

Leaf fossils of Proteaceae tribe Persoonieae from the Late Oligocene–Early Miocene of New Zealand

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Abstract. Fossils from the Newvale lignite mine, Southland, are the first substantiated foliar records of Proteaceae subfamily Persoonioideae. The fossils possess very large stomata, a probable synapomorphy for Persoonioideae, and within Proteaceae the combination of this feature and more or less parallel-aligned, brachyparacytic stomatal complexes and undulate anticlinal epidermal cell walls is uniquely found in this subfamily. The new genus *Persoonieaephyllum* is described to recognise affinity of the fossil leaves and cuticles with tribe Persoonieae of Persoonioideae and their distinction from its only other extant representative, *Placospermum*. Two new species are described. *P. ornatum* is represented by linear leaves less than 20 mm wide and possessing more or less parallel-aligned major veins. These leaves closely match those of extant hypostomatic, broad-leaved species of tribe Persoonieae and are distinct from *Placospermum* in venation and several cuticular details. *P. villosum* has so far been recovered only as cuticular material in disaggregated lignite. It is distinct from *P. ornatum* in having abundant trichome bases, an absence of surface tubercules, and even larger stomata (guard cells often >70 µm long). The fossils extend the known record of Persoonioideae in the New Zealand–New Caledonia region by ~20 million years.

Introduction

The large southern hemisphere family, Proteaceae, has long been of biogeographic, ecological and evolutionary interest. Within Proteaceae, subfamily Persoonioideae and *Bellendena* (subfamily Bellendenoideae) are of great phylogenetic significance, being sister groups to all other taxa (Hoot and Douglas 1998; Weston and Barker 2006; Barker *et al.* 2007; Sauquet *et al.* 2009). Persoonioideae includes *Placospermum coriaceum* C.T. White & W.D. Francis, the sole representative of tribe Placospermeae, and considered by Johnson and Briggs (1975) to appear to preserve the greatest number of primitive character states in the family. This species is sister to tribe Persoonieae, which contains the monotypic genera *Acidonia*, *Garnieria* and *Toronia*, as well as *Persoonia*, one of the larger Australian plant genera, with 100 species (Weston 1995, 2003). The genera of Persoonieae have always been regarded as closely related, and indeed *Acidonia* and *Toronia* were formerly included in *Persoonia* (Johnson and Briggs 1975). Weston (2003) and Weston and Barker (2006) also mentioned evidence that *Persoonia* is polyphyletic, and this view is supported by the most recently published molecular phylogeny of Proteaceae (Sauquet *et al.* 2009). Here, *Toronia* is strongly supported as sister to the rest of Persoonieae, but although the positions of *Acidonia* and *Garnieria* are not well resolved, these genera appear to be nested in *Persoonia*. Adding data from the

three species of the *P. rufiflora* group of Weston (2003) to the study of Sauquet *et al.* (2009) would alter their tree to show that this group is in fact sister to *Toronia* (Weston 2003; Weston, pers. comm.).

Despite its apparent antiquity and the good fossil record of other Proteaceae (Hill *et al.* 1995; Dettmann and Jarzen 1998), Persoonioideae has a very poor fossil record, and we know of no prior reports of credible or adequately justified macrofossils (see also Johnson and Briggs 1975). A dispersed cuticle type from the Miocene of New Zealand was suggested by Pole (2008) to represent an extinct species of *Placospermum*, but he also noted that this cuticle had some obvious differences from that of *P. coriaceum*, and no trichome bases were present that might strengthen a case even for Proteaceae. In Australia, there are several fossil pollen types that are comparable with extant *Persoonia*, including fossils from Late Cretaceous sediments in south-eastern Australia (Dettmann and Jarzen 1996), and from the Eocene of Central Australia (Kemp 1976). Martin (1995) regarded the Eocene specimens as ‘almost unquestionably of or closely related to’ extant *Persoonia*. However, it may be that such grains lack derived morphological features that would allow their unequivocal assignment at this level (Sauquet *et al.* 2009).

Placospermum coriaceum is a large tree species confined to rainforests of north-eastern Queensland, whereas most

Persoonieae are shrubby and typically occur in non-rainforest habitats, notably the nutrient impoverished Mediterranean climate heathlands and sclerophyll woodlands of south-western Australia (Weston 1995, 2003). *Acidonia* is endemic to this region. *Toronia* is common in the *Agathis* (kauri) forests that are confined to the North Island of New Zealand on mostly low-fertility soils (Dawson 1988), and *Garnieria* is found only in New Caledonia, mostly in the shrubby maquis vegetation that typifies the widespread nutrient-poor ultrabasic soils of the main island (Virot 1968). The presence of *Toronia toru* (A.Cunn.) L.A.S. Johnson & B.G. Briggs in New Zealand is particularly interesting because it is one of only two extant species of Proteaceae there, and because although New Zealand has a long and diverse fossil pollen and foliar record of Proteaceae (Pole 1998; Raine *et al.* 2008), pollen attributed to *Toronia* first appears very late (the early Late Pliocene, ~2.8 million years ago) (Mildenhall 1985). This is also the only extra-Australian record of fossil Persoonieae.

The aim of the present study was to describe and discuss new fossil foliage from the Newvale Mine of the Gore Lignite Measures in Southland, South Island, New Zealand, and justify its assignment to tribe Persoonieae, subfamily Persoonioideae of Proteaceae.

Materials and methods

Fossil site and age

All fossils are from a thin leaf-litter bed from 5 m below the top of the 17-m thick Seam W6 of the middle Gore Lignite Measures (GLM), Newvale Mine, Waimumu, Southland (Lee *et al.* 2007; Ferguson *et al.* in press). Here, the GLM consist of 10 major seams or seam groups separated by sandstone and mudstone which are overlain by 60 m or more of quartzose sandy conglomerate (Isaac and Lindqvist 1990: fig. 63). Lee *et al.* (2007) concluded on the basis of palynological evidence (Pocknall and Mildenhall 1984; Pocknall in Isaac and Lindqvist 1990) and the age of marine sediments intercalated with the lignites (Isaac and Lindqvist 1990) that the Newvale fossils are of Late Oligocene to Early Miocene age (Waitakian on the New Zealand scale: 25.2–21.7 million years ago). Fossiliferous sediments of the very extensive GLM apparently accrued in coastal deltaic swamps on the southern coast of New Zealand (Wood 1956; Isaac and Lindqvist 1990) surrounded by vegetation that is interpreted to have been growing in a warm, ever-wet, fire-free environment (Pole 2008; Pole *et al.* 2008). Ferguson *et al.* (in press) concluded that the leaf beds of the Newvale lignites formed in highly acidic ponds within raised mire settings. These authors and Isaac and Lindqvist (1990) reported an abundance of conifer resin and foliage in the lignitic material, and Lee *et al.* (2007) described some of this foliage as having affinity to the New Zealand endemic *Agathis australis* (D. Don) Lindl. Recent studies of mining cores that intersect the GLM at other sites in eastern Southland have revealed diverse foliar (mostly cuticular) material of Lauraceae (Pole 2007a), gymnosperms (Pole 2007b), monocots (Pole 2007c), Myrtaceae (Pole *et al.* 2008) and a range of other taxa (Pole 2008). However, it is important to note that Pole's material did not come from the vicinity of the Newvale mine, nor from lignites, and floristic differences may therefore be expected. For instance,

there is as yet no evidence for Lauraceae or Myrtaceae macrofossils at Newvale (Ferguson *et al.* in press).

Methods

The Newvale lignites are comprised of densely packed plant fragments, as described and illustrated by Lee *et al.* (2007) and Ferguson *et al.* (in press). Complete and nearly complete mummified leaves are common in this matrix on some bedding planes, but the dense packing often makes it very difficult to discriminate individual specimens. Several more or less complete leaves recognisable as Persoonieae were recovered, as well as portions displaying complete leaf width and/or venation details. Numerous other fragmentary specimens and cuticle envelopes were recovered by sieving following disaggregation of lignite pieces in warm hydrogen peroxide. Cuticle preparations from both the leaf specimens on the lignite blocks and from the specimens recovered from sieved residues were made by soaking leaf fragments with gentle heating either in 30% hydrogen peroxide to which a few crystals of sodium pyrophosphate were added, or in household bleach (sodium hypochlorite 42 g L⁻¹). The cuticles were then rinsed, cleaned with a fine paintbrush if necessary, and mounted on glass slides in glycerine jelly after staining with crystal violet or Safranin O for viewing with transmitted light microscope. Cuticles were photographed with an Olympus DP11 (Tokyo, Japan) digital camera mounted on a Zeiss Axioskop (Jena, Germany) microscope at the University of Adelaide, or with a Diagnostic Instruments Spotflex (Sterling Heights, MI) digital camera mounted on a Leica DMLB (Wetzlar, Germany) microscope at the Queensland Herbarium (BRI). Other pieces of cuticle were placed on aluminium stubs and carbon/gold coated for scanning electron microscopy with a Philips XL 20 (Eindhoven, The Netherlands) SEM operated at 10 kV. Individual fossil-leaf and cuticle specimens were catalogued with OU prefixes for the Department of Geology, University of Otago, and all leaf specimens are housed there. Cuticle specimens on microscope slides and SEM stubs are currently housed at the School of Earth and Environmental Sciences, University of Adelaide.

