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EARLY EOCENE DISPERSED CUTICLES AND MANGROVE TO RAINFOREST VEGETATION AT STRAHAN-REGATTA POINT, TASMANIA

Mike Pole

Mike Pole. Queensland Herbarium, Toowong, Qld 4066, Australia. murihiku@yahoo.com

ABSTRACT

Early Eocene plant-fossil assemblages (mostly of dispersed cuticle) from Strahan-Regatta Point, Tasmania, Australia, record evidence of mesothermal rainforest (mean annual temperatures between 12 and 20ºC) and mangrove vegetation surrounding an estuary, which grew close to the polar circle. Plant taxa represented by cuticle include: *Bowenia* (Cycadales), conifers, including *Acmopyle, Agathis*, *Araucaria*, *Dacrycarpus*, *Libocedrus*, *Prumnopitys*, and a gnetalean. Fifty- five taxa of angiosperms are recognised from cuticle, including Winteraceae, 11 Lauraceae (including an unusual toothed species) and seven Proteaceae as well as *Gymnostoma*, Aquifoliaceae, and Rhipogonaceae. There is also a Rhizophoraceae, which is interpreted as another mangrove, in addition to the mangrove palm *Nypa,* which has been described previously. In an Australasian context the absence of Myrtaceae is notable.

Multivariate analysis of the fossil distribution suggests that a significant amount of the variation can be attributed to whether they accumulated in the mangrove mud (or associated tidal sand flat) or in a freshwater facies.

KEY WORDS: Early Eocene, cuticle, stomata, mangrove, biodiversity, paleoclimate

INTRODUCTION

The Early Eocene includes two periods of globally warm temperatures where thermophilic vegetation (among other biota) extended its range significantly towards the poles; these were the Paleocene-Eocene Thermal Maximum (sometimes known as the Late Paleocene Thermal Maximum) and the Early Eocene Climatic Optimum (Katz et al. 1999; Zachos et al. 2001, 2005). Today the world is also undergoing profound warming due to anthropogenic greenhouse gases (Intergovernmental Panel on Climate Change 2007) and understanding the effects this will have on the biota and local climates has become a key research goal. To test the accuracy of global climate models for future terrestrial climates in a high-greenhouse state, we must identify an analogous period in the

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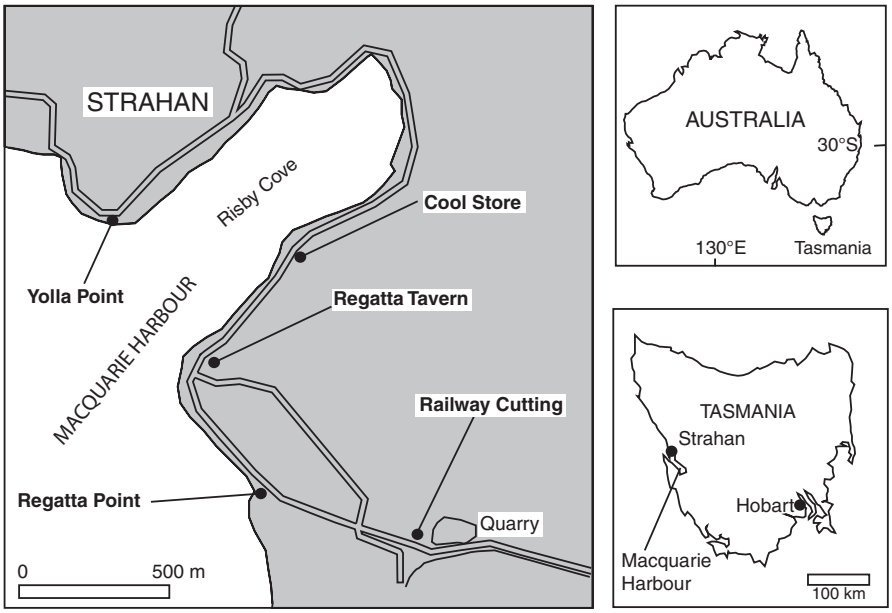

Figure 1. Locality map.

past and analyse its plant fossils. With a few exceptions, most of the terrestrial climate data for the early Eocene come from the northern hemisphere and from mid-latitudes. This paper attempts a detailed documentation of the vegetation from a high-latitude Southern Hemisphere Early Eocene locality. It mostly uses the evidence of leaf cuticle as a taxonomic tool. While this technique has been used for more than 50 years in parts of Europe, and has become standard in Australasia (e.g., Hill and Carpenter 1991; Jordan et al. 1998; Pole 2007a), its use in the Cenozoic of North and South America is still almost non-existent. Part of the problem may be the lack of broad, critical treatments of cuticle morphology, which give a researcher a basic framework to start within. This paper contributes toward filling this knowledge gap.

The township of Strahan lies on the edge of Macquarie Harbour on the wet, western side of Tasmania at 42 ºS (Figure 1) and a variety of plate tectonic reconstructions (e.g., Veevers et al. 1991; Li and Powell 2001) place it near the Polar Circle (66º) in the Early Eocene. The natural vegetation is a mixture of cool rainforest (the mean annual temperature is about 12ºC; Australian Bureau of Meteorology 2007 [Mike: should this be in the reference section?]) dominated by *Nothofagus*, and conifers of the Podocarpaceae family, wet sclerophyll forest and shrub land.

The fossils described in this paper come from sediments, which accumulated within the Macquarie Harbour Graben. This is a NW-SE trending basin, which probably resulted from extensional forces during separation of the Australian and East Antarctic plates (Colhoun 1989). Strahan, and the study area, lie at the seaward end of the basin.

Sediments exposed around the edges of the harbour in road cuts and in quarries are placed in the *Malvacipollis diversus* Zone of Stover and Partridge (1973) with a most likely age of late Early Eocene (54.9-48.5 Ma; A.D. Partridge personal commun. in Pole and Macphail 1996). The first paleontological work on the site was by Cookson and Eisenack (1967), who described the pollen *Monosulcites prominatus*, which was later recognised as representing *Nypa* by Churchill (1973). Today *Nypa* is the only mangrove palm, with a single, tropical species, *N. fruticans*. Previously described macrofossils include the conifers *Araucarioides linearis* and *A. sinuosa* (Bigwood and Hill 1985); *Araucaria readiae* (Hill and Bigwood 1987; Hill 1990); *Acmopyle glabra, Dacrycarpus linifolius and D. mucronatus* (Hill and Carpenter 1991), a possible cycad *Pterostoma* (Hill and Pole 1994), and the angiosperm *Eucryphia* (Hill 1991). There are also overlying fossiliferous Pleistocene sediments (Hill and Macphail 1985; Jordan 1997).

Nypa macrofossils, including fronds, cuticle, and fruits at Regatta Point were described by Pole and Macphail (1996). These are thought to be the highest latitude *Nypa* known, as the Early Eocene paleolatitude of Tasmania was close to the polar circle (66 ºS; Lawver and Gahagan 2003). The study was then extended to the broader stratigra-

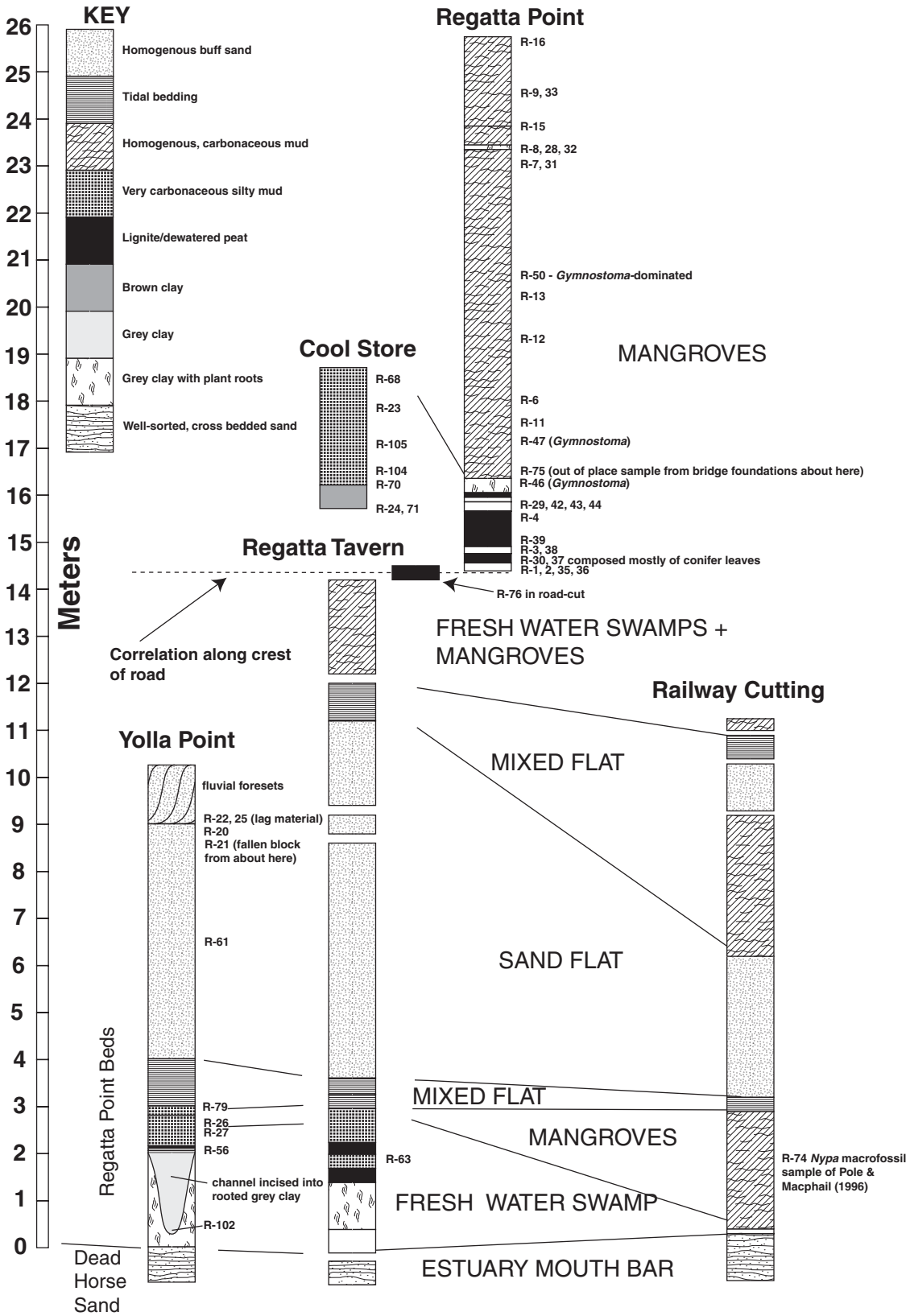

Figure 2. Stratigraphic section showing location of samples. Based on Pole (1998a) with the addition of the Cool Store Section, modifications to the Strahan Point Section, and removal of non-fossiliferous samples. Facies correlation between sections indicated by horizontal/diagonal lines.

phy and sedimentology. Based on sedimentary features and the presence or absence of *Nypa* pollen or dinoflagellates, it was concluded that the Early Eocene environment was a tidal estuary and that basic elements of such a system, a tidal bar, mixed flats, sand flats, mangrove swamps and freshwater swamps, could be identified (Figure 2; Pole 1998a). This was important in confirming that the fossils identified as *Nypa* really did occur in a mangrove environment.

Subsequent to the sedimentological study, research has focussed on the fossil cuticle and developing a reference database of extant leaf cuticle to help identify the fossils. This study aims to build on the environmental interpretation of Pole (1998a), by documenting the dispersed cuticle from the samples and then to see if discrete taxonomic assemblages can be recognised and related to their spatial/ecological distribution within the framework provided by Pole (1998a). The discovery of *Nypa* strongly suggests that other mangrove species will also be present (Duke et al. 2002), so the search for other mangrove fossils was a further goal of this study.

METHODS

Outcrop is visible in five places, termed 'sections'; the Railway Cutting, Regatta Point, Regatta Tavern, Yolla Point, and Cool Store sections. Sediment samples were taken from potentially fossiliferous horizons and numbered sequentially with an "R-" prefix in the order they were collected on repeat trips over the course of five years (1991-1996). Some stratigraphic horizons were sampled several times. Samples were typically of about 500 g, except for sample R-74, which was the *Nypa* macrofossil sample in Pole and Macphail (1996). Several kilograms of this were collected, and about 1 kg was prepared for cuticle. Preparation of dispersed cuticle follows a standard procedure of sediment disaggregation in hydrogen peroxide and hot water followed by sieving to retain all material greater than approximately 0.5 mm maximum dimension, and remaining silicates are removed with hydrofluoric acid. At this stage the plant material is usually a hash of opaque plant fragments, and small, three-dimensional items, such as shoots of conifers, may be picked out. Final reduction of fragments to cuticle involves immersion in aqueous chromium trioxide for several hours, or heating in concentrated hydrogen peroxide. This later technique gave better results for conifer leaves, which tended to shred in the chromium trioxide. Cuticle was then washed and stained in safranin, then mounted in thymol glycerine jelly on microscope slides for transmitted light microscopy (TLM) or on aluminium stubs and either gold or (more recent years) platinum coated for scanning electron microscope (SEM) viewing.

Catalogue numbers for material mounted on microscope slides is prefixed with "SB" or "SL" and SEM stubs are prefixed with "S-". Cuticle preparations of extant herbarium material cite the original herbarium sheet number ("AQ" refers to catalogue numbers of specimens in the Queensland Herbarium, Brisbane, "CANB" of specimens in the Australian National Herbarium, Canberra), and material in my own reference herbarium is prefixed with "OPH". All other material is stored in the State Herbarium of Queensland, Brisbane.

The taxonomic philosophy is to place fossils in the Linnean hierarchy to the level where it is possible. This is routine with conifer and cycad fragments where epidermal details are often sufficient to either place a fossil into an extant genus, or recognise that it must be an extinct taxon. For the much more diverse angiosperms, a different approach is used; each different morphology is assigned a parataxon code consisting of the prefix "CUT-" followed by a string of letters. Nomenclaturaly these are like species without a genus, for purposes of biodiversity they can be regarded as species. For each parataxon a Reference Specimen is nominated, which is the equivalent of the holotype in Linnean taxonomy. The detailed description of each parataxon is presented in Appendix 1. The taxa are presented first in taxonomic order for those cuticle parataxa that may be placed within families, and then the remainder are presented in order that they appear in a key, which groups morphologically similar taxa.

Epidermal terminology is based on the standard works of Stace (1965), Baranova (1987, 1992), Dilcher (1974), Hewson (1988), Payne (1978), and Wilkinson (1979). Carpenter (2005) is followed in the use of stoma (stomata pl.) to refer to the stomatal pore and the pair of guard cells, and stomatal complex for the stoma plus subsidiary cells. "Networking" (Pole 1998b) describes the situation where contact or subsidiary cells are shared between stomatal complexes.

A Bray-Curtis dissimilarity was used to perform a Non Metric Multidimensional Scaling on the presence-absence data for the taxa (Figure 3). The sites were plotted in the first two axes of the analysis to represent graphically the ordination of the samples. An Analysis of Similarity was performed using the same Bray-Curtis dissimilarity matrix to

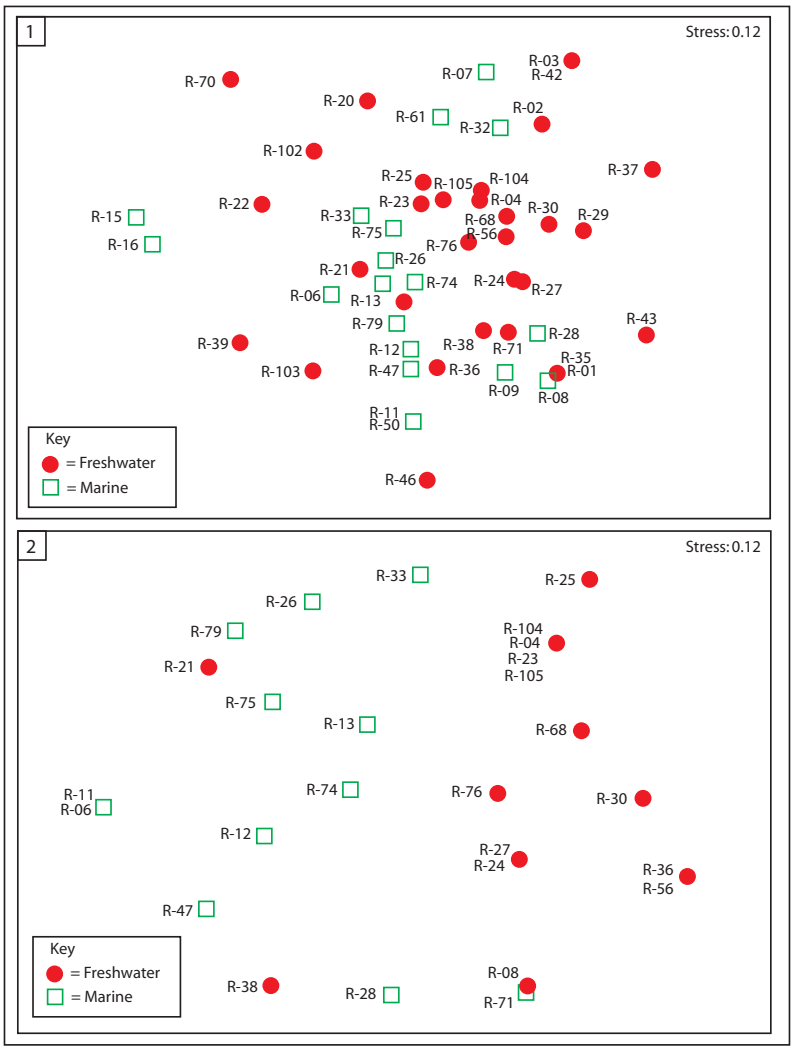

Figure 3. Ordination diagrams. **1.** Analysis based on all species. Scatter plot of the sites plotted in the first two axis of a Multidimensional Scaling calculated using Bray Curtis dissimilarity. ANOSIM results: R = 0.028, P 0.222; **2.** Results for taxa present in at least 20% of the samples (six taxa in 27 samples). Scatter plot of the sites plotted in the first two axis of a Multidimensional Scaling calculated using Bray Curtis dissimilarity. ANOSIM results: R = 0.292, P 0.03.

determine if the factor environment (freshwater or saltwater) affected the ordination. All multivariate analyses were completed using Primer 5 version 5.2.4.

RESULTS

Plant-Fossil Assemblages

The fossils found based on dispersed cuticle include a cycad (*Bowenia*) and a possible cycad (*Pterostoma*), a gnetalean, three families of conifers; Podocarpaceae (including *Acmopyle* and *Dacrycarpus, Prumnopitys*), Araucariaceae (including *Araucaria*, *Araucarioides* and *Agathis*), and Cupressaceae (including *Libocedrus*), and 55 angiosperm taxa. These include the Lauraceae, Proteaceae, Winteraceae, Aquifoliaceae, Rhizophoraceae, Rhipogonaceae, and other monocots. The mangrove palm, *Nypa*, was clearly an important element based on its pollen presence (Pole and Macphail 1996), but its delicate cuticle does not survive bulk preparation, but occasional scraps indicate other palms were present as well. *Gymnostoma* also rarely survives bulk cuticle preparation, but its woody articles often survive the initial sediment disaggregation and sieving and were common in some samples. The taxonomic affinities of these plants are consistent with a rainforest (sensu Bowman 2000; no charcoal is present in palynological preparations, pers. obs.) and mangrove vegetation.

An absence of Myrtaceae in this study is notable, given its prominence in Australia today, and its presence in most extant Australian rainforests, but is consistent with other evidence from the early Eocene on the Australian mainland (e.g., Martin 1994; Sluiter 1991; Carpenter et al. 2004). Myrtaceae cuticle can typically be identified by the presence of paired lid cells (Lange 1980; Christophel and Lys 1986). Clearly the timing and nature of the spread of Myrtaceae into Australian vegetation may be more complex than generally thought.

The highest diversity was found in sample R-75, which had 19 taxa in all, including 15 angiosperm taxa as well as Araucariaceae, Podocarpaceae, and *Bowenia*. *Bowenia* was widespread, occurring in 16 (33%) of the samples. Conifers occurred in 36 of the 49 samples (74%). Podocarpaceae were the most widespread group, occurring in 33 (67%) of the samples. Some samples have only conifer remains, and these are probably the result of weathering or taphonomic processes resulting in the destruction of all but the typically robust conifer cuticle. However, sample R-30 is visibly packed with conifer remains and was probably genuinely conifer-dominated vegetation.

Sample R-21 stands out as having the second highest diversity (12 taxa) yet is one of the few samples with no conifer remains at all. The most diverse angiosperm groups recognised are Lauraceae (11 taxa) and Proteaceae (eight taxa; see personal commun. in Jordan et al. 1998). The most widespread angiosperm was CUT-Z-JAE, occurring in 11 samples.

On Strahan Point, sample R-102 is from a layer of leaf fragments lying at the base of a small clay-filled channel, about 2 m deep, that is cut into a bed of clay penetrated by many small nodulated roots. These roots are probably remains of Podocarpaceae, which grew on waterlogged, gleyed soils above the high tide levels. However, the channel itself preserves an entirely angiosperm flora (without *Gymnostoma*). This suggests that there may have been segregation at high taxonomic levels across the broader environment. Conifer-dominated vegetation may have been more a feature of waterlogged habitats closest to the mangrove zone. A rise in relative sea-level then flooded these swamps, and the vegetation was replaced by mangroves, including *Nypa* and Rhizophoraceae. At the top of this section, a bed of metre-high foresets in sand with a lag of leaf and wood fragments at its base is interpreted to represent a fluvial channel that migrated into the tidal sand flat. Sample R-25 from this lag has both conifers and angiosperms.

The highly carbonaceous zones near the base of Regatta Point and Regatta Tavern are interpreted as freshwater swamps (Pole 1998a) where conifers were dominant and generally diverse. In both locations they are overlain within a metre of section by mangrove mud, so it is likely they grew immediately adjacent mangrove vegetation, just above high tide level. Because of their highly carbonaceous nature, the fossils are inferred to have accumulated in situ with little likelihood of contaminant material being washed in from elsewhere. Taxa that are found together in these facies are likely to have grown together. Sample R-30, from this facies, had all three conifer families (but no cycads), and had the highest conifer diversity of 10 species. Its angiosperm diversity was low, only three species, and not including any Lauraceae. The high diversity of conifers agrees well with previous work indicating extraordinary levels of conifer diversity in Tasmania's Paleogene (Pole 1992a; Hill and Brodribb 1999).

The presence of Rhizophoraceae cuticle (CUT-Z-JAG) with affinities to extant *Bruguiera*, *Ceriops*, and *Rhizophora,* clearly indicates a further mangrove taxon. It is present in sample R-74 in association with the *Nypa* described by Pole and Macphail (1996), and also within the mangrove mud on Regatta Point (R-12, 130, and overlying the freshwater swamp facies on Strahan Point (R-26). In this later sample it is associated with dinoflagellates (Pole 1998a) but no *Nypa* was found. This was interpreted as being the edge of a freshwater swamp, where saltwater incursions may have washed dinoflagellates in. Rhizophoraceae cuticle suggests that mangroves fringed the freshwater swamps here.

It is highly unlikely that some of the other plants found in mangrove facies in association with *Nypa* macrofossil, pollen and dinoflagellates, also grew as mangroves. For instance, *Bowenia* occurs with *Nypa* macrofossils in R-74 but today it grows as a small plant in the understory of rainforest. For instance, it grows within a rainforest only a metre from the upper limit of mangrove vegetation along the Mardja walk, in Cape Tribulation National Park (pers. obs.).

Gymnostoma is abundant in three samples (R-46, 47, 50) from mangrove mud on Regatta Point, where it is found with a number of other angiosperms but almost no conifers. Like *Bowenia*, *Gymnostoma* is unlikely to have been a mangrove, although today members of the Casuarinaceae can

dominate regions adjacent to mangroves. The abundance of *Gymnostoma* in some samples suggests that it was, as members of the family often are today, typically gregarious. Members of the Casuarinaceae host nitrogen-fixing bacteria, and as such they are well-suited to be pioneering plants after a disturbance, perhaps on a fluvial point bars.

Other than CUT-Z-JAG (Rhizophoraceae) none of the cuticle morphologies appear similar to any known mangrove, and those that have been identified, like Lauraceae and Proteaceae, do not have mangrove taxa today. Whereas it can not be ruled out that some of these taxa may have had mangrove representatives in the past, some taphonomic mixing must surely have occurred. It is likely that many of these were plants growing along the edge of supra-tidal, freshwater reaches of rivers, which were washed into the mangrove environment. It is possible that some of the cuticle parataxa of unknown affinities represent extinct mangrove taxa, perhaps in families which today do not include mangroves. This would certainly be difficult to prove, but identifying taxa consistently restricted to mangrove facies would be a start.

Based on Figure 2 samples were allocated simply to either “freshwater’ or “marine” (mangrove mud and sand flat) facies. Multivariate analysis based on the presence-absence data for all species (Figure 3.1) does not give significant results in terms of this environmental partition. However, most taxa are only present in one or two samples and are likely just introducing noise into the analysis. When the analysis was limited to taxa that are present in at least 20% of the samples, the results were significant (Figure 3.2), and suggest that the broad facies difference accounts for about 30% of the variability between samples. Samples from the “marine” facies probably include taxa from both mangrove and immediately adjacent vegetation.

Paleoclimate

As a genuine lowland and coastal Early Eocene site, Regatta Point could provide globally important paleoclimatic data. However, the method of foliar physiognomy (Wolfe 1979, 1995) is of limited use at Regatta Point as intact leaves are uncommon. Carpenter et al. (1994) included an average leaf length for Regatta Point fossils on a chart as about 70 mm, with a corresponding mean annual temperature of about 17ºC. However, none of the specimens that this figure was based on (number unknown) could be located, and in the four years of this study only a single partially complete angiosperm leaf impression (no cuticle could be isolated) was found, with an original length of about 100 mm.

Rainfall levels are even harder to estimate, and annual totals are almost worthless without knowing how this was seasonally distributed. Like the Regatta Point Eocene, there are also high diversities of (mainly Podocarpaceae) in the microthermal rainforests of Tasmania and New Zealand today (e.g., Jarman et al. 1984; Reid et al. 1999), but without the diversity of Lauraceae and Proteaceae in the fossil assemblages. This is likely to be a function of very wet conditions and poor soils. The abundance of conifer remains at Regatta Point likewise may suggest very wet conditions throughout the year, but this needs to be balanced against the general lack of almost any coal. Several of the cuticle taxa at Regatta Point have surface papillae or pronounced ridges, which might have some climatic significance. However, their significance is ambiguous. Hill (1998) argued that the firmest evidence for xeromorphy included the presence of individually protected stomata (by being “surrounded by raised epidermal structures”). But he also argued that these could be evidence of wet conditions, and Carpenter et al. (2004) listed trichomes, papillae, and ridging as characters that obscured the stomata, some of which “would also be advantageous in generally wet conditions …”. Clearly some data on extant plants are needed to clarify this issue. This leaves floristics as a further climatic indicator. Nix (1982) classified “thermal regimes” as mean annual temperatures (MAT) of >24ºC = megatherm, >14<20ºC = mesotherm, and <12ºC = microtherm. In a broad sense, the prominence of conifers (especially Podocarpaceae), Lauraceae, and Proteaceae compares well with extant mesothermal rainforest vegetation, which is found in mid-montane altitudes of the tropics, and which extends down towards sea level at higher latitudes (Whitmore 1984; Richards 1996). Conifers are important in some tropical swamp situations, for example the low-nutrient raised peat-swamps of Borneo where they can compete with angiosperms (e.g., Brünig 1974). However, they do not dominate these communities, and there is no suggestion that the Regatta Point environment included raised peat swamps. The other ‘dry-land’ taxa that have been identified at Regatta Point are consistent with this interpretation. The mere presence of broad-leaved Lauraceae in Tasmania, where they do not occur today, suggests warmer conditions than the present. In Australasia the Lauraceae reach their southern limit near the southern margin of mainland Australia, and at similar lati-

tudes in New Zealand (Pole 2007a). This is likely to be a temperature-related limit. At these limits today the Lauraceae are present at low diversities (for instance 1-2 species in a local flora). The 11 species occurring at Regatta Point suggest temperatures were well above the cold-limit for the family, and reflect a high overall tree diversity. A similar southern limit on the Australian mainland exists for mangroves and palms (Duke et al. 2002; Cameron 1987). Greenwood et al.'s (2003) characterisation of *Ilex* as a "megathermal" taxon is simply incorrect. As summarised by Martin (1977) it has wide limits, and in fact in a biomass sense, is probably more characteristic of microthermal conditions. However, superimposed on this essentially mesothermal combination is the presence of the mangrove palm, *Nypa. N. fruticans* lives today within about 15º of the equator, i.e., it is wholly tropical and would seem to provide an excellent indicator for tropical, or megathermal temperatures. In the fossil record the broad history of the genus confirms that it has always been a plant of relatively warm conditions (e.g., Gee 1990, 2001; Collinson 1993). But there is a clear danger of extrapolating too far from a single extant species. The Tasmanian *Nypa australis* is specifically different from the extant species (Pole and Macphail 1996) and is likely to have had different environmental tolerances. The fact that the fossil *Nypa* occurs with a variety and abundance of conifers should warn against assuming the environment as megathermal, although the presence of palms, cycads, and the mangrove life-style indicates a largely frost-free environment (e.g., Wing and Greenwood 1993).

Finally, Carpenter et al. (2004) noted that an unusual proportion of their Proteaceae taxa had average stomata; lengths less than 20 µm. Jordan et al. (1998) proposed this was a general phenomenon for Palaeogene Proteaceae from Tasmania and linked it to high carbon dioxide levels. This phenomenon is not apparent in the Proteaceae studied here, and only one taxon (CUT-P-EJD) has an average stomatal length less than 20 µm.

To summarise, temperatures at Regatta Point in the Early Eocene were warmer than today (12), despite the locality being 20º of latitude or further south (perhaps as far south as the Polar Circle at 66 ºS). Mean annual temperatures somewhere in the middle of the mesothermal range (between 14 and 20ºC) were likely and rainfall was continuously high (probably similar to much of Tasmania today).

DISCUSSION

The Regatta Point beds were deposited during or close to the warmest known interval of the Tertiary—the Early Eocene Climatic Optimum (Zachos et al. 2001). The distinct Southern Ocean water masses and fronts of the present day had not evolved, and 'cool subtropical' water flowed to high latitudes (Nelson and Cooke 2001). There is heightened interest in this period as a potential analogue of the enhanced greenhouse warming that the world is currently experiencing (e.g., Wing et al. 2003). In Australia, there have been several publications covering the Early Eocene climate (Greenwood and Christophel 2004), although primary published data are limited.

Pioneering oxygen isotope studies of the Southern Ocean (Shackleton and Kennett 1975) suggested sea surface temperatures for the southern Australian Early Eocene of around 15-17ºC. There have been a much broader range of estimates since, from climate modelling and palaeobotanical evidence. For instance, Nix (1982) argued that southern Australia may have been borderline mesothermal (c. 14ºC) around the Early Eocene.

Early Eocene plant macrofossil sites on the southeastern Australian mainland lie about 4-5º of latitude further north than Regatta Point today–as they would have in the Eocene. Based on low Early Eocene thermal gradients (e.g., Greenwood and Wing 1995) sea surface temperatures in this region would have been no more than 2ºC warmer than Tasmania. Early Eocene mainland sites include Hotham Heights, Brandy Creek, and Deans Marsh. Greenwood et al. (2003) published MAT estimates for Hotham Heights of 17.9ºC, based on the proportion of entire-margined leaves (the Australian relationship later published as Greenwood et al. 2004) in an unpublished taxonomy, and 17.8ºC, based on leaf length and the current relationship between leaf length and MAT in Australian forests. The stated average length of leaves for this deposit of 78 mm is approximately the boundary between the microphyll and notophyll classes of leaf size (Webb 1959). Greenwood et al. (2003) extrapolated their results from Hotham Heights and other localities to infer that MAT for the lowland of southeastern Australia around the Early Eocene was in the 20-25ºC range. They noted that this conclusion was "consistent with the observation by Macphail et al. (1994) that the early Eocene was the acme of development of lowland megathermal species-rich rainforest in southeastern Australia," and further that this was "much higher" than recent computer

climate model suggestions of MAT of <10ºC (Sewall et al. 2000; Shellito et al. 2003).

Greenwood and Christophel (2004, their figure 18.1) acknowledged that coastal communities around Tasmania included the "mesothermal-megathermal to megathermal mangrove palm *Nypa*" but mapped the dry-land vegetation as "Microphyll Fern Forest" (Webb et al. 1984 give the present-day average MAT of this forest type as about 12-13ºC) and "Broad–leaved deciduous forest and temperate mixed conifer" (BDF). The basis of this decision is unclear. Greenwood and Christophel (2004) mapped the south-eastern Australian mainland as having notophyll-mesophyll vine forest (which they equated with "mesothermal-megathermal rainforest").

Carpenter et al. (2004) published an overview of Hotham Heights, which they regarded as preserving vegetation growing in an upland region, approximately 800 m above sea level. In terms of overall diversity, the prominence of Lauraceae and Proteaceae, and the absence of Myrtaceae macrofossils, the site is similar to Regatta Point. A similar diversity of conifers was reported for Hotham Heights (although without Cupressaceae) but they were apparently generally uncommon elements. The abundance of the cycad *Bowenia* in Tasmania contrasts with the absence of cycads at Hotham Heights. They concluded that "all lines of evidence are consistent for the prevalence of a wet, mesotherm environment at Mt Hotham in the Early Eocene" and that the lowlands had an "abundance of taxa that indicate the presence of vegetation with a megatherm character."

The evidence cited above indicates a surprising level of uncertainty about Early Eocene temperatures in southern Australia: ranging from a cool 10ºC (or less) to about 17ºC from modelling and oxygen isotope results, and up to as much as 25ºC based on palaeobotany. Greenwood et al.'s (2004) Australian-based leaf margin calibration is a welcome addition to our knowledge, and they stated that previous estimates of MAT for Australian floras based on the east Asian correlation should be revised, for the Early-Middle Eocene essentially downwards by around six degrees (Interestingly, at around the same time, Kowalski and Dilcher, 2003, suggested that "current methods of inferring paleotemperatures from fossil floras yield underestimates of 2.5–10ºC). However, Greenwood et al. (2004) also stated that the "most conservative approach" would be to use the Australian relationship as a minimum, and non-Australian as a maximum. Thus, leaf margin analysis using their MAT figures and their stated standard error of about 2ºC, suggests Hotham Heights MAT ranged between around 15.9 and 25.8ºC, and lowland temperatures 4–5ºC warmer still.

The actual evidence for megathermal temperatures ever being experienced in the southeastern Australian lowlands is slim. Despite the "megathermal" conclusions attributed to Macphail et al. (1994) above, in reality he wrote of "megathermal in character," to which a potentially broader range of MATs might be attributed. Various workers (e.g., Basinger et al. 1994; Plaziat et al. 2001) have emphasised that in an essentially ice-free world, the winter temperature minima which probably control the polewards limits of many apparently "tropical " taxa today, would have been relaxed. Thus this aspect of climate, rather than MAT, is more relevant. It is hard to reconcile Greenwood and Christophel's (2004) conclusion of (presumably sea-level) microphyll forest existing on Tasmania, while notophyll-mesophyll forest was on the south-eastern mainland. This would imply a higher thermal gradient than today.

The precision of leaf-length based estimates of MAT in Greenwood et al. (2003) also needs to be considered carefully. Leaf length is also a function of precipitation (e.g., Wilf et al. 1998) and the relationship which holds today in Australia may not have held in the past, or indeed, elsewhere today. For example, Schneider et al. (2003) documented rainforest vegetation from 2950 m in Venezuela which is, based on species or individuals, equally dominated by microphyll and notophyll sized leaves (similar to Hotham Heights). They cited the MAT in their area to be 14.9ºC at 2300 m. Based on a lapse rate of 0.55–0.60ºC per 100 m (Meyer 1992), the MAT at 2950 m would be about 11ºC.

