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REPRODUCTIVE STRUCTURES OF THE GLOSSOPTERIDALES IN THE PLANT FOSSIL COLLECTION OF THE AUSTRALIAN MUSEUM

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SUMMARY

A new, Late Permian *Glossopteris* fructification genus *Squamella* is erected. It comprises cones (the 'terminal buds' of Walkom, 1928) which are aggregations of 'scale-fronds' bearing sporangia or seeds. The cones are borne terminally on branchlets which had foliage leaves in whorls or close spiral arrangement, and modified, gangamopteroid leaves preceded the cones. Scale-fronds were composed of a deciduous scale (the 'squamae' of *Glossopteris* assemblages) and a laminal segment. Fructifications were attached to the scale-fronds at the line of junction of scale and lamina. Three new species of the genus are described: *Squamella australis*, which is the male cone of *Glossopteris linearis* McCoy and is known in attachment to a leaf whorl of that species; *Squamella ampla*, which is referred to *Glossopteris ampla* Dana; and *Squamella ovulifera*, which is a female cone whose foliage is unknown. "*Lidgettonia australis* White 1964" is redescribed and emended and is incorporated in *Squamella australis*.

The description of *Glossopteris linearis* McCoy is amplified, on vegetative, reproductive and internal anatomical evidence.

Two new species of *Partha* are described, as well as examples of *Eretmonia*, *Rusangea* and *Lidgettonia*.

Multiovulate fructifications referable to *Dictyopteridium*, *Scutum*, and *Plumsteadia* (*Cistella*) are included, and a controversial fructification which may be referable to *Vannus*. Some specimens of *Rigbya arberioides* which might possibly be glossopteridalean are illustrated.

Part 1: Review of '*LIDGETTONIA AUSTRALIS* White' and formation of *SQUAMELLA* GEN NOV.

In 1964 (White, 1964) a series of progressively modified leaves, believed to be referable to *Glossopteris angustifolia* Bgt. was described, culminating in fertile 'scale-fronds' which bore fructifications at the line of junction of scale and lamina. The series and the fertile scale-fronds were named *Lidgettonia australis* as there was insufficient evidence available from the limited number of specimens from the Bowen Basin, Queensland, to create a new genus. The genus *Lidgettonia* Thomas 1958 was, at that time, the only glossopteridalean fructification which involved a modified small leaf.

Recently a great deal of research has been done in India (summarised by Surange and Chandra, 1975) and in Africa (summarised by Lacey et al., 1975) and a number of genera have been described in which reproductive structures are borne on small, modified leaves or scales.

In the Plant Fossil Collection of the Australian Museum are many fructifications referable to most *Glossopterid* reproductive structure genera so far described, and in addition, much material of '*Lidgettonia australis*'. The information is unusually complete and it is possible to describe the reproductive structures in detail, to show them attached

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Records of The Australian Museum, 1978, Vol. 31, No. 12, 473-505, Figures 1-68

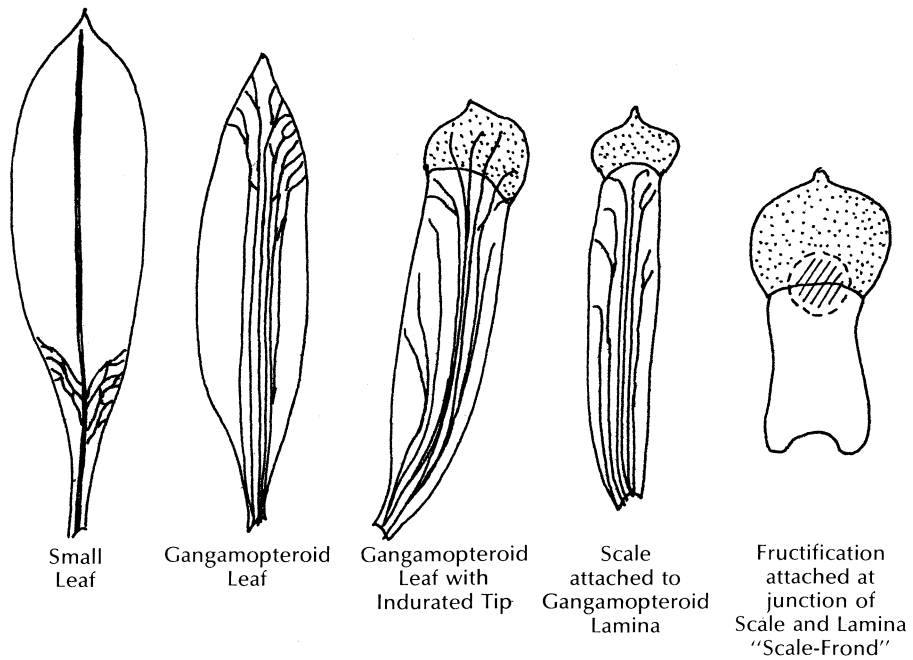


Fig. 1. Diagrammatic representation of "*Lidgettonia australis*." Progressive modification from small leaves; to gangamopteroid small leaves; to gangamopteroid leaves with indurated tips which become squamous; to scale-fronds. Scale-fronds have a gangamopteroid laminal segment and attached squama and the fructification is attached at the junction of scale and lamina.

to the plant, and to investigate the stem structure of a branchlet bearing the same leaves as those associated with the fertile phase. It is necessary to erect a new genus and to incorporate *Lidgettonia australis* in it.

The progressive modification from small leaves to scale-fronds as described by White, 1964, is shown to be valid. Whereas *Lidgettonia*, *Partha*, *Denkania* and *Glossotheca* have a modified, gangamopteroid leaf bearing cupules or sporangia on forking pedicels, and *Eretmonia* bears similar forked pedicels on the petiole of its intermediate-type scale like, modified leaf, the new genus here described has distinct differences. The concave scales are deciduous and as fossils normally occur detached. The texture of the scales was presumably papery or woody. Sporangial clusters were made from an aggregation of forking 'threads' of sporangia attached along the line of junction of the scale and lamina.

Scale-fronds are aggregated into cones which are borne at the ends of foliage-bearing branchlets with leaves in whorled or close-spiral formation. Modified small, gangamopteroid leaves precede the cone structures.

Because the scales associated with the reproductive structures are squamae and not leaf-like, the name *Squamella* is given to the genus. In the Australian Museum Collection, material of *Squamella australis* occurs at many localities in Late Permian strata, always associated with a *Glossopteris* with long, narrow leaves, and in one specimen attached to a stem bearing leaves of this type. The Bowen Basin material (White, 1964) was described as being the fertile phase of *Glossopteris angustifolia* Bgt. As determination of similar leaves is still unsatisfactory on gross morphology, a problem arises in naming the vegetative leaves of the specimens under discussion. A specimen in which a whorl of leaves is attached to a stem whose internal structure was preserved was referred to *Glossopteris linearis* McCoy 1874 by Etheridge (1894). *Squamella australis* is referred to *Glossopteris linearis* so as not to imply that all the many leaves referred to *Glossopteris angustifolia* are from plants whose reproductive phase was *S. australis*.

Type material of "*Lidgettonia australis* White" was kindly lent by the Bureau of Mineral Resources, Canberra, for re-examination. Figures 10-13 illustrate specimens which now become paratypes for *Squamella australis*. In accordance with the procedure laid down in "Principles of Palaeontology" (Raup & Stanley, 1971) a holotype, the most complete specimen, and a series of paratypes is used to express the concept of the species, and to show the elements of the composite structures involved.

An understanding of *Squamella australis* has led to the identification of *Squamella ampla*, which is described in (b) of Part 1 below and is illustrated in Figures 27-31. It is believed to be the cone structure of *Glossopteris ampla* Dana whose very large leaves are in keeping with the size of the cone and its component parts.

Genus **Squamella** gen. nov.

Type species *Squamella australis* (White)

Syn. *Lidgettonia australis* White 1964

DIAGNOSIS: Reproductive structure genus of *Glossopteris*.

Cones formed by aggregation of squamous scale-fronds, each composed of a scale and a laminal segment, and each bearing a reproductive structure at the line of junction of scale and lamina. The "terminal buds" of Walkom, 1928, are complete *Squamella* cones. The scale-fronds of *Lidgettonia australis* White 1964 are incorporated in *Squamella*. There are small, gangamopteroid, sterile leaves associated with the cones,

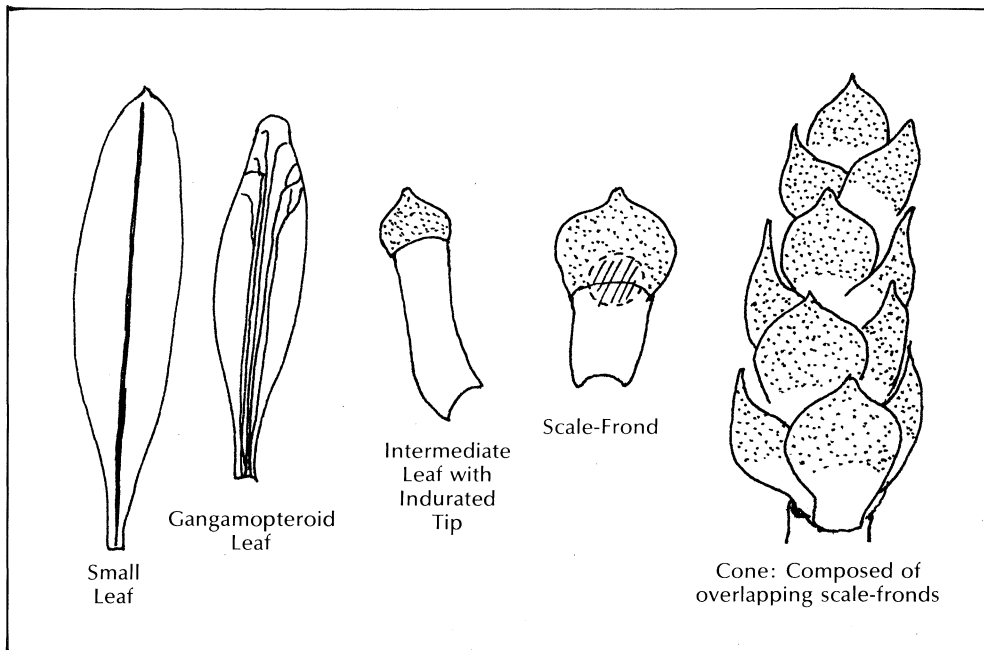


Fig. 2. Diagrammatic Representation of *Squamella australis*. Progressive modification from small leaf; to gangamopteroid small leaf; to gangamopteroid lamina with squamous tip; to scale-frond consisting of squama and laminal segment with fructification attached at junction of lamina and scale; the scale fronds are aggregated into cones.

and some of these show serial modification towards scale-fronds with induration of tips. Squamae are deciduous and are mostly fossilised separately from the laminal segments, sporangial clusters, and residual cores. The cones were borne at the ends of branchlets which had leaves in whorls or close spirals. Modified leaves formed a whorl between the cone and the foliage leaves. There is evidence that ripening of the cones and shedding of the sporangia was achieved by elongation of the laminal sections of scale-fronds.

In *S. australis* the reproductive structures are male sporangia of *Arberiella* type (Pant & Nautiyal, 1960). In *S. ampla* they are assumed to be male. A specimen described as *S. ovulifera* is described in (c) below. It bears stalked seeds at junction of scale and lamina.

***Squamella australis* (White)**

DIAGNOSIS: Cones composed of scale-fronds in which the scales are pointed, pear-shaped, often deeply concave. The complete cone measures 6 cm. long, is widest at the base, maximum width 2 cm, and tapers to an acute apex. Scales overlap in close spiral arrangement, three to each slightly oblique whorl. Laminal segments were as long as, or shorter than, the scale. Sporangial clusters contained more than fifty sporangia.

At the base of the cone, gangamopteroid small leaves and small leaves modified to the extent that they had an indurated tip (intermediate between scale-fronds and gangamopteroid leaves) formed a whorl or whorls. Foliage leaves with characteristic form and appearance of *Glossopteris linearis* McCoy formed a whorl below these.

DESCRIPTION OF SPECIMENS: Holotype F 57342, 57341. (F 57343 counterpart of lower portion of F 57342).

On specimen F 57342 (Figure 3) is a whorl of leaves of *Glossopteris linearis* McCoy. In the centre of the whorl is a *Squamella australis* scale in situ (A). This represents the base of a cone. The cone has been broken up into its component parts. Scale-fronds and sporangial masses lie near the leaf whorl (C) associated with gangamopteroid small leaves (B), and forming a dense aggregation on the lower part of the specimen (D). Figure 4 shows an enlargement of the centre of the leaf whorl on the counterpart F 57341.

Paratypes F 57655, 57316, 57645, 57625, 57626, 57659, 57315, 43706, 57667, 46445, 25729, 44461, 43659, 14948. B.M.R. CPC 4369, 4366, 4375, 4363 M.M.F. 18918, 17100.

