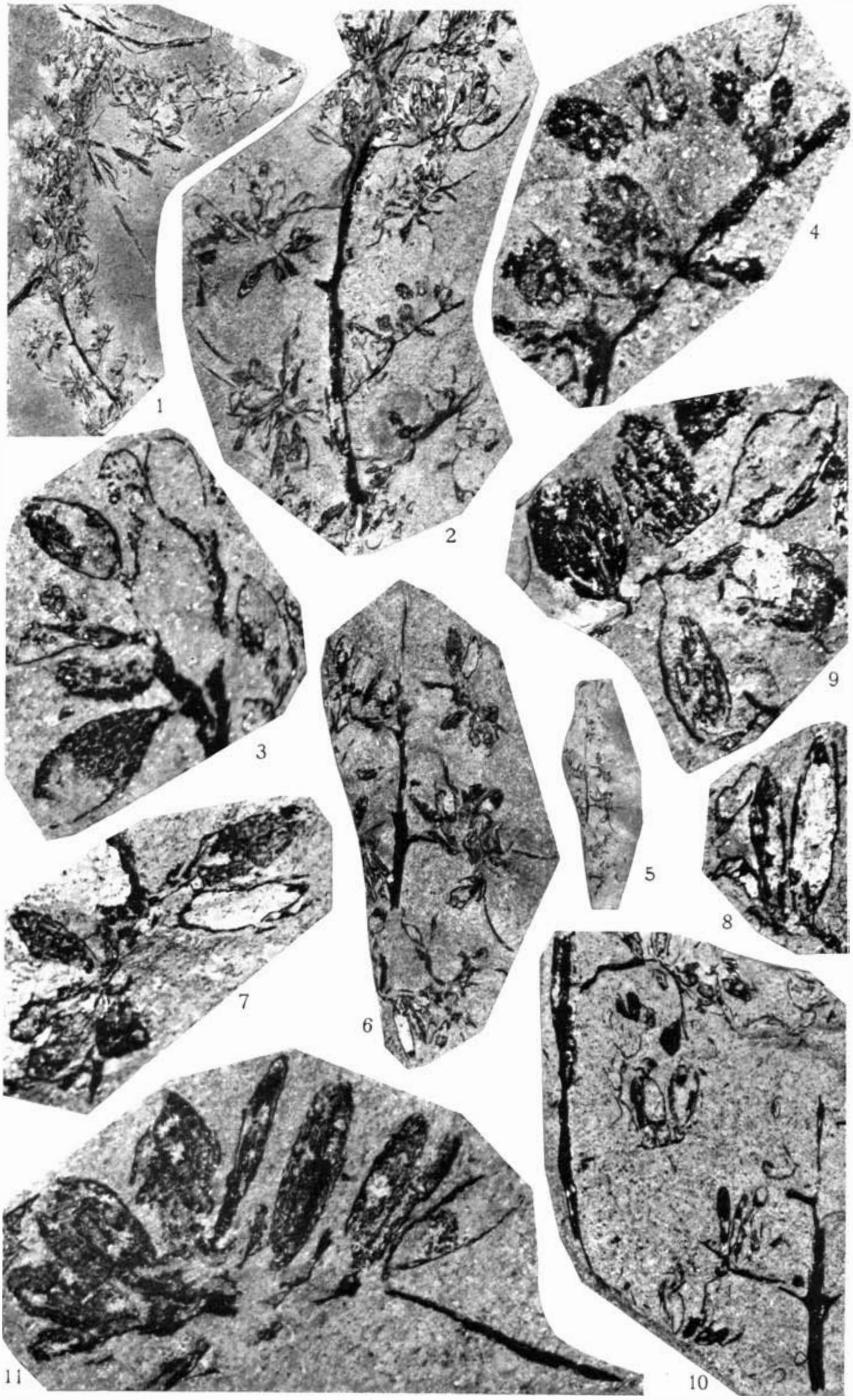
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Plate XXXI


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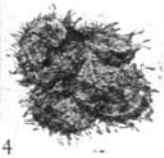
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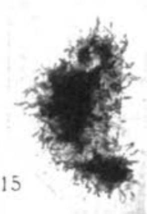
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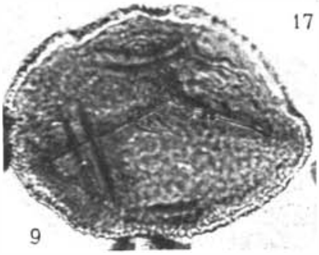
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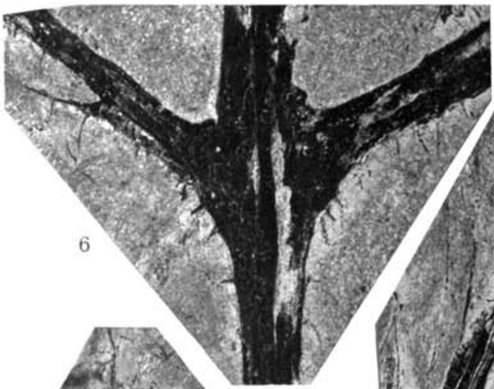
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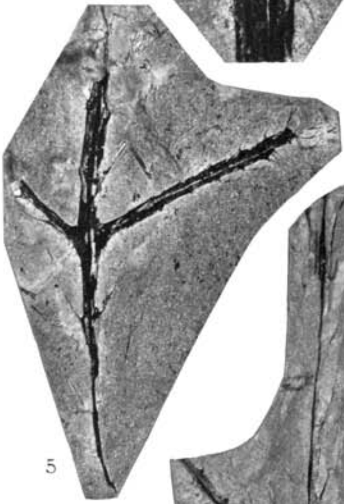
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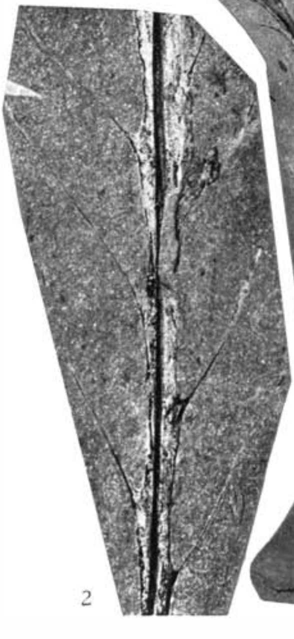
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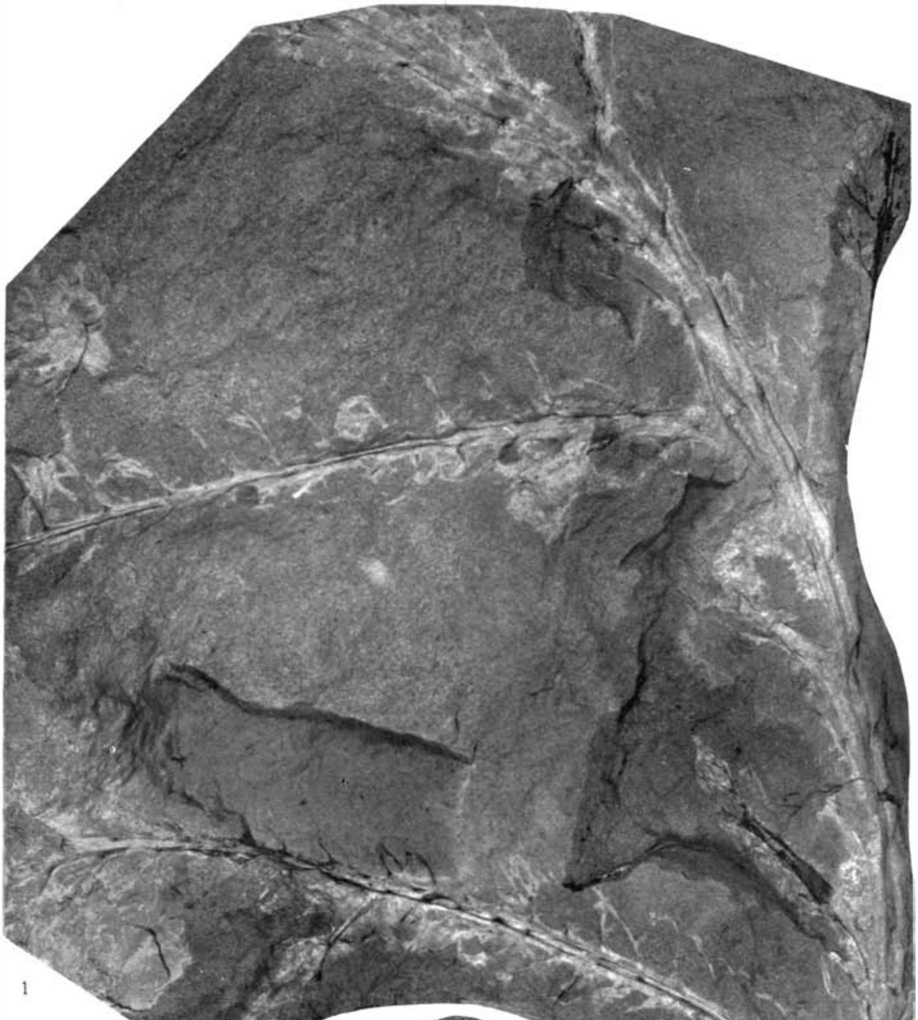

