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A NEW ASSEMBLAGE OF PLANT FOSSILS
FROM MILORGFJELLA, DRONNING MAUD LAND

By

EDNA P. PLUMSTEAD, D.Sc., F.R.S.(S.A.)

*Bernard Price Institute for Palaeontological Research,
University of the Witwatersrand, Johannesburg,
Republic of South Africa*



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ABSTRACT

IN this paper a number of Antarctic plant fossils, from a new area in Dronning Maud Land east of the Weddell Sea, are described. They were collected by members of the British Antarctic Survey during the period 1964-67, and include several genera and species which have not been found previously in Antarctica. They fill a gap in the early Permo-Carboniferous records of plant life in that continent. The paper is in three parts: the first part describes briefly the geological succession and geographical environment of the plant-fossil sites; the second part is a detailed description of the plants, and in the third part the composition, affinities, age and significance of the flora are discussed. The plant fragments were transported and the preservation is poor. There are fragments of lycopod, *Paracalamites* and fern stems, but the vast majority of the fossils are of woody stems and leaves whose closest affinities are with four different groups of gymnosperms: the cordaitean, ginkgoalean, coniferalean and glossopteridean classes. The dominance of such varied gymnospermous plants in this area at so early a stage is regarded as being highly significant in plant-distribution studies.

It was a cold-climate flora, established in the closing stages of the Southern Hemisphere Palaeozoic glaciation, and can be compared with those of the Needle Shales of the Talchirs in India, the Upper Dwyka Shales of South Africa and possibly the Bacchus Marsh beds of Victoria, Australia, and is therefore of late Carboniferous or early Permian age. Like those described earlier from Antarctica, the flora emphasizes the uniformity and near contemporaneity of each stage of plant life throughout Gondwanaland.

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I. INTRODUCTION

THE plant fossil assemblage described in this paper was collected between 1964 and 1967 by members of the British Antarctic Survey from Milorgfjella which is east of the Weddell Sea in east Antarctica. It provides an interesting corollary to earlier work on the fossil floras of Antarctica (Plumstead, 1962) which was based on a number of plant fossils collected from isolated sites and outcrops by the geologists of the Trans-Antarctic Expedition, 1955-58. All earlier palaeobotanical work in Antarctica was summarized in that publication, but a number of papers have since appeared describing the fossil plants of areas explored more recently. Each of them has enriched our knowledge and our understanding of the earlier plant life of this still largely unexplored continent, and has confirmed its close association with other Southern Hemisphere areas in a vast "Gondwana" floral province.

The position of Milorgfjella in relation to other areas in east Antarctica from which fossil plants have been collected is shown in Fig. 1.

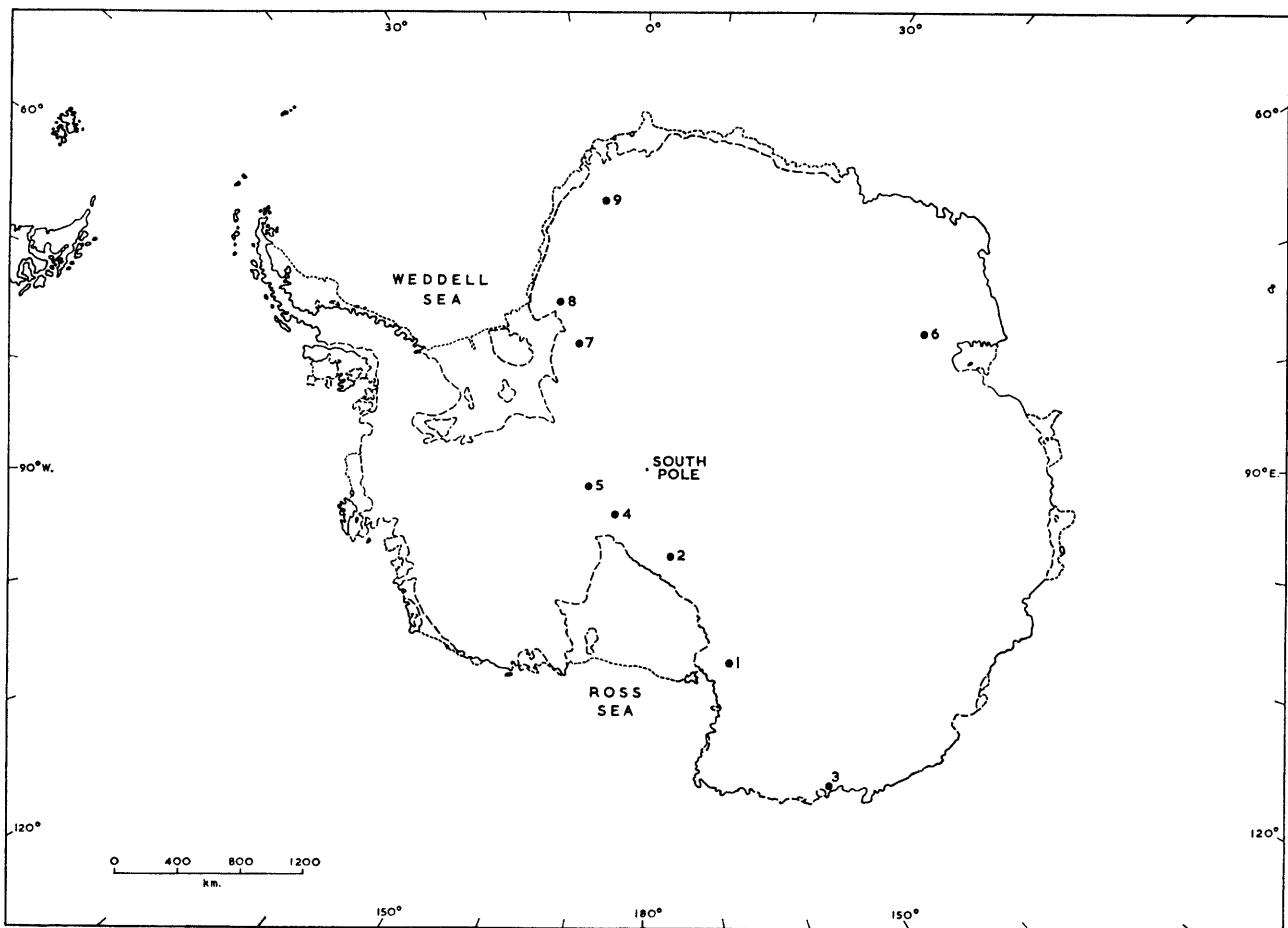


FIGURE 1

Sketch map of Antarctica showing the position of Milorgfjella (9) in relation to other areas in east Antarctica from which Permian fossil plants have been collected.

- | | |
|------------------------|------------------------|
| 1. Ferrar Glacier. | 6. Amery Formation. |
| 2. Mount Buckley. | 7. Whichaway Nunataks. |
| 3. King George V Land. | 8. Theron Mountains. |
| 4. Mount Weaver. | 9. Milorgfjella. |
| 5. Horlick Mountains. | |

A. LOCATION AND GENERAL GEOLOGY OF THE FOSSIL SITES

The geology of Milorgfjella has been described in detail by the field geologist (Juckes, 1972). The following short description is based on his notes which are summarized here to provide the necessary information about the geographical and geological environment of the fossils.

All the plant fossils were collected from a comparatively small area of Milorgfjella situated in approximately lat. $74^{\circ} 17' 40''$ S., long. $09^{\circ} 38'$ W. (Fig. 2). Milorgfjella is the north-eastern extension of Heimefrontfjella, of which the south-western end (nearer the Weddell Sea) is known as Tottanfjella. The exposures of Milorgfjella constitute a string of isolated outcrops which mark the position of the highest points of the mountain range projecting through the ice. They indicate the presence of a north-west-facing escarpment, approximately 610 m. in height, which forms the boundary in this area between the higher part of the ice sheet and a lower level. Where it is exposed, the rocky escarpment is often very steep and difficult to investigate, but many of the larger outcrops have the form of rocky spurs which extend north-westward from the escarpment. On top of the escarpment there are also some exposures and it was in these areas that the main collecting was possible.

An examination of the exposures proved that the mountain range consists primarily of ancient basement rocks, including granites, gneisses and schists, but that in a few areas there is a capping of near-horizontal sediments of the Beacon Supergroup. (The Beacon Supergroup of Antarctica corresponds to the Gondwana System of India, the Karroo System of South Africa and similar successions in Australia and eastern South America. To all these, collectively, the general term "Gondwana" is now applied for they have proved to have many characteristics in common.) It was from the two largest of these sedimentary outcrops that the plant fossils were collected at an approximate altitude of 1,700 m. For the purpose of this paper they will be called the "eastern" and "western" sites. According to Juckes, the western one is about 8 km. south-west of the main or eastern site and about 40 m. above the base of the Beacon Supergroup in that area. The maximum thickness of the sediments is about 160 m. at the western site (to the west of station Z.354), while at the eastern site the maximum exposed thickness is only 5–6 m. If there are no faults between the western site and a small outcrop about 8 km. to the south-east, the total thickness of the succession could approach 500 m.

The general sedimentary sequence is described below. A basal conglomerate, attaining 5 m. in thickness, is normally present. It rests with marked unconformity on an uneven surface of ancient rocks into which, in at least two areas, deeper valley troughs have been cut. These hollows, which are 30 and 15 m. wide, respectively, and about 5 m. deep, are filled with coarse conglomerates which, in the more easterly one, appear to rest upon a glacially polished and striated *roche moutonnée*. Although the actual contact was obscured by snow and rubble, it seems very unlikely from the field relations that the *roche moutonnée* could be younger than the adjacent sediments (Juckes, 1972). This is supporting evidence that the basal conglomerate itself and at least some of the fossiliferous sediments overlying it could be of glacial and fluvio-glacial origin, respectively. The conglomerate is overlain by 20–30 m. of finely banded siltstones and sandstones which grade upwards into a succession of sandstones and siltstones forming the upper part. A dolerite sill, approximately 10 m. in thickness, occurs in one area about 30 m. above the base of the sediments, but it has caused only local contact metamorphism. The beds of sandstone above this are normally about 6 m. thick and the finer intercalations are about 1 m. The latter consist largely of siltstones with thin beds of sandstone, shale, and in the upper part of the section, occasional thin coal seams. Most of the coal seams are only 2–10 cm. thick, although there is one near the top of the succession with a thickness of about 0.5 m. The siltstones adjacent to the coal often contain fragmental plant remains but only one of these specimens was examined.

The sediments are undisturbed and any irregularity can be attributed to local unevenness of the floor on which they rest. In the area of maximum thickness a gentle dip of $3-4^{\circ}$ to the south-east can be measured and this would imply a greater thickness of sediments on the plateau. However, Juckes has recorded that to the south-east of this area the sedimentary succession is overlain by at least 300 m. of basic lavas.

The lavas of Milorgfjella are Jurassic in age, like those in other parts of east Antarctica (Juckes, 1972) and in many other areas of the larger Gondwanaland. Hence there must be a considerable time gap between the sediments and the lavas to account for the great reduction in the thickness of Gondwana rocks in this area.

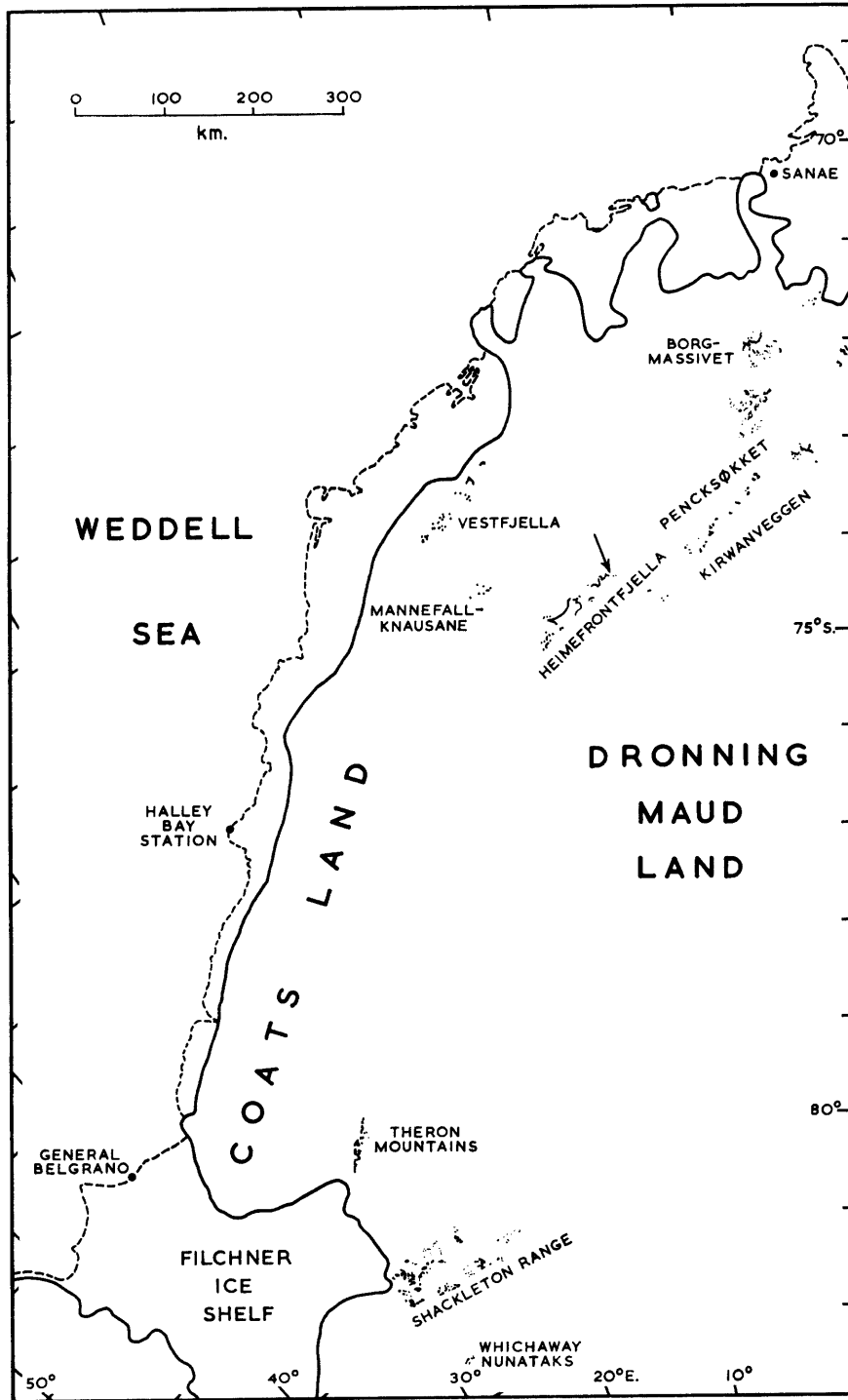


FIGURE 2

Sketch map of part of east Antarctica showing the position of Heimfrontfjella, Dronning Maud Land, and the locality in Milorgfjella (arrowed) where plant fossils were collected.

Numbering of the specimens

Numbering is done in the field, when each specimen receives the number of the site according to the time when it was collected. This is customary geological practice but it is particularly important in Antarctica where the thickness and position of the snow cover may vary considerably from time to

time and so expose different parts of the same horizon. The success of collecting at any particular time depends on these factors. The eastern site, which proved to be by far the best fossil area, was visited four times and therefore the fossils bearing the station numbers Z.342, 392, 393 and 399A must be regarded as having come from almost the same horizon but at different times.

In addition, each rock specimen was given an individual serial number. In both the tables and the descriptions which follow, the specimen number quoted refers to the face on which the number was marked. Where fossils are described from the reverse side, (R) is placed behind the serial number. Where two or more parts have been split in the laboratory from an original block, or where specimens bearing different numbers have been glued together to complete a stem or leaf, the fact has been noted in the text.

B. DETAILED DESCRIPTION OF THE FOSSIL HORIZONS

1. *The eastern site; Holstnuten (Z.342, 392, 393 and 399A)*

Here the fossiliferous horizon is very close to the base of the succession. The basal member is formed by about 1 m. of mudstone, finely laminated in its upper part and containing many scattered pebbles, cobbles and boulders, particularly near the base. This grades into the fossiliferous bed which is overlain by a bed of light-coloured sandstone about 1–2 m. thick.

This area was examined in the 1964–65 summer season when it was noted that very poorly preserved impressions of whole leaves and stems occur in the sandstones. Only one impression was observed to show any detail and this was collected (Z.342.3). In the following season, the area was re-examined in the hope that better specimens might be found, and a thin horizon containing identifiable remains was eventually discovered by R. Rhys Jones about 15 m. west of station Z.342 and about 2 m. lower stratigraphically. The specimens were numbered Z.392. The impressions of leaves and stems occur in a rather soft, dark sandy siltstone with fine partings of micaceous shale. This horizon is about 2–3 m. thick and extends over a distance of 30 m. Where the prominent overlying sandstone bed is re-exposed about 100 m. to the west, the siltstones and shales below it no longer contain plant fossils.

The fossils were found to be most abundant in the upper part of the siltstones, directly beneath the sandstone bed. The impressions were more easily seen in the unweathered rock where they stand out as carbonaceous traces. Most of them are of scattered leaves and fragments of stems. Where whole leaves are preserved they are often matted. Unfortunately, the rock did not always split cleanly along the bedding planes owing to its rather soft and sandy nature.

Since the time for collecting was short, the area was re-visited 1 month later and the specimens marked station Z.393 were collected. Once again the time for collecting was limited, so several large slabs were collected from what appeared to be the most prolific zone in the hope that better specimens might be revealed if these were split.

Equisetales are abundant in some specimens, usually with a distinct preferred orientation. Unfortunately, this was not noticed in the field during the hurried collecting operations.

Finally, in the 1966–67 summer season, G. Lovegrove collected the largest batch of 25 specimens, which are numbered station Z.399A, from the same site but these only arrived in South Africa in March 1968. In the same season, Lovegrove was able to complete more accurate mapping on which Fig. 2 is based.

The above record reflects some of the difficulties of fossil hunting in Antarctica as well as the perseverance of the field party.

2. *The western site; Helsethorga (Z.352 and 354)*

Fossil specimens from two higher horizons at the western site were collected by Juckes during the 1964–65 summer.

Station Z.352 is an horizon in the upper beds of the sequence, just above the dolerite sill. Only one fossil (Z.352.1) was found at this site; it is the hollow mould of what appears to be a lycopod stem (Plate Id) preserved in a very coarse grit. Juckes has stated that gritty and pebbly beds are present in the sandstones but that the finer intercalations which are probably present are covered by snow.

Station Z.354 is the highest horizon from which any fossils were collected. It is a shale associated with thin coal seams and bears some stem impressions. Only one specimen from this horizon was examined.

3. *Preservation and conditions of burial of the plant remains*

Unfortunately, the preservation is poor and the plant fossils are fragmentary but despite this there are representatives of a number of different classes of plant. There is a wider assortment than might be expected from so few specimens and from so limited an area, especially as most of the fossils came from an horizon only a few metres above the "tillite".

The specimens have one advantage which was lacking from all the plant fossils collected by the Trans-Antarctic Expedition; none of them exhibits the effects of thermal metamorphism due to their proximity to intrusive dolerite sills or dykes. In consequence, preliminary tests have shown that a number of microfossils can be obtained from the rock by maceration. These will be described later and should provide interesting comparisons with other areas.

