

ECOLOGY OF PALEOCENE-EOCENE VEGETATION AT KAKAHU, SOUTH CANTERBURY, NEW ZEALAND

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ABSTRACT

A plant-fossil bearing sequence at Kakahu, south Canterbury, New Zealand, probably extends from the late Paleocene to the Early Eocene (palynological Zones PM3-MH1). One of the leaf macrofossil assemblages previously published from this locality as Paleocene (J38/f58), is here regarded as coming from very close to, and probably just above the Paleocene – Eocene boundary. Palynology indicates there was a major change in vegetation throughout the Kakahu sequence from conifer to angiosperm (possibly Casuarinaceae) dominance, which is similar to elsewhere in New Zealand. In this study a palynological “interzone” is identified that separates these two extremes. It may correspond to rapid vegetation-climate change over the Paleocene–Eocene boundary. Fossil leaf cuticle is of low diversity, but includes locally common Podocarpaceae conifers, Gnetaceae, at least four species of Lauraceae, and a possible Aquifoliaceae. An important conclusion based on the presence of ubiquitous charcoal is that there was significant landscape burning throughout the sequence. This is likely to reflect climatic conditions but also the character of the vegetation, as controlled by soil conditions, may be implicated. It is consistent with studies in the Northern Hemisphere, which also find significant charcoal around the Paleocene–Eocene boundary. Using leaf margin relationships based on Australian rainforests, the mean annual temperature for two previously published assemblages is remarkably cool – around 4–8 °C – although leaf size suggests warmer conditions, perhaps around 12–20 °C.

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INTRODUCTION

One of the major foci of current climate research involves the Paleocene–Eocene Thermal Maximum and the longer-lasting peak of warmth within the Early Eocene. At these times thermo-

philic plant lineages extended far poleward of their current extent, and rainforest of a broadly tropical nature reached its maximum extent (Morley 2000). Most of the research on plant macrofossils for these time periods has been on Northern Hemisphere localities while data from the more ocean-

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dominated Southern Hemisphere are scarce. Two areas where organically preserved plant remains, including leaf cuticle, are located are southeastern Australia and New Zealand. This paper examines the plant fossil record from one region in southern New Zealand.

The New Zealand region rifted away from the Gondwana margin from the Late Cretaceous until the mid Paleocene (Laird 1994; Laird and Bradshaw 2004). Then, for a time in the Paleocene, no plate boundary existed through New Zealand, and it settled into a tectonically quiescent period. With crustal cooling and an absence of major tectonism, the land surface sank, and there was a regional transgression (with higher frequency sea-level changes superimposed). The east coast of the South Island contains a stratigraphic record of transgression across the paleo-east coast from the Late Cretaceous until perhaps as late as the earliest Miocene. The coastal plain which developed (the Taratu Formation, sensu Carter 1988) includes frequent coal and an often abundant plant macrofossil record. The changing vegetation of this landscape is slowly being pieced together. In one of the earliest works on New Zealand plant fossils, Ettingshausen (1887, 1891) documented leaves from the Late Cretaceous of Shag Point. From the same locality, Bose (1975) described the first fossil cuticle from New Zealand. Further Late Cretaceous plant remains were described by Pole (1992, 1995) and Pole and Douglas (1999) from Shag Point and the more southerly locality of Kaitangata. Macrofossils and cuticle from a new Cretaceous-Cenozoic boundary section at Cave Stream have recently been described by Pole and Vajda (2009). A Paleocene macrofossil assemblage from Mount Somers was described by Pole (1998a), and in the Eocene Rozefelds et al. (1992) described *Lygodium* fossils from the Kakahu area. More material from Kakahu was described by Pole (1997). A further Eocene assemblage from Livingstone was described by Pole (1994). The palynology of samples from the Taratu Formation been documented in several publications, including Couper (1953, 1960), McIntyre (1965, 1968), and Raine and Wilson (1988). Pocknall (1990) included discussion of the Taratu Formation in a synthesis of New Zealand's Eocene.

Kakahu lies to the west of Geraldine, a small town in southern Canterbury (Figure 1). It is a mixture of farmland and bush, in which sedimentary outcrop is poor, with the exception of limestone bluffs. The local Palaeozoic-Mesozoic basement includes a tectonic melange including a block of

Carboniferous marble – the first record of the Carboniferous in New Zealand (Jenkins and Jenkins 1971). The basement is directly overlain by Paleogene coal measures, which were mined at several localities in the 19th century. Associated 'pipeclay' deposits are still exploited. The coal measures are overlain by marine sediments, including Oligocene limestone, which forms the steep scarps of the surrounding ridges.

The regional geology was documented by Wellman (1953), who considered that about 120 m of 'coal measures' were present. Along Bush Creek, the strata dip to the east at 45-65° and along Rapuwai Road the strata dip to the south at 12-20°. The lowest marine strata, a band of corals in the bed of Bush Creek, are Bortonian (Middle Eocene) in age.

Raine (1988) briefly described the palynology of a sample of the Kakahu coal measures. Based on key taxa and the scarcity of *Haloragacidites harrisii* (Couper) a Teurian (Paleocene) age was assigned, "for at least part of the sequence." Two leaf fossil assemblages were described by Pole (1997) with 15 taxa in one and 13 in the other. With the exception of some conifers, a Proteaceae (*Lomatia novae-zelandiae*) and some scraps of Lauraceae, these fossils were impressions without cuticle.

At the invitation of one of the local landowners, Ian Morrison, research has continued in the area. The aim of subsequent visits has been to search for new fossil localities, particularly those which may preserve cuticle, and document the fossils ecologically and stratigraphically.

METHODS

This study is mostly based on sediment samples (prefixed with "Kakahu-") of about 300-500 g, although more was collected where macrofossils were obvious. The material which was published by Pole (1997) was collected by G. Mason around 1987-89, and by myself and J.D. Campbell in 1990. I have visited the area in most years since but the two original localities have since been trampled by livestock, weathered, and overgrown. Therefore, in 2003 a mechanical ditch-digger was employed to dig a hole at one of these localities (Wellman's "Clay Pits") to try and relocate the richly fossiliferous horizon. The digger removed mud which had accumulated over the bottom of the old pit and then dug about 2 m into in-situ sediment. The main fossil horizon was not rediscovered. However, scattered plant fossils were found preserved as dark, carbonaceous layers, with some cuticle pre-

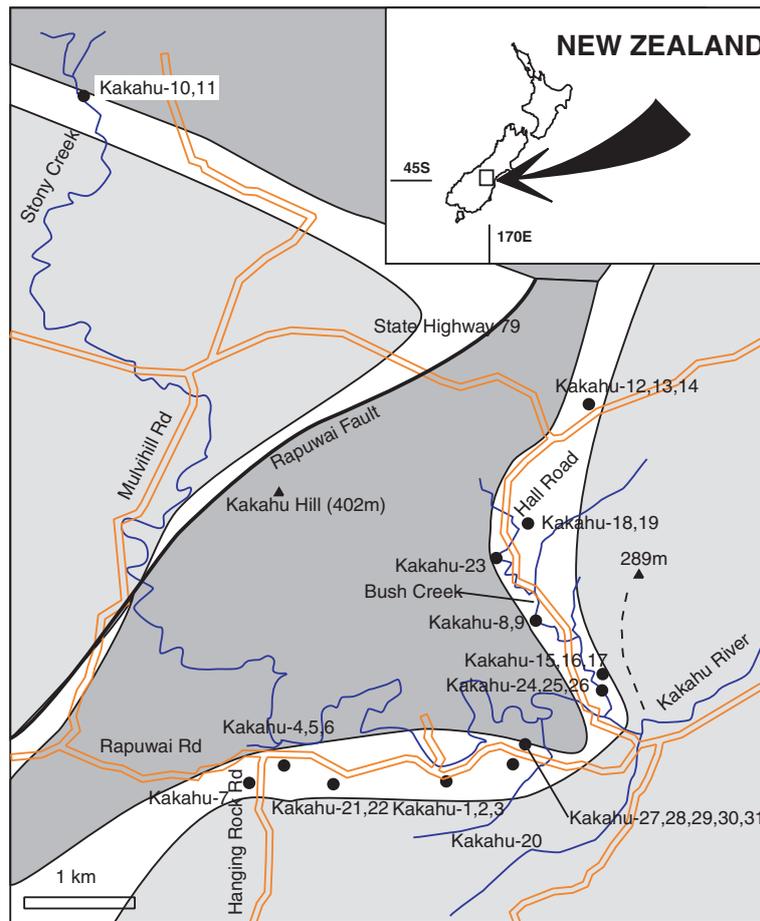


FIGURE 1. Locality map and basic geology (following Wellman 1953). Palaeozoic-Mesozoic basement is shown in dark grey, the coal measures are not toned, and the overlying Cenozoic marine is shaded light grey. Sample locations indicated by black dots.

served. These included dense layers (about 10 mm thick) of conifer leaves. Angiosperm leaf fragments tended to be scattered individually or concentrated on single bedding surfaces. The fossils in this material appear to lie within Wellman's (1953) K3 zone of dark clay. Wellman's K7 zone of 'leaf beds' from the Clay Pits lies about 35 m stratigraphically higher and has not been relocated.

Wellman (1953) published a stratigraphic column for the 'Clay Pits' locality on Rapuwai Road, which covers samples Kakahu-20 and 27-31, and for the roadside 400 m to the west, which includes samples Kakahu 1-3. Wellman's stratigraphy had an advantage of being partially based on numerous boreholes, and in the years since there has been a reduction of outcrop and quarrying, and some of his stratigraphic details are difficult to recognise now. The relative stratigraphic positions of some samples are therefore difficult to determine precisely due to lack of outcrop continuity, but Fig-

ure 2 summarises stratigraphic understanding. From their general location in the valley of Bush Creek, it is clear that samples Kakahu 15, 16, 17 and Kakahu 24, 25, 26 will be among the youngest, lying very close to the coral bed of the overlying marine sequence, while sample Kakahu-23 is likely to be one of the oldest. Sample Kakahu-1 is considered to be from the lignite indicated near the base of Wellman's (1953) column 400 m to the west of the Clay Pits.

In 1990 leaf material was also collected from fallen blocks at the base of a cliff forming Wellman's (1953) locality, "Road-side 20 chains west of Clay Pits." Several hours in 2003 were spent on the end of a rope trying to collect in situ leaf material from the mudstone horizon in the cliff, but this was also unsuccessful. Wellman correlated the leaf beds at this locality with his leaf beds at the Clay Pits.

New macrofossil localities were searched for but with the exception of *Lygodium* fronds and monocot leaves on one bedding surface in the quarry by Hanging Rock Road, no more were located.. Details of these localities are given in Table 1.

To prepare leaf cuticle, samples were broken down into a sludge using hot water and hydrogen peroxide and the resulting material sieved, retaining what did not pass through a 1 mm mesh. The remaining organically preserved plant fossils could be cleaned in hydrofluoric acid, or be reduced to cuticle using a 10% solution of aqueous Chromium Trioxide and stained with Crystal Violet. Cuticle fragments were mounted on microscope slides in Thymol Glycerine-jelly, or mounted on Electron Microscope stubs with double-sided tape and platinum coated. As the affinities of most angiosperm cuticle taxa are not known, and there is no established way of grouping the morphologies hierarchically, they described using a parataxon code, consisting of a string of letters. These are essentially species without genera. For previous use of this system see Pole (2007).

Palynological samples were processed using a standard procedure of hydrofluoric acid, nitric acid, and were mounted on microscope slides in thymol glycerine jelly. Individual pollen grains are located using England Finder coordinates. Charcoal grains >20 µm in length were also counted (Singh et al. 1981; Martin 1996). These were identified as very black, highly reflective, angular fragments, often with well-preserved cellular detail and a homogenous, translucent sheen in TLM. To confirm this identification, a sub-set of samples was boiled in concentrated nitric acid for one hour and washed with 5% ammonium hydroxide solution. Cell-wall structure of some specimens was also observed under SEM and noted to be homogenised.

All material is stored in the Queensland Herbarium (AQ).

RESULTS

The palynological record is summarized in Figure 3, the charcoal record in Figure 4.1 and the cuticle record in Figure 4.2. A diverse flora was present with prominent ferns, Araucariaceae, Podocarpaceae, and angiosperms including a prominent Casuarinaceae and Proteaceae component. Charcoal is almost ubiquitous. Only one of the pollen samples (Kakahu-17) contained no charcoal. In six of the samples (Kakahu 1, 8, 19, 23, 24, 25)

there were more fragments of charcoal than pollen and spores.

Nineteen taxa were recognized based on leaf cuticle (Figure 4.2, 5-14, Appendix 1). There included three forms of conifer (all of which are regarded as Podocarpaceae), one gnetalean, two monocots, five Lauraceae, and a further eight types which are probably dicotyledons.

DISCUSSION

Biostratigraphy

The palynological samples show a striking variation in overall dominance and taxonomic composition. They clearly range from the (at least) mostly Paleocene PM3 to the Early Eocene MH1 assemblage zones of Raine (1984). Zone PM3 is conifer-dominated with *Phyllocladites mawsonii* Cookson ex Couper (1953) usually as the dominant species. The angiosperm *Tricolpites secarius* McIntyre (1965) was common in some samples - its first appearance defines the lower boundary of the PM3 Zone and it extends up into the mid-late Eocene. The uppermost part of Zone PM3 is indicated by the appearance of *Malvacipollis subtilis* Stover in Stover and Partridge (1973) and *Cupanieidites orthotheichus* Cookson and Pike (1954). *Spinizonocolpites prominatus* (McIntyre) Stover and Evans (1973), representing the mangrove palm, *Nypa*) appears at about the Paleocene-Eocene boundary in the North Island (Crouch and Visscher 2003), and thus in latest PM3 time. It is found in younger sediments elsewhere in New Zealand (Raine 1984; Pocknall 1990). The lower boundary of Zone MH1 is "provisionally taken as the lowest level of" *Myricipites harrissi* (Couper) Dutta and Sah (1970) "in abundance" (Raine 1984), and there is a clear increase in this taxon to outright dominance at Kakahu. Zone MH1 is also characterized by diverse Proteaceae, while gymnosperms are not usually common. At Kakahu there are pollen assemblages lying between those clearly belonging to the PM3 and MH1 Zones, which do not clearly belong in either. The samples lack both dominance by conifers and *M. harrissi* and therefore are here provisionally placed into an 'interzone'.