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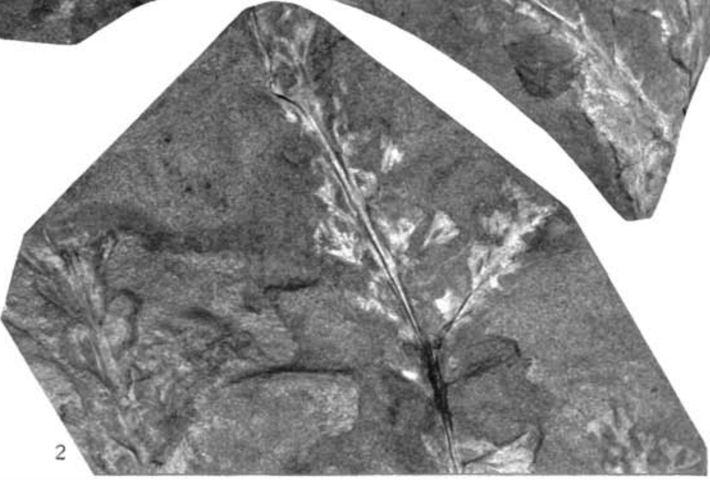

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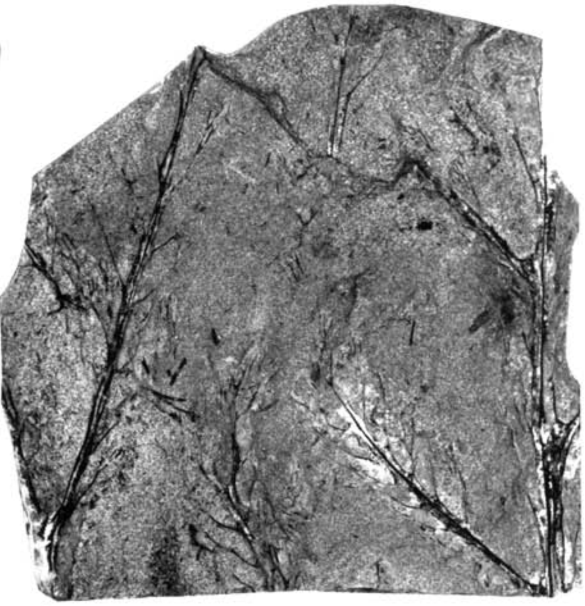

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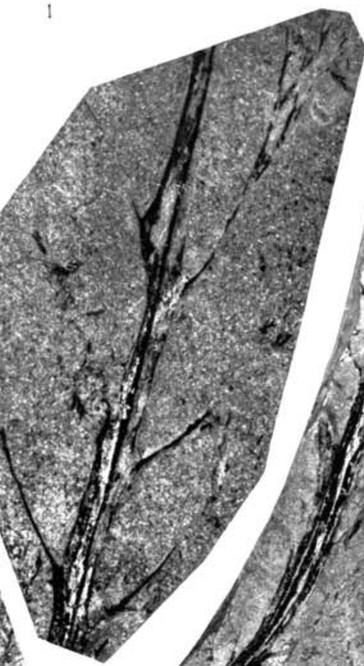

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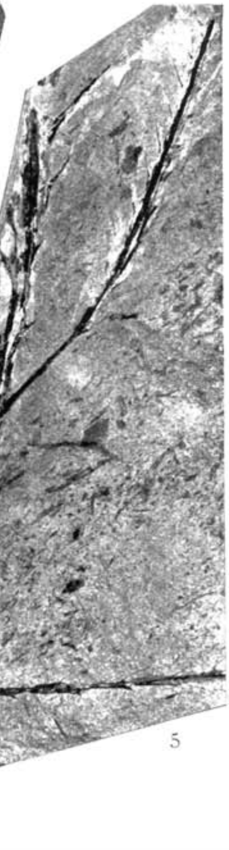

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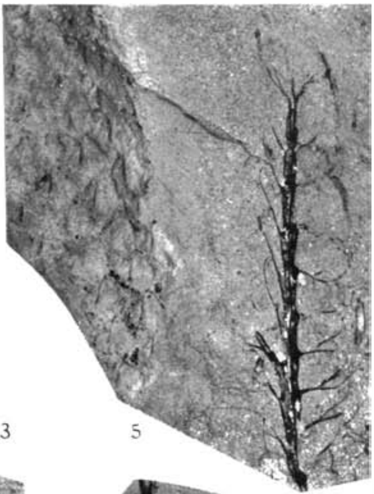
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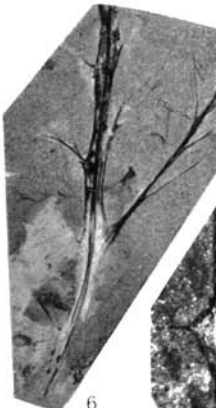
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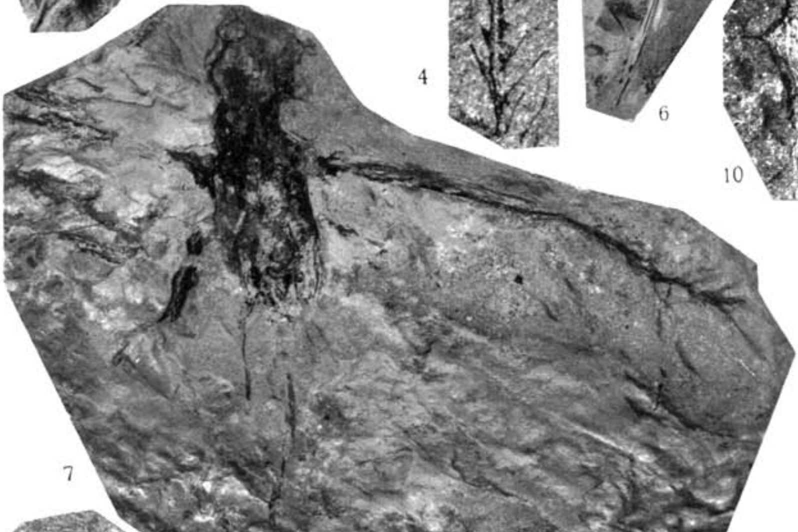
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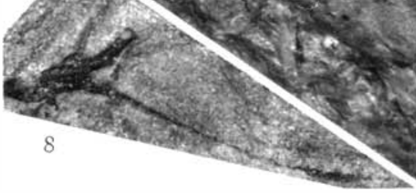
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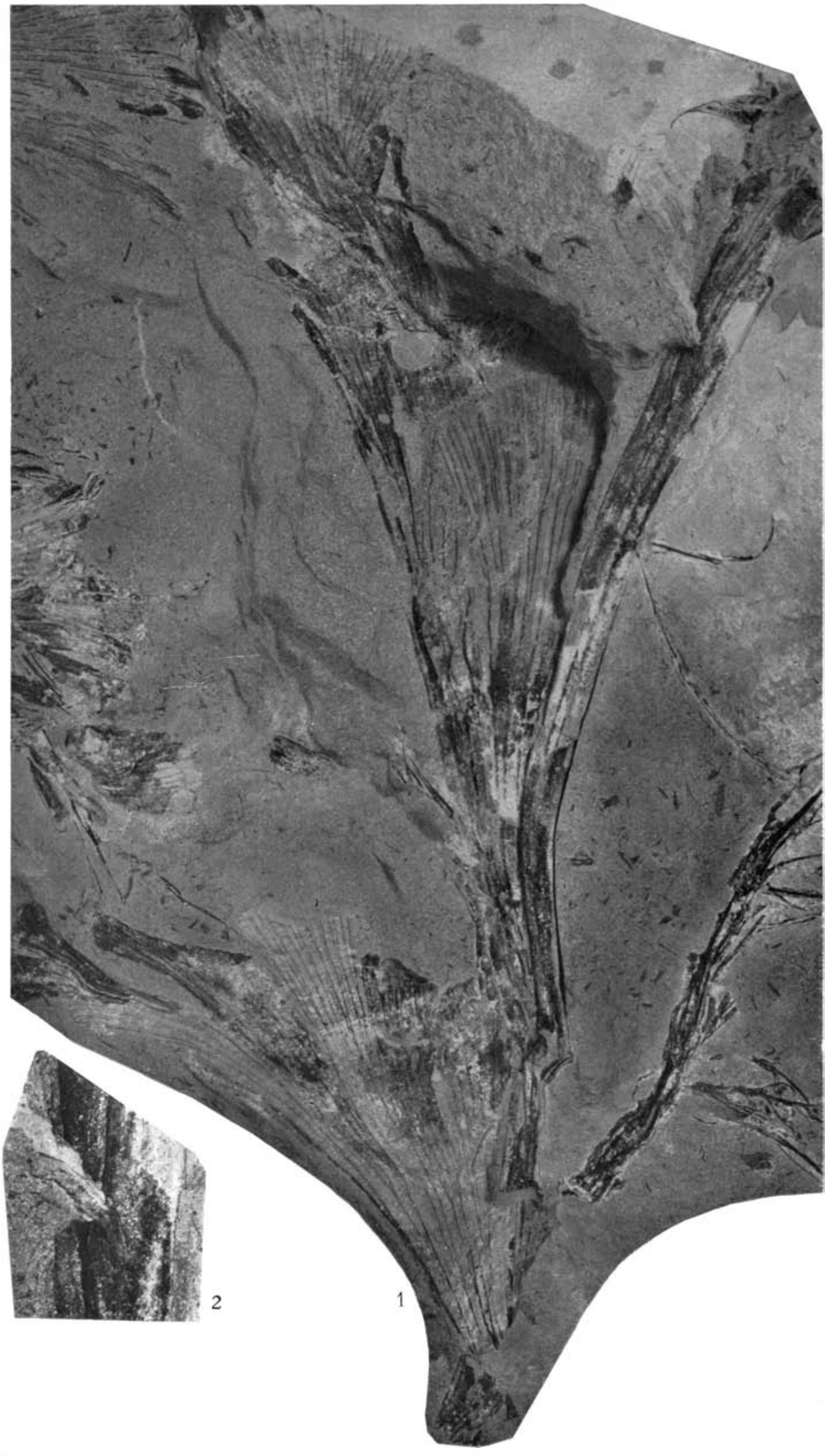