Fossil identifications and comparisons with extant taxa

Fossil taxa were recognised as Proteaceae on the basis of the combined presence of brachyparacytic stomatal complexes (i.e. where there are two subsidiary cells flanking the sides of the guard cells but not completely enclosing them: Dilcher 1974) and distinctive annular trichome bases that often encompass more than one underlying epidermal cell (Carpenter *et al.* 2005). The placement of the Newvale fossils within the extant subfamily Persoonioideae was based on presumed synapomorphies identified from studies of extant specimens and comparison with published phylogenies of the family (Hoot and Douglas 1998; Weston and Barker 2006; Barker *et al.* 2007; Sauquet *et al.* 2009). Extant species examined for gross leaf form included the Proteaceae herbarium specimens housed at the University of Adelaide and at BRI. Cuticles from all extant genera of Proteaceae (Douglas 1995; Weston and Barker 2006) and ~400 species housed at the University of Adelaide were also compared with the fossils. These included the species of subfamily Persoonioideae listed in Table 1, comprising all four monotypic

Table 1. List of Persoonioideae species for which cuticles were examined under light microscope
Guard-cell sizes are mean lengths rounded to whole µm based on measurements from at least 10 stomata per specimen

Species and authority	Specimen details	Tribe/species group <i>sensu</i> Weston (2003)	Guard-cell size
<i>Placospermum coriaceum</i> C.T.White & W.D.Francis	AU RJC collection	Placospermeae	66
<i>Toronia toru</i> (A. Cunn.) L.A.S.Johnson & B.G.Briggs	HO 42173	Persoonieae	68
<i>Garnieria spathulaefolia</i> Brongn. & Gris	NSW 239093	Persoonieae	62
<i>Acidonia microcarpa</i> (R.Br.) L.A.S.Johnson & B.G.Briggs	AQ 483614	Persoonieae	95
<i>Persoonia brevifolia</i> (Benth.) L.A.S.Johnson & P.H.Weston	HO 82986	Persoonieae/ <i>P. lanceolata</i> group eastern	62
<i>P. brevirhachis</i> P.H.Weston	NSW 484152	Persoonieae/ <i>P. ruffiflora</i> group	80
<i>P. confertiflora</i> Benth.	HO 48060	Persoonieae/ <i>P. laurina</i> group	67
<i>P. falcata</i> R.Br.	HO 116009	Persoonieae/ <i>P. teretifolia</i> group	70
<i>P. gunnii</i> Hook. f. var. <i>gunnii</i>	HO 106309	Persoonieae/ <i>P. gunnii</i> group	62
<i>P. hirsuta</i> Pers.	HO 93224	Persoonieae/ <i>P. lanceolata</i> group eastern	64
<i>P. inconspicua</i> P.H.Weston	NSW 508738	Persoonieae/ <i>P. ruffiflora</i> group	82
<i>P. juniperina</i> Labill.	HO 117425	Persoonieae/ <i>P. lanceolata</i> group eastern	69
<i>P. lanceolata</i> Andrews	HO 93218	Persoonieae/ <i>P. lanceolata</i> group eastern	65
<i>P. levis</i> (Cav.) Domin	HO 78867	Persoonieae/ <i>P. lanceolata</i> group eastern	72
<i>P. linearis</i> Andrews	HO 117898	Persoonieae/ <i>P. lanceolata</i> group eastern	61
<i>P. longifolia</i> R.Br.	AU RJC collection	Persoonieae/ <i>P. longifolia</i> group	74
<i>P. media</i> R.Br.	BRI 142068	Persoonieae/ <i>P. lanceolata</i> group eastern	63
<i>P. media</i> R.Br. (syn. <i>P. attenuata</i> R.Br.)	E/NE/007	Persoonieae/ <i>P. lanceolata</i> group eastern	54
<i>P. moscalii</i> Orchard	HO 117427	Persoonieae/ <i>P. gunnii</i> group	70
<i>P. muelleri</i> subsp. <i>angustifolia</i> (Benth.) L.A.S.Johnson & P.H.Weston	HO 89722	Persoonieae/ <i>P. gunnii</i> group	74
<i>P. nutans</i> R.Br.	HO 106912	Persoonieae/ <i>P. lanceolata</i> group eastern	53
<i>P. pungens</i> W.Fitzg.	HO 115126	Persoonieae/ <i>P. lanceolata</i> group western	57
<i>P. quinquenervis</i> Hook.	HO 78404	Persoonieae/ <i>P. quinquenervis</i> group	76
<i>P. ruffiflora</i> Meisn.	NSW 432616	Persoonieae/ <i>P. ruffiflora</i> group	66
<i>P. saundersiana</i> Meisn.	HO 64274	Persoonieae/ <i>P. teretifolia</i> group	68
<i>P. sericea</i> A. Cunn. ex R.Br.	HO 105086	Persoonieae/ <i>P. lanceolata</i> group eastern	60
<i>P. silvatica</i> L.A.S.Johnson	HO 111843	Persoonieae/ <i>P. laurina</i> group	65
<i>P. striata</i> R.Br.	HO 20732	Persoonieae/ <i>P. quinquenervis</i> group	69
<i>P. virgata</i> R.Br.	HO 105141	Persoonieae/ <i>P. lanceolata</i> group eastern	71

genera plus representatives of the large genus *Persoonia* that occur widely within the 11 informal species groups recognised by Weston (1994, 1995, 2003). Unpublished morphological and molecular evidence suggests that these informal species groups are natural (Weston 2003, unpubl. data). Taxonomy follows Weston and Barker (2006). Persoonieae leaves similar to the fossils were photographed at BRI.

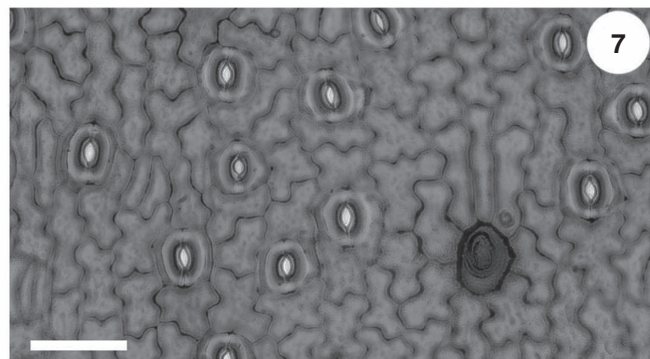
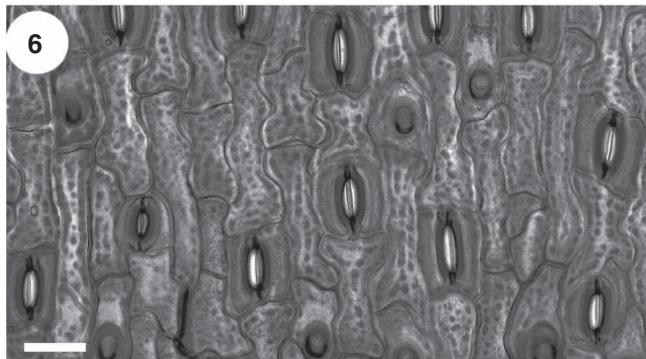
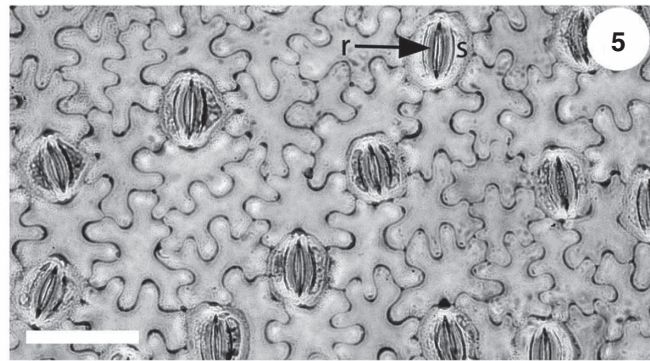
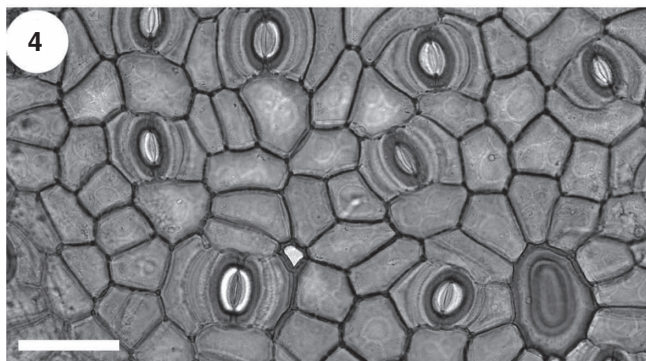
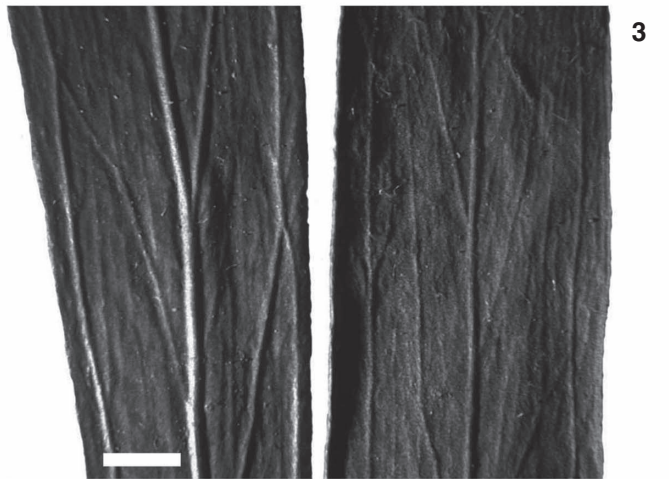
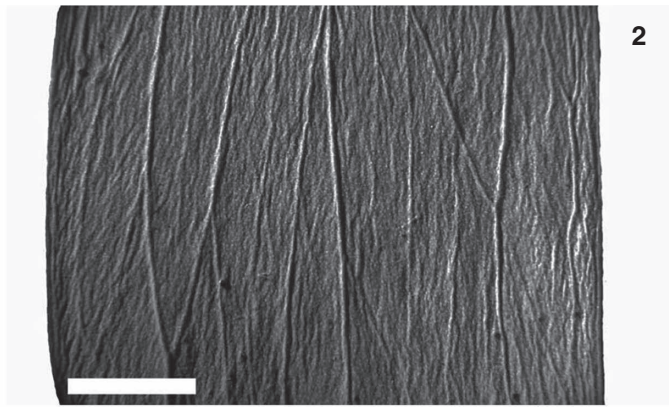
Results

