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KONG CHRISTIAN DEN X's LAND UDFØRT
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UNDER LEDELSE AF LAUGE KOCH

THE FOSSIL FLORA OF SCORESBY
SOUND EAST GREENLAND

PART 5: STRATIGRAPHIC RELATIONS OF THE PLANT BEDS

BY

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WITH 1 PLATE AND 5 FIGURES IN TEXT AND 3 TABLES

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INTRODUCTION

This paper completes the account of the fossil plants collected in 1926—27 on the Danish expedition to East Greenland.

It is divided into two parts. The first is devoted to a review of the species described in the previous paper (together with additional information about some of them). The second deals with stratigraphy — the plant-bearing rocks are described, the flora is correlated in detail with other floras and the whole question of the stratigraphy of the plant-bearing *facies* of the Rhaetic and Lower Liassic is discussed.

A complete list of the papers describing this Greenland Flora will be found in the bibliography under the names of HARTZ and HARRIS.

Part 1. Floristic Review.

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Algae.

1. *Confervites vaucherioides* HARRIS.

See HARRIS 1931(b), p. 3.

Thaumatopteris zone at 25 m; 1 locality.

Hepaticae.

Genus *HEPATICITES* WALTON.

Four liverworts are now known from Scoresby Sound; it is interesting that they appear similar to the thalloid *Jungermanniales* — none of them give any sign of Marchantiaceous air chambers. The Palaeozoic

liverworts also appear nearest to the Jungermanniales and possibly the same may be true of the Mesozoic *Marchantites erectus* and even of *Palaeohepatica rostofenskii* RACIBORSKI, in which, though air chambers are described, they are minute and might possibly represent the indistinct patterns produced by crushing several similar layers of cells. In the Tertiary, on the other hand, there are some undoubted Marchantiales.

2. *Hepaticites rosenkrantzi* sp. nov.

Pl. 1, figs. 1—5, 6, 8.

1931(b): *Thallites* sp. HARRIS, p. 4; Pl. 1, figs. 1, 2, 5.

Type-specimen HARRIS 1931(b), Pl. 1, figs. 1, 5.

Thaumatopteris zone at 25 m, 1 locality (Neill Cl., Liverwort Bed).

Diagnosis. Thallus attaining a length of over 2 cm; typically 3 mm wide (5 mm in widest parts, 1 mm in narrowest apical branches). Branching dichotomous and nearly equal, occurring at irregular and often long intervals; margin entire or only very slightly lobed. Midrib absent but margins of the thallus usually appearing a little thinner than the middle. Ventral scales absent. Thallus showing two layers of rather similar, parenchymatous cells; cells isodiametric to slightly elongated tending to be placed in longitudinal rows along the middle of the thallus but rows arching outward towards the margin. Actual margins in the apical region possibly only one cell thick but whole of the rest of the thallus showing two distinct layers of cells. Occasional cells of lamina somewhat enlarged and with considerably thickened walls; such cells occurring singly or in patches of three or four, and being most numerous towards the middle of the lamina.

Surface of thallus (? upper) bearing round or oval cups 1.5—3 mm in diameter; margins of cup formed of a delicate cellular wall 0.3 mm high, wall directed upwards from the thallus sometimes overhanging the cup, sometimes pointing slightly outwards, margin entire but seldom well preserved.

Base of cup formed of at least two layers of cells, one of these layers and also the sides of the cup being very largely composed of cells with thickened walls. Nature of cup unknown.

Discussion. The original specimens consisted of the Type (HARRIS 1931b, Pl. 1, figs. 1, 5, which was rather ill preserved but recognisable) and another (1931b), Pl. 1, fig. 2), which I now realise is distinct and possibly belongs to *H. amauros*. The new specimens were discovered late in the investigation as a result of splitting up a discarded rock fragment; they are rather better preserved than the Type and were made into balsam transfers.

The existence of two layers of cells in nearly all parts of the thallus can be readily demonstrated wherever the preservation allows; it is

impossible to say whether any internal cells were present in the middle of the thallus, certainly there is no trace of them near the margin. Rhizoids are not satisfactorily preserved but I think I have recognised a rhizoid base and half a millimetre from it a piece of a rhizoid which has become detached from the balsam. The wall of this possible rhizoid is smooth.

The cups on the surface of the thallus are an interesting feature; they might be compared with the gemma cups of *Marchantia* or with the round patches of antheridia or archegonia found on the surface of the thallus of various existing liverworts.

H. rosenkrantzi is distinguished from *H. laevis*, *H. amauros* and *H. glebosus* by having no midrib; it is also distinguished by the narrowness of the young branches, by the presence of at least two layers of cells in the thallus and by the cups on its surface.

3. *Hepaticites glebosus* HARRIS.

See HARRIS 1931(b), p. 4.

Thaumatopteris zone, 25 m; 1 locality.

Some additional specimens of this liverwort were found which agree with those previously described in showing oval swellings in the midrib with a slightly rough surface.

4. *Hepaticites laevis* HARRIS.

See HARRIS 1931(b), p. 5.

Thaumatopteris zone at 42 m; 1 locality.

Marchantites yabei KRYSHTOFOVICH (1933) appears to be rather similar in habit, but differs in having a broader thallus, but a narrower and more sharply defined midrib.

Thallites uralensis KRYSHTOFOVICH and PRINADA (1933b) is indistinguishable from *H. laevis* and may well belong to the same species. Its age is probably rather similar.

5. *Hepaticites amauros* sp. nov.

Pl. 1, figs. 7, 9.

Both the figures represent the Type specimen.

C. Stewart, *A. hartzi* Bed (*Thaumatopteris* zone at an estimated level of 50 m).

Diagnosis (based on Type specimen alone). Thallus 1.5—2.5 mm wide, branching by equal dichotomy every 3 mm or less; apices rounded, not markedly attenuated, margins entire. Midrib a rather narrow and well defined dark strip, not projecting on the surface. Ventral scales absent. Substance of thallus thick, apparently formed by a good many

layers of cells which, when pressed together, give no indication of cell-rows.

Discussion. The Type-specimen was made into a balsam transfer. Only one rhizoid was seen and this could not be traced with certainty to its point of attachment, but it appears from its position to belong to this plant. It is unbranched, unseptate and has evenly thickened walls.

H. amauros is distinguished from the other Greenland species by its frequent dichotomy, narrow midrib and very thick substance.

Equisetales.

Genus **EQUISETITES** v. STERNBERG.

In discussing this genus (HARRIS 1931b, p. 13) I came to the conclusion that the Mesozoic fossils agreed with the living genus in all fundamental characters of gross and minute structure except that there were twice as many vascular bundles as leaf-teeth, instead of an equal number. This conclusion was not the result of direct observation but was inferred from the fact that the nodal diaphragm (especially in *E. muensteri* and *E. laevis*) shows a ring of dots which are twice as numerous as the leaf-teeth, and these dots I interpreted as the imprints of bundles.

As a result of a study of the stems of living species from which I have prepared artificial fossils by allowing them to rot and by crushing I have now come to a different conclusion. I now consider that the dots on the diaphragm do not represent the internodal bundles themselves, but instead they are formed by the little masses of metaxylem into which the bundles divide below a node and from which the bundles of the next internode are formed. These metaxylem masses in recent stems are rather substantial and on compression stand out as little tubercles; as there are two to every bundle they give exactly the appearance shown in the fossil diaphragms. On this interpretation there is agreement in the number of bundles.

The 'artificial fossil' *Equisetum* stems have given some interesting suggestions about the bundle structure. It may be remarked that in few, if any, *Equisetites* stems with well preserved leaf-teeth is there any sign of bundles in the internode, though in other genera — *Neocalamites* — the bundles are exceedingly obvious.

The vascular bundle in most species of *Equisetum* has a large (water conducting) carinal canal and only a vestige of metaxylem. If the internode is allowed to rot under water the bundles and all the other internal tissues of the internode breakdown to a pulp enclosed by the rigid epidermis + hypodermis; at the node the diaphragm and the

metaxylem masses prove resistant (in certain species). On crushing such a stem the diaphragm rotates into the plane of compression and a preparation of the surface + diaphragm is obtained which matches the fossils almost perfectly.

If the internode is crushed without previous rotting under a fairly high pressure (about 10 tons per sq. cm in my experiments) a similar result is obtained; the carinal canals collapse and the bundles scarcely form ridges at all, since there is no more cell-wall material here than elsewhere.

Turning to the cone of *Equisetites* (e.g. *E. muensteri*) vascular bundles are quite distinct in the fossil; this again has its parallel in *Equisetum*, where in the cone the bundles have plenty of metaxylem in contrast with those of the internode. The cone in consequence, when crushed, behaves quite differently from the internode — the woody bundles stand out as distinct ridges just as in the fossil cone.

It will be seen from this work that certain apparent differences in vascular structure between *Equisetites* and *Equisetum* can be explained as the result of the process of fossilisation; in fact, a plant of the structure of *Equisetum* must on fossilisation give a specimen of the appearance of *Equisetites*; the apparent differences when investigated lead to the recognition of the important similarity in bundle structure as well as in their number. There is, in fact, complete agreement between *Equisetites muensteri*, etc. and *Equisetum* in everything but mere size.

In *Neocalamites*, where the internode is strongly striated, it seems legitimate to conclude that the bundles were woody like those of the *Calamites*, but unlike those of *Equisetum*, possessing plenty of metaxylem and a relatively unimportant carinal canal. There are a good many fossil Equisetalean stems which have lost their leaves, but show the imprints of vascular bundles which alternate at the node as in *Equisetum*. It is certainly possible that these stems are rightly referred to *Equisetites*; but in the substantial nature of their bundles they agree better with *Neocalamites* than with anything yet recognised in the living *Equisetum* or reliably determined fossil *Equisetites* stems.

The almost exact agreement between *E. muensteri* and the living *Equisetum* indicates that it should be placed in the same genus. I have only refrained from doing this because this is a step which should not be taken without a careful review of all the fossil species.

Certain petretied Tertiary fossils are known; *Equisetum stellare* and *E. noviodunense* which agree fully in anatomy with the living species (FRITEL and VIGUIER 1909, FRITEL 1910).

6. *Equisetites muensteri* v. STERNBERG.

See HARRIS 1931(b), p. 7; also 1926(b), p. 52, also HARTZ 1896, p. 233.

Lepidopteris zone, all levels; *Thaumatopteris* zone at 10—25 m and probably in lower part. 14 localities (and probably two others where the determination is uncertain).

Localities not previously mentioned: — Vardekloft, *Neocalamites* Bed; C. Stewart *E. laevis* Bed; ? at Lejr R., *Thaumatopteris* Bed (unconfirmed field record).

E. muensteri is one of the best characterised species of its genus; it occurs throughout both zones in Greenland; elsewhere it is chiefly known from the *Thaumatopteris* zone. The cone is less characteristic than the stem; *E. sibiricus* (HEER) NATH., from considerably younger Jurassic rocks (see KRYSHTOFVICH 1933) is very similar indeed.

E. muensteri occurs at several localities in the German, English and French Liasso-Triassic 'Grenzschieht' floras; it also occurs in Sweden, Poland and Bornholm, and possibly Austria in beds either definitely belonging to the *Thaumatopteris* zone, or with a flora of this general character (see HARRIS 1931(b), p. 7).

7. *Equisetites laevis* HALLE.

See HARRIS 1931(b), p. 14; 1926(b), p. 53.

Lepidopteris zone at all levels; lower half of the *Thaumatopteris* zone: 12 localities.

E. laevis occurs in the following localities in addition to those previously mentioned:

C. Hope, *A. minor* Bed (*Lepidopteris* zone).

Ammonite Mtn.; Coal at 50 m (lower part of *Thaumatopteris* zone).

C. Stewart; above the *A. hartzi* Bed (middle of *Thaumatopteris* zone).

Although this species extends up into the *Thaumatopteris* zone, it is far more abundant in the *Lepidopteris* zone and is a very useful zone indicator. *E. laevis* occurs in Sweden at one or two localities in the *Lepidopteris* zone (HALLE 1908, p. 14).

8. *Equisetites sarrani* (ZEILLER) HARRIS.

1903. *Equisetum Sarrani* ZEILLER, p. 144, Pl. 39, figs. 1—13.

1926(b). *Equisetites* sp. B cf. *sarrani* (ZEILLER) HARRIS, p. 54; Pl. 2, figs. 2, 3.

? 1924. *Equisetites* sp. CHOW. P. 2; Pl. 1, fig. 1 (poor specimen).

1931(b). *Equisetites doratodon* HARRIS, p. 16. Pl. 3, figs. 1, 2, 4—6, 9, 11, 13, 14, 16, 18; Text-fig. 3 F.

1933(a). *Equisetum sarrani* ZEILLER, SZE, p. 20; Pl. 3, fig. 10.

Thaumatopteris zone at 6—25 m; possibly at 54 m; 4 localities — + 1 doubtful.

In describing the present material, I originally named it *E. cf.*

sarrani; afterwards I regarded it as a distinct species, and am now inclined to refer it to *E. sarrani* again. One of the main differences which I supposed existed between my specimens and *E. sarrani* lay in the structure of the diaphragm, which was rather different in my specimens from the minute ones figured by ZEILLER. SZE (1933a) has, however, figured a diaphragm determined as *E. sarrani*, which is exactly like mine. The other supposed difference lay in the number of leaf-teeth (about 16 in mine, number stated to be 20 or 30 in ZEILLER's diagnosis of *E. sarrani*). SZE's specimen shows probably not more than twenty, and reference to ZEILLER's figures suggests that none of his figured specimens have much over 20, and some probably only 18 (e. g. that shown in ZEILLER, Pl. 39, fig. 3). There is no difference I can recognise in the sculpturing or shape of the leaf-teeth between the Greenland and Tonkin specimens and I must therefore identify the two. The cone is unknown from Greenland.

There are several other species which resemble *E. sarrani*; notably *E. praelongus* and *E. grosphodon* (with which the Greenland specimens have been compared by HARRIS 1931b, p. 18), *E. scanicus* HALLE (1908), which has rather more leaf-teeth, and also *E. conicum* STERNB. (or *E. platyodon* BRONGN.) and *E. arenaceum*, with which ZEILLER (1903) compares his specimens. The existence of so many similar species suggests that *E. sarrani* is unlikely to be much use as a zone fossil as there is too great a risk of incorrect determination. The same difficulty deprives the identification of the Greenland specimens with this *E.* Asiatic species of much of its geographical significance.

E. sarrani is confined to the *Thaumatopteris* zone in Greenland; its age in E. Asia cannot be stated precisely in terms of the European plant zones but must be Upper Trias or Lower Lias.

9. *Equisetites grosphodon* HARRIS.

See HARRIS 1931(b), p. 18; also HARRIS 1926(b), p. 54 as *E. sp. A* cf. *praelongus*.

Lepidopteris zone at 65—80 or 90 m. 8 localities. New locality: C. Stewart, *A. minor* Bed.

This species is confined to the Greenland *Lepidopteris* zone; but cannot be regarded as a very reliable zone fossil as it is extremely like *E. ferganensis* SEWARD (see HARRIS 1931(b) for references), which is of rather younger age.

10. *Neocalamites hoerensis* (SCHIMPER) HALLE.

Additional references: See HARRIS 1931(b), p. 22; also HARRIS 1926(b), p. 51.

1931. *N. hoerensis* (HIS.), FRENTZEN, p. 78 (German Rhaetic, no figure).

1933. *N. hoerensis* (HIS.), KRYSHTOFVICH, Pl. 5, fig. 3 (Older Mesozoic of Russia).

The specimen determined by SZE (1931, p. 51) as *N. hoerensis* was later referred by him to *N. carrerei* ZEILLER.

Lepidopteris zone at all levels, 10 localities.

This species is by no means easy to distinguish from many of those referred to *N. carrerei* ZEILLER, and *N. ferganensis* KRYSHTOFOVICH (1933). It is not therefore likely to be a good zone fossil unless the material is abundant enough to show the range of variation. KAWASAKI (1927, p. 16) has recently discussed the specific characters of *N. hoerensis*.

11. *Lobatannularia carcinoides* (HARRIS) n. comb.

1908. *Equisetites scanicus* (? non v. STERNBERG) HALLE pars; p. 22; Pl. VIII, figs. 1—5; Pl. IX, figs. 16, 17.
 1926(b). *Neocalamites* cf. *inopinata* (NON ZEILLER) HARRIS, p. 51; Pl. 4, fig. 7; Pl. 9, figs. 1, 4.
 1931(b). *Neocalamites carcinoides* HARRIS, p. 25, Pl. 4, figs. 2, 3, 5—7; Pl. 5, figs. 1—5; Pl. 6, figs. 1—6; Text-fig. 5 A—D.
 1934. *Neocalamites carcinoides* HARRIS, KAWASAKI. Pp. 65—71 (discussion of this and other species).

Thaumatopteris zone at 4—25 m; 16 localities (often as only species). The record of this species at Primula R. (HARRIS 1931(b), p. 25) is unconfirmed and may be erroneous.

KAWASAKI (1934, pp. 65—71) has given a good account of *Lobatannularia* and its differences from *Neocalamites* and questions whether this species would not be better transferred to *Lobatannularia*. I agree with his arguments and have made the change; the great variability of this species causes difficulty wherever it is classified.

I have previously pointed out that some of the pith casts figured by HALLE from the Swedish Liassic show the same structure as similarly preserved specimens of *N. carcinoides*. The dot-like leaf trace to every occasional bundle agrees with the genus *Neocalamites* rather than *Equisetites*, while the occurrence of as many as five longitudinal bundles between a pair of leaf traces is in agreement with this species alone. It has previously been pointed out that conspicuous bundles are not usually seen in the internode of *Equisetites*, p. 8.

Lobatannularia is a characteristic genus of the uppermost Palaeozoic and older Mesozoic of E. Asia, where it is represented by many species, from all of which it is fairly readily distinguished by its longer and differently shaped leaves. The occurrence of this genus in the basal Lias of Greenland and probably Sweden is obviously of considerable interest. *L. carcinoides* is a most useful zone fossil of the upper half of the *Thaumatopteris* zone in Greenland; the Swedish specimens referred to above are of the same age.

KRYSHTOFOVICH and PRINADA (1933b) have compared *L. carcinoides* with the somewhat similar species *Neocalamites nordenskioldi* (HEER) KR. and P.

Lycopodiales.

See HARRIS 1935, p. 151.

12. *Grammaephloios ichtha* HARRIS.

See HARRIS 1935, p. 152.

Thaumatopteris zone 25 m; 1 locality.

13. *Lycostrobus scotti* NATHORST.

See HARRIS 1935, p. 153; 1926(b), p. 50.

Thaumatopteris zone at 22 m down to a bed transitional between this and the *Lepidopteris* zone; 3 localities.

This species occurs in the *Thaumatopteris* zone of Sweden at Helsingborg (NATHORST 1908(a), p. 3).

14. *Triletes rexargenteus* HARRIS.

See HARRIS 1935, p. 156; 1926(b), p. 51 as 'Megaspore Type 3'.

Lepidopteris zone at 62 m to near base, 6 localities.

15. *Triletes areolatus* HARRIS.

See HARRIS 1935, p. 158.

Thaumatopteris zone from 10 m down to a bed transitional to the *Lepidopteris* zone; 8 localities.

An undescribed megaspore somewhat resembling *T. areolatus* but distinguishable by being smaller and having stronger triradiate scars is very common in the Lower Oolite (Middle Estuarine) of Grinstead Bay, Yorkshire, England.

16. *Triletes litchi* HARRIS.

See HARRIS 1935, p. 159.

Lepidopteris zone, 62—75 m; 2 localities.

17. *Triletes myrmecodes* HARRIS.

See HARRIS 1935, p. 160; 1926(b), p. 50 as 'Megaspore 2'.

Lepidopteris zone at 62 m to near base; 5 localities.

18. *Triletes mensura* HARRIS.

See HARRIS 1935, p. 160.

Lepidopteris Zone at 62—85 m; 3 localities.

19. *Triletes tylosus* HARRIS.

See HARRIS 1935, p. 162.

Lepidopteris Zone at 85 m; 1 locality.

20. **Triletes ales** HARRIS.

See HARRIS 1935, p. 165.

Bed at about level of transition from *Lepidopteris* to *Thaumatopteris* Zone, 1 locality.

21. **Triletes aurantium** HARRIS.

See HARRIS 1935, p. 164.

Lepidopteris Zone at 62—85 m; 5 localities.

22. **Triletes persimilis** HARRIS.

See HARRIS 1935, p. 165.

Lepidopteris Zone at 85 m; 1 locality.

23. **Triletes pedinacron** HARRIS.

See HARRIS 1935, p. 165.

Lepidopteris Zone at 69 m; 1 locality.

24. **Triletes pinguis** HARRIS.

See HARRIS 1935, p. 165.

Lepidopteris Zone, level unknown; 1 locality.

25. **Triletes ionthus** HARRIS.

See HARRIS 1935, p. 166.

Lepidopteris Zone, 62—69 m; 2 localities.

26. **Triletes stenoxysmatodes** HARRIS.

See HARRIS 1935, p. 167.

Lepidopteris Zone at 62 m; 1 locality.

Filicales.

Genus **TODITES** SEWARD.

1900. *Todites* SEWARD p. 86.

The genus *Todites* was proposed for fossil ferns which resemble in all the known characters of their sterile and fertile leaves the recent genus *Todea*: its only distinction is its age. One of the names used for this genus is *Acrostichites* GOEPPERT; but although earlier this name is not in my opinion valid. GOEPPERT (1836) defined his genus thus "*Frons vel pinnata, nervis secundariis obliquis dichotomofurcatis, vel digitata, nervis secundariis anastomosantibus. Sori rotundi inferiorem frondis paginam occupantes.*" Three species were included — *A. williamsonis* (now *T. williamsoni*), *A. phillipsi* and *A. inaequilatera* (now *Sagenopteris*). The diagnosis refers first to *Todites*, then to *Sagenopteris*: in the

second sentence fits neither; and in my opinion *Acrostichites* GOEPPERT cannot be a valid genus. There is no rule of nomenclature about the validity of the very numerous names of genera and form-genera distinguished by their age, some (like *Cladophlebis* for the Mesozoic Pecopterids) are generally used; others (like *Equisetites*, *Ginkgoites* and *Todites*) are not, and some might prefer to use *Todea* for the fossils.

In my previous account I merged *Cladotheca* HALLE with *Todites* on the grounds that the sporangia were identical in structure and insertion. I think it is only possible to maintain *Cladotheca* as a sub-generic section of *Todites*, of which there appear to be three groups of species. These are as follows:—

- § 1. *T. princeps*. Small and delicate leaves with Sphenopterid venation; leaves often partly fertile, partly sterile.
- § 2. *T. williamsoni-goepperti* group. Large leaves with Alethopterid or Neuropterid venation; leaves often partly fertile, partly sterile.
- § 3. *Cladotheca* group. Large leaves with more or less Pecopterid venation; as far as known wholly fertile or wholly sterile.

I do not consider it advisable to raise *Cladotheca* to generic rank: no complete fertile leaf of any species of this section is known. It should be pointed out that the name *Todites* applies primarily to a fertile leaf, and it is, according to the views of many palaeobotanists, wrong or at any rate inadvisable to use the same generic designation for different categories of plant organs. The sterile leaf should therefore be referred to *Cladophlebis* as formerly. It may be argued that in the species with partially fertile leaves, sterile and fertile leaf fragments are not 'different categories of organs' and may all be conveniently described by the same name; but in those species where the leaves appear to have been wholly fertile or sterile different names should be used. This is not the course I adopted previously, but I have been convinced by discussion at the Sixth International Botanical Congress that it is right.

As it happens, the sterile *Cladophlebis* leaves are so numerous and confused as to have little scientific interest apart from the fertile leaves, and I have not thought it necessary to give any new names to the sterile leaves.

The type species of *Cladotheca* (*C. undans*), which was first described by BRONGNIART as *Phlebopteris undans*, and later by HALLE (1911, 1921) and by WALTON (1923) as *Cladotheca undans* and by me as "fertile *Todites denticulatus*" becomes *Todites undans* (BRONGN.) n. comb.; the sterile leaf remains *Cladophlebis denticulata*.

It may be pointed out that fertile pinnae are very common in association with *Cladophlebis* but they appear rather like ill preserved

sterile specimens and their true nature is only revealed by the preparation of a transfer. Among the many figures of *Cladophlebis* in the literature, there are a good many which I feel certain are fertile leaves (with the sporangia immersed in the rock).

27. **Todites goeppertinus** (MÜNSTER) KRASSER.

See HARRIS 1931(b), p. 31 (as *Todites goeppertianus*; also HARRIS 1926(b) as *Todites* cf. *Williamsoni*; also HARTZ 1896 as *Todites Williamsoni*.

Lepidopteris and *Thaumatopteris* Zones at all levels. 12 certain localities and 2 doubtful.

As previously pointed out, *T. goeppertianus* is so like various upper Triassic and Jurassic species that it has little stratigraphic value.

OISHI (1932a, p. 274) has described some specimens very like the Greenland ones as *Todites roesserti* ZEILLER (non PRESL).

While I agree with his identification, I cannot accept this as a valid name. ZEILLER himself stated (1903, p. 38) that his specimens were identical with *Neuropteris goeppertianus* MÜNSTER and in this it seems to me he was correct. The specific name *roesserti* ZEILLER (non PRESL) is therefore a synonym of *goeppertianus* MÜNSTER; the original specific name *roesserti* PRESL was applied to an indeterminable fragment which appears, however, to be different from the leaves under discussion.

28. **Todites princeps** (PRESL) GOTHAN.

See HARRIS 1931(b), p. 35; also HARRIS 1926(b), p. 56.

Thaumatopteris Zone 15—54 m. 4 localities.

This species is confined to the *Thaumatopteris* Zone of Greenland; and occurs probably in the same Zone of Germany and Poland. The same species, or a species at present indistinguishable, occurs in much younger Middle Jurassic rocks of England and parts of Russia and Siberia. It also occurs in E. Asia in rocks of approximately Rhaetic age which cannot be precisely correlated with the European plant zones (ZEILLER 1903; OISHI 1932a). Its utility as a zone fossil is thus very slight.

29. **Todites recurvatus** HARRIS.

1931(b). *Todites recurvatus* HARRIS, p. 39. Pl. 9, figs. 1—4, 6—8, 9; Pl. 10, figs. 1—7.

Sterile leaves attributed to this species: — HARRIS 1931(b), Text-figs. 10, 11; Pl. 10, fig. 7.

Thaumatopteris Zone at 22 and about 50 m; 2 localities.

The name *A. recurvatus* should apply primarily to the fertile specimens which are quite different from any hitherto described. The sterile ones attributed to this species are very like many species of *Cladophlebis*, in particular *C. nebbensis* as interpreted by many authors (see *T. hartzi*).

30. *Todites scoresbyensis* HARRIS.

1931(b). *Todites Scoresbyensis* HARRIS; HARRIS, p. 42, Pl. VIII.

Sterile leaves attributed to this species:—HARRIS 1931(b), Text-fig. 12; HARRIS 1936(b), p. 59, Pl. 11, fig. 4; Text-fig. 4 A—D.

Lepidopteris Zone at 72 m; 1 locality. (Sterile leaves of the type attributed to *T. scoresbyensis* are widespread in the *Lepidopteris* Zone.)

This name applies primarily to the fertile leaf, though it is very probable indeed that the sterile leaf attributed to it does, in fact, belong to the same species. This sterile leaf is very like certain specimens determined by various authors as *Cladophlebis nebbensis* and *C. denticulata*, and only differs slightly from the sterile leaves attributed to *Todites hartzi*, *T. recurvatus* and *Osmundopsis plectrophora*, though the fertile leaves are very distinct (see below under *T. hartzi*).

31. *Todites hartzi* HARRIS.

1931(b). *Todites hartzi* HARRIS, p. 44, Pl. 10, figs. 1—6.

Sterile leaves attributed to this species:—HARRIS 1931(b), p. 44; Text-figs. 13, 14; HARTZ 1896, p. 228; Pls. 7, 8, 9, 10, 12, fig. 1 (as *Cladophlebis Roesserti* v. *groenlandica*).

Thaumatopteris Zone at about 25 m; 4 localities.

The name *T. hartzi* should apply primarily to the fertile leaf, but from the invariable association of the one particular type of sterile *Cladophlebis* leaf with it, there can be no doubt that the two belong to the same species.

OISHI (1932a, p. 286) considers that the sterile leaf of *T. hartzi* is indistinguishable from *Cladophlebis nebbensis*. Though it never shows small entire nearly rectangular pinnules like the type-specimen of *C. nebbensis*, it is true that it is very like some of those which have been identified with *C. nebbensis* by other authors. The chief reasons, why it would be a mistake to identify this with *C. nebbensis* is firstly that it is different from BRONGNIART's original figure and secondly that there are several leaves all more or less of the *C. nebbensis* type differing only slightly from one another (the sterile leaves of *T. hartzi*, *T. scoresbyensis*, *T. recurvatus*, *Osmundopsis plectrophora*) but with considerably different fertile leaves. If any of these is to be identified with *C. nebbensis* it should be that of *T. recurvatus*, which is certainly the least different; but even this should, I think, be left until the fertile leaf of *C. nebbensis* from the type locality has been identified.

T. hartzi is characteristic of the *Thaumatopteris* Zone of Greenland.

Genus *OSMUNDOPSIS* HARRIS.

It is very probable that the leaves of *O. plectrophora* were dimorphic, i. e. completely fertile or sterile and not as in the recent genus *Osmunda*,

but there is no evidence whether the leaves of the other Mesozoic species of *Osmundopsis* were dimorphic too.