Specimens F 57655, F 57316 and F 57645, Figures 5, 6, and 7 show aggregations of scales, sporangial masses and gangamopteroid leaves from broken up cones. In Figure 7 an *Eretmonia* type gangamopteroid leaf lies next to squamae and sporangia (A). It is probably a modification form referable to *S. australis*, intermediate between the squamous scale-fronds of the cone and the gangamopteroid leaves. Laminal segments of scale-fronds are elongated in Figure 5. The implication is that in young cones (as seen in Figures 8 and 9) the cone was compact with scale-fronds with short laminal segments closely overlapping and concealing and protecting the sporangia. In a ripening cone, elongation of the laminal segments allowed the sporangia to hang out. The scales would have been deciduous when the spores were ready to disperse and protection was no longer necessary.

Figures 8 and 9 illustrate specimen F 57625 and counterpart 57626. A segment of bore core from the Elecom Wyong DDH 6 Bore was presented by the Joint Coal Board in 1966. When it was split in 1975 the specimen was revealed. It represents a young cone broken up into its component parts of scale-fronds with short, wide laminal segments and large sporangial clusters containing very numerous sporangia. The squamae are deeply

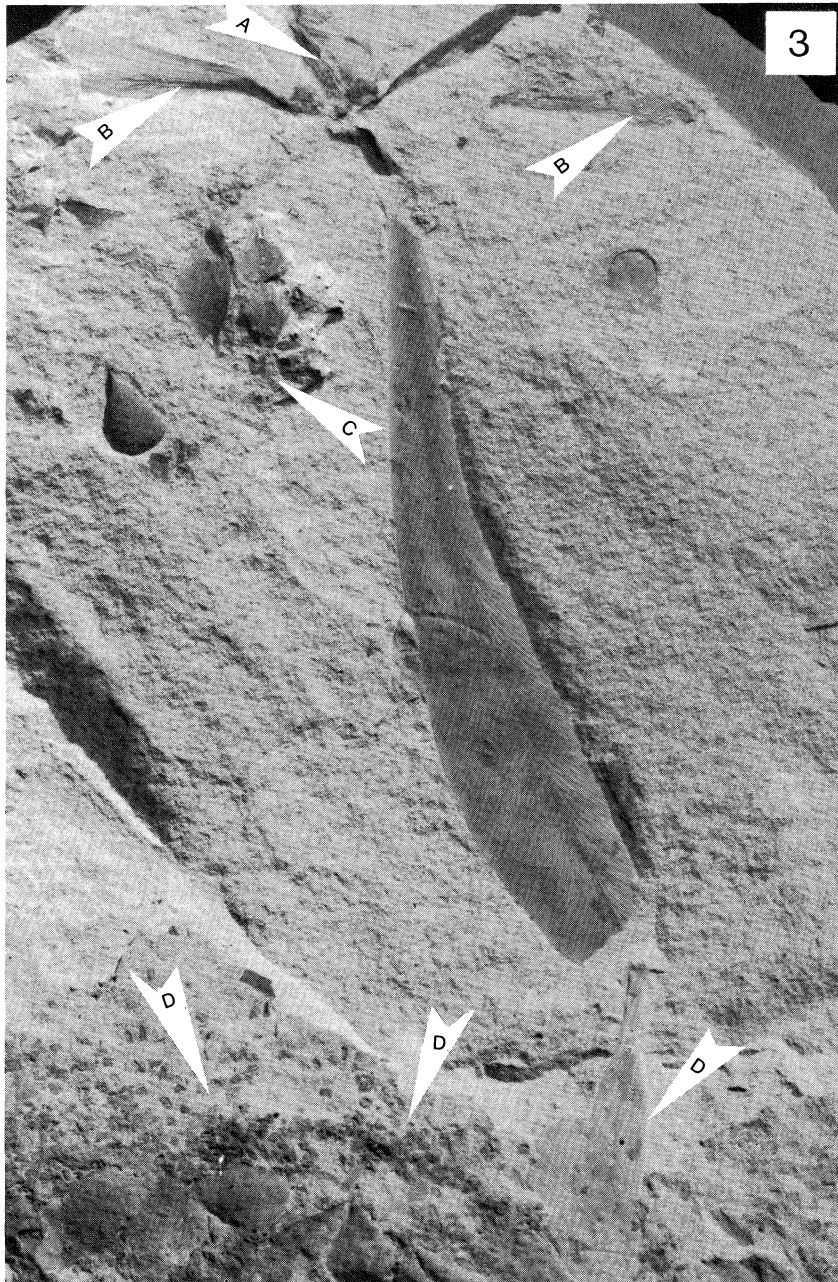


Fig. 3. *Squamella australis* (White). Specimen F 57341. Magn. X 1.3. Whorl of leaves of *Glossopteris linearis* McCoy with *Squamella australis* scale-frond at centre (A); gangamopteroid leaves (B); scale-fronds and sporangia from broken cone near whorl (C); and mass of scale-fronds, sporangial clusters and gangamopteroid leaves from broken cone forming dense deposit on lower portion of specimen (D).

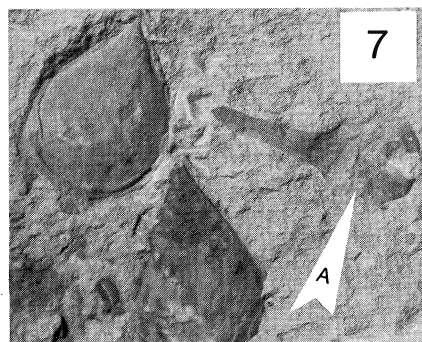
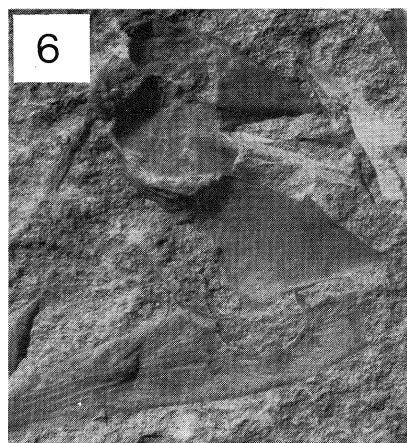
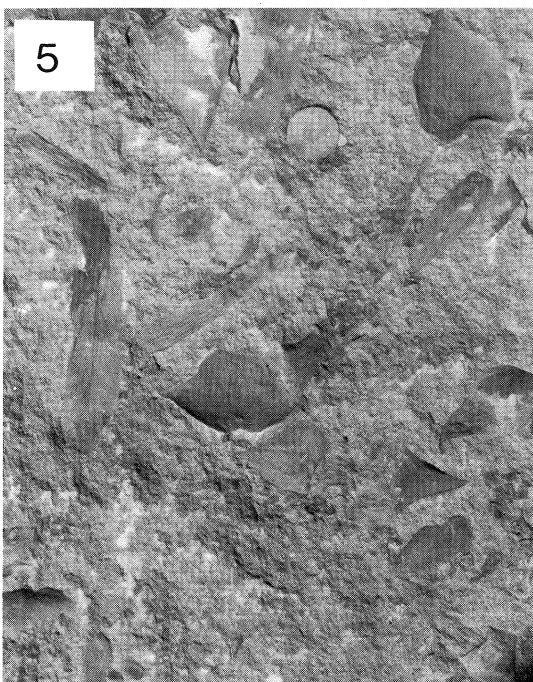


Fig. 4. *Squamella australis* (White). Specimen F 57342. Magn. X 3. Base of cone in situ in centre of whorl of leaves. Fig. 5. Specimen F 57655. Magn. X 1.5. Scale-fronds, sporangial clusters and gangamopteroid small leaves from broken up cone. Fig. 6. Specimen F 57316. Magn. X 2. Gangamopteroid small leaf and scale-fronds. Fig. 7. Specimen F 57645. Magn. X 1.5 Squamae and *Eretmonia* type gangamopteroid leaf (A).

concave. Comparison of this specimen with the B.M.R. specimen CPC 4369 illustrated in Figure 10 shows that "*Lidgettonia australis*" was in fact an example of incomplete or immature *Squamella* scale-fronds with only an indication of where the sporangial masses had been or would be (A, B, C). The interpretation of the fructifications as cupules was incorrect. Figures 10, 12 and 13 show B.M.R. type specimens CPC 4366, 4375 and 4363 which illustrate the serial modification from small leaves to scale-fronds.

Specimen F 57659, Figure 14 shows a scale-frond and sporangial masses on part of a cone axis, and Figure 15 of F 57315 depicts a scale-frond with sporangial cluster at junction of scale and lamina.

The attachment of sporangia to scale-fronds is shown clearly in Figures 16, 17 and 18. Specimen F 43706 (Figs. 16 and 17) shows a concave squama, laminal segment detached, and sporangia borne on forking threads on the line where scale and lamina joined. In F 57667, Fig. 18, there is a sporangial cluster below a squama and one thread is seen attached.

Figure 19 of F 46445 shows a scale-frond in which the apex is indurated. This is an intermediate modification stage.

The nature of complete *Squamella* cones is illustrated in Figures 20 and 21. Of these two Mining Museum specimens illustrated by Walkom (1928) as terminal buds, MMF 18918 is referred to *Squamella* sp. as it is bulkier than those recognised as *S. australis* and the scales are not typical. It is of particular interest, however, as it shows what is believed to be an aggregation of sporangia at the base of a scale on the side of the specimen. Figure 20A illustrates this feature. Specimen MMF 17100 shows a finer, smaller cone with scales of the sort identified as *S. australis*.

There are no *Squamella* cones in the Australian Museum Collection as complete as those illustrated from the Mining Museum. However, F 25729, Figure 22, shows part of a cone with a number of overlapping scales and F 44461, Figure 23, shows a cone apex. In specimen F 43659, Figure 24, is a cone axis from which scale-fronds have fallen, and a similar axis is seen in Figure 25 of F 14948. Both axes have absciss scars of scale-fronds and impressions from the sporangial masses which had been addressed.

***Squamella ampla* gen. et sp. nov.**

DIAGNOSIS: Large cones, length much in excess of the 10 cm sections preserved in the only fairly complete specimen. Cone axis had a diameter of more than 1 cm. Scale-fronds attached to axis in close spiral arrangement. Squamae are broad, shallow and only slightly concave. Laminal segments were approximately three times longer than the scales. Entire scale-fronds were woody in mature cone. Cones referred to *Glossopteris ampla* Dana.

DESCRIPTION OF SPECIMENS: Holotype F 8836. Paratypes F 40459, 28040, 25668, 26063. Associated with very large leaves of *Glossopteris ampla* Dana at a number of localities are broad, shallow squamae, believed to be the scale part of scale-fronds. Figure 27 of specimen F 40459 illustrates one of these squamae. A complete scale-frond in which the squamae and laminal segment are still attached is seen in Figure 28 of F 28040. A woody laminal segment of a scale-frond from which the squama has fallen is shown in Figure 29 of F 25668.

