

# Proteaceae leaf fossils from the Oligo–Miocene of New Zealand: new species and evidence of biome and trait conservatism

Raymond J. Carpenter<sup>A,E</sup>, Jennifer M. Bannister<sup>B</sup>, Daphne E. Lee<sup>C</sup> and Gregory J. Jordan<sup>D</sup>

<sup>A</sup>School of Earth and Environmental Sciences, University of Adelaide, Adelaide, SA 5005, Australia.

<sup>B</sup>Department of Botany, University of Otago, PO Box 56, Dunedin 9054, New Zealand.

<sup>C</sup>Department of Geology, University of Otago, PO Box 56, Dunedin 9054, New Zealand.

<sup>D</sup>School of Plant Science, University of Tasmania, Private Bag 55, Hobart, Tas. 7001, Australia.

<sup>E</sup>Corresponding author. Email: [raymond.carpenter@adelaide.edu.au](mailto:raymond.carpenter@adelaide.edu.au)

**Abstract.** At least seven foliar taxa of Proteaceae occur in Oligo–Miocene lignite from the Newvale site. These taxa include two new species of the fossil genus *Euproteaciphyllum*, and previously described species of tribe Persoonieae and *Banksia*. Other specimens from Newvale are not assigned to new species, but some conform to leaves of the New Caledonian genus *Beauprea*, which is also represented in the lignite by common pollen. Two other *Euproteaciphyllum* species are described from the early Miocene Foulden Maar diatomite site. One of these species may belong to *Alloxylon* (tribe Embothrieae) and the other to tribe Macadamieae, subtribe Gevuininae. Ecologically, the species from Newvale represented important components of wet, oligotrophic, open vegetation containing scleromorphic angiosperms and very diverse conifers. In contrast, Proteaceae were large-leaved and rare in Lauraceae-dominated rainforest at the volcanic Foulden Maar site. Overall, the Oligo–Miocene fossils confirm that Proteaceae was formerly much more diverse and dominant in the New Zealand vegetation, and provide fossil evidence for biome conservatism in both leaf traits and lineage representation.

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## Introduction

New Zealand has only two extant species of Proteaceae, *Knightia excelsa* R.Br. and *Toronia toru* (A.Cunn.) L.A.S. Johnson & B.G. Briggs. Pollen and cuticular fragments provide evidence that the diversity of Proteaceae in New Zealand was much higher in the Paleogene and early Neogene than it is today (Pole 1998; Lee *et al.* 2001). However, there are few reports of well preserved leaf fossils, which can provide much superior information for taxonomic and ecological interpretations.

Within most phylogenetic lineages, species occupy similar biomes, suggesting strong trait conservatism and ancient fidelity to particular vegetation and physiognomies (Crisp *et al.* 2009). In Proteaceae, the extant subfamilies are likely to have evolved in the Late Cretaceous (Johnson and Briggs 1975; Sauquet *et al.* 2009a, 2009b), and the presence of dense clusters of rootlets (or ‘proteoid roots’) in all taxa with the exception of subfamilies Persoonioideae and Symphionematoideae (where the rootlets were probably secondarily lost; Weston and Barker 2006; Weston 2007) indicates that the common ancestor of the family evolved in a nutrient-poor (oligotrophic) situation (Johnson and Briggs 1975). Species of Proteaceae are now well known as significant representatives of Mediterranean-climate heathland and woodland communities on mostly oligotrophic, in some cases seasonally swampy, substrates in Australia and South Africa. Crisp *et al.* (2009) included these communities as part of a wider sclerophyll biome. Other Proteaceae of this biome occur commonly in New Caledonian

maquis vegetation, which is an open form of scrub or woodland that dominates on ultramafic, oligotrophic substrates in the prevailing wet, subtropical climate of the south-eastern part of the main island (Jaffré 1980). Most species of Proteaceae of the sclerophyll biome are scleromorphic shrubs, and typically feature small leaves, with, for example, reduced, more-or-less parallel venation and amphistomaty (Johnson and Briggs 1975). Despite the obvious species richness of this biome, however, the greatest generic diversity of Proteaceae exists in the rainforests of the Wet Tropics of Queensland (especially the granite uplands), where several species have distinctive, very large, commonly lobed leaves (Carpenter 1994). Crisp *et al.* (2009) included this rainforest as part of a wider wet forest biome defined as exhibiting a closed canopy of trees, typically in high-precipitation climates.

Lee *et al.* (2001) attributed most extinctions of Proteaceae and numerous other lineages in New Zealand to the effects of Neogene climatic cooling, increasing geographical isolation and tectonism. Most important was probably the pronounced global cooling event that began in the middle Miocene following the Miocene climatic optimum (~17 million–15 million years ago; Zachos *et al.* 2001). Paucity of Proteaceae diversity in modern New Zealand vegetation allows only very limited ecological inferences with respect to the ecology of taxa in deep time. Both extant species occupy a variety of seral vegetation types in broadleaved–conifer forest on a range of soils (Wardle 1991), and neither species has leaves that approach the extreme forms of

those found in the sclerophyll or wet forest biomes. Thus, important questions are first whether the extinct species of Proteaceae of New Zealand were indeed specialists in oligotrophic environments, and second, whether there were taxa that more obviously had typical features of the sclerophyll and wet forest biomes that now host numerous species outside New Zealand. Indications that New Zealand's vegetation formerly included elements belonging to lineages that typify the extant Australian sclerophyll biome were provided by recently described fossil leaf species of subfamily Persoonioideae tribe Persoonieae (Carpenter *et al.* 2010a) and *Banksia* (Carpenter *et al.* 2010b).

The aim of the present study is to report on new fossil foliar specimens of Proteaceae from the Oligo–Miocene Newvale site, Southland, New Zealand, and from the potentially coeval Foulden Maar diatomite site, Central Otago, where no Proteaceae species have previously been recognised (Pole 1996). These fossils are discussed in terms of their importance to understanding the ecological role of the family across time.

## Methods and materials

### Fossil sites and ages

#### Newvale

Fossils are from the same Oligo–Miocene leaf beds within Seam W6 of the middle Gore Lignite Measures, Newvale Mine, Waimumu Coalfield, Southland, that were described by Lee *et al.* (2007, 2012) and Ferguson *et al.* (2010). This lignite was dated as being of probable Waitakian age of the New Zealand scale (Lee *et al.* 2007), which corresponds to 25.2 million–21.7 million years old. The locality is registered as F45/f0394 in the New Zealand Fossil Record File administered by the Geoscience Society of New Zealand. The NZ Map Grid reference on Infomap Series NZMS 260 is F45/817434 (46.1427°S, 168.7518°E).

#### Foulden Maar

The diatomite formed in a volcanic maar lake and features well preserved fossils of plants and animals (e.g. Pole 1993, 1996; Bannister *et al.* 2005, 2012; Lindqvist and Lee 2009; Conran *et al.* 2009, 2010; Lee *et al.* 2007, 2010, 2012). Palynostratigraphic dating (Bannister *et al.* 2005) and radiometric dating of nearby volcanic basalts (23.2 million years old; Lindqvist and Lee 2009) imply that the lake formed in the earliest Miocene. The locality is registered as I43/f8503 in the New Zealand Fossil Record File,

and the NZ Map Grid reference is I43/929166 (45.5271°S, 170.2218°E).

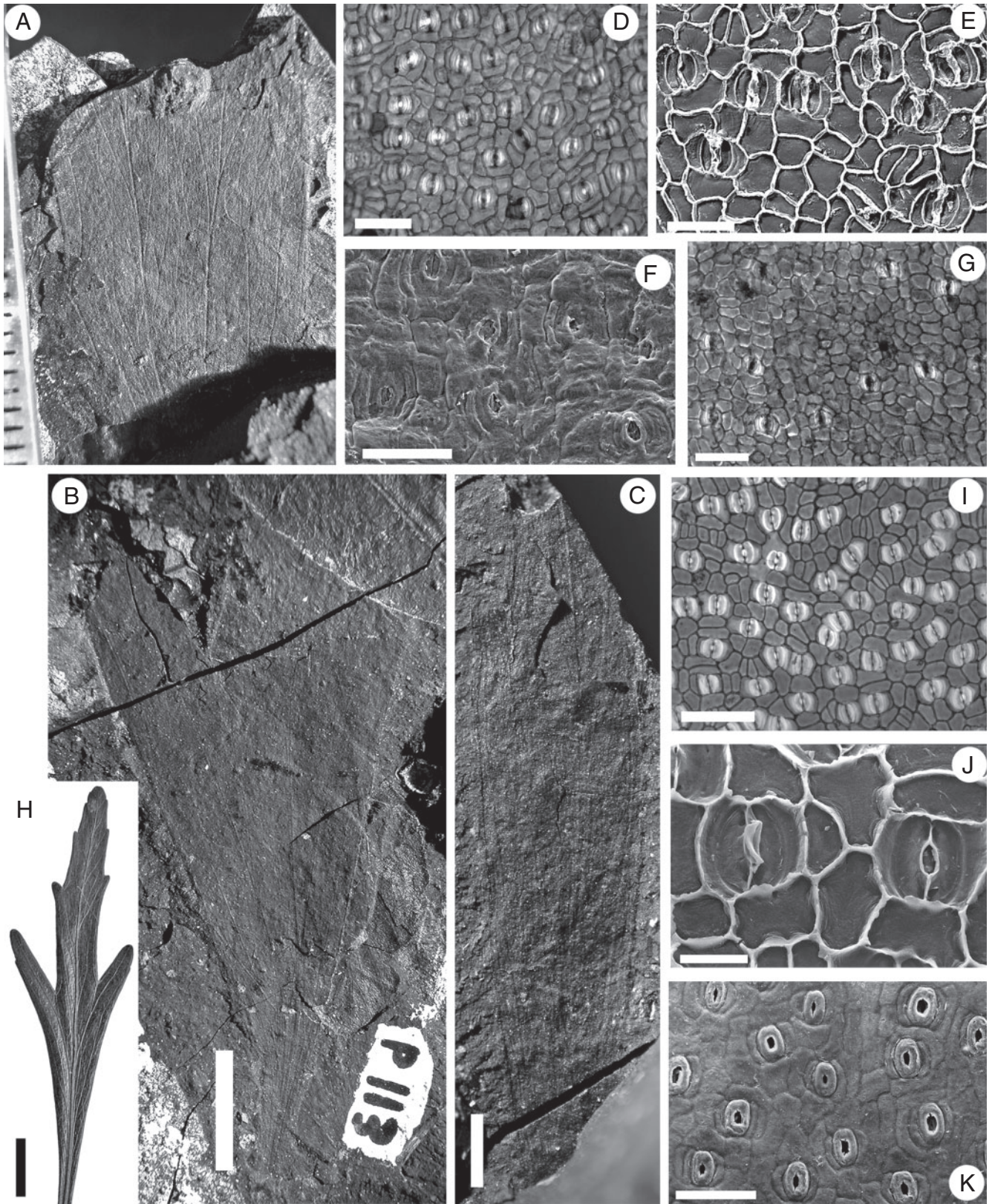
### Preparation of specimens and identifications

The lignite from Newvale contains mummified leaves and leaf fragments (Lee *et al.* 2007). No complete Proteaceae leaves were recognised among the ~20 small blocks of lignite that were examined, although several specimens bear leaf fragments with complete widths and venation details. Numerous other fragmentary specimens were recovered by sieving following disaggregation of lignite pieces in warm hydrogen peroxide. Two specimens of relatively complete and well preserved proteaceous leaves were recovered from Foulden Maar. They were cleared of diatomite with a paintbrush and water.

