Taxonomy and palaeoecology of Early Cretaceous (Late Albian) angiosperm leaves from Alexander Island, Antarctica

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Abstract

Seven species of angiospermous leaves from the mid to Late Albian of Alexander Island, Antarctica provide further evidence of angiosperm radiation into high southern palaeolatitudes. The leaves have both palmate (three species) and pinnate (four species) venation. Entire margined leaves with brochidodromus venation are interpreted as belonging to the Magnoliidae, and possibly include members of the Laurales. Palmately veined forms representing the Laurales occur as do palaeoherbs. Other taxa have marginal teeth comparable to those found in the Rosidae. Palaeoecological analysis indicates that *Hydrocotylophyllum alexandri* sp. nov. was a herbaceous streamside coloniser; *Gnafalea jeffersonii* gen. et sp. nov. was a small shrubby plant growing adjacent to levee banks. The other angiosperms, *Araliaephyllum quinquelobatus* sp. nov., *Timothyia trinervis* gen. et sp. nov., *Gnafalea binatus* sp. nov., *Ficophyllum palustris* sp. nov., *Dicotylophyllum lobatus* sp. nov., occur infrequently in swamp deposits and probably represent a scattered understorey of trees and shrubs amongst a conifer and pentoxylalean overstorey.

1. Introduction

The earliest accepted record of angiospermous plants comes from pollen that occurs in the Hauterivian of Israel (Brenner, 1984) and southern England (Hughes and McDougall, 1987; Hughes et al., 1991). The diversification of angiosperms at low palaeolatitudes, and their subsequent radiation and dispersal polewards, during the mid-Cretaceous has been well documented for the Northern Hemisphere (Brenner, 1976; Hickey and Doyle, 1977; Lidgard and Crane, 1988, 1990; Crane and Lidgard, 1989). Isolated parts of both macro- and microfloras give congruent results suggesting a real reflection of evolutionary pattern (Lidgard and Crane, 1990). This pattern of radia-

tion from the equatorial regions polewards can also be demonstrated in the Southern Hemisphere for microfloras (Drinnan and Crane, 1990), but less well so for the macrofloral remains. This largely stems from an incomplete knowledge of fossil floras from these regions.

Angiosperms are widely reported from Late Cretaceous sediments of the Antarctic Peninsula (Truswell, 1991). In the northern Antarctic Peninsula, floras on Snow Hill Island (Fig. 1), first described by Halle (1913), are now believed to be Campanian in age. Angiosperm floras are also known now from both James Ross Island and Seymour Island (Dettmann and Thomson, 1987; Askin, 1983, 1989) (Fig. 1). More recently angiosperm leaves (Rees and Smellie, 1989) and wood
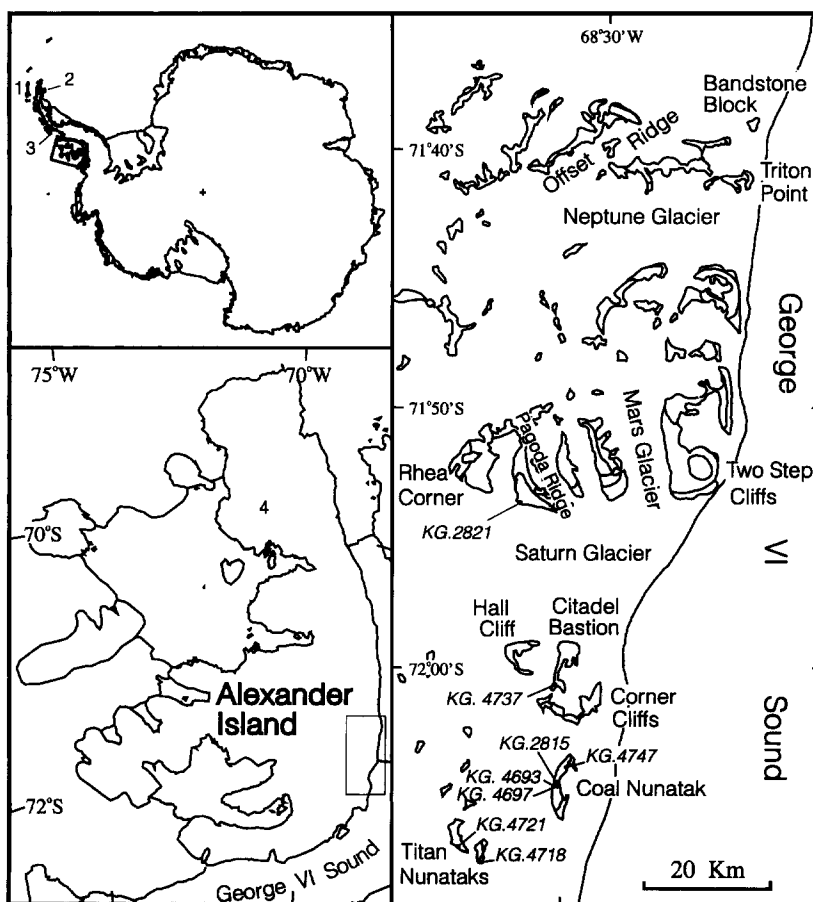
Fig. 1. Locality map for Alexander Island, Antarctica. *1* = South Shetland Islands; *2* = James Ross, Snow Hill and Seymour islands; *3* = Adelaide Island; *4* = Elgar Uplands.

(Torres and Lemoigne, 1989; Chapman and Smellie, 1992) were recorded from Williams Point (Livingston Island, South Shetland Islands) (Fig. 1). The few palynomorphs recovered from the sediments indicate a Cenomanian to early Campanian age (Chapman and Smellie, 1992). Further south on Adelaide Island, large angiospermous leaves with ?craspedodromous venation occur in sedimentary rocks, previously believed to be Upper Jurassic (Jefferson, 1980). The form of the leaves and the presence of poorly preserved tricolpate (cf. *Psilatricolpites*) and six colpate pollen (cf. *Psilastephancolpites*) suggested an Late Cretaceous to early Tertiary age (Jefferson, 1980). However, age assignments are still uncertain, uppermost limits being provided only by cross

cutting plutons yielding ages of 60 ± 2 and 62 ± 3 Ma (Pankhurst, 1982). On Alexander Island (Elgar Uplands) large simple, serrate, craspedodromous leaves occur in tuffs interbedded with lavas (Thomson and Burn, 1977). Recent $^{40}Ar/^{39}Ar$ dating of the lavas indicates an Early Tertiary age (J. McCarron, pers. commun., 1995).

Unfortunately these Late Cretaceous/early Tertiary floras post date the postulated angiosperm diversification through the Antarctic Peninsula region. The oldest known angiospermous leaves come from Alexander Island, where they occur in the Triton Point Member (Neptune Glacier Formation, Fossil Bluff Group) (Jefferson, 1981). These sediments were suggested to be Albian on the basis of the angiosperms alone (Jefferson,

1981). Recent biostratigraphic studies on marine strata above, and below, the sequence at Triton Point indicate a Late Albian age (Kelly and Moncrieff, 1992). Sedimentary rocks referred to the Triton Point Member occur in a broad band extending southwards from Triton Point to the south, cropping out on Pagoda, Phobos ridges and in the southern nunataks (Coal and Titan nunataks, Citadel Bastion) of Alexander Island (Fig. 1). Investigations into the sedimentology and macrofossil flora during the 1992/1993 field season revealed the presence of a diverse (7 species) angiospermous component. Certain taxa were confined to particular sedimentary settings. The description of the leaves and their palaeoecological interpretation forms the basis of this paper.

2. Material and methods

New material collected from outcrops at Coal Nunatak, Citadel Bastion and Titan Nunataks (Fig. 1) supplement existing specimens from Pagoda Ridge, Phobos Ridge, and Coal Nunatak. The material is preserved as impressions in medium- to fine-grained sandstones and siliceous siltstones. No cuticles are preserved but details of venation can be seen, especially in material preserved in siltstones. Few whole leaves were found and most taxa are represented by largely fragmentary material. Descriptions are based on a composite picture from a number of specimens. Primary and secondary venation is commonly observed, but tertiary and higher-order venation is rarely distinguishable due to preservation. In many cases it is difficult to interpret the higher-order venation due to leaf degradation prior to fossilisation. Leaves often show signs of folding and in a number of instances are covered in traces that possibly represent impressions of roots in the leaf litter (Plate IV, 1). Material was examined using strong low-angle lighting to give maximum contrast and photographed using a Olympus SZH10 stereo dissecting microscope with Kodak Technical Pan (2415) film, or with a Nikon FG camera and ring flash. Line drawings were made using a drawing attachment.

The description of fossil angiosperm leaves in the late 1800s and early 1900s was hampered by a lack of an evolutionary framework for leaf morphological characters. This lead to "picture matching" (Wolfe, 1973) techniques for the identification of fossil leaves causing predominantly incorrect assignments of leaf taxa to extant families and genera (e.g. Fontaine, 1889; Lesquereux, 1892; Berry, 1911). The use of names with modern connotations (e.g. *Ficophyllum* Fontaine, *Eucalyptophyllum* Fontaine) has often lead to erroneous assumptions about the affinities of the fossil material; this has severely hampered our understanding of evolutionary change in this important group (see Dilcher, 1974; Hickey and Wolfe, 1975; Hickey and Doyle, 1977, for a full discussion). More recently, re-examination of extant plants has allowed recognition that leaf morphological features such as venation and marginal tooth type are of taxonomic importance (Hickey, 1973, Hickey and Wolfe, 1975). Morphological terminology follows Hickey (1973, 1979) and Hickey and Wolfe (1975). Leaves were divided into two main groups based on venation patterns; palmate and pinnate. Although a number of early names coined by Fontaine (1889) have been applied to the leaves described here, they are used as artificial form-genera and are not meant to imply affinities with modern families or species. All specimens are housed at the British Antarctic Survey and have been assigned British Antarctic Survey numbers (prefix KG.).

3. Stratigraphy

Lower Jurassic to Lower Cretaceous sedimentary rocks crop out extensively in eastern Alexander Island where they form part of a thick forearc basin sequence, the Fossil Bluff Group (Taylor et al., 1979; Butterworth et al., 1988). Although predominantly marine, the upper part of the Fossil Bluff Group contains a prograded wedge of non-marine fluviatile sediments referred to as the Triton Point Member of the Neptune Glacier Formation (Moncrieff and Kelly, 1993). At Triton Point the non-marine sediments are constrained by marine faunas above and below that indicate a Late Albian age (Kelly and

Moncrieff, 1992). The Triton Point Member can be traced southwards from Triton Point through Pagoda and Phobos ridges to the southern nunataks (Moncrieff and Kelly, 1993, fig. 1). The material examined in this study comes from Pagoda Ridge, Citadel Bastion, Titan Nunataks and Coal Nunatak (Fig. 1).

4. Palmately veined leaves

4.1. Actinodromous venation

Hydrocotylophyllum alexandri Cantrill, *sp. nov.*

Holotype: KG. 4697.2 from Coal Nunatak, Alexander Island; Triton Point Member, Neptune Glacier Formation, Fossil Bluff Group; Late Albian (Plate I, 3).

Material examined: Whole leaves KG. 2815.171 (three leaves), KG. 4697.2 (holotype 2a, three leaves), .9 (paratype 9a, four leaves), .27 (two whole and eight fragments), .31 (three whole and seven fragments). Fragmentary leaves KG. 4697.15, .26, .29, .32 (seven fragments) all from the Coal Nunatak, Triton Point Member, Neptune Glacier Formation, Fossil Bluff Group; Late Albian.

Etymology: Named after Alexander Island, first sighted in 1820 and named in honour of the Russian Czar by Thaddeus Bellingshausen.

Diagnosis: Leaves petiolate, flabellate; base asymmetric, acute; margin crenate. Venation loosely actinodromous to irregularly palinactinodromous; primary veins terminate medially within a crenation. Gland terminating each crenation; gland venation comprising a medial primary vein and two lateral, marginal, accessory veins.

Description: Leaves small, flabellate to cordate, 15–35 mm long, 25–30 mm wide (Plate I, 1, 2). Leaf apex rounded, indistinct, base asymmetric acute ending in a narrow petiole. Petiole 2 mm wide and up to 14 mm long (Plate I, 3). Margin crenate, crenations 1–3 mm wide and up to 2 mm deep, apex of each crenation with a small nipple-like projection, sinuses rounded (Plate I, 4).