CONCLUSION

The Early Eocene environment at Strahan, Tasmania, was centred on a tidal estuary with mean annual temperatures that were mostly likely mesothermal. The mangrove palm *Nypa* flanked the tidal reaches of river channels and was associated with a species of Rhizophoraceae with affinities to the extant mangroves in the genera *Bruguiera*, *Ceriops*, and *Rhizophora*. *Gymnostoma* was likely a pioneer plant along the banks of the river away from saltwater influence. Forests rich in and dominated by conifers (including *Acmopyle, Agathis*, *Araucaria*, *Dacrycarpus*, *Libocedrus*, *Prumnopitys*) grew in the freshwater swamps flanking the mangroves. There was also a broad-leaved gnetalean. Angiosperm-dominated vegetation may

have occupied the better drained flood basin areas. The angiosperm flora was also rich, with 55 taxa of angiosperms recognised from cuticle. These include 11 Lauraceae (including an unusual toothed species), seven Proteaceae, Aquifoliaceae, and Winteraceae,

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REFERENCES

Bandulska, H. 1926. On the cuticles of some fossil and recent Lauraceae. *Journal of the Linnean Society of London (Botany)*, 47:383-425.

Baranova, M. 1987. Historical development of the present classification of morphological types of stomates. *The Botanical Review,* 53:53-79.

Baranova, M. 1992. Principles of comparative stomatographic studies of flowering plants. *The Botanical Review*, 58:49-99.

Barnes, R.W. and Jordan, G.J. 2000. *Eucryphia* (Cunoniaceae) reproductive and leaf macrofossils from Australian Cainozoic sediments. *Australian Systematic Botany*, 13:373-394.

Bartling, F.G. 1830. *Ordines Naturales Plantarum.* Dieterich, Göttingen.

Basinger, J.F., Greenwood, D.R., and Sweda, T. 1994. Early Tertiary vegetation of Arctic Canada and its relevance to paleoclimatic interpretation, p. 175-198. In Boulter, M.C. and Fisher, H.C. (eds.), *Cenozoic Plants and Climate of the Arctic*. NATO ASI Series.

Bigwood, A.J. and Hill, R.S. 1985. Tertiary Araucarian macrofossils from Tasmania. *Australian Journal of Botany*, 33:645-656.

Bowman, D.M.J.S. 2000. *Australian Rainforests: Islands of Green in a Land of Fire*. Cambridge University Press, Cambridge.

Brown, R. 1814, Appendix 3, p. 571. In Flinders, M. *Voyage of the Terra Australis 2*. G. and W. Nicol, London.

Brünig, E.F. 1974. Ecological Studies in the Kerangas Forests of Sarawak and Brunei, 1237. Borneo Literature Bureau, Kuching.

Cameron, D.G. 1987. Temperate rainforests of East Gippsland, p. 33-46. In Werren, G. and Kershaw, A.P. (eds.). The rainforest legacy. Australian national rainforests study. Vol. 1. Australian Government Publishing Service, Canberra.

Carpenter, K.J. 2005. Stomatal architecture and evolution in basal angiosperms. *American Journal of Botany*, 92:1595-1615.

Carpenter, R.J. 1994. Cuticular morphology and aspects of the ecology and fossil history of North Queensland rainforest Proteaceae. *Botanical Journal of Linnean Society*, 116:249-303.

Carpenter, R.J., Hill, R.S., and Jordan, G.J. 1994. Cenozoic vegetation in Tasmania: macrofossil evidence, p. 276-298. In Hill, R.S. (ed.), *History of the Australian Vegetation: Cretaceous to Recent*. Cambridge University Press, Cambridge.

Carpenter, R.J., Hill, R.S., Greenwood, D.R., Partridge, A.D., and Banks, M.A. 2004. No snow in the mountains: Early Eocene plant fossils from Hotham Heights, Victoria, Australia. *Australian Journal of Botany*, 52:685-718.

Carpenter, R.J. and Pole, M.S. 1995. Eocene plant fossils from the Lefroy and Cowan paleodrainages, western Australia. *Australian Systematic Botany*, 8:1107-1154.

Christophel, D.C. and Lys, S.D. 1986. Mummified leaves of two new species of Myrtaceae from the Eocene of Victoria, Australia. *Australian Journal of Botany,* 34:649-662.

Christophel, D.C. and Rowett, A.I. 1996. Leaf and cuticle atlas of Australian leafy Lauraceae. *Flora of Australia Supplementary Series*, 6:1-217.

Christophel, D.C., Kerrigan, R., and Rowett, A.I. 1996. The use of cuticular features in the taxonomy of the Lauraceae. *Annals of the Missouri Botanical Garden,* 83:419-432.

Churchill, D.M. 1973. The ecological significance of tropical mangroves in the Early Tertiary floras of southern Australia. *Special Publication of the Geological Society of Australia,* 4:79-86.

Colhoun, E.A. 1989. Cainozoic geomorphology, p. 403-409. In Burrett, C.F. and Martin, E.L. (eds.) *Geology and mineral resources of Tasmania*. *Special Publication of the Geological Society of Australia*, 15.

Collinson, M.E. 1993. Taphonomy and fruiting biology of recent and fossil *Nypa*. *Special Papers in Palaeontology*, 49:165-180.

Cookson, I.C. and Eisenack, A. 1967. Some early Tertiary microplankton and pollen grains from a deposit near Starhan, western Tasmania. *Proceedings of the Royal Society of Victoria,* 80:131-140.

Conran, J. and Clifford, H.T. 1985. The taxonomic affinities of the genus *Ripogonum*. *Nordic Journal of Botany*, 5:215-219.

Cronquist, A. 1981. *An Integrated System of Classification of Flowering Plants*. Columbia University Press, New York.

Dahlgren, R.M.T. and Clifford, H.T. 1982. *The Monocotyledons: a comparative study*. Academic Press, London.

de Laubenfels, D. 1969. A revision of the Malesian and Pacific rainforest conifers, I. Podocarpaceae, in part. *Journal of the Arnold Arboretum*, 50:315

Dilcher, D.L. 1974. Approaches to the identification of angiosperm leaf remains. *The Botanical Review,* 40:1-157.

Dilcher, D.L., Christophel, D.C., Bhagwandin, H.O., Jr. and Scriven, L.J. 1990. Evolution of the Casuarinaceae: morphological comparisons of some extant species. *American Journal of Botany*, 77:338-355.

Duke, N.C., Lo, E.Y.Y., and Sun, M. 2002. Global distribution and genetic discontinuities of mangroves - emerging patterns in the evolution of *Rhizophora*. *Trees. Structure and Function*, 16: 65-79.

Endlicher, S. 1847. *Synopsis coniferarum*. Scheitlin and Zollikofer, Sankt-Gallen, Switzerland.

Engler, A. 1924. *Syllabus der Pflanzenfamilien.* Borntraeger, Berlin.

Farjon, A. 2005. A monograph of Cupressaceae and Sciadopitys. Royal Botanic Gardens, Kew.

Faroqui, A. 2001. Micromorphology and Adaptation of leaf epidermal traits in Rhizophoraceae to Coastal Wetland Ecosystem. *Palaeobotanist*, 50:295-309.

Florin, R. and Boutelje, J.B. 1954. External morphology and epidermal structure of leaves in the genus *Libocedrus*, s.lat. *Acta Horti Bergiani*, 17:7-37.

Gee, C.T. 1990. On the fossil occurence of the mangrove palm *Nypa*, p. 315-319. In Knobloch, E. and Kvacek, Z. (eds.), *Paleofloristic and Paleoclimatic Changes in the Cretaceous and Tertiary*. Geological Survey Publications, Prague.

Gee, C.T. 2001. The mangrove palm *Nypa* in the geologic past of the New World. *Wetlands Ecology and Management*, 9:181-194.

Greenwood, D.R. and Christophel, D.C. 2004. The Origins and Tertiary History of Australian “Tropical” Rainforests, p. 336-373. In Bermingham, E., Dick, C.W., and Moritz, C. (eds.), *Tropical Rainforests: Past, Present, and Future*. University of Chicago Press, Chicago.

Greenwood, D.R. and Wing, S.L. 1995. Eocene continental climates and latitudinal temperature gradients. *Geology*, 23:1044-1048.

Greenwood, D.R., Moss, P.T., Rowett, A.I., Vadala, A.J., and Keefe, R.L. 2003. Plant communities and climate change in southeastern Australia during the early Paleogene, p. 365-380. In Wing, S.L., Gingerich, P., Schmitz, B., and Thomas, E. (eds.), *Causes and Consequences of Globally Warm Climates in the Early Paleogene*.

Greenwood, D.R., Wilf, P., Wing, S.L., and Christophel, D.C. 2004. Paleotemperature estimation using leaf-margin analysis: is Australia different? *Palaios*, 19:129-142.

Greguss, P. 1968. Xylotomy of the living cycads. Akademiai Kiado, Budapest.

Henkel, J.B. and Hochstetter, W. 1865. Synopsis der Nadelhölzer, deren charakteristischer Merkmale nebst Andeutungen über ihre Cultur und Ausdauer in Deutschlands Klima XVII. Cotta, Stuttgart.

Hewson, H.J. 1988. Plant Indumentum - A Handbook of Terminology. *Australian Flora and Fauna Series*, 9:1-25.

Hill, R.S. 1978. Two new species of *Bowenia* Hook. ex. Hook. from the Eocene of eastern Australia. *Australian Journal of Botany*, 26:837-846.

Hill, R.S. 1980. Three new Eocene cycads from eastern Australia. *Australian Journal of Botany*, 28:105-122.

Hill, R.S. 1986. Lauraceous leaves from the Eocene of Nerriga, New South Wales. *Alcheringa*, 10:327-351.

Hill, R.S. 1990. *Araucaria* (Araucariaceae) species from Australian Tertiary sediments - a micromorphological study. *Australian Systematic Botany*, 3:203-20.

Hill, R.S. 1991. Leaves of *Eucryphia* (Eucryphiaceae) from Tertiary sediments in south-eastern Australia. *Australian Systematic Botany*, 4:481-497.

Hill, R.S. 1998. Fossil evidence for the onset of xeromorphy and scleromorphy in Australian Proteaceae. *Australian Systematic Botany*, 11:391-400.

Hill, R.S. and Bigwood, A.J. 1987. Tertiary gymnosperms from Tasmania: Araucariaceae. *Alcheringa*, 11:325-335.

Hill, R.S. and Brodribb, T.J. 1999. Turner Review No. 2 - Southern conifers in time and space. *Australian Journal of Botany*, 47:639-696.

Hill, R.S. and Carpenter, R.J. 1991. Evolution of *Acmopyle* and *Dacrycarpus* (Podocarpaceae) foliage as inferred from macrofossils in south-eastern Australia. *Australian Systematic Botany*, 4: 449-479.

Hill, R.S. and Macphail, M.K. 1985. A fossil flora from rafted Plio-Pleistocene mudstones at Regatta Point, Tasmania. *Australian Journal of Botany*, 33:497-517.

Hill, R.S. and Pole, M.S. 1992. Leaf and shoot morphology of extant *Afrocarpus*, *Nageia* and *Retrophyllum* (Podocarpaceae) species, and species with similar leaf arrangement, from Tertiary sediments in Australasia. *Australian Systematic Botany*, 5:337.358.

Hill, R.S. and Pole, M.S. 1994. Two new species of *Pterostoma* R.S. Hill from Cenozoic sediments in Australasia. *Review of Palaeobotany and Palynology,* 80:123-130.

Hooker, J.D. 1863. *Botanical Magasine* 89: 5398.

Horaninow, P.F. 1834. Primae Lineae Systematis Naturae. Karoli. Krajanis, St. Petersburg.

Intergovernmental Panel on Climate Change. 2007. *IPCC Fourth Assessment Report* (AR4). Available from World Wide Web: <http://www.ipcc.ch/>

Jarman, S.J., Brown, M.J., and Kantvilas, G. 1984. *Rainforest in Tasmania*. National Parks and Wildlife Service, Tasmania, Hobart.

Jordan, G.J., Carpenter, R.J., and Hill, R.S. 1998. The Macrofossil Record of Proteaceae in *Tasmania: a Review with New Species.* Australian Systematic Botany, 11:465-501.Jordan, G.J. 1997. Evidence of Pleistocene plant extinction and diversity from Regatta Point, western Tasmania, *Australia. Botanical Journal of Linnean Society,* 123:45-71.

Johnson, L.A.S. 1980. Notes on Casuarinaceae. *Telopea* 2:83-84.

Jussieu, A.L. 1789. *Genera Plantarum secundum ordines naturales disposita*. Herissant and Barrois, Paris.

Katz, M.E, Pak, D.K., Dickens, G.R., and Miller, K.G. 1999. The Source and Fate of Massive Carbon Input During the Late Paleocene Thermal Maximum. *Science,* 286:1531-1533.

Kitzberger, T. and Veblen, T.T. 1999. Fire-induced changes in northern Patagonian landscapes. *Landscape Ecologym* 14:1-15.

Kowalski, E.A. and Dilcher, D.L. 2003. Warmer paleotemperatures for terrestrial ecosystems. *Proceedings of the National Academy of Sciences*, 100:167-170.

Lange, R.T. 1978. Some Eocene leaf fragments comparable to Proteaceae. *Journal of the Royal Society of Western Australia*, 60:107-14.

Lange, R.T. 1980. Evidence for lid-cells and host-specific microfungi in the search for Tertiary *Eucalyptus*. *Review of Palaeobotany and Palynology*, 29:29-33.

Lawver, L.A. and Gahagan, L.M. 2003. Evolution of Cenozoic seaways in the circum-Antarctic region. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 198:11-37.

Li, Z.X. and Powell, C. Mc A. 2001. An outline of the palaeogeographic evolution of the Australasian region since the beginning of the Neoproterozoic. *Earth-Science Reviews*, 53:237-277.

Lindley, J. 1830. *An Introduction to the Natural System of Botany.* Longman, London.

Lindley, J. 1834. *Botanical Register* 20.

Macphail, M.K., Alley, N., Truswell, E.M., and Sluiter, I.R.K. 1994. Early Tertiary vegetation: evidence from spores and pollen, p. 189-262. In Hill, R.S. (ed.), *History of the Australian Vegetation: Cretaceous to Recent*. Cambridge University Press, Cambridge.

Martin, H.A. 1977. The history of *Ilex* (Aquifoliaceae) with special reference to Australia: evidence from pollen. *Australian Journal of Botany,* 25:655-673.

Martin, H.A. 1994. Australian Tertiary phytogeography: evidence from palynology, p. 104-142. In Hill, R.S. (ed.), *History of the Australian Vegetation: Cretaceous to Recent*. Cambridge University Press, Cambridge.

Meyer, H.W. 1992. Lapse rates and other variables applied to estimating paleoaltitudes from fossil floras. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 99:71-99.

Nautiyal, D.D., Singh, S., and Pant, D.D. 1976. Epidermal structure and ontogeny of stomata in *Gnetum gnemon*, *G. montanum* and *G. ula*. *Phytomorphology*, 26:282-296.

Nelson, C.S. and Cooke, P.J. 2001. History of oceanic front development in the New Zealand sector of the Southern Ocean during the Cenozoic - a synthesis. *New Zealand Journal of Geology and Geophysics,* 44:537-555.

Nix, H. 1982. Environmental determinants of biogeography and evolution in Terra Australis, p. 47-66. In Barker, W.R. and Greenslade, P.J.M. (eds.), *Evolution of the fauna and flora of arid Australia*. Peacock Publications, Fremville, South Australia.

Paliwal, G.S., Rampal, G.C., and Paliwal, N. 1974. A Compariative Light and Scanning Microscopic Study of the Epidermis in Gnetopsida. *Acta Botanica Indica*, 2:37-43.

Payne, W.W. 1978. A glossary of plant hair terminology. *Brittonia*, 30:239-255.

Persoon, C.H. 1807. *Synopsis Plantarum*, 2. Cramer, Paris.

Philippi, R.A. 1861. Zwei neue Gattungen der Taxineen aus Chile. *Linnaea, 3*0:730-735.

Pilger, R.K.F. 1903. Taxaceae, p. 117, In Engler, H.G.A. (ed.), *Das Pflanzenreich* 18. Wilhelm Engelmann, Leipzig.

Plaziat, J.-C., Cavagnetto, C., Koeniguer, J.-C., and Baltzer, F. 2001. History and biogeography of the mangrove ecosystem, based on a critical reassessment of the paleontological record. *Wetlands Ecology and Management*, 9:161-179.

Pole, M.S. 1992. Eocene vegetation from Hasties, northeastern Tasmania. *Australian Systematic Botany*, 5:431-75.

Pole, M.S. 1996. Plant macrofossils from the Foulden Hills Diatomite (Miocene), Central Otago, New Zealand. *Journal of the Royal Society of New Zealand*, 26:1-39.

Pole, M.S. 1997a. Miocene conifers from the Manuherikia Group, New Zealand. *Journal of the Royal Society of New Zealand*, 27:355-370.

Pole, M.S. 1997b. Paleocene plant macrofossils from Kakahu, south Canterbury, New Zealand. *Journal of the Royal Society of New Zealand*, 27:371-400.

Pole, M.S. 1998a. Early Eocene estuary at Strahan, Tasmania. *Australian Journal of Earth Sciences*, 45:979-985.

Pole, M.S. 1998b. Paleocene gymnosperms from Mount Somers, New Zealand. *Journal of the Royal Society of New Zealand*, 28:375-403.

Pole, M.S. 1998c. The fossil flora of Melville Island, Northern Australia. *The Beagle*, 14:1-28.

Pole, M.S. 2000. Mid-Cretaceous conifers from the Eromanga Basin, Australia. *Australian Systematic Botany*, 13:153-197.

Pole, M. 2007a. Lauraceae Macrofossils and Dispersed Cuticle from the Miocene of Southern New Zealand. *Palaeontologia Electronica* 10, Issue 1; 3A:38p, 65MB; http://palaeo-electronica.org/paleo/2007_1/zealand/index.html

Pole, M.S. 2007b. Conifer and Cycad distribution in the Miocene of southern New Zealand. *Australian Journal of Botany*, 55:143-164.

Pole, M.S. and Macphail, M.K. 1996. Eocene *Nypa* from Regatta Point, Tasmania. *Review of Palaeobotany and Palynology*, 92:55-67.

Ramassamy, V. and Kannabiran, B. 1996. Leaf epidermis and taxonomy in Rhizophoraceae. *Indian Forester*, 122:1049-1061.

Reid, J.B., Hill, R.S., and Hovenden, M.J. (eds.), 1999. Vegetation of Tasmania. Series Flora of Australia supplementary series, 8. Australian Biological Resources Study, Canberra.

Richard, A. 1828 *Nouveaux élémens de Botanique et de Physiologie vegétale*. Bechet Jeune., Paris.

Richards, P.W. 1996. The Tropical Rainforest, an ecological study. Cambridge University Press, Cambridge.

Salisbury, R.A. 1807. The characters of several genera in the Natural Order Coniferae. *Transactions of the Linnean Society, London* 8:308-318.

Schneider, J.V., Zipp, D., Gaviria, J., and Zizka, G. 2003. Successional and mature stands in an upper Andean rain forest transect of Venezuela: do leaf characteristics of woody species differ? *Journal of Tropical Ecology*, 19:251-259.

Schultz, S. 1832. *Natürliches System des Pflanzenreich*. Schlesinger, Berlin.

Scriven, L.J. and Hill, R.S. 1995. Macrofossil Casuarinaceae: their identification and the oldest macrofossil record, *Gymnostoma antiquum* sp. nov., from the Late Paleocene of New South Wales, Australia. *Australian Systematic Botany*, 8:1035-1053.

Setoguchi, H., Kosuge, K., and Tobe, H. 1999. Molecular Phylogeny of Rhizophoraceae Based on rbcL Gene Sequences. *Journal of Plant Research*, 112:443-455.

Sewall, J.O., Sloan, L.C., Huber, M., and Wing, S. 2000. Climate sensitivity to changes in land surface characteristics. *Global and Planetary Change*, 26:445-465.

Shackleton, N.J. and Kennett, J.P. 1975. Paleotemperature history of the Cenozoic and the initiation of Antarctic glaciation: oxygen and carbon isotope analyses in DSDP sites 277, 279, and 281. *Initial Reports of the Deep Sea Drilling Project,* 29:743-55.

Shellito, C.J., Sloan, L.C., and Huber, M. 2003. Climate model sensitivity to atmospheric CO_2 levels in the early-middle Paleogene. *Palaeoceanography, Palaeoclimatology, Palaeoecology*, 193:113-123.

Sluiter, I.R. 1991. Early Tertiary vegetation and paleoclimates, Lake Eyre region, northeastern South Australia. In Williams, M.A.J., Deckker, P. De, and Kershaw, A.P. (eds.), *The Cainozoic of the Australian Region*. *Geological Society of Australia Special Publication*, 18:99-118.

Stace, C.A. 1965. Cuticular studies as an aid to plant taxonomy. *Bulletin of the British Museum (Natural History), Botany*, 4:1-78.

Stebbins, G.L. and Khush, G.S. 1961. Variation in the organization of the stomatal complex in the leaf epidermis of monocotyledons and its bearing on their phylogeny. *American Journal of Botany*, 48:51-59.

Stockey, R.A. and Atkinson, I.J. 1993. Cuticle micromorphology of *Agathis* Salisbury. *International Journal of Plant Sciences*, 154:187-225.

Stover, L.E. and Partridge, A.D. 1973. Tertiary and Late Cretaceous spores and pollen from the Gippsland Basin, southeastern Australia. *Proceedings of the Royal Society of Victoria,* 85:237-286.

Tomlinson, P.B. 1974. Development of the stomatal complex as a taxonomic character in the Monocotyledons. *Taxon*, 23:109-128.

Upchurch, G.R., Jr. and Dilcher, D.L. 1990. Cenomanian angiosperm leaf megafossils, Dakota Formation, Rose Creek locality, Jefferson County, southeastern Nebraska. *U.S. Geological Survey Bulletin*, 1915:1-52.

Vadala, A.J. and Greenwood, D.R. 2001. Australian Paleogene vegetation and. environments: evidence for palaeo-Gondwanic elements in the fossil records of Lauraceae and Proteaceae, p. 201-226. In Metcalfe, I., Smith, J.M.B., Morwood, M., and Davidson, I. (eds.), *Faunal and floral migration and evolution in SE Asia-Australasia*. A.A. Balkema, Lisse.

Veblen, T.T., Kitzberger, T., Villalba, R., and Donnegan, J. 1999. Fire history in northern Patagonia: The roles of humans and climatic variation. *Ecological Monographsm* [Mike , should this be Monographism?] 69:47-67.

Veevers, J.J., Powell, C.M., and Roots, S.R. 1991. Review of seafloor spreading around Australia. I. Synthesis of the patterns of spreading. *Australian Journal of Earth Sciences*, 38:373-389.

von Berchtold F. and Presl, J.S. 1820. *O Prirozenosti Rostlin*. J. Krause, Prague.

Webb, L.J. 1959. A physiognomic classification of Australian rainforests. *Journal of Ecology*, 47: 551-70.

Webb, L.J., Tracey, J.G., and Williams, W.T. 1984. A floristic framework of Australian rainforests. *Australian Journal of Ecology*, 9:169-198.

Wells, P.M., and Hill, R.S. 1989. Leaf morphology of the imbricate-leaved Podocarpaceae. *Australian Systematic Botany*, 2:369-386.

Whitmore, T.C. 1984. *Tropical Rain Forests of the Far East*. English Language Book Society/Oxford University Press, Oxford.

Wilf, P., Wing, S.L., Greenwood, D.R., and Greenwood, C.L. 1998. Using fossil leaves as paleoprecipitation indicators: an Eocene example. *Geology*, 26:203-206.

Wilkinson, H.P. 1979. The plant surface (mainly leaf), pp. 97-157. In Metcalfe, C.R. and Chalk, L. (eds.), *Anatomy of the Dicotyledons Vol. 1*. Clarendon Press, Oxford.

Wing, S.L. and Greenwood, D.R. 1993. Fossils and fossil climate: the case for equable continental interiors. *Philosophical Transactions Royal Society, London*, B, 341:243-252.

Wing, S.L., Harrington, G.J., Bowen, G.J., and Koch, P.L. 2003. Floral change during the Initial Eocene Thermal Maximum in the Powder River Basin, Wyoming. *Geological Society of America Special Paper*, 369:425-440.

Wolfe, J.A. 1979. Temperature parameters of humid to mesic forests of eastern Asia and their relation to forests of other regions of the northern Hemisphere and Australasia. *U.S. Geological Survey Professional Paper*, 1106:1-37.

Wolfe, J.A. 1995. Paleoclimatic estimates from Tertiary leaf assemblages. *Annual Review Earth and Planetary Science*, 23:119-142.

Zachos, J.C., Pagani, M., Sloan, L., Thomas, E., and Billups, K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to Present. *Science*, 292:686-693.

Zachos, J.C., Röhl, U., Schellenberg, S.A., Sluijs, A., Hodell, D.A., Kelly, D.C., Thomas, E., Nicolo, M., Raffi, I., Lourens, L.J., McCarren, H., and Kroon, D. 2005. Rapid Acidification of the Ocean during the Paleocene-Eocene Thermal Maximum. *Science,* 308:1611-1615.

APPENDIX. TAXONOMIC DESCRIPTIONS

Gymnospermae Engler 1924
Cycadophyta Engler 1924
Pterostoma Hill 1980
Pterostoma hirsutus Hill and Pole 1994
Figure 4.1

Referred specimens and occurrence: S-283, R-70; SL5381, R-102.

Distinguishing features: Hill and Pole (1994) described *Pterostoma hirsutus* from the Cool Store Section. It is distinguished from other *Pterostoma* by the ornamentation of thick cuticular ridges.

?*Pterostoma* sp
Figure 4.2-4.4

Referred specimens and occurrence: SB0384, R-77; SB0690, R-105.

Distinguishing features: Two specimens have deeply sunken, gymnospermous stomata with some resemblance to *Pterostoma*, but without the surface ornamentation of *P. hirsutus*. They are included here for convenience, although they may represent some other form of non-coniferous gymnosperm, like a ginkgophyte.

Zamiaceae Horaninow 1834
Bowenia Hooker 1863
Bowenia eocenica Hill 1978
Figure 4.5-4.6

Referred specimens and occurrence: SL5190, R-04; SL5256, R-13; SL5059, R-21; SL5072, R-23; SL5081, R-24; SL5086, R-25; SL5097, R-26; SL5099, R-27; SL5152, R-32; SL5166, R-33; SL5016, R-61; SL5274, R-68; SL5400, R-74; SB0373, R-75; SL5265, R-76; SL5287; SL5420, R-79; R-104; SL5310, R-105.

Distinguishing features: This cuticle is identified as *Bowenia* on the basis of having stomates and epidermal cells in rows, stomates with irregularly shaped and typically elongate subsidiary cells, fusiform epidermal cells having periclinal walls of variable thickness (e.g., Greguss 1968) and by direct comparison with material published by Hill (1978), who described *Bowenia papillosa* and *B. eocenica* from the Eocene of New South Wales and Victoria. The Tasmanian fossils are identified with *B. eocenica* on the basis of absence of papillae.

Pinophyta Engler 1924
Araucariaceae Henkel and Hochstetter 1865
Agathis Salisbury 1807
Agathis sp.
Figure 5.1

Reference specimen and occurrence: SL5083, R-25; SL5354, R-30; SL5409, R-34; SL5021, R-68; SL5027, R-71; SL5283, R-104.

Distinguishing features: *Agathis* is identified on the basis of rounded, coniferous stomatal complexes which are obliquely oriented and under TLM have a strongly thickened ring of cuticle around the stomatal pore, which appears 'suspended' by radiating flanges (Bigwood and Hill 1985; Hill and Bigwood 1987; Stockey and Atkinson 1993; Pole 2007b).

Araucaria Jussieu 1789.
Araucaria sp. A
Figure 5.2

Reference specimen and occurrence: SL5077, R-24; SL5163, R-33.

Distinguishing features: In this study, *Araucaria* cuticle is recognised as araucarian cuticle with obliquely oriented stomatal complexes and elongate epidermal cells. See Pole (2000) for further discussion of these features.

Araucaria sp. B
Figure 5.3

Referred specimens and occurrence: SL4995, R-43.

Distinguishing features: A single fragment has typical araucarian structure but with stomatal complexes that are aligned to the long axis of the leaf.

Araucarioides Bigwood and Hill 1985
Araucarioides sp.
Figure 5.4

Referred specimens and occurrence: SL5191, R-04; SL5207, R-08; SL5075, R-23; SL5115, R-30 ; SL5178, R-38; SL4997, R-47; SL5279, R-68; SL5026, R-71; SB0331, R-74; SL5033, R-75; SL5263, R-76; SL5290, R-104; SL5308, R-105.

Distinguishing features: In this study, *Araucarioides* cuticle is recognised as araucarian cuticle with obliquely oriented stomatal complexes and isodiametric epidermal cells. See Pole (2000) for further discussion. Bigwood and Hill (1985) described *Araucarioides linearis* and *A. sinuosa* from Regatta Point. All material found in this study has straight, rather than sinuous epidermal cell walls. Although sinuous epidermal cells walls were noted in the

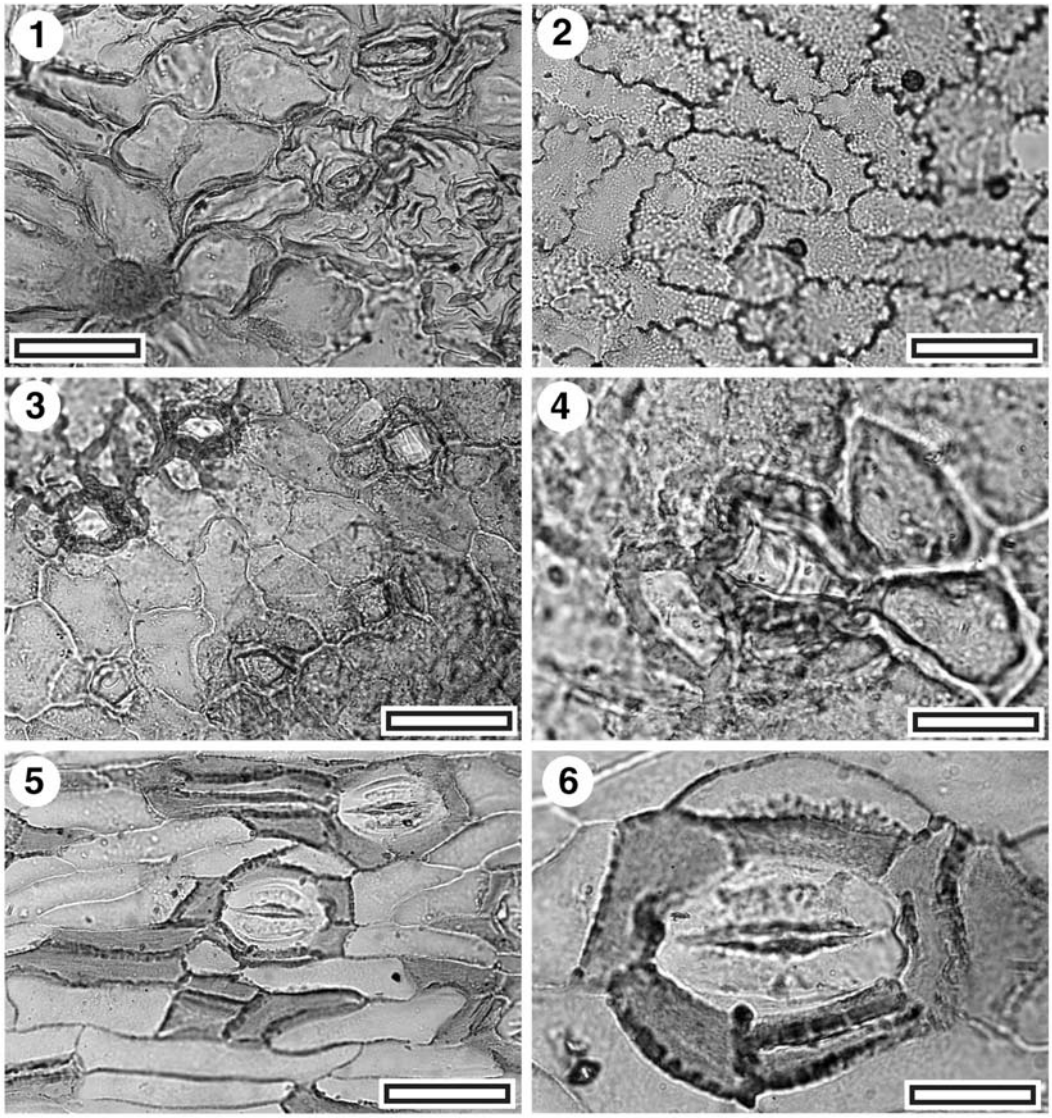

Figure 4. *Pterostoma* sp. and *Bowenia* sp. **1.** *Pterostoma hirsurtus*. TLM view showing stomata at right, surrounded by prominent ridges of cuticle, and, lower left, a trichome base (SL5381, scale-bar = 50 µm); **2.** ?*Pterostoma*. TLM view showing a single stomatal complex (SB0384, scale-bar = 50 µm); **3.** ?*Pterostoma*. TLM view showing five stomatal complexes (SB0690, scale-bar = 50 µm); **4.** ?*Pterostoma*. TLM detail of a single stomatal complex. Note massively thickened ring around stomatal pore (SB0690, scale-bar = 20 µm); **5.** Bowenia. TLM view showing two stomatal complexes. Note differently thickened peristomatal walls of epidermal and subsidiary cells (SL5059, scale-bar = 50 µm); **6.** CUT-Z-ACB. TLM detail of a single stomatal complex (SL5335, scale-bar = 20 µm).

etymology of *A. sinuosa*, this featured is not mentioned in the diagnosis and is not apparent in Bigwood and Hill's (1985) figures.

Cupressaceae Bartling 1830
Libocedrus Endlicher 1847
Libocedrus sp.
Figure 5.5

Reference specimen and occurrence: SL5128, R-30.