Specimens from both sites were photographed with a Nikon D70 digital SLR (Tokyo, Japan) or a Canon Powershot A480 digital camera (Tokyo, Japan). Cuticle preparations were made by soaking leafy material in either dilute hydrogen peroxide or household bleach (sodium hypochlorite 42 g L<sup>-1</sup>) until all mesophyll was cleared. The cuticles were then rinsed and, if necessary, cleaned with a fine paintbrush. Some cuticle pieces were mounted on glass slides in glycerine jelly after staining with either 0.1% crystal violet or 1% safranin O for viewing with transmitted light microscopy. Other pieces were placed on double-sided adhesive tape on aluminium stubs and either sputter coated with carbon and gold, and examined and photographed using a Philips XL 30 field emission gun scanning electron micrograph (FEGSEM) (Eindhoven, the Netherlands) operated at 10 kV at Adelaide University or coated with gold and palladium and examined using a Cambridge S360 Stereoscan electron microscope (Cambridge, UK) at Otago University.

The fossils were compared with descriptions of extant genera (e.g. McCarthy 1995, Hyland *et al.* 2010) and living specimens sourced from the field and Australian herbaria. Leaf venation terminology follows Ellis *et al.* (2009) and taxonomy follows Weston and Barker (2006). Cuticles were compared with the large collection of Proteaceae material housed at the University of Adelaide that incorporates at least one species from every extant genus, and ~400 species in total. Most of the new fossils were recognised as Proteaceae on the basis of the presence of brachyparacytic stomata and distinctive annular trichome bases that commonly encompass more than one underlying epidermal cell (Carpenter *et al.* 2005). However, none of these fossils could be included in extant genera, because of an apparent lack of phylogenetically informative features. The fossil genus *Euproteaciphyllum* was erected to house such specimens that

**Fig. 1.** A–G. *cf. Beuprea* sp. from Newvale Mine. H–K. Extant *Beuprea*. A. Incomplete leaf specimen showing weakly linear venation (OU32742); scale bar in millimetres. B. Incomplete leaf specimen showing a lobe and weak veins (OU33343); scale bar = 10 mm. C. Incomplete leaf specimen showing a tooth (at upper left) and weak veins (OU33342); scale bar = 2 mm. D. Light micrograph (LM) showing stomata on abaxial leaf surface (OU32125). Note near-parallel stomatal placement, and T-pieces at poles of guard cells; scale bar = 100 µm. E. Scanning electron micrograph (SEM) showing inner abaxial cuticle (OU33343). Note near-parallel stomatal placement, T-pieces at poles of guard cells and smooth periclinal walls; scale bar = 50 µm. F. SEM showing outer abaxial cuticle (OU33343). Cell outlines and ledges over the guard-cell regions are visible; scale bar = 50 µm. G. LM showing more sparsely distributed stomata on the adaxial surface (OU32125); scale bar = 100 µm. H. Part of a *B. pancheri* (NOU015984) leaf, showing lobing and teeth similar to those of the fossils, but differing venation, with the single principal veins running into the apices; scale bar = 10 mm. I. LM showing stomata on abaxial leaf surface (*B. balansae*). Note the same type of near-parallel stomatal placement and T-pieces at poles of guard cells as in the fossils; scale bar = 100 µm. J. SEM of the inner surface of abaxial cuticle, showing two stomata (*B. balansae*). Note similarities to fossil (Fig. 1E), including T-pieces; scale bar = 20 µm. K. SEM of the outer abaxial surface (*B. montisfontium* Guillaumin). Note similarities to fossil (Fig. 1F), including cell outlines, scale bar = 100 µm.



are clearly Proteaceae (Carpenter and Jordan 1997; Jordan *et al.* 1998). In previous studies, some leaf fossils lacking clear apomorphic evidence but with strong similarity to leaves of an extant taxon of Proteaceae in gross morphology, venation details, stomatal complexes, trichome-base types and cuticular ornamentation have been assigned to that taxon. This approach is best reserved for very well preserved fossils with distinctive features (Carpenter and Jordan 1997). Other leaf fossils that very closely resemble leaves of an extant taxon, but without distinctive features, are best regarded as likely to belong to the extant taxon, but should not be formally placed there. This was the case for the *Beauprea*-like leaf remains in the present study.

All fossils are held in the collections of the Geology Museum (OU), University of Otago, Dunedin, New Zealand. Some microscope slides and scanning electron micrograph (SEM) stubs with material derived from the specimens are currently housed at the University of Adelaide.

## Results

Leaf and cuticle specimens from the Newvale lignite were separable into seven taxa of Proteaceae. Three species have previously been described. These are two species of subfamily Persoonioideae in the new genus *Persooniaephyllum* (Carpenter *et al.* 2010a), and also *Banksia novae-zelandiae* R.J.Carp., G.J. Jord., D.E.Lee & R.S.Hill (Carpenter *et al.* 2010b). New fossils are consistent with extant *Beauprea*, but are not formally assigned to *Beauprea* because the leaves of this genus lack unique features, and are apparently entirely glabrous. These *Beauprea*-like fossils also cannot be included in *Euproteaciphyllum* because the diagnosis for this genus includes a requirement for trichome bases (Carpenter and Jordan 1997). Three of the other Newvale taxa exhibit the typical stomata and trichome bases of Proteaceae but, on current understanding, lack features that might enable them to be assigned to extant groups. Two of these taxa were sufficiently well preserved to be assigned to *Euproteaciphyllum*, whereas the third is so far represented by a single cuticle fragment and is therefore attributed to family level only. Two further Proteaceae specimens were recovered from Foulden Hills, and assigned to *Euproteaciphyllum*.

## Taxonomy

### Family Proteaceae

cf. *Beauprea* sp. (Fig. 1A–G)

*Specimens examined*: OU32061, OU32065, OU32067, OU32068, OU32069, OU32070, OU32076, OU32116, OU32117, OU32118, OU32122, OU32125, OU32132, OU32742, OU33342, OU33343.

