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# ON *GANGAMOPTERIS WALKOMII* SP. NOV.

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Plates 25-27. Text Fig. 1

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## Abstract

*Gangamopteris walkomii* sp. nov. is erected to contain certain small *Gangamopteris*-like leaves from the Permian of New South Wales. These leaves grew spirally on long and short shoots, and were deciduous.

## Introduction

A large number of specimens bearing the proposed species were found at Duncan's Pass, Narrowneck, near Katoomba, New South Wales, by two collecting expeditions in 1949. Messrs H. O. Fletcher and R. O. Chalmers collected the specimens. From the way in which the specimens were grouped together, it is probable that all were derived from the same plant. The collection is now housed at the Australian Museum, Sydney, N.S.W. All specimens bear a registered fossil number of the Museum's collection.

## *Gangamopteris walkomii* sp. nov.

### DIAGNOSIS

Leaves, obovate, becoming elliptical then rhombic at maturity; apex obtuse to rounded; leaf base narrowing gradually to a short, thick petiole; margin entire; primary venation absent in the mature leaf, secondary venation dichotomously branching and anastomosing forming elongate reticulate meshes arising from a central region of strongly developed parallel veins, or a midrib in the developing leaf; venation strongly arcuate intersecting margin in the upper third at 90 degrees, varying to less than 30 degree near petiole. Leaves arising from a closely packed spiral as tufts along a stem of unknown identity; abscission apparently occurring before the number of leaves exceeded 12 or slightly more, although leaves grew from more than one point along the stem at any one time. No stem elongation occurring after expansion of leaves of short shoots. Short shoot branching from within axil of leaf on shoot of unlimited growth. Stomata absent from adaxial leaf surface.

*Type specimen*: Australian Museum, F43563, the leaf as designated in the caption to fig. 7.

*Paratype*: Australian Museum, F43564, designated to show the long and short shoots, and habit.

*Locality*: Duncan's Pass, Narrow Neck, near Katoomba, New South Wales.

*Horizon*: Lithgow Coal Measures, of Permian age.

*Specific name*: The species is named in honour of Dr A. B. Walkom, of Sydney, N.S.W., palaeobotanist, and one time director of the Australian Museum, Sydney.

## DESCRIPTION

*Habit*

A number of the specimens showed tufts of leaves attached to a branch, and in a few there was more than one tuft on a branch.

The leaves were spirally arranged, and fell leaving a small polygonal leaf scar. The average single twist of the spiral appeared to have 8 leaves. Later leaves were attached above earlier leaves where a greater number of leaves was visible. This happened commonly. The greatest number of leaves in any tuft was 12, on F43529 (fig. 2).

F43564 (fig. 8) shows a branch bearing leaves, and branching from it a small shoot bearing two tufts of leaves. The small shoot branched from within a leaf axil of the branch. Only 4 of the leaves that formed part of the leaf clump on the branch can be seen.

The medial tuft of leaves on the shoot has 5 leaves visible on the counterpart F43563 (fig. 16) and the terminal cluster has 8 leaves visible.

The shoot leaves the branch at an angle of 30 degrees, but this angle probably has been foreshortened by compression of the shoot on to the branch during burial. There is a decided bending of the shoot near the medial tuft. The longitudinal ribbing on the shoot has been distorted just below the medial tuft. This gives the impression that the shoot was straight during life. There is also a limited amount of distortion just above the medial tuft, here too, the shoot was probably straight during life. This shoot is considered to be comparable with the short shoot of a gymnosperm as there is no evidence of growth occurring at the terminal tuft.

Some stems lay across bedding planes. The stems were only ribbons of carbon when cut, e.g. specimen F43590 (not figured). There was a suggestion of a *Vertebraria*-like segmentation in these stems, e.g. the stem on F43563, reverse (fig. 16), where it is well developed, and in the largest stem of the collection F43529, reverse (fig. 20), where it is indistinct. Cross sections of stems appeared on specimen F43588, reverse (fig. 15), where they have been compressed to give stellate sections.

Leaves grew spirally along the short shoots. Specimen F43562 (fig. 9) shows that the leaves did not all grow in the same plane. This specimen shows a tuft compressed axially. The three petioles attached to cushions visible on the lower tuft of specimen F43568 (fig. 13) arose in a diagonal row typical of a closely adpressed spiral. The cushions show a spiral arrangement on specimen F43528 (fig. 17) and less clearly on the counterpart, F43529, obverse (fig. 2). Where leaf scars are visible, neighbouring attached leaves are generally elliptical.

The petiole expanded markedly just above the abscission layer into a rounded, almost triangular cushion. This shows best in the three lower petioles shown on fig. 13 (specimen F43568). There is no evidence to suggest any form of sheath, stipule or scale grew at the base of the leaf. Scars are absent from most stems, or if present are found only just below a tuft of leaves.

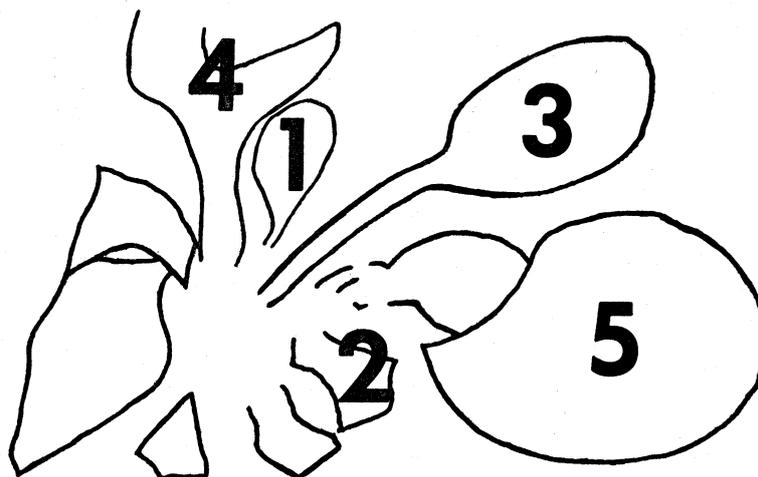
A single undifferentiated pit was obvious on most cushions. This was surrounded by a double row of small protuberances, 16 were counted on one cushion.

If abscission occurred after only a small number of leaves had expanded, then leaf fall would have occurred continuously throughout the growing season. It is possible that this specimen (i.e. the whole plant) was buried during the period of leaf fall. This may account for the tufted arrangement of leaves on shoots, but would not explain the number of young leaves present. I think that leaf fall must have continued throughout the growing season, although there might have been a time of the year when it was heavier.

The upper right hand spray on specimen F43529 (fig. 2) shows leaves arising at one per rib of the stem. This suggests that the ribbed stem is decorticated and represents a stele.

*Leaf*

It appears that leaves were at first erect, then after they expanded, they drooped. Text fig. 1 is a representation based on the tuft of leaves shown as fig. 17, and its counterpart, the lower left hand tuft of fig. 2. This will be used to illustrate leaf expansion.



Text Fig. 1

The series of leaves labelled 1 to 5 probably illustrates the normal mode of expansion. The term "leaf axis" is used to refer to the central portion of the leaf that would normally be occupied by a midrib, were one present.

The earliest stages of growth can only be postulated, that is from development in a primordium and initial expansion into a leaf. No evidence of this stage was found, such as a bud.

The size of the areoles formed by the secondary venation does not appear to differ markedly between the smallest and the largest of the leaves in the collection. Compare the areoles of the small leaves of specimens F43535 and F43587 (figs 6 and 11) with those of fully expanded leaves on the majority of figured specimens, e.g. F43562 (figs 4 and 5). The major difference between these two groups of leaves is that the smaller leaves appear to have a midrib, whereas the larger leaves have a series of stout parallel veins along the leaf axis.

The parallel central veins that form the leaf axis dichotomise, but do not anastomose. There are up to 7 of these veins across the width of a petiole. The divergent venation develops from the dichotomies of the axial venation. It is arched towards the margin. It dichotomises and anastomoses frequently. There is little or no decrease in width of areoles between the central and marginal portions of the leaf. The length of an areole may decrease by up to half over the same distance.

The following mode of expansion of the leaves is probable. Elongation of a primordial leaf into a thin, strap-like organ with an expanded head, possibly resembling a very small spoon. Lateral expansion of the strap-like organ into a leaf blade started near the expanded head, then extended downwards towards the attachment. The developing leaf continued to increase in length until approximately half of the total length of the leaf had expanded laterally. Thereafter, increase in length was slight, but lateral expansion continued downwards until only a short length of petiole remained. This was noticed in a number of tufts, but is illustrated best by the tuft shown as text fig. 1. As expansion continued, the tissue between the ribbing of the

midrib itself expanded so that the midrib dissolved into a series of strongly developed secondary veins that lay along the leaf axis. The *Glossopteris* juvenile leaf thus became a *Gangamopteris*.

The final stage in expansion appeared to be the development of a rhombic outline. This seemed to be most common in drooping leaves—leaves that no longer had the support of a coherent midrib. The lowermost leaf visible on fig. 16 is a leaf that was developing the rhombic outline. The leaves figured on the upper part of fig. 7, including the type specimen, its counterpart, fig. 5, and on figs. 1 and 4 have a well developed rhombic outline.

The leaf shown at the left of fig. 12 (specimen F43531) is unusual, it was the only oblong leaf found. In this specimen the leaves of the upper tuft had fallen, but the stem had not become decorticated as scars are visible between the upper and lower tufts.

TABLE I  
Dimensions in Millimetres of Leaves Designated in Text Fig. 1

	Leaf Number				
	1	2	3	4	5
Length of leaf .. .. .	7	?	14	16	21
Width of half leaf .. .. .	2.7	2.4	5.0	7.0	8.5
Length of petiole .. .. .	5	4	11	6	5 est.
Width of petiole .. .. .	0.8	1.0	1.4	2.0	1.9
Veins per 2 mm at margin half way along leaf .. .. .	9	7	9	7	6

Some organs described and illustrated occasionally in the literature probably represented juvenile leaves for the mode of expansion suggested, e.g. Johnston (1888) plate VIII, figs 10-14. Johnston described his specimens as "Impressions of young fronds resembling *Gangamopteris obliqua*; probably the rudimentary leaves of *Gangamopteris spatulata*."

The resemblance of fig. 10 of Johnston to *Nephropsis tomiensis* Zalessky and his figs 13 and 14 to *Nephropsis elongata* Neuburg is striking. An observational difference between the above leaves and *Glossopteris* scale leaves on one hand and *Nephropsis* on the other, is also found in a comparison of *Glossopteris* and *Gangamopteris* with *Pursongia* and *Zamiopteris*. This is that the veins in anastomoses fuse in the Gondwana genera, but do not in the Angara genera.

Halle (1911) illustrated "an unusual form of *Gangamopteris*, or perhaps, rather a scale frond of a *Glossopteris*" (plate 8, fig. 10) that could be a juvenile leaf undergoing expansion into a normal *Gangamopteris* leaf. It appears to resemble *Nephropsis*. Many other scale leaves of *Glossopteris* resemble *Nephropsis cordata* Radczenko. This similarity between these *Nephropsis* species (a cordaitalean leaf) and juvenile or apparently juvenile forms of *Gangamopteris* and *Glossopteris* appears remarkable, particularly as some of the wood associated with occurrences of Lower Gondwana floras is of a cordaitalean type. This might tend to further support the idea of a parallel development of floras in Gondwanaland and Angaraland, as suggested by Neuburg (1954), rather than connection between the two areas.

The taeniopteroid leaf fragments shown on fig. 10 occurred commonly throughout the collection. As only fragments were seen, no attempt at identification was made.

### Microstructures

Although many leaves had what appeared to be original coaly leaf material present, no cuticle could be recovered. Under reflected light very few leaves showed signs of microstructure (fig. 19).

Leaves of the lower whorl of specimen F43568 (fig. 13) and of specimen F43528 (fig. 17) showed cuticular structure of the upper epidermis. In both the cell pattern formed elongate-polygonal cells elongated along the direction of the venation. Cells along veins were more elongate than those between veins. Stomata appeared to be absent. Cell walls appeared to be straight.

Average dimensions of cells are 25-40 $\mu$  long by 12-20 $\mu$  wide along veins and 25-60 $\mu$  long by 25-40 $\mu$  wide between veins.

A number of specimens has tracheids visible within the veins. All such leaves appeared to be exposing the ventral surface. Specimen F43586 (leaf, top left of fig. 14, and enlarged in fig. 18) showed bundles of tracheids dividing and recombining with bundles of tracheids from adjacent veins at anastomoses. When tracheid bundles combined, the separate identity of the joining veins becomes completely lost. Tracheids appeared to be less than 10 $\mu$  wide, and some in excess of 200 $\mu$  long. Preservation precluded determination of the type of thickening present, or of the presence of pits. No cell structure was visible in interveinal regions.

### Comparison

In a comparison with other species, it seems that *Gangampteris walkomii* may be compared with other species of *Gangampteris* in adult leaves only. For the comparison to be complete, the juvenile leaves must be compared with *Glossopteris* leaves. The habit must be considered separately too.

### Adult leaves

The frequent anastomoses of the venation and the rhombic leaf shape separates *Gangampteris walkomii* from all other species of *Gangampteris*.

### Juvenile leaves

The small ovate leaves have a venation pattern similar to that of *Gangampteris castellanosii* Archangelsky in disposition, but the Australian leaves are very much smaller, and have an apparent midrib. The leaves are similar in shape, and only slightly smaller than figured leaves of *Glossopteris orbicularis* White. In *Gangampteris walkomii* the venation arches outwards similar to the arching of the secondary venation in *Glossopteris browniana*, but in *Glossopteris orbicularis* it arches upwards towards the apex.

### Microstructure

Insufficient is known to give any valid separation from other species.

### Habit

The leaves are arranged into tightly adpressed spirals. This seems to be characteristic of many *Glossopteris* and *Gangampteris* species. Pant (1962) has recorded all previously reported attached specimens. The nature of the scars on the specimen described by Etheridge (1894) is very much broader compared with length than the scar in specimens of this collection. The specimen of Etheridge has deteriorated somewhat apparently because of dehydration, so only the scars shown by his pl. XVIII fig. 2 are still readily discernable. *Gangampteris walkomii* has elliptical to rhombic leaves and lacks a midrib whereas the specimen of Etheridge (1894) along with others listed by Pant (1962) are lanceolate and have a midrib.

Plumstead (1959) discussed the habit of various glossopterids. Some of her postulates require review because of the evidence of habit shown by *Gangampteris walkomii*. These are dealt with under the same headings as she used.

*Evidence of habit from leaves*

- (a) Banks of fossilized leaves; and
- (b) The evidence . . . concerning the mixed sizes of leaves.

Most clusters of leaves of *Gangamopteris walkomii* showed a mixture of leaves of different sizes growing together. Although leaves frequently were shed in clusters, these clusters were not broken during transport or burial under the prevailing conditions at Narrownneck. Plumstead suggested leaves might be shed in clusters and, during burial, the clusters broken or intermingled with many other clusters to form into matted bands. No bank of leaves occurred associated with this species, but it has been recognized only at this locality.

- (c) New evidence of attached leaf clusters.

This is yet another species that had spirally arranged leaves that formed tufts or clusters.

- (d) Suggested reasons for the paucity of evidence of *Glossopteris* in a position of growth.

*Gangamopteris walkomii* leaves and clusters were small enough to be readily recognizable in clusters on small slabs of rock, whereas most other glossopterid leaves were sufficiently big for clusters to be broken when the rock was split.

- (e) Reconstruction of the leaf growth habit.

In common with other recorded clusters, leaves varied in size. This was to be expected when leaves expanded in succession along the shoot.

No fructifications were found associated with any of the leaves. There is no evidence where on a shoot the fructification may have developed, or whether it developed on a special fertile shoot.

Plumstead suggested that "clusters were normally shed as a whole, leaving probably a single large oval, or pear-shaped scar, and that in many cases the leaves remained together until they were buried." This is not so in *Gangamopteris walkomii* where leaves appeared to have been shed singly (figs 12 and 13). It would appear that were clusters shed as a whole, each cluster would represent a short shoot. In this species a terminal cluster would have to be shed, but not a short shoot, to give rise to fossil leaf clusters. The wood would have to be brittle and break at points of leaf growth, otherwise specimens such as shown on figs 1, 2, 6, 7, 8, 12, 13, and 16 would be common in many species. If the wood in this species had been sufficiently brittle to shed only terminal tufts, then preservation of specimens such as F43564 (fig. 8) would not be likely. It is possible that *Gangamopteris walkomii* had an unusually long short shoot. In other species tufts of leaves occur only in the form shown by *Gangamopteris walkomii* on fig. 9.

She then discussed the role of the scale leaf. There is no evidence here to suggest or favour any particular function of these organs, as scales were not found attached to shoots of *Gangamopteris walkomii*. She was apparently unaware of the shoots figured by Walkom (1928) showing scales attached in a position of growth (figs 1 and 2). From the spacing of the scales along the stem his shoots could not have been associated with vegetative shoots of *Gangamopteris walkomii*. His shoots bore *Nephropsis*-like scales.

The specimen of *Glossopteris* ? *angustifolia* shown as fig. 3 is from Thornley, N.S.W. These leaves are arranged in a tuft similar to *Gangamopteris walkomii* and the specimen figured by Etheridge (1894). He described his specimen as "undoubtedly comes near to *G. linearis*, McCoy, in a general habit of the leaves, and *G. Clarkei*, Feist., in the venation." It was found in the Permian outcrop near Cooyal (determined from Etheridge, 1904). Hence three species of glossopterid leaves were borne spirally on branches, besides the curious specimen described as *Glossopteris browniana* by Dana (1849; pl. 12, fig. 13c).

#### ACKNOWLEDGMENTS

Thanks are due to the former Director of the Australian Museum, Sydney, Dr. J. W. Evans, for permission to borrow and describe this collection; and to the former Deputy Director, Mr H. O. Fletcher, for arranging this permission, and for information concerning the locality and other pertinent matters. The examination was carried out in the laboratories of the Department of Geology, University of Newcastle, N.S.W.

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## LEGEND

**Gangamopteris walkomii** sp. nov.

All specimens are held by the Australian Museum, Sydney, N.S.W. All figures are approximately natural size, unless otherwise noted.

## PLATE 25

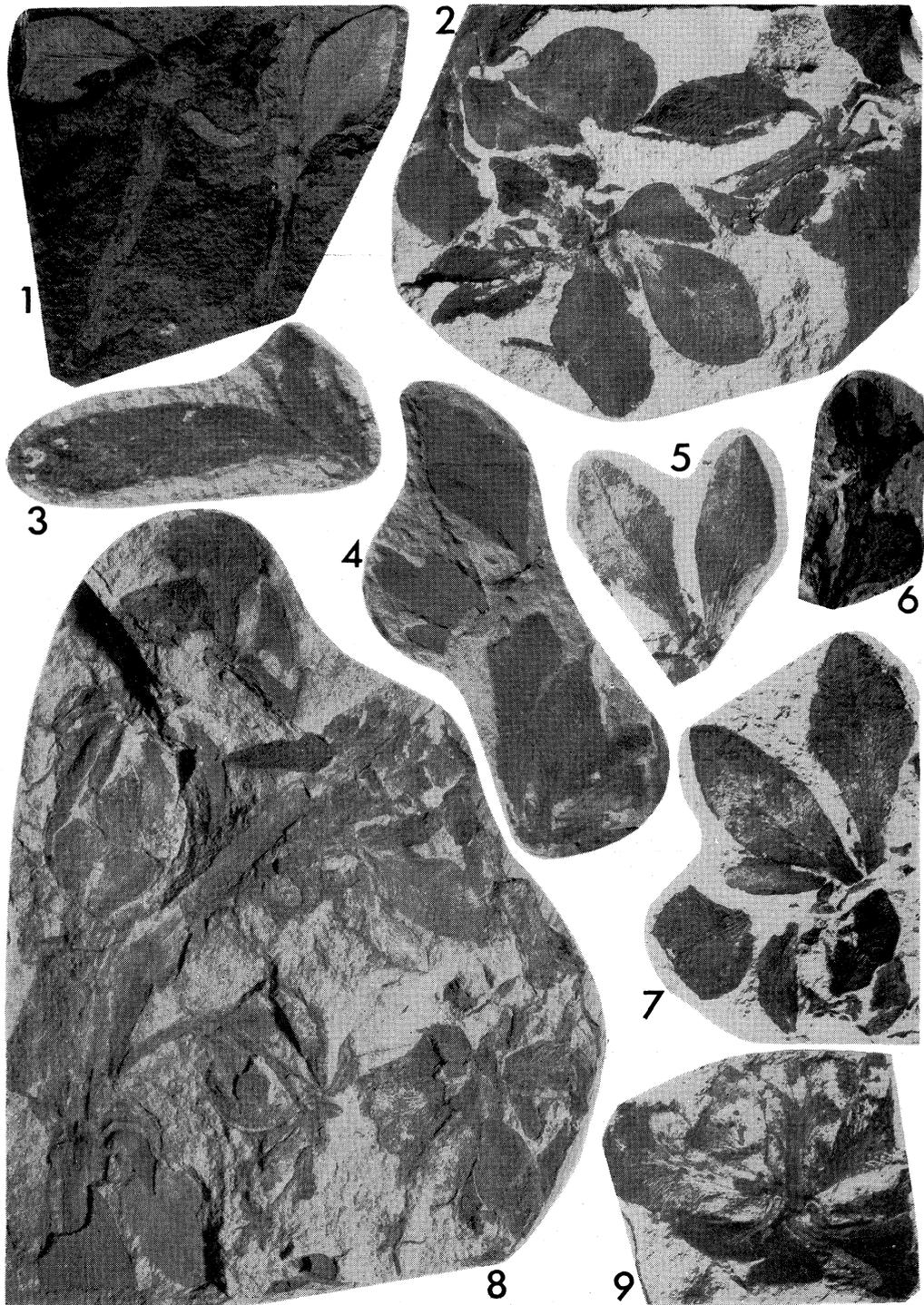
- Fig. 1—Two shoots showing terminal groups of leaves. Specimen F43535.
- Fig. 2—A number of groups of leaves showing how the closely addressed phyllotaxy gives a verticillate appearance. The leaves have fallen from the branch in the upper right without leaving scars or cushions, but only a longitudinally striated stem. Specimen F43529 (obverse) (counterpart, enlarged, is shown as fig. 17).
- Fig. 3—*Glossopteris*? *angustifolia* Brongniart. Leaves showing probable similar arrangement to *Gangamopteris walkomii*. Specimen from unregistered collection 582, Mining Museum, Sydney, N.S.W. Enlarged  $\times 1\frac{1}{4}$ .
- Fig. 4—Leaves, some isolated. The uppermost leaf still shows a midrib although it has developed a rhombic shape. Specimen F43562 (reverse).
- Fig. 5—Counterpart of the type specimen is shown on the left. Specimen F43562 (see also fig. 9) (counterpart to fig. 7).
- Fig. 6—Juvenile leaves, broadly elliptical to almost circular, with a distinct midrib. Specimen F43535.
- Fig. 7—Type specimen. The leaf vertically placed nearest to fig. 6 has been selected. Midrib has expanded into a series of coarse longitudinal veins. Other leaves of this specimen also show the longitudinal veins. Specimen F43563 (obverse) (counterpart to fig. 5).
- Fig. 8—Paratype showing long and short shoots. The short shoot (lower centre) arose within a leaf axil of the long shoot. Leaves at the base of the short shoot droop backwards along the stem. Specimen F43564 (counterpart to fig. 16).
- Fig. 9—Leaf cluster showing that leaves did not arise in a verticil, but in a closely addressed spiral. Specimen F43562 (see also fig. 5).

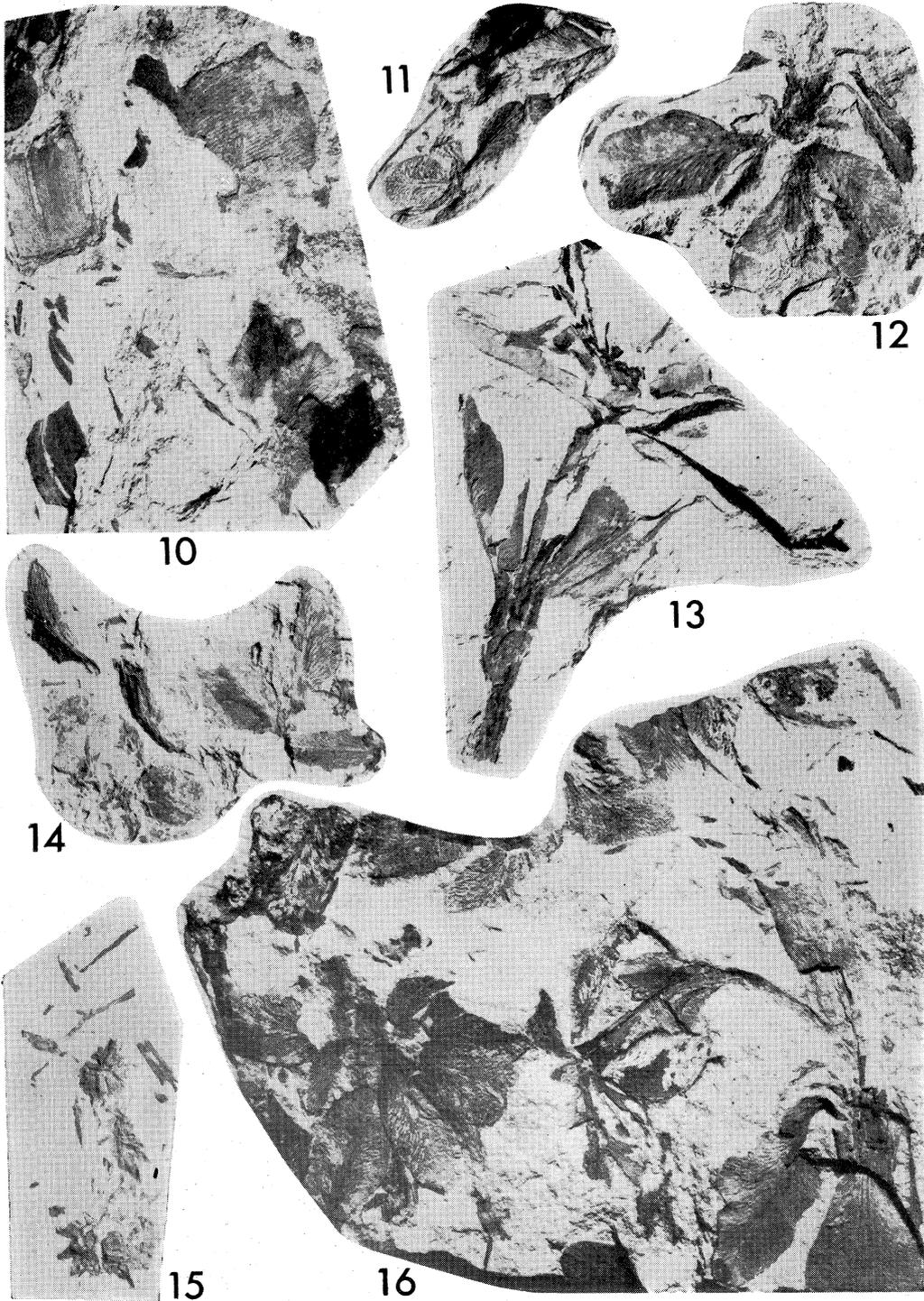
## PLATE 26

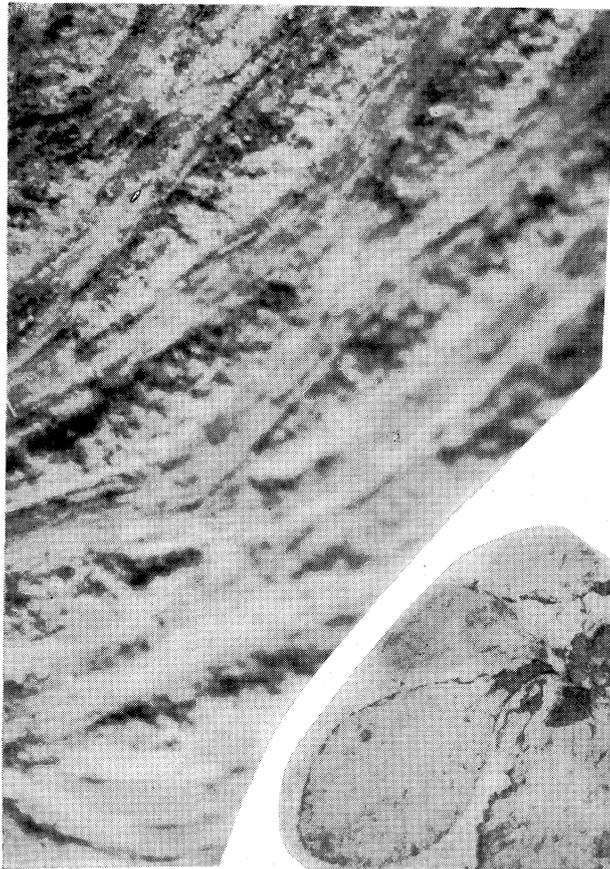
- Fig. 10—Juvenile leaves and leaf fragments. The taeniopteroid fragments are common in the collection. Specimen F43584.
- Fig. 11—Distorted juvenile leaves. The nature of the anastomosis of the secondary venation shows most clearly in the lowest leaf. Specimen F43587.
- Fig. 12—Stem showing closely grouped, spirally arranged leaf cushions. The shape of the left hand leaf is unusual. Specimen F43531.
- Fig. 13—Broadly expanded leaf bases are shown attached to the stem. The position of the abscission layer appears as a notch. Although these leaves are not small, they still appear to be stem clasping. The upper structure at right angles to the stem is a whorl that was damaged during splitting. Specimen F43568.
- Fig. 14—Juvenile leaf fragments that have venation anastomosis of identical dimensions to that of adult leaves. Specimen F43586 (part of leaf at top left has been enlarged as fig. 18).
- Fig. 15—Cross sections of stems. Specimen F43588 (reverse).
- Fig. 16—Long and short shoots. The short shoot has been slightly bent below the lower leaf tuft. The stem of the short shoot is longitudinally ribbed. No leaf scars are visible. Specimen F43563 (reverse) (counterpart to paratype, fig. 7).

## PLATE 27

- Fig. 17—Tuft of leaves showing cushions left when leaves have fallen. Enlargement  $\times 1\frac{1}{4}$  of specimen F43528 (counterpart to fig. 2).
- Fig. 18—Leaf surface, assumed dorsal, enlarged to show tracheids of veins. Enlargement  $\times 16$  of specimen F43586 (leaf shown natural size as fig. 14).
- Fig. 19—Ventral surface of leaf enlarged  $\times 25$  to show outline of cells. No stomata appear present. Specimen F43528.
- Fig. 20—Stem fragment. Specimen F43529 (reverse).



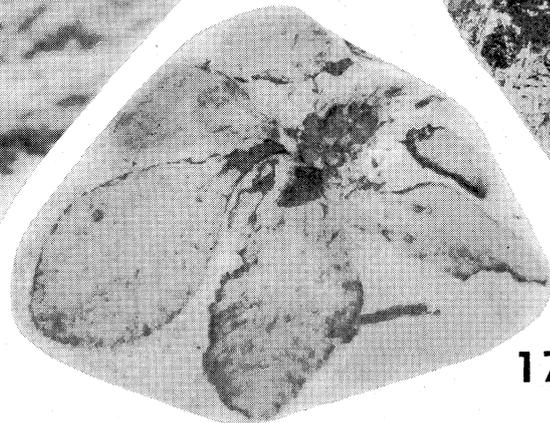




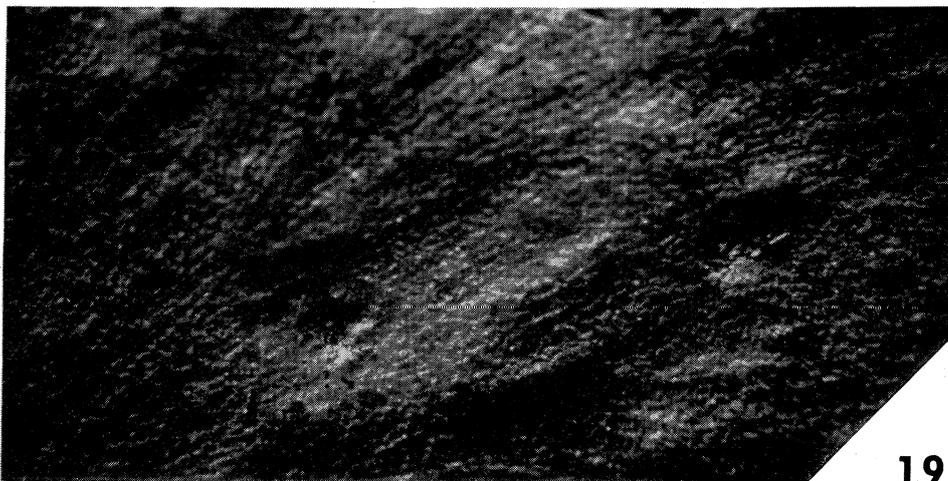
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