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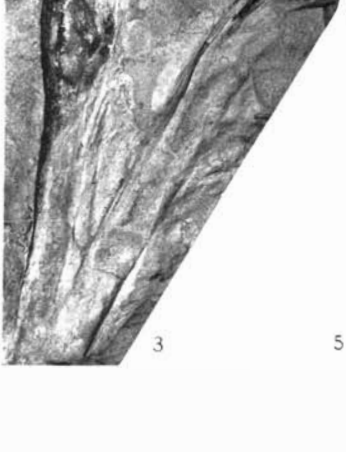
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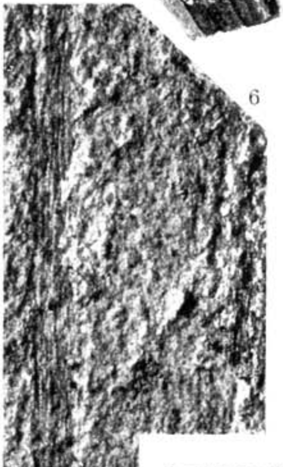
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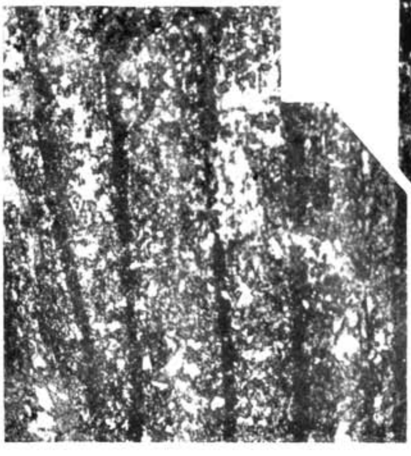
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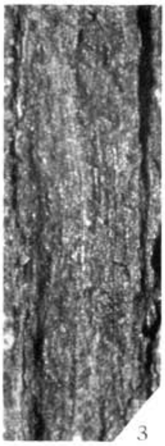
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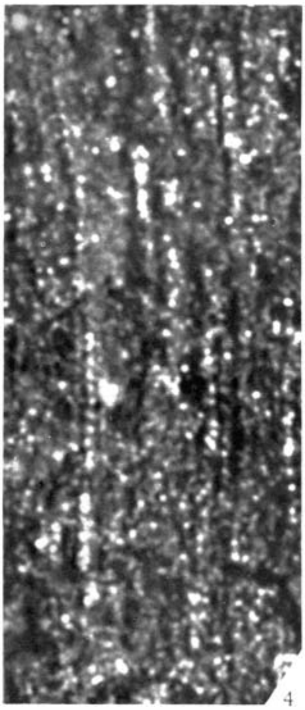
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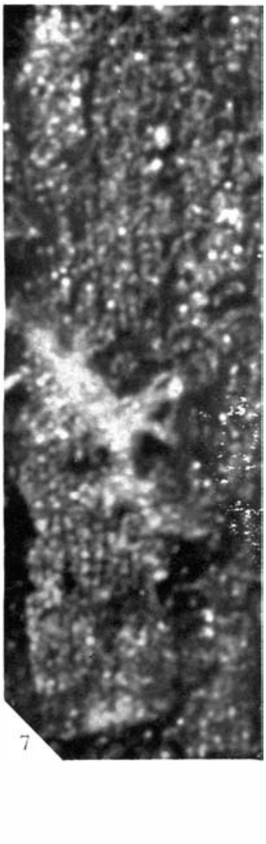
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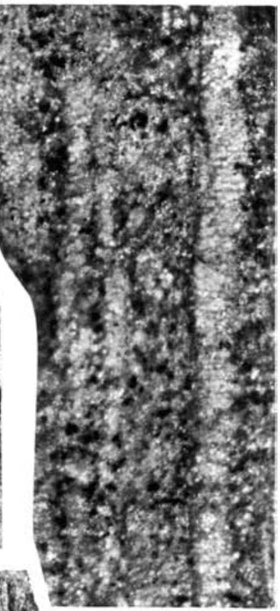
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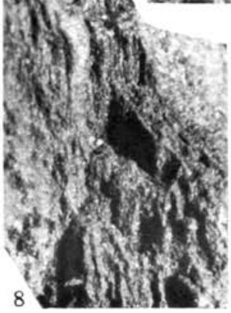
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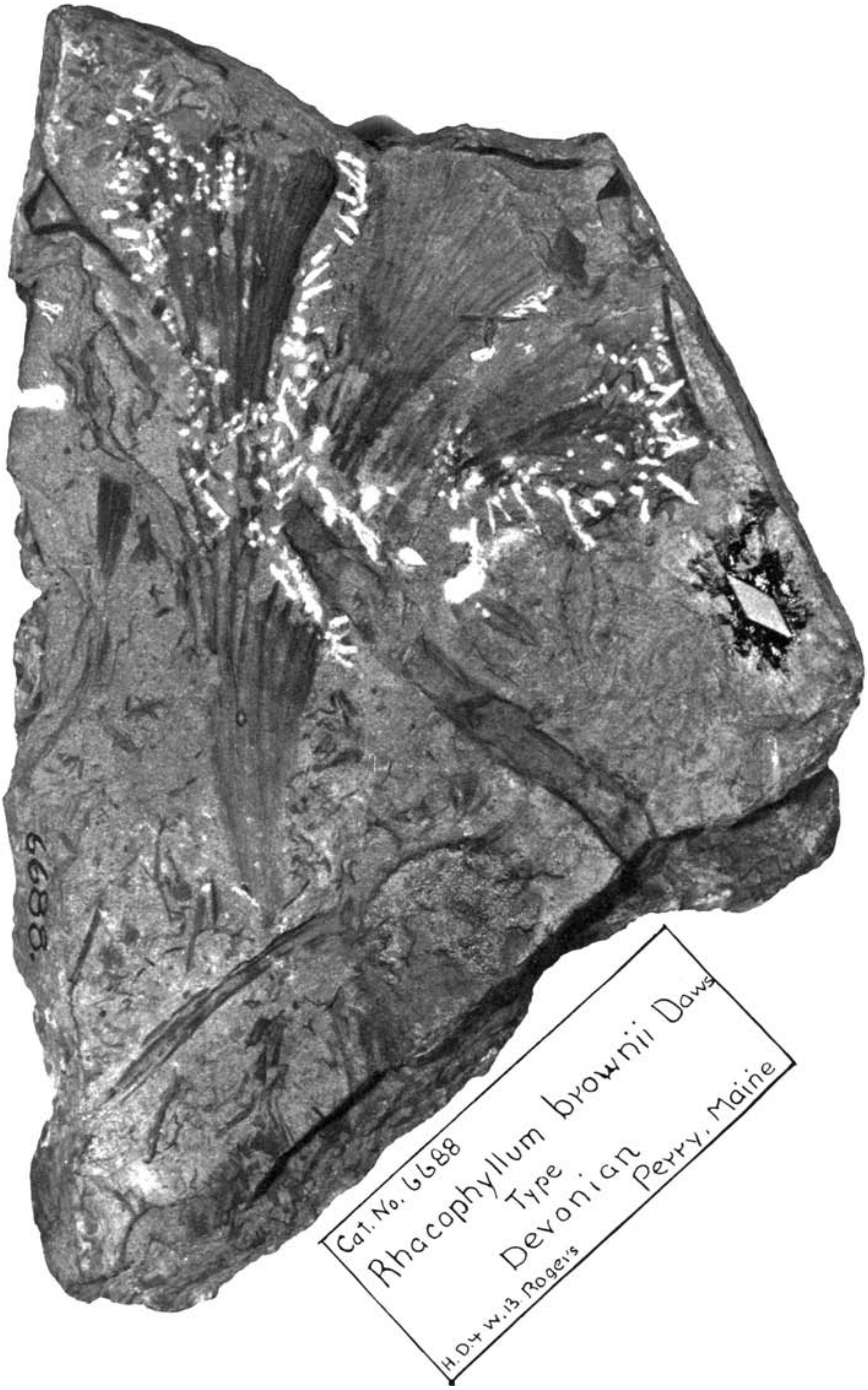
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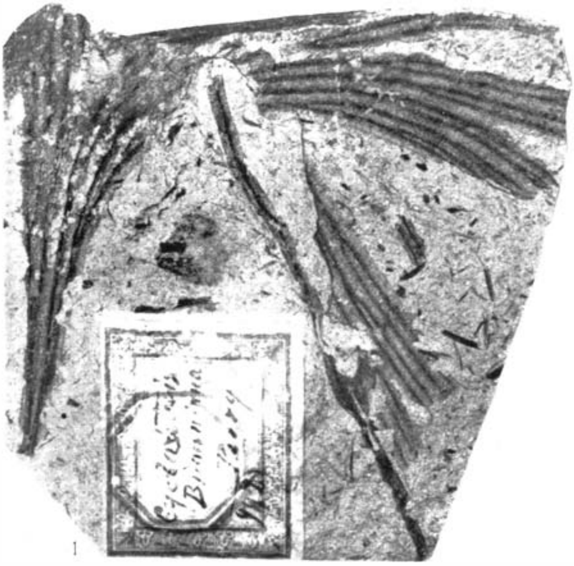
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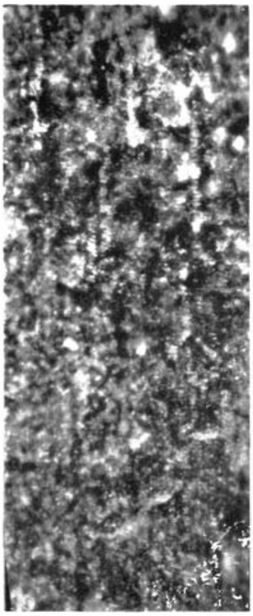
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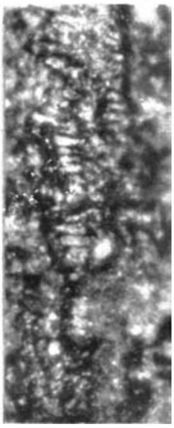
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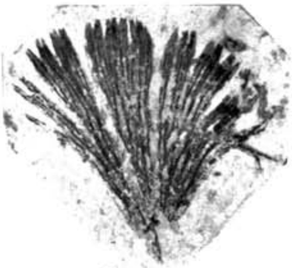