Raine (1984) regarded the Paleocene-Eocene boundary as lying within the PM3 palynological zone. The boundary between his PM3 and the overlying MH1 Zone lies within the New Zealand Waipawan Stage. The Paleocene-Eocene boundary has been placed at the boundary of the Teurian and Waipawan local stages by Hollis (2006) but

TABLE 1. Sample details.

Sample	Grid reference	Locality description
Kakahu-1	J38/560704	Mudstone, c. 50 cm below coal seam, roadside cliffs, west of the clay pits.
Kakahu-2	J38/560704	Coal seam, roadside cliffs, west of the clay pits.
Kakahu-3	J38/560704	Prominent fissile mudstone unit c. 20 m above coal, roadside cliffs, west of the clay pits,
Kakahu-4	J38/544705	Mudstone below coal seam in Kakahu School quarry
Kakahu-5	J38/544705	Mudstone below coal seam in Kakahu School quarry
Kakahu-6	J38/544705	Coal seam in Kakahu School quarry
Kakahu-7	J38/542702	Mudstone in Hanging Rock road quarry
Kakahu-8	J38 568719	Mudstone in channel of Bush Stream, c. 2-3 m stratigraphically above Kakahu-9
Kakahu-9	J38 568719	Mudstone in channel of Bush Stream, c. 2-3 m stratigraphically below Kakahu-9
Kakahu-10	J38 566527	Isolated coal cropping out in Stony Creek
Kakahu-11	J38 566527	Isolated coal cropping out in Stony Creek
Kakahu-12	J38 574739	Coal seam, McMurtrie's Pit
Kakahu-13	J38 574739	Coal seam, McMurtrie's Pit
Kakahu-14	J38 574739	Coal seam, McMurtrie's Pit
Kakahu-15	J38 574713	Coal seam, Hargreave's Pit
Kakahu-16	J38 574713	Coal seam, Hargreave's Pit
Kakahu-17	J38 574713	Coal seam, Hargreave's Pit
Kakahu-18	J38 567728	Coal seam in Park Gate coal mine
Kakahu-19	J38 567728	Coal seam in Park Gate coal mine
Kakahu-20	J38/565706	Mudstone immediately below coal seam, Insulators clay pits
Kakahu-21	J38 548704	Coal seam in O'Leary's Pit
Kakahu-22	J38 548704	Coal seam, O'Leary's Pit
Kakahu-23	J38 565725	Creek by Morrison's house
Kakahu-24	J38/574713	200 m upstream from Fossil Bank
Kakahu-25	J38/574713	200 m upstream from Fossil Bank
Kakahu-26	J38/574713	200 m upstream from Fossil Bank
Kakahu-28	J38/568707	Mudstone in re-excavated clay pit, on south side of road from the Insulators clay pits
Kakahu-29	J38/568707	Mudstone in re-excavated clay pit, on south side of road from the Insulators clay pits
Kakahu-30	J38/568707	Mudstone in re-excavated clay pit, on south side of road from the Insulators clay pits
Kakahu-31	J38/568707	Mudstone in re-excavated clay pit, on south side of road from the Insulators clay pits

has also been regarded as lying within the Waipawan Stage (Edwards 1982) or within the latest Teurian Stage (McGowran et al. 2004). This uncertainty reflects the fact that the Paleocene-Eocene boundary is apparently not prominently marked by palynological changes in New Zealand.

This conclusion was supported by Crouch and Visscher (2003) who documented the palynology across the boundary in marine sediments of the North Island. They found little appreciable taxonomic change, with *Dilwynites granulatus* Harris (1965) dominant throughout, along with spores of

POLE: PALEOCENE-EOCENE OF KAKAHU

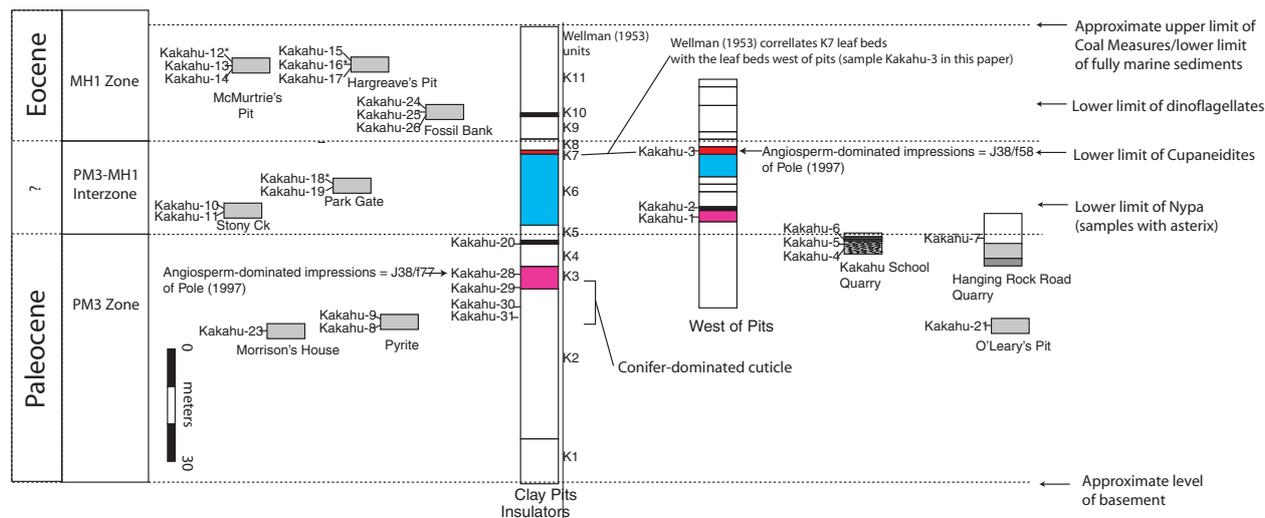


FIGURE 2. Stratigraphic location of samples and zonation. Coal seams are black, dominantly carbonaceous mud sequences are grey, other non-carbonaceous sediments are not toned.

Cyatheaceae, Gleicheniaceae, and bisaccate Podocarpaceae. *Haloragacidites* and *Phyllocladidites mawsonii* were uncommon, sometimes not appearing in a count at all. Proteaceae were also uncommon, forming only 1-2% of some counts. Crouch and Visscher (2003) noted that these results supported conclusions elsewhere in the world, and that the period of greatest vegetation change lies within the Early Eocene, rather than at the Paleocene-Eocene boundary. However, Raine (in Cooper 2004) regarded the lowest occurrence of *Cupaneidites orthotheichus* as approximating the Paleocene/Eocene boundary and used it to define the latest part of Zone PM3 as an Eocene Subzone PM3b. *C. orthotheichus* is present in samples Kakahu-12, 14, and 16, which are clearly zone MH1. It is also present in Kakahu-3 and 19, which fall into the interzone as recognised here, and a concerted search in sample Kakahu-2, about 18 m below Kakahu-3, failed to locate any. It is also absent in all samples within and below the coal seam at the Insulators Pit. It is possible therefore that the Paleocene-Eocene boundary at Kakahu falls within the interzone. It could further be speculated that as the interzone is a relatively transient phase between the PM3 and MH1 Zones, it may represent an equally transient or unstable climate, which was fundamental to the PM3 - MH1 boundary. Thomas et al. (2006) suggested that the Early Eocene Climate Optimum may have been a time of alternating warm and very warm conditions – which might yet hold a key to the disagreements over the

precise location of major vegetation and biodiversity changes with respect to the boundary.

Pocknall (1990) summarised the palynology of the Early-Middle Eocene of New Zealand and discussed other samples, including Waipara River, Otaio Gorge, Waihao River, and Boundary Creek. The nearest quantitative comparison for the Paleocene is provided by the Mt Somers Coal Mine (Raine and Wilson 1988), which was considered to fall entirely within Zone PM3, although the upper part of the sequence was regarded as close to the upper boundary of the zone, and probably within the Waipawan zone. Mt. Somers shows a typical dominance by saccate coniferous pollen, contrasting strongly with the typically less than 10% in the succeeding MH1 Zone. Raine and Wilson (1988) did not record any *Araucariacites australis*, (Cookson 1947) although *Dilwynites granulatus* made a low-abundance appearance in their uppermost samples. Casuarinaceae was about 5% or less, and no samples showed any sign of dominance by *Tricolpites secarius*. The presence or absence of charcoal was not reported.

Throughout New Zealand, the lower boundary of the MH1 appears to be within the Waipawan. In Canterbury, coal measures at Boundary Ck are dominated by Podocarpaceae, Liliaceae, and *Nypa*, and rare *Phyllocladidites* and Casuarinaceae (McIntyre 1965; Raine 1984, Pocknall 1990), are overlain by well-dated Waipawan marine sediments dominated by Casuarinaceae (Couper 1960; Pocknall 1990).

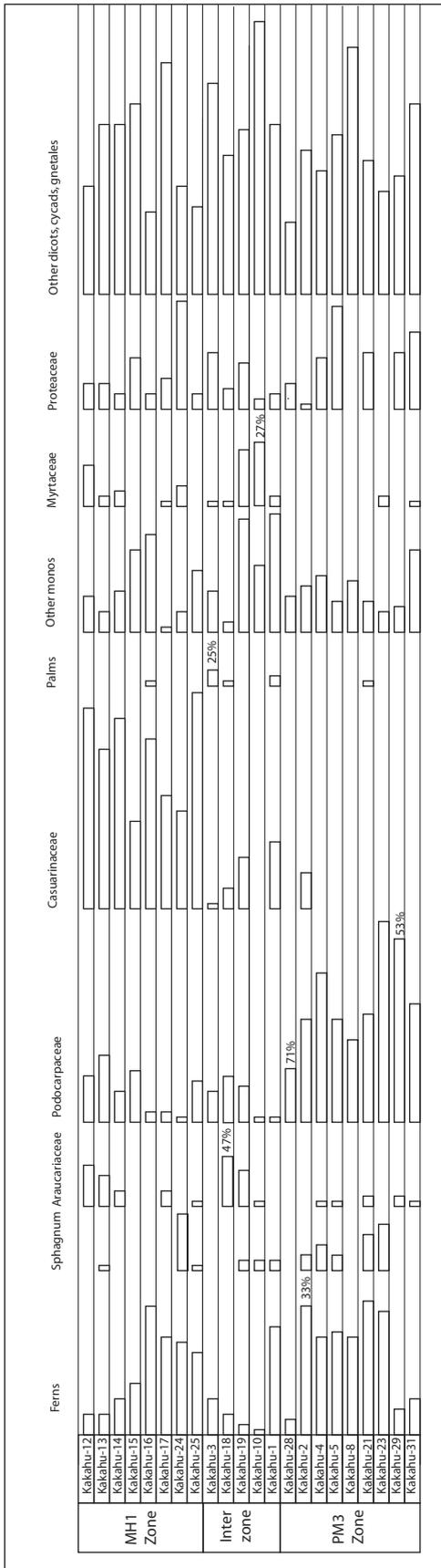


FIGURE 3. Simplified composition of palynological samples (poor preparations are omitted). Raine's (1984) original distinction between a conifer-dominated Zone PM3 and a *Myricipites harrisi*-dominated Zone MH1 is indicated, separated by an 'interzone' in which neither are dominant. Raine's later (in Cooper 2004) distinction of a Subzone PM3b, as conifer-dominated but with *Cupaneidites* present, cannot be indicated on this figure. The lowest occurrence of *Cupaneidites* is in Kakahu-3.

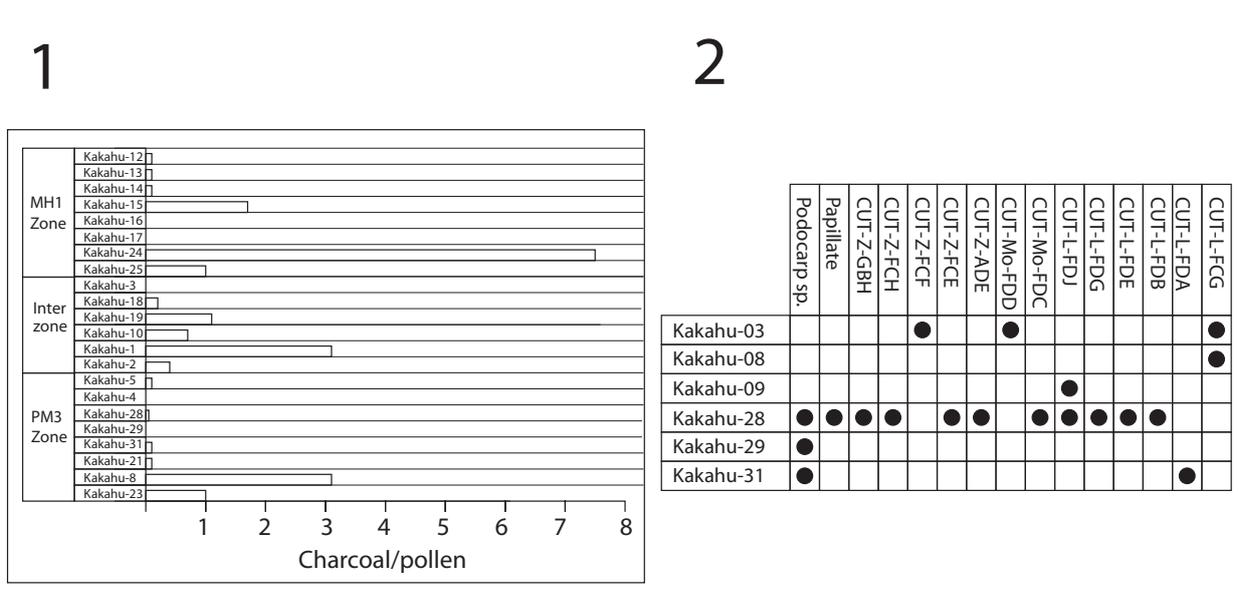


FIGURE 4. (1). Ratio of charcoal fragments to pollen and spores. (2). Distribution of cuticle parataxa by samples.

