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New Species of *Banksiaeformis* and a *Banksia* ‘Cone’ (Proteaceae) from the Tertiary of Central Australia

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Abstract

Silicified leaf impressions attributed to the tribe Banksieae (Proteaceae) are reported from a new Tertiary macroflora from near Glen Helen, Northern Territory and from the Miocene Stuart Creek macroflora, northern South Australia. The fossil leaf material is described and placed in *Banksiaeformis* Hill & Christophel. *Banksiaeformis serratus* sp. nov. is very similar in gross morphology to the extant *Banksia baueri* R.Br. and *B. serrata* L.f. and is therefore representative of a leaf type in *Banksia* that is widespread geographically and climatically within Australia and that is unknown in *Dryandra* or other genera of the Banksieae. The leaf material from Stuart Creek and Woomera represents the lobed leaf form typical of Paleogene macrofloras from southern Australia, but one species, *B. langii* sp. nov., is closely similar in gross form to *Banksiaephyllum taylorii* R.J.Carpenter, G.J.Jordan & R.S.Hill *et al.* from the Late Paleocene of New South Wales and similarly may be sclerophyllous. Also reported are impressions of *Banksia* infructescences, or ‘seed cones’, in Neogene sediments near Marree and Woomera, South Australia. These fossils demonstrate the presence of Banksiinae in central Australia in the mid-Tertiary, potentially indicating the former existence of linking corridors between now widely separated populations of *Banksia*.

Introduction

The modern genus *Banksia* L.f. (Proteaceae, subtribe Banksiinae of Banksieae) is a common component of sclerophyllous heaths and other modern Australian sclerophyllous vegetation. *Banksia* has about 76 species and is generally restricted to oligotrophic soils but occurs over a wide climatic range, with annual rainfall from 300 to 2500 mm (Holliday and Watton 1990; Thiele and Ladiges 1996; George 1999a). *Banksia* has a disjunct east–west distribution, with major centres of diversity in south-western and south-eastern Australia. The centre of the continent and the Nullarbor Plain today do not support populations of *Banksia* or related taxa, most likely due to a lack of suitable climate in these areas. Few species of *Banksia* occur in northern Australia, with only *B. dentata* occurring outside of Australia on the island of New Guinea and the Aru Islands (George 1999a). However, even though the fossil record of the tribe Banksieae is extensive, only three fossil species of *Banksia* s.s. have been described (McNamara and Scott 1983; Jordan and Hill 1991; Hill *et al.* 1995; Greenwood *et al.* 2000). As *Banksia* and *Dryandra* cannot be distinguished solely on leaf architectural features, fossil leaves architecturally matching either genus are assigned to *Banksiaephyllum* Cookson and thus, by definition, are attributed to the Banksiinae (Blackburn 1981; Vadala and Drinnan 1998). However, some previously described *Banksiaephyllum* species have cuticular features that indicate affinity to the subtribe Musgraveinae, or do not indicate affinity to the Banksieae and/or Proteaceae (Carpenter and Jordan 1997).

Tertiary macrofloras within Australia are primarily known from near the coastal margin and particularly from the southern half of the continent and Tasmania (Greenwood 1994; Greenwood *et al.* 2000). Information on palaeovegetation, phytogeography and

palaeoclimate for central Australia is therefore largely known from the microfloral record and geological features (Truswell and Harris 1982; Benbow *et al.* 1995). Palaeobotanical data have emphasised the presence of rainforest taxa in central Australia throughout much of the Cenozoic (Truswell and Harris 1982; Greenwood 1996; Barnes and Hill 1999). Limited macrofloral evidence suggests, however, that important evolutionary innovation within key Australian genera, such as *Banksia* and *Eucalyptus*, may have been occurring much earlier in central Australia than in the coastal fringes (Lange 1978, 1982, 1986; Greenwood *et al.* 1990; Greenwood 1994, 1996). Fossil evidence in the form of banksioid leaves (*Banksiaeformis* and *Banksiaephyllum* species), wood, pollen (*Banksiaeidites elongatus* Cookson) and *Banksia* fruiting cones are known from Paleocene to Pleistocene sediments throughout the modern range of *Banksia* (Redaway 1858; Smyth 1873, 1875; Cookson and Duigan 1950; Pike 1953; Patton 1957; Blackburn 1981; Hill and Macphail 1983; McNamara and Scott 1983; Hill 1988; Hill and Christophel 1988; Jordan and Hill 1991; Hill and Merrifield 1993; Carpenter *et al.* 1994; Vadala and Drinnan 1998), but have also been reported from central Australian localities (Chapman 1937; Greenwood *et al.* 1990; Greenwood 1996).

George (1981, 1999a) proposed an evolutionary series in *Banksia* based on cone and floral morphology and Hill and Christophel (1988) provided scenarios of inter-relationships between extant and fossil species of Banksiinae on the basis of leaf morphology. Hill and Christophel (1988) suggested that further records of fossil species over a wider geographic range were required to determine the ancestral leaf form and direction of evolution within the group. The present disjunct distribution of *Banksia* and the fossil record of Banksieae suggest that *Banksia* did occur in central Australia in the middle Tertiary. Hitherto the central Australian records of Banksiinae have not been discussed systematically. The classification of *Banksia* has recently been revised, incorporating leaf and infructescence morphological characters (Thiele and Ladiges 1996; George 1999a), some of which are referable to fossil material. Vadala and Drinnan (1998) provided a review of *Banksiaephyllum* and commented on the relationship of fossil Banksieae to the subtribe Banksiinae. This paper describes new records of Banksieae, including leaf impressions from Glen Helen near Alice Springs in the Northern Territory and Stuart Creek in northern South Australia and *Banksia* infructescences from Woomera and Poole Creek in northern South Australia. Where possible, these fossil taxa are incorporated within the infrageneric classification of *Banksia* provided by Thiele and Ladiges (1996).

Materials and Methods

The Fossil Sites

Glen Helen

The Glen Helen macrofloral locality consists of a small outcrop of flat-lying sediments situated 119 km west of Alice Springs and 5 km east of Glen Helen tourist camp in the southern part of the Northern Territory (23°S, 132°E; Fig. 1). It lies unconformable over an irregular basement of dipping Amadeus Basin sediments and similar outcrops extend from this site for about 95 km to the west-north-west, along a broad valley within the MacDonnell Ranges. The sequence was first mapped by Prichard and Quinlan (1962) who suggested a Cretaceous age on the basis of lithological correlations with subsurface sediments beneath the Burt Plain to the north. However, the dating of the Burt Plain sediments was later shown to be in error (Lloyd 1968) and the unit described here has been classified as Tertiary on all subsequent maps. Warren and Shaw (1995) consider these outcrops as a correlative of the Waite Formation, which contains an early Miocene vertebrate fauna in its type area 230 km to the north-east (Woodburne 1967). As there is no fossil evidence for this correlation and there are significant differences in lithology between the respective

