THE TRIASSIC FLORA OF LIVINGSTON ISLAND, SOUTH SHETLAND ISLANDS

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ABSTRACT. A rich Triassic flora is described from new collections made on Livingston Island, South Shetland Islands. The flora contains at least 18 taxa, including probable bryopsids; pteropsids, cycadopsids and coniferopsids, as well as indeterminable wood, stems, roots, leaf fragments, and some micro-fossils. Several specimens show a lignitic form of preservation, in some cases with internal structure. Two new taxa are described: *Pterophyllum dentatum* sp. nov. and *Hexagonocaulon minutum* gen. et sp. nov. The flora is probably Ladino–Carnian (upper Middle to lower Upper Triassic) in age.

THIS paper presents the main results of a study of a new collection of fossil plants from the Triassic of Livingston Island. The collection is of exceptional interest in adding considerably to the present knowledge of the flora in Antarctica. Many of the taxa strengthen correlations between this continent and other parts of Gondwanaland (Lucas, 1979).

The plants described here came from a sequence of thin-bedded fine-grained volcanic sandstones, mudstones and vitric tuffs that is best exposed at the back of the beach on the western side of the Williams Point headland (Fig. 1). Because of coastal reefs and a capping sill of basalt, which forms precipitous cliffs, the sedimentary sequence there is poorly accessible. However, parts of it are also present on the top of the headland, where they have been transported to the surface in giant squeeze-up structures through the sill (e.g. locality B), and in a small exposure of horizontal strata beneath the sill on the north side of Dragon Cove (locality C). Although it was previously believed (Hobbs, 1968; Orlando, 1968) that the loose plant-bearing fragments at locality A were derived from nearby conglomeratic rocks (presumably either the true conglomerates at locality D or the vent agglomerate of Sayer Nunatak), further field work has indicated that they are weathered out of rocks caught in a squeeze-up as at locality B and they do not have an exotic origin.

EARLIER WORK ON TRIASSIC PLANTS FROM LIVINGSTON ISLAND

The only previous study is that of Orlando (1968) on a single collection made for the British Antarctic Survey by G. J. Hobbs in 1959 (designated by the station number P.101).

This material was regarded by Orlando (1968) as Lower to Middle Triassic in age, based on the following six determinations of plant taxa (of which it should be noted that two are new species):

Asterotheca crassa Orlando
Rachis of Osmundaceae
Coniopteris distans Orlando
Frond of Dipteridaceae
Thinnfeldia sp.
Xylopteris cf. *elongata* Frenguelli

LOCALITIES

New material was collected in 1975 for the British Antarctic Survey by M. R. A. Thomson and J. L. Smellie from three of four known fossil sites on Williams Point (Fig. 1). Although most of the material was collected from locality A (the same locality from which the first collection, described by Orlando (1968), was made), good specimens were also obtained from locality C. Locality B yielded only very poor specimens and, although carbonized log and twig moulds were seen at locality D, none was collected.

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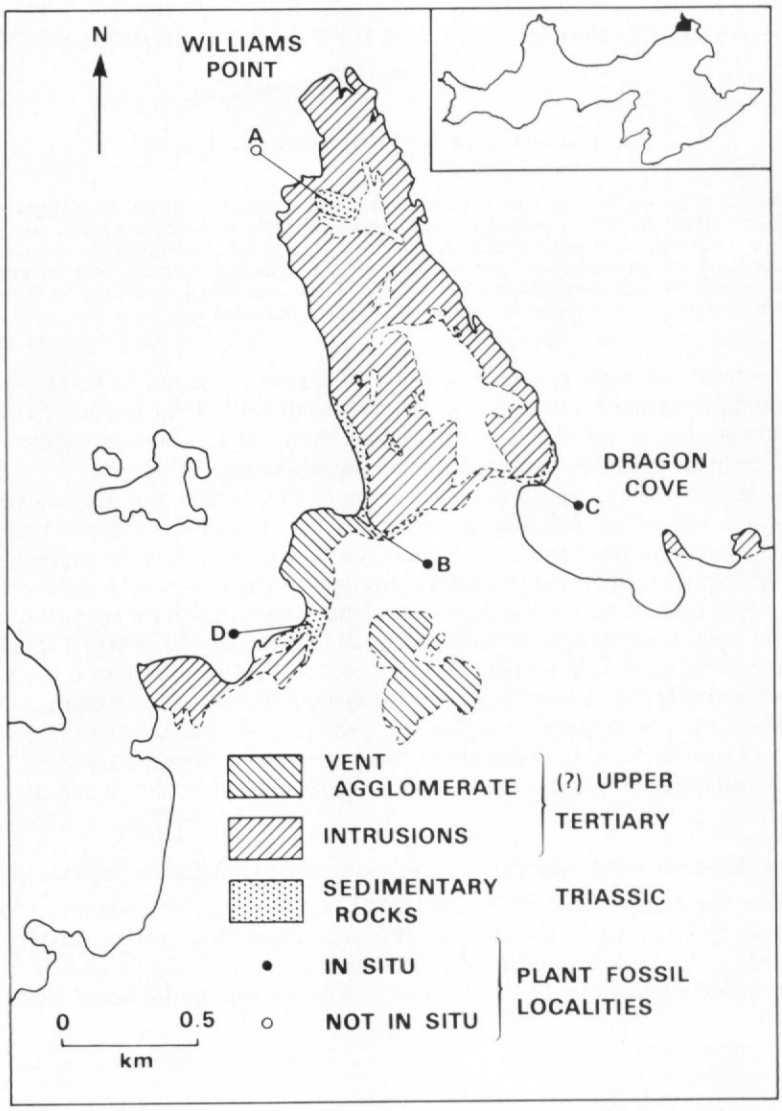

Fig. 1. Map of Williams Point, Livingston Island, showing the positions of the four fossil localities.

Material and Methods

In total, 65 hand specimens were collected from the three localities A, B and C, the bulk of the material (almost 50 specimens) coming from locality A.

The petrological data, which have been supplied by J. L. Smellie, are as follows. The plant fossils are preserved in either a buff-coloured, fine-grained mudstone or sandstone containing silt-sized grains of quartz, feldspar, epidote and carbonaceous matter (localities A and B) or a grey coarse muddy siltstone composed of vitric tuff, a volcaniclastic rock formed of colourless fragments of flattened pumice in an abundant yellow-brown matrix (locality C).

Specimens were studied using a Nikon zoom binocular microscope with strong low-angle unilateral illumination from a Vickers focussing bench lamp. Slide preparations, where possible,

were made using the standard peel technique (Joy and others, 1956) and examined with a Vickers microscope.