Dinoflagellate spores are common in the stratigraphically highest samples, consistent with other evidence that deposition was in a near-coastal environment, and that the area was submerged under a regional marine transgression. Sporadic pollen of the palm *Nypa* (*Spinozonocolpites prominatus*) confirms that mangrove vegetation was present. The sedimentological relations of this pollen type along with associated macrofossil material in the Early Eocene of Tasmania (Pole and Macphail 1996) support the interpretation of similar mangrove ecology of the fossils to extant *Nypa*. The pollen is a rare component of those Kakahu samples in which it is found but this is a widespread phenomenon discussed by Frederiksen (1985), who noted that only a few pollen grains may still be indicative of a broad belt of *Nypa* mangroves.

Leaves and Cuticle

Although leaf cuticle was abundant in some samples, it was always low in diversity, or at least overwhelmingly dominated by one type. It showed nothing of the diversity which the leaf impression assemblages of Pole (1997) suggested. It is possible that in some cases weathering has removed all but the most robust cuticles. However, in some samples cuticle is abundant and well-preserved, and the sediment is an organic-rich grey mud with no sign of any strong weathering. This suggests that at least in these cases, the low diversity is genuine. One of these, sample Kakahu-09, consists

entirely of small Lauraceae leaves, and another, Kakahu-28, is overwhelmingly dominated by conifers. This in turn suggests that there may have been a broad ecological/spatial distinction between angiosperm and conifer-dominated vegetation within the floodbasin. There is no evidence that this was related to sedimentary facies, but perhaps is due to water-table level, or successional status. For instance the low diversity may be a function of a “backswamp” habitat – as noted in modern environments (e.g., Frye and Quinn 1979). In the Paleocene of the Clark’s Fork basin of the USA, Hickey (1980) found assemblages from the backswamps to be dominated by conifers and low in diversity, contrasting with the better drained habitats nearer the river channels. However, Wing et al. (1995) in the USA found the diversity difference to be insignificant in the Bighorn Basin of comparable age.

Charcoal

Fragments of charcoal are abundant in most palynological preparations and occasionally are large enough to be seen in the field. They show the homogenized cells walls which are one of the diagnostic characters of charcoal (Jones and Chaloner 1991) (Figure 15.1). Among the relatively uncommon fragments which show structure, the most common morphology is angiosperm with scalariform pitting. Some fragments of perforation plates have more than 20 bars, which is regarded as a uncommon feature and therefore of taxonomic

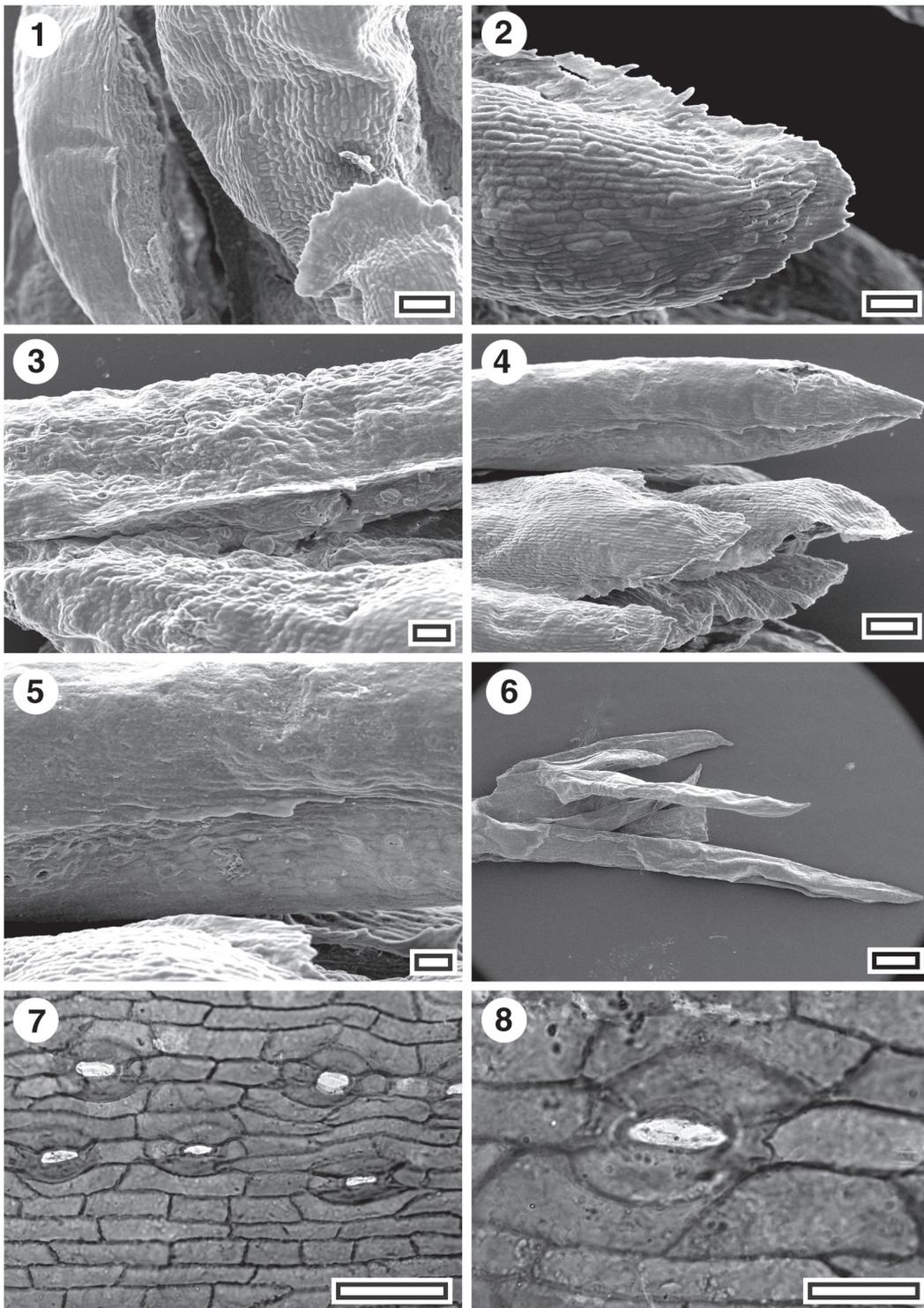


FIGURE 5. Podocarpaceae; (1-6) cf. *Dacrycarpus*, (7-8) *Kakahu Podocarp* sp. A; (1) Outer SEM view (S-1163, scale = 50 μm); (2) Outer SEM view (S-1164, scale = 50 μm); (3) Outer SEM view (S-1164, scale = 50 μm); (4) Outer SEM view (S-1164, scale = 100 μm); (5) Outer SEM view (S-1164, scale = 50 μm); (6) Outer SEM view (S-1165, scale = 0.5 mm); (7) TLM view of stomata complexes (SL5498, scale bar = 50 μm); (8) TLM detail of stomatal complex (SL5498, scale bar = 20 μm).

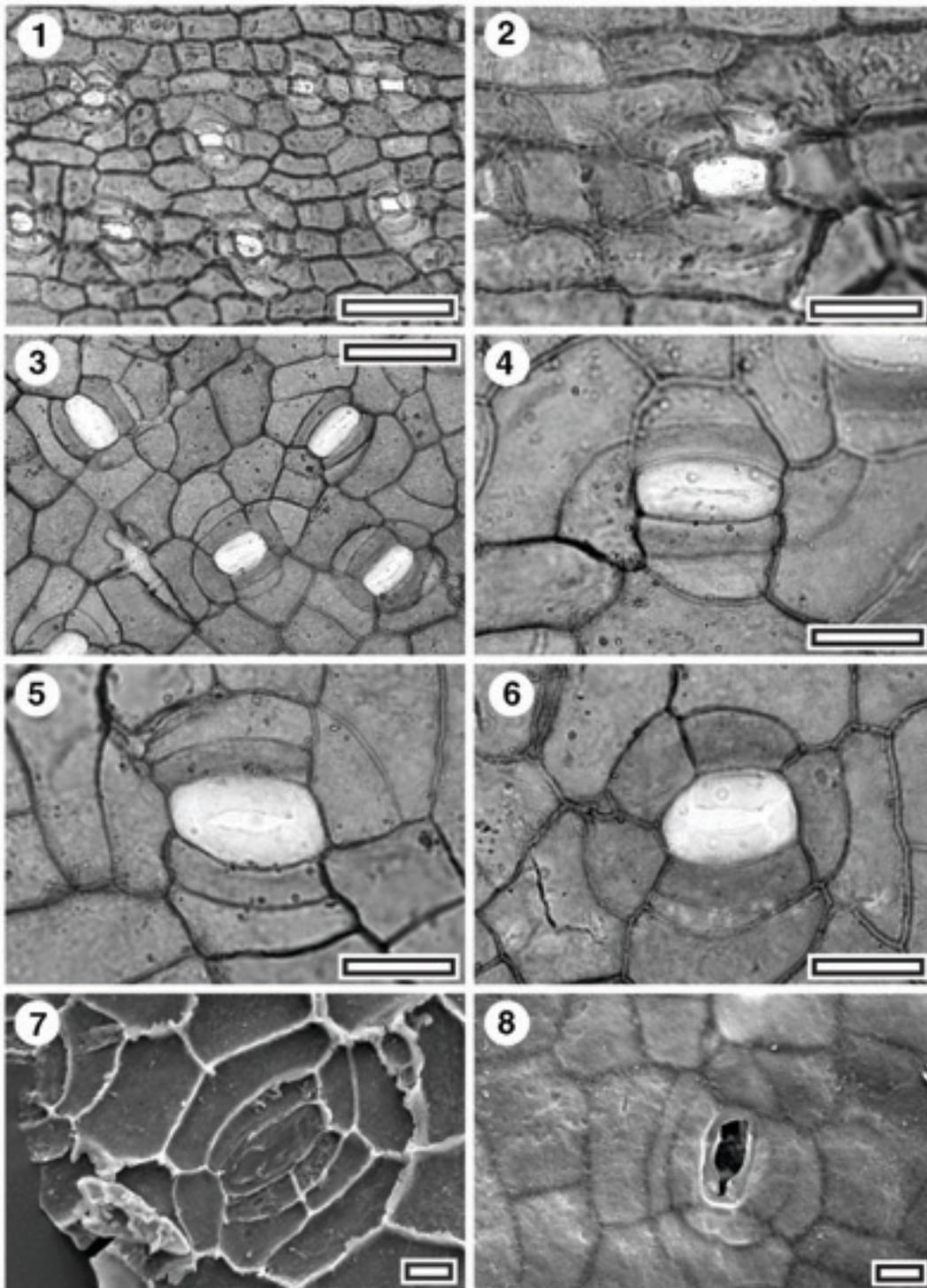


FIGURE 6. Podocarpaceae and CUT-Z-ADE (Gnetale); (1) Kakahu podocarp sp. B, TLM view of stomatal complexes (SL5490, scale bar = 50 μm) (2) Kakahu podocarp sp. B, TLM detail of stomatal complex (SL5490, scale bar = 20 μm) (3) CUT-Z-ADE, TLM view of five stomatal complexes (SL2727, scale bar = 50 μm); (4) CUT-Z-ADE, TLM detail of stomatal complex. Note complete ring of subsidiary cells (SL2727, scale bar = 20 μm); (5) CUT-Z-ADE, TLM detail of stomatal complex. Note undivided contact cell in polar region at lower right (SL2727, scale bar = 20 μm); (6) CUT-Z-ADE, TLM detail of stomatal complex (SL2727, scale bar = 20 μm); (7) CUT-Z-ADE, inner SEM view of stomatal complex (S-1642, scale bar = 10 μm); (8) CUT-Z-ADE, outer SEM view of stomatal complex (S-1642, scale bar = 10 μm).