Distinguishing features: Very small scale-like leaves which have monocyclic stomatal complexes and calcium oxalate crystals within the cuticle of the epidermal cells clearly belong in Cupressaceae sensu stricto. They are most likely a species of *Libocedrus* (Florin and Boutelje 1954). Ruling-out the closely related *Austrocedrus* (not distinguished from *Libocedrus* by all botanists) would require more complete material, although there is a broad habitat difference, with *Libocedrus* predominant in

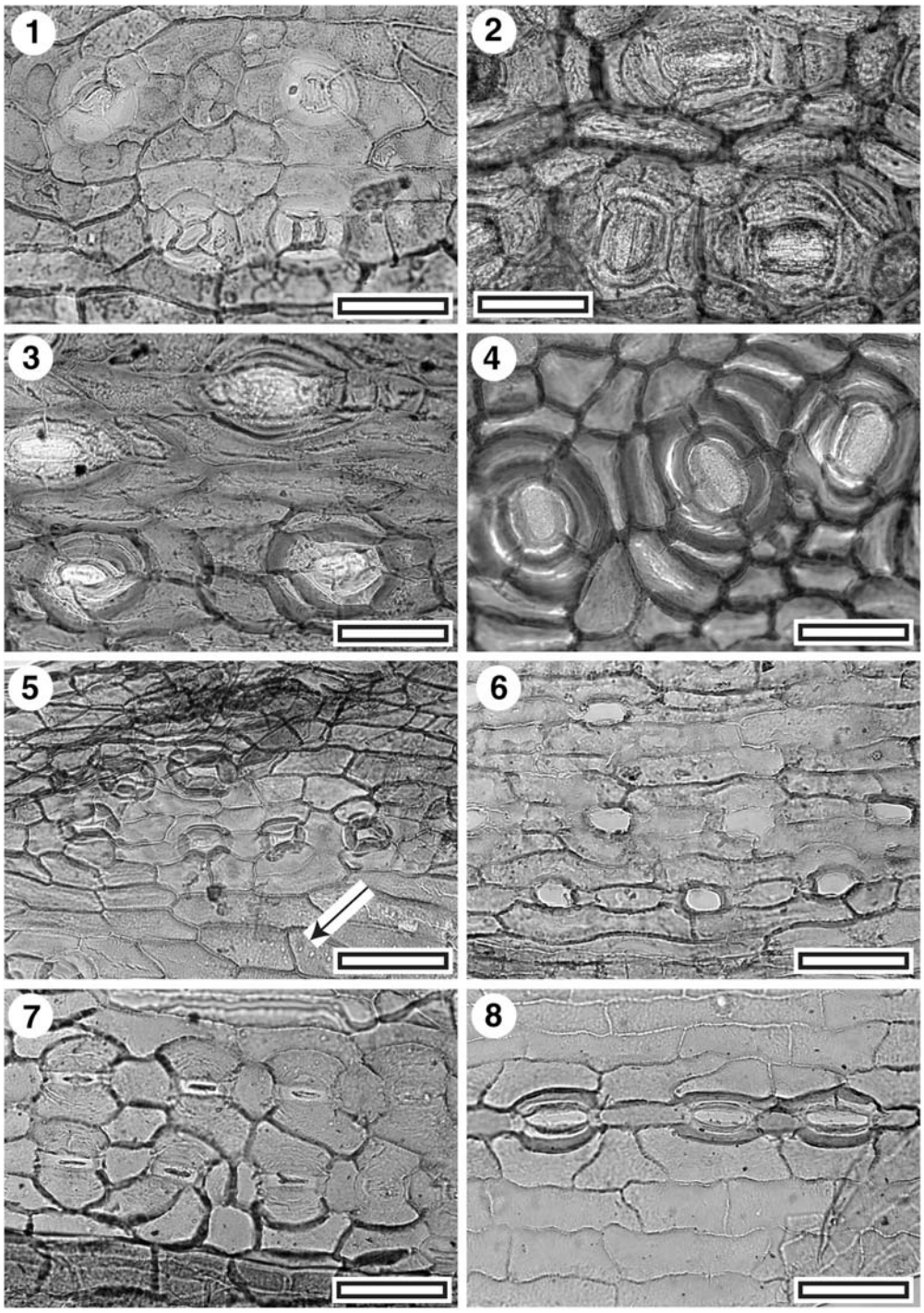

Figure 5. Conifers. **1.** *Agathis* sp. TLM view showing two rows of stomatal complexes (SL5021, scale-bar = 50 µm); **2.** *Araucaria* sp. A. TLM view showing two rows of stomatal complexes (SL5077, scale-bar = 50 µm); **3.** *Araucaria* sp. B. TLM view showing two rows of stomatal complexes (SL4995, scale-bar = 50 µm); **4.** *Araucarioides* sp. TLM view showing a row of stomatal complexes (SL5178, scale-bar = 50 µm); **5.** *Libocedrus* sp. TLM view showing a patch of stomatal complexes. Note networking. Arrow indicates group of calcium oxalate crystals (SL5128, scale-bar = 50 µm); **6.** Cupressaceae sp. A. TLM view showing three rows of stomatal complexes. Note common sharing of subsidiary cells between complexes (SL5122, scale-bar = 50 µm); **7.** *Acmopyle sp*. TLM view showing two rows of stomatal complexes. Note distinctive small stomata and broad lateral subsidiary cells with sloping walls (SL5183, scale-bar = 50 µm); **8.** *Dacrycarpus sp*. TLM view showing a single row of chained stomatal complexes (SL5114, scale-bar = 50 µm).

very wet rainforest habitat (Farjon 2005), and *Austrocedrus* common in drier, sometimes woodland habitats and perhaps with more of a fire-association than *Libocedrus* (Kitzberger and Veblen. 1999; Veblen et al. 1999).

Cupressaceae Bartling 1830
Cupressaceae sp. A.
Figure 5.6

Reference specimen and occurrence: SL5122, R-30.

Distinguishing features: This has a very distinctive morphology of monocyclic stomatal complexes, which are in rows and where there is a high degree of networking. Lateral subsidiary cells are often shared between two or even three stomatal complexes in the same row, and subsidiary cells are sometimes shared between stomatal complexes in adjacent rows. These characters identify it as Cupressaceae sensu stricto. A papillate rim around the stomatal aperture is not pronounced and there are no calcium oxalate crystals. However, neither of these characters is ubiquitous within Cupressaceae.

Podocarpaceae Endlicher 1847
Acmopyle Pilger 1903
Acmopyle glabra Hill and Carpenter 1991
Figure 5.7

Referred specimens and occurrence: SL5183, R-01; SL5209, R-08; SL5211, R-09; SL5258, R-12; SL5247, R-13; SL5080, R-24; SL5101, R-27; SL5103, R-28; SL5108, R-29; SL5147, R-30; SL5156, R-35; SL5171, R-36; SL5008, R-56; SL5275, R-68; SL5029, R-71; SB0333, R-74; SL5036, R-76.

Distinguishing features: *Acmopyle* has very characteristic stomatal complexes under TLM; the lateral subsidiary cell walls slope gradually from the periclinal to anticlinal position and vary a lot in shape and number (Hill and Carpenter 1991; Pole 1997a). The polar subsidiary cells are often shared, and there are typically many incompletely formed stomatal complexes. *Acmopyle glabra* was described from Regatta Point by Hill and Carpenter (1991) and has the distinctive stomatal structure of the genus, but lacks the trichomes which are found in some species.

Dacrycarpus de Laubenfels 1969
Dacrycarpus sp.
Figure 5.8

Referred specimens and occurrence: SL5114, R-29; SL5276, R-68.

Distinguishing features: *Dacrycarpus* has elongated stomatal complexes in chains, which are present in zones of typically only one–three rows, and associated with smooth, elongate epidermal cells (Hill and Carpenter 1991; Pole 1992).

Prumnopitys Philippi 1861
Prumnopitys sp.
Figure 6.1

Referred specimens and occurrence: SL5110, R-29; SL5131, R-30; SL5414, R-37; SB0356, R-75; SL5261, R-76; SL5303, R-105.

Distinguishing features: *Prumnopitys* has distinctive stomatal complexes where the subsidiary cells tend to bulge out from their common walls, and a distribution where the nearest neighbouring complex is usually in an adjacent row (Pole 1992a, 1997a)

Indet. Podocarpacae

The following taxa are all regarded as most likely Podocarpaceae based on longitudinally-oriented, dicyclic and paratetracyclic stomata (e.g. Wells and Hill 1989; Hill and Carpenter 1991; Hill and Pole 1992; Hill and Brodribb 1999) and their biogeographic context.

Podocarpaceae sp. A
Figure 6.2

Referred specimens and occurrence: SL5186, R-02; SL5195, R-04; SL5074, R-23; SL5082, R-25; SL5140, R-30; SL5165, R-33; SL5410, R-34; SL5169, R-36; SL5005, R-56; SL5272, R-68; SL5281, R-104; SL5306, R-105.

Distinguishing features: This cuticle type has some resemblance to *Acmopyle*, but the more crowded bands of stomatal complexes and their more angular outline differ from *A. glabra*. The generic identification is not certain.

Podocarpaceae sp. B
Figure 6.3

Referred specimens and occurrence: SL5237, R-12.

Distinguishing features: This cuticle morphology has rows of very isodiametric epidermal cells. They may be partially formed stomatal complexes, as

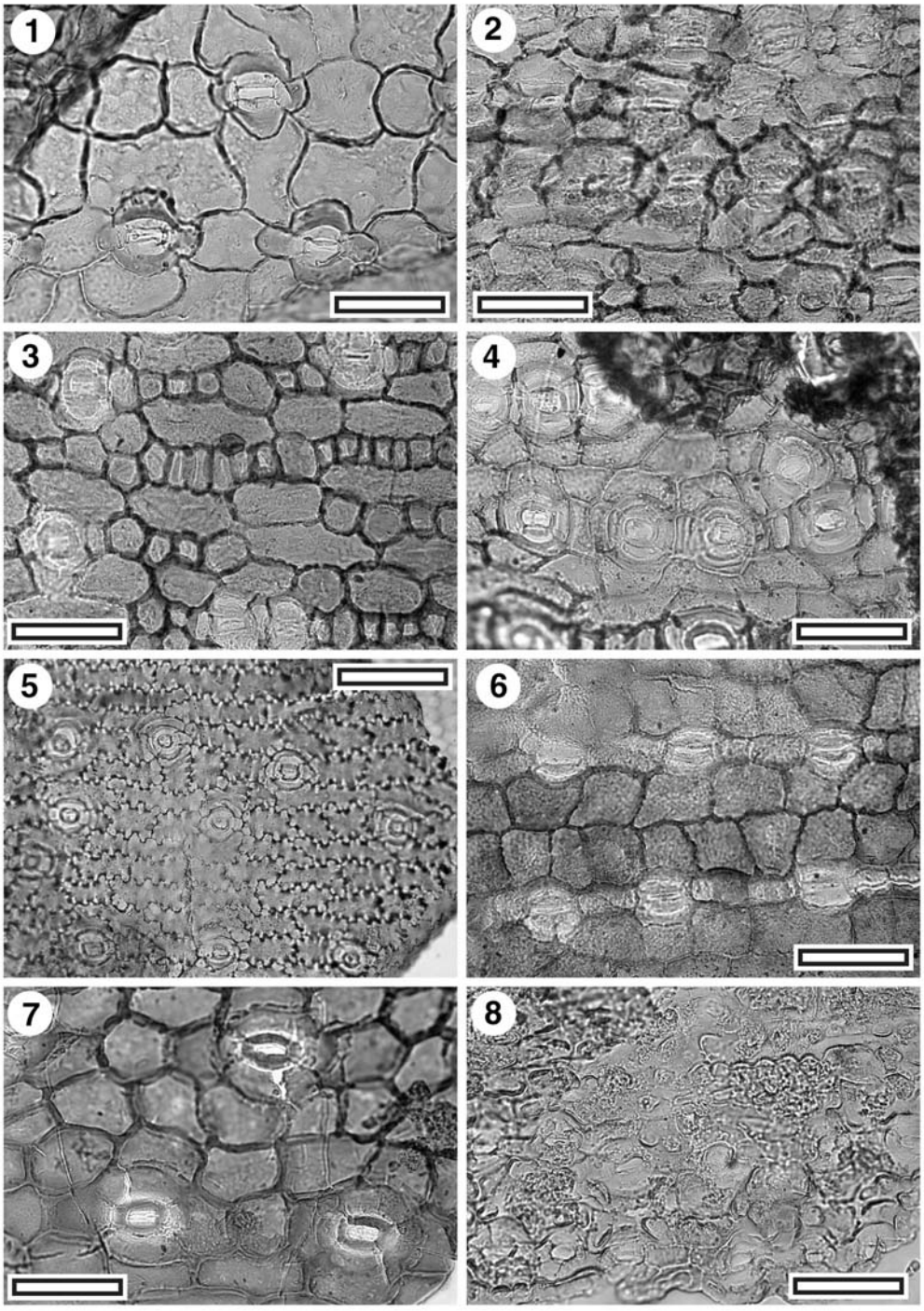

Figure 6. Conifers. **1.** *Prumnopitys* sp. TLM view showing two overlapping rows of stomatal complexes. Note typical bulging outline of complexes (SL5131, scale-bar = 50 µm); **2.** Podocarpaceae sp. A. TLM view showing several crowded rows of stomatal complexes (SL5186, scale-bar = 50 µm); **3.** Podocarpaceae sp B. TLM view showing stomatal complexes and rows of small, isodiametric cells (SL5237, scale-bar = 50 µm); **4.** Podocarpaceae sp. C. TLM view showing two rows (and one partially obscured) of stomatal complexes. Note narrow subsidiary cells (SL5142, scale-bar = 50 µm); **5.** Podocarpaceae sp. E. TLM view showing scattered stomatal complexes. Note prominent buttressing and sinuous walls (SL5020, scale-bar = 50 µm); **6.** Podocarpaceae sp. F. TLM view showing two rows of stomatal complexes. Note broad cells flanking complexes (SL5240, scale-bar = 50 µm); **7.** Podocarpaceae sp. G. TLM view showing three stomatal complexes (SL5159, scale-bar = 50 µm); **8.** Taxaceae? TLM view showing overlapping rows of stomatal complexes and prominent papillae (SL5132, scale-bar = 50 µm).

found in *Acmopyle*, but the stomatal form is very distinct.

Podocarpaceae sp. C
Figure 6.4

Referred specimens and occurrence: SL5142, R-30.

Distinguishing features: This cuticle morphology has rows of very circular stomatal complexes in which subsidiary cells are often very thin.

Podocarpaceae sp. E
Figure 6.5

Referred specimens and occurrence: SL5020, R-68.

Distinguishing features: The highly sinuous and buttressed epidermal cells of this morphology are very distinctive. The stomatal distribution and, to a lesser degree, outline, suggest *Prumnopitys*.

Podocarpaceae sp. F
Figure 6.6

Referred specimens and occurrence: SL5214, R-11; SL5240, R-12; SL5091, R-26; SL5351, R-30; SL4994, R-43.

Distinguishing features: This cuticle is recognised by small and narrow stomatal complexes in chains with very broad cells flanking the lateral subsidiary cells, and in zones at least seven stomatal rows wide.

Podocarpaceae sp. G
Figure 6.7

Referred specimens and occurrence: SL5159, R-33; SL5200, R-06; SL5242, R-13; SL5369, R-15; SL5370, R-16.

Distinguishing features: This is a more generalised morphological of Podocarpaceae cuticle with more isodiametric epidermal cells and with a distinctively thickened ring of cuticle around the stomatal pore. Further study may show that some of the specimens listed above come from distinct taxa.

Taxaceae? von Berchtold & Presl 1820
Figure 6.8

Referred specimens and occurrence: SL5132, R-30.

Distinguishing features: The distinctive feature of this cuticle is the papillae found on the subsidiary and epidermal cells. In this respect and in general morphology it resembles *Kahahuia* (Pole 1997b), which has been placed in the Taxaceae (Pole 2007b). Similar material was illustrated by Carpenter et al. (2004).

Gnetalaceae Lindley 1834
CUT-Z-GDB
Figure 7

Reference specimen and locality: SL5298, R-104.

Referred specimens and occurrence: SL5187, R-02; SL5189, R-03; SL5205, R-07; SL5111, R-29; SL5145, R-30; SL5153, R-32; SL4993, R-42; SL5018, R-68.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread on stomatal surface, isolated, randomly oriented, essentially brachyparacytic, but also with subsidiary cells modified by a tangential division, giving two lateral and two polar cells at right angles to stomatal axis, size range unimodal, at same level as normal epidermal cells. Subsidiary cell periclinal walls same thickness as normal epidermal cells. Guard cell pair outline distinctly elongate-rectangular, outlined by a well-defined anticlinal wall, length 27–37 µm (medium), at same level as subsidiary cells (exposed on surface), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge not apparent, outermost cuticle possibly lying directly over guard cells, much thinner than normal epidermal cells, often broken away, with a slit-like pore.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, normal cells typically elongate, larger than the stomata, cells over veins not differentiated, anticlinal walls wavy, unbuttressed, unornamented.

Indumentum. Glabrous.

Distinguishing features. Distinguished by the distinctive shape of the guard cell pair; elongated rectangles, with no division at the polar ends, with very thin cuticle overlying them, and a slit-like pore.

Identification. This very distinctive shape of the guard cells links this taxon with *Gnetum* in the Gnetaceae (Figures 7.2, 7.4, and see Paliwal et al. 1974; Nautiyal et al. 1976). However, all the extant *Gnetum* appear to have purely brachyparacytic stomatal complexes, whereas the fossil commonly has a pair of polar subsidiary cells as well as a pair of lateral subsidiary cells. This suggests CUT-Z-GDB represent an extinct genus of Gnetaceae.

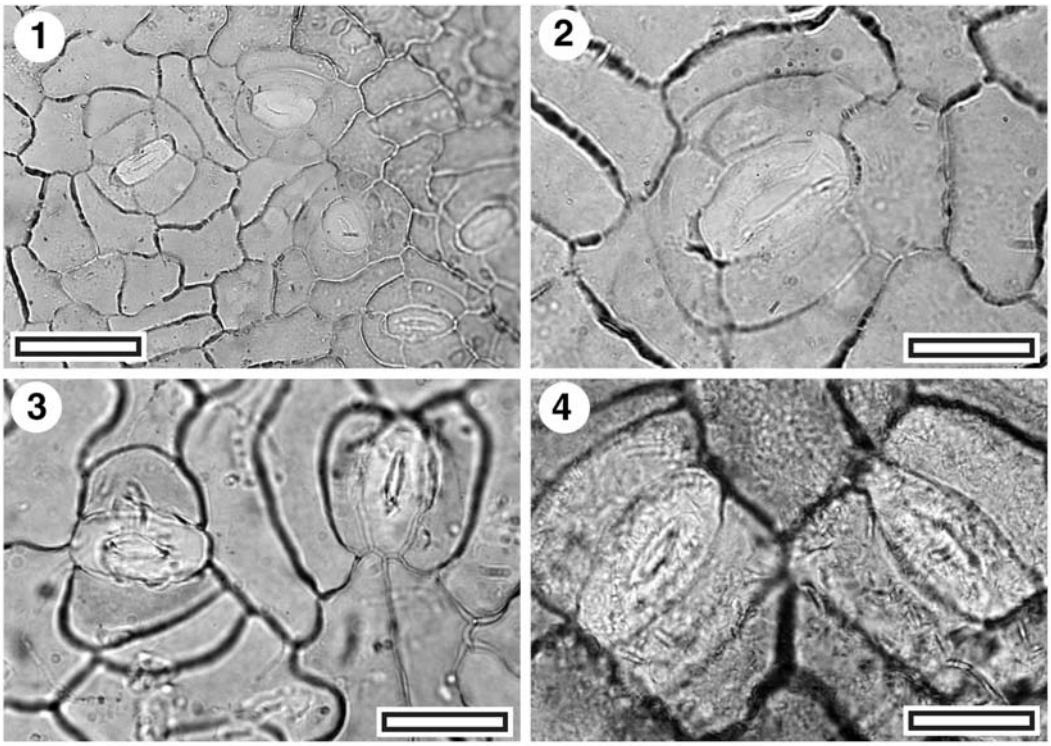

Figure 7. Fossil and extant Gnetales. **1.** CUT-Z-GDB. TLM view showing five stomatal complexes (SL5298, scale-bar = 50 µm); **2.** CUT-Z-GDB. TLM detail of a single stomatal complex. Note the much thinner cuticle over the guard cells (SL5298, scale-bar = 20 µm); **3.** Extant *Gnetum gnemon* (AQ142124, scale-bar = 20 µm); **4.** *G. microcarpum* (AQ142225, scale-bar = 20 µm).

Magnoliospida Cronquist 1981
Winteraceae Lindley 1830
CUT-Z-DDD
Figure 8.1-8.5

Reference specimen and locality: SB0756, R-102.

Referred specimens and occurrence: SB0360, R-75.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, brachyparacytic, size range unimodal. Subsidiary cells typically elongate tangential to stomata and often longer than the stomata, periclinal walls of same thickness as normal epidermal cells, unornamented. Guard cell pair outline elliptical, outlined by a well-defined anticlinal wall, length 25-35 µm (medium). Outer stomatal ledge elliptical, extending from outer edge of stoma, same thickness as normal epidermal cells, pore elliptical.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, highly variable from isodiametric to elongate, approximately the same size, or slightly smaller than the stomata, anticlinal walls straight to curved, unbuttressed, coarsely granular, unornamented.

Indumentum. Glabrous. Lid-cells present, consisting of four cells slightly smaller than normal epidermal cells, but with thinner cuticle.

Distinguishing features. Paracytic subsidiary cells and coarsely granular cuticle.

Identification. The brachyparacytic stomatal complexes, prominent outer stomatal ledges and coarsely granular epidermal cells suggest this as Winteraceae (Figures 8.6-8.8), although the lack of granular plugging of the stomatal pore (typical of extant species) introduces an element of doubt. One of the only two specimens (SB0360) has what is interpreted as a four-parted complex of lid cells (forming a lid over a gland). There is no ridge or scar on this structure which might indicate it was some form of trichome base. The presence of lid cells is intriguing, only one taxon of Winteraceae is known to me to have lid cells, *Bubbia semecarpoides*, but these are single-celled.

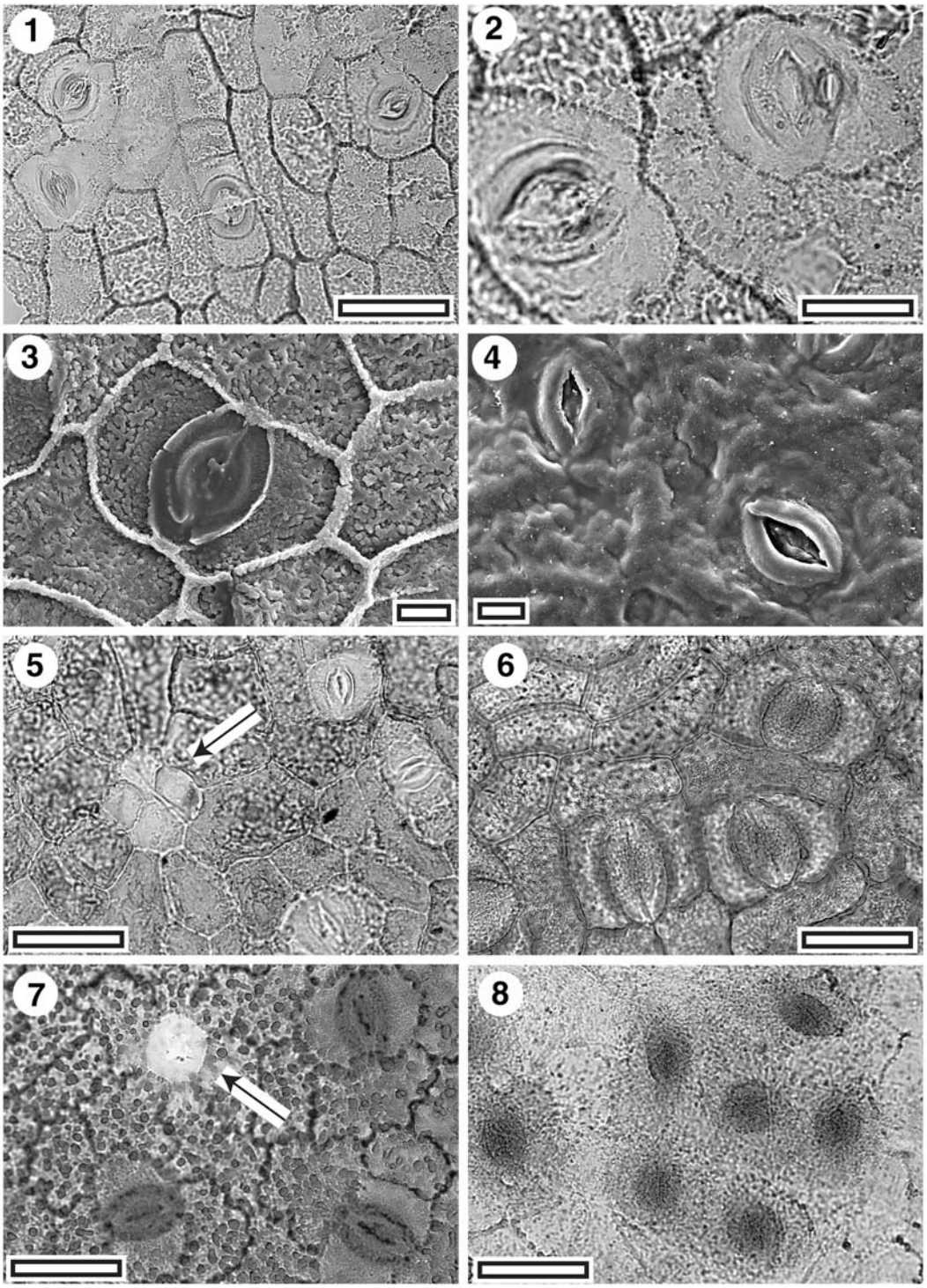

Figure 8. Winterceae, fossil and extant. **1.** CUT-L-DDD. TLM view showing stomatal complexes (SB0756, scale-bar = 50 µm); **2.** CUT-L-DDD. TLM view showing two stomatal complexes (SB0756, scale-bar = 20 µm); **3.** SEM view of inner cuticular surface showing single stomatal complex. Note very granular surface of epidermal cells (S-1537, scale bar = 10 µm); **4.** SEM view of outer cuticular surface showing two stomatal complexes. Note prominent outer stomatal ledges, but without plugged pores (S-1537, scale-bar = 10 µm); **5.** CUT-L-DDD. TLM view showing lid cell complex indicated with an arrow (SB0360, scale-bar = 50 µm); **6.** Extant *Zygogynum balansae*, TLM view showing three stomatal complexes. (AQ391241, scale-bar = 50 µm); **7.** Extant *Bubbia semecarpoides*, TLM view showing lid cell indicated with an arrow (AQ546547, scale-bar = 50 µm); **8.** Extant *Belliolum burttianum*, TLM view showing a group of stomatal complexes. (AQ463392, scale-bar = 50 µm).

Monocots

Parallel-veined monocot cuticle is identified on the basis of stomatal complexes which are aligned along the long axis of the leaf, and typically have a paratetracytic structure, or some derivative of it (Stebbins and Khush 1961; Tomlinson 1974; Dahlgren and Clifford 1982). Some conifers have this structure but differ from monocots in having guard cells overarched by the subsidiary cells. The cuticle of the net-veined monocots is fundamentally different and is identified by direct comparison with living taxa.

Key to Parallel-veined Monocot cuticle

1. Trichome bases present. **CUT-Z- JJG** (Arecaceae)
1. Trichome bases absent. 2.

2. Cuticle very thin, outer stomatal ledges thickest part of cuticle. **CUT-Z-JBC**
2. Stomatal complexes large and subsidiary cell cuticle robustly thickened. **CUT-Mo-GCE**

Rhipogonaceae Conran and Clifford 1985
CUT-Z-JAI (*Rhipogonum* sp.)
Figure 9.1-9.2

Reference specimen and locality: SB0388, R-75.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, brachyparacytic, size range unimodal. Subsidiary cells irregularly shaped, periclinal walls same thickness as normal epidermal cells, ornamented with a more or less continuous ridge flanking the outer stomatal ledge. Guard cell pair outline circular, outer margin obscured under TLM by surface ornamentation, length 25–33 µm (medium), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge a distinctive 'lemon' shape, broad in the middle, and narrowing sharply at either end, thicker than normal epidermal cells, extending over inner edge of stoma, pore elliptical - subcircular.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate, typically slightly larger than the stomata, cells over major veins more elongate, anticlinal walls markedly sinuous, unbuttressed, unornamented.

Indumentum. Glabrous.

Distinguishing features. Brachyparacytic stomatal complexes with highly sinuous epidermal cell walls.

Identification: The cuticle is identified as *Rhipogonum* based firstly on the distinctive brachyparacytic stomatal complexes, and highly sinuous epidermal cell walls. The rather similar *Smilax* tends to have smaller stomata and more diffuse epidermal cell walls, although there is some overlap. A very similar form of cuticle is present on Early Miocene leaves in New Zealand with *Rhipogonum* leaf architecture (Pole 1996). Along with impressions of the family from Melville Island, furthest north Australia, which are likely of early Tertiary age (Pole 1998c) these are the earliest record of the family in Australia.

Arecaceae Schultz 1832
CUT-Mo-JJG
Figure 9.3-9.4

Reference specimen and locality: SB0744, R-70.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, isolated, aligned parallel to long axis of leaf, brachyparacytic, size range unimodal. Subsidiary cells typically elongate tangential to stomata, periclinal walls same thickness as normal epidermal cells, ornamented by a ridge above the distal wall. Guard cell pair outline narrowly elliptic, outlined by a well-defined anticlinal wall, length 20–23 µm (medium), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge not clear, same thickness as normal epidermal cells, pore elliptical.

Epidermal Cells. Epidermal cell flanges somewhat diffuse, approximately the same size, or slightly smaller than the stomata, anticlinal walls sinuous, unbuttressed, unornamented.

Indumentum. With sparse scars of trichome bases (trichomes deciduous), inserted between epidermal cells, with a thickened poral rim.

Distinguishing features. Monocot cuticle with trichome insertion scars with smooth, thickened poral rims.

Identification. Based on the trichome insertion scars this is regarded as Arecaceae.

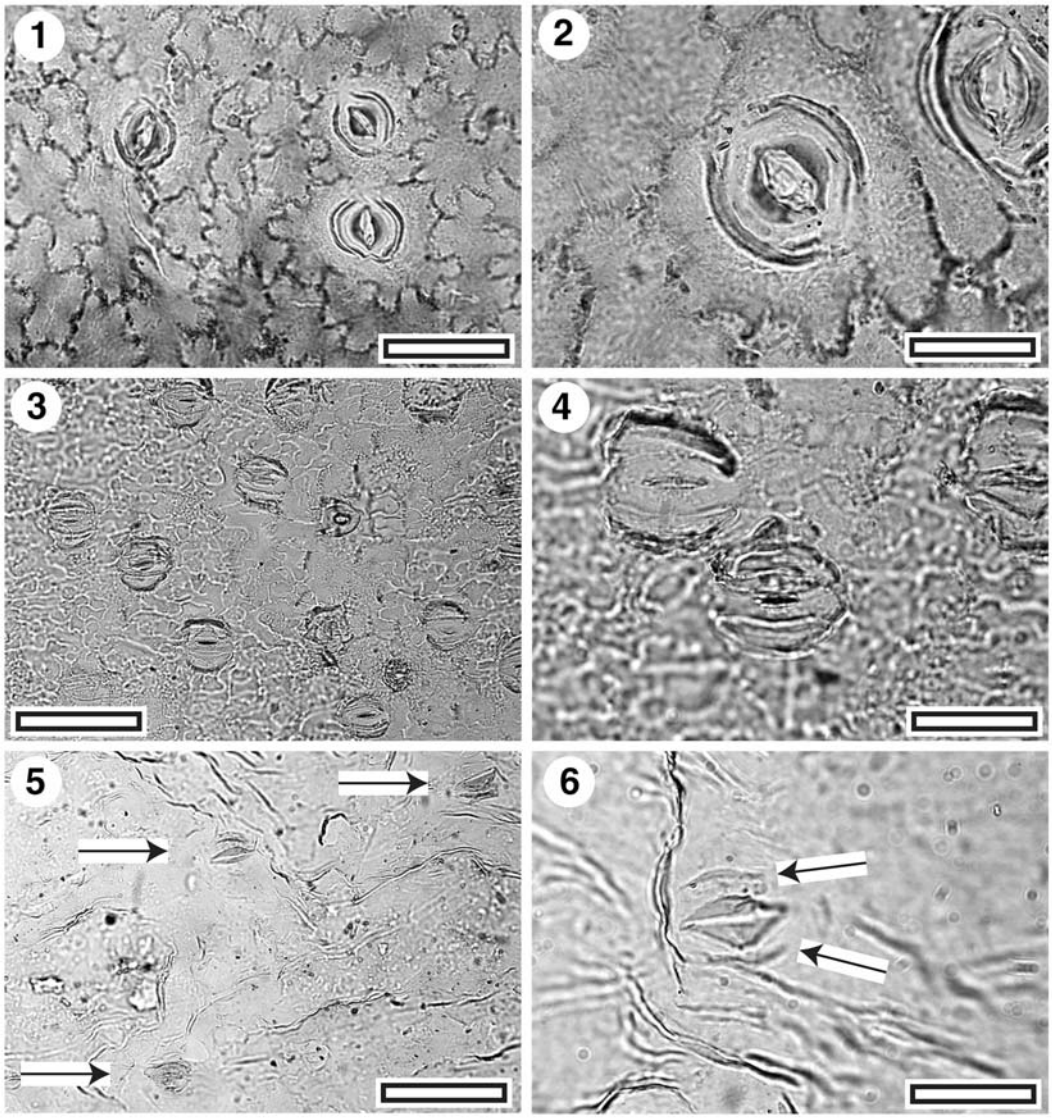

Figure 9. Monocots. **1.** CUT-Z-JAI. TLM view showing three stomatal complexes (SB0388, scale-bar = 50 µm); **2.** CUT-Z-JAI. TLM detail of two stomatal complexes (SB0388, scale-bar = 20 µm); **3.** CUT-Mo-JJG. TLM view showing several stomatal complexes, and (to right of centre) a smooth, thickened trichome insertion scar (SB0744, scale-bar = 50 µm); **4.** CUT-Mo-JJG. TLM view showing three stomatal complexes (SB0744, scale-bar = 20 µm); **5.** CUT-Mo-JBC. TLM view showing (arrowed) three stomatal complexes (SB0393, scale-bar = 50 µm); **6.** CUT-Mo-JBC. TLM detail of a single stomatal complex with (arrowed) flanking ridges of cuticle (SB0393, scale-bar = 20 µm).

Indet. Monocots
CUT-Mo-JBC
Figure 9.5-9.6

Reference specimen and locality: SB0393, R-75.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, showing a clear trend towards alignment, size range unimodal. Subsidiary cells difficult to count under TLM, periclinal walls same thickness as normal epidermal cells. Guard cell pair outline difficult to distinguish, length 25–28 µm (medium). Outer stomatal ledge narrowly elliptic, thicker than normal epidermal cells, extending over inner edge of stoma, pore slit-like.

Epidermal Cells. Epidermal cell flanges very thin or absent (anticlinal walls of epidermal cells not clear under TLM), normal cells elongated, anticlinal walls straight to curved, unbuttressed, unornamented.

Indumentum. Glabrous.

Distinguishing features. Monocot cuticle which is very thin with only the narrowly elliptic outer stomatal ledges being prominent. Sometimes with single ridges of cuticle flanking the outer stomatal ledges.

CUT-Mo-GCE
Figure 10

Reference specimen: SL4999, R-47.

Referred specimens and occurrence: SL5199, R-06; SL5238, R-12; SL5255, R-13; SL5052, R-21; SL4999, R-47; SL5430, R-74; SL5425, R-79.

Description. Epidermis not divided into costal and intercostal zones (stomata evenly spread). Stomatal complexes paratetracytic, with four subsidiary cells (two polar and two lateral, the lateral subsidiary cells, or both the lateral and polar subsidiary cells have much thicker anticlinal walls than normal epidermal cells), with a typically angular outline, not in rows or chains, but widely scattered (nearest neighbour often to the side), longitudinally oriented. Subsidiary cells with periclinal walls thinner than those of normal epidermal cells, not papillate. Outer stomatal ledge 30–43 µm long, distinctly elliptical, with elongate aperture, cuticle thicker than normal epidermal cells. Epidermal cells clearly visible under TLM, in clear rows, elongate, straight-walled, unbuttressed, glabrous, not papillate.

Distinguishing features. Typical monocot cuticle but with subsidiary cells with prominently thickened anticlinal walls.

Lauraceae Jussieu 1789

Lauraceae cuticle is identified on the basis of paracytic stomatal complexes with guard cells embedded within the subsidiary cells, and the presence of cuticular scales, or flanges between them (Bandulska 1926, Hill 1986, Christophel et al. 1996, Vadala and Greenwood 2001). Lauraceae have simple, deciduous, trichomes with poral bases. This clearly distinguishes them from Myristicaceae which have a similar stomatal structure, but multi-celled trichome bases (Upchurch and Dilcher 1990, Pole, pers. obs.) Identification with extant genera of Australasian Lauraceae is based on Christophel and Rowett (1996).