32. *Osmundopsis plectrophora* HARRIS.

HARRIS 1931(b), p. 49, Pl. 12, figs. 2, 4—10.

Sterile leaf attributed to this species: — HARRIS 1931(b), p. 49, Text-figs. 15, 16.

Thaumatopteris Zone at about 25 m; 2 localities.

The name *Osmundopsis plectrophora* should apply primarily to the fertile specimens which appear to have been entirely fertile (unlike the living species of *Osmunda*).

The sterile leaf is usually rather well distinguished from all hitherto described species of *Cladophlebis* by the little 'spur' on the basal pinules; but near the top of the leaf this is feebly developed or absent, and such specimens are scarcely distinguishable from many of those determined by various authors as *C. nebbensis* (see p. 16).

The fossil sterile and fertile leaf fragments which have recently been described by KRYSHTOFOVICH and PRINADA (1933b) as *Osmundites prigorovskii* KR. and P. appears to be congeneric with *O. plectrophora* and should therefore be named *Osmundopsis prigorovskii* (KRYSHTOFOVICH and PRINADA) n. comb. It differs from *O. plectrophora* in having obtusely pointed sterile pinnules without marginal teeth even in their upper parts, and very probably in having smaller sporangia.

Form-genus *CLADOPHLEBIS* BRONGN.

The addition in the literature of several new species and the figures of many specimens referred to known species of *Cladophlebis* every year only makes determination increasingly difficult; and I think that it may almost be said that the very common group centring round *C. nebbensis* and *C. denticulata* are now so difficult as to make their determination almost without geological significance. I have, in fact, made absolutely no use of them in correlating the Greenland flora; I recognise, however, that they might become significant if systematically revised (presumably in relation to their corresponding fertile leaves).

33. *Cladophlebis scariosa* HARRIS.

See HARRIS 1931(b), p. 52, also HARRIS 1926(b), p. 57.

Lepidopteris Zone at about 70 m. 2 localities.

Apart from the probable fact that this leaf was a sort of 'filmy fern' — comparable to *Todea hymenophylloides*, this leaf has little interest. In spite of its excellent preservation, it cannot be clearly distinguished from imperfectly known specimens described by other authors as *C. roesserti* and *C. nebbensis*, but is quite distinct from the other Greenland species.

34. *Cladophlebis ingens* HARRIS.

See HARRIS 1931(b), p. 55; probably also HARRIS 1931(b), p. 56 as '*C. sp. A*'.

Thaumatopteris Zone at 25 and about 50 m; 2 localities.

The following specimens are very similar to *C. ingens* and may be identical: —

C. halleiana SZE 1931, p. 32, Pl. 8, figs. 1, 2.

C. fukienensis SZE 1933b, p. 49, Pl. 8, figs. 1—3.

This species varies to some extent in the different parts of the leaf and the discovery of some new specimens has shown that the specimens I previously distinguished as *C. sp. A* are very probably identical with those figured previously as *C. ingens*.

Certain specimens of *C. ingens* appear to be exactly like SZE's two species mentioned above. I do not know whether his name *halleiana* or mine, *ingens*, has priority (both papers are dated 1931) but as his was held up for some years, and only reached me in 1933, I assume that the name *ingens* is the earlier.

The narrow forms of *C. ingens* (figured as *C. sp. 'A'*) are very like *C. raciborskii* ZEILLER (recently figured by OISHI 1932a) but the veins make a slightly larger angle with the midrib, and the form with coarse pinnules differs more decidedly in the wavy margins of the pinnules, as well as in their breadth. It is also very similar to certain specimens determined as *C. haiburnensis* from various horizons, and is certainly not sharply enough distinguished from the other species to have stratigraphic value.

35. *Cladophlebis svedbergi* JOHANSSON.

See HARRIS 1926(b), p. 56.

Thaumatopteris Zone at 25 m; 1 locality.

The Greenland specimens agree exactly with the Swedish Type-specimens of *C. svedbergi* from beds situated near the transition region between the *Lepidopteris* and *Thaumatopteris* Zones of Sweden. They also agree very well with *C. fangtzuensis* SZE (1933b, p. 35; Pl. 6, fig. 1) and with certain specimens figured by other authors as *C. nebbensis*. I do not attribute any stratigraphic significance to this determination.

36. *Rhinopteris concinna* (PRESL) HARRIS.

See HARRIS 1931(b), p. 58.

Lepidopteris Zone at 69 m; 1 locality.

The name *Rhinopteris* refers primarily to the fertile specimens. This fern appears to belong to the large group of Palaeozoic Marattiales with Pecopterid leaves and *Asterotheca* fruits. This group appears to

have been most abundant in the early Permian, but is not uncommon in the Trias. This and *Asterotheca cottoni* ZEILLER, also Rhaetic, are among the last known survivors of this group. The corresponding sterile leaf is known from the 'Grenzschrift' flora of S. W. Germany though I do not know in which zone it occurs. As it only occurs in one locality in Greenland the limits of its vertical range are doubtful.

37. **Marattiopsis hoerensis** (SCHIMPER) THOMAS.

See HARRIS 1931(b), p. 60.

Thaumatopteris Zone at 25 m and probably at about 50 m; 1 locality + 2 where the determination is doubtful.

It only seems to be possible to distinguish *M. hoerensis* from *M. muensteri* and other allied species (see HARRIS 1931(b), p. 66) by the bases of the pinnae, which for some reason do not often seem to have been preserved. I cannot therefore be sure that the Greenland specimens from Astarte R. and C. Stewart belong to this species rather than to *M. muensteri*, but I have assumed that they are the same as the abundant material from Dinosaur R., which is undoubtedly *M. hoerensis*.

Of the recently described specimens, those figured by PRINADA (1933) show a pinna base which agrees definitely with *muensteri* rather than *hoerensis*, but those figured by PRINADA (1931) and KRYSHTOF-VICH (1933) could, I think, belong to either species. The fragmentary specimens determined by OISHI (1931b, 1932a) as *M. muensteri* may, as OISHI points out, belong to either species.

The difficulty of distinguishing these two species does not, however, remove their stratigraphic value since both in Europe belong to the *Thaumatopteris* Zone (basal Lias). The existence of the very similar *M. anglica* from the middle Jurassic is a more serious difficulty in the use of fossils of this genus as Zone indicators; and it is very possible that ZEILLER's Tonkin species (which has a leaf base like *M. hoerensis*, but more crowded veins) belongs to a slightly older horizon.

38. **Gleichenites nitida** HARRIS.

See HARRIS 1931(b), p. 67; also HARRIS 1926(b), p. 61 (as '*G. microphyllus* SCHENK').

Thaumatopteris Zone at 25 m; 4 localities.

The only known ferns which can be confused with *G. nitida* are some of the finely divided, sterile *Coniopteris* leaves, and none of these have exactly similar veins.

Genus **PHLEBOPTERIS** HIRMER and HOERHAMMER.

I previously expressed my doubt of the morphological view expressed by HIRMER that in the leaf of the Matoniaceae there is a 'main

pinna'. I take this opportunity of saying that the evidence now put forward by HIRMER and HOERHAMMER appears to me to prove their case convincingly.

39. **Phlebopteris muensteri** (SCHENK) HIRMER and HOERHAMMER.

See HARRIS 1931(b), p. 70 (as *Laccopteris brauni*), also HARRIS 1926(b), p. 62 (as *L. groenlandica*). The specimen figured by HARRIS 1931(b) on Pl. 14, fig. 13 also may belong to this species.

Thaumatopteris Zone at 12—50 m; 7 localities. Additional localities not previously mentioned:

Lejr R., Coal Bed.

C. Stewart, *A. hartzii* Bed.

This fern is one of the most characteristic fossils of the Greenland *Thaumatopteris* Zone.

As a result of the discovery of several much better specimens in the same bed, I have come to the conclusion that a specimen from C. Stewart (referred to above), which I determined as a fragment of a fertile pinna of *P. angustiloba*, belongs to this species. The fragment in question agrees in dimensions with this species, but in its uneven surface with *P. angustiloba*.

MAKAREWICZOWNA (1928) figures a fragment as *L. muensteri* from the Lower Lias of Poland.

HIRMER and HÖRHAMMER (1936) have thoroughly revised this species, and have concluded that there are in the German Liasso-Rhaetic the two rather similar but distinct species — *P. brauni* and *P. muensteri* (which I had previously united). They have re-figured the best German specimens and I am convinced that this conclusion is right.

As I now interpret the two species, *P. brauni* has short wedge-shaped pinnules which are usually crowded and united with their neighbours for 1—2 mm. The veins are usually crowded and make an angle of 45° or less with the midrib. *P. muensteri*, on the other hand, has long, almost parallel-sided pinnules which are seldom crowded and free to near their bases, or only united for 1 mm. The veins usually appear less crowded and the basal branches at least make an angle of more than 45° with the midrib. *P. brauni* is also distinguished by having only about seven main pinnae, while a large leaf of *P. muensteri* has about thirteen. *P. brauni* is scarcely, if at all, known in the fertile condition, but the form of the leaves of the young plant is known; *P. muensteri* is well known in the fertile condition but its young stages are unknown.

I do not agree, however, in their reference of certain specimens

from other countries to these species. In particular, I consider that all the Greenland specimens are best referred to *P. muensteri*, none to *P. brauni*. It is true that certain specimens are intermediate, and, taken by themselves could be placed in *P. brauni* (particularly the specimen refigured by HIRMER and HOERHAMMER in their Text-fig. 4. This specimen is rather extreme in the shortness of its pinnules but even this specimen will be seen to be nearly identical with that figured by HIRMER and HOERHAMMER in Pl. III, fig. 6 (as *P. muensteri*) and considerably different from their *P. brauni* on Pl. II, fig. 1.

The transference of these Greenland specimens leaves '*P. brauni*' without any fertile leaves but it makes the two species much more definite, in my opinion.

In their list of synonyms, HIRMER and HOERHAMMER cite many specimens which I have excluded. Reference to the original figures will show that these are mostly poorly preserved or poorly figured specimens which cannot be definitely excluded from this species but at the same time do not show the details of leaf form, sorus and venation needed for full identification. For the purpose of establishing the reliable geological range, it is best to exclude all but the specimens which show the full characters and these are confined to the Lower Liassic (or perhaps Rhaeto-Liassic). The Cretaceous specimens from W. Greenland, for example, figured by SEWARD (1926) as *L. rigida* are leaves with similar pinnules; the veins are not indicated in most figures but in two they are shown and are different from those of *P. muensteri*. Even if SEWARD's figures represent two species, those without veins do not prove the occurrence of *P. muensteri* in the Cretaceous.

List of references:—

1. The German Rhaeto-Liassic specimens cited by HIRMER and HOERHAMMER, 1936, pp. 17, 18. These are: — GOEPPERT, 1936, figs. 5, 6; BRAUN, 1843, Pl. 9, figs. 3, 7, 8, 10, 11; SCHENK, 1867, Pl. 18, figs. 6, 8, 10; Pl. 24, figs. 1—3, 6—10; Pl. 25, figs. 1, 2; SCHIMPER, 1869—74, Pl. 39, figs. 4, 5, 17—20; HIRMER, 1927, figs. 761, 763. The most important of these specimens are refigured in HIRMER and HOERHAMMER, 1936, together with new ones.
2. The Austro-Hungarian specimens of ANDRAE, 1855, Pl. 7, figs. 1—3 (not 2 C).
3. Probably the Polish specimens of MAKAREWICZOWNA (1928), Pl. 10, figs. 2, 2a.
4. The Greenland specimens figured by HARRIS (see above).

All of these specimens of Rhaeto-Liassic age and indeed all may belong to the basal Liassic. Besides these specimens, there are many showing some degree of similarity from the Cretaceous, Oolite and

Triassic (mentioned by HIRMER and HOERHAMMER) but I am unwilling to accept these as definite proof of the occurrence of this species outside the basal Liassic.

40. **Phlebopteris angustiloba** (PRESL) HIRMER and HOERHAMMER.

See HARRIS 1931(b), p. 74 (as *Laccopteris angustiloba*).

All specimens but the one figured on Pl. 14, fig. 13.

Thaumatopteris Zone at 54 m; 1 locality.

This species was recorded from two localities but the record from C. Stewart depended on a fragmentary and rather exceptional specimen. This I now regard as probably wrongly determined because a number of better but similarly preserved specimens agreeing with *P. muensteri* have since been found in the same bed.

In their revision of *Phlebopteris* HIRMER and HOERHAMMER give many figures of German specimens of this species. Their synonymy of this species as of others includes a good many poorly figured specimens which, though perhaps rightly named, do not establish the existence of *P. angustiloba* at a particular epoch. Well characterised specimens are only known from the basal Liassic, for which the species is a valuable zone fossil.

41. **Phlebopteris polypodioides** BRONGNIART.

See HARRIS 1931(b), p. 77 (as *Laccopteris affinis*).

Lepidopteris Zone at 69 m; 1 locality.

HIRMER and HOERHAMMER (1936, p. 37) have revised this species and consider that it ranges from the Rhaetic to the Cretaceous.

42. **Dictyophyllum exile** (BRAUNS) NATH.

See HARRIS 1931(b), p. 80; also HARRIS 1926(b), p. 64.

Lepidopteris Zone, all levels (up to base of the *Thaumatopteris* Zone. 17 localities + 3 doubtful. According to my field notes this species occurs at Astarte R. in the *Pterophyllum hanesi* Bed.

This species, when fairly complete leaves are available, can be determined with certainty and is one of the most useful zone fossils of the *Lepidopteris* Zone. It occurs in S.W. Germany and in S. Sweden; in both being apparently confined to this zone.

The Liassic fossil determined by SAPORTA (1873, p. 320) as *Thaumatopteris exilis* is undoubtedly different from *D. exile*, but may possibly be a form of *D. muensteri*.

43. **Dictyophyllum nilssoni** (BRONGN.) GÖPP.

See HARRIS 1931(b), p. 81; also HARRIS 1926(b), Text-fig. 7 A only (as *D. exile* in part).

Thaumatopteris Zone 25—50 m; 4 localities.

D. nilssoni varies greatly and different specific names have been

given to several different forms; *D. spectabile* to the largest; *D. nilssoni*, *D. acutilobum* and *D. obtusilobum* to certain of the smaller ones. It resembles the Middle Jurassic species *D. rugosum* both in its sterile and fertile leaves, and is not unlike *D. remauri* ZEILLER of approximately Rhaetic age. It is hardly distinguished from *D. carlsoni* NATHORST (1878a), an imperfectly known fossil from the *Lepidopteris* Zone of Sweden. *D. nilssoni* is confined to the *Thaumatopteris* Zone in the Europe-Greenland area; but its stratigraphic value is lessened by the difficulty which may exist in determining it.

Excellent specimens of the typical form have been figured by OISHI (1932a); and also associated with them fragments of the large *spectabile*-form of this species which he describes as *D. spectabile*. More fragmentary specimens agreeing with certain of the smaller forms have been recently figured by SZE 1933b; TURITANOVA KETOVA (1930) and FRENTZEN (1932, as *D. acutilobum*). The *acutilobum*-form has recently been figured by MAKAREWICZOWNA (1928) from the Polish Liassic.

44. *Dictyophyllum muensteri* (GOEPPERT) NATH.

See HARRIS 1931(b), p. 85.

Thaumatopteris Zone at 25 m and possibly at 50 m; 1 locality + 1 where the determination is doubtful.

OISHI (1932a) has figured a number of specimens, some of which are typical examples of this species (e. g. his Pl. 36, fig. 7; Pl. 37, figs. 2, 4—7) and others which seem intermediate between this species and *D. nilssoni* (e. g. his Pl. 36, figs. 3—6; Pl. 27, figs. 1, 3). The Liassic fossil determined as *Thaumatopteris exilis* by SAPORTA (1873, p. 320) is undoubtedly distinct from *D. exile* but may belong to this species.

This species is a useful indicator of the *Thaumatopteris* Zone, the only one with which it is likely to be confused, being *D. nilssoni* (in its smaller forms), but as this is the same age, confusion of them would not be serious. The spores of the two species distinguish them with certainty.

45. *Clathropteris meniscoides* BRONGN.

See HARRIS 1931(b), p. 88.

Throughout the *Lepidopteris* and *Thaumatopteris* Zones at all levels. 20 localities. The two localities previously given as doubtful are now confirmed.

Specimens of this species have been figured recently by MAKAREWICZOWNA (1928), FRENTZEN (1932), SZE (1931), and as *C. platyphylla* by KRYSHTOFOVICH and PRINADA (1933a).

Two interesting and undoubtedly distinct species are figured by OISHI (1932a) as *C. obovata* OISHI and *C. meniscoides* v. *elegans* (the

latter, if correctly placed in *Clathropteris*, I think distinct enough to be worthy of specific rank).

C. meniscoides is hardly to be distinguished from certain Keuper leaves, and appears to range well into the Lias.

46. *Thaumatopteris schenki* NATHORST.

See HARRIS 1931(b), p. 93.

Thaumatopteris Zone at all levels down to top of *Lepidopteris* Zone. 5 localities. The specimens of *T. schenki* from Dinosaur R. were collected from the *L. carcinoides* Bed, not the *Marattiopsis* Bed as previously stated.

This species, which is very well distinguished by its strongly lobed pinnules, is one of the most useful indicators of the *Thaumatopteris* Zone.

OISHI (1931b, 1932a) has referred some Japanese specimens to *T. schenki*, which show pinnules with almost or quite straight margins. The absence of lobes he explains as being due to the youth of his specimens (the basal pinnules also of *T. schenki* have straight margins) and compares them with some very similar fronds of young plants figured by NATHORST (1907). Until typically lobed specimens (such as greatly predominate in European floras) are discovered in the Japanese floras, it is at least equally possible that his specimens belong to a species such as *T. brauniana*, which never develops lobes; and therefore though they may be correctly determined they do not as yet afford proof of the existence of this species in Japan. OISHI and YAMASITA (1936) have reviewed the genus *Thaumatopteris*.

47. *Thaumatopteris brauniana* POPP.

See HARRIS 1931(b), p. 94; also HARRIS 1926(b), Text-fig. 7c as "*Hausmannia* sp. 1").

Thaumatopteris Zone at 25—50 m; 5 localities.

OISHI (1932a) has figured a poorly preserved Japanese specimen as cf. *T. brauniana*, which certainly appears to agree with this species; and has also determined some well preserved specimens as a new species — *T. elongata*. These specimens agree in outline and in the distribution of their sori with the European and Greenland specimens of *T. brauniana*, and also in their main veins and in the fact that the finest veins are indistinct. OISHI considers that the finest meshes of his specimens ($\frac{1}{3}$ to $\frac{1}{2}$ mm wide) are smaller than in mine, but they seem to me to agree. It should perhaps be pointed out that in my figure of the veins (HARRIS 1926(b), Text-fig. 7 C as '*Hausmannia* sp. 1') only veins actually visible in the preparation are drawn, and as they are only seen clearly in a few places, this results in the venation appearing in many parts a good deal coarser than it really is. The finest meshes are less than half a millimetre wide in my specimens.

48. *Hausmannia* sp. indet. A.

See HARRIS 1931(b), p. 97; HARRIS 1926(b), p. 66 (as *Hausmannia* sp. '2' or 'B').

Thaumatopteris Zone; 3 localities.

It is still uncertain whether the specimens previously figured by me represent one or two species. OISHI and YAMASITA (1936) have recently revised this genus.

Seed plants.

The plants grouped together here include a great many which are not definitely known to have borne seeds but which show some seed plant character such as a resistant cuticle. Their classification is tentative but has been brought up to date in accordance with the work of THOMAS (1933) and FLORIN (1933a). The following provisional classes are adopted:—

1. Cycadales including the *Ctenis* series; also *Nilssonina*.
2. Pteridosperms including the *Thinnfeldia* series.
3. Bennettitales.
4. Ginkgoales.
5. Coniferales.
6. Genera not assigned to the previous classes.

Cycadales.

See FLORIN 1933a, p. 120.

Besides *Ctenis*, *Pseudoctenis* and *Doratophyllum*, a good many leaves of imperfectly known, but probably similar structure are tentatively included here. I have placed *Nilssonina* in this group because its stoma is of the same fundamental type as that of the Cycads and its reproductive organ (*Beania*) appears on the available evidence to be similar to that of *Zamia*.

49. *Ctenis minuta* FLORIN.

See HARRIS 1932(a), p. 8 (as *C. fallax*) and HARRIS 1926(a) (as *Anthrophyopsis crassinervis* in part, Text-fig. 11 A—D only).

See FLORIN (1933a p. 68) for full references.

Lepidopteris Zone at 62—80 m; 54 localities. Additional localities not previously mentioned:

Astarte R., Bed C.

C. Hope, A. minor Bed.

This species, which represents part of NATHORST's '*C. fallax*', has been thoroughly discussed by FLORIN. It is a well defined species and

should be a useful zone fossil. In Sweden, as in Greenland, it occurs in the *Lepidopteris* Zone.

C. latepinnata FLORIN (1933(a), p. 70) has a similar cuticle to *C. minuta* but is distinguished by its much broader pinnae (up to 7.2 cm wide as against 2.2 cm).

FLORIN has, as I think rightly, rejected the name *fallax* NATH., which might have been applied to this species, as a *nomen confusum*.

50. *Ctenis stewartiana* HARRIS.

See HARRIS 1932(a), p. 12.

Thaumatopteris Zone at 12—about 50 m; 5 localities. Additional locality: Dinosaur R., *L. carcinoides* Bed.

This species has been found in Sweden by FLORIN (1933a), who has figured it and compared it with other species. It is well distinguished by the sinuous outlines of the cells of the upper epidermis. The age of its occurrence in Sweden (in the Lias of Hör) agrees with that in Greenland.

51. *Ctenis nilssoni* (NATH.) HARRIS.

See HARRIS 1932 (b), p. 14, p. 88.

Lepidopteris Zone at 62—90 m; 5 localities.

This species has been re-investigated by FLORIN (1933a), who, as a result of the study well preserved cuticles (especially in microtome sections), has investigated their structure closely. He has interpreted the cells round the stoma differently from the way I had done. Compare, for example, my figure 36 B, C with his 21a. His interpretation is based on sections and is certainly correct.

OISHI (1932a) has described a *Ctenis* of similar appearance and venation but with unknown cuticle structure as *C. japonica* OISHI. A good many other specimens of *Ctenis* are known (described under various names), which cannot be satisfactorily distinguished from *C. nilssoni*, which is chiefly characterised by its microscopic structure.

MAKAREWICZOWNA (1928) has identified a fragment (which appears to me indeterminable macroscopically) as being identical with both this species and *Anthrophyopsis crassinervis* Nath.

C. nilssoni is known from the lowest Rhaetic of Bjuf in Sweden. In Greenland it occurs throughout the Rhaetic.

C. laxa FLORIN (1933a, p. 73) has a similar cuticle to *C. nilssoni* but differs somewhat in its gross features; the single known specimen, which is an isolated pinna, is a little broader than the widest referred by FLORIN to *C. nilssoni* (3.7 as against 3.2 cm) and has wider vein meshes (3.5 mm as against a maximum of 3 mm). The Greenland specimens agree in these dimensions with the Swedish *C. nilssoni* rather than with *C. laxa*.

52. ? *Ctenis* sp. A.

See HARRIS 1932(a), p. 15.

Lepidopteris Zone at about 80 m; 1 locality.53. *Quervainia spectabilis* HARRIS.

See HARRIS 1932(a), p. 16.

Lepidopteris Zone at 75 m; 1 locality.Genus *PSEUDOCTENIS* SEWARD.

Pseudoctenis is here used for leaves agreeing macroscopically with *Pterophyllum* but possessing stomata of the 'haplocheilic' (ordinary Gymnosperm) type. It may well include several natural genera. *Pseudopterophyllum* FLORIN (1933a) is a particular type belonging to this complex, which is distinguished by its evenly distributed and longitudinally placed stomata and by other characters. Whether the Greenland species are rightly included can only be settled by the study of the cuticle of the type species of *Pseudoctenis*.

54. *Pseudoctenis spectabilis* HARRIS.

See HARRIS 1932(a), pp. 20, 86; also HARRIS 1926(a), p. 70 (as 'Leaf A').

Lepidopteris and *Thaumatopteris* Zones at all levels; 12 localities.

Additional localities not previously mentioned:—

Neill Cliff, *Clathropteris* Bed, Coal Bed.

This species is possibly represented in Sweden: the leaves figured by JOHANSSON (1922, Pl. 6, figs. 4—6) and determined by him (with some doubt) as *Pterophyllum aequale* agree in their form with small leaves of this species, and, as previously stated (HARRIS 1926b, p. 71), they have a very similar cuticle.

P. spectabilis is equally common in the *Lepidopteris* and *Thaumatopteris* Zones.

55. *Pseudoctenis depressa* HARRIS.

See HARRIS 1932(a), p. 25.

Thaumatopteris Zone at 25 m; 1 locality.56. *Drepanozamites nilssoni* (NATHORST) HARRIS.1878(c). *Adiantites Nilssoni* NATHORST p. 26 (as *Otozamites Nilssoni*); p. 53; Pl. 3, fig. 11.1879, 1886. *A. Nilssoni* NATHORST p. 57 (as *A. agnitus*), p. 120; Pl. 11, figs. 11, 11a.1932(b). *Drepanozamites nilssoni* (NATH.). HARRIS p. 83; Pl. 7, Pl. 8, figs. 1, 2; Text-figs. 44, 45.1933(b). *Rhacopteris*(?) *gothani* SZE p. 42; Pl. 11, figs. 1—3.

See HARRIS 1932(b), p. 14, p. 88.

Lepidopteris Zone at 70—80 m; 2 localities + 1 doubtful (specimen lost).

SZE (1933b, p. 42) has recently described some Chinese specimens under the name *Rhacopteris*(?) *gothani* which agree exactly both in form and venation with the Greenland specimens and are probably identical with them.

He compares this species (which was only known to him in a fragmentary condition) with various Palaeozoic leaves (*Rhacopteris*, etc.) and concludes that no satisfactory distinction could at present be found. It may, however, be remarked that the leaf is only once pinnate (by which it differs from most species of *Adiantites* and that it has a definite cuticle which makes it rather unlikely that it should belong to a fern at all.

According to my field notes this leaf occurs at Zamites R., but the specimen was lost.

57. *Macrotaeniopteris* sp. indet.

See HARRIS 1932(b), p. 18 (as *M. cf. gigantea*); see also FLORIN 1933a, p. 49.

Lepidopteris Zone at 62 m; 1 locality.

This large leaf is too poorly preserved for determination. It is definitely distinct from NATHORST's *T. gigantea* (now *Bjuvia simplex* FLORIN) with which I previously compared it. *B. simplex* FLORIN (1933a, p. 48) has a thicker cuticle of somewhat different structure.

58. *Anthrophyopsis crassinervis* NATH.

See HARRIS 1932(a), p. 28 (as *Glossopteris crassinervis* and HARRIS 1926(b), p. 74 in part; all but Text-fig. 11 A—D and the description of this text-figure).

SZE (1931, p. 5) has recently described a very similar leaf from the Lias of China and has reached the following conclusions:—

1. That the Swedish material of *A. crassinervis* is both generically and specifically indeterminable;

2. that the Greenland leaf is identical with the Chinese, which he renames *Macroglossopteris leeiana* gen. et sp. nov.

Both conclusions are contested by FLORIN (1933a, p. 55), who re-instates the genus *Anthrophyopsis* and renames SZE's specimen *A. leeiana* (SZE) FLORIN. SZE (1933b, p. 41) has since figured another specimen as cf. *M. leeiana*. I agree with both of FLORIN's conclusions.

A. leeiana is distinguished by its tuberculate rachis; while *A. crassinervis* has a longitudinally striated rachis.

A. crassinervis is only known from Greenland and from Bjuf (layer 2) in Sweden.

59. *Amdrupia stenodonta* HARRIS.

See HARRIS 1932a, p. 29.

Lepidopteris Zone at 72 m; 1 locality.

60. *Doratophyllum astartensis* HARRIS.

See HARRIS 1932(a), p. 36.

Lepidopteris Zone at 70—90 m; 6 localities. Two new localities; *Lepidopteris* R., *Lepidopteris* Bed and *Astarte* R., Bed C.

This appears to be a satisfactory species as a zone fossil. FLORIN (1933 a, p. 89; Pl. 13, figs. 2—7) has found *D. astartensis* in rocks of the same age in Sweden and also a second species with a slightly different cuticle structure which is not known from Greenland.

Genus NILSSONIA BRONGN.

Specimens of *Nilssonina* seem to me very difficult to determine specifically even when they have well preserved cuticles, and without cuticles their determination is usually impossible. Owing to this difficulty their stratigraphic value is slight and I have placed no reliance on them in correlating the Greenland flora with other floras.

61. *Nilssonina undulata* HARRIS.

See HARRIS 1932 (a), p. 41.

Thaumatopteris Zone at about 25 m, 4 localities + 1 where the determination is doubtful.

This species possibly occurs in the Swedish Lower Liassic.

62. *Nilssonina obtusa* (NATHORST) HARRIS.

See HARRIS 1932(a), p. 41.

Thaumatopteris Zone at 20 and about 45 m; 2 localities.

This species possibly occurs in the Swedish Rhaetic.

63. *Nilssonina polymorpha* SCHENK (sensu stricto).

See HARRIS 1932(a), p. 46; HARRIS 1926(b), p. 73 in part, Text-fig. 10 A, C only.