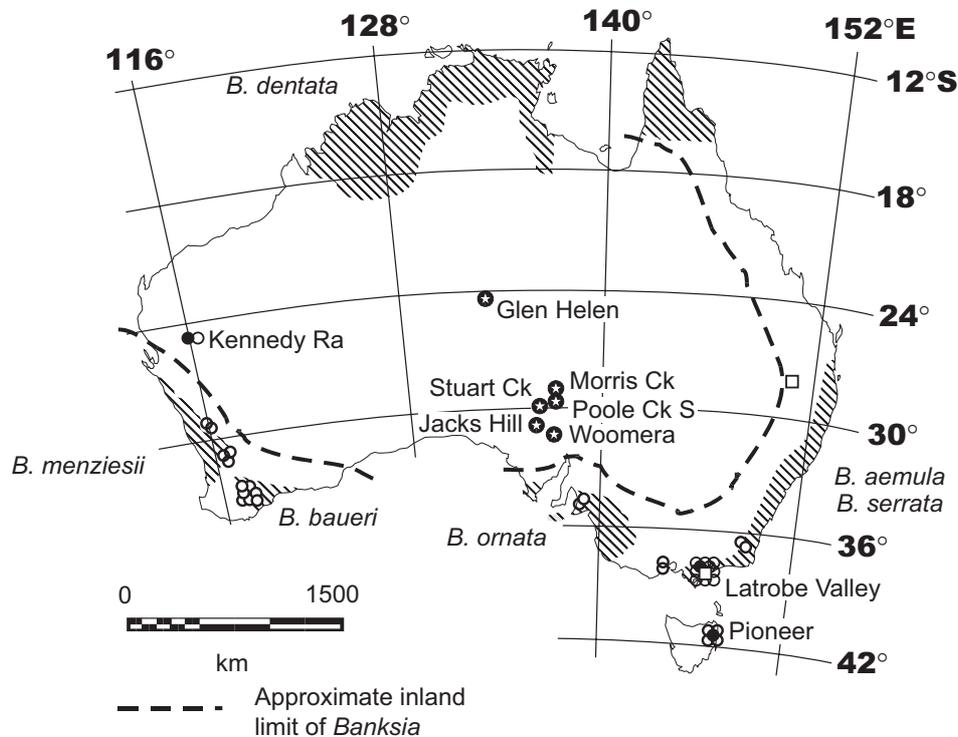


Fig. 1. Map of Australia showing distribution of selected species of *Banksia* today (shading) and location of the mid-Tertiary Glen Helen and Poole Creek macrofloral sites (⊕) and other localities mentioned in the text. Tertiary fossil occurrences of *Banksia* cones (●), wood (□) and *Banksia* leaves (○) are indicated. The total distribution of *Banksia* today is only slightly greater than that shown for the *Banksia* spp., but extending further up the east coast.

localities we regard the correlation as speculative and so only suggest a mid-Tertiary age for the Glen Helen flora. The outcrop near Glen Helen reaches about 15 m in thickness, mostly comprising weakly consolidated and poorly exposed gravel, sand and silt, apart from a 2–3-m capping of well-silicified sandstone (silcrete). Plant fossils are largely confined to the lower, somewhat ferruginised part of this silicified cap and dominated by moulds of wood fragments (rarely up to 0.5 m long), bark and twigs. Leaves are generally sparse or confined to local concentrations in single beds. The sediments were probably deposited fluviially and the predominance of detrital quartz, in comparison with modern alluvium in the area, suggests a warm, humid environment and deep weathering at the time of deposition.

Poole Creek

An impression of a *Banksia* infructescence or 'seed cone' was discovered in late November 1988 by one of us (D. R. G.), D. J. Barrett and B. Gare (at the time at Mines and Energy South Australia) *in situ* on a boulder in a creek-bed exposure of a silicified unit of the Miocene Etadunna Formation (29°37'S, 137°43'E), in the Southern Lake Eyre Basin near the Oodnadatta Track in the Poole Creek Palaeochannel (Greenwood *et al.* 1990; Greenwood 1996). The specimen remains *in situ* (Fig. 1). A mould of a *Banksia* infructescence collected near Woomera (see below) is considered conspecific with the Poole Creek specimen and is designated the holotype. The exposure of the silicified unit was sparsely fossiliferous, with

common poorly preserved cones of *Casuarina* (Fig. 1), coniferous shoots and small angiosperm leaves, including some that may be *Banksiaeiformis*. Owing to the size of the boulders on which these impressions occurred, collection of the specimens was not possible.

The *Banksia*-cone mould preserved a three-dimensional impression of the external morphology of half of the structure, including the mature follicles (Figs 12 and 13). The mould was photographed in the field in natural light with 35-mm Ektachrome 100 ASA colour positive (slide) film. Black and white photographs were produced from these slides for the Figures here. The original slides are housed in the collection of the Mineral Resources Group of Primary Industry and Resources South Australia (PIRSA). As the *Banksia* specimen was not collectable, measurements were taken from photographs of the mature cone for comparison with infructescences from modern species of *Banksia* and fossil infructescences.

Stuart Creek, Jacks Hill, Woomera and Morris Creek

Material from Stuart Creek, Jacks Hill and Woomera represents collections made by various workers, including Tate (in Chapman 1937), Lange (1982, 1986) and Greenwood *et al.* (1990). Much of this material was collected from surface float of silicified Willalinchina Sandstone at the Willalinchina Hut locality near Stuart Creek Station homestead (29°45'S, 136°45'E), or at sites near this area in the Billa Kalina Basin. Specimens are also considered from Morris Creek in the southern Lake Eyre Basin (Greenwood *et al.* 1990; Greenwood 1996) and from South Australian Museum collections labelled 'Eyre Formation' from Koolymilka near Woomera (30°58'S, 136°33'E) and at several sites in the Stuart Range near Mt Eba Station, such as Jacks Hill (30°12'S, 135°42'E). The age of the Stuart Creek macrofloras and putative Eyre Formation at sites near Woomera and Jacks Hill are problematic and these floras have been assigned Eocene–Oligocene or Miocene ages (Ambrose *et al.* 1979; Wells and Callen 1986; Krieg *et al.* 1991; Callen *et al.* 1995). Sandstone from the Stuart Range and related sites was often formerly labelled 'Eyre Formation', but is now named Mount Sarah Sandstone, a rock unit potentially equivalent to the upper part of the Eyre Formation (and thus Eocene), but some outcrop of Mt Sarah Sandstone may be equivalent to the Oligocene–Miocene Etadunna or Doonbara formations (Callen *et al.* 1995). Biostratigraphic and lithological correlation of silcrete floras in the Billa Kalina Basin, however, indicates that the Willalinchina Sandstone, and thus the Stuart Creek flora, is Late Miocene (Callen *et al.* 1995). Specimen numbers for Stuart Creek material other than those in the South Australian Museum follow the PIRSA unique rock sample (RS) system, which ties each specimen to its collection locality according to 1 : 250 000 map sheets. Specimens from earlier collections (Chapman 1937; Lange 1982) were also examined, including material from additional sites (e.g. Morris Creek) for which little stratigraphic information is presently available. These are housed in the South Australian Museum (SAM) and are cited using SAM specimen numbers.

Modern Comparative Material

The cladistic analysis of *Banksia* by Thiele and Ladiges (1996) provides a useful starting point in the systematic analysis of the fossil material as these authors used leaf features, such as leaf margin and/or lobation type and mature infructescence characters, such as the gross shape of the axis and follicle shape. Several of their diagnostic characters can be observed on the fossils. Vadala and Drinnan (1998) provide a detailed compilation of leaf architectural and epidermal characters of extant *Banksia* and *Banksiaephyllum*–*Banksiaeiformis* species. While no attempt is made here to apply a cladistic analysis of the fossil material, the characters used by Thiele and Ladiges (1996) and by Vadala and Drinnan (1998) are used to compare the fossil species described here with previously described fossil species of *Banksia* and to extant species of *Banksiinae*. Additional information on leaf and infructescence morphology is derived from Hill and Christophel (1988), Hill (1990), Holliday and Watton (1990), Jordan and Hill (1991) and George (1999a, 1999b) and from both field-collected modern material and herbarium material (MEL).

Leaf and infructescence material of *Banksia integrifolia*, *B. marginata*, *B. ornata*, *B. serrata* and *B. spinulosa*, was collected from natural populations in Victoria. This material was scored for morphometric characters of leaves and the infructescence to assess intra-specific and infra-specific level variation in these organs. In particular, the size and shape of leaves of similar form to the fossils and both infructescence and follicle size and shape and the number and position of follicles were assessed.

