SCIADOPITYTES VARIABILIS N.SP. FROM THE ARCTIC OF CANADA

BY

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Abstract. *Sciadopitytes variabilis* n. sp. is described in considerable detail on the basis of a well preserved material of numerous detached leaves from Padloping Island, North West Territories, Arctic Canada. The age is supposed to be Lower Cretaceous. The chief interest of the new species lies in the distribution of stomata and papillae in the stomatal groove, which shows a great variation.

Introduction.

A sample of coaly shale in small pieces and weighing altogether about half a pound was sent to Professor T. M. HARRIS, the University of Reading, by Dr. WAYNE L. FRY of the Department of Mines and Technical Surveys, Canada. The material was passed on to me for examination. The collection was made by Mr. D. J. KIDD of the Arctic Institute in 1953 from the coal seams of Padloping Island on the north side of Cumberland Peninsula, Baffin Island. The age of these beds is supposed to be Lower Cretaceous.

Embedded in these shales were found a large number of compressed *Sciadopitytes* leaves. The leaves could be detached from the rock by ordinary water maceration. Thus separated they were fairly thick, brittle and black in colour. For microscopic examination they were treated with nitric acid. When treated with Schulze's mixture or even with concentrated nitric acid they behaved differently from the cuticle of most other fossil plants. They turned brown and extremely brittle. Such brittle leaves became very slimy when treated with even dilute alkali and in most of the cases the stomatal groove separated from the leaves, dividing the lower side into two. I therefore found it better to replace the concentrated nitric acid by dilute nitric acid (50 %) and, when the maceration was complete, to treat the leaves with very dilute ammonia. The best result, however, was obtained by boiling the leaves for an hour or so in 15 % hydrogen peroxide. When the leaves assumed a brownish yellow colour they were treated with nitric acid (50 %) till the maceration was fully complete. Finally they were treated with dilute ammonia.

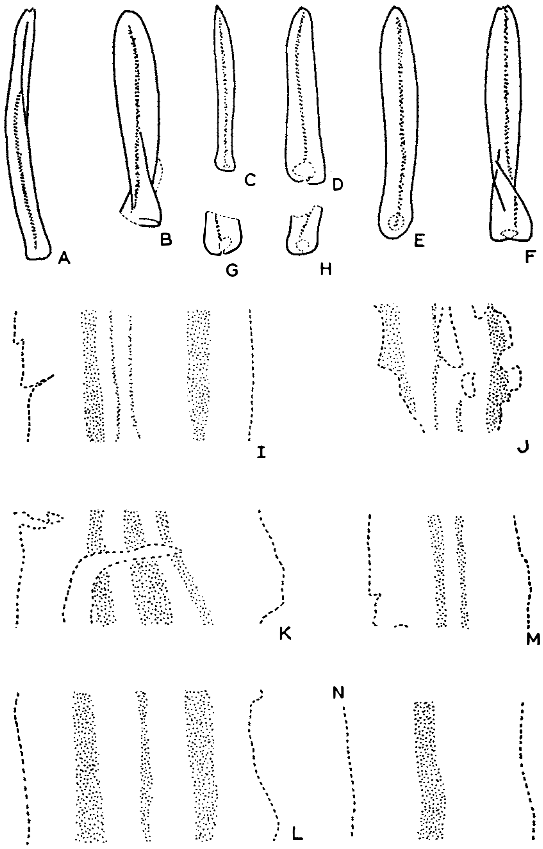
An attempt was made to find out the number and position of veins. In such cases a few leaves were made translucent (or slightly opaque) by boiling with hydrogen peroxide. Then they were washed and mounted with a thick coating of Canada balsam. The slides were examined under strong red light. In some cases, then, the position of the veins could be made out. A better result was obtained by taking photographs in infra-red light. In none of the cases veins were actually seen, but their position could be marked out in few instances.

Besides the maceration of the detached leaves, a few pieces of shale were macerated in bulk with strong nitric acid. In this the majority of the *Sciadopitytes* leaves were destroyed. The maceration, however, yielded minute pieces of cuticles belonging to other plants and quite a good number of pollen grains and spores. Besides the leaves of *Sciadopitytes* only *Sciadopitys*-like pollen grains and a few cone-scales have been described in the present paper. The other microflora isolated will form the subject of a second paper.

Description.