Thaumatopteris Zone at 22 m; 1 locality.

Specimens agreeing with the Greenland ones occur in the Swedish and in the German Liassic.

64. *Nilssonina fragilis* HARRIS.

See HARRIS 1932(a), p. 47.

Lepidopteris Zone at 70—90 m; *Thaumatopteris* Zone at 30—50 m; 6 localities.

65. *Nilssonina minor* HARRIS.

See HARRIS 1932(a), p. 49.

Lepidopteris Zone at 65—90 m; 4 localities + 6 where the determination is doubtful.

Specimens agreeing with the Greenland ones occur in the Swedish Rhaetic.

66. *Nilssonia incisoserrata* HARRIS.

See HARRIS 1932(a), p. 50.

Thaumatopteris Zone 20—45 m; 2 localities.

The fructification which I consider to belong to this species I now describe under a separate name as *Beania kochi* sp. nov.

Genus **BEANIA.**

The type species of *Beania* occurs in the Yorkshire Jurassic; it consists of a long axis bearing megasporophylls which appear to be spirally placed; each megasporophyll consists of a stalk bearing a pair of inverted seeds. It has been attributed to the Ginkgoales, but according to information supplied by Dr. H. H. THOMAS there is evidence from both structure and association that it belongs to *Nilssonia*. *B. kochi* is a similar sporophyll and also probably belongs to a *Nilssonia*, but its axis is unknown.

The isolated seeds described by various authors as belonging to *Nilssonia* may probably have been borne in *Beania* fructifications and it is very likely that some species of *Stenorachis* are species of *Beania*.

67. *Beania kochi* sp. nov.

1932(a). *Nilssonia incisoserrata* (in part), seed only, HARRIS, p. 52; Pl. 5, figs. 1—7, 15, Text-figs. 26 C—G, I, J.

Type-specimen HARRIS 1932(a), Pl. 5, figs. 3, 5.

Thaumatopteris Zone at 10 and about 50 m; 2 localities.

Diagnosis. Main axis unknown; lateral branches slender, slightly expanded distally and bearing two seeds; seeds about 10 mm long $\times$ 7 mm wide, surface covered with prominent swellings caused by the presence of resin. Cuticle of outside of integument thick, showing straight-sided cells; cuticles of inside of integument and of nucellus delicate, showing straight cell outlines.

Discussion. *B. kochi* has been described and discussed before; it is probably the female reproductive organ of *Nilssonia incisoserrata*.

68. *Taeniopteris tenuinervis* BRAUNS.

See HARRIS 1932(a), p. 34.

Lepidopteris Zone from its top to 69 m; 3 localities.

Leaves like *T. tenuinervis* BRAUNS, though specially common in the Rhaetic, range the mesozoic and doubtless belong to a whole series

of species which at present are undistinguished and have no stratigraphic value. OISHI (1932a) gives a useful list of such specimens. Among recently described specimens resembling the Greenland *T. tenuinervis* are those figured by PRINADA (1934) and OISHI (1932a) (as *T. tenuinervis* and as *T. lanceolatus*).

69. **Taeniopteris** sp. A.

See HARRIS 1932(a), p. 34.

Lepidopteris Zone at 72 m; 1 locality.

2. Pteridosperms.

See THOMAS 1933.

Genus **THINNFELDIA** Ett.

1852. *Thinnfeldia* ETTINGSHAUSEN, p. 2.

The genus *Thinnfeldia* had a peculiar distribution in Europe in Rhaeto-Liassic times; it is abundant in France and Germany, somewhat rare in most of the rest of Europe, e. g. Sweden and Poland, and, until the fragment described below was found, not known at all from Greenland. This extreme rarity in Greenland is remarkable because the other elements of this flora are very similar to those of Sweden and Germany.

The single fragmentary specimen was determined generically by the structure of the cuticle. The features mentioned below, especially the very highly developed ring of subsidiary cells together with what is known of the venation is characteristic of many species of this genus. It is not, however, possible to determine it specifically; it might possibly belong to any of the three Swedish species though it differs from the figured specimens (ANTEVS 1914a) in various details.

70. **Thinnfeldia** sp.

Text-fig. 1.

Occurrence. C. Stewart, probably from the *G. minuta* bed; *Lepidopteris* Zone.

Description. A small fragment, about 2 mm square, of a leaf was found in a bulk maceration which shows the cuticle characters of various *Thinnfeldia* species (e. g. *T. major* RACIB. as interpreted by ANTEVS (1914(a), p. 35; Pl. 3, fig. 1). The fragment shows an indication of three veins at intervals of 0.45 mm, which meet the margin at an angle of 45°.

Both cuticles are very thick. The upper is without stomata and gives no clear indication of veins. It shows the outlines of polygonal

cells with very thick straight walls. The cells are for the most part arranged irregularly, but here and there with an indication of a longitudinal row. The cells are without papillae and hairs are probably absent, but occasional cells are much thickened and may be the bases of hairs, but more probably are a traumatic effect (cf. ANTEVS 1914(b), p. 6).

The surface is probably without sculpture.

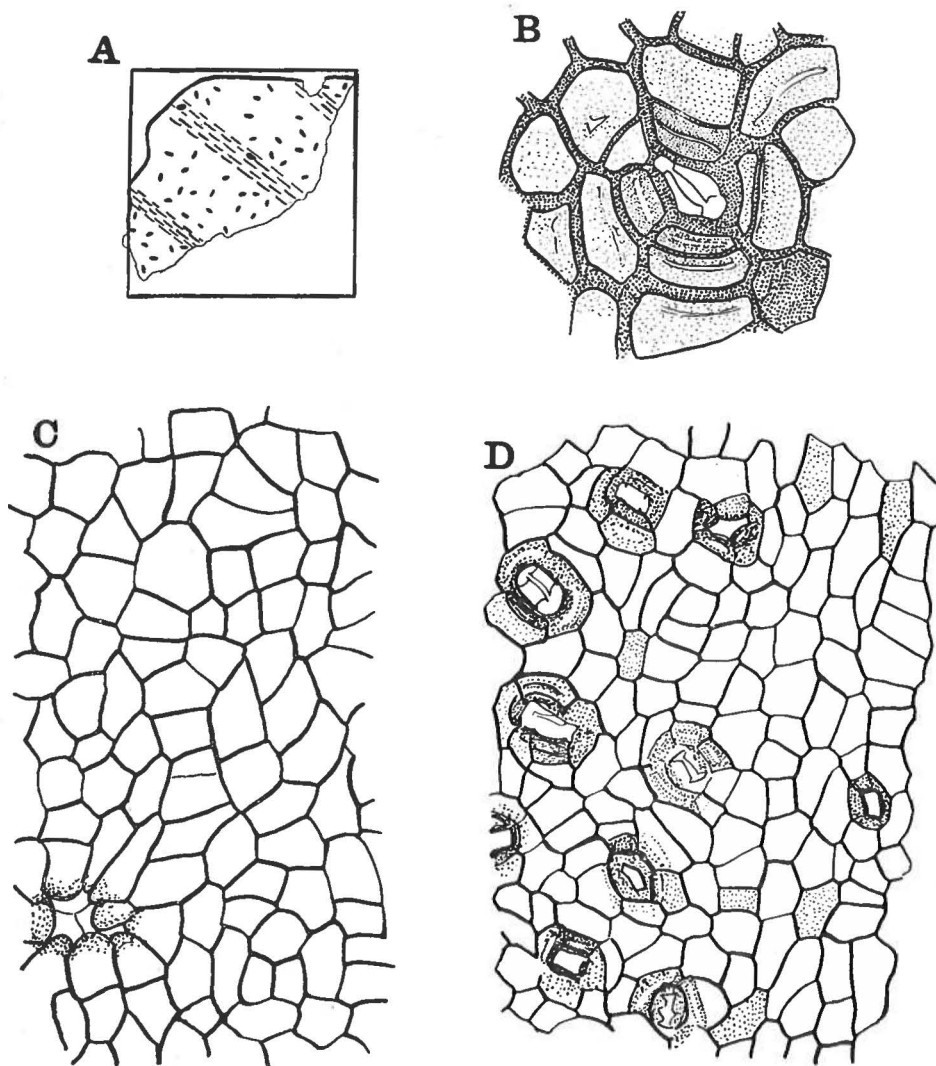
The cuticle extends inwards a considerable distance along the lateral walls of the cells as far as the base of the cells, where it is rather irregularly developed and gives an indication of a second layer of cells (hypodermal) of similar size and shape to the epidermal cells.

The lower cuticle is also thick, but slightly thinner than the upper. The stomata are arranged in broad strips between the veins with only occasional ones along the veins. The epidermal cells are polygonal and straight-sided with extensions of the cuticle along their margins forming very conspicuous cell-outlines. The periclinal wall is either evenly thickened or has slight and irregular pitting; often there is a thin straight strip along the middle of a cell forming a pale stripe. Occasional cells still possess thickened inner periclinal walls, such cells appearing very dark. No hairs or papillae occur in any part of this fragment.

Between the veins there is no indication of cell rows and the cells are isodiametric; along the veins they tend to be rectangular and form rather indefinite longitudinal rows.

The stomata are evenly scattered and are in the areas between the veins and are not arranged in longitudinal rows. They are irregularly orientated, and just as many appear to be placed transversely as longitudinally. They are haplocheilic and dicyclic. The guard cells are sunken and rather thinly cutinised; the aperture is 12μ long and appears to be at a good deal lower level than the poles of the guard cells. The guard cells are surrounded by a rather regular ring of 4—6 subsidiary cells which are narrower and usually more thickly cutinised than the other epidermal cells. The thin strips on the surface of these cells are particularly prominent and run parallel with the stomatal pit. The subsidiary cells form the stomatal pit which is occasionally circular but more commonly is narrow and elongated in the direction parallel with the aperture. The mouth of the stomatal pit is open and not protected by any cutinised ingrowths of the subsidiary cells; the margin of the pit, however, is heavily cutinised.

Encircling cells occur opposite almost all the subsidiary cells; sometimes they are a little thicker but more commonly are exactly like the other epidermal cells and are only distinguished by their position. The thin strips of these cells also run parallel with the stomatal pit margin.



Text-fig. 1. *Thinnfeldia* sp.

A, distribution and orientation of the stomata in a fragment of the lower cuticle. The square is 1 sq. mm. B, stoma, $\times 400$. C, upper cuticle, $\times 200$. D, lower cuticle, $\times 200$. All the figures drawn from Slide No. 1190.

71. *Lepidopteris ottonis* (Göpp.) Schimper.

See HARRIS 1932(a), p. 58; 1926(b), p. 67.

Lepidopteris Zone at all levels from its base up to the base of the *Thaumatopteris* Zone. 15 localities.

New locality not previously mentioned: Neill Cliff Coal Bed; this bed is transitional between the *Lepidopteris* and *Thaumatopteris* Zones. Also according to field notes, Astarte R., *Pterophyllum hanesi* Bed.

This species appears to be the most valuable zone fossil of the *Lepidopteris* Zone (Rhaetic) in the region of Europe and Greenland. It has recently been found in China (SZE 1933a) and has been compared with a similar species, *L. nataliensis*, by THOMAS (1933).

The microsporophyll is mentioned here under the name *Antevsia zeilleri* (p. 35), and the seed-bearing organ as *Peltaspermum rotula* (below). I have previously pointed out the reasons (HARRIS 1932(a), p. 62) why I am unable to accept ANTEVS's record of *L. ottonis* from the Liassic of Hör.

Genus **PELTASPERMUM** gen. nov.

Type species *P. rotula* HARRIS.

Diagnosis. Seed bearing fructification consisting of an axis with lateral branches terminating in peltate discs. Under surface of discs bearing a ring of seeds. Seeds with a prominent micropyle, a free and cutinised nucellus and a cutinised megaspore membrane.

Cuticle of axis and of seed-bearing discs wrinkled or blistered. Stomata haplocheilic, guard cells at the bottom of a pit formed by the subsidiary cells and protected by the papillae of the subsidiary cells.

This genus is put forward to include the seed-bearing organs referred to *Lepidopteris* which are known in *L. ottonis* and in *L. nataliensis* THOMAS. The name is based on the 'Peltaspermaceae' of THOMAS a family made for *Lepidopteris*.

72. **Peltaspermum rotula** sp. nov.

1886. undetermined fossil, NATHORST p. 113, Pl. 25, fig. 17.

1932(a). *Lepidopteris ottonis* in part; HARRIS, p. 65; Pl. 6, figs. 3—9; Pl. 7, figs. 3—9; Pl. 8, figs. 1—3, 5, 6, 9, 10; Text-fig. 28.

Type-specimen HARRIS 1932(a), Pl. 6, figs. 3—6.

Lepidopteris Zone at 62—85 m; 5 localities. Additional locality, Zamites R.

Diagnosis. Peltate seed-bearing head 10—12 mm in diameter; margin lobed; under-surface probably bearing about twenty seeds; micropyle of seed curved. Surface of axis and of peltate head covered with blister-like swellings; cuticle of exposed surface of peltate head thick.

This fossil, the seed-bearing organ of *Lepidopteris ottonis*, has been discussed by HARRIS (1932(a)), THOMAS (1933, p. 254), HIRMER (1936). The specific name is from *rotula*, a little wheel.

Peltaspermum thomasi sp. nov.

1933. *Lepidopteris nataliensis* in part, THOMAS, p. 254; Pl. 24, fig. 78 and Text-fig. 55 (Type-specimen).

Diagnosis. Peltate seed-bearing head 3—5 mm in diameter, margin not definitely lobed, probably bearing less than ten seeds of which only a few came to maturity; micropyle of seed nearly straight; cuticle of axis and peltate heads rather thin, surface of axis and head without any prominent blister-like swellings.

The only specimen was collected by THOMAS in the ?Middle Triassic (Molteno Series) of South Africa and was described by him. I have named it after him.

ANTEVSIA Gen. nov.

Type-species *A. zeilleri* (Nath.).

Diagnosis. Microspore-producing organ consisting of an axis about 10 cm long bearing pinnately arranged branches about 2 cm long. Branches themselves dichotomising in various planes, ultimate branches bearing one or more, usually two, rows of pollen sacs. Pollen sacs oval, about 2 mm long, unilocular, dehiscing by a longitudinal slit. Pollen grains oval, 30μ long with smooth walls. Surface of axis covered with blisterlike swellings, cuticle well developed, showing polygonal cells and sunken stomata surrounded by an irregular ring of subsidiary cells; subsidiary cells possessing flattened papillae which project inwards over the aperture and overlap rather irregularly.

Discussion. This name has been instituted for *Antholithus zeilleri* on the grounds that *Antholithus* is not a genus at all but only a designation for fossil 'flowers' in general. This fossil, which is the pollen-bearing organ of *Lepidopteris*, should be described under a separate name and is well enough characterised to merit a generic name of its own.

The genus is named after Dr. ANTEVS, who added greatly to our knowledge of this organ.

73. *Antevsia zeilleri* (NATH.) n. comb.

1908b. *Antholithus zeilleri* NATHORST, p. 20; Pl. 2, figs. 59, 60; Pl. 4.

1914b. *Antholithus zeilleri* NATH., ANTEVS, p. 10; Pl. 3, figs. 1—16.

1922. *Antholithus zeilleri* NATH., JOHANSSON, p. 28, Pl. 1, figs. 11—13.

1932(a). *Lepidopteris ottonis* (in part) — microsporophyll, HARRIS, p. 62, Pl. 7, figs. 1, 2, 10, 11.

Lepidopteris Zone at 62—85 m; 4 localities.

See HARRIS 1932(a), p. 62.

74. *Ptilozamites nilssoni* NATHORST.

See HARRIS 1932(a), p. 71; 1926(b), p. 69.

Lepidopteris Zone; all levels to base of *Thaumatopteris* Zone; 13 localities. New locality; C. Stewart, *Ginkgoites minuta* Bed (*Lepidopteris* Zone).

This species appears to be an excellent zone fossil of the European Rhaetic.

FRENTZEN (1932) has refigured SALFELD's "*Nilssonia propinqua*" as *Keraiaphyllum suevicum* n. gen. et sp. and gives a restoration of the whole leaf, which appears to agree perfectly with this species. A fragmentary Japanese specimen has also been referred, provisionally, to this species by OISHI (1932a, p. 322).

The 'microsporophyll', *Hydropterangium marsilioides*, is held to belong to this species.

75. *Hydropterangium marsilioides* HALLE.

See HARRIS 1932(b), p. 122 (misspelt as '*Hydropteridangium*').

Lepidopteris Zone at 85 m; 1 locality.

This is very probably the microsporophyll of *Ptilozamites*. It is known also from Bjuf in Sweden.

76. *Stenopteris dinosaurensis* HARRIS.

Text-fig. 2; Pl. 1, fig. 10.

1924. *Baiera cf. angustiloba* (non HEER) CHOW, p. 10, Pl. 1, fig. 21.

1932(a). *Stenopteris dinosaurensis* HARRIS, p. 75; Pl. 8, fig. 4, Text-fig. 31.

1935. *Stenopteris dinosaurensis* HARRIS, p. 35, Pl. 5, figs. 8, 9; Text-fig. 18.

Thaumatopteris Zone from 20 m down to beds transitional between this and the *Lepidopteris* Zone; 9 localities.

The following two localities had not previously been mentioned:—Storgaard R. and C. Stewart, *Todites* Bed.

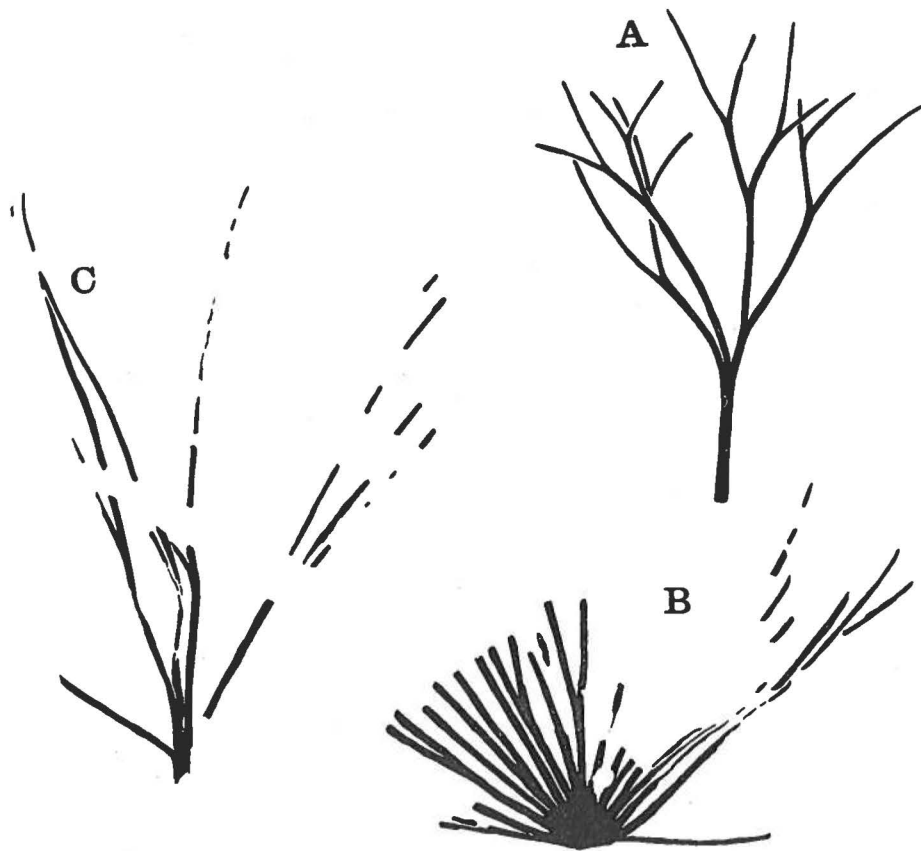
This species proves to be widespread though by no means abundant in the *Thaumatopteris* Zone of Greenland. Fragments, such as are generally found, are just like fragments of rather broad *Czekanowskia* leaves and are only to be distinguished by their cuticles. Even the cuticle shows in its strong gymnospermous features a certain resemblance to the Ginkgoales, though it has certain features which distinguish it as a species, at least, from all known Ginkgoales.

During the investigation it was realised that specimens of *S. dinosaurensis* had been overlooked as imperfect specimens of *Czekanowskia*. The cuticle of every *Czekanowskia* fragment was therefore prepared (several hundreds in all) and as a result a good many fragments of *S. dinosaurensis* were discovered and, in addition, three additional specimens of nearly complete leaves.

S. dinosaurensis proves to vary both in form and in cuticle, but I consider that all the forms belong to one species. The new information makes a re-diagnosis desirable.

The variation in form is between the extremes illustrated in Text-

fig. 2; one extreme is a leaf with a rather slender petiole branched dichotomously in its upper part; the other, a leaf apparently with no petiole but a triangular central region from which diverge a considerable number of dichotomous branches. The Type-specimen (HARRIS 1932(a), p. 76) and the specimen shown in Pl. 1, fig. 10 are intermediate in showing a rather elongated central region with laterally placed seg-



Text-fig. 2. *Stenopteris dinosaurens*.

A, complete leaf, No. 1132, 1133, Dinosaur R. B, nearly complete leaf, C. Stewart, *Todites* Bed, No. 1121. C, fragmentary leaf, Storgaard R., No. 1123. All the figures are natural size.

ments. Probably those shown in HARRIS 1935(a), p. 36, are of this form too. These differences, though great, are comparable to the differences which exist between, for example, the radicle and cauline leaves of *Capsella bursa-pastoris* L. and occur also even in woody plants at different parts of the same shoot.

The differences in cuticle are between leaves with cells as long as broad and ones with cells several times longer than broad, leaves with

rather sparsely and weakly developed epidermal papillae, and stomata with little indication of papillae on their subsidiary cells to others surrounded and overhung by very large papillae. Most of these differences — at least as regards the stomata — can be found in a single specimen.

Diagnosis (based on all available specimens). Leaf of varying form, consisting of a petiole which may be up to 1.5 cm long but may be undeveloped and a central portion bearing lateral segments in more or less crowded opposite pairs. Number of segment pairs varying from about six down to one (when the petiole dichotomises), typically about three placed at intervals of 2 mm. Segments 5–10 cm long, 1–2 mm wide, branched dichotomously one to three times. Substance of leaf very hard and thick, segments showing a single dark central strand or 'vein'. Apices of segments acute. 'Mesophyll' often forming transverse plates; resin bodies absent. Cuticle very thick, usually of the same thickness on the two sides of the leaf; position of vein either unrecognisable or only faintly indicated in the cuticle. Epidermal cells with straight, strongly marked lateral walls; elongated in some parts of the leaf, almost square in other parts but placed in longitudinal rows. Surface of cells appearing finely granular but without definite pitting; typically with occasional cells developed as a very prominent hollow papilla, the majority of cells without papillae, but in other specimens all cells with similar, rather weakly developed median papillae, and in others with weak papillae only discernable in a few cells. Extent to which papillae are developed often differing on two sides of leaf. Stomata rather sparse but equally numerous on the two sides of the leaf, placed in several short longitudinal rows, the rows commonly giving no indication of the vein, but occasionally tending to be grouped in two main sets on one side (? the under). Stomata sunken, surrounded by five or six subsidiary cells which are commonly smaller than the other epidermal cells. Surface of the subsidiary cell occasionally no thicker than the other epidermal cells, but usually more or less thickened, sometimes strongly thickened. Subsidiary cells almost invariably bearing a local thickening which often takes the form of a conspicuous slightly hollow papilla more or less overhanging the stomatal pit. In other stomata the papillae are produced in the middle of the subsidiary cells as in other epidermal cells; in others they are united to form a more or less even ridge round the stomatal pit. Stomatal pit round or oval, about $20\mu \times 16\mu$; stomatal aperture usually placed longitudinally, about 20μ long. Surface of guard cells thinly cutinised except near the aperture, where it is fairly thick. Encircling cells absent or very occasionally and irregularly produced. Trichomes (apart from the epidermal papillae) absent.

Comparison. *S. dinosaurensis* is distinguished from *S. astartensis*

by its broader and more crowded leaf segments, by its epidermal papillae and by its larger stomata in which the cuticle of the subsidiary cells seldom, if ever, forms a rim with a round hole over the aperture. From *Thinnfeldia schwarzi* GOTHAN (1914) it differs in its more crowded and branched segments, while its stomata look very different owing to its subsidiary cells having no central thin region. *S. desmomera* SAPORTA (1873) has also less crowded segments; its cuticle is unknown. There are possibly a good many species of '*Stenopteris*' in the older Mesozoic rocks of the southern hemisphere but they most or all differ in showing an initial dichotomy of the rachis and then unbranched, or pinnately branched, segments. Their cuticles, where known, are different (see THOMAS 1933, p. 249).

S. dinosaurensis is a characteristic fossil of the *Thaumatopteris* Zone of Greenland and also probably of Sweden.

77. *Stenopteris astartensis* HARRIS.

See HARRIS 1932(a), p. 77.

Lepidopteris Zone at 85 m; 1 locality.

An additional specimen was obtained which agreed closely with the one figured.

Caytoniales.

78. *Sagenopteris nilssoniana* (BRONGN.) WARD.

See HARRIS 1932(b), p. 5; 1933, p. 104; 1926(b), p. 77.

Thaumatopteris Zone, 20—54 m; 4 localities.

See also *Caytonia* and *Caytonanthus*.

MAKAREWICZOWNA (1928) has figured a leaflet of this species from the Lias of Poland. Her "*S. phillipsi*" matches such specimens of *S. nilssoniana* as that figured by HARRIS 1932(b), Text-fig. 1 D and in all probability belongs to *S. nilssoniana*. *S. nilssoniana* is characteristic of the *Thaumatopteris* Zone (basal Liassic of Greenland and various parts of Europe). It is only distinguished with certainty by the structure of its cuticle taken in conjunction with the range of form of fairly numerous specimens. A small specimen from Japan is provisionally identified as *S. nilssoniana* by OISHI and TAKAHASI (1936).

79. *Caytonia thomasi* HARRIS.

See HARRIS 1933, p. 97; 1926(b), p. 77.

Thaumatopteris Zone from 20 m to the top of the *Lepidopteris* Zone (60 m); 4 localities.

New localities: Neill Cliff Coal Bed (this bed is transitional between

the two zones) and probably in C. Stewart, *Todites* Bed. Both of these localities refer to isolated seeds obtained in bulk macerations.

In macerating the Neill Cliff Coal I obtained six seeds which I refer to this species. They are a little shorter than most, but by no means all, seeds of *C. thomasi*, but agree perfectly in structure. With them was a fragment of an unripe anther of the *Caytonanthus arberi* type. No *Sagenopteris* leaves were found, but this was not surprising as the cuticle of this leaf is delicate and unless very abundant is usually lost in bulk maceration.

Genus **CAYTONANTHUS** gen. nov.

Type-species *C. arberi* (THOMAS).

Diagnosis. Pollen-bearing fructification consisting of a slender 'axis' probably only two or three centimetres long, bearing short lateral branches which are arranged irregularly but probably confined to the horizontal plane. Lateral branches themselves branched irregularly but in one plane and terminating slight spatulate expansions, either produced singly on short branches or in groups of two or three where the ultimate branches are weakly developed. Each expansion bearing on its surface a single sessile 'anther' or synangium consisting of four (occasionally three) elongated pollen sacs arranged radially round a central core of tissue. Pollen sacs rounded in section, wall of pollen sacs thin. Anther typically 3—10 mm long, 1—2 mm wide with a pointed apex.

Cuticle of main 'axis' delicate, showing straight-walled cells of slightly different dimensions on the two sides (i. e. dorsiventral). Cuticle of lateral branches showing elongated cells, anther-bearing expansions showing isodiametric straightwalled cells. Cuticle of anther very delicate and without hairs. Thickened cells bearing a short hair occurring on the 'axis' and branches.