Specimen F 8836, designated the holotype for *Squamella ampla*, is illustrated in Figure 30. It shows a number of woody scale-fronds composed of shallow squamae and broad laminal segments, overlapping in ascending spiral formation. They have obviously

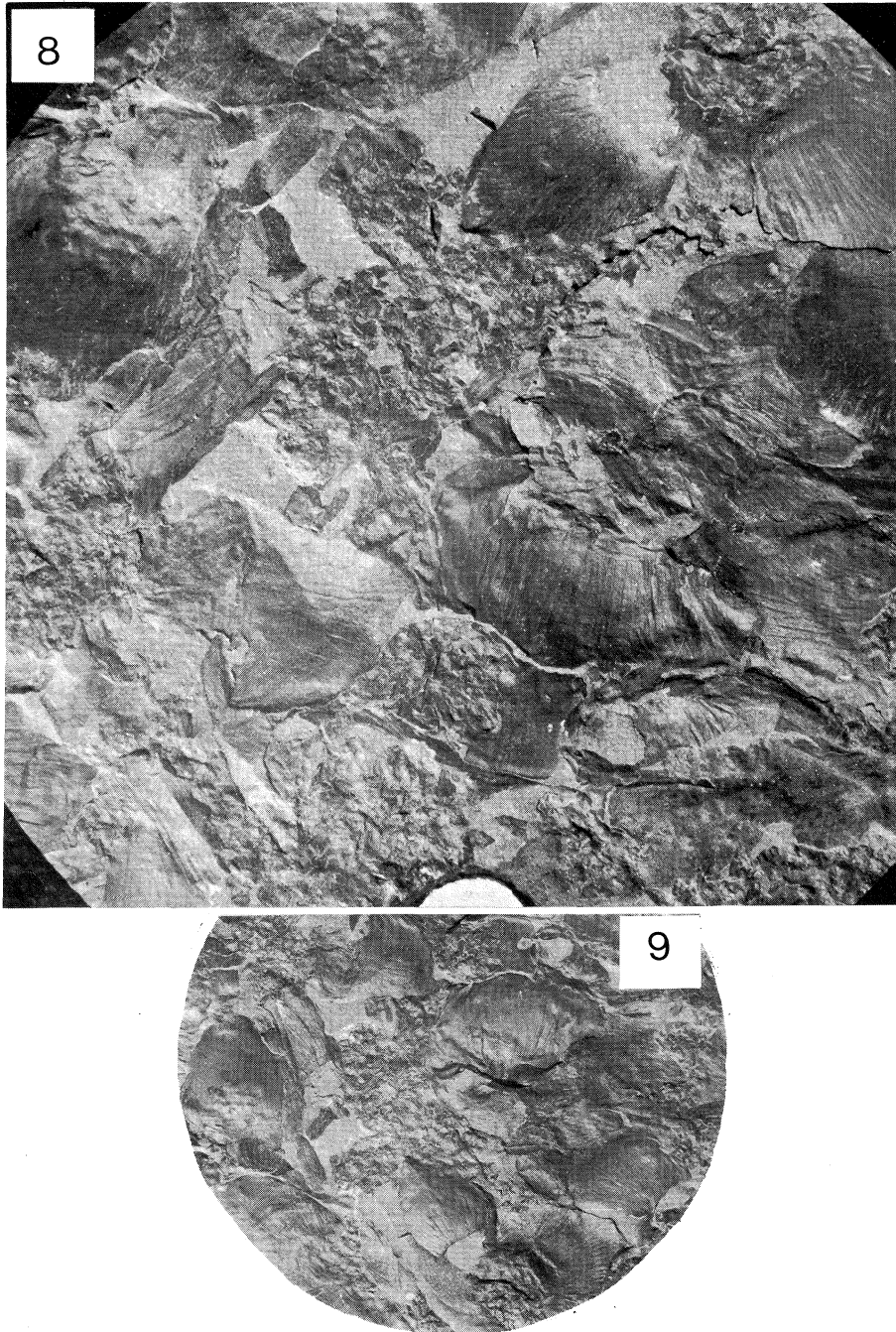


Fig. 8. *Squamella australis* (White). Specimen F 57625. Magn. X 3. Scale-fronds and sporangial clusters from broken up cone. Fig. 9. Specimen F 57626. Magn. X 1.5. Part of counterpart of Figure 8.

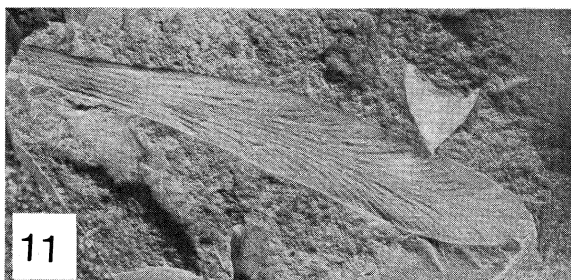
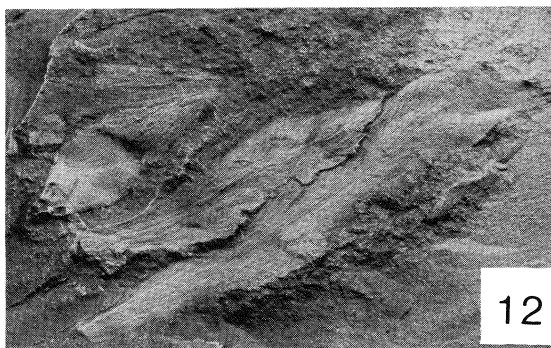
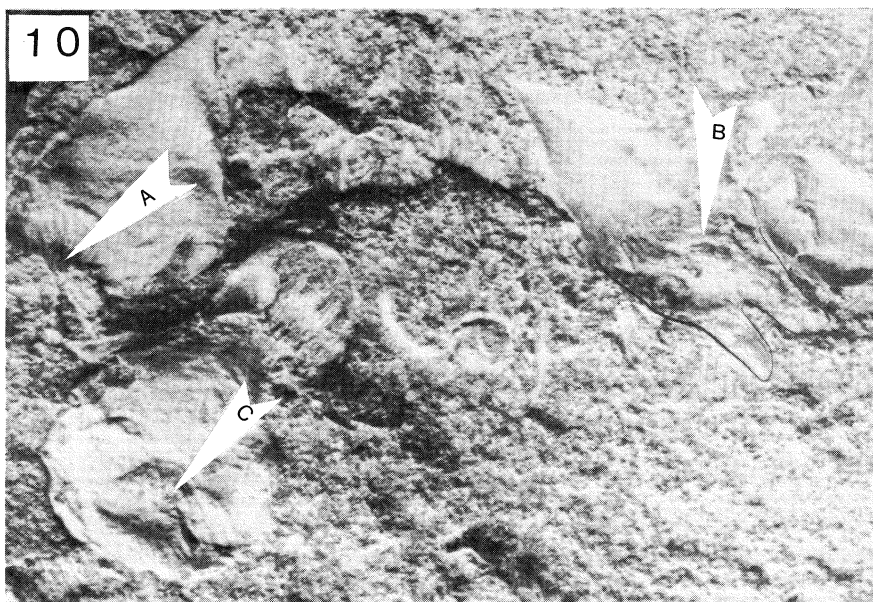


Fig. 10. "*Lidgettonia australis* White." Specimen B.M.R. C.P.C. 4369. Magn. X 4. Scale-fronds with fructifications attached at (A), (B), (C). Fig. 11. Specimen B.M.R. C.P.C. 4366. Magn. X 2. Gangamopteroid small leaf, concave squama. Fig. 12. Specimen B.M.R. C.P.C. 4375. Magn. X 2. Gangamopteroid small leaves with indurated tips. Fig. 13. Specimen B.M.R. C.P.C. 4363. Magn. X 4. Scale-frond of long, gangamopteroid lamina with small scale attached.

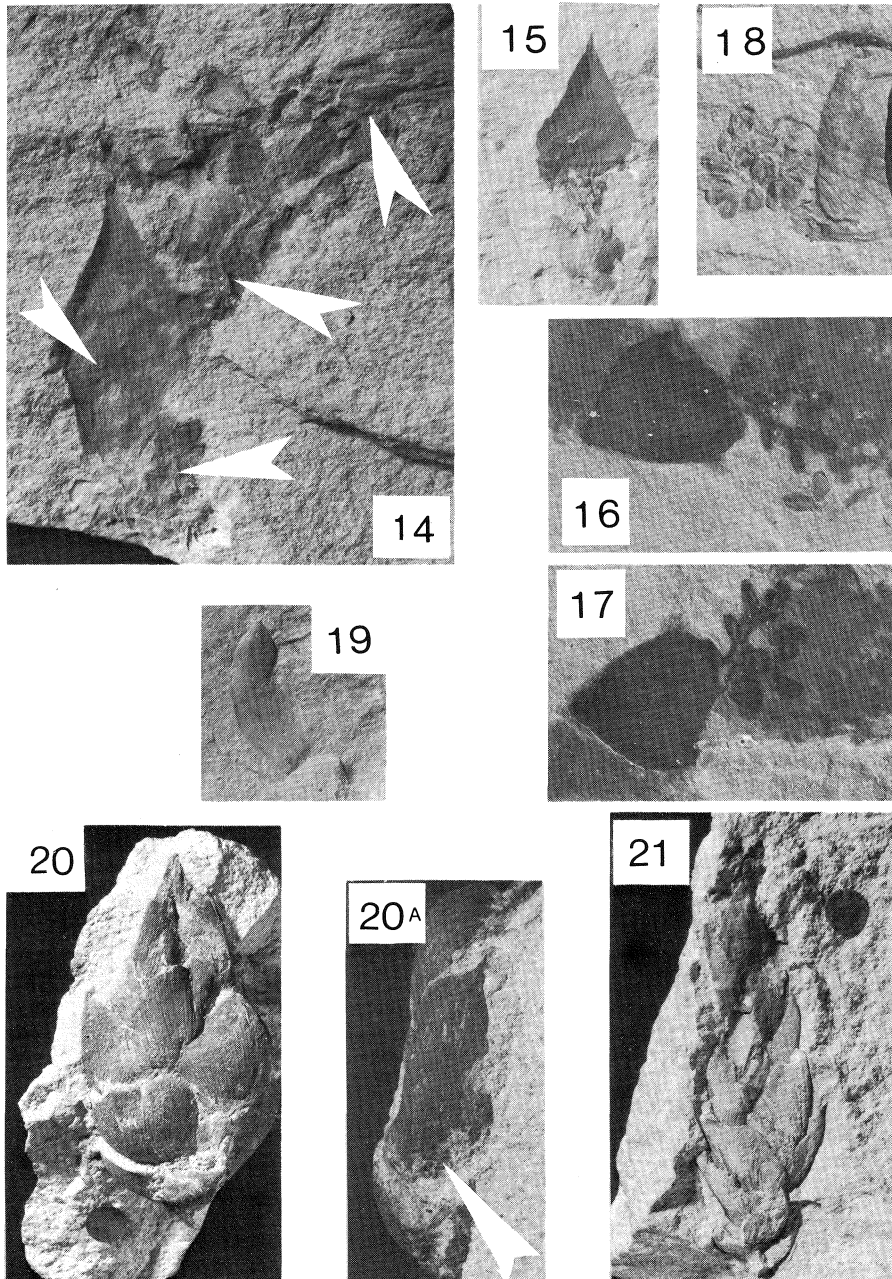


Fig. 14. *Squamella australis* (White), Specimen F 57659. Magn. X 3. Scale-fond and sporangial clusters (arrowed) on part of cone axis. Fig. 15. Specimen F 57315. Magn. X 1.5. Scale-frond with sporangial mass at junction of squama and laminal segment. Figs. 16-17. Specimen F 43706. Magn. X 4. Squama without laminal segment; sporangia borne on forking threads attached on line of junction with lamina. Fig. 18. Specimen F 57667. Magn. X 4. Sporangial mass attached to junction of lamina and squama. Fig. 19. Specimen F 47445. Magn. X 1. Gangamopteroid small leaf with indurated tip. Intermediate between gangamopteroid leaf and scale-frond. Fig. 20. Specimen MF 18918. Magn. X 1. *Squamella* sp., complete cone. "Terminal bud" of Walkom 1928. Fig. 20A. Specimen MF18918. Magn. X 2. Cone viewed from the side. Sporangia at arrow. Fig. 21. Specimen MF 17100. Magn. X 1. Complete *Squamella australis* cone.