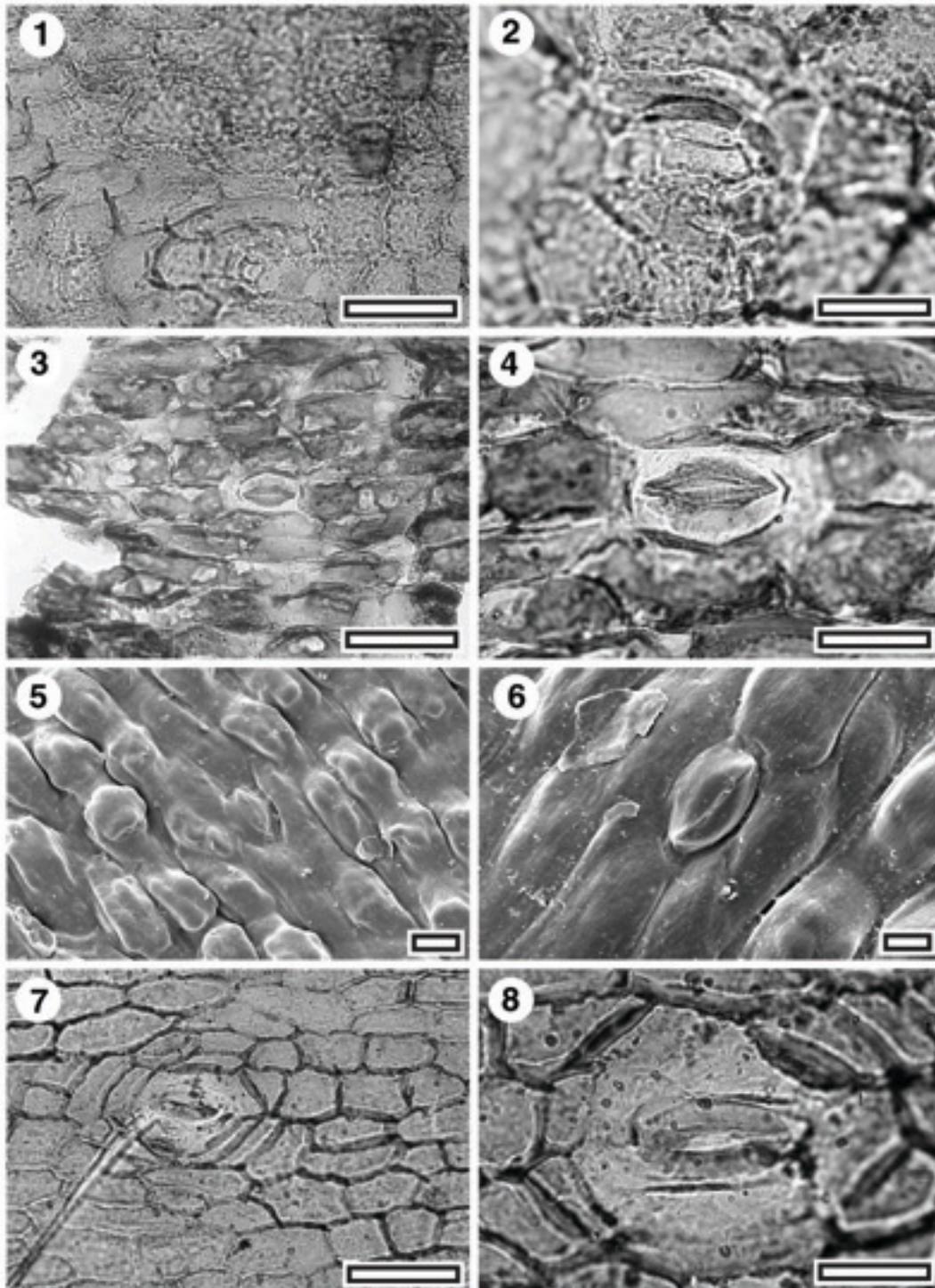


FIGURE 7. Kakahu podocarp sp. B and monocots; (1) Kakahu podocarp sp. B, TLM view showing two trichome bases (upper right) and a stomatal complex (lower centre) (SL2756, scale bar = 50 µm); (2) Kakahu podocarp sp. B, TLM detail of stomatal complex (SL2756, scale bar = 20 µm); (3) CUT-Mo-FDD, TLM view of stomatal complex and surrounding epidermal cells. Note the epidermal cells are broadly raised as papillae (SL2723, scale bar = 50 µm); (4) CUT-Mo-FDD, TLM detail of stomatal complex (SL2723, scale bar = 20 µm); (5) Outer SEM view (S-1428, scale bar = 20 µm); (6) Outer SEM view (S-1428, scale bar = 10 µm); (7) CUT-Mo-GED, TLM view of stomatal complex (SL5515; scale bar = 50 µm); (8) CUT-Mo-GED, TLM detail of stomatal complex (SL5515; scale bar = 20 µm).

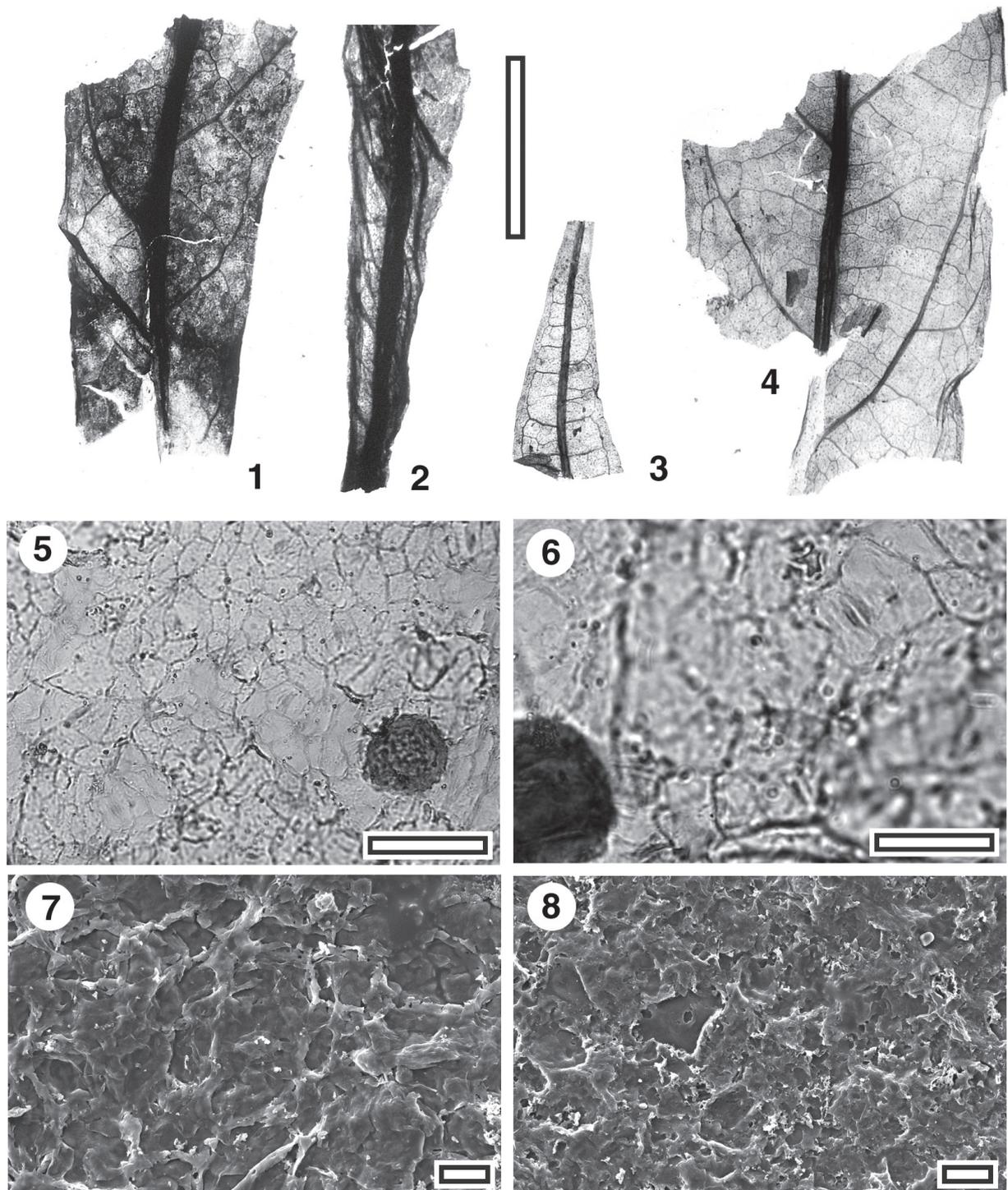


FIGURE 8. Lauraceae leaf fragments and cuticle. 1-5 all to same scale (scale bar = 5 mm); (1) SL2797; (2) SL2793; (3) SL2786; (4) SL2785; (5) CUT-L-FDJ, TLM of stomatal complexes and trichome bases (SL2788, scale bar = 50 μ m); (6) CUT-L-FDJ, TLM of stomatal complexes and trichome bases (SL2788, scale bar = 20 μ m); (7) Inner SEM view with poorly preserved stomatal complexes visible (S-1499, scale = 10 μ m); (8) Outer SEM view showing no obvious stomatal pores (S-1499, scale = 10 μ m).

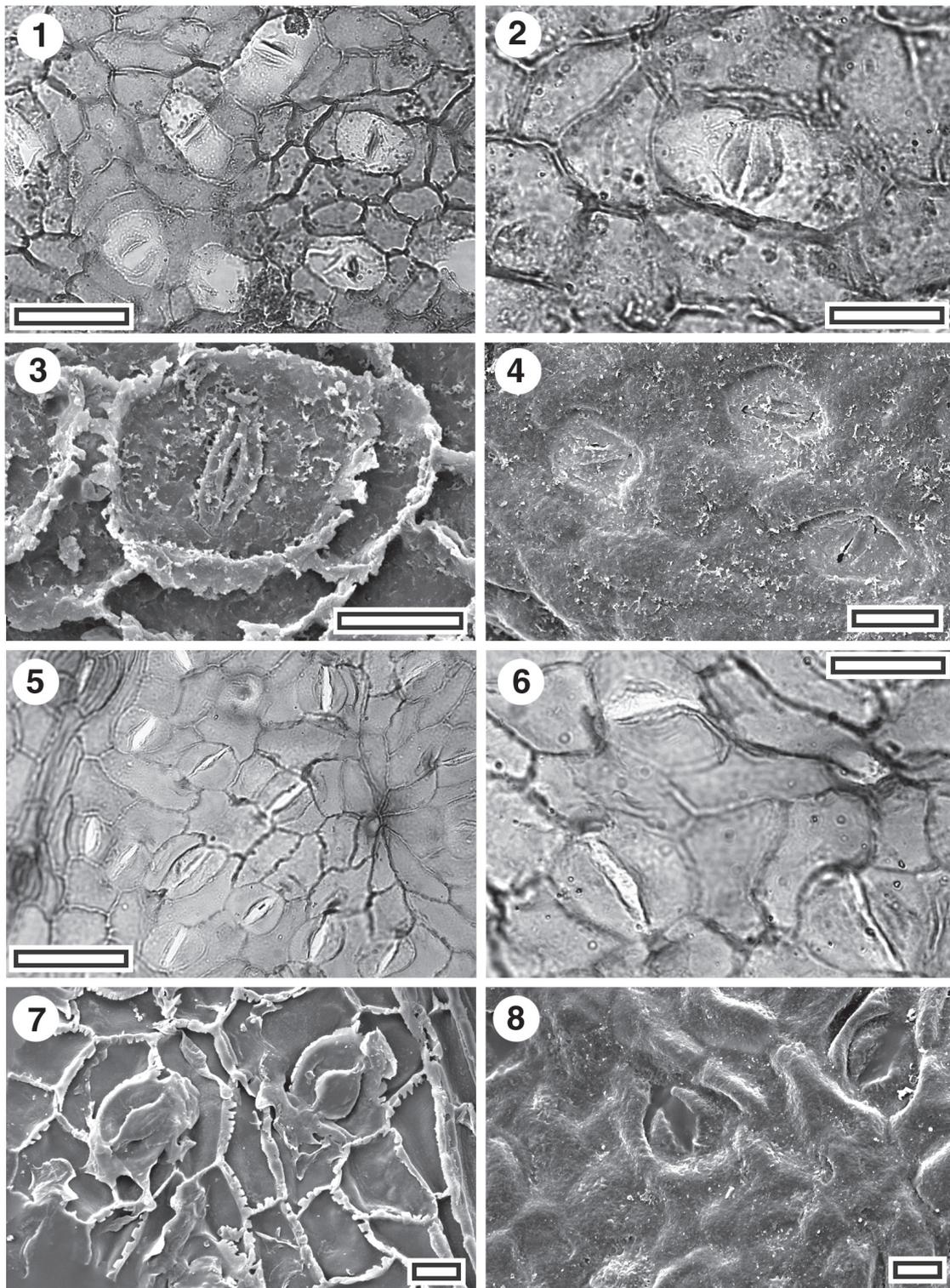


FIGURE 9. Lauraceae; (1) CUT-L-FDJ, TLM view of stomatal complexes and trichome bases (SL1115, scale bar = 50 μm); (2) CUT-L-FDJ, TLM detail of stomatal complex (SL1115, scale bar = 20 μm); (3) CUT-Z-CDG, TLM view showing robust papillae obscuring stomatal pores (SL2743, scale bar = 50 μm); (4) CUT-Z-CDG, TLM detail of stomatal complex (SL2743, scale bar = 20 μm); (5) CUT-L-FDB, TLM view of stomatal complexes and trichome bases, (SL2751, scale bar = 50 μm); (6) CUT-L-FDB, TLM detail of stomatal complex (SL2751, scale bar = 20 μm).