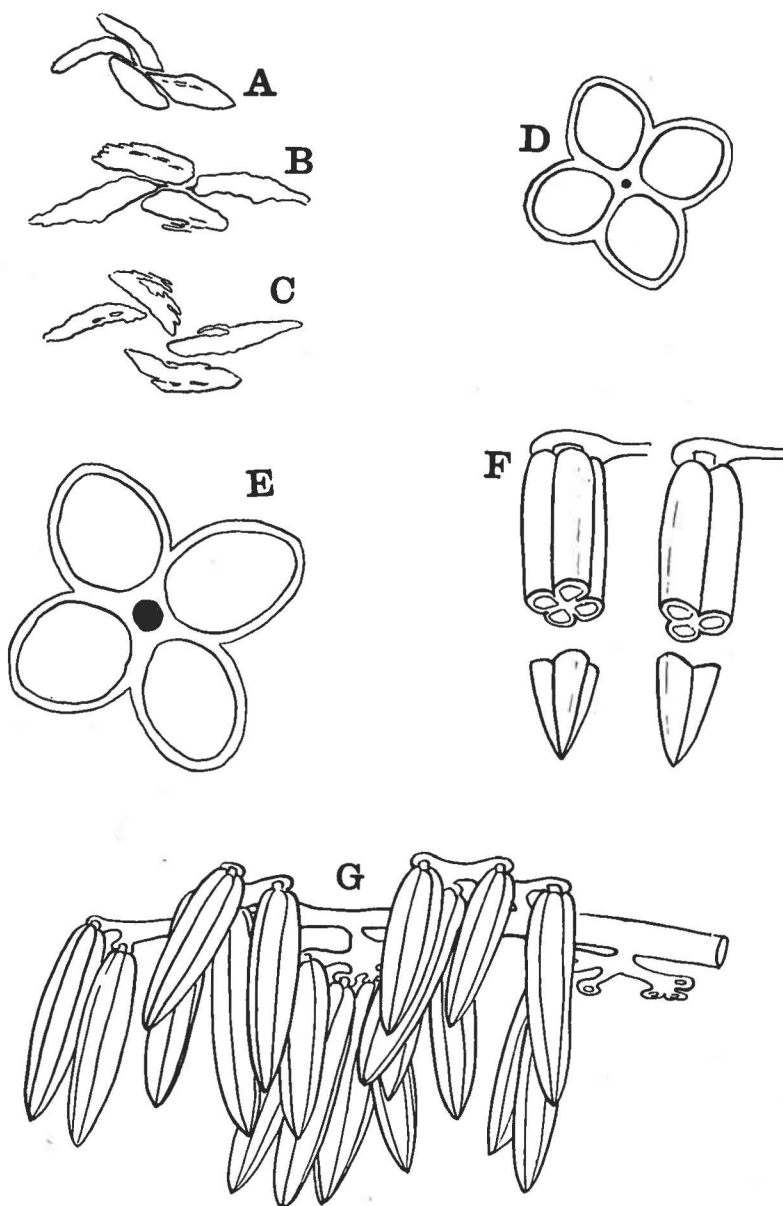
Pollen grains very numerous, often appearing to be packed in longitudinal rows in immature anthers. Pollen grains transversely elongated, consisting of a central cell and two lateral 'air sacs'. Air sacs placed slightly asymmetrically, the central cell being slightly wedge-shaped; the pollen grain thus appearing curved when viewed from the side but straight from above or below. Pollen grains of the order of 20—30 μ from wing to wing and 12—20 μ across.

The name is from Cayton Bay and *anthus*, a flower.

Discussion. This fossil is well enough characterised to merit a generic name — *Antholithus* is merely an artificial group name for fossil 'flowers'.

Some new information has been obtained as a result of re-investigation of the Greenland material, and also certain conclusions put forward tentatively by THOMAS (1925) have been confirmed.

1. Sections through immature anthers (Text-fig. 3 A—C) strongly support THOMAS's view (expressed in his restoration) that the anther was radially symmetrical. When allowance is made for crushing — by



Text-fig. 3. *Caytonanthus kochi*.

A, B, C, microtome sections through a macerated anther; A, from near the apex, B from the middle and C near the base; D, restoration of A; E, restoration of C; all $\times 40$, Slide 705—708. F, restoration of two anthers, one with four, one with three loculi, $\times$ about 10. G, restoration of the end of the microsporophyll, $\times$ about 6.

magnifying the width of the pollen sacs by about 3 in the direction of their compression — the four sacs appear equal and to be radially placed round a central core presumably occupied by vascular tissue. This central core is fairly thick at the base of the anther but tapers towards the apex.

2. Certain anthers have only three pollen sacs, but these, as far as can be seen, are placed radially. About a dozen anthers were examined and of these two had three, the rest four, sacs.

3. The anthers are attached superficially — not terminally — on the spatulate ends of the branches. As far as is known they are all borne on the same side of the branch. In my restoration, they are represented as being on the lower side, but there is as yet no evidence of this.

4. The anthers were attached singly on each ultimate branch, or at most in groups of two or three where the branches are partly concrescent, not in bunches or tassels as in Dr. THOMAS's restoration. This is shown clearly by the structure of the branches in *C. kochi*, but seems equally to be the case in *C. arberi* (see SEWARD 1919, Text-fig. 654, which THOMAS identifies as *C. arberi*).

5. *C. kochi* is satisfactorily distinguished from *C. arberi* by the detailed structure of the pollen. Associated with *C. arberi* is a second hitherto undescribed species. It is probable that *C. kochi* belongs to *Caytonia thomasi* and *Sagenopteris nilssoniana*; it may be presumed that the two types of pollen in Yorkshire belong to the two associated species of Caytoniales.

It may be pointed out that it is not yet known how the *Caytonanthus* anthers dehisced, nor is it known whether they were produced on the upper or under-side of the branches. A re-examination of the Yorkshire specimens of *Caytonanthus* is needed to show which belongs to which of the fruit species.

Caytonanthus and the systematic position of the Caytoniales.

The difference between *Caytonanthus* and any type of Angiosperm stamen or flower appears to me to have been increased by the new points brought out above. The 'anther' appears to be a radially symmetrical synangium of the *Asterotheca* type, while in almost all flowering plants it is a bilaterally symmetrical organ with a connective (occasionally strongly developed) and two lateral thecae. There is no similarity between the way the anthers of *Caytonanthus* and the flowering plant are borne on their filaments, but, on the other hand, if they were borne on the lower side they had a considerable resemblance to the type of fructification seen in certain ferns and Pteridosperms. The difference between their male organs added to the differences between their female organs

suggests strongly that the Caytoniales should at present be considered as having no definite phylogenetic relationship to the flowering plants, their angiosperm-like pollination being a convergent development which may yet have great evolutionary significance as indicating the path of evolution of the flowering plants.

80. *Caytonanthus kochi* sp. nov.

Text-figs. 3, 4 H—J.

?1908(b). Pollen grains; NATHORST, Pl. 2, figs. 56, 58.

1926(b). *Sagenopteris nilssoniana* stamen and pollen; HARRIS, p. 77; Pl. 8, figs. 4, 5, 9; text-fig. 12 B.

1932(b). *Antholithus* sp. aff. *A. arberi*; HARRIS, p. 14; Text-fig. 2 A—E.

1933. *Sagenopteris nilssoniana* stamen and pollen. HARRIS, p. 103; Text-fig. 11, 12; and pollen grains in seed, Pl. V, fig. 4.

Occurrence. Vardekløft, *P. agardhianus* Bed (*Sagenopteris* shale at the base of this bed).

Neill Cliff, Coal Bed (new record).

C. Stewart, *A. hartzi* Bed.

The Neill Cliff bed is transitional, the other two belong to the *Thaumatopteris* Zone; 25 to 50 m.

Diagnosis. Main 'rachis' not known. Lateral branches attributed to *C. kochi*, about 0.4 mm wide, reaching a length of at least 3 mm, ultimate branches produced alternately or in irregular groups. Scar of attachment of anther 0.2 mm wide. Cuticle delicate, showing narrow straight-sided cells towards the distal end, the cells becoming isodiametric and about 30μ wide. Hairs occurring fairly frequently, especially at the distal ends, consisting of a more thickly cutinised cell about 30μ wide, bearing a unicellular cutinised hair 40μ long, 15μ wide. Stomata not observed. Anther cylindrical or ovate, 2.5—6.5 mm long, commonly 4 mm long, about 0.8—1.2 mm broad; base abruptly contracted; apex pointed. Cuticle of anther delicate, showing narrow straight-sided cells.

Pollen grains commonly 30μ from wing to wing, 18μ in diameter (limits of variation in length 33μ and 26μ), fairly thickly cutinised. Walls separating central cell from wings strongly marked. Surface of central cell smooth; surface of wings nearly smooth, showing only the most indistinct thickenings and pits.

Comparison. The form of the antherophore of *C. kochi* is, so far as is known, the same as in *C. arberi*; the anthers differ in being slightly narrower (1.5—2 mm broad in *C. arberi*). The pollen grains of *C. kochi* are well distinguished both from *C. arberi* and *C. sp. A.* *C. kochi* has large grains with a rather thick wall which is almost without sculpturing; *C. arberi* is equally large, the wall is rather thinner and the surface of

the wings is finely and fairly regularly pitted. *C. sp. A* has small thinly cutinised grains with a rather indistinct, coarse and irregular pitting. *C. kochi* (basal Liassic) is attributed to *Sagenopteris nilssoniana* and *Caytonia thomasi*; *C. arberi* and *C. sp. A* presumably belong to *Gristhorpia nathorsti*, perhaps to *Caytonia sewardi* and the two species of leaf called *Sagenopteris phillipsi*.

Notes on the pollen of some Jurassic Caytoniales.

For comparison some pollen was prepared from the Lower Oolitic shale forming the famous plant bed of Cayton and Gristhorpe bays, Yorkshire. I am indebted to Dr. M. BLACK for the material.

Caytonanthus arberi (THOMAS) n. comb.

Text-fig. 4 D—G (English Material).

1900. *Ginkgo*, male flower; SEWARD, text-fig. 45.

1900. *Ginkgo* male flower; SEWARD and GOWAN, Pl. 9, fig. 28.

1919. *Ginkgo* male flower; SEWARD, Text-fig. 654.

1925. *Antholithus arberi* THOMAS, p. 327, Pl. 14, figs. 33—40; Text-figs. 9 A, 10.

The pollen determined as *C. arberi* (Text-fig. 4 D—G) is very well preserved. A very large number of grains were measured; the dimensions are as follows: average size $29\mu \times 17\mu$; extreme measurements from wing to wing, highest 36μ , lowest 24μ ; the most slender spore measured was $31\mu \times 12\mu$.

The spore is clearly divided by a thin wall into a central cell and two wings; the wings are sculptured, the central cell typically smooth, but the cuticle of the wings may overlap the central cell, and occasionally fine sculpturing is visible on the central cell.

The sculpture under a fairly low magnification has the appearance of granules but at higher magnification consists of fine, more or less circular pits separated by somewhat irregular ridges which are occasionally developed as small granular thickenings. While there is some variation in the pitting, all spores show a considerable portion of their wings at least which is regularly pitted. Occasionally the whole wing is as clearly and regularly pitted as the shell of certain diatoms. The pitting is most conspicuous in water mounts, but still clearly shown in glycerine.

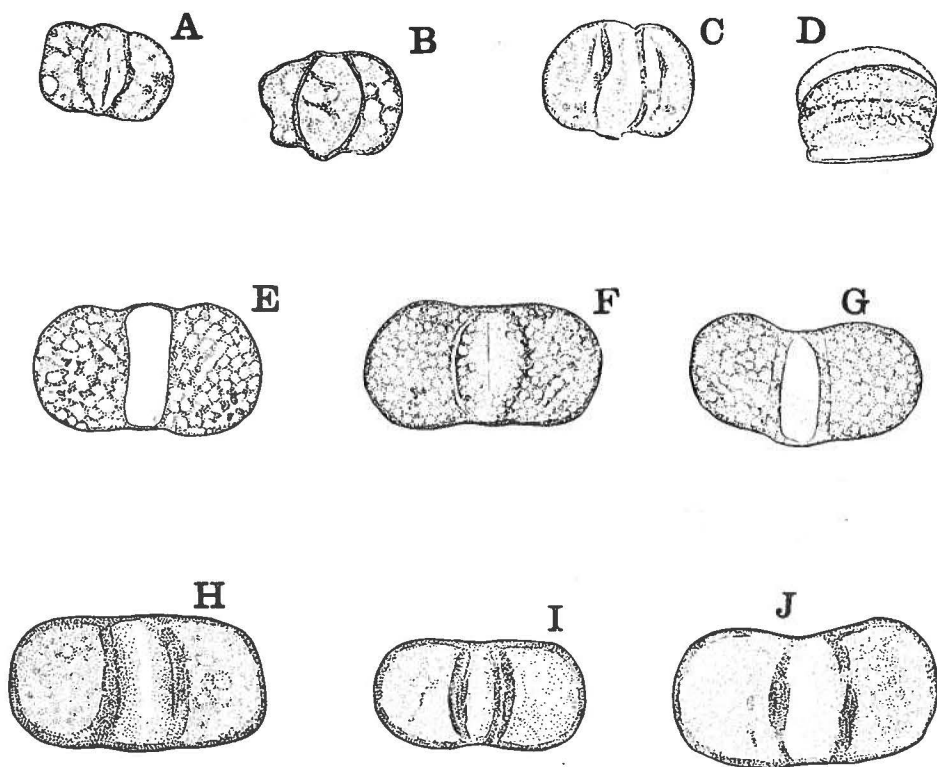
Caytonanthus sp. 'A'.

Text-fig. 4 A—C.

The pollen described as *C. sp. A* consists of smaller and usually less well preserved grains than *C. arberi*. The dimensions are average size $20\mu \times 13\mu$; extreme measurements from wing to wing, highest 21μ , lowest 18μ ; relatively widest spore measured $18\mu \times 17\mu$.

The wall is thin and in most cases had collapsed somewhat, but a few excellently preserved specimens were studied. The central cell is only a little smaller than that of *C. arberi*, but the wings are much shorter, and their surface has only rather vague indications of sculpture which may take the form of coarse and very irregular pitting. The delicacy of the wall of *C. sp. A* and the consequent ill preservation makes it a less satisfactory species than *C. arberi*.

The possibility was considered that these spores might be an ill



Text-fig. 4. *Caytonanthus* spp.; pollen grains.

A—C, *C. sp. A*; D—G, *C. arberi*; H—J, *C. kochi*; Slide 93, Hartz Collection. All the pollen grains are figured at a magnification of 1000; those of *C. arberi* and *C. sp. A* were obtained from the Gristhorpe Bay plant bed (Jurassic, Yorkshire, England); those of *C. kochi* are adhering to a leaf of *Sagenopteris nilssoniana*.

preserved state of *C. arberi*. This view was rejected because very few spores were seen which could not at once be referred to one or other type, differing, as will be seen, in thickness of wall, shape, dimensions and sculpture.

In the Greenland spores of *C. kochi*, which are associated with one sort only of leaf and of fruit and therefore presumably belong to

a single species, the form and dimensions of the spore coat are rather constant, a fact which is in agreement with the view that the very varied Yorkshire spores belong to more than one species. Although I consider *C. sp. A* distinct I have refrained from naming it in the hope that it may ultimately be described from better material.

81. **Sagenopteris serrata** HARRIS.

See HARRIS 1932(b), p. 11.

Lepidopteris Zone at about 70—85 m; 2 localities.

82. **Sagenopteris hallei** HARRIS.

See HARRIS 1932(b), p. 10.

Thaumatopteris Zone at about 25 and at 54 m; 2 localities. Additional Locality: C. Hope, Coal.

In my diagnosis the size of the vein meshes, actually 6 mm $\times$ 0.4 mm, is wrongly stated as 6 mm $\times$ 4 mm.

The new specimen is a fragment of well preserved cuticle obtained by bulk maceration.

83. **Amphorispermum rotundatum** HARRIS.

See HARRIS 1932(b), p. 17.

Lepidopteris Zone at 63—85 m; 5 localities.

84. **Amphorispermum major** HARRIS.

See HARRIS 1932(b), p. 17.

Thaumatopteris Zone, 20 m to base; 5 localities.

A. major has been found in the following localities in addition to those previously mentioned: — Astarte R., *T. brauniana* Bed; Neill Cl., Coal Bed (which is transitional between the *Lepidopteris* and *Thaumatopteris* Zones).

This species appears to be a useful zone fossil of the *Thaumatopteris* Zone.

85. **Amphorispermum ellipticum** HARRIS.

See HARRIS 1932(b), p. 15; HARRIS 1926(b), p. 128 (as Seed E).

Lepidopteris Zone 62—85 m; 9 localities.

Additional locality, Astarte R., *Equisetites* Bed. This bed is at the base of the *Lepidopteris* Zone.

This seed appears to be a useful zone fossil of the *Lepidopteris* Zone.

Bennettitales. 1. Leaves.

86. *Anomozamites marginatus* (UNGER) NATHORST.

(*A. gracilis* NATHORST).

See HARRIS 1932(b), p. 21.

Thaumatopteris Zone; probably in upper part, at 54 m and at base; 3 localities.

Additional locality: Neill Cliff Coal Bed (transitional between *Lepidopteris* and *Thaumatopteris* Zones).

This species is satisfactorily distinguished from small specimens of *A. minor* by its cuticle, but in the absence of a cuticle definite distinction may be impossible. The Rhaetic leaf ascribed to *A. gracilis* by FRENTZEN, while more typical in general form of that species, could also belong to *A. minor*. For this reason, until the identification of this specimen is confirmed by a study of its cuticle I would prefer not to accept this as a record of this species in the Rhaetic (*Lepidopteris* Zone); and the species remains characteristic of the *Thaumatopteris* Zone.

87. *Anomozamites hartzi* HARRIS.

See HARRIS 1932(b), p. 24; HARRIS 1926(b), p. 86.

Thaumatopteris Zone 32 m to base; 3 localities.

Additional locality, Neill Cliff Coal Bed. This is transitional between the *Lepidopteris* and *Thaumatopteris* Zones.

This species is variable in form but has a characteristic cuticle. It cannot at present be satisfactorily distinguished from various large but imperfectly known *Anomozamites* leaves (e. g. *A. major* as figured by ANTEVS (1919) and may ultimately prove identical with them, though this can only be decided by an investigation of the cuticle of *A. major*. The Greenland leaves described as cf. *A. major* on p. 49 are quite distinct from *A. hartzi* having very much more delicate cuticles. Under the circumstances the correct course appears to distinguish this leaf of known cuticle structure as a definite species, leaving ones of similar form but unknown structure as *A. cf. major* (BRONGN.).

A. hartzi occurs in the lower half of the *Thaumatopteris* Zone of Greenland.

88. *Anomozamites minor* NATHORST (non BRONGN.).

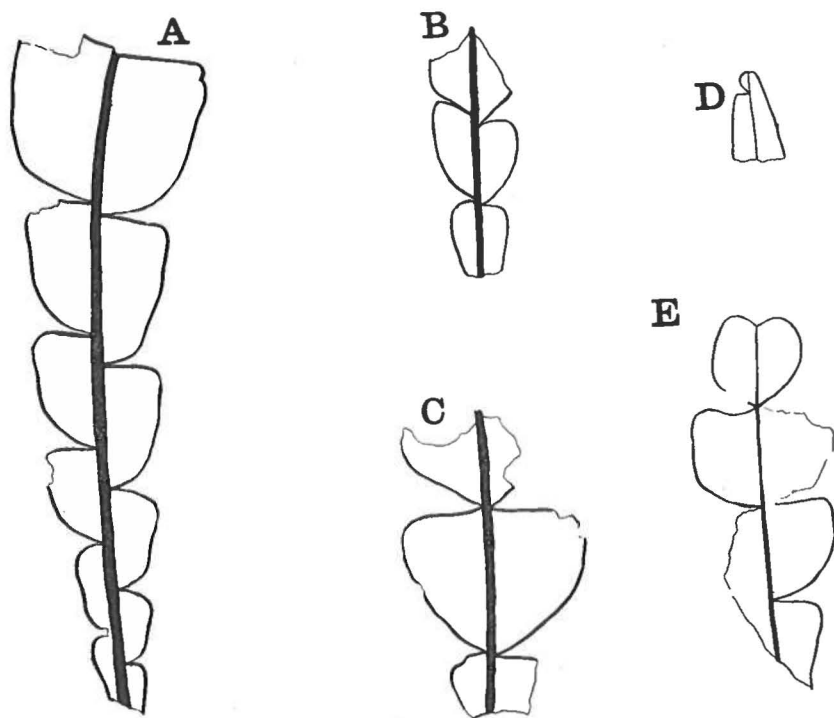
See HARRIS 1932(b), p. 29; HARRIS 1926(b), p. 80.

Lepidopteris Zone, all levels; 18 localities + 2 where the determination is doubtful. In addition to the previous records a fragment which may belong to this species was found in Neill Cliff Coal Bed.

As stated above, I consider that the leaves recently described

by FRENTZEN (1932) as *A. gracilis* may be small leaves of *A. minor*. SZE (1933 b) has found this species in China and KRYSHTOFOVICH and PRINADA (1933a) state that it occurs in the Upper Triassic (? Rhaetic) of Armenia. FLORIN (1933d) has recently figured the stoma of a Swedish specimen.

A. minor is one of the most useful zone fossils of the Rhaetic. I have



Text-fig. 5. *Anomozamites cf. major*.

A, lower part of a leaf, Nos. 1575, 1576. B, lower part of a very small leaf, No. 1577. C, fragment of a leaf with triangular segments, No. 1578. D, apex of a leaf, No. 1579. E, apex of a very small leaf, No. 1580. All the figures are natural size and were collected from Astarte R., Bed A.

previously given reasons why the leaves from Hör described as *Pterophyllum minus* BRONGN. should not be regarded as the type specimens of *A. minor*.

89. *Anomozamites nitida* HARRIS.

See HARRIS 1932(b), p. 30.

Lepidopteris Zone at 85 m; 1 locality.

90. *Anomozamites* sp. cf. *A. major* (Brongn.).

Text-fig. 5.

See *Anomozamites amdrupiana* HARRIS 1932(b), p. 33; *A. cf. major* HARRIS 1926(b), p. 86.

Lepidopteris Zone at 69—72 m; 2 localities. New locality, Astarte R., Bed A.

I have found a number of additional specimens which appear to be identical with those I described before. While some of the new specimens are exactly like those already figured; others differ in having almost triangular segments. It was impossible to obtain any information about the cuticle structure, apart from the conclusion that it must be very delicate — much more delicate than that of the associated *Pterophyllum kochi* leaves, where it is by no means thick. The existence of the form with triangular segments removes the only known difference between the Greenland specimens and the original ones of *A. major* from Hör (ANTEVS 1919). Under the circumstances it appears to me to be the best course to describe them as cf. *A. major*, though from the difference in age it is unlikely that they will ultimately prove to be the same (i. e. have the same structure). Meanwhile it is clear that leaves agreeing in gross features with the type *A. major* occur both in the Rhaetic and Lower Lias and therefore until their structure is known provide no indication of exact age.

SZE (1933b, pp. 30, 57) has figured some Chinese specimens as *A. cf. major* which are indistinguishable from the Greenland ones.

A. cf. major occurs in Greenland near the base of the *Lepidopteris* Zone; *A. major* (BRONGN.) in the *Thaumatopteris* Zone at Hör.

Genus NILSSONIOPTERIS NATHORST.

The nomenclature of this genus is complicated by the fact that some of NATHORST's original specimens were *Taeniopteris vittata* and others *Nilssonina orientalis*, and none was selected as a type. FLORIN (1933a, p. 12) is of the opinion that the description and therefore the name refers solely to '*Taeniopteris vittata*', though of this I am doubtful; but there can be no doubt that the description of the cuticle refers solely to *T. vittata* and accordingly I am inclined to accept this name. *Taeniozamites* HARRIS therefore becomes a synonym.

91. *Nilssoniopteris groenlandica* (HARRIS) FLORIN.

1926(b). *Taeniopteris groenlandica* HARRIS, p. 97.

1932(b). *T. groenlandica* HARRIS, p. 34.

1933(b). *Nilssoniopteris groenlandica* (HARRIS) FLORIN, p. 5.

Lepidopteris Zone at 70—80 m; 2 localities.

92. *Nilssoniopteris jourdyi* (ZEILLER) FLORIN.

See HARRIS 1932(b), p. 36.

Lepidopteris Zone at about 85 m; 2 localities.

This species is placed in *Nilssoniopteris* by FLORIN (1933(a), p. 5).

PRINADA (1934) has described a poorly preserved leaf from the Pamir region as cf. *Taeniopteris jourdyi*.

93. *Nilssoniopteris ajorpokensis* (HARRIS) FLORIN.

See HARRIS 1932(b), p. 39.

In transitional region between *Lepidopteris* and *Thaumatopteris* Zones at about 60 m; 1 locality.

FLORIN has described a species, *N. glandulosa*, from the Lias of Bornholm which is very close indeed to *N. ajorpokensis*, but is distinguished by the prevalence of trichomes with multicellular bases (in *N. ajorpokensis* the bases are mostly unicellular), the cell outlines are more distinct in *N. glandulosa*. Another slight difference is that the rachis of *N. glandulosa* is almost smooth, while in *N. ajorpokensis* it is transversely wrinkled — a feature doubtless caused in preservation, but one which is often characteristic of a species.

94. *Pterophyllum hanesianum* HARRIS.

See HARRIS 1932(b), p. 40.

Lepidopteris Zone at 78 and 85 m; 2 localities.

Various fragments of large *Pterophyllum* leaves have been described as *P. braunsi* SCHENK (BRAUNS 1866 and as *P. maximum*; SCHENK 1867; PRINADA 1934) and it is possible that *P. hanesianum* is identical with one or more of them but it seems best to keep it separate because its veins branch once or twice in the lamina of *P. hanesianum*, while in the figures of *P. braunsi* (especially that of PRINADA), they appear to be quite unbranched. The cuticle of '*P. braunsi*' is unknown.

95. *Pterophyllum astartense* HARRIS.

See HARRIS 1932(b), p. 44.

Lepidopteris Zone at 85 m; 1 locality.

P. astartense is one of several species of the *Lepidopteris* Zone which seem to resemble those of the rather older Lunz flora. It is possible that the bract, *Bennettitolepis dictylota*, p. 56, belongs to this plant. OISHI and TAKAHASHI (1936) have described a leaf with rather less crowded veins, but of very similar aspect as *P. yamanoiensis* Y. & T.

96. *Pterophyllum schenki* ZEILLER.

- See HARRIS 1932(b), p. 49; 1926(b), p. 88, and possibly p. 93, as *Pterophyllum* sp. B.
 ? 1878(a)—1886. *P. aequale* NATHORST (? non BRONGN.) probably some of the specimens in Pl. 15 as *P. aequale* and *P. affine*.
 ? 1878(b). *P. aequale* NATHORST (? non BRONGN.) possibly some of the specimens in Pl. 2 and Pl. 6 as *P. aequale*.
 1886. *Anomozamites schenki* ZEILLER, p. 460; Pl. 24, fig. 9; and *Pterophyllum* cf. *Falconeri*, p. 460.
 1903. *Pterophyllum schenki* ZEILLER, p. 181, Pl. 43, fig. 7.
 1922. *P. aequale* JOHANSSON (? non BRONGN.), in part Pl. 1, figs. 14—16; Pl. 8, figs. 20, 21 (not Pl. 6, figs. 4—6).
 1926(b). *P. schenki* ZEILLER, HARRIS, p. 88, Text-fig. 16 A—H; possibly also *P. sp. B*, p. 93, Text-fig. 19 A—F.
 1932(b). *P. schenki* ZEILLER, HARRIS p. 49; Pl. 6, figs. 1, 2; Text-figs. 22—24.
 1932(a). *P. schenki* ZEILLER, OISHI p. 310; Pl. 40, figs. 2—7.

Lepidopteris Zone from 62 m to base, 12 localities.

Through the courtesy of Dr. FLORIN I have been able to examine the cuticles of the Swedish specimens described by JOHANSSON as *P. aequale*. They agree closely with typical Greenland *P. schenki* and I consider them identical. JOHANSSON (1922) states that specimens of '*P. aequale*' from Bjuf and from Bosarp also have the same sort of cuticle. On the other hand, other specimens which have from time to time been described as '*P. aequale*' have decidedly different cuticles and I am sure that a large number of totally different plants are known by this name, only a few being identical with *P. schenki* ZEILLER.

This determination of *P. schenki* in Sweden removes one of the few types in the Greenland flora which appeared to be characteristic of E. Asia. *P. schenki* must probably be regarded as widespread in the Rhaetic.

There is evidence of association suggesting that the reproductive organs *Bennettistemon bursigerum* and *Bennetticarpus exiguus* may belong to this species.

97. *Pterophyllum rosenkrantzi* HARRIS.

See HARRIS 1932(b), p. 53; 1932(a), p. 96; 1926(b), p. 92.

Lepidopteris Zone at about 70 m; 2 localities + 1 where the determination is doubtful.

98. *Pterophyllum pinnatifidum* HARRIS.

See HARRIS 1932(b), p. 55; 1926(b), p. 96 as *P. sp. D*; HARTZ 1896, p. 235, as *Ptilozamites* sp. and as *Anomozamites* cf. *inconstans*.

Lepidopteris Zone at 65—85 m; 6 localities.

99. **Pterophyllum kochi** HARRIS.

See HARRIS 1932(b), p. 58; 1926(b), p. 89.

Fructification ascribed to this leaf — *Vardekloeftia sulcata*, p. 55.
Lepidopteris Zone at about 70 m; 3 localities.

100. **Pterophyllum ptilum** HARRIS.

See HARRIS 1932(b), p. 61; 1926(b), Text-fig. 17 *F—I* (as *P. kochi* in part).

Lepidopteris Zone from 62 m—90 m, 11 localities + 2 where the determination is doubtful.

Additional locality not previously mentioned; C. Stewart, *Ginkgoites minuta* Bed.

A small fragment of cuticle agreeing rather closely with *P. ptilum* was found in C. Hope Coal, which is in the *Thaumatopteris* Zone; apart from this doubtful record, the species is characteristic of the *Lepidopteris* Zone.

P. ptilum is very like *P. bavieri* ZEILLER (see ZEILLER 1903, PRINADA 1934) in its general appearance but is distinguished by the bases of the leaf segments which are always contracted in *P. ptilum* but according to ZEILLER not at all contracted and even expanded in *P. bavieri*.

101. **Pterophyllum zygotacticum** HARRIS.

See HARRIS 1932(b), p. 64; 1926(b) Text-fig. 17 *J* (as *Pterophyllum kochi* in part); p. 117 as *Podozamites* sp. *B*.

Lepidopteris Zone 62 m — base; 3 localities + one where the determination is doubtful.

102. **Pterophyllum xiphipterum** HARRIS.

See HARRIS 1932(b), p. 69.

Lepidopteris Zone — near base; 3 localities.

103. **Pterophyllum subaequale** HARTZ.