It is possible to make certain generalizations about the fossil collection. In composition it includes a large number of stems, most of which are of woody plants and a number of isolated leaves, mostly fragmental, and notably of resistant species. There are no fructifications, no fragile leaves or stems and no attached foliage of any kind. The sediment changes rapidly from lenses of coarse sand to thin layers of carbonaceous mud, in which the plant fragments occur and along which the rock can be split but the lamination is very uneven. Considerable quantities of mica are present and isolated larger mineral and rock fragments, 1-2 cm. in diameter, are not uncommon and may well have been dropped from floating ice. All this suggests an active environment of rapid current action, in which only the tougher stems and leaves could survive and these were often torn. Some of the stems are twisted together as though a woody shrub had been torn from the ground. The fossils in fact reflect rough handling or storm conditions rather than the accumulation, in quiet pools, of leaves and twigs from deciduous plants, during autumn. Plate XV is an exception.

II. DESCRIPTION OF PLANT FOSSILS FROM MILORGFJELLA

BECAUSE very few geologists and botanists, interested in Antarctic fossil floras, will have the opportunity of visiting the original sites and only a small proportion will be able to examine the collection of specimens when it is returned to the United Kingdom, it is desirable that the descriptions should be accompanied by representative illustrations. To provide as full a record as possible, these must include some imperfect specimens which otherwise would not have been included in a description of material from more accessible areas.

Several of the fossils have not been recorded previously from Antarctica and a few exhibit features which have not been noticed previously in collections from other Gondwana areas. These specimens have been illustrated somewhat freely because their bearing on the evolution of the *Glossopteris* flora and on plant distribution generally is of considerable interest. Besides these, the importance of the collection lies mainly in its overall composition and in the percentage of each component which can be used to indicate the age of the occurrence and also for comparison with other areas. For a statistical approach, all the fossil fragments on every specimen should be recorded, but it was found in practice that this was impossible because so many were indeterminable, even generically, that any attempt would have been inaccurate and served no useful purpose. Instead, each group of plants has been recorded, affinities suggested as accurately as preservation allowed, and the illustrations listed (Table I, p. 8-9).

The most obvious grouping of the Milorgfjella flora is into stems and leaves, for these are the only fossils found with the exception of one small coniferous shoot and some fungal patches. There are no roots, no fructifications and no instances of stems and leaves organically connected. Stems will be described first and then the separate leaves, followed by a discussion of possible relationships between them.

All of the photographs used for the illustrations were taken in the Geology Department of the University of the Witwatersrand, with the assistance of Mr. M. Hudson. Strong but very oblique artificial lighting was used to emphasize relief. Parts of the prints were shaded in some cases to bring out additional detail, but no re-touching has been done.

A. FOSSIL STEMS FROM MILORGFJELLA (Plates I-VIII)

1. *Discussion*

For the size of the collection from Milorgfjella the number of fossil plant stems is exceptionally large. They occur on 37 of the 52 rock specimens collected and belong to at least eight different kinds of plant,

but both in size and in number gymnospermous stems are dominant. To a certain extent the high percentage of stems may be attributed to the harsh climatic and environmental conditions prevailing at the time of preservation, but which must have been mild in comparison with those of the same areas at the present day. I believe that they also reflect the relative importance of the various elements of the flora, and, in particular, the predominance of woody plants. There are some records of lower-order plants which will be described first.

TABLE I
MAIN ELEMENTS OF THE FOSSIL FLORA FROM MILORGFJELLA

<i>Division or group</i>	<i>Affinity</i>	<i>Specimen number</i>	<i>Illustration</i>
STEMS			
Lower-order plants			
Lycopodophyta	<i>Lycopodiopsis pedroanus</i> (Carr.) Edwards	Z.352.1	Plate Id
Arthrophyta	<i>Paracalamites</i> Zalessky cf. <i>Phyllothea australis</i> Brong.	Z.393.1, 3, 4 Z.399A.10A(R) Z.399A.22A(R)	Plate Ia and b
Pterophyta or Pteridospermophyta	Indeterminate small branched stem	Z.392.15	Plate Ic
Uncertain affinity	Stem with small round scars (probably leaf scars)	Z.399.22A(R)	Plate Ia(2)
	Hollow mould with grooved spiral markings	Z.399A.40	Plate Ie Plate XIVa
Woody probably gymnospermous stems			
Group 1	cf. Cordaitales	Z.399A.18 Z.399A.19 Z.392.6(R)	Plate IIa-c Plate IIIa Plate IIId
Group 2	cf. Glossopteridae	Z.399A.32 Z.393.2 Z.399A.42(R) Z.392.28 Z.399A.18 plus other fragments	Plate IIIb Plate IIIc Plate VIIa Plate VIIIa Plate IIa
Group 3	cf. Ginkgophyta Long shoots	Z.399A.7(R) Z.399A.7A Z.399A.7 Z.399A.7(R) Z.399A.22 Z.399A.22A	Plate Vd Plate Ve Plate Vf Plate Vg Plate VIa and b Plate VIc and d Plate Va-c
	Short shoots		
	Modern <i>Ginkgo biloba</i> for comparison		
Group 4	cf. Coniferophyta	Z.399A.42(R) Z.399A.36B	Plate VIIa and b Plate VIIc
Micro-structure of wood	Probably of group 1	Z.399A.18; (4) on Plate IIa	Plate IVa-g
Concentric marks possibly of pathogenic origin		Z.399A.18	Plate IIa(2) and (3), and b and c

TABLE I—continued

Division or group	Affinity	Specimen number	Illustration
LEAVES			
<i>With reticulate venation</i>	<i>Gangamopteris</i> McCoy <i>G. obovata</i> Carr. (<i>G. cyclopteroides</i> var. <i>attenuata</i> Feist.)	Z.392.2(R) Z.399A.10(R) Z.392.20 Z.392.13(R)	Plate IXa Plate IXb Plate IXc Plate IXd
	<i>G. cyclopteroides</i> Feist.	Z.399A.10C Z.392.16 Z.392.7(R) Z.392.7	Plate Xa and b Plate Xc and d
	<i>G. sp.</i>	Z.399A.40 Z.399A.18 etc.	Plate XIVa Plate IIa
<i>With bifurcating venation</i>	cf. <i>Walikalia</i> Høeg and Bose <i>W. jukesii</i> sp. nov.	Z.392.15C Z.392.15(R) Z.392A.5C Z.399A.28(R) Z.392.6(R) Z.392.24(R)	Plate XIa Plate XIb Plate XIc Plate XIId Plate XIe Plate XIf
	cf. <i>Euryphyllum</i> Feist. <i>E. antarcticum</i> sp. nov.	Z.399A.28(R) Z.399A.29A Z.392.8(R) Z.399A.29 Z.399A.28A Z.392.24(R) Z.399A.22A Z.399A.28(R)	Plate XIIa and b Plate XIIa Plate XIIc Plate XIIId Plate XIIId Plate XIIIa Plate XIIIb
	<i>E. sp.</i>	Z.399A.22A(R)	Plate XIVc and d
<i>With parallel venation</i>	<i>Noeggerathiopsis</i> Feist. <i>N. hislopi</i> (Bunb.) Feist.	Z.392.24	Plate XIVe
	<i>N. spathulata</i> (?) Dana	Z.399.31A(R)	Plate XIVf and g
	cf. <i>Palaeovittaria</i> Feist	Z.392.5A	Plate XIVh
Coniferous twig		Z.399A.40	Plate XIVa and b
Mixed foliage, etc.		Z.392.16R	Plate XV
Fungi	Spots on <i>Gangamopteris</i> leaf	Z.392.20	Plate IXc

The remainder of the specimens (18 in all) have less well preserved fragments of the leaves and stems mentioned above, in addition to many undeterminable plant remains. There are no attached stems and leaves with the exception of the small coniferous shoot, and no fructifications of any kind were found in the collection.

2. Stems of lower-order plants (Plate I)

On Plate I five types of stem of lower-order plants are illustrated. They include one lycopod, the largest of a small number of equisetalean axes, a probable fern or pteridosperm axis and two stems of uncertain affinity.

LYCOPODOPHYTA

cf. *Lycopodiopsis pedroanus* (Carr.) Edwards

Plate Id

There is one very poorly preserved specimen of a lycopod in the whole collection. It was the only plant fossil found at station Z.352, a high horizon of the western site.

Specimen Z.352.1 has the shallow mould of a stem, measuring 11 cm. by 2·3 cm., on the lower part of which regularly arranged, round to oval carbon patches, averaging 5 cm. by 4 mm. and fairly uniform in size, indicate the former positions of leaf cushions. There is no detail preserved on the scars but their arrangement in a fairly tight spiral, and their size and proximity could belong to no other plant. In the upper part there is faint ribbing but no scars remain. The size of the individual scars suggests one of the earlier southern lycopods, e.g. *Lepidodendron pedroanum* (Carruthers) Zeiller, which Edwards (1952) later included, with a number of other Southern Hemisphere lepidophytes, in a composite species *Lycopodiopsis pedroanus*. It included *Cyclodendron* which has much smaller scars but the paper served to draw attention to the unique character and probable separate development of Gondwana lycopods.

The matrix in which the plant mould occurs is a particularly coarse-grained feldspathic grit. The specimen is about 5 cm. in thickness, and on the underside the grit has merged into a small-pebble conglomerate in which the larger inclusions are most irregular in shape, size and composition. They include fragments of brown shale, sandstone, vein quartz and feldspar, ranging up to 2 cm. in size. Such unsorted sediment could not have been transported far and most of it must have been derived from a granite source.

Comparison. Palaeozoic lycopod fossils are rare in most Gondwana sediments and of these the commonest genus with larger scars is *Lycopodiopsis pedroanus*. It occurs in Lower Gondwana beds in South Africa (Seward and Leslie, 1908, pl. IX, fig. 1), in Brazil (Maack, 1947) and Western Australia (Edwards, 1952, pl. I, fig. 4).

ARTHROPHYTA

Paracalamites Zalesky

Plate Ia and b

Small lengths of narrow, ribbed and jointed equisetalean stems occur on a number of specimens, e.g. Z.392.15 (7·5 cm. by 4 mm.) and shorter ones on Z.393.1, 3, 4 and 399A.10A(R). Most of the stems are only several millimetres wide. The broadest is 2·5 cm. and it can be seen on specimen Z.393.1, but unfortunately only a short length of it has been preserved and most of the detail is obscured. No attached leaves or leaf sheaths remain on any stem. By far the best-preserved and longest stem occurs on specimen Z.399A.22A(R) (Plate Ia and b). The stem lies diagonally across Plate Ia and a part of it is enlarged in Plate Ib. It is 13·5 cm. long and approximately 8 mm. in width. Nine internodes can be seen varying in length from 2 to 1·5 cm., being broadest near the nodes and shrunken in the middle. The ridges and grooves, where it is possible to count them, appear to be 12 in number and the ridges are opposite one another in adjacent internodes. The nodes are marked clearly both by a change of relief and by the remains of carbon in the hollows, but the details are indistinct.

There is no evidence of leaf whorls on this stem and it must therefore be classified as *Paracalamites* sp. Zalesky. This genus was proposed by Zalesky (1932) to include equisetalean stems of Permian age in the Angara floral province which exhibited the features normally associated only with Lower Carboniferous *Asterocalamites*, of having the ribs and furrows of adjacent sections opposite one another. More recently, Rigby (1966) has extended the term to include equisetalean stems in the Gondwana floral province which exhibit the same character. While agreeing with Rigby that a general term for such stems is most useful, I doubt whether the choice of *Paracalamites* is a wise one because it implies relationship with Northern Hemisphere arthrophytes of this age for which there is no direct evidence at present. However, as the term has been used already both in Australia and in India, I have used it myself pending a decision by the Committee on Nomenclature.

cf. Phyllothea australis Brong.

Plate Ic

It is suggested that the small tapering objects occurring in radiating groups on the surface of specimen Z.392.15 may have been the foliage of the stems described above.

There is no evidence of whorls of attached leaves or of leaf sheaths on any of the stems, but the surfaces of a number of specimens exhibit areas where many small tapering acicular objects can be seen,

singly and in radiating groups. These suggest that the now leafless stems were a species of *Phyllothea* which bore very finely divided leaf whorls. Of these, *Phyllothea australis* Brong. is the most probable for it is common in all Lower Gondwana rocks, and the size of the stems as well as the short internodes agree with those of the stem illustrated in Plate Ia and b.

P. australis was created by Brongniart (1828) for the most common Australian Palaeozoic species, and *P. indica* by Bunbury (1861) for the common Indian form. Both species bore finely divided leaves and many geologists expressed difficulties in distinguishing between them, e.g. Feistmantel (1890), Seward (1898, p. 288), Arber (1905, p. 21), Du Toit (1932*a, b*), Surange (1955), Townrow (1956) and Rigby (1966), but it was only in 1968 that Maheshwari formally proposed the merging of the two as *P. australis*.

Comparison. In addition to the Indian, Australian and South African specimens mentioned above, comparable specimens from the Congo were illustrated by Høeg and Bose (1960, pl. II, III, figs. 3 and 4).

PTEROPHYTA OR PTERIDOSPERMOPHYTA

Plate Ic(2)

The small branched stem indicated on the same surface as equisetalean (?) leaves (Z.392.15) is one of a small number of fern or pteridosperm axes preserved. Its size and delicacy suggest the former and also explain the paucity of such remains in a deposit formed under rough conditions. Although so rarely preserved, the small stems demonstrate the existence of such plants in the flora of Milorgfjella.

Indeterminate stems

Plate Ia(2) and e

Two stems of uncertain affinity are described below.

Specimen Z.399.22A(R) (Plate Ia(2)). The relationship of the small curved stem marked "2" is uncertain. It measures 6.5 cm. by 6 mm., is curved and was probably herbaceous and pliable when buried. The surface is smooth and has a number of small round raised scars with a central hole. When magnified, the surface of the stem exhibits fine striae which bend slightly outwards around each scar, indicating that they are probably leaf scars but no clear phyllotaxy can be determined. It may have been spiral but, if so, the position of some of the scars is now masked by imperfect preservation. Alternatively, the now irregularly arranged scars might be the remains of two rows of leaf scars where fern pinnules were inserted on the upper surface of a rachis. Two other small specimens with similar scars occur in the collection. One can be seen at the top of Plate XIe.

Specimen Z.399A.40 (Plate Ie). This is another indeterminate stem which is the only one of its kind in the collection. It is a hollow mould with grooved spiral markings. The latter may be part of the stem structure or may conceivably be worm or insect trails formed during the period of burial, but the former explanation is more likely. There are no carbon remnants but the stem may have been woody.

On the right-hand side, in contact with the stem, there is the base of a large *Gangamopteris* leaf and the mould of a small coniferous shoot. These can be seen more clearly in Plate XIVa and b. No relationship between them is suggested but the association is of interest.

3. Woody gymnospermous stems (Plates II–VIII)

There are records of fossilized stems being found in many areas of Gondwanaland, including some from Antarctica, but they are usually dismissed as unidentifiable—as indeed they are—except where slow petrification has permitted the preservation of anatomical details which can be studied in thin section. In consequence there is a considerable amount of literature describing and illustrating petrified, mainly silicified, wood most of which is either Permian or Mesozoic in age. It is customary to refer to all Gondwana fossil wood of Palaeozoic age as *Dadoxylon*, a form genus for wood with araucarian affinities. However, as a result of the work of Sahni, Kräusel, Walton and others, a number of different genera are now recognized, but of the foliage borne by these trees practically nothing is known because silicified wood and fossil leaves are very rarely found in the same areas.

Illustrations and even brief descriptions of woody stems of Southern Hemisphere Palaeozoic floras, other than the petrified wood discussed above, are extremely rare and yet collectively they could present a considerable amount of evidence about the composition of the flora and the percentages of its different components. Where leaves are preserved in addition, their association with the stems may be significant even though no connection can be demonstrated.

Such indeterminate plant records constitute the majority of the plant fossils from Milorgfjella; for most of the woody stems, even generic determination is improbable but a broad classification has been attempted based mainly on external form.

Means of classifying woody stems on external evidence. Most of the woody stems from Milorgfjella represent tangential sections at different levels through the wood and few are of outer surfaces. Despite this, there are various features exhibited by groups of stems which distinguish them from the rest and it is suggested that on a broader basis some classification may be possible. Four such groups will be described and, as far as possible, these have been illustrated.

Group 1. Twisted and branched woody stems

Plates II and III

Fragments of such stems occur on many specimens but the largest and most important can be seen on Plate IIa.

Specimen 399A.18 (Plate IIa) is approximately 30 cm. square and could only be illustrated at half size. On this surface a mass of stems is displayed. They lie in approximately the same direction and from this a current direction might be inferred.

The largest stem, which can be seen just above the specimen number, increases in width just before branching from 5 to 10.5 cm. within a length of 10 cm. This division of the stem at a wide angle resembles more closely the spreading of a woody shrub or bush close to the ground rather than a simple bifurcation. The smaller stems are normally straighter and smoother, but all display inner woody surfaces suggesting that they were partly decomposed at the time of burial. The carbonized tissue, which must have been present when the specimen was excavated, has crumbled and been lost in transit but strips of shining black vitrain at the edges of stems indicate its previous presence on many surfaces; no outer surfaces of these stems have been identified.

Two large convex stems, which can be seen on the left-hand margin, offered the possibility of sectioning but when lifted from the slab for that purpose they proved to be only hollow layers of wood covering sediment and plant debris. The base of a broad *Gangamopteris* leaf, which lay beneath one of them, was the only identifiable foliage on the slab but no connection is implied.

There is a large round scar on the branched stem, marked with an arrow but whether it is a leaf, short shoot or branch scar cannot be determined.

Specimen Z.399A.19 (Plate IIIa). On this specimen two twisted stems, which may at one time have been connected, can be seen. The right-hand stem appears to be branching in the upper half; the left-hand stem has a scar marked by the arrow.

Specimen Z.392.6(R) (Plate III d) is a much smaller stem but with a similar surface and the same twisted wide-angled branching.

Micro-structure (Plate IV). On Plate IIa two small woody fragments are marked by an arrow (4). The wood appeared to be less altered than the rest and a small piece was taken for maceration. Although treatment was prolonged for some time and the wood disintegrated into splinters, none of them showed any degree of transparency. Bordered pits arranged in single straight rows were visible in some of the fragments. There were also some much larger cells that could be seen in section. I should like to thank Mrs. H. M. Anderson for the preparation of the slides. A selection of the woody splinters is shown under various magnifications in Plate IV. They represent the only available anatomical evidence of fossil wood from this site but it is not adequate for accurate generic determination. Neither the uniseriate contiguous pitting of the tracheids nor the larger cells—probably of medullary rays—can indicate more than a general gymnospermous classification into the broad form genus *Dadoxylon*. Kräusel (1962), p. 134), who described the woods of the Trans-Antarctic Expedition, stated with reference to Permo-Carboni-

ferous woods from south Victoria Land in east Antarctica: "The secondary wood of many Palaeozoic gymnosperms is fairly uniformly built (*Dadoxylon* type)—but the pith and primary structures are very variable and offer diagnostically valuable criteria for differentiation." Even where a large piece of wood was available but which lacked the pith and primary wood, Kräusel retained the non-committal form genus but gave a new specific name *Dadoxylon allani*. In the same publication, he commented that the fossil wood which Seward (1914) had described from the much earlier Scott expedition, and had named *Antarcticoxylon priestleyi*, was too imperfect to warrant such classification. Seward had considered that the structure revealed was an infallible criterion of *Cordaites* and, although so much more is now known, a cordaitalean affinity can still be claimed for the *Dadoxylon* wood type. Where only fragments of secondary wood of this type are available, the form genus *Dadoxylon* Endlicher is still applicable (see also Florin, 1940, 1951; Kräusel and others, 1962).

The piece of wood from which the micro-evidence was obtained was similar in appearance to the surfaces of the twisted branched stems near it, so that identity is probable but not definite.