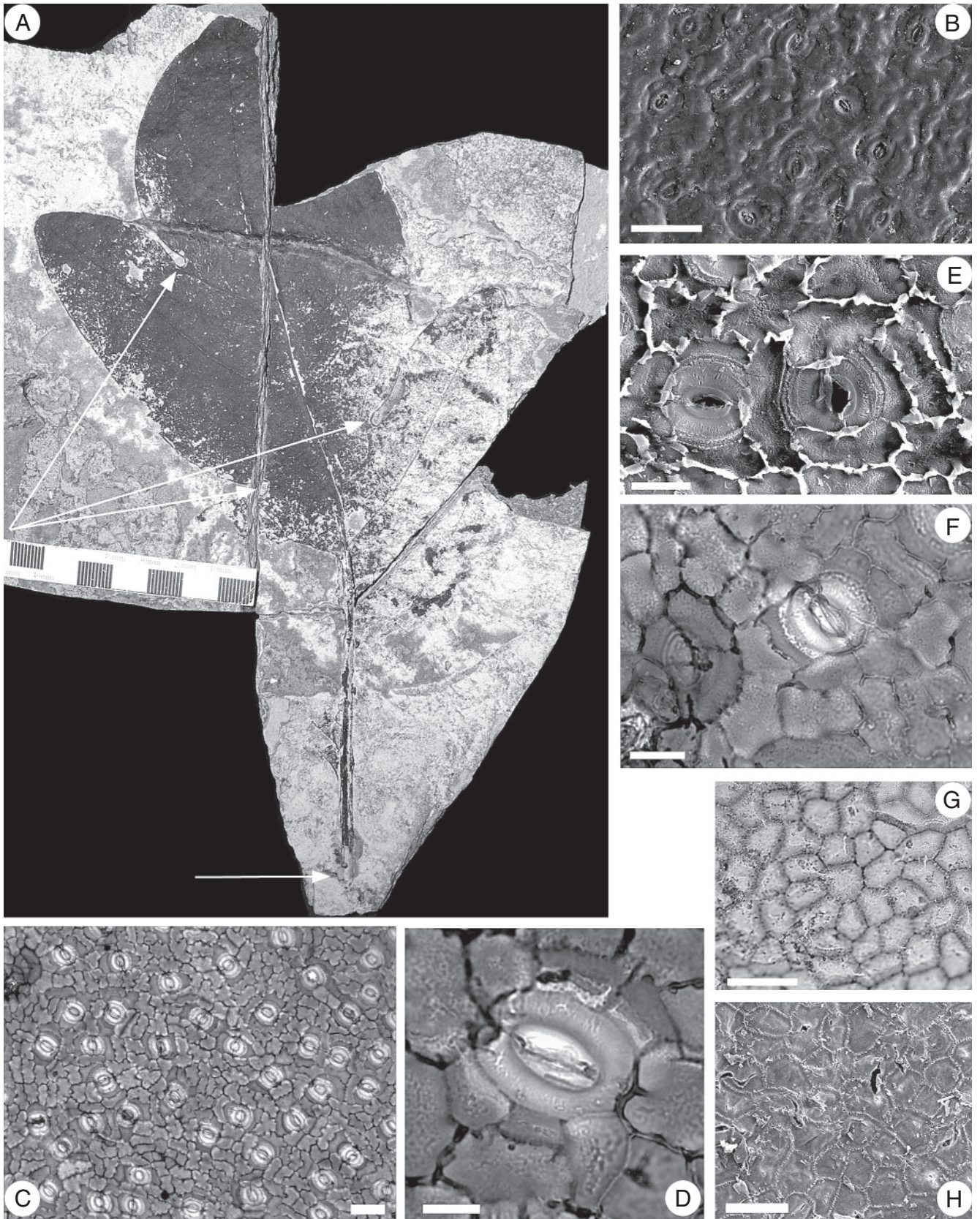
## Description

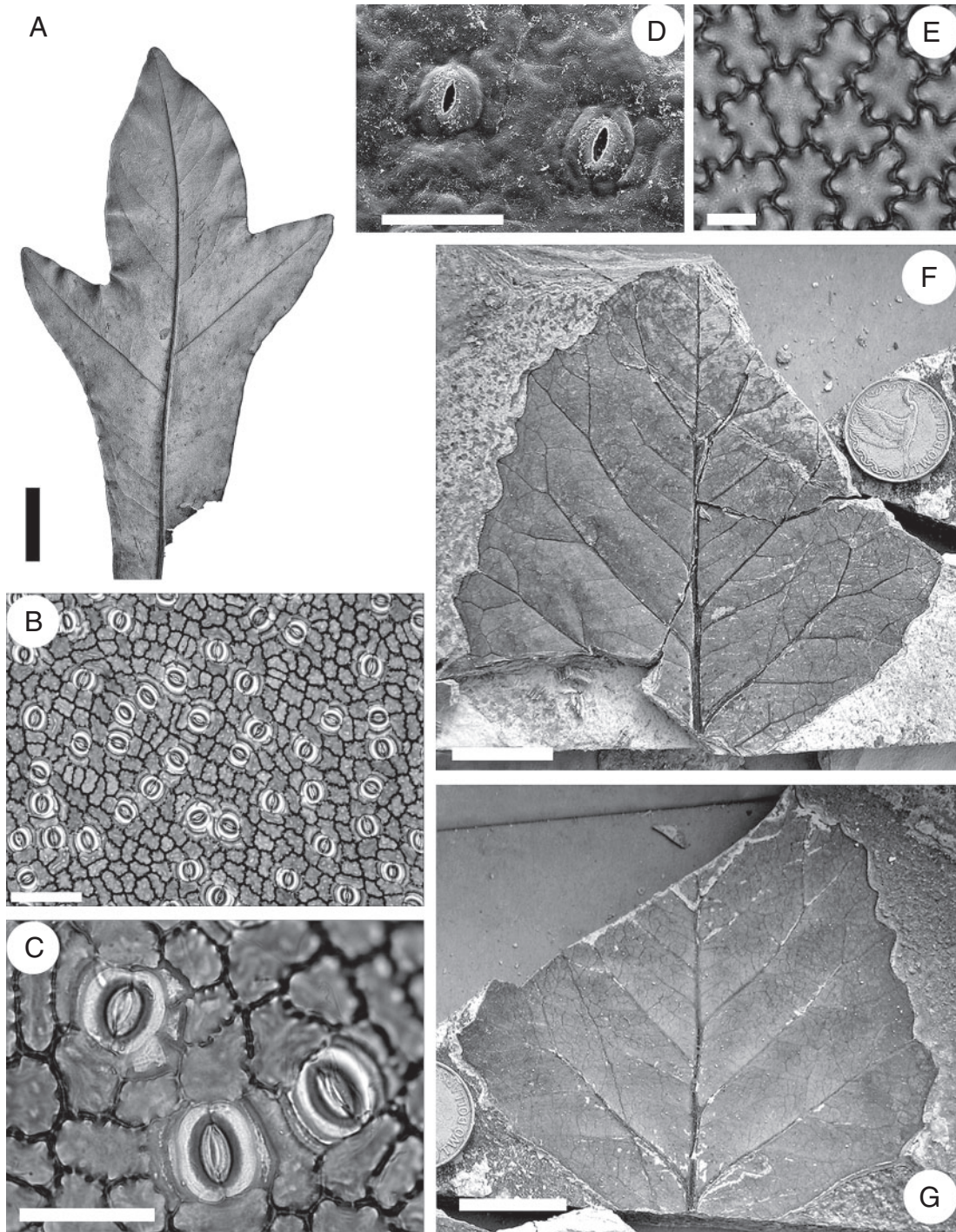
Foliage specimens incomplete, but one specimen (OU32742) is 14 mm wide (Fig. 1A), and another (OU33343) is 23 mm wide and shows a prominent tapering lobe (Fig. 1B). All specimens lack evidence of a strong, central primary vein; rather, they show several quasi-parallel, weakly defined (narrow) veins that have higher-order interconnecting veins (Figs 1A–C). Stomata (Fig. 1D–G) brachyparacytic, mostly distributed with guard-cell pairs aligned parallel to the long axes of the specimens. Stomata on both leaf surfaces (amphistomatic), but much more abundantly so abaxially. Adaxial stomata of variable density. Mean guard-cell length variable among specimens, ~30–40 µm, with T-pieces of thickened cuticle obvious at poles of guard cells (Fig. 1D, E). Trichome bases absent.

## Comments

This Newvale taxon (assumed to represent a single species) is characterised by the presence of parallel distributed stomata with T-pieces at the poles of the guard cells, variable but very unequal amphistomaty and an absence of trichome bases. Incomplete specimens with gross morphological details were available, together with numerous cuticle specimens showing both leaf surfaces. Specimen OU33343 represents a leaf base, with a portion of a lobe on one side (Fig. 1B), Specimen OU33342 a section of leaf with a smaller lobe or tooth (Fig. 1C) and specimen OU32742 a short section of leaf without lobes (Fig. 1A). All three of these specimens show more-or-less parallel but not prominent venation. The lobing and relatively small stomatal sizes clearly separate this taxon from Persoonieae, so the amphistomatic leaves with clearly parallel distributed stomata indicate affinity with Proteoideae or possibly Grevilleoideae with reduced leaves (Carpenter and Jordan 1997). Within extant Proteoideae, several taxa exhibit leaf lobing and venation similar to those of the fossil, including species of *Beauprea*, *Petrophile* and *Stirlingia*. The fossils are strikingly similar to extant *Beauprea* leaves, including that they lack evidence of trichome bases (Carpenter and Jordan 1997) and surface ornamentation. Many *Beauprea* leaves are also variably lobed (Viro 1968), although these appear to have stronger primary veins (Fig. 1H) than in the fossils. Absence of laminar trichomes appears to be a synapomorphy for *Beauprea*, because trichomes are found in the apparent nearest relatives of the genus (*Protea* and *Faurea*; Sauquet *et al.* 2009a), widely elsewhere in the family, and in the sister family Platanaceae. All extant *Beauprea* species have the same type and arrangement of abaxial stomata as in the fossils (Fig. 1I–K), and specimens of at least one species (*B. pancheri* Brongn. & Gris) also exhibit unequal amphistomaty (R. J. Carpenter, unpubl. data). Many species have tightly sinuous or buttressed anticlinal cell walls,

**Fig. 2.** *Euproteaciphyllum alloxylonoides* sp. nov. (OU32728) from Foulden Maar. A. Large, lobed leaf specimen. The petiole base and lobe sinuses are arrowed. B. Scanning electron micrograph (SEM) showing outer abaxial cuticle; scale bar = 50 µm. C. Light micrograph (LM) showing distribution of commonly amphibrachyparacytic stomata on abaxial leaf cuticle, and sinuous and buttressed anticlinal walls. A trichome base is at upper left; scale bar = 50 µm. D. LM showing a stoma with unusual, non-brachyparacytic subsidiary-cell arrangement (i.e. two or three cells instead of one); scale bar = 10 µm. E. SEM of inner abaxial cuticle showing two stomata. Note T-pieces at poles of guard cells, narrow subsidiary cells with relatively granular cuticle, and ragged anticlinal wall cuticle with buttressing; scale bar = 20 µm. F. LM showing a stoma on abaxial surface and a trichome base associated with four epidermal cells; scale bar = 20 µm. G. LM of adaxial cuticle; scale bar = 50 µm. H. SEM of the inner adaxial cuticle. Note relatively straight, weakly developed anticlinal walls without buttressing; scale bar = 50 µm.





**Fig. 3.** A–E. Extant *Alloxylon*. F, G. Fossil *Euproteaciphyllum pacificum* sp. nov. (OU32875) from Foulden Maar. A. Large (incomplete), lobed leaf specimen of *A. flammeum* (cult., Brisbane); scale bar = 20 mm. B. Light micrograph (LM) showing distribution of stomata on abaxial cuticle (*A. brachycarpum*). Note similarity to fossil *E. alloxylonoides* cuticle (Fig. 2C); scale bar = 100 µm. C. LM showing three stomata (*A. brachycarpum*). The stoma at upper left has the same type of unusual subsidiary-cell arrangement as in the fossil *E. alloxylonoides* (Fig. 2D); scale bar = 50 µm. D. Scanning electron micrograph of outer abaxial cuticle showing two stomata (*A. flammeum*). Note similar surface features as in the fossil *E. alloxylonoides* (Fig. 2B); scale bar = 50 µm. E. LM showing distinctly sinuous and buttressed adaxial cuticle (*A. brachycarpum*). Contrast to adaxial cuticle of *E. alloxylonoides* (Fig. 2H); scale bar = 20 µm. F. Part specimen. G. Counterpart specimen. Note asymmetry of lamina, rounded, glandular teeth and venation detail; scale bars = 25 mm.

although especially in *B. balansae* Brongn. & Gris (Fig. 11) and the abaxial surface of *B. pancheri*, they are relatively straight, as in the fossils.

