TERTIARY PROTEACEAE IN AUSTRALIA: A RE-INVESTIGATION OF *BANKSIA ADUNCA* AND *DRYANDRA URNIFORMIS*

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The specimens described by Deane (1925) as *Banksia adunca* and *Dryandra urniformis* from Upper Oligocene–Lower Miocene coals at Morwell, Victoria have been re-examined and their cuticular morphology examined for the first time. *Banksia adunca* is considered to be conspecific with *Banksieaephyllum fastigatum* (Dean) Cookson & Duigan. *D. urniformis* is also transferred to *Banksieaephyllum* and is considered to be closely related to *B. elongatum* Hill & Christophel, 1988 from the Upper Oligocene–Lower Miocene at Loy Yang. These *Banksieaephyllum* species are particularly important in tracing the history of the development of sclerophylly and xeromorphy in Australian plants.

MACROFOSSILS of the Proteaceae are well represented in Australian Tertiary sediments, leaves and reproductive structures of a range of genera having been described (Cookson & Duigan 1950, Pike 1953, Lange 1978, Blackburn 1981, McNamara & Scott 1983, Christophel 1984, Carpenter & Hill 1988, Hill & Christophel 1988). Amongst the Proteaceae the most common and diverse macrofossils belong to the tribe Banksieae.

The coals of the Latrobe Valley in Gippsland, Victoria contain a diversity of macrofossils in the Banksieae, nine species based on vegetative material having been described by Deane (1925), Cookson & Duigan (1950) and Hill & Christophel (1988). Following Ettingshausen (1888), Deane (1925) adopted the convention of placing serrate leaves in *Banksia* and pinnate leaves in *Dryandra* but he was aware that this distinction is invalid amongst living species. Cookson & Duigan (1950) concluded that extant species of these two genera cannot be separated on leaf form alone and thus erected the form genus *Banksieaephyllum* for fossil leaves with the characteristics of *Banksia* and/or *Dryandra*. They transferred *Banksia fastigata* Deane to *Banksieaephyllum* on the basis of the original specimen and new collections. The other two species described by Deane, *Banksia adunca* and *Dryandra urniformis*, were listed by Cookson & Duigan amongst species requiring re-investigation to establish their affinities. Hill & Christophel (1988) noted that leaves should not be placed in *Banksieaephyllum* unless the cuticular morphology was sufficiently well preserved to support the assignment.

The type specimens of *Banksia adunca* and *Dryandra urniformis* were examined recently in the Museum of Victoria (specimen numbers with prefix NMV), and it was determined that in both specimens the cuticle was preserved. The specimens have been re-investigated and their cuticular morphology studied to determine whether their placement in the tribe Banksieae is valid, and if so whether they should be transferred to the form genus *Banksieaephyllum*. Both fossil species were collected from the Morwell coal (Deane 1925) which spans the Upper Oligocene to Lower Miocene (Stover & Partridge 1973), but the precise horizon from which the specimens came is uncertain.

MATERIAL AND METHODS

The material of each species consists of only part of the leaf. Extreme care was required in preparing the cuticle since only a small amount of leaf tissue is available. Before any attempt was made to remove leaf fragments, the specimens were photographed using an Olympus OM-4 camera with bellows and reflected light. Both leaves appear to have been coated with some type of varnish for protection, and this was successfully removed by soaking small fragments of the leaves in acetone for several hours. Following this treatment the leaf fragments were placed in 10% chromic acid until the internal leaf tissue had dissolved. The cuticular fragments were then washed, neutralised in 5% ammonia, stained in 1% aqueous safranin O, and mounted on microscope slides in phenol glycerine jelly. Cuticles were examined using a Zeiss Axioskop compound microscope.

Both specimens yielded well preserved cuticle, although the stomatiferous surface of *Banksia adunca* could not be cleaned completely despite a number of attempts. It is possible that other methods may be successful in cleaning this cuticle, but given the small amount available it was considered that the risk of damaging the cuticle was too great to persevere.

Both species clearly belong to the tribe Banksieae of the Proteaceae. They contain a combination of characters listed by Cookson & Duigan (1950) and Hill & Christophel (1988) as being typical of the tribe (stomata with paired subsidiary cells parallel to the pore (brachyparacytic), serrations with prominent veins ending in the apices, and distinctive trichome types). Like other fossil leaves of this type, however, they cannot be placed with certainty in either *Banksia* or *Dryandra*, and so must be transferred to the form genus *Banksieaephyllum*.