See HARRIS 1932(b) p. 74; 1932(a) p. 96; 1926(b), p. 95 as *P. sp. C* and p. 91 as *P. subaequale*; HARTZ 1896, p. 236.

Thaumatopteris Zone 10—50 m; 11 localities. Additional localities not previously mentioned: — C. Hope, Coal Bed; Neill Cliff, Coal Bed.

The reproductive organ *Cycadolepis rugosa* (p. 56) is considered to belong to *P. subaequale*.

The leaves described as *P. andraeanum* SCHIMP. by PRINADA (1934) are very like *P. subaequale* in the shape of their pinnae.

The specimens described from Poland by MAKAREWICZOWNA (1928) as *Pterophyllum polonicum* n. sp., and also perhaps those de-

scribed as *P. nathorsti* and *P. sp.* are quite indistinguishable on their macroscopic characters from *P. subaequale* and might, in the absence of microscopic detail, be assigned provisionally to this species. So also may many of the large *Pterophyllum* leaves described by ANTEVS (1919) from Hör — especially those figured on Pl. 3 under the names *P. propinquum* and *P. aequale* and also possibly a few of the smaller ones described as *P. angustum* and *P. intermedium* (in part), which closely match the smallest Greenland leaves of *P. subaequale*. This can only be settled by a study of the cuticle without which it is certainly impossible to determine a *Pterophyllum* of this type.

104. **Otozamites sp. A** HARRIS.

See HARRIS 1932(b), p. 79.

Lepidopteris Zone, near its base; 1 locality.

Bennettitales — reproductive organs.

105. **Wielandiella angustifolia** NATHORST.

See HARRIS 1932(b) p. 86; 1926(b) p. 82.

Lepidopteris Zone 62 m to base; 15 localities (includes some where the identification is based on small fragments).

FLORIN (1932(c), p. 13) has recently figured and discussed the stoma of this plant.

106. **Bennettistemon amblum** HARRIS.

See HARRIS 1932(b), p. 98.

Lepidopteris Zone at 85 m; 1 locality.

107. **Bennettistemon bursigerum** HARRIS.

See HARRIS 1932(b), p. 99.

Lepidopteris Zone at 60—80 m; 2 localities.

This microsporophyll is associated with *P. schenki* and may belong to it.

108. **Bennettistemon ovatum** HARRIS.

See HARRIS 1932(b), p. 100.

Lepidopteris Zone at 85 m; 1 locality.

109. **Bennetticarpus exiguus** HARRIS (emend.).

1932(b). *Bennetticarpus exiguus* HARRIS, p. 102, Pl. 14, figs. 8—10, 12—16; Text-fig. 48 C.

1932(b). *Bennetticarpus oxylepidus* HARRIS, p. 101, Pl. 14, figs. 1—6, 11; Text-fig. 48 D—F.

Lepidopteris Zone 60—85 m; 4 localities. Additional locality: Astarte R., *Lepidopteris* Bed.

Diagnosis (emended). Bennettitalean gynaecium; in immature stage 1.5 cm long, 1 cm in diameter, surface showing very slightly convex heads of interseminal scales 0.2 mm in diameter. Cuticle of head of scale not very thick, showing uniform straight-sided cells with clearly marked outlines, surface of cell flat (except at sides of scale, where it may bulge outwards); middle of cell not locally thickened. Stomata occurring near margins, curved cutin plates 30—35 μ long. Micropyles not projecting, outer cuticle delicate, forming a tube 0.3 mm long, cuticle of micropylar canal.

At ripe stage, fruit falling to pieces. Cutinised heads of scale 0.4—0.8 mm in diameter consisting of the part seen at the younger stage and 1—5 long projections at the corners. Cells in middle of scale now rather thick-walled and occasionally bulging; those towards the margin more or less thick-walled and radially elongated. Stomatal region now forming a zone half way between the centre and margin of the scale. Micropyle of seed occasionally still adhering to a scale; forming a tube now 0.5 mm long $\times$ 0.25 mm wide with a cuticle which is rather thick near the free end but becoming delicate below, showing outlines of small, nearly isodiametric cells. Cuticle of micropylar canal delicate, collapsed to a mere strand in upper part of micropyle but expanded below as a tube 60 μ wide, showing elongated straight-walled cells. Lower part of seed unknown.

I am convinced that '*B. exiguus*' and '*B. oxylepidus*' as previously described are merely two stages of development of the same fruit. The main difference between them lay in the presence in *B. oxylepidus* of an outer margin including sharp points on the cutinised head of the scale which was not found in *B. exiguus*. The discovery of some scales which show the character of '*exiguus*' in one part and '*oxylepidus*' in another strongly suggested that the lateral part was formed later from the margin of the scale (exactly as in *Vardekloeftia* and other Bennettitales, see HARRIS 1932(b), Text-fig. 50 A, B, p. 114. The close agreement between the cells of the middles of the scales in the two and also between their micropyles confirms this.

The union of the two species simplifies the evidence of their association, which provides some evidence for attributing this fruit to *Pterophyllum schenki*. This association is analysed below.

In all four localities *B. exiguus* is associated with an abundance of *P. schenki* leaves. In one (Astarte R., *Lepidopteris* Bed) this association has no particular significance because many other Bennettitalean leaves and fructifications occur; but in the other three *P. schenki* is much the commonest Bennettitalean leaf; of the others associated *Anomoza-*

mites minor and its fructification *Wielandiella* may be dismissed and there remain only *Pterophyllum ptilum* (rare in all three localities), *P. zygotacticum*, rare in one, absent from the other two and the fruit *B. crossospermus* present in one. The leaf *P. schenki* is, it is true, known from several other localities, but in these it is relatively uncommon.

The cuticle of the scale shows no very definite characters of agreement with any particular species of leaf: it appears rarely to do so in the Bennettitales (see FLORIN 1933c). This evidence of association is not sufficient to convince me that the two fossils belong to the same plant, but is sufficient to make the possibility worth bearing in mind. Should the bulk-maceration of the rocks of other countries containing *P. schenki* yield *B. exiguus* the evidence would, of course, be greatly strengthened.

There is similar but less strong evidence suggesting that the microsporophyll *Bennettistemon bursigerum* belongs to the same plant; it is associated in two localities with this leaf and its stomata have some peculiarities in common with those of the leaf.

110. **Bennetticarpus crossospermus** HARRIS.

See HARRIS 1932(b), pp. 103, 113, 115; HARRIS 1926(b), p. 82 as '*Wielandiella* sp.' in part.

111. **Bennetticarpus tylotus** HARRIS.

See HARRIS 1932(b), p. 106.

Thaumatopteris Zone at about 20 m; 1 locality.

112. **Vardekloeftia conica** HARRIS.

See HARRIS 1932(b), p. 107.

Lepidopteris Zone at 85 m; 1 locality.

113. **Vardekloeftia sulcata** HARRIS.

See HARRIS 1932(b), pp. 109, 113, 115; 1926(b), pp. 98, 125 (as 'Interseminale scale A' and 'Seed A').

Lepidopteris Zone at 63—75 m; 4 localities + 1 doubtful.

On the grounds of its very striking association with *Pterophyllum kochi* I refer this fruit to the same plant as that leaf species.

114. **Cycadolepis psila** HARRIS.

See HARRIS 1932(b), p. 91.

Lepidopteris Zone 70—90 m; 4 localities + 1 where the determination is doubtful.

115. **Cycadolepis rugosa** JOHANSSON.

See HARRIS 1932(b), p. 93.

Thaumatopteris Zone 10—50 m; 3 localities.

This scale very likely belongs to *Pterophyllum subaequale*.

116. **Bennettitolepis dactylota** (HARRIS) FLORIN.

See HARRIS 1932(b), p. 97 (as *Cycadospadix dactylota*).

Lepidopteris Zone at 85 m; 1 locality.

FLORIN (1933(a), p. 34) makes the new genus *Bennettitolepis* for this fossil which I placed in *Cycadospadix*. It is impossible to state any difference between it and *Cycadospadix* (beyond the 'seed pedicels' of *Cycadospadix*, which are suppositious and therefore scarcely a diagnostic character); but I freely admit that the evidence for identifying them is also meagre. It is possible to accept FLORIN's genus if *Cycadospadix* be regarded as a form genus in which the cuticle is unknown and *Bennettitolepis* a genus of scales of similar form whose cuticle is definitely Bennettitalean, and this course appears to be the most convenient one. The existence of *Palaeocycas integer* FLORIN, which is without doubt a Cycad-like megasporophyll, on the one hand, and *Bennettitolepis dactylota* on the other, which is equally probably a Bennettitalean bract, shows that the nature of the *Cycadospadix* species is entirely open.

Ginkgoales Leaves.

See FLORIN 1936a, 1936b.

117. **Ginkgoites obovatus** (NATH.) SEWARD.

See HARRIS 1935, p. 3.

Lepidopteris Zone at about 85 m; 2 localities.

This species occurs in the *Lepidopteris* Zone of Sweden at Bjuf (NATHORST, 1886, p. 93). FLORIN (1936b) has fully redescribed the Swedish specimens.

118. **Ginkgoites fimbriatus** HARRIS.

See HARRIS 1935, p. 6.

Lepidopteris Zone at 62—85 m; 2 localities.

119. **Ginkgoites acosmius** HARRIS.

See HARRIS 1935, p. 8.

Lepidopteris Zone at 69 m; 1 locality.

For a seed possibly belonging to this plant, see *Allicospermum striatum*, p. 59.

120. **Ginkgoites hermelini** (HARTZ) HARRIS.

See HARRIS 1935, p. 15.

Thaumatopteris Zone at 15—42 m; 9 localities.

This species occurs in the *Thaumatopteris* Zone of Sweden at Sofiero and probably also at Stabbarp, but this leaf, which is variable, is difficult to distinguish from *G. taeniata* (cf. CHOW 1924, p. 8; JOHANSSON 1922, p. 45 as *B. longifolia*, etc.).

Some of the specimens figured by MAKAREWICZOWNA (1928) (especially Pl. 11, figs. 4, 7) as *G. sibirica* and *G. digitata* may well belong to this species, but in the absence of precise details of the cuticle are indeterminable.

121. **Ginkgoites taeniatus** (BRAUN) HARRIS.

See HARRIS 1935, p. 19.

Thaumatopteris Zone at 15—about 50 m; 3 localities.

This species is known from S. W. Germany; but I am very doubtful whether the Swedish specimens determined as '*taeniata*' do in fact belong to this species. Some at least of them are more like *G. hermelini*. A leaf of similar form but with not quite identically lobed apices is known from Japan (OISHI 1932(a)). See also p. 59 for the seed *Allicospermum xystum*, which may belong to this species.

KRYSHTOFOVICH and PRINADA (1933b) have recently figured a leaf as *B. taeniata* Braun, which agrees very well in shape with the Greenland specimens. One of their specimens (on Pl. 11, fig. 5) determined as *G. sibirica* HEER is also comparable.

MAKAREWICZOWNA (1928) also figures a similar leaf from the Lias of Poland.

122. **Baiera minuta** NATH.

See HARRIS 1935, p. 11 as *Ginkgoites minuta*; 1926(b), p. 101 (as *B. muensteriana*)
FLORIN 1936a, p. 108.

Lepidopteris Zone 62—90 m; 7 localities + 2 doubtful.

This species is also known from Bjuf in Sweden (*Lepidopteris* Zone, NATHORST 1886, p. 93; LUNDQUIST 1918, p. 493). It is difficult to distinguish from *B. muensteriana* PRESL (*Thaumatopteris* Zone) and consequently has limited stratigraphic value.

123. **Sphenobaiera spectabilis** (NATH.) FLORIN.

See HARRIS 1935, p. 25; 1926(b), p. 99 (as *Baiera spectabilis*; FLORIN 1926a p. 108,
1936b, p. 38.

Thaumatopteris Zone 10—25 m; 10 localities.

This species is characteristic of the upper half of the *Thaumatopteris* Zone in Greenland; in Sweden it is only definitely known from a bed

belonging to the lower half of this zone, but may also occur in several localities in the upper part of this zone. See also p. 60 for the reproductive organ, *Bernettia phialophora*, which may probably belong to this species. FLORIN (1936b) has described and figured the cuticle of Swedish specimens of this species.

124. ? **Sphenobaiera boeggildiana** (HARRIS) N. comb.

See HARRIS 1935, p. 28 (as *Baiera*).

Lepidopteris Zone at 85—89 m; 2 localities. Additional locality, Astarte R., *Equisetites* Bed.

As FLORIN remarks, this species is difficult to place in a genus. In the general form of its leaf it rather resembles *Arctobaiera* FLORIN 1936, p. 118, but from this genus it differs in possessing resin.

125. **Sphenobaiera leptophylla** (HARRIS) FLORIN.

See HARRIS 1935, p. 30; 1926(b), p. 103 as '*Baiera* sp. A'. FLORIN 1936a, p. 108.

Lepidopteris Zone at 62—85 m; 6 localities.

The doubtful record of this species at Astarte R., Bed A is now confirmed by the discovery of a better preserved and typical specimen.

126. **Sphenobaiera amalloidea** (HARRIS) FLORIN.

See HARRIS, 1935, p. 32; FLORIN 1936a, p. 118.

Lepidopteris Zone at 62 m; 1 locality.

Genus **CZEKANOWSKIA** HEER.

See FLORIN 1936a, p. 128.

127. **Czekanowskia hartzii** HARRIS.

See HARRIS 1935, p. 38; 1926(b) p. 104; HARTZ 1896, p. 241 as *C. rigida* and *C. setacea*.

Thaumatopteris Zone at 15—25 m; 15 localities.

This species is very characteristic of the upper part of the *Thaumatopteris* Zone in Greenland. See also p. 59 for the reproductive organ, *Leptostrobus longus*, which probably belongs to this species.

128. **Czekanowskia nathorsti** HARRIS.

See HARRIS 1935, p. 40.

Thaumatopteris Zone at 15 m down to beds transitional between this and the *Lepidopteris* Zone; 8 localities + 1 doubtful.

This species is rather characteristic of the lower part of the *Thaumatopteris* Zone. It occurs in Sweden at Stabbarp in the lower part of

the *Thaumatopteris* Zone (NATHORST 1906, p. 11; JOHANSSON 1922, p. 49, determined as *C. rigida*). FLORIN (1936) has recently figured the cuticle of Swedish specimens of this species.

129. **Hartzia tenuis** HARRIS.

See HARRIS 1935, p. 42; 1926(b), p. 107 as *Phoenicopsis tenuis*. See also below for the reproductive organ, *Staphidiophora secunda*, which probably belongs to this species.

Lepidopteris Zone 63—80 m; 4 localities.

130. **Pseudotorellia ephela** (HARRIS) FLORIN.

See HARRIS 1935, p. 46; FLORIN 1936a, p. 142.

Thaumatopteris Zone at 12 m; 1 locality.

Reproductive organs attributed to the Ginkgoales.

131. **Staphidiophora secunda** HARRIS.

See HARRIS 1935, p. 114.

Lepidopteris Zone at 75 m; 1 locality.

This fruit is thought to belong to *Hartzia tenuis*, with which it is associated and shows agreement in cuticle structure.

132. **Staphidiophora(?) exile** HARRIS.

See HARRIS 1935, p. 116.

Lepidopteris Zone at about 75 m; 1 locality.

133. **Allicospermum xystum** HARRIS.

See HARRIS 1935, p. 121.

Thaumatopteris Zone at 15—50 m; 3 localities.

This seed is associated with *G. taeniata* and may probably belong to that species.

134. **Allicospermum(?) striatum** HARRIS.

See HARRIS 1935, p. 114.

Lepidopteris Zone at 62 m; 1 locality.

This seed is associated with and may belong to *G. acosmia*.

135. **Leptostrobus longus** HARRIS.

See HARRIS 1935, p. 138.

Thaumatopteris Zone at about 25 m; two localities.

This cone is thought to be the male cone of *Czekanowskia hartzi*. OISHI & TAKAHASI (1936) have recently described a Japanese specimen of *Leptostrobus* resembling *L. longus*.

136. **Bernetta phialophora** HARRIS.

See HARRIS 1935, p. 140.

Thaumatopteris Zone at 15—25 m; 3 localities.

This fossil is a male cone and may belong to *Sphenobaiera spectabilis*.

Conifers-leaves, shoots and attached cones.

137. **Stachyotaxus elegans** NATH.

See HARRIS 1935, p. 52; 1926(b), p. 119; HARTZ 1896, p. 242 (as *S. septentrionalis*)
— foliage male and female cones and seeds.

Lepidopteris Zone all levels from about 85 m up to beds transitional to the *Thaumatopteris* Zone; 14 localities.

This species (i. e. the one with the larger leaves and cones) probably occurs in four localities in Sweden in the *Lepidopteris* Zone, Bjuf, Höganäs, Stabbarp, Skromberga. I have pointed out that the nomenclature of this species and of *S. septentrionalis* is by no means clear.

Both species are confined to the *Lepidopteris* Zone, so that confusion between them is not serious stratigraphically; the small cone, *Callipitys leptoderma*, of the *Thaumatopteris* Zone, however, a good deal resembles that of *S. septentrionalis* in its general appearance.

138. **Stachyotaxus septentrionalis** (? non AGARDH) NATH.

See HARRIS 1935, p. 56.

Lepidopteris Zone at about 85 m; 2 localities (foliage and female cone and seed).

This species (i. e. the one with the smaller leaves and cones) occurs at Hyllinge in Sweden and possibly also at Bjuf, but I think that most of the earlier specimens called *S. septentrionalis* belong to *S. elegans*.

139. **Storgaardia spectabilis** HARRIS.

See HARRIS 1935, p. 58; p. 172. (Name corrected from '*Storgaadia*').

Thaumatopteris Zone at 15—25 m; 4 localities.

140. **Elatocladus patens** HARRIS.

See HARRIS 1935, p. 61.

Thaumatopteris Zone at top and at base; 2 localities.

141. **Elatocladus pachyteichus** HARRIS.

See HARRIS 1935, p. 61.

Thaumatopteris Zone at 54 m; 1 locality.142. **Elatocladus perforatus** HARRIS.

See HARRIS 1935, p. 64.

Lepidopteris Zone at 62 m; 1 locality.143. **Elatocladus stenostomus** HARRIS.

See HARRIS 1935, p. 65.

Lepidopteris Zone at 62 m; 1 locality.144. **Elatocladus lacunosus** HARRIS.See HARRIS 1935, p. 65; 1926(b), p. 123 as *Taxites* sp. A.*Lepidopteris* Zone at 75 m; 1 locality.145. **Elatocladus punctatus** HARRIS.

See HARRIS 1935, p. 68.

Lepidopteris Zone, 62—85 m; 2 localities.146. **Elatocladus nitidus** HARRIS.

See HARRIS 1935, p. 68.

Lepidopteris Zone at unknown level; 1 locality.147. **Elatocladus oligostomus** HARRIS.

See HARRIS 1935, p. 69.

Thaumatopteris Zone at 54 m; 1 locality.148. **Elatocladus tuberculatus** HARRIS.

See HARRIS 1935, p. 69.

Thaumatopteris Zone at a high level; 1 locality.149. **Elatocladus amblus** HARRIS.

See HARRIS 1935, p. 70.

Thaumatopteris Zone, from top to bottom; 3 localities.150. **Elatocladus molopicus** HARRIS.

See HARRIS 1935, p. 73.

Lepidopteris Zone at 62 m; 1 locality.

151. **Elatocladus polystictus** HARRIS.

See HARRIS 1935, p. 75.

Lepidopteris Zone at 62—75 m; 3 localities.152. **Elatocladus physetus** HARRIS.

See HARRIS 1935, p. 76.

Lepidopteris Zone at 75 m; 1 locality.153. **Elatocladus eurystomus** HARRIS.

See HARRIS 1935, p. 76.

Lepidopteris Zone at 62 m; 1 locality.154. **Elatocladus sp. A.**

See HARRIS 1935, p. 74.

Lepidopteris Zone at 69 m; 1 locality.155. **Elatocladus sp. B.**

See HARRIS 1935, p. 74.

Lepidopteris Zone at 85 m; 1 locality.156. **Elatocladus sp. C.**

See HARRIS 1935, p. 77.

Thaumatopteris Zone at 20 m; 1 locality.157. **Ontheodendron sternbergi** (NILSSON) HARRIS.

See HARRIS 1935, p. 78.

Lepidopteris Zone from top to near base; 5 localities (shoots, female cones and isolated seeds).

This species occurs in the *Lepidopteris* Zone of Sweden in two localities (NATHORST 1886, p. 107; 1878(c), p. 28). Though confined to the *Lepidopteris* Zone, its stratigraphic usefulness is diminished by the delicacy of the cuticle of its leaf, making determination difficult.

Form-genus **PODOZAMITES.**

In our present state of knowledge the species of *Podozamites* appear to have no reliable stratigraphic value.

158. **Podozamites stewartensis** HARRIS.

See HARRIS 1935, p. 84; 1926(b), p. 113.

Lepidopteris Zone at 63 m to near base; 4 localities.

159. ***Podozamites astartensis* HARRIS.**

See HARRIS 1935, p. 87.

Lepidopteris Zone at 65—69 m; 2 localities.160. ***Podozamites punctatus* HARRIS.**

See HARRIS 1935, p. 89.

Thaumatopteris Zone at 15 m; 1 locality.161. ***Podozamites* cf. *distans* (PRESL) BRAUN.**

See HARRIS 1935, p. 95; 1926(b), p. 110.

Lepidopteris Zone 62 m to near base; 5 localities + 2 where the determination is doubtful.Fossils closely resembling *P. distans* occur in most parts of the world in rocks of Upper Triassic and Jurassic age.162. ***Podozamites* sp. B. cf. *P. distans*.**

See HARRIS 1935, p. 95.

Lepidopteris Zone at about 90 m; 1 locality.163. ***Podozamites mucronatus* HARRIS.**

See HARRIS 1935, p. 96.

Bed transitional between *Lepidopteris* and *Thaumatopteris* Zones. 1 locality.164. ***Podozamites* spp. indet. (narrow-leaved forms).**See HARRIS 1935, p. 92; 1926(b), p. 115 (as *P. schenki*) and p. 112 (as *P. agardhianus*).

All levels in both zones; about 60 localities.

Similar leaves are known from nearly all parts of the world in rocks of Upper Triassic and Jurassic age.

Coniferates — detached reproductive organs.**Genus CYCADOCARPIDIUM NATHORST.**

OISHI and TAKAKASI (1936) point out a difficulty in accepting the view that this sporophyll belongs to *Podozamites*: while *Podozamites* occurs throughout the Mesozoic, *Cycadocarpidium* is only associated with it in the Rhaetic and Liassic (being, in fact, almost confined to the Rhaetic). I suggest that the explanation is that the accepted polymorphic 'species' of *Podozamites*, e. g. *P. lanceolatus*, consist of the superficially similar foliage of several widely different genera of plants.

One of these genera has the *Cycadocarpidium* sporophyll, perhaps another the *Swedenborgia* type; while the reproductive organs of the majority apart from those of the Liasso-Rhaetic, are of still other and unrecognised types. This suggestion is supported by the diversity of structure found among the Liasso-Rhaetic *Podozamites* material, but can only be proved by a closer investigation than my material has permitted.

165. ***Cycadocarpidium swabi* NATHORST (sensu lato).**

See HARRIS 1935, p. 101.

Lepidopteris Zone, 69 m to base; 5 localities.

I have already stated my opinion that *C. swabi* must be regarded as an aggregate of several similar species and not at present definitely separable from a second group known as *C. erdmanni* NATH. The *Cycadocarpidium*-type of sporophyll is, however, characteristic of the *Lepidopteris* Zone in the European area, only *C. redivivum* NATH. being known from the lower part of the *Thaumatopteris* Zone. Species of *Cycadocarpidium* are known from Sweden (NATHORST 1886; 1902; 1911); Central Asia TURUTANOVA-KETOVA (1930); Cochin China (COUNILLON 1914), China (SZE 1931) and Japan (Ozawa 1925, OISHI 1932, OISHI & TAKAHESI 1934).

The slender type of axis (Type B) is recorded in my field notes from Primula R., Lower plant bed, but the specimen was lost.

166. ***Cycadocarpidium erdmanni* NATH. (sensu lato).**

See HARRIS 1935, p. 105; for discussion see *C. swabi* above.

Lepidopteris Zone all levels from the base up to beds transitional to the *Thaumatopteris* Zone; 3 localities.

KRYSHTOFOVICH and PRINADA (1933) have recently figured specimens of *C. erdmanni* from the Urals, where it appears to be associated with *Podozamites lanceolatus*. Another fossil possibly belonging to this species has recently been figured by OISHI and TAKAHASI (1936).

167. ***Swedenborgia cryptomerioides* NATHORST.**

See HARRIS 1935, p. 108.

Thaumatopteris Zone 25 m down to base (beds transitional between this and the *Lepidopteris* Zone; three localities + 1 doubtful. Additional locality: C. Hope, just below the *Jamesoni* horizon (discovered in 1935 by A. Rosenkrantz).

The three species of *Swedenborgia* only differ from one another in their dimensions. From the stratigraphic point of view their distinction is unimportant as they are all confined to the *Thaumatopteris* Zone.

This species is known from two localities in Sweden (NATHORST 1876, p. 66 or 1878(b), p. 30; ANTEVS 1919, p. 48).

S. cryptomerioides has been recently discovered in Japan by OISHI and YAMASETA (1935), where it is also associated with narrow-leaved species of *Podozamites*.

168. **Swedenborgia major** HARRIS.

See HARRIS 1935, p. 109.

Thaumatopteris Zone at about 25 m; 3 localities.

This species has been discovered in Japan by OISHI (1935).

169. **Swedenborgia minor** HARRIS.

See HARRIS 1935, p. 109.

Thaumatopteris Zone at about 50 m; 1 locality.

170. **Callipitys leptoderma** HARRIS.

See HARRIS 1935, p. 110.

Thaumatopteris Zone at 25 m; 1 locality.

171. **Araucarites charcoti** HARRIS.

See HARRIS 1935, p. 113.

Lepidopteris Zone at 62—85 m; 2 localities.

Unclassified seed plants.

In this group there are a few leaves, one of which, *Furcula*, is of great interest because it has the form, venation and structure of a dicotyledon. There are also a good many reproductive organs.

172. **Furcula granulifer** HARRIS.

See HARRIS 1932(a), p. 4.

Lepidopteris Zone at about 70—90 m; 2 localities + 1 where the determination is doubtful.

No other fossil is known which closely resembles this leaf; its coarser venation is somewhat like that of *Yabeiella* OISHI (1931a) but it is readily distinguished by its finer venation (which is not unlike that of species of *Gigantopteris*).

173. **Scoresbya dentata** HARRIS.

See HARRIS 1932(a), p. 38.

Thaumatopteris Zone at 25 m; 1 locality.

174—176. **Desmiophyllum** spp.

See HARRIS 1935, pp. 98, 99.

Type 1. *Thaumatopteris* Zone at 15—25 m; 3 localities.Type 2. *Thaumatopteris* Zone at 15—25 m; 6 localities.Type 3. *Lepidopteris* Zone at 75 m; 1 locality.

These fossils are imperfectly known and have therefore little stratigraphic value.

177. **Allicospermum obscurum** HARRIS.

See HARRIS 1935, pp. 104, 125.

Lepidopteris Zone, level uncertain; 1 locality.This is probably the isolated seed of a form of *Cycadocarpidium swabi*.178. **Brightonia arota** HARRIS.

See HARRIS 1932(b), p. 119.

Lepidopteris Zone at 69 m; 1 locality.179. **Ourostrobos nathorsti** HARRIS.

See HARRIS 1935, p. 116.

Thaumatopteris Zone at about 25—32 m; 6 localities.

This species probably occurs in Sweden (NATHORST 1878(b), Pl. 16, fig. 4).

180. **Sphaerostrobos clandestinus** HARRIS.

See HARRIS 1935, p. 143.

Lepidopteris Zone at 62 and 85 m; 2 localities.181. **Amydrostrobos groenlandicus** HARRIS.

See HARRIS 1935, p. 148.

Lepidopteris Zone at 75 m; 1 locality.

182. 'Male cone sp. A' HARRIS.

See HARRIS 1935, p. 149; 1926(b), p. 124.

Thaumatopteris Zone at 25 m; 1 locality.

183. 'Male cone sp. B' HARRIS.

See HARRIS 1935, p. 151.

Bed transitional between *Thaumatopteris* and *Lepidopteris* Zones at 58 m; 1 locality.184. **Ixostrobos groenlandicus** HARRIS.

See HARRIS 1935, p. 147.

Thaumatopteris Zone at 25 and 42 m; 2 localities.

This fossil may be identical with *I. siemiradzki* RACIBORSKI 1891a, 1892, which occurs in rocks of similar age in Poland.

KRYSHTOFOVICH and PRINADA (1933b) have described a cone as *Stenorachis* sp. cf. *Ixostrobis siemiradzki* RACIB., which may be comparable but appears to differ to some extent in having more crowded sporophylls.

185. **Sorosaccus minor** HARRIS.

See HARRIS 1935, p. 146.

Thaumatopteris Zone at about 25 m; 1 locality.

186. **Sorosaccus gracilis** HARRIS.

See HARRIS 1935, p. 145.

Thaumatopteris Zone at 15—25 m; 2 localities.

187. **Stenomischus athrous** HARRIS.

See HARRIS 1935, p. 144.

Thaumatopteris Zone at 25 m; 1 locality.

188. **Chitospermum stereococcus** HARRIS.

See HARRIS 1935, p. 134; 1926(b), p. 129 as 'Seed F'.