Transfer preparations were made from some of the better incrustations and bulk macerations were carried out on selected specimens for spore and cuticle extraction (Lacey, 1963).

Systematic Description of the Flora, including a Revision of Earlier Work

Bryopsida ?

Genus *Thallites* Walton 1925

Thallites sp. A

Fig. 2a

The collection from locality A includes dichotomously branched thalloid remains measuring 3–4 mm wide and possessing an indistinct midrib almost 1 mm wide. In section, the midrib is up to 93 μm thick in contrast to the much thinner lamina which is no more than 7 μm thick. Pores and rhizoids could not be identified with any certainty.

The nearest comparisons can be made with *Thallites uralensis* described by Kryshtofovich and Prynada (1933) from Lower Jurassic deposits in the East Ural mountains of the USSR; less so with *Thallites sewardii* (Berry) Lundblad (1954) from the Lower Cretaceous of Maryland, USA.

However, the material cannot be identified beyond the genus *Thallites*.

Thallites sp. B

Fig. 2b

Locality A also yielded a single specimen of a different thalloid plant. It measures 2 mm wide by up to 22 mm long, with a single dichotomy and more conspicuous midrib 0.7 mm wide. In the lower half of the specimen small protrusions are found to either side of the midrib and the lamina appears to break up into separate lobes. Although there is slight similarity to some members of the Jungermanniales, the apparent lobing may be the result of preservation and not an original feature.

Sphenopsida

Equisetales

Genus *Equisetites* Sternberg 1833

Equisetites sp.

A large number of fragmented small axes, many preserved *in situ*, measuring 0.5–2.5 mm in diameter, up to 46 mm long and with apparent internodes of between 4 and 10 mm have been recovered at all three localities.

In nearly all cases these axes are hollow tubular structures composed of a single (rarely double) layer of cells. Nodal sheaths were unfortunately not preserved, indicating that they were probably small and delicate.

Cellulose acetate peel sections yielded fragments of rhizome, roots, tracheids and cuticle.

Comparisons can be made with *Equisetites burchardti* Dunker (Seward, 1900) from the British Wealden, *E. fertilis* Frenguelli (Jain and Delevoryas, 1967) from the Middle Triassic of Argentina and with *E. minuta* Arber (1917) from the Mesozoic of New Zealand, but the new material does not conform to any of these taxa and is here recorded as *Equisetites* sp.

Genus *Neocalamites* Halle 1908

Neocalamites sp.

Two specimens were found at locality C, one possessing a constricted node and the other the remains of a possible leaf whorl. The specimens measure 31 and 38 mm long by 19 and 15 mm

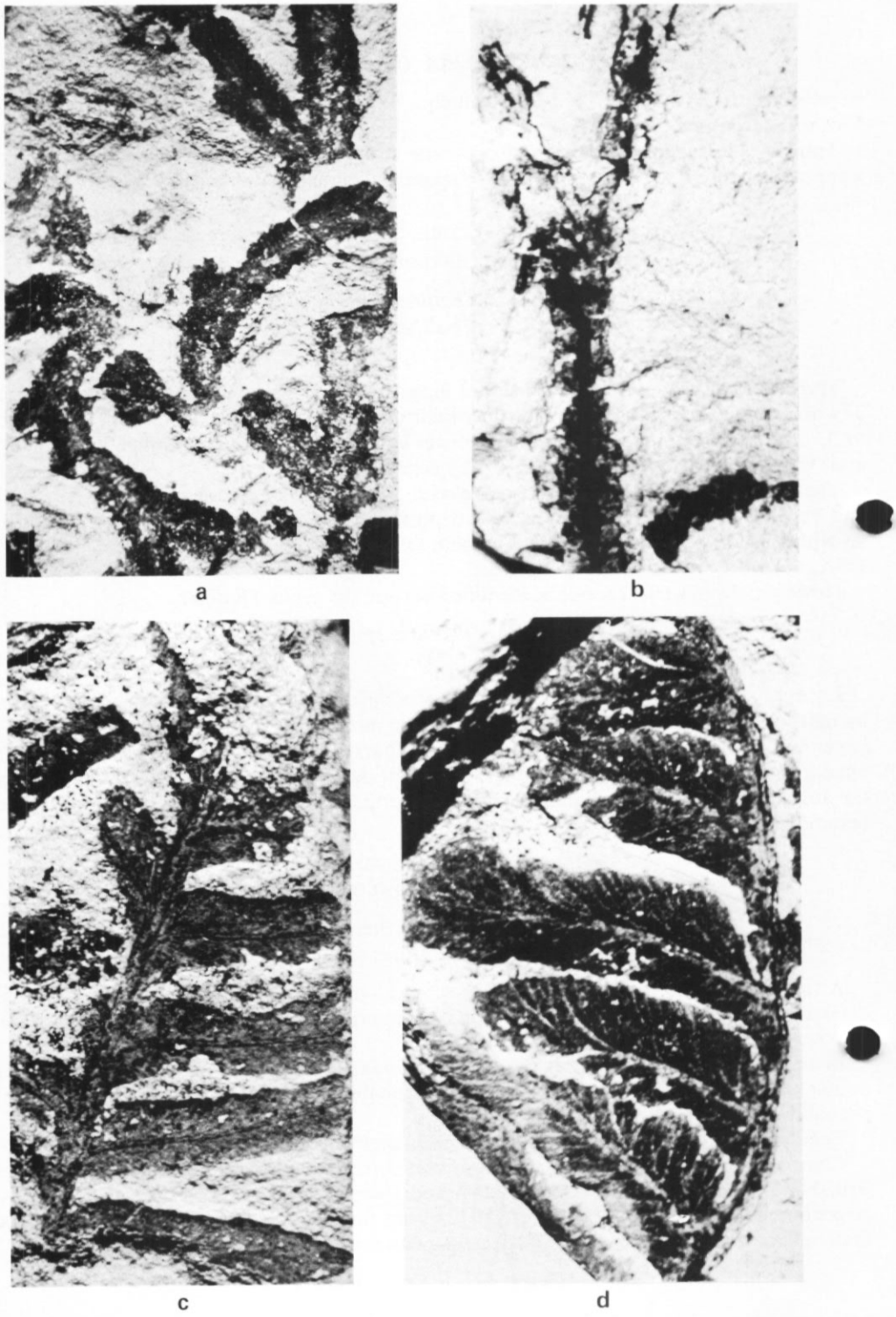

Fig. 2. a. *Thallites* sp. A. Dichotomous plant body with indistinct midrib; locality A (P.224.21; × 2.5).
b. *Thallites* sp. B. Note the more conspicuous midrib and suggestion of lobing at the base; locality A (P.224.21; × 4.0).
c. *Dicroidium* cf. *lancifolium* (Morris) Gothan. Note the lanceolate pinnule (at base of the photograph) and the conspicuous midrib; locality A (P.224.38; × 4.5).
d. *Dicroidium* cf. *lancifolium* (Morris) Gothan. Note the dichotomous lateral veins in the pinnules; locality A (P.224.38; × 5.0).

wide, respectively. The free segments of the whorl measure 11–18 mm long by 2.5 mm wide, are lanceolate in shape and have a single median vein. The ridges on the axes are opposite (continuous) from one internode to the other.