Systematic Palaeobotany

Family Proteaceae

Subfamily Grevilleoideae

Tribe Banksieae

Genus *Banksiaeformis* Hill & Christophel (1988)***Banksiaeformis serratus*** Greenwood, Haines & Steart, sp. nov. (Figs 2 and 3)*Diagnosis*

Simple bilaterally symmetrical leaves; leaf base and apex unknown. Leaf greater than 9 cm long and 2.5 cm wide, margin serrate, teeth regular, apically directed and acute. Leaf rachis massive, venation pinnate, craspedodromous, more than 30 secondary veins, secondary veins *c.* 90–70° from the midvein, generally straight but diverging apically near the margin and a single vein entering each marginal tooth; secondary veins between teeth bifurcating prior to sinus.

Location: unnamed Tertiary unit (cf. Waite Formation) at Glen Helen, Northern Territory.

Holotype: P36575, stored in the South Australian Museum.

Collector: Peter W. Haines.

Etymology: the specific epithet is derived from the regular serrate margin.

Remarks

The leaf architecture (Figs 2 and 3) matches that of some extant species of *Banksia* (subtribe Banksiinae). According to Hill and Christophel (1988), fossil leaves with this morphology but lacking epidermal detail (i.e. lacking cuticle) should be placed in the organ-genus *Banksiaeformis*. These authors also considered that such leaves represent now extinct species within the tribe Banksieae of Proteaceae (which includes the modern subtribes, Musgraveinae (*Austromuelleria* and *Musgravea*) and Banksiinae). The banksioid leaf type with a simple undivided lamina and dentate margins is common in *Banksia* (Table 1, Fig. 4), but is unknown in *Dryandra* and the Musgraveinae and so *B. serratus* is considered to represent Banksiinae, and probably *Banksia*.

Banksiaeformis serratus resembles *B. dentatus* Hill & Christophel, from the Tasmanian Oligocene Cethana macroflora, and to a lesser degree the organically preserved Middle–Late Eocene species, *Banksiaephyllum attenuatum* Hill & Christophel (1988) from Loch Aber in Tasmania and the Oligocene species, *B. fastigatum* (Deane) Cookson & Duigan (1950) from Yallourn in Victoria (Table 1). *Banksiaeformis serratus* differs from *B. dentatus* in the bifurcation of secondary veins prior to the sinus between the marginal teeth; the two species are otherwise very similar. Carpenter and Jordan (1997) suggested that *Banksiaephyllum attenuatum* may not represent Banksieae or perhaps may not even be a member of Proteaceae. The presence of epidermal information for *Banksiaephyllum attenuatum* and *B. fastigatum* and the lack of such detail for *Banksiaeformis serratus* restricts a complete comparison between these species; however, the secondary veins of *B. attenuatum* do not bifurcate at the sinus and this species is only superficially similar in general leaf form to *Banksiaeformis serratus*. *Banksiaephyllum longifolium* Hill & Merrifield (1993) from the Middle Eocene–Oligocene West Dale flora in Western Australia is entire-margined with brochidodromous venation and so is quite unlike the Glen Helen

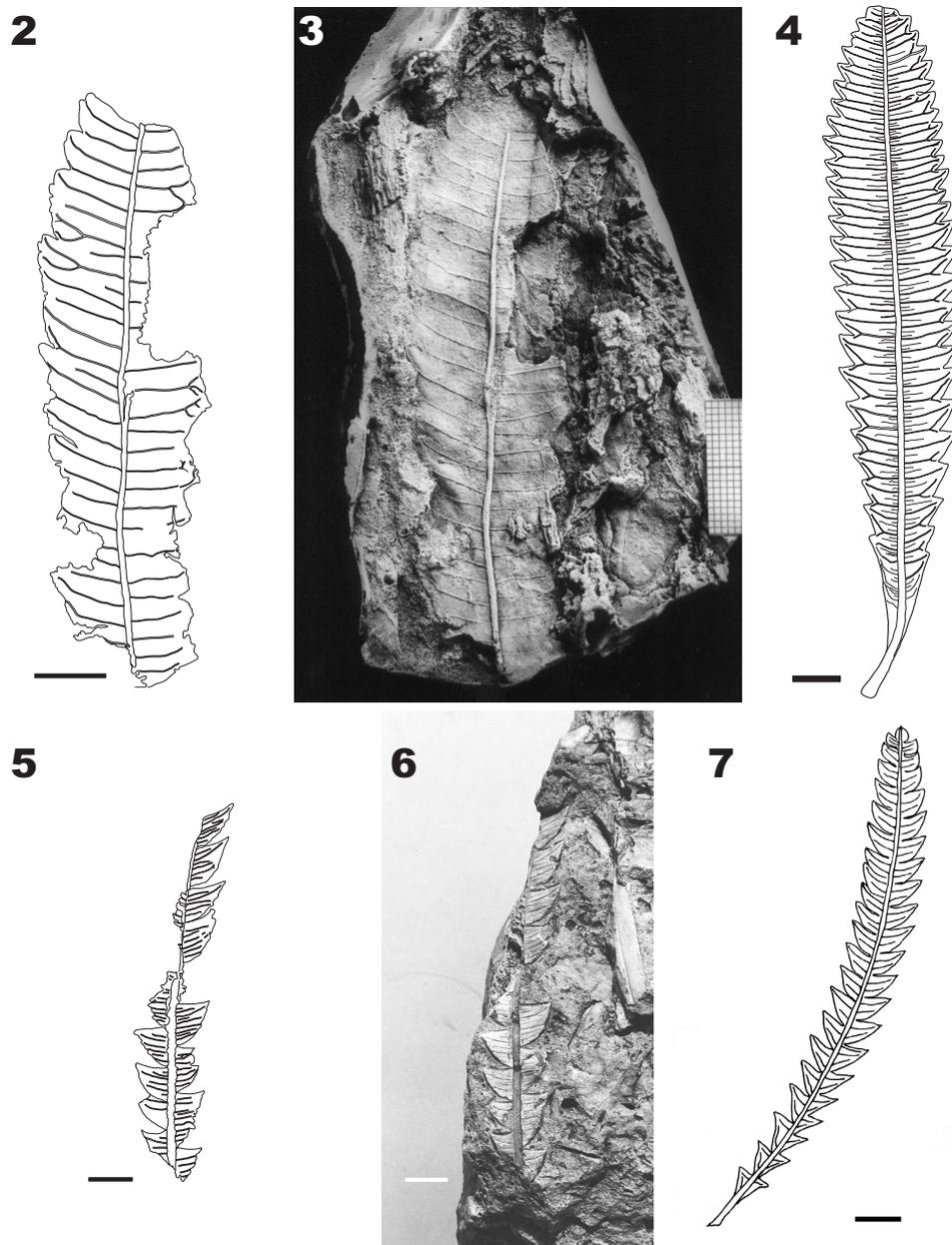


Fig. 2. Line drawing of *Banksiaeiformis serratus* from the Glen Helen macroflora. Scale bar = 10 mm. (Drawing by A. Vadala from the photo by P. Haines.) **Fig. 3.** Photo of *Banksiaeiformis serratus* from the Glen Helen macroflora. Scale bar = 10 mm. (Photo by P. Haines from a latex cast of the original specimen.) **Fig. 4.** Line drawing of extant *Banksia serrata* from field collected material. Scale bar = 10 mm. (Line drawing by A. Vadala.) **Fig. 5.** Line drawing of *Banksiaeiformis langii* (6238 RS 122) from the Stuart Creek macroflora. Scale bar = 10 mm. (Drawing by A. Vadala from the PIRSA photo 39035.) **Fig. 6.** Photo of *Banksiaeiformis langii* (6238 RS 122) from the Stuart Creek macroflora. Scale bar = 10 mm. (PIRSA photo 39035.) **Fig. 7.** Line drawing of extant *Dryandra formosa* by D. Steart from cultivated material. Scale bar = 10 mm.