Lepidopteris Zone at 63 m to about 75 m; 3 localities.

189. **Bysmatospermum macrotrachelum** HARRIS.

See HARRIS 1935, p. 132.

From *Thaumatopteris* Zone at about 50 m to lower part of *Lepidopteris* Zone; 4 localities.

190. **Samaropsis chalcos** HARRIS.

See HARRIS 1935, p. 129.

Lepidopteris Zone about 75 m; 2 localities.

191. **Samaropsis nathorstiana** HARRIS.

See HARRIS 1935, p. 129.

Lepidopteris Zone at about 75 m; 1 locality.

192. **Allicospermum ooides** HARRIS.

See HARRIS 1935, p. 128.

Thaumatopteris Zone at about 20 m; 1 locality.

193. **Allicospermum fragilis** HARRIS.

See HARRIS 1935, p. 127; 1926(b), p. 128 as 'Seed D'.

Lepidopteris Zone 62 m(?) to base; 3 localities + 2 doubtful. Additional locality (determination doubtful), Vardekloft, *N. hoerensis* Bed.

194. **Allicospermum hartzii** HARRIS.

See HARRIS 1935, p. 125; 1926(b), p. 126 as 'Seed B'.

Lepidopteris Zone? 63 m and at 75 m; 2 localities.

195. **Tmematostrobos eremus** HARRIS.

See HARRIS 1935, p. 119.

Lepidopteris Zone at 62 m to base; 4 localities.

196. **Androlepis hartzii** HARRIS.

See HARRIS 1932(b), p. 121; 1926(b), p. 124 (as *Androlepis* sp.).

197. **Microcheiris enigma** HARRIS.

See HARRIS 1935, p. 117.

Thaumatopteris Zone at about 15 m; 1 locality.

PART 2. STRATIGRAPHY

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A. THE GREENLAND RHAETO-LIASSIC PLANT BEDS

§ 1. General Stratigraphy.

The general relations of the Triassic and Jurassic rocks of Scoresby's Sound have been described by ROSENKRANTZ in KOCH (1929); ROSENKRANTZ (1930); NOE-NYGAARD (1934), (1934) and by KOCH (1929a), (1929b), (1930), (1934), (1935); it will merely be necessary to describe the stratigraphy of the beds adjacent to the plant-bearing series.

These beds are as follows:—

Neill Cliff Formation (Marine Lias)	{ Various sandstones and limestones The <i>Jamesoni</i> horizon	{ 200 m
Cape Stewart Formation (Freshwater Lower Lias and Rhaetic)	{ Plant-bearing series — 90 m Barren sandstone — 85 m	{ 175 m
Klitdahl Formation (Con- tinental Trias)	{ Red marl Gypsum Arkose	{ over 200 m

The upper part of the Klitdahl formation (which is probably identical with Koch's Kap Biot Formation) is non-marine and consists largely of red marly shales, but it has thick bands of coarser grits, greenish or purplish sandstones and at least one bed of Gypsum. Its general character agrees with much of the 'New Red Sandstone' of N.W. Europe and it may be presumed to have been deposited under similar, prevailing arid conditions.

The sediments are well bedded and must have been laid down in fairly still water (i. e. lakes), but the very frequent layers with ripple marks show that the water was shallow and the numerous layers with sun cracks show that such lakes often dried up. No fossils (apart from entirely problematical 'fucoids', etc.) were found and the sediments are not even penetrated by vertical roots, a very significant fact in view of the abundance of such roots in the C. Stewart formation.

The prevailing red colour of the shale indicates a completely oxidised sediment, such as would be formed under arid conditions. The occasional presence of greenish rock (usually coarser grained than the red marl) does, however, suggest the occasional arrival of material with sufficient organic matter to reduce the iron, though even here fossils are absent.

At the top of this formation cross-bedded sandstones appear and soon predominate and this level is taken as the upper boundary of the Klitdahl formation and the C. Stewart formation, though in the absence of fossils this boundary may not be precise.

The prevailing type of deposition is evidently changing from that of a desert basin to that of the delta of a river; occasional red or green sediments of the Klitdahl type, which are found in the C. Stewart formation (as at Dinosaur R.) are probably redeposited sediments derived from the underlying rocks.

The sediment shows no widespread change through the C. Stewart formation, but the formation is divided by its fossils into an upper plant-bearing half (the plant-bearing series) and a lower barren half. The lack of plants (and of old land surfaces with roots) in the lower

half must be due to some peculiarity in the conditions of deposition. (A few pieces of petrified wood lying on the surface of the barren series may belong there or may have been derived from them or the overlying Jurassic rocks).

The only difference between the two parts is due to the presence of plant beds and of old land surfaces in the upper part, but these plant beds only constitute a small fraction of the total thickness which is composed largely of more or less cross-bedded and barren sandstone or grit. The Klitdahl type of sediment (green or red marls) becomes rarer in the upper part of the series, but local bands are found even at the top.

There are innumerable breaks and violent unconformities in this series, but none of them appear to extend any great distance laterally or to have any general significance.

The rocks of the C. Stewart formation sometimes show a certain local uniformity of character which extends over a great vertical range. Thus at C. Stewart calcareous and garnet-bearing sandstones predominate; at Dinosaur R. the sandstones are greenish and have to an unusual extent the character of the Klitdahl formation; elsewhere yellow, non-calcareous sandstone predominates. These local differences indicating great differences in the materials carried by neighbouring river channels suggest the existence of a number of rather small rivers bringing material from nearby rather than the distributaries of a very large one, and the coarseness of the prevailing sediments suggests rapid flow.

The plant-bearing beds are discussed more fully later; the conclusion being reached that some of them contain autochthonous plants and that they represent lagoons formed by disused parts of river channels where much finer sediments were deposited.

The Neill Cliff formation is a marine formation of estuarine character with occasional horizons rich in fossil animals but its plants are few and ill preserved. From Cape Stewart to the end of Hurry Inlet the base of this formation is formed by a hard richly fossiliferous limestone (the *Jamesoni* horizon) or "Pecten Limestone", which formed an easily recognisable boundary to the plant-bearing series. This horizon was used as the base line for determining the levels in the plant bearing series. There is sometimes (as A. ROSENKRANTZ informs me exists at C. Hope) an angular unconformity at the base of the *Jamesoni* horizon, but sometimes (as at Astarte R.) there is no apparent unconformity. No significance can yet be given to this occasional unconformity because the plant bearing series has numberless local unconformities.

The actual character of the sediments shows a dozen abrupt changes in the few metres between the highest plant bed and the

marine fossils, but these are no more frequent than in other parts of the plant bearing series. There is neither a widespread pebble bed nor a horizon with vertical roots below the *Jamesoni* horizon and there is thus no geological evidence of any considerable gap between the freshwater and marine formations. A rather interesting layer sometimes found at the boundary is a ripple-marked sandstone with the cavities partly filled with black material; such sandstones are otherwise rare in the plant series and were only noticed in Lejr R., where a few marine fossils occur in association with it. Such sediments are widespread on the intertidal zones of present day sandy estuaries and other types of sea beach, but I have not noticed them in purely freshwater deposits. I think that in Scoresby Sound it possibly marks a very shallow marine transgression and that it, rather than the overlying limestone, is the real beginning of the Neill Cliff formation.

Summary. The conditions in Scoresby Sound during this period may be pictured as follows:—

During late Triassic Scoresby Sound was part of a continental area with an arid climate and Jameson Land formed a shallow desert basin in which sediments were laid down in temporary lakes; at one period near the end of the Triassic such a lake was sufficiently permanent to deposit a considerable thickness of Gypsum. Shortly before the Rhaetic the climate became wet and the basin became occupied and rapidly filled up by coarse sediments laid down in the combined delta of a number of rivers; by the Rhaetic most of the surface was built up as land and occupied by marsh plants and probably by forest.

The land was subsiding during the whole of the Rhaetic and Lower Liassic time. The rate of the subsidence was slow enough for the surface of the delta to be maintained nearly everywhere at just above sea level. At one stage (marking the Liasso-Rhaetic boundary) there was a slowing of subsidence (p. 92) which seems to have been widespread over Europe and may have been caused by a slight general change of sea level. At the end of the Lower Liassic times (*Jamesoni* Zone) the land subsided rapidly and was occupied by sea though the presence of much plant material in the rocks and the prevailing coarse texture and cross-bedding of the rocks suggests coastal and probably estuarine conditions.

§ 2. The Plant Beds.

The plant bearing beds occur at all levels of the plant bearing series, though their total thickness is never more than a small fraction of the whole series, which is largely formed of nearly barren sandstones. The number of beds in a section varies from place to place; there are thirteen

at Astarte R., the richest place, and none in parts of Ammonite Mtn.; as a rule there are two or three in a section. Plant beds are decidedly more frequent at two levels than elsewhere — about 20 m and at about 75 m below the *Jamesoni* horizon and in the important middle part of the series between 40 and 60 m they are rare, though because this region was specially studied the rarity is not apparent in Table 1.

Many plant beds are composed of several horizons with rich and different floras alternating with barren layers and such beds can either be regarded as large composite beds or a series of many thin ones. The number of the major plant beds studied was about seventy; but if the local horizons which were studied separately be considered the number would be very much greater.

The levels of the plant bearing beds were determined by aneroid barometer readings in relation to the base of the *Jamesoni* limestone. Considerable care was taken to secure accuracy by repeating the readings and I think that most of the levels given below should be correct to within ± 5 m. North of Hurry Inlet, where the *Jamesoni* Bed is undeveloped and at other places where it could not be recognised, the level could only be roughly estimated. In the subsequent account all levels are given as a number of metres *below* the base of the *Jamesoni* horizon.

The plant bearing beds are of two extreme types. There is the type composed of fine, very perfectly bedded sediment and containing large and even undamaged leaves; there is the type with coarse grits and either showing hollow casts of broken twigs or fragments of leaves, stems, etc. preserved as compressions. In the first type of bed the absence of water-worn fragments and the marked local dominance of certain species indicate a flora preserved very near where it grew — that is, almost autochthonous.

In some beds dominated by the Equisetales these plants are actually autochthonous, the rhizomes and intact roots are found in the lower part of the bed, and from the rhizomes erect stems arise; these are broken off after a few centimetres and the upper part of the bed is full of the broken remains of the aerial stems of the same species.

The other type of plant bed was less studied but yielded results of interest. When the rock is disintegrated by bulk-maceration it yields cuticles of many tough-leaved species, some of them of known types but many unknown in the autochthonous floras. Though often too fragmentary for description, this material indicates the existence of many species at present unknown, perhaps living inland.

Certain plant beds (e. g. Astarte R., Bed C) provide a mixture of large specimens of presumably local origin and very occasional fragments of many other species.

The plant beds vary greatly in horizontal extent, the smallest being less than a metre wide, the largest a kilometre or more; typically they are 100 m wide and 1 m thick at the middle, tapering towards the ends. The sediments of the plant beds themselves are horizontal — never cross-bedded — and their lens-shaped form suggests that they may have been formed in lagoons left by disused river channels in the delta.

§ 3. Coal.

Coal seams of several types occur in the plant-bearing series. A thin shaly coal found at Vardekloft is composed of innumerable fossil leaves pressed together with very little rock matrix, and this coal yields a great number of cuticles on maceration. At Ammonite Mtn. is a coal composed of fusainised wood and parenchyma (i. e. fossil charcoal) embedded in sandstone. The fragments are small and angular and I am inclined to believe that they are true charcoal washed down from a forest fire. Occasional pieces of similar fusain are to be found in many other plant beds.

There is also some bituminous coal, especially in the upper part of the series, which locally attains a thickness of up to 50. cm The smallest seams of this bituminous coal can be seen to be constituted from the trunks of trees 50 cm or more in diameter and it is probable that the largest seams are composed of large numbers of similar tree trunks. Maceration of this coal yields a very few cuticles of leaves and fruits, etc., but these are well preserved. In spite of its thinness this coal is valued by the Eskimos and quarried by them.

§ 4. The fossil animals of the plant bearing series.

Despite a close search very few fossil animals were found in the plant bearing series. The following is a complete list: —

1. A fish spine (*Hybodus* sp.) from just below the Lejr R. *Thaumatopteris* Bed (probably a little below the middle of the plant bearing series); see ROSENKRANTZ 1934, p. 119. Some indeterminable fragments of fairly large bones were associated with the fish spine.
2. A very thin shelled lamellibranch is abundant in a bed immediately below the fish spine bed.
3. *Estheria* sp. cf. *E. minuta* from the C. Stewart *Anomozamites minor* Bed, which is situated near the base of the plant bearing series.
4. A fossil resembling a beetle elytron, from the same bed as 3.
5. Two specimens of insect wings from Vardekloft *P. agardhiana* Bed.

It will be seen that only one of these fossils (*Hybodus*) is definitely marine, and that none of them except possibly the *Estheria* are likely to have any stratigraphic value. *Estheria minuta*, or very similar species,

ranges through the upper half of the Trias and is often common in the Rhaetic.

The chief interest of the occurrence of *Hybodus* is that it provides evidence that the land surface was liable to be temporarily flooded by the sea and therefore that it was normally only just above sea level.

§ 5. Horizontal distribution of the fossil flora.

The plant bearing series extends from C. Hope and C. Stewart in the south probably as far as Antarctic Harbour. It was investigated in detail only as far as the south end of Carlsberg Fjord and it can be said that there is no significant change in the flora over this distance. Rather fewer species were found in the northern localities, but this is presumably because they were less fully investigated owing to lack of opportunity.

§ 6. Vertical distribution of the fossil flora; the plant zones.

a. The Major Divisions.

There is a very important change in the flora in passing up through the plant bearing series, this change occurs between the levels 50 and 60 m below the *Jamesoni* horizon; above this level is one flora, below it a flora almost completely different, while mixing occurs over the intervening few metres.

Each of these floras contains about a hundred species, but any particular plant bed contains as a rule only a few and these seem as though selected at random. One or two of these species are overwhelmingly abundant in a bed, but an entirely different species will dominate an adjacent bed, or even another part of the same bed. It thus follows that a first survey seems to indicate the existence of an indefinitely great number of plant zones, or perhaps no underlying principal of distribution but when the floras of a good number of beds are brought together the principle of the distribution of species becomes very obvious (Table 1).

Certain features of Table 1 need explanation. The levels of the beds on the left represent the number of metres at which a bed is situated *below* the top of the series (measured from the *Jamesoni* horizon). Where no figure is given no measurement could be made but in all cases a rough estimate of the vertical position could be formed on other evidence. The vertical order of the beds in the table is therefore that of their occurrence in the section.

To avoid unduly stretching the table, plant beds were lumped together as far as possible. That is to say, beds at the same level and with substantially the same flora but occurring in adjacent sections have been reckoned as the same bed and also where several plant bearing

shales alternate with rather thin unfossiliferous layers these again have been reckoned as a single plant bed, though this had only been done where their floras were almost the same.

Determinations of which I feel certain are represented by a black dot, those which because of poor preservation admit of doubt by rings. The thick vertical lines are merely lines drawn connecting the limits of distribution and represent the total range.

In Table 1 only well defined species or genera are included (difficult genera like *Podozamites*, *Cladophlebis*, *Cycadolepis* and *Nilssonina* are left out) and also only the more commonly occurring species are included, since the vertical range of rare ones is problematical.

In this table, and throughout my work, I have tried to define species rather narrowly (preferring a 'splitting' to a 'lumping' basis). I have, however, constructed similar tables to the one given in which the difficult genera and rare species are included and in which all fossils which could possibly be identified with one another were so identified, but these differences in method hardly affect the table beyond adding somewhat to the species which range the entire flora and in my opinion making the table less reliable.

It will be seen in Table 1 that the two plant zones are distinguished by a great number of species. They have already been defined (briefly by HARRIS 1931a, p. 157; and with complete species lists by KOCII, 1935) and a list of the more important species of each zone is given by Table 1.

The beds lying between 50 and 60 m are of special importance because mixing of the two floras occurs in them. It should be emphasised that real mixing occurs, not merely an abrupt change. The two sets of plants will be seen on the same bedding plane and they continue to be found together from top to bottom of one of these beds; or if a coal layer at this level is macerated it yields cuticles of both sets of species.

b. Subdivision of the Zones.

Table 1 shows that two zones can be distinguished satisfactorily; it also shows that each of these zones is essentially a unit and not made up of well defined parts. I have nevertheless searched for signs of a stratigraphic division in each.

The *Lepidopteris* Zone, which is only 30 m thick, is the more uniform. I can find no distinctive character in the flora of its upper beds (those just below the transition region); but its lowest beds have a few species found in more than one locality which may have stratigraphic significance, though the evidence is incomplete. I give the list of these characteristic species (p. 78) not as of established significance but in the hope that their distribution in other countries may be found to

coincide with that in Greenland and establish a zonal significance for some of them. These lowest beds are only distinguished by the presence of these particular species; the rest of their flora is the same as that of higher beds.

I estimate the thickness of the rock where the *Lepidopteris* and *Thaumatopteris* floras are mixed at about 5 m. In no section is more than one bed with a mixed flora found; but at Astarte R. there is a typical *Lepidopteris* flora at c. 62 m; a mixed flora at c. 58 m and a typical *Thaumatopteris* flora at c. 54 m, and these measurements may be taken as accurate in relation to one another. In Neill Cliff a mixed flora occurs at c. 50 m, but as this is in a section some way from Astarte R. the errors of determination (± 5 m) would allow it to be below the Astarte R. '54 m' bed, though it is less likely to be below the '58 m' bed. Although the great bulk of the *Lepidopteris* Zone species cease at this level one or two extend a good deal higher up, though they become very rare indeed. Presumably with completer knowledge this will be found true of other species.

There are no species characteristic of the transition region. Like almost every plant bed in Greenland, each of those of the transition region provides a few species not known elsewhere, but since these species are not shared by the transition beds of other localities there is no reason to regard them as characteristic of this region. The absence of a characteristic flora at this stage means that there is no missing zone between the *Lepidopteris* and *Thaumatopteris* Zones. This is important because so far as we know in Sweden and in Germany there is a complete break between the floras of the *Lepidopteris* and *Thaumatopteris* Zones and apart from the evidence from Greenland it might have been supposed that a whole stage in the Rhaetic-Liassic plant sequence had been left out. I have suggested later (p. 92) that the rapidity of the change in flora in passing up the rock is due to a comparative lack of deposition at this time causing the sequence to be telescoped together and not due to any sudden revolution in the flora.

The *Thaumatopteris* Zone, which is nearly twice as thick as the *Lepidopteris* Zone, shows a slight though more definite indication of a division into two parts. There are six species which are fairly general in the top 20 or 30 m but do not occur below, and there are two which occur in the lower 40 m but seem to be absent in the top 20 m.

The species most characteristic of the *Lepidopteris* Zone of Greenland are given in Table 1 (species 31—54). A very large number of other species — many rare ones and some ill-defined ones of difficult genera also occur and a complete list of these is given in Koch (1935). In this and in my previous papers in describing the species I have stated the zone where each occurs.

The basal beds of the *Lepidopteris* Zone contain the following in addition to the normal members of this zone and species peculiar to one locality:

<i>Furcula granulifer</i> HARRIS	<i>Pterophyllum xiphipterum</i> HARRIS
<i>Drepanozamites nilssoni</i> (NATH.)	<i>Nilssonniopteris jourdyi</i> (ZEILLER)
<i>Sagenopteris serrata</i> HARRIS	<i>Ginkgoites obovata</i> (NATH.)
<i>Pterophyllum hanesianum</i> HARRIS	<i>Stachyotaxus septentrionalis</i> NATH.

The following species are characteristic of the *Thaumatopteris* Zone: Nos. 1—25 in Table 1 together with a very large number of rarer species and some ill-defined ones, a complete list of which is given by KOCH (1935).

The following species are confined to the upper 25 m: — Nos. 1—6 in Table 1; *Sphenobaiera spectabilis* extends down to 32 m. In addition, this region has the rare species *Bernettia phialophora* (probably belonging to *S. spectabilis*) and *Osmundopsis plectrophora*, both of which are found in two or more localities. As some of these species are very abundant in this region their absence lower down appears to be significant.

The following species are only found in the lower 40 m of the *Thaumatopteris* Zone (20 m downwards): *Czekanowskia nathorsti*, *Anomozamites hartzi*. Unfortunately my records of the distribution of *C. nathorsti* at Dinosaur R. are not precise, but I believe that it is as stated in the table, confined to the lower part of the complex of plant beds which occur in that locality between 6 and 25 m

B. THE STRATIGRAPHY OF COMPARABLE AREAS IN EUROPE

§ 1. Introduction.

The most similar flora to that of Scoresby Sound is the very rich one of S. Sweden. It is also geographically the nearest. A similar flora is the famous 'Grenzschrift' flora of S. W. Germany. In other parts of Europe — France, Bornholm, Poland, and the former Austro-Hungarian Empire — there are floras which resemble the younger half of the Greenland flora. Outside Europe, there is a chain of floras extending across Asia to Japan which have much in common with that of Greenland though the assemblage of species is rather different. South of this chain is another, less similar, extending across Asia to Tonkin with much less but still something in common.

In the southern hemisphere and in India floras are known which must be of rather similar age but their character is entirely different and I am inclined to believe that their resemblances are even less close than has been commonly stated.

The correlation of a flora depends ultimately on correlation with the marine rocks. The type areas for the Triassic and Rhaetic are in

Central Europe, notably in the Alps; the area in which the Lias was first described fully was in southern England. It will be necessary to discuss the marine rocks of these areas briefly.

During the Triassic much of the Alps was occupied by sea under which an enormous marine series was laid down, containing a varied fauna including Ammonites, which have provided the basis for the distinction of a good many zones. The Triassic sea continued into the Rhaetic when a great thickness of sediment was deposited. This is, however, rather poor in fossils, but has provided a basis for the recognition of three Ammonite zones. It is clear that the Rhaetic is a great formation representing a considerable portion of the Triassic period, and is by no means the almost negligible passage series which it has sometimes been regarded.

North of the Alps the Triassic submergence was less considerable, and the marine Trias (Muschelkalk) was preceded and succeeded by rocks laid down under terrestrial and largely arid conditions, thus forming the basis for the famous threefold division from which the Trias is named:—

Keuper — often reddish marls

Muschelkalk — marine limestone

Bunter — often reddish sandstone

The marine transgression became briefer as one traces the Trias northward and did not reach England, where the Trias is divided simply into the Keuper and Bunter. It is clear that the beginning of the 'Keuper' is altogether indefinite, varying in age in different places. The Keuper has few fossils of any sort, and nearly all of these are without precise zonal significance.

At the end of the Carnic stage of the Trias, that is, at the beginning of the Rhaetic, a marine transgression took place which involved much of northern Europe, and this sea continued to exist in Europe through the Jurassic. In the area of this submergence the Rhaetic would be most naturally included in the Jurassic, but in its much better development in the Alps it belongs more naturally to the Triassic because its ammonites in particular belong to Neo-Triassic families and are different from those predominating in the Lower Liassic.

The Rhaetic transgression was shallow and began irregularly; in England, for example, an archipelago of small islands escaped submergence during the first half of the period but were submerged later and it may be presumed to have begun irregularly elsewhere too. These Rhaetic marine sediments are a shallow water facies poor in fossils, apart from a few small lamellibranches; ammonites are absent. One of the most characteristic lamellibranches, *Pteria contorta*, is confined

to the lower half of the shallow water Rhaetic, which is correlated with the lower half of the Alpine Rhaetic. There is much uncertainty about the separation between the Rhaetic and the Lias, some of the upper beds commonly regarded as Rhaetic being perhaps a rather barren development of the lowest Lias (SPATH 1934).

In several places one of the celebrated 'bone beds' is developed, consisting largely of teeth of fish and reptiles. This was formerly ascribed to catastrophic slaughter, but almost certainly is due merely to the absence of sedimentation over a very long period during which these very resistant organs alone accumulated.

The Liassic period is represented by a thick series of marine limestones in which ammonites are often abundant and have been worked out in the greatest detail. The succession of the main ammonite zones found in Europe of the older Lias, the Rhaetic and the younger Trias is given below; the information being taken from SPATH (1934) and from LANG (1914).

Stage	Zone
"Middle Lias or Pleinsbachian or Charmouthian	Domerian { <i>spinatus</i>
	{ <i>marginatus</i>
	{ <i>davaei</i> (= <i>Capricornus</i> zone)
	Carixian { <i>ibex</i>
	{ <i>jamesoni</i>
Lower Lias or Sinemurian	{ <i>armatus</i>
	 <i>raricostatus</i>
	 <i>oxynotus</i>
	 <i>obtusus</i>
	 <i>semicostatum</i>
	 <i>bucklandi</i>
	 <i>angulata</i>
Rhaetic	 <i>planorbis</i>
	Eopsiloceratan { <i>Planorboides</i> Beds
	Rhaetitan { <i>Rhaetites</i> Beds
Norian	 { <i>Choristoceras haeri</i> Beds
	Pinaco- { <i>Sirenitis argonauti</i>
	ceratan { <i>Pinacoceras metternichi</i>
	Haloritan { <i>Cyrtopleurites bicrenatus</i>
	{ <i>Sagenites giebeli</i>
Carnian	{ <i>Heinrichites paulckeri</i>
	Tropitan { <i>Tropitilles subbulatus</i>
	Carnitan { <i>Carnites floridus</i>
	Trachyce- { <i>Trachyceras aonides</i>
	ratan { <i>Trachyceras aon</i>

In a few areas, notably S. Sweden and S. W. Germany, estuarine conditions existed and instead of the thin series of fine grained shales which commonly represent the Rhaetic north of the Alps is a variable thickness of rock which is often coarse grained but with local bands of coarse or fine material containing fossil plants. In both of these areas occasional marine bands also occur, and provide small faunas of the usual non-alpine type (i. e. lacking ammonites). In so far as the age of the plant beds is correlated with the ordinary marine time scale, this correlation depends on these bands.

§ 2. Germany.

SCHENK (1867) discussed the age of the important 'Grenzschiefer' flora at considerable length and ultimately decided to regard it as Rhaetic though he did so without any great assurance, and up till recently it has been taken as a standard Rhaetic flora without the evidence being questioned. After a long interval several papers followed; SALFELD (1907) supported the Rhaetic age of most localities, but recognised that a few were Lower Liassic; SCHÜSTER (1911) strongly supported the view that the floras he was describing belonged to the oldest Rhaetic (a view which as a result of more evidence must now be considered incorrect).

GOTHAN (1914) made an exceedingly important contribution when he recognised the existence of two distinct floras in the 'Grenzschiefer', the older of which he regarded as Rhaetic, the younger, which is much more abundantly represented, he regarded as basal Liassic (belonging to the *Planorbis* Zone). I am in complete agreement with GOTHAN's conclusions.

SCHÜSTER (1928) quoted in HÖRHAMMER 1933, while not definitely opposing GOTHAN's main conclusions, prefers to leave the division of the Grenzschiefer in abeyance and speaks of it 'for practical purposes' as Rhaetic, or Upper Keuper, while HÖRHAMMER (1933 p. 27), who also leaves it in abeyance, terms it the *Rhaeto-Liassic*. FRENTZEN (1932), who has recently described a small flora from marine Rhaetic rocks, expresses agreement with GOTHAN's conclusions. GOTHAN (1935) has restated his views.

So far as I am aware no section shows both of GOTHAN's floras, and in many places the beds both above and below the plant-bearing series are entirely without fossils and therefore undated.

The best sections in this area appear to be approximately as follows:—

1. for the older (Rhaetic) flora (SALFELD, FRENTZEN).

Marine basal Liassic rock (*angulatus* or *planorbis* Zone)

5 m Marine Rhaetic sandstone with lamellibranches (*Pteria contorta* etc.) and occasional plants.

Unfossiliferous Keuper Marl.

2. for the younger flora (GOTHAN, SCHÜSTER)

Marine Liassic (*angulatus* Zone).

15 m Non-marine sandstone with local plant beds.

30 - Marine sandstone with Rhaetic fish.

30 - Unfossiliferous Keuper Marl.

It will be seen that the age of the older flora is definitely that of the *Pteria contorta* beds; that is, it belongs to the zone of the older Rhaetic. The age of the younger flora is open, the existence of Rhaetic fossils underneath merely shows that it cannot belong to the oldest Rhaetic, but it might belong to the younger Rhaetic or to the *planorbis* Zone of the Lias, or both. Its age has indeed been assumed to be Liassic.

GOTHAN's older flora is according to him characterised by the presence of *Dictyophyllum exile* and *Lepidopteris ottonis* and to these we may add *Ptilozamites nilssoni* (FRENTZEN's *Keraiaphyllum suevicum*). A good many species characteristic of the younger flora have been reported by FRENTZEN in the Rhaetic beds — *Anomozamites gracilis*, etc. — but these are based on very small and imperfect specimens which, so far as I can judge from the figures, could equally well have been referred to a species more characteristic of the Rhaetic.

The younger flora (which I identify with the *Thaumatopteris* flora) is better known than the older; it includes at least fifty species, the majority of which are based on well preserved specimens.

It is characterised by the following well-defined species which, so far as I know, are confined to floras of this age:— *Todites princeps*, *Phlebopteris muensteri*, *P. angustiloba*, *Selenocarpus muensterianus*, *Thaumatopteris schenki*, *T. brauniana*, *Dictyophyllum nilssoni*, *D. muensteri*, *Norimbergia brauni*, *Thinnfeldia rhomboidalis*, *T. schwarzi*, *Sagenopteris nilssoniana*, *Thinnfeldia belhofensis*, *T. hartmanniana*, *Nilssonia acuminata*, *N. minima*, *Anomozamites marginatus*, *Pterophyllum angustum*, *P. nathorsti*, *Otozamites brevifolius*, *Campylophyllum hoermanni*, *Ctenopteris wolfiana*, *C. cycada*, *Ginkgoites taeniata*, *Baiera muensteriana*, *Cheirolepis muensteri*.