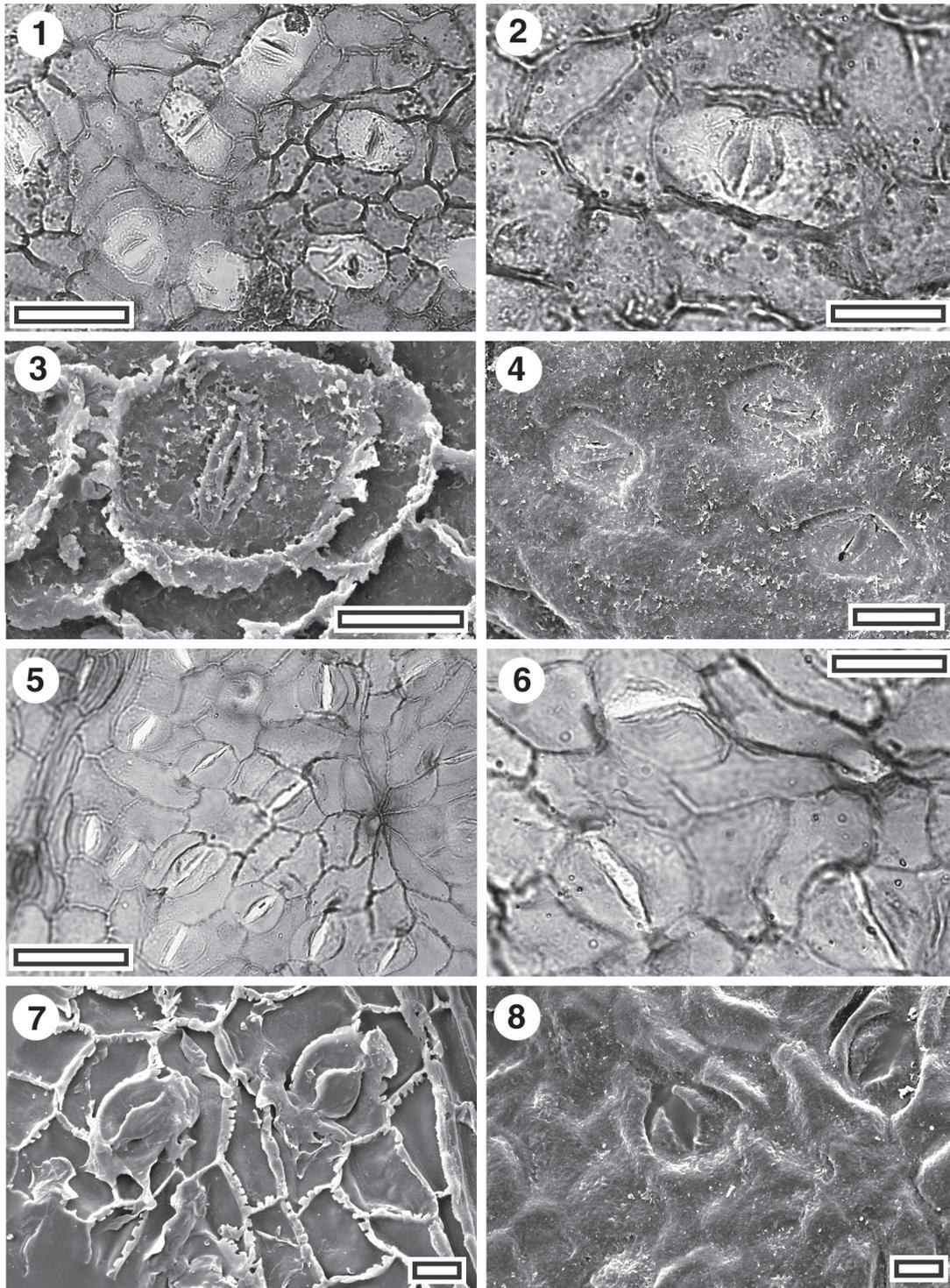


FIGURE 10. Lauraceae; (1) CUT-L-FCG, TLM view of stomatal complexes. Note cuticle over stomatal complexes is much thinner than over epidermal cells (SL2757, scale bar = 50 μm); (2) CUT-L-FCG, TLM detail of stomatal complex (SL2757, scale bar = 20 μm); (3) Inner SEM view of single stomatal complex. Note 'double' cuticular flanges (S-1427, scale bar = 10 μm); (4) Outer SEM view of three stomatal complexes (S-1427, scale bar = 20 μm); (5) CUT-L-FDG, TLM of stomatal complexes and (centre right) a trichome base (SL2772, scale bar = 50 μm); (6) CUT-L-FDG, TLM detail of three stomatal complexes and a trichome base (SL2772, scale bar = 20 μm); (7) Inner SEM view of stomatal complexes (S-1429, scale bar = 10 μm); (8) Outer SEM view of two stomatal complexes (S-1429, scale bar = 10 μm).

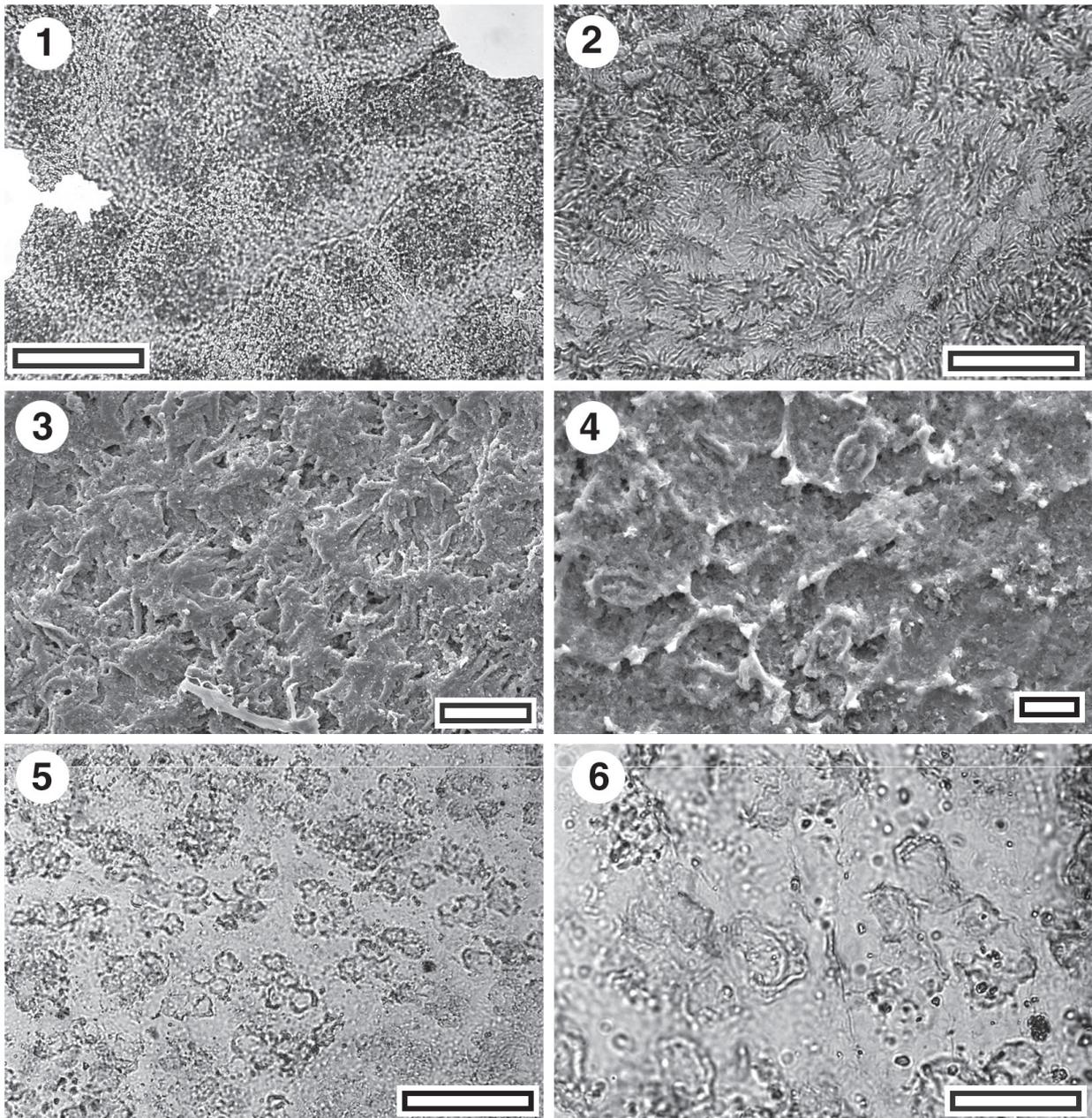


FIGURE 11. CUT-Z-FCF, and GBI; 1) CUT-Z-FCF, TLM view showing patches of stomatal complexes obscured by peltate extensions (SL2758, x10); (2) CUT-Z-FCF, TLM detail of two patches of stomatal complexes (upper left and lower right) with venal cells in between (SL2758, scale bar = 50 μm); (3) Outer SEM view of trichomes (S-1425, scale bar = 20 μm); (4) CUT-Z-FCF, inner SEM view showing stomatal complexes (S-1641, scale bar = 10 μm); (5) CUT-Z-GBI, TLM view showing clusters of papillae probably obscuring stomatal complexes (SL4931, scale bar = 50 μm); (6) CUT-Z-GBI, TLM detail of papillae, possibly obscuring a stomatal complex (SL4931, scale bar = 20 μm).

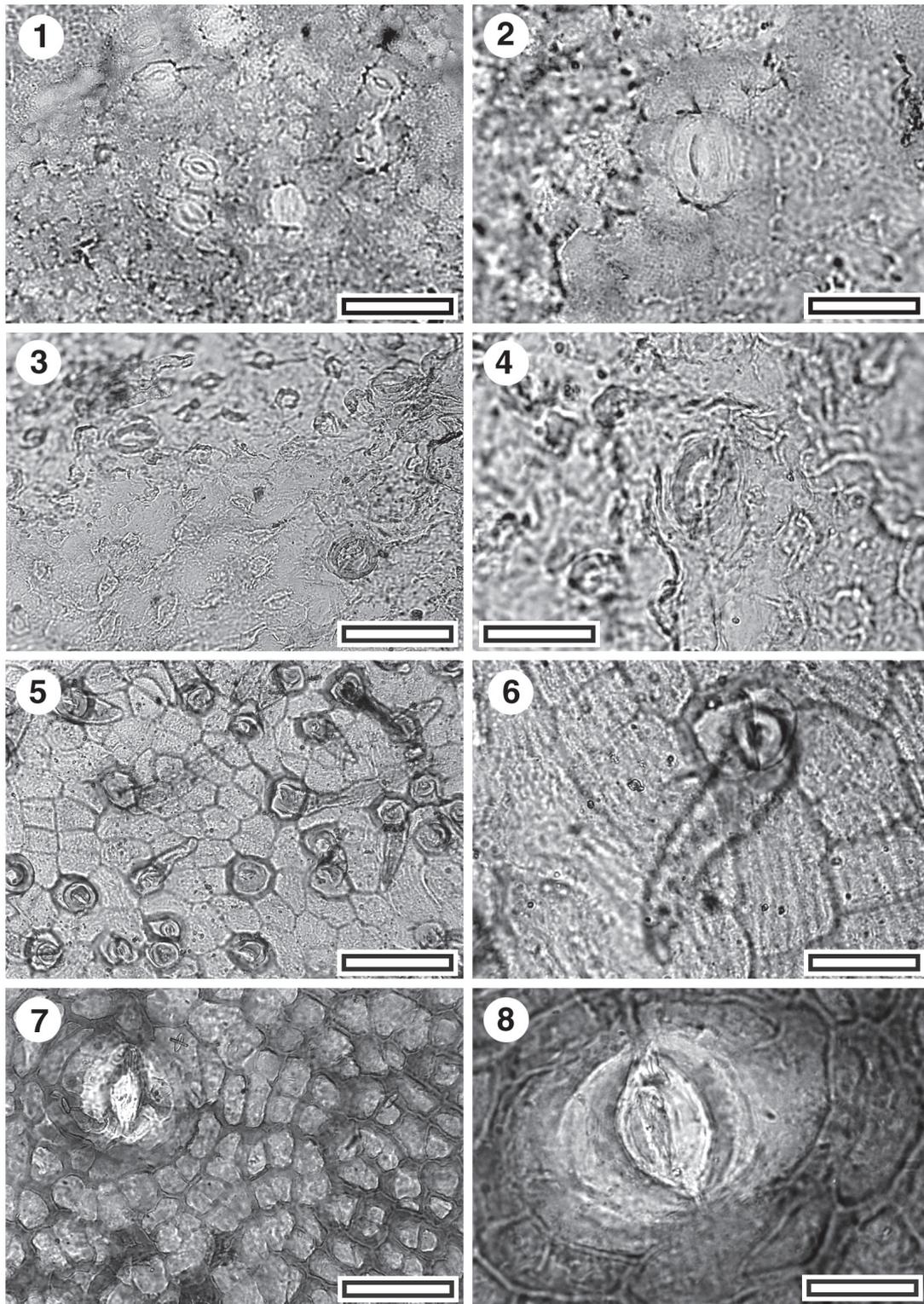


FIGURE 12. CUT-Z-FCH, FCI, and GBG; (1) CUT-Z-FCH, TLM of stomatal complexes (SL1114, scale bar = 50 μm); (2) CUT-Z-FCH, TLM detail of stomatal complex (SL1114, scale bar = 20 μm); (3) CUT-Z-FCI, TLM of stomatal complexes. Note papillate epidermal cells (SL2755, scale bar = 50 μm); (4) CUT-Z-FCI, TLM detail of stomatal complex. Note papillae on surrounding cells (SL2755, scale bar = 20 μm); (5) CUT-Z-GBG, TLM of trichomes (SL4932, scale bar = 50 μm); (6) CUT-Z-GBG, TLM detail of trichome (SL4932, scale bar = 20 μm).

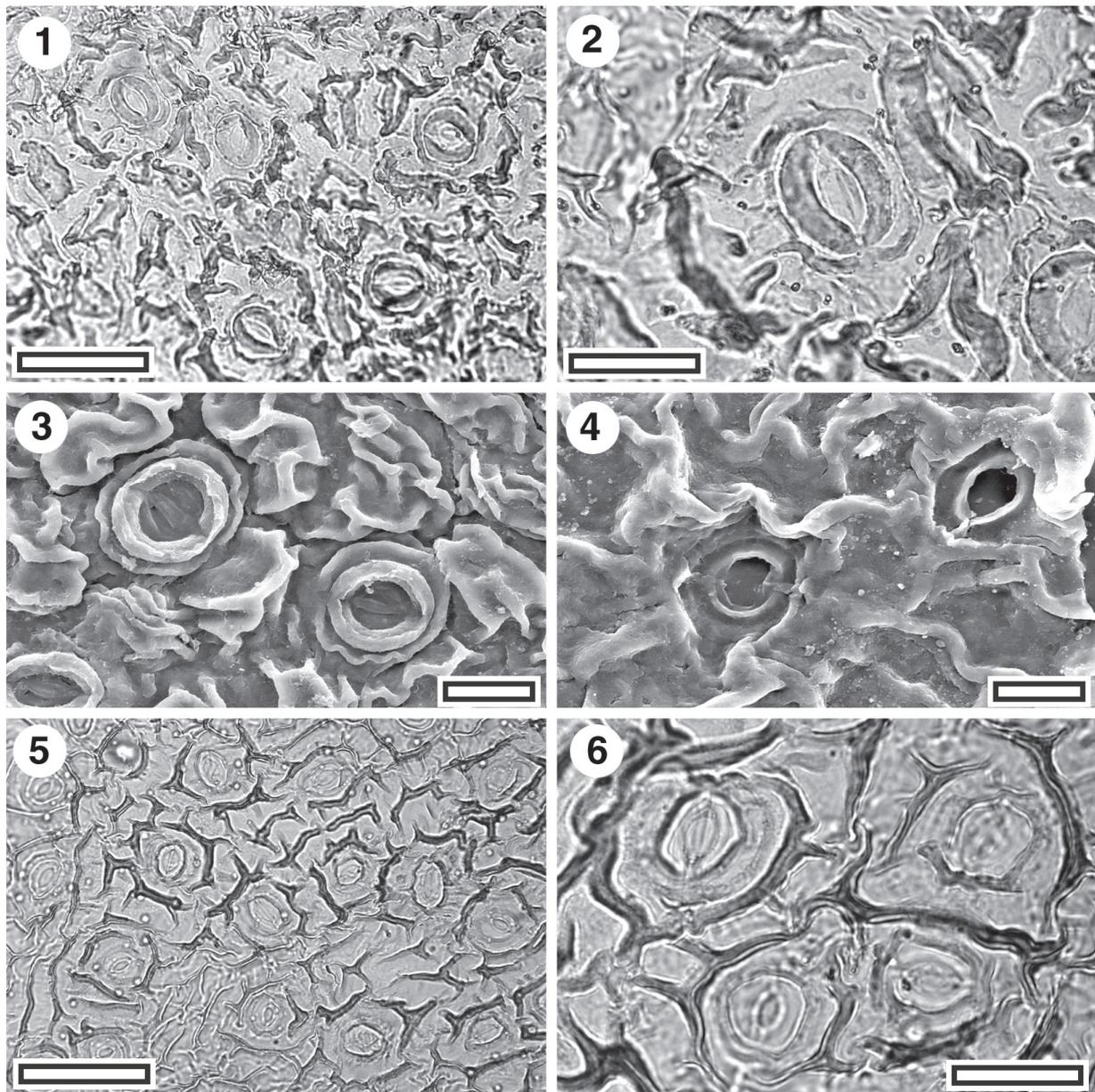


FIGURE 13. CUT-Z-FCE and extant Aquifoliaceae; (1) CUT-Z-FCE, TLM of stomatal complexes. Note cusped ridges approximating cell boundaries (SL1069, scale bar = 50 μm); (2) CUT-Z-FCE, TLM detail of stomatal complex. Note almost complete peristomatal ring (SL1069, scale bar = 20 μm); (3) Outer SEM view of stomatal complexes (S-1161, scale bar = 20 μm); (4) Inner SEM view of stomatal complexes (S-1161, scale bar = 20 μm); (5) extant *Nemopanthus mucronata*, TLM of stomatal complexes. Note cusped ridges approximating cell boundaries (AQ214666, scale bar = 50 μm); (6) extant *N. mucronata*, TLM detail of stomatal complexes (AQ214666, scale bar = 20 μm).