Pole (2007) reported leaf cuticular remains from Pliocene sediments in the South Island of New Zealand that are similar to the taxon described here, and which he referred to *Beauprea*. He based this conclusion in part on the evidence that associated sediments contained *Beaupreaidites* pollen. *Beaupreaidites* and *Beauprea* pollen share clearly defined colpoid apertures, a unique state in Proteaceae (Cookson 1950; Milne 1998) that is of phylogenetic significance (Sauquet *et al.* 2009a, 2009b). The Gore Lignite Measures, which include the Newvale lignite, also contain quite abundant *Beauprea*-like pollen (mostly as *Beaupreaidites elegansiformis* Cookson; Pocknall and Crosbie 1988). However, although we consider it likely that the Newvale fossils are indeed *Beauprea* foliage, we prefer the more conservative approach of identifying the specimens as comparable with *Beauprea* only.

*Beauprea* is a New Caledonian endemic genus that is most commonly encountered in maquis vegetation and open forest types (Viro 1968). A much more extensive past range is indicated by the presence of *Beauprea*-like pollen in sediments from not only New Zealand but also Australia, subantarctic Campbell Island, Antarctica and the Antarctic Peninsula, with a total age range of Campanian (Late Cretaceous) to Pleistocene (e.g. Pocknall and Crosbie 1988; Milne 1998; Truswell and Macphail 2009). *Beaupreaidites* is one of several fossil pollen taxa that suggest the former presence of New Caledonian genera in New Zealand as recently as the Pleistocene (e.g. Pocknall and Crosbie 1988; Lee *et al.* 2001).

Genus ***Euproteaciphyllum*** G.J.Jord., R.J.Carp. & R.S.Hill

***Euproteaciphyllum alloxylonoides*** R.J.Carp., Bannister, D.E.Lee & G.J.Jord., *sp. nov.* (Fig. 2).

*Holotype*: OU32728 (only specimen, includes material on microscope slides and SEM stubs), Geology Museum, University of Otago, Dunedin, NZ.

*Type locality*: Foulden Maar, Otago, registered as I43/f8503 in the New Zealand Fossil Record File administered by the Geological Society of New Zealand and GNS Science (NZ Map Grid Infomap I43 reference 929166: 45.5271°S, 170.2218°E).

#### *Species diagnosis*

Leaves pinnately lobed. Venation within lobes brochidodromous. Stomatal alignment random, stomata not clearly within areoles. Subsidiary cells typically narrow, but with further epidermal cells lateral to each subsidiary cell. Stomatal complexes rarely not brachyparacytic. Trichome bases associated with two to eight epidermal cells uncommon on both leaf surfaces. Outer cuticle surfaces not striated, inner surfaces granular. Inner abaxial epidermal cell anticlinal wall cuticle flanged, buttressed. Adaxial walls straighter, not buttressed.

#### *Description*

Leaf (Fig. 2A) multi-lobed, not toothed, with the terminal lobe strongly asymmetrical. Leaf large, ~24.7 cm long × 13.1 cm

wide. Apparently two lobes per side. Lateral lobe apices acute, rounded, lobe sinuses rounded. Principal veins within lobes running centrally. Venation within lobes brochidodromous, veins looping well inside the margin, and with festooned loops outside these. Stomata confined to abaxial surface, in some cases marked by slightly raised ledges over the guard-cell regions (Fig. 2B). Most stomata randomly aligned (Fig. 2C), not obviously within areoles. Mean guard-cell length ~32 µm, T-pieces of thickened cuticle typically at poles of guard cells (Fig. 2D–F). Stomatal complexes commonly amphibrachyparacytic, with narrow subsidiary cells each typically flanked by wider cells (Fig. 2C). Subsidiary-cell cuticle thinner (less darkly staining) than the dark-staining cuticle of outer flanking cells (Fig. 2C, F). Subsidiary cells usually more obviously granular than normal epidermal cells (Fig. 2C–F). Rare stomatal complexes with two or three subsidiary cells instead of one (Fig. 2D). Trichome bases uncommon on both surfaces, bases associated with two to eight epidermal cells, some of which have thicker (more darkly staining) cuticle than do normal epidermal cells (Fig. 2F). Adaxial and abaxial (Fig. 2B) external cuticle not striated or otherwise ornamented, but with slightly raised regions over epidermal cells. Abaxial cuticle associated with anticlinal epidermal cell walls appearing ragged, in many cases slightly sinuous, and buttressed at the junctions with the periclinal walls (Fig. 2C–F). Periclinal-wall cuticle slightly granular (Fig. 2E). Adaxial cuticle associated with anticlinal epidermal cell walls not well-developed and not buttressed at periclinal junctions (Fig. 2G, H).

#### *Etymology*

In recognition of similarities to *Alloxylon* leaves.

#### *Comments*

Neither of the two extant New Zealand species has large, lobed leaves. Within extant Proteaceae, such leaves similar in overall shape to the fossil and without teeth are known only in low-latitude rainforest species of northern Queensland (species of *Alloxylon*, *Buckinghamia*, *Darlingia*, *Grevillea*, *Musgravea*, *Placospermum* and *Stenocarpus*; see McCarthy 1995; Hyland *et al.* 2010), Asia/New Guinea (*Heliciopsis*; see Sleumer 1955) and New Caledonia (*Virotia*; see Viro 1968). Of these taxa, *Alloxylon* spp., *Stenocarpus sinuatus* (Loudon) Endl., and species of *Heliciopsis* and *Virotia* have broadly similar overall morphology and cuticular features, whereas features of the other genera are clearly distinct. In *Alloxylon* (tribe Embothriaceae, subtribe Embothriinae), leaf lobing and venation similar to those of the fossil are known in *A. flammeum* P.Weston & Crisp (Weston and Crisp 1991) (Fig. 3A). The fossil cuticles are also similar to those of *Alloxylon* species (Fig. 3B–E). Most interestingly, *A. brachycarpum* (Sleumer) P.H.Weston & Crisp of New Guinea and the Aru Islands shares the same type of divided subsidiary cells as in the fossil (Fig. 3C). The most obvious differences are that all of the extant *Alloxylon* species have extremely rare trichome bases and have clearly sinuous and commonly buttressed adaxial anticlinal walls (Fig. 3E).

***Euproteaciphyllum pacificum*** R.J.Carp., Bannister, D.E.Lee & G.J.Jord., *sp. nov.* (Figs 3F, G, 4A–F)

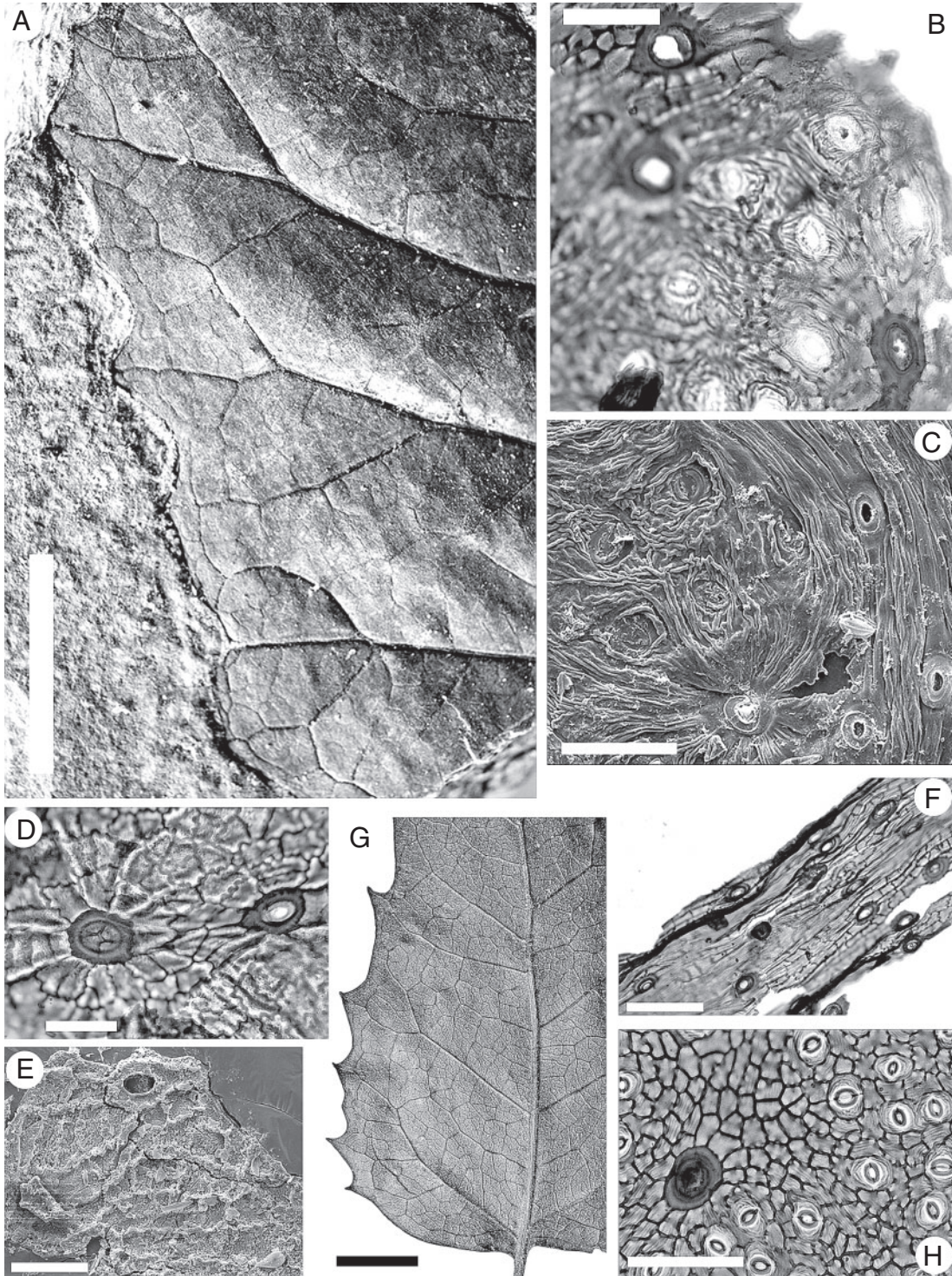
*Holotype*: OU32875 (only specimen, includes part and counterpart, and material on microscope slides and SEM stubs), Geology Museum, University of Otago, Dunedin, NZ.

*Type locality*: Foulden Maar, Otago, registered as I43/f8503 in the New Zealand Fossil Record File administered by the

Geological Society of New Zealand and GNS Science (NZ Map Grid Infomap I43 reference 929166: 45.5271°S, 170.2218°E).