In addition it contains species which occur outside this zone in other parts of Europe or in Greenland, namely *Clathropteris meniscoides*, *Todites goeppertianus*, *Equisetites muensteri*, and a good many that are ill-defined such as species of *Cladophlebis* and *Podozamites*.

§ 3. Sweden.

The Rhaeto-Liassic rocks of Sweden form a series of very considerable thickness. They begin by being prevailingly freshwater deposits and end by being prevailingly marine. The rocks are exposed in a good

many sections, but as this area is disturbed by faulting and the character and thickness of the rocks varies from place to place, it is only possible to recognise levels in the series in different regions by the fossils themselves. As in Germany and Greenland, the series often rests on unfossiliferous Mesozoic red marls and sandstone referred tentatively to the Keuper, or else it rests unconformably on Palaeozoic rocks: thus the only indication of the date of the beginning of the series is that provided by the fossils (plants) of its lowest fossiliferous bed. The general character of the plant-bearing series seems to be remarkably like that of Greenland; the prevailing rock is sandstone or sandy shale with bands of soft fine-grained sediment containing exquisitely preserved plants. At intervals are seams of coal, these being a little more numerous and much thicker than in Greenland.

Knowledge of this formation is due to NATHORST and others as a result of whose work the stratigraphic scheme below was put forward, and this has stood with scarcely any alteration till recently, when TROEDSSON re-investigated the evidence forming the basis of this scheme and made some considerable alterations. As the Swedish floras have been taken as the stratigraphic basis for correlations over the whole world, TROEDSSON's conclusions deserve the closest attention.

The stratigraphic conclusions which held up till recently are set forth below:

Zone	{	15 <i>Cardium</i> Bank— <i>Bucklandi</i> Zone	
“Lower Liassic”	{	14 <i>Ammonite</i> Bank	{ <i>angulatus</i> and <i>planorbis</i> Zones. The Liassic floras of Hör, etc. are contemporaneous with part of this series.
	{	13 <i>Avicula</i> Bank	
	{	12 <i>Ostrea</i> Bank	
	{	11 <i>Cyclas Nathorsti</i> Bank	
	{	10 <i>Cardinia</i> Bank	
	{	9 <i>Mytillus</i> Bank	
“Rhaetic”	{	8 <i>Nilssonina polymorpha</i> Zone.	
	{	7 <i>Dictyophyllum acutilobum</i> Zone.	
	{	6 <i>Pullastra</i> Bank.	
	{	5 <i>Thaumatopteris schenki</i> Zone.	
	{	4 <i>Equisetites gracilis</i> Zone.	
	{	3 <i>Lepidopteris ottonis</i> Zone.	
	{	2 <i>Camptopteris spiralis</i> Zone.	
	{	1 <i>Dictyophyllum exile</i> Zone.	

The number of these "zones" is strikingly large, and has been the envy of many stratigraphers working in other areas. Reference, however, to the original accounts makes it clear that they are not what are termed "zones" nowadays but correspond much more nearly with

the term "Beds". NATHORST's "zones" are, as he makes clear, local beds characterised by the abundance of the species after which it is named. They do not correspond to the whole vertical distribution of the species, thus NATHORST identified *Nilssonia polymorpha* in every one of his plant zones, and the distribution of the other species is similarly extensive. Probably NATHORST at first considered that this abundance of species was characteristic of particular period; but he may have changed his views later, for in the important floras described later (by JOHANSSON in 1922) beds were referred to a particular zone though the "zone species" was absent.

Comparison with the Greenland flora suggests that the local abundance of a species has no more than local significance, and may not even be characteristic of the whole extent of a single plant bed.

I attempted to recognise "zones" in the modern sense — that is, rocks characterised by a certain assemblage of species (HARRIS 1931a) and concluded that there were two such zones in the Swedish flora; these zones being closely similar to the two in Greenland. The break between the two floras occurs at NATHORST's Zone 4. These conclusions are supported and developed further by TROEDSSON.

TROEDSSON in 1930 pointed out that NATHORST's 'zone' 6 occurred at some distance above 'zone 7' but made no other important change. In 1934 he went much further. He states that many of the 'zones' in the old stratigraphic table are merely local fossiliferous horizons which are unrecognisable in other localities and also have unknown stratigraphic relation to the fossiliferous beds elsewhere. He gives a revised stratigraphic table for the coast section in the Helsingborg region as follows (freely translated from the Swedish):

320 m				
300 -	Döshult sandstone, coarse, ferruginous	{	14, Ammonite Bank(?)	} Liassic
280 -			13, Avicula Bank	
260 -			12, Ostrea Bank	
240 -				
220 -			14, Ammonite Bank(?)	
200 -				
180 -				
160 -	Ramlösa Bed		6, Pullastra Bank	
140 -	Pålsjö series	{	NATHORST's zones 8—11	
120 -				
100 -	Hälsingborg Series	{	Sandstones at Hålsövägen and Halalid	
80 -			Coal beds at Tågaborg and the 'Hälsingborg flora'	
60 -			(5 and 7)	

40 m	} Mine Series, with useful coal	} NATHORST'S ZONES 1—4	} Rhaetic
20 -			
0 -			
Kågeröd Formation			{ Trias or older

The relation of this table to NATHORST'S will be apparent from the numbers of the 'zones'. The chief changes affecting the flora is raising zone 6 into the Liassic and lowering the Rhaeto-Liassic boundary from between 'zones 8 and 9' to between 4 and 5. Several important floras — at Pålshö, Stabbarp, Hälsingborg, etc. — which have hitherto been regarded as Rhaetic become Liassic. Nearly half of the species which were regarded as zone species of the Rhaetic now become exclusively Liassic and it is certain that had this result been known earlier a great number of the world's floras which have been correlated as Rhaetic would have been placed in the Liassic.

The Kågeröd formation consist of variously coloured unfossiliferous sandstones and marls. It was formerly regarded as Keuper, but now, according to TROEDSSON, may be older. In Table 2, I have attempted to plot the vertical range of species in the Swedish flora in the same way as I have done for Greenland. Although the Swedish Liasso-Rhaetic flora is one of the most closely studied Mesozoic floras in the world, the flora as a whole has never been critically revised and the floras of many localities have never been described or listed. In constructing Table 2, I have had to judge of the validity of many specific determinations on the very imperfect evidence offered by early descriptions and figures, and it is probable that the Table may embody some mistakes. It would be a considerable service to Palaeobotany if such a table of vertical distribution could be worked out by some one undertaking both critical revision of the stratigraphy and of the specific determinations in the flora; meanwhile it is necessary for my purpose to put forward this table imperfect though it is.

Where my conclusion about the identity of a specimen is in disagreement with that of the Swedish author I have mentioned the supposed occurrence, giving my reasons for rejecting it in the descriptive part of my previous papers. I have had to assign definite positions to certain plant bearing beds in this table where the author left the question of the precise age open, though I have never placed a bed in disagreement with an author's conclusions. Certain beds also have been described under different names by different authors and this had led to some difficulty in placing them in the table though I think it will not have led to any serious error.

It will be seen at once that the species belong to three groups — an older group, a younger group, and a group ranging the whole flora.

These groups distinguish the two zones, and it is shown later (p. 90) that these two zones correspond remarkably well to the *Lepidopteris* and *Thaumatopteris* Zones of Greenland. No locality in Sweden shows a transitional flora, but the two localities where NATHORST recognised his 'zone 4' have small floras with so little in common with either the older or younger flora that it is impossible for me to say from their flora what relation they have to the transition.

Table 2 not only shows the existence of two zones, but shows that these are all that can, on present evidence, be safely recognised in the flora.

There is a suggestion that the upper flora, though without any marked floral break, might be divisible; there is no indication of a division in the older flora. This is exactly the position in Greenland.

§ 4. France.

In France (SAPORTA 1873—1878) there are small floras in the *Pteria contorta* (Rhaetic) shales; in the *planorbis* shales (basal Liassic) and a more considerable one in the *bucklandi* beds (Lower Liassic) of Hettange. Very few Keuper plants are known.

The 'Rhaetic' flora includes two species, *Danaeopsis marantacea* and *Equisetites arenaceus*, which are more characteristic of the upper Keuper; a few species peculiar to this flora or of no stratigraphic value and the two fossils, *Equisetites muensteri* and *Clathropteris meniscoides*, which occur equally in the Rhaetic and Lower Lias.

The *planorbis* zone flora includes a few tough-leaved plants — Conifers, Bennettitales, etc. — which appear very similar to those of the *angulatus* Zone.

The *angulatus* Zone has a fairly large flora in which tough-leaved plants again predominate, though fragments of a few fern leaves occur — *Dictyophyllum nilssoni*, *D. muensteri*? (determined as *Thaumatopteris exilis*); *Clathropteris meniscoides*. The commonest plants appear to be Conifers of the *Brachyphyllum* type; *Ctenopteris*, *Thinnfeldia*, *Otozamites* and *Cycadites*. The general character of this flora is very like that of the upper 'Grenzschrift' flora of S.W. Germany with most of the more delicate leaves omitted and with the genera *Otozamites* and *Brachyphyllum* increased. It is probable that the rarity of delicate leaves is due to their failure to be preserved in these marine beds. On the other hand, the prevalence of characteristically Oolitic genera (*Otozamites*, *Brachyphyllum*) may be due to the slightly younger age of the French flora than the Liassic floras of Greenland, Sweden and Poland, where this element is almost absent or only weakly represented as in Germany and Austria-Hungary. Re-investigation of the French flora might pro-

vide interesting information about the subsequent development of the *Thaumatopteris* flora; at present, however, it is unsafe to use it as a basis for any such conclusions.

§ 5. Poland.

Several floras which together make a moderately large one are known from Poland. They were originally regarded as upper Rhaetic (NATHORST's 'zone 5' of *T. schenki*) by RACIBORSKI (1890, 1891, 1892); but are now regarded by MAKAREWICZOWNA (1928) as Lower Liassic. There is no real difference between the two views, since NATHORST's Zone 5 is now referred by TROEDSSON to the Liassic, the essential fact is that the flora includes hardly any *Lepidopteris* Zone species, but many which belong to the *Thaumatopteris* Zone and perhaps younger stages. Leaving aside doubtfully determined specimens, particularly those of *Podozamites*, the flora may be analysed as follows:—

Species confined to the *Lepidopteris* Zone:

None (see below).

Species common to the *Lepidopteris* and *Thaumatopteris* Zones:

Equisetites muensteri; *Clathropteris meniscoides*; "*Todites William-soni*" agg.

Species confined to the *Thaumatopteris* Zone or younger zones:

Phlebopteris muensteri, *P. angustiloba*, *Dictyophyllum nilssoni*, ?*Hausmannia forchhammeri*, *Todites princeps*, *Sagenopteris nilssoniana*, *Nilssonina acuminata*, ?*Pterophyllum subaequale*, *Ginkgoites taeniata*, ?*G. hermelini*, *Czekanowskia* (the genus), *Ixostrobus siemiradzkii*, *Cheirolepis muensteri*, *Schizolepis brauni*.

A few species are identified with Jurassic species but to judge from the figures they might almost equally well belong to Lower Liassic ones.

A few specimens have from time to time been identified with species of the *Lepidopteris* Zone. These include *Ctenis fallax* and *Neocalamites hoerensis*, which, to judge from the figures, are almost indeterminable; *Dictyophyllum exile* and *Lepidopteris ottonis*, which MAKAREWICZOWNA rejects; *Nilssonina simplex*, which, though identified, is stated to be in all probability wrongly identified.

The Polish flora is very similar indeed to the *Thaumatopteris* floras of Greenland, Sweden and Austria; nearly all its species are found in the German flora, but it differs in lacking a large *Thinnfeldia* element which is so prominent in both Germany and France.

§ 6. The former Austro-Hungarian empire.

A considerable flora occurs in various places but unfortunately it has been very inadequately figured in recent times (KRASSER 1922). It is said to be of *angulatus* Zone age, though I do not know whether the evidence exists for all the localities. It appears to show very close similarities with the *Thaumatopteris* Zone flora of Germany, Sweden and Greenland, having twenty species in common and does, in fact, contain but a single species identified with an exclusively *Lepidopteris* Zone fossil — *Ptilozamites acuminatus*. This determination undoubtedly needs revision since the type specimen of *P. acuminatus* is a tiny and scarcely determinable fragment.

§ 7. Bornholm.

In Bornholm (BARTHOLIN 1892, 1894; HJORTH 1899; MÖLLER 1902, 1903) there may be one or perhaps several horizons with fossil plants: unfortunately the localities appear to be isolated and are dated by their plants. Although a very large number of species have been determined, reference to the original figures will show that most of them are based on small fragments which have not been microscopically investigated. There appears to me to be no single species which can be identified with the *Lepidopteris* zone or true Rhaetic: the few which have been e. g. *Stachyotaxus* are impossible to determine at all from the figures.

There are a good many fossils which are identified with those belonging to the *Thaumatopteris* (Liassic) flora, and which even if wrongly determined specifically seem to preclude an age as old as the Rhaetic — e. g. *Marattiopsis*; *Sagenopteris* of a type resembling *S. nilssoniana*; *Dictyophyllum* c. f. *nilssoni*. One small flora — that of Velengsbj is composed entirely of such species and may well be of *Thaumatopteris* zone age (basal Liassic) though it is also possible that it may belong to a rather younger stage in the Liassic.

There is another group of fossils which agree generically with those of the floras of the Lower Oolite and have in some cases been identified with them specifically, though not convincingly. The most interesting group — because the best preserved or most fully investigated consists of species peculiar to this flora, though their genera are widespread. Their peculiarity can almost certainly be attributed to their being of an age not represented among the plant bearing rocks of any neighbouring region, see p. 90.

C. § 1. Triassic.

Our knowledge of the European "Lower and Middle Keuper" or Middle Neo-Triassic flora is unsatisfactory. There is the rich and well preserved flora of Lunz, which has never been completely described,

and there are a good many small and mostly ill preserved floras scattered over Germany and France (Lettenkohle and the slightly younger Schilfsandstein). The work on these latter floras is brought together by FRENTZEN (1922); later papers on particular plants of this flora include those by FRENTZEN (1933); v. LILIENSTERN (1928); LINNELL (1932, 1933). A very similar flora presumed to be of the same age is known from Thuringia (COMPTER 1911, 1918).

These floras of the Lettenkohle and Schilfsandstein (which may be conveniently considered together) have a great deal in common with the Lunz flora and with the Virginian Keuper flora (FONTAINE), but not much in common with the Rhaetic. Apart from some aggregate species with a long time range (*Todites* cf. *Williamsoni*; *Clathropteris* cf. *meniscoides*) they have few or no species in common unless '*Lepidopteris stuttgartensis*' should, when better known, prove to be indistinguishable from *L. ottonis*. Most of the genera of Gymnosperms are, however, represented in Rhaetic or Liassic floras, but the ferns are remarkably different, various *Asterotheca*-like and *Danaea*-like fructifications being abundant in these Keuper floras and very rare in the European Rhaetic, and absent in younger floras.

There is a break in our knowledge of the European flora between the stage of the Neo-Triassic represented by the above mentioned floras and the Rhaetic, but the occurrence of a few Triassic types, such as *Asterotheca*, as rare species in the Rhaetic, suggests that completer knowledge might show a simple transition from the Triassic to the Rhaetic flora. I think it unlikely that any considerable intervening flora distinct from either remains to be discovered. Our ignorance of the transition is unsatisfactory because it prevents our being able to say how far down into the Trias the Rhaetic type of flora extends; for convenience we may place the beginning of the *Lepidopteris* flora at the commencement of the marine Rhaetic, but this is pure assumption.

§ 2. Lias.

The rich floras of the European basal Liassic beds has been already discussed.

The European Lias contains even in its marine beds a good many scattered fossil plants which together make a considerable list, but do not give us much idea either of any one typical Liassic flora or of the sequence of floras in the Liassic. Deltaic deposits with plants are poorly developed during the interval between the basal zones of the Lias and the uppermost, the only large flora being that of Bornholm, which although not studied in its entirety by recent methods and not precisely dated is of great importance.

In Bornholm (p. 88) various stages of marine Lias are represented in somewhat small blocks near the coast bounded by faults, and among these are areas containing plant beds of one or perhaps various ages. As far as I know the correlation of the beds depends entirely on the plants; certain localities (Vellengsby) which have been called Rhaetic agree in flora with the *Thaumatopteris* Zone of Sweden (formerly called Upper Rhaetic and Lower Lias, but now regarded as purely basal Liassic). The other floras — those of Bagaa etc. are intermediate in general character between the European basal Liassic floras on the one hand and the upper Liassic flora of Poland or the similar Lower Oolitic flora of England and Italy, etc. On the grounds of this intermediate character it may be regarded as belonging to a period in the middle of the Liassic. It is remarkable that the Bornholm Middle Liassic flora contains few or no genera which are not represented in either the basal Liassic, or in the Oolite; many of its ferns have been identified with those of other floras, but the majority of its gymnospermous species (I believe all whose cuticle have been investigated by FLORIN) are peculiar to this flora. I am inclined to think that equally close investigation of its ferns would establish their specific distinction, but the fact of their general similarity to those of one or other period is incontestable. This intermediate flora gives me the impression that there was, in N. Europe, a very gradual change from the Lower Liassic to the Upper Liassic and Oolitic floras, and that while it is certainly possible to recognise one intermediate stage — that developed in Bornholm, it will be very difficult to recognise many other intermediate stages by the plants. I think that plants in the European Mesozoic at least have probably rather long time ranges and are only reliable for somewhat coarse correlation. It is impossible for me to say how far into the Lias the *Thaumatopteris* Zone extends before it became so much altered that a new zone can be established, but certainly it may be said to have ended before the Bagaa (Bornholm) flora was preserved.

D. COMPARISON OF THE FLORAS OF GERMANY, SWEDEN AND GREENLAND

The three floras are compared in Table 3 where the more characteristic and widespread plants of the *Lepidopteris* and *Thaumatopteris* floras are recorded. In the *Thaumatopteris* Zone the three floras agree very well and one can scarcely say that one pair has more in common than another; in the *Lepidopteris* Zone, on the other hand, Sweden and Greenland have much more in common than either with Germany, but this probably results from the *Lepidopteris* flora being less well known in Germany.

The transition region of Greenland only is shown in the table since there is nothing comparable in the other two regions.

In the middle of the table species are given which range both zones. Some of these are confined to one zone in one country but occur in both in an other; the absence of such a species does not constitute a serious difference, the floras are too incompletely known. It is remarkable that there are no misfits such as would be caused by a species being characteristic of one region in the Rhaetic, another in the Liassic. This coincidence is astonishing and its perfection may well be in part the result of a lucky accident, but I think that the general agreement concerns so many species that it is safe to stand closer investigation.

To sum up: we have in the European early Mesozoic a Middle Keuper flora, then a gap; a Rhaetic (*Lepidopteris*) flora followed immediately by a Basal Liassic (*Thaumatopteris*) flora, and then another gap; a flora belonging to some period in the middle of the Lias in Bornholm and then after another interval a sequence of floras in the Upper Lias and Lower Oolites. Of the Rhaetic and Basal Liassic — the floras with which I am immediately concerned I may say:—

For the *Lepidopteris* flora:—

The Rhaetic (*Pteria contorta* Zone) age of certain localities in Germany is established, but it is not known whether the *Lepidopteris* Zone corresponds in its limits with the marine Rhaetic.

For the *Thaumatopteris* flora:—

The Basal Liassic (*planorbis* and perhaps *angulatus* Zones) age of certain localities in Sweden, Germany and France is established, but again we cannot set its limits.

However, I think it probable that the transition from the *Lepidopteris* to the *Thaumatopteris* flora coincided with the end of the Rhaetic and beginning of the Liassic (see p. 92). As the two floras are very different — correlation by means of plants, in Europe, is fairly easy, but up till the publication of TROEDSSON's conclusions in 1934 we had to assume that the transition took place in the Middle Rhaetic and it was therefore impossible to distinguish an 'Upper Rhaetic' flora from one of the Lower Lias.

The rather rapid transition from the *Lepidopteris* to the *Thaumatopteris* flora is remarkable. In Greenland it has been shown to occur in less than ten metres of rock — perhaps in less than five metres out of the 90 m of the plant-bearing series; in Sweden and Germany we have no evidence, but from the absence of any described floras showing clear evidence of mixing it also is probable that the transition took place in a thin layer of rock, or it may indeed be unrepresented.

One could account for the change in flora at the top of the *Lepidopteris* Zone in a considerable number of ways, among which might be mentioned:—

1. Establishment of a land bridge allowing many fresh species to reach the Europe-Greenland area.
2. Change of climate causing a change in dominant types.
3. Gradual change with time in the composition of the flora owing to steady immigration (or evolution) of new types.

Suggestion 1 has nothing to be said in its favour; the *Thaumatopteris* flora does not happen to be known anywhere in pre-Liassic time, but as this flora is itself used for correlation its recognition as pre-Liassic would be difficult.

Suggestion 2 is, I think, unlikely. The general aspect of the flora — size of leaf, proportion of delicate leaved plants, e. g. ferns, is about the same in the two floras in Greenland, and the few species which range through both show leaves of the same size in both. No change in land level in relation to the sea occurred during the Liasso-Rhaetic of sufficient size to affect climate.

Suggestion 3, I consider the most useful hypothesis. The relatively rapid change in flora is most naturally accounted for by assuming that there was a lag in deposition over a rather long period, so that a great interval of time is represented in a very thin series of rocks. This type of interruption appears to be very common even in apparently continuous marine series and in a deltaic deposit where the rate of deposition depends on the rate of subsidence it is to be expected. Since the land surface of the Rhaeto-Liassic deltas in Sweden, Germany and Greenland was probably almost at sea level throughout the period a very slight general change in sea level — for example, the flooding of a desert basin — would affect all three at the same time and in the same way. If a long interval of time is represented in these few metres of rock it is probable that they may include not only the Rhaetic-Liassic transition but a considerable portion of one or both formations as well, in which case the *Lepidopteris* flora would be wholly pre-Liassic; the *Thaumatopteris* flora wholly post-Rhaetic as TROEDSSON has taken to be the case.

E. OTHER FLORAS OF UPPER TRIASSIC TO LOWER LIASSIC AGE

Floras determined as Rhaetic are found all over the world; there are a good many also determined as Lower Liassic, but very few regarded as rather older than the Rhaetic. I believe that this preponderance of the 'Rhaetic' is due to error arising from difficulties of correlation and

to no real geological cause. Unfortunately there is no complete description of the well-preserved Lunz flora which would supply a standard for the Middle or Upper Keuper though the recent description by FRENTZEN of German Keuper floras goes a long way to remedy this lack. The 'Rhaetic flora' has been known fairly well since SCHENK's and NATHORST's early work, and both of these have been revised, the German by GOTHAN in 1914, the Swedish by TROEDSSON in 1934, and much which was taken as standard Rhaetic must now be standard Liassic.

For the Liassic we had formerly only a little in Germany though now the greater part of the German flora and the large Hör flora of Sweden; the imperfectly dated Bornholm floras again partly regarded as Rhaetic; and the large Rajmahal flora (now regarded by some as of younger than Liassic age).

With these difficulties before us, it will be plain that comparison with these more distant floras is better able to give results of interest from the point of view of plant distribution than help in dating the Greenland flora.

It is only in Europe and Greenland that two distinct assemblages of plants (the *Lepidopteris* and the *Thaumatopteris* floras) are known; elsewhere there is a preponderance of the *Thaumatopteris* species, or else a mixture without any stratigraphic evidence of zonation. Floras of the '*Thaumatopteris*' or intermediate type are known all round the world; not scattered indiscriminately, but grouped in a belt of the earth's surface which takes an oblique course from Greenland at 70° N.; Europe from Sweden to Austria (46°—56° N.); through Russia and Siberia at about the same latitudes and finally in Japan at about 35° N. North of this belt Liasso-Rhaetic floras are unfortunately unknown, but south of it there are many fossiliferous localities.

In the lands of the southern hemisphere and also in India — that is, in Gondwanaland — there is a succession of floras which, though changing, retain throughout the Triassic and Lower Jurassic strong characters uniting them as a group but distinguishing them from all northern floras. Intermediate in geographical position, but different in floral character from either, there appears to be a middle province extending again as an oblique belt from Armenia to South China (Tonkin). It will be convenient to consider these three floral provinces separately.

§ 1. The Northern Province.

Siberia, Afghanistan and Central Asia. There are many rich Jurassic floras in this vast area, and some which include a good many plants of Liasso-Rhaetic aspect, though, as KRYSHTOFOVICH points out, they need much closer investigation than they have yet received.

Such species are recorded as *Neocalamites hoerensis*, *Camptopteris spiralis*, *Dictyophyllum nilssoni*, *Hausmannia crenata*, *Marattiopsis muensteri*, *Baiera spectabilis*, *Nilssonia acuminata*; some belonging to the *Lepidopteris* but most to the *Thaumatopteris* Zone. From these and other similar species it would appear that the *Thaumatopteris* flora at least extended from Greenland across North Europe and Central and Northern Asia.

For recent papers on these floras see: — KRYSHTOFOVICH 1933; KRYSHTOFOVICH and PRINADA 1932; PRINADA 1928, 1931, 1933, 1934.

E. Asia. 1. Japan. During the last few years our knowledge of the fossil floras of Rhaeto-Liassic aspect from Japan has been very greatly increased.

The correlation of these beds depends entirely on their fossil plants; even the plant-bearing beds of the Nariwa district, which were formerly supposed to be overlain by marine beds with Upper Triassic shells, are now definitely stated to be without known relation to the marine beds (OISHI 1932 b, p. 371).

The various Japanese floras have been collected from very numerous localities, the exact stratigraphic relations of which to one another have not been described. For the purposes of a very general comparison it is therefore advantageous to consider the various floras together.

A remarkably high proportion of the Japanese fossils are like European ones, and even if investigation of their spores and cuticles should show that many of them are distinct, the resemblance in general appearance will remain.

Among the species which make up the Japanese flora are a very few identified with those of the European Trias; rather more identified with the European *Lepidopteris* flora; a still larger number identified with the European *Thaumatopteris* flora and a few identified with younger European floras, in particular those of the Lower Oolites.

The Oolitic species are, I think, without exception ones which are very difficult to determine — *Podozamites lanceolatus*, *Cladophlebis haiburnensis*, *C. denticulata*, *Todites williamsoni*, etc., and all are species which closely resemble others known from the Rhaetic. I think these identifications are therefore without important zonal significance.

The only species definitely pointing to an age older than the Rhaetic is *Pterophyllum jaegeri*, which has been described by YABE and OISHI (1929) and by OISHI (1931, 1932 b) from China and Japan. The specimens are rather fragmentary and while they certainly match certain Triassic ones very well, appear to me to agree equally with some basal Liassic ones of *P. subaequale*.

The many determinations of species characteristic of *Lepidopteris*

and *Thaumatopteris* zone floras of Europe seem to me to have a much surer foundation.

Of the *Lepidopteris* flora there appear to be at least half a dozen reliable species or genera, namely:—

Neocalamites hoerensis
Hausmannia crenata
Ptilozamites
Cycadocarpidium swabi
Baiera paucipartita
Pterophyllum schenki,

all of which but *Cycadocarpidium* occur in the Nariwa flora.

Of the *Thaumatopteris* flora, there are rather more species, namely: —

Marattiopsis muensteri
Thaumatopteris brauniana
Dictyophyllum nilssoni
D. muensteri
Todites princeps
Nilssonia acuminata
N. muensteri
Baiera taeniata
B. muensteriana
Campylophyllum hörmanni,

all of which occur in the Nariwa flora. The evidence available is not adequate to show the existence of any zonation in this flora; but at the same time there may be a possible indication of it: for example, some of OISHI's localities in the Nariwa district (e. g. his 'No. 1') appear to show a preponderance of the *Lepidopteris* Zone flora, while others ('No. 49') have more of the *Thaumatopteris* flora.

Considering their relative geographical closeness, the Japanese floras have extraordinarily little in common with the Tonkin flora. Excluding species of whose determination the Japanese authors were doubtful and the various species which seem to me unsatisfactory as zone indicators, there are only *Neocalamites carrerei*, which has apparently a considerable range, *Pterophyllum schenki*, and *Todites princeps*, which appears to range from the basal Lias to the Oolite; all of which occur in many other parts of the world too.

Among the doubtfully determined species, however, are some more characteristic of the Tonkin flora, namely:—

Annulariopsis inopinata
Otozamites indosinensis
Baiera guilhaumati
Dictyophyllum nathorsti.

(I think the Tonkin *Marattiopsis* is a distinct species, but the Japanese *M. muensteri* is probably rightly determined.)

There is no reason to suppose that there is any considerable difference in age between the Japanese and Tonkin floras; but rather the difference indicates a different floral province. In view of the agreement between the Japanese and European floras this may indicate the existence of a climatic zone which would have great palaeogeographical significance.

§ 2. Middle Province.

China and Indo-china. The flora of Tonkin described by ZEILLER (1903) remains the most important 'Rhaetic' flora in this region.

This flora was obtained from a good many different points and as far as I know their exact stratigraphic relation to one another remains undetermined; certain localities, however, have been shown to contain lamellibranches of Rhaetic type (DEPRAT 1914).