Key to Lauraceae cuticle

1. Stomatal complexes aligned. **CUT-L-DDE**
1. Stomatal complexes randomly oriented. 2.

2. Surface ornamented with prominent striations. **CUT-L-DDC**
2. No striations. 3.

3. Papillae present. 4.
3. Papillae not present. 5.

4. Whole surface of epidermal cells surfaces raised in "bubble-like" fashion. **CUT-L-JEC**
4. Papillae distinct, with the margins of the epidermal cell. **CUT-L-GCI**

5. Anticlinal walls of subsidiary cells and those cells in contact with subsidiaries are markedly thickened. **CUT-L-DCG**
5. Anticlinal wall thickness of subsidiary and ordinary epidermal cells similar. 6.

6. Epidermal cells sinuous or markedly wavy. **CUT-L-DCD**
6. Epidermal cells polygonal or only slightly wavy. 7.

7. Epidermal cells immediately surrounding stomatal complex typical in an anisocytic pattern (and often stain slightly darkly than normal epidermal cells). **CUT-L-DCI**
7. Epidermal cells immediately surrounding stomatal complex not in any discernable pattern (and all epidermal cells staining similarly). 8.

8. Subsidiary cells of distinctly different thickness (staining differently) than normal epidermal cells. 9.
8. Subsidiary cells staining similarly to or less than epidermal cells. 10.

9. Subsidiary cells staining less than epidermal cells. 14.
9. Subsidiary cells staining more than epidermal cells, trichome bases present and strongly thickened. **CUT-L-DCF**

10. Cuticular scales distinctly ‘double’. **CUT-L-DDJ**
10. Cuticular scales not ‘double’. 11.

11. Stomatal complex large. **CUT-L-DCH**
11. Stomatal complex small-medium. 12.

12. Stomatal complex medium, cuticle of moderate thickness.
12. Stomatal complexes small, cuticle very thin. 13.

13. Outline of stomatal complex slightly overgrown by cuticle. **CUT-L-JBI**
13. Outline of stomatal complex not overgrown by cuticle. **CUT-L-JBA**

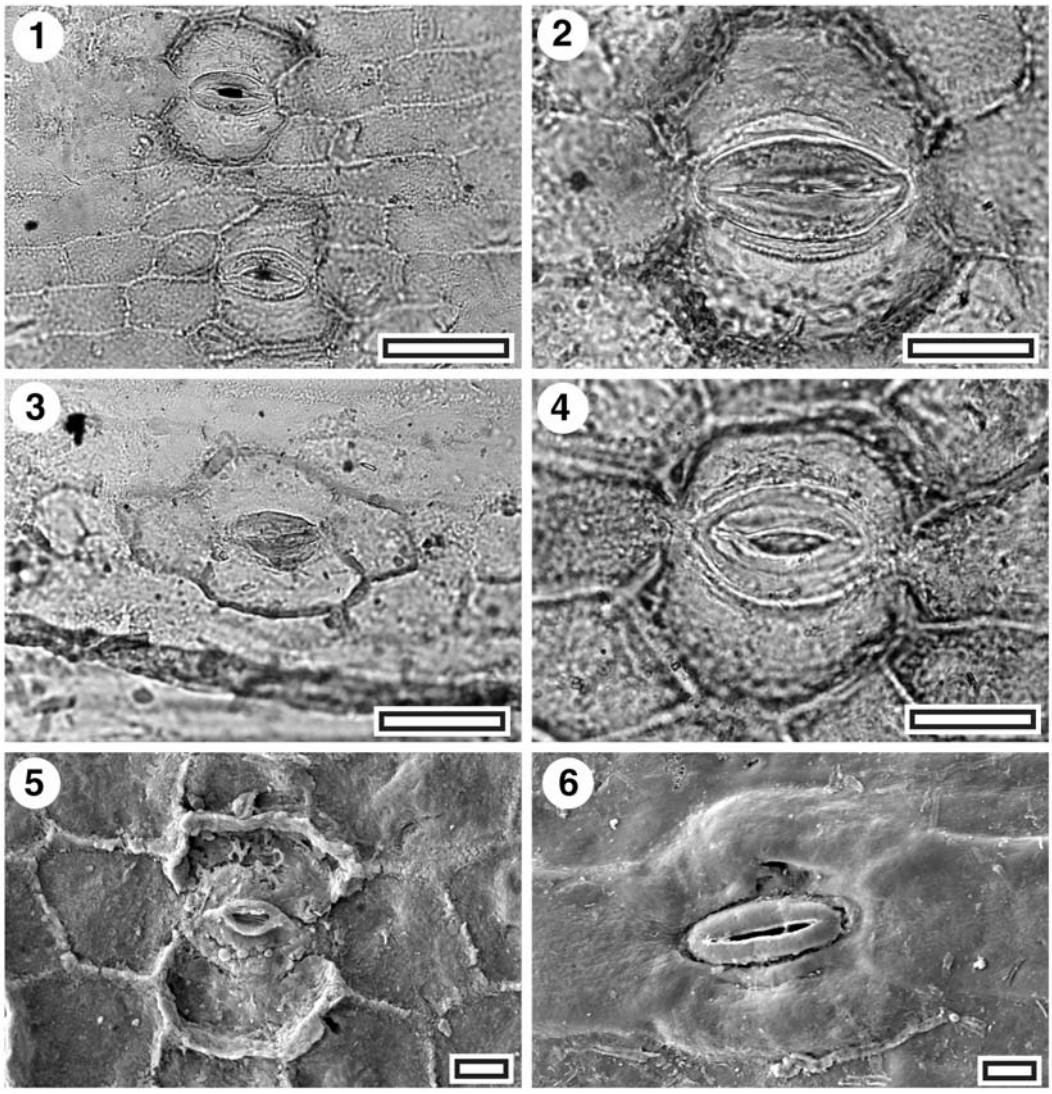

Figure 10. Indeterminate monocot. **1.** CUT-Mo-GCE. TLM view showing two stomatal complexes with thickened lateral subsidiary cell walls (SL4999, scale-bar = 50 µm); **2.** CUT-Mo-GCE. TLM detail of a single stomatal complex (SL4999, scale-bar = 20 µm); **3.** CUT-Mo-GCE. TLM view showing a stomatal complex with thickened lateral and polar subsidiary cell walls (SL5199, scale-bar = 50 µm); **4.** CUT-Mo-GCE. TLM detail of a single stomatal complex (SL5062, scale-bar = 20 µm); **5.** SEM view of inner cuticular surface showing single stomatal complex. Note thickened walls of lateral subsidiary cells (S-1682, scale-bar = 10 µm); **6.** SEM view of outer cuticular surface showing single stomatal complex. Note prominent elliptical outer stomatal ledges (S-1682, scale-bar = 10 µm).

14. Essentially glabrous. CUT-L-GCG
14. With prominent trichome insertion scars. CUT-L-GCH

CUT-L-DDE
Figure 11.1-11.2

Reference specimen and locality: SB0730, R-16.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, evenly spread, isolated, transversely oriented, paracytic, outline typically broader than long, length 28–38 µm (medium). Subsidiary cell periclinal cuticle thinner than over normal epidermal cells. Cuticular scales narrow.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, cells over veins not distinguished by shape, normal epidermal cells isodiametric, walls straight, unbuttressed.

Indumentum. Glabrous, unornamented.

Distinguishing features. Lauraceae cuticle with stomatal complexes transverse to the long axis of the leaf.

CUT-L-DDC
Figure 11.3-11.6

Reference specimen and locality: SB0670, R-23.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, Stomatal complexes evenly spread, isolated, randomly oriented, paracytic, outline polygonal, length 28–38 µm (medium). Subsidiary cell periclinal cuticle thinner than over normal epidermal cells. Cuticular scales narrow.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, cells over fine venation poorly distinguished as 'venal' (elongated), normal epidermal cells isodiametric, walls straight to curved, unbuttressed.

Indumentum. With scars of trichome bases, ornamented with bands of ridges joining some stomatal complexes and radiating from trichome bases. Trichome insertion scars common (trichomes deciduous and therefore trichome type unknown), inserted between epidermal cells, modified with thickened poral rim and radial walls. Epidermal cells around trichome scar form a distinct ring of isodiametric foot cells.

Distinguishing features. Lauraceae cuticle with an ornamentation of ridges and with very thickened trichome insertion poral rims.

CUT-L-JEC
Figure 12.1-12.4

Reference specimen and locality: SL0719, R-102.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, Stomatal complexes in clear areoles, isolated, randomly oriented, paracytic. Cuticular scales not clear.

Epidermal Cells. Epidermal cell flanges generally hidden by papillae, cells over fine venation distinguished as 'venal' (elongated), normal epidermal cells isodiametric, walls curved or wavy, unbuttressed.

Indumentum. With trichome insertion scars and papillose, unornamented. Papillae present over all epidermal cells, formed by the entire outer surface of the epidermal cell projecting upwards in a bubble-like fashion, smooth. Trichome insertion scars common (trichomes deciduous and therefore trichome type unknown), inserted between epidermal cells. Epidermal cells around trichome scar radially elongated as distinct foot cells, unthickened.

Distinguishing features. Papillate Lauraceae cuticle with bubble-like papillae and with trichome scars.

CUT-L-GCI
Figure 12.5-12.6

Reference specimen and locality: SL5372, R-102.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, Stomatal complexes in clear areoles, isolated, randomly oriented, paracytic length 15-18 µm (medium). Cuticular scales not clear.

Epidermal cells. Epidermal cell flanges not in TLM (cuticle thin), cells over fine venation distinguished as 'venal' (elongated), normal epidermal cells isodiametric, walls curved or wavy, unbuttressed.

Indumentum. With trichome insertion scars and papillose, unornamented. Papillae present over all epidermal cells, smooth, discrete, about one half to two thirds of the diameter of the epidermal cell. Trichome insertion scars common (trichomes deciduous and therefore trichome type unknown), inserted between epidermal cells. Epidermal cells around trichome scars radially elongated as distinct foot cells, with thickened radial walls and pore.

Distinguishing features. Papillate Lauraceae cuticle with discrete papillae.

CUT-L-DCG
Figure 13

Reference specimen and locality: SB0346, R-74.

Referred specimens and occurrence: SL5198, R-06; SL5215, R-11; SL5223, R-12; SL5049, R-21; SL5105, R-28; SL5017, R-61; SB0346, R-74; SB0352, R-75; SL5421, R-79; SL5270, R-103.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown. Stomatal complexes evenly spread, isolated, randomly oriented, paracytic, length 18–23 µm (medium). Subsidiary cell anticlinal walls, including walls forming the stomatal pore, markedly thickened, periclinal cuticle not distinct in thickness from normal epidermal cells. Cuticular scales narrow.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, cells over veins not distinguished by shape, normal epidermal cells isodiametric,

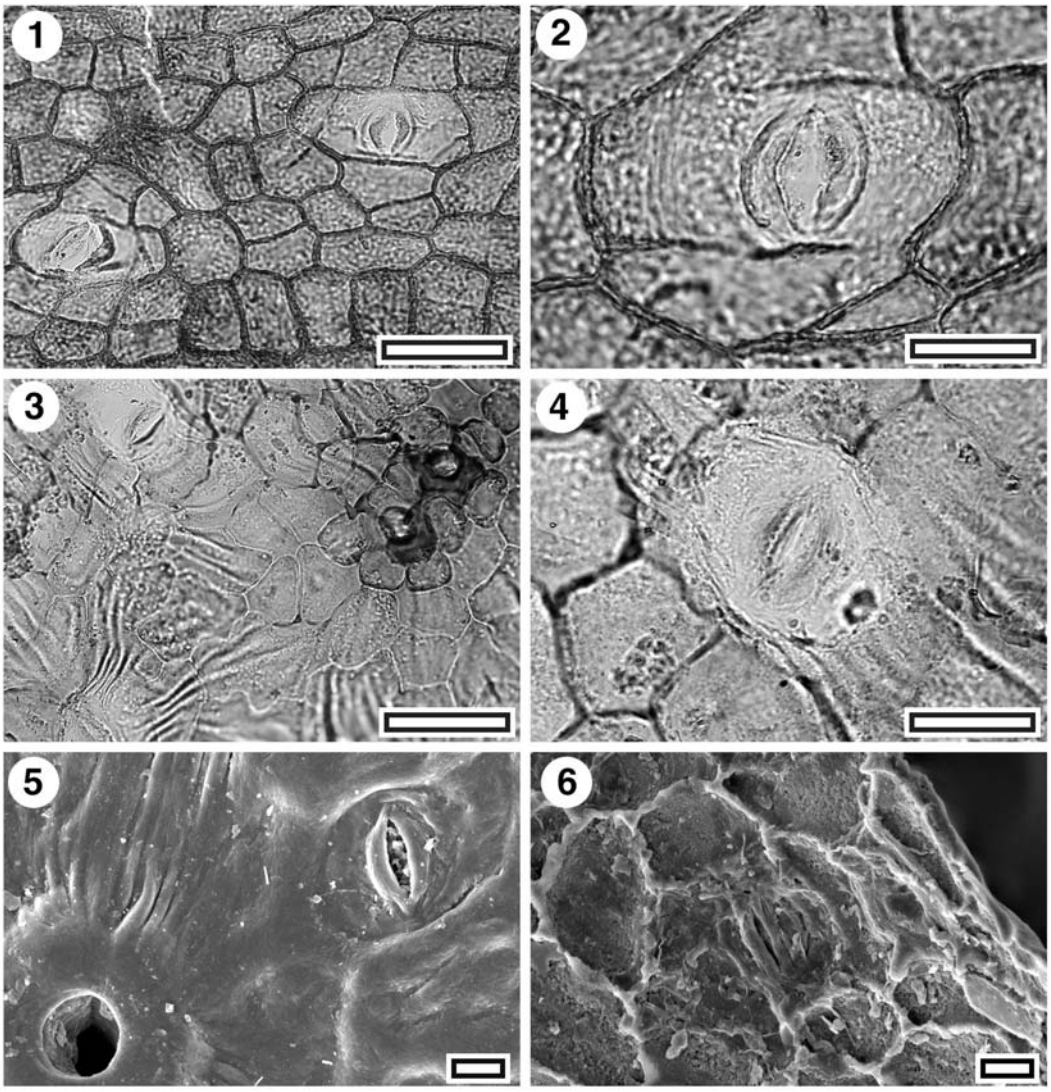

Figure 11. Lauraceae. CUT-L-DDE, and CUT-L-DDC, **1.** CUT-L-DDE. TLM view showing two stomatal complexes (SB0730, scale-bar = 50 µm); **2.** CUT-L-DDE. TLM detail of a single stomatal complex (SB0730, scale-bar = 20 µm); **3.** CUT-L-DDC. TLM view showing a stomatal complex (upper right) and two massively thickened trichome insertion scars (upper right) (SB0670, scale-bar = 50 µm); **4.** CUT-L-DDC. TLM detail of a single stomatal complex (SB0670, scale-bar = 20 µm); **5.** SEM view of outer cuticular surface showing trichome insertion scar (lower left) and stomatal complex (upper right) (S-1544, scale-bar = 10 µm); **6.** SEM view of inner cuticular surface showing a single stomatal complex (S-1544, scale-bar = 10 µm).

walls straight to curved, unbuttressed. Epidermal cells near the stomatal complex may have thickened anticlinal walls. **Indumentum.** Persistent uniseriate trichomes inserted over 1-3 epidermal cells.

Distinguishing features. Lauraceae cuticle readily distinguished by the remarkable thickening of anticlinal walls within and sometimes around the stomatal complex.

CUT-L-DCD
Figure 14.1-14.4

Reference specimen and locality: SB0349, R-74.

Referred specimens and occurrence: SL5098, R-27.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, Stomatal complexes in clear areoles, isolated, randomly oriented, paracytic, outline rounded, but irregular, length 13–30 µm, (small-medium). Subsidiary cell periclinal cuti-

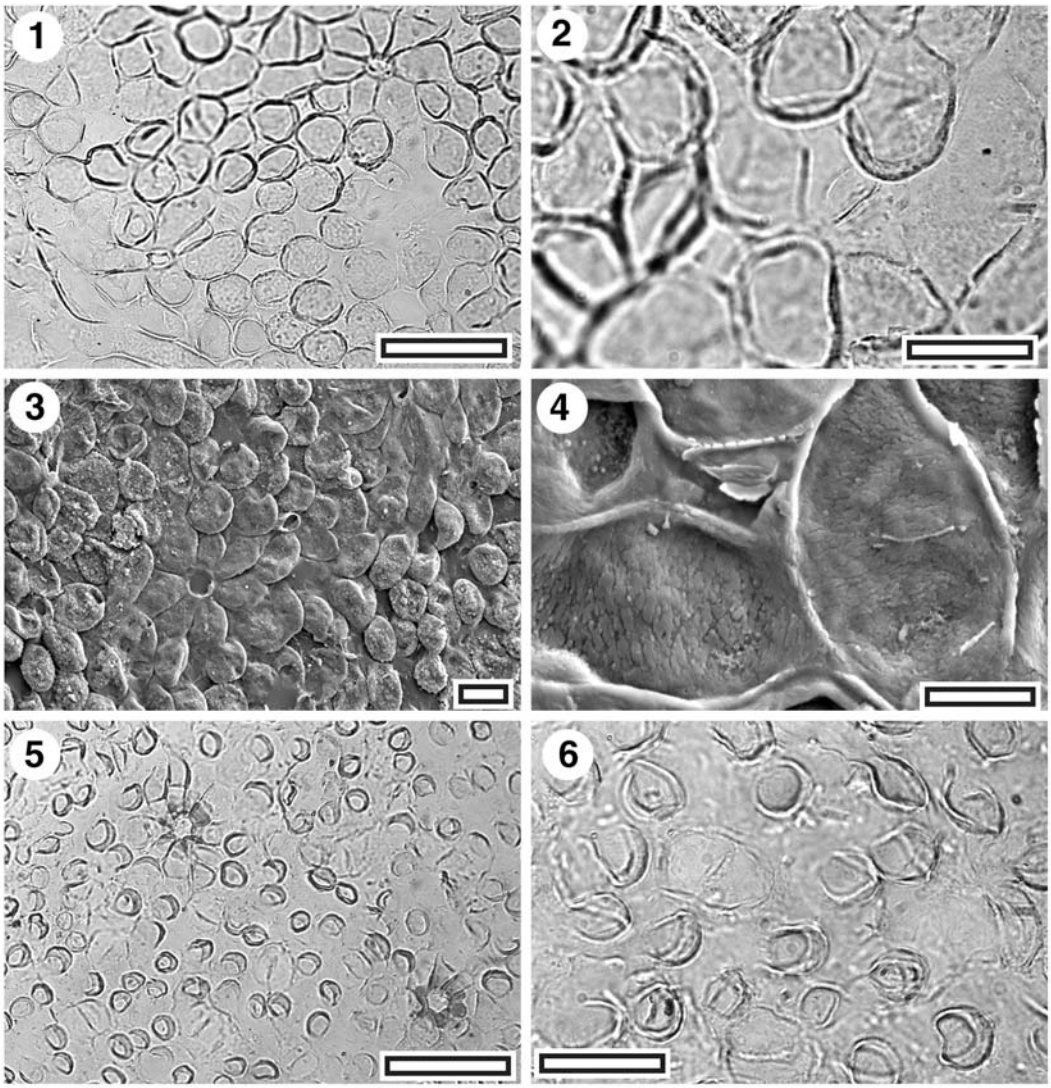

Figure 12. Lauraceae. CUT-L-JEC, and CUT-L-GCI. **1.** CUT-L-JEC. TLM view showing papillae, and (upper right) a trichome insertion scar with a distinct ring of foot cells (SB0719, scale-bar = 50 µm); **2.** CUT-L-JEC. TLM detail of a single stomatal complex (right of centre) surrounded by papillae (SB0719, scale-bar = 20 µm); **3.** SEM view of outer cuticular surface showing trichome insertion scar with prominent foot cells (left of centre) and papillae obscuring stomata (S-1684, scale bar = 20 µm); **4.** SEM view of inner cuticular surface showing a possible stomatal complex (just above centre) (S-1684, scale-bar = 10 µm); **5.** CUT-L-GCI. TLM view showing papillae and two trichome insertion scars with prominent thickening around the pores (SL5372, scale-bar = 50 µm); **6.** CUT-L-GCI. TLM detail with a stomatal complex visible (centre left) SL5372, scale-bar = 20 µm).

cle not distinct in thickness from normal epidermal cells. Cuticular scales 'butterfly-like'.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, cells over fine venation distinguished as 'venal' (elongated), normal epidermal cells highly variable from isodiametric to elongate, walls sinuous, unbuttressed.

Indumentum. With trichome insertion scars, unornamented. Trichome scars sparse (trichomes deciduous), inserted between epidermal cells, Epidermal cells around trichome scar radially elongated as distinct foot cells, unthickened.

Distinguishing features. Lauraceae cuticle with sinuous epidermal cell anticlinal walls and butterfly-like scales.

CUT-L-DCI
Figure 14.5-14.8

Reference specimen and locality: SB0672, R-102.

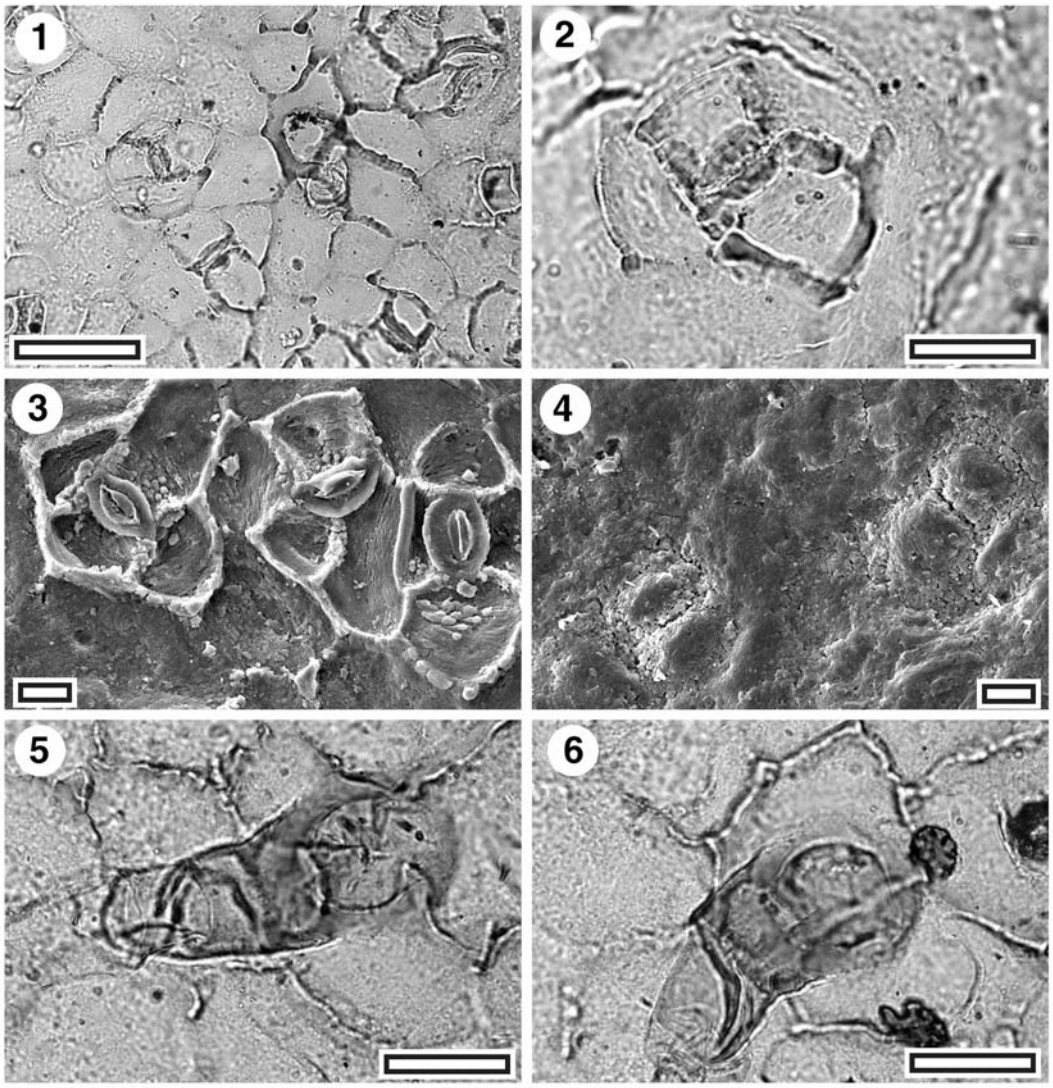

Figure 13. Lauraceae. CUT-L-DCG, **1.** TLM view showing five stomatal complexes around a trichome (to right of centre) inserted over two epidermal cells (SB0346, scale-bar = 50 µm); **2.** TLM detail of a single stomatal complex. Note massive thickening around stomatal pore and subsidiary cells (SB0346, scale-bar = 20 µm); **3.** SEM view of inner cuticular surface showing three stomatal complexes. Note prominent thickening of subsidiary cell walls (S-1544, scale-bar = 10 µm); **4.** SEM view of outer cuticular surface showing two stomatal complexes. Subsidiary cells are visible and the stomatal pore is slit-like and largely plugged (S-1544, scale-bar = 10 µm); **5.** TLM view of a trichome over junction of two epidermal cells (SL5049, scale-bar = 20 µm); **6.** TLM view of a trichome over junction of two epidermal cells. Note epiphyllous germling (SL5049, scale-bar = 20 µm).

Referred specimens and occurrence: SL5332, R-20; SL5343, R-23; SL5084, R-25; SB0672, R-27; SB0399, R-75; SL5432, R-102; SL5313, R-105.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, Stomatal complexes evenly spread, isolated, randomly oriented, paracytic, outline rounded but with flattened poles, length 15–25 µm (medium). Subsidiary cell periclinal cuticle thicker than over normal epidermal cells. Cuticular scales narrow.

Indumentum. With trichome insertion scars, unornamented. Trichome scars common, (trichomes deciduous), inserted between epidermal cells. Epidermal cells around trichome scar modified to form a thickened poral rim.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, cells over fine venation distinguished as 'venal' (elongated), normal epidermal

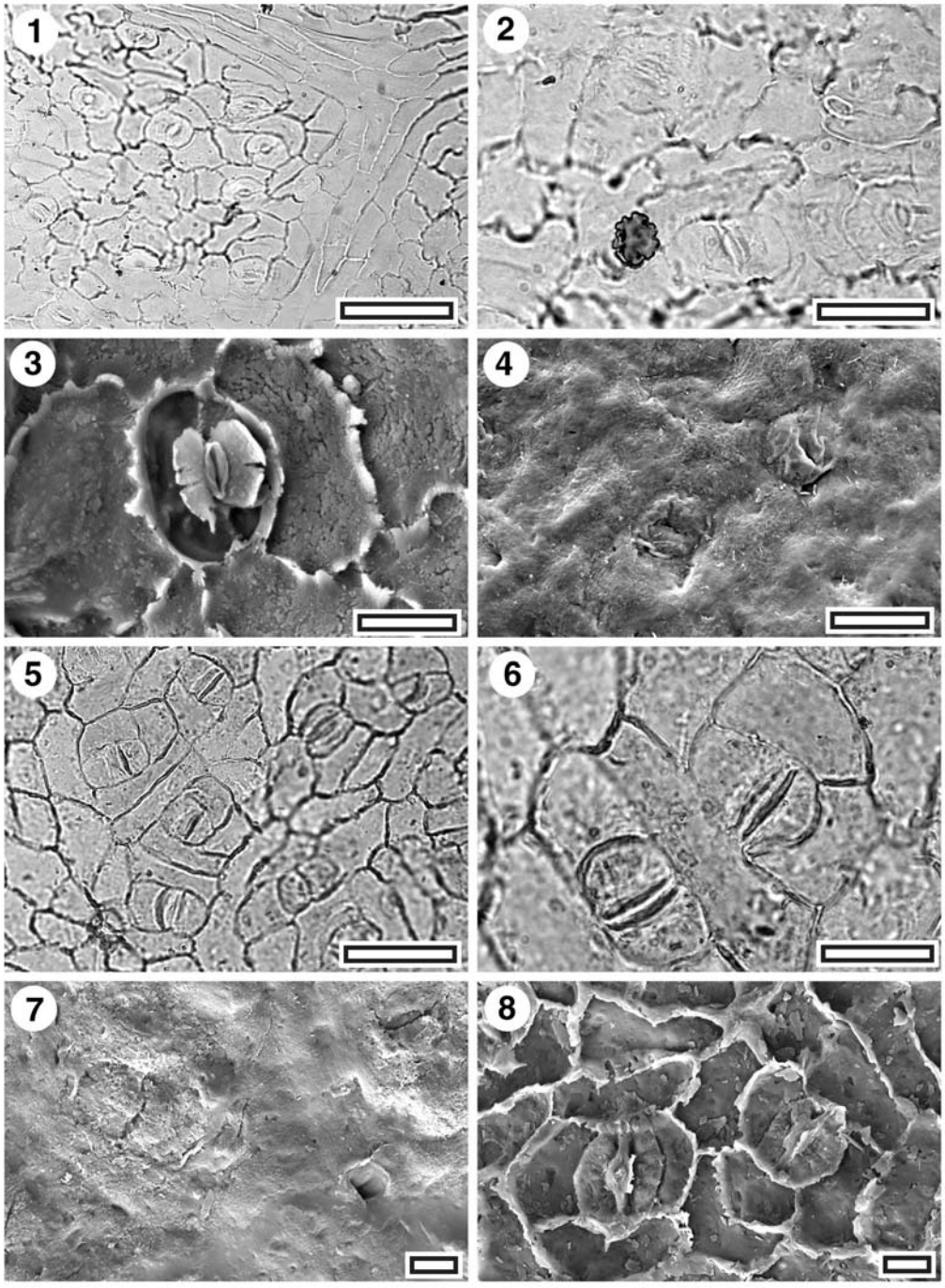

Figure 14. Lauraceae. CUT-L-DCD and CUT-L-DCI. **1.** CUT-L-DCD. TLM view showing several stomatal complexes and (upper right) the junction of two fine veins indicated by distinct venal epidermal cells (SB0349, scale-bar = 50 μm); **2.** CUT-L-DCD. TLM detail of a four stomatal complexes (note epiphyllous germling at lower left) (SB0349, scale-bar = 20 μm); **3.** UT-L-DCD. SEM view of inner cuticular surface showing a single stomatal complex. Note “butterfly” cuticular scales (S-1683, scale-bar = 10 μm); **4.** CUT-L-DCD. SEM view of outer cuticular surface showing two stomatal complexes, barely distinguished from the surrounding topography (S-1683, scale-bar = 10 μm); **5.** CUT-L-DCI. TLM view showing several stomatal complexes and (lower left) a trichome insertion scar. Note distinctive “anisocytic' pattern around the complexes (SB0672, scale-bar = 50 μm); **6.** CUT-L-DCI. TLM detail of a two stomatal complexes (SB0672, scale-bar = 20 μm); **7.** CUT-L-DCI. SEM view of outer cuticular surface showing two stomatal complexes (left of centre and upper right) where the subsidiary cells are visible and the pore slit-like, and a trichome insertion scar (lower right) (S-0302, scale-bar = 10 μm); **8.** CUT-L-DCI. SEM view of inner cuticular surface showing two stomatal complexes (S-0302, scale-bar = 10 μm).

cells highly variable from isodiametric to elongate, walls straight to curved, unbuttressed. Cells immediately around the paracytic stomatal, complex are arranged in an anisocytic manner, with three and sometimes four cells.

Distinguishing features. Lauraceae cuticle with cells around the stomatal complex arranged in an anisocytic pattern.

CUT-L-DCF
Figure 15

Reference specimen and locality: SB0666,R-22.

Referred specimens and occurrence: SL5045, R-21; SB0731, R-22; SL5341, R-23; SB0348, R-74; SL5271, R-103.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, Stomatal complexes evenly spread, isolated, randomly oriented, paracytic, outline rounded but with flattened poles, length 15–23 µm (medium). Subsidiary cell periclinal cuticle markedly thicker than over normal epidermal cells. Cuticular scales double.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, cells over fine venation distinguished as 'venal' (elongated), normal epidermal cells highly variable from isodiametric to elongate, walls straight to curved, unbuttressed.

Indumentum. With trichome insertion scars, unornamented. Trichome scars common, (trichomes deciduous), inserted between epidermal cells. Epidermal cells around trichome scar modified to form thickened poral rim and radial walls.

Distinguishing features. Lauraceae cuticle with periclinal walls of subsidiary cells distinctly thicker than normal epidermal cells, and with massively thickened poral rims of trichome insertion scars.

Identification: Although the stomatal structure is entirely consistent with, and in terms of extant plants, unique to Lauraceae, several leaf fragments indicate that the margin was toothed (Figure 15.5-15.8). Teeth are unknown in extant Lauraceae (Sassafras is lobed). It is possible that Lauraceae once included taxa with teeth, and it is also possible that this represents a related, but extinct family. For convenience, the cuticle is included here as Lauraceae. The ‘double’ cuticular scales recall *Endiandra* (Christophel and Rowett 1996) but the shape of the stomatal complexes and the thicker subsidiary cell cuticle are further evidence of at least generic difference.

CUT-L-DDJ (*Endiandra* sp.)
Figure 16.1-16.4

Reference specimen and locality: SB0398, R-75.

Referred specimens and occurrence: SL5319, R-06; SL5331, R-20; SL5094, R-26; SB0398, R-75; SL5305, R-105.

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic, Stomatal complexes evenly spread, isolated, randomly oriented, paracytic, outline rounded but with flattened poles, length 18–23 µm (medium). Subsidiary cell periclinal cuticle thinner than over normal epidermal cells. Cuticular scales double.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, cells over fine venation distinguished as 'venal' (elongated), normal epidermal cells highly variable from isodiametric to elongate, walls curved or wavy, unbuttressed.

Indumentum. With trichome insertion scars, unornamented. Trichome scars common, (trichomes deciduous), inserted between epidermal cells. Epidermal cells around trichome scar irregularly elongated as foot cells, unthickened.

Non-stomatal surface. Non-Stomatal Surface Epidermal cells isodiametric, wavy and slightly buttressed. Simple trichome insertion scars present.

Distinguishing features. Lauraceae cuticle with ‘double’ cuticular scales and slightly buttressed epidermal cells.

Identification. The ‘double’ cuticular scales, stomatal complex outline and thinner subsidiary cell cuticle than epidermal cells is completely consistent with this being an *Endiandra* (Christophel and Rowett 1996).

CUT-L-DCH
Figure 16.5-16.6

Reference specimen and locality: SB0728, R-6.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, Stomatal complexes evenly spread, isolated, randomly oriented, paracytic, outline rounded but with flattened poles, length c. 45 µm (medium). Subsidiary cell periclinal cuticle not distinct in thickness from normal epidermal cells. Cuticular scales 'butterfly-like'.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, cells over veins not distinguished by shape, normal epidermal cells isodiametric, walls straight, unbuttressed.