*Species diagnosis*

Toothed leaves or leaflets. Venation craspedodromous to semicraspedodromous. Teeth glandular, not spinose, typically





two per secondary vein. Stomatal alignment random, stomata not clearly within areoles. Abaxial outer cuticle surface prominently ornamented with striations. Annular trichome bases associated with numerous thickened epidermal cells frequent on both leaf surfaces. Inner cuticle surfaces granular. Epidermal-cell anticlinal-wall cuticle tightly sinuous, commonly irregularly thickened and buttressed.

#### Description

Leaf (Figs 3F, G, 4A) or leaflet ovate, serrately toothed, slightly asymmetrical. Leaf of mesophyll size, estimated to reach 13.5 cm long × 12.3 cm wide (actual specimen [part] 12.1 cm long × 12.3 cm wide). Apex and base absent, apex likely be obtuse. Venation craspedodromous to semicraspedodromous, approximately six secondary veins per side arising at ~45° from the primary vein, with some intersecondary veins that form loops with secondary veins, tertiary venation random reticulate. Typically, two simple teeth per secondary vein (Fig. 4A). Teeth rounded at apex, evidently glandular. Abaxial external cuticle prominently ornamented with striations (Fig. 4B, C). Striations radiating from some trichome bases on the adaxial surface. Stomata brachyparacytic, confined to abaxial surface, with ropy striations over the subsidiary cell regions (Fig. 4B, C). Stomata mostly randomly aligned, not obviously within areoles. Mean guard-cell length ~23 µm. Anticlinal epidermal cell-wall cuticle on both inner surfaces appearing tightly sinuous (Fig. 4B, D), obviously buttressed at the junctions with the periclinal walls of many cells, especially on the abaxial surface (Fig. 4B). Periclinal-wall cuticle granular (Fig. 4E). Trichome bases abundant on both surfaces, each appearing as a large, donut-like ring associated with numerous epidermal cells with thickened (dark-staining) cuticle (Fig. 4B–F). This complex is suggestive of a platform with a crimped margin (on the inner cuticle), which may be especially evident under light microscopy along veins where normal venous cells have straight walls (Fig. 4F).

#### Etymology

In recognition that the fossil possesses leaf features of subtribe Gevuininae, which comprises closely related taxa that are distributed across the Pacific Ocean region.

#### Comments

Neither of the two extant New Zealand species has leaves that are similar to those of this fossil. However, the fossil leaf architecture, teeth and cuticle are consistent with the foliage of species that occur in tribe Macadamieae, subtribe Gevuininae (Fig. 4G, H). In particular, the fossil possesses a type of trichome

base that may be a synapomorphy for the clade comprising all the species of Gevuininae except *Cardwellia* (Mast *et al.* 2008). These distinctive trichome bases (Fig. 4H) have been observed widely in this clade (Carpenter 1994; Carpenter and Pole 1995). Further features of the fossil cuticle that are shared in these Gevuininae are outer-surface striations and inner-surface granulations (Carpenter 1994). Leaf material of this type has previously been recorded from the late middle Eocene of Western Australia (Carpenter and Pole 1995), the early Oligocene of Tasmania (*Euproteaciphyllum gevuinoides* G.J.Jord., R.J.Carp. & R.S.Hill: Carpenter and Jordan 1997; Jordan *et al.* 1998), and the early Miocene Manuherikia Group of southern New Zealand (Carpenter 1994; Pole 1998). Here, we consider that the latter fossils probably belong to *E. pacificum*, in part because the relevant Manuherikia Group sediments are geographically close to Foulden Maar, and probably almost contemporaneous (Pole 1993). The asymmetrical nature of the fossil suggests that it may have been derived from a compound leaf. Paripinnate to imparipinnate or tripinnate adult leaves are widely found in subtribe Gevuininae (Weston 2007). The clade contains mostly rainforest species in eastern Australia–New Guinea, Vanuatu, New Caledonia, Fiji and South America (Mast *et al.* 2008).

***Euproteaciphyllum pinnatum*** R.J.Carp., Bannister, D.E.Lee & G.J.Jord., *sp. nov.* (Fig. 5)

*Holotype*: OU33344 (only specimen, includes material on microscope slides and SEM stubs), Geology Museum, University of Otago, Dunedin, NZ.

*Type locality*: Seam W6, middle Gore Lignite Measures, Newvale Mine, Waimumu Coalfield, Southland, New Zealand. The NZ Map Grid reference on Infomap series is NZMS 260 F45/817434 (46.1427°S, 168.7518°E).

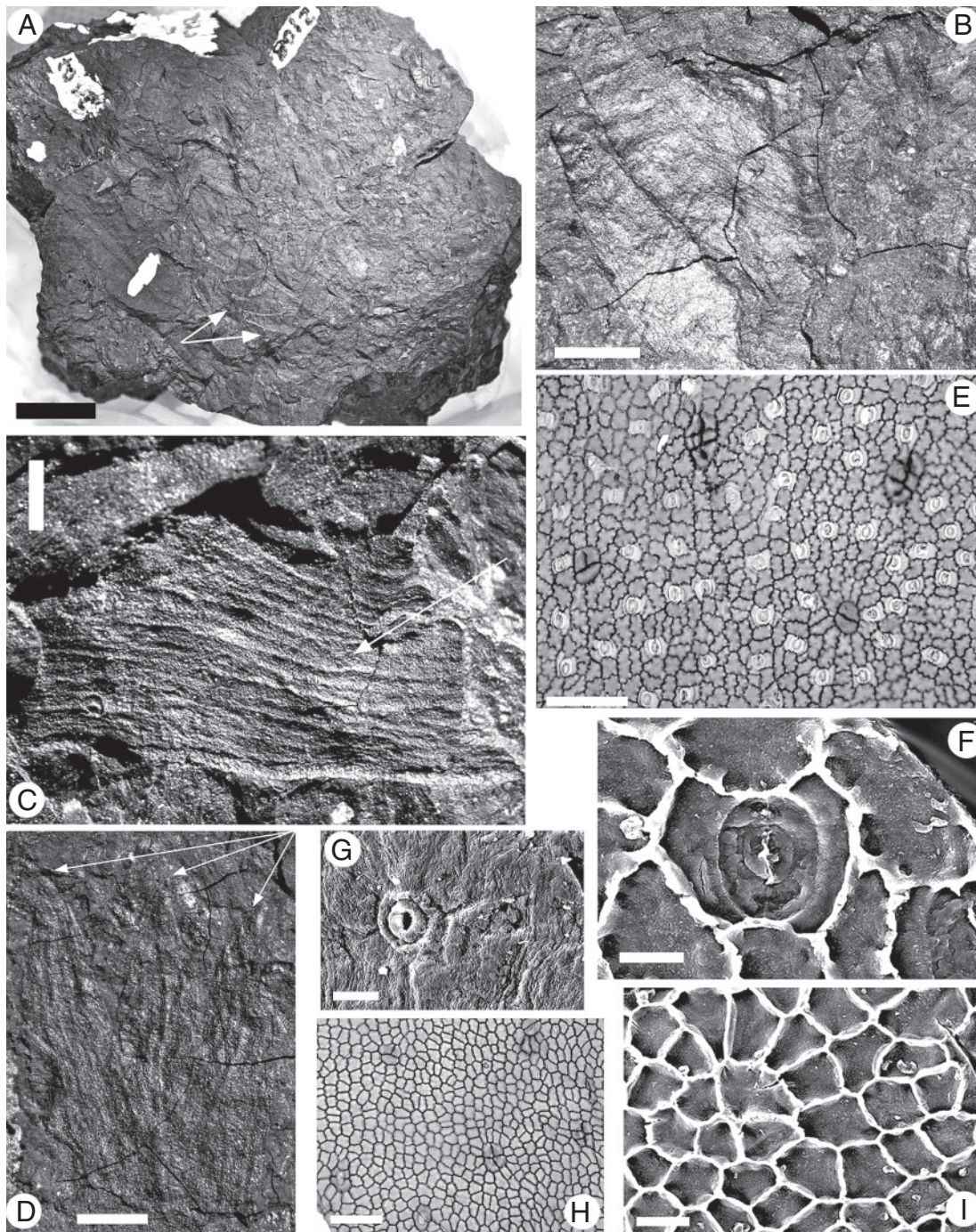
#### Species diagnosis

Foliage pinnately lobed. Lobes small, more-or-less triangular or falcate. Stomatal distribution more-or-less parallel, subsidiary cells typically appearing butterfly-winged. Anticlinal epidermal-wall cuticle variably buttressed and sinuous at junctions with periclinal walls. Trichome bases common on both leaf surfaces, associated with two or more epidermal cells.

#### Description

Interpretation of the foliage that has so far been observed on one small block of lignite is complicated because of distortion and overlapping, apparently by foliage of the same species in some regions, and by other material (Fig. 5A). However, pinnate lobing is inferred from the consecutive placement of lobe segments

**Fig. 4.** *Euproteaciphyllum pacificum* sp. nov. (OU32875) A–F. From Foulden Maar. G. Extant Gevuininae foliage. H. Extant *Euplassa incana* (Klotzsch) I.M.Johnst. cuticle. A. Enlarged section of leaf margin, showing teeth and vein detail; scale bar = 20 mm. B. Light micrograph (LM) of abaxial cuticle, showing distribution of stomata, striations, tightly sinuous anticlinal walls and thickened (dark-staining) trichome bases; scale bar = 50 µm. C. Scanning electron micrograph (SEM) of abaxial cuticle surface, showing stomata, ropy striations and trichome bases (three on vein at right); scale bar = 50 µm. D. LM of adaxial cuticle, showing two trichome bases and tightly sinuous anticlinal walls; scale bar = 50 µm. E. SEM showing a trichome base (top, centre) and evidence of granulations on inner adaxial cuticle; scale bar = 50 µm. F. LM of venous region showing numerous thickened trichome bases, with evidence of crimping; scale bar = 100 µm. G. Leaflet from unidentified species, Mount Panie, New Caledonia. Note asymmetrical base, and similarity of venation details to that of fossil *E. pacificum* (Figs 3F, G, 4A); scale bar = 10 mm. H. LM showing stomata, a thickened (dark-staining) trichome base, striations and sinuous and buttressed anticlinal walls. Note similarity to fossil *E. pacificum* cuticle (Fig. 4B); scale bar = 100 µm.