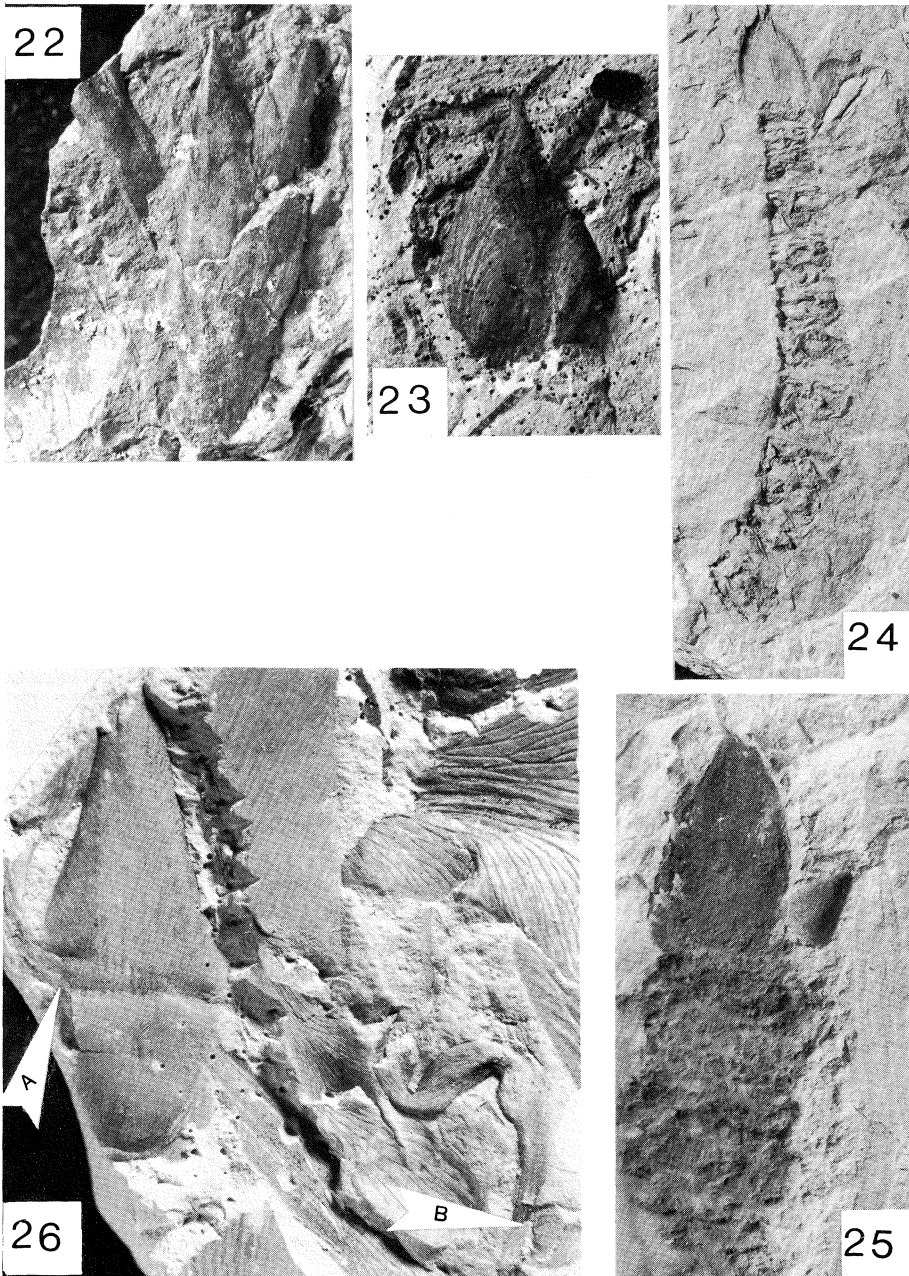


Fig. 22. *Squamella australis* (White). Specimen F 25729. Magn. X 2. Cone. Fig 23. Specimen F 44461. Magn. X 2. Apex of cone of *Squamella australis*. Fig. 24. F 43659. Magn. X 2. Axis of Cone. Fig. 25. Specimen F 14948. Magn. X 3. Axis of cone. Fig. 26. *Squamella ovulifera* (White). Specimen F 26227. Magn. X 2. Pointed squama of scale-frond attached to short laminal segment. Pedicel attached at (A) on line of junction of scale and lamina. Separate fleshy pedicel with seed (B), gangamopteroid leaves in centre of specimen.

been disarranged from a cone. Part of a leaf of *Glossopteris ampla* lies below the scale-fronds. *Glossopteris ampla* is used in a narrow sense, comprising only the large leaves, which in some cases must have been half a metre in length, which are associated with the scale fronds and squamae described above.

Etheridge (1904) described a specimen F 26063 as a caudex of *Glossopteris*. This specimen, illustrated in Figure 31 of this paper, shows what Etheridge described as leaf base scars in ascending spiral formation. The scars can now be seen to be the squamae of scale-fronds of *Squamella ampla* and the specimen represents a cone, not a caudex. The oval (compressed cylinder) core of the specimen can be seen at one end of the specimen. The cone scales, or scale-fronds, are seen to be displaced from one side of the core, a feature substantiating the nature of the organ. Specimen F 8836 (Figure 30) in which only a few scale-fronds of the cone are preserved, could not be confused with a caudex. The evidence of separate squamae, laminal segments and compound structure of scale-frond as illustrated in Figures 27-29 confirms the diagnosis of specimen F 26063 as *Squamella ampla*.

A diagrammatic representation of *Squamella ampla* is seen in Figure 32.

***Squamella ovulifera* gen. et sp. nov.**

DIAGNOSIS: Holotype F 26227. Cones in which scale-fronds were acutely pointed. The laminal segment was short, about half the length of the squama, and seeds were borne on fleshy pedicels attached at junction of scale and lamina.

DESCRIPTION OF SPECIMEN: In specimen F 26227, illustrated in Figure 26, a pointed scale is seen in attachment to a short, broad laminal segment. A pedicel is attached laterally at the point of junction of scale and lamina (A). A seed (B) is attached to a long, fleshy pedicel above, and there is a small, modified, gangamopteroid leaf present. There are many of these pointed scales free in material from Late Permian strata at Newcastle and elsewhere, and it seems likely that they were aggregated into cones as in *Squamella australis* and *Squamella ampla*.

They were female cones and the name *ovulifera* is appropriate.

In Lacey et al. 1975, p. 406, specimen MN 1419 shows a scale-frond which appears to have the squama indurated and a line of seeds attached at junction of the scale and laminal segment. This may be a female *Squamella* scale-frond which has sessile seeds.

PART II: *GLOSSOPTERIS LINEARIS* McCOY

INTERNAL STRUCTURE OF STEM

Specimen F 48156, Figure 33, was described by Etheridge (1894) as a rare example of *Glossopteris* leaves in attachment to a stem. He was under the impression that no internal structure had been preserved in the stem, part of which is fossilised as a solid cylinder. A transverse section of the stem (at arrow) was found to have some preservation of cell structure. Figure 34 shows the arrangement of tissues in the stem.

There is a central core of primary xylem, or xylem and pith (A) surrounded by a uniform zone of secondary xylem composed of small-diameter tracheids in very regular rows (B). A dark zone of tissue representing the phloem and cambium follow (C), and the outer region is composed of leaf bases. Vascular bundles can be seen in some of the leaf bases, but preservation is poor.

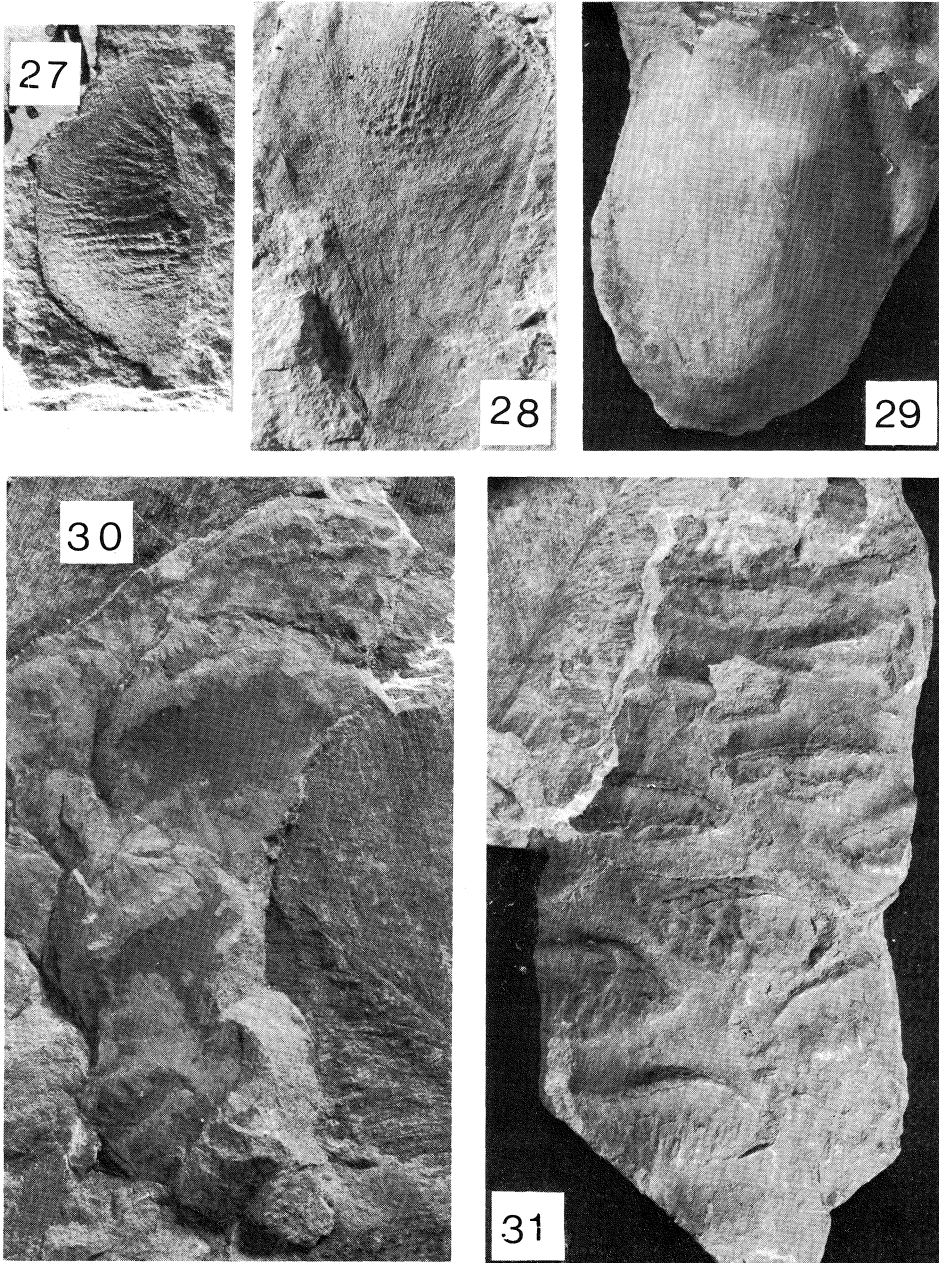


Fig. 27 *Squamella ampla* White. Specimen F 40459. Magn. X 2. Shallow, concave scale, detached from laminal section of scale-frond. Fig. 28. Specimen F 28040. Magn. X 2. Complete scale-frond with squama and laminal segment united. Fig. 29. Specimen F 25668. Magn. X 2. Laminal segment of scale-frond. Fig. 30. Specimen F 8836. Magn. X 1.5. Overlapping scale-fronds of mature cone. Lamina and squama obviously substantial and woody. Venation of *Glossopteris ampla* Dana to the right of the cone scales. Fig. 31. Specimen F 26063. Magn. X 1.5. Portion of cone. Squamae of scale-fronds in ascending spiral.

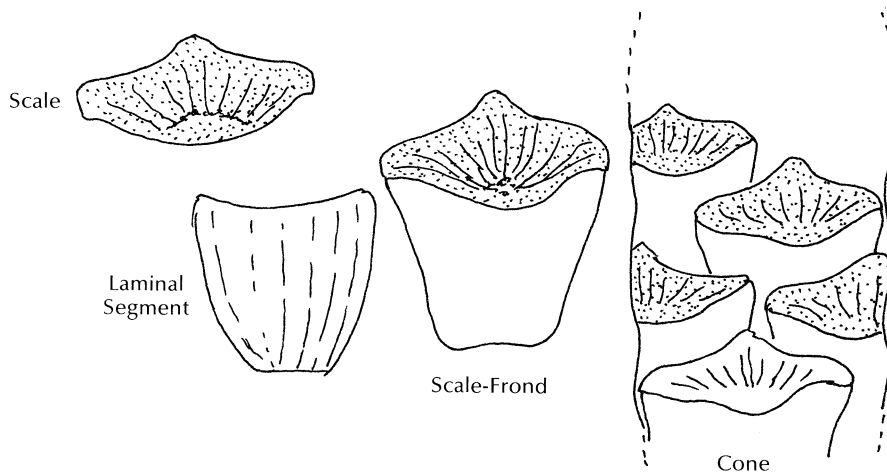


Fig. 32. Diagrammatic representation of *Squamella ampla*. Scale-fronds composed of shallow, woody squama, elongated laminal segment, arranged in ascending spiral on axis to form a cone.

Leaf bases can be seen to the right of the arrow in Figure 33 in impression, and on the outside of the petrified cast to the left of the arrow. The leaves appear to have been sessile with an absciss layer. Whether or not this leaf-bearing branchlet is a short shoot, is not indicated in the specimen.

DESCRIPTION OF *GLOSSOPTERIS LINEARIS* AS GIVEN BY McCOY, 1847.

"S. char.: Leaves very long, narrow, with nearly parallel sides: Midrib very large, secondary veins fine, forming an angle of about 50° with the midrib, anastomosing occasionally from the midrib to the margin.

It is only with *Glossopteris angustifolia* Bgt. from the Indian coal fields of Rana-Gunge, near Rajemahl, that this long, parallel-sided frond could be confounded and it is distinguished easily from that species by the fineness of the neuration which is as remarkably delicate as that of the other is coarse; the neuration of *G. angustifolia* is also distinguished by its great obliquity, forming an angle of about 30° with the midrib, while the nerving of the present species is not more oblique than that of *G. browniana* or *G. nilssoniana*. In this species also, from the anastomosing being continued up to the margin, it results that the nerves are little closer at the margin than in the middle of the leaf, while in *G. angustifolia* the anastomosing is confined to the central portion, and the dichotomising goes on to the margin, where in consequence the neuration is finer and closer than towards the midrib."

DESCRIPTION OF *GLOSSOPTERIS LINEARIS* McCOY AS A WHOLE PLANT.

McCoy (1847) described detached leaves of the species. Additional information is now available on the structure and appearance of the plant which bore the leaves.