The affinity of group 1 woody stems with the Cordaitales is however possible.

Small concentric marks of pathogenic (?) origin

Plate IIb and c

Specimen Z.399A.18. One more feature of unusual interest, on the same large specimen, is the presence on a number of the stems of groups of small round concentric markings. They occur in patches which do not appear to be confined to any particular area of the stem. The individual markings vary considerably both in size (average 1–2 mm.) and in the number of rings. One with nine evenly spaced surrounding rings is illustrated in Plate IIc. Where carbon remains in the centre or within the rings, they can be seen clearly but there are other areas where the "structures" occur in relief only, as though etched into the surface. One such area is indicated by an arrow in Plate IIb. The illustrations are from the stems in Plate IIa marked by arrows "3" and "4". The nature of these structures is difficult to determine. No anatomical significance or explanation can be suggested, although the ring markings apparently occur at various depths within the woody stems. The most plausible explanation seems to be that of a pathogenic origin in which the growth of bacteria or fungus commenced after the partial disintegration of the stems. Such marks have not, to my knowledge, been recorded previously from any Palaeozoic woods and I have not seen them on comparable South African fossil woods. I doubt very much that they could be of modern origin in the present disease-free environment. Botanists whom I consulted could offer no solution.

I have collected from the veld near an old colliery shaft at Vereeniging portions of fossil tree trunks in which annual rings can still be distinguished. The trunks are now completely replaced by pisolitic haematite. I believe that their post-burial history may have been similar to that of the wood described above.

Group 2. Straight woody stems with elongated raised and tapered marks

Plates IIa (top left), IIb and c, VIIa (left-hand side) and VIIIa

These stems are straight and of uniform thickness. They exhibit a general longitudinal striation which in some areas is very fine and parallel (see the base of specimen Z.393.2 in Plate IIIc), but the most characteristic features are small elongated ridges (up to 2 cm. in length) and tapered at either end which are scattered across the surface. Such stems are known to be associated with the class Glossopteridae. In a paper discussing the habit of growth of Glossopteridae (Plumstead, 1958*b*), a number of closely comparable stem surfaces from South Africa and Rhodesia were illustrated—some with leaves of Glossopteridae attached. In that paper the raised marks were called "streaks" for lack of a better term. They were shown to be characteristic of a sub-surface layer of the stem and are possibly due to stretch marks caused by expansion during growth. It was suggested that the Glossopteridae were deciduous woody plants of arborescent or woody-shrub habit and that the leaves grew in clusters of short shoots at fairly wide intervals on the stems, which left a scar when the leaves were shed in autumn. A round scar which is large enough to have supported a leaf cluster can be seen at the top of specimen Z.393.2 (Plate IIIc). An enlargement of this scar did not provide any further detail and has not been included.

Specimens Z.399A.32 (Plate IIIb) and 399A.42(R) (Plate VIIa; left-hand side) show no scars and none of the three specimens is branched.

A stem on specimen Z.399A.18 (Plate IIa; top) shows the "streaks" clearly on the left-hand side but it merges into a rougher surfaced stem on the right-hand side which may represent the true outer surface. It suggests that similar stems in the collection may also be members of Glossopteridae although lacking the clearly defined tapered "streaks".

Specimen Z.392.28 (Plate VIIIa) has been illustrated because it is the largest stem in the collection but it is incomplete on the right-hand side. It is preserved in a coarse sandstone and is now only a carbonaceous impression but the elongated "streaks" are clearly visible.

There are many other fragments of the group 2 type of stem in the collection but only the clearest have been figured.

The affinity of group 2 is with the Glossopteridae. It is not known whether this type of stem belonged exclusively to Glossopteridae in the Permo-Carboniferous but this may have been the case.

Group 3. Woody stems with the leaf scars of long and short shoots

Plates V and VI

Long shoots can be seen on specimens Z.399A.7 and 7(R), and a smaller part is on Z.399A.7A. All of these are illustrated in Plate V. The short shoots are shown in Plate VI.

This habit of growth occurs in some conifers, some Cordaitales and it is well exemplified in the "living fossil" *Ginkgo biloba*.

A 3 year old woody twig of *Ginkgo biloba* from the University of the Witwatersrand campus is shown in Plate Va-c for comparison. Long shoots occur on the main stem and each represents a former terminal shoot from which the stem continues its growth the following season. The zone of leaf scars is restricted in area; one or more isolated scars may occur a short distance below or above the main zone and these can be seen in both the modern and the fossil stems. The length of stem between two long shoots is devoid of leaf scars but it bears so-called "short" shoots like the one in Plate Vc. They may be shed at the end of a season, leaving only a small *round* scar or they may continue growing and give rise to a new branch. The recent and the fossil twigs compare very closely in every particular save one. The *Ginkgo* leaf scars exhibit only two small round vascular scars while the fossil stem has four on each leaf scar. This difference is an important one because all fossil *Ginkgoites* leaves, as well as those of the modern plant, have two major veins entering the base of the leaf and thereafter bifurcating frequently.

Specimen Z.399A.7(R) (Plate Vd) has two stems whose surfaces compare quite closely and also with that of the modern stem. The right-hand stem has a part of a long shoot preserved, while that on the left has only two small *round* scars near the top. These can be compared with the round scars left on a *Ginkgo* stem after a short shoot has been shed. Unfortunately, none is visible in the photographs above.

On the modern stem the distances between four long shoots (representing former terminal shoots) are 25, 6.5 and 16 cm. to the present tip. The intervals between them bear short shoots or their scars, but there are portions on which neither is visible. The short shoots never grow in a whorl nor in approximately the same zone around the stem.

A much longer "long" shoot can be seen in Plate Vf (Z.399A.7) and a small part of its counterpart enlarged $\times 2$ in Plate Ve (Z.399A.7A).

In Plate Vg a part of a wide stem can be seen. It occurs on the same rock surface as the two stems in Plate Vd and represents, I think, the "contracted" long-shoot zone of an older and wider stem.

In addition to the specimens figured, a fragment of a long shoot occurs on specimen Z.399A.29A where the faint impression of a group of similar leaf scars can be seen on the left-hand side of the fossil stem next to the specimen number. It is on the same surface as a *Ginkgo*-like leaf.

Short shoots. The short shoots of *Ginkgo* in Plate Va and b, but especially in Plate Vc, can be compared similarly with those in Plate VIa and b and the counterpart, Plate VIc and d, from specimens Z.399A.22 and 399A.22A. Once again, the fossils have four cicatrices on each leaf scar as opposed to two on the *Ginkgo* stem.

Comparison. I know of no records of fossil leaf bases arranged in long and short shoots as clearly preserved as these from Milorgfjella, but three partly comparable ones are listed below.

Feistmantel (1890, pl. XXI, figs. 1 and 2) illustrated a fossil stem fragment which he named *Caulopteris adamsi*. It was from the Newcastle Beds of Australia (Permian) and exhibited well-spaced scars, somewhat similar in appearance, but with five cicatrices on each scar. Feistmantel was doubtful about its relationship but suggested a fragment of a fern trunk.

Arber (1905, p. 151–53) referred to Feistmantel's illustration and stated that he could see no resemblance to the European fern stems of that name but, since he had not seen the original, he placed the name in brackets. The fossil stem was quite possibly that of a gymnosperm.

The affinity of group 3 woody stems could be with Ginkgoales—possibly another genus.

Group 4. Woody stems with branch scars arranged in whorls

Plate VIIa–c

Among the woody stems from Milorgfjella there are several which have branch scars arranged in whorls separated by fairly wide intervals. Since this type of branching is characteristic of modern conifers, including the Southern Hemisphere *Araucaria*, the feature is probably of diagnostic importance.

Specimen Z.399A.42(R) has three woody stems, of which only that on the right-hand side exhibits branch scars. Two scars are visible at the base. The following whorl is 6–7 cm. higher and has three scars visible; the one on the left margin is indicated by the bending of the grain of the wood around it. A fourth scar is likely to have been present at the back of the stem. An interval of 13 cm. follows without any sign of branching; the overlapping sediment on the left was lifted subsequent to the photograph being taken to confirm this. There is an indication that the stem was broken just below a third branch zone, because a bending of woody structure on the right-hand margin indicates another scar at this point. The best-preserved scar of the middle zone is shown magnified five times in Plate VIIb but no reliable evidence of structure is displayed. The stem shows marked shrinkage between the branch whorls. Its rough surface, too, differs from those of the previous three groups but this may not be significant, for groups 1 and 2 represented different levels of decortication.

Specimen Z.399A.36B (Plate VIIc) has two small stems of similar surface appearances, and which may have been connected. Only the right-hand one has two branch scars in a zone which approximates to a whorl.

Branch scars also occur on the other woody stem groups but in each case only one is visible, e.g. on the branched woody stems in Plates IIa and IIIa large scars are indicated by arrows, and on the group 2 stem a large scar can be seen at the top of the specimen in Plate IIIc.

Comparison. The only comparable specimen known to me was illustrated by Kurtz (1921, pl. VII, fig. 65). It is a wide strip of bark, obviously from a woody plant, on which three holes indicate branch scars of a similar size to those on the Antarctic wood. They occur in a single whorl and the grain bends around them in each case on the rest of the stem; there are no others. The fossil was named *Euryphyllum whitty anum* Feist., (?) a *Walchia*. It came from Bajo de Velis in the province of San Luis, Argentina.

There were no other scars on the rest of the stem. In Feistmantel's original illustration of *Euryphyllum whitty anum* (Feistmantel, 1879, pl. XXI), two large single scars are shown, some distance apart, on a large stem but a third scar is indicated by the curvature of the wood on the left-hand margin in the same zone, or whorl, as the lower scar. There might also have been others since the right-hand side of the stem was missing. Feistmantel believed that this plant was allied to conifers.

The affinity of group 4 is with conifers, e.g. *Araucaria*.

4. Summary of woody stems

The fragmental, often decorticated, poorly preserved woody stems from the Milorgfjella flora provide enough evidence to separate them into four groups on positive evidence. The negative evidence is less convincing but not contradictory, e.g. it might be argued that the absence of whorls of branches (like group 4) or of intervals of leaf scars (like group 3) from the Glossopteridae stems of group 2 is not proof that these might not yet be found. This, of course, is true even if improbable because in each case comparatively large pieces of stem were available. It is also true that small parts of stem from each of the four groups could be selected which would look very similar, but as a rule the general appearance of each is distinctive. I feel it is significant that the distinctive characters of each group of stems and the

comparisons which they suggested, lead to four different gymnospermous groups—the Cordaitales, Glossopteridae, Ginkgoales and Coniferales, respectively. It would be ridiculous on the strength of such slender evidence to allocate the groups to the orders mentioned, but a separate trend has been indicated and must be borne in mind. This subject will be re-opened on p. 24, after the evidence of the leaves in the collection has been considered and when the whole fossil flora can be reviewed.

B. FOSSIL LEAVES FROM MILORGFJELLA (Plates IX–XV)

Seven different leaves have been recorded. They occur in varying numbers but in some cases they are represented by a single but distinctive leaf. There are many fragments of leaves but they are all too small or too imperfect to be determined. In addition, there is one small coniferous shoot.

The separate leaves fall naturally into two categories: those with reticulate venation and those with bifurcating venation. The latter are in the majority by five to two. This ratio is most unusual in any Gondwana flora where reticulate leaves normally greatly outnumber all others. One other feature is remarkable and that is the complete absence of *Glossopteris*. Both facts are indicative, I believe, of a very early stage in the development of the *Glossopteris* flora—when *Gangamopteris* only was found and other elements were plentiful.

1. Leaves with reticulate venation (Plates IX and X)

Gangamopteris McCoy

Plates IX and X

Two species of *Gangamopteris* occur; each is represented by a number of specimens in which the external characters are clearly defined. In addition, there are many fragments, some of which obviously belong to different species but which cannot be determined. All the fossils are impressions only and no cuticular evidence is available.

The genus has been defined and re-defined so often since its inception in 1847, and the merits and demerits of the various classifications discussed in great detail, so that it is unnecessary to repeat the whole argument here, especially since agreement has not been reached. It is desirable, however, that a summary of the position should be presented here, because it is especially relevant to Antarctica where different international teams are, severally, collecting palaeontological evidence and where the knowledge gained should be co-ordinated, as far as possible, rather than dissipated by nomenclatorial differences. The main trends of the argument have revolved around three points.

First, should *G. obovata* Carr. or *G. cyclopteroides* Feist. be used for the most common and widely distributed species? The first had priority but the second was more commonly used. Both were regarded as synonymous.

Secondly, were all the varieties of *G. cyclopteroides* proposed by Feistmantel, in his well-known studies (1879–90) of the Gondwana flora, valid and should they be raised to specific rank? Furthermore, how many of the more recently erected species were of local distribution only?

Lastly, the study of cuticles has been used in recent years, especially in India, as a basis for classification. This has complicated the problem further, because, where cuticular evidence is present, it may differ quite considerably on median and marginal parts as well as on upper and lower leaf surfaces, and leaves of Glossopteridae are large so that evidence based on fragments may be utterly misleading. Experience has shown that in a number of cases it has cut across specific and even generic denominations based on external characters. The result has been a considerable nomenclatorial expansion which is of little practical value because, in the vast majority of cases, no cuticular evidence has remained.

The latest contender is P. K. Maithy, of the Birbal Sahni Institute, who has made a gallant effort to sort out the difficulties. He has re-defined the genus to include cuticular evidence with the result that it has become unwieldy and almost too general for practical purposes (Maithy, 1966). He has suggested that the disputed *G. obovata* and *G. cyclopteroides* are not synonymous but are different species and, finally, he has proposed yet another tentative scheme for classifying *Gangamopteris* on external characters only, in which he accepts 19 species. For the field geologist, the position is hopeless and untenable. At the same time, every student with more than a superficial knowledge of the *Glossopteris* flora is aware

that considerable differences exist in the composition of the genus as expressed both in space and in time. The present difficulties are due, in part, to a healthy revival of interest in the flora in many parts of the Southern Hemisphere. Careful recording, both descriptive and illustrative, is essential and should be confined to evidence from complete, or nearly complete, leaves. Accurate stratigraphic information is equally important. Classification should be on a broad and for some further period on a tentative basis, and both undue "lumping" or "splitting" should be avoided. In due course a general evolutionary trend, which is evident already in some areas, will become apparent throughout the huge Gondwana Province, while lesser differences between locally endemic species will be recognized as such. The resolution of such problems is one of the objects of the current series of meetings in different Gondwana countries, by the Sub-commission of Gondwana Stratigraphy and Palaeontology, under the auspices of the International Union of Geological Sciences. It is hoped that the discussion will produce satisfactory results.

***Gangamopteris obovata* Carr.**

Plate IXa-d

This species, which for the present I continue to regard as synonymous with *G. cyclopteroides* var. *attenuata* Feist. and which is the most widely distributed of all *Gangamopteris*, has now been found at Milorgfjella. Specimen Z.392.2(R) is the best preserved from the point of view of venation and is shown in Plate IXa magnified twice. It presents the salient features of the species very clearly, viz. an elongate obovate leaf with broadly rounded apex, tapering base and entire margin. The venation consists of a median region of a number of prominent sub-parallel veins, at the base, which gradually fan outwards at a steep angle towards the margin, curving, bifurcating and reticulating to form a long narrow network of veins. The specimen would have been placed by Feistmantel in var. *attenuata* because of the pronounced tapering.

Specimen Z.399A.10(R) (Plate IXb) is a more complete leaf but the venation is less clear (note the large pieces of grit, indicative of poorly sorted sediment).

Specimen Z.392.20 (Plate IXc) is an impression on sandstone, like the leaf in Plate IXa, but only the general shape and venation are visible. It has been included here to illustrate the fungal mark clearly visible at the base.

Specimen Z.392.13(R) (Plate IXd) is incomplete but it demonstrates the narrow base and sessile nature of the leaf.

Other examples of the species occur in the collection but these demonstrate the characteristic features.

Comparison. There are so many examples of the species that only a couple can be mentioned from each country:

India: e.g. Feistmantel (1879, pl. XIV, fig. 1, 1886, pl. VIIIA, fig. 1).

Africa: Transvaal (Seward and Leslie, 1908); Congo (Høeg and Bose, 1960); Uganda (Du Toit, 1932b).

Australia: e.g. Queensland (Walkom, 1922).

South America: e.g. Brazil (White, 1908); Argentina (Archangelsky, 1957).

Antarctica: south Victoria Land (Plumstead, 1962).

G. obovata can be regarded as the zone fossil of the Lower Gondwana in every area, and in South Africa it has been found below tillite in the Transvaal (Leslie, 1922), thus demonstrating its low temperature tolerance.

Comparison of leaf fungus. Leaf fungi have been described from South Africa (Plumstead, 1958a, p. 71) and from the Whichaway Nunataks, Antarctica (Plumstead, 1962). As long ago as 1867, Tate figured similar marks on a leaf from the Cape Province, believing them to be fern sori.

***Gangamopteris cyclopteroides* Feist.**

Plate X

Specimen Z.399A.10C (Plate Xa) is one of a number of similar leaves, all remarkably uniform in size, shape and venation. The shape approximates to a regular oval with entire margin and rounded apex. It is abruptly tapered at the base to a short sessile, slightly embracing proximal end.

The venation is coarser than in Plate IX and anastomoses throughout. There is no sub-parallel median area but general arching towards the margin where the mesh is much finer. In Plate Xb the same specimen is enlarged to demonstrate the venation. On the counterpart of the same specimen, Z.399A.10C, only a part of the leaf is preserved but the venation is clearer and the anastomoses distinct.

On specimen Z.392.16 at least five of the overlapping leaves are of this species and there is very little difference in size between them.

The two small leaves (Plate Xc and d) both occur on specimen Z.392.7(R). They are included to illustrate a small change of shape with the same venation. The largest leaf 8.3 cm. by 5.5 cm. occurs on the numbered side, Z.392.7, of the same specimen.

Comparison. The leaves illustrated in Plate X appear to me to approximate closely to what Feistmantel called his original type form, from the Talchir, and which he stated were far more rare than the varieties he created.

The type form was shorter than most of the varieties and he illustrated a number of specimens including some very small leaves. Among these (Feistmantel, 1886, pl. VIIIA, fig. 6, pl. XIVA, fig. 1) are small and large examples of his "type form". Both are from the Talchir of western Bengal.

Similar small leaves on pl. XIII A, fig. 4 and pl. XII A, figs. 16–18 of the same publication are named *G. cyclopteroides* var. *attenuata* and *cordifolia*, respectively, and they serve to demonstrate the difficulties attendant on classifying this genus.

Other *Gangamopteris*

The presence of larger species at Milorgfjella is indicated by the very large bases of leaves, which can be seen on specimen Z.399A.40 (Plate XIVa) and can also be found on specimen Z.399A.18 (Plate IIa) underneath the loose stem on the left-hand side. These fragments are not large enough to offer specific identification.

2. *Leaves with bifurcating venation* (Plates XI–XIV)

Genus *Walikalia* Høeg and Bose

Among the leaves from Milorgfjella are some broad, almost round ones which are not closely comparable with any described up to now from any parts of the Gondwana floral province. The nearest resemblance is to the genus *Walikalia*, created by Høeg and Bose (1960) for organs which they described as large and thick scale-like bodies of oval or circular shape. Four specimens of *Walikalia cahenii* were found in the oldest fossiliferous beds of the former Belgian Congo—the Permo-Carboniferous "schistes noirs de Walikale (W.4)". All other fossils which have a few features in common with the Antarctic species are either much younger in age or their geographical origin is even more distant. Since the Antarctic fossils are not identical with the Congo fossils but may be related, I propose to name them *Walikalia* (?) *jucklesii* after the young geologist who first found them.