**Fig. 5.** *Euproteaciphyllum pinnatum* sp. nov. (OU33344) from Newvale Mine. A. Lignite block showing evidence of pinnate foliage (some arrowed); scale bar = 10 mm. B. Magnification of foliage showing the two lobes arrowed in Fig. 5A at left, attached to midvein; scale bar = 2 mm. C. Magnification of lobe, showing weak, more-or-less parallel veins and evidence of vein interconnection (arrowed); scale bar = 1 mm. D. Apical region of pinnate foliage segment, showing a central apex with lateral pinnae (all arrowed); an overall tridentate form; scale bar = 1 mm. E. Light micrograph (LM) of abaxial cuticle, showing more-or-less parallel distribution of stomata, sinuous and buttressed anticlinal walls and several trichome bases; scale bar = 100 µm. F. Scanning electron micrograph (SEM) of inner abaxial cuticle, showing anticlinal wall buttressing and a stoma with 'butterfly-wing' subsidiary cells; scale bar = 20 µm. G. SEM of outer abaxial cuticle, showing a stoma with a surrounding double round ledge; scale bar = 20 µm. H. LM showing adaxial cuticle with several trichome bases; scale bar = 100 µm. I. SEM showing inner surface of adaxial cuticle. Note evidence of a trichome base associated with five epidermal cells at left, and some butressing at anticlinal and periclinal junctions; scale bar 20 = µm.

along a section of midvein that is ~0.8 mm wide (Fig. 5B). The segments have a broad basal attachment (i.e. the foliage is pinnatisect *sensu* Ellis *et al.* 2009), decurrent to the midvein on the lower margins, which are typically broadly rounded. Apical margins are gently curved (concave) from the base to the tip, and with apices that are acute but rounded, and typically inclined upwards (Fig. 5B). The segments are up to ~10 mm long, and each appears to bear ~12 equispaced fine veins that run in nearly parallel courses towards the apex, with evidence of interconnections (Fig. 5C). A preserved leaf apex appears tridentate (Fig. 5D), as is seen in some similarly small, lobed extant *Banksia* species formerly included in *Dryandra*. Leaf cuticle within lobe segments well preserved, hypostomatic, stomata mostly distributed parallel to the veins, although veins lack evidence of differentiated venous cells (Fig. 5E). Abaxial anticlinal epidermal-wall cuticle sinuous, variably buttressed at junctions with periclinal walls (Fig. 5E, F). Subsidiary cells typically appearing butterfly-winged (Fig. 5E, F), with cuticle generally less darkly staining than that of normal epidermal cells (Fig. 5E). Guard-cell cuticle also not darkly staining, but with rounded dark-staining central regions (Fig. 5E) that correspond with thickened surface rims overlying the guard cells (Fig. 5G). Central surface rim surrounded by second rim (Fig. 5G). Mean guard-cell length ~22  $\mu\text{m}$ . Stomata rarely not brachyparacytic (not figured). Adaxial anticlinal-wall cuticle less sinuous and buttressed than abaxial cuticle, periclinal walls quite smooth (Fig. 5H, I). Trichome bases large, common on both surfaces, associated with two to six epidermal cells (Fig. 5E, H, I).

#### Etymology

In recognition of the pinnate lobing of the leaf.

#### Comments

This species is represented by distinctive leaves, with no features that suggest a link to any living taxon, even at the subfamily level. The foliage is similar to that of the co-occurrent *B. novae-zelandiae*, but the cuticle is clearly unlike that of this species, and that of any other Banksieae. Interestingly, the foliage is also architecturally very similar to Oligocene foliage from Tasmania and New South Wales that was referred to the bennettitalean genus *Ptilophyllum* by McLoughlin *et al.* (2011). These Australian specimens of *Ptilophyllum* unfortunately lacked supportive evidence from cuticle. However, *E. pinnatum* can most readily be distinguished from them in showing evidence of vein interconnections.

***Euproteaciphyllum amphistomaticum*** R.J.Carp., Bannister, D.E.Lee & G.J.Jord., *sp. nov.* (Fig. 6A–D)

*Holotype*: OU32064 (Figs 6B–D) Geology Museum, University of Otago, Dunedin, NZ. *Additional specimens*: OU32057, OU32060, OU32062, OU32063, plus other material on slides and SEM stubs retrieved from dispersed cuticle preparations, University of Adelaide.

*Type locality*: Seam W6, middle Gore Lignite Measures, Newvale Mine, Waimumu Coalfield, Southland, New Zealand. The NZ Map Grid reference on Infomap series is NZMS 260 F45/817434 (46.1427°S, 168.7518°E).

#### Species diagnosis

Fossil foliage, in some cases toothed. Stomata abundant on both leaf surfaces, unequally amphistomatic. Stomata aligned more-or-less parallel. Trichome bases associated with mostly one, but up to four epidermal cells, abundant on both leaf surfaces.

#### Description

No complete leaves have been observed, whereas numerous fragments, including one showing an apex with a lateral tooth (Fig. 6A), have been observed. Maximum leaf width at least 8 mm. Mean guard-cell length ~32  $\mu\text{m}$ . Leaves amphistomatic, stomata slightly more abundant on the (presumed) abaxial surface (Fig. 6B). Stomata distributed more-or-less parallel with the long axis of the leaf (Fig. 6B, C). Subsidiary and guard-cell cuticle clearly thinner (much less darkly staining) than that of normal epidermal cells (Fig. 6C, D). Trichome bases abundant on both surfaces, overwhelmingly (>96%) associated with one epidermal cell, rarely two (~3%), very rarely three or four (Fig. 6C, D). Cuticle of epidermal cells associated with trichome bases not especially thickened.

#### Etymology

In recognition of the obvious amphistomaty of the foliage.

#### Comments

Despite the fossils so far being represented only by small fragments, a new species is established in recognition of the distinctive features of the fossils, and to highlight that neither of the two extant New Zealand species has remotely similar leaves, nor have any other fossil taxa, including the dispersed cuticles described by Pole (1998, 2008) from Southland, New Zealand. Macrofossils of *E. amphistomaticum* are abundant in the leaf-bed in the Newvale lignite. Amphistomaty with clearly parallel-distributed, relatively small stomata (i.e. much smaller than in Persoonioideae) indicates possible affinity with subfamily Proteoideae (Carpenter and Jordan 1997). Similar Proteoideae include species of the Australian genera *Adenanthos* (Fig. 6E), *Isopogon* and *Petrophile*. The fossils show many trichome bases associated with only one epidermal cell or rarely more, the overwhelmingly typical state in similar extant Proteoideae (Carpenter and Jordan 1997). Some Grevilleoideae species with reduced leaves and of open habitats also show amphistomaty, especially *Hakea* and some species of *Stenocarpus*. However, although some *Stenocarpus* cuticles are similar to the fossils, *Hakea* (and *Grevillea*) have very distinct stomatal complexes and trichome bases (Carpenter 1994).

Finally, although we conclude from the above discussion that it is not possible to determine modern affinities of the fossils with any confidence, we note that pollen grains morphologically consistent with those of certain Australian sclerophyllous Proteoideae (e.g. Dettmann and Jarzen 1998; Milne 1998; Milne and Martin 1998) are diverse and locally abundant in the Gore Lignite Measures (Pocknall and Mildenhall 1984).

**Proteaceae** sp. (Fig. 6F–H)

*Specimens examined*: OU32206 (only specimen: cuticle only).

### Description

Specimen hypostomatic, most stomata distributed more-or-less parallel, not obviously within areoles (Fig. 6F). Stomata with pronounced, thick (strongly stained), round, donut-like ledges over the guard-cell regions (Fig. 6F–H). Guard cells with T-pieces of strongly thickened cuticle at poles (Fig. 6H). Mean guard-cell length  $\sim 32\ \mu\text{m}$ . Abaxial cuticle associated with anticlinal epidermal cell walls irregularly sinuous, unevenly thickened and buttressed (Fig. 6F, H); sinuosity and buttressing less evident on adaxial side (not figured). Trichome bases infrequent on both surfaces, associated with two to four epidermal cells (Fig. 6F). Abaxial cuticular surface with irregular ornamentation, including raised regions and broad striations associated with some stomata (Fig. 6G).

### Comments

The cuticle is clearly distinct from all other taxa at Newvale. The most obvious feature is that of the pronounced, thick (strongly stained), rounded donut-like ledges over the guard-cell regions of the stomata. In this respect, and in the type of sinuosity and buttressing of the cell-wall cuticle, this taxon is similar to *Knightia excelsa*. However, the stomata of *K. excelsa* are confined to small areoles (not distributed in a more-or-less parallel arrangement as in the fossil), and the veins in particular of *K. excelsa* are covered in numerous trichomes. Pole (2007) referred dispersed cuticle specimens from the Pliocene of the South Island to *Knightia*. However, his descriptions and illustrations of the fossils do not strongly support this. In particular, his illustrations of the fossil stomata (see fig. 16A, B in Pole 2007) do not show thickened ledges, nor could he show that the stomata are confined to small areoles.

### Discussion

Overall, the combined evidence from the Newvale lignite and the Foulden Maar diatomite supported the hypothesis that Proteaceae have had a long history of strong association with oligotrophic habitats. Moreover, there is evidence of biome conservatism in Proteaceae from >20 million-year-old leaf fossils found in a region where the family is largely extinct. The fossils exhibit both physiognomic and taxonomic features that are typical of modern sclerophyll and wet forest biomes.