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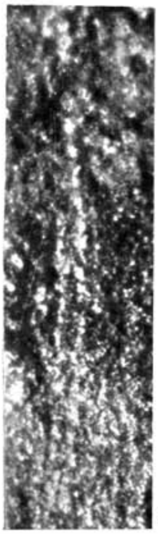

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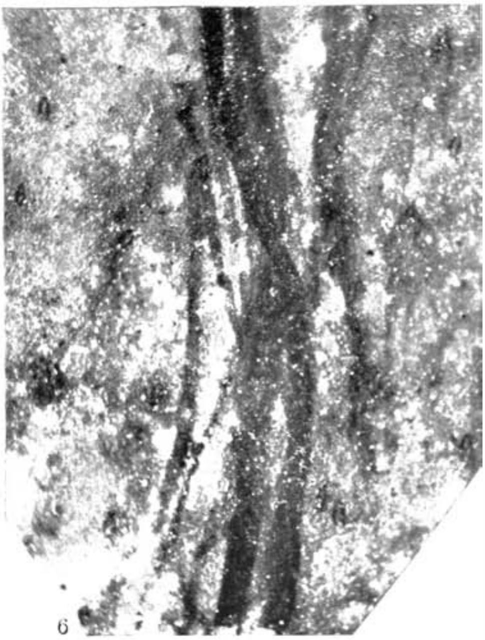