Glossopteris linearis McCoy was a woody plant with gymnospermous internal structure. It bore its linear-lanceolate leaves in whorls or close spiral arrangement on branchlets which were substantial, with considerable development of secondary wood. The leaves were deciduous, and were borne sessile on the stem with an absciss layer from which they fell, leaving a small cushion of tissue which formed an ornamentation on the outside of the stem.

The male reproductive phase of the plant comprised cones which terminated leaf-bearing branchlets. A whorl of modified, gangamopteroid, small leaves preceded the cone, between it and the normal foliage leaves. Cones were aggregations of scale-fronds, each consisting of a squama and a laminal segment. The squamae were deciduous. On the line of junction between squama and laminal segment in each scale-frond, clusters of sporangia of *Arberiella* type were attached. The sporangia were borne on fine, branching threads.

In the young male cones the scale-fronds were closely packed and had short laminal segments, and the sporangial masses were protected by the overlapping squamae. Ripening was accompanied by elongation of laminal segments, resulting in a lax cone with easy spore distribution even before the squamae fell off.

The female phase of the plant is unknown.

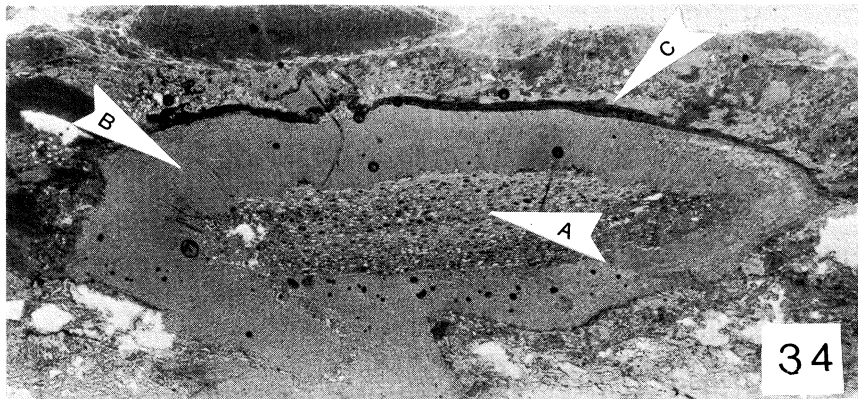


Fig. 33. *Glossopteris linearis* McCoy. Specimen F 48156. Magn. X .5. Whorl of leaves of *Glossopteris linearis* McCoy attached to top of a branchlet. Leaf base ornamentation of stem, which is petrified as a flattened cylinder with some cell preservation to the left of the arrow, and seen in impression to the right. Fig. 34. Specimen F 48156. Transverse section of stem, magn. approx. X 20 showing central region (A) of primary xylem or xylem and pith, regular tracheids of secondary xylem (B) and dark-stained cambial and phloem layer (C). Leaf bases form outer regions.

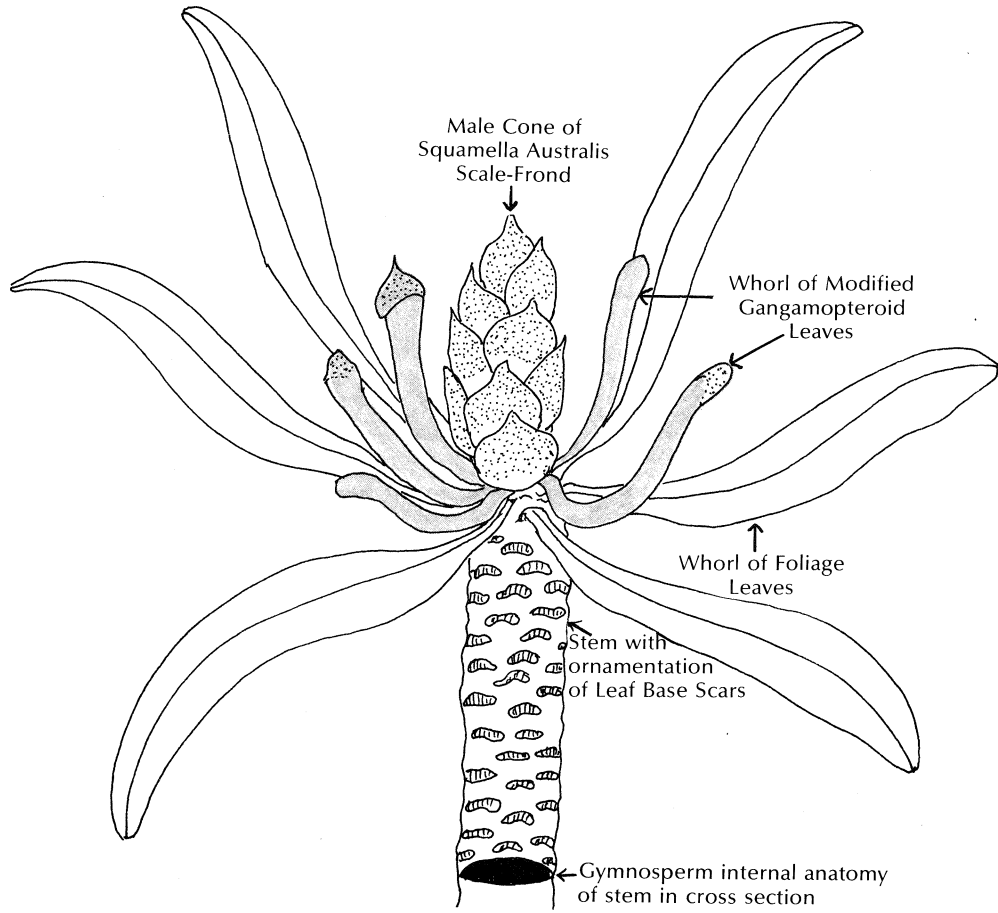


Fig. 35. Diagrammatic representation of *Glossopteris linearis* McCoy.

PART III: GENUS *PARTHA* SURANGE & CHANDRA 1973

Surange and Maheshwari (1970) described a new glossopteridalean fructification as *Lidgettonia indica*. Surange and Chandra (1973) erected the genus *Partha* which is described as being a fertile "scale" which is oval-spathulate in shape, has gangamopteroid venation and bears four pedicels. They incorporated *Lidgettonia indica* in *Partha*. The pedicels were attached to the mid-vein in the stalk region of the fertile leaf, and each bore four seeds or single-seeded cupules.

(a). ***Partha belmontensis*** sp. nov.

DIAGNOSIS: Small gangamopteroid leaves 3 cm long, spatulate in form with a maximum width of 0.5 cm near the top of the lamina. Apex rounded. Venation of three or four strands in the centre of the lamina, reticulation towards margins. Lower third of lamina narrowed into a stalk. Pairs of pedicels on each side of median line of lamina, each forking and bearing two single-seeded cupules, attached where the lamina narrows into a stalk.

DESCRIPTION OF SPECIMENS: Holotype: F 46525, Paratypes: F 39925, 41095, 57391. F 46525, illustrated in Figures 36 and 37, was collected from the Insect Horizon (Late Permian) at Belmont, N.S.W. It is excellently preserved and shows a small gangamopteroid leaf 3 cm long with a stranded midrib and reticulated lamina. It bears seeds, or single-seeded cupules, which are oval in outline, 0.5 cm long and 0.4 cm maximum width. These seeds are borne in pairs on branchlets attached near the midline of the leaf, apparently two branches on each side. It is referable to *Partha* and is the holotype for a new species which is named *belmontensis* after the locality from which it was collected. The Insect Horizon at Belmont (Lake Macquarie) is a well known stratigraphical unit and its insect fossils of Late Permian age have been reported on by Riek (1953).

Detached seeds or cupules which may be referable to *Partha belmontensis* are illustrated in Figures 38, 39 and 40 of specimens F 39925, 41095 and 57391.

(b). ***Partha sessilis*** sp. nov.

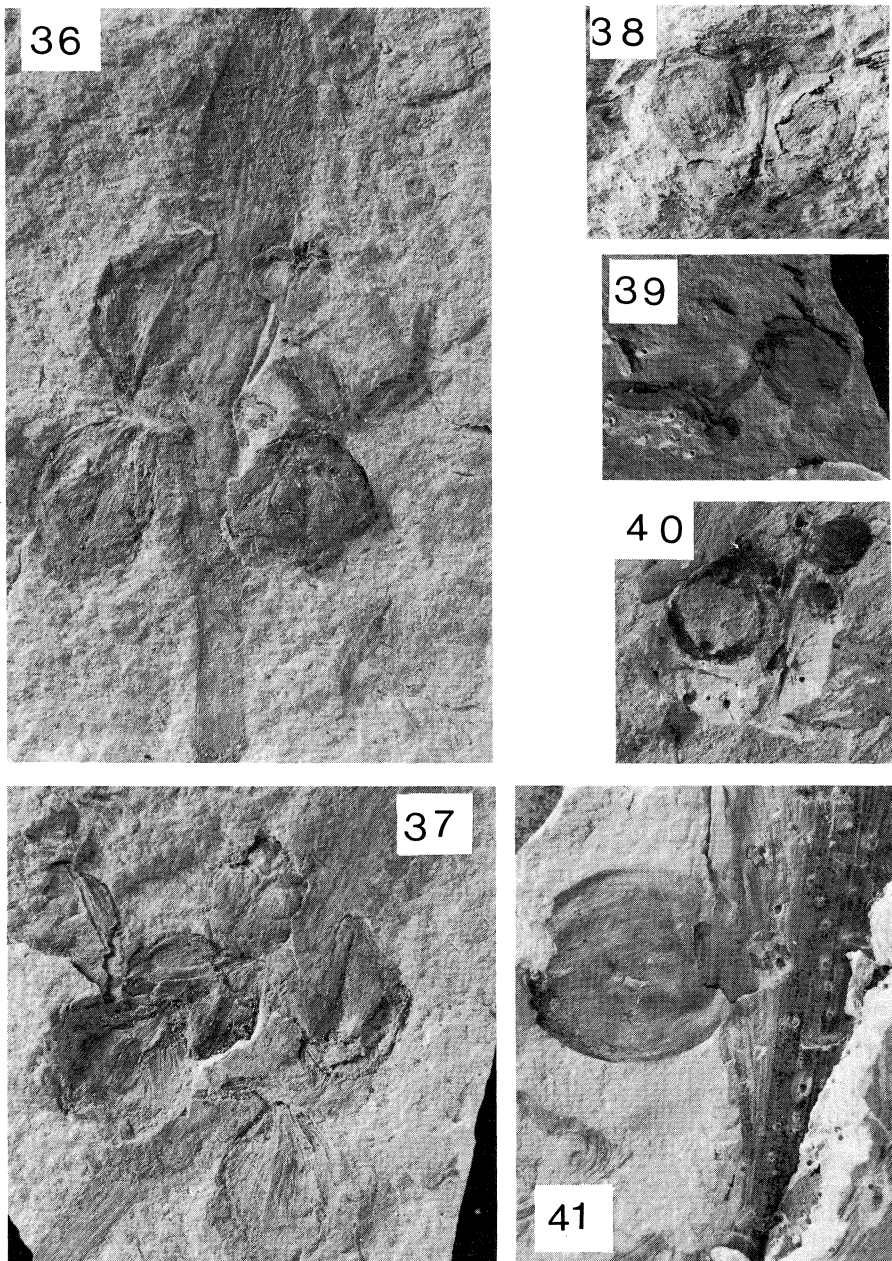
DIAGNOSIS: Gangamopteroid small leaves bearing seeds or single-seeded cupules singly on the leaf margin. The small leaves are similar to those in *Partha belmontensis*.

DESCRIPTION OF SPECIMENS: Holotype: F 29741. F 29741 (Figure 41) shows the base of a gangamopteroid leaf with a sessile seed clearly attached to its margin. A similar leaf base fragment with seed attached to the margin was described and illustrated by White (1965, Plate 5, Fig. 5) in a Bureau of Mineral Resources collection from Agate Creek Volcanics, Queensland.

Partha sessilis is particularly interesting in view of Endrody-Kovaks (1974) description of Glossopteris leaves bearing seeds sessile on the midrib.

(c). ***Rusangea elegans*** Lacey et al. 1975

Lacey et al. 1975 describes gangamopteroid fertile leaves in which seeds or cupules are borne on scale-like projections attached to the leaf margins. The attachment of the seeds to a scale and not directly to the leaf margin differentiates this species from *Partha sessilis*.



Figs. 36-37. *Partha belmontensis* sp. nov. Specimen F 46525. Magn. X 3. Small, gangamopteroid leaf bearing forking pedicels with pairs of single-seeded cupules. Fig. 38, 39, 40. Specimens F 39925, 41095 and 57391. Magn. X 3. Detached cupules of *Partha belmontensis*. Fig. 41. Specimen F 29741. Magn. X 3. *Partha sessilis* White. Seed attached to margin of small, gangamopteroid leaf.

Specimen F 57663 (Figure 42) is tentatively determined as *Rusangea elegans* Lacey et al. This is a scale-like gangamopteroid leaf and at the base on either side are depressions which could represent scales or seeds.