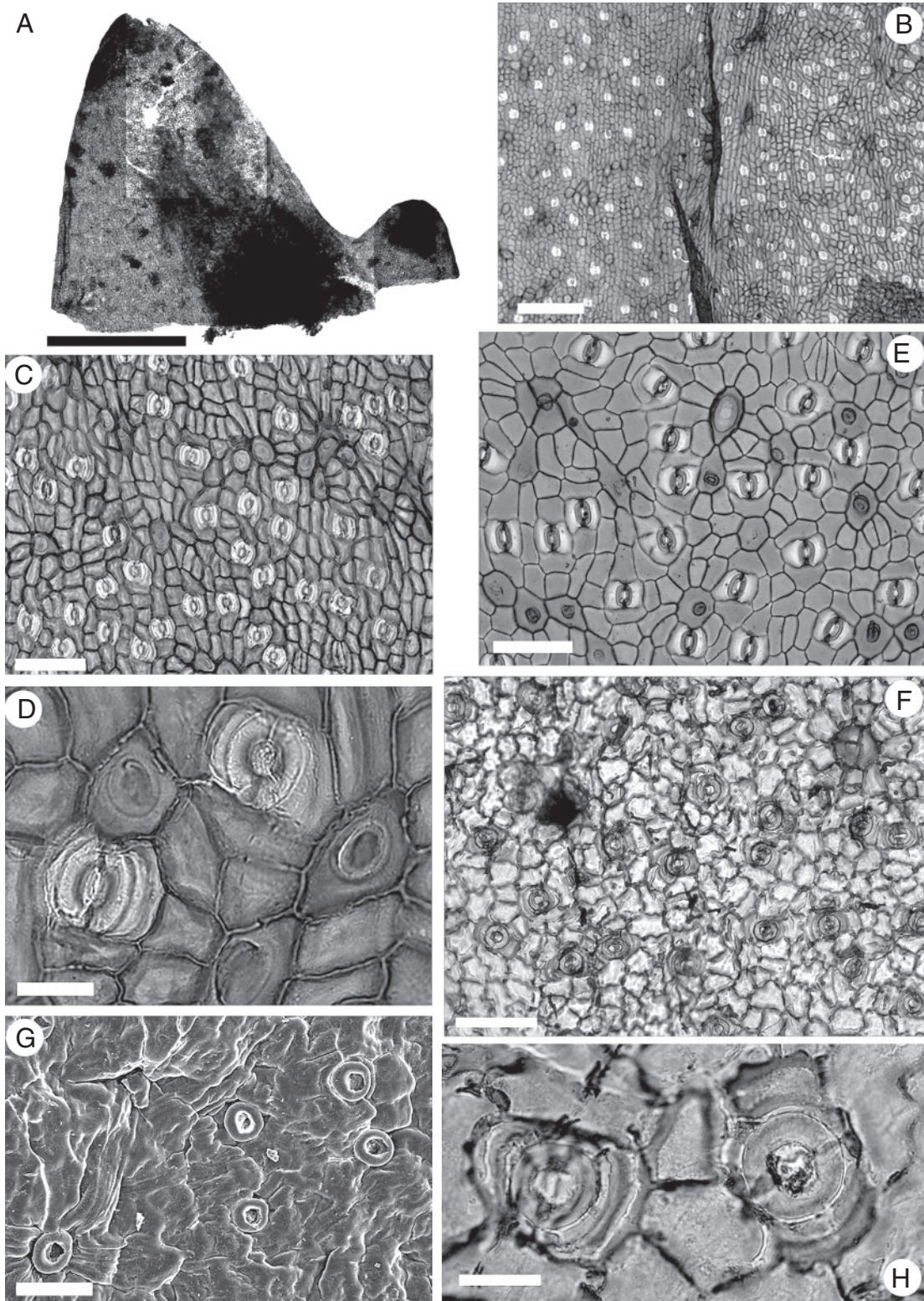
The Newvale environment has been reconstructed as comprising low, open swamplands in a very oligotrophic region that included raised mires with acidic blanket peats and a diverse conifer flora (Isaac and Lindqvist 1990; Lee *et al.* 2007, 2012; Ferguson *et al.* 2010; Carpenter *et al.* 2011; Jordan *et al.* 2011). Proteaceae remains were common and also diverse, and at least some of the seven taxa so far recognised belong to lineages

that are important in oligotrophic habitats of Australia and New Caledonia today (i.e. fossils of *Banksia*, Persoonieae, probably *Beauprea*, possibly *Adenanthos* or similar Proteoideae). The fossils also exhibit leaf traits that are consistent with those observed in Proteaceae of modern heathland communities of the sclerophyll biome (see Johnson and Briggs 1975). These traits include overall small leaf-sizes, lobing, quasi-parallel venation and amphistomaty. In addition, proteoid roots (Purnell 1960), which are specialised structures that markedly increase root-system surface area and act to maximise phosphorus uptake from soils of low fertility (Lambers *et al.* 2006), are abundant in the lignite (Carpenter 2012). Further traits that appear to be typical of Proteaceae in open, sclerophyllous habitats are exhibited in the fossil cuticles. The type of prominent cuticular papillae that occur in the Newvale *Banksia*, *B. novae-zelandiae*, are reconstructed among Proteaceae as having evolved in high-light environments (Jordan *et al.* 2005), and none of the seven taxa exhibits the prominent cuticular striations that typify the leaves of rainforest Proteaceae (see Carpenter 1994).

The Foulden Maar palaeovegetation was a very diverse, Lauraceae-dominated mesotherm rainforest that most probably grew on rich basaltic soils surrounding the crater-lake site of deposition (Pole 1996; Bannister *et al.* 2012). Among the >700 fossil leaves so far recovered (Bannister *et al.* 2012), only the two specimens described here can be referred to Proteaceae. Both leaves are morphologically consistent with forms now mostly found in rainforests of the wet forest biome, and both probably belong to lineages that are largely restricted to this biome. However, the rarity of Proteaceae at Foulden Maar is notable, and is interpreted as evidence that the high diversity and abundance of the family at Newvale did not extend to much more fertile sites in the Oligo–Miocene of southern New Zealand (see also Pole 1996). Association of past Proteaceae with oligotrophic environments is also apparent at fossil sites in Australia. For instance, the most diverse proteaceous macroflora so far known was linked to infertile, quartz-derived soils at Cethana, Tasmania, in the early Oligocene (Carpenter and Jordan 1997), and Itzstein-Davey (2004) found that Western Australian Eocene sediments that contained highly diverse Proteaceae pollen also yielded low concentrations of nitrogen and phosphorus.

Interestingly, even though Proteaceae species are characteristic elements of modern mesotherm forests (at least in Australia), they are still less likely to be found at sites of higher fertility. This is exemplified in the Wet Tropics of northern Queensland, where very high phylogenetic and species diversity is found in the granitic uplands of the Atherton Tableland region (Carpenter 1994; Carpenter *et al.* 2004), compared with on its recent volcanic soils.

**Fig. 6.** *Euproteaciphyllum amphistomaticum* sp. nov. A–D. From Newvale Mine. E. Extant *Adenanthos acanthophyllum* A.S.George cuticle. F–H. Proteaceae sp. cuticle from Newvale Mine. A. Dispersed leaf fragment showing an apparent apex and tooth; scale bar = 1 mm. B. Light micrograph (LM) of cuticle (holotype, OU32064), showing amphistomaty (adaxial and abaxial surfaces at left and right respectively); scale bar = 100  $\mu\text{m}$ . C. LM of abaxial cuticle (holotype OU32064) showing more-or-less parallel distribution of stomata and numerous trichome bases, most being associated with only one epidermal cell; scale bar = 100  $\mu\text{m}$ . D. LM of abaxial cuticle (holotype OU32064), showing detail of two stomata and three trichome bases; scale bar = 25  $\mu\text{m}$ . E. LM of abaxial cuticle showing strong similarity to fossil *E. amphistomaticum* (Fig. 5B–D); scale bar = 100  $\mu\text{m}$ . F. LM showing stomata, sinuous and buttressed anticlinal walls and a trichome base at upper right; scale bar = 100  $\mu\text{m}$ . G. Scanning electron micrograph showing outer surface of cuticle. Note evidence of irregular surface ornamentation and stomata with prominent donut-like ledges over the guard-cell regions; scale bar 50  $\mu\text{m}$ . H. LM showing two stomatal complexes. Note the prominent donut-like ledges over the guard-cell regions; scale bar = 20  $\mu\text{m}$ .



The leaf fossil record of Proteaceae is one of the best of any angiosperm family, and as demonstrated here, can provide material evidence of the antiquity, diversification and trait characteristics of lineages within distinct past communities.