Walikalia (?) *jucklesii* sp. nov.

Plate XIa–f

The type specimen Z.392.15C was separated from specimen Z.392.15(R). It is illustrated at natural size, in Plate XIb and is shown ($\times 2$) as a separate specimen in Plate XIa. It is now numbered Z.392.15C. The fossil is a cast in sandstone of a thick, convex scale-like leaf which measures 5 cm. in length by 4.6 cm. in breadth and is fan-shaped. The veins radiate upwards and outwards from the whole wide base, so that the maximum width is attained well within the lower half, after which an entire margin follows a smooth deep arc. The veins maintain an almost uniform distance apart, by bifurcating, as they spread with small outward curvature towards the margin. There is the possibility of an occasional reticulation but bifurcation is clearly visible, and seems to occur several times, at equal distances from the leaf base, and in this way the size of the leaf is increased along arcs of increasing diameter. One of these can be seen clearly in the upper part of specimen Z.392A.5C (Plate XIc), where it is accompanied

by a small change of level, but it is still the same leaf. This specimen also illustrates the very wide, almost straight base of 2 cm.

Specimen Z.392.6(R) in Plate XIe is less well preserved and the venation in the upper half is masked. The upper margin appears to be divided but this may be due to preservation—otherwise the general features are constant.

Specimen Z.392.24(R) (Plate XI f) is a small and obviously young and unexpanded leaf. The shape and venation suggest that it belongs to the same species.

All of the above specimens are convex and indicative of a thick, tough scale-like leaf. There is one other specimen, Z.399A.28(R) and its counterpart Z.399A.28B, on which a slightly smaller and decidedly flatter but otherwise identical leaf can be seen (Plate XI d). The apparent division of the upper margin is due to slight undulation and consequent uneven overlapping of sediment, but it has to be cleaned to show that the leaf is almost round (4.2 cm. by 4 cm.) and the margin entire. The overlapping sediment on the lower left-hand side in Plate XI d was cleaned later and the true shape can be seen, a little less than half size, in Plate XII a. The counterpart has not been figured but it is equally clear. This resembles a vegetative leaf far more closely, but I think there can be no doubt about its specific identity with the others. It is possible that the plant bore vegetative leaves and also very large scale leaves which differed in texture. The resistant nature of the scale leaves would explain why more of them have been preserved in this particular environment. Both kinds of leaves appear to have been sessile for, although the preservation of the base is less clear than the rest of the leaf, in each case there is no indication of any petiole.

Comparison. *Walikalia cahenii* from the former Belgian Congo (Høeg and Bose, 1960, pl. XIII). There is undoubtedly some resemblance between the Congo and the Antarctic fossils. Of the four specimens of the former which were found, all were a little larger and three were more oval in shape than the present leaves. All were convex but one had a concave side preserved as well. The base was narrower and the radiating veins were straight, or curved slightly inwards, but the venation was not as clear as in the present scale leaves. The greatest breadth was in the middle, or above it rather than in the lower half. Like the Antarctic leaves, the margin was entire and the leaves sessile. The Congo and Antarctic fossils may be regarded provisionally as representing two species of the same genus. They are of the same age and the floras of which they form part are very similar.

Systematic affinities of the genus Walikalia. In their original description, Høeg and Bose (1960) were unable to suggest relationship with any known plant, and although it was necessary to create a new genus, they felt that the available evidence did not indicate affinity on any broader basis. The present fossils provide a little more detail and, because of their Antarctic isolation, invite a wider investigation of possible affinities. The fossil Cycadales, Glossopteridales and Ginkgoales provide the best links and each, in turn, is considered briefly.

Cycadales. The thick scale leaves suggest comparison with the various fossil species of *Cycadolepis*. Early records of these from Gondwana deposits in India have been reviewed recently by Bose and Jain (1964) and new illustrations provided. Their pl. I, fig. 3 is nearest in shape and size but the resemblance is only superficial and all the Indian examples are from Upper Gondwana formations and of Jurassic age.

From South Africa, Seward (1903) described a similar fossil from the Uitenhage Series which is likewise of Jurassic or lowest Cretaceous age.

Sewardia latifolia (Saporta) Zeiller (see Seward, 1919, p. 104, fig. 674) also falls into this category as a thick, more or less round, entire-margined, sessile leaf-like organ, but it was borne on stems in the axil of "stout, recurved spinous processes" which suggested to Seward that they might be phylloclades. He regarded the affinity of the plant with cycads as uncertain. These fossils too were of Wealden age.

Glossopteridae. The possibility of affinity with *Gangamopteris* cannot be entirely ruled out because of the occasional anastomoses seen in the "vegetative" leaf and because scale leaves are known to have been associated with these plants, but I believe it is improbable. No scale leaves of the size and venation of these have ever been recorded and round leaves with comparable venation are not known. The nearest

for purposes of comparison are *G. clarkeana* from the Bacchus Marsh Beds of Victoria, Australia (Feistmantel, 1890, pl. XX, fig. 3), and also from the Permo-Carboniferous lower coal measures of the Transvaal, South Africa (Plumstead, 1963, pl. 1), but the resemblance is to the rounded apical part only, for the species has a long tapering basal part. Also, the veins of *G. clarkeana* are more widely and evenly spaced. Another leaf which is comparable in shape and size is *Gangamopteris intermedia* Maithy (1965c, pl. 3 and 4, figs. 21 and 24, text-fig. 5) but the reticulate venation separates it from the Antarctic leaves.

Affinity with Ginkgoales. In many ways this offers the best prospects especially as far as the vegetative leaf is concerned. The size, shape, the undulating upper margin and straight lower margin, and the uniformly distributed spreading, bifurcating venation are all comparable but *Ginkgoites* Seward is always petiolate, and all of the Antarctic leaves are sessile. Moreover, none of them is lobed and there is no indication of the characteristic marginal veins of *Ginkgoites*. *Ginkgoites* and related leaves are known from Lower Gondwana rocks and have been recorded from various areas. Høeg and Bose (1960, pl. X) described *Ginkgoites*, *Ginkgophyton* and *Baira plumosa* from Lower Permian beds of the Congo, and Plumstead (1961, pl. 8) described a larger and more closely comparable leaf from the Permo-Carboniferous of the Transvaal.

The related genus *Psymphyllum* is known from the Lower Gondwana of Kashmir (Seward, 1912) and *P. kidstoni* from the Transvaal (Seward, 1903).

Seward (1919, p. 83, fig. 666) illustrated a *P. flabellatum* from the Coal Measures of Great Britain in which several anastomoses were shown. They were caused by the bifurcation of two adjacent veins and led to the expansion of the leaf fan-wise along the same arc as in the Antarctic leaf in Plate XIc. In his text-book, Seward (1919) devoted three chapters to a consideration of Ginkgoales, and other fossil "genera of uncertain position", which had been classed with them and placed *Psymphyllum* in the latter category. Since that time it has become increasingly evident that the features originally attributed to Ginkgoales were characteristic in the Devonian period of a branch of broad-leafed plants. Høeg (1942) drew attention to them and Andrews (1961) called them "megaphyllous leaves of unknown affinity". This leaf type persisted in the Carboniferous period. The surviving *Ginkgo biloba* may be a relict of this ancient time and there is a long series of evidence to suggest that it was but, if so, many branches and transitional forms have become extinct *en route*. At present the characters of Carboniferous and Permo-Carboniferous fossil plants, which have so often been correlated with those of *Ginkgo*, may be indicative of their early stage of development in an evolutionary sense rather than one of direct relationship. The broad-leafed plant, with bifurcating venation and possibly a gymnospermous type of wood, originated in the Devonian at a time before floral provinces became demarcated. A similar but not identical trend developed in both Northern and Southern Hemispheres. Høeg and Bose (1960, p. 41, 42), in discussing this question, suggested that if the Southern Hemisphere or Gondwana plants in this category were more fully known they would be found to constitute a natural genus of their own. They proposed that provisionally the Kashmir species *Psymphyllum haydeni* (Seward, 1912), *P. hollandi* (Seward, 1907b) and *P. kidstoni* from the Transvaal (Seward, 1903) should be placed in the form genus *Ginkgophyton* Zalesky.

This discussion has been interposed because several of the remaining leaf types from Milorgfjella have bifurcating venation. Similarities with the Angara Upper Palaeozoic flora will be discussed on p. 27.

Genus *Euryphyllum* Feist.

This genus was instituted by Feistmantel (1879, p. 26, pl. XXI) based on a single large woody stem with round leaf scars and two leaves, which, although not attached to the stem, were lying in positions that justified his supposition that they belonged to it. He named the plant *Euryphyllum whittyanum*. The specimen was from the Karharbari coalfield where, according to Feistmantel, the shales of the two lower seams contain the most interesting fossil flora of the Indian coal-bearing rocks. A few isolated leaves were found at that same time but thereafter have not been recorded from India, or any other part of the Gondwana floral province for many years. In fact, Arber (1905), when reviewing the *Glossopteris* flora, concluded that it was not a separate genus and re-named the plant *Noeggerathopsis whittiana*. It was, however, reinstated by Seward and Sahni (1920) in their revision of Indian Gondwana plants. Recently,

Maithy (1965*b*, pl. I, figs. 9 and 10) has illustrated two leaves from the Karharbari Beds of the Giridih coalfield, India.

Feistmantel (1879) described the leaves as being "broad, attenuate at base, veins coming out strongly from the base and then many times divergingly furcate. The leaves appear thinly coriaceous." He regarded *Euryphyllum* as being related to conifers.

Euryphyllum (?) *antarcticum* sp. nov.

Plates XIIa-d and XIIIa and b

From one area and probably one horizon of the eastern site of Milorgfjella a number of leaves have been collected which I believe can be included in this genus. Of the station Z.399 specimens collected by Lovegrove, four can be fitted together, viz. Z.399A.2, 28A, 28B(R) and 29, to form one large surface, while Z.399A.29A and 399.28(R) join to form a part of the counterpart. Parts of these surfaces can be seen on Plate XIIa and d, which are a little less than half natural size. Notice the *Walikalia* "vegetative" leaf on the left of Plate XIIa.

On the former slab at least eight leaves occur and, judging by size, shape and angle of venation, they are of one species.

On specimen Z.392.8(R) (Plate XIIc), collected by Jukes in the previous season, there are two of these leaves which are less damaged than some of the others. These are shown at natural size.

Another specimen (Z.399A.22A) can be seen in Plate XIIIa on which the short shoot (illustrated previously in Plate VI) also occurs.

All of these separate leaves lie in approximately the same direction which must have been controlled by moving water. They give the impression of being long narrow *Gangamopteris* leaves but, on closer examination, every leaf in Plate XII can be seen to have the lateral margins folded over, or under, on each side so that where the folded part is visible the venation is in reversed direction (see the margins of the leaves in Plate XIIb and c). The folding has two effects: the leaves appear to be linear and narrow instead of obovate, and also, where the lateral margins are folded, the leaf develops a deep median groove, or ridge, according to whether it is part or counterpart. This is obviously the result of pressure on the folded leaf after burial. The groove does not extend into either the base or the apex, which were narrow and were not folded. The median part of the leaf is occupied by about ten strong sub-parallel veins which cover about one-third of the leaf surface. On either side of this the veins diverge at a steep angle and curve towards the margin, bifurcating at intervals but very rarely anastomosing. The veins are thinner than in the median region and the lamina softer. Feistmantel stated that the leaves were not as rigid as those of *Noeggerathiopsis* and that they were rather soft or of a thin leathery consistency. Their texture is certainly not nearly as tough and rigid as that of the vast majority of the Glossopteridae, whose normal thick texture and reticulate venation protect them from folding and usually from tearing. In Plate XIII the leaves are not folded and, as a result, the lateral margins of every leaf are worn and frayed, sometimes into single veins, and only by tracing these can the true width of the leaves be estimated, e.g. the leaf in Plate XIIIa, just below the short shoot, has a half width of 3 cm. in the upper half and it may have been more for the margin is not well demarcated. The lengths of the leaves vary. They are normally incomplete and approximately 10 cm. long but one of 16 cm. was measured. Not one complete or even nearly complete leaf can be seen. The shape, size and venation have to be determined from the group as a whole. The result of this detailed investigation leads to the conclusion that the features are not those of any known *Gangamopteris*—the curvature of the lateral veins excludes *Noeggerathiopsis* but the combined characters closely resemble those attributed to *Euryphyllum* save for the presence of an occasional anastomosis. In the absence of complete leaves and despite their large number, I propose to place these leaves, only provisionally, into this genus and have given a specific name of *antarcticum* to record their origin and to indicate that there are small deviations from Feistmantel's type specimen.

Comparison. In the type specimen, Feistmantel did not find even an occasional mesh in the venation. Both leaves showed a tendency to curl over at the edges but the full effect probably only developed after separation. Numbers of folded leaves have been illustrated by several authors. They are particularly common in the oldest Gondwana sediments and are rarely seen in the middle or upper sediments. In

some of those illustrated by Feistmantel no indication of reticulation is visible and, if the drawing is accurate, they may have been of this genus but others are true *Gangamopteris*.

Høeg and Bose (1960, pl. VII, figs. 1 and 4) illustrated two turned over leaves, which they called *G. cyclopteroides*. One of them shows a sharp keel as in the Milorgfjella specimens and the clear venation in the upper half seems remarkably free from reticulation but it is impossible to be certain. The specimen on the left exhibits asymmetry, which could be due to the folding over of one half more than the other. Asymmetry was a feature of *Euryphyllum* mentioned by Feistmantel but it could not be determined in the incomplete Antarctic specimens.

Euryphyllum (?) sp.

Plate XIVc and d

One more leaf from Milorgfjella is included provisionally in this genus. It can be seen at natural size in Plate Ia on the left-hand side of the equisetalean stem on specimen Z.399A.22A(R) and is illustrated in Plate XIVc and d. The right-hand margin of this small leaf is folded under giving the leaf an elongated hexagonal appearance but on the left-hand side the lamina extends out, somewhat frayed, to almost twice the width of the other. The median sub-parallel venation is less developed than in *E. antarcticum* and the secondary venation is stronger, but the steep angle of the bifurcation and the rarity of anastomoses are similar.

Comparison. The leaf bears a fairly close resemblance to the single leaf on which Maithy (1965a, pl. I, fig. 5) has based a new species *Rubidgea lanceolatus* from the Karharbari Beds of the Giridih coalfield of India. The illustration is not clear but judging from his description there is a similarity. I should like, however, to take this opportunity of stating that I disagree with Maithy in reinstating the genus *Rubidgea* Tate by placing in it two new species from India: one, *R. obovata*, based on three incomplete small leaves, and the second, *R. lanceolatus*, based on a single leaf. Much as I should like to perpetuate the name of Dr. Rubidge, who played an important role in early palaeontology in South Africa, it should be remembered that the genus was established in 1867 on the basis of a drawing by a Mr. McKay of East London which was sent by Dr. Rubidge to Tate in London together with two leaf specimens showing what Mr. McKay and Dr. Rubidge believed were fructifications. The small oval objects on the leaf were carefully drawn but I doubt whether the details of the background venation, on which so much evidence has been based, were more than sketchily drawn. The spots were undoubtedly of fungal origin like the one shown in Plate IXc. They occur on many Glossopteridae in different parts of the Southern Hemisphere (Plumstead, 1962). The leaves themselves were both from Lower Beaufort horizons of Middle Permian age where fine-veined *Glossopteris* of this shape is not uncommon but it does have a reticulate mesh. The specimens are no longer in existence, and Seward (1907a) long ago cast doubt on the accuracy of the diagnosis and of the drawing. In any case, the Giridih leaves, which are at present too rare to justify specific rank, can be accommodated more easily in Feistmantel's genus *Euryphyllum*.

Genus *Noeggerathiopsis* Feist.

There have been endless discussions about this genus since its inception by Feistmantel in 1879. The Palaeozoic Gondwana leaves, which superficially at least resemble *Cordaites* of the Euramerican Province, have been separated and re-united with them a number of times. It is apparent in Africa, at least, where the genus has not been revised for some time that the common species *N. hislopi* includes a number of different plants. In India, several authors have created new species on the basis of both external features and cuticular studies. In the latest of these, Maithy (1965b) has made a somewhat sweeping revision of the genus throughout Gondwana territories, accepting four species and one additional variety based on external features and four species with different names based on cuticular studies. I do not propose to comment on his classification here for I have not made a detailed study of the genus and only two imperfect specimens have been found at Milorgfjella. Maithy's account of the history of the genus to date should be useful to those readers who have little access to the original Gondwana literature.

***Noeggerathiopsis hislopi* (Bunb.) Feist.**

Plate XIve

On specimen Z.392.24 the upper half of a small leaf is preserved as an impression in sandstone on which no cuticle remains. The fossil appears to belong to this species. The leaf is narrow, symmetrical and linear with entire margin and obtusely rounded apex. The venation is fine, parallel and quite straight, exhibiting occasional bifurcation. There is no anastomosing and no crowding in the median section. There are approximately 18 veins per cm.

Comparison. Feistmantel's (1879, pl. XIX, fig. 5) illustration is one example of many which could be chosen. It is of comparable size and from Lower Gondwana Karharbari Beds of India, and his pl. XIX, fig. 1 is from the Talchir Shales. Further comparisons are unnecessary in view of the incompleteness of the leaf.

It also resembles *N. hislopi* (Høeg and Bose, 1960, pl. VIII, figs. 1 and 5) from the Congo except that the apex of the Antarctic specimen is more rounded. However, Lele and Maithy (1964) have placed this Congo specimen in *N. gondwanensis* on the basis of the cuticular structure described by the original authors, while the *N. hislopi* described by Zeiller (1896) from the Transvaal has been placed by the same authors in another new species, *N. zeilleri*.

All this serves to emphasize the problems attendant upon any attempt to classify this important member of the early Gondwana floras.

Meyen (1963, 1964) has suggested that the genus *Noeggerathiopsis* Feist. was wrongly founded and that most leaves from both the Angara and Gondwana Provinces are actually *Cordaites* but that there are others from both provinces, distinguished by the arrangement of their stomata in dorsal furrows, which cannot be classed as *Cordaites* but should be placed in a new genus *Ruffloria* Meyen. He also believed that the genus *Crassinervia*, which has similar dorsal furrows, was borne on the same plants. These thick scale leaves have, superficially at least, much in common with *Walikalia* of the Gondwana Province. I have continued to use *Noeggerathiopsis* in this paper because I do not think enough work has been done in the Gondwana Province to justify discarding it.

***Noeggerathiopsis* sp.**

Plate XIVf and g

On specimen Z.399.31A(R) the upper part of an asymmetrical leaf is preserved. It has a more acute apex and the venation is straight, occasionally bifurcating and slightly divergent as well as coarser than on the common *N. hislopi*. The specimen is shown at natural size and $\times 2$ in Plate XIVf and g.

Comparison. The leaf can be compared with one from Tasmania, now in the British Museum (Nat. Hist.) and illustrated by Arber (1905, pl. VI, fig. 2). It agrees also with the emended diagnosis of *N. spathulata* Dana as given by Maithy (1965b) and which included a spathulate shape, acute apex and more divergent veins to distinguish it from *N. hislopi*. Arber (1905) had merged *N. spathulata* with *N. hislopi*. I have not seen Dana's original paper, and on the basis of a single specimen it is preferable to label the specimen *Noeggerathiopsis* sp. and to record the differences photographically.

cf. *Palaeovittaria* Feist.

Plate XIVh

Only one other leaf with straight bifurcating venation remains to be described. It is the upper part of a comparatively large leaf with an acute apex (of which the tip is missing) and with straight veins diverging from the median region towards the margin at a wider angle than in the *Noeggerathiopsis* sp. just described. There is no midrib and apparently no anastomoses. In *Noeggerathiopsis* the veins originate at the base and broaden upwards by bifurcation. Straight veins diverging from a median region are more characteristic of the genus *Palaeovittaria* than of *Noeggerathiopsis*, but from a single incomplete specimen no accurate determination is possible. There is an oval swelling at the base similar to those of immature fructifications of Glossopteridae but it is too indefinite to claim it as such.

Comparison. The venation is finer than on Feistmantel's type specimen but it is similar in angle and direction. The tentative determination is primarily to draw attention to existing differences between this and the specimens described previously.

Coniferous shoot

Plate XIVa and b

Specimen Z.399A.40 (Plate XIVa, natural size; Plate XIVb, $\times 2$) illustrates the only record of conifer foliage from Milorgfjella. It is the hollow mould of a part, possibly the apical part, of a small-leaved conifer. The moulds of about 16 small leaves can be seen. They appear to have been arranged in spiral order on the stem and must have been fairly rigid to have been buried and left so perfect a mould.

Comparisons. These have to be confined to foliage shoots of approximately the same size and age for no other evidence is available. Among such, the following can be cited to illustrate similar fossils in the Lower Gondwana formations of other areas:

Kurtz (1921, pl. XIII, fig. 134); a small shoot which was named *Walchia*; from La Rioja, Argentina. Høeg and Bose (1960, pl. VI); "foliage shoots" from the Congo; poorly preserved.

Feistmantel (1886, pl. XIIA, figs. 3, 4 and 4a); from the Talchir of Karanpura; small shoots which were called equisetaceous or coniferous branchlets.

Feistmantel (1879, pl. XXV, fig. 2); *Voltzia heterophylla*; see the small leafed twig on this figure.

3. A mixed plant assemblage (Plate XV)

To conclude the description of the fossils, specimen Z.392.16(R) (Plate XV) has been illustrated as the best composite example of leaves from Milorgfjella. Several species of *Gangamopteris* can be seen with *G. cyclopteroides* like those in Plate X predominating. A part of the coarse radiating venation of *Walikalia* can be seen on the left-hand side. The surface is from an outcrop and no remnant of carbonized tissue remains on the leaf impressions. The layers are too hard and undulating to be split without damaging it and little would be gained because all the leaves overlap to such an extent that specific identifications of simple leaves would be unreliable. The specimen is interesting because it is the only good example from this area of what I have called elsewhere (Plumstead, 1958b) an "autumnal bank of deciduous leaves" which are such a feature of the best Gondwana floral sites. The leaves had collected in quiet water where they were first dropped and I believe they reflect the mixed plant assemblage in the immediate vicinity.

III. SUMMARY OF THE COMPOSITION OF THE FOSSIL FLORA OF MILORGFJELLA: ITS ENVIRONMENT, AFFINITIES, AGE AND SIGNIFICANCE

A. COMPOSITION OF THE FLORA

Most of the fossil plants collected from Milorgfjella were poorly preserved and fragmentary but despite this it has been possible to gain a comprehensive idea of its composition. It includes very few lower-order plants, namely, one lycopod, a few *Paracalamites* stems and a few fragments of fern stems. It consists mainly of stems and leaves of gymnospermous affinities, namely, a large number of woody stems which, on external and a very little microscopic evidence, fall into four groups with cordaitan, ginkgoalean, coniferalean and glossopteridean affinities. The leaves include two species of *Gangamopteris*, two of *Walikalia* (one of scale leaves and one vegetative), two species of (?) *Euryphyllum*, two of *Noeggerathiopsis* and one of cf. *Palaeovittaria*; of these only two species are new. In addition, there is one coniferous shoot and some evidence of fungal disease.

The linking together of particular stems with particular leaves would be entirely speculative, but it is interesting to note that the leaves too can be allocated to the four gymnospermous classes mentioned above. There must, inevitably, have been at that time many transitional and also many hybrid forms

of which very few would survive. Later finds may lead to a clearer view of the plants concerned, but, in the interval, the large variety of gymnospermous plants, almost to the exclusion of all others, and at so early a stage (probably late Carboniferous), is of considerable significance in plant-distribution studies.

B. ENVIRONMENT OF THE FLORA

It was a cold-climate flora. The Milorgfjella flora provides evidence, from one more continent, of the nature of the plant life established in the closing stages of the Palaeozoic glaciation, since at the eastern site the basal tillite grades upwards within a few metres into the fossiliferous beds.

The thin coal seams, associated with the upper sediments of the western site at Milorgfjella, are likewise additional examples of the development of coal in a cold climate. Coal was at one time considered to be the product of tropical plant growth only, but the number of coal seams known to be associated with cold temperate and even frigid climates, in the Southern Hemisphere especially, is increasing as new areas are explored. The geological evidence provided by Jukes suggests that, at the eastern site, no interval of erosion separated the tillites from the overlying fossiliferous sediments into which they grade. From the western site also, the few specimens from the two highest horizons support the belief that they were very little younger and were still subject to cold climatic conditions. The only lycopod record is one of these, for the plant itself is possibly of Upper Carboniferous age. In addition, the coarseness of the sediments, and the large pieces of unweathered feldspar in the matrix indicate the continuance of a cold climate as well as proximity to Basement Complex outcrops. In fact, from the evidence preserved in the succession of rocks exposed, it would not have been surprising had a recurrence of glaciation in the area been revealed.

All of the plants were apparently cold tolerant and because of this they were able to multiply and to establish themselves during a long cool post-glacial period without competition from less hardy plants. The influence of this pattern persisted for a considerable time and this is possibly the reason why the Pteridophyta only played a minor role in the flora of the late Palaeozoic of Gondwana countries compared with those of Europe and North America.

C. AGE OF THE FLORA

The Beacon Supergroup in Milorgfjella represents only a fraction of the stratigraphical succession displayed elsewhere in east Antarctica, and is apparently the northern rim of a basin of deposition which increases in thickness southward and eastward. There is no underlying succession of Devonian and Lower Carboniferous sediments as in parts of Victoria Land, and the rocks explored reveal only a comparatively thin tillite grading into an early stage of plant-bearing beds which are overlain, at some distance to the south-east, by the uppermost volcanic member of the succession.

Stratigraphically, the Milorgfjella plant-bearing beds may be correlated in east Antarctica with the Mackellar Formation, which overlies the Pagoda Tillite in the Beardmore Glacier area and is itself partly glacial, and with the Discovery Ridge Formation overlying the Buckeye Tillite of the Horlick Mountains but, up to now, no fossils have been found in either (see Grindley, 1963).

In the absence of any absolute age determination from the area, the age of the Milorgfjella deposits can only be estimated from the close association with the late stages of glaciation and also from the composition of the flora. Both of these support a late Carboniferous age and indicate that the fossiliferous beds are older than those from any stage of the *Glossopteris* flora discovered up to now in Antarctica.

The predominance of the gymnospermous woody plants, the prevalence of leaf species with bifurcating venation and, finally, the presence of *Gangamopteris* as the only representative of reticulate-veined *Glossopteridae* bear witness that this Antarctic fossiliferous deposit was formed during the early stages of development of the *Glossopteris* flora. It must be borne in mind, however, that this stage could not have been contemporaneous in every part of the province, but would have been dependent on the fluctuations of the final glaciation in each area. There appears to be general agreement, throughout the Southern Hemisphere, that this occurred during the Upper Carboniferous period.

The formation can be compared with the Needle Shales of the Talchir Stage in India, the Upper Dwyka Shales of South Africa and possibly the Bacchus Marsh Beds of Victoria, Australia.

D. AFFINITIES OF THE FLORA

1. *Comparison with other early Gondwana floras*

The closest comparisons of the Milorgfjella fossil flora are to be found with India and Africa. These are considered as follows:

India. In the past, several palaeobotanists have suggested a direct connection between the southern Permo-Carboniferous glaciation and the origin of the *Glossopteris* flora with the result that the search for the earliest Glossopteridae has excited a number of Gondwana geologists, among whom the late Professor Birbal Sahni was particularly enthusiastic. He encouraged his students to hunt for both mega- and micro-plant fossil evidence in the Talchir boulder beds of India and in their immediate vicinity. Recently, Lele (1966) has reported on the present position of the search. As far as India is concerned, it has proved fruitless up to now within the tillites themselves, but the overlying sediments, which are still regarded as being part of the Talchir Group, have been investigated in a number of coalfields. The maximum thickness of the Talchir Stage in India is 275 m., which is found in the Raniganj coalfield, but this decreases westward and is comparable with the succession exposed at Milorgfjella. Up to now the earliest record of the *Glossopteris* flora in India is from the West Bokara coalfield, where spores have been found in shales immediately above the boulder beds. In this coalfield, too, Lele drew attention to the appearance of a second boulder bed nearer the top of the Talchir Stage. This is possibly significant in view of the dropped pebbles and the unoxidized nature of the feldspars in some of the higher horizons in Milorgfjella. The earliest known mega-fossils, of the Gondwana System in India, came from Talchir Needle Shales in the Giridih coalfield; these included two species of *Noeggerathiopsis* and *Gangamopteris cyclopteroides* (Surange and Lele, 1955).

In the Singrauli coalfield, the South Rewa basin, the Karampura area and a number of others, plant fossils have been found at various levels in the Talchir sediments. In every case, *Gangamopteris* and *Noeggerathiopsis* are either dominant or the only genera present. Lele (1966, p. 93, table 2) gave a list of 28 known mega-plant species from all exposures of Talchir Stage rocks in India. It included 12 of *Gangamopteris*, two of *Noeggerathiopsis*, some equisetaceous stems and coniferous shoots, three species of *Glossopteris* and some seeds.

Of the 13 Talchir localities quoted by Lele in his table, *Glossopteris* occurred in only three and always in the higher horizons.

It is significant that this list bears a marked relationship to that of Milorgfjella.

In the other Gondwana areas similar records have not been kept in quite the same way, but work is in progress.

Africa. South Africa is the only country from which mega-plants have been found, in the past, actually within the tillites. Du Toit (1908) and Leslie (1922) found *Gangamopteris* within boulder beds in the Cape Province and Transvaal, respectively, and in the former case it was associated with a small woody stem with circular scars. More recently, Plumstead (1966) has described an assemblage of leaves, which she regarded as Protoglossopteridae, and many small fragments of moss interbedded with thick glacial deposits, in a bore-hole core in the Transvaal. Among the Protoglossopteridae, leaves with bifurcating venation heavily outnumbered those with net venation. Intermediate stages were represented by a few leaves with only an occasional reticulation.

From South West Africa, also, there is evidence of large gymnospermous trees in the Dwyka Series, between the boulder beds or tillite and the White Band, which marks the top of the Dwyka Series and is considered to be the top of the Carboniferous.

The "fossil forest" of South West Africa is of this age and Kräusel (1956*a, b*) has described some of the silicified wood.

Du Toit (1932*a*) recorded *Gangamopteris* from a well and an adjacent bore hole at Artesia siding (Botswana) and commented that it was the farthest north that the genus had been found in South Africa. The fossils were found at depths up to 180 m., which in that area could not have been far above the boulder beds. They were of large leaves of *G. cyclopteroides* with a few of *G. var. attenuata*. He concluded with the words "curiously *Glossopteris* is unrepresented". In the same volume, Du Toit (1932*b*) recorded the species from Uganda, north of the Equator, not far above a glaciated pavement. Both horizons are comparable with that of the present collection.

Attention has already been drawn to the close similarity between the Milorgfjella flora and the lower of the Gondwana floras from Walikali in the Congo, described by Høeg and Bose (1960).

From Australia and from South Africa, Virkki, at the instigation of Professor Sahni, recovered spores from within the Bacchus Marsh Tillites of Victoria, Australia, and the Dwyka Tillite of South Africa, respectively. I understand that in 1963 Macchiavelle recorded similar evidence from Uruguay but I have not seen this paper. The accumulation of data from all these areas is sufficient to establish the existence of elements of the *Glossopteris* flora in Gondwana countries during the final stages of the great southern ice age. The new evidence of the comparatively large flora from Milorgfjella, within so short a distance of a glacial conglomerate, is therefore of considerable importance. Supporting evidence from microfossils will be awaited with interest.

2. Comparison with contemporaneous Euramerican flora

The composition of this flora differed widely from contemporary fossil floras of Europe and North America, for it was dominated by woody gymnospermous plants. Both wood and leaves, whose closest affinities are with Cordaitales, Ginkgoales and Coniferales are conspicuous and, in addition, the new class of Glossopteridae dominated the fossil leaf deposits in the number of individual leaves but not in the number of species.

In contradistinction, plants of lower orders played a very minor role which was due partly, but by no means entirely, to the rough and harsh conditions in which most of the plant remains were accumulated. The absence of the typical northern arboreal forms of lycopods and arthropytes is conspicuous and the only records of the dominant pteridosperms and ferns of the northern "Age of Ferns" are to be found in a couple of fragile branched axes.

3. Comparison with the Angara flora of the southern U.S.S.R.

Throughout the text comparisons have been drawn, almost entirely, with other Gondwana plants but there is also a general resemblance to the Angara floral province of the southern U.S.S.R., which may be of significance when attempting to reconstruct the Gondwanaland of the late Palaeozoic. It was a flora dominated by Cordaitales and Ginkgoales but conifers and a group of plants, which early Russian palaeobotanists linked with Glossopteridae, also occurred.

I do not think that the Cordaitales ever dominated any part of the Gondwana Province, as they did the Angara, but there is a similarity great enough to imply possible contact between the two for a limited time.

In perusing the work of Zalessky (1937*a, b*), Neuberg (1948, 1965) and Meyen (1963, 1964), admittedly more from a pictorial than literary point of view because of language difficulties, it is evident that the four gymnospermous elements Cordaitales, Ginkgoales, Coniferales and some leaf species, which resemble *Gangamopteris* and which may be Glossopteridae, all play a prominent part.

In particular, the identity of the species *Paracalamites* Zalessky and *Ruffloria* Meyen have already been mentioned, as well as the resemblance between the coarse Angara *Crassinervia* and the Gondwana scale leaves *Walikalia*.

A part of a long shoot with leaf scars, which Neuberg (1948, pl. LVI, fig. 3) attributed to *Noeggerathiopsis latifolia*, can be compared with the group 3 stems of Milorgfjella.

Coniferous twigs are common to both floras, as well as to other provinces, so that they are less significant, cf. *Walchia peremiana* Zalessky (1937*a*, p. 75, fig. 40). In addition, a number of simple entire-margined leaves with bifurcating venation occur in the Angara flora, e.g. *Pursongia asiatica* Zalessky (Neuberg, 1948, pl. XLIV) was originally called *Glossopteris amalitzkii* by Zalessky, while *Zamiopteris glossopteroides* Schmalhauzen (Neuberg, 1948, pl. LXV) was called *Gangamopteris glossopteroides* in 1918, and *Glottophyllum* Zalessky (Neuberg, 1948, pl. LXIII) was once *Ginkgo cuneata*.

The earlier terminology used in Russia indicates the thinking of the authors. The leaves, while resembling Glossopteridae in size and shape, have bifurcating rather than anastomosing venation. The veins approach one another closely in some illustrations but do not actually join.

However, I have seen leaves from this area, collected by Wagner (1962) which showed anastomoses

and were more like true Glossopteridae. I have also drawn attention elsewhere (Plumstead, 1963) to the similarities between a new *Gangamopteris* fructification *Vannus* and Neuberg's *Vojnovskyales*.

None of these general resemblances can, however, be compared with the identities, even at the specific level, which are common between floras from different parts of Gondwanaland.

E. SIGNIFICANCE OF THE MILORGFJELLA FLORA

As with all Antarctic fossil floras, the most significant thing about it is that it is there at all—in the ice- and snow-bound east Antarctica where at present no vascular plant is known to grow.

The second important fact is that it represents a new stage in the records of fossil plant life of Antarctica and, when added to those already known, it emphasizes the unity and near contemporaneity of each stage of the *Glossopteris* flora throughout Gondwanaland.

Thirdly, it has drawn attention to the overwhelming number of woody gymnospermous plants in all Palaeozoic Gondwana floras, but particularly at Milorgfjella, where the harsh conditions during preservation destroyed the more delicate plant fragments and emphasized the woody and tough-leaved gymnosperms.

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PLATE I

Stems—mainly of lower-order plants.

- a. (1). *Paracalamites* Zalesky. The best example in the collection.
(2). Stem of uncertain affinity with scattered round scars. (Z.399A.22A(R); $\times 1$)
- b. Part of stem in a(1) to show detail of nodes. (Z.399A.22A(R); $\times 2$)
- c. (1). A small branched fern or pteridosperm axis.
(2). The fine acicular curved impressions found on the left of this and on a number of surfaces suggest that the stem in a(1) and others like it bore narrow-leaved foliage, e.g. *Phyllothea australis*. (Z.392.15; $\times 2$)
- d. The hollow mould of a lycopod stem. Note the coarse grit. (Z.352.1; $\times 1$)
- e. Hollow mould of a stem with spiral marks; of uncertain affinity. Base of a large *Gangamopteris* and a small coniferous twig on the right (see Plate XIVa). (Z.399A.40; $\times 1$)

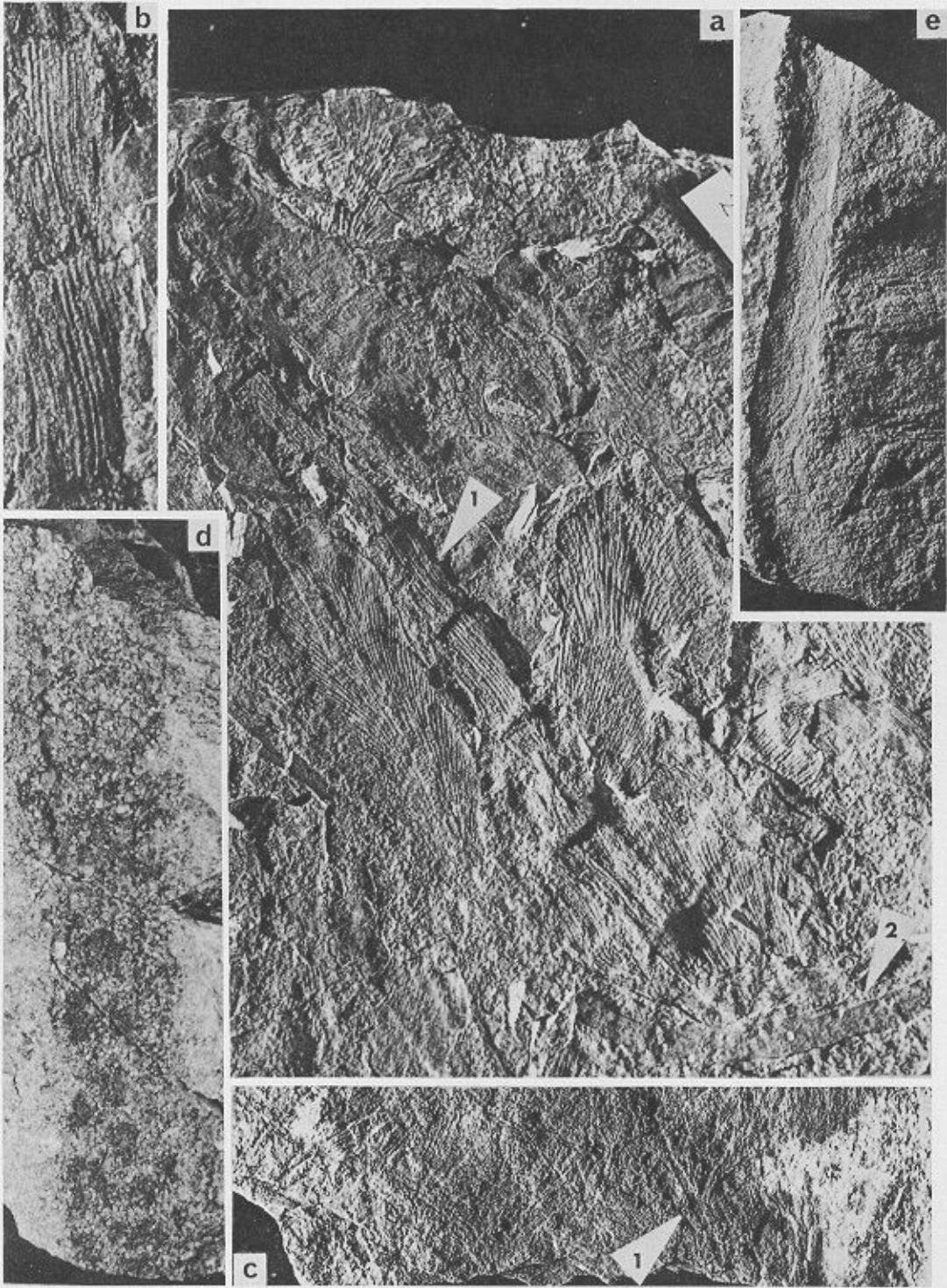


PLATE II

The largest specimen of woody stems.

- a. Woody stems of group 1. Branched and twisted, possibly of cordaitalean affinity. Arrows indicate:
- (1). Large branch scar.
 - (2) and (3). The stems on which the concentric marks in (b) and (c) were photographed.
 - (4). Piece of wood from which macerated fragments of Plate IV were obtained.
 - (5). Woody stem of group 2, probably Glossopteridae. (Z.399A.18; $\times 0.5$)
- b. An area showing groups of the concentric marks which occur on many stems—origin unknown but possibly pathogenic. Arrow indicates an area where the marks are etched into the surface and no carbon remains. (Z.399A.18; $\times 5$)
- c. A similar area of concentric markings, one with nine rings. (Z.399A.18; $\times 5$)



PLATE III

Woody stems of groups 1 and 2.

- a. Branched and twisted stems of group 1. Note the branch scar on the left-hand stem and the wide-angled branching of the right-hand stem. (Z.399A.19; $\times 1$)
- b. Woody stem of group 2. Note the raised and tapered elongated "streaks" on the surface showing glossopteridean affinity and the straight growth. (Z.399A.32; $\times 1$)
- c. A wider woody stem of glossopteridean affinity. Note the tapering streaks, the very fine parallel striae visible along the lower edge of the stem and the large branch scar at the top. (Z.393.2; $\times 1$)
- d. A much smaller branched and twisted woody stem of group 1. Note the wide angle of branching and the grain of the wood as in Plate IIa and in (a) above. (Z.392.6(R); $\times 1$)

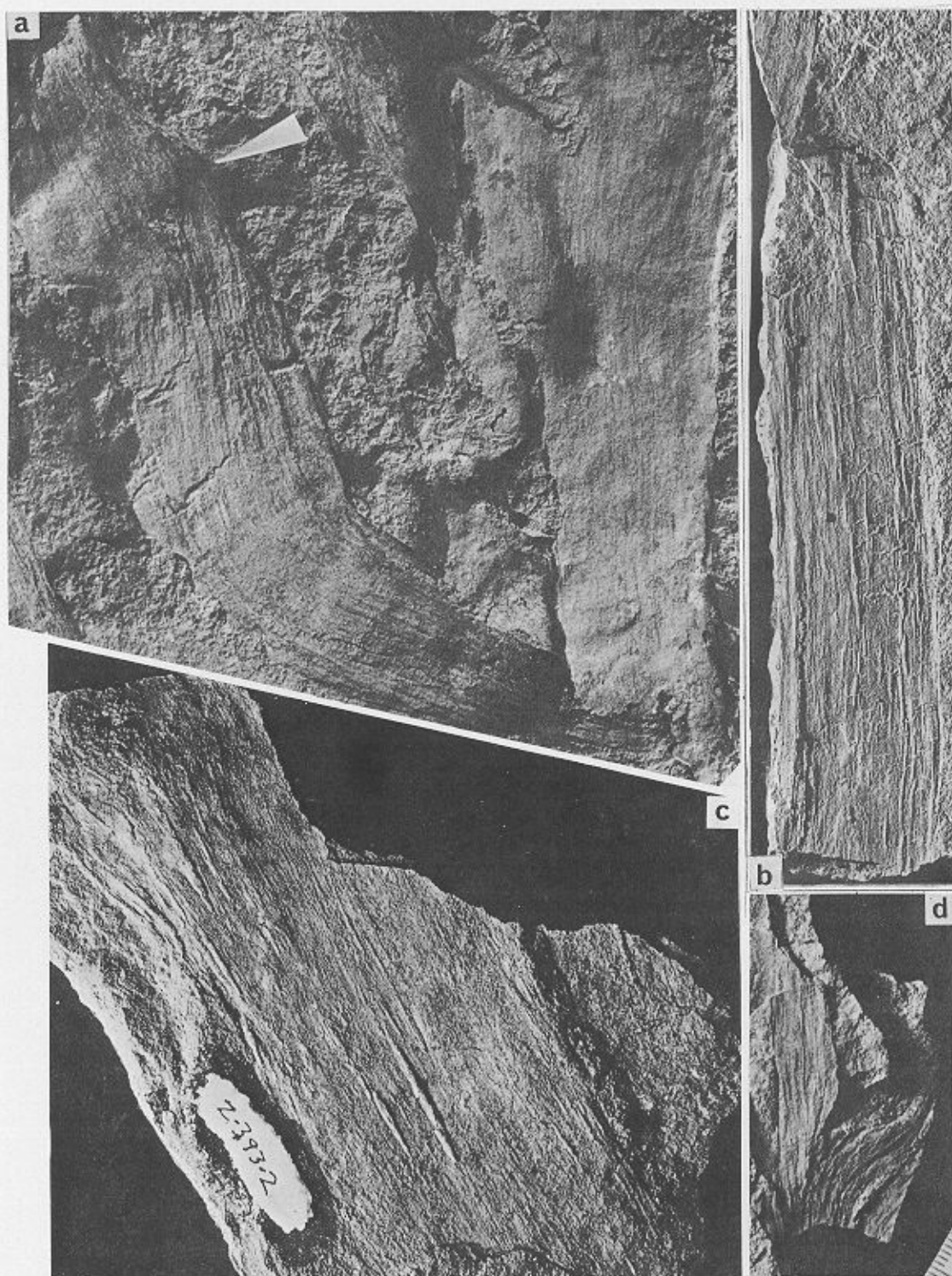


PLATE IV

a-g. Micro-structure of wood of group 1 of woody stems. Obtained from wood marked 4 on Plate IIa after long maceration. (Z.399A.18; a and b $\times 200$; c-g $\times 500$)

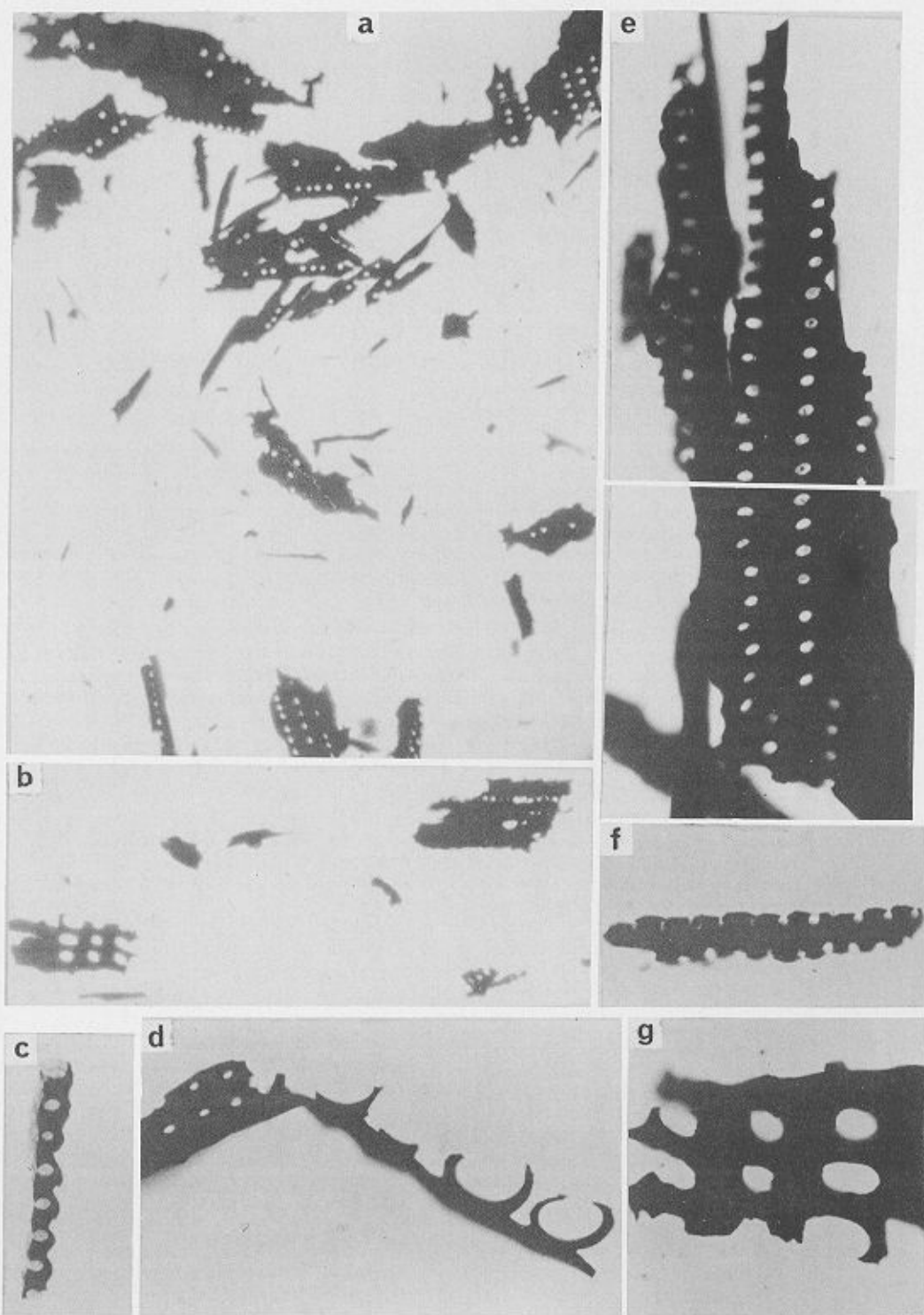


PLATE V

Dry twig of *Ginkgo biloba* for comparison with woody stems of group 3.

- a. Woody twig from the "living fossil" *Ginkgo biloba* growing on the University of the Witwatersrand campus. Note the long shoot which was a former terminal shoot and also parts of four damaged short shoots, about to fall. These would leave a small round scar. ($\times 1$)
- b. Another part of the *Ginkgo biloba* stem showing details of the long shoot. Note the two small punctures signifying vascular scars on each leaf scar and also an odd leaf scar or two just below and just above the main long shoot zone. ($\times 2$)
- c. Part of the *Ginkgo biloba* stem to show details of a short shoot. Note the crowded arrangement of the leaf scars and the presence of two vascular scars on each. Note also the texture of the unscarred stem. ($\times 2$)
- d. Woody stems of group 3. Note part of a long shoot on the right-hand stem with an isolated leaf scar below the main zone. The apparent large round scar at the base is only a shadow. The left-hand stem is not connected but has a similar surface and it is thought to be from the same plant. Note the two small round scars in the upper half which resemble short-shoot scars on the modern plant; cf. also the surface appearance of the stem with that in (c). (Z.399A.7(R); $\times 1$)
- e. Part of the counterpart of the long shoot in (f). Note the small double-edged ridges which surround each leaf scar on both living and fossil stems which appear as grooves in this counterpart. (Z.399A.7A; $\times 2$)
- f. A particularly long "long shoot". Note parts of impressions of leaf bases can be seen in a few places and also on (e). Wherever vascular scars are clearly preserved, there are four of them instead of the two normally developed on each *Ginkgo* leaf scar. (Z.399A.7; $\times 1$)
- g. A small impression resembles a compressed zone of a long shoot on an older and wider woody stem. It occurs on the same surface as the stems on (d). (Z.399A.7(R); $\times 1$)

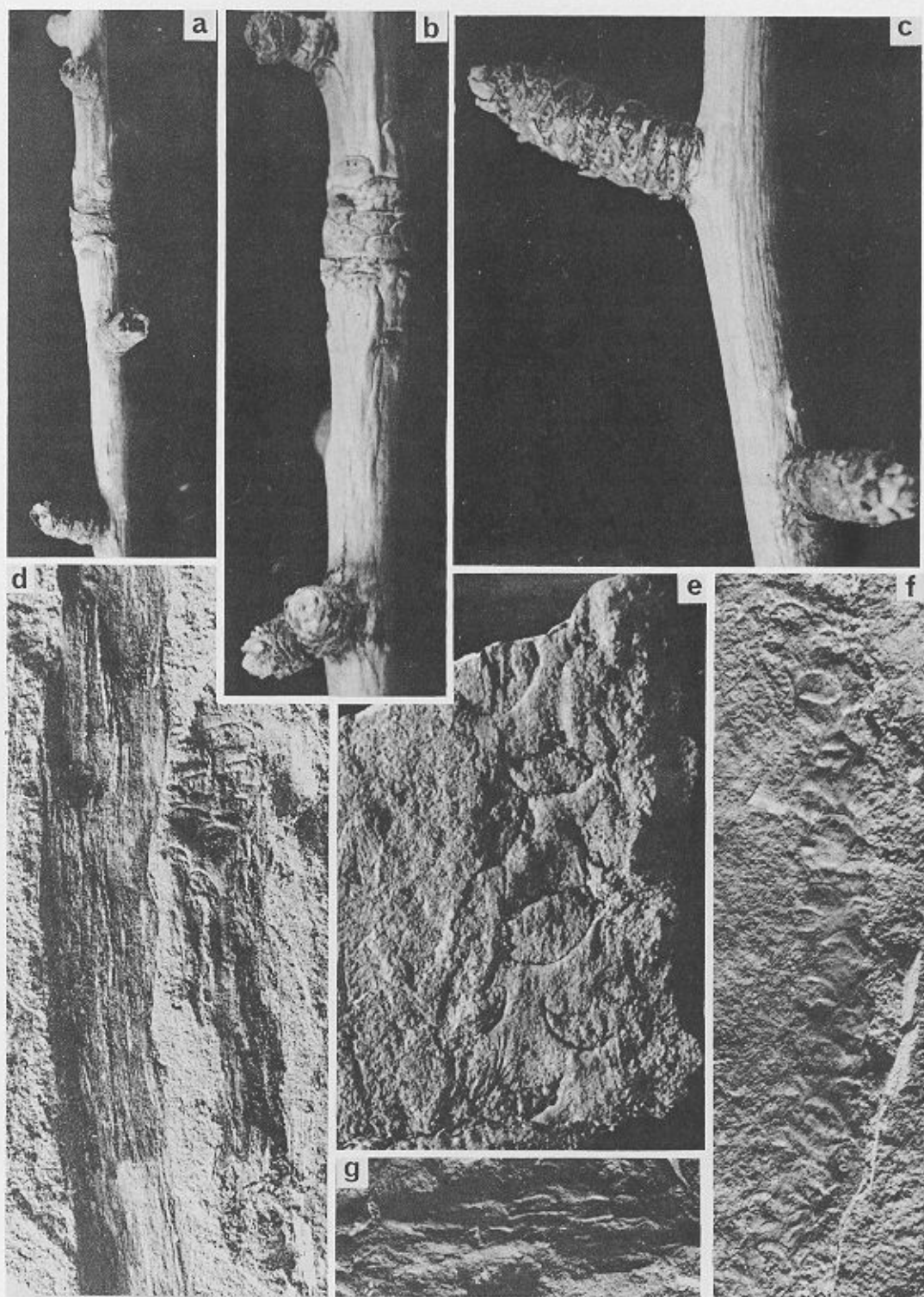


PLATE VI

Short shoots of stems of group 3.

- a. A short shoot which is believed to be from the same plant as the long shoots in Plate V. The stem below it was cleaned but no evidence of connection could be seen; cf. short shoot of *Ginkgo* (Plate Vc). (Z.399A.22; $\times 1$)
- b. The same short shoot as in (a). (Z.399A.22; $\times 2$)
- c. The counterpart of (a). (Z.399A.22A; $\times 1$)
- d. The counterpart of (a). (Z.399A.22A; $\times 2$)

Note. In all photographs there are four vascular strands on each of the well-preserved leaf scars.

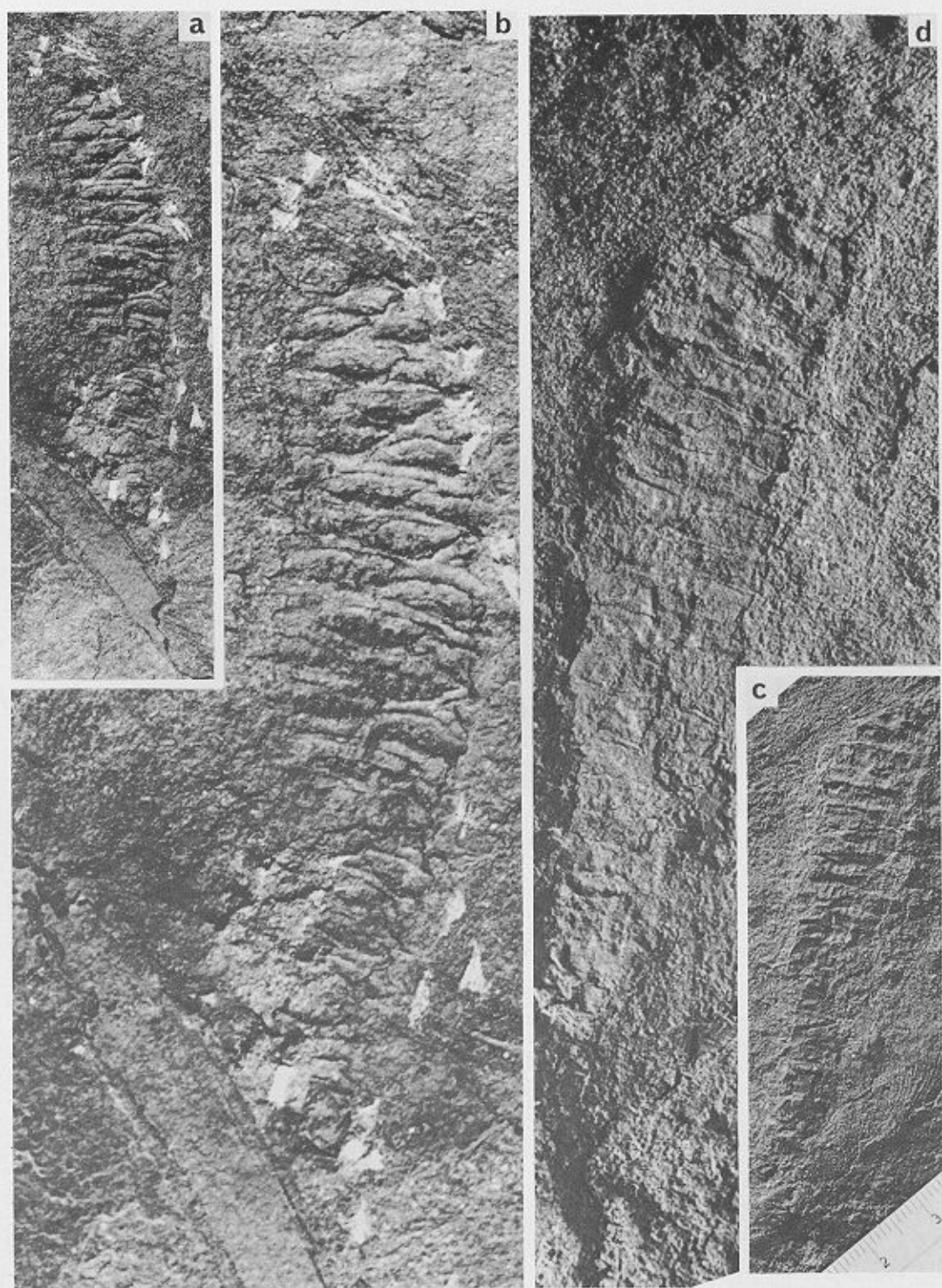


PLATE VII

Woody stems of group 4 and one of group 2.

- a. Three stems of which that on the left is of group 2—Glossopteridae, while the other two on the right are of group 4. On the right-hand stem there are two whorls of branch scars, one at the base and one nearer the middle. There is an indication of a third at the top of the stem. The affinities of these stems are believed to lie with conifers. (Z.399A.42(R); $\times 1$)
- b. The large branch scar on the right of (a). (Z.399A.42(R); $\times 5$)
- c. Two much smaller stems of which the right-hand one has a zone of branch scars and is of group 4. There is less certainty of the left-hand stem but it may be the same. (Z.399A.36B; $\times 1$)

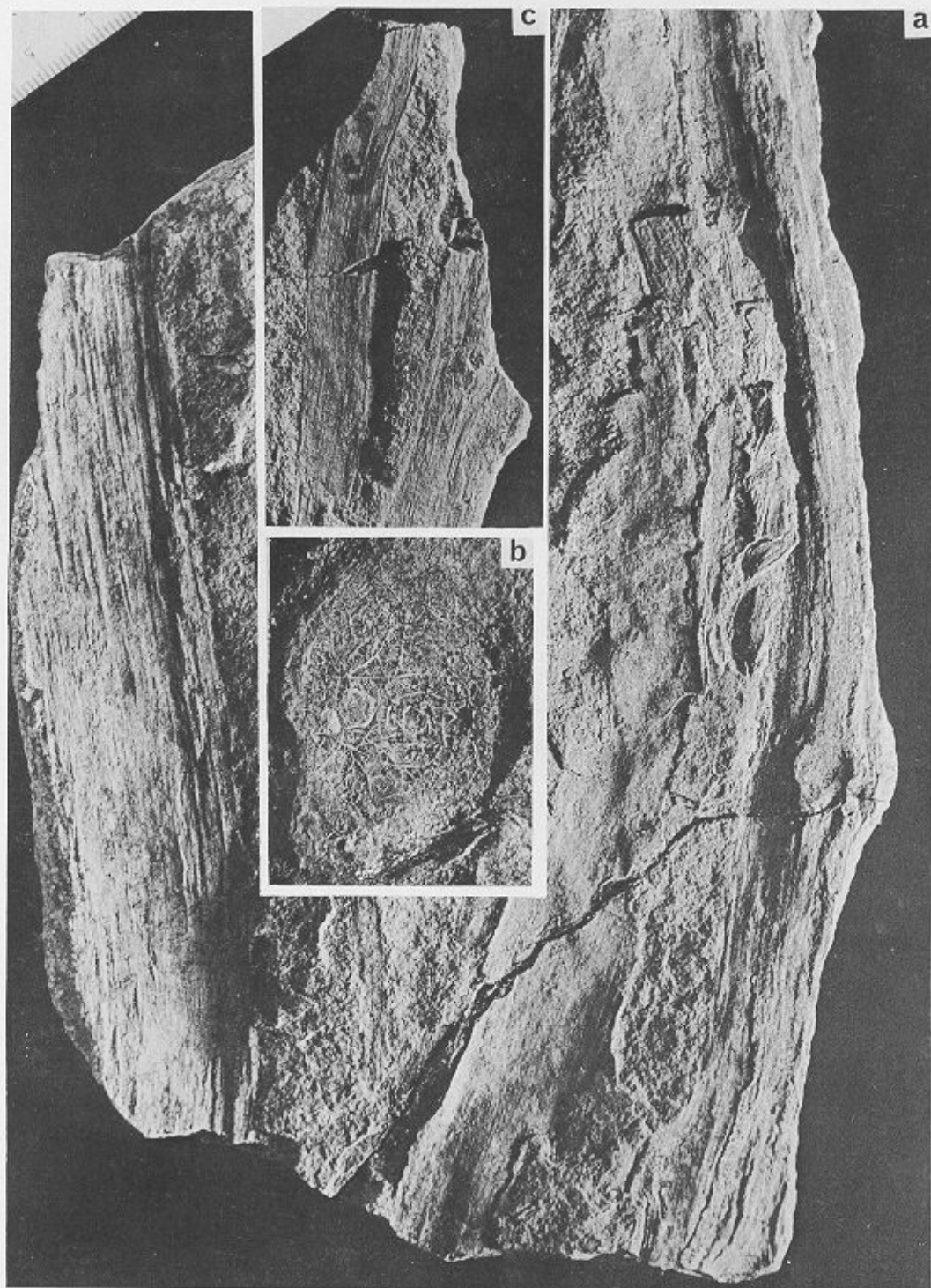


PLATE VIII

The largest stem in the collection and a small one with concentric rings.

- a. The largest stem in the collection. It is incomplete on the right-hand side and is part of a larger stem. The straight growth and hollow tapered streaks on the mould impression in sandstone suggest group 2—Glossopteridae. (Z.392.28; $\times 1$)
- b. A small shrunken stem on which a carbon ridge indicates its woody nature. Note the patches of small concentric marks like those on Plate IIb and c. The apparent branch on the left is due to a shadow. (Z.392.19; $\times 1$)

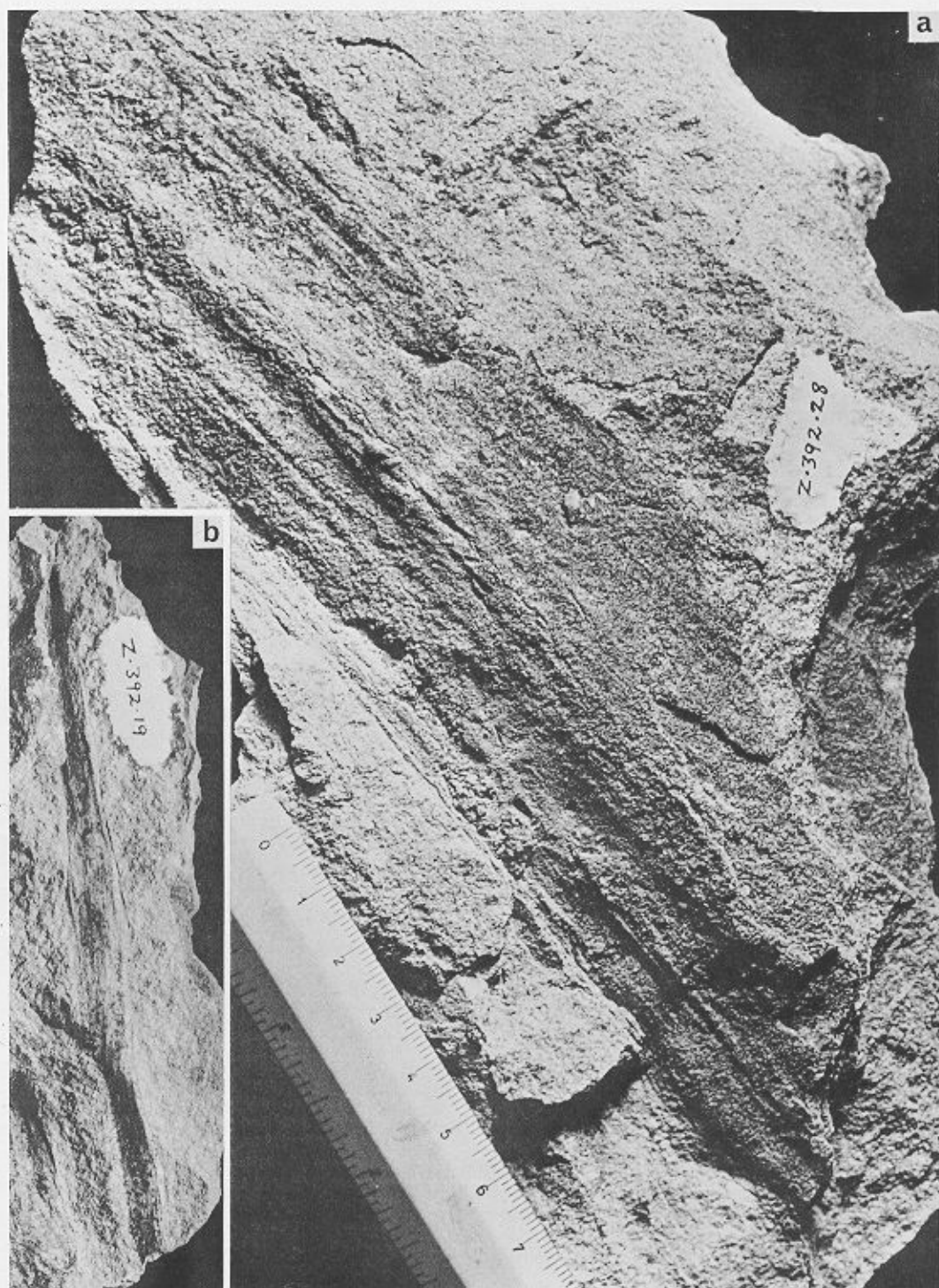


PLATE IX

Gangamopteris obovata Carr. (*G. cyclopteroides* var. *attenuata* Feist.).

- a. Part of a leaf showing characteristic shape and venation. (Z.392.2(R); $\times 2$)
- b. A similar tapered leaf. Note the small irregular rock chips on the upper left of the leaf and on its right base. (Z.399A.10(R).; $\times 1$)
- c. A small leaf on sandstone. The leaf shape and disposition of the main veins are those of *G. obovata*. This specimen is figured in order to record the fungal spots. Note the large oval patch near the base and smaller growths on the upper left-hand side. (Z.392.20; $\times 2$)
- d. The narrow tapered base of a sessile leaf, probably of *G. obovata*. (Z.392.13(R); $\times 1$)

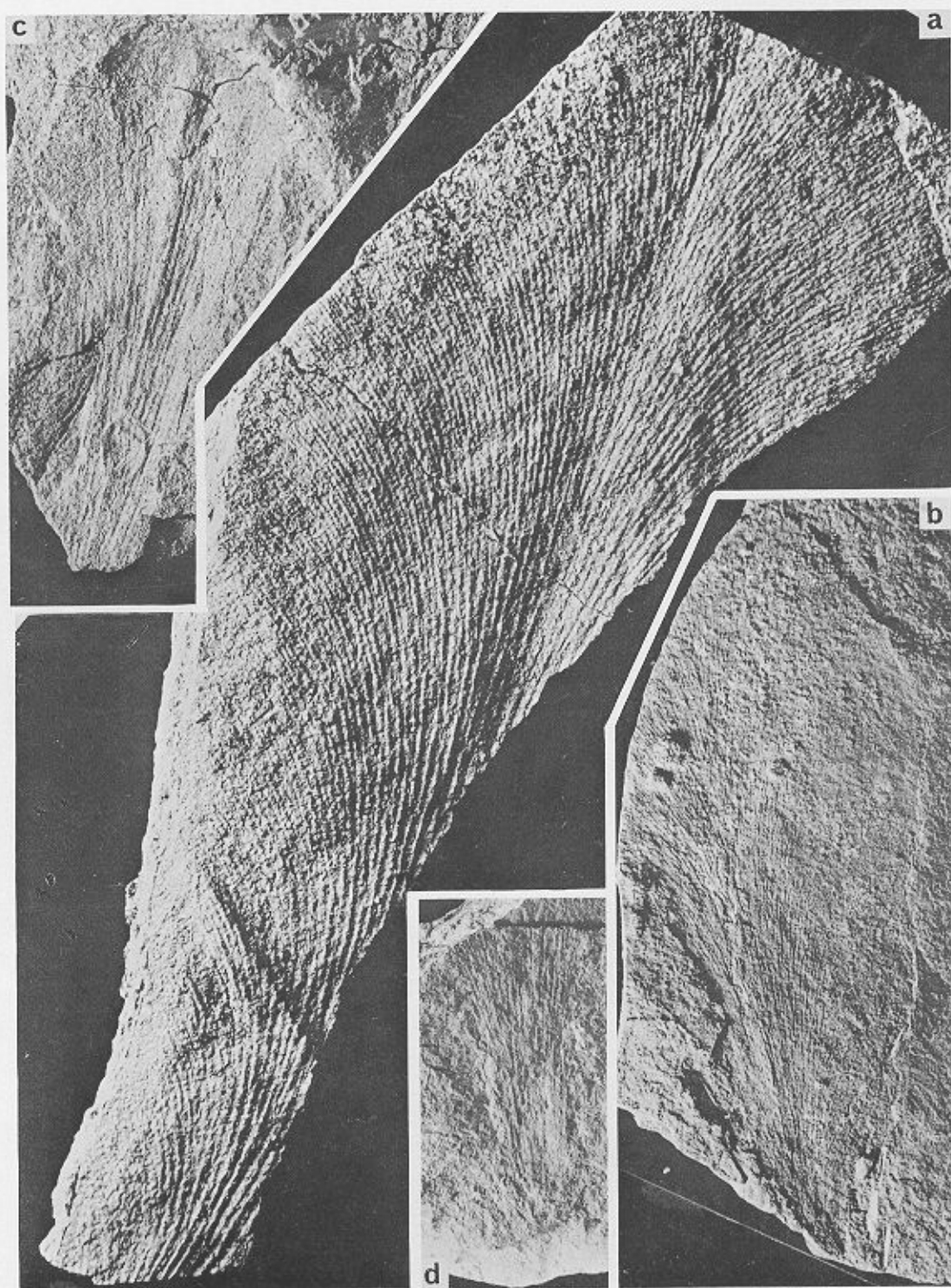


PLATE X

Gangamopteris cyclopteroides Feist.

- a. *Gangamopteris cyclopteroides* Feist.—resembles closely his “type form” but all the examples from Milorgfjella are small. Note the oval shape, embracing base, and absence of sub-parallel median veins. (Z.399A.10C; $\times 1$)
- b. The same specimen as in (a) to show venation detail. (Z.399A.10C; $\times 2$)
- c and d. Two smaller specimens probably of the same species. They occur on the same surface. (Z.392.7(R); $\times 1$)

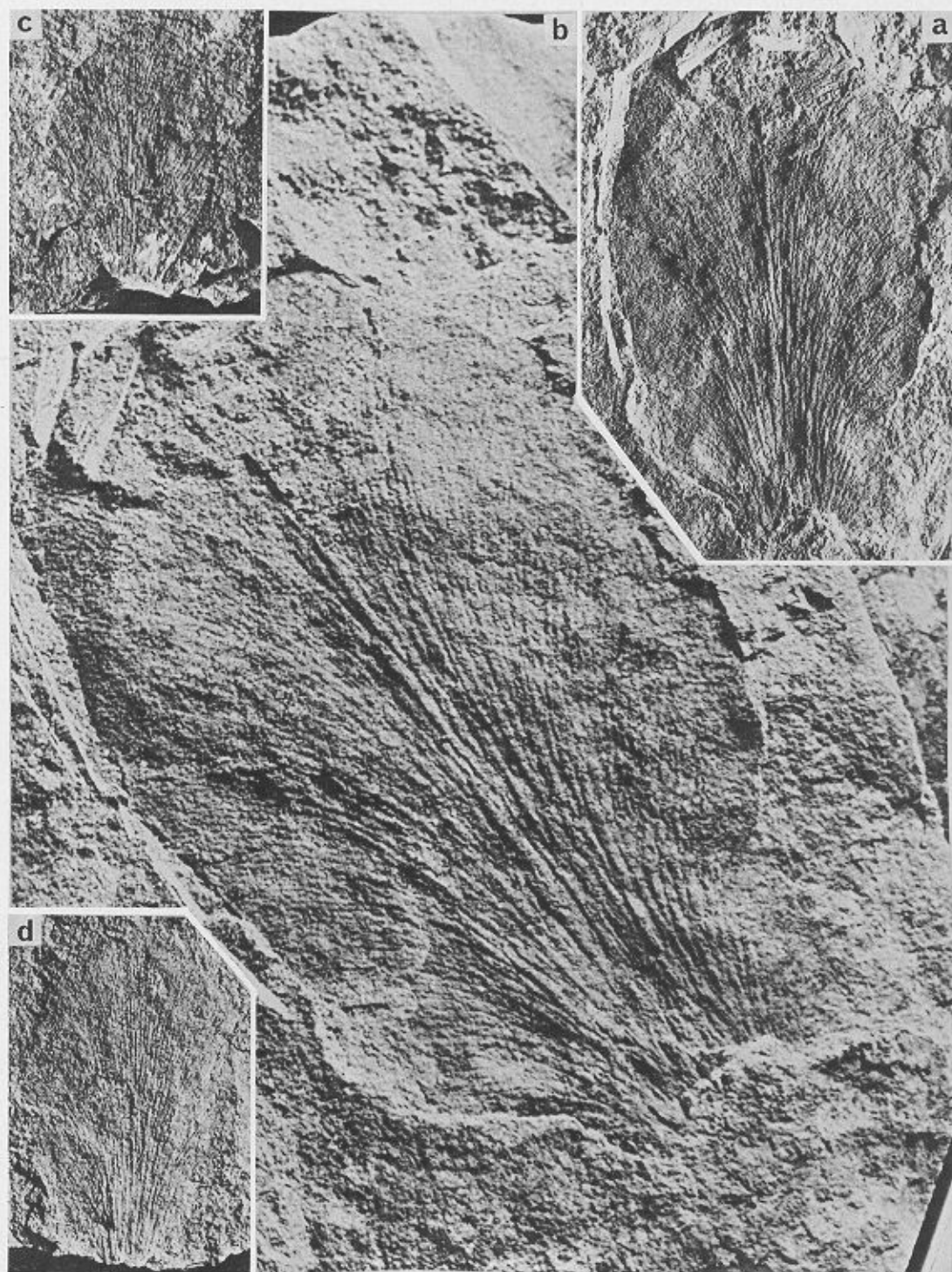


PLATE XI

- Thick scale leaves—cf. *Walikalia* Høeg and Bose, and a related (?) vegetative leaf.
- a. *Walikalia jukesii* sp. nov. Imprint of an almost round thick convex scale leaf with radiating veins, broad sessile base, straight obtuse-angled lower margin and an entire deep arc upper margin. Anastomoses very doubtful. (Z.392.15C; $\times 2$)
 - b. The same leaf as in (a) before it was separated from the original. It is overlain by a very fine-veined leaf fragment which has coarser mesh on the left and may possibly be part of a *Glossopteris* leaf, a genus which is otherwise completely absent from the Milorgfjella fossil flora. (Z.392.15(R); $\times 1$)
 - c. *Walikalia jukesii* sp. nov. Another less complete specimen illustrating the same characters. The sessile base is more complete. Note also the zone of bifurcating veins near the top which account for leaf surface expansion in a concentric arc. (Z.392A.5C; $\times 2$)
 - d. A leaf similar in shape but flat instead of convex. This is believed to be the vegetative leaf of the plant which bore the thick scale leaves. The undulating margin gives a false impression of being lobed. (Z.399A.28(R); $\times 1$)
 - e. Another specimen less well preserved. Note the small fern (?) stem with round scars above the leaf, cf. Plate 1a(2). (Z.392.6(R); $\times 1$)
 - f. A small and obviously unexpanded leaf with broad base and prominent radiating veins. It is possibly of the same species. (Z.392.24(R); $\times 1$)

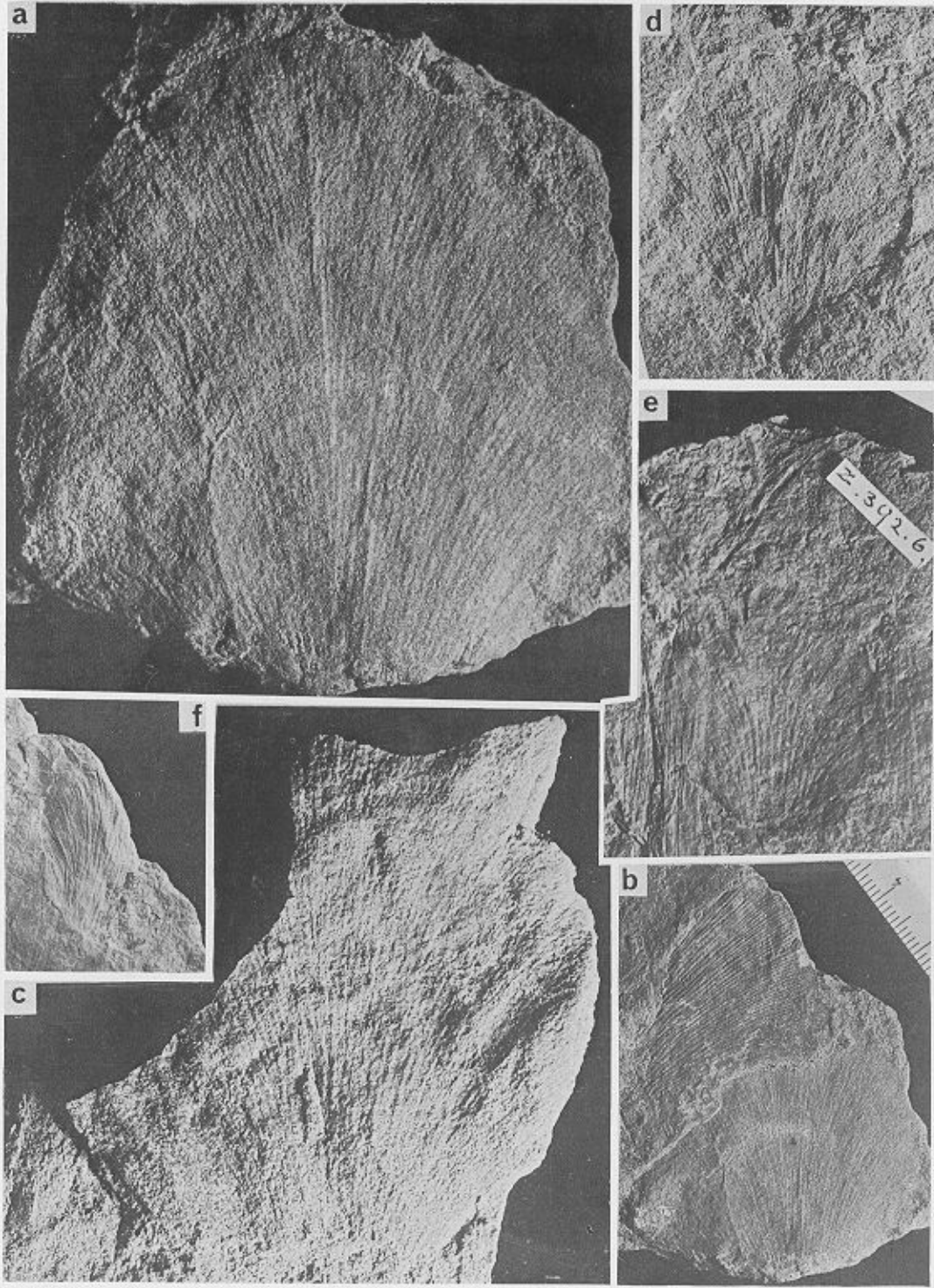


PLATE XII

Euryphyllum antarcticum sp. nov.

- a. Leaves of *Euryphyllum* showing directional deposition. Most of them have the lateral margins folded inwards—either below or above the surface, showing reversed direction of venation and emphasizing a groove or a ridge in the median region. The round leaf on the left is a vegetative leaf of *Walikalia* (see Plate XI d), while next to the curved leaf on the right-hand side there is the faint impression of the leaf scars as on the long shoots (Plate V f). Specimen Z.399A.28(R) on the left joined to specimen Z.399A.29A on the right. ($\times < 0.5$)
- b. A leaf showing the broad sub-parallel median zone and margins turned under. Reversed venation can be seen on the upper left-hand margin where the upper surface of the leaf is destroyed. (Z.399A.28(R); $\times 1$)
- c. Two leaves with margins folded underneath and so giving the false impression of a long narrow form. Reversed venation can be seen on both margins of the left-hand leaf—where the upper leaf surface has been destroyed. The leaf on the right-hand side shows the median hollow caused by subsequent pressure on the folded leaf. (Z.392.8(R); $\times 1$)
- d. A number of leaves from part of the counterpart of (a). They can be seen best from the side. All exhibit the same features. Parts of three specimens joined. (Z.399A.29; Z.399A.28A; Z.399A.28B; $\times < 0.5$)

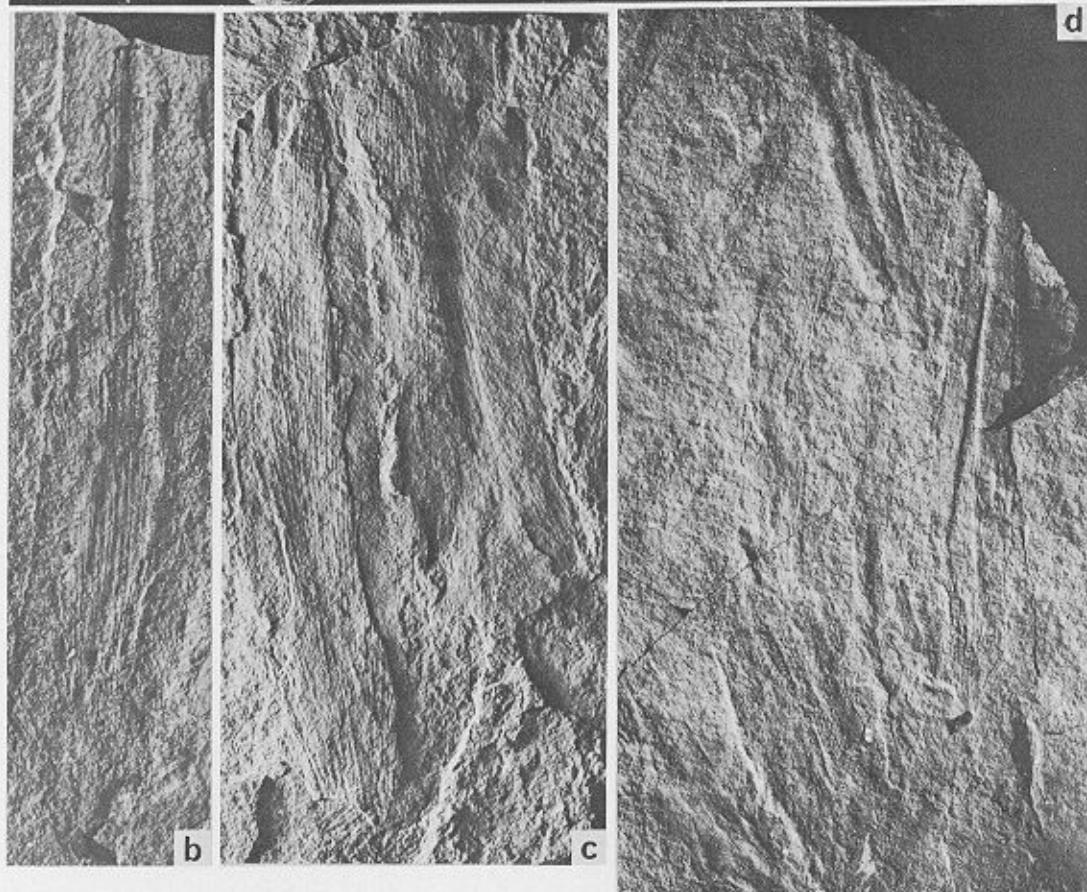
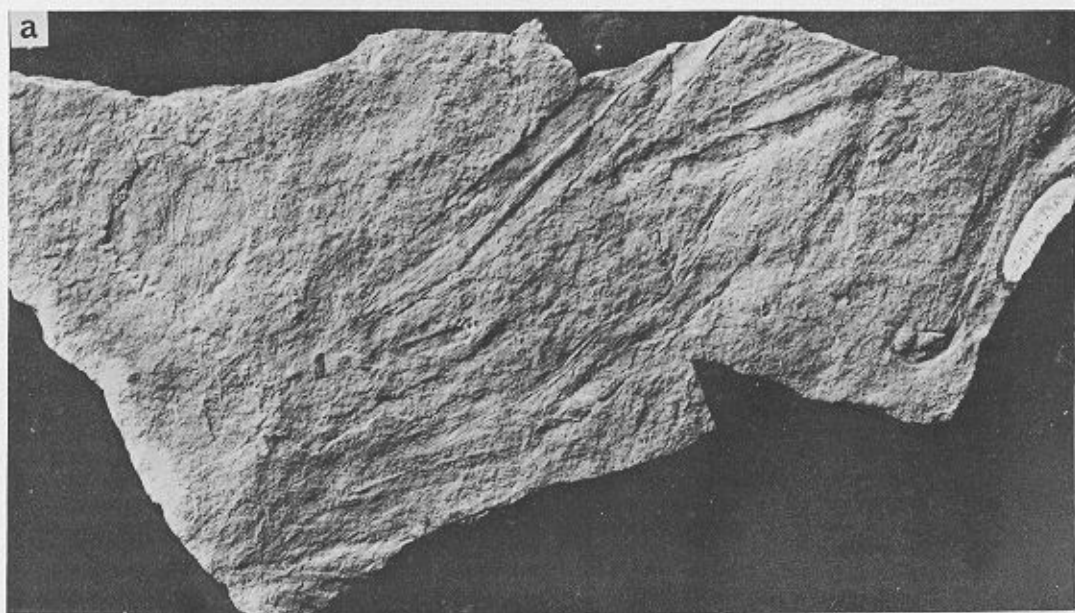


PLATE XIII

Euryphyllum (?) *antarcticum* sp. nov.

- a. A number of leaves which have not been folded but of which the thin textured lamina is bent and badly frayed, sometimes into single veins. Best viewed from the side. (Z.399A.22A; $\times 1$)
- b. Similar frayed leaves; anastomoses are extremely rare or absent in all leaves. (Z.399A.28(R); $\times 1$)

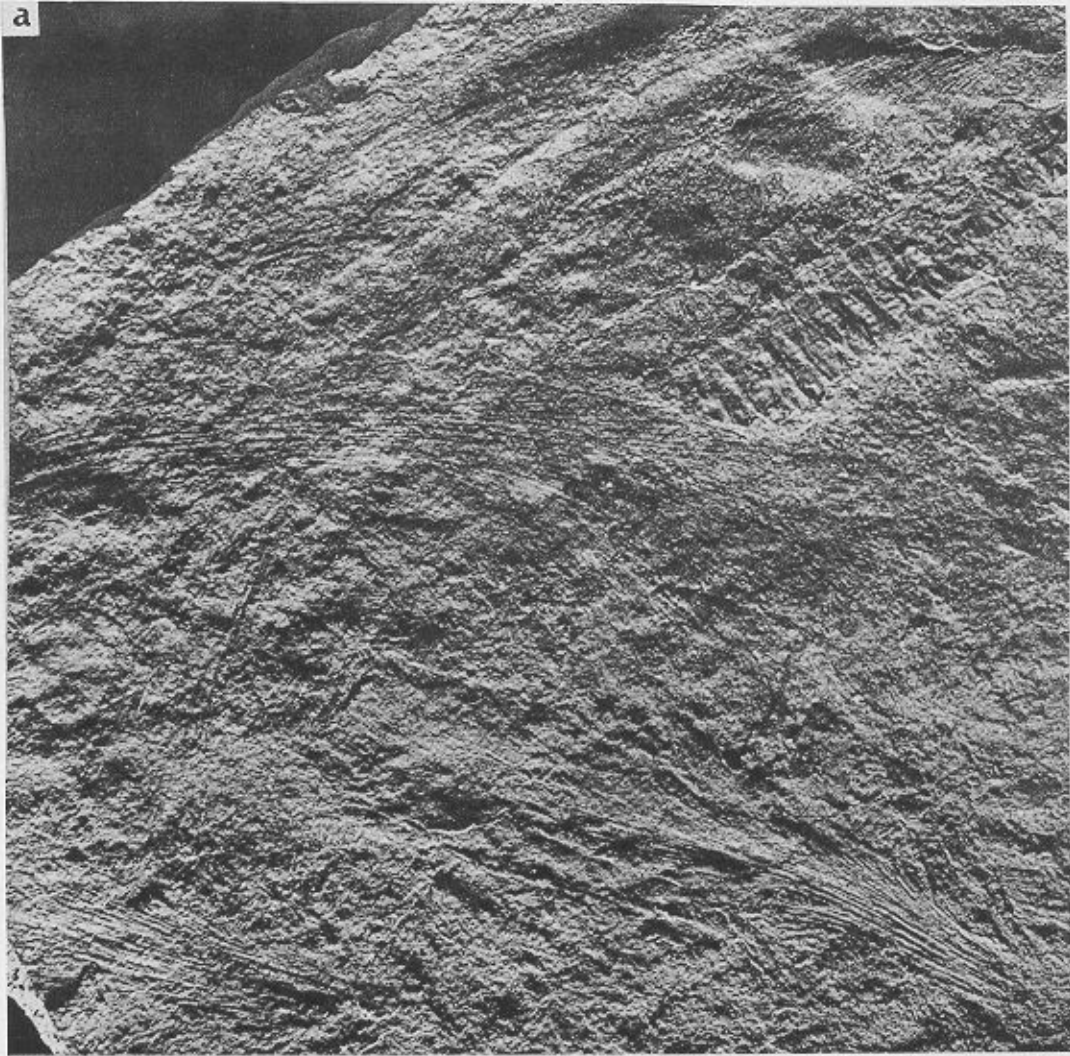


PLATE XIV

Isolated specimens.

- a. The hollow mould of a small coniferous shoot, on the right of the base of a very large *Gangamopteris* leaf of indeterminable species. (Z.399A.40; $\times 1$)
- b. Coniferous shoot as in (a) enlarged to show detail. (Z.399A.40; $\times 2$)
- c. *Euryphyllum* (?) sp. (Z.399A.22A(R); $\times 1$)
- d. *Euryphyllum* (?) sp. (Z.399A.22A(R); $\times 2$)
- e. *Noeggerathiopsis hislopi*. (Z.392.24; $\times 2$)
- f. *Noeggerathiopsis spathulata* (?). (Z.399.31A(R); $\times 1$)
- g. *Noeggerathiopsis spathulata* (?). (Z.399.31A(R); $\times 2$)
- h. cf. *Palaeovittaria*. (Z.392.5A; $\times 1$)

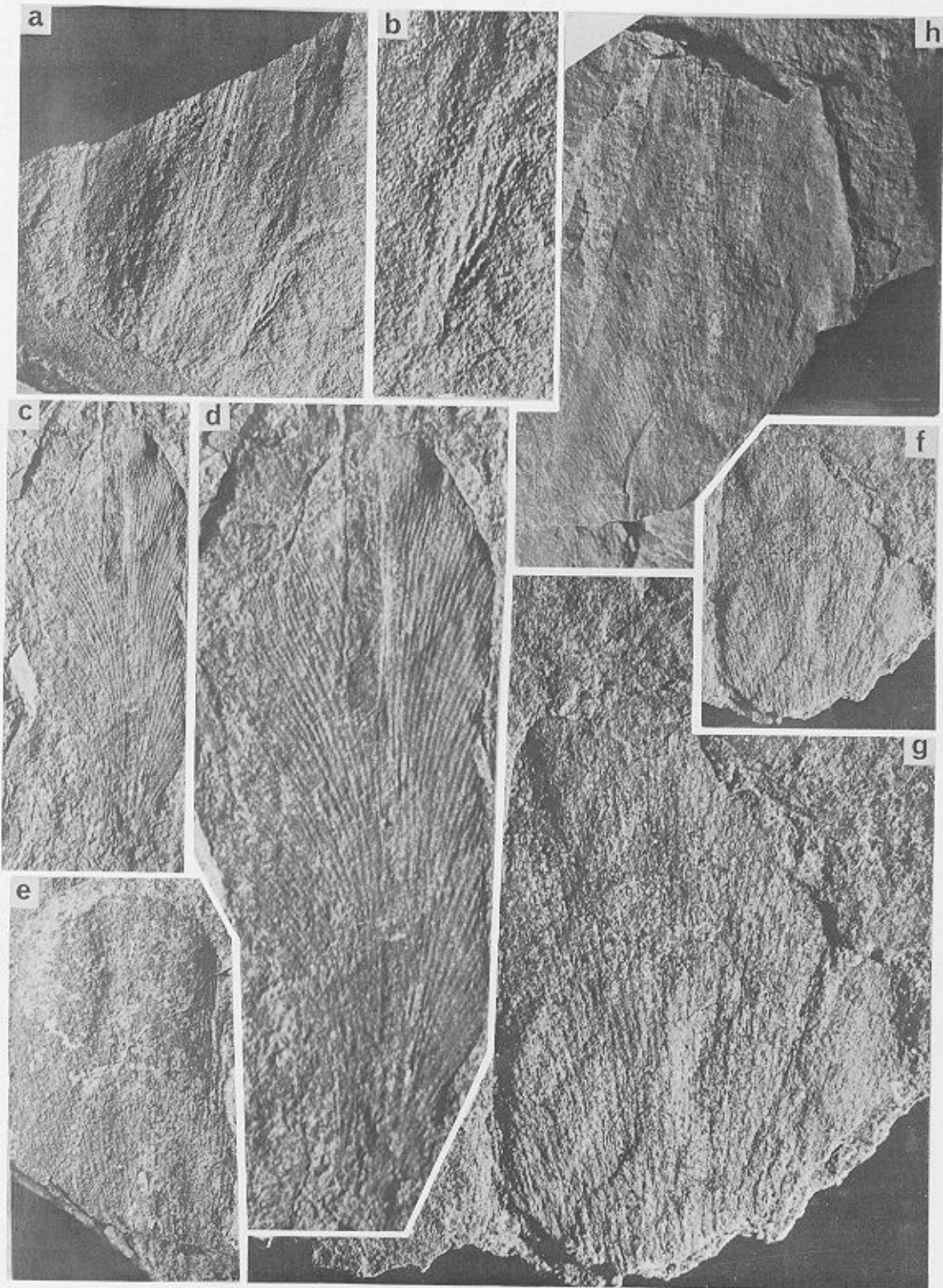


PLATE XV

Leaf impressions of several species in an "autumnal bank". Specimen Z.392.16(R) is the only good example from Milorgfjella of an autumnal collection of leaves which accumulated in a quiet pool at the end of a season. They reflect the mixed plant assemblage in the vicinity. ($\times 1$)