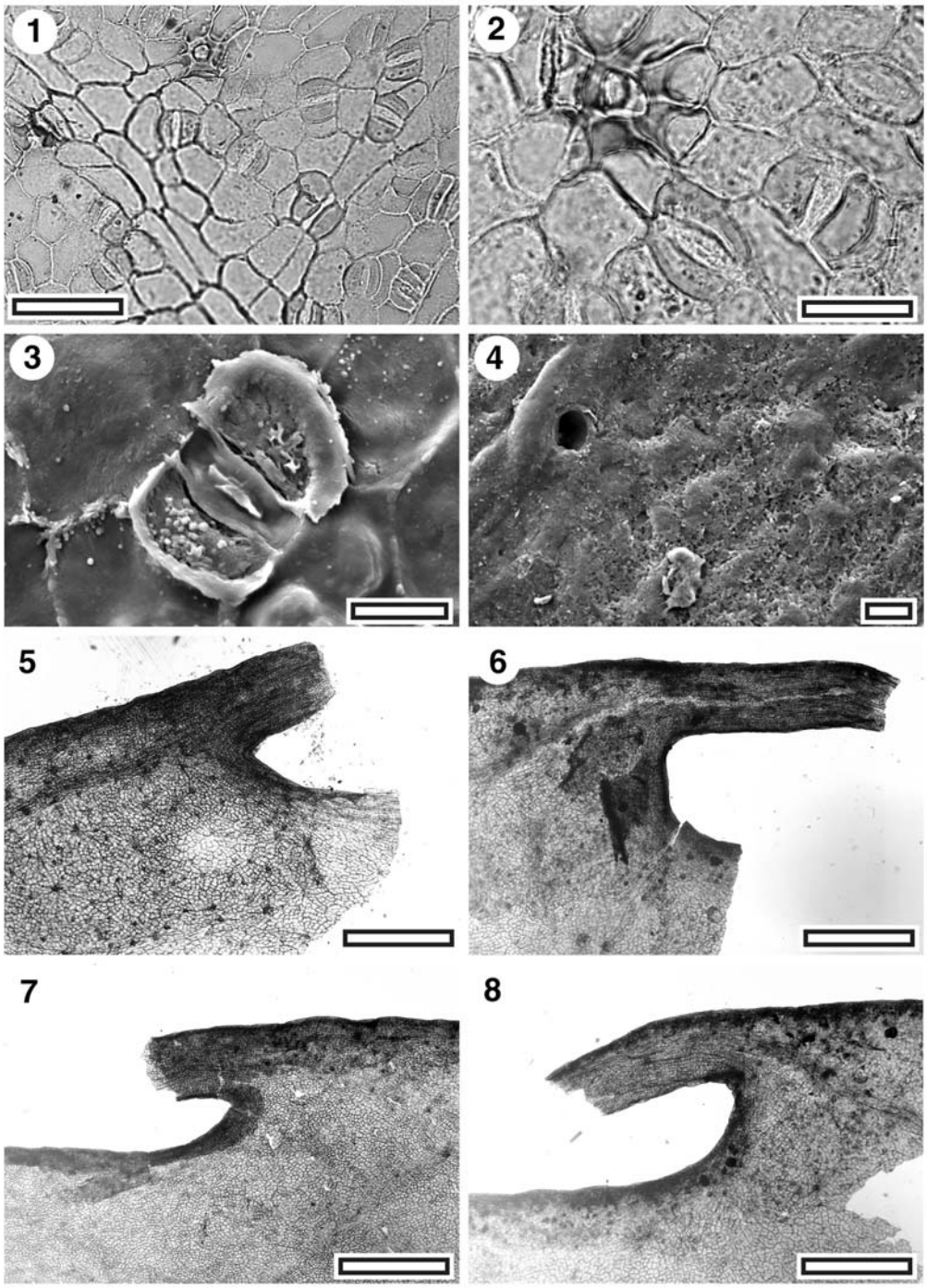

Figure 15. Toothed ?Lauraceae, CUT-L-DCF. **1.** TLM view showing several stomatal complexes and (upper centre) a massively thickened trichome insertion scar. Note much thicker cuticle over subsidiary cells (SB0666, scale-bar = 50 µm); **2.** TLM detail of a two stomatal complexes and (upper left) a massively thickened trichome insertion scar (SB0666, scale-bar = 20 µm); **3.** SEM view of inner cuticular surface showing single stomatal complex. Note the straight, parallel cuticular scales. The granular material is often present in subsidiary cells, but is found elsewhere and may be artifactual (S-1679, scale-bar = 10 µm); **4.** SEM view of outer cuticular surface showing a prominent trichome insertion scar (upper right) and several stomatal complexes to the right, completely obscured by granular cutin (S-1679, scale-bar = 10 µm); **5.** TLM view of a tooth (SB0731, scale-bar = 50 µm); **6.** TLM view of a tooth (SL5387, scale-bar = 50 µm); **7.** TLM view of a tooth (SL5375, scale-bar = 50 µm); **8.** TLM view of a tooth (SL5386, scale-bar = 50 µm).

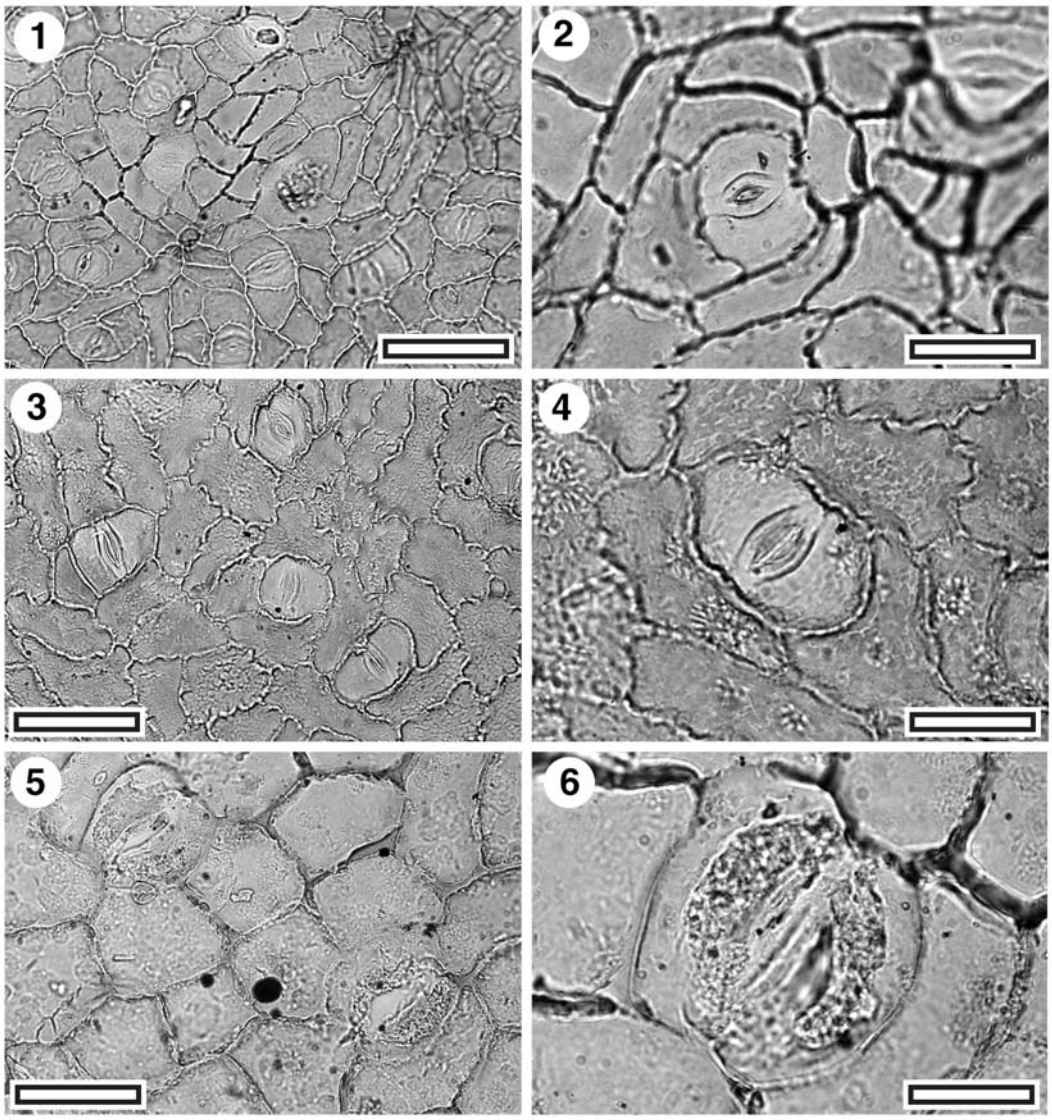

Figure 16. Lauraceae. CUT-L-DDJ and CUT-L-DCH, **1.** CUT-L-DDJ. TLM view showing several stomatal complexes and (upper right) a trichome insertion scar (SB0397, scale-bar = 50 µm); **2.** CUT-L-DDJ. TLM detail of a single stomatal complex. Note 'double' cuticular scales (SB0397, scale-bar = 20 µm); **3.** CUT-L-DDJ. TLM view showing four stomatal complexes (SL5325, scale-bar = 50 µm); **4.** CUT-L-DDJ. TLM detail of a single stomatal complex. Note 'double' cuticular scales (SL5325, scale-bar = 20 µm); **5.** CUT-L-DCH. TLM view showing two stomatal complexes (SB0728, scale-bar = 50 µm); **6.** CUT-L-DCH. TLM detail of a single stomatal complex (SB0728, scale-bar = 20 µm).

Indumentum. Glabrous, unornamented.

Distinguishing features. Lauraceae cuticle with large stomatal complexes.

Note. The apparent cuticular scales on this taxon may be an artefact of preservation. The stomatal complex size is unusually large for Lauraceae. It is placed here until further and perhaps better preserved specimens clarify this point.

CUT-L-JBI
Figure 17.1-17.4

Reference specimen and locality: SB0700, R-102.

Referred specimens and occurrence: SL5028, R71.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, Stomatal complexes in clear areoles, isolated, randomly oriented, paracytic, outline rounded, but irregular, length 13–18

µm, (small-medium). Subsidiary cell periclinal cuticle not distinct in thickness from normal epidermal cells, anticlinal walls particularly strong and in TLM view appear to slightly overhang the stomatal complex. Cuticular scales butterfly-like.

Epidermal cells. Epidermal cell flanges not clearly visible under TLM, cells over fine venation distinguished as 'venal' (elongated), normal epidermal cells highly variable from isodiametric to elongate, walls curved or wavy, unbuttressed.

Indumentum. With trichome insertion scars, unornamented. Trichome scars common, (trichomes deciduous), inserted between epidermal cells. Epidermal cells around trichome base radially elongated to form distinct foot cells and thickened to form a poral rim.

Distinguishing features. Lauraceae cuticle which is very thin, and with stomatal complexes sunken into individual pits and surrounded by an irregular rim.

CUT-L-JBA
Figure 17.5-17.6

Reference specimen and locality: SB0391, R-75.

Referred specimens and occurrence: SL5065, R-21; SL5345, R-23.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, Stomatal complexes evenly spread, isolated, randomly oriented, paracytic, outline rounded, but irregular, length 25–28 µm (medium). Subsidiary cell periclinal cuticle not distinct in thickness from normal epidermal cells. Cuticular scales narrow.

Epidermal cells. Epidermal cell flanges very thin or absent (anticlinal walls of epidermal cells not clear under TLM), cells over fine venation distinguished as 'venal' (elongated), normal epidermal cells unclear, walls curved or wavy, unbuttressed.

Indumentum. Glabrous, unornamented.

Distinguishing features. Very thin Lauraceae cuticle.

CUT-L-GCG
Figure 18.1-18.4

Reference specimen and locality: SL1023, R-21.

Referred specimens and occurrence: SL5324, R-06; SL5228, R-12; SL5244, R-13; SL5269; SL5423, R-79; R-103; SL5307, R-105.

Stomatal complexes. Stomatal distribution hypostomatic, stomatal complexes evenly spread, isolated, randomly oriented, paracytic, outline rounded but with flattened poles, length 15–25 µm (medium). Subsidiary cell periclinal cuticle thinner than over normal epidermal cells (occasionally not apparent). Cuticular scales narrow, but with prominent triangular flaps of cuticle at the polar ends.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, cells over fine venation distinguished as 'venal' (elongated), normal epidermal cells highly variable from isodiametric to elongate, walls straight to curved, unbuttressed.

Indumentum. Essentially glabrous, but very rarely simple, poral trichome insertion scars present.

Distinguishing features. Lauraceae cuticle with subsidiary cell cuticle thinner than normal epidermal cell cuticle and glabrous. The basic form and size of the stomatal complexes is rather similar to CUT-L-DCI, but lacks the anisocytic pattern of epidermal cells around the stomatal complex.

CUT-L-GCH
Figure 18.5-18.6

Reference specimen and locality: SL5374, R-102.

Stomatal complexes. Stomatal distribution unknown, stomatal complexes in distinct, small clusters within areoles, isolated, randomly oriented, paracytic, outline rounded but with flattened poles, length 15–25 µm (medium). Subsidiary cell periclinal cuticle much thinner than over normal epidermal cells. Cuticular scales butterfly-like.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, cells over fine venation distinguished as 'venal' (slightly elongated), normal epidermal cells highly variable from isodiametric to elongate, walls straight to curved, unbuttressed.

Indumentum. With trichome insertion scars, unornamented. Trichome scars common, (trichomes deciduous), often inserted over the junction of three epidermal cells. Epidermal cells around trichome base radially elongated to form distinct foot cells and slightly thickened to form a poral rim and radiating walls.

Distinguishing features. Lauraceae cuticle with subsidiary cell cuticle thinner than normal epidermal cell cuticle and with prominent trichome insertion scars.

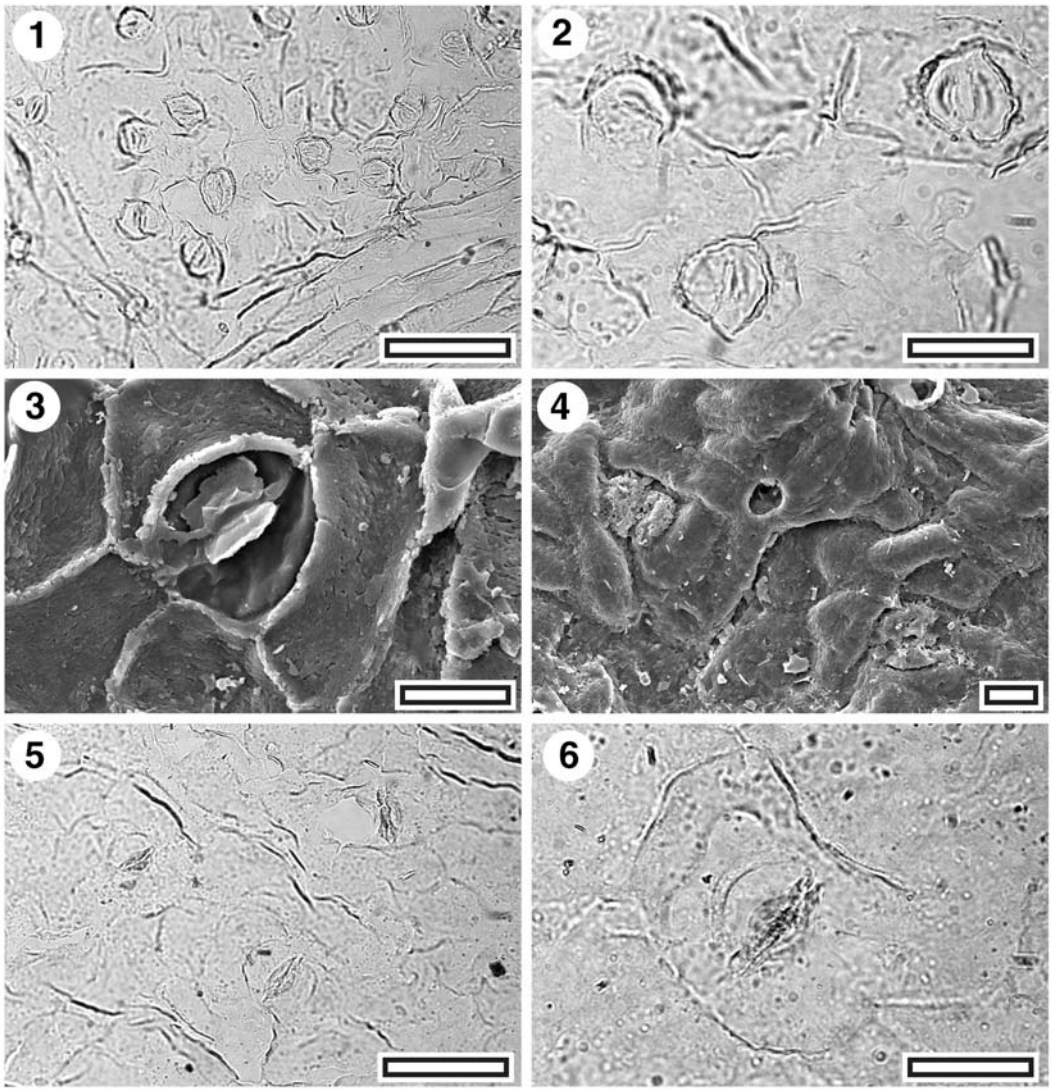

Figure 17. Lauraceae. CUT-L-JBI and CUT-L-JBA, **1.** CUT-L-JBI. TLM view showing several stomatal complexes and (lower left) a trichome insertion scar over venal epidermal cells (SB0700, scale-bar = 50 µm); **2.** CUT-L-JBI. TLM detail of three stomatal complexes. Note cuticular thickening surrounding complexes (SB0700, scale-bar = 20 µm); **3.** SEM view of inner cuticular surface showing single stomatal complex. Note "butterfly" cuticular scales (S-1538, scale bar = 10 µm); **4.** SEM view of outer cuticular surface showing two stomatal complexes (centre left and lower right) and two trichome insertion scars (centre and upper right) (S-1538, scale-bar = 10 µm); **5.** CUT-L-JBA. TLM view showing three stomatal complexes (SB0391, scale-bar = 50 µm); **6.** CUT-L-JBA. TLM detail of a single stomatal complex (SB0391, scale-bar = 20 µm).

Proteaceae Jussieu 1789

Proteaceae cuticle is identified on the basis of brachyparacytic stomatal structure and rounded trichome scars, at leats some of which overlie more than one epidermal cell (Lange 1978, Carpenter 1994, Carpenter et al. 2004)

Key to Proteaceae cuticle

1. Cuticle with prominent surface striations. 2.
1. Cuticle without striations, or striations subdued. 4.

2. Epidermal cell walls sinuous. **CUT-P-EJG**
2. Epidermal walls curved or indistinct. 3.

3. Trichome base outline diffuse, surface ornamentation of striations in flowing bands. **CUT-P-EJF**

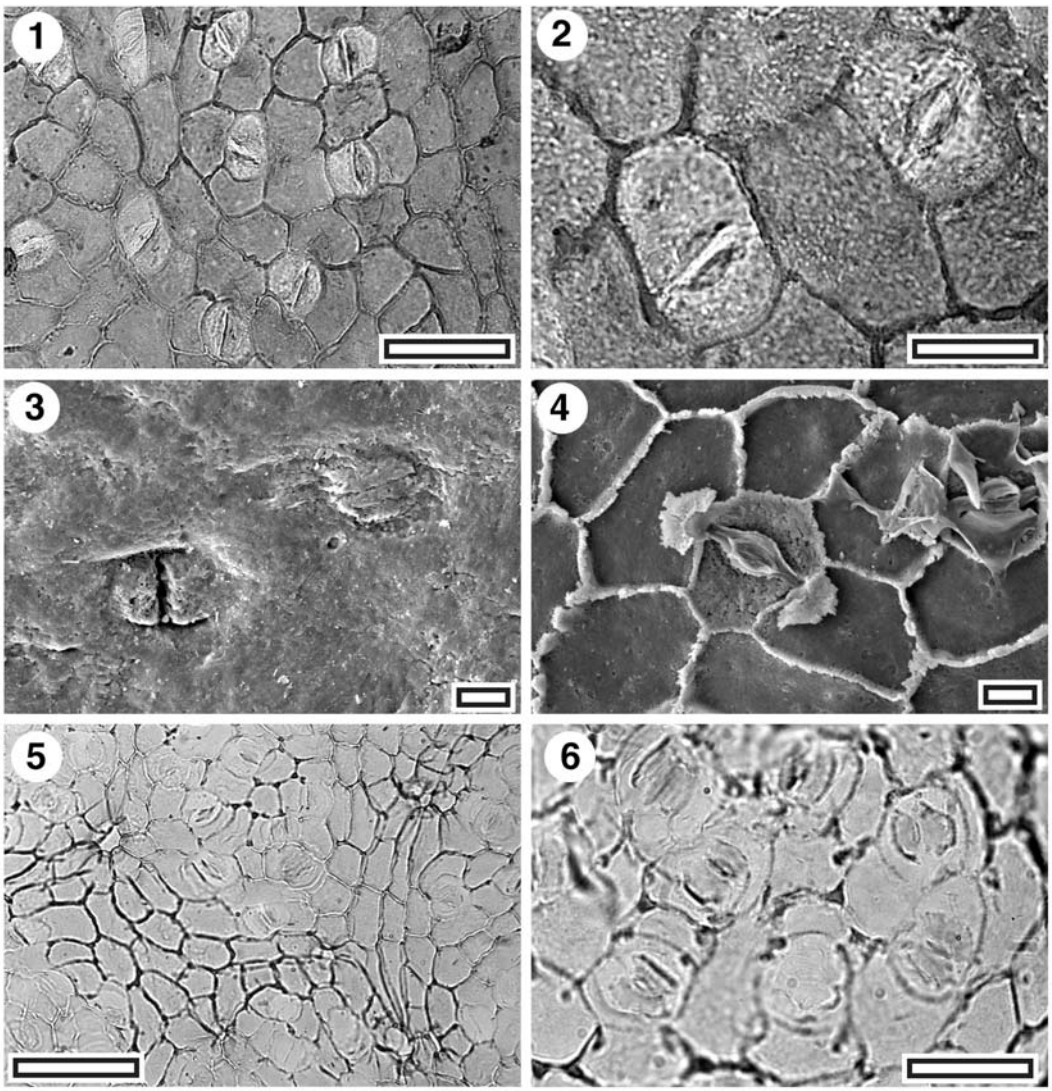

Figure 18. Lauraceae. CUT-L-GCG and CUT-L-GCH. **1.** CUT-L-GCG. TLM view showing several stomatal complexes. Note typically thinner cuticle over subsidiary cells (SL1023, scale-bar = 50 μm); **2.** CUT-L-GCG. TLM detail of two stomatal complexes (SL1023, scale-bar = 20 μm); **3.** SEM view of outer cuticular surface showing two stomatal complexes with slit-like pores (S-1690, scale-bar = 10 μm); **4.** SEM view of inner cuticular surface showing two stomatal complexes. The central specimen clearly shows the triangular flaps of cuticle at the polar ends of the complex (S-1690, scale-bar = 10 μm); **5.** TLM view showing several stomatal complexes and three trichome insertion scars over venal epidermal cells (SL5374, scale-bar = 50 μm); **6.** TLM detail of a group of stomatal complexes. Note very thin cuticle of the subsidiary cells, and clear "butterfly" shaped cuticular scales (SL5374, scale-bar = 20 μm).

3. Trichome base outline well-defined, surface ornamentation of ridges above epidermal cell anticlinal walls. **CUT-P-EJE**

4. Epidermal surface ornamented with papillae. 5.
4. Epidermal surface smooth or without prominent ridging. 6.

5. Papillae elongate. **CUT-P-EJH**
5. Papillae circular and with a diameter distinctly smaller than their epidermal cell. **CUT-P-GDJ**

6. Trichome bases prominent, stomata with random orientation. 7.
6. Trichome bases not prominent, stomata with a trend towards alignment. **CUT-P-EAA**

6. Trichome bases surrounded by radially elongate cells, epidermal cell walls clear, Prominent T-pieces at guard cell poles. Stomatal complexes generally parallel **CUT-P-EJI**
6. Trichome bases not surrounded by radially elon-

gate cells, epidermal cell walls often indistinct, No T-pieces, epidermal cells polygonal. **CUT-P-EJD**

CUT-P-EJG
Figure 19.1-19.4

Reference specimen and locality: SB0674, R-104.

Referred specimens and occurrence: SL5361, R-20; SL5050, R-21; SB0750, R-23; SL5007, R-56; SL5277, R-68; SB0389, R-75; SL5264, R-76.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, brachyparacytic, size range unimodal. Subsidiary cells typically elongate tangential to stomata, periclinal walls same thickness as normal epidermal cells, ornamented with many fine ridges parallel with, and on either side of the stomata. Guard cell pair outline elliptical, length 25–33 µm (medium), with prominent polar rods. Outer stomatal ledge elliptical, extending from outer edge of stoma, thicker than normal epidermal cells, pore elliptical.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, normal cells elongated, approximately the same size as the stomata, cells over veins not distinguished by shape, anticlinal walls markedly sinuous; slightly buttressed, ornamented with 'flowing' pattern of many prominent ridges.

Indumentum. With trichome insertion scars, and basal part of trichome persistent. Trichome scars common, annular and multicellular, inserted over 1–2 modified epidermal cells, diameter similar in size to normal epidermal cell. Epidermal cells under trichome base modified to form a thick, raised circular platform, on top of which sits a smooth, thick hollow collar.

Distinguishing features. Proteaceae cuticle with prominent surface striations and persistent trichomes.

CUT-P-EJF
Figure 19.5-19.6

Reference specimen and locality: SB0679, R-6.

Referred specimens and occurrence: SB0740, R-25.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, brachyparacytic, size range unimodal. Subsidiary cell number and shape unclear. Guard cell pair outline elliptical, not outlined by a clear anticlinal wall, length about 20 µm (medium), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge elliptical, extending from outer edge of stoma, same thickness as normal epidermal cells, pore elliptical.

Epidermal cells. Epidermal cell flanges from clearly defined to indistinct, normal cells highly variable from isodiametric to elongate, approximately the same size as the stomata, cells over veins not distinguished by shape, anticlinal walls curved, unbuttressed, ornamented with 'flowing' pattern of many prominent ridges.

Indumentum. With trichome insertion scars (trichomes deciduous). Trichome scars sparse, annular and multicellular, inserted over 1–2 modified epidermal cells, diameter similar in size to normal epidermal cell. Epidermal cells under trichome base modified to form a thick, raised circular platform, on top of which sits a smooth, thick hollow collar.

Distinguishing features. Proteaceae cuticle which is thin, but with prominently thickened trichome bases and an ornamentation of flowing ridges.

CUT-P-EJE
Figure 20.1-20.2

Reference specimen and locality: SB0680, R-70.

Referred specimens and occurrence: SL5068, R-21; SL5006, R-56; SB0680, R-70.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, showing a clear trend towards alignment, brachyparacytic, size range unimodal. Subsidiary cells typically elongate tangential to stomata, periclinal walls same thickness as normal epidermal cells, ornamented with 1–2 ridges parallel with, and on either side of the stomata. Guard cell pair outline elliptical, outlined by a well-defined anticlinal wall, length 23–25 µm (medium), clearly separated by polar walls. Outer stomatal ledge elliptical, extending from outer edge of stoma, same thickness as normal epidermal cells, pore elliptical - sub circular.

Epidermal cells. Epidermal cell flanges distinct (although may be partly obscured by surface topography), normal cells elongated, approximately the same size as the stomata, cells over veins not distinguished by shape, anticlinal walls curved, unbuttressed, ornamented with strong ridges above the epidermal cell anticlinal walls.

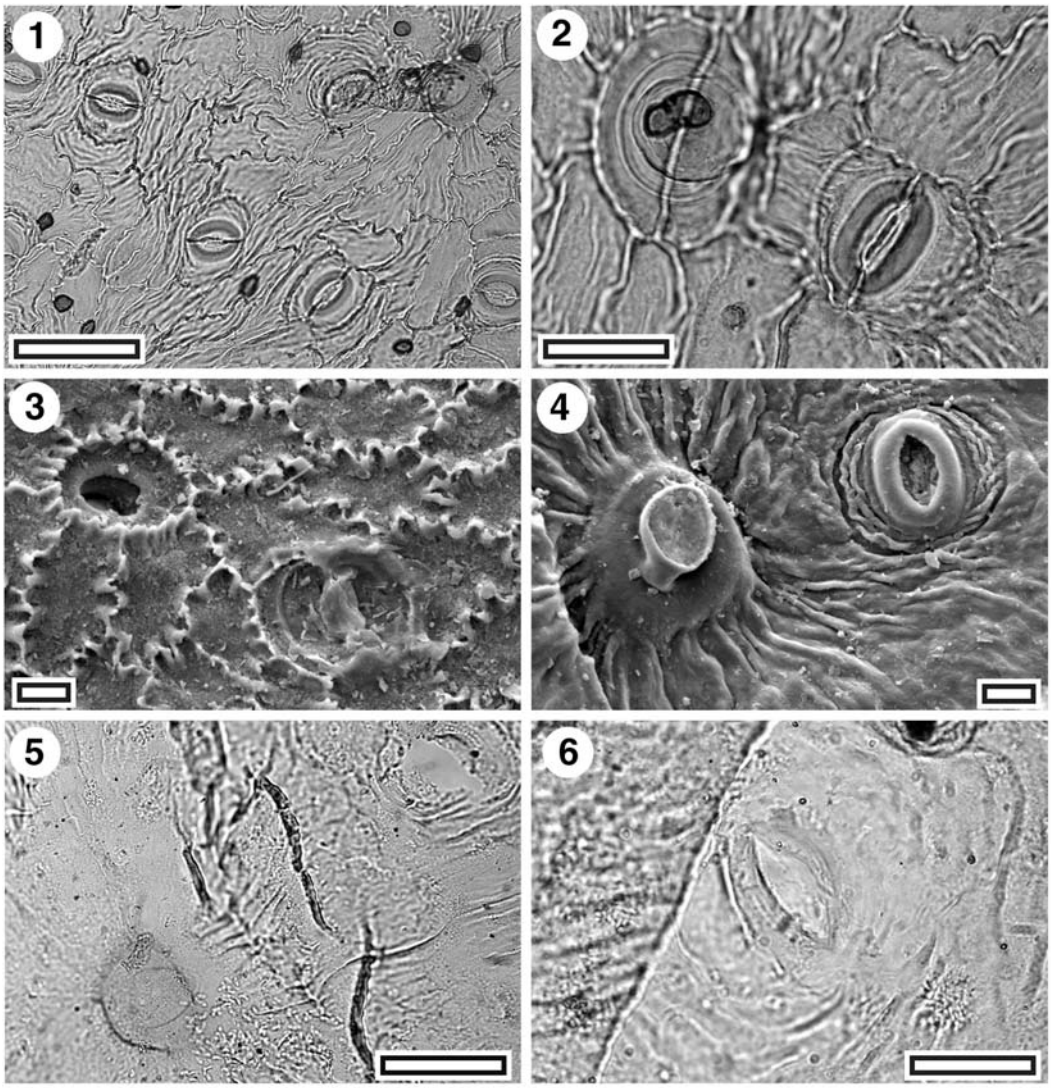

Figure 19. Proteaceae. CUT-P-EJG and CUT-P-EJF. **1.** CUT-P-EJG. TLM view showing several stomatal complexes and (upper right) a persistent trichome (SB0674, scale-bar = 50 µm); **2.** CUT-P-EJG. TLM detail of a trichome base over two epidermal cells (left) and a stomatal complex (right) (SB0674, scale-bar = 20 µm); **3.** CUT-P-EJG. SEM view of inner cuticular surface showing a trichome base (upper left) and a stomatal complex (lower right) (S-1696, scale-bar = 10 µm); **4.** CUT-P-EJG. SEM view of outer cuticular surface showing a trichome base (centre left) and a stomatal complex (upper right) (S-1696, scale-bar = 10 µm); **5.** CUT-P-EJF. TLM view showing a trichome base (lower left) and (upper right) a stomatal complex with the guard cell cuticle broken away (SB0679, scale-bar = 50 µm); **6.** CUT-P-EJF. TLM detail of a single stomatal complex (SB0679, scale-bar = 20 µm).

Indumentum. With trichome insertion scars (trichomes deciduous). Trichome bases common, annular and multicellular, inserted over 1–2 modified epidermal cells. Diameter similar in size to normal epidermal cell. Epidermal cells under trichome base modified to form a thick, raised circular platform, on top of which sits a smooth, thick hollow collar. Trichome platform is granular and frilled with a markedly thickened collar.

Distinguishing features. Proteaceae cuticle with pronounced ridges over the epidermal cell anticlinal walls.

CUT-P-EJH
Figure 20.3-20.6

Reference specimen and locality: SB0677, R-76.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread,

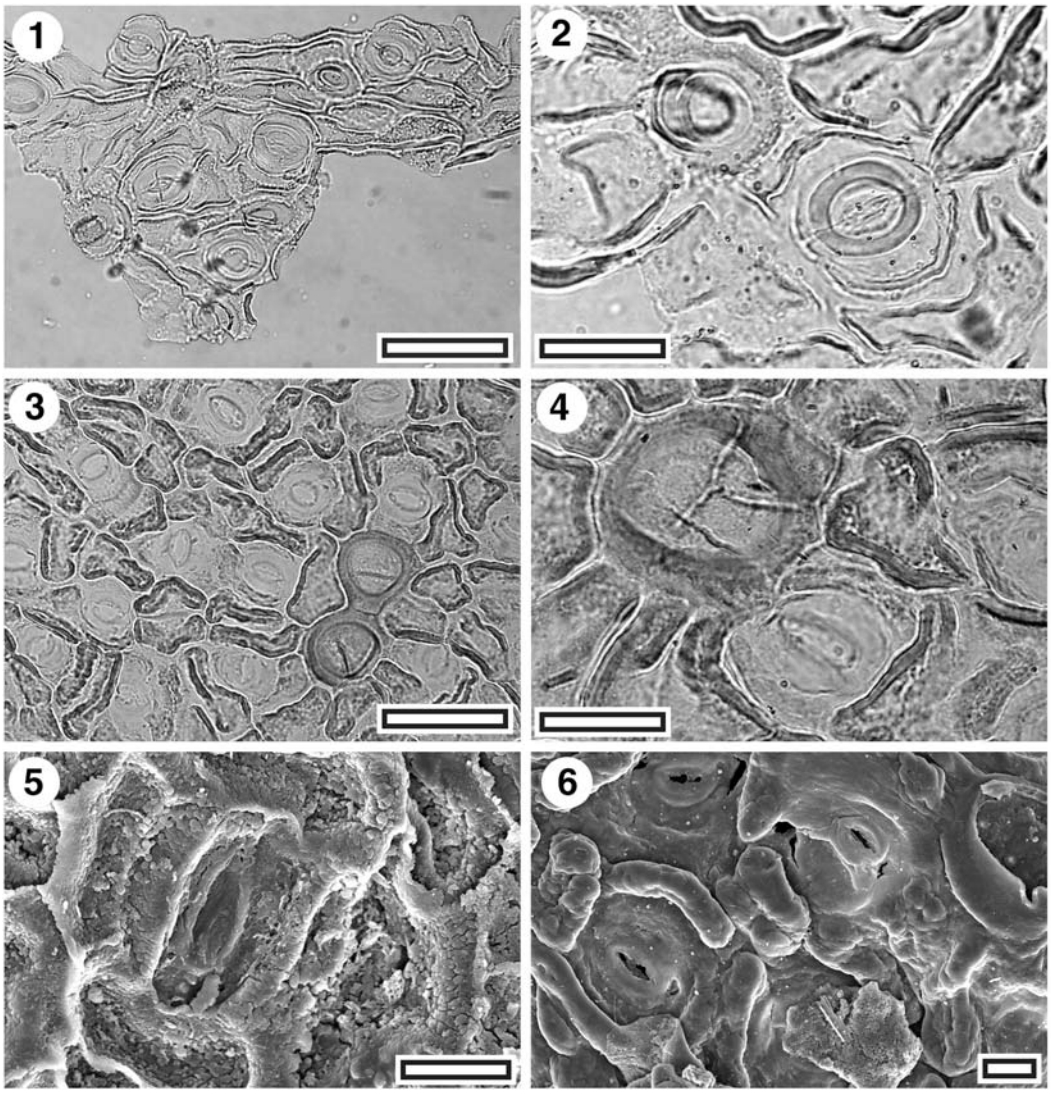

Figure 20. Proteaceae. CUT-P-EJE and CUT-P-EJH, **1.** CUT-P-EJE. TLM view showing several stomatal complexes and (Lower left and upper right) trichome bases (SB0680, scale-bar = 50 µm); **2.** CUT-L. TLM detail of a trichome base (upper left) and a stomatal complex (right) (SL4740, scale-bar = 20 µm); **3.** CUT-P-EJH. TLM view showing several stomatal complexes and paired trichome bases (lower right). Note elongate papillae (SB0677, scale-bar = 50 µm); **4.** CUT-P-EJH. TLM detail of a trichome base over three epidermal cells (upper left) and a stomatal complex (lower centre) (SB0677, scale-bar = 20 µm); **5.** CUT-P-EJH. SEM view of inner cuticular surface showing a single stomatal complex (S-1533, scale-bar = 10 µm); **6.** CUT-P-EJH. SEM view of outer cuticular surface showing there stomatal complexes and (upper right) a trichome base (S-1536, scale-bar = 10 µm).

isolated, randomly oriented, brachyparacytic, size range unimodal. Subsidiary cells typically elongate tangential to stomata, periclinal walls same thickness as normal epidermal cells, unornamented. Guard cell pair outline elliptical, outlined by a well-defined anticlinal wall, length 20–25 µm (medium), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge elliptical, extending from outer edge of stoma, thinner than normal epidermal cells, pore elliptical.