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## References

- Bannister JM, Lee DE, Raine JI (2005) Morphology and palaeoenvironmental context of *Fouldenia staminosa*, a fossil flower with associated pollen from the Early Miocene of Otago, New Zealand. *New Zealand Journal of Botany* **43**, 515–525. doi:10.1080/0028825X.2005.9512972
- Bannister JM, Conran JG, Lee DE (2012) Lauraceae from rainforest surrounding an early Miocene maar lake, Otago, southern New Zealand. *Review of Palaeobotany and Palynology* **178**, 13–34. doi:10.1016/j.revpalbo.2012.03.015
- Carpenter RJ (1994) Cuticular morphology and aspects of the ecology and fossil history of North Queensland rainforest Proteaceae. *Botanical Journal of the Linnean Society* **116**, 249–303. doi:10.1111/j.1095-8339.1994.tb00434.x
- Carpenter RJ (2012) Proteaceae leaf fossils: phylogeny, diversity, ecology and austral distributions. *Botanical Review* **78**, 261–287. doi:10.1007/s12229-012-9099-y
- Carpenter RJ, Jordan GJ (1997) Early Tertiary macrofossils of Proteaceae from Tasmania. *Australian Systematic Botany* **10**, 533–563. doi:10.1071/SB96016
- Carpenter RJ, Pole M (1995) Eocene plant fossils from the Lefroy and Cowan Paleodrainages, Western Australia. *Australian Systematic Botany* **8**, 1107–1154. doi:10.1071/SB951107
- Carpenter RJ, Hill RS, Greenwood DR, Partridge AD, Banks M (2004) No snow in the mountains: Early Eocene plant fossils from Hotham Heights, Victoria, Australia. *Australian Journal of Botany* **52**, 685–718. doi:10.1071/BT04032
- Carpenter RJ, Hill RS, Jordan GJ (2005) Leaf cuticular morphology links Platanaceae and Proteaceae. *International Journal of Plant Sciences* **166**, 843–855. doi:10.1086/431806
- Carpenter RJ, Bannister JM, Jordan GJ, Lee DE (2010a) Leaf fossils of Proteaceae tribe Persoonieae from the Late Oligocene–Early Miocene of New Zealand. *Australian Systematic Botany* **23**, 1–15. doi:10.1071/SB09015
- Carpenter RJ, Jordan GJ, Lee DE, Hill RS (2010b) Leaf fossils of *Banksia* (Proteaceae) from New Zealand: an Australian abroad. *American Journal of Botany* **97**, 288–297. doi:10.3732/ajb.0900199
- Carpenter RJ, Jordan GJ, Mildenhall DC, Lee DE (2011) Leaf fossils of the ancient Tasmanian relict *Microcachrys* (Podocarpaceae) from New Zealand. *American Journal of Botany* **98**, 1164–1172. doi:10.3732/ajb.1000506
- Conran JG, Bannister JM, Lee DE (2009) Earliest orchid macrofossils: Early Miocene *Dendrobium* and *Earina* (Orchidaceae: Epidendroideae) from New Zealand. *American Journal of Botany* **96**, 466–474. doi:10.3732/ajb.0800269
- Conran JG, Kaulfuss U, Bannister JM, Mildenhall DC, Lee DE (2010) *Davallia* (Polypodiales: Davalliaceae) macrofossils from Early Miocene Otago (New Zealand) with *in situ* spores. *Review of Palaeobotany and Palynology* **162**, 84–94. doi:10.1016/j.revpalbo.2010.06.001
- Cookson IC (1950) Fossil pollen grains of proteaceous type from Tertiary deposits in Australia. *Australian Journal of Scientific Research, Series B: Biological Sciences* **3**, 166–177.
- Crisp MD, Arroyo MTK, Cook LG, Gandolfo MA, Jordan GJ, McGlone MS, Weston PH, Westoby M, Wilf P, Linder HP (2009) Phylogenetic biome conservatism on a global scale. *Nature* **458**, 754–756. doi:10.1038/nature07764
- Dettmann ME, Jarzen DM (1998) The early history of the Proteaceae in Australia: the pollen record. *Australian Systematic Botany* **11**, 401–438. doi:10.1071/SB97022
- Ellis B, Daly DC, Hickey LJ, Johnson KR, Mitchell JD, Wilf P, Wing SL (2009) ‘Manual of Leaf Architecture.’ (Cornell University Press: New York)
- Ferguson DK, Lee DE, Bannister JM, Zetter R, Jordan GJ, Vavra N, Mildenhall DC (2010) The taphonomy of a remarkable leaf bed assemblage from the Late Oligocene–Early Miocene Gore Lignite Measures, southern New Zealand. *International Journal of Coal Geology* **83**, 173–181. doi:10.1016/j.coal.2009.07.009
- Hyland BPM, Whiffin T, Zich FA, Duffy S, Gray B, Elick R, Venter F, Christophel D (2010) ‘Australian Tropical Rainforest Plants.’ Edn 6. (CSIRO) Available at <http://www.anbg.gov.au/cpbr/cd-keys/rfk/index.html> [Verified 30 October 2012]
- Isaac MJ, Lindqvist JK (1990) Geology and lignite resources of East Southland Group, New Zealand. *New Zealand Geological Survey Bulletin* **101**, 1–202.
- Itzstein-Davey F (2004) A spatial and temporal Eocene palaeoenvironmental study, focusing on the Proteaceae family, from Kambalda, Western Australia. *Review of Palaeobotany and Palynology* **131**, 159–180. doi:10.1016/j.revpalbo.2004.03.008
- Jaffré T (1980) Étude écologique du peuplement végétal des sols dérivés de roches ultrabasiques en Nouvelle Calédonie. *Travaux et Documents de l'ORSTOM* **124**, 1–274.
- Johnson LAS, Briggs BG (1975) On the Proteaceae – the evolution and classification of a southern family. *Botanical Journal of the Linnean Society* **70**, 83–182. doi:10.1111/j.1095-8339.1975.tb01644.x
- Jordan GJ, Carpenter RJ, Hill RS (1998) The macrofossil record of Proteaceae: a review with new species. *Australian Systematic Botany* **11**, 465–501. doi:10.1071/SB97020
- Jordan GJ, Dillon RA, Weston PH (2005) Solar radiation as a factor in the evolution of scleromorphic leaf anatomy in Proteaceae. *American Journal of Botany* **92**, 789–796. doi:10.3732/ajb.92.5.789
- Jordan GJ, Carpenter RJ, Bannister JM, Lee DE, Mildenhall DC, Hill RS (2011) High conifer diversity in Oligo–Miocene New Zealand. *Australian Systematic Botany* **24**, 121–136. doi:10.1071/SB11004
- Lambers H, Shane MW, Cramer MD, Pearse SJ, Veneklaas EJ (2006) Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. *Annals of Botany* **98**, 693–713. doi:10.1093/aob/mcl114
- Lee DE, Lee WG, Mortimer N (2001) Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to palaeogeography and climate. *Australian Journal of Botany* **49**, 341–356. doi:10.1071/BT00031
- Lee DE, Bannister JM, Lindqvist JK (2007) Late Oligocene–Early Miocene leaf macrofossils confirm a long history of *Agathis* in New Zealand. *New Zealand Journal of Botany* **45**, 565–578. doi:10.1080/00288250709509739
- Lee DE, Bannister JM, Raine JI, Conran JG (2010) Euphorbiaceae: Acalyphoideae fossils from early Miocene New Zealand: *Mallotus–Macaranga* leaves, fruits, and inflorescence with *in situ* *Nyssapollenites endobalteus* pollen. *Review of Palaeobotany and Palynology* **163**, 127–138. doi:10.1016/j.revpalbo.2010.10.002

- Lee DE, Conran JG, Lindqvist JK, Bannister JM, Mildenhall DC (2012) New Zealand Eocene, Oligocene and Miocene macrofossil and pollen records and modern plant distributions in the southern hemisphere. *Botanical Review* **78**, 235–260. doi:10.1007/s12229-012-9102-7
- Lindqvist JK, Lee DE (2009) High-frequency paleoclimate signals from Foulden Maar, Waipiata Volcanic Field, southern New Zealand: an Early Miocene varved lacustrine diatomite deposit. *Sedimentary Geology* **222**, 98–110. doi:10.1016/j.sedgeo.2009.07.009
- Mast AR, Willis CL, Jones EH, Downs KM, Weston PH (2008) A smaller *Macadamia* from a more vagile tribe: inference of phylogenetic relationships, divergence times, and diaspore evolution in *Macadamia* and relatives (tribe Macadamieae; Proteaceae). *American Journal of Botany* **95**, 843–870. doi:10.3732/ajb.0700006
- McCarthy P (Ed.) (1995) 'Flora of Australia. Volume 16 – Elaeagnaceae, Proteaceae 1.' (Australian Biological Resources Study and CSIRO Publishing: Melbourne)
- McLoughlin S, Carpenter RJ, Pott C (2011) *Ptilophyllum muelleri* (Ettingsh.) *comb. nov.* from the Oligocene of Australia: last of the Bennettitales? *International Journal of Plant Sciences* **172**, 574–585. doi:10.1086/658920
- Milne LA (1998) Tertiary palynology: *Beaupreaidites* and new Conospermeae (Proteoideae) affiliates. *Australian Systematic Botany* **11**, 553–603. doi:10.1071/SB97013
- Milne LA, Martin ARH (1998) Conospermeae (Proteoideae) pollen morphology and its phylogenetic implications. *Australian Systematic Botany* **11**, 503–552. doi:10.1071/SB97035
- Pocknall DT, Crosbie YM (1988) Pollen morphology of *Beauprea* (Proteaceae): modern and fossil. *Review of Palaeobotany and Palynology* **53**, 305–327. doi:10.1016/0034-6667(88)90037-1
- Pocknall DT, Mildenhall DC (1984) Late Oligocene–early Miocene spores and pollen from Southland, New Zealand. *New Zealand Geological Survey Paleontological Bulletin* **51**, 1–66.
- Pole MS (1993) Miocene broad-leaved *Podocarpus* from Foulden Hills, New Zealand. *Alcheringa* **17**, 173–177. doi:10.1080/03115519308619601
- Pole M (1996) Plant macrofossils from the Foulden Hills Diatomite (Miocene), Central Otago, New Zealand. *Journal of the Royal Society of New Zealand* **26**, 1–39. doi:10.1080/03014223.1996.9517503
- Pole M (1998) The Proteaceae record in New Zealand. *Australian Systematic Botany* **11**, 343–372. doi:10.1071/SB97019
- Pole M (2007) Plant-macrofossil assemblages during Pliocene uplift, South Island, New Zealand. *Australian Journal of Botany* **55**, 118–142. doi:10.1071/BT06055
- Pole M (2008) Dispersed leaf cuticle from the Early Miocene of southern New Zealand. *Palaeontologia Electronica* **11**, 15A.
- Purnell HM (1960) Studies of the family Proteaceae. I. Anatomy and morphology of the roots of some Victorian species. *Australian Journal of Botany* **8**, 38–50. doi:10.1071/BT9600038
- Sauquet H, Weston PH, Barker NP, Anderson CL, Cantrill DJ, Savolainen V (2009a) Using fossils and molecular data to reveal the origins of the Cape proteas (subfamily Proteoideae). *Molecular Phylogenetics and Evolution* **51**, 31–43. doi:10.1016/j.ympev.2008.12.013
- Sauquet H, Weston PH, Anderson CL, Barker NP, Cantrill DJ, Mast AR, Savolainen V (2009b) Contrasted patterns of hyperdiversification in Mediterranean hotspots. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 221–225. doi:10.1073/pnas.0805607106
- Sleumer H (1955) Proteaceae. *Flora Malesiana ser. 1* **5**, 147–206.
- Truswell EM, Macphail MK (2009) Polar forests on the edge of extinction: what does the fossil spore and pollen evidence from east Antarctica say? *Australian Systematic Botany* **22**, 57–106. doi:10.1071/SB08046
- Virot R (1968) Protéacées. *Flore de la Nouvelle Calédonie et Dépendances* **2**, 1–254.
- Wardle P (1991) 'Vegetation of New Zealand.' (Cambridge University Press: Cambridge, UK)
- Weston PH (2007) Proteaceae. In 'The families and genera of vascular plants, vol. 9'. (Ed. K Kubitzki) pp. 364–404. (Springer: Berlin)
- Weston PH, Barker NP (2006) A new suprageneric classification of the Proteaceae, with an annotated checklist of genera. *Telopea* **11**, 314–344.
- Weston PH, Crisp MD (1991) *Alloxylon* (Proteaceae), a new genus from New Guinea and eastern Australia. *Telopea* **4**, 497–507.
- Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292**, 686–693. doi:10.1126/science.1059412