Venation comprising a main vascular "trunk" entering and extending into the leaf base for up to

3 mm before dividing into a loosely actinodromous to irregularly palinactinodromous pattern (Plate I, 1, 3; Fig. 2A,B). Primary veins dichotomising and diverging through lamina, each primary vein terminating medially within a crenation. Secondary veins arising subopposite to alternate. The most apical secondary veins from adjacent primaries fuse at or near the sinus of each crenation to form a marginal vein (Plate I, 4). Marginal vein fusing with primary vein at the apex of each crenation to form a glandular tooth (Plate I, 5; Fig. 2C). Tertiary and higher-order veins irregular forming polygonal aeroles; aeroles from tertiary veins elongate at an acute angle to secondary veins (Fig. 2C).

Remarks: Jefferson (1981) grouped small crenate leaves in a hughesian palaeotaxon DICTYOPHL-PHOBOS, now referred, in part, to *Hausmannia papilio* Feruglio, a dipteridaceous fern (Cantrill, 1995). The small leaves differ substantially from *Hausmannia* Dunker. No evidence of square net-like veins are present, the leaf has a distinct marginal vein, at least four orders of veins were recognised, and each crenation terminates in a distinct gland or tooth. On this basis, these small leaves were separated from *Hausmannia* and identified as angiospermous.

Few leaves are well enough preserved to reveal details of secondary venation. Most reveal a pattern of actinodromous to weakly palinactino-dromous primary veins (Plate I, 1) dichotomising through the lamina similar to primary veins in the fern *Hausmannia*. However, four specimens yielded details of secondary and tertiary veins which form a more organised pattern. Towards the leaf margin the secondary veins diverge acutely from the medial vein and pass directly towards the sinus of the leaf margin. At the sinus, secondary veins from adjacent primaries fuse and produce a marginal vein. The marginal vein in turn fuses at the apex of each crenation with a primary vein (Plate I, 4, 5). This region at the apex of each crenation is characterised by a distinct discoloured region (Plate I, 1). In better preserved specimens the region of vein fusion is marked by a larger area of more darkly coloured and distinctly carbonised material. This area is interpreted as a glandular structure with the discolouration of the rock being due to contents of the glands.

PLATE I
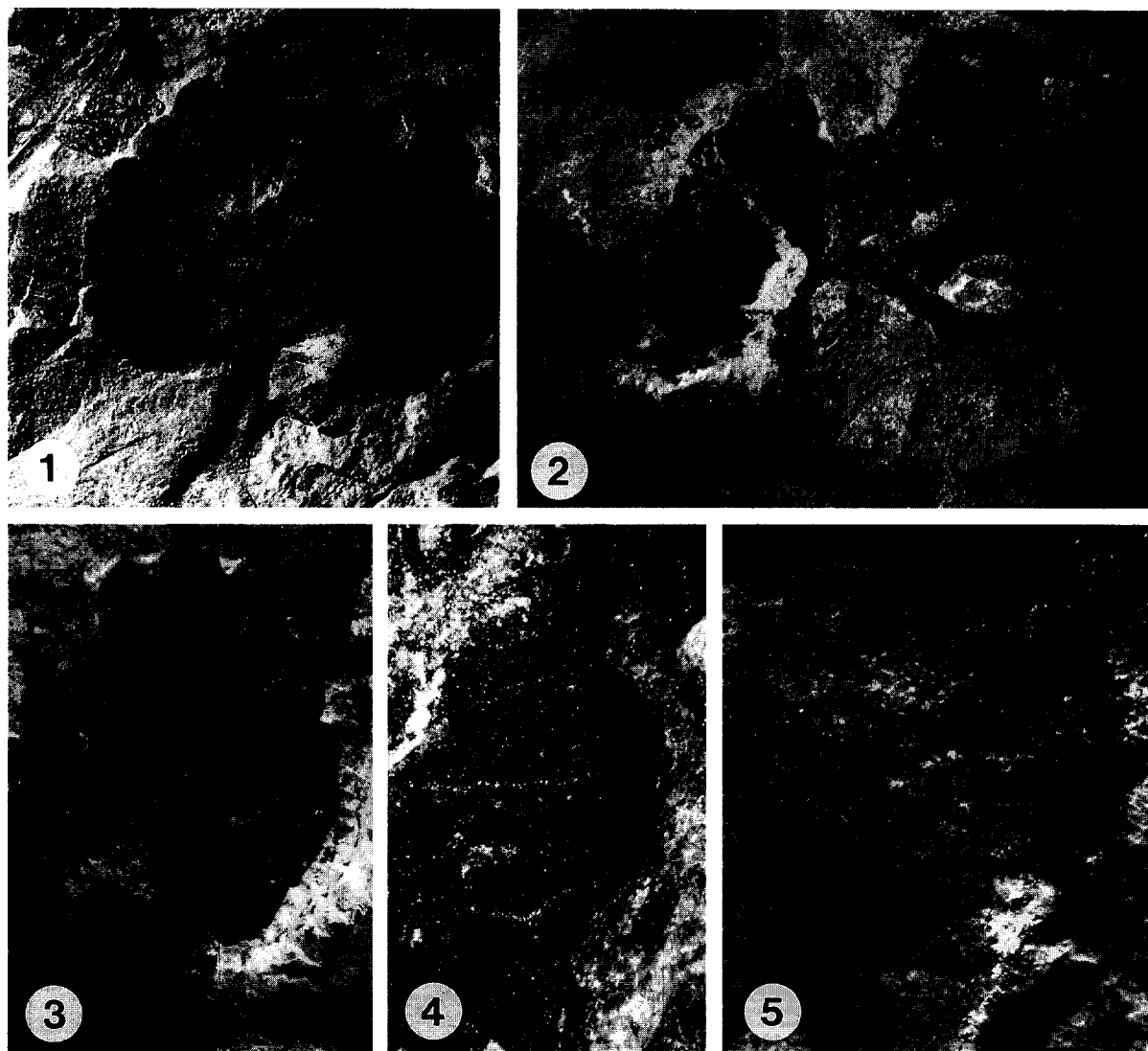
Hydrocotylophyllum alexandri Cantrill, *sp. nov.*

1. KG. 2815.171a, whole leaf showing palmate primary veins and crenately toothed margin. × 2.5.
2. KG. 4697.27a, fragmented whole leaf attached to a creeping rhizome? × 2.5.
3. KG. 4697.2a, holotype. Whole leaf illustrating asymmetric base and crenate toothed margin. × 2.5.
4. KG. 4697.2b, leaf margin showing fusing of lateral marginal vein with primary vein at apex of tooth. × 7.
5. KG. 4697.9a, details of secondary and higher-order veins forming venation patterns similar to that seen in chloranthoid teeth (compare to Fig. 3D). × 7.

The venation pattern of each crenation (Fig. 2C), with a medial primary vein, and two lateral marginal accessory veins, is similar to that observed in the Chloranthaceae, and the teeth are regarded as chloranthoid. However, chloranthoid teeth in extant angiosperms lack strong accessory veins (e.g. Hickey and Wolfe, 1975; Fig. 2A,B) like those seen in *Hydrocotylophyllum alexandri*. Chloranthoid teeth with strong accessory veins do however, characterize Lower Cretaceous leaves
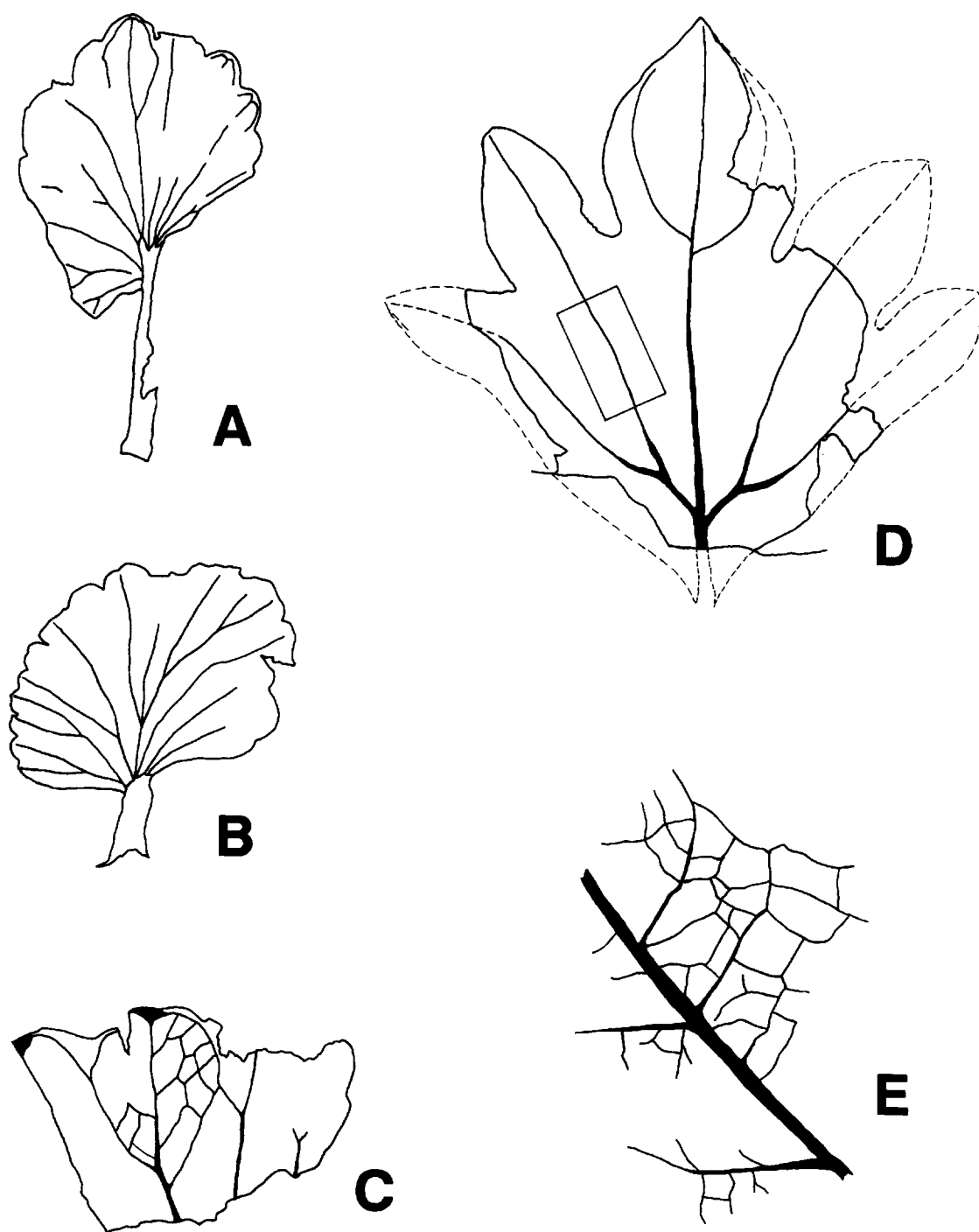
Fig. 2. Line drawings of *Hydrocotylophyllum alexandri* Cantrill, *sp. nov.* (A–C) and *Araliaephyllum quinquelobatus* Cantrill, *sp. nov.* (D, E). Solid lines observed features, dashed lines interpretative. (A) KG 4697.2a, ×2, (B) KG 2815.171a. ×2. Whole leaves illustrating the palmate venation and crenate margins. (C) KG. 4737.9a, line drawing of higher-order vein patterns and marginal gland interpreted as a chloranthoid tooth (illustrated in Plate I, 5), ×4. (D) KG. 4693.16, whole leaf showing primary venation pattern, ×2. (E) KG. 4737.8, close up of equivalent area marked in square box on (D), illustrating high-order venation pattern, ×4.

described as *Moutonia quetamensis* (Pons, 1988) from Colombia, and simple craspedodromous leaves (Drewys Bluff leaf type 1) from the Potomac Group in North America (Upchurch, 1984a). Both taxa differ in leaf shape and primary venation pattern from *H. alexandri*.

Leaves of similar shape to *H. alexandri* occur in Lower Cretaceous sedimentary rocks of Australia (Douglas, 1965; Drinnan and Chambers, 1986; Taylor and Hickey, 1990), Portugal (Teixeria, 1947, 1948), and North America (Fontaine, 1889; Doyle and Hickey, 1976; Hickey and Doyle, 1977). Fontaine (1889) described leaves from the Cretaceous of North America which he assigned to a new genus, *Proteaephyllum* Fontaine, 1889, recognising seven species. Only *Proteaephyllum dentatum* Fontaine, 1889, *P. reniforme* Fontaine, 1889, and *P. orbiculare* Fontaine, 1889, are similar in leaf shape to the material from Alexander Island. Despite the morphological similarity the venation patterns differ; primary veins cannot be distinguished from secondary or higher-order veins as all are of equal thickness, and the veins form a reticulate pattern with the aeroles elongated parallel to the leaf length. In contrast the tertiary vein areolation in *Hydrocotylophyllum alexandri* forms elongate areas at an angle to the midvein (Plate I, 5; Fig. 2C). This type of areolation is rare within extant angiosperms, and has only been described for *Ascarina* within the Chloranthaceae. Extinct fossil genera such as *Moutonia* Pons, 1988 and *Eucalyptophyllum* Fontaine also have this type of areolation. *Proteaephyllum dentatum* is the only dentate species. Hickey and Doyle (1977) reported *P. dentatum* as having A-1 type teeth with a large apical glandular area. The syntypes examined here (USNM 3902, 3196) have apical glands. However, the venation supplying these glands differs from that seen in the Alexander Island material and the latter does not conform to *Proteaephyllum*.