LEAVES

Linear leaves of conifer-like habit, typically 12—15 mm long (range noted 6—24 mm). Fairly thick, oval or circular in cross-section. When dorsiventrally flattened typically 2—2·5 mm broad (range noted 1—4 mm). Apex acute or obtuse. Base swollen. A little above the base the leaf is slightly narrow and often twisted (in fossil condition). Petiole absent. Mode of attachment to the stem unknown. The area of attachment to the stem represented by an oval or circular opening at the base. Sometimes the area of attachment lies a little above the base on the upper side (Text-fig. 1, G—H). On the lower



Text-fig. 1.

A—F detached leaves Nos. 6702.8, 6702.1, 6702.9—12. In all these torn margins and the area of attachment at the base are shown by broken lines. x 2.

G—H bases of two leaves showing the area of attachment (shown by broken lines). No. 6702.13. x 2.

I—J portions of stomatal groove with four stomatal bands. Nos. 6702.14—15 In these and other stippled area shows the position of the bands and the broken lines indicate torn margins. x 10.

K—L stomatal grooves with three stomatal bands. Nos. 6702.16, 6702.2. x 10.

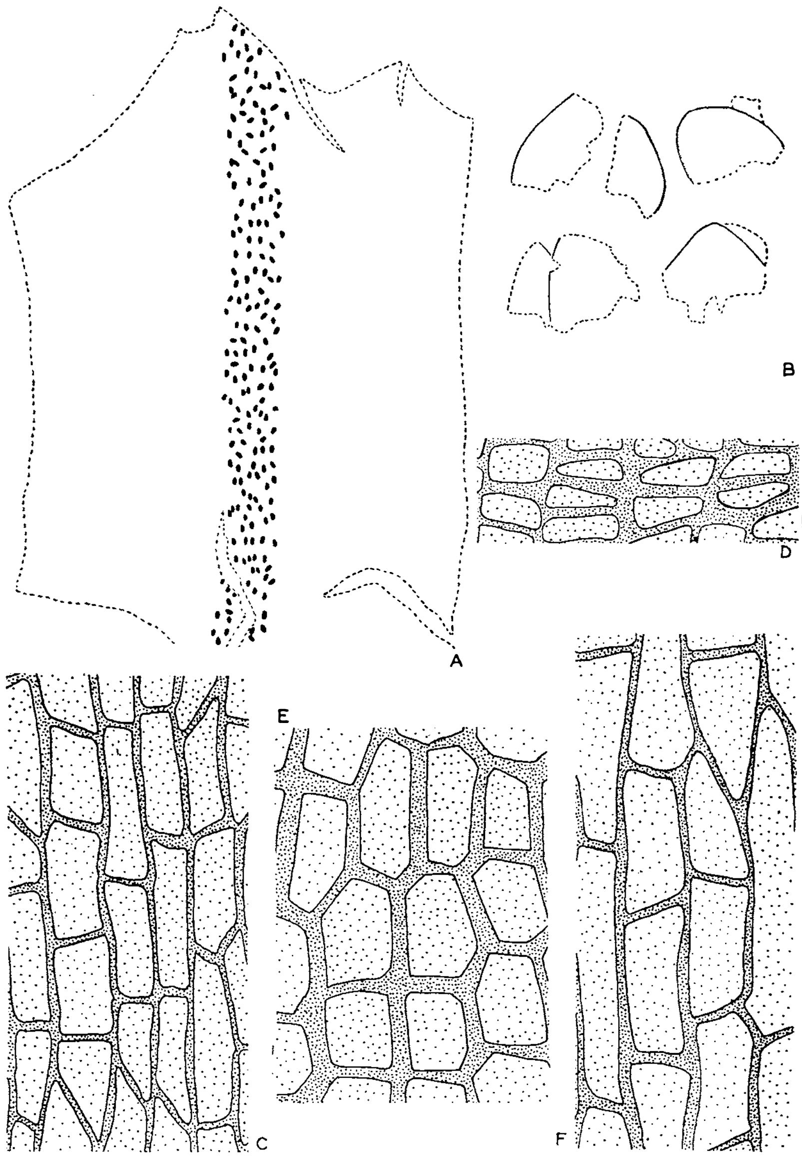
M stomatal groove with two stomatal bands. No. 6702.17. x 10.