Comparative morphology of extant Persoonioideae

Leaves

Placospermum coriaceum has large, deeply lobed leaves in the juvenile phase and smaller entire leaves in the adult phase (Weston 1995). Venation is clearly pinnate and brochidodromous, with quite weakly defined secondary veins that arise at relatively high angles from the midvein and form loops near the leaf margin (see image in Hyland *et al.* 2003). In Persoonieae, a variety of generally much smaller leaf forms occur across the numerous species, ranging from very small and terete to flat and relatively broad. As described by Weston (1994, 1995, 2003), venation types also vary, from brochidodromous to

acrodromous to parallelodromous and hypodromous (*sensu* Hickey 1979). In many species, secondary veins diverge from the midvein at low angles and connect to veins that run more or less parallel to the leaf margin. Numerous other parallel-running veins interconnect with these major veins (Figs 1–3). This venation type can be envisaged as being ultimately derived from leaves similar to those of *Placospermum* by changes associated with reduction and narrowing of the leaf lamina. This type of evolution to narrow leaves with subparallel venation has evidently occurred widely in Proteaceae (Johnson and Briggs 1975). To our knowledge, no modern species of Persoonieae has the combination of large leaf size and clearly brochidodromous venation with high-angle secondary veins, and this fact alone enables *Placospermum* leaves to be readily distinguished from all Persoonieae. Within Persoonieae, however, there do not appear to be any gross leaf or venation characters that might help define phylogenetically the species groups or clades recognised by Weston (2003). The wide distribution of reduced leaf forms across these groups or clades suggests a convergent response to similar selective pressures, and probably reflects speciation during the Neogene as the Australian climate became increasingly seasonal and arid.



Cuticles

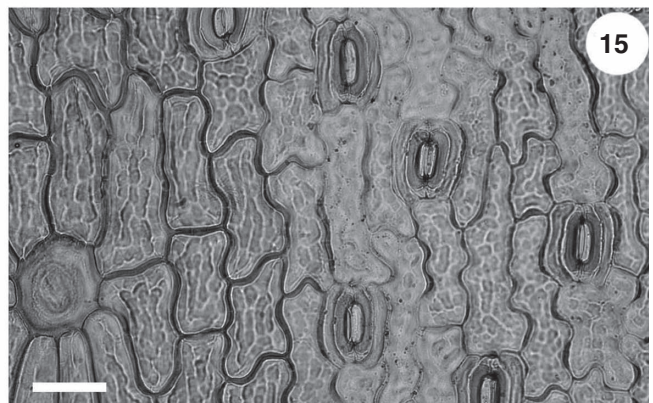
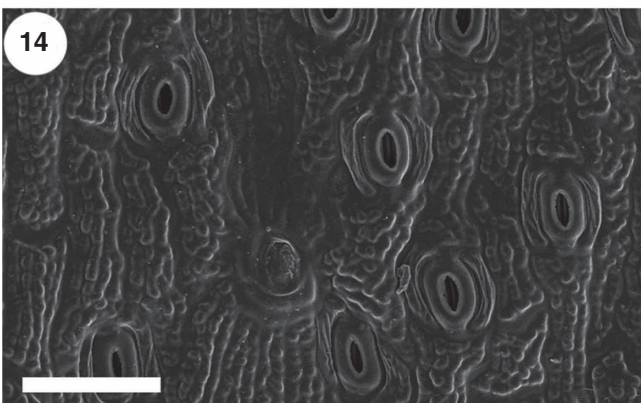
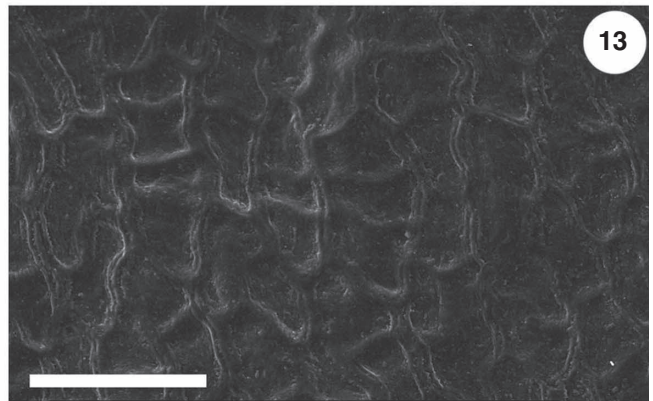
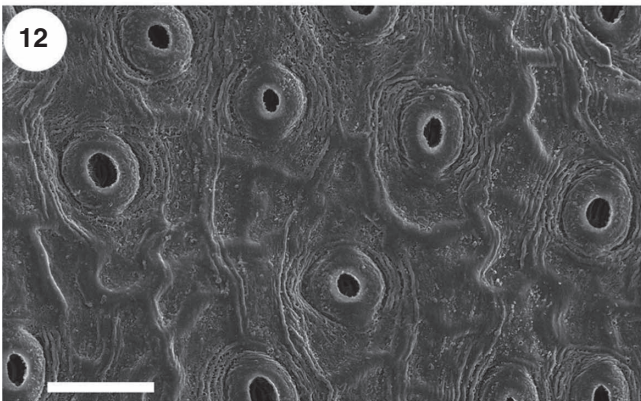
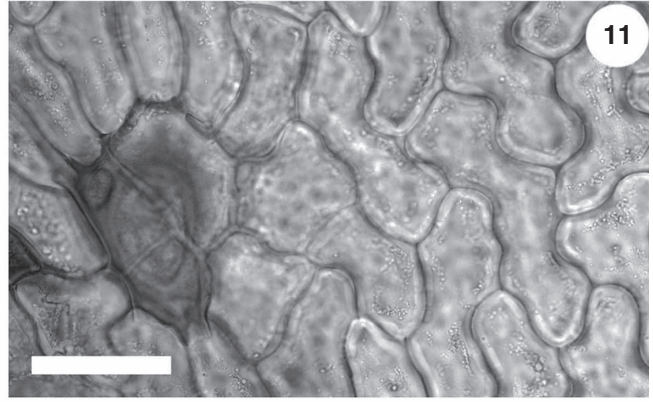
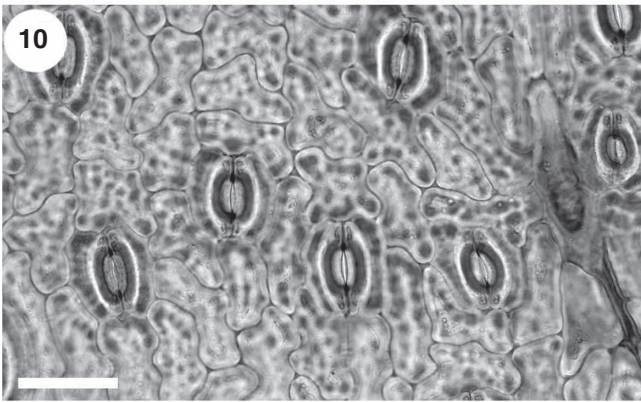
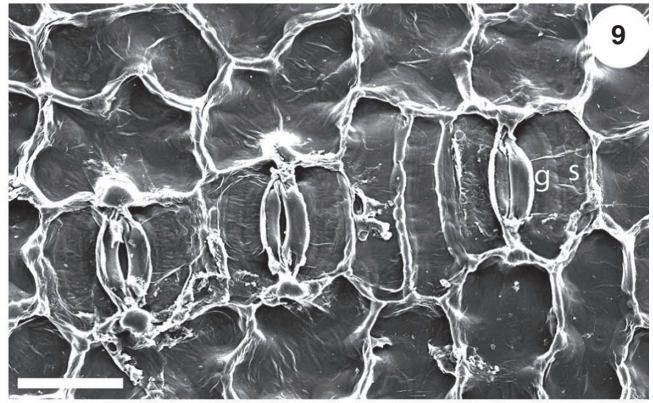
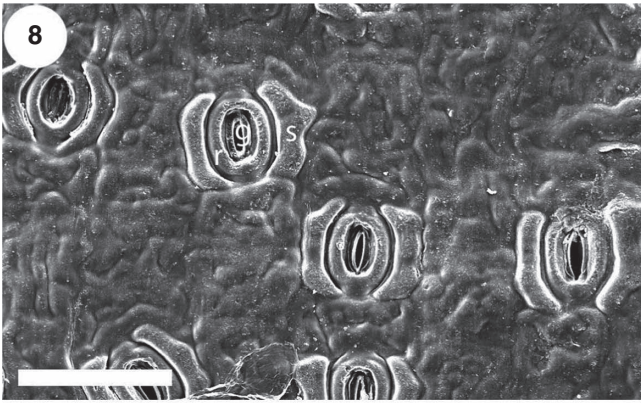
Persoonioideae are united by the presence of very large stomata, with guard cells consistently in the range of 50–80 µm long or even larger (Table 1; Carpenter 1994; Jordan *et al.* 1998). The extremely large chromosomes observed in Persoonioideae are regarded as synapomorphic for the subfamily (Johnson and Briggs 1975; Weston 1994; Stace *et al.* 1998; Weston and Barker 2006), and we reach the same conclusion for large stomatal size. It is in fact likely that large chromosomes and large stomatal sizes are correlated, given the known association between the total DNA volume and guard cell size (Masterson 1994; Knight and Beaulieu 2008). Other features of Persoonioideae cuticle are that the stomata in all species are clearly aligned, with their long axes more or less parallel to the long axis of the leaf, and the epidermal-cell anticlinal walls of many species are undulate to highly sinuous (Carpenter 1994; Carpenter and Jordan 1997). These features may also be of phylogenetic significance, and require further study. Mostly parallel-aligned stomata are also found in subfamily Bellendoideae and most species of subfamilies Proteoideae and Symphionematoideae, regardless of leaf size and shape. Elsewhere in Proteaceae, this arrangement is also found in *Sphalmium*, but very rarely in other Grevilleoideae (Carpenter 1994; Carpenter and Jordan 1997), and then only in species with very narrow leaf laminae, such as *Lomatia tinctoria* R.Br. (Carpenter and Hill 1988). Stomatal sizes within the range observed in Persoonioideae were seen in many species of *Protea*, but only very rarely in other Proteoideae (*Orothamnus zeyheri* Pappe ex Hook. and some species of *Aulax* and *Petrophile*), Bellendoideae (the largest stomata of some specimens of *Bellendena montana* R.Br.), Symphionematoideae (*Agastachys odorata* R.Br.) and Grevilleoideae (*Strangea linearis* Meissn.). However, all of these taxa with large, mostly parallel-aligned stomata differ from Persoonioideae in other ways. Most obviously, the stomatal complexes of *Bellendena* are not clearly brachyparacytic (Carpenter *et al.* 2005), and in *Protea* and the other species, anticlinal walls are more or less straight with angular junctions (Fig. 4), not undulate to sinuous as in most Persoonioideae.