Epidermal cells. Epidermal cell flanges distinct (although may be partly obscured by surface topography), normal cells elongated, typically as long as, although narrower than typical epidermal cells, cells over veins not distinguished by shape, anticlinal walls curved, unbuttressed, unornamented.

Indumentum. With trichome insertion scars (trichomes deciduous) and papillae. Trichome scars common, annular and multicellular, inserted over 2–3 modified epidermal cells, basal diameter similar or distinctly larger size than normal epidermal cells. Epidermal cells under trichome base modified to form a thick, raised circular platform, on top of which sits a smooth, thick hollow collar. Trichome bases sometimes paired. Papillae present over all epidermal cells, laterally elongate, formed by formed by the entire outer surface of the epidermal cell projecting outwards, although they are very 'lumpy' and are probably many papillae fused together.

Distinguishing features. Proteaceae cuticle with laterally elongate papillae. CUT-P-EJH is very similar to CUT-P-004 published by Carpenter and Pole (1995) from the Middle Eocene of Western Australia. It is regarded here as distinct by having a broader rim around the trichome insertion scar, and by the papillae on each cell being more fused and projecting more.

Identification. Based on the similarity to CUT-P-004 (Carpenter and Pole 1995) CUT-P-EJH is regarded is *Telopea*.

CUT-P-GDJ
Figure 21.1-20.4

Reference specimen and locality: SL5412, R-37.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, with a trend towards alignment, brachyparacytic, size range unimodal. Subsidiary cells not visible under TLM, periclinal walls same thickness as normal epidermal cells, unornamented. Ornamented with discontinuous ridges of cuticle concentric about the stomatal pore. Guard cell pair length 18–23 µm (medium). Outer stomatal ledge elliptical, extending from outer edge of stoma, thinner than normal epidermal cells, pore elliptical.

Epidermal cells. Epidermal cell flanges distinct, normal cells isodiametric, cells over fine veins not distinguished by shape, anticlinal walls straight, unbuttressed, unornamented.

Indumentum. With trichome insertion scars (trichomes deciduous) and papillae. Trichome scars common, annular and multicellular, inserted over 2–3 epidermal cells with periclinal walls slightly thicker than normal epidermal cells, basal diameter similar or distinctly larger size than normal epidermal cells. Papillae present over all epidermal cells, round, smooth, about half the diameter of their epidermal cell.

Distinguishing features. Proteaceae cuticle with round papillae.

CUT-P-EAA
Figure 21.5-21.6

Reference specimen and locality: SB0688, R-68.

Referred specimens and occurrence: SB0687, R-23; SL5011, R-56.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, showing a clear trend towards alignment, brachyparacytic, size range unimodal. Subsidiary cells typically elongate tangential to stomata, periclinal walls thinner than over normal epidermal cells, unornamented. Guard cell pair outline varying from distinctly elongate to very broad, outlined by a well-defined anticlinal wall, length 15–23 µm (medium), with prominent T-piece thickenings at polar ends. Outer stomatal ledge elliptical, extending from outer edge of stoma, thinner than normal epidermal cells, pore elliptical.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric, approximately the same size as the stomata, cells over veins not distinguished by shape, anticlinal walls sinuous, buttressed, unornamented.

Indumentum. With trichome insertion scars (trichomes deciduous), Trichome bases common, annular and multicellular, inserted over 1–2 modified epidermal cells. Diameter similar in size to normal epidermal cell. Epidermal cells under trichome base forming an irregular platform (by thickening of the periclinal walls) which contains the trichome scar.

Distinguishing features. Proteaceae cuticle with stomatal complexes with a clear trend towards alignment, and buttressed epidermal cell walls.

CUT-P-EJI
Figure 22.1-22.4

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented or may show some alignment, brachyparacytic, size range unimodal. Subsidiary cells typically elongate tangential to stomata, periclinal walls same thickness as normal epidermal cells, unornamented. Guard cell pair outlined typically with flattened poles, outlined by a well-defined anticlinal wall, length 25–35 µm

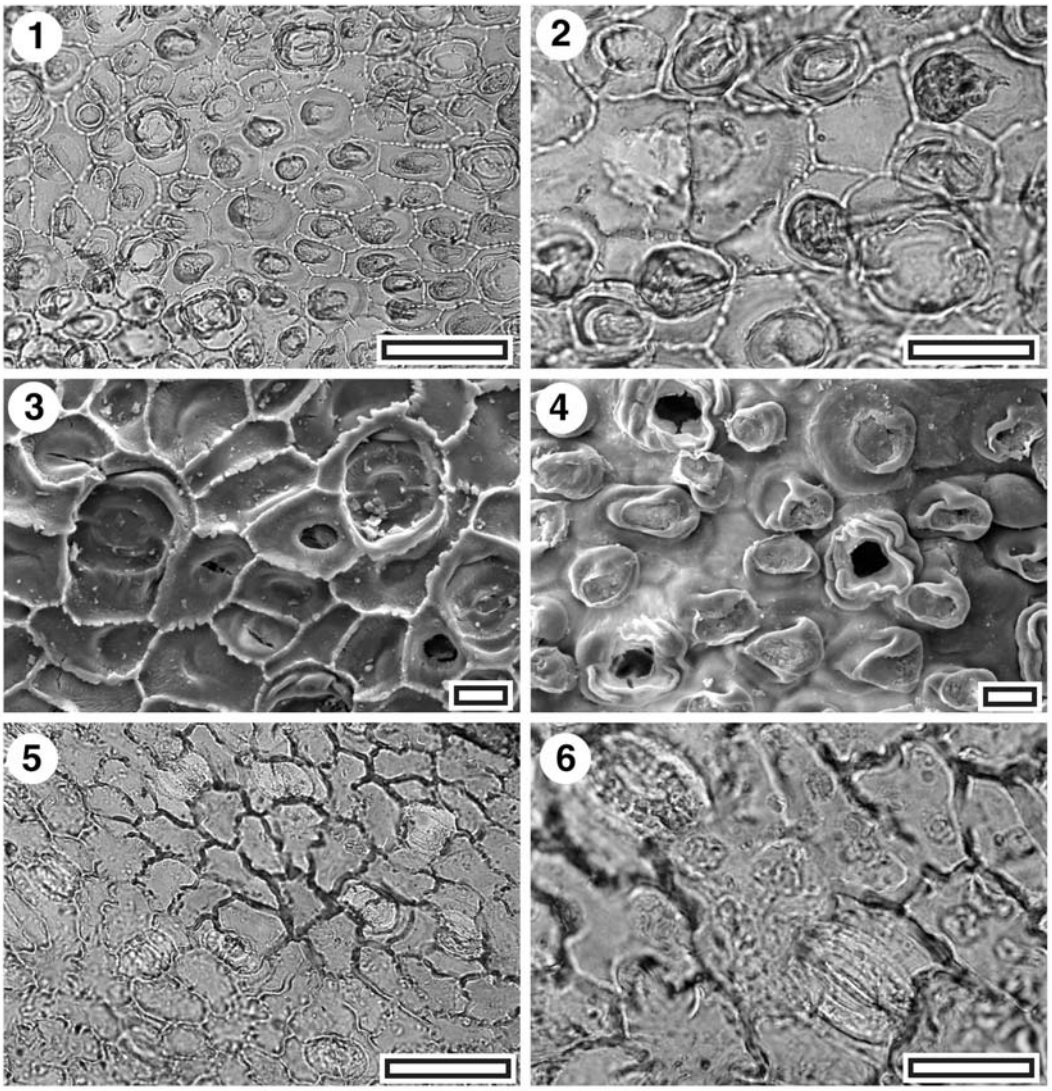

Figure 21. Proteaceae. CUT-P-GDJ and CUT-P-EAA. **1.** CUT-P NEW. TLM view showing several stomatal complexes (SL5412, scale-bar = 50 µm); **2.** CUT-P NEW. TLM detail of a trichome base over two epidermal cells (left of centre), a stomatal complex (lower right). Other dark objects are mostly papillae (SL5412, scale-bar = 20 µm); **3.** SEM view of inner cuticular surface showing four stomatal complexes, and papillate epidermal cells (S-1698, scale-bar = 10 µm); **4.** SEM view of outer cuticular surface showing three stomatal complexes (note the irregular ridges surrounding them), papillate epidermal cells, and (upper right) a trichome base (S-1698, scale-bar = 10 µm); **5.** CUT-P-EAA. TLM view showing several stomatal complexes (SB0688, scale-bar = 50 µm); **6.** CUT-P-EAA. TLM detail of a two stomatal complexes (SB0688, scale-bar = 20 µm).

(medium), with prominent polar rods, cuticle thinner than normal epidermal cells. Outer stomatal ledge extending from outer edge of stoma, pore elliptical.

Reference specimen and locality: SB0676, R-16; SL5411, R-34; SB0686, R-102.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate, approximately the same size as the stomata, cells over veins not distinguished by shape, anticlinal walls curved to sinuous, unbuttressed, unornamented.

Indumentum. With trichome insertion scars (trichomes deciduous), Trichome bases common, annular and multicellular, inserted over 2–4 modified epidermal cells. Diameter similar in size to normal epidermal cell. Epidermal cells around trichome base modified into radially elongate foot-cells. Epidermal cells under trichome base modi-

fied to form a thick, raised circular platform, on top of which sits a smooth, thick hollow collar.

Distinguishing features. Proteaceae cuticle with wavy to sinuous epidermal cell walls.

CUT-P-EJD
Figure 22.5-22.8

Reference specimen and locality: SB0675,R-76, SL5431, R-102.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, brachyparacytic, size range unimodal. Subsidiary cells typically elongate tangential to stomata, periclinal walls same thickness as normal epidermal cells, ornamented with many fine ridges parallel with, and on either side of the stomata. Guard cell pair outline elliptical, not outlined by a clear anticlinal wall, length 15–20 µm (medium), little polar development between guard cells (guard cells appear as continuous ring), cuticle same thickness as normal epidermal cells, Outer stomatal ledge extending from outer edge of stoma, pore elliptical.

Epidermal cells. Epidermal cell flanges not distinct under TLM and obscured by surface ridging which develops over the flanges, normal cells highly variable from isodiametric to elongate, approximately the same size as the stomata, cells over veins not distinguished by shape, anticlinal walls curved to sinuous; slightly buttressed, ornamented with discontinuous ridges above the epidermal cell anticlinal walls.

Indumentum. With trichome insertion scars (trichomes deciduous), Trichome bases common, annular and multicellular, inserted over 6–8 modified epidermal cells. Diameter much larger than normal epidermal cell. Epidermal cells under trichome base modified to form a thick, raised circular platform, on top of which sits a smooth, thick hollow collar. By far the thickest parts of the cuticle are under the trichome bases.

Distinguishing features. Proteaceae cuticle which is thin, but with very thickened trichome bases and no surface ornamentation. The thin cuticle but prominent trichome bases are similar to CUT-P-EJF.

Casuarinaceae Brown 1814

Casuarinaceae stem and cuticle morphology has been described by Dilcher et al. (1990) and Scriven and Hill (1995). *Gymnostoma* is identified on the basis of having four-sided articles and rows of stomata which are not protected within grooves.

Gymnostoma Johnson 1980
Gymnostoma sp.
Figure 23

After initial sample disaggregation articles were noted in samples: R-6, R-11, R-12, R-36, R-38, R-46, R-47, R-50, R-71. No dispersed cuticle survived further processing.

Rhizophoraceae Persoon 1807

CUT-Z-JAG
Figure 24.1-24.4

Reference specimen and locality: SB0338, R-74.

Referred specimens and occurrence: SL5230, R-12; SL5251, R-13; SL5064, R-21; SL5089, R-26; SB0338, R-74; SB0363, R-75; SL5424, R-79.

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic, stomata evenly spread, isolated, showing a clear trend towards alignment, cyclocytic, size range unimodal. Subsidiary cells hard to count under TLM as radial flanges of subsidiary cells are not well developed), periclinal walls thinner than over normal epidermal cells, unornamented. Guard cell pair outline elliptical, not outlined by a clear anticlinal wall, length 38–45 µm (large). Outer stomatal ledge narrowly elliptic, typically separated at polar ends, thicker than normal epidermal cells, extending over inner edge of stoma, pore narrowly elliptic.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric, distinctly smaller than the stomata, anticlinal walls straight, unbuttressed, unornamented.

Indumentum. Glabrous.

Distinguishing features. Cyclocytic stomatal complexes with a trend towards alignment and distinctly larger than epidermal cells.

Identification. Identification of Rhizophoraceae is based on the large, cyclocytic stomatal complexes, which have a trend towards alignment, and which are placed within isodiametric epidermal cells which are distinctly smaller than the dimensions of the stomatal complex (see also Ramassamy and Kannabiran 1996, Farooqui (Jennifer: references spell it “Faroqui”) 2001). The family Rhizophoraceae includes both terrestrial and mangrove species, but this combination of epidermal characters (Figures 24.5-24.7) appears to be unique to *Bru-*

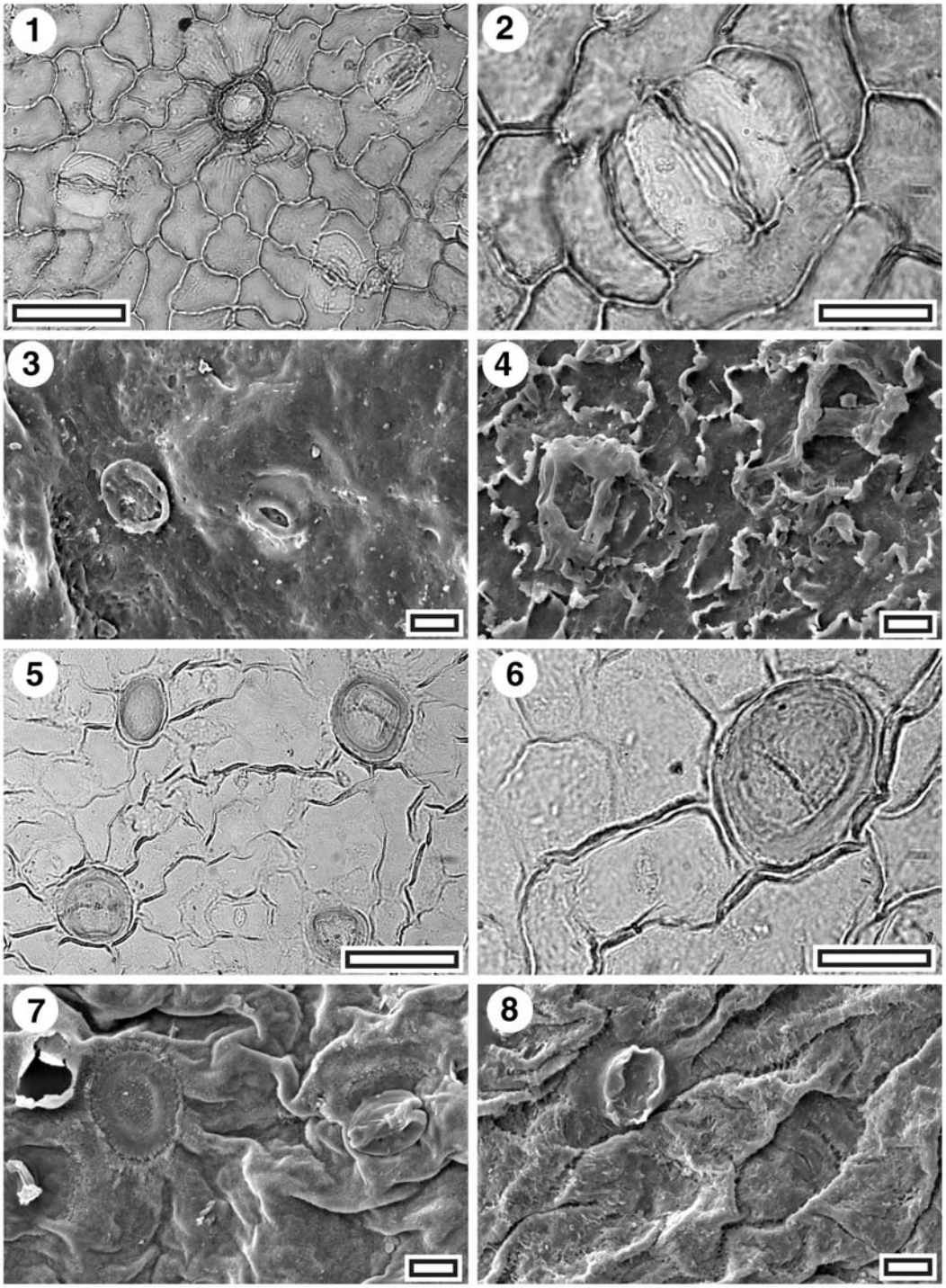

Figure 22. Proteaceae. CUT-P-EJI and CUT-P-EJD, **1.** CUT-P-EJI. TLM view showing three stomatal complexes and a trichome base (SB0676, scale-bar = 50 µm); **2.** CUT-P-EJI. TLM detail of a single stomatal complex (SB0676, scale-bar = 20 µm); **3.** SEM view of outer cuticular surface showing a trichome insertion scare (left of centre) and a stomatal complex (to right) (S-1691, scale-bar = 10 µm); **4.** SEM view of inner cuticular surface showing two stomatal complexes (S-1691, scale-bar = 10 µm); **5.** CUT-P-EJD. TLM view showing several stomatal complexes (indistinct) and four dark trichome bases (SB0675, scale-bar = 50 µm); **6.** CUT-P-EJD. TLM detail of a stomatal complex (lower left) and a dark trichome base (upper right) (SB0675, scale-bar = 20 µm); **7.** CUT-P-EJD, SEM view of inner cuticular surface showing a trichome base (left) and a stomatal complex (right). Note virtual absence of epidermal cell anticlinal walls (S-1686, scale-bar = 10 µm); **8.** CUT-P-EJD, SEM view of outer cuticular surface showing a trichome base (upper left) and a sunken stomatal complex (right) (S-1686, scale-bar = 10 µm).

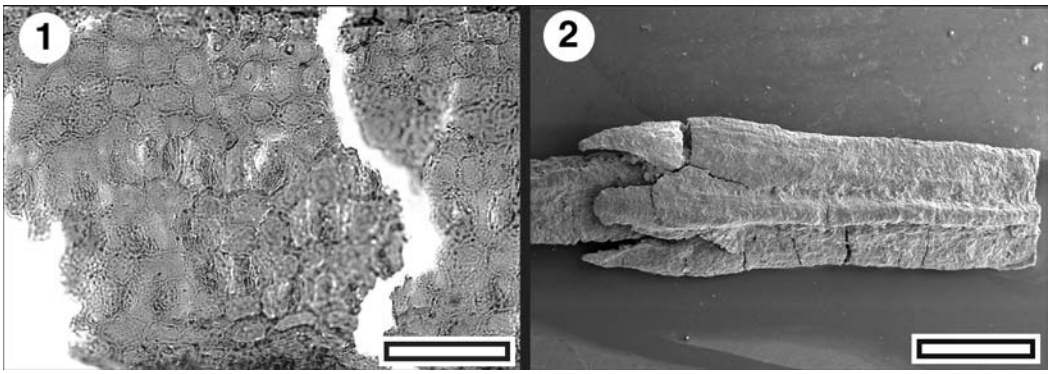

Figure 23. *Gymnostoma* sp. **1.** TLM view showing three stomatal rows (SL5429, scale-bar = 50 µm); **2.** TLM view of a stem with a leaf whorl (S-1714, scale-bar = 0.5 mm).

guiera, *Ceriops*, and *Rhizophora* which are closely related genera within the mangrove tribe Rhizophoreae within the Rhizophoraceae (Setoguchi et al. 1999). *Pelliciera* (Pellicieraceae) a mangrove in the tropical American region has the aligned stomatal complexes and small epidermal cells, but the stomatal complex morphology is distinctly different (Figure 24.8). Other Rhizophoraceae species available in the reference collection have very different epidermal morphologies. CUT-Z-JAG is therefore regarded as a mangrove of the family Rhizophoraceae.

Aquifoliaceae Richard 1828
CUT-Z-JJC
Figure 25.1-25.4

Reference specimen and locality: SB0694, R-20.

Referred specimens and occurrence: SB0693, R-20.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, unclear, bimodal size range with occasional giant stomata. Subsidiary cells (3–4) irregularly shaped, (generally not possible to count under TLM because of surface ornamentation), periclinal walls same thickness as normal epidermal cells, ornamentation continuous with that of epidermal cells. Guard cell pair outline circular, outer margin obscured under TLM by surface ornamentation, length 28–45 µm, (medium-large), with prominent polar rods. Outer stomatal ledge elliptical, thicker than normal epidermal cells, extending from outer edge of stoma, pore elliptical.

Epidermal cells. Epidermal cell flanges not distinct under TLM because of surface ornamentation, normal cells highly variable from isodiametric to elongate, approximately the same size as the stomata, anticlinal walls curved to sinuous, unbuttressed, ornamented with 'flowing' pattern of many fine ridges.

Indumentum. Trichome insertion scars sparse, with slightly thickened poral rims.

Distinguishing features. Having subsidiary and epidermal cells entirely covered by flowing fine ridges.

Identification. *Ilex cornuta* (Aquifoliaceae) has a similar ornamentation of fine, flowing ridges, and has giant stomata (Figures 25.5-25.6). However, its epidermal cell flanges are distinct, despite the ornamentation, and the subsidiary cells are smaller and more adpressed to the guard cells.

CUT-Z-JJB
Figure 26.1-26.3

Reference specimen and locality: SB0395, R-75.

Referred specimens and occurrence: SB0737, R-12.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, unclear, size range bimodal, with distinct 'giant stomata' present, (distinguished by being much narrower and longer and by having bands of fine ridges flowing away from them). Subsidiary cells difficult to count under TLM because of ornamentation of short, cuspate ridges which are concentric about the stoma, periclinal walls same thickness as normal epidermal cells, ornamented with 3–4 ridges parallel with, and on either side of the stomata. Guard cell pair outline elliptical, outlined by a well-defined anticlinal wall, clearly separated by polar walls, length 23-38 µm. Outer stomatal ledge elliptical, extending from

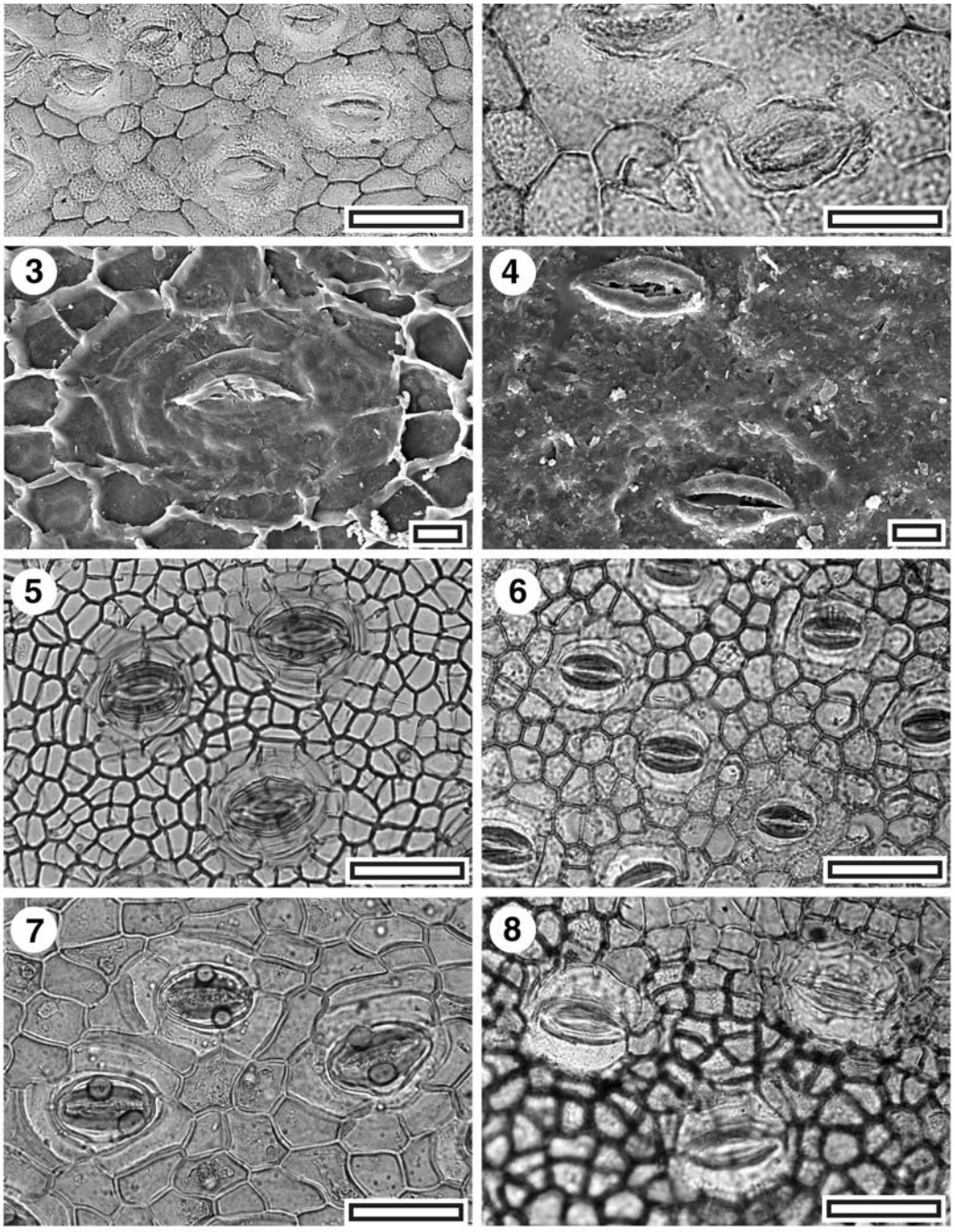

Figure 24. Rhizophoraceae, fossil and extant. **1.** CUT-Z-JAG. TLM view showing several stomatal complexes (note alignment and relatively small epidermal cells) SL5251, scale-bar = 50 µm); **2.** CUT-Z-JAG. TLM detail of two stomatal complexes (SL5251, scale-bar = 20 µm); **3.** CUT-Z-JAG. SEM view of inner cuticular surface showing single stomatal complex. Note most of subsidiary cell walls have collapsed (S-1545, scale-bar = 10 µm); **4.** CUT-Z-JAG. SEM view of outer cuticular surface showing two stomatal complexes. Note prominent elliptical outer stomatal ledges (S-1545, scale-bar = 10 µm); **5.** Extant *Rhizophora mangle.,* TLM view showing three stomatal complexes (note alignment and relatively small epidermal cells) OPH3063, scale-bar = 50 µm); **6.** Extant *Bruguiera sexangula*, TLM view showing several stomatal complexes. Note alignment and relatively small epidermal cells (CANB 231858, scale-bar = 50 µm); **7.** Extant *Pelliciera rhizophorae*, TLM view showing three stomatal complexes. Note alignment and relatively small epidermal cells (OPH7495, scale-bar = 50 µm); **8.** Extant *Ceriops tagal,* TLM view showing three stomatal complexes. Note alignment and relatively small epidermal cells (AQ109064, scale-bar = 50 µm).

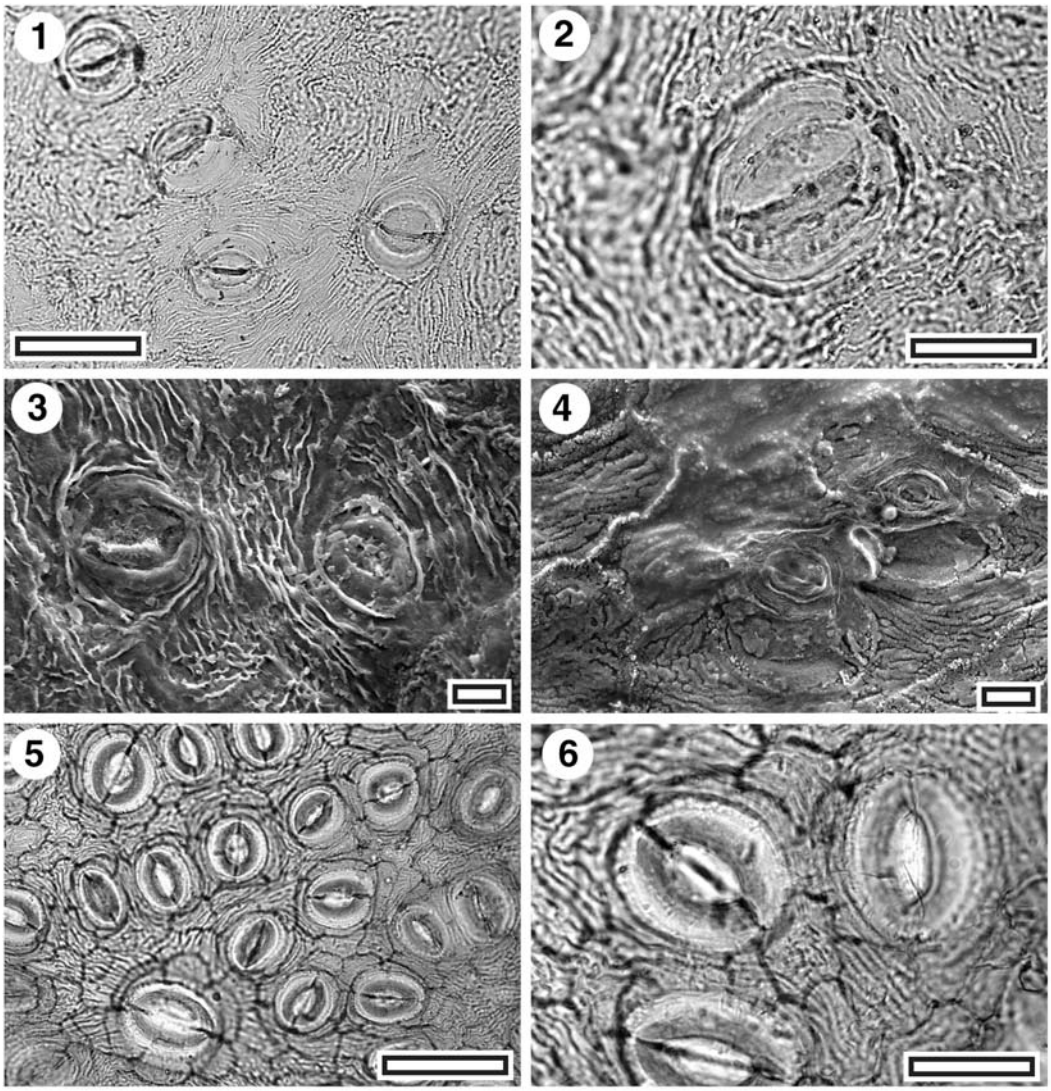

Figure 25. Aquifoliaceae, fossil and extant. CUT-Z-JJC. **1.** CUT-Z-JJC. TLM view showing four stomatal complexes (SB0694, scale-bar = 50 µm); **2.** CUT-Z-JJC. TLM detail of a single stomatal complex (SB0694, scale-bar = 20 µm); **3.** CUT-Z-JJC. SEM view of outer cuticular surface showing two stomatal complexes (S-0326, scale-bar = 10 µm); **4.** CUT-Z-JJC. SEM view of inner cuticular surface showing two stomatal complexes (S-0326, scale-bar = 10 µm); **5.** Extant *Ilex cornuta*, TLM view showing several stomatal complexes. Note "giant" stomatal complex (lower left) (AQ447358, scale-bar = 50 µm); **6.** Extant *Ilex cornuta*, TLM detail of three stomatal complexes (AQ447358, scale-bar = 20 µm).

outer edge of stoma, same thickness as normal epidermal cells, pore elliptical.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate, approximately the same size as the stomata, anticlinal walls curved, unbuttressed, ornamented with discontinuous, cuspate, thick ridges.

Indumentum. Glabrous.

Distinguishing features. Having a prominent ornamentation of discontinuous, cuspate ridges.

Identification. The extant *Nemopanthus mucronata* (Aquifoliaceae, Figure 26.4) has a similar ornamentation of short, cuspate ridges, as well as having 'giant stomata' which are longer and narrower than normal stomata and have ridges flowing away from them. Identification is suggested to be with Aquifoliaceae.

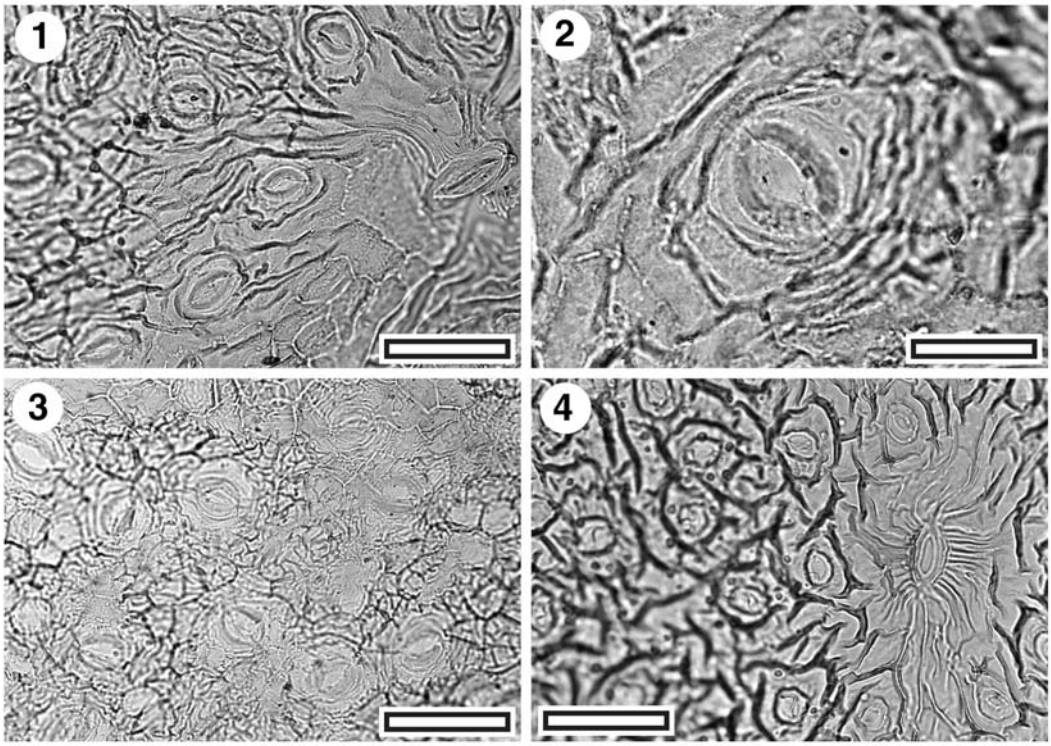

Figure 26. Aquifoliaceae, fossil and extant. **1.** CUT-Z-JJB. TLM view showing several stomatal complexes, and longer and narrower "giant" stomatal complex (centre right)., SB0737, scale-bar = 50 µm); **2.** CUT-Z-JJB. TLM detail of a single stomatal complex (SB0737, scale-bar = 20 µm); **3.** CUT-Z-JJB. TLM view showing a slightly different morphology than in 1 (SB0395, scale-bar = 50 µm); **4.** Extant *Nemopanthus mucronata*, TLM view showing several stomatal complexes, and longer and narrower "giant" stomatal complex (centre right). Compare with 1. (AQ214666, scale-bar = 50 µm).