N stomatal groove with scattered stomata and without any stomatal band. No. 6702.18. x 10.

side there is a median groove almost reaching the base and the tip but never touching them. In very rare cases the groove goes up to the tip. Veins two, one on each side of the groove, fairly thick.

Cuticle thick, about 6 μ, on both sides, except in the groove on the lower side where it is fairly thin. Stomata occurring only on the lower side in a well developed median dorsal groove. In most cases the groove is widened inwards as in *Sciadopitytes Crameri* (Heer) Halle (1915) and the stomata inside the groove are protected by papillae in the same way, except that in the present case often even the ordinary epidermal cells inside the groove are also provided with papillae. Width of the stomatal groove varying. In most of the leaves the stomata are irregularly scattered, not forming longitudinal rows or files. Sometimes, however, inside the groove the stomata are placed in definite bands — mostly three in number, but varying from two to four. Their arrangement inside these bands is irregular.

Epidermal cells of the upper side almost uniform in shape. They are serially arranged and are rectangular to trapezoidal in outline. Lateral and end walls very clearly marked, fairly thick and almost straight. Surface wall unspecialized. Cells near the apex mostly polygonal in shape. The cells surrounding the area of attachment rather small and rectangular. Cells on the lower side like those of the upper side, except in the median groove and a few layers of cells lying close to it. Such cells near the margins of the groove are generally rather elongated. The cuticle here and also inside the groove is thinner than on the rest of the leaf, as mentioned above. Due to this fact the stomatal groove during maceration mostly gets torn out of the leaves. Ordinary epidermal cells in the groove irregular in shape, mostly isodiametric, only sometimes rectangular. Lateral and end walls thick. Surface wall with or without papillae. Papillae mostly cylindrical or conical with rounded or pointed tips, greatly varying in shape and size. In some cases they are very well developed, in others they are feebly developed, in the form of blunt projections or only slight bulges on the surface wall. Papillae most common on the slopes of the groove. Very rarely they are altogether absent from the whole leaf. The epidermal cells separating the stomatal bands of the groove rectangular and their arrangement and shape similar to the epidermal cells lying outside the groove but slightly smaller in size and never papillate.



Text-fig. 2.

A stomatal groove with stomata in actual position and orientation. No. 6702.18. x 25.

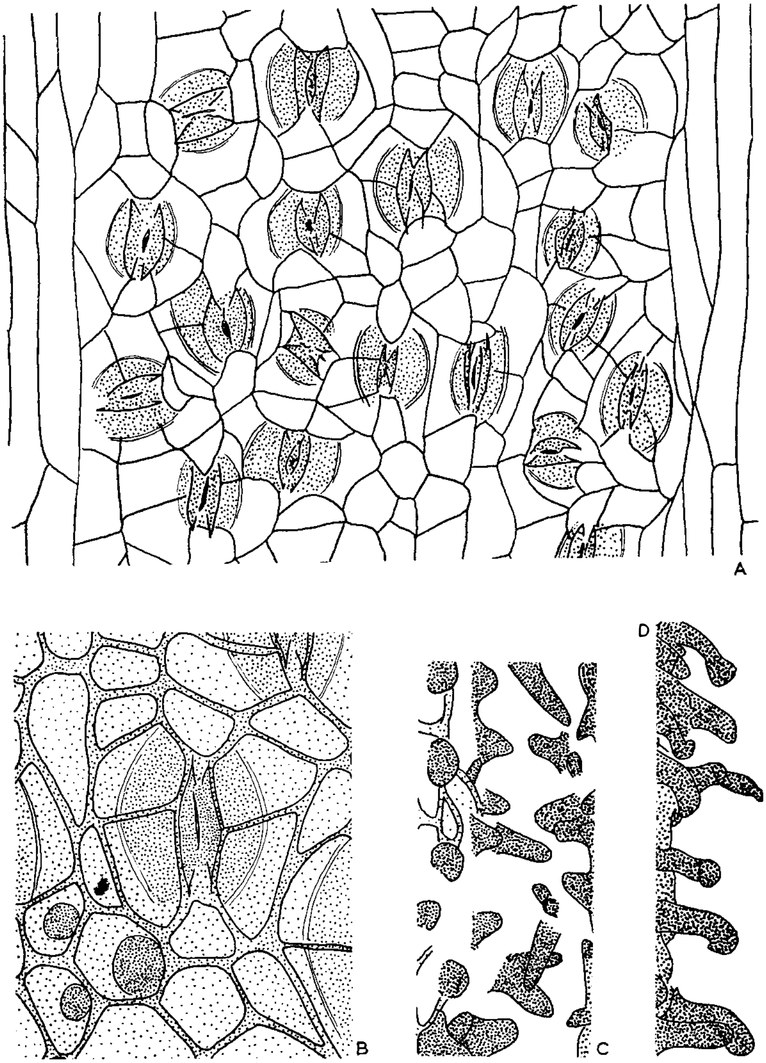
B cone-scales (?) obtained from macerated matrix. No. 6702.19. x 10.