The specimens have some similarity to *Neocalamites hörensis* (Schimper) Halle from the Esk Formation in Queensland, Australia (Rigby, 1977). However, as preservation is poor, they are recorded here as *Neocalamites* sp.

PTEROPSIDA
EUSPORANGIATAE
MARATTIALES
ASTEROTHECACEAE Stur.

Genus *Asterotheca* Presl 1845
cf. *Asterotheca crassa* Orlando
Fig. 3d

The new collections from localities A and C include poorly preserved sterile fragments of fronds, comparable to those described by Orlando (1968) as *Asterotheca crassa*. The fronds measure 5–25 mm long by 2 mm wide.

A re-examination of the original material from the Orlando (1968) collection has provided additional information on this taxon. Sections of the rachis were prepared from the better-preserved specimens bearing the characteristic foliage and these revealed a central "C"-shaped vascular strand (Fig. 3a and b). This same anatomy is characteristic of many defoliated axes observed in the new collections, suggesting these probably have affinities with *A. crassa* (Fig. 3d). A very small rachis with a similar vascular anatomy was referred by Orlando (1968) to the Osmundaceae (see Fig. 3c). In the light of the new information, the latter has been included within cf. *A. crassa*.

LEPTOSPORANGIATAE
FILICALES
DICKSONIACEAE

Genus *Coniopteris* Brongniart 1849
Coniopteris distans Orlando

Since no specimens were found in the new collections, no additional comments are made.

CYCADOPSIDA
PTERIDOSPERMALES
CORYSTOSPERMACEAE

Genus *Dicroidium* Gothan 1912
Dicroidium cf. *lancifolium* (Morris) Gothan
Fig. 2c and d

Two incomplete frond compressions and the fragment of a third were recorded from the same hand specimen collected from locality A. The two better specimens measure 24 and 23 mm long by 18 and 12.5 mm wide, respectively, with alternately arranged lanceolate pinnules up to 11.5 mm long by 3 mm wide. The pinnules have a conspicuous midrib which gives off dichotomizing secondary veins at an angle of 45°.

On external morphology only, these fronds compare favourably with *D. lancifolium* and to a lesser extent with *D. narrabeenense* (Walkom) Frenguelli. *D. lancifolium* was treated as a synonym of *D. odontopteroides* (Morris) Gothan by Townrow (1957) but given specific rank by Du Toit (1927), Lacey (1976) and Retallack (1977).

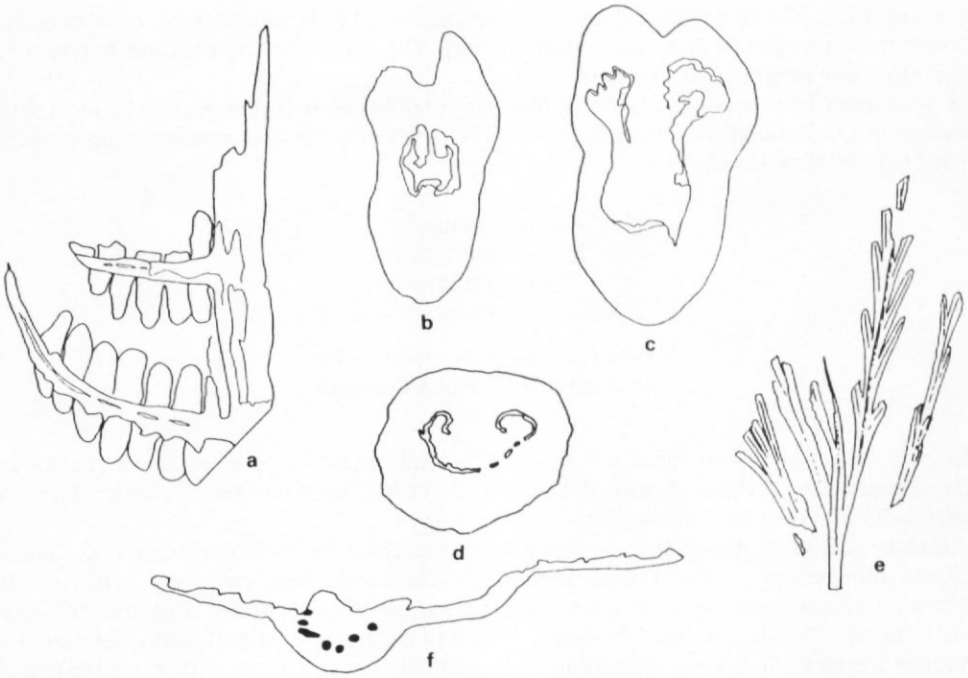

Fig. 3. a. *Asterotheca crassa* Orlando. Fragment of a rachis and two pinnae; locality A (P.101.16; × 3.5).
b. *Asterotheca crassa* Orlando. Transverse section of a rachis from Fig. 3a; locality A (P.101.16; × 15.5).
c. cf. *Asterotheca crassa* Orlando. Line drawing of "rachis of Osmundaceae" from Orlando (1968); locality A (P.101.4; × 7.0).
d. cf. *Asterotheca crassa* Orlando. Transverse section of a defoliated axis (rachis); locality A (P.224.25; slide No. 31; × 9.9).
e. *Dicroidium* cf. *spinifolia* (Frenguelli) Archangelsky; locality A (P.224.37; × 0.9).
f. *Pterophyllum dentatum* sp. nov. Composite transverse section of a rachis and lamina—note arrangement of vascular strands; locality C (P.426.6; slide Nos. 37–40; × 23.2).

The specimen described by Orlando (1968) as *Thinnfeldia* sp. resembles the *D. lancifolium/D. narrabeenense* form and is included under *Dicroidium*. However, since the pinnules and venation are poorly preserved, it is referred to here as *Dicroidium* sp.

Dicroidium cf. *spinifolia* (Frenguelli) Archangelsky

Fig. 3e

Collections from localities A and C include three examples of this taxon, although only two were reasonably well preserved.