Light-microscope and SEM images of Persoonioideae cuticles are shown in Figs 5–15. The large, mostly parallel-aligned stomata of *Placospermum* are very distinctive. The complexes of guard cells plus subsidiary cells are oval in shape and the guard-cell pairs are narrow and elongate (Fig. 5). Also, the outermost apertures of the stomata appear only as very narrow slits between the elongate cuticular rims that lie over the guard cells (Fig. 5, see also Fig. 6 in Carpenter 1994).

By contrast, the complexes of guard and subsidiary cells in Persoonieae often appear more or less square or rectangular in overall shape and on the cuticular surface there are always much broader, often squarish rims around the stomatal apertures (Figs 6–10, 12, 14, 15). Hereafter, stomatal complexes of this type are referred to as ‘broad’. *Placospermum* cuticle is also very thin and slightly granular on its inner periclinal surfaces under SEM (Carpenter 1994), whereas the Persoonieae examined have thicker cuticles, with no evidence of granulations. *Placospermum* is hypostomatic, whereas almost all species of Persoonieae are amphistomatic. Hypostomaty in Persoonieae has been observed only in *Toronia* (Figs 8–11) and *Garnieria* (Figs 12, 13) and a few species of *Persoonia* from several subgeneric species groups. These include *P. confertiflora* Benth. (*P. laurina* group), *P. volcanica* P.H.Weston & L.A.S.Johnson (*P. lanceolata* group) and *P. tropica* P.H.Weston & L.A.S.Johnson (unique group). *Placospermum* cuticle is quite smooth on its outer surfaces, apart from the rims associated with the stomatal apertures (Carpenter 1994), whereas Persoonieae cuticle may exhibit surface ornamentation, including waxiness. Rough leaf surfaces may be attributed to persistent protruding trichome stalk cells or papillae/tubercles (Figs 14, 15) (Weston 1994), and in some species cuticular surface striations or regulations occur, especially over the subsidiary cell regions (Fig. 12). Most species of Persoonieae have trichomes on their immature leaves, but these are lost at or before maturity (Weston 1994). Trichome base scars on mature leaves of *Placospermum*, *Toronia* and *Garnieria* cuticles are very rare, whereas they are abundant in some species of *Persoonia*. As noted by Carpenter (1994) and Carpenter and Jordan (1997), Persoonioideae trichome bases appear to be associated with only one (Figs 6, 7, 15), or more rarely, two underlying epidermal cells, although three such cells have been observed in *Toronia* (Fig. 11).

Overall, there is a combination of cuticular characters that are uniquely found in subfamily Persoonioideae of Proteaceae. This is the presence of large, parallel-aligned, brachyparacytic stomatal complexes and sinuous or undulate epidermal-cell anticlinal wall cuticle (Figs 5–15). Within Persoonioideae, *Placospermum* cuticle can be distinguished from Persoonieae in having only narrow stomatal complexes. Persoonieae cuticle is also generally thicker with smooth inner surfaces, and many species exhibit outer surface features not found in *Placospermum*, including evidence of abundant trichomes. However, as for leaf morphology, there does not appear to be evidence that there are cuticular features that might help define phylogenetically the species groups or clades of Persoonieae recognised by Weston (2003).

Figs 1–7. Images of portions of Persoonieae leaves similar to Newvale leaf fossils (Figs 1–3) and light microscope images of abaxial Proteaceae (see Table 1 for Persoonioideae specimens) cuticles with large, parallel-aligned stomata (Figs 4–7). Scale bars = 2 mm (Figs 1–3), 100 µm (Figs 4–7). **Fig. 1.** *Persoonia media* (BRI QH204214), showing more or less parallel principal veins of similar thickness and higher-order interconnecting veins. **Fig. 2.** *P. levis* (BRI QH046883), showing more or less parallel principal veins of similar thickness and higher-order interconnecting veins. **Fig. 3.** Adaxial (left) and abaxial views of *Toronia toru* (BRI QH354984), showing more or less parallel venation with a central principal vein and higher-order interconnecting veins. **Fig. 4.** *Protea aurea* (Burm.f.) Rourke (Adelaide University E/2185), showing straight anticlinal walls with distinctly angular junctions. **Fig. 5.** *Placospermum coriaceum*, showing highly sinuous anticlinal walls and oval-shaped complexes of guard cells plus subsidiary cells (s). Also, note the slit-like apertures between the narrow cuticular rims (r) that lie over the guard cells. **Fig. 6.** *Acidonia microcarpa*, showing undulate anticlinal cell walls and broad, squarish complexes of guard cells plus subsidiary cells. Note also several round trichome bases and that guard-cell length may reach ~100 µm. **Fig. 7.** *Persoonia media*, showing undulate anticlinal cell walls. Note trichome base at right.



The fossils

Numerous entire-margined Proteaceae leaves and leaf fragments with variably evident, more or less parallel venation (Figs 16–19) and with the same cuticle type were recognised from the Newvale lignites. The leaves are typically linear to falcate in shape and ~10–20 mm wide. The most complete specimens suggest that overall leaf length was ~85–100 mm (Fig. 16). The normally robust cuticles show large, broad, mostly parallel-aligned stomatal complexes that are confined to one surface (Figs 20–24), and undulating anticlinal cell walls (Figs 20–27). The abaxial surface, in particular, of the leaf specimens is covered in small tubercles (Figs 20–22, 24) that give a rough appearance to the leaves under binocular microscope. The inner cuticle surfaces do not show evidence of granulations (Figs 23, 26). Trichome bases are almost always absent, but one specimen shows a typical proteaceous base on the abaxial surface and another shows such a base on the adaxial surface (Fig. 25). Both bases are associated with four epidermal cells.

Cuticular material of a similar but clearly distinct taxon also occurs within the lignites, although so far no whole leaves with venation details have been observed on the leafy bedding planes where the blocks split most readily. The cuticle of this taxon also exhibits undulate anticlinal cell walls (Figs 28–35) and broad, parallel-aligned stomatal complexes (Figs 28, 30–33) that are confined to one surface (Figs 28, 29). However, it can readily be distinguished from the first taxon by its even larger stomata (Figs 30–33), non-tuberculate outer surfaces (Figs 30, 34) and generally abundant trichome bases on both surfaces that are associated with one or less commonly two epidermal cells (Figs 31, 33, 35).

The two taxa are recognised as two new species of a new fossil genus of tribe Persoonieae of Proteaceae.

Taxonomy

Family **Proteaceae**

Subfamily **Persoonioideae** L.A.S.Johnson & B.G.Briggs

Tribe **Persoonieae** Rchb

Persoonieaephyllum R.J.Carp., J.M.Bannister, G.J.Jord. & D.E.Lee, gen. nov. (Figs 16–35)

Type species: Persoonieaephyllum ornatum R.J.Carp., J.M.Bannister, G.J.Jord. & D.E.Lee, sp. nov. (Figs 16–27).

Type locality: Newvale Mine, Waimumu Coalfield, Southland. Site registered as F45/f0394 in the New Zealand

Fossil Record File administered by the Geological Society of New Zealand. The NZ Map Grid reference on Infomap series is NZMS 260 F45/817434 (46.1427°S, 168.7518°E).