C epidermal cells from the above. No. 6702.19. x 250.

D upper epidermal cells around the area of attachment. No. 6702.13. x 240.

E upper epidermal cells near the apex. No. 6702.20. x 250.

F lower epidermal cells. No. 6702.21. x 250.



Text-fig. 3.

A a few stomata in the stomatal groove. No. 6702.18. x 250.
B a single stoma and parts of three others. No. 6702.22. x 500.
C bottom of a stomatal groove with papillae. No. 6702.23. x 250.
D papillae from the sides of a stomatal groove. No. 6702.26. x 250.

Stomata rather crowded in the stomatal groove. Width of stomatal groove very variable, typically 5—8 stomata wide. In leaves with stomata in two bands in the groove, each band is about 4—6 stomata wide. When there are three bands in the groove, the outer two are about 4—5 stomata wide and the central one 4—7 stomata wide; in this case the breadth of the middle one is rather varied. When in four bands the outer two about 3—5 stomata wide and the width of the inner two varied, 1—3 stomata wide. But on the whole the width of the different stomatal bands is not constant. Stomata mostly longitudinally orientated but some oblique and transverse. Subsidiary cells of neighbouring stomata lying in contact or separated by small epidermal cells, very rarely two stomata sharing a subsidiary cell. Subsidiary cells rather big, 4—6 in number (2 polar and 4 lateral ones), rarely 7. The lateral subsidiary cells much thickened towards the region surrounding the guard cells (Text-fig. 3, B). Polar subsidiary cells unspecialized. Both lateral and polar subsidiary cells devoid of papillae. Guard cells highly thickened, mostly fusiform in shape, sometimes crescent-shaped. They are not sunken below the surrounding subsidiary cells. Pore slit-like or narrowly elliptical.

MALE CONE-SCALES (?)

From the partially macerated rock sample a few closely packed scale-like bodies were obtained. They were broadly triangular in shape and approximately 1 mm long. *Sciadopitys*-like pollen grains were found sticking to some of them. In order to examine their cuticular structure they were further macerated. They were found to possess epidermal cells like those of the leaves, the cells on both sides being serially arranged, rectangular or trapezoidal in shape, with thick and straight lateral and terminal walls and unspecialized surface wall. Stomata, however, were lacking on both sides.

When these scales were finally mounted on the slide most of the pollen grains were lost and only one or two were left behind. At present I am unable to say whether the pollen originally belonged to the scales or came to lie on them during the maceration. The shales contain a large number of pollen grains of this type. They were even found in some of the finished slides of the cuticular preparations of the leaves. Therefore, there is a possibility that the pollen grains got themselves attached to these scales during the maceration.

In shape and size these scales are somewhat similar to the male cone-scales of the recent *Sciadopitys verticillata* Sieb. et Zucc. The latter, however, are mostly, but not always, provided with a few stomata.

It is impossible to say with full certainty whether these scales belong to the same plant as the leaves and whether they really are male cone-scales, but the facts mentioned indicate that they may possibly be so.

POLLEN GRAINS

Almost spherical in polar view (Pl. 1, fig. 4), diameter from 30—48 μ. In lateral view slightly oval. Ektexine thick and provided with coarse verrucose sculpturing. In some grains there is a narrow slit-like area (seen in lateral view only) where the surface is smooth and thin, suggesting that perhaps the grains were monocolpate.

A great similarity exists between these and the pollen of the modern plant *Sciadopitys verticillata*. In the fossils there is some variation in the sculpturing of the ektexine. A similar variation, however, is also seen in the recent *Sciadopitys* pollen grains according to the description by INGWERSEN (1954).