Table 1. Gross leaf characteristics of some extant species of *Banksia* and *Dryandra* used for systematic analysis of fossils

Data for extant species from George (1981, 1999a, 1999b), Taylor and Hopper (1988), Holliday and Watton (1990), Thiele and Ladiges (1996) and specimens in MEL; data for fossil species from original descriptions of each taxon, as indicated in the text. Lobation incision is given as a 3-point scale where 0 = no lobes; 1 = <1/3 incision from margin to midrib; 2 = >1/3 incision; 3 = incision through to midrib (or apparently so). Where lobes are pungent or apiculate (i.e. with a sharp point), they are considered to represent 'teeth'

Species	Length (cm)	Width (cm)	L : W	Lobed	Incision	Teeth or apiculate lobes	Apex
<i>Banksia</i> subgenus <i>Banksia</i>							
Series <i>Tetragonae</i>							
<i>B. lemanniana</i> ^A	5–10	1.5–4	2–3	–	0	+	blunt
Series <i>Banksia</i>							
<i>B. aemula</i> ^A	8–22	1–2	8–11	–	0	+	round
<i>B. menziesii</i> ^A	15–30	2–4	7–8	–	0	+	round
<i>B. ornata</i>	5–8	2–3	2–3	–	0	+	round
<i>B. serrata</i> ^A	8–22	2–4	4–6	–	0	+	blunt
<i>B. speciosa</i> ^B	20–40	1.5–2.5		+	3	+	terminal lobe
Incertae sedis							
<i>B. baueri</i> ^A	7–13	1–2	6–7	–	0	+	round
Series <i>Salicinae</i>							
<i>B. dentata</i> ^A	10–25	2–8	3–5	–	0	+	Blunt or round
<i>B. robur</i> ^A	<30	<10	3	–	0	+	round
Series <i>Prostratae</i>							
<i>B. chamaephyton</i> ^C	20–50	4–15		+	3	±	terminal lobe
Series <i>Grandes</i>							
<i>B. grandis</i>	20–50	8–15		+	3	+	blunt
Series <i>Dryandroides</i>							
<i>B. dryandroides</i> ^B	5–15	1		+	3	+	blunt
<i>Dryandra</i> subgenus <i>Dryandra</i>							
<i>D. formosa</i>	7–16	0.6–1.1	>10	+	3	+	blunt
<i>D. idiogenes</i>	15–37	1.2–3.8	4–10	+	3	+	acute or blunt
Fossil species							
<i>Banksiaeformis decurrens</i>	c. 7	c. 1	c. 7	+	3	+	not known
<i>B. dentatus</i>	6	1	6	–	0	+	not known
<i>B. langii</i>	>8.5	1.2–1.6	5–7	+	3	+	acute
<i>B. praegrandis</i>	8–16+	2–8	2–4	+	3	±	acuminate
<i>B. serratus</i>	>9	c. 2.5	c. 4	–	0	+	not known
Kennedy Ra <i>Banksia</i> leaves							
<i>Banksiaephyllum attenuatum</i>	c. 6	≤ 1.5	c. 4	–	0	+	attenuate
<i>B. cuneatum</i>	>12	≤ 4	c. 3	+	3	+	not known
<i>B. elongatum</i>	>6	≤ 1	c. 6	+	3	+	not known
<i>B. fastigatum</i>	>3	1.5	>3	–	0	+	not known
<i>B. longifolium</i>	>7.5	1	7	–	0	–	?acute or blunt
<i>B. regularis</i>	c. 4	c. 0.8	c. 4	–	0/1	+	acute
<i>B. taylorii</i>		c. 2		+	3	+	acute
<i>B. urniforme</i>		≥ 0.6		+	3	–	not known
<i>B. westdaliense</i>		0.3		+	3	+	not known

^ASpecies most similar to *Banksiaeformis serratus* sp. nov.

^BSpecies most similar to *B. langii* sp. nov.

^CSpecies most similar to *B. praegrandis*.

material. An undescribed *Banksieaeformis* from Western Australia matches *B. serratus* in most details, but has a bluntly denticulate margin (S. McLoughlin, pers. comm.; McLoughlin and Hill 1996), whereas *B. serratus* is serrate-margined. McNamara and Scott (1983) noted without illustration the presence of two poorly preserved *Banksia*-like leaves associated with *Banksia archaeocarpa*, commenting that these leaves matched in many respects those of the extant species *B. menziesii*.

Strap-like dentate- to serrate-margined leaves are found in several species of *Banksia*, most notably in Series *Banksia* and Series *Salicinae* (Table 1). The extant species, *B. aemula* R.Br., *B. baueri* R.Br., *B. menziesii* R.Br., *B. ornata* F.Muell. and *B. serrata* L.f. (Series *Banksia*) and *B. dentata* L.Fill., *B. oblongifolia* Cav. and *B. robur* Cav. (Series *Salicinae*), are comparable with *Banksieaeformis serratus*. Of these extant species, the morphology of the fossil leaf is closest to that of the leaves of *Banksia serrata* (Fig. 4). The teeth of *Banksia ornata* are quite prominent and apiculate, much more so than in *Banksieaeformis serratus*. The secondary veins in *Banksia robur* either terminate in marginal teeth or terminate within the blade; in *B. oblongifolia* and *B. dentata* intra-tooth secondary veins bifurcate at the sinus and loop back to fuse with the secondary vein terminating in the tooth; in *B. menziesii* and *B. serrata* the intra-tooth secondary veins bifurcate without fusing with the vein terminating in the tooth, as seen in *Banksieaeformis serratus*. The shape and prominence of the teeth in *Banksieaeformis serratus* are closer to those seen in *Banksia serrata* than those in *Banksia menziesii*.

Banksieaeformis langii Greenwood, Haines & Steart, sp. nov. (Figs 5 and 6)

Diagnosis

Leaves bilaterally symmetrical, pinnately lobed; lobes acute and apically directed. Apical side of lobe usually concave, rarely straight; basal side convex, sinuses acute; leaf base and apex unknown. Leaf length greater than 8.5 cm, width 1.2–1.6 cm; lobes typically with 4 veins, rarely 5, with a pronounced vein leading to the apex of the lobe and ramifying prominently. Leaf rachis massive.

Location: Willalinchina Sandstone, Stuart Ck and ?Eyre Formation (Mt Sarah Sandstone) near Woomera and at Jacks Hill, all in South Australia.

Holotype: 6238 RS 122, stored in the PIRSA Core Library.

Collector: unknown.

Other specimens: R368928 & 6238 RS 129, both specimens stored in the PIRSA Core Library; P17965B & P13568, stored in the South Australian Museum.

Etymology: the specific epithet recognises R. T. Lange, who played a significant role in the discovery and scientific exploration of the Stuart Creek site.

Remarks

Banksieaeformis langii corresponds to ‘*Banksieaeformis* I’ in Greenwood *et al.* (1990, fig. 3B) and was figured as a line drawing in Greenwood (1996, fig. 4H). The *Banksia*-like leaf type with arcuate lobes incised fully to the rachis is common in the *Banksiinae*, but is unknown in the *Musgraveinae* (Hill and Christophel 1988; Carpenter *et al.* 1994; George 1999a, 1999b). Specimens of *Banksieaeformis langii* have a massive rachis and the lobes appear quite thick and coriaceous, suggesting scleromorphy. Carpenter *et al.* (1994)

suggest that *Banksiaephyllum taylorii*, which has leaves with an architecture similar to *Banksiaeformis langii*, likely represents antecedents of the modern sclerophyllous Banksiinae and not the rainforest Musgraveinae and so *B. langii* is considered here to also represent Banksiinae. *Banksiaeformis langii* is locally common at some Stuart Creek sites (e.g. Willalinchina Hut) and has been collected in putative Eyre Formation sediments at Jacks Hill (P13568) and near Woomera (P17956B). The latter material is on display in the South Australian Museum.