Hydrocotylophyllum Teixeria, 1947, originally described from the Lower Cretaceous of Portugal, is comparable to *Proteaephyllum* (Teixeria, 1947, 1948). However, the material figured in Teixeria (1947, 1948) differs from *Proteaephyllum* in having primary palmate veins that can be easily distinguished from higher-order veins. *Hydrocotylophyllum lusitanicum* Teixeria, 1947 comprises

small, petiolate, cordate leaves with crenate margins. Although Teixeria (1947, 1948) described the venation as weakly pinnate, the illustrations show a primary actinodromous to weakly palinactinodromous venation pattern. The material from Alexander Island conforms to the primary venation pattern, leaf size and shape, and crenate margins, of *H. lusitanicum*. However, the Alexander Island leaves are slightly larger, 25–30 mm in diameter, as opposed to up to 25 mm in *H. lusitanicum*, and have coarser crenations. There is little variation in crenation size in *H. alexandri* whereas the crenations in *H. lusitanicum* decrease in size from the leaf apex towards the leaf base. This difference in characters, along with the lack of details on secondary or higher-order veins in *H. lusitanicum*, suggest that the Alexander Island material is best placed in a new species, *H. alexandri*.

Douglas (1965) ascribed material from a Lower Cretaceous borehole in Victoria to *Hydrocotylophyllum lusitanicum*. This material is also similar in leaf form and primary venation to the material described herein, but differs in the form of the crenations. The crenations lack glandular terminations, and the higher-order venation is loosely organized into irregularly brochidodromous loops. Neither the material illustrated by Teixeria (1947, 1948) or the material described by Douglas (1965) have secondary or higher-order venation patterns preserved that appear similar to those seen in *H. alexandri*. Also occurring in the Victorian Cretaceous is a small leaf with a loosely and irregularly palinactinodromous venation pattern (Taylor and Hickey, 1990) that is similar to the material from Alexander Island. However, the leaf margin is folded over the lamina of the leaf obscuring the margin and the marginal venation, although a fimbrial vein appears to be present (Taylor and Hickey, 1990). Based on the leaf characters and attached inflorescence, this plant is considered to be closely allied to Chloranthaceae or Saururaceae, Aristolochiaceae, Piperaceae (Taylor and Hickey, 1990).

The leaf morphology and primary venation pattern seen in *H. alexandri* is similar to that found in families such as Saururaceae, Aristolochiaceae, and Piperaceae.

4.2. Palinactinodromous venation

Araliaephyllum Fontaine

Araliaephyllum quinquelobatus Cantrill, *sp. nov.*

Holotype: KG. 4693.16 from Coal Nunatak, Alexander Island; Triton Point Member, Neptune Glacier Formation, Fossil Bluff Group; Late Albian (Plate II, 1).
*Material examined*: KG. 4693.16 (holotype, whole leaf), isolated leaf lobes KG. 4693.4, fragmentary leaves KG. 4737.7, .8, .34, .53, .54, .70, .73, .86, .93, .141. All from the Triton Point Member, Fossil Bluff Group; Late Albian.
Etymology: From Latin *quinque* meaning five and *lobatus* meaning lobed; referring to the common five-lobed leaf margin that is distinctive of this taxon amongst the Alexander Island angiosperms.
Diagnosis: Leaves palmate, three- to five-lobed. Primary venation palinactinodromous, weakly decurrent; secondary veins rarely forming brochi-

PLATE II
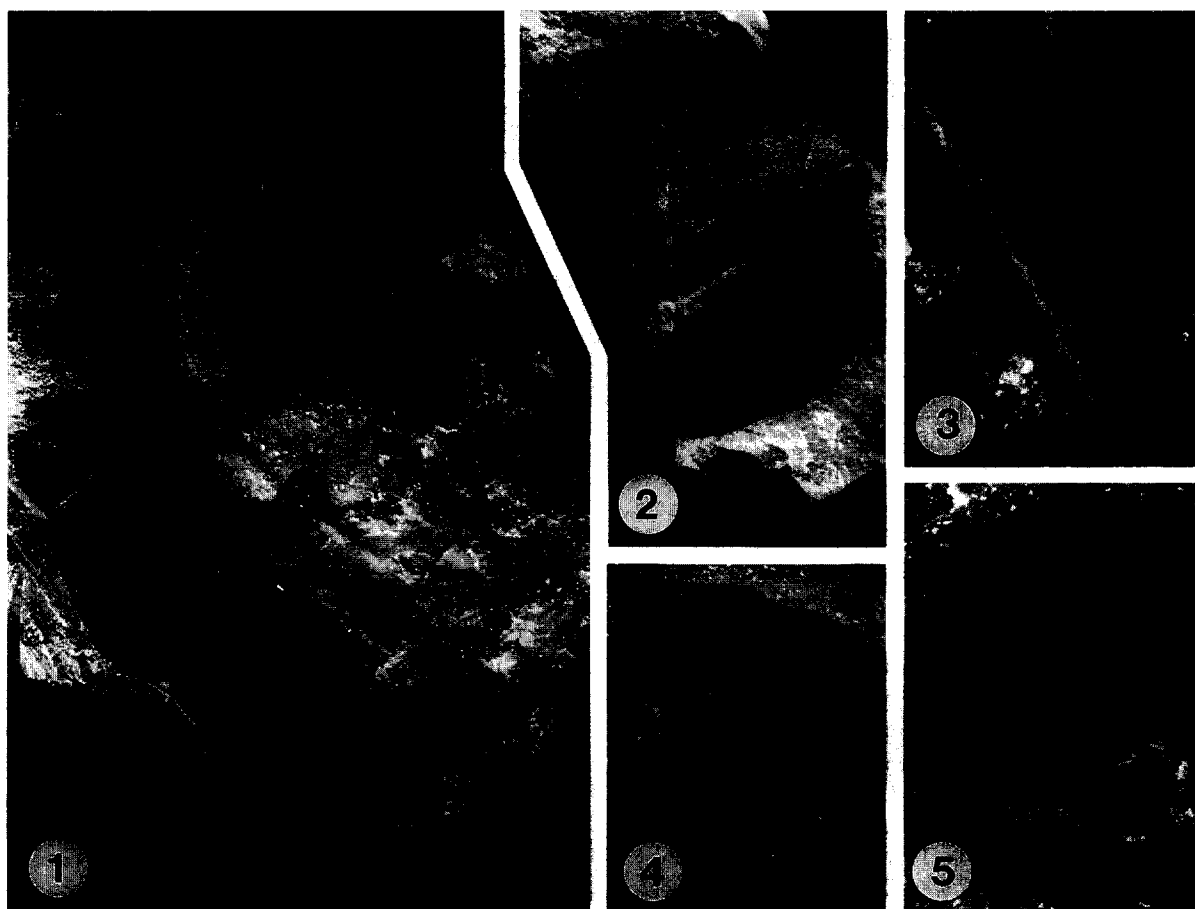
1–3, 5 *Araliaephyllum quinquelobatus* Cantrill, *sp. nov.*
1. KG. 4693.16, holotype. Illustrating the palinactinodromous venation and five leaf lobes. × 2.
2. KG. 4737.54, three-lobed leaf note rare brochidodromous loops in the secondary veins. × 2.
3. KG. 4737.53, close up of leaf surface with faint striations interpreted as possible hairs. × 7.
5. KG. 4737.8, faint details of tertiary and higher-order veins. × 7
4. *Timothyia trinervis* Cantrill, *gen. et sp. nov.* KG. 4737.97, holotype. × 2.5.

dodromous loops; tertiary and higher-order veins more irregular.

Description: Leaves palmate, three to five lobes; leaves 28–40.5 mm long and 25–32 mm wide (Plate II, 1, 2; Fig. 2D). Smaller leaves three-lobed. Leaf lobes 12–15 mm long, 8–16 mm wide, apex acute, base constricted. Sinus between lobes rounded, margin entire. Lower leaf surface possibly covered in hairs (Plate II, 3).

Primary veins palinactinodromous, three to five, weakly decurrent, diverging between 24 and 31°, each primary vein terminating apices of leaf lobe. Secondary veins opposite to subopposite, arising 45–60° to primary vein, not reaching leaf margin, rarely forming indistinct brochidodromous loops. Tertiary and higher-order veins disorganised (Plate II, 5; Fig. 2E).

Remarks: Few intact leaves were found, most consist of isolated lobes or whole leaves fragmented so that the parts are lying close to each other. It is the only leaf within the Triton Point Member that has a strongly palinactinodromous venation pattern.

No Lower Cretaceous palmately lobed leaves are known from the Southern Hemisphere. However, there are a few records in Upper Cretaceous sediments from South America. Berry (1937) identified palmately lobed leaves from the Upper Cretaceous of Patagonia which he assigned to *Sterulia sehuensis* Berry. This taxon is three-lobed, with a basally palinactinodromous venation. Secondary veins forming brochidodromous loops and higher-order veins appear to be well organised and on this basis *S. sehuensis* is not similar to the material from Alexander Island.

Palinactinodromous palmately lobed leaves are widespread in Northern Hemisphere late Early Cretaceous and Late Cretaceous sediments (Crabtree, 1987). Within the Cretaceous Potomac succession, palinactinodromous palmately lobed leaves show a progressive trend in ordering of venation patterns (Hickey and Doyle, 1977). The earliest recognised leaf, *Araliaephyllum obtusifolium* Fontaine, has only moderately ordered secondary veins and weak irregular development of tertiaries. Morphological evolution of these palmate leaves resulted in more regular development of lobes and the ordering of secondary veins into

brochidodromous loops (e.g. "*Sassafras*" *potomacensis* Fontaine). These type of leaves are succeeded in the fossil record by leaves with well developed and percurrent tertiary veins. The leaves described here from Alexander Island are intermediate in development between the earliest stages. The tertiary veins ramify, and only rarely form brochidodromous loops. This is in distinct contrast to "*Sassafras*" *potomacensis* which has prominent brochidodromous loops in secondary and tertiary veins. On this basis the Alexander Island leaves are best assigned to *Araliaephyllum* Fontaine, 1889.

The Potomac Group palmate leaves have generally been allied to the platanoids (Doyle and Hickey, 1976; Hickey and Doyle, 1977), and platanoid flowers are known from Cretaceous sediments (Friis et al., 1988). However, the platanoid complex recognised by Hickey and Doyle (1977) has been shown to contain leaves with affinities to the Laurales (Upchurch, 1984b; Upchurch and Dilcher, 1990). The case for lauraceous affinity of some of the leaves is strengthened by the discovery of lauraceous flowers (Drinnan et al., 1990) and wood (Herendeen, 1991) in Cenomanian sedimentary rocks, and it appears that the Laurales were more important in Cretaceous floras than previously thought.

Affinity of leaves with either the platanoids or Laurales can be confirmed through differences in leaf morphology and venation patterns. Distinct morphological features that characterize Laurales are strongly decurrent primary veins, primary veins recurving apically, the leaf sinus being braced by a secondary vein that arises from the midvein and passes to the sinus where it bifurcates into a marginal vein (Upchurch and Dilcher, 1990). In contrast, platanoid leaves tend to have non-decurrent primary veins, the course of the primary veins is straight, and they lack a sinus bracing vein; the leaf sinuses tend to be braced by brochidodromous vein loops. In *Araliaephyllum quinquelobatus* the primary veins are slightly decurrent and recurved, and the sinuses appear to be braced by a secondary vein that arises from the primary vein and recurves to the leaf sinus where it bifurcates into a marginal vein (Plate II, 2). The morphological features seen in *A. quinquelobatus* appear to be more consistent with a lauralean interpretation.

Cretaceous three-lobed leaves with a similar sinus bracing pattern have been assigned to *Pabiania* (Upchurch and Dilcher, 1990; Upchurch et al., 1994). However, *A. quinquelobatus* lacks the strongly decurrent primary veins seen in *Pabiania* and cannot be assigned to this genus.

4.3. Acrodromous venation

TIMOTHYIA Cantrill, *gen. nov.*

Type species: *Timothyia trinervis* Cantrill and Nichols, *sp. nov.* from the Triton Point Member, Neptune Glacier Formation, Fossil Bluff Group; Late Albian.