CUT-Z-ACB
Figure 27.1-27.6

Reference specimen and locality: SB0335, R-74.

Referred specimens and occurrence: SL5326, R-06; SL5254, R-13; SB0720, R-21; SL5164, R-33; SB0334, R-74.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, anisocytic, size range unimodal. Subsidiary cells (2–4) irregularly shaped, periclinal walls same thickness as normal epidermal cells, ornamented with thick ridges concentric about the stomata. Guard cell pair outline elliptical, outlined by a well-defined anticlinal wall, with prominent T-piece thickenings at polar ends, length 40–55 µm (large). Outer stomatal ledge elliptical, same thickness as normal epidermal cells, extending from outer edge of stoma, pore elliptical.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate, typically as long as, although narrower than typical epidermal cells, anticlinal walls curved, unbuttressed, unornamented.

Indumentum. Glabrous.

Distinguishing features. Large anisocytic stomatal complexes with an ornamentation of concentric ridges restricted to subsidiary cells.

Identification. Large, anisocytic stomatal complexes with an ornamentation of relatively thick ridges over the subsidiary cells suggests Aquifoliaceae (Figures 27.7-27.8). Finer ridges would be more indicative of Myrsinaceae.

Other Angiosperm Taxa
Key to Miscellaneous angiosperm cuticle

1. Cuticle has distinct papillae. **Group A.**
1. Cuticle does not have distinct papillae. 2.

2. Cuticle has distinct surface striations. **Group B.**
2. Cuticle does not have distinct striations. 3.

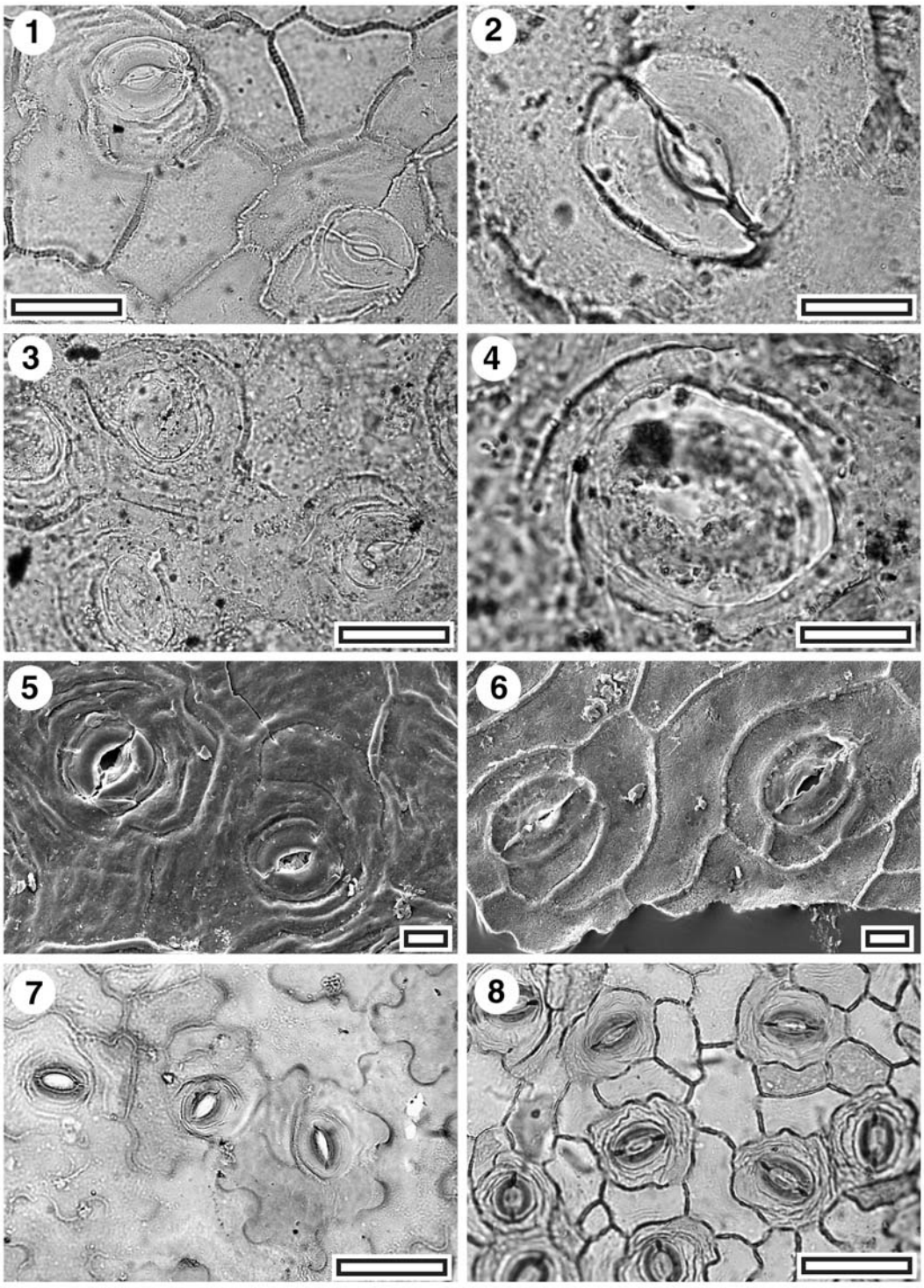

Figure 27. Aquifoliaceae, fossil and extant. **1.** CUT-Z-ACB. TLM view showing two stomatal complexes, SB0335, scale-bar = 50 µm); **2.** CUT-Z-ACB. TLM detail of a single stomatal complex (SB0335, scale-bar = 20 µm); **3.** CUT-Z-JAF. TLM view showing four stomatal complexes, SB0347, scale-bar = 50 µm); **4.** CUT-Z-JAF. TLM detail of a single stomatal complex (SB0347, scale-bar = 20 µm); **5.** CUT-Z-ACB. SEM view of outer cuticular surface showing two stomatal complexes (S-1680, x600); **6.** CUT-Z-ACB. SEM view of inner cuticular surface showing two stomatal complexes (S-1680, x600); **7.** Extant *Ilex godajam* TLM view showing three stomatal complexes (AQ503240, scale-bar = 50 µm); **8.** Extant *Ilex alternifolia,* TLM view showing several stomatal complexes (AQ214721, scale-bar = 50 µm).

3. Stomatal orientation is aligned. **Group C.**
3. Stomatal orientation is random. **Group D.**

Group A.
Cuticle with distinct papillae

1. Papillae ridged, No trichomes or trichome scars present. **CUT-Z-JBB**
1. Papillae not ridged. 2.

2. Papillae over whole epidermis. **CUT-Z-GDA**
2. Papillae distinct only around stomata. 3.

3. Papillae smooth, discrete, large, multicellular trichome insertion scars present. **CUT-Z-GCF**
3. Papillae broad, cuticle glabrous. **CUT-Z-JAD**

Group B.
Cuticle with prominent striations or grooves.

1. Cuticle very thin, epidermal cell outlines not clear. **CUT-Z JJE**
1. Epidermal cell outlines clear under TLM. 2.

2. Striations confined to, or most prominent in area around stomata. 3.
2. Striations spread over whole cuticle. 4.

3. Striations thick, forming two or three very discontinuous rings around stomata, cuticle glabrous. **CUT-Z-JCF**
3. Striations thin and many, cuticle with many persistent trichome bases. **CUT-Z-JCC**

4. Epidermal cells sinuous. **CUT-Z-JJA**
4. Epidermal cells polygonal or slightly wavy. **CUT-Z-JJB**

Group C.
Stomatal orientation is aligned.

1. Thick, simple trichome bases present. **CUT-Z-JEB**
1. No trichome bases. 2.

2. Epidermal cell outlines obscured by granularity of cuticle. **CUT-Z-JEJ**
2. Epidermal cell outlines clear. **CUT-Z-JEA**

Group D.
Cuticle without papillae, striations or aligned stomatal complexes.

1. Stomatal complex paracytic. **CUT-Z-JCA**
1. Stomatal complex not paracytic. 2.

2. Stomatal complex anisocytic, largest subsidiary cell in complex much larger than guard cell pair. 3.
2. Stomatal complex not anisocytic. 4.

3. Epidermal and subsidiary cell walls straight. **CUT-Z-JJF**
3. Epidermal and subsidiary cell walls wavy. **CUT-Z-JEF**

4. Epidermal cells sinuous. 5.
4. Epidermal cells not sinuous.6.

5. Trichome bases common, fine venation reflected in shape of epidermal cells. **CUT-Z-JCJ**
5. Trichome bases essentially absent, fine venation not reflected in shape of epidermal cells. **CUT-Z-JJH**

6. Stomatal aperture surrounded by a massively thickened ring. **CUT-Z-JDH**
6. Stomatal aperture not surrounded by a massively thickened ring. 7.

7. Stomata without prominent outer stomatal ledge. 8.
7. Stomata with very prominent outer stomatal ledge. 10.

8. Stomatal complexes infrequent, surrounded by a double ring of subsidiary cells. **CUT-Z-JAA**
8. Stomatal complexes common, not surrounded by a double ring of subsidiary cells. 9.

9. Stomata round, subsidiary cell arrangement highly variable, their cuticle of same thickness as normal epidermal cells. **CUT-Z-JJI**
9. Stomata elliptical, typically four subsidiary cells disorganised, thinner than normal epidermal cells. **CUT-Z-JAE**

10. Stomatal complexes staurocytic, stomatal pore slit-like. **CUT-Z-JEE**
10. Stomatal complexes not staurocytic, stomatal pore elliptical or sub-circular 11.

12. Epidermal cells isodiametric, small poral trichome bases present. **CUT-Z-JED**
12. Epidermal cells irregular to elongate, glabrous. **CUT-Z-JBH**

Group A.

CUT-Z-JBB
Figure 28

Reference specimen and locality: SB0378, R-75.

Referred specimens and occurrence: SL5208, R-08; SB0377, R-75; SB0710, R-76, SL5371, R-102.

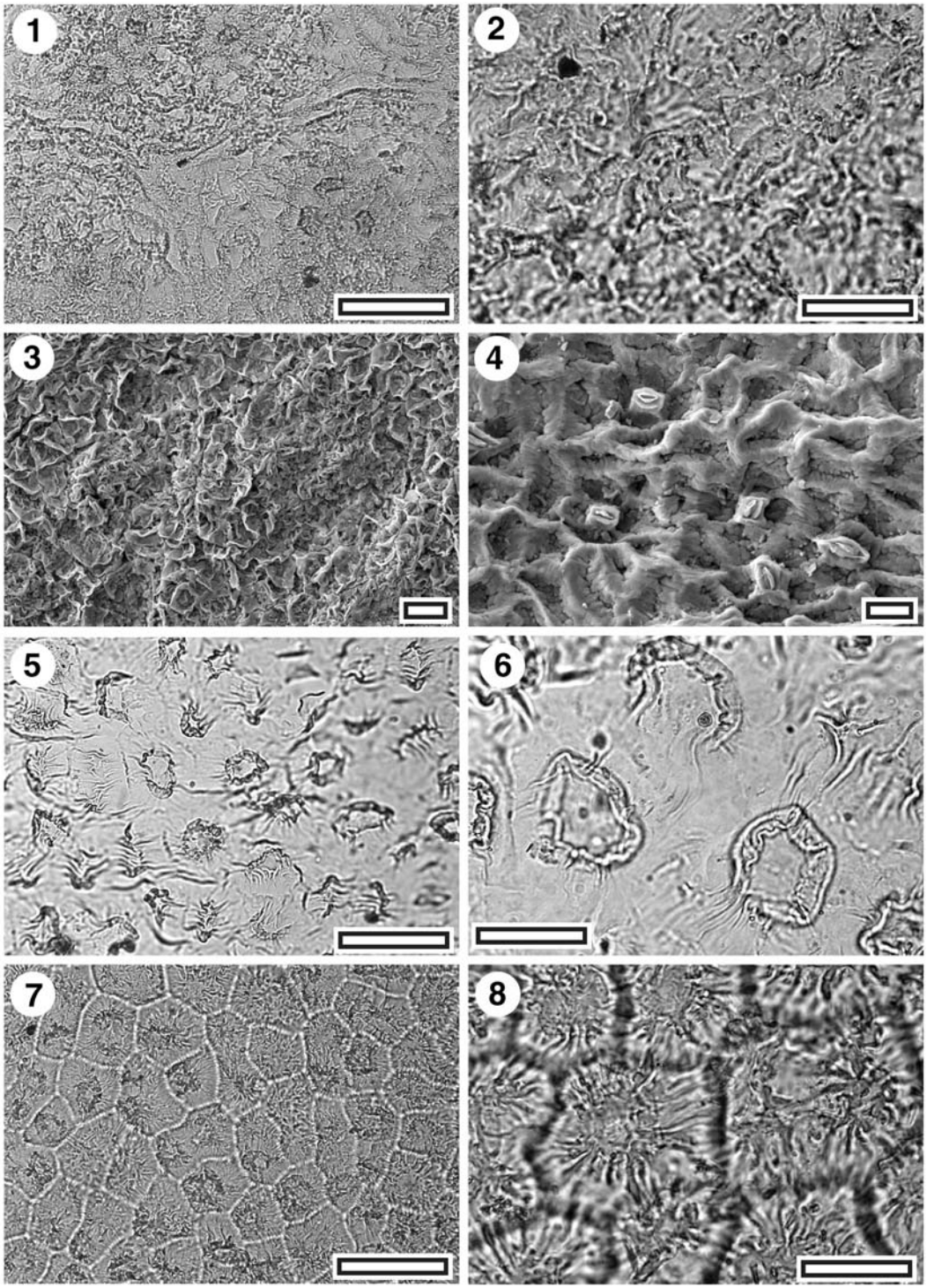

Figure 28. CUT-Z-JBB, **1.** TLM view showing three areoles with papillae-covered cells separated by venal epidermal cells (SL5371, scale-bar = 50 µm); **2.** TLM detail of papillae, with completely obscured stomatal complexes (SL5371, scale-bar = 20 µm); **3.** SEM view of outer cuticular surface showing papillae entirely obscuring stomatal complexes (S-1699, x600 scale-bar = 20 µm); **4.** SEM view of inner cuticular surface showing five deeply sunken stomata (S-1699, scale-bar = 10 µm); **5.** TLM view showing widely-spaced papillae (SB0378, scale-bar = 50 µm); **6.** TLM detail of widely-spaced papillae (SB0378, scale-bar = 20 µm); **7.** TLM view showing closely-spaced papillae (SB0710, scale-bar = 50 µm); **8.** TLM detail of closely spaced papillae (SB0710, scale-bar = 20 µm).

Stomatal complexes. Stomatal distribution in clear areolar groups, isolated, randomly oriented, cyclocytic or anomocytic, size range unimodal, length about 5-7 µm (small).

Epidermal cells. Flanges often indistinct under TLM (because of ornamentation of papillae), isodiametric, walls straight. From the centre of each normal epidermal and sometimes on venal epidermal cells, projects a single, longitudinally ridged papilla, which expands distally either slightly, or to cover the entire epidermal cell.

Indumentum. Glabrous.

Distinguishing features. Having longitudinally ridged papilla, which expand slightly, distally.

Identification. This cuticle is regarded as the same as that published by Hill (1991) as *Eucryphia*. Barnes and Jordan (2000) did not believe Hill's (1991) identification of the fossils to *Eucryphia* was correct. Hill described *E. microstoma* as brachyparacytic (a feature of extant *Eucryphia*) although this is not apparent in his figures.

CUT-Z-GDA
Figure 29.1-29.4

Reference specimen and locality: SL5433, R-102.

Stomatal complexes. Stomatal distribution unknown, isolated, randomly oriented, brachyparacytic, size range unimodal, length 20–22 µm (medium). Subsidiary cells not papillate, not obscured by papillae.

Epidermal cells. Flanges often indistinct under TLM (because of ornamentation of papillae), isodiametric, walls straight. Surface of each normal epidermal cell projecting outwards to form a single, smooth papilla.

Indumentum. With persistent, simple trichomes (staining much darker than normal epidermal cuticle under TLM), surrounded by epidermal cells radially elongated, and either papillae-free or with subdued papillae, forming foot-cells.

Distinguishing features. Having papillae and persistent simple trichomes.

CUT-Z-GCF
Figure 29.5-29.6

Reference specimen and locality: SB0371, R-75.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata in clear areolar areas between veins, isolated, randomly oriented, size range probably bimodal. Each stomata is surrounded by a ring of papillae (4-6) projecting from the subsidiary cells, one from each cell. Normal stomata completely obscured by papillae, but larger ones have the guard cells visible, typical length about 13 µm (small) but up to about 25 µm (medium).

Epidermal cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric, approximately the same size as the stomata, anticlinal walls curved, unbuttressed, unornamented but papillate, each cell with a single smooth papilla formed from most of the cell surface. Epidermal cells over fine veins distinguished by being more rectangular and not papillate.

Indumentum. Trichome insertion scars common (trichomes deciduous), situated over veins, consisting of a sub-circular opening with a smooth; Slightly thickened rim, 25–45 µm in diameter, leading to a chamber flanked by many cells with walls thicker than typical venal epidermal cells.

Distinguishing features. Having large papillate epidermal cells and distinctive compound trichome insertion pits.

CUT-Z-JAD
Figure 29.7-29.8

Reference specimen and locality: SB0725, R-23.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread. isolated, randomly oriented, size range unimodal, length around 25 µm (medium). Pore massively thickened, slit-like. Subsidiary cells 4-5, periclinal walls raised up as bubble-like papillae, anticlinal walls thicker than normal epidermal cells.

Epidermal cells. Isodiametric, rounded, granular, raised up slightly as papillae, but less than the subsidiary cells.

Indumentum. Glabrous.

Distinguishing features. CUT-Z-JAD is similar to CUT-L-DCG with regard to the massive thickening around the stomatal pore and subsidiary cells. However, it is distinct on the basis of papillae and higher number of subsidiary cells.

Group B.

CUT-Z-JJE
Figure 30.1-30.2

Reference specimen and locality: SB0732, R-6.

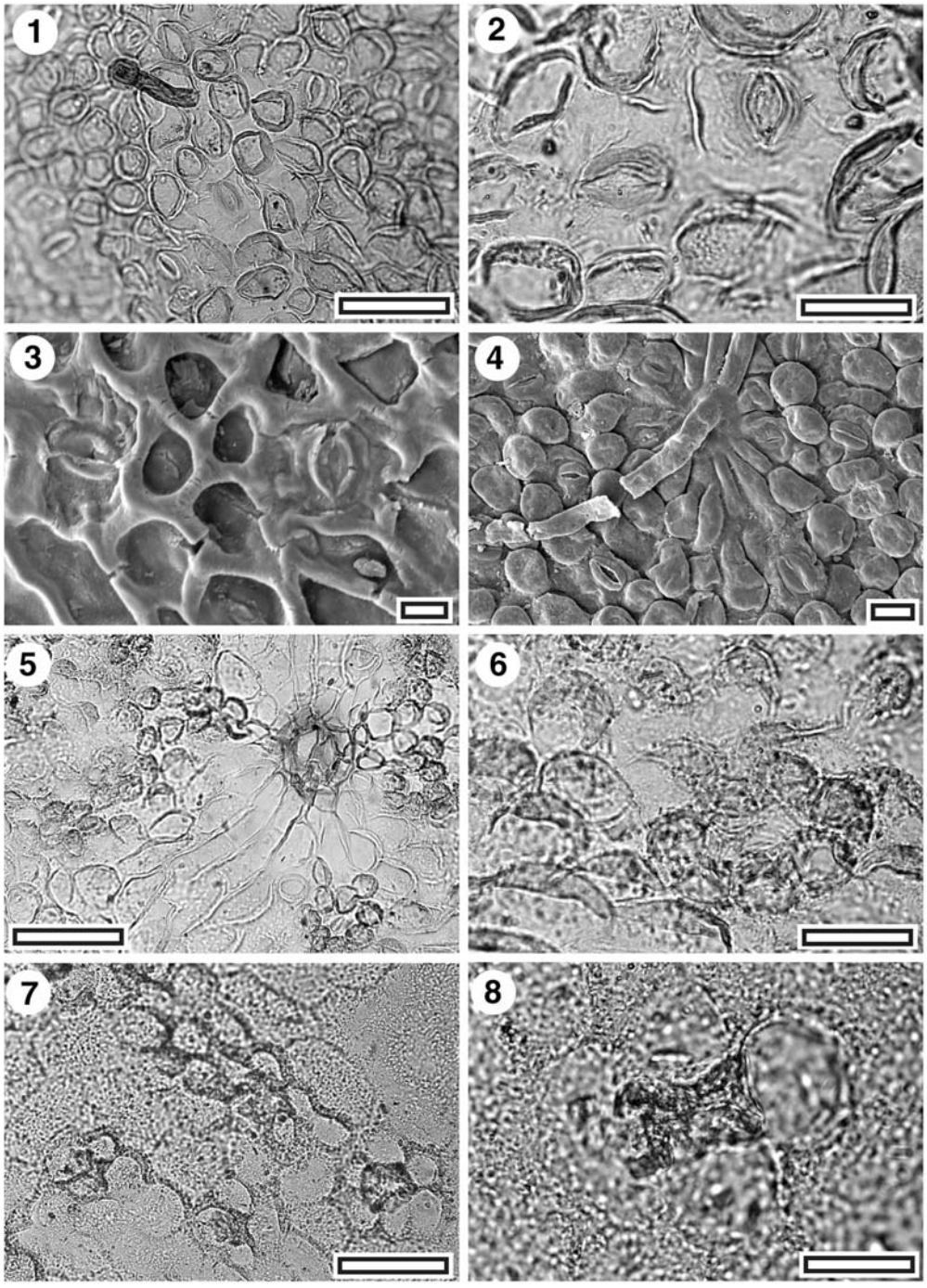

Figure 29. CUT-Z-GDA, CUT-Z-Z-GCF, and CUT-Z-Z-JAD, **1.** CUT-Z-GDA. TLM view showing scattered stomatal complexes and (upper left) a darkly staining persistent trichome (SL5433, scale-bar = 50 μm); **2.** CUT-Z-GDA. TLM detail of two stomatal complexes (SL5433, scale-bar = 20 μm); **3.** CUT-Z-GDA. SEM view of inner cuticular surface showing two stomatal complexes (S-1688, scale-bar = 10 μm); **4.** CUT-Z-GDA. SEM view of outer cuticular surface showing persistent trichome (upper centre) and several stomatal complexes surrounded by papillate epidermal cells (S-1688, scale-bar = 10 μm); **5.** CUT-Z-GCF. TLM view showing clusters of papillae surrounding stomatal complexes and a large trichome insertion scar in the middle of venal epidermal cells (SB0371, scale-bar = 50 μm); **6.** CUT-Z-GCF. TLM detail showing a ring of papillae around a stomatal complex (lower right) (SB0371, scale-bar = 20 μm); **7.** CUT-Z-JAD. TLM view showing several stomatal complexes surrounded by subdued papillae (SB0725, scale-bar = 50 μm); **8.** CUT-Z-JAD. TLM detail of a single stomatal complex. Note massive thickening around pore (SB0725, scale-bar = 20 μm).

Referred specimens and occurrence: SB0704, R-12; SB0734, R-22.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, size range unimodal. Subsidiary cell number and shape unclear, periclinal walls same thickness as normal epidermal cells, ornamented with fine ridges concentric about the stomata. Guard cell pair outline elliptical, not outlined by a clear anticlinal wall, length 23–40 µm, (medium-large). Outer stomatal ledge elliptical, thicker than normal epidermal cells, extending over inner edge of stoma, pore narrowly elliptic.

Epidermal cells. Epidermal cell periclinal and anticlinal walls very thin (anticlinal walls of epidermal cells not clear under TLM), unornamented.

Indumentum. With sparse trichome insertion scars (trichomes deciduous and therefore trichome type unknown), inserted between epidermal cells, with a massively thickened poral rim and radiating walls.

Distinguishing features. Very thin cuticle, but with massively thickened poral trichome insertion scars.

CUT-Z-JCF
Figure 30.3-30.4

Reference specimen and locality: SB0727, R-6.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, size range unimodal. Subsidiary cells not distinguished under TLM and therefore construction unclear, periclinal walls same thickness as normal epidermal cells, ornamented with a more or less continuous ridge immediately external to the outer stomatal ledge, and further out by 2–3 very discontinuous ridges concentric about the stomata. Guard cell pair outline elliptical, length 23–40 µm (medium-large). Outer stomatal ledge elliptical, same thickness as normal epidermal cells, extending from outer edge of stoma, pore elliptical.

Epidermal cells. Epidermal cell flanges somewhat diffuse, normal cells highly variable from isodiametric to elongate, approximately the same size as the stomata, anticlinal walls curved, unbuttressed, unornamented.

Distinguishing features. Having 2–3 very discontinuous ridges concentric about the stomata.

Indumentum. Glabrous.

CUT-Z-JCC
Figure 31.1-31.4

Reference specimen and locality: SB0741,R-30.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, brachyparacytic, size range unimodal, Subsidiary cells irregularly shaped, periclinal walls same thickness as normal epidermal cells, ornamented with fine ridges concentric about the stomata. Outer margin obscured under TLM by surface ornamentation, length 25–30 µm (medium). Outer stomatal ledge elliptical, same thickness as normal epidermal cells, extending from outer edge of stoma, pore elliptical.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate, approximately the same size as the stomata, anticlinal walls straight, unbuttressed, unornamented.

Indumentum. Hirsute, with abundant, simple, persistent trichomes inserted between epidermal cells. Epidermal cells around trichome base unmodified.

Distinguishing features. Brachyparacytic stomatal complexes and persistent trichomes.

CUT-Z-JJA
Figure 31.5-31.8

Reference specimen and locality: SB0723, R-7.

Referred specimens and occurrence: SB0723, R-7; SL5320, R-06; SL5206, R-07; SB0765, R-22; SL5373, R-102.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, isolated, randomly oriented, size range unimodal. Subsidiary cells (4–6) irregularly-shaped, difficult to distinguish by shape from epidermal cells, but with more granular inner cuticular surface, construction variable from actinocytic to possibly only one subsidiary cell, periclinal walls as thick as or often distinctly thinner than normal epidermal cells, ornamented by many fine ridges radiating from or flowing around the stomata. Guard cell pair outline elliptical, outlined by a well-defined anticlinal wall, length 15–28 µm (medium), clearly separated by polar walls. Outer stomatal ledge elliptical, same thickness as normal epidermal cells, extending from outer edge of stoma, pore elliptical.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate, distinctly larger than the stomata, anticlinal walls sinuous, unbuttressed,

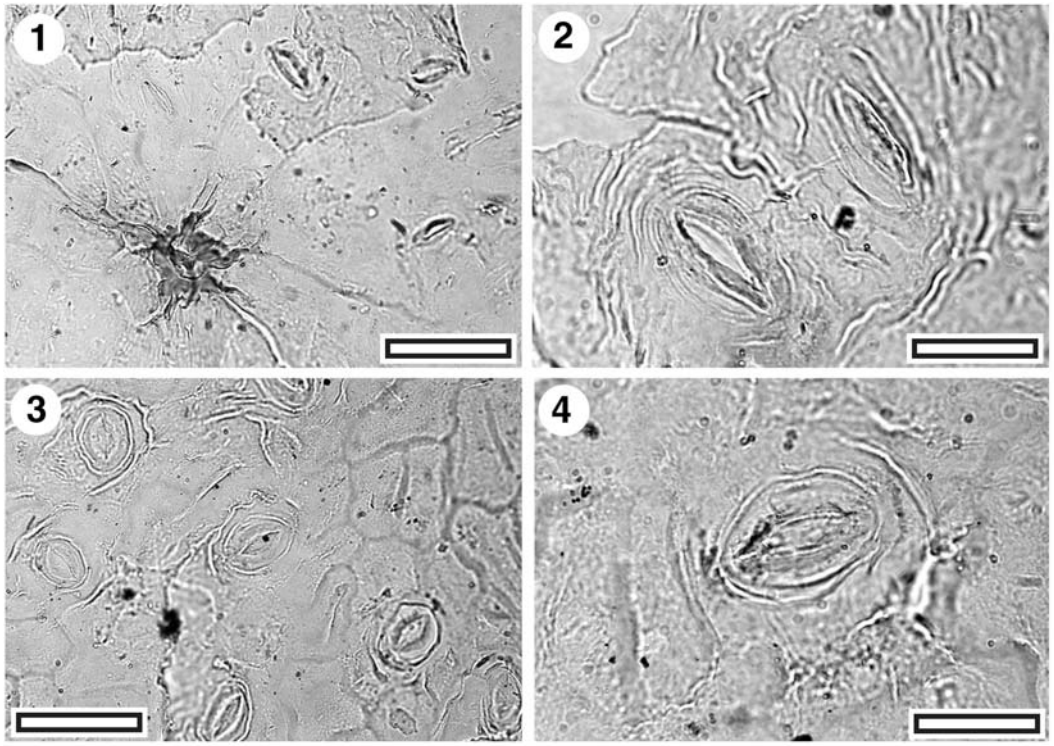

Figure 30. CUT-Z-JJE and CUT-Z-Z-JCF. **1.** CUT-Z-JJE. TLM view showing three stomatal complexes (upper right) and massively thickened trichome attachment scar (lower left) (SB0704, scale-bar = 50 μm); **2.** CUT-Z-JJE. TLM detail of two stomatal complexes (SB0704, scale-bar = 20 μm); **3.** CUT-Z-JCF. TLM view showing six stomatal complexes (SB0727, scale-bar = 50 μm); **4.** CUT-Z-JCF. TLM detail of a single stomatal complex (SB0727, scale-bar = 20 μm).

ornamented with 'flowing' pattern of many fine ridges.

Indumentum. Glabrous.

Distinguishing features. Elliptical stomata, sinuous epidermal cells and an ornamentation of fine flowing ridges.

Group C.

CUT-Z-JEB
Figure 32.1-32.2

Reference specimen and locality: SB0753, R-76.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, showing a clear trend towards alignment, unclear, size range unimodal. Subsidiary cells difficult to count under TLM, periclinal walls same thickness as normal epidermal cells, unornamented. Guard cell pair outline elliptical, outlined by a well-defined anticlinal wall, length 30–45 μm, (medium-large), some wall development between guard cells, and sometimes development of T-piece thickenings at the poles. Outer stomatal ledge elliptical, same thickness as normal epidermal cells, extending from outer edge of stoma, pore elliptical.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells elongated, approximately the same size as the stomata, anticlinal walls straight, unbuttressed, unornamented.

Indumentum. With trichome insertion scars (trichomes deciduous). Trichome scars sparse, inserted between epidermal cells. Epidermal cells around trichome scar mostly radially elongate, often modified by tangential divisions to form an irregular sub-circular zone of foot cells, poral rim massively thickened and frill-like.

Distinguishing features. Having a massively thickened and frill-like trichome poral rim.

CUT-Z-JEJ
Figure 32.4-32.5

Reference specimen and locality: SB0726,R-22.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, showing a clear trend towards alignment,

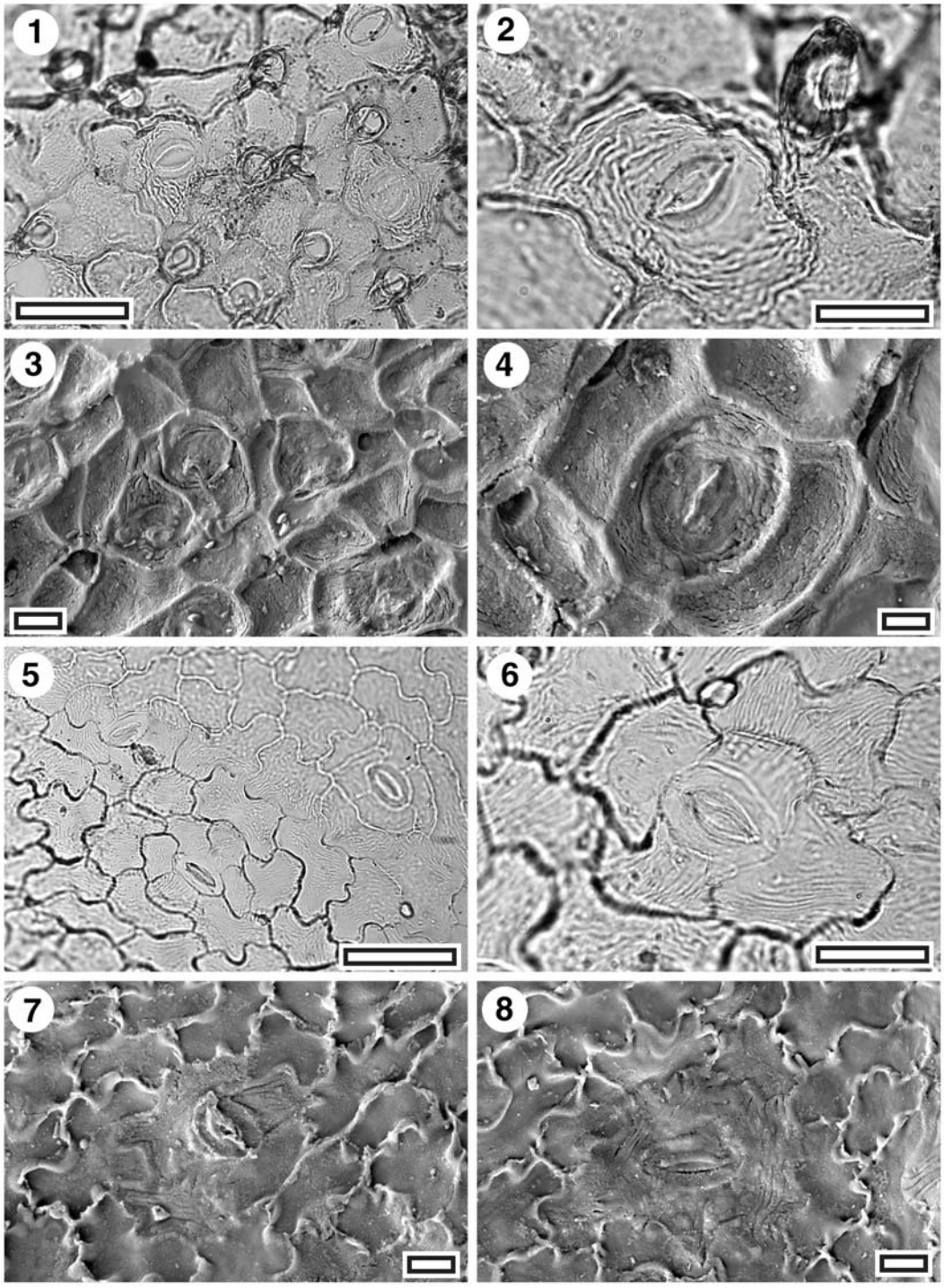

Figure 31. CUT-Z-JCC and CUT-Z-Z-JJA, **1.** CUT-Z-JCC. TLM view showing several stomatal complexes and persistent trichomes at intersections of epidermal cells (SB0741, scale-bar = 50 µm); **2.** CUT-Z-JCC. TLM detail of a single stomatal complex (note ornamentation of fine ridges on the subsidiary cells) and (upper right) a trichome (SB0741, scale-bar = 20 µm); **3.** SEM view of inner cuticular surface showing several stomatal complexes (S-0328, x600 scale-bar = 20 µm; **4.** SEM view of inner cuticular surface showing a single stomatal complex (S-0328, scale-bar = 10 µm); **5.** CUT-Z-JJA. TLM view showing three stomatal complexes (SB0723, scale-bar = 50 µm); **6.** CUT-Z-JJA. TLM detail of a single stomatal complex (SB0723, scale-bar = 20 µm); **7.** CUT-Z-JJA. SEM view of inner cuticular surface showing a single stomatal complex (S-0313, scale-bar = 10 µm); **8.** CUT-Z-JJA. SEM view of inner cuticular surface showing a single stomatal complex (S-0313, scale-bar = 10 µm).