importance (Wheeler and Baas 1998; Carlquist 2001; see McIver 1999 fig. 9 for similar material in the Canadian Paleocene). This morphology is most typical of relatively primitive angiosperms and would be consistent with the Lauraceae, which is so prominent in the cuticle fraction. The range of morphology (Figure 15.2-15.3) within this charcoal

type could reflect the difference between the perforation plate and lateral wall within a single species (e.g., Carlquist 2001; Meylan and Butterfield 1972). Smaller and more scattered pits (Figure 15.4-15.6) may represent cross-field pitting, or other species. Conifer charcoal is uncommon and represented by cells with large, uncompressed, circular, bordered

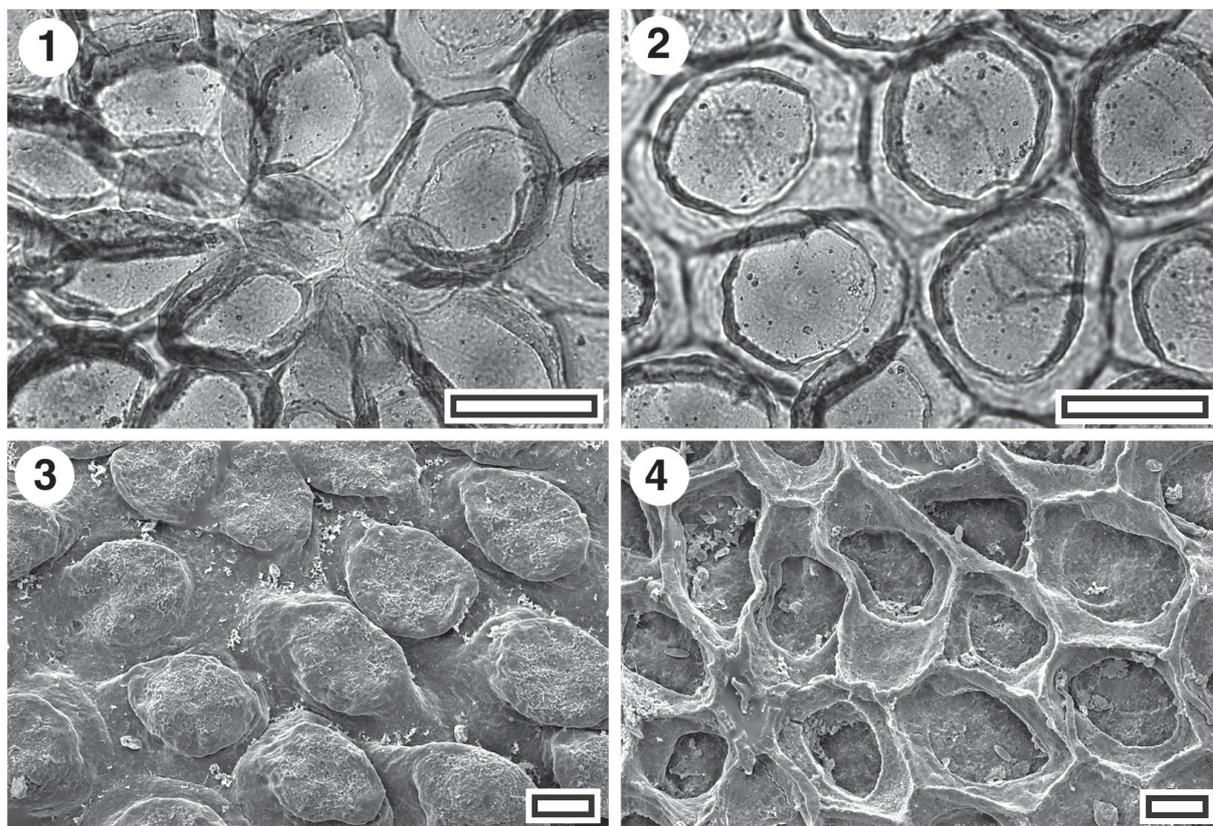


FIGURE 14. CUT-Z-GBH; (1) CUT-Z-GBH, TLM view of papillae possibly obscuring a stomatal complex (SL2759, scale bar = 50 µm); (2) CUT-Z-GBH, TLM view of papillae (SL2759, scale bar = 50 µm); (3) Outer SEM view of papillae (S-1423, scale bar = 20 µm); (4) Inner SEM view of papillae (S-1423, scale bar = 20 µm).

pits, consistent with (but not limited to) Podocarpaceae (Figure 15.7-15.8), and smaller bordered pits which may be cross-field pits.

The abundant presence of charcoal in many of the Kakahu samples was surprising and has ecological and possible climatic implications. Fire in New Zealand has been a relatively unusual event. For instance, charcoal is abundant in the Cretaceous of Horse Range and Kaitangata (Pole, pers. obs.), although it seems to be mainly detrital fragments of a few millimeters dimension, rather than the ubiquitous microscopic size range found at Kakahu. It is clear that fire was an important environmental factor influencing the Kakahu vegetation. Fire then seems to have been absent throughout much of Eocene times (Pole, unpublished data). New Zealand's forests in the Oligocene-early Miocene did not burn, as charcoal is essentially absent, although burning did resume later in the Miocene (Mildenhall 1989), probably near the Middle Miocene boundary (Pole and

Douglas 1998; Pole 2003). New Zealand forests today often have a high gymnosperm component, but they are ever-wet, and although they will burn with anthropogenic intervention, natural fires as a result of lightning strikes, are rare and localized (McGlone 1988).

Where structural elements of the charcoal allow identification it can be seen to be overwhelmingly angiosperm. Most identifiable fragments are angiosperm vessels with many scalariform perforations, which are taxonomically uncommon. Conifer charcoal is much rarer. Thus it appears to have been mainly angiosperm vegetation which was burning. The burning was a feature of the landscape for a considerable period of time as the charcoal extends across at least two palynological zones and the putative interzone. There is no clear pattern to the amounts of charcoal. Sample Kakahu-17, in which no charcoal was recorded, is stratigraphically close to samples Kakahu-15, which has more charcoal than pollen, and 16, in

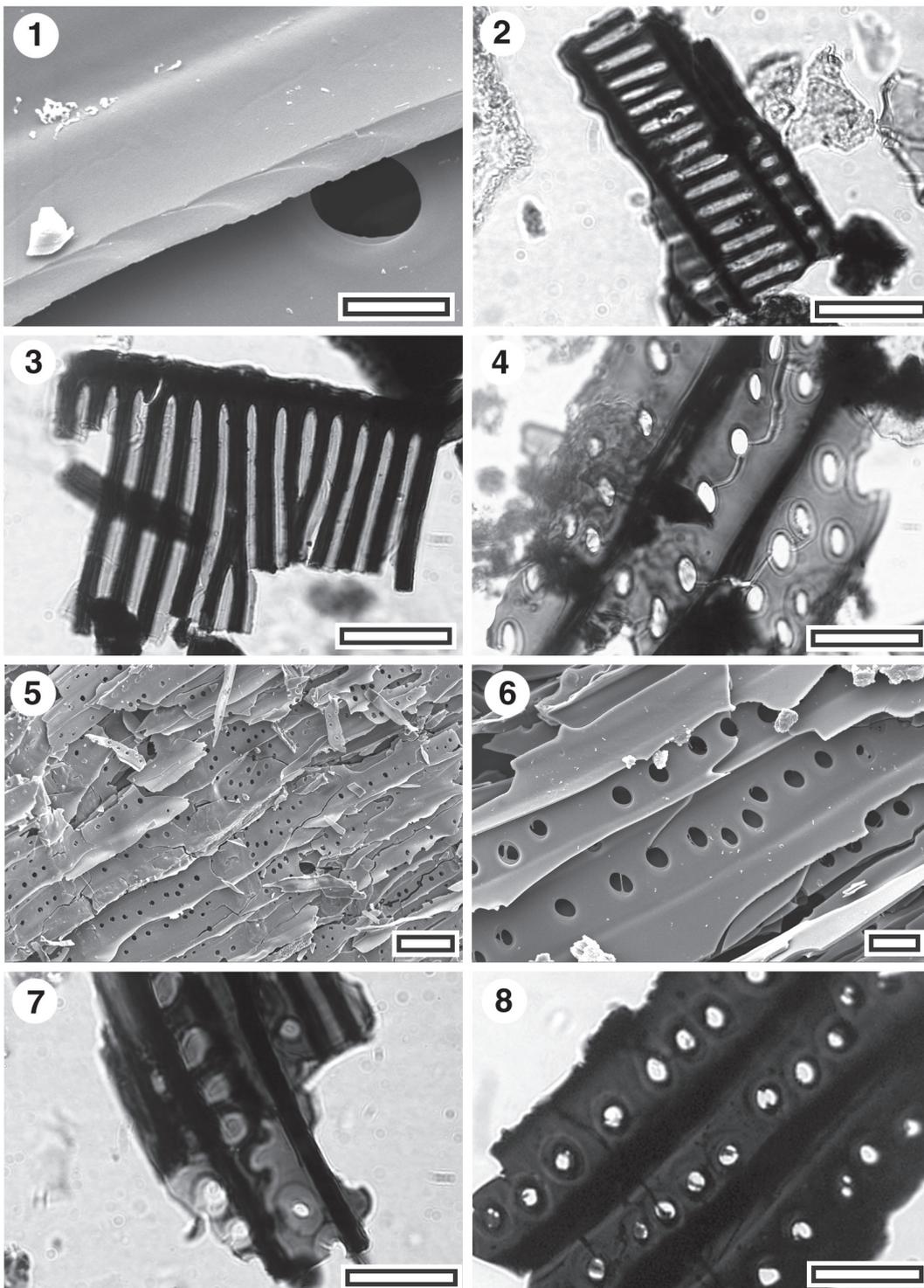


FIGURE 15. Charcoal; (1) SEM detail of homogenised cell walls (S-1596, scale bar = 5 μm); (2) TLM view showing scalariform pitting (P0584), scale bar = 20 μm); (3) TLM view showing scalariform pitting (P0595, N42.3, scale bar = 20 μm); (4) TLM view showing uniseriate and biseriate bordered pits in xylem, (P0612, O32.1, scale bar = 20 μm); (5) SEM of xylem cells. Note unfilled, three-dimensional preservation, (S-1596, scale bar = 50 μm); (6) SEM of xylem cells. Note unfilled, three-dimensional preservation (S-1596, scale bar = 10 μm); (7) TLM view showing uniseriate bordered pits in xylem (P0588, L23.2, scale bar = 20 μm); (8) TLM view showing uniseriate bordered pits in xylem (SL5545, scale bar = 50 μm).

which it is common. Each of the three palynological zones has a sample in which the amounts of charcoal are very high (Kakahu-1, 8, and 24). The diverse, angiosperm-dominated impression assemblages of Kakahu-3, and 28 both have charcoal, although in relatively small amounts, as does the conifer-dominated cuticle assemblage of Kakahu-28. In general, a persistent fire regime appears to have been present, at least for some component of the Kakahu ecosystem. Further study might be able to identify which parts of the landscape were burning. After much debate it is now clear that peat-forming mires (i.e., the precursors of coal) have a long history of fire (Scott 1989, 2000; Scott and Jones 1994). They are inherently flammable and are prone to drying-out. It might be speculated that the Kakahu peat-mires burnt frequently, while the vegetation on the levees and back-swamps was relatively fire-free.

Prominent amounts of charcoal across the P-E boundary have been reported in England by Collinson et al. (2003, 2007), who interpreted it in terms of repeated fires in a flowering plant dominated vegetation. Similar material has been recorded elsewhere, for instance Crodale et al. (2002) reported large amounts of inertinite (fire-induced) in more broadly dated Paleocene coals from far eastern Russia. It is intriguing to think that these fires may have been one of the environmental responses to the events of the Paleocene-Eocene Thermal Maximum. Based on a study of the global carbon and sulfur cycles, Kurtz et al. (2003) have suggested that the prominent negative carbon isotopic excursion near the Paleocene-Eocene Thermal Maximum may result from a "global conflagration," essentially the sustained burning of accumulated Paleocene peat, which may have been triggered by a change to a drier climate. However, neither Collinson et al. (2003, 2007) nor this study found burnt Paleocene peat, but as those authors pointed out, widespread burning of standing vegetation may still be implicated in the changes across the P-E boundary.