Diagnosis: Leaves ovate to circular. Leaf apex obtuse; base rounded, petiolate. Venation acrodromous, imperfect, basal to suprabasal; midvein with two lateral decurrent primaries. Admedial secondary veins brochidodromous.

Etymology: Named in honour of Dr. Timothy H. Jefferson, who first recognised angiosperm leaves within the Triton Point Member.

Timothyia trinervis Cantrill, *sp. nov.*

Holotype: KG. 4737.97 from Citadel Bastion, Triton Point Member, Neptune Glacier Formation, Fossil Bluff Group, Late Albian (Plate II, 4).

Material examined: KG. 4737.5, .44, .97 (holotype); all from the Triton Point Member, Fossil Bluff Group; Late Albian.

Etymology: From the Latin *tri* meaning three and *nervis* meaning vein; referring to the three acrodromous veins.

Diagnosis: As for genus.

Description: Leaves ovate to circular, 14–16 mm long and up to 16 mm wide (Plate II, 4; Fig. 4C). Leaf apex obtuse, base rounded to obtuse, petiolate; petiole up to 2 mm wide and 2 mm long. Margin entire.

Venation acrodromous, imperfect, basal to suprabasal, midvein 0.5 mm wide, tapering to 0.2 mm, persisting to leaf apex; two lateral primary veins arising acutely, 40–45° to main vein, decurrent, up to 0.5 mm wide, traversing three quarters of the distance to the leaf apex, tapering, recurved (Plate II, 4; Fig. 4C). Secondary veins indistinct, those derived admedially from the lateral primaries forming brochidodromous loops. Higher-order venation not distinguishable.

Remarks: *Timothyia trinervis* is known from only three leaves. However, it is distinctive being the only leaf with acrodromous venation from Alexander Island.

Amongst living angiosperms, acrodromous venation patterns are found within the Laurales (Hernandiaceae, some Lauraceae) and Piperales (Hickey and Wolfe, 1975). The morphology of *T. trinervis* with well developed lateral decurrent primary veins, that are free from the midvein to the base of the lamina, is similar to core families of the Laurales such as Hernandiaceae (e.g. *Illigera*), and so *T. trinervis* is regarded as lauralean. During the latest Albian? to Cenomanian, leaf floras from North America suggest this order was well established (Upchurch and Dilcher, 1990). By the latest Cretaceous at least three leaf morphotypes assignable to Laurales can be recognised (Upchurch and Wolfe, 1987). Support for the importance of

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PLATE III

1–3, 6. *Gnafalea jeffersonii* Cantrill, *gen. et sp. nov.*
1.   KG. 4718.1, holotype. Note faint outlines of secondary veins and slightly crenate margin ×2.5.
2.   4718.23, note paired secondary veins arise from stout midrib. ×2.5.
3.   KG 4718.64, base of small crenate leaf with petiole. ×2.5.
6.   KG. 4718.95, leaf margin with primary tooth. ×4.
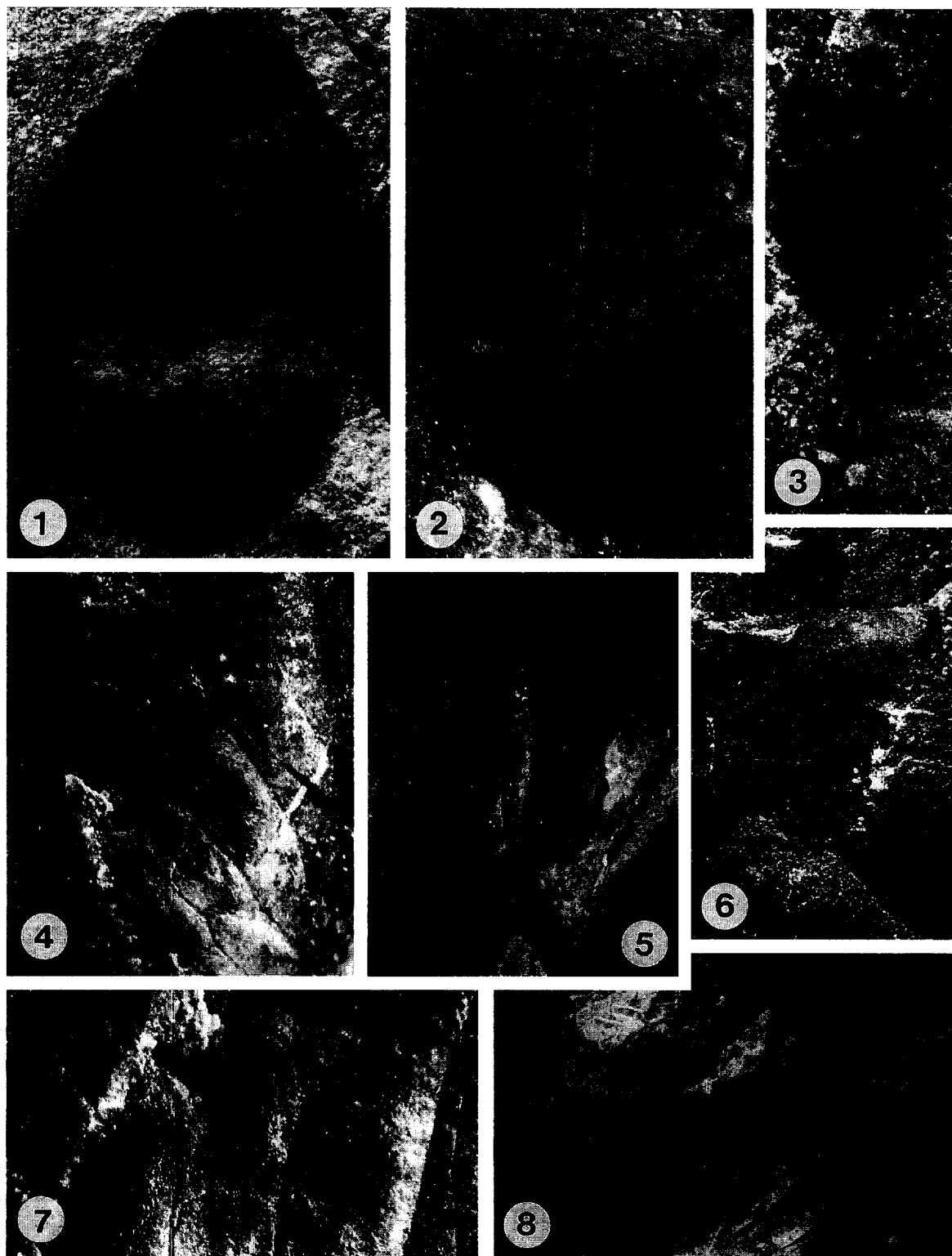4, 5, 7, 8. *Gnafalea binatus* Cantrill, *sp. nov.*
4.   KG. 4737.135, holotype illustrating the leaf margin. ×4.
5.   4737.135. ×2.
7.   4737.135, details of teeth type and venation. ×7.
8.   4737.134 ×2.

PLATE III

Laurales in Early Cretaceous floras comes from well-preserved flowers (Retallack and Dilcher, 1981; Drinnan et al., 1990). *Mauldinia* flowers, described from the Potomac Group (Cenomanian), are attributed to the Lauraceae (Drinnan et al., 1990). Drinnan et al. (1990) pointed out that this family is advanced within the Laurales and so representatives of cladistically more basal families were probably present in Early Cretaceous times. One reason for the lack of recognition of this group is the low preservation potential of Lauraceae pollen which would lead to an underestimation of abundance and diversity of this group in Early Cretaceous times (Drinnan et al., 1990). This may partly account for the large discrepancy in diversity of leaf floras in comparison to microfloras (Lidgard and Crane, 1990) during the Early Cretaceous (Drinnan et al., 1990).

5. Pinnately veined leaves

5.1. Craspedodromous venation

GNAFALEA Cantrill, *gen. nov.*

Type: *Gnafalea jeffersonii* Cantrill and Nichols, *sp. nov.* from Titan Nunatak, Alexander Island; Triton Point Member, Neptune Glacier Formation, Fossil Bluff Group; Late Albian.
Diagnosis: Leaves lanceolate to ovate; leaf apex acute; leaf base petiolate. Venation simple, pinnate, craspedodromous, margin dentate.
Etymology: An anagram of fagalean; a leaf type for poorly preserved pinnate veined leaves from the Southern Hemisphere.

Gnafalea jeffersonii Cantrill, *sp. nov.*

Holotype: KG. 4718.1 from Titan Nunatak; Triton Point Member, Neptune Glacier Formation, Fossil Bluff Group; Late Albian (Plate III, 1).
Material examined: Whole leaf specimens KG. 2820.64, KG. 2821.44, KG. 4718.1 (holotype), .32 (three leaves), .34, .43, .47, .70, KG. 4721.2, .5, KG. 4737.67?. Almost intact leaves KG. 4718.2, .9, .13, .14, .20, .27, .31, .37, .39, .69, .102. Fragmentary leaves with attached petioles KG.

4718.4, .50, .92, .107, .120. Fragmentary material KG. 4718.3, .5, .6, .11, .15, .16, .18, .21, .22, .24–26, .28, .30, .33, .41, .46, .49, .51–55, .57, .59, .65, .68, .74, .75, .78, .83–88, .91, .98–101, .112, .122, .125. All from the Triton Point Member, Neptune Glacier Formation, Fossil Bluff Group; Late Albian.
Etymology: After Dr. T.H. Jefferson, who first recognised angiosperm leaves within the Triton Point Member of Alexander Island.
Diagnosis: Leaves elliptical to ovate; leaf apex acute to retuse; leaf base petiolate. Venation pinnate, craspedodromous, secondary veins less pronounced than midvein. Leaf margin dentate, margin divided into primary, secondary and rarely tertiary teeth. Each tooth supplied by a primary, secondary or tertiary vein, respectively.
Description: Leaves elliptical to ovate; 15–47 mm long and 10–28 mm wide (Plate III, 1–3; Fig. 3A). Length typically 22–30 mm, width typically 12–18 mm. Leaf apex acute, occasionally retuse, base variable from acute to obtuse, rarely asymmetric. Petiolate, petiole 0.5–1.2 mm wide, 4–7 mm long, base slightly expanded (Plate III, 3). Margin dentate; teeth compound comprising a primary convex/convex tooth, secondary teeth basal convex/convex (Plate III, 6). Rare tertiary teeth present. Each tooth with an apical vein (Plate IV, 4), primary tooth with a secondary vein; secondary and tertiary teeth with tertiary veins.