Diagnosis

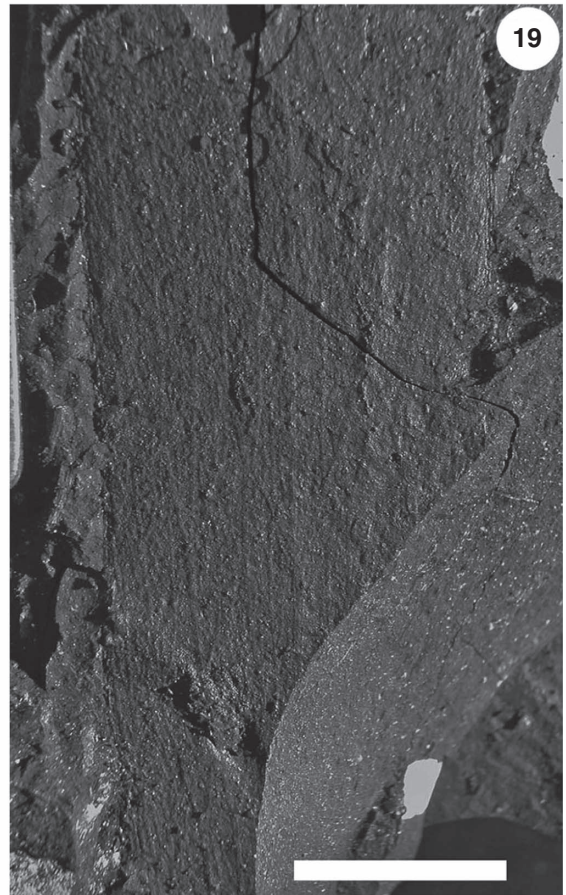
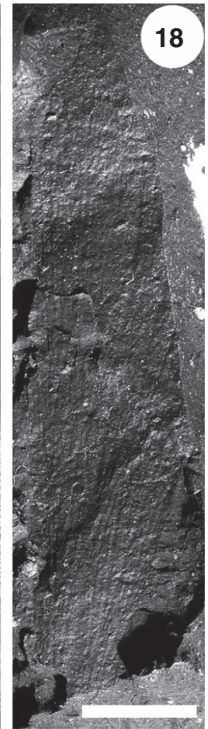
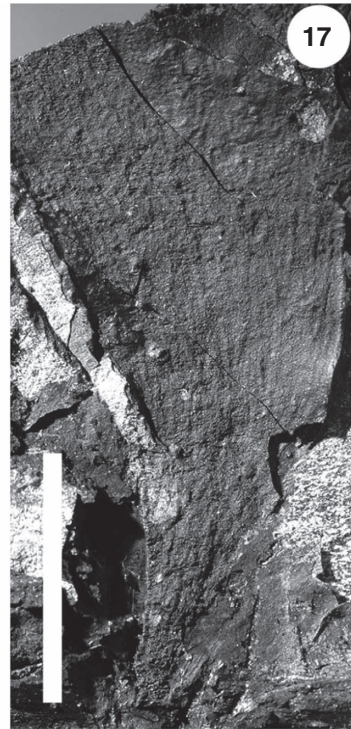
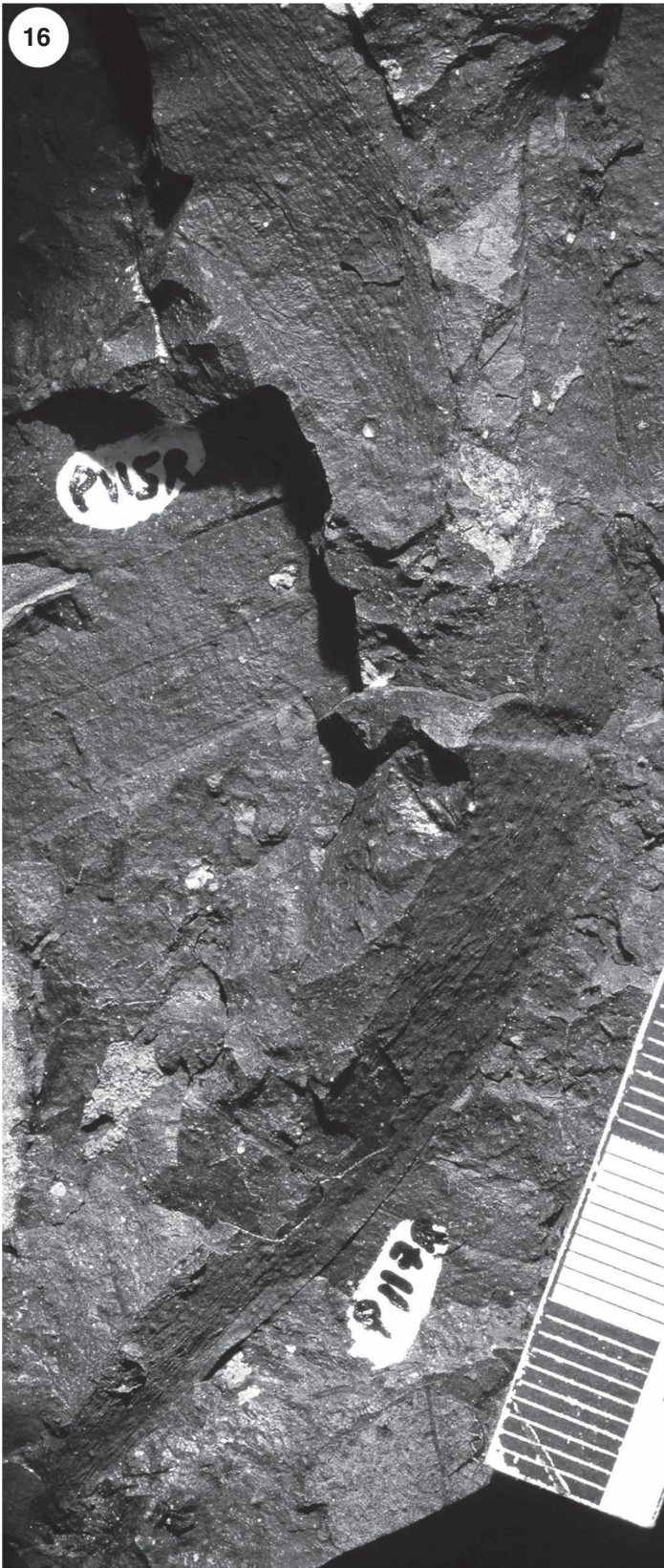
Proteaceous leaf material with broad, mostly parallel-aligned, brachyparacytic stomatal complexes. Stomata large, guard cells typically greater than 50 µm long. Cuticular extensions between epidermal-cell anticlinal walls undulate to sinuous, not straight with angular junctions. Trichome bases associated with up to four epidermal cells. Venation, where known, with more or less parallel-aligned major veins and numerous higher-order interconnecting veins.

Discussion of *Persoonieaephyllum*

The Newvale fossils were recognised as belonging to Persoonioideae on the basis of features now uniquely found in the subfamily in combination. This is the presence of parallel-aligned brachyparacytic stomatal complexes and undulate anticlinal cell walls and the synapomorphy of large stomatal size. The fossils are assumed to belong to the crown group of Persoonioideae because their available features are entirely consistent with those of extant tribe Persoonieae. A feature shared by all specimens of the Newvale fossils and extant Persoonieae but distinct from *Placospermum* is the presence of broad stomatal complexes. Fossil specimens that are represented by leaves with venation details are also distinct from *Placospermum* in having subparallel v. brochidodromous venation. Further evidence justifying the placement of the fossils in Persoonieae is that the cuticles are relatively thick and smooth on their inner surfaces, and show ornamentation or abundant trichome bases on their outer surfaces. However, placement of the fossils in the crown group of Persoonieae is problematic because they do not appear to possess features that are synapomorphic for any of its subclades. Therefore, the new genus *Persoonieaephyllum* is erected for fossil leaves with cuticle and isolated cuticular specimens that conform entirely to tribe Persoonieae of Persoonioideae in available details, but that could represent stem taxa of the tribe.

We recognise that extensive extinctions are likely to have occurred in Persoonioideae and its apparent sister group, the monotypic subfamily Bellendenoideae (Weston and Barker 2006; Barker *et al.* 2007; Sauquet *et al.* 2009), and that it is theoretically possible that fossils showing apomorphies for subfamily Persoonioideae may be extinct stem taxa of this subfamily or even of Bellendenoideae (see Magallón 2004). This problem is compounded by the fact that it is difficult to draw inferences concerning morphological synapomorphies in

Figs 8–15. Images of cuticles of specimens (see Table 1 unless specified) of *Toronia toru* (Figs 8–11), *Garnieria spathulaefolia* (Figs 12, 13) and *Persoonia virgata* (Figs 14, 15). Scale bars = 100 µm (Figs 8, 10, 11, 13, 14), 50 µm (Figs 9, 12, 15). **Fig. 8.** Scanning electron microscopic (SEM) image of the outer abaxial surface. The positions of the subsidiary cells (s) are particularly clear, and there are broad rims (r) surrounding the stomatal apertures and underlying guard cells (g). **Fig. 9.** SEM image of the inner abaxial surface. Note the broad, brachyparacytic arrangement of guard (g) and subsidiary (s) cells and evidence of undulate epidermal cell anticlinal walls. Thick cuticle associated with the guard cells surrounds the stomatal apertures. **Fig. 10.** Light microscopic (LM) image of abaxial cuticle, showing large parallel-aligned stomata, undulate anticlinal walls and a trichome base at right. **Fig. 11.** LM image of adaxial cuticle, showing a trichome base associated with three epidermal cells and undulate anticlinal walls. Stomata are absent (cult., Dunedin Botanic Garden). **Fig. 12.** SEM image of outer abaxial surface, showing raised outlines marking the positions of epidermal cells, and weak striations over the subsidiary cells. **Fig. 13.** SEM image of outer adaxial surface, showing raised outlines marking the positions of epidermal cells. **Figs 14, 15.** SEM (Fig. 14) and LM (Fig. 15) images of abaxial surface, showing stomata, tuberculate surface ornamentation and trichome bases.



such ecologically and morphologically disparate species as *Placospermum coriaceum* and *Bellendena montana*, a Tasmanian mountain shrub, especially given that molecular evidence indicates that the Persoonioideae and *Bellendena* lineages diverged in the Late Cretaceous (Barker *et al.* 2007; Sauquet *et al.* 2009).

Much more study of cuticular characters in Proteaceae is required overall; however, placement of the Newvale fossils in stem group Bellendenoideae might be possible if large stomatal size, and perhaps other character states including parallel-aligned stomata, undulate anticlinal cell walls and subparallel venation, are in fact synapomorphic for the *Bellendena* + Persoonioideae clade. Assuming a synapomorphy of brachyparacytic stomatal complexes for Proteaceae, this would imply that the unusual state of the stomatal complexes of *Bellendena* (Carpenter *et al.* 2005) is derived. It would also imply that the relatively large leaves with brochidodromous venation in *Placospermum* are independently derived with respect to similar leaf forms in other subfamilies of Proteaceae. However, it is probable that as for other of its unusual features (Johnson and Briggs 1975), the small leaf type with subparallel venation of *Bellendena* is associated with evolution into high-latitude subalpine habitats in Tasmania, not the state of the common ancestor of *Bellendena* and Persoonioideae. We also assume that the brochidodromous venation type of *Placospermum* is ancestral in Persoonioideae as it probably is for Proteaceae in general (Johnson and Briggs 1975), and the state of reduced leaves with subparallel venation in Persoonieae is independently derived. Thus, although other potential placements for the Newvale fossils exist, we conclude that they are unlikely to belong anywhere but on the stem or crown of tribe Persoonieae.