FUNGAL REMAINS

Some of the leaves were found to be full of fungal hyphae, especially in the stomatal grooves. They seem to lie superficially and not penetrating into the leaves. Along with the hyphae are a few very small and rounded spores. It seems that the fungus grew on the leaves without doing any damage as there is no obvious sign present. Besides these hyphae, disc-like bodies as shown in Pl. 1, fig. 3 are also commonly met with on some of the leaves. They represent more than one genus and suggest microthyraceous affinites. Fungal remains somewhat similar to these have been described by COOKSON (1947) from Tertiary deposits in Kerguelen Archepelago, Australia, and New Zealand. They are known to be mostly saprophytic but in some cases they live superficially on the living leaves as well. In the present case it is not known whether these fungi grew on the leaves during life or on the fallen leaves. I am continuing the study of these fungal remains and will come back to them in a second paper.

Comparison.

Sciadopitytes variabilis is easily distinguished from all other *Sciadopitytes* in its great variation in the structure of papillae in the stomatal groove and also in having, in some leaves, definite stomatal bands inside the groove. In these characters it also stands out from the living *Sciadopitys verticillata* Sieb. et Zucc. and the fossil *Sciadopitys tertiara* Menzel first described by MENZEL (1913) from Herzogenrath near Aachen and then redescribed by FLORIN (1922). In the latter two there is a distinct non-stomatiferous groove on the upper side as well and the stomata on the lower side have papillate subsidiary cells. In *S. variabilis* there is no groove on the upper side and the subsidiary cells are never papillate.

Among the various species of *Sciadopitytes* so far described, the Greenland species *S. Crameri* (Heer) HALLE (1915) is closest to *S. variabilis.* The size of the leaves, the epidermal cells, and to some extent the stomata are similar in both. In *S. Crameri* the guard cells are crescent-shaped, while in *S. variabilis* they are mostly fusiform. In *S. Crameri* papillae do not occur inside the stomatal groove, whereas in *S. variabilis* papillae are commonly met with inside the groove as well. *S. Nathorstii* Halle, from Greenland, can be readily distinguished from the present species by its shape and size alone, besides the characters in which it differs from *S. Crameri*. In *S. Nathorstii,* like the present species, the guard cells are fusiform. *S. Hallei* Florin, found along with *S. Crameri,* is much larger and has a distinct non-stomatiferous groove on the upper side (?) as well; the stomatiferous groove on the lower side lacks papillae. The other Greenlandic species, *S. Olafiana* (Heer) Florin, is characterized by longitudinal rows of stomata inside the groove and also the needles are larger. *S. Lagerheimii* Joh. and *S. persulcata* Joh., both described by JOHANSSON (1920), are distinct from *S. variabilis,* as their subsidiary cells are papillate and they have also a non-stomatiferous groove. The Scottish species *S. scotica* Florin is readily distinguished by its mere size. In this respect the Spanish species described by GOTHAN (1954) is also different.

Discussion.

The possibility of the existence of more than one species was considered. The character and shape of the stomata are essentially the same in all leaves and so are the epidermal cells both on the upper and lower sides. In the majority of cases the stomata are irregularly scattered in a groove. In some, however, they are in distinct bands, but within the bands they are again irregularly scattered. The relation of the size and shape of the leaves with stomata scattered inside the groove and the leaves with distinct stomatal bands in the groove was studied. In this respect there is no clear distinction. In the majority of cases it was, however, found that the grooves with stomatal bands were slightly broader than grooves without such bands, and so were the leaves. But this distinction is not always constant, as quite a good many leaves with scattered stomata in the groove were found to be equally broad. As far as the length is concerned there exists no such distinction. In both the cases the leaves are approximately of the same size. It may be mentioned that the largest leaf so far obtained is one with scattered stomata inside the groove. The number of stomatal bands in the groove is from 2 to 4 but there is a great variation as to the breadth of the individual bands; there is also a great variation as to the presence or absence of papillae in the groove and as to their shape and size. These variations are so great from leaf to leaf that if we consider all the possible combinations more than dozen species will crop up. So in view of all these facts I have placed all the variations under one species.

FORM AND ATTACHMENT OF THE LEAVES

The leaves in the fossil condition are dorsiventrally flattened and in most cases the stomatal groove occupies a median position. But there are also cases when the groove, instead of lying in the middle, is placed slightly obliquely. In extreme cases flattening took place quite near the region of the groove. The leaves are all swollen at the base and a little above the base they are invariably slightly narrow and twisted. All these facts suggest that the leaves were thick and oval if not cylindrical.