TAXONOMIC DESCRIPTIONS

Family PROTEACEAE
Subfamily GREVILLIOIDEAE
Tribe BANKSIEAE

Genus **Banksieaephyllum** Cookson & Duigan

Banksieaephyllum urniforme (Deane) Hill, comb. nov.

Figs 1A–D, 2A

Dryandra urniformis Deane 1925: 495, pl. 62, fig. 9.

Holotype. NMV P15127.

Emended diagnosis. Leaves bilateral, at least 6 mm wide, pinnately lobed. Lobes acute and apically directed; apical and basal sides of lobes convex, apical side much shorter than basal side. Leaf base and apex unknown. Secondary venation pattern craspedodromous, with a number of secondary veins per lobe. Stomata brachyparacytic, superficial. Trichome bases of two types abundant on stomatiferous epidermis. Large trichome bases usually associated with one but sometimes with two or three epidermal cells; trichome small, unicellular. Small trichome bases associated with one epidermal cell; trichome basal cell thickly cutinized, cylindrical; apical cell(s) not preserved. Trichome bases absent from upper epidermis.

Discussion. This species is represented by only a fragment of a single leaf but the cuticle is well-preserved. The leaf has characteristic urn-shaped pinnae which are similar to those described in *Banksieaephyllum elongatum* Hill & Christophel (1988). Hill & Christophel (1988) commented on this similarity but considered the pinnae of *B. urniforme* and *B. elongatum* to be consistently of a different shape. The specimen of *B. urniforme* was not studied by Hill & Christophel, however, and its cuticular morphology was therefore not considered. The cuticle of *B. urniforme* is similar to that of *B. elongatum* but differs from it most notably in lacking small, simple trichome bases on the upper epidermis.

The remaining fossil species of Banksieae with pinnate leaves are much larger in size than *Banksieaephyllum urniforme*, and have very distinct cuticular patterns (*Banksieaephyllum cuneatum* Hill & Christophel, 1988 and *B. incisum* Blackburn, 1981), distinctive leaf bases (*Banksieaeformis decurrens* Hill & Christophel, 1988), or distinctively rounded pinnae (*Banksieaephyllum pinnatum* Cookson & Duigan, 1950).

Banksieaephyllum elongatum Hill & Christophel, 1988

Banksieaephyllum elongatus Hill & Christophel 1988: 212–214, figs 24–29.

Emended diagnosis. Leaves bilateral, at least 60 mm long and up to 10 mm wide, pinnately lobed. Lobes acute and apically directed; apical side of lobe usually straight or slightly concave, much shorter than basal side; basal side convex. Leaf base cuneate, apex unknown. Secondary venation pattern craspedodromous, with a variable number of secondary veins per lobe. Stomata brachyparacytic, superficial. Trichome bases of two types abundant on stomatiferous epidermis. Large trichome bases usually associated with one but sometimes with two or three epidermal cells; trichome small, unicellular. Small trichome bases associated with one epidermal cell; trichome basal cell thickly cutinized, cylindrical; apical cell(s) not preserved. Small, unicellular trichome foot cells scattered on upper epidermis; trichomes unknown.

Discussion. An emended diagnosis of *B. elongatum* is given here because in the original diagnosis the small unicellular trichome bases on the upper epidermis were not included. This is one of the most important characters separating this species from *B. urniforme*.

Banksieaephyllum fastigatum (Deane) Cookson & Duigan

Figs 1E–H, 2B

Banksia fastigata Deane 1925: 494, text-fig. 140, pl. 61, figs 1, 4, pl. 62, figs 6, 7?, pl. 63, fig. 13.
Banksia adunca Deane 1925: 494–5, text-fig. 141, pl. 62, fig. 10, pl. 64, fig. 18.
Banksieaephyllum fastigatum.—Cookson & Duigan 1950: 153, pl. 6, figs 43–48.

Holotype of Banksia adunca. NMV P15128.