Venation pinnate, craspedodromous, midvein prominent, 0.4–0.9 mm wide, extending to leaf apex, tapering slightly (Plate III, 1, 2). Secondary veins straight, rarely slightly apically recurved, opposite to alternate, five to seven pairs, arising from midvein at angles of 37–54°. Distance between secondaries 2.5–5 mm decreasing towards the leaf apex and base. Secondary veins traversing two thirds of the way towards leaf margin before dividing, apical division terminating apex of primary tooth, basal division terminating apex of secondary tooth. Apices of teeth with a distinct, small, 0.25 by 0.25 mm, carbon-rich area, setaceous (Plate IV, 4) to spherulate. Tertiary veins irregular, higher-order veins not distinguishable.
Remarks: All intact leaves have poorly delineated tertiary and higher vein order venation. In addition they lack petioles; it was more common to find
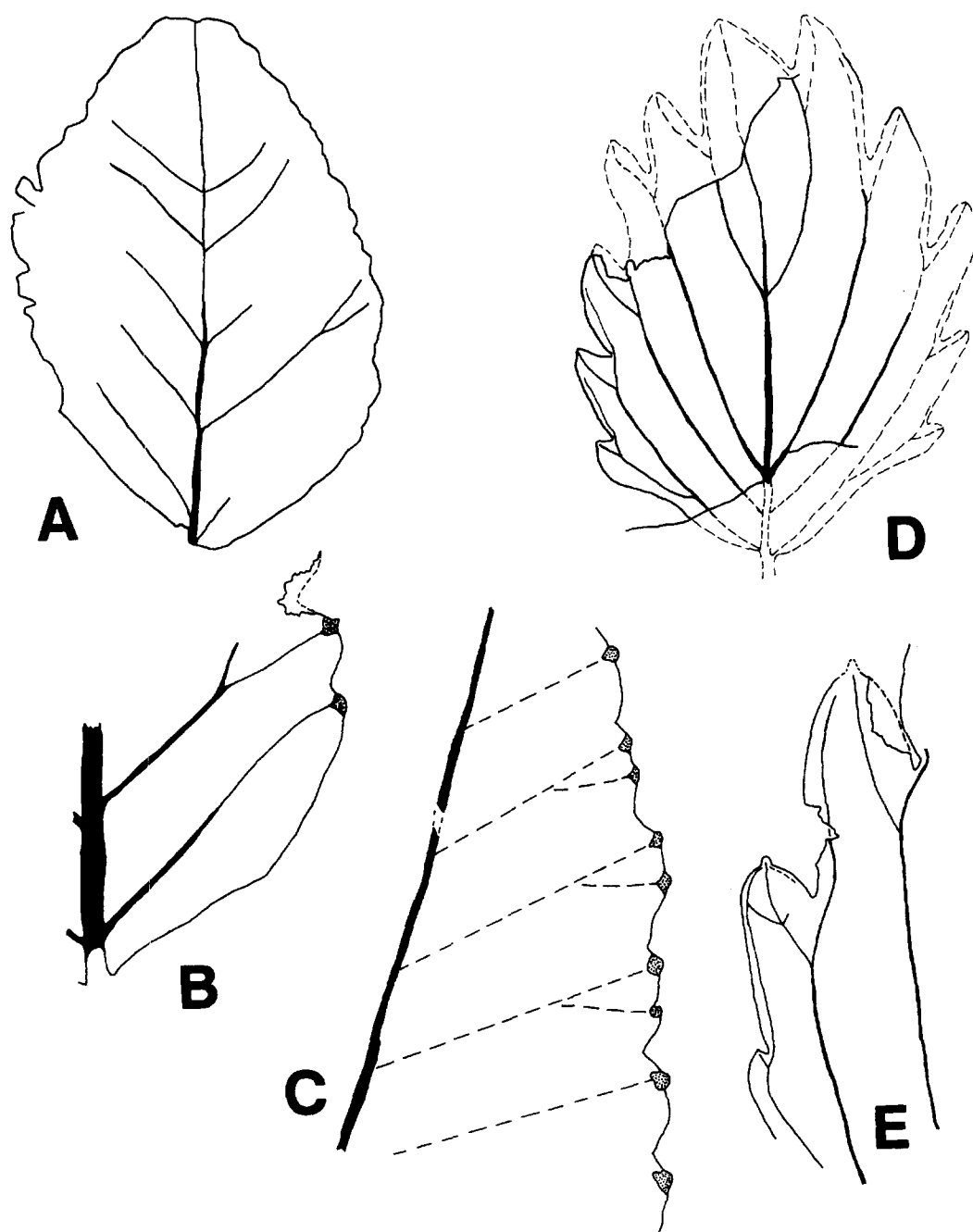
Fig. 3. Line drawings of *Gnafalea* Cantrill, *gen. nov.* (A–C) *G. jeffersonii* Cantrill, *gen. et sp. nov.* (A) KG. 4718.1, holotype, illustrating the pinnate craspedodromus venation, ×2. (B) KG. 4718.23 illustrating the leaf margin and venation, ×4. (C) KG. 2821.44 marginal teeth with glandular apices. Secondary venation inferred, ×4. (D, E) *G. binatus* Cantrill, *sp. nov.* (D) KG. 4737.134, inferred leaf shape, ×2. (E) KG. 4737.134, illustration of tooth type and venation pattern, ×4.

PLATE IV
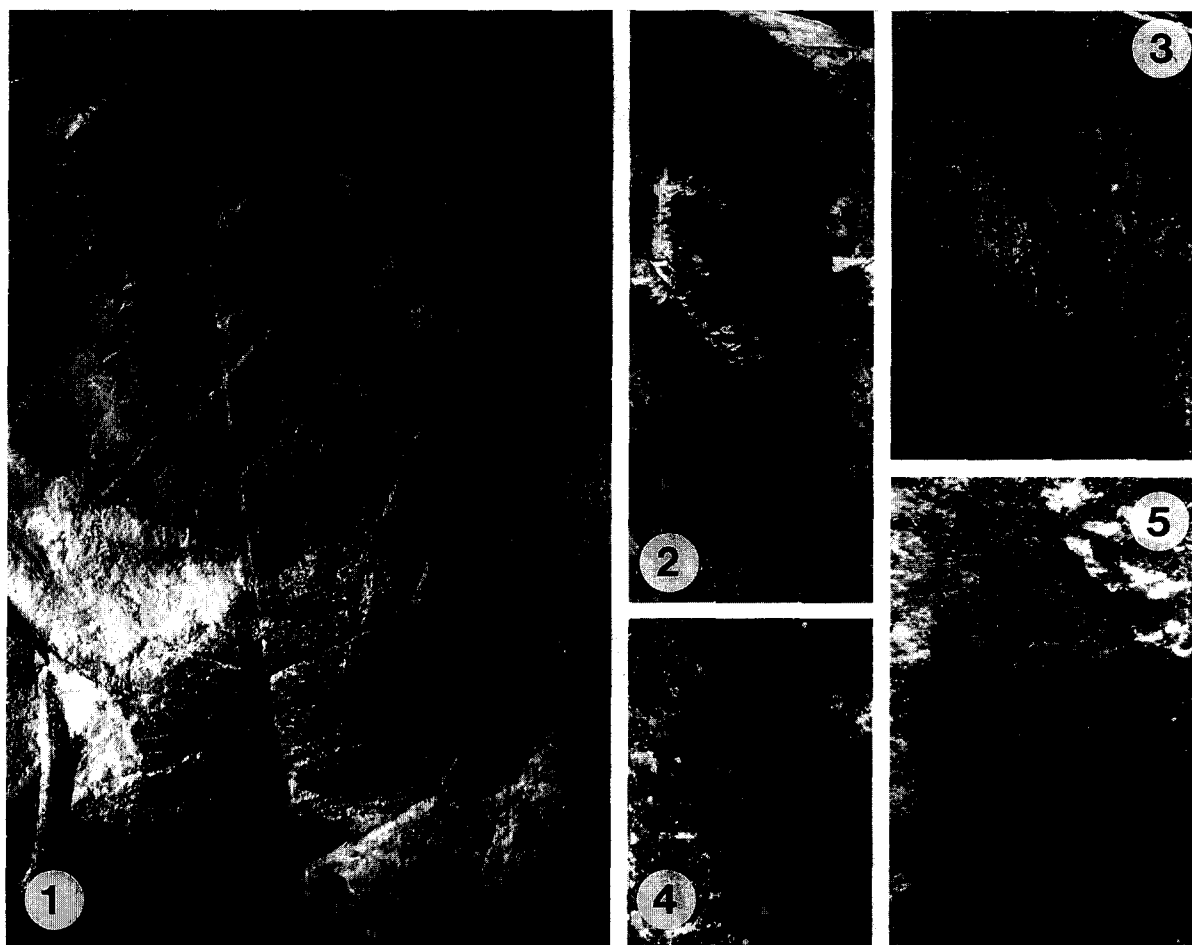
1–3, 5 *Ficophyllum palustris* Cantrill, *sp. nov.*
1. KG. 4747.84, holotype. ×2.
3. KG. 4747.71, leaf apex with prominent tip and marginal teeth. Note strongly looped secondary veins. ×2.
2. KG. 4747.99, small lanceolate leaf. ×2.
5. KG. 4747.99, close up of leaf margin illustrating small nipple like teeth which terminate veins. ×7.
4. *Gnafalea jeffersonii* Cantrill, *sp. nov.* KG. 4718.23 close-up of teeth type which appear similar to those of *Ficophyllum palustris* Cantrill, *sp. nov.* ×7.

almost intact leaves or the basal parts of leaves with attached petioles. The leaf margin varies from dentate to almost entire. Venation patterns were established from almost intact and fragmentary leaves. However, preservation in dark siltstones made it difficult to delineate high order venation. The only specimen with tertiary or higher orders was identified by Jefferson (1981), who assigned it to the hughesian palaeotaxon RETIPHYLL-

PAGODA. This specimen (KG. 2821.44) is preserved in a tuffaceous horizon and impressions of volcanic fragments have disrupted the leaf surface. Despite this, some tertiary and higher-order veins were observed but, it was not possible to establish the venation pattern. This specimen has small marginal teeth with distinct discoloured apical region interpreted as a gland (Fig. 3C). The teeth appear to terminate secondary and higher-order veins

(Fig. 3C). Similar teeth (Plate IV, 4) were seen on a few of the specimens from KG. 4718 (Fig. 3B) but because of the preservation mode this was difficult to establish. Due to the poor preservation and the lack of detail of high order veins it is difficult to compare the teeth seen in *G. jeffersonii* to angiospermous teeth described in Hickey and Wolfe (1975).

Poorly preserved angiospermous leaves with craspedodromous venation from the Southern Hemisphere have tended to be allied to the southern beech, *Nothofagus* (e.g. Jefferson, 1980; Thomson and Burn, 1977). Although such poorly preserved leaves do superficially appear similar to the Fagaceae, pinnate venation of the simple craspedodromous type is widespread amongst the "higher" Hamamelidae including Fagales, Betulales, Eupetales, Eucommiales, and amongst some of the lower pinnate Dilleniidae (Actinidiaceae, Saururaceae) (Hickey and Wolfe, 1975). The leaves from Alexander Island lack obvious tertiary veins and so do not compare well to the above groups which, in general, have well organised percurrent tertiary veins.

Gnafalea binatus Cantrill, *sp. nov.*

Holotype: KG.4737. 135 from Citadel Bastion, Alexander Island; Triton Point Member, Neptune Glacier Formation, Fossil Bluff Group; Late Albian (Plate III, 5).
Material examined: KG. 4737.50, .134 (paratype), .135 (holotype) from Citadel Bastion; Triton Point Member, Neptune Glacier Formation, Fossil Bluff Group; Late Albian.
Etymology: From the Latin *binatus* meaning paired; after the strongly pronounced and paired secondary veins that is diagnostic of this species.
Diagnosis: Leaves ovate; leaf apex acute; leaf base petiolate. Venation pinnate, craspedodromous, midvein and secondaries equally prominent. Leaf margin dentate. Secondary vein branching in tooth sinus one branch passing to the tooth apex the second branch becomes marginal and extends to the apex? of the superadjacent tooth.
Description: Leaves ovate, at least 35 mm long and 28 mm wide (Plate III, 5, 8; Fig. 3D). Leaf apex acute, base obtuse? to rounded, assumed to be

petiolate (Fig. 3D). Margin toothed; teeth 2–5 mm long and 1.5–3.5 mm wide, basal and apical side of teeth convex, sinuses rounded (Plate III, 4, 7).

Venation pinnate, craspedodromous, midvein and secondaries equally prominent. Secondary veins moderate, opposite, arising 27–35°, incurved, divergence angle decreasing apically. Secondary vein branching just below tooth, each branch thinner than secondary vein. Basal branch entering the tooth and extending to tooth apex; apical branch curving into the adjacent apical tooth sinus, becoming marginal and possibly extending to adjacent apical tooth apex (Plate III, 7; Fig. 3E).
Remarks: This leaf type is rare within the sequence and is represented by two almost intact leaves and a small part of a leaf apex (KG. 4737.50). It is easily distinguished from the other leaf types by the consistently opposite and pronounced secondary veins, and the type of marginal teeth.

The interpretation of the tooth venation is limited by the small sample size and the preservation style. The vein course generally comprises a secondary vein that arches towards the apex and branches near the tooth sinus. The course of the basal branch is clear, taking a direct course to the tooth apex. However, the course of the apical branch is less clear, the vein branch initially passes towards the tooth sinus where it becomes marginal. The vein then either passes marginally towards the adjacent apical tooth apex or disappears. This style of branching has been reported as widespread in the Rosidae (Hickey and Wolfe, 1975) and can most closely be compared with the cunonioid tooth of Hickey and Wolfe (1975). Cunonioid teeth are widespread in Rosidae and are considered to be primitive within this subclass (Hickey and Wolfe, 1975). On this basis, *Gnafalea binatus* can possibly be assigned to the Rosidae.

5.2. Brochidodromous venation

Ficophyllum Fontaine

Ficophyllum palustris Cantrill, *sp. nov.*

Holotype: KG. 4747.84 from Coal Nunatak; Triton Point Member, Neptune Glacier Formation, Fossil Bluff Group; Late Albian (Plate IV, 1).

Material examined: KG. 4747.71 (paratype), .84 (holotype), .93 (two leaves), .99 all from the Triton Point Member, Neptune Glacier Formation, Fossil Bluff Group; Late Albian.

Etymology: From Latin *palustris* meaning swampy; referring to the occurrence of this leaf in swamp sediments.

Diagnosis: Leaves ovate; leaf apex acute to acuminate, margin toothed. Teeth apparently not supplied by veins. Venation brochidodromous, secondary veins sparse, enclosing isodiamteric regions.