Etymology

In reference to leaf fossils that can be assigned only at the level of the tribe Persoonieae, and not to any one genus within the tribe.

Persoonieaephyllum ornatum R.J.Carp., J.M.Bannister, G.J.Jord. & D.E.Lee, sp. nov. (Figs 16–27)

Holotype: OU32765, stored at Otago University Geology Department.

Type locality: Newvale Mine, Waimumu Coalfield, Southland.

Diagnosis

Leaves linear to falcate, hypostomatic. Outer abaxial cuticle covered in small tubercules. Trichome bases extremely rare, associated with four epidermal cells.

Discussion of *P. ornatum*

Several leaves of *P. ornatum* co-occur in close proximity, suggesting that detached foliage shoots may have been deposited. *P. ornatum* clearly shows features of extant species of Persoonieae, but on current understanding it is not closely similar to any one species. Its leaves are up to ~100 mm long and typically 14–19 mm wide, and some clearly show evidence of venation (Figs 16–19). The main veins are always more or less parallel to the long axis of the leaf (sometimes with a discernible central primary vein that is slightly stronger than the other veins), and are linked by a meshwork of bifurcating and anastomosing higher-order veins. This leaf type and size is seen widely in extant Persoonieae, including numerous broad-leaved species of *Persoonia* (e.g. *P. media* R.Br., Fig. 1 and *P. levis* (Cav.) Domin, Fig. 2), *Toronia* (Fig. 3) and *Garnieria*. As discussed previously, the state of hypostomaty seen in *P. ornatum* is not common in Persoonieae, but does occur in *Toronia* and *Garnieria*. Mean guard-cell size in *P. ornatum* is ~53 µm. Although very large with respect to most Proteaceae other than Persoonioideae, this is at the lower end of the range observed in Persoonieae (Table 1). The state of the subsidiary cell positions being clearly evident on the cuticle surface (Fig. 22) is typical of many Persoonieae, including *Toronia* (Fig. 8). The cuticle of *P. ornatum* appears to have some variation in thickness and the development of surface ornamentation (Figs 21, 24). Several extant species, including *P. virgata* R.Br., also exhibit forms of tuberculate ornamentation of the abaxial surface (Figs 14, 15). The only trichome bases observed on the cuticle of *P. ornatum* were associated with four epidermal cells (Fig. 25), a state so far not seen in extant Persoonieae, although three such cells have been observed on both cuticular surfaces of *Toronia* (Fig. 11).

The diagnosis of *P. ornatum* is a composite based on numerous leaf and/or cuticular specimens, because trichome bases are usually absent and not all specimens provide gross leaf details. Specimens should therefore be assigned to this species with caution.

Etymology

Named for the ornate, tuberculate appearance of the leaf surface.

Specimens examined

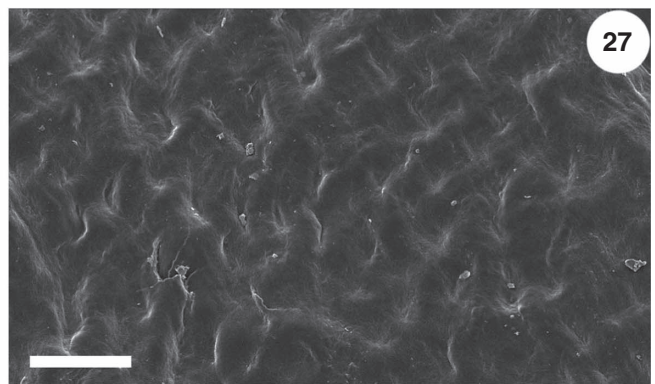
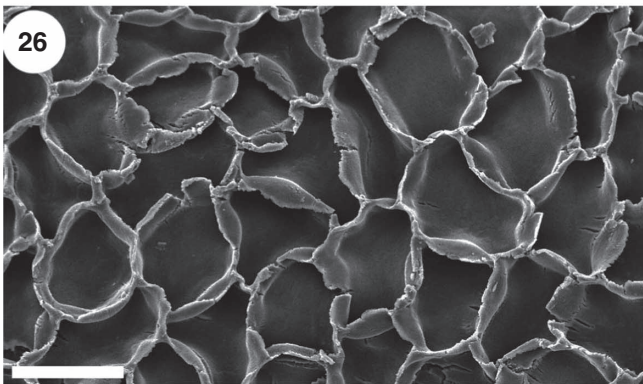
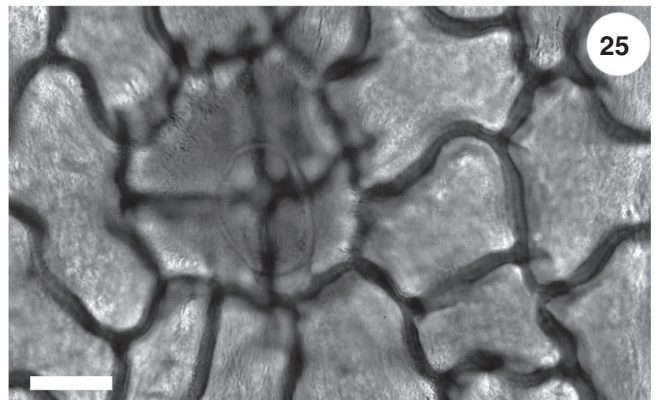
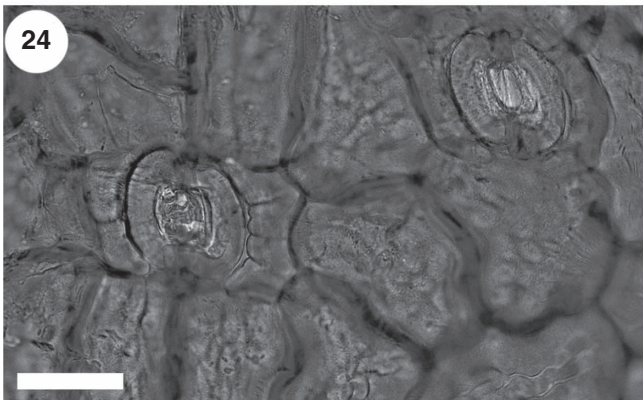
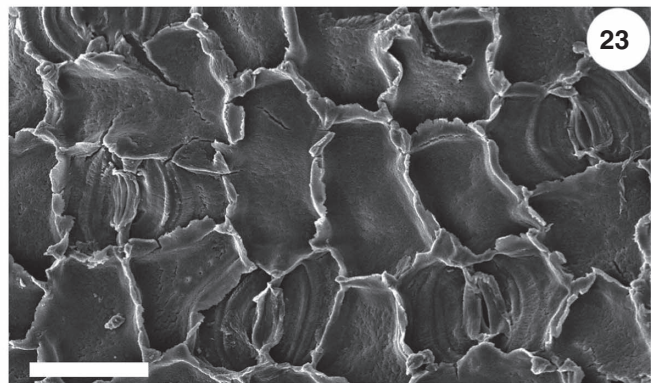
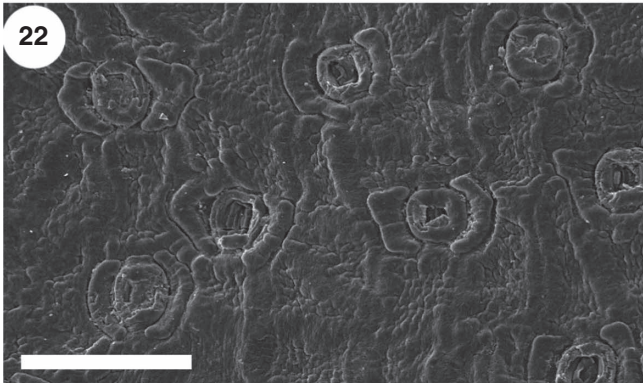
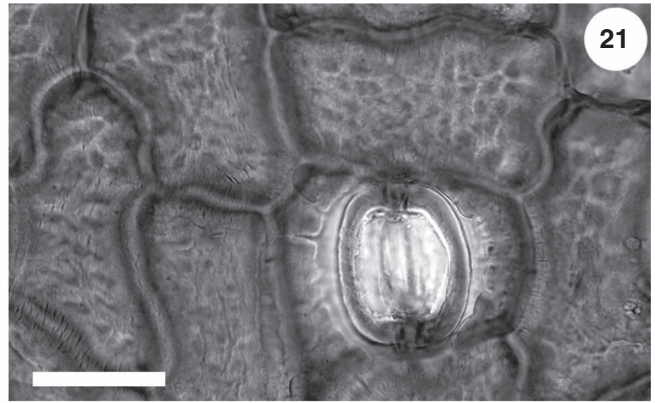
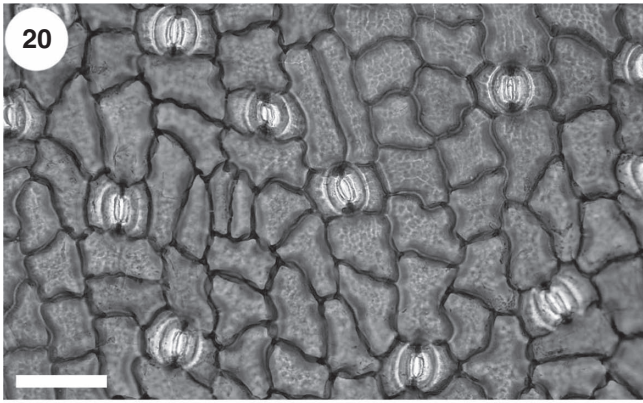
Leaves with cuticle: OU32745–OU32765. Cuticles only: OU32058, OU32077, OU32082, OU32174–OU32176.

Persoonieaephyllum villosum R.J.Carp., J.M.Bannister, G.J.Jord. & D.E.Lee, sp. nov. (Figs 28–35)

Holotype: OU32079, stored at the Department of Plant Science, University of Adelaide.

Type locality: Newvale Mine, Waimumu Coalfield, Southland.