Emended diagnosis. Leaves long, regularly serrate, about 15 mm wide and tapering at both base and apex. Serrations curved towards apex of leaf; sinuses about 1/3 width from midvein to apex of serration. Secondary veins upwardly curved, with one terminating in each serration and one near each sinus. Cuticular pattern suggests that areoles are well-developed. Stomata situated in slight depressions, long axes of which tend to be oriented in one direction. Individual stomata appear to be slightly sunken below surface of surrounding epidermis. Lying parallel to pore of each stoma are two inconspicuous subsidiary cells, over which neighbouring epidermal cells may project slightly. Stomatal apparatus surrounded by 3–6 narrow cells which stain deeply. Epidermal parenchyma not uniform; most of its cells of medium size, with straight or curved, very thin and pitted walls in stomatal areas, and similar but somewhat thicker walls above veins. Amongst cells of parenchyma are scattered exceptionally small cells 4–6 µm in diameter, supporting hair bases of similar size. Cells over midvein small, square to quadrangular, with moderately thick, unpitted walls; small hair bases sparsely developed. Cuticle longitudinally ridged. Upper epidermal cells above veins somewhat smaller than those of areas enclosed by veins; all have rather thin, unpitted, straight or slightly curved walls.

Discussion. Banksia adunca is distinct from 10 of the 13 previously described fossil species, which either have entire leaf margins (*Banksieaephyllum acuminatum* Cookson & Duigan, 1950, *B. laeve* Cookson & Duigan, 1950 and *B. obovatum* Cookson & Duigan, 1950), leaves that are divided into the midvein (*Banksieaephyllum cuneatum, B. incisum, B. elongatum, B. pinnatum* and *Banksieaeformis decurrens*), or leaves that are serrate with more than one secondary vein per serration (*Banksieaephyllum regulare* Hill & Christophel, 1988 and *B. angustum* Cookson & Duigan, 1950).

Banksia adunca is similar in leaf morphology and venation pattern to *Banksieaephyllum attenuatum* Hill & Christophel, 1988, *B. fastigatum* and *Banksieaeformis dentatus* Hill & Christophel (1988). The comparison with *B. dentatus* can be carried no further, since this species is not organically preserved (and hence is placed in a separate genus). Hill & Christophel (1988) noted the similarity between *Banksieaephyllum attenuatum* and *B. fastigatum*, with the major difference being the superficial stomates in the former in comparison with the sunken stomates in the latter. In this and all other features observed, *Banksia adunca* is very similar to *Banksieaephyllum fastigatum* and its cuticular morphology is identical. Deane (1925) described differences in serration morphology but differences such as these commonly occur within extant species. It is concluded, therefore, that *Banksia adunca* and *Banksieaephyllum fastigatum* are synonymous. The name *Banksieaephyllum fastigatum* is retained for the species because this name was used by Cookson & Duigan (1950) and more recent authors (e.g. Blackburn 1981, Hill & Christophel 1988), and its continued use will avoid confusion for future workers. Since *Banksia fastigata* and *B. adunca* were described in the same paper, the choice is one of convenience since neither name has priority.

The diagnosis of *B. fastigatum* provided by Cookson & Duigan (1950) has been emended to accommodate the slightly different shape of the serrations in the holotype of *Banksia adunca*.

DISCUSSION

The coals of the Latrobe Valley have yielded eight species of *Banksieaephyllum*, three of them (*B. laeve, B. obovatum* and *B. pinnatum*) being widespread and relatively common in both the Yallourn and Morwell coal (Blackburn 1985), the others occurring infrequently and in some cases being known only from single specimens. It is clear, however, that this group was an important part of the vegetation which contributed to coal formation, and a study of the leaf form of these species is of major importance in understanding the environmental conditions under which the plants were growing.