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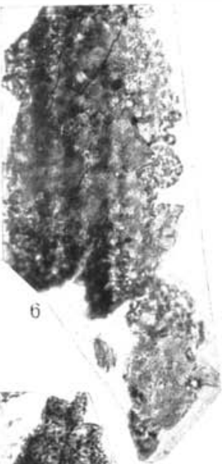
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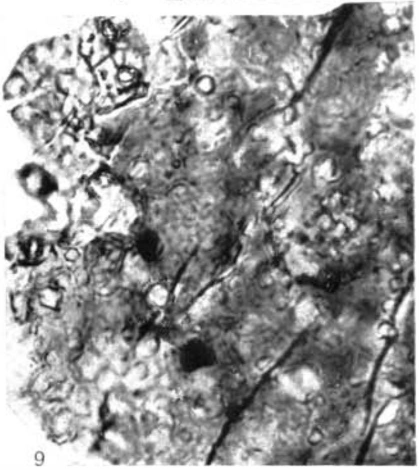
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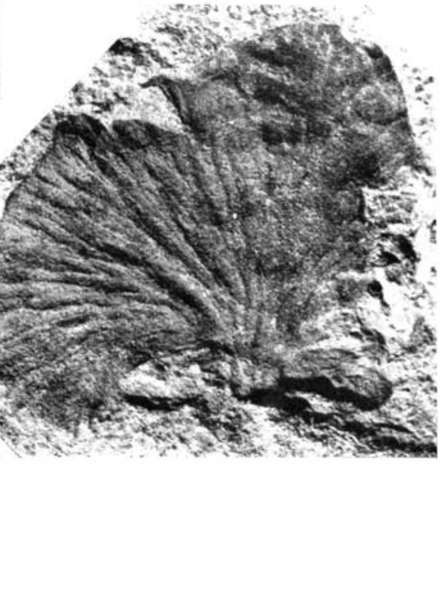
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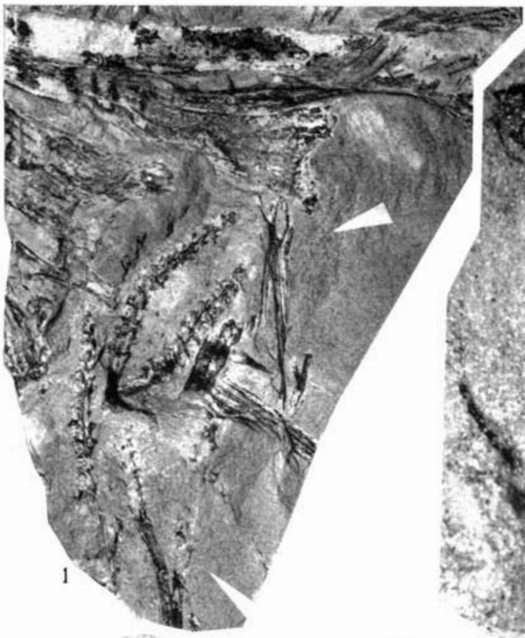
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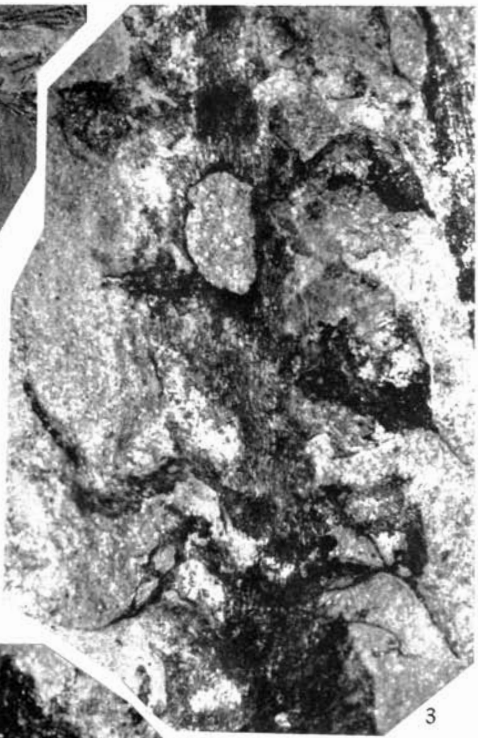
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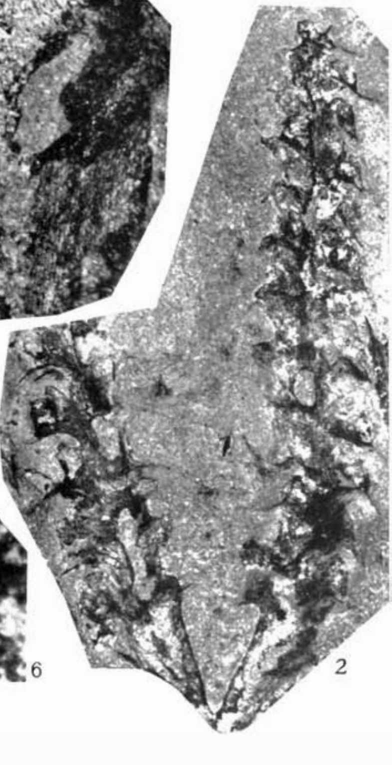
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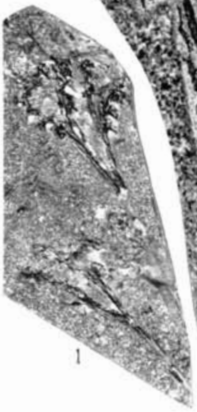
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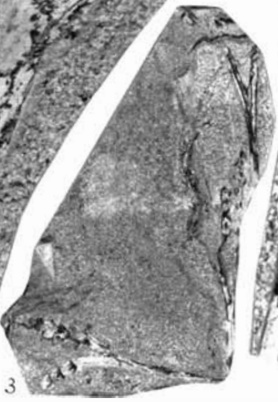
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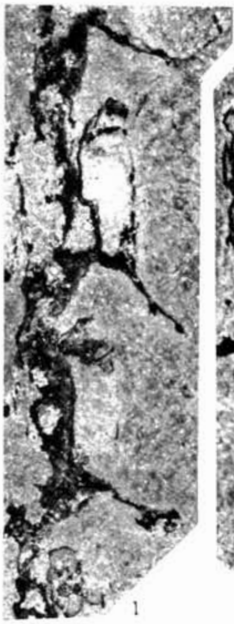
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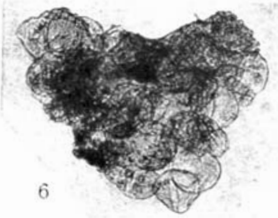
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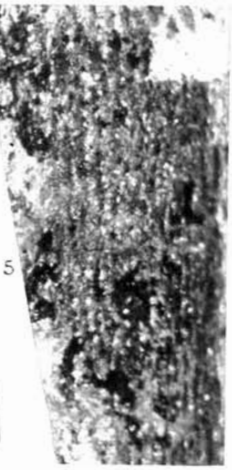
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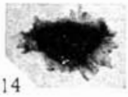
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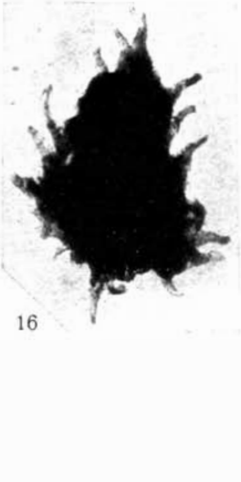
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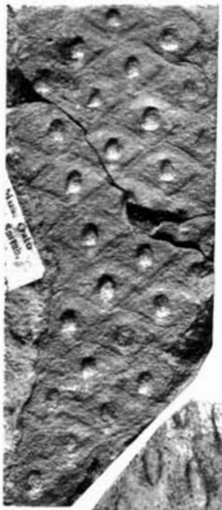
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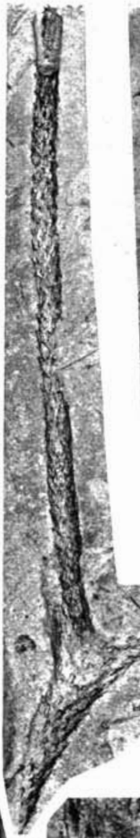
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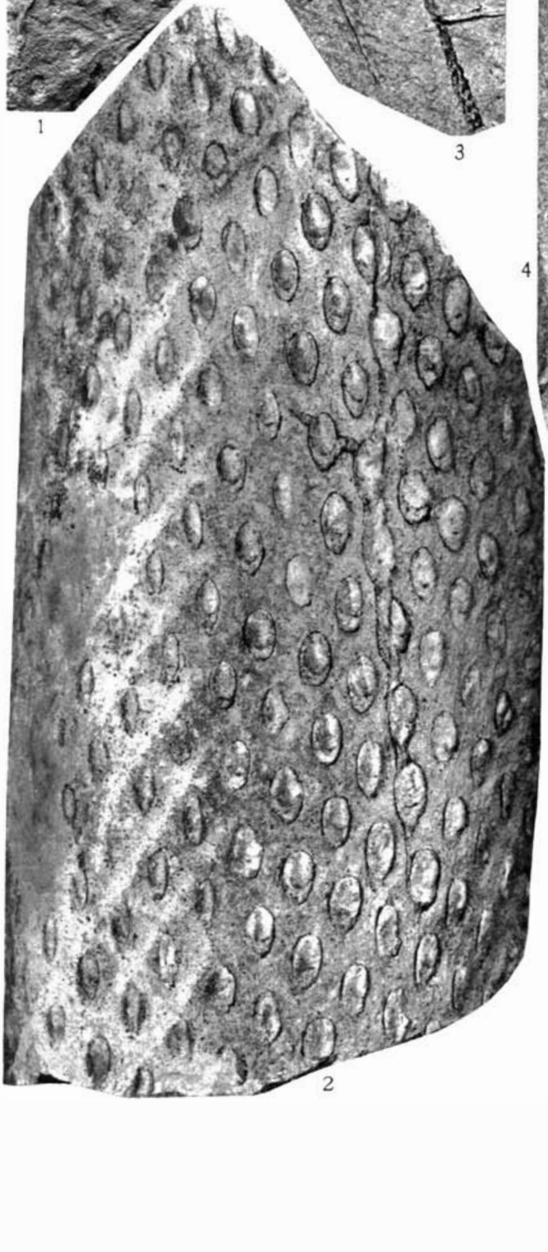
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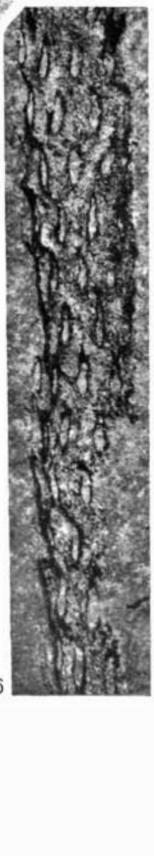
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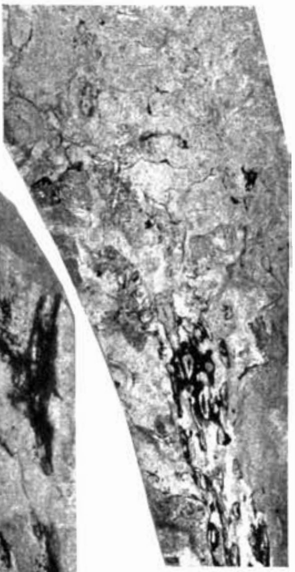
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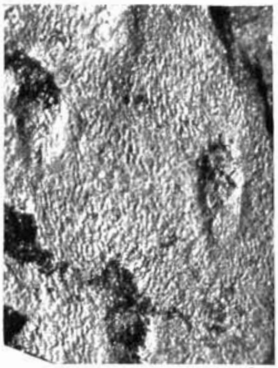
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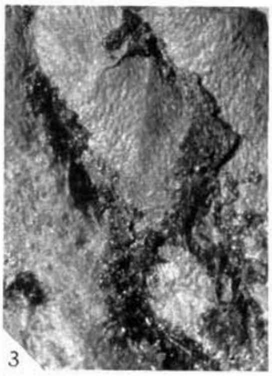
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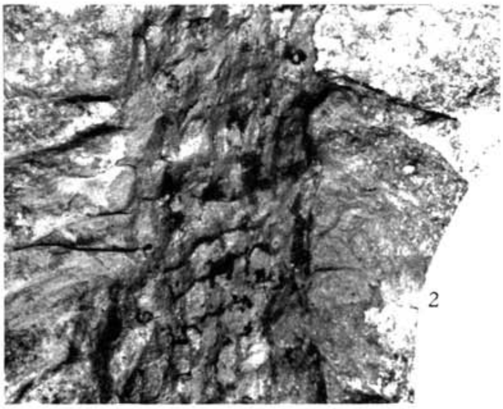
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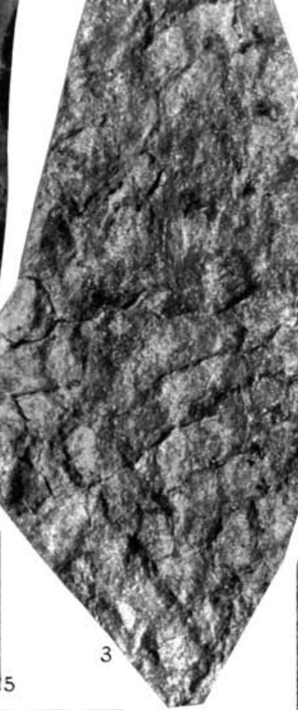
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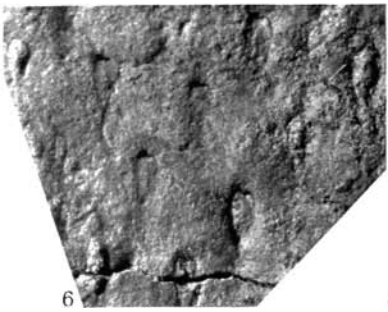
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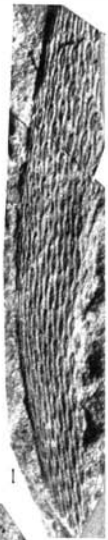
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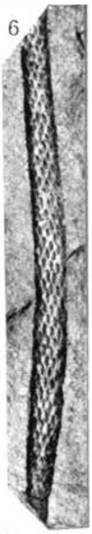
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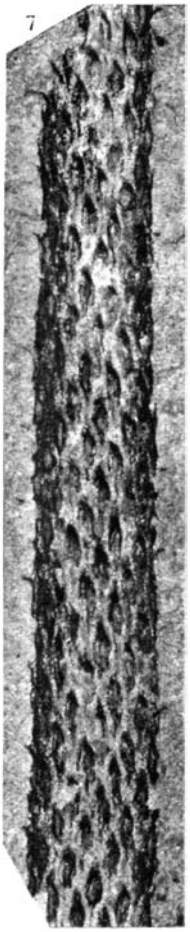
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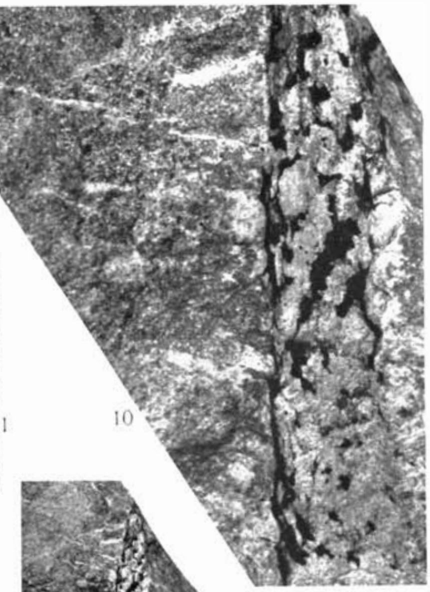
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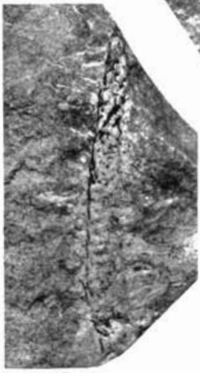
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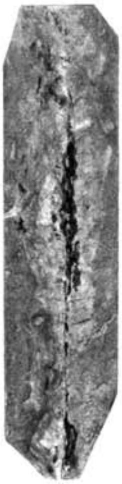
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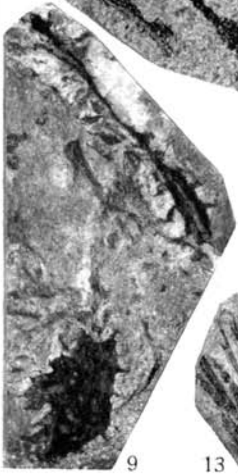
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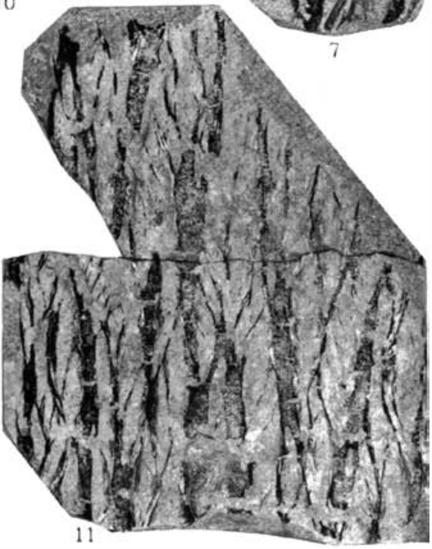
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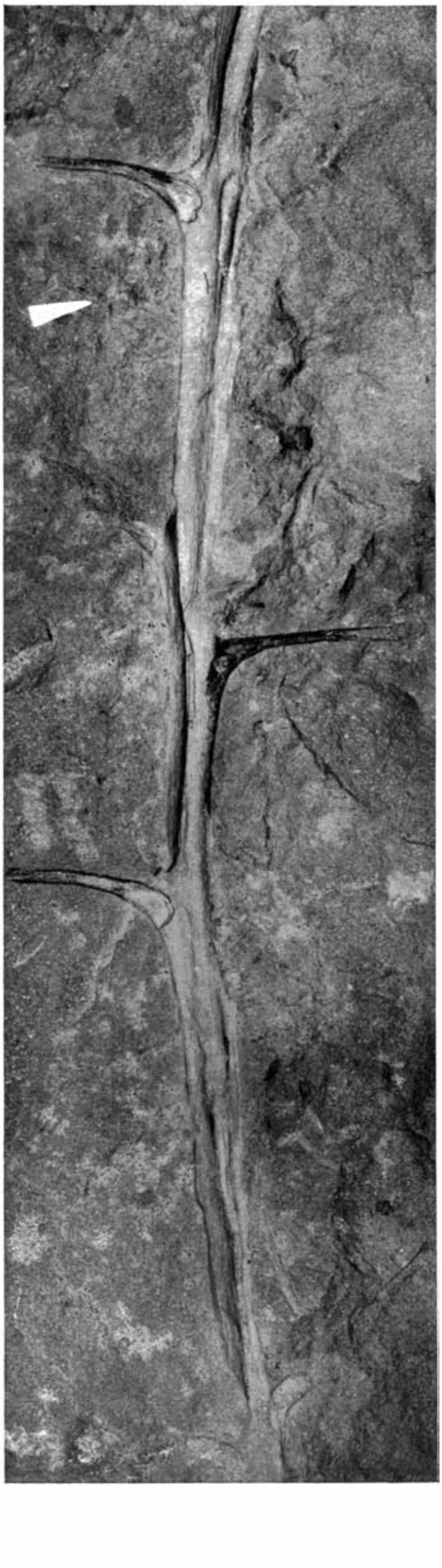