The best specimen (Fig. 3e) is a slender bi-pinnate frond, 65 mm long with each pinna bearing sub-opposite pinnules 1.3 mm wide by up to 11 mm long. Each pinnule possesses a distinct median vein which persists almost to the apex.

The second example appears to be the remains of a single pinna with four alternately branched pinnules, each showing a distinct median vein. The specimen measures 42 mm long with the pinnules borne 13–15 mm apart.

Both these specimens compare more closely with *Dicroidium spinifolia* than either *D. tripinnata* (Jones and De Jersey) Archangelsky or *D. elongata* (Frenguelli) Archangelsky described by Jones and De Jersey (1947) from the Ipswich coal measures of Queensland, Australia.

All of these species possess the characteristic median vein in the pinnules and differ from one another only in the degree of branching.

Dicroidium cf. *elongata* (Frenguelli) Archangelsky

Orlando (1968) recorded this taxon as *Xylopteris* cf. *elongata* but no specimens were found in the new collection, so no comments can be added.

BENNETTITALES
WILLIAMSONIACEAE

Genus *Pterophyllum* Brongniart 1828
Pterophyllum dentatum sp. nov.
Figs 3f and 4b–f

Description

Three specimens, including one part and counterpart, have been found at locality C. The most complete frond (Fig. 4b) measures 30 mm long by 36 mm wide and bears opposite to sub-opposite pinnae each possessing four or five parallel veins.

Complete pinnae measure between 18 and 20 mm in length by 1.3–3.0 mm wide and the apex is dissected into four or five elongated teeth.

Under a binocular microscope the abaxial pinna surface revealed small protuberances measuring 40–53 μm long by 34–53 μm wide and spaced half to three widths apart. These structures are occasionally in irregular rows between and parallel to the veins of the pinna and may represent the remains of stomata, pits or hair bases.

Both transverse and longitudinal sections of the rachis were made using the standard peel technique (Joy and others, 1956). In transverse section, the rachis measures approximately 0.75 mm wide by 0.5 mm thick and appears to possess seven bundles in a flattened "V" shape (Fig. 3f). In addition to the vascular bundles, the section shows a crushed epidermis, a two-layered cortex and a poorly preserved parenchymatous pith (Fig. 4c and d).

In longitudinal section, the tracheid pitting is mostly reticulate, although sometimes scalariform (Fig. 4e and f).

Comparison

The closest comparison with the present material is *Pterophyllum incisum* described by Sahni and Rao (1933) from the Mesozoic of India, although the frond of that species is larger, has a greater number of veins in the pinna and the apex is incised once or twice, resulting in a maximum of only three lobes. These differences indicate we are dealing with an undescribed taxon, regarded as a new species for which the name *Pterophyllum dentatum* is proposed.

Specific diagnosis

Frond pinnate, pinnae linear with parallel margins, usually 1.5–3.0 mm wide by about 20 mm long; veins parallel, unbranched 4 or 5 in each pinna; tips of the pinnae incised 3 or 4 times in an unequal manner, resulting teeth bluntly pointed and veins appear to stop short of these teeth. Probable stomata in rows between veins on the abaxial surface.

Rachis approximately 0.75 mm wide by 0.5 mm thick with a thin epidermis, cortex (hypodermis), undifferentiated pith (ground tissue) and at least seven vascular bundles arranged in a flattened "V" shape. Tracheids with reticulate, rarely scalariform pitting. Cuticle and reproductive structures unknown.

Locality: Williams Point Beds, Livingston Island, South Shetland Islands.
Horizon: Ladino–Carnian (upper Middle to lower Upper Triassic).
Holotype specimen: P.426.5.