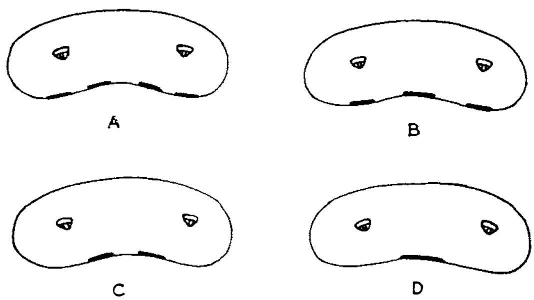
The leaves are without petiole and their area of attachment is represented by an oval or circular opening at the base, suggesting, perhaps, that the leaves were attached directly to the axis. But in quite a good many leaves this area of attachment lies a little above the base on the upper side (Text-figs. 1, C, E, G-H) which makes the question of attachment slightly complicated. I have tried some of the possibilities with plasticine models but so far I have failed to come to any conclusions. One of the possibilities may be that the leaves were attached to some sort of projection from the stem.

The side on which the area of attachment lies is always devoid of any stomata; this being the natural upper side I have come to the conclusion that the lower side is the one which has a median stomatal groove.

MORPHOLOGICAL NATURE

In *Sciadopitytes* two distinct forms of "leaves" are known, the one with only a median stomatiferous groove on the lower (?) side and the other with a distinct non-stomatiferous groove on the upper (?) and a stomatiferous groove on the lower (?) side. The latter form is close to *Sciadopitys verticillata*, where the morphological nature of the "leaves" (short shoots) has been a matter of great discussion in the past. Regarding them there are two views, the one put forth by DIXON (1866) who regarded them as phylloid shoots or cladodes, while the other is that of von MOHL (1871) who considered them as symphyllods or double needles. In accordance with the latter view, which has been more commonly accepted, the fossil "leaves" of *Sciadopitytes* have been described as double needles by various authors. The shape of the present "leaves" with entire, acute or obtuse apex does not suggest a double nature. This has also been mentioned by HALLE (1915) in the case of *S. Crameri* and *S. Nathorstii*. As we know too little about the history of the genus to say if the double needle theory (in the form usually stated) is the best way of looking at the thing, I have accepted the terminology of Halle, that is, I have described them as "leaves of conifer-like habit."

As far as the distribution of the stomata in the groove is concerned, in the present case, there is a possibility that the commonest type of groove with irregularly scattered stomata is the result of merging of four distinct stomatal bands. The whole thing could be explained if we suppose that originally the leaves were with four stomatal bands and inside each band stomata were placed irregularly, but that later development resulted in the fusion and supression of the inner two, while the outer two bands fused together to give rise to the type of groove with irregular distribution of the stomata (Text-fig. 4, A—D). In support of this I have found the following stages in the stomatal groove.



Text-fig. 4.

A—D shows the changes which may have taken place during the formation of the commonest type of stomatal groove with irregularly scattered stomata. Broad lines on the lower side indicate the position of the stomatal bands in fig. A—C, in fig. D it shows the position of the stomatal groove with irregularly scattered stomata.

1. Stomatal groove with four distinct bands; here the inner two have a varying breadth, but are mostly 1—3 stomata wide (Text-fig. 1, I—J).
2. Stomatal groove with three distinct bands, showing a great variation in the width of the central band (Text-fig. 1, K—L).
3. Stomatal groove with two distinct bands of practically equal size (Text-fig. 1, M).
4. Stomatal groove with irregularly scattered stomata (Text-fig. 1, N).

Inside each band the stomata are irregularly scattered as is seen in the last case and the shape of the epidermal cells found between the stomata is also similar to the epidermal cells of the stomatal groove with irregularly scattered stomata. But the epidermal cells between the bands are different: they are similar to those found outside the groove which again supports the idea that originally the stomata were placed in distinct bands.

GEOLOGICAL AGE

The material has come from that part of Padloping Island of which we know very little or nothing about the stratigraphy. The area is completely unknown and only now it is beginning to be explored. The age is only supposed to be Lower Cretaceous. This, of course, is supported by the presence of *Sciadopitytes* leaves which are most common in the upper Jurassic and Lower Cretaceous of the Arctic regions. The complete absence of angiospermic pollen grains in the matrix speaks in favour of its being Lower Cretaceous or older. Moreover, the maceration has yielded minute pieces of Bennettitalean leaf cuticle which again shows that the flora is not younger than Lower Cretaceous.