Banksiaeformis langii resembles only superficially *B. decurrens* Hill & Christophel and the organically preserved species, *Banksiaephyllum cuneatum* Blackburn, both from the Eocene Maslin Bay flora (Blackburn 1981; Hill and Christophel 1988; Table 1). *Banksiaeformis langii* differs from both *Banksiaeformis decurrens* and *Banksiaephyllum cuneatum* in its much smaller size and more symmetrical individual leaf lobes and also in the presence of a well-developed cuneate base in both of the Maslin Bay species, a feature not observed on any of the Stuart creek material. Architecturally, there is a close resemblance between *Banksiaephyllum taylorii* Carpenter *et al.* (1994) from the Late Paleocene Lake Bungarby flora (NSW), *B. westdaliense* Hill & Merrifield (1993) from the Middle Eocene–Oligocene West Dale flora (WA) and *Banksiaeformis langii* (Table 1). Both *Banksiaephyllum taylorii* and *Banksiaeformis langii* lack a cuneate leaf base and these two species and *Banksiaephyllum westdaliense* have a similar lobe shape. The *Banksiaephyllum taylorii* and *B. westdaliense* leaves are smaller than those of *Banksiaeformis langii* and have three rather than four veins in each lobe, but these differences alone may not be of systematic importance as the two species of *Banksiaephyllum* are differentiated from each other primarily on the basis of cuticular characters. In the absence of cuticular information for the Stuart Creek material, *Banksiaeformis langii* is maintained as a separate species of *Banksiaeformis*. *Dryandra benthami* Ett. and *D. praeformosa* Ett., from Late Eocene florules of the Vegetable Creek macroflora (Ettingshausen 1888) have gross vegetative morphology that is closely comparable with *Banksiaeformis langii*. However, Cookson and Duigan (1950) and others (Hill 1988; Carpenter *et al.* 1994) consider that these species lack sufficient taxonomic information for comparison with other fossil species. The acute lobes of *B. langii* (Figs 5 and 6) differentiate it from the remaining lobed-leaved fossil Banksiinae, such as *Banksiaephyllum pinnatum* Cookson & Duigan and *B. urniforme* (Deane) Hill (Hill 1990), as the latter have rounded- or blunt-tipped lobes, respectively.

The modern species, *Banksia speciosa* R.Br., is comparable with *Banksiaeformis langii* (Table 1); however, the former differs from the fossil by having more-or-less symmetrical acute lobes, whereas *B. langii* has lobes that are apically directed. A closer affinity may be with the extant species, *Dryandra formosa* R.Br. (see fig. 44 in Hill and Christophel 1988; Fig. 7 herein), which strongly resembles *B. langii* (Figs 5 and 6). Carpenter *et al.* (1994) also considered that *Banksiaephyllum taylorii* was architecturally indistinguishable from *Dryandra formosa*, but noted marked differences in cuticular anatomy between these two species. The close similarity between the Stuart Creek (and both Woomera and Jacks Hill), Lake Bungarby and modern species, may therefore indicate a common lineage of proto-sclerophyllous Banksiinae across southern Australia in the Early Tertiary (see discussion in Carpenter *et al.* 1994). A *Banksia* infructescence on the same block (P17956) as *Banksiaeformis langii* may have come from a *B. langii* plant and so assignment of this taxon to *Banksia* may be appropriate. In the absence of attachment between these organs, assignment to *Banksiaeformis* is retained and assignment to *Banksia* must remain conjectural.

Banksieaeformis praegrans (Tate) Greenwood, Haines & Steart, comb. nov. (Figs 8 and 9)

Synonymy: *Banksia praegrans* Tate in Chapman, *Trans. Roy. Soc., South Austr.* 61: 1–16 (1937); *Banksieaeformis praegrans* in Greenwood, *Aust. Syst. Bot.* 9: 95–112 (1996).

Emended Diagnosis

Leaves bilaterally symmetrical, pinnately lobed; lobes generally narrowly triangular with a narrowly rounded apex and apically directed. Apical side of the lobes straight to slightly concave, rarely strongly concave; basal side straight, but curving to produce a broad attachment to the rachis. Leaf base unknown, apex consisting of a terminally directed modified lobe (single specimen). Lobes opposite in some specimens, but becoming alternate further along the rachis in other specimens; some specimens fully alternate. Leaf length 8 to >16 cm, width across spread of lobes up to 8 cm (estimated), but may be as small as 2.0 cm. Individual lobes 0.8–2.7 cm wide at the midrib. Lobes typically with 2 prominent veins, rarely 1 or 3 or 4 on the one specimen, with a single vein leading to the lobe apex. Tertiary veins in a loose reticulate net. Leaf midrib massive.

Location: Eyre Formation at Morris Creek and Mt Alford and Willalinchina Sandstone at Stuart Creek and Elizabeth River, all in South Australia.

Holotype: P1198, stored in the South Australian Museum.

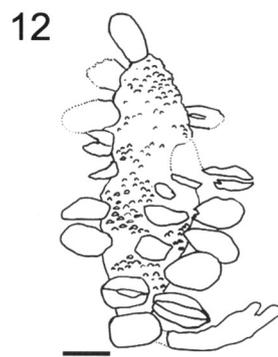
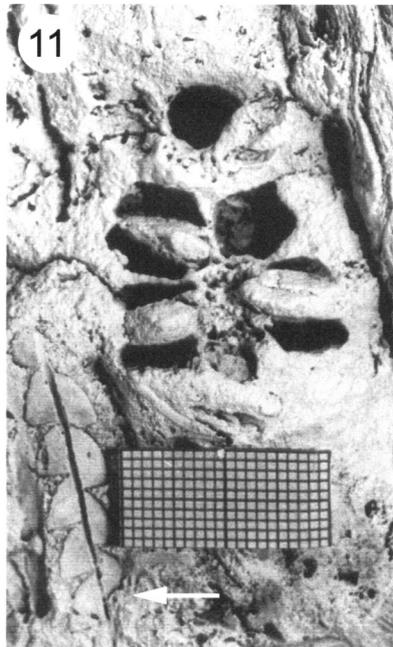
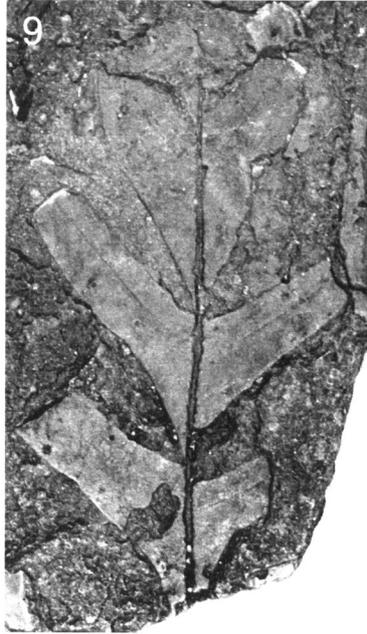
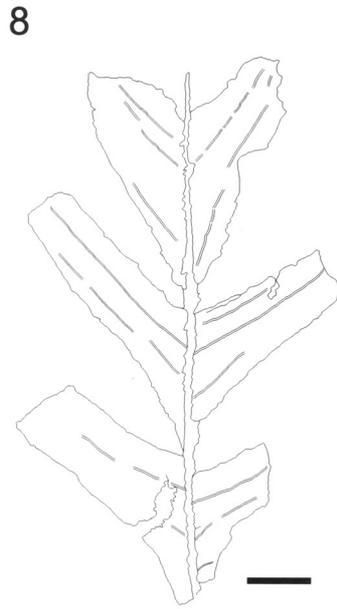
Other material: 6438 RS 534, RS 484; 6439 RS 150, RS 194, RS 039; 6238 RS 129, stored in the PIRSA Core Library.