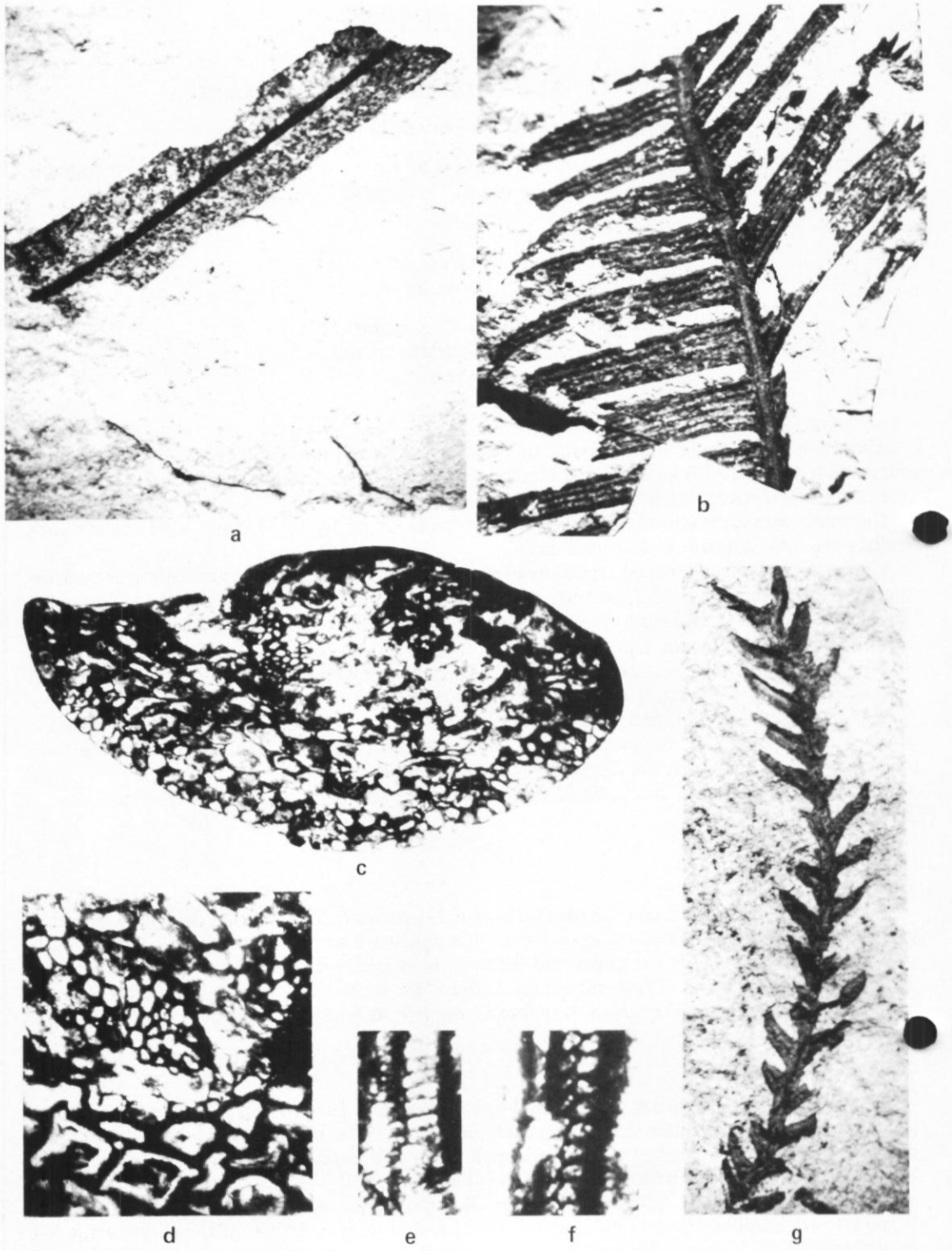

Fig. 4. a. *Doratophyllum tenison-woodsi* (Etheridge) Harris. Fragment of a leaf in surface view and two transverse sections—note well-defined prominent midrib; locality A (P.224.36; × 3.0).
b. *Pterophyllum dentatum* sp. nov. The most complete specimen showing the incised tips of the pinnae; locality C (P.426.5; × 2.0).
c. *Pterophyllum dentatum* sp. nov. Transverse section of a complete rachis (see also Fig. 3f); locality C (P.426.6; slide No. 40; × 110).
d. *Pterophyllum dentatum* sp. nov. Transverse section of a rachis showing the remains of two vascular bundles and cortex; locality C (P.426.6; slide No. 39; × 270).
e. and f. *Pterophyllum dentatum* sp. nov. Longitudinal section of tracheids showing scalariform and reticulate (? bordered) pitting; locality C (P.426.6; slide No. 45; × 650).
g. *Pagiophyllum* sp. Leafy shoot—note falcate leaves; locality A (P.224.42; × 3.5).

CYCADALES

Genus *Doratophyllum* Harris 1932
Doratophyllum tenison-woodsi (Etheridge) Harris

Figs 4a, 5a and b

Five specimens were contained on a single hand specimen from locality A. The best-preserved frond measures 26.5 mm long by 5 mm wide, has a prominent grooved midrib and sparse secondary venation (Fig. 5a). These veins are mainly unbranched (only two veins possess dichotomies and these occur near the midrib), spaced 1.0–1.25 mm apart at an angle of 65° to the midrib.

Sections of the frond (Figs 4a and 5b) give measurements of 5–10 mm for the width of the lamina and 0.65–1.4 mm wide by 0.4–0.6 mm thick for the midrib, which is prominent abaxially and conspicuously grooved adaxially.

In general appearance, the specimens resemble species of the genera *Taeniopteris* Brongniart and *Yabiella* Oishi, although closer examination shows that the marginal vein characteristic of the latter genus is not present. A close comparison can be made with *Doratophyllum (Taeniopteris) tenison-woodsi* described by Jones and De Jersey (1947) from the Ipswich coal measures, Australia, and with a specimen of *Taeniopteris tenison-woodsi* (No. V21371) from Denmark Hill, Australia, in the British Museum (Nat. Hist.), London.

The new specimens have been included in this species with reasonable confidence.

CONIFEROPSIDA

Genus *Pagiophyllum* Heer 1881
Pagiophyllum sp.

Figs 4g, 5c and d

Large numbers of conifer shoots, measuring 10–70 mm in length, 2–7 mm wide, with spirally arranged falcate leaves up to 5 mm long and 1 mm wide are present in the material from locality A.

The leaves have decurrent leaf bases, may or may not be depressed to the main stem and appear to be arranged in a 3/8 phyllotaxy (Fig. 5c).

In section, the leaves are four-sided (rhomboidal; see Fig. 5d) and composed of a dark uniform carbonaceous material in which anatomical details are not visible.

Although reproductive organs were not identified with any certainty, the remains of two possible cones were recognized. Both specimens are borne laterally and appear to be composed of tightly packed spirally arranged scale leaves. The first measures 3.5 mm long by 1.8 mm wide and the second 1.5 mm in diameter.

These leafy shoots are most similar superficially to *Rissikia apiculata* (Townrow, 1967*b*) from Southern Hemisphere Triassic deposits and to *Nothodacrium warreni* (Townrow, 1967*c*) from the Jurassic of East Antarctica. In both of these the reproductive organs show only slight resemblances to the possible cones of the Livingston Island material.

Pagiophyllum heerianum Saporta from the Jurassic of West Antarctica (Halle, 1913) and *Pagiophyllum setosum* Phill. from the Jurassic of India (Jacob and Shukla, 1955) also show some similarities to the new material.

As no cuticle details are available and as the reproductive organs have not been identified with certainty, it is proposed to include all of the new material under *Pagiophyllum* sp.

CONIFEROPSIDA
GINKGOALES
GINKGOACEAE

Genus *Ginkgoites* Seward 1919
Ginkgoites sp.
Fig. 5e and f

Three specimens were identified in the collection from locality A, one of which was found during a re-examination of the original material studied by Orlando (1968).

All specimens show dichotomous venation, one (Fig. 5e) shows the remains of a petiole and another (Fig. 5f) shows an apical notch in the lamina. These characteristics suggest ginkgoalean affinity and indicate this material should be included in the genus *Ginkgoites* rather than the more dissected types such as *Baiera* Braun, *Arctobaiera* Florin and *Windwardia* Florin.

As cuticles are not preserved, comparisons are limited to gross morphology only. Although the material compares with many species of *Ginkgoites*, it could well be included in the near cosmopolitan species *G. digitata* (Seward, 1919), which exhibits a great range of morphological variation.

With the limited information available, the material has been recorded simply as *Ginkgoites* sp.