GEOLOGICAL HISTORY

The geological history of the Sciadopitineae was first described by Florin in 1922. Since then, besides the one described here, only one new species of *Sciadopitytes* has been added, by GOTHAN (1954) from the Upper Jurassic or Wealden of the Spanish East Pyrenees. But in the pollen literature there has been a considerable addition. Many new species of *Sciadopitys*-like pollen grains have since been described especially from the Tertiary lignites of Germany. On the evidence of these Thiergart (1949) rediscussed the geological history of Sciadopitineae. According to him they existed in the Central Europe during the Triassic period but later they migrated towards the north and finally they again moved south during the Upper Oligocene period. Thiergart has mainly based his conclusions on the evidence of pollen findings. If we consider the leaves alone they do not support this view of double migration. The earliest known *Sciadopitytes*, as far as I know, is from the Middle Jurassic, as now I understand from Professor Florin that *S. scanica* earlier described by him from the Rhaetic of Scania is of uncertain affinity. In a letter to me he writes: "....In respect to "*Sciadopitytes scanica*" I would say that I have long regarded my interpretation as too uncertain to be of any value. It was based on a very small and not very well preserved fragment, which I received by macerating a piece of rock, and should never have been given any name or on the whole been described. I was too optimistic at that time as to the possibility of interpreting fragmentary material of fossil plants." The present record only shows the marked occurrence of *Sciadopitytes* from the Middle Jurassic to the Lower Cretaceous and to a lesser extent in the Middle Cretaceous in the Arctic region including northern Scandinavia, and the occurrence of true *Sciadopitys* in Western Germany and Silesia from the Upper Pliocene till the end of Tertiary when the Sciadopitineae finally disappeared from Europe. From this we can only infer that they moved southwards from the Arctic region and northern Scandinavia at the end of the Mesozoic or the beginning of the Tertiary period. But even this does not hold true when we consider the existence of *Sciadopitytes* as far south as Spanish East Pyrenees during the Upper Jurassic or Wealden and the *Sciadopitys*-like pollen grains in older Tertiary formation of West Spitsbergen as reported by Manum (1954). So from these records it is quite evident that we still know too little to form any definite opinion regarding the movement of these plants in the past.

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I wish to express my deep-felt gratitude to Professor O. A. HØEG for his keen interest in the present work as well as for his personal kindness to me on various occasions. I am grateful to Professor T.M. HARRIS for entrusting me with the present material. My sincere thanks are also due to the Director of the Geological Survey of Canada and to Dr. WAYNE L. FRY for the loan of the material and some necessary information regarding the locality. To Professor R. FLORIN my thanks are due for his permission to quote his letter and for kindly examining some of my slides. I am extremely grateful to the Norwegian Ministry of Foreign Affairs for the financial aid which enabled me to carry out the work at the University of Oslo. To Mr. S. MANUM I am grateful for help in photography, and to Professor K. FÆGRI, Botanical Garden of the University of Bergen, and Mr. O. REISÆTER, Norwegian College ot Agriculture, for providing living material of *Sciadopitys verticillata* for comparison.

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PLATE I

Sciadopitytes variabilis n. sp.

Fig. 1: Piece of shale with a few embedded leaves. No. 6702. x 1.

Fig. 2: A detached leaf. Type Specimen No. 6702.1. x 1.

Fig. 5: Lower cuticle of a leaf with three stomatal bands in the groove. No. 6702.2. x 15.

Fig. 6: Lower portion of a leaf showing the positions of the two veins. Photographed in infra-red light. No. 6702.3. x 10.

Fig. 7: Part of lower surface of a leaf, showing the stomatal groove with papillae. No. 6702.4. x 150.

Fig. 8: A few stomata inside the groove. No. 6702.5. x 150.

Pollen grain.

Fig. 4: Sciadopitys-like pollen grain. No. 6702.6. x 500.

Fungal remain.

Fig. 3: Microthyriaceous fungal remain as seen on the surface of a leaf. No. 6702.1. x 200.

All the figured specimens and slides are preserved at the Geological Survey of Canada, Ottawa.

PLATE I