The fossil record suggests that New Zealand's vegetation in the Paleogene had a significant component of what would be regarded as 'sclerophyll' in the Australian sense, and probably 'pyrophytic' as well. This may also have encouraged the ignition of fires in an essentially ever-wet climate. It is clear from the charcoal record that both woody gymnosperms and angiosperms were burning. However, burning did cease later in the Cenozoic, when many of these sclerophyll elements were still present.

There are clear peaks of charcoal in the mid-part of the Kakahu sequence, although more samples would be needed to understand if this actually reflected a more fire-ridden landscape at the time. There is no indication of a relationship with overall floristic content. Perhaps more important is the observation that charcoal is present throughout the sequence.

Climate

The Paleocene-Eocene has long been considered to represent an important transition in vegetation, associated with the rise to the peak in global warmth in the Early Eocene. However, the boundary is often not obviously marked and the biotic changes associated with it are mostly gradual. The abrupt, but transient Paleocene-Eocene Thermal Maximum (PETM) or Initial-Eocene Thermal Maximum (IETM, Schmitz et al. 2001) is now regarded as marking the P-E boundary at about 55 Ma (it was earlier thought to lie within the late Paleocene and was then termed the "Late Paleocene Thermal maximum," or LPTM; Zachos et al. 1993). The actual peak of global warmth is thought to have been about 52-53 Ma, about 2-3 Ma into the Eocene (Wing 1987).

The presence of a Paleocene-Eocene boundary section in New Zealand, containing plant fossils, is potentially important in helping to understand what happened over this period. At Kakahu, the foliar physiognomy of the leaf impressions described by Pole (1997) may help quantify the paleoclimate in the latest Paleocene (locality J38/f77) and in the interzone, close to the Paleocene-Eocene boundary (J38/f058). Since that publication, Greenwood et al. (2004) have published leaf margin-mean annual temperature (MAT) regressions based on species inventories for the rainforests of eastern Australia. They suggested that they be used in addition to those of Wolfe (1979), Greenwood (1992), Wing and Greenwood (1993) and Wilf (1997). The use of several equations would have the effect of broadening the range of MAT estimates. On this basis, the leaf assemblage from J38/f058 (12 species, 33% entire-margined) suggests a MAT of 7-9 °C (Greenwood et al. 2004 equation) or 11-12 °C (Wilf 1997; Greenwood 1992; Wolfe 1979; Wing and Greenwood 1993 equations). However, the low number of species it is based upon means the sampling error (Wilf 1997) is in the order of 4 °C. Similarly, the assemblage from J38/f077 (10 species, 30% entire-margined) suggests a MAT of 6-8 °C or 11 °C and a comparable sampling error. The MAT estimates

from both assemblages are not statistically distinct. Both assemblages are well below the 20, or even 30 species generally regarded as necessary for reasonable accuracy. Combined, the two assemblages contain 18 species, with 22-28% entire margins, giving a MAT of 4-8 °C or 8-11 °C and a sampling error nearer to 3 °C. The overall suggestion is thus of cool to mild temperatures (1-15 °C). Despite this estimate being so broad, it is still distinctly cooler than the 20-25 °C estimated for the Late Paleocene-Early Eocene by Hornibrook (1992).

The average leaf length is approximately 76 ±5 mm, which is close to the boundary between the microphyll and notophyll leaf size classes (Webb 1959). According to both Greenwood (1992) and Carpenter et al.'s (1994) data for eastern Australian rainforest leaf litter, this correlates with mean annual temperature of about 17 °C (although with a broad range of accuracy of around 12-20 °C). Thus there is overlap with the estimates from leaf margin proportions, but it also suggests caution. Leaf litter size may be suggesting warmer temperatures than inventory-based leaf margin data.

There are no clear features which allow identification of the paleosols in the manner of Retallack (2001) (the soils may be too immature), and the chemical and microscopic features which Retallack (1997) indicated had become necessary to classify paleosols into the current US Soil taxonomy are beyond the scope of this project. However, the grey muds in the lower part of the section (including samples Kakahu-08 and Kakahu-28) are best interpreted as gleyed, reducing, anoxic soils of the poorly-drained backswamps. The coals are the relatively raised peats of the interfluvial areas. The fissile mudstones with the leaf impression assemblages of Pole (1997) are associated with fluvial channels and are considered to preserve vegetation growing on the relatively richest soils of the region situated on the levees. This is unlikely to be such an extremely poor situation that would significantly alter the foliar physiognomy, such as reducing leaf size. In one of the more profound conclusions for paleobotany Burnham (1994) found that the proportion of a species leaf area in litter is proportional to its trunk basal area in the source forest. With a total of 18 leaf taxa distinguished from a collection of about 45 specimens, the levee vegetation of Pole (1997) was certainly diverse.

Further estimates of climate are suggested by key taxa. Extant *Nypa* is restricted to truly tropical locations, and the presence of *Nypa* in the New

Zealand fossil record is generally taken to indicate conditions of peak warmth in the overall Cenozoic succession. However, temperatures were clearly less than truly tropical. The record of *Nypa* from Tasmania (Pole and Macphail 1996) emphasises that the *Spinizonocolpites prominatus* (McIntyre 1965) Stover and Evans (1973) pollen morphology, in addition to the living species, covers at least one extinct species, *Nypa australis*, and that this had a cooler, temperature tolerance to the extant species, *Nypa fruticans* (Pole and Macphail 1996).

Despite the evidence for burning, rainfall was evidently high at times, based on the presence of coal. A key taxon also supporting this is the pollen type *Phylocladidites mawsonii*, which was often important in the early Cenozoic of the Australasian region. Based on its highly distinctive morphology, it has been linked to the extant conifer *Lagarostrobos* (Playford and Dettmann 1979), which is currently restricted to the wettest habitats of Tasmania. However, increasing macrofossil data are suggesting that this pollen type may have been produced by other, extinct genera (Pole 1998a). Nevertheless, in Australia, *P. mawsonii* contracts southwards over the Cenozoic as the bulk of the country dried out (Kershaw 1988). So, whatever its botanical affinities, it still appears to be an indicator of cool, very wet conditions. The appearance of *Cupaneidites* is usually taken as the onset of relatively warm conditions in New Zealand. Muller and Leenhouts (1976) regard this pollen type as representing their pollen group B of tribe Cupanieae in the Sapindaceae, including genera currently extending from the tropics to subtropics in Australia.

It is possible that climate thresholds, which resulted in major vegetation change, occurred at different places in different latitudes. In New Zealand, the switch to a *Haloragacidites harrisii*-dominated pollen-rain is dramatic (Raine 1984; Pocknall 1990). In Australia expansion of *H. harrisii* can be detected, but it is no-where near as obvious, at least not enough for it to warrant being used there as a palynological zone boundary (Harris 1965). In North America and Europe there was a general shift to warmer types of vegetation, and deciduous vegetation was restricted to >70° N, or to the continental interiors. In other places deciduous was replaced by evergreen. Recent work by Wing et al. (1995) focusing on the Paleocene-Eocene boundary has highlighted some interesting phenomena, for instance that mammal diversity increased, while plant diversity dropped. They argued that although global climate warmed, in theory promoting higher

diversity, because of the rate of climate change, the initial result may have been a drop in biodiversity.

In New Zealand the shift from conifer-dominated vegetation to one dominated by angiosperms, and specifically by Casuarinaceae, probably reflects warming and drying into the Early Eocene. This is supported by the large amounts of charcoal, which indicate that fire was a major component of the ecology. The initial conifer-dominated vegetation was probably a closed forest, but the nature of what followed it is much less certain. If the pollen species *Halorgacidies harrissii* does represent Casuarinaceae, then its dominance in Zone MH1 suggests dry woodland. This is unlikely, given that elsewhere in New Zealand it dominates in samples from coal and thus grew in a wet climate. The Casuarinaceae is predominantly a family of dry vegetation, but it does include *Gymnostoma*, which is sometimes referred to as the 'rainforest casuarina'. *Gymnostoma* is the most primitive genus (Johnson and Wilson 1989) and both Australian, New Zealand and South American macrofossil evidence supports that at least some of the *Halorgacidies harrissii* pollen was produced by this genus (the pollen produced by the different genera is practically indistinguishable). However, it typically grows as a small component of rainforest. The dominance of this pollen type throughout New Zealand for a period of several million years suggests that the parent plant was more than a minor component. In recent pollen assemblages in Australia today, those that are dominated by Casuarinaceae pollen, were deposited under Casuarinaceae-dominated vegetation. This raises a question, does this pollen assemblage represent a unique vegetation dominated by *Gymnostoma*, or was the pollen produced by Casuarinaceae at all? While the affinities of *Halorgacidies harrissii* are generally accepted as Casuarinaceae, other possibilities exist, such as *Canacomyrca*, of the Myricaceae (listed as pollen from the New Zealand Cenozoic by Mildenhall 1980) which, like the Casuarinaceae, is an essentially nitrogen-fixing pioneer. Some fossil leaves from Kakahu (*Dryandroides comptoniaefolia* Ettingshausen 1887 = Parataxon TARA-34 Pole 1997) are remarkably similar to extant *Comptonia peregrina* (L.) Coulter (1894), also of the Myricaceae, and it is unfortunate that no cuticle has been obtained from the fossils. That the fossils have such a delicate cuticle is suggestive that they are not Proteaceae (see further discussion of this taxon in Pole 1998b), in which it is typically robust.

A palynological sequence of comparable age to Kakahu is present in South Australia (Harris 1965). It also shows a shift away from conifer dominance and a rise in Casuarinaceae, which is thought to correlate with that in New Zealand (Raine 1984). However, there are significant differences as Casuarinaceae never reaches the overwhelmingly dominant amounts that it does all over New Zealand, and the conifers still remain important. This suggests that South Australia remained wetter than New Zealand, possibly because of its more southerly situation. In Tasmania the Paleocene-Eocene boundary is not known, but Early Eocene sediments at Regatta Point preserve a conifer-dominant vegetation, which grew inland of a belt of *Nypa*-mangroves (Pole and Macphail 1996; Pole 2007). Thus temperatures were warm, but the abundance and diversity of conifers suggests it was still very wet, and there is no sign of charcoal.

CONCLUSIONS

Sediments exposed at Kakahu were probably deposited from the Paleocene into the Early Eocene. The boundary itself is probably represented by an "interzone" reflecting a transient vegetation and climate. Organically-preserved plant macrofossils indicate that low diversity communities of conifers and angiosperms existed, although localized leaf-impression assemblages suggest some higher diversity communities may also have been present. Paleoclimate details are difficult to interpret as more comparative information is needed on the physiognomy of extant vegetation. However, leaf margin analysis suggests temperate conditions, much cooler conditions than subtropical temperatures suggested by leaf size. An important conclusion of this work is that fire seems to have been an integral part of much of the environment for an extended period of time.

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APPENDIX

Taxonomy of cuticle fragments

Podocarpaceae
cf. *Dacrycarpus*
Figure 5.1-5.6

Reference specimen and locality: SL5498, Kakahu-28.

Referred specimens and occurrence: SL2589, Kakahu-29; SL5509, Kakahu-30; SL5511, Kakahu-30; SL2744, Kakahu-31; SL5521, Kakahu-33.

Description: Loosely imbricate, awl-like leaves up to about 2.5 mm long, 0.25- 0.50 mm in diameter, rounded in cross section, or perhaps also with some bilateral or bifacial flattening, often with a distinct frill of ctenoidally oriented cells along the junction of the adaxial and abaxial surface. Stomatal complexes in four stomatal zones, longitudinally oriented, paratetracytic, elongate. Epidermal cell walls elongate, smooth, straight-walled, unbuttressed, often with oblique end-walls, with periclinal walls often bulging slightly outwards, sometimes markedly so on the adaxial surface.

Notes: This conifer has characters which have been used to place some fossils in *Dacrycarpus* (e.g., Wells and Hill 1989) These include loosely imbricate, awl-like leaves, which have four zones of longitudinally oriented, elongate stomatal complexes, and unbuttressed epidermal cell walls. However, the absence of the distinctive tri-saccate pollen type from both Mt Somers and from Kakahu, despite the abundance of the macrofossils, strongly suggests those leaf morphological characters may be generalised and have probably be present in more than one genus. The bulging epidermal cells periclinal walls are not known from any certain *Dacrycarpus*. For now, the generic affinities of this Kakahu conifer are left open.

Kakahu Podocarp sp. A
Figure 5.7-5.8

Reference specimen and locality: SL5490, Kakahu-28.

Notes: A single fragment of podocarp cuticle is distinguished from cf. *Dacrycarpus* by its rounder stomatal complexes, in which the lateral subsidiary cells are more frequently divided in two.

Kakahu Podocarp sp. B
Figure 6.1-6.2

Reference specimen and locality: SL2756, Kakahu-28.

Notes: A single fragment of cuticle with typically Podocarpaceae stomatal morphology also contains the bases of persistent trichomes. However, the rounded and narrowly paratetracytic stomatal morphology is very distinct from *Acmopyle*, the only Cenozoic - Recent conifer currently known to have trichomes (Hill and Carpenter 1991). The fossil probably represents an undescribed genus.

Gnetalaceae Lindley 1834
CUT-Z-ADE
Figure 6.3-6.8

Local reference specimen and locality: SL2727, Kakahu-03.

Referred specimens and occurrence: SL1089, Kakahu-28.

Notes: This cuticle taxon is widely distributed, being known from the Miocene of Central Otago (Pole 2008), and an extremely similar form from the Early Eocene of Tasmania (Pole 2007). Its distinctively rectangular-shaped guard cells suggest it is probably an extinct genus of the Gnetales. The pollen species *Ephedrapites notensis*, present in the Kakahu assemblages, is further evidence that the Gnetales were present in the vegetation. The pollen and cuticle type may have been produced by the same plants.

Monocots
CUT-Mo-FDD
Figure 7.3-7.4

Reference specimen and locality: SL2723, Kakahu-03.