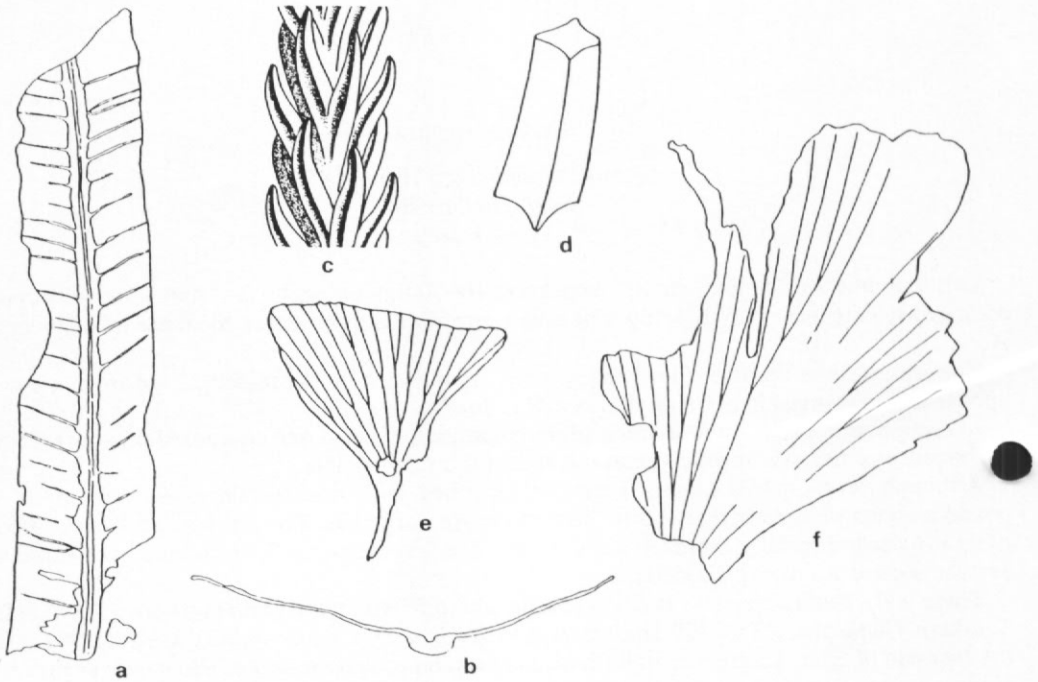

Fig. 5. a. *Doratophyllum tenison-woodsi* (Etheridge) Harris; locality A (P.224.36; × 3.1).
b. *Doratophyllum tenison-woodsi* (Etheridge) Harris. Tranverse section—note conspicuous adaxial groove in the prominent midrib; locality A (P.224.36; × 6.2).
c. *Pagiophyllum* sp. Reconstruction of a leafy shoot; locality A (× 5.4).
d. *Pagiophyllum* sp. Reconstruction of part of a leaf, adaxial ridge to left; locality A (× 13.1).
e. *Ginkgoites* sp. Note the dichotomous venation and petiole; locality A (P.224.27; × 2.3).
f. *Ginkgoites* sp. Note the dichotomous venation and central notch; locality A (P.101.25; × 2.7).

INCERTAE SEDIS

Hexagonocaulon minutum gen. et sp. nov.

Figs 6a–e and 7a–m

Description

Large numbers of radially symmetrical axes, preserved *in situ* and characterized by a hexapartite form have been found in the material from locality A.

The axes measure between 0.5 and 4.0 mm wide, and possess one or two concentric outer layers surrounding a hollow hexagonal stele up to 1 mm in diameter. The stele shows isodiametric to slightly radial elongate cells in transverse section and some evidence of annular or helical thickening in longitudinal section.

Surrounding the stele and connecting it to the outer layers occurs poorly preserved parenchyma. This tissue is rarely seen in transverse section but in longitudinal section it can be observed as plates (diaphragms) usually two (up to four) cells thick and dividing the axis up into compartments (see Figs 6e and 7j–l).

The outer part of the axis may consist of two layers of tissue folded into six lobes, from which a whorl of three scale-like appendages is given off, one appendage to each pair of lobes (see Fig. 6a–c and the reconstruction, Fig. 7m).

Comparisons

Superficial comparisons can be made with *Psilotum* with regard to stele and axis shape but close comparisons can only be made with *Equisetites* and *Ephedra* (see Table I).

The fossil record of *Equisetites* extends back to the Carboniferous. No macro-fossils of *Ephedra* have been found, although spores referred to *Ephedra* have been recorded by Scott (1960) from the Upper Triassic Chinle Formation, USA.

In view of the uncertainty of identification, it is proposed to name the axis *Hexagonocaulon minutum* gen. et sp. nov. ("very small six-angled stem") until more evidence can be accumulated.

Combined generic and specific diagnosis

Small, slender six-angled axes, at least 10 mm long and 0.5–4.0 mm wide with internodes 2–4 mm long, bearing alternating whorls of three scale-like bilobed appendages (? leaves) at the nodes. Stele hollow, hexagonal, with annular or helically thickened tracheids, connected to the outer cortical tissue at the nodes by parenchymatous diaphragms 2–4 cells thick. Reproductive organs unknown.

Locality: Williams Point Beds, Livingston Island, South Shetland Islands.
Horizon: Ladino–Carnian (upper Middle to lower Upper Triassic).
Holotype specimen: P.224.25 (slide No. 25).

SUMMARY OF FLORA IN THE NEW COLLECTIONS

Locality A (P. 224.17–55)
Thallites sp. A
Thallites sp. B
Equisetites sp.
cf. *Asterotheca crassa* Orlando
Dicroidium cf. *lancifolium* (Morris) Gothan
Dicroidium cf. *spinifolia* (Frenguelli) Archangelsky
Doratophyllum tenison-woodsi (Etheridge) Harris
Pagiophyllum sp.
Ginkgoites sp.