Remarks

This leaf taxon has been previously described and illustrated by Chapman who used a name proposed by Tate; *Banksia praegrans* Tate (Chapman 1937). The material viewed by Chapman (1937, figs 2 and 6) was collected near Elizabeth River, northern South Australia. *Banksieaeformis praegrans* was illustrated and named by Greenwood (1996, fig. 4H) but not formally transferred to *Banksieaeformis* and corresponds to ‘*Banksieaeformis* II’ in Greenwood *et al.* (1990, fig. 3A). This species possesses the gross leaf morphology typical of modern members of the tribe Banksieae of the Proteaceae (e.g. Figs 8–10) and so this taxon is formally transferred to *Banksieaeformis*. The original material illustrated by Chapman (SA Museum, P1198) is conspecific with the specimens from Stuart Creek and Morris Creek. Material referable to *B. praegrans* has been collected from localities at Stuart Creek, Morris Ck, at Mt Alford and Woomera (Lange 1986; Greenwood 1996; SAM collections).

Banksieaeformis praegrans differs from all previously described *Banksieaeformis* or *Banksieaephyllum* species by its long, narrow, widely spaced apiculate pinnae. The

Fig. 8. Line drawing of *Banksieaeformis praegrans* from the Stuart Creek macroflora. Scale bar = 10 mm. (Line drawing by A. Vadala from PIRSA photo 39034.) **Fig. 9.** Photo of *Banksieaeformis praegrans* from the Stuart Creek macroflora. Scale bar = 10 mm. (PIRSA photo 39034.) **Fig. 10.** Line drawing of extant *Banksia chamaephyton* redrawn from Fig. 31C in George (1999a). **Fig. 11.** *Banksia longicarpa* infructescence impression (P17956a) from Koolymilka, near Woomera. Scale bar = 10 mm. *Banksieaeformis* cf. *B. langii* leaf (P17956b) arrowed. (Photo by P. Haines.) **Fig. 12.** Line drawing of *Banksia longicarpa* infructescence impression from Poole Creek south. Scale bar = 10 mm. (Line drawing by D. Steart from photo by D. Greenwood.) **Fig. 13.** Photo of *Banksia longicarpa* infructescence impression from Poole Creek south. Scale bar = 10 mm. A *Casuarina* infructescence mould is indicated by an arrow. (Photo by D. Greenwood.)



morphology of *Banksiaeformis praegrans* is most similar to leaves of the extant *B. chamaephyton* A.S.George (Fig. 10) and *B. blechnifolia* F.Muell. (Series *Prostratae*) and only superficially so to *Banksia grandis* (Table 1). There is a superficial resemblance to *Dryandra idiogenes* A.S.George (George 1999b, fig. 49). The rounded apices of the lobes of *Banksiaeformis praegrans* and the general tendency for each pair of lobes to be opposite (Figs 8 and 9) was noted by Chapman (1937, fig. 6). This is unusual for the Banksiinae, although is present in *Banksia grandis* Willd. (Hill and Christophel 1988, fig. 36) and some specimens of both *B. chamaephyton* (Fig. 10) and *D. idiogenes*. However, the lobes in several fossil specimens are not paired and show a tendency to become progressively alternate, as seen in modern leaves of *Banksia* and *Dryandra*. Chapman (1937) observed that each lobe in his specimen had six secondary veins, but specimens from Stuart Creek had from one to four prominent veins (Fig. 9), depending on the degree of preservation, with additional lesser veins present on some specimens. *Banksiaeformis praegrans* differs from *Banksia chamaephyton* by having lobes that are quite broad at the base, whereas the extant species always has linear lobes (Fig. 10). The fossil species differs from *D. idiogenes* by having generally longer lobes (they are much shorter triangles in *D. idiogenes*), with the extant species also having much longer leaves than *Banksiaeformis praegrans* (Table 1).

Tribe Banksieae
 Subtribe Banksiinae
 Genus *Banksia* L.f.
 Subgenus *Banksia*

Banksia longicarpa Greenwood, Haines & Steart, sp. nov. (Figs 11–13)

Diagnosis

Infructescence an elongate cylinder, abruptly tapering distally. Floral bracts not in rows. Follicles very prominent, few in number and concentrated in the lower portion of the axis; valves ovoid and robust; smooth; suture straight.

Location: ?Eyre Formation (Mt Sarah Sandstone) at Koolymilka, near Woomera and Etadunna Formation at BMR 3, Poole Creek south, all in South Australia.

Holotype: P17956a, stored in the South Australian Museum.

Etymology: The specific epithet is derived from the tall cylindrical form of the infructescence.

Remarks

The infructescence is elongate and the axis was probably cylindrical in life (Figs 11–13). The specimen from Woomera (Fig. 11) would appear to represent the top half of a cone, but as this specimen is curated in a museum it is designated the type. The mature bi-valved follicles are few in number and are irregularly arranged on both specimens and attached to a regularly textured massive cylinder (the woody axis). The regular patterning of the axis in the Poole Creek specimen is interpreted as indicating that the perianths were shed by the inflorescence at maturity, but may also reflect combustion of the perianths during a fire. Each element of the textured surface of the axis is an irregular polygon, similar to the

perianth base commonly persistent on *Banksia* infructescences, representing unfertilised individual flowers. Follicles are sparse, concentrated in the lower part of the axis, very prominent and broadly elliptic (defined here as ‘domed’).

The infructescences of *Banksia* and *Dryandra* R.Br. are similar in their common possession of woody bi-valved follicles attached to a central woody axis (George 1999a, 1999b). The infructescences of *Dryandra* typically have a very short axis with a low number of mature follicles. Infructescences with short axes are found in *Banksia* (subgenus *Isostylis*, e.g. *B. ilicifolia* R.Br.); however, the majority of modern species of *Banksia* have long axes sometimes bearing 10–20 mature follicles (Table 2). The specimens from Woomera and Poole Creek are clearly of the type found only in *Banksia* and so comparisons are restricted to species of that genus. Pike (1953) dismissed infructescence size as a diagnostic character for *Banksia*, basing her systematic analyses on cuticular characters. The Woomera and Poole Creek material are moulds and lack any epidermal detail. McNamara and Scott (1983) suggest that *Banksia* species can be distinguished on the basis of the overall shape of the inflorescence and follicle and bract form. Of the characters listed by Thiele and Ladiges (1996) for their analysis, seven characters of the infructescence may be preserved in fossil material. Comparisons between extant and fossil *Banksia* infructescences on the basis of gross morphological characters are presented in Table 2.

Thiele and Ladiges (1996) differentiated mature *Banksia* infructescences only as being spherical (subgenus *Isostylis*) or ovoid to elongate (subgenus *Banksia*). On this basis, *B. longicarpa* may be placed in subgenus *Banksia* (Table 2). Using the descriptions in George (1981, 1999a) and Holliday and Watton (1990) and herbarium collections, we differentiated five categories of infructescence shape (Table 2). Several extant species intergrade across more than one shape category, but none includes more than two categories. Intergradation may reflect imperfect development or in some cases phenotypic plasticity, or taxonomic imprecision in existing taxa. The shape of the mature follicles in plan view was considered by both McNamara and Scott (1983) and Thiele and Ladiges (1996) as a character in their analysis; follicle shape in longitudinal view was considered here morphometrically with length and width measurements on unopened follicles.