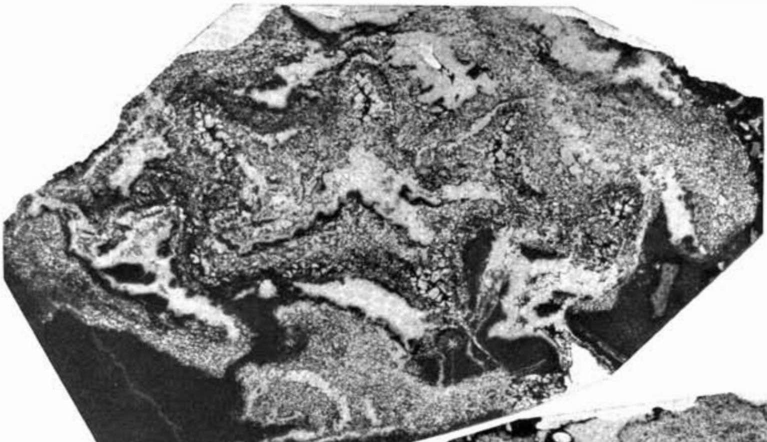
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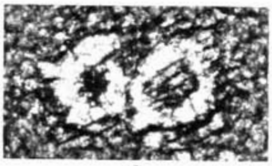
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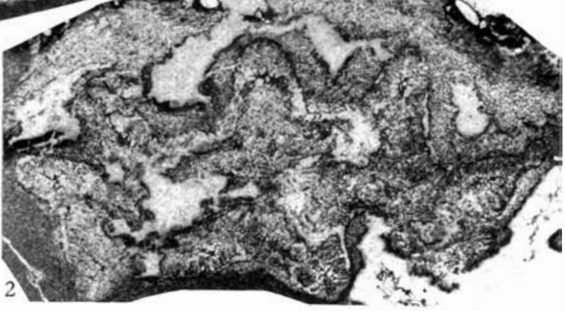
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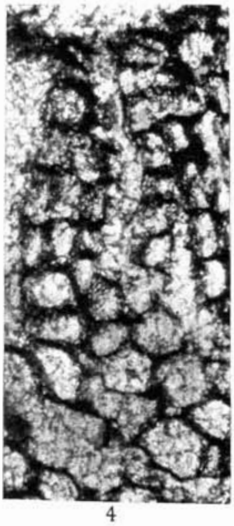
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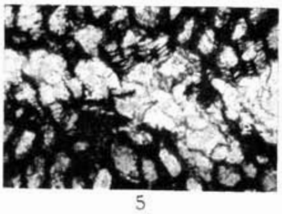
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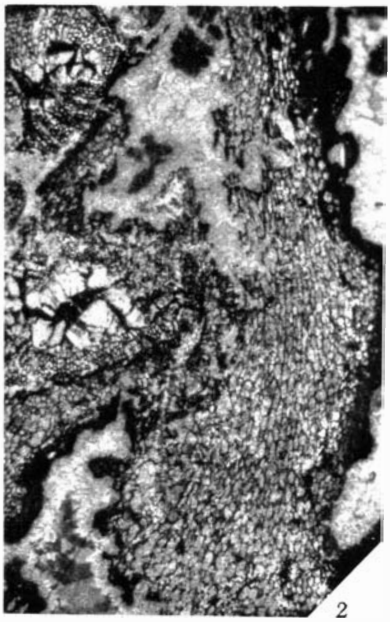