The leaves of all these species are relatively sclerophyllous in nature, a condition which is a

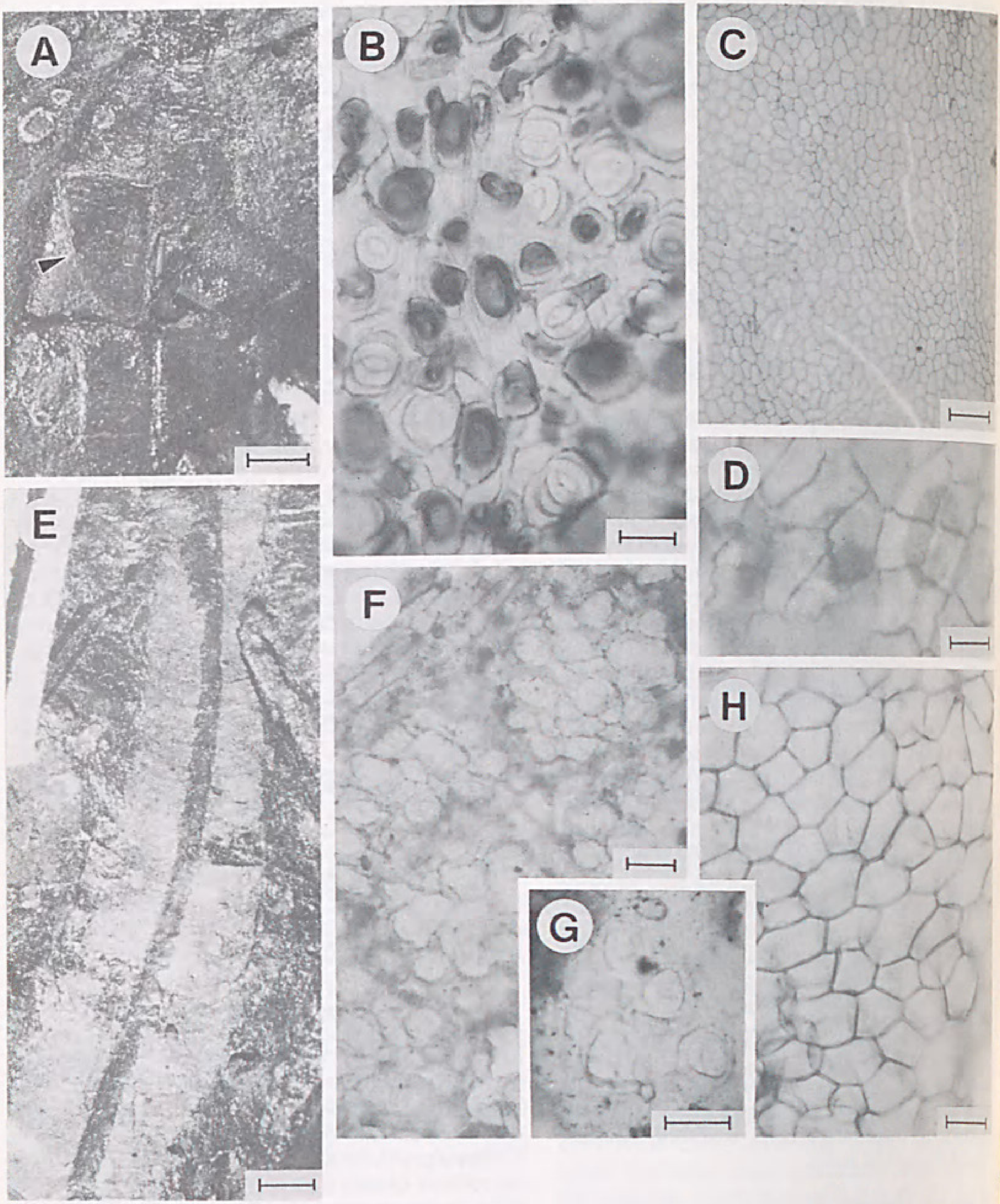

Fig. 1. A-D, *Banksieaephyllum urniforme*, holotype, NMV P15127. A, entire specimen; note single well preserved lobe of leaf (arrowed); scale = 2 mm. B, lower epidermis showing stomates and two common trichome base types; scale = 25 µm. C, upper epidermis; note absence of trichomes; scale = 100 µm. D, two multicellular trichome bases near leaf margin; these bases are characteristic of Proteaceae; scale = 25 µm. E-H, *Banksieaephyllum fastigatum*, NMV P15128, holotype of *Banksia adunca*. E, entire leaf; scale = 2 mm. F, lower epidermis; cuticle is not completely clean but it can be seen that trichome bases are lacking; scale = 25 µm. G, lower epidermis; stomates with small brachyparacytic subsidiary cells visible; scale = 25 µm. H, upper epidermis; scale = 25 µm.