Infructescences of *Banksia* have been reported from Eldorado and Creswick in Neogene deep leads (Redaway 1858; Smyth 1873, 1875; Pike 1953), Miocene lignites of the Latrobe Valley (Cookson and Duigan 1950; Pike 1953), Victoria (summarised in Greenwood *et al.* 2000), Eocene sandstones from the Kennedy Range in Western Australia (McNamara and Scott 1983) and from both Oligocene and Pleistocene sediments from Tasmania (Hill and Macphail 1983; Jordan and Hill 1991; Fig. 1). All these fossil *Banksia* infructescences appear to represent subgenus *Banksia*, as all have dense condensed woody axes that are ovoid to elongate (Table 2). *Banksia longicarpa* and *B. archaeocarpa* McNamara & Scott have a similar number of follicles that are of similar size and shape, but *B. longicarpa* differs from *B. archaeocarpa* primarily in that the former possesses a tall cylindrical axis, whereas the Western Australian species has the form of an elongated ovoid. The un-named *Banksia* cones from Eldorado and Yallourn in Victoria (Cookson and Duigan 1950; Pike 1953) are squat and cylindrical in shape, with abundant fertile follicles and strongly flattened valves and so represent a separate species to *B. longicarpa*. A *Banksia* infructescence described from Melaleuca Inlet in Tasmania associated with *B. kingii* leaves (Jordan and Hill 1991) is of a similar size to *B. longicarpa* and has similar-shaped mature follicles, but is much stouter than the latter species and has more regularly spaced mature follicles.

Table 2. Infructescence characteristics of extant and fossil species of *Banksia*

Data from Holliday and Watton (1990), McNamara and Scott (1983), Thiele and Ladiges (1996) and specimens in MEL and NMV. Not all modern species are listed. Lengths and widths are ranges. 1, long cylinder; 2, short cylinder; 3, barrel to ovoid; 4, globular; 5, irregular

Species	Cone length (cm)	Cone width (cm)	Cone shape					Follicle
			1	2	3	4	5	
Subgenus <i>Isostylis</i>	1–2	2–4						X flattened
Subgenus <i>Banksia</i>								
Series <i>Tetragonae</i>	7–16	7–12			X	X		domed
Series <i>Lindleyanae</i>	10–15	7–10			X			
Series <i>Banksia</i>	5–40	4–12	X	X	X	X	X	Domed or flattened
<i>B. serrata</i>	8–16	5–18	X					domed
Series <i>Prostratae</i>	6–20	5–8	X	X	X			domed or flattened
Series <i>Cyrtostylis</i>	7–30	5–10	X		X			domed or flattened
Series <i>Ochraceae</i>	7–13	6–10		X	X	X		flattened
Series <i>Grandes</i>	8–30	8–12	X		X			flattened
Series <i>Salicinae</i>	4–25	2–8	X	X	X			domed or flattened
<i>B. integrifolia</i>	7–15	4–8	X					flattened
<i>B. marginata</i>	4–10	4–6	X					flattened
Series <i>Spicigeræ</i>	5–25	4–9	X	X				domed or flattened
<i>B. spinulosa</i>	5–20	4–9	X					domed
Series <i>Quercinae</i>	5–15	4–7	X					domed or flattened
Series <i>Dryandroides</i>	4–5	4			X	X		flattened
Series <i>Abietinae</i>	4–20	4–15	X	X	X	X		domed or flattened
Fossil species								
<i>B. archaeocarpa</i>	11	4			X			domed
<i>B. lignitica</i>	5.5	3		X				flattened
<i>B. kingii</i>	6.2	4.6		X				domed
<i>B. 'eldorado'</i>	4–7.5	2.5–3.5		X				flattened
<i>B. 'pioneer'</i>					X			
<i>B. longicarpa</i>	3–7	2–2.2	X					domed

Elongate infructescence axes are absent from Series *Tetragonae*, *Lindleyanae*, *Ochraceae*, *Dryandroides* and *Abietinae* of Genus *Banksia*, are rare in Series *Banksia* and *Grandes*, but they are typical of Series *Prostratae*, *Cyrtostylis*, *Salicinae*, *Spicigeræ* and *Quercinae* (Table 2). Of the elongate taxa, small to moderate size similar to that of *B. longicarpa* is also seen in Series *Prostratae*, *Salicinae*, subseries *Occidentales* of Series *Spicigeræ* and Series *Quercinae*. The small number of large, prominent, thick follicles in the fossil species is quite similar to those in *B. serrata* (Series *Banksia*), but unlike those in *B. integrifolia*, *B. marginata* (Series *Salicinae*) or *B. spinulosa* (Series *Spicigeræ*) as the latter taxa have follicles that are quite flat and not domed into a substantial woody structure. The follicles of *B. longicarpa* (Figs 11–13) are smaller and less flattened dorsiventrally than

those in *B. serrata*, but otherwise similar. While placement of these fossils in Series *Banksia* is not suggested at this stage, it is likely that the closest match to *B. longicarpa* may be found by more detailed comparisons with taxa from Series *Banksia*.

Discussion

Banksia is an important and distinctive component of some sclerophyllous vegetation types in the modern Australian flora. The evolutionary history of *Banksia* is, however, poorly known despite the common presence of *Banksia*-like leaves (*Banksiaephyllum* and *Banksiaeformis*) in many Tertiary macrofloras (Fig. 1). This lack of insight into *Banksia* evolution from leaf fossils results in part from systematic uncertainty in the status of *Banksia*-like leaves (e.g. Carpenter and Jordan 1997, but see also Vadala and Drinnan 1998). The presence of *Musgraveinanthus* in the same sediments as *Banksiaephyllum* at Golden Grove in South Australia (and even within the same block of matrix; Barrett and Christophel 1990) prompted Christophel and Greenwood (1987) to suggest that in some Eocene macrofloras *Banksia*-like leaves may have represented the foliage organs of a plant from the related Subtribe Musgraveinae, rather than *Banksia* (Subtribe Banksiinae). Carpenter *et al.* (1994) concluded on the basis of cuticular information and the possession of cuneate bases, that these Eocene taxa had a greater affinity to *Musgravea* than to *Banksia*. However, Hill and Christophel (1988), Carpenter *et al.* (1994) and Vadala and Drinnan (1998) suggested that some members of *Banksiaephyllum* probably represented *Banksia* or a related taxon on the basis of more sclerophyllous epidermal features on these fossil leaves. On the basis of diagnostic epidermal features Carpenter and Jordan (1997) have also raised doubts that all *Banksia*-like Tertiary leaves are Proteaceae. The leaf material described here, however, lacks epidermal detail and matches closely with some modern species of *Banksia* (i.e. matches the diagnosis for *Banksiaeformis*) and so accordingly is assigned to *Banksiaeformis*. It is very likely that the fossil taxa *Banksiaeformis langii* and *B. serratus* represent *Banksia* specifically. In the absence of cuticular information, the affinity of *Banksiaeformis praegrandis* within the Banksieae remains speculative.

Reports of remains of *Banksia s.s.* from areas outside the main range of the extant genus are rare (Fig. 1), as most previous reports of *Banksia*-like leaves, *Banksia* cones and fossil wood attributed to *Banksia* are from Tertiary deposits in southern Australia and Tasmania (Cookson and Duigan 1950; Pike 1953; Patton 1957; Blackburn 1981; Hill and Macphail 1983; Hill 1988; Hill and Christophel 1988; Carpenter *et al.* 1994; Hill 1994; Vadala and Drinnan 1998; Greenwood *et al.* 2000). Previous reports of *Banksia*-like leaves and the tips of the fruiting spike of *Banksia* from silcrete near Lake Eyre South in South Australia lacked systematic precision or were anecdotal (Chapman 1937; Lange 1986; Greenwood *et al.* 1990; Greenwood 1996). The presence of *Banksia* cones at Poole Creek and near Woomera are therefore an indisputable record for the genus in northern South Australia and, together with the Kennedy Range fossils (McNamara and Scott 1983), provide a significant extension of the Tertiary geographical range of *Banksia*. *Banksia longicarpa* material lacks sufficient detail to allow a comprehensive systematic analysis, but matches most closely with members of Series *Banksia* and perhaps *B. serrata* most closely of all.