Description: Stomatal complexes aligned to long axis of leaf, paratetracytic, scattered. Outer stomatal ledge prominent, narrow elliptical, pore narrow. Epidermal cells with straight-walls, not buttressed, with periclinal walls raised as broad, often compound papilla. Glabrous.

CUT-Mo-GED
Figure 7.7-7.8

Reference specimen and locality: SL5515, Kakahu-31.

Description: Stomatal complexes aligned to long axis of leaf, scattered, probably basically paratetracytic but modified by radial divisions to subsidiary cells and by tangential divisions to sometimes give two rings of narrow cells. Outer stomatal ledge prominent, blunt-ended, pore narrow. Epidermal cells with straight-walls, not buttressed, not papillate Glabrous.

Lauraceae
Leaves
Figure 8

Leaves are all fragmentary, but all narrowly lanceolate, microphyllous, about 5-10 mm wide and perhaps reaching 100 mm long, with an acute apex, acute base, and entire margin. The midrib is prominent and the lateral veins form several loops, and the finest venation forms a tight mesh.

CUT-L-FDJ
Figure 9

Reference specimen and locality: SL2788, Kakahu-09.

Referred specimens and occurrence: SL2763, Kakahu-28; SL5507, Kakahu-30; SL5512, Kakahu-31.

Description: Stomatal distribution hypostomatic. Stomatal complexes in clear areoles between veins; isolated; randomly oriented; paracytic; outline irregular, typically with flat polar regions and curved sides; stomatal size range unimodal with a small range; shape and size highly irregular; not distinct in thickness from normal epidermal cells; unornamented. Guard cell overarched by subsidiary cells; cuticular scales narrow; very small. Epidermal cell flanges clearly visible using TLM. Normal epidermal cells isodiametric; cells over major veins have clear anticlinal walls, those over fine veins have indistinct walls; walls wavy; unbuttressed; with scars of trichome bases; unornamented. Trichomes common; scattered over venal and non-venal regions but slightly more common over veins; deciduous (and therefore trichome type unknown); inserted between epidermal cells; diameter much smaller than a normal epidermal cell. Epidermal cells around trichome base (5-6) modified only slightly to form a thickened poral rim. Non stomatal surface epidermal cells isodiametric; polygonal; cells over major veins distinguished. Trichomes present and sparse (same morphology as stomatal surface).

CUT-L-FCG
Figure 10.1-10.4

Reference specimen and locality: SL2757, Kakahu-03.

Referred specimens and occurrence: SL2581, Kakahu-08; SL2722, Kq-A1; SL5536, Kakahu-09.

Description: Stomatal complexes evenly spread, isolated; randomly oriented; paracytic; outline typically broader than long; size range unimodal (but broad); cuticle thinner than over normal epidermal

cells; unornamented. Guard cells overarched by subsidiary cells; cuticular scales narrow; very small. Epidermal cell flanges clearly visible using TLM. Normal epidermal cells isodiametric, cells over major veins distinguished as 'venal' (elongated), walls straight, unbuttressed (or possibly slightly buttressed); with scars of trichome bases; unornamented. Trichomes sparse; scattered over venal and non-venal regions but slightly more common over veins; deciduous (and therefore trichome type unknown); inserted between epidermal cells; diameter similar in size to a normal epidermal cell; cells around trichome base (4-5) modified with thickened poral rim.

CUT-L-CDG
Figure 9.3-9.4

Reference specimen and locality: SL4845, Cave-30 (Pole and Vajda 2009).

Local reference specimen and locality: SL2743, Kakahu-31.

Notes: A single cuticle fragment is identified as a morphology previously described from earliest Palaeocene sediments at Cave Stream (Pole and Vajda 2009). The cuticle has epidermal cells with single large, thick, slightly angular papillae, which are discrete, but almost as large as the epidermal cell outline. The stomata; complexes have distinctive thickenings.

CUT-L-FDB
Figure 9.5-9.6

Reference specimen and locality: SL2751, Kakahu-33.

Description: Stomatal complexes in clear areoles between veins; isolated; randomly oriented; paracytic; outline unclear, cuticle thinner than over normal epidermal cells (usually broken); unornamented. Guard cell overarched by subsidiary cells; cuticular scales narrow. Epidermal cell walls curved, unbuttressed; with scars of trichome bases; unornamented. Trichomes attachment scars common; scattered over venal and non-venal regions but slightly more common over veins.

CUT-L-FDG
Figure 10.5-10.8

Reference specimen and locality: SL2772, Kakahu-28.

Referred specimens and occurrence: SL5537, Kakahu-09; SL5518, Kakahu-33.

Description: Stomatal complexes in clear areoles between veins; isolated; randomly oriented; paracytic; outline irregular, typically with flat polar

regions and curved sides; stomatal size range unimodal with a small range; not distinct in thickness from normal epidermal cells; unornamented. Guard cell overarched by subsidiary cells; cuticular scales narrow; very small. Epidermal cell flanges clearly visible using TLM. Normal epidermal cells highly variable from isodiametric to elongate; cells over major veins distinguished as 'venal' (elongated); walls wavy; unbuttressed; with scars of trichome bases; unornamented. Trichomes common; scattered over venal and non-venal regions but slightly more common over veins; deciduous (and therefore trichome type unknown); inserted between epidermal cells; diameter much smaller than a normal epidermal cell. Epidermal cells around trichome base (5-8) modified with thickened poral rim and radial walls.

CUT-Z-FCF
Figure 11.1-11.4

Reference specimen and locality: SL2758, Kakahu-03.

Referred specimens and occurrence: SL1085, J38/f58.

Description: Under TLM all cell outlines are obscured by ridged, peltate extensions of the epidermal cells. Stomatal complexes grouped into areoles, clearly distinguished as patches of thicker (darker-staining) cuticle. Normal stomata overarched almost completely by peltate extensions from about five surrounding cells, except for a few 'giant stomatal complexes'. No subsidiary cells are distinguished. Glabrous.

CUT-Z-GBI
Figure 11.5-11.6

Reference specimen and locality: SL4931, Kakahu-31.

Description: Stomatal complexes difficult to distinguish under TLM (cuticle very thin). Epidermal cell walls not clearly visible under TLM, but papillate with irregular, compound papillae. Glabrous.

CUT-Z-FCH
Figure 12.1-12.2

Reference specimen and locality: SL1114, Kakahu-33.

Description: Stomatal complexes evenly spread; isolated; randomly oriented; possibly anomocytic. Outer stomatal ledge very thin. Epidermal cell outlines wavy, buttressed, but often poorly distinct. Glabrous.

CUT-Z-FCI
Figure 12.3-12.4

Reference specimen and locality: SL2755, Kakahu-28.

Referred specimens and occurrence: SL5505, Kakahu-29; SL5508, Kakahu-30.

Description: Stomatal complexes evenly spread, anticlinal walls not clear and no distinct subsidiary cells apparent. Outer stomatal ledges clear, prominent, continuous ring about half with of the guard cells. Epidermal cells papillate, papillae discrete and slightly flanged, apparently centred well within the outlines of the epidermal cell. Venal cells not distinguished. Strongly thickened trichome attachment scars common.

CUT-Z-GBG
Figure 12.5-12.6

Reference specimen and locality: SL4932, Kakahu-31.

Description: Adaxial cuticle only, stomatal complexes not known. Epidermal cells isodiametric, straight-walled, periclinal surface ornamented with flowing pattern of many fine, subdued ridges. Persistent trichomes common, simple, with multicelled bases.

CUT-Z-GEE
Figure 12.7-12.8

Reference specimen and locality: SL5519, Kakahu-33.

Description: Stomatal complexes very scattered, randomly oriented. Cyclocytic with two or three rings of tangentially oriented subsidiary cells. Outer stomatal ledge prominent. Epidermal cells isodiametric, distinctly smaller than the stomatal complexes, straight-walled, unbuttressed. Glabrous.

CUT-Z-FCE
Figure 13.

Reference specimen and locality: SL1069, Kakahu-33.

Referred specimens and occurrence: SL1128, Kakahu-28; SL5506, Kakahu-29.

Description: Stomatal complexes evenly spread; isolated; randomly oriented; possibly anomocytic. Not distinct in thickness from normal epidermal cells (but all cells within areole are much thinner than venal cells). Ornamented with prominent, discontinuous, distinctly cusped ridges which appear to be centred over cell borders. Guard cell pair outline circular; periclinal walls same thickness as normal epidermal cells. Outer stomatal ledge a broad ridge covered about half the width of the guard cells, but notched at the polar ends. Epidermal

cells unbuttressed; ornamented with discontinuous ridges, probably corresponding to walls of epidermal cells. Venal cells not distinguished. Glabrous.

Identification: The cuticle morphology shows a remarkable similarity to an extant species off Aquifoliaceae, *Nemopanthus mucronata* (L.) Trelease (1889) the American Mountain holly. On this basis the fossil is suggested to belong in the family.

CUT-Z-GBH Smoothly papillate cuticle
Figure 14.

Reference specimen and locality: SL2759, Kakahu-28.

Referred specimens and occurrence: SL5524, Kakahu-33.

Description: Adaxial cuticle only known. Epidermal cells isodiametric, rounded, raised into prominent, smooth papillae. Trichome attachment scars present surrounded by a ring of cells.

Charcoal types
Figure 15.

Two types are present; angiosperm, with scalariform pitting ad multiple (more than twenty bars), and podocarp, with mostly uniseriate, circular bordered pits.

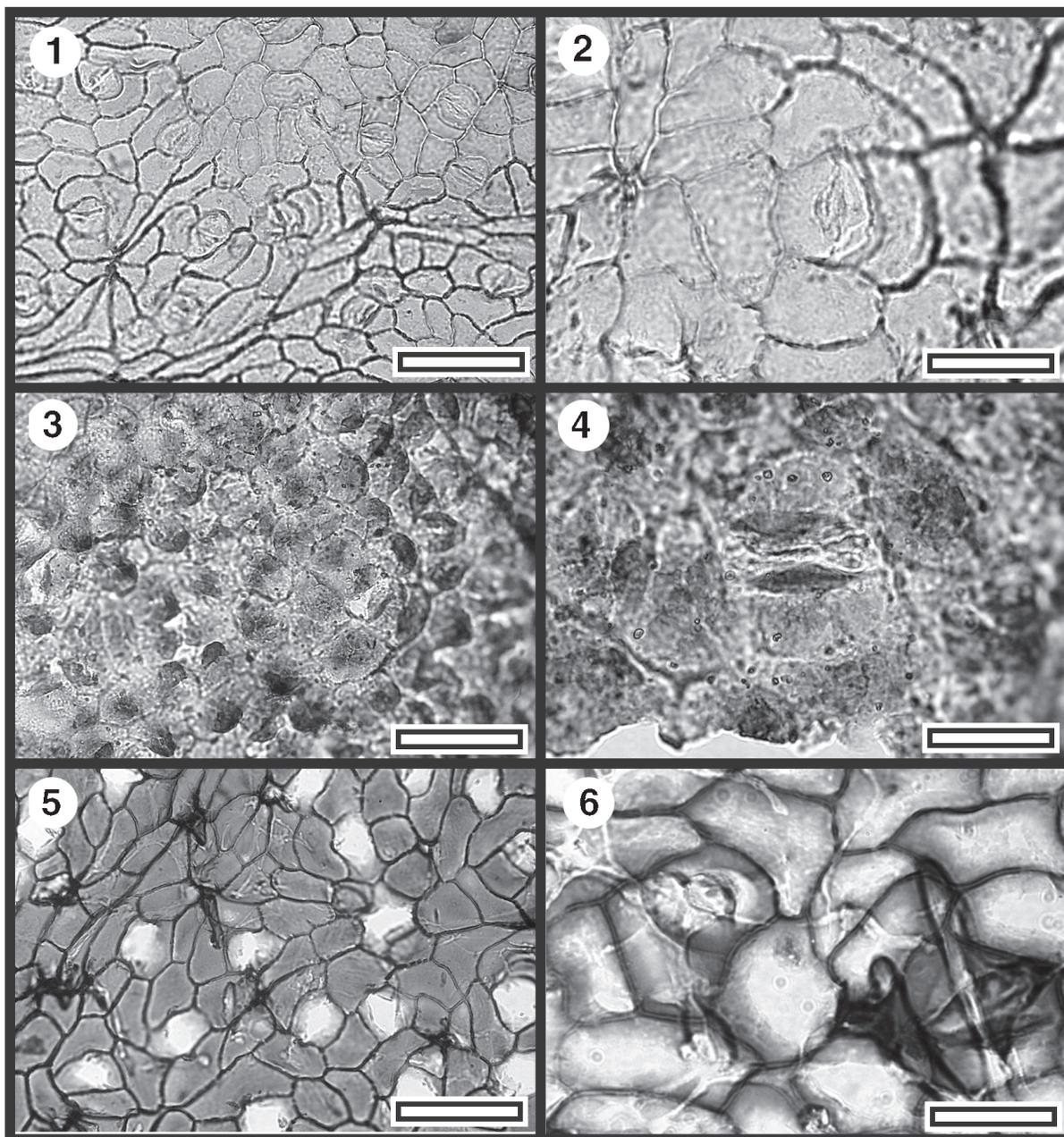


FIGURE 9. Lauraceae; (1) CUT-L-FDJ, TLM view of stomatal complexes and trichome bases (SL1115, scale bar = 50 μm); (2) CUT-L-FDJ, TLM detail of stomatal complex (SL1115, scale bar = 20 μm); (3) CUT-Z-CDG, TLM view showing robust papillae obscuring stomatal pores (SL2743, scale bar = 50 μm); (4) CUT-Z-CDG, TLM detail of stomatal complex (SL2743, scale bar = 20 μm); (5) CUT-L-FDB, TLM view of stomatal complexes and trichome bases, (SL2751, scale bar = 50 μm); (6) CUT-L-FDB, TLM detail of stomatal complex (SL2751, scale bar = 20 μm).

PE ERRATUM: An incorrect figure was placed in the PDF version of 13.2.14A, in Volume 13, Issue 3. The correct version of Figure 9 can be seen here.