Figs 16–19. Images of *Persoonieaephyllum ornatum* sp. nov. leaf and leaf fragments. Scale bars = 1 cm. **Fig. 16.** Specimen OU32763 (at right). Note the narrow, falcate leaf form. Another *P. ornatum* specimen on the same bedding plane is located at upper left. **Figs 17–19.** Incomplete leaf specimens, showing more or less parallel venation with higher-order interconnecting veins. Compare with extant Persoonieae species (Figs 1–3). **Fig. 17.** Specimen OU32749. This is the base of a leaf. **Fig. 18.** Specimen OU32758. Part of the base of a leaf. Note the slightly stronger central vein. **Fig. 19.** Specimen OU32765 (Holotype). Note the central vein.



Diagnosis

Leaves hypostomatic. Trichome bases abundant on at least the adaxial surface, associated with one or two epidermal cells. Epidermal cells clearly delineated on both outer cuticular surfaces. Stomata extremely large, mean guard-cell length ~71 μm .

Discussion of *P. villosum*

Although no whole-leaf specimens of *P. villosum* have been recovered, several cuticular envelopes show that this species was hypostomatic. The type specimen OU32079 shows most of the tip of an apparently acute leaf apex (Figs 28, 29). Another cuticular envelope specimen (OU32071) is 9 mm wide and 20 mm long, and indicates that the source leaf was at least this large, and possibly of similar size as *Persooniaephyllum ornatum*. All of the cuticular material of *P. villosum* conforms overwhelmingly with extant Persoonieae. Indeed, if the specimens here assigned to *P. ornatum* were represented only by cuticle, an even stronger case could be made for *P. villosum* having affinities with Persoonieae than that for *P. ornatum*. This is partly because the stomata of *P. ornatum* are at the lower end of the size range seen in extant species, and thus more similar to other Proteaceae, whereas those of *P. villosum* are the typical very large size of most extant Persoonieae (Table 1). The cuticular surface delineation of the epidermal cells by raised ridges (Figs 30, 34) is also identical to that seen in many Persoonieae, especially in species with little ornamentation such as *Garnieria spathulaefolia* Brongn. & Gris (Figs 12, 13). *P. villosum* most obviously differs from *Garnieria* and *Toronia* (Figs 8–11) in possessing abundant trichome bases, a feature now found only in Australian Persoonieae. In one specimen of *P. villosum* (OU32071), the trichome bases do not appear to occur on the abaxial surface. This is regarded as variation, because in all other respects the cuticle is identical to that of the other specimens. Also, Weston (1994) noted that there may be variation in trichome density within the species of extant *Persoonia*. Identical trichome bases to that of the fossils occur in several species of *Persoonia*, including *P. virgata* (Fig. 14).

Etymology

Named for the abundant trichome bases that suggest the source leaves were hairy during at least some life stage(s).

Specimens examined

OU32059, OU32066, OU32071, OU32073, OU32078, OU32079.

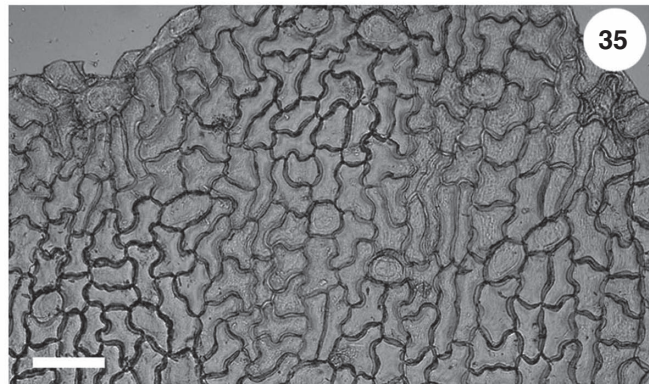
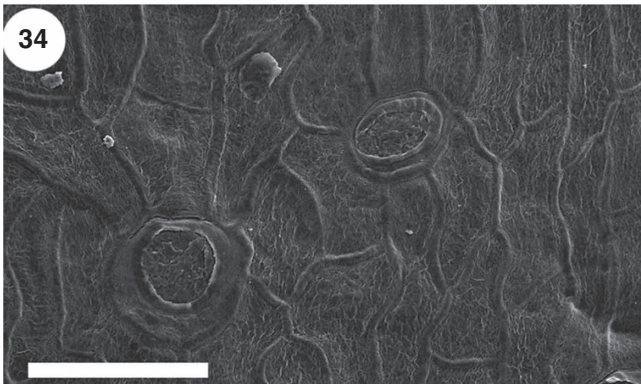
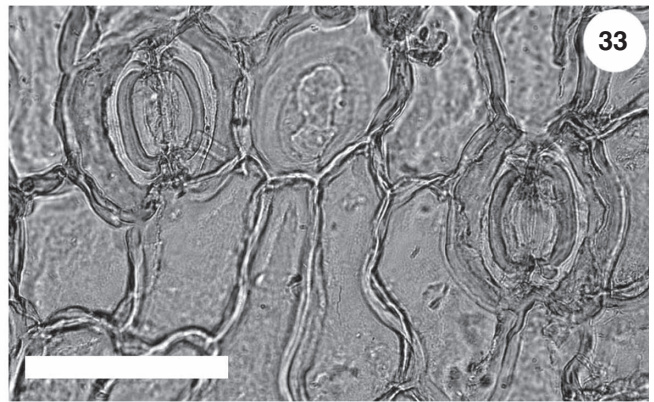
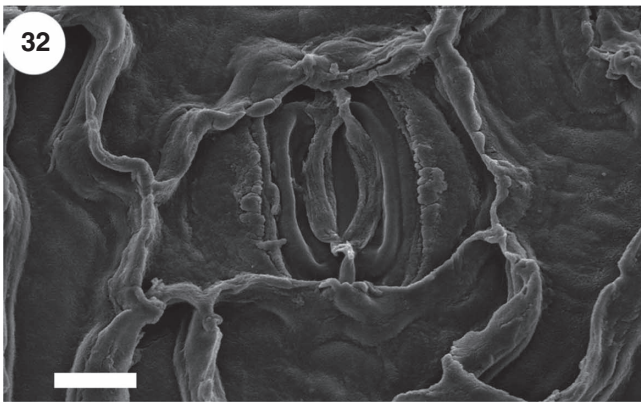
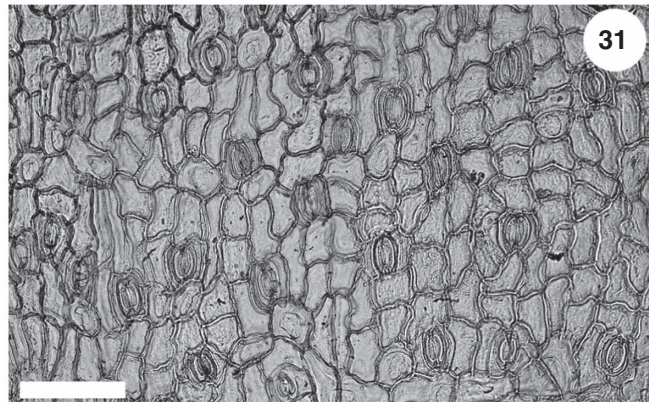
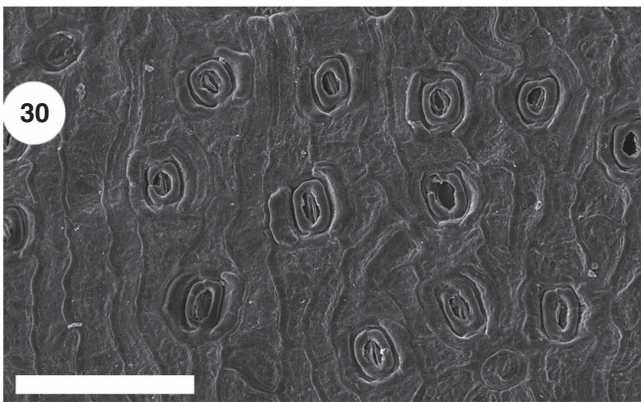
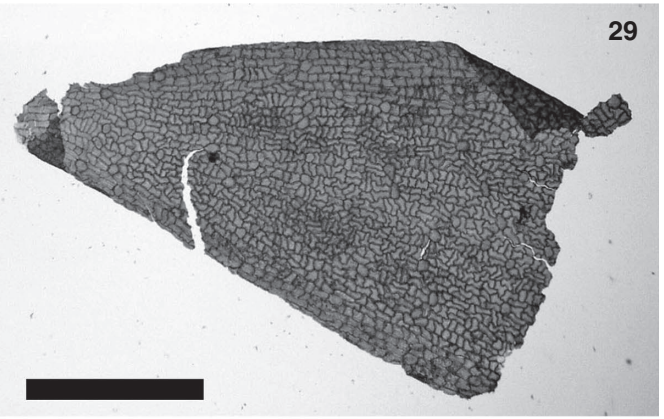
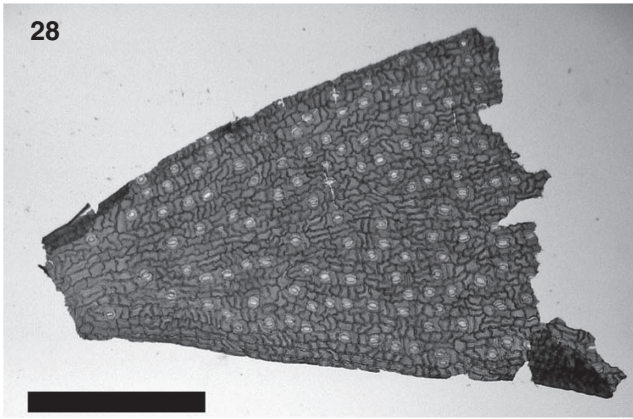
Discussion

Biogeographic and phylogenetic implications of the fossils

The fossils not only represent the first substantiated macrofossil records of Persoonioideae, but also demonstrate the presence of this subfamily in the Oligo–Miocene of southern New Zealand long before the first New Zealand pollen records (of *Toronia*) in the Late Pliocene, perhaps 20 million years later. Molecular-based estimates by Barker *et al.* (2007) dated the divergence between *Placospermum* and *Toronia* as Late Cretaceous, whereas Sauquet *et al.* (2009, their supporting information table S2), by using a much larger dataset of extant Persoonieae, dated the divergence between *Placospermum* and *Toronia* + the rest of Persoonieae within 66.4–32.8 million years ago, and the split between *Toronia* and the rest of Persoonieae within 31.5–11.6 million years ago. The Newvale fossils thus fall within the range of the estimated crown group age of Persoonieae. However, although the fossils are clearly similar to leaves of extant taxa, and one or both species may belong in the crown group, this cannot be determined unequivocally on the available evidence.