Specimen F 41109 (Figure 43) illustrates a scale with a pair of seeds attached to the median vein. This is similar to specimens described by Lacey et al. from South Africa. Its affinities are not known.

PART IV: GENUS *ERETMONIA* DU TOIT 1932

Eretmonia natalensis (du Toit) emend. Lacey et al. 1975.

Du Toit (1932) described small, spoon-shaped leaves with sporangial clusters as *Eretmonia natalensis*. Much additional information on the species has been supplied by investigations in recent years. Lacey et al. 1975 give an emended diagnosis of the genus and the species after analysis of all the evidence. Great variation is shown to exist within the species and the three additional species described by Surange and Maheshwari (1970) are within the range and are therefore discarded. Sporangia are borne in two pedicillate clusters, one on either side of the stalk near the point of expansion of the lamina.

Figures 45-49 illustrate examples of *Eretmonia natalensis* in the Australian Museum Collection.

Specimens F 39934 and F 57657 (Figures 45 and 46) show spoon-shaped leaves with sporangial clusters. F 41553 (Figure 47) shows a leaf in which the scale-like lamina is elongated into a stalk and two sporangial clusters lie to one side. F 57624 (Figure 48) shows the petiolar region on an *Eretmonia* leaf with a sporangial cluster attached to one side, another broken up above. This specimen looks like the reconstruction of *Eretmonia cooyalensis* Holmes 1974 but re-examination of Holmes' type specimen F 55031 shows it in fact to be a poorly preserved specimen of *Partha* sp. (probably *P. indica*). The pedicels bear seeds and not sporangial clusters. The free sporangial cluster in F 55032 which Holmes interpreted as being the fructification of "*Eretmonia cooyalensis*" is referable to *Eretmonia natalensis* (du Toit) Lacey et al.

Specimen F 57662 (Figure 49) shows a forking pedicel bearing sporangial clusters.

Eretmonia sp.

Specimens F 57658 and F 57661 (Figures 50 and 51) show two examples of fertile leaves bearing pedicillate sporangial clusters. They may fall within the range accepted by Lacey et al. as *Eretmonia natalensis* or may represent a separate species.

PART V: GENUS *LIDGETTONIA* THOMAS 1958

Specimen F 57622, 57623 illustrated in Figures 52 and 53, contains a pointed scale with three peltate discs bearing cupules attached where it narrows into a laminal region. Preservation of the specimen is poor but it appears to be referable to *Lidgettonia*.

PART VI: MULTIOVULATE AND OTHER FRUCTIFICATIONS, NOT BORNE ON MODIFIED SMALL LEAVES OR SCALES

1. *Dictyopteridium sporiferum* (Feist.) Surange and Chandra 1975.

Surange and Chandra (1975) give a full account of the species in its emended form. Much information has been obtained from many authors since Feistmantel first

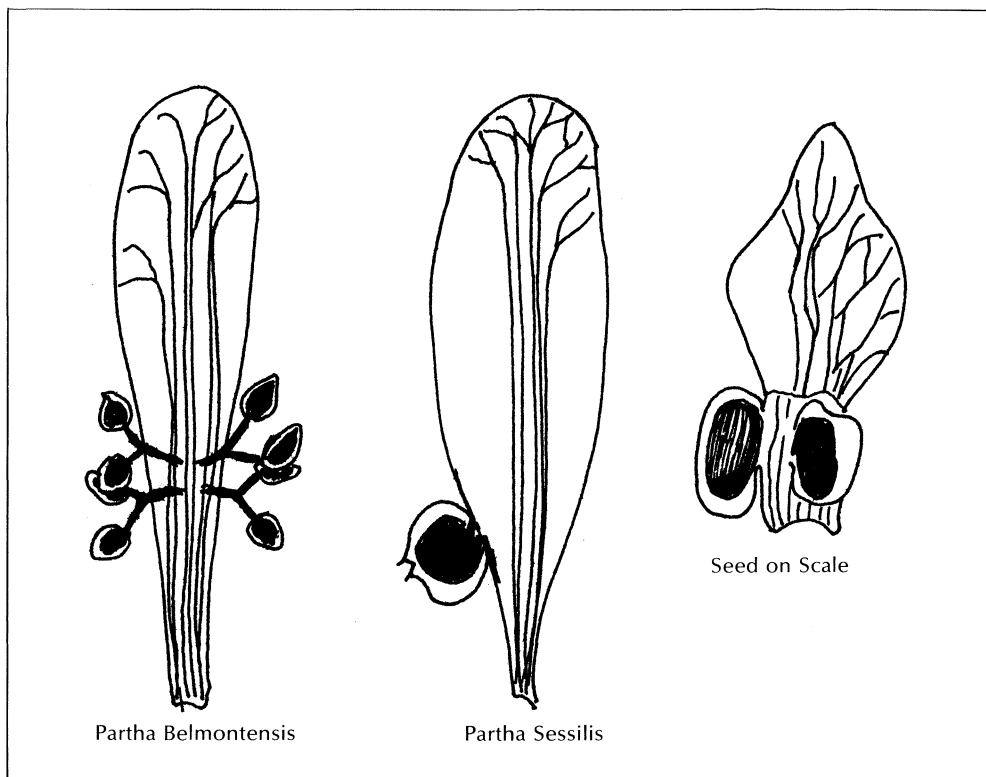


Fig. 44. Diagrammatic representation of *Partha belmontensis*, *P. sessilis* and *Rusangea elegans*.

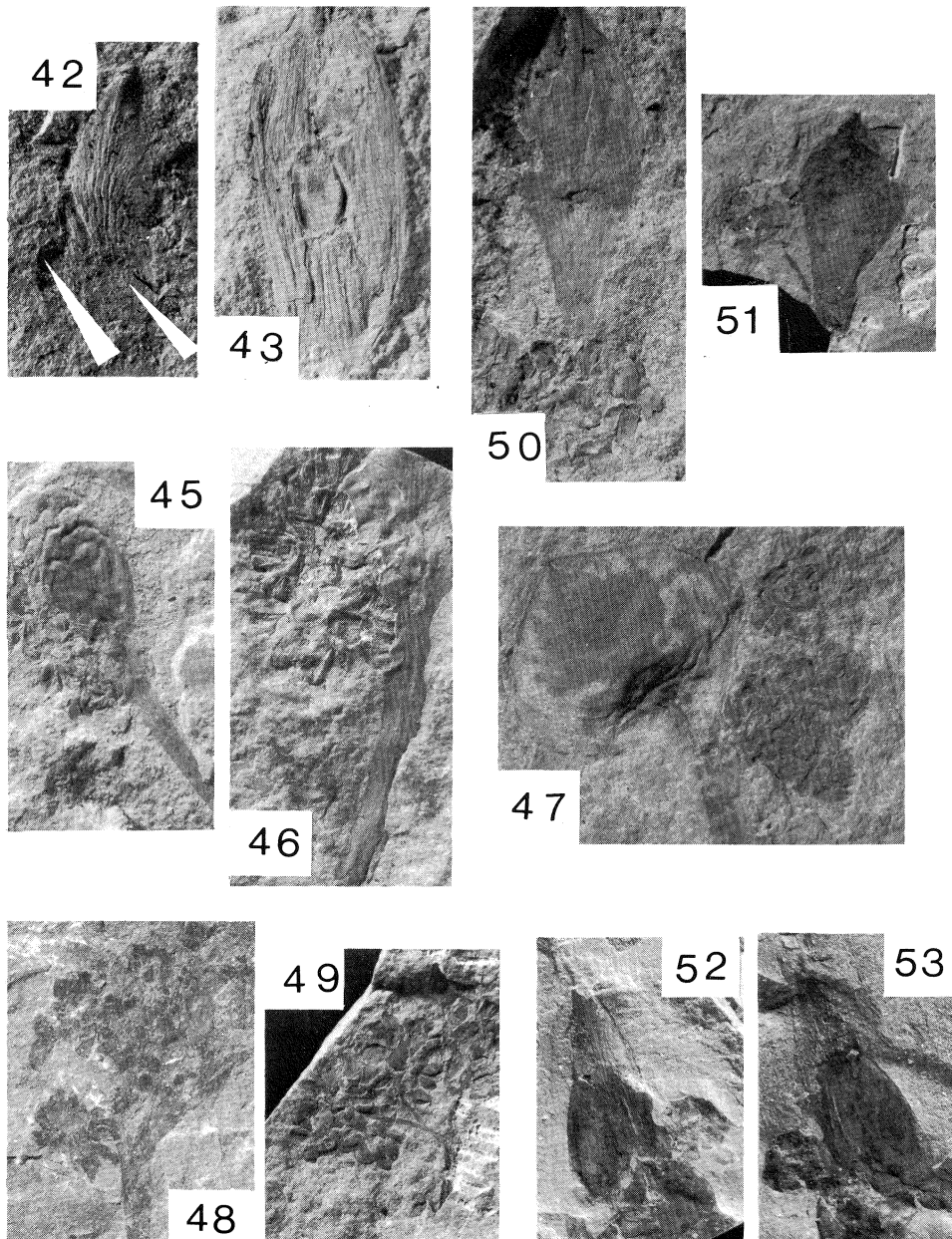


Fig. 42-53 (excluding Fig. 44). *Rusangea*, *Eretmonia* and *Lidgettonia*. Fig. 42. Specimen F 57663. Magn. X 3. *Rusangea elegans* Lacey et al. Small, gangamopteroid leaf with two depressions at base. Fig. 43. Specimen F 41109. Magn. X 3. Small scale with two seeds attached at midline. Figs. 45 to 49. *Eretmonia natalensis* du Toit. Fig. 45. Specimen F 39934. Magn. X 3. Spoon-shaped gangamopteroid leaf with sporangial cluster attached at point of narrowing into stalk. Fig. 46. Specimen F 57567. Magn. X 3. Fig. 47. Specimen F 41553. Magn. X 3. Fig. 48. Specimen F 57624. Magn. X 3. Fig. 49. Specimen F 57662. Magn. X 3. Forking pedicel bearing sporangial clusters. Figs. 50-51. *Eretmonia* sp. Fig. 50. Specimen F 57658. Magn. X 3. Scale-like leaf with sporangial clusters at base. Fig. 51. Specimen F 57661. Magn. X 3. Scale-like leaf with sporangial cluster on long stalk. Figs. 52-53. *Lidgettonia* sp. Specimen F 57622, 57623. Magn. X 3. Sharply pointed scale with three stalked cupules attached to midvein of lower portion.

described this species and a full understanding of the structure of the fructification has now been reached.

Dictyopteridium sporiferum is a female reproductive organ which consists of a cylindrical receptacle or axis bearing small ovules on round cushions in close spiral arrangement. The whole ovule-bearing receptacle is naked in the sense that there are no ovuliferous scales or megasporophylls. The receptacle is borne in the axil of a scale leaf, which, being protective, closely fits on one side of the fructification. Understanding the structure of the organ enables interpretation of the different forms seen as fossils.

The commonest form of *Dictyopteridium sporiferum* in the Collection is illustrated by Figure 55 of specimen F 25655. In this the elongated, narrow organ is patterned with small, circular markings from which the seeds have fallen. In Figure 56, specimen F 44074 shows an organ seen from the protective leaf side with the venation of the leaf superimposed on the receptacle and the marginal seeds appearing as a regular, fluted wing. Figure 57 of F 26130 is particularly interesting as it shows long thin seeds in situ along the left margin of the receptacle, and the rest of the receptacle is patterned with small spots from which the seeds have fallen.

Surange and Chandra (1974) include Rigby's 1972 genus *Isodictyopteridium* in *Dictyopteridium sporiferum*, a conclusion justified by evidence in this collection. Holmes (1974) describes as *Isodictyopteridium costatum* sp. nov. examples of *Dictyopteridium* which have a prominent midrib (specimens F 55033, 55034). These are examples in which the protective leaf is more evident than usual. The interesting feature of the specimen illustrated by Holmes in Figure 13, Plate 8 (Holmes 1974) is that three leaves occur together and were clearly borne in a whorl.

2. *Scutum* Plumstead, 1958.

Surange and Chandra 1975 explain and clarify the structure of *Scutum*. It is a female reproductive organ which is structurally and functionally gymnospermous. A fertile scale bears a seed-bearing receptacle in its axil, with ovules in close-spiral arrangement. The receptacle and protective scale are borne in the axil of a foliage leaf.

(a). *Scutum sahnii* Surange and Chandra 1975

Figure 58 (F 4219) shows a *Scutum* fructification, seen from the protective leaf side, attached to the base of a leaf of *Glossopteris conspicua* Feist. It is referable to *S. sahnii*. A detached cover leaf of the same appearance occurs in specimen F 25642 and is illustrated in Figure 59.

(b). *Scutum* sp.