Each of the *Banksiaeformis* species described here, some species of *Banksiaeformis* and *Banksiaephyllum* from Oligocene sediments in Tasmania and Western Australia and the Paleocene *B. taylorii* from New South Wales, are very similar in architecture to extant species, whereas common *Banksia*-like leaves in Eocene–Miocene floras from south-eastern Australia appear to represent extinct lineages with cuneate bases that may be more

closely allied to the Musgraveinae than the Banksiinae (Hill and Christophel 1988; Carpenter *et al.* 1994; Vadala and Drinnan 1998). The presence of Tertiary *Banksia*-like leaves that may not represent Proteaceae (Carpenter and Jordan 1997) further emphasises the need for caution in interpreting phylogeny on the basis of single organs.

On the weight of available stratigraphic evidence, both *Banksiaeformis serratus* and *B. langii* are mid-Tertiary in age (Krieg *et al.* 1991; Callen *et al.* 1995; Warren and Shaw 1995), and thus their close similarity with extant species is perhaps to be expected. The remaining species, *Banksiaeformis praegrans*, is known from both Eocene (Mt Sarah Ss. at Woomera and Eyre Formation at Mt Alford and Morris Creek) and Miocene sediments (Willalinchina Sandstone at Stuart Creek). The Woomera, Mt Alford and Morris Creek samples of *B. praegrans* have broader, shorter lobes, but are otherwise indistinguishable from the Miocene examples from Stuart Creek and so were treated here as belonging to the same species. The significant temporal separation of these specimens is not considered problematic, as there appears to be no sound systematic reason for creating two separate taxa. The age difference may also be an artefact of current stratigraphic interpretation (Greenwood *et al.* 1990; Callen *et al.* 1995).

Palaeoecology

The use of individual fossil taxa as climatic indicators is problematic, as climatic tolerances evolve over time and taxonomic relationships based on single organs may underestimate phylogenetic distance. Nevertheless, the climatic envelopes of the nearest living relatives of fossil taxa may be informative, particularly in comparison with estimates derived from other sources. Greenwood (1996) estimated mean annual rainfall for the Lake Eyre Basin Middle Eocene Poole Creek and Nelly Creek macrofloras as 1100 and 1360 mm, respectively, but with large uncertainties attached to these estimates. He suggested that floristic and foliar physiognomic differences between the Poole and Nelly Creek floras (which contain a majority of broad-lamina taxa) and the Stuart Creek flora (which is dominated by stenophyllous forms) may reflect either a drier climate (through climate change over time) or perhaps poor soils in the Stuart Creek area promoting greater xerophylly and/or sclerophylly in the local flora there. It is likely that the Lake Eyre area was no wetter in the Late Miocene than in the Middle Eocene, and may even have been drier (Truswell and Harris 1982; Benbow *et al.* 1995). Most extant species of *Banksia* occur on sites where annual rainfall is between 500 and 1000 mm (all but *B. plagiocarpa* <1500 mm per year; based on 75 spp. for which rainfall values were provided in Taylor and Hopper 1988 and Holliday and Watton 1990). The extant saw tooth-lobed species most similar to *Banksiaeformis langii* (e.g. *Banksia speciosa* and *B. dryandroides*) are both found on sites with rainfall <800 mm per year and the extant species most similar to *Banksiaeformis praegrans* (i.e. *Banksia chamaephyton*) occurs on sites <600 mm per year. This data suggests that the Stuart Creek flora grew under an annual rainfall of <1000 mm per year. The presence of *Banksiaeformis* spp. at Stuart Creek, Morris Creek and sites in the Stuart Range is therefore consistent with a lowering of annual rainfall between the Middle Eocene (1100–1360 mm year⁻¹) and Miocene for sites in the Lake Eyre area. However, at the lower range of uncertainty for the Middle Eocene rainfall estimates, or broadened tolerances in the past for the taxa (reflecting also taxonomic uncertainty), there is no or little change in rainfall indicated. Also the record of *Callicoma serratifolia* from the Stuart Creek flora (Barnes and Hill 1999) is inconsistent, with rainfall in the Late Miocene being much lower than 1000 mm per year, as this extant species is found in wet sclerophyll forest and warm temperate to subtropical rainforest along the east coast of Australia. Other taxa reported for

the Stuart Creek flora, such as Casuarinaceae aff. *Gymnostoma* and *Brachychiton*, are consistent with annual rainfall of about 1000 mm (Greenwood 1996).

McNamara and Scott (1983) speculated that damaged follicles on *B. archaeocarpa* may be evidence of insect attack and predation on these insects by birds (possibly parrots). Hill (1994) also suggested that other Tertiary Proteaceae inflorescences might demonstrate the development of animal pollination vectors. The development of a robust woody axis in *Banksia* inflorescences would seem to be an adaptation to mammalian pollination, but may also be a consequence of seroteny. The fossil record of honey possums (Tarsipedidae) is quite sparse; however, Miocene faunas in Etadunna Formation in the Lake Eyre area contain evidence of two possum families, the Phalangeroidea and Petauridae (Rich 1991), modern species of which are known to feed on *Banksia* inflorescences. It is therefore possible that *B. longicarpa* was pollinated by possums. The robust character of the follicles in *B. longicarpa* is possibly an adaptation to allow seeds to survive fire (serotiny), a common characteristic in modern species.

Conclusions

Without doubt, *Banksia* occurred formerly outside of its present range. The character, location and time frame of central Australian populations of *Banksia* may provide important insight into the phytogeography and evolution of this important genus of Australian plants. The fossil records presented here indicate that *Banksia* occurred in northern South Australia in the Miocene (*Banksia longicarpa*) and that Banksiinae, possibly *Banksia*, occurred near Alice Springs in the mid-Tertiary. The leaves of *Banksieaeformis serratus* from Glen Helen are quite similar to those of the species occurring in both south-western (*Banksia baueri* and *B. menziesii*, Series *Banksia*) and south-eastern Australia (*B. serrata* and *B. aemula*, Series *Banksia*) and also the sole Northern Territory species, *B. dentata* (Series *Salicinae*), whereas the northern South Australian *Banksieaeformis praegrans* and *B. langii* reflect taxa restricted to Western Australia (e.g. *Banksia chamaephyton*, Series *Prostratae* and *B. speciosa*, Series *Banksia*, respectively), and in the case of *Banksieaeformis praegrans* may not represent Banksiinae. The '*Banksia speciosa*' leaf type of *Banksieaeformis langii* is also known from the Paleocene of New South Wales (i.e. *Banksieaephyllum taylori*), indicating an ancient and widespread occurrence of this leaf type. This pattern of occurrence may reflect a former set of connected populations, or equally so, may reflect common leaf forms as adaptations to particular circumstances. Available fossil evidence suggests that a wide range of leaf morphologies were present early in the Tertiary, but that infructescences primarily represent subgenus *Banksia*; this supports suggestions of mosaic evolution within Banksiinae, with some leaf characters evolving independently of infructescence form in separate lineages. While estimates of rainfall presented here on the basis of taxa must be considered speculative, the *Banksieaeformis* species from the Lake Eyre region are consistent with a climatic drying between the Middle Eocene and the Miocene in this area, but do not conclusively indicate drying. Conversely, these taxa may indicate local vegetational mosaicism involving sclerophylly and/or fire (e.g. putative serotinous cone of *B. longicarpa*), as other taxa in the Stuart Creek macroflora (e.g. *Callicoma* and *Brachychiton*) at least are indicative of seasonally wet conditions.

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