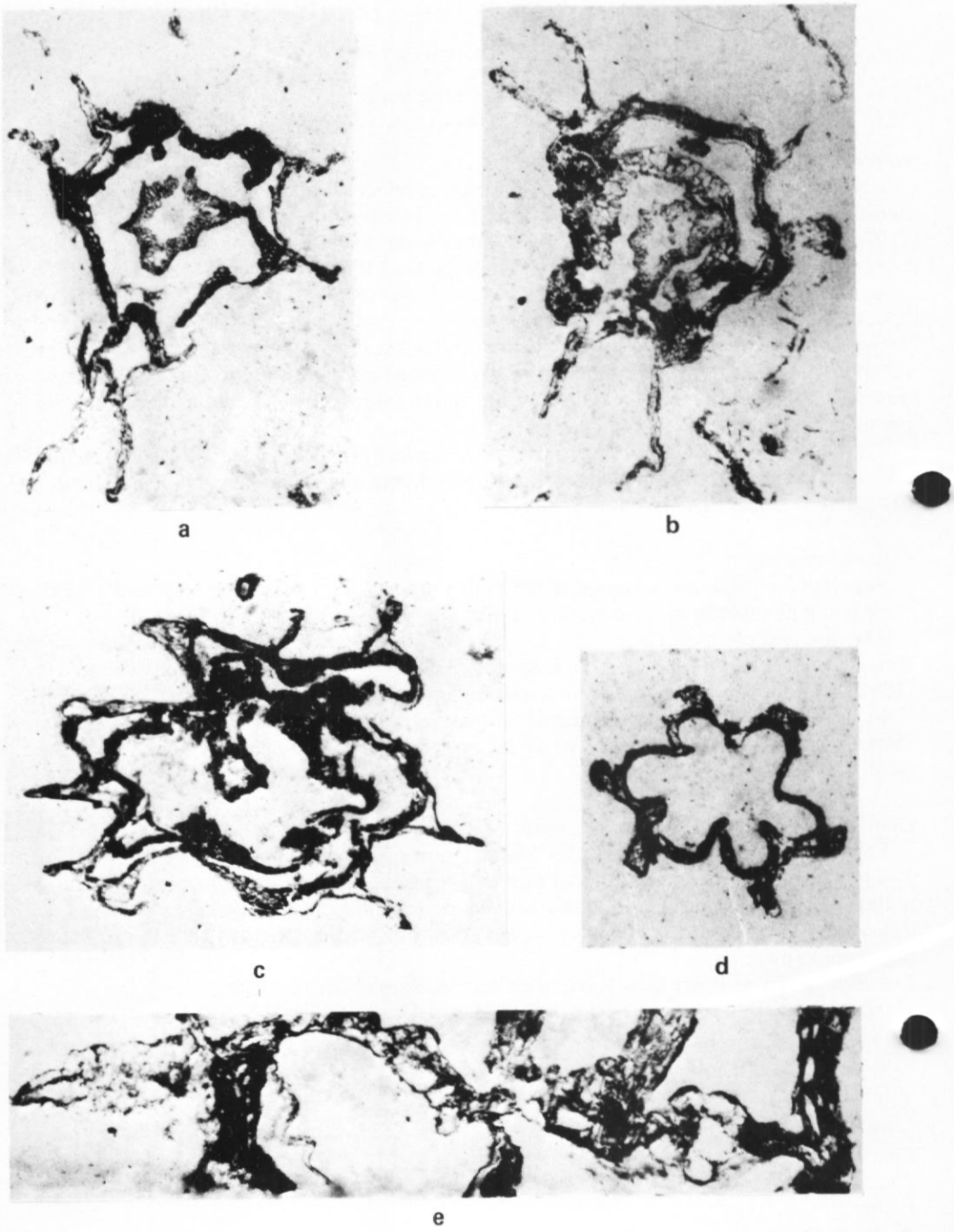

Fig. 6. a–d. *Hexagonocaulon minutum* gen. et sp. nov. Selected transverse sections showing stele with central cavity, inner cortical tissue (with some large-celled tissue preserved in Fig. 6b), small-celled more resistant outer cortex and whorl of three scale-like appendages (each showing two flanges; see reconstruction in Fig. 7m); locality A (P.224.25, 27 and 29; slide Nos. 17, 18, 24 and 25; × 20).

e. *Hexagonocaulon minutum* gen. et sp. nov. Longitudinal section, showing stele appearing in two parts (centre upper side and centre left lower side), diaphragm, outer cortical tissue (right and left) and scale-like appendages (extreme left) (see Fig. 7k); locality A (P.224.27; slide No. 21; × 60).

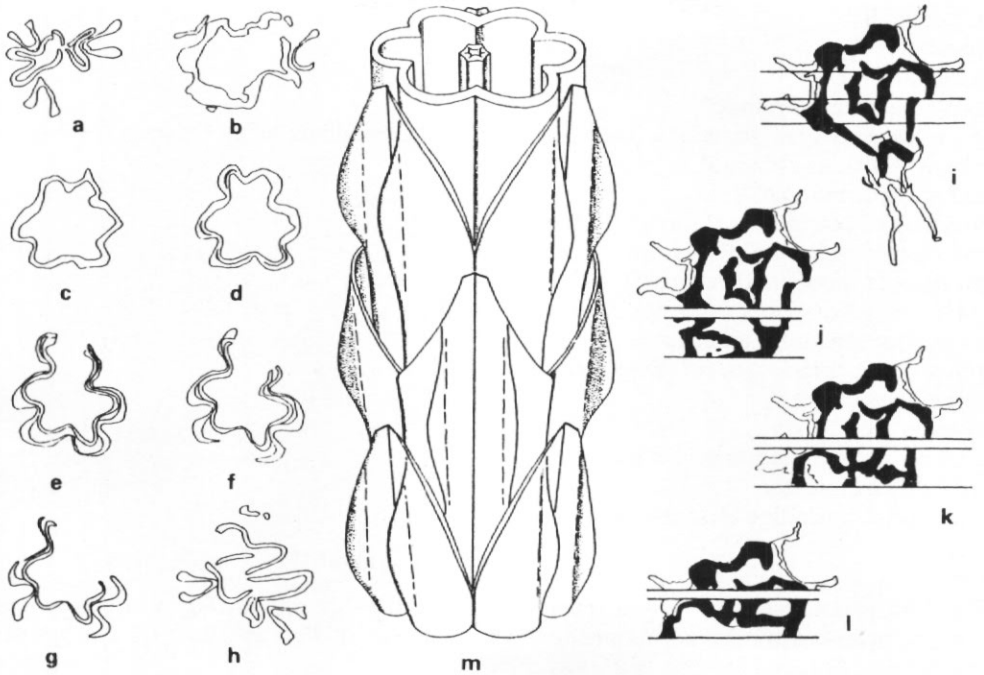

Fig. 7. a–h. *Hexagonocaulon minutum* gen. et sp. nov. Outline drawings of selected transverse sections showing the departure and alternation of scale-like appendages: locality A (P.101.14; slide Nos. 0.13 to 0.18; × 7.4).
i. Transverse section showing position of Fig. 7j–l reading from below upwards; locality A (P.224.27; slide No 18; × 13.2).
j–l. Drawings of combined transverse and longitudinal sections showing evidence for the presence of a diaphragm; locality A (P.224.27; slide Nos. 17 and 18; × 13.2).
m. Reconstruction showing central stele, cortical cavity, outer tissue and alternating scale-like appendages; locality A (× 11.0).

Hexagonocaulon minutum gen. et sp. nov.
Micro-fossils (including Desmidioideae)

Locality B (P. 224.2–16)

cf. *Equisetites* sp.
Dicroidium cf. *spinifolia* (Frenguelli) Archangelsky

Locality C (P. 426.4–13)

Neocalamites sp.
Equisetites sp.
cf. *Asterotheca crassa* Orlando
Pterophyllum dentatum sp. nov.

There is no evidence that these collections came from significantly different horizons and they are therefore treated as a single unit. The complete flora, including a revision of the earlier material described by Orlando (1968), is listed below.