A cover leaf from a *Scutum* fructification of a different species is seen in Figure 60 (F 57348).

An incomplete fructification at the base of a *Glossopteris* leaf is illustrated in Figure 61 (F 28183).

Figure 62 (F 57455) shows a small *Scutum* cone enclosed in a protective leaf at the base of a *Glossopteris* leaf.

3. *Ottakaria* Zeiller, 1902.

Zeiller (1902) described a structure consisting of a lobed disc on a slender stalk and believed it to be a vegetative structure. Seward and Sahni (1920) realised it was a fructification. Many authors have added information on its structure in recent years.

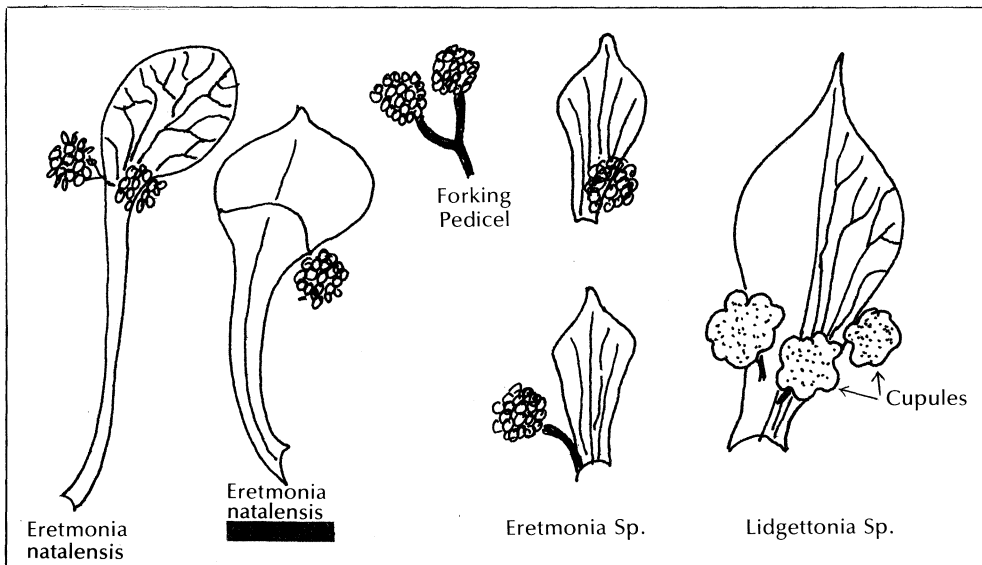
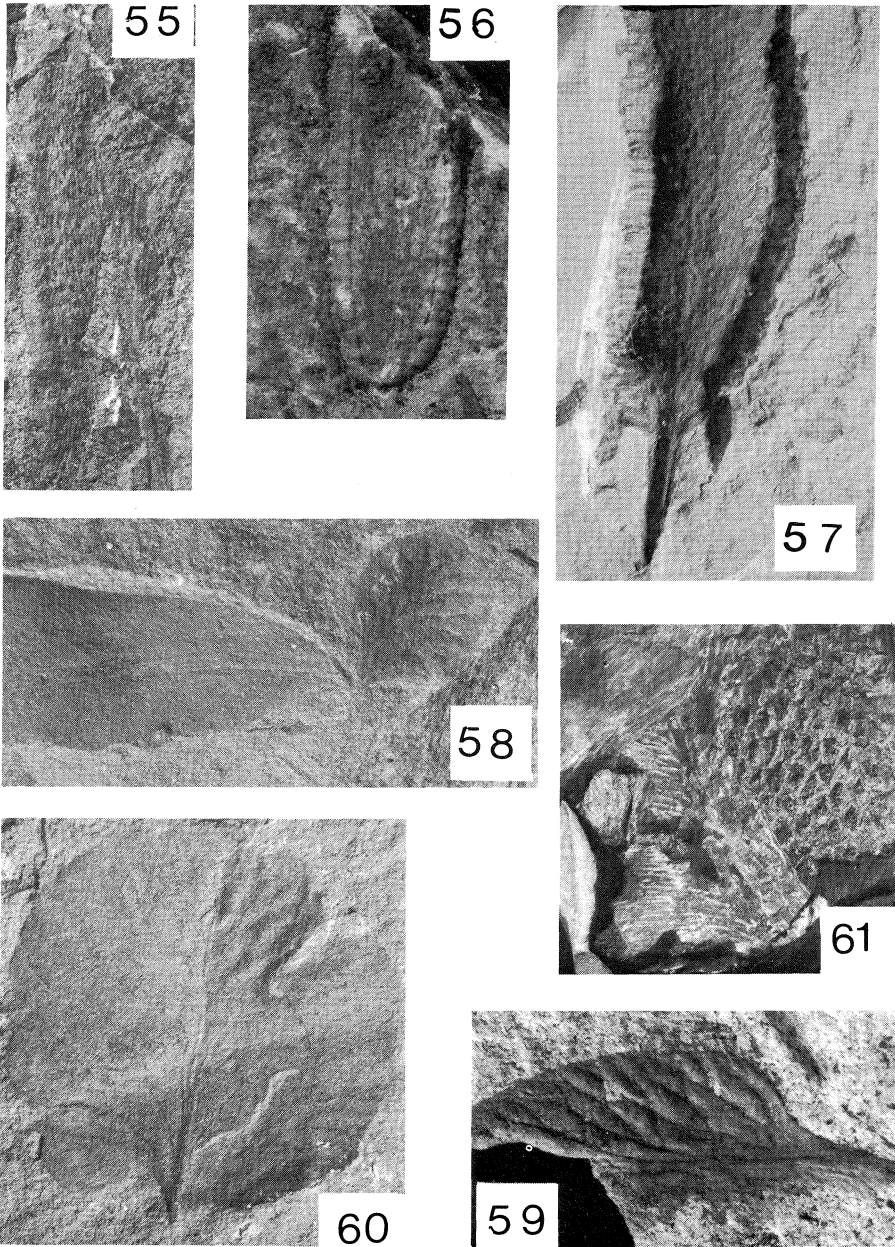


Fig. 54. Diagrammatic representation of *Eretmonia* and *Lidgettonia*.



Figs. 55-57. *Dictyopteridium sporiferum* Feist. Fig. 55. Specimen F 25655. Magn. X 1.5. Elongated receptacle with small, circular scars. Fig. 56. Specimen F 44074. Magn. X 1.5. Receptacle covered by protective leaf. Fluted wing effect round outer edge is a line of seeds. Fig. 57. Specimen F 26130. Magn. X .2. Long, narrow seeds in situ along left margin. Receptacle patterned with circular scars from which seeds have been shed. Fig. 58: *Scutum sahnii*, specimen F 4219. Magn. X 1.5. Leaf of *Glossopteris conspicua* Feist with *Scutum* fructification, seen from protective leaf side, attached at base. Fig. 59: *Scutum* protective leaf. Specimen F 25642. Magn. X 2. Fig. 60. Specimen F 57347. Magn. X 3. *Scutum* protective leaf of another species. Fig. 61. *Scutum* sp. Specimen F 28183. Magn. X 1.5. Fructification at base of *Glossopteris* leaf.

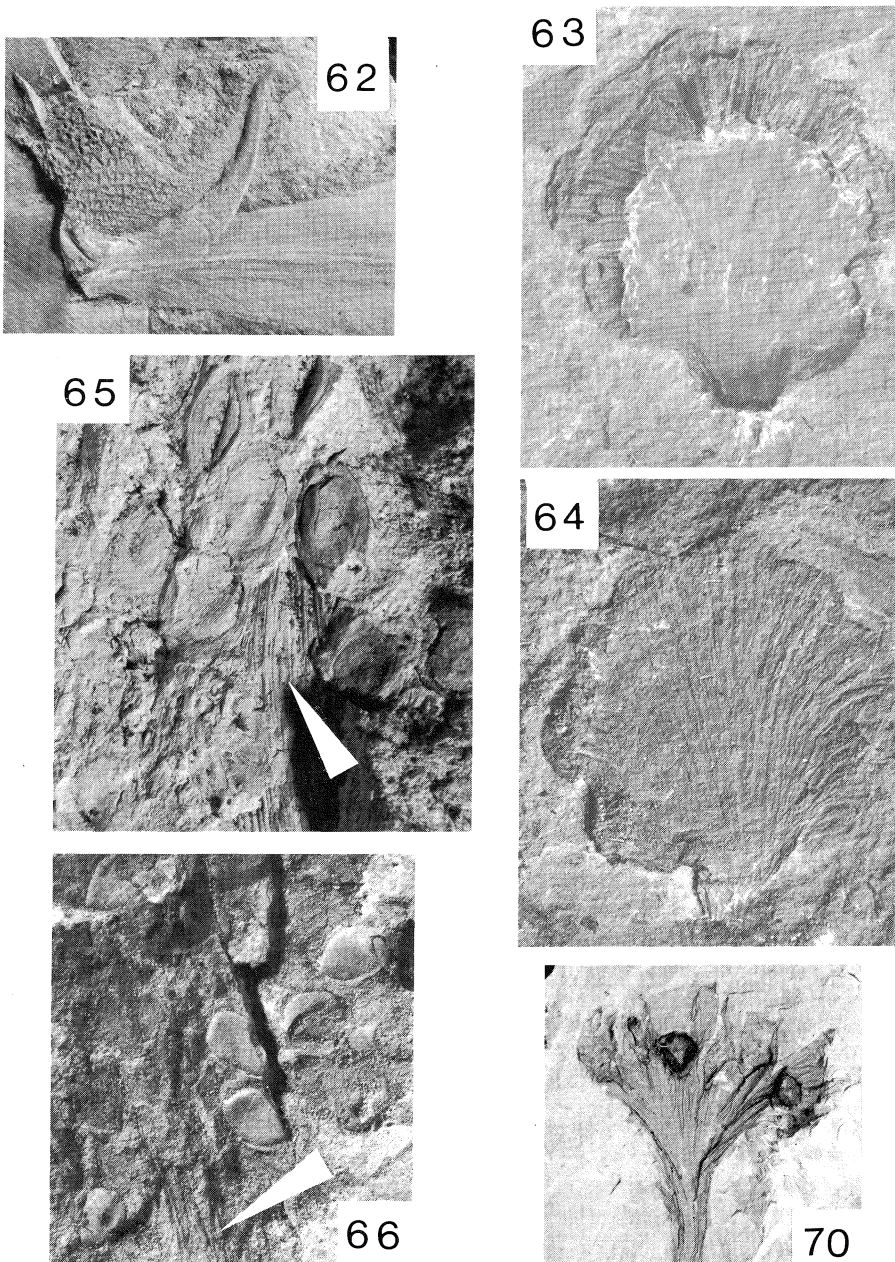
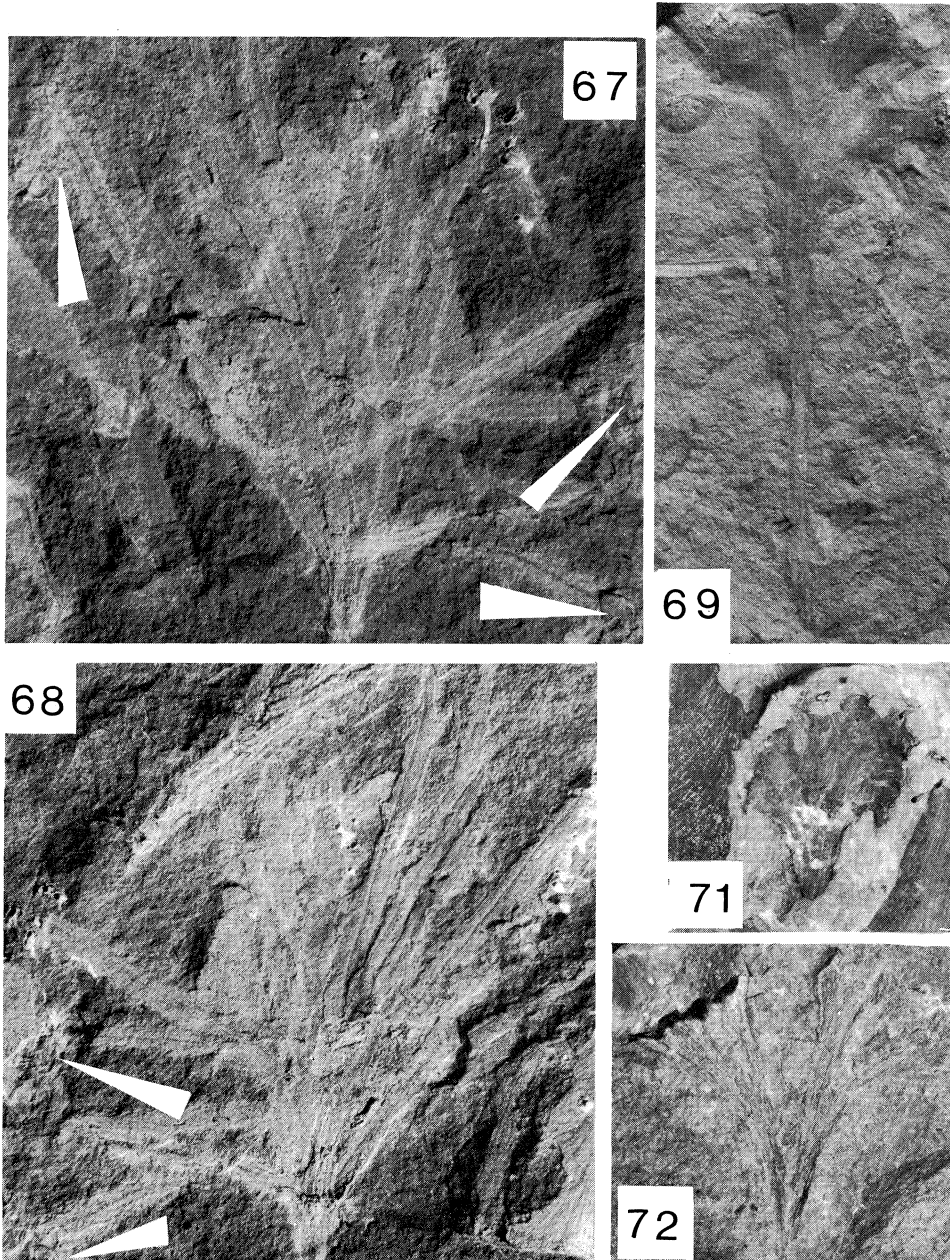