Description: Leaves ovate, greater than 70 mm long and ranging from 11 to 50 mm wide (Plate IV, 1; Fig. 4A). Leaf apex narrowly acute to acuminate (Plate IV, 3), base rounded. Margin toothed, teeth 2.5–4.5 mm apart in mid-leaf region, 5–7 mm apart at the leaf apex (Plate IV, 3). Teeth 1.7–4.5 mm long and 0.2–0.7 mm deep, concave to straight apically, convex basally, apex acute, sinus angle 55–78°.

Venation brochidodromous (Plate IV, 1). Midvein massive to stout, persisting to leaf apex, 0.25–0.95 mm wide, tapering slightly apically. Secondary veins sub-opposite, 10–15 mm apart, distance between veins decreasing apically; arising at 29–75° to main vein, origin angle decreasing apically. Secondary veins straight for 0.5–0.66 leaf width before recurving apically and adjoining superadjacent secondary vein at an acute to right angle. Tertiary veins indistinct, imperfect looped aeroles. Venation of teeth not clear, apparently without veins or glands.

Remarks: Of the five fragmentary leaves were recognised, KG. 4747.84 is the most intact, but lacks the apical portion of the leaf. The apex is best illustrated in KG. 4747.71 (Plate IV, 3; Fig. 4B) which is designated as a paratype. Secondary venation is reasonably well-preserved in a number of specimens, but numerous probable root traces (Plate IV, 1) obscure detail of tertiary and higher-order veins, making interpretation of secondary vein courses difficult. Although four of the leaves are similar in shape, a small lanceolate leaf (Plate IV, 2) is also assigned to this taxon on the basis of its similar venation pattern and marginal teeth. It differs not only in size from the other specimens but also in a more acute origin of the secondary veins (29–42°). However, the marginal teeth in all specimens are distinctive with straight/convex margins and acute apices. Despite relatively well-preserved material no veins supplying these teeth were observed and the apices lack glands.

Large leaves with well developed brochidodromus vein loops are amongst the earliest well-organised vein patterns to appear in the angiosperm fossil record. Within the Potomac Group these leaves were variously assigned to *Ficophyllum*, *Ficus* Tournef., or *Rogersia* Fontaine, 1889 (Fontaine, 1889; Wolfe et al., 1975). The assignment of the leaves to extant taxa is incorrect as pointed out by Wolfe (1973), and the specimens described here are best accommodated amongst those taxa described as *Ficophyllum*. Wolfe et al. (1975 p. 815) suggested that the grade of venation in *Ficophyllum*, *Ficus*, *Salix*, and *Rogersia* is most similar to that seen in the Magnoliidae and in particular the Magnoliales (e.g. Winteraceae, Himantrandraceae and Canellacaceae). Within the *Rogersia* group of leaves, Wolfe et al. (1975, p. 815) also recognised two toothed forms where the teeth lacked glands and the venation did not reach the outermost part of the tooth. Unfortunately, these leaves were not figured or fully described which precludes further comparison. The similarities of *F. palustris* to the leaves discussed by Wolfe et al. (1975) in vein organisation, teeth lacking glands, and veins not reaching the outermost part of the teeth suggests that *B. palustris* belongs to the Magnoliales.

Dicotylophyllum lobatus Cantrill, *sp. nov.*

Holotype: KG. 4737.48 Citadel Bastion; Triton Point Member, Neptune Glacier Formation, Fossil Bluff Group; Late Albian (Plate V, 2).

Fig. 4. Line drawings of *Ficophyllum palustris* Cantrill, *sp. nov.* (A, B), *Dicotylophyllum lobatus* Cantrill, *sp. nov.* (D), and *Timothyia trinervis* Cantrill, *gen. et sp. nov.* (C). A. KG. 4747.84, holotype, illustrating preserved part of leaf and interpreted leaf shape, ×2. (B) KG. 4747.71, paratype illustrating the leaf apex and venation pattern. Note the small marginal teeth apparently lacking venation, ×2. (C) KG. 4737.97 ×1.5. (D) KG. 4737.45, leaf lobe with details of high order veins, ×2.
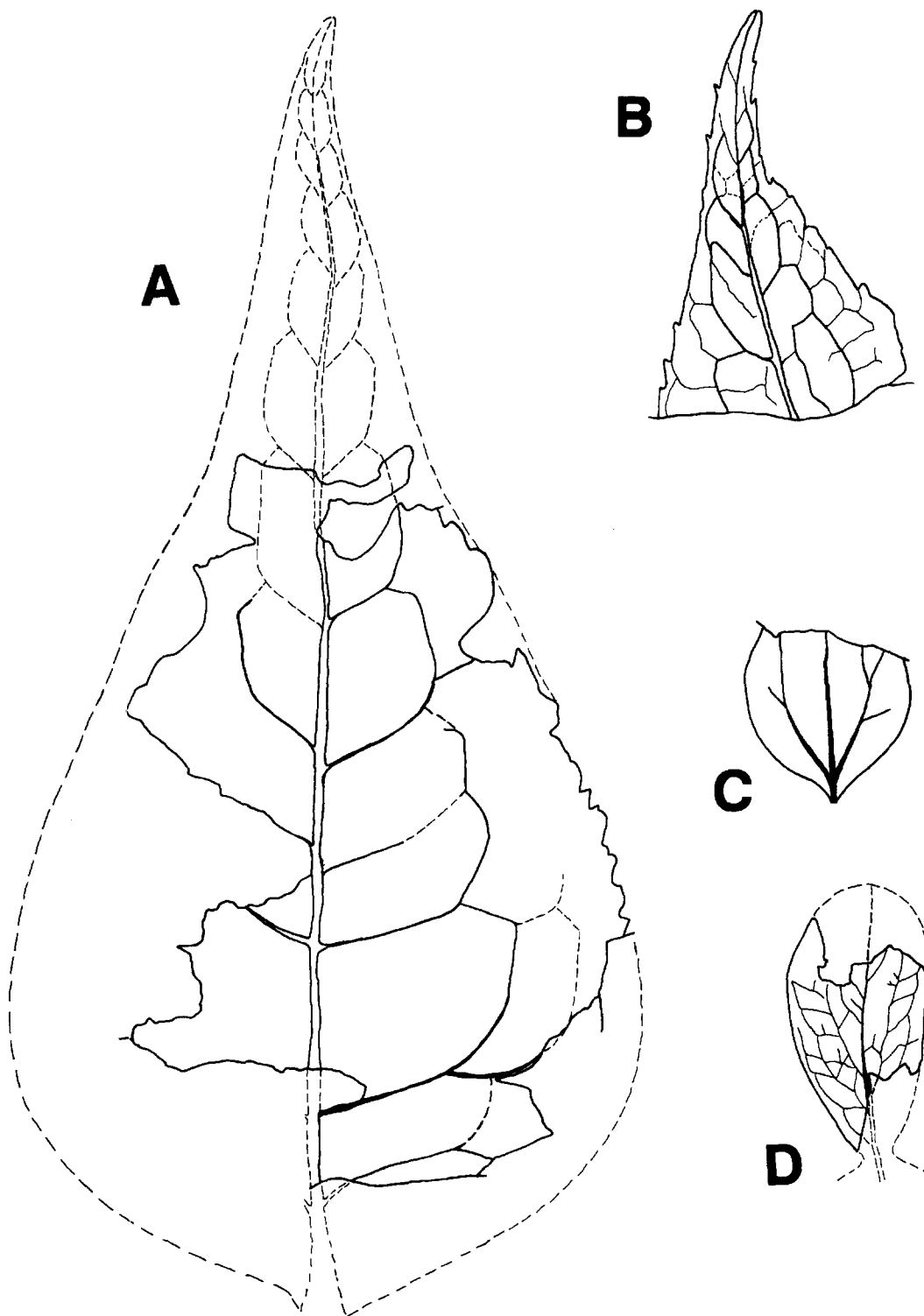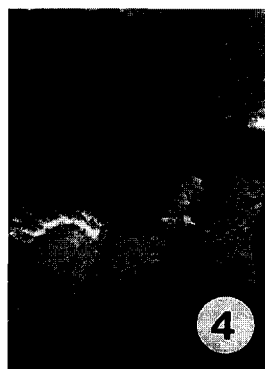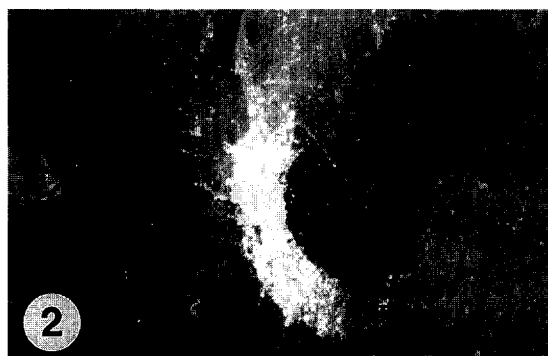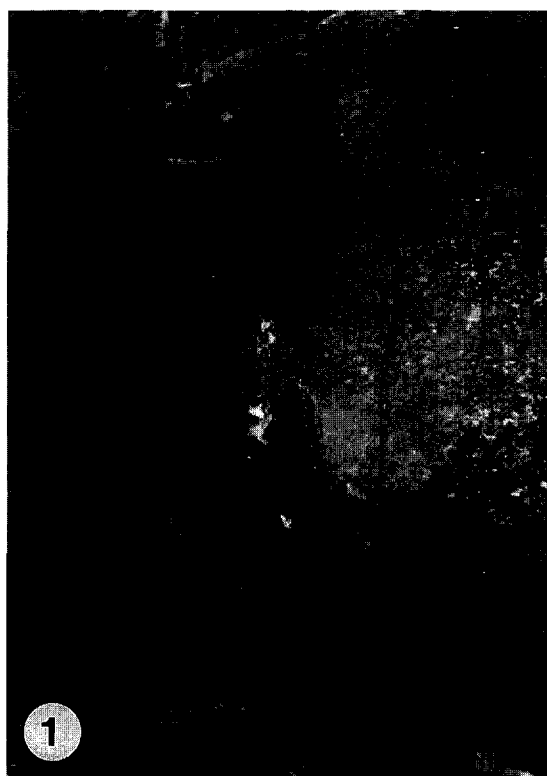
Material examined: KG. 4737.44 (four leaves), .45 (paratypes, two leaves), .46 (two leaves), .47, .48 (holotype), .49, .51 (three leaves), .52. All from the Triton Point Member, Fossil Bluff Group; Late Albian.

Etymology: From the Latin *lobatus* meaning lobed; referring to the lobed nature of these leaves.

Diagnosis: Leaf lobed; lobes thick, coriaceous; apices acute; margins entire. Venation brochidodromous; tertiary veins forming irregular areoles, higher-order veins not distinguished.

Description: Fragmentary leaves preserved as ultimate lobes (Plate V, 2). Leaf lobes thick, coriaceous (Plate V, 3), lanceolate to ovate, 11–27 mm long, 7–16 mm wide. Leaf lobes apices acute to rounded, occasionally retuse, base constricted, margin entire.

Venation brochidodromous, midvein extending almost to leaf apex (Plate V, 1). Secondary veins arising 32–48°, recurved apically into a series of loops. Lower secondaries joining superadjacent secondaries at obtuse to right angles; often enclosed in secondary and tertiary arches by higher-order veins (Plate V, 1, 4; Fig. 4D). Tertiary veins arising between secondaries forming irregular aeroles. Higher-order veins not distinguished.

Remarks: The form-genus *Dicotylophyllum* Saporta was used originally for small fan-shaped leaves from the Cretaceous of Portugal. However, in recent times this genus has been used for a broad range of poorly known dicotyledonous leaf types with various venation patterns (e.g. Upchurch and Dilcher, 1990; Upchurch et al., 1994). The leaf morphology of *Dicotylophyllum lobatus* indicates that it is derived from a larger leaf. However, it is unclear whether they are

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PLATE V

Dicotylophyllum lobatus Cantrill, *sp. nov.*

1. KG 4737.45, close up of leaf illustrating the brochidodromous secondary veins and irregular higher order veins. × 7.
2. KG. 4737.48, most complete leaf preserved illustrating the lobed nature of the foliage. Note the apparent lack of venation. × 2.5.
3. KG. 4737.42, small lobe with prominent transverse wrinkles indicating the thick coriaceous nature of the foliage. × 2.5.
4. KG. 4737.49, counterpart to 2 above illustrating the brochidodromous secondary veins. × 2.5.

derived from compound leaves or from lobed palmate leaves. Some specimens suggest a palmate arrangement. For example, in KG. 4737.48 (Plate V, 2) two leaf lobes lie on slightly different planes, but appear from their juxtaposition, to join forming part of a palmate leaf. The interpretation of the leaves as thick and coriaceous is based on the consistent features seen in parts and counterparts. When splitting the rock to reveal the specimens, one part is transversely wrinkled with no details of venation (Plate V, 3) whereas the other (Plate V, 4) is smooth with details of the venation.