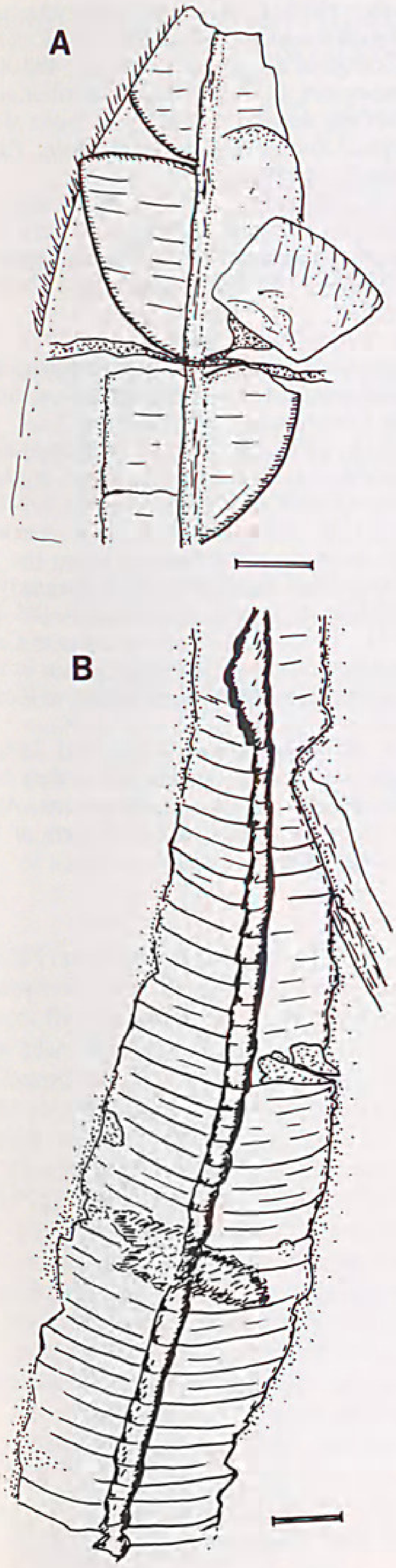

Fig. 2 A, drawing of holotype of *Banksieaephyllum urniforme*, NMV P15127, see Fig. 1A; scale = 2 mm. B, drawing of specimen of *B. fastigatum* shown in Fig. 1E, NMV P15128); scale = 2 mm.

response to low nutrient levels in the soil, particularly low phosphorus (Beadle 1966). There has often been confusion about the interaction of nutrient levels and climate (in particular low rainfall) as contributing factors to sclerophylly. Many sclerophyllous characters are also useful xeromorphic adaptations (e.g. small leaf size, thick cuticle), and with features such as these it is difficult if not impossible to determine whether low nutrients or a dry climate was the causal factor. There are some leaf characters, however, which can be described as xeromorphic and are distinct from scleromorphy. Most prominent amongst these are adaptations directed towards protecting the stomates, so that the boundary layer resistance is increased (e.g. sunken stomates, stomates in pits, revolute leaf margins, hairs around the stomates, etc.). It is the presence or absence of these characters which should allow an interpretation of the factor(s) most affecting leaf form in *Banksieaephyllum* (Hill in press).

Although all species of *Banksieaephyllum* described from the Latrobe Valley coal are sclerophyllous, only some have adaptations which can be considered as solely xeromorphic. *B. angustum* and *B. acuminatum* are the most xeromorphic species, having strongly recurved leaf margins, stomata sunken in pits, and very hairy stomatal leaf surfaces. Blackburn (1985) noted these xeromorphic features and their relationship to the darker coals which accumulated in the drier environments. Some of the other species (e.g. *B. laeve, B. obovatum*) exhibit almost no xeromorphic adaptations, and the remaining species are intermediate in form. Even the most xeromorphic species are not as strongly adapted to preventing water loss as are some of the extant *Banksia* and *Dryandra* species, and they may be in a transitional state towards this development. Thus it can be concluded that these fossils offer the earliest fossil evidence of xeromorphy in Australia, even though *Banksieaephyllum* is recorded from the Palaeocene onwards. This suggests that these coal floras are an important site for the study of the way in which the morphological adaptations to the Mediterranean climate evolved in Australia. Future studies on other taxonomic groups should refine these conclusions.

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