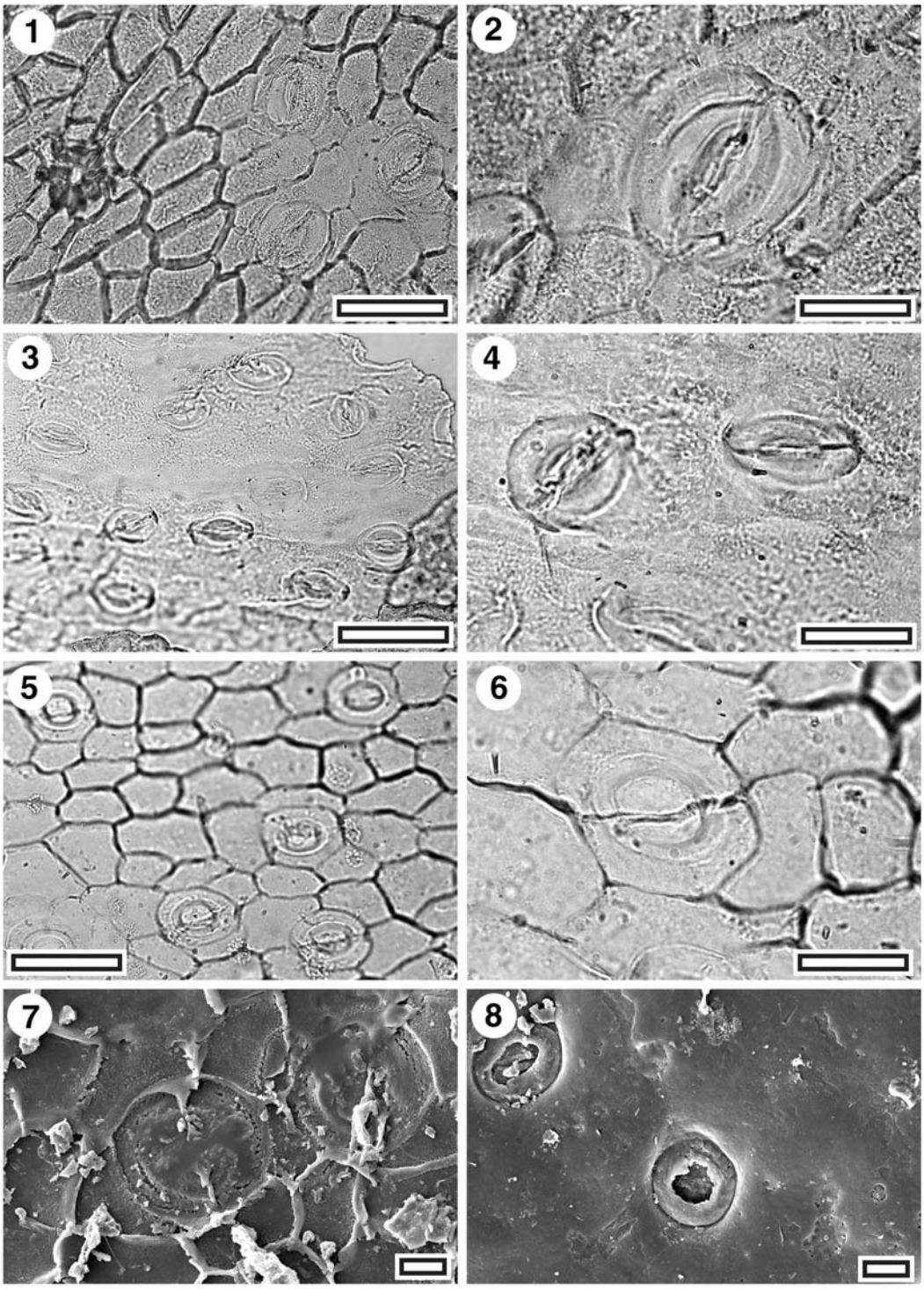

Figure 32. CUT-Z-JEB, CUT-Z-Z-JEJ, and CUT-Z-Z-JEA, **1.** CUT-Z-JEB. TLM view showing three stomatal complexes and (centre left) a massively thickened trichome insertion scar (SB0753, scale-bar = 50 µm); **2.** CUT-Z-JEB. TLM detail of a single stomatal complex (SB0753, scale-bar = 20 µm); **3.** CUT-Z-JEJ. TLM view showing several stomatal complexes (SB0726, scale-bar = 50 µm); **4.** CUT-Z-JEJ. TLM detail of two stomatal complexes (SB0726, scale-bar = 20 µm); **5.** CUT-Z-JEA. TLM view showing several stomatal complexes (SB0717, scale-bar = 50 µm); **6.** CUT-Z-JEA. TLM detail of a single stomatal complex (SB0717, scale-bar = 20 µm); **7.** CUT-Z-JEA. SEM view of inner cuticular surface showing two stomatal complexes (S-1541, scale bar = 10 µm); **8.** CUT-Z-JEA. SEM view of outer cuticular surface showing two stomatal complexes. Note very circular outer stomatal ledge (S-1541, scale-bar = 10 µm).

construction unclear, size range unimodal. Subsidiary cells not possible to count under TLM because of surface ornamentation, periclinal walls same thickness as normal epidermal cells, unornamented. Guard cell pair outline elliptical, not outlined by a clear anticlinal wall, length 18–35 µm (medium), with prominent T-piece thickenings at polar ends. Outer stomatal ledge elliptical, extending from outer edge of stoma, thicker than normal epidermal cells, pore elliptical.

Epidermal cells. Epidermal cell flanges not distinct under TLM because of surface ornamentation, unornamented.

Indumentum. Glabrous.

Distinguishing features. Elliptical stomata with a clear trend towards alignment and prominent T-pieces.

CUT-Z-JEA
Figure 32.6-32.8

Reference specimen and locality: SB0717, R-12.

Referred specimens and occurrence: SL5322, R-06; SB0717, R-12; SL5245, R-13; SL5047, R-21; SL5181, R-38; SL4998, R-47; SL5266, R-76.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated (but very rare networking noted), showing a clear trend towards alignment, anomocytic, size range unimodal. Subsidiary cells (4–5) irregularly shaped, periclinal walls same thickness as normal epidermal cells, unornamented. Guard cell pair outline circular, outlined by a very well-defined anticlinal wall, length 30–43 µm (medium-large), clearly separated by polar walls. Outer stomatal ledge sub circular, extending over centre of stoma, thicker than over normal epidermal cells, but surrounded by a very narrow thin zone, pore broad, sub-circular.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate, approximately the same size, or slightly smaller than the stomata, anticlinal walls straight to curved, unbuttressed, unornamented.

Indumentum. Glabrous.

Distinguishing features. Circular stomata showing a clear trend towards alignment.

Group D.

CUT-Z-JCA
Figure 33

Reference specimen and locality: SB0764, R-21.

Referred specimens and occurrence: SB0762, R-25.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, brachyparacytic, size range unimodal. Subsidiary cells typically elongate tangential to stomata, often longer than the stomata, unequally sized, periclinal walls same thickness as normal epidermal cells, unornamented. Guard cell pair outline elliptical, outlined by a well-defined anticlinal wall, length 18–35 µm (medium), clearly separated by polar walls. Outer stomatal ledge elliptical, extending over inner edge of stoma, thicker than normal epidermal cells, pore narrowly elliptic.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate, approximately the same size as the stomata, anticlinal walls sinuous, unbuttressed, unornamented.

Indumentum. Glabrous.

Distinguishing features. Brachyparacytic stomatal complexes, sinuous anticlinal walls and glabrous.

CUT-Z-JJF
Figure 34.1-34.4

Reference specimen and locality: SB0739, R-9.

Referred specimens and occurrence:

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, anisocytic (largest subsidiary cell is three to four times larger than the stoma), size range unimodal. Subsidiary cell periclinal walls same thickness as normal epidermal cells, unornamented. Guard cell pair outline circular, outlined by a well-defined anticlinal wall, length 15–20 µm (medium), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge sub circular, extending from outer edge of stoma, same thickness as normal epidermal cells, pore elliptical.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate, from approximately the

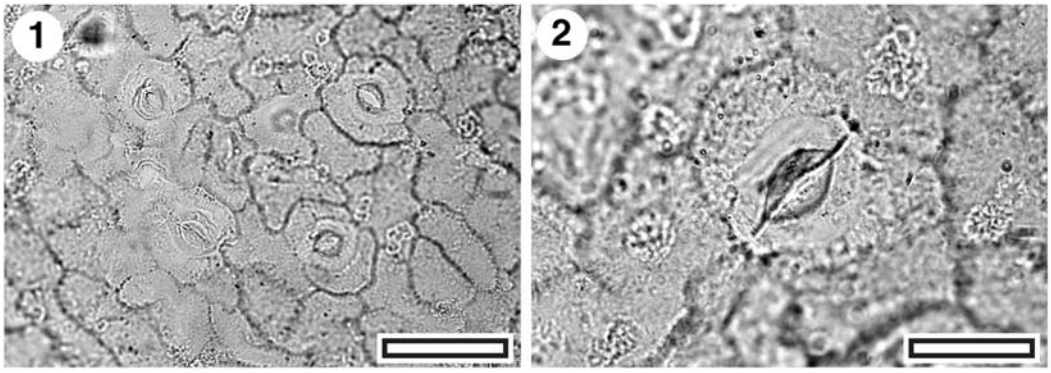

Figure 33. CUT-Z-JCA, **1.** TLM view showing several stomatal complexes (SB0764, scale-bar = 50 µm); **2.** TLM detail of a single stomatal complex (SB0764, scale-bar = 20 µm)

same size as the stomata to distinctly larger, anticlinal walls straight, unbuttressed, unornamented.

Indumentum. Glabrous.

Distinguishing features. Anisocytic stomatal complexes in which the largest subsidiary cell is three to four times larger than the stomata and with straight epidermal cell anticlinal walls. Differs from CUT-Z-JEF by having straight rather than sinuous walls.

CUT-Z-JEF
Figure 34.5-34.8

Reference specimen and locality: SL5426, R-34; SB0698, R-76.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, anisocytic (largest cell is three-four times larger than the stoma), size range unimodal. Subsidiary cell periclinal walls same thickness as normal epidermal cells, unornamented. Guard cell pair outline circular, outlined by a well-defined anticlinal wall, length 20–25 µm (medium), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge sub circular, extending from outer edge of stoma, same thickness as normal epidermal cells, pore elliptical.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, normal cells elongated, from approximately the same size as the stomata to distinctly larger, anticlinal walls sinuous, unbuttressed, unornamented.

Indumentum. Glabrous.

Distinguishing features. Anisocytic stomatal complexes in which the largest subsidiary cell is three to four times larger than the stomata and with sinuous epidermal cell anticlinal walls. Differs from CUT-Z-JJF by having sinuous rather than straight walls.

CUT-Z-JCJ
Figure 35.1-35.2

Reference specimen and locality: SB0763, R-102.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, often networked, randomly oriented, anomocytic, size range unimodal. Subsidiary cell periclinal walls same thickness as normal epidermal cells, unornamented. Guard cell pair outline circular, outlined by a well-defined anticlinal wall, length 15–28 µm (medium), clearly separated by polar walls. Outer stomatal ledge sub circular, extending over centre of stoma, thicker than normal epidermal cells, pore elliptical - sub circular.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, though cuticle generally thin, normal cells elongated, approximately the same size as the stomata, anticlinal walls sinuous, unbuttressed, unornamented.

Indumentum. With trichome insertion scars. Trichome scars common (trichome deciduous), inserted between epidermal cells. Epidermal cells around trichome scar modified into radially-elongate foot-cells (6–8), and thickened to form a poral rim and radial walls.

Distinguishing features. Circular stomata with sinuous epidermal cells and common simple trichome insertion scars. Differs from CUT-Z-JJH by the presence of trichome insertion scars.

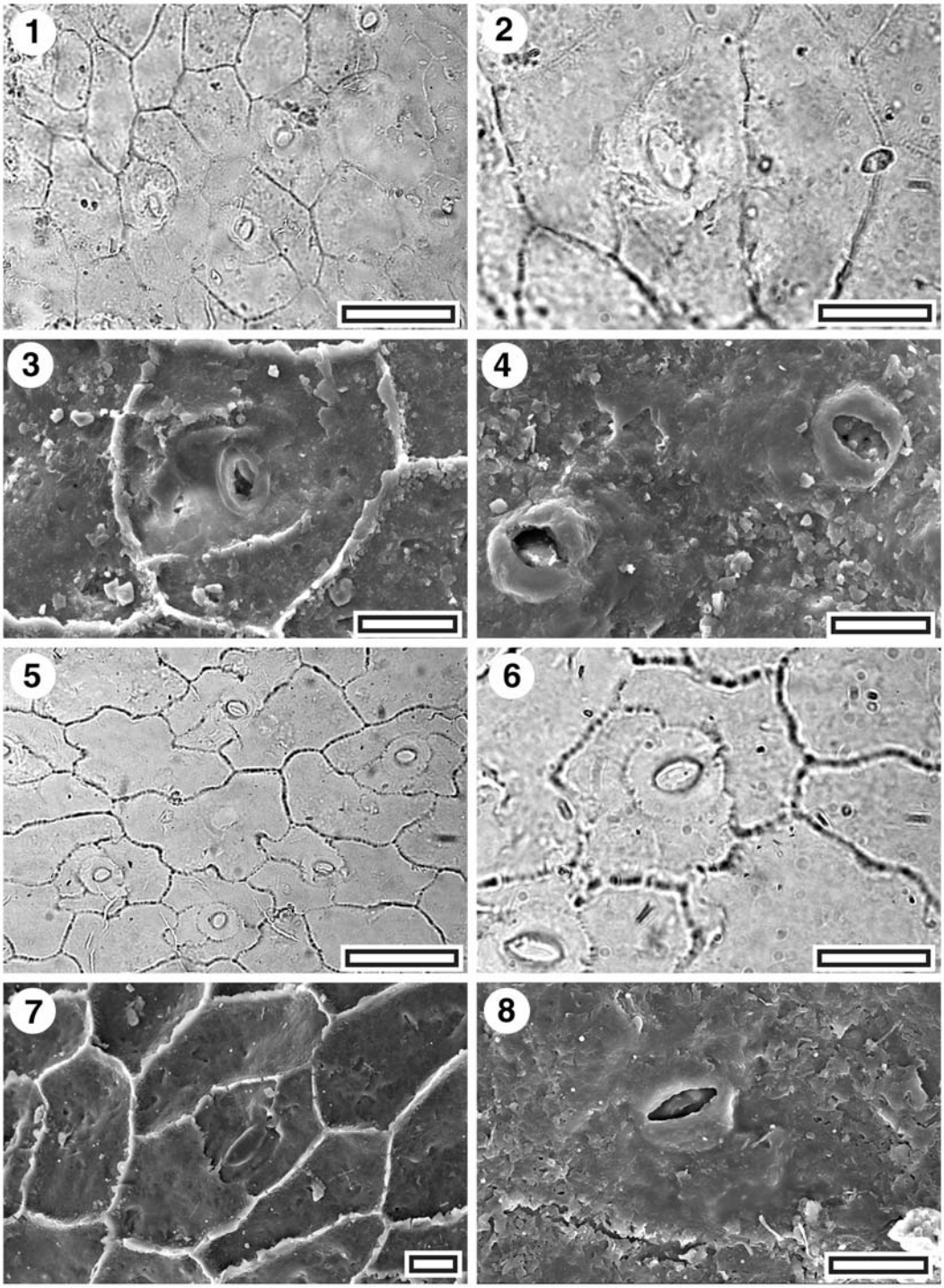

Figure 34. CUT-Z-JJF and CUT-Z-Z-JEF, **1.** CUT-Z-JJF. TLM view showing several stomatal complexes (SB0739, scale-bar = 50 µm); **2.** CUT-Z-JJF. TLM detail of a single stomatal complex (SB0739, scale-bar = 20 µm); **3.** SEM view of inner cuticular surface showing a single stomatal complex (S-1549, scale-bar = 10 µm); **4.** SEM view of outer cuticular surface showing two stomatal complexes (S-1549, scale-bar = 10 µm); **5.** CUT-Z-JEF. TLM view showing several stomatal complexes (SB0698, scale-bar = 50 µm); **6.** CUT-Z-JEF. TLM detail of two stomatal complexes (SB0698, scale-bar = 20 µm); **7.** CUT-Z-JEF. SEM view of inner cuticular surface showing a single stomatal complex (S-1534, scale-bar = 10 µm); **8.** CUT-Z-JEF. SEM view of outer cuticular surface showing a single stomatal complex (S-1534, scale-bar = 10 µm).

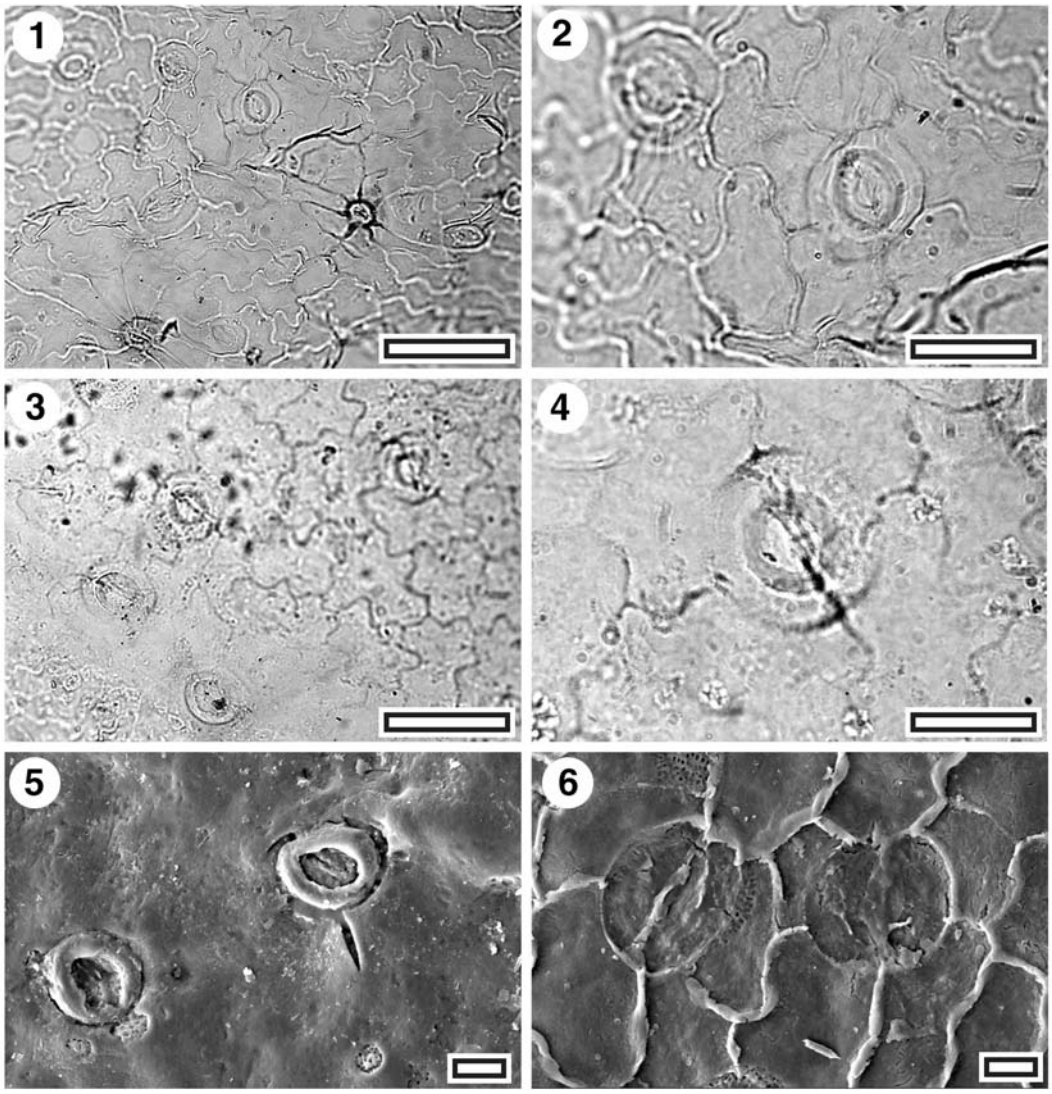

Figure 35. CUT-Z-JCJ and CUT-Z-Z-JJH, **1.** CUT-Z-JCJ. TLM view showing several stomatal complexes and two trichome attachment scars (SB0763, scale-bar = 50 μm); **2.** CUT-Z-JCJ. TLM detail of two stomatal complexes (SB0763, scale-bar = 20 μm); **3.** CUT-Z-JJH. TLM view showing TLM view showing four stomatal complexes. Note the pair to left of centre is networked - sharing a single contact cell (SB0701, scale-bar = 50 μm); **4.** CUT-Z-JJH. TLM detail of a single stomatal complex (SB0701, scale-bar = 20 μm); **5.** CUT-Z-JJH. SEM view of outer cuticular surface showing two stomatal complexes (S-1689, scale-bar = 10 μm); **6.** CUT-Z-JJH. SEM view of outer cuticular surface showing two stomatal complexes (S-1689, scale-bar = 10 μm).

CUT-Z-JJH
Figure 35.3-35.6

Reference specimen and locality: SB0701, R-26.

Referred specimens and occurrence: SL5346, R-11; SL5055, R-21; SB0748, R-23; SL5088, R-25; SB0701, R-26; SL5336, R-50; SL5329, R-75.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, anomocytic, size range unimodal. Subsidiary cell periclinal walls same thickness as normal epidermal cells, unornamented. Guard cell pair outline circular, outlined by a well-defined anticlinal wall, length 28–35 μm (medium), some wall development between guard cells, and sometimes development of T-piece thickenings at the poles. Outer stomatal ledge sub circular, extending from outer edge of stoma, thicker than normal epidermal cells, pore elliptical - sub circular.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate, from approximately the

same size as the stomata to distinctly larger, anticlinal walls sinuous, unbuttressed, unornamented.

Indumentum. Glabrous.

Distinguishing features. Circular stomata with sinuous epidermal cells and absence of trichome insertion scars. Differs from CUT-Z-JCJ by the absence of trichome insertion scars.

CUT-Z-JDH
Figure 36.1-36.2

Reference specimen and locality: SB0712, R-25.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, unclear, size range unimodal. Subsidiary cell periclinal walls same thickness as normal epidermal cells, ornamented with a very broad, massive, and lumpy peristomatal rim. Guard cell pair outline difficult to distinguish, outer margin obscured under TLM by surface ornamentation, length 25–28 µm (medium). Outer stomatal ledge elliptical, extending from outer edge of stoma, same thickness as normal epidermal cells, pore elliptical.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric, distinctly smaller than the stomata, anticlinal walls straight, unbuttressed, unornamented.

Indumentum. With trichome insertion scars (trichomes deciduous). About 7 ft cells surround scar; slightly radially elongated.

Distinguishing features. Having a very broad, massive and lumpy peristomatal rim.

CUT-Z-JAA
Figure 36.3-36.4

Reference specimen and locality: SB0350,R-74.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, cyclocytic, appears to be two rings of subsidiary cells, size range unimodal. Subsidiary cell periclinal walls thinner than over normal epidermal cells, unornamented. Guard cell pair outline elliptical, not outlined by a clear anticlinal wall, length 25–38 µm (medium), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge not clear, thinner than normal epidermal cells, pore elliptical.

Epidermal cells. Epidermal cell flanges clearly visible using TLM but of varying thickness, normal cells isodiametric, approximately the same size, or slightly smaller than the stomata, anticlinal walls straight, unbuttressed, unornamented.

Indumentum. Glabrous.

Distinguishing features. Sparse stomatal complexes with apparently two rings of subsidiary cells.

CUT-Z-JJI
Figure 36.5-36.6

Reference specimen and locality: SB0754, R-76.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata in areoles, sometimes networked, randomly oriented, size range unimodal, construction very variable from apparently anomocytic to having one or two subsidiary cells (distinguished by being narrower than normal epidermal cells). Subsidiary cell periclinal walls same thickness as normal epidermal cells, unornamented. Guard cell pair outline elliptical, outlined by a well-defined anticlinal wall, length 15–20 µm (medium), some wall development between guard cells, and sometimes development of T-piece thickenings at the poles. Outer stomatal ledge elliptical, extending from outer edge of stoma, same thickness as normal epidermal cells, pore elliptical.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, though cuticle generally thin, normal cells highly variable from isodiametric to elongate, approximately the same size as the stomata, cells over both major and fine venation more elongate, anticlinal walls curved, unbuttressed, unornamented.

Indumentum. Glabrous.

Distinguishing features. Thin cuticle with thin outer stomatal ledges and stomatal complexes varying from anomocytic to having one or two subsidiary cells.

CUT-Z-JAE
Figure 37

Reference specimen and locality: SL5071, R-21.

Referred specimens and occurrence: SL5201, R-06; SL5217, R-11; SL5225, R-12; SL5253, R-13; SL5066, R-21; SB0718, R-26; SL5161, R-33; SL5182, R-39; SL5001, R-47; SB0345, R-74; SB0374, R-75.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, cyclocytic, size range unimodal. Subsidiary cells (4–5) with periclinal

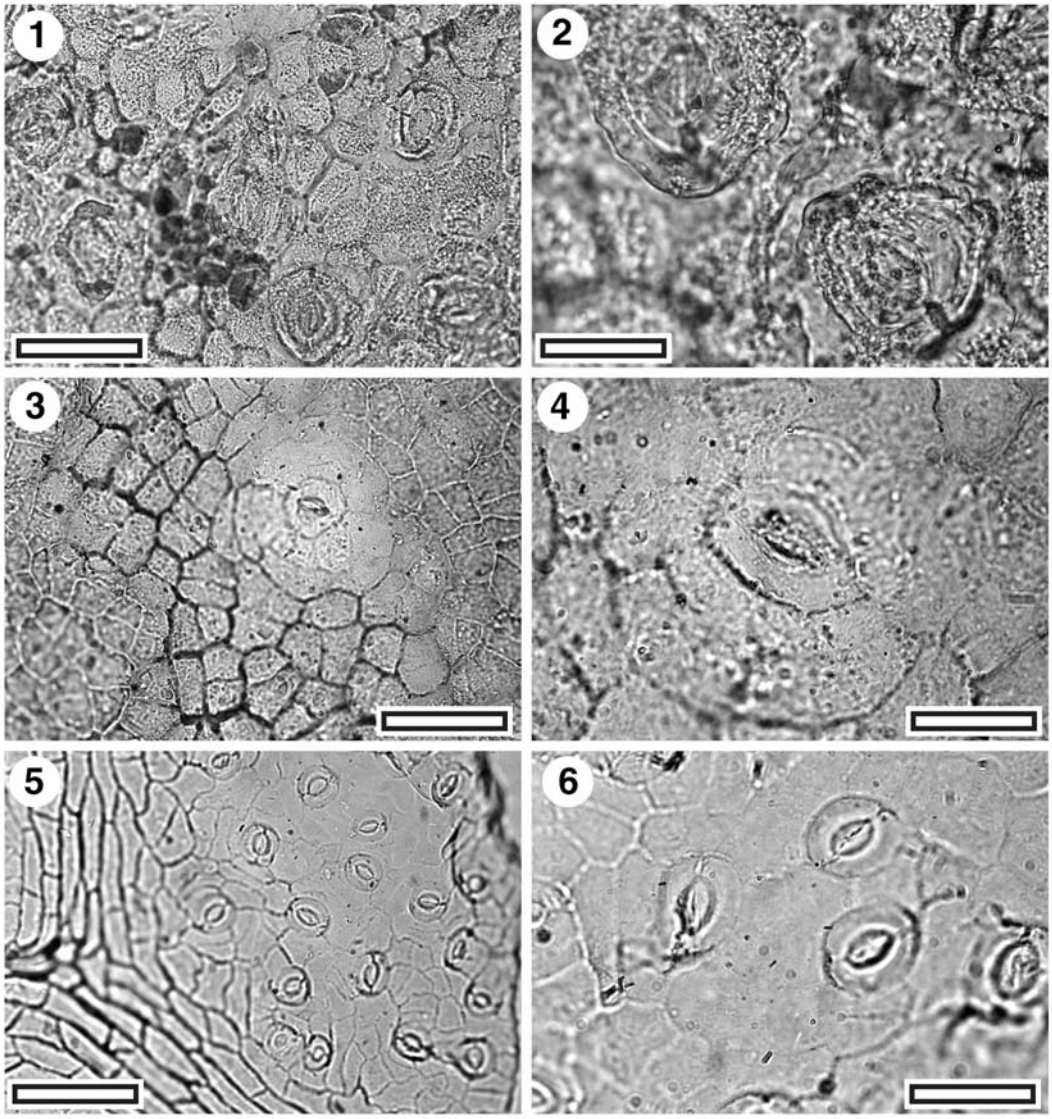

Figure 36. CUT-Z-JDH, CUT-Z-Z-JAA, and CUT-Z-Z-JJI, **1.** CUT-Z-JDH. TLM view showing several stomatal complexes (SB0712, scale-bar = 50 µm); **2.** CUT-Z-JDH. TLM detail of two stomatal complexes. Note massive rings of cuticle surrounding each. (SB0712, scale-bar = 20 µm); **3.** CUT-Z-JAA. TLM view showing a single stomatal complex (SB0350, scale-bar = 50 µm); **4.** CUT-Z-JAA. TLM detail of a single stomatal complex (SB0350, scale-bar = 20 µm); **5.** CUT-Z-JJI. TLM view showing several stomatal complexes and (at left) a vein reflected in the shape of venal epidermal cells (SB0754, scale-bar = 50 µm); **6.** CUT-Z-JJI. TLM detail of four stomatal complexes (SB0754, scale-bar = 20 µm).

walls as thick as, or sometimes slightly thicker than normal epidermal cells, but also with a distinctly thinner zone around the outer stomatal ledge, unornamented. Guard cell pair outline elliptical, not outlined by a clear anticlinal wall, length 15–25 µm (medium), some wall development between guard cells, and sometimes development of T-piece thickenings at the poles. Outer stomatal ledge elliptical, extending from outer edge of stoma, thinner than normal epidermal cells, pore elliptical.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate, from approximately the same size as the stomata to distinctly larger, anticlinal walls thick, straight to curved, unbuttressed, unornamented and with a particularly smooth texture.

Indumentum. With trichome insertion scars (trichomes deciduous). Trichome scars sparse, inserted between epidermal cells. Epidermal cells

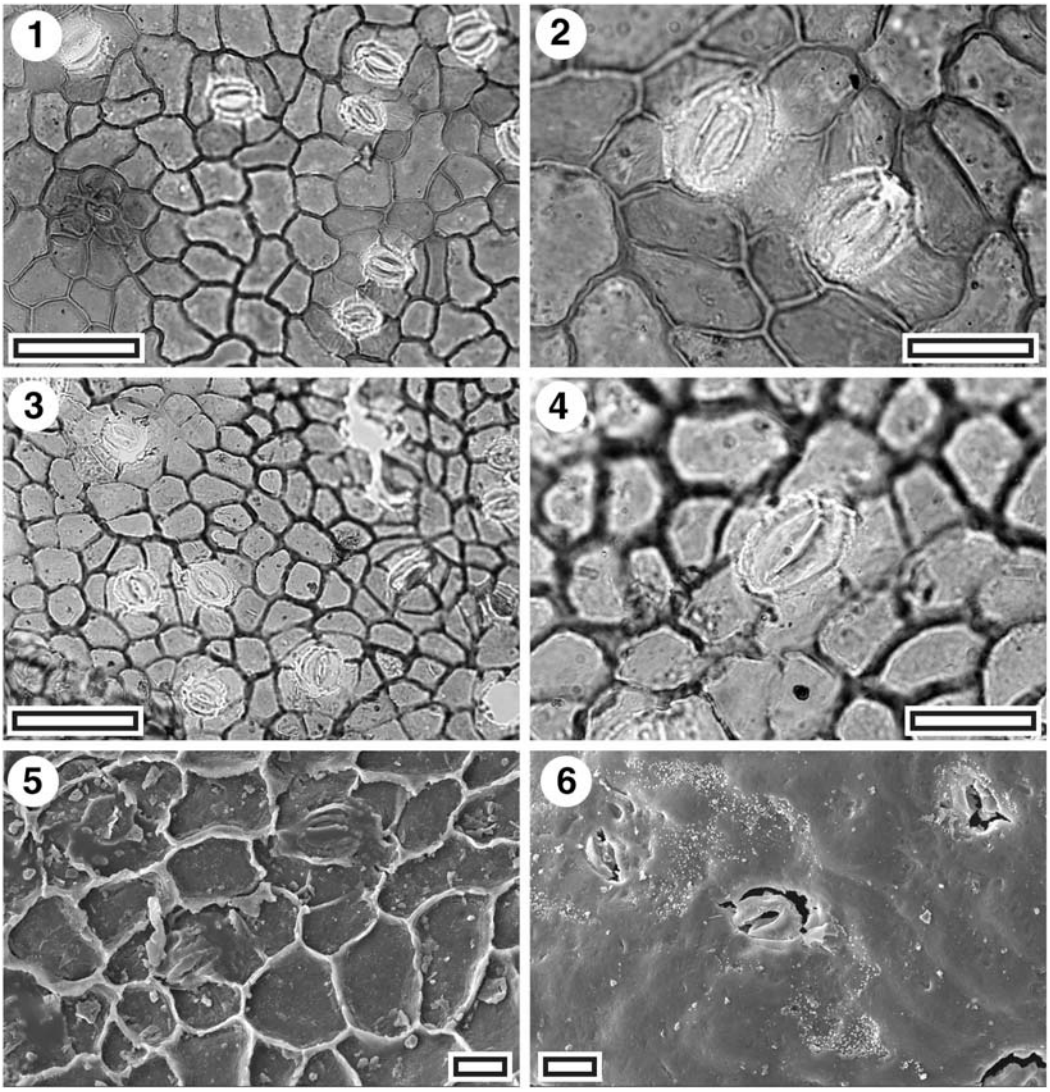

Figure 37. CUT-Z-JAE, **1.** TLM view showing several stomatal complexes and (centre left) a trichome insertion scar (SL5071, scale-bar = 50 µm); **2.** TLM detail of two stomatal complexes (SL5071, scale-bar = 20 µm); **3.** TLM view showing several stomatal complexes (SB0742, scale-bar = 50 µm); **4.** TLM detail of a single stomatal complex (SB0742, scale-bar = 20 µm); **5.** SEM view of inner cuticular surface showing three stomatal complexes (S-1542, scale-bar = 10 µm); **6.** SEM view of outer cuticular surface showing four stomatal complexes (S-1542, scale-bar = 10 µm).

around trichome scar modified by tangential divisions to form a sub-circular zone of foot cells (5–6), and thickened to form a poral rim and radial walls.

Distinguishing features. Cyclocytic stomatal complexes and epidermal cells with a particularly smooth texture

CUT-Z-JEE
Figure 38.1-38.4

Reference specimen and locality: SB0738, R-29.

Referred specimens and occurrence: SB0342, R-74; SB0375, R-75.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, staurocytic-cyclocytic, size range unimodal. Subsidiary cells (4–5) isodiametric-elongate tangential to stoma, periclinal walls same thicker than normal epidermal cells, unornamented. Guard cell pair outline difficult to see under TLM, length about 38–50 µm (medium to mostly large). Outer stomatal ledge prominent, sub