Dicotylophyllum lobatus can be separated from the only other brochidodromous leaf, *F. palustris*, by its smaller size, lanceolate shape and entire margin. Entire margined leaves with brochidodromous venation patterns are widespread amongst species in Magnoliidae and Dilleniidae (Hickey and Wolfe, 1975). However, whereas Magnoliidae tend to have entire margins, many Dilleniidae are toothed (Hickey and Wolfe, 1975).

6. Discussion

6.1. Palaeoenvironments

In the southern nunataks of Alexander Island, the Triton Point Member of the Neptune Glacier Formation is estimated to be over 1 km thick, and is represented by approximately 470 m of section at Citadel Bastion, 175 m at Titan Nunataks, and 200 m at Coal Nunatak. Strata are inclined from 4 to 10° dipping towards the south or southeast. Stratigraphically this suggests that the oldest beds are exposed on Citadel Bastion and are overlain by those at Titan Nunatak with the youngest beds occurring on Coal Nunatak. This interpretation is also supported by changes in the sedimentary facies (Fig. 5).

Citadel Bastion and Titan Nunatak

Two broad lithofacies are recognised. Very coarse sandstone with thin conglomerate beds form prominent cliffs which are separated by less well exposed units of thinner-bedded, fine to medium sandstone and siltstone. The thick coarse units have scoured bases overlain by granule or pebble conglomerate; the bulk of each unit is made up of trough cross-bedded (0.5–1.0 m sets), very coarse sandstone, fining up in some cases to coarse sandstone (Fig. 5). These units range from 6 to 10 m thick (Fig. 5) and vary in lateral extent from at least 100 m to over 300 m; the full width cannot be determined because of the nature of the exposure. Finer-grained facies associations consists of beds 0.2 to 1.5 m thick of medium or fine sandstone (Fig. 5), sometimes normally graded, but more commonly with ripple cross lamination or horizontal laminae. Siltstone beds are 0.1–0.4 m thick, dark and rich in plant remains. Rootlet horizons occur at the tops of some siltstone beds.

Fining-up successions of trough cross-bedded coarse sandstone and conglomerate are typical of bedload-dominated, braided rivers (Cant and Walker, 1976; Miall, 1978). The cross-bedded sands arranged into lenticular sets separated by bounding surfaces are reminiscent of that described by Allen (1983) as deposits of individual bar forms in a braided river channel. On this basis they are interpreted as mid-channel bar deposits, although individual barforms could not be identified in outcrop. The coarse grain size, scale of cross-bedding and lateral extent of the coarse facies suggest deposition by sandy to pebbly braided rivers within a broad channel belt on the alluvial plain. The thickness of these coarse sand and conglomerate units can be used to imply channel depths of 6–10 m at Citadel Bastion and shallower channels of 4–8 m at Titan Nunatak.

Finer sandy and silty facies would have been deposited on areas of the alluvial plain beyond the channel belt; deposition by periodic floods which carried sand at high velocities (indicated by the planar stratification) across the flood plain is suggested.

Coal Nunatak

The lowermost 75 m of section at Coal Nunatak contains the same facies seen at Citadel Bastion and Titan Nunatak (Fig. 5), and so is interpreted as representing a similar environment. However, strata in the upper part of Coal Nunatak are distinct from all lower beds, being composed of generally finer-grained material, with a more lensoid geometry to the sandstone beds. Exposure is

Fig. 5. Summary log through the Triton Point Member (Neptune Glacier Formation) for the southern nunataks, with detailed sedimentary logs of the key angiosperm localities.

poorer than in the lower parts of the Triton Point Member in this area, with at least three-quarters of the surface of the upper part of the nunatak is covered by scree. From a distance, some of the sandstone beds can clearly be seen to be in lenticular units 1.5–3.0 m thick and a few tens of metres wide. Individual beds within these lenses are typically sharp-based, normally-graded and show cross-bedding in 0.1–0.2 m sets, ripple-cross-lamination and planar, horizontal laminae. Thinner (0.1–1.0 m), and in some places finer, sandstone beds occur interbedded with siltstone and mudstone beds which are generally less than 0.1 m thick. Ripple and planar lamination is common in the thinner, finer beds and rootlets occur in places, along with abundant plant debris on bedding planes.

The lenticular sandstone bodies are interpreted as fluvial channel fill units and the interbedded thin sandstones and very thin mudstones as overbank facies. In comparison to the fluvial facies in the lower parts of the Triton Point Member, the individual channels were shallower, with a narrower channel belt; a lower flow velocity is indicated by the predominance of ripple cross-lamination over larger scale cross-bedding and a grain size ranging up to 1 mm maximum. The presence of narrow channel belts suggests either a greater stability of individual channels or a higher frequency of channel avulsion (Leeder, 1978; Bridge and Leeder, 1979). Low-angle surfaces within one medium sandstone body, parallel to the channel margin, may be lateral accretion surfaces or epsilon cross-bedding (Allen, 1965), indicative of a meandering channel form. However, exposure is too limited to demonstrate that all channels were sinuous and meandering. Exposure of the overbank is poor, and probably biased towards coarser beds; logged sections include a high proportion of decimetre-scale, medium sandstone beds with ripple and planar lamination. This suggests that overbank flood events were of relatively high energy, able to deposit sheets of sand over the floodplain.

Synthesis

The lower horizons at Citadel Bastion and Titan Nunatak are within a braided river system which was decreasing in gradient and channel size through time; broad channel belts formed by migration of braided channels over the alluvial plain, possibly forming a braidplain environment (Fig. 6A). Overbank flooding events beyond the channel belts were high energy and deposited medium to coarse sand on the floodplain (Fig. 6A). This braidplain environment evolved into a lower-energy river system, possibly meandering (Fig. 6B), but also with floodplain deposits of similar grain size to the in-channel component on Coal Nunatak.

Broad channel belts in the braided channel facies and the relatively coarse floodplain deposits throughout the Triton Point Member suggest that the rivers had weak banks (Friend, 1978), easily breached by floodwaters which periodically inundated the alluvial plain with strong flows to deposit decimetre scale sand beds. Rootlet horizons and abundant plant debris within the overbank facies show that there was sufficient time between flooding events for communities of plants to become established.

6.2. Palaeoecology

Three stages can be recognised in the formation of fossil leaf assemblages: (1) leaf abscission and accumulation; (2) transport; and (3) burial and preservation (Burnham et al., 1992). A number of studies (e.g. Burnham, 1993, 1994; Ferguson, 1985; Greenwood, 1991, 1992) have addressed the first phase of formation through the examination of extant forests. From these studies we can conclude that forest litter represent accumulations of local vegetation (Ferguson, 1985) and that the distance of leaf fall from any individual tree is generally restricted to a radius of canopy height (Burnham, 1994). This holds true in closed canopy forests but transport from the parent tree becomes more significant the more open the vegetation type, with the abundance of leaf remains declining along an approximate negative exponential function (Ferguson, 1985). In general, more accurate estimates of diversity are obtained from leaf litter in temperate climates and this decreases towards the tropics (Burnham, 1993, 1994). Overall, however, litter composition consistently underestimates
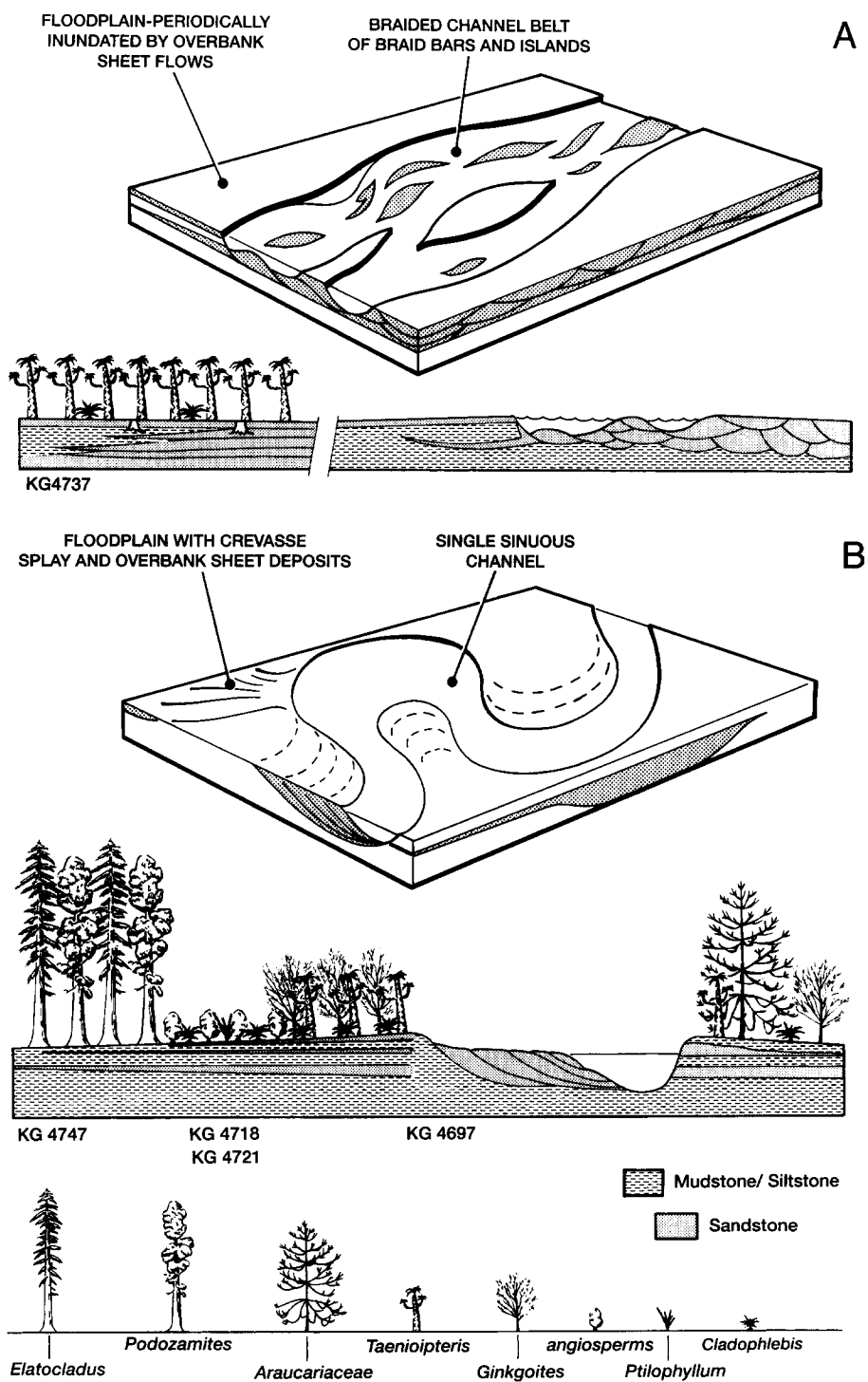
Fig. 6. Suggested relationships between sedimentary environments and vegetation. (A) Depositional setting for the Triton Point Member at Citadel Bastion, Titan Nunatak and the lower part of Coal Nunatak. (B) Depositional setting for the upper part of Coal Nunatak.

canopy diversity by up to a factor of 3.5 (Burnham, 1993, 1994), due to differential breakdown of some taxa and other biotic biases (Ferguson, 1985; Burnham, 1993, 1994). Thus, although leaf litter can be used to accurately assess the diversity of the forest canopy, it is a better predictor of forest productivity, accounting for up to 99% of the biomass produced.

The second and third phases in the formation of fossil leaf assemblages are more problematic. The degree of transport and how this filters the resulting leaf assemblages is no doubt important in assessing transported assemblages. However, many assemblages in the fossil record represent in-situ leaf litter accumulations (e.g. Wing et al., 1993) and so reflect the local vegetation.

Qualitatively, a number of criteria can be used to interpret fossil leaf litter. Overstorey species contribute larger quantities of leaf litter, due to the size of the organism, that is spread over a wider area. On this basis, leaf taxa that are widespread over the whole bedding surface are interpreted as overstorey species. However, as leaves generally occur within a radius of canopy height a wide spacing along bedding of sample points is needed to evaluate this. Burnham (1994) suggested that samples 12.5 m apart will give a good indication of canopy diversity in diverse rainforest communities. Species that show localized abundances over individual bedding planes may be taken to indicate smaller plants such as shrubs and the lateral distribution may also give some estimate of size. In addition to these general criteria, the physiognomic features of the fossil leaves often suggest life habit.

Although the angiosperm material described above appears abundant, only six of the 72 localities yielding plant fossils contained angiospermous leaves. Of these localities KG. 4721 and KG. 4693 yielded two leaves each and KG. 4747 yielded five leaves, despite an abundant megaflora of bryophytes, ferns, cycadophytes and conifers. Only three localities (KG. 4697, 4737, 4718) had both an abundant megaflora and a significant number of angiosperm leaves.