On the basis of the current distribution of Persoonioideae, its molecular phylogeny and the existing fossil record of *Persoonia*-like pollen, the presence of Oligo–Miocene Persoonieae in New Zealand can probably best be explained by dispersal from Australia. The mostly west to east trans-Tasman dispersal of many other taxa throughout the Cenozoic is well known from the fossil pollen record in particular (Mildenhall 1980; Macphail *et al.* 1994). Foliar and cuticular evidence unfortunately do not allow any resolution as to the closeness of the relationship of the Newvale fossil species to each other or to *Toronia* or the large clade containing most Australian *Persoonia* species and the New Caledonian *Garnieria*. However, although it may be an ancestral state of stomatal distribution in Persoonieae, both species of *Persooniaephyllum* share hypostomaty with *Toronia* and *Garnieria*, and *P. ornatum* and *Toronia* are the only Persoonieae that have trichome bases associated with more than two epidermal cells. Thus, this fossil evidence makes it plausible that *Toronia* is the last member of a clade that has been present in New Zealand since at least the beginning of the Miocene, and also plausible that the ancestor of *Garnieria* reached New Caledonia from New Zealand, not directly from Australia. Multiple dispersals of Persoonieae to Zealandia (the landmass now comprising New Zealand, New Caledonia, Lord Howe Island and associated ridges and islands) are assumed since the extant sister taxa of both *Toronia* and *Garnieria* appear to be Australian *Persoonia* species that are not closely related (Weston 2003). An alternative explanation for past and present distributions involving a

Figs 20–27. Images of *Persooniaephyllum ornatum* sp. nov. cuticles under light microscope (Figs 20, 21, 24, 25) and scanning electron microscope (Figs 22, 23, 26, 27). Scale bars = 100 μm (Figs 20, 22, 27), 50 μm (Figs 21, 23, 24, 26) and 25 μm (Fig. 25). **Fig. 20.** Specimen OU32745. Abaxial surface, showing more or less parallel alignment of large stomata, tuberculate ornamentation and undulate anticlinal walls. **Fig. 21.** Specimen OU32745. Enlargement of single stoma, showing brachyparacytic arrangement of subsidiary cells. **Fig. 22.** Specimen OU32765 (Holotype). Outer abaxial surface, showing more or less parallel alignment of stomata, tuberculate ornamentation, and raised outlines marking the positions of epidermal and subsidiary cells. **Fig. 23.** Specimen OU32058. Inner abaxial cuticle surface, showing brachyparacytic stomatal complexes. **Fig. 24.** Specimen OU32751. Abaxial cuticle, showing stomata. The cuticle is thicker than in other specimens such as OU32745 (Figs 20, 21). **Fig. 25.** Specimen OU32175. Adaxial cuticle, showing a trichome base associated with four basal cells. **Fig. 26.** Specimen OU32058. Inner adaxial surface, showing that the epidermal cell walls are undulate. **Fig. 27.** Specimen OU32058. Outer adaxial surface.



New Zealand origin of the whole of Persoonieae should not be dismissed out of hand, but would imply dispersal to Australia of both the ancestor of the *P. ruffiflora* group of south-western Australia and that of the large Australian clade of Persoonieae, a less parsimonious explanation of modern distributions than dispersal of the ancestor of *Toronia* from eastern Australia to Zealandia or New Zealand.

Although there is paucity of experimental evidence for distance dispersal, Persoonieae have drupes suited to dispersal by birds (Johnson and Briggs 1975). Although Weston and Crisp (1995) concluded that the drupes of both *Toronia* and *Garnieria* are and have always been too large (notably up to 3.5 cm long in *Garnieria*; Viroit 1968) to be dispersed over ocean gaps by birds, there is an impressive list of very large fossil frugivorous bird species from Pacific Islands (Balouet and Olson 1989; Steadman 1997; Worthy 2001), including giant pigeons that could easily have swallowed Persoonieae fruits and potentially have dispersed them. Also, the fruit sizes of the ancestors of *Toronia* and *Garnieria* were not necessarily as large as in their extant descendants. This is apparent in the Hawaiian Islands where many plant species display fruit-size gigantism with respect to their ancestors that must have reached these islands via long-distance dispersal (Carlquist 1966).

Assuming that all past Persoonieae produced pollen recognisable as such, the absence of *Toronia* pollen or similar types from the Newvale lignites so far studied and in sediments older than the Late Pliocene in New Zealand generally is not readily explainable. This is usually regarded as evidence of a very recent arrival of *Toronia* in New Zealand, as is the case for many other taxa (e.g. Pole 1994). However, although it appears unlikely for palynological records as comprehensive as that of New Zealand, long periods of absence of some taxa may be attributable to low pollen production associated with specialised insect pollination. This could be pertinent for Persoonieae, because extant species are strongly under-represented in modern pollen assemblages, even where flowering plants are known to occur near traps (Itzstein-Davey 2003). Furthermore, the first records of *Toronia* pollen in the Pliocene of New Zealand may reflect markedly increased abundance of the source plants in a flora clearly otherwise decimated by climatic factors during the Neogene (e.g. Lee *et al.* 2001). Studies of the pollination ecology of both *Toronia* and *Garnieria* would be of interest with respect to that of *Persoonia* in Australia, where it is apparent that small colletid bees of *Leioproctus* subgenus *Cladocerapis* are very important pollinators (Bernhardt and Weston 1996; Wallace *et al.*

2002). *Leioproctus* is now depauperate in New Zealand and particularly in New Caledonia and is believed to have also reached these regions by dispersal from Australia (Donovan 1983).

Newvale vegetation in the Oligo–Miocene

There is no doubt that the overall climate of southern New Zealand in the Early Miocene was much warmer than that of today (Pole *et al.* 2003; Pole 2008), and other authors have emphasised that Miocene pre-uplift soils in general in New Zealand were probably strongly weathered and infertile under the warm, humid conditions that prevailed (Lee *et al.* 2001). At Newvale, Ferguson *et al.* (in press) concluded that *Dacrydium*, *Agathis* and other conifers and many sclerophyllous angiosperms were growing on the margins of raised mires in highly acidic environments. *Persoonieaephyllum* can similarly be envisaged as a component of local sclerophyllous heath or woodland vegetation, because most extant Persoonieae are typical of such habitats on infertile acid soils (Weston 1994). Further evidence for the presence of relatively open, sclerophyllous vegetation at Newvale is that fossil epicarid (Ericaceae) leaves (Jordan *et al.* 2010), Casuarinaceae and at least four other taxa of Proteaceae have been recovered. The Proteaceae leaves include *Banksia* (Carpenter *et al.* 2010) and two amphistomatic taxa. Amphistomaty in Persoonieae requires further study with respect to habitat, although in other Proteaceae (Carpenter 1994) and in angiosperms generally, it is strongly linked to growth in open habitats, where it has been proposed that it enables an increase in maximum leaf conductance to CO₂, an adaptive advantage for plants growing in full sun and in conditions of rapidly fluctuating or continuously available soil moisture (Mott *et al.* 1982). The possibility that sclerophyll vegetation with a character now typically Australian was established at oligotrophic sites in southern New Zealand in the Oligo–Miocene will be explored in ongoing studies of the Newvale lignites. The assemblage offers the opportunity of reconstructing the vegetation of a peat swamp with only *in situ* or very local input of plant organs (Ferguson *et al.* in press). Interestingly, vast coal reserves in the Latrobe Valley of south-eastern Australia that evidently formed under similar conditions are of the same age and also feature abundant foliage of *Dacrydium*, Araucariaceae, Casuarinaceae and sclerophyllous Proteaceae (Duigan 1966; Blackburn and Sluiter 1994).

Figs 28–35. Images of *Persoonieaephyllum villosum* sp. nov. cuticles under light microscope (Figs 28, 29, 31, 33, 35) and scanning electron microscope (Figs 30, 32, 34). Scale bars = 1 mm (Figs 28, 29), 200 μm (Figs 30, 31), 100 μm (Figs 33–35) and 20 μm (Fig. 32). **Fig. 28.** Specimen OU32079. Mostly complete tip of leaf apex, abaxial side with parallel-aligned stomata. **Fig. 29.** Specimen OU32079. Mostly complete tip of leaf apex, adaxial side. **Fig. 30.** Specimen OU32079. Outer abaxial surface, showing more or less parallel-aligned, broad stomatal complexes and raised outlines marking the positions of epidermal cells. Note round trichome base scars at top left and bottom right. **Fig. 31.** Specimen OU32078. Abaxial cuticle, showing parallel-aligned stomata, undulate anticlinal walls and abundant trichome bases, most associated with one basal epidermal cell. **Fig. 32.** Specimen OU32079. Inner abaxial surface, showing a single stoma and undulate anticlinal walls. **Fig. 33.** Specimen OU32078. Abaxial surface, showing two stomata and a trichome base associated with a single epidermal cell. **Fig. 34.** Specimen OU32073. Outer adaxial surface, showing raised outlines marking the positions of epidermal cells and two trichome bases. **Fig. 35.** Specimen OU32078. Adaxial surface, showing numerous trichome bases and undulate anticlinal cell walls.

Acknowledgements

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