Composition of the Williams Point Flora

The following is a list of taxa recorded up to the present:

Thallites sp. A‡

Thallites sp. B‡
Equisetites sp.§
Neocalamites sp. ‡
Asterotheca crassa Orlando*
cf. *Asterotheca crassa* Orlando*§ (including "rachis of Osmundaceae" of Orlando (1968))
Coniopteris distans Orlando*
Frond of Dipteridaceae*
Dicroidium cf. *lancifolium* (Morris) Gothan‡
Dicroidium cf. *spinifolia* (Frenguelli) Archangelsky‡
Dicroidium cf. *elongata* (Frenguelli) Archangelsky*
Dicroidium sp.* (as *Thinnfeldia* sp. in Orlando (1968))
Pterophyllum dentatum sp. nov.‡
Doratophyllum tenison-woodsi (Etheridge) Harris‡
Pagiophyllum sp.§
Ginkgoites sp.§
Hexagonocaulon minutum gen. et sp. nov.§
Wood† (indeterminate)
Micro-fossils‡ (including Desmidioideae)

Botanical Considerations

The flora is dominated by *in-situ* remains of *Equisetites* sp. and *Hexagonocaulon minutum* gen. et sp. nov. and by drifted, fragmented conifer shoots of *Pagiophyllum* sp. Pteropsids are much less abundant and are also of a fragmented nature.

Table I. Comparison of *Hexagonocaulon* with *Equisetites* and *Ephedra*

Hexagonocaulon	*Equisetites*	*Ephedra*
Apparent monopodial branch system	Monopodial branch system	Monopodial at first
Small, slender six-angled axes (0.5 to 4.0 mm wide)	Ridged axes (1.0 mm to several centimetres wide)	Ridged axes (0.5 mm to several centimetres wide)
Specimens at least 10 mm long with internodes measuring 2.0 to 4.0 mm	Large range of size (internodes measure from 3.0 mm to several centimetres)	Large range of size (internodes measure from 4.0 mm to several centimetres)
Alternating whorls of three scale-like appendages at nodes	Alternating whorls of scale-like leaves fused in a sheath, sometimes in threes, at nodes	Alternating whorls of scale-like leaves fused in a sheath, sometimes in threes at nodes
Hollow (? medullated) hexagonal stele (position of protoxylem unknown)	Medullated stele with endarch protoxylem	Medullated stele with endarch protoxylem
Apparent (?) leaf traces to appendages	Leaf traces extend through entire internode	Leaf traces extend throughout entire internode
Annular or helically thickened primary xylem tracheids	Annular or helically thickened primary xylem tracheids	Annular or helically thickened primary xylem tracheids, secondary xylem includes vessels
Nodal diaphragms (2–4 cells thick)	Nodal diaphragms with primary xylem ring	Nodal cortical tissue with primary xylem ring
Large internodal spaces	Large internodal spaces	Small spaces present
Reproductive organs unknown	Terminal strobili	Dioecious with compound strobili

* Recorded by Orlando (1968).
† Recorded only in 1959 material after re-examination.
‡ Recorded only in new collection.
§ Recorded in both new and old collections after re-examination of 1959 material.

All of the remaining taxa are uncommon and some of them occur only on single hand specimens.

Possible reproductive organs are rare and seeds entirely absent.

Several types of micro-fossil are present and those which could be determined appear to belong to the unicellular algae (Desmidioideae).

Geological Considerations

The Livingston Island flora as revised here includes many taxa characteristic of the Lower Mesozoic and a number of these indicate that it is of undoubted Triassic age. It is the richest Triassic flora described so far from Antarctica, the best known hitherto being Townrow's (1967*a*) account of seven taxa, including four species of *Dicroidium* from Allan Nunatak, Mount Bumstead and Shackleton Glacier in mainland Antarctica.

Triassic floras from other parts of Gondwanaland which have the most in common with the Livingston Island flora are:

i. The Upper Anisian to Lower Norian Molteno floras of southern Africa (Du Toit, 1927; Anderson, 1974; Lacey, 1970, 1976).
ii. The Upper Ladinian to Upper Norian Ipswich flora of Queensland, Australia (Jones and De Jersey, 1947; Retallack, 1977).
iii. The early Carnian to early Norian Marayes flora and the early Norian to Upper Norian Ischigualasto flora of Argentina (Archangelsky, 1968; Stipanicic and Bonetti, 1969).

All of these floras contain *Dicroidium lancifolium, D. elongata* and *D. spinifolia.* Retallack (1977) stated that *D. lancifolium* ranges from Smithian to Rhaetian, and *D. spinifolia* from Anisian to Norian in eastern Australia. Stipanicic and Bonetti (1969) stated that *D. spinifolia* and *D. elongata* are common in the Middle to Upper Triassic of Argentina. Additionally, *Doratophyllum (Taeniopteris) tenison-woodsi* occurs in the Ipswich flora (Upper Ladinian to Upper Norian) of eastern Australia (Jones and De Jersey, 1947) and Orlando (1968) stated that *Coniopteris* is common in the Middle Triassic of Argentina.

These comparisons suggest that the Livingston Island flora could range from Upper Anisian to Upper Norian in age, but it appears to have most in common with Ladino–Carnian floras elsewhere. It is therefore suggested that the Livingston Island flora is approximately of Ladino–Carnian (upper Middle to lower Upper Triassic) age.

Palaeoenvironment

In-situ plants

The probable liverworts described as *Thallites* spp. A and B appear to be sterile and this often indicates favourable conditions for vegetative growth. The plants themselves are reasonably undamaged, suggesting that they were preserved in the place of actual growth or were transported only a short distance.

Other *in-situ* plants include *Equisetites* sp. (with root-bearing rhizomes) and *Hexagonocaulon minutum,* suggesting that the sedimentary basin in which this material was preserved may represent part of the original habitat which underwent periodic inundation.

Fragmentary plants

These no doubt represent some of the surrounding vegetation which grew some distance from the sedimentary basin and were transported to the site by wind or water. The remains are dominated by conifer shoots, which were either easily transported, preserved better or were a dominant constituent of the hinterland vegetation.

Micro-fossils

Only fossil desmids could be recognized with any certainty from the bulk macerated samples made and these suggest a fresh-water lacustrine environment.

Conclusion

The general picture which emerges from a consideration of the fossil flora is one of an undulating terrain with muddy or silty, probably temporary, brackish or fresh-water pools, supporting a growth of bryopsids, sphenopsids and *Hexagonocaulon* at the shallower margins and on the banks, with fragments of pteropsids, cycadopsids and coniferopsids drifted in from more distant higher ground. The absence of fern spores and coniferous pollen grains, which might have been expected to occur, is rather surprising.

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