KG. 4697

Occurring marginal to a lenticular sandstone body (channel deposit) the sediments at KG. 4697 comprise ripple and planar laminated very fine sandstones to coarse siltstones ranging from 5 to 30 cm thick. Occasional thin rootlet horizons (1–2 cm) occur at the tops of these beds. This site is interpreted as representing overbank deposits marginal to a river channel.

The flora occurring within the siltstones and on top of the individual beds mainly comprises *Taeniopteris* Brongniart (9%), *Ginkgoites* Seward (32%) and *Cladophlebis* Brongniart (35%). Both *Taeniopteris* and *Ginkgoites* are large up to 30 cm long by 4 cm wide and 16 cm long by 12 cm wide, respectively. These leaves are larger than at other localities where *Taeniopteris* and *Ginkgoites* occur, and this is taken to indicate a more riparian habitat rather than different species. For example, the *Taeniopteris* leaves at KG. 4737 are up to 15 cm long by 1.5 cm wide and *Ginkgoites* leaves at KG. 4718 are 5–6 cm long and 4–5 cm wide. Minor components of the vegetation at KG. 4697 include *Brachyphyllum*, and the angiosperm *Hydrocotylophyllum alexandri*. The angiosperm leaves occur scattered in large numbers over individual bedding planes. Some specimens appear to be rhizomatous or with creeping stems (Plate I, 2) and individual plants appear to be herbaceous. It is suggested that the vegetation at KG. 4697 comprised an overstorey of *Taeniopteris* and *Ginkgoites* with an understorey of *Cladophlebis*. Freshly deposited overbank sediments marginal to the river channel were colonised by the herbaceous angiosperm *H. alexandri*.

KG. 4737

This fossil horizon is sandwiched at the interface between a 100 cm thick, medium sandstone and an overlying 150 cm thick siltstone. The siltstone has a non-erosive base, contains low angle current ripples at its base and evidence of flow around in situ plants; towards the top of the bed laminations become planar. The underlying sandstone is characteristic of a sheet flood deposit. This deposit has engulfed a pre-existing vegetation, as evidenced by casts of tree stumps in growth position (Plate VI, 2). The development of roots in the top of this sandstone, penetrating up to 10 cm, the presence of palaeorelief, and an abundant layer of fossilised leaves, interpreted here as leaf litter, all identify
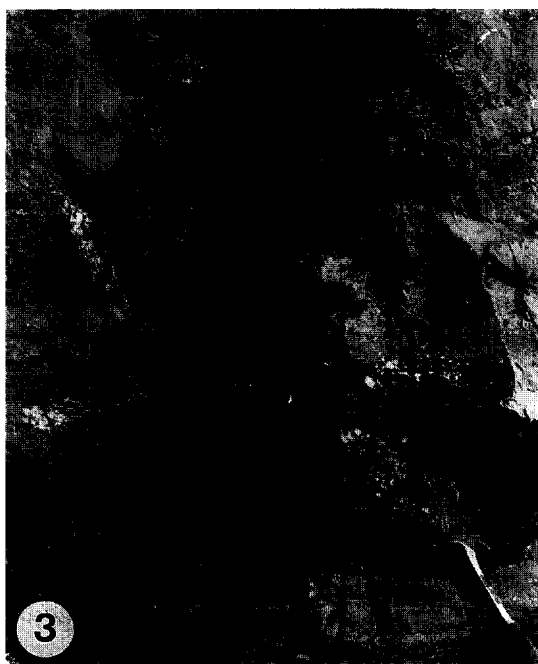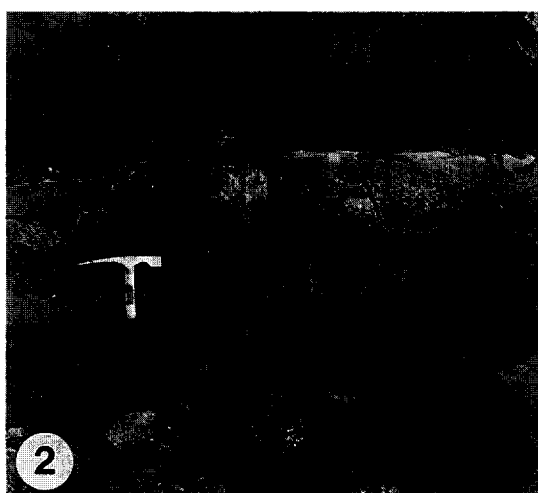
KG. 4737 as a fossil soil horizon. The vegetation developed on this soil was buried by a low-energy flood event as evidenced by the preservation of palaeotopography, small grain size and ripple laminations. This suggests that the channel was more distal than during the deposition of the lower sheet flood sands. Rapid burial of the leaf litter close to the parent plant is supported by the lack of leaves, except in the basal 10 cm of the siltstone bed, indicating minimal transport.

Over 200 m of lateral exposure was available for examination. *Taeniopteris* comprised the dominant taxon varying between 60 and 100% of specimens per slab. Its abundance and widespread nature indicates that it was probably the major overstorey plant. Other taxa make up less than 40% (usually less than 5%) abundance but have distinct associations along strike, indicating deposition close to the parent plant. *Cladophlebis* abundance increased in proximity to raised mounds on the soil surface bearing stems (Plate VI, 3) rising from 0% to up to 40%. The raised mounds are interpreted as the base of the *Cladophlebis* plant with the foliage being buried nearby. Frond bases can be traced vertically through bedding (Plate VI, 3) Many extant ferns have either an erect rhizome or produce a small "trunk" (e.g. Osmundaceae, Blechnaceae, *Blechnum nudum* (Labillardière) Mettenius ex Luerssen). In the former type of plants the close proximity of leaf bases served to act as a sediment and leaf litter trap producing raised mounds where the plant grows. A similar habit is envisaged for the fern bearing *Cladophlebis* foliage.

Between the raised mounds, local abundances of thalloid liverworts and ferns (cf. *Coniopteris*, *Hausmannia papilio*) occur. Away from the base

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PLATE VI

Locality KG. 4737.
1. Base of plant bearing *Cladophlebis* fronds note the raised surface mound produced by this plant.
2. Underlying sheet flood sandstone with cast of in-situ tree. KG. 4737 is a soil developed on this unit.
3. In-situ plant base buried by siltstone note the radiating vertical cracks. These are developed around compressed frond material.

of the bed, in the upper 30 cm, rare fern foliage (*Aculea* Douglas) and cone scales (*Araucarites* Presl) are found. Their rarity and occurrence in the upper part of the siltstone suggests that they are transported elements of the regional flora.

Angiosperm leaves occurred in isolated pockets or as isolated leaves along bedding. The morphology of *Araliaephyllum quinquelobatus* suggests a tree-like habit and its sparse but widespread occurrence suggests that it was scattered in distribution amongst the overstorey. The small leaves of *Dicotylophyllum lobatus* and *Timothyia trinervis* occur in small localised quantities. Given the coriaceous nature of *D. lobatus* it seems most likely that this represents an evergreen shrub, whereas *T. trinervis* was either a small herbaceous plant or shrub. Conversely they could be elements of the regional vegetation.

KG. 4737 is interpreted as a back swamp site that is occasionally flooded by either ponding due to water table rise or overspill of channels. The small grain size and low-energy conditions suggest a distal position to channel deposition. *Taeniopteris* probably formed an extensive overstorey. The understorey comprised mounds formed by ferns (*Cladophlebis*) with other smaller ferns and liverworts growing scattered between the mounds. The rare angiosperm leaves are suggestive of significant transport or rare local elements of the local flora.

KG. 4718

This locality occurs within a 1 m sequence of medium bedded fine sandstones siltstones and mudstones. The sandstones and siltstones have low-angle ripples or are plane laminated and are interpreted as overbank deposits. KG. 4718 is a thin soil horizon, as evidenced by shallow roots penetrating bedding by up to 3 cm below an overlying leaf litter. The soil is overlain by further fine sandstones and siltstones. Plant material is common at the interface between the two units and incorporated in the overlying siltstone bed. This site is interpreted as overbank deposits in a more distal environment than KG. 4697 as evidenced by the thinner sandstone beds and the greater abundance of fine sediments.

The plant taxa represented include ferns (*Cladophlebis*, *Aculea*), Ginkgoales (*Ginkgoites*),

Cycadophytes (*Ptilophyllum* Morris) and Conifers (*Brachyphyllum* Heer). *Gnafalea jeffersonii* is particularly common making up 40% of the flora by abundance. However, this abundance is largely restricted to isolated pockets extending for some 30 to 195 cm along strike. Cosmopolitan species along strike include the *Brachyphyllum* and *Ginkgoites* whereas *Ptilophyllum* and the ferns are patchy in their occurrence.

The sedimentology indicates that KG. 4718 was more distal to the river channel than KG. 4697. This is indirectly supported by the presence of small *Ginkgoites* leaves. At KG. 4697 large *Ginkgoites* leaves occur (up to 16 cm long by 12 cm wide). In contrast, KG. 4718 contains smaller *Ginkgoites* (6 cm by 5 cm) leaves. Roth and Dilcher (1978) and Ferguson (1985) have demonstrated that the smaller leaves on a tree are most likely to be transported further. This is due to two reasons; firstly the outer leaves in the canopy tend to be smaller as they are exposed to stronger sunlight, whereas the shade leaves (larger) tend to be closer to the centre of the canopy. As a result shade leaves tend to accumulate closer to the parent plant. Secondly, smaller leaves are more easily transported (Ferguson, 1985) and so are found farther from the parent plant.

The vegetation at KG. 4718 is interpreted as comprising low shrubs of *Ptilophyllum*, *Gnafalea* and ferns (*Cladophlebis*, *Aculea*) with scattered *Ginkgoites* trees towards the river channel.

KG. 4747

This locality contains a transported assemblage of leaves, fossils occurring in a thin 3 cm siliceous siltstone. This siltstone occurs within a sequence of fine sand and muds. Most beds are thinly bedded, with planar laminations; however, occasional slightly thicker units with low angle current ripples, invertebrate trackways and tool/drag marks all attest to low current conditions and slow settling. The depositional setting is similar to KG. 4737, and KG. 4747 is interpreted as a distal backswamp deposit with ponding, rare levels of flooding, and a wet waterlogged environment. However, unlike KG. 4737 the flora is remarkably different, comprising largely *Podozamites* (Brongniart) Braun (46%) and *Elatocladus*

Halle (41%) with minor ferns (*Cladophlebis*, *Sphenopteris*, BREVIPTERIS-RHOMBOID) liverworts (cf. *Hepaticites*) and rare angiosperm leaves (*Ficophyllum palustris*). This assemblage of fossil plants is interpreted as a conifer canopy of *Podozamites* and *Elatocladus* with a diverse understorey of ferns, liverworts and rare angiosperms.

This is a similar setting to *Ficophyllum* leaves in the Potomac Group which form minor components in conifer dominated assemblages. Doyle and Hickey (1976) interpreted *Ficophyllum* as an understorey tree, based on leaf form and sparse association in a coniferous leaf assemblage. The similarity in leaf morphology to the Potomac Group leaves suggests that *F. palustris* may have had a similar role in the community.

6.3. Summary: the ecological distribution of angiospermous plants

At least five associations of leaf foliage and angiosperm leaves can be recognised within the Triton Point Member. These vegetative associations occur in different sedimentary settings suggesting that they reflect real variations of vegetation types. Near-channel riparian plant communities were dominated by *Ginkgoites* and *Taeniopteris* with an understorey of *Cladophlebis* (Fig. 6B). Freshly deposited sediments were colonised by *Hydrocotylophyllum alexandri* (Fig. 6B) More distal to the river channels low shrubby communities of *Ptilophyllum*, *Gnafalea jeffersonii*, *Cladophlebis*, and *Aculea* occurred. Backswamps were occupied by an overstorey of either *Taeniopteris* dominated communities or mixed *Podozamites* and *Elatocladus* communities (Fig. 6B). The understorey of the former contained mixed associations of mound ferns (*Cladophlebis*) with smaller ferns and bryophytes occupying the spaces between.

The angiosperms that occur in the Triton Point Member comprise approximately 12% of the overall species diversity. This compares well with other Cretaceous floras of similar age and palaeolatitude (Drinnan and Crane, 1990). Although at this stage in the Cretaceous the angiosperms fail to dominate plant associations, they do reach significant numbers, making up to 40% by abundance of the

leaves recorded in the overbank deposits adjacent to river channels. However, despite this lack of dominance in terms of primary productivity or floral diversity they occupy a diverse suite of ecological sites.

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