The general character of this flora, which shows a striking number of '*Taeniopteris*' leaves, is considerably different from any European flora. There are, however, a number of closely similar or identical species with some which characterize the *Lepidopteris* Zone in Europe and Greenland, namely:—

Nilssoniopteris jourdyi,

Pterophyllum schenki, both of which occur in the *Lepidopteris* Zone of Greenland, and some which characterize the *Thaumatopteris* zone or younger floras:—

Todites princeps

Woodwardites microlobus

Equisetites sarrani

Marattiopsis sp. nov. (*M. hoerensis* of ZEILLER),

a genus not known before the *Thaumatopteris* Zone in Europe.

In addition, there are species of *Podozamites* which at present have no zonal significance; some species of *Pterophyllum* and *Taeniopteris*, which, though determined as Rhaetic or basal Liassic species, need confirmation by their cuticles, and long ranged types like *Todites* of the *T. williamsoni* group and *Clathropteris*.

ZEILLER was only able to make rather tentative suggestions about the relative age of his different localities and no very definite zonation was established. It is interesting, however, that the species which characterize the *Lepidopteris* and *Thaumatopteris* Zones respectively of Europe here appear to be mixed together. This fact is referred to later.

Apart from the Tonkin flora there are only a few quite small floras in China of definitely Rhaetic aspect, but these include certain European

species, *Lepidopteris ottonis* and *Cycadocarpidium erdmanni*, both characteristic of the *Lepidopteris* zone; see SZE (1933 a); also HALLE (1927). As would be expected from their intermediate position, these small floras appear to have some species of the Northern floral region and others of the Southern (Tonkin).

Persia. The flora of the Elburz Mountains (Albours Kette) has been described in 1887 by SCHENK and KRASSER (1891). The general aspect of the flora is very like that of European Rhaeto-Liassic floras and a preponderance of the species were identified with those of the German 'Grenzschiefer flora' (basal Liassic), which was then regarded as Rhaetic, and in consequence the Persian flora has been ever since referred to as Rhaetic. ZEILLER (1905) pointed out that some of SCHENK's species are more similar to those of the Tonkin flora (*Dictyophyllum nathorsti*, *Pterophyllum bavieri*).

While no help can be obtained from the Persian flora for exact correlation, the fact that it has leaves agreeing best with those of the Tonkin flora is interesting from a geographical point of view, particularly as *P. bavieri* occurs again in the Pamir flora (PRINADA 1934), one of the most southerly of the Central Asiatic floras so far studied.

Caucasus. PRINADA (1934) has described a flora from Armenia which appears to be of approximately Rhaetic age. As far as can be judged from the rather imperfect specimens the author's conclusions that this flora has most in common with the Persian, Pamir and Tonkin floras (that is, with the Middle province) are justified.

The Pamir flora. A considerable number of plants are described by PRINADA (1934) from about 38° N. latitude; they were obtained from a good many localities but all are regarded as being of similar age. The general aspect of the flora agrees, as PRINADA points out, with Rhaeto-Liassic floras of other parts of the world rather than with the geographically nearer Jurassic floras of the U.S.S.R. A very interesting feature is the presence of *Pterophyllum bavieri* ZEILLER, a Tonkin and Persian species; and the relative abundance of Cycad-like leaves — *Pterophyllum*, etc. — and rarity of Ginkgoalean and coniferous ones, in which also it agrees with the Tonkin flora.

America. No flora of Rhaetic type is known from North America, though there is the important Virginian Triassic flora, which shows striking agreement with the Triassic flora of Lunz. In Jurassic times, however, floras are known from Alaska which resemble European floras of similar age, and in Mexico there is a large flora correlated with

the Liassic (WIELAND 1916). This flora contains many species which are almost certainly peculiar to it, but a number which are identified with those of other floras though in no case is the identification confirmed by an agreement in microscopic structure. In this Mexican flora "Cycadean" leaves show a most extraordinary preponderance; Ginkgos and Conifers are in abeyance; to this extent at least it agrees with the Tonkin type of flora rather than with the N. European type of Liassic flora.

A small flora supposed to be Rhaetic has been described from British Honduras (NEWBERRY 1888), but no conclusions can be safely based on it.

In Europe the 'middle province' is not represented in the Liasso-Rhaetic though a possible approach to it is shown by the South German flora, which is to some extent intermediate between the Swedish and the Persian and Pamir floras in some of its species of *Pterophyllum* and in the comparative rarity of its Ginkgoales.

§ 3. Southern Province.

South Africa, etc. There is a very important flora in the Molteno beds of the Stormberg series of the Karoo system of South Africa, and a similar flora in the Forest sandstone series of S. Rhodesia; the most recent general account of the flora being given by DU TOIT (1927). This flora was formerly regarded as Rhaetic but DU TOIT points out that this conclusion rests on insecure evidence. He says "there is no doubt that the majority of the Eurasian species — mainly fern-like plants and Ginkgoales are Rhaetic"; but there is a Triassic and an important Permian element, so that "the flora of the Molteno beds shows an anomalous mixture of (a) Eurasian Rhaetic genera and species, (b) European Keuper types, (c) European Permian elements, (d) representatives of the Glossopteris Flora with Permo-Triassic characters". He draws the conclusion that "it would seem more probable that the Molteno Flora must be regarded as essentially of Upper Triassic — Keuper — age".

THOMAS (1933) expresses the opinion that "the flora of the Molteno beds is Triassic in character, but it is very doubtful whether it is safe to go beyond this", but considers it likely that it may belong to the Middle rather than the Upper Trias. Of some of DU TOIT's determinations he says "It must be noted that the species which DU TOIT regards as Rhaetic in type are mainly forms which cannot be identified with any great certainty at the present time from their external form". This conclusion I would endorse strongly.

THOMAS points out also that the South African flora has considerable agreement with the Permian flora of Arizona (WHITE 1929).

In most cases I would be prepared to agree that DU TOIT's determination of European Rhaeto-Liassic species may be correct; but in no case do I feel convinced that it must be correct. Thus *Cladophlebis roesserti* and *C.* or *Todites goeppertiana* are a type of fern which ranges with only the slightest changes from the Middle Trias to the Middle Jurassic of Europe; and both appear to be based on sterile specimens. The sterile fragment named *C. nebbensis* is again a very difficult species (see p. 16); while his *C. concinna* seems to me definitely distinct from SCHENK's *Pecopteris concinna*.

Ginkgoites digitata (BRONGN.) is a name of a group of species of a certain general form which occurs throughout the Mesozoic. His *Pterophyllum* cf. *braunianum* GOEPP. and *Pterophyllum inconstans* (BRAUN) belong to a group of leaves which seem to me almost indeterminable unless it is possible to take their cuticles into consideration as well as their macroscopic details. I cannot therefore attach any great weight to these determinations at present. Of the other determinations the specimen of "*Marattiopsis muensteri*" has been named *Yabeiella?* *du toiti* by OISHI. The genus *Yabeiella* is Triassic or "Rhaetic" and distinctly older than *Marattiopsis*; while THOMAS states that DU TOIT's "*Sagenopteris*" is a *Glossopteris* and that his "*Thinnfeldia rhomboidalis*" is almost certainly a *Dicroidium*.

If one is prepared to place no reliance on these Rhaeto-Liassic determinations, the result is that DU TOIT's argument that the flora is Triassic rather than Rhaetic is very greatly strengthened. I would be inclined to say of the flora that it contains few or no species of the European Rhaetic flora. The same remarks apply equally to its supposed agreement with the Persian "Rhaetic" flora.

On the other hand, the agreement is better between the Molteno flora and those of the Parsora stage of the Rajmahal series of India and with the East Asiatic flora, in particular that of Tonkin. The Parsora flora is regarded as Lower Triassic or even rather older (SEWARD 1933); the E. Asiatic floras as "Rhaetic".

Most important of all is the agreement with the Ipswich floras of Australia, and in particular with the flora of Tasmania and the "Rhaetic" (or older) flora of Argentina (see DU TOIT 1927, p. 305). These floras agree not only in the species as determined but, what is more important, in the general aspect of the flora; in particular in their peculiar forked "*Pteridosperm*" leaves, *Dicroidium*, "*Pachypteris*", "*Stenopteris*", "*Danaeopsis*", etc.

Judging by the general aspect of the fossils and without placing particular reliance on any one determination, the evidence would seem to me to favour a Middle, or even Lower, rather than Upper Triassic age for this flora; for a large element seems to me to recall the Permian

rather than the Rhaetic. An age as old as the Permian is, however, excluded by the large admixture of purely Mesozoic genera.

Australia. In Queensland there are two distinct and important floras, the older (Ipswich), being correlated with the Upper Triassic or Rhaetic; the younger (Walloon) with the Lower Jurassic, (WALKOM 1915—1917, 1924). Although a good many species are compared or identified with those of other countries there are extraordinarily few which seem certainly identical with the European Rhaeto-Liassic flora. The younger flora may be ruled aside as being younger than Rhaetic; the older, which may well be of Upper Triassic age, has only one species of whose identity with European Rhaetic species I feel convinced, namely *Neocalamites hoerensis*; while *Sagenopteris rhoifolia* and a species of *Coniopteris* would point to a Liassic age and *Dictyophyllum rugosum* to the Oolite.

The Esk series (WALKOM 1924, 1928), which is also supposed to be Upper Triassic, has a flora very like that of the Ipswich series, but the identification of its species affords even less proof of a Rhaetic age; as their names stand at present in WALKOM's papers there appear to be three or four S. African Triassic species, one European Rhaetic, two European inferior oolitic and about six aggregate species which range the Jurassic.

The resemblance of these floras and also those of other parts of Australia and, in particular, Tasmania to the Molteno flora (?Middle Triassic age) seem to me important, for not only are many more species the same, but the whole character of the flora is similar.

The stratigraphy of the Australian floras has been recently summarised by WHITEHOUSE (1931).

Argentina. There is a flora of "Rhaetic" type in Argentina but which is still very inadequately known. The most recent and useful list of species is given by DU TOIT (1927, p. 305). It shows, as DU TOIT emphasizes, extremely close resemblance to the Australian Ipswich flora, etc. and very considerable resemblance to the S. African Karoo flora. It may well, therefore, be rather older than the Rhaetic. It has no real affinity with the Northern floras.

Discussion of the distribution of floras in the Liasso Rhaetic.

It is very difficult to distinguish the effects produced by age and climate in determining the character of a fossil flora; even if all other possible factors be disregarded. This difficulty is intensified by the great doubt one must hold of all specific determinations. The study of microscopic structure does not, of course, make determination safe,

but it does frequently prove specimens of similar gross appearance to be entirely different and so makes determination less liable to error. Although an increasing proportion of the specimens being determined and figured nowadays have been investigated microscopically, this proportion, even where preservation is good, remains less than half. At present the evidence suggested by the existing names certainly seems far better than it really is; in making comparisons the possibility of error in every determination must be borne in mind, and also a great difference in value must be assigned to different determinations. Often in comparing floras I have had to disregard all names and to compare the general impressions given by the figured specimens; the results being as vague as the evidence.

It is thus with considerable hesitation that I put forward my conclusions which coincide with those of some others who have worked on this subject, namely that there are three floral provinces — a northern, a southern and a middle one — and that the northern and middle provinces at least occupy a zone which does not follow existing climate and latitude zones but runs obliquely. It is interesting that this is in fair agreement with KOEPPEN's and WEGENER's (1922) maps of the Triassic and Jurassic; but I do not feel that the facts are sure enough to give much support to the theory of continental drift.

The recognition of the *Lepidopteris* and *Thaumatopteris* zones of Europe and Greenland, and their general correspondence with the Rhaetic and basal Liassic is, however, much surer, because it is based on specimens identified both by form and by microscopic structure (cuticle, spores, etc.), and the work I have done after first recognising these two zones has served to make their recognition more certain. They are indeed so well marked that one would expect to find them everywhere but this is not the case. In the large floras of E. Asia, the sequence of the plant beds is little known and it is therefore out of the question to work out their zonation, but there seems to be no doubt that certain beds contain a mixture of species which in Europe characterize the *Lepidopteris* zone with others of the *Thaumatopteris* zone. This might be due to the flora being of intermediate age, a thing which is very possible if I am right in supposing that the middle part of the Greenland and European sequence is poorly developed; but the possibility must also be recognised that the same species might make their appearance in different order in regions far apart. The establishment of such differences would set a limit to the use of plants for correlation.

F. CONCLUDING REMARKS.

The Greenland Liasso-Rhaetic flora is one of the largest floras of its age known at the present time, and it should be as possible to draw

general conclusions from it as from any in the world. It has, in fact, been possible to show, as a result of the simplicity of the geological section and abundance of fossiliferous horizons that very well marked zones are distinguishable in the floras of this period.

It might also be possible from the abundant data to draw some conclusions about the climate prevailing in Greenland during the Rhaetic. For this we must, I think, assume that plants and the other things used as evidence then behaved as similar things do now; the question then becomes one of deciding how far the things concerned are similar. SEWARD suggested that the plants of the past may have been more independent of their environment than now; passing "from a phase of vigorous youth to a state of senescence when the living mechanism is more sensitive to external factors and less tolerant of fluctuations in temperature" (1935, p. 13). For the present I will take the opposite hypothesis, namely that plants have changed but little in their reactions to climate and that local climates may have changed greatly.

The evidence bearing on the climate in the Liasso-Rhaetic as far as Greenland is concerned is as follows:—

In the period preceding the Rhaetic, red marls, arkoses and gypsum were laid down, the rocks thus resemble those of the W. European Triassic and presumably like them were deposited under arid conditions. Since great elevation is probably out of the question it may be supposed that the climate was then dry and possibly rather warm, such as prevails near the present desert belts of the earth. The marine Liassic sandstones following the Liasso-Rhaetic are also prevailingly yellow or reddish, but perhaps no conclusion can be drawn from this fact. Nowhere in the Upper Palaeozoic or Mesozoic of Greenland or any neighbouring land is there any sign of glaciation.

Animals. The enormously rich fauna of the *Jamesoni* horizon, which occurs just after the end of the plant-bearing series suggests at least temperate conditions, since arctic faunas at the present day are comparatively poor. On the other hand, the absence of any sort of coral reef at any stage is definitely against the conditions being tropical.

Plants. 1. Fair sized (gymnosperm) trees grew throughout the Rhaetic and Liassic; their wood shows annual rings with moderate (1—3 mm) annual growth. At present no trees grow in Scoresby Sound, probably because the growing season is too cold and the storms too violent; the occurrence of such trees suggests that the climate was at least as favourable as in the present northern tree belt, where even if the winter is long and extremely cold the summer is very favourable

to plant growth and no season is stormy enough to tear trees to pieces. The large number of different plant species discovered — which can only represent a minute fraction of the whole flora of Greenland — suggests fairly warm conditions. The general character of the vegetation also suggests rather luxuriant conditions of growth; the great reedy Equisetales must have attained the dimensions of fairly large subtropical bamboos and greatly exceeded any cool temperate or arctic marsh plants in size; many of the ferns (*Dictyophyllum*, etc.) had very large and somewhat delicate leaves, as also had *Anthrophyopsis*. No such leaves occur in arctic plants at the present day.

It is rather striking that although the Gymnosperms show a range of from heavily cutinised leaves with protected stomata to others with thinly cutinised leaves and more exposed stomata, the thinly cutinised types predominate; in the conifers in particular the thinly cutinised leaves of *Podozamites*, *Stachyotaxus*, etc. are often the commonest fossils in a bed while leaves of the protected species are very rare indeed.

It may be noticed that all these points suggest a favourable growing season; nothing excludes the possibility that the winter may have been cold.

Comparison with other floras suggests that there was a broad belt of floras (the Northern floral province) where the climate was sufficiently uniform to allow a nearly uniform flora to grow. (See also BERRY 1930.)

In 1926 I drew the following conclusions from the evidence then available:—

1. The conditions were certainly not arctic, but there is no reason to suppose that they were tropical rather than temperate.
2. There was a plentiful water supply.

From the evidence given above I am inclined to support these conclusions, but I would not go beyond them.

From the floristic point of view I believe the Greenland flora, or the fraction of it which grew in an estuarine marsh, is fairly well known. During the beginning of my field work every new locality gave many new species, but towards the end, though I investigated new localities which were really just as rich, there was very little that was new. Another season spent collecting, even if many new localities were found — and I doubt if many would be in the area which ROSENKRANTZ and I studied — would probably yield comparatively few new species by the methods I employed. I have deposited manuscript notes on the localities with the collection in Copenhagen in the hope they may be of some help to a future collector.

Though the flora may be largely known, the plant localities are far from fully worked out. I think it is true to say for early Mesozoic plants in general that apart perhaps from a few ferns and a couple of conifers, we know less than the full set of structural facts we have a right to expect to learn from plants preserved as 'compressions' by the application of present day technique. From the point of view of plant morphology the Greenland plant beds are far from worked out but just well enough known to be interesting.

SUMMARY

In the first part the entire flora of the Greenland Liasso-Rhaetic is brought under review. The stratigraphic value of many species is discussed.

The following new species and genera are described for Greenland plants:—

Hepaticites rosenkrantzi sp. nov., previously undescribed.

Hepaticites amauros sp. nov., previously undescribed.

Beania kochi sp. nov. (for the fruit of *Nilssonina incisoserrata*).

Peltaspermum gen. nov. (type-species *P. rotula*).

Peltaspermum rotula sp. nov. (for the fruit of *Lepidopteris*).

Antevsia gen. nov. (type-species *A. zeilleri* (NATH.)), for *Antholithus arberi* NATH., the microsporophyll of *Lepidopteris*.

Caytonanthus gen. nov. (type-species *C. arberi* (THOMAS)).

Caytonanthus kochi sp. nov. for the microsporophyll described by HARRIS as *Sagenopteris nilssoniana*.

The genus *Thinnfeldia* has been found in Greenland.

The following changes are made in the names of Greenland plants:—
Neocalamites carcinoides changed to *Lobatannularia carcinoides* (HARRIS) n. comb.

Equisetites doratodon is identified with *E. sarrani* ZEILLER.

Bennetticarpus oxylepidus HARRIS is identified with *B. exiguus* HARRIS; a new diagnosis of *B. exiguus* is given.

New data are given about the structure of *Caytonanthus*, about the vascular structure of *Equisetites*, and about the variation of the leaf of *Stenopteris dinosaurensis* HARRIS, of which an emended diagnosis is given.

The following fossils belonging to other floras are considered:—

The seed-bearing organ described as *Lepidopteris natalensis* THOMAS from the Trias of S. Africa is named *Peltaspermum thomasi* HARRIS.

The Caytonialean microsporophyll *Antholithus arberi* THOMAS is re-named *Caytonanthus arberi* (THOMAS). Pollen identified with this species and also that of a second species, *C. sp. A* obtained from the Jurassic of Yorkshire, England, is described and figured.

The name *Todites undans* (BRONGN.) n. comb. is substituted for *Cladotheca undans* (BRONGN.) HALLE.

In the second part the stratigraphy of the E. Greenland Liasso-Rhaetic is described and discussed in relation to that of other areas. The two plant zones are distinguished, recognised in other floras and correlated with the Rhaetic and basal Liassic. The difficulty of recognising any exactly corresponding stages outside the area of Greenland and Europe is pointed out.

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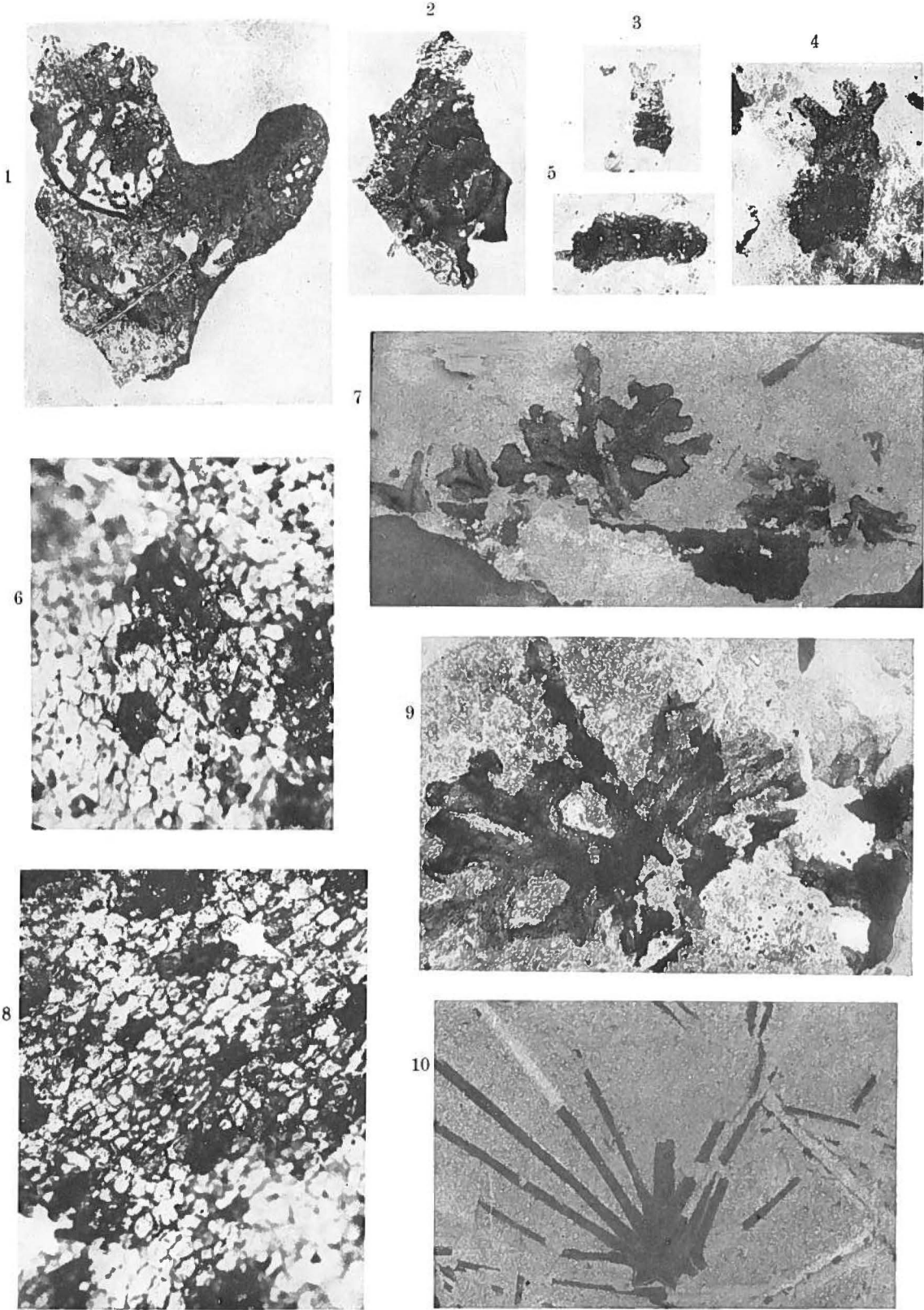
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PLATE AND TABLES

Plate 1.

- Fig. 1. *Hepaticitis rosenkrantzi*, drawing of the thallus bearing a 'cup', $\times 10$.
Fig. 2. *H. rosenkrantzi*, drawing of a thallus with a 'cup', slide 1b, $\times 10$.
Fig. 3, 5. *H. rosenkrantzi*, photographs of thallus, $\times 2$.
Fig. 4. *H. rosenkrantzi*, photograph of transfer of specimen shown in Fig. 3, slide 1b, $\times 4$.
Fig. 6. *H. rosenkrantzi*, photograph of thallus tissue, slide 1b, $\times 100$.
Fig. 7. *H. amauros*, drawing of the type specimen, $\times 2$.
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Fig. 9. *H. amauros*, photograph (by infra red light) of the transfer of the type specimen, slide 8a, $\times 4$.
Fig. 10. *Stenopteris dinosaurensis*, basal part of leaf, No. 1133, $\times 1$. The specimen was obtained from Dinosaur R.



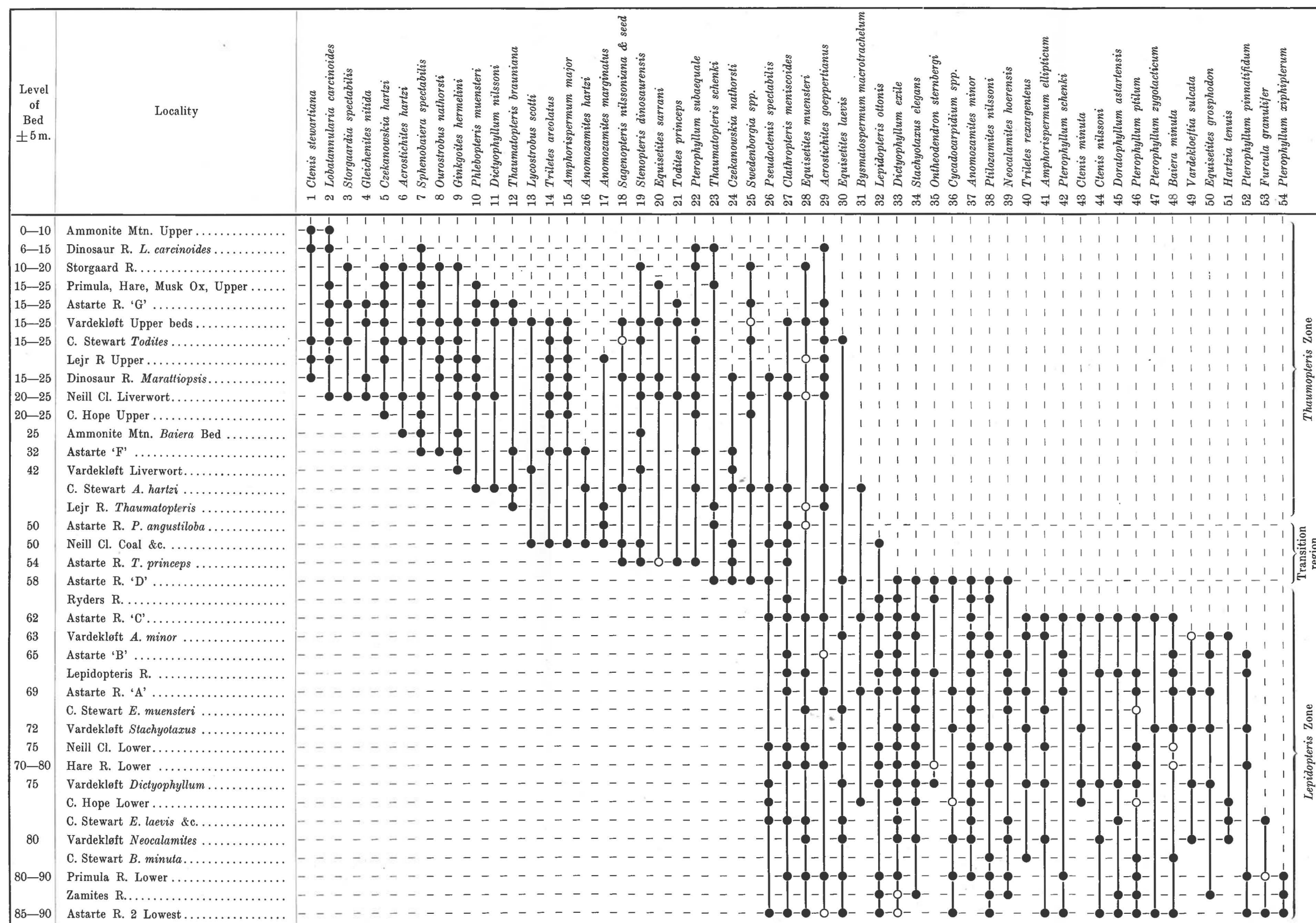


TABLE 1. Vertical distribution in Greenland.

● = occurrence of a species; ○ = probable occurrence of a species but determination doubtful.

Troedson's Zones		Nathorst's Zones		Locality	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43							
Liasic	Liasic	Liasic	Liasic	Hör	○	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●						
				Sofiero.....	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●				
				Dompäng	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●			
				Rödalsberg	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●			
				Munka Tågarp	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●				
				<i>Nilssonina polymorpha</i> { Palsjö	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●			
				<i>Dictyophyllum acutilobum</i> { Helsingborg	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●			
				Höganäs (Upper)	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●			
				<i>Thaumatopteris schenki</i> { Stabbarp J. Molin	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		
				<i>Equisetites gracilis</i> { Stabbarp N. U. G.	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Skromberga Upper.....	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●				
Rhaetic	Rhaetic	Rhaetic	Rhaetic	<i>Lepidopteris ottonis</i> { Bjuf 4.....	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●				
				Bosarp; Billesholm.....	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●			
				Hyllinge	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	
				Bjuf 2 & 3	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	
				<i>Camptopteris spiralis</i> { Skromberga Lower.....	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	
				Stabbarp 'Ton 10'	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	
				Höganäs Lower.....	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	
				Bjuf 1.....	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	
				<i>Dictyophyllum exile</i> { Bjuf α.....	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●

TABLE 2. Vertical distribution of species in Sweden.

● = accepted record; ○ = doubtful record; × = rejected record.

TABLE 3.

[illegible]

TABLE 3. Comparison of the floras of Greenland, Sweden and Germany.

G = Greenland; S = Sweden; F = Franconia or other part of Germany.

Note. Species of the genera *Nilssonia*, *Cladophlebis* and *Podozamites* are excluded because their determination is at present too uncertain.