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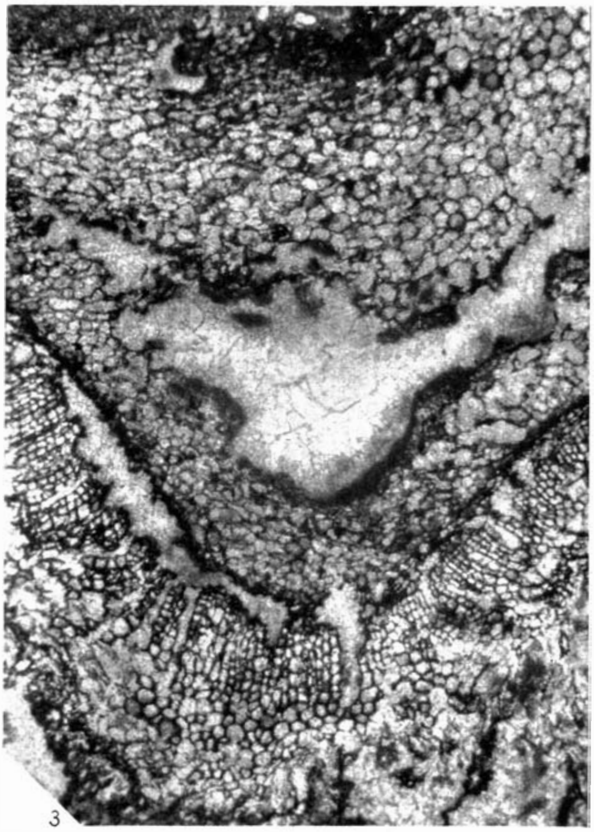

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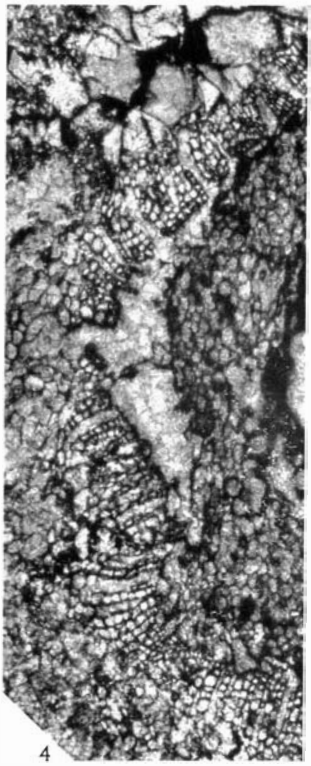

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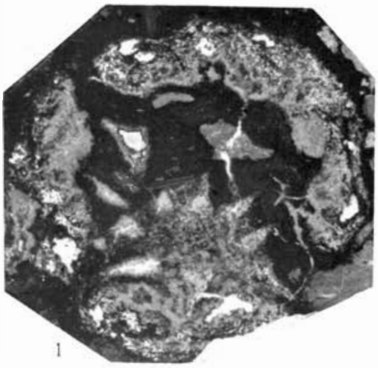
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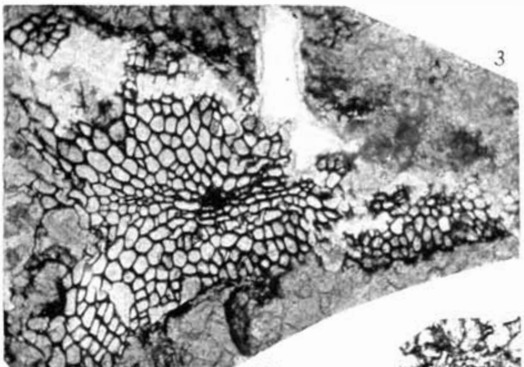
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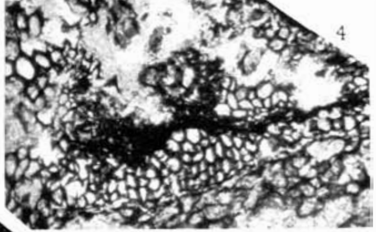
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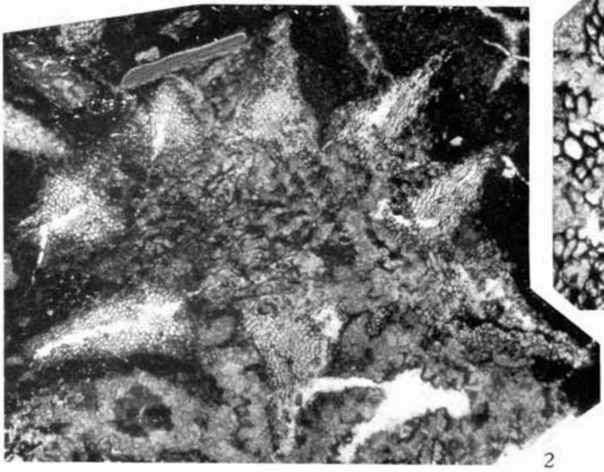
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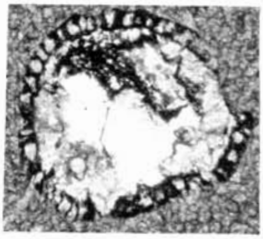
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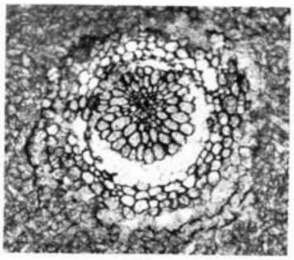
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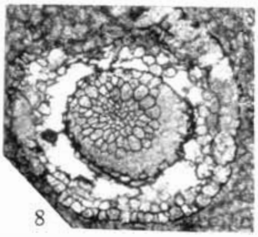
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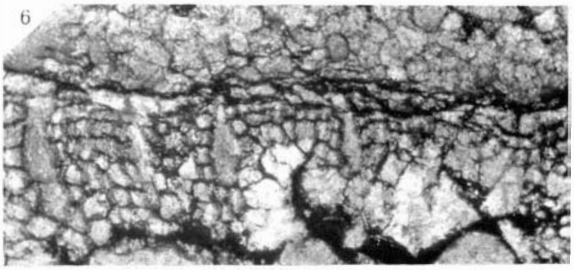
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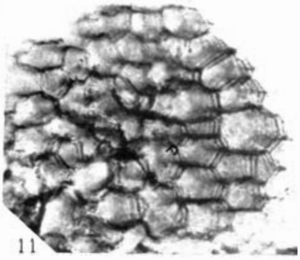
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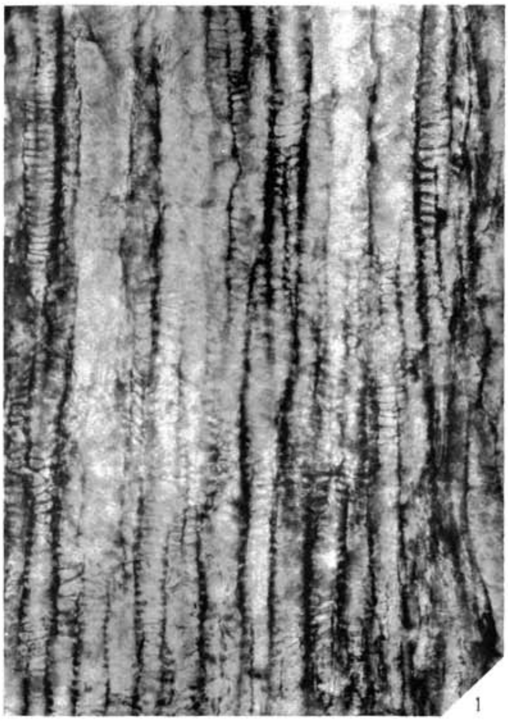

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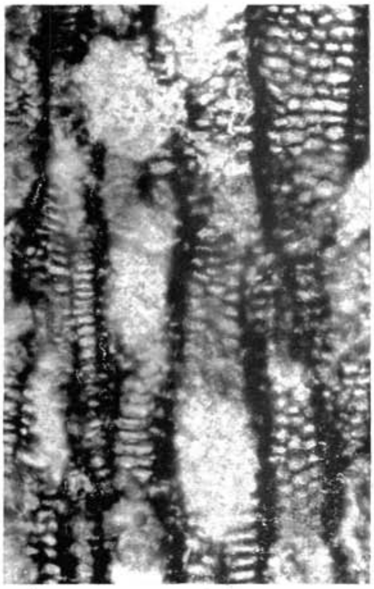

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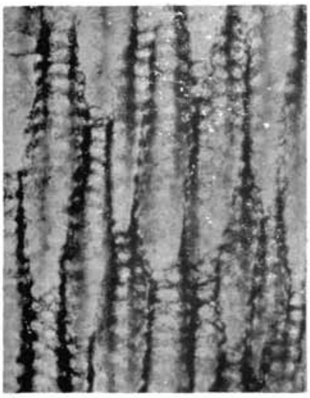

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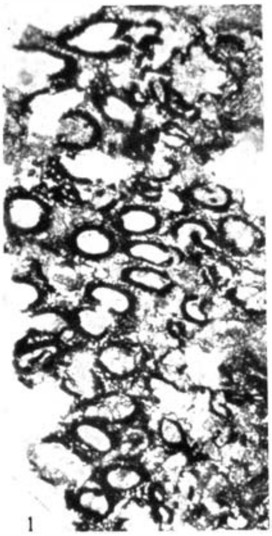
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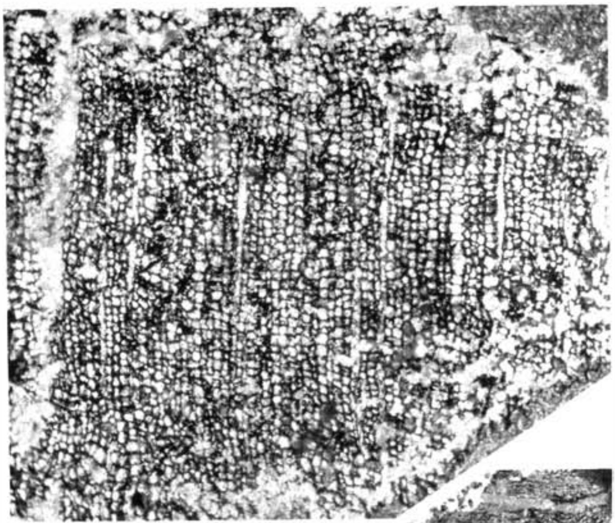
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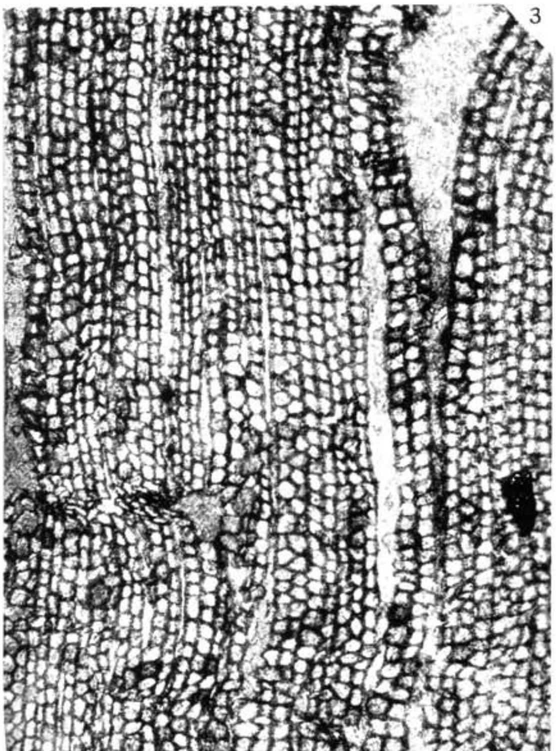
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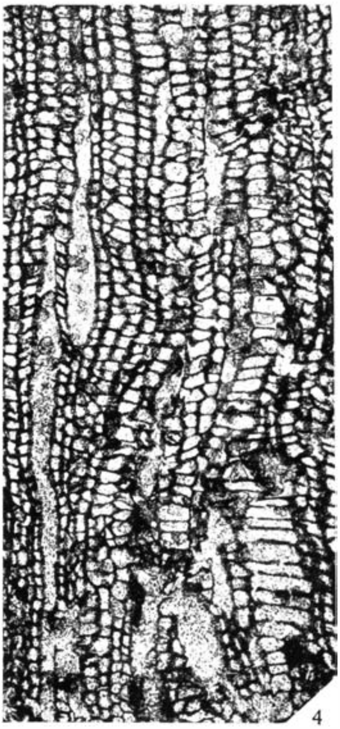
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Charts:

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