Fig. 62-66, 70. *Scutum*, *Ottokaria*, *Cistella* and *Rigbya*. Fig. 62. Specimen F 57485. Magn. X 1.5. *Scutum* fructification inside protective leaf at base of *Glossopteris*. Fig. 63. Specimen F 19713. Magn. X 3. *Ottokaria* fructification in concavity of protective leaf. Fig. 64. Specimen F 19714. Counterpart F 19713. Flat protective leaf which covered *Ottokaria* fructification from other side. Fig. 65. Specimen F 48163. Magn. X 1.5. *Cistella ampla* White. Large seeds in fleshy head on broad stalk (arrowed). Fig. 66. Specimen F 48173. Magn. X 1.5. *Cistella ampla* White. Seeds in head, stalk (arrowed). Fig. 70. Specimen F 57666. Magn. X 2. *Rigbya arberioides*, Lacey et al. Lobed head with seeds attached.



Vannus
 Figs. 67-68. [redacted] Specimen F 57347, 57348. Magn. X 3. Fan of linear bracts with clusters of sporangia (arrowed). Figs. 69, 71, 72. *Rigbya arberioides* Lacey et al. Fig. 69. Specimen F 29086. Magn. X 2. Lobed head on long stalk. Fig. 71. Specimen F 37390. Magn. X 2. Immature. Fig. 72. Specimen F 57653. Magn. X 2. Bifurcating, lobed head.

Surange and Chandra (1975) summarise the evidence and conclude that it is a multiovulate receptacle borne in the axil of a protective leaf, as in *Scutum*.

Specimen F 19713, 19714 illustrated in Figures 63 and 64 is of particular interest as it shows that the receptacle was in fact covered from both sides. It fitted into a convex protective leaf on one side and was covered from the other by a flat, protective leaf. Both had crenulated margins. The structure is, therefore, considerably different from *Scutum*. If other examples of *Ottokaria* are definitely not organised in this way, it will be necessary to create a new genus for this specimen.

4. *Cistella* Plumstead, 1958

Rigby (1968) states that Plumstead gave the name *Cistella* to some glossopteridalean fructifications in ignorance of the fact that the generic name had already been used. He proposed the name *Plumsteadia* instead of *Cistella*.

Cistella ampla White, 1964

White (1964) described large, fleshy cone-like bodies with seeds clearly embedded in their tissue as *Cistella ampla*. They were associated with *Glossopteris ampla* Dana. They were described as having a smooth integument on one side of the fructification. This feature is in keeping with the protective leaf which is now known to be a feature of *Scutum*, *Dictyopteridium* and *Cistella* type fructifications.

Two examples of large cones of the species are present in the Australian Museum Collection. F 48163 and F 48173 have large seeds embedded in the matrix of the cones (Figures 65 and 66).

5. *Vannus* Plumstead, 1962

A fructification of uncertain affinities is referred tentatively to the genus *Vannus*.

Specimen F 57347, F 57348 seen in Figures 67 and 68, consists of a whorl or fan-shaped arrangement of linear leaves or bracts arising from a stem apex. The segments each have a median vein. Clusters of sporangia are borne near the apices of some of the bracts (arrowed) and in some areas sporangia can be seen attached singly to the margins of the linear organs. The sporangia are of *Arberiella* type similar to those of *Glossopteris*.

Plumstead describes *Vannus gondwanensis* as a fan of bract-like organs attached to a *Gangamopteris* leaf. No sporangia were detected and the nature of the organ was unknown. Perhaps it was a sporangium-bearing organ and the specimen here described is a *Vannus* and referable to the *Glossopteridales*.

In this connection, *Vojnovskya paradoxa* Neuberg 1955, illustrated by Andrews 1961 (p. 352) is also of interest. This plant has micro- and megasporangial organs arranged in a crown on a short shoot. The seeds borne by the female bracts were *Samaropsis* seeds, one of the types recognised as being Glossopteridalean. Perhaps *Vojnovskya* has developed from the *Glossopteridales*.

6. *Rigbya* Lacey et al. 1975

Lacey et al. 1975 create a new genus for fructifications which consist of a slender stalk which is expanded into a flattened head composed of several seed-bearing scales. They believe that these fructifications are referable to the *Glossopteridales*.

There are several examples of *Rigbya arberioides* Lacey et al. in the Collection.

F 29086, Figure 69, shows a specimen in which a long pedicel has its head expanded into six regular lobes. F 57653, Figure 70, shows an irregularly lobed head with two seeds in situ. Figure 71 of F 37390 is an immature example, and F 57666 (Figure 72) shows a bifurcating, lobed head.

There is no evidence at all, apart from that of association, that these fructifications are glossopteridalean.

PART VII: GENERAL DISCUSSION

The information on glossopteridalean fructifications supplied by specimens in the Australian Museum Collection is interesting and important in several respects. In the case of *Squamella* gen. nov. it explains the squamae which have been a controversial feature of the *Glossopteris* flora since earliest authors noted their regular association with the leaves. It is extremely fortunate that specimens were present which show that squamae were part of scale-fronds, that scale-fronds were aggregated into cones, and how the cones were borne on the plant. To have leaves, cones and branchlets with internal structure preserved all clearly of the same species is most unusual, and to have details of the scale-fronds of the cones so explicitly demonstrated, including attachment of the sporangia, is added good fortune. Considering that the Collection is a small one and much of the material has been undetected since it was stored away at the turn of the century, it has been a most rewarding study.

The information obtained on *Partha*, *Eretmonia* and other genera involving small modified leaves or scales in reproduction is useful as added knowledge, and mostly new for Australia.

In the case of the multiovulate fructifications, in *Dictyopteridium* and similar genera the evidence confirms interpretations of structure made by other authors. In the case of *Ottokaria* new information may have been supplied. A controversial fructification is included in *Vannus* to stimulate discussion, and *Rigbya* is included because other authors consider its affinities are with *Glossopteris*.

LIST OF SPECIMEN NUMBERS AND LOCALITY INFORMATION FOR FIGURED SPECIMENS

Figure	Specimen	Locality	Age or Horizon
3.	57342	Flagstaff Hill, Newcastle	Late Permian
4.	57341	Flagstaff Hill, Newcastle	Late Permian
5.	57655	Bowenfels, near Lithgow, N.S.W.	Illawarra Coal Measures
6.	57316	Bowenfels, near Lithgow, N.S.W.	Illawarra Coal Measures
7.	57645	Bowenfels, near Lithgow, N.S.W.	Illawarra Coal Measures
8.	57625	Elecom Wyong DDH 6 Bore, Tuggerah Lake, N.S.W.	Late Permian
9.	57626	Elecom Wyong DDH 6 Bore, Tuggerah Lake, N.S.W.	Late Permian
10. BMR	CPC 4369	Bowen Basin, Queensland	Late Permian
11. BMR	CPC 4366	Bowen Basin, Queensland	Late Permian
12. BMR	CPC 4375	Bowen Basin, Queensland	Late Permian
13. BMR	CPC 4363	Bowen Basin, Queensland	Late Permian
14.	57659	Bowenfels, near Lithgow, N.S.W.	Illawarra Coal Measures
15.	57315	Bowenfels, near Lithgow, N.S.W.	Illawarra Coal Measures
16.	43706	Belmont, N.S.W.	Insect Beds, Late Permian
17.	43706	Belmont, N.S.W.	Insect Beds, Late Permian

18.	57667	Belmont, N.S.W.	Insect Beds, Late Permian
19.	46445	Belmont, N.S.W.	Insect Beds, Late Permian
20. MMF	18918	Glouchester, N.S.W.	Permian
20A.	18918	Glouchester, N.S.W.	Permian
21. MMF	17100	Glouchester, N.S.W.	Permian
22.	25729	Merewether Beach, Newcastle, N.S.W.	Permian
23.	44461	Burraborang Valley, N.S.W.	Illawarra Coal Measures
24.	43659	Belmont, N.S.W.	Insect Beds, Late Permian
25.	14948	Tryphinia, Queensland	Late Permian
26.	26227	Newcastle, N.S.W.	Late Permian
27.	40459	Belmont, N.S.W.	Insect Beds, Late Permian
28.	28040	Belmont, N.S.W.	Insect Beds, Late Permian
29.	25668	Crandaces Hill, Newcastle, N.S.W.	Late Permian
30.	8836	Little Red Head, Newcastle, N.S.W.	Late Permian
31.	26063	Shepherd's Hill, Newcastle, N.S.W.	Late Permian
33.	48156	Mudgee, N.S.W.	Illawarra Coal Measures
34.	48156	Mudgee, N.S.W.	Illawarra Coal Measures
36.	46525	Belmont, N.S.W.	Insect Beds, Late Permian
37.	46525	Belmont, N.S.W.	Insect Beds, Late Permian
38.	39925	Belmont, N.S.W.	Insect Beds, Late Permian
39.	41095	Belmont, N.S.W.	Insect Beds, Late Permian
40.	57391	Newcastle, N.S.W.	Late Permian
41.	29741	Merewether Beach, Newcastle, N.S.W.	Late Permian
42.	57663	Belmont, N.S.W.	Insect Beds, Late Permian
43.	41009	Belmont, N.S.W.	Insect Beds, Late Permian
45.	39934	Belmont, N.S.W.	Insect Beds, Late Permian
46.	57657	Warner's Bay, N.S.W.	Insect Beds, Late Permian
47.	41553	Belmont, N.S.W.	Insect Beds, Late Permian
48.	57624	Elecom Wyong DDH 4 Bore, Tuggerah Lakes, N.S.W.	Late Permian
49.	57662	Belmont, N.S.W.	Insect Beds, Late Permian
50.	57658	Warner's Bay, N.S.W.	Insect Beds, Late Permian
51.	57661	Belmont, N.S.W.	Insect Beds, Late Permian
52.	57622	Elecom Wyong DDH 6 Bore, Tuggerah Lakes, N.S.W.	Late Permian
53.	57623	Elecom Wyong DDH 6 Bore, Tuggerah Lakes, N.S.W.	Late Permian
55.	25655	No locality information, N.S.W.	
56.	44074	Talbragar, N.S.W.	Permian
57.	26130	Newcastle, N.S.W.	Late Permian
58.	4219	Joadja Creek, near Mittagong, N.S.W.	Permian
59.	25642	Belmont, N.S.W.	Insect Beds, Late Permian
60.	57348	Warner's Bay, N.S.W.	Insect Beds, Late Permian
61.	28183	Jamberoo, N.S.W.	Permian
62.	57485	Mudgee, N.S.W.	Illawarra Coal Measures
63.	19713	Warner's Bay, N.S.W.	Insect Beds, Late Permian
64.	19714	Warner's Bay, N.S.W.	Insect Beds, Late Permian

65.	48163	Werris Creek, N.S.W.	Permian
66.	48173	Hamilton River, Queensland	Permian
67.	57348	Belmont, N.S.W.	Insect Beds, Late Permian
68.	57347	Belmont, N.S.W.	Insect Beds, Late Permian
69.	29086	Newcastle, N.S.W.	Late Permian
70.	57666	Warner's Bay, N.S.W.	Insect Beds, Late Permian
71.	57390	Newcastle, N.S.W.	Late Permian
72.	57653	Belmont, N.S.W.	Insect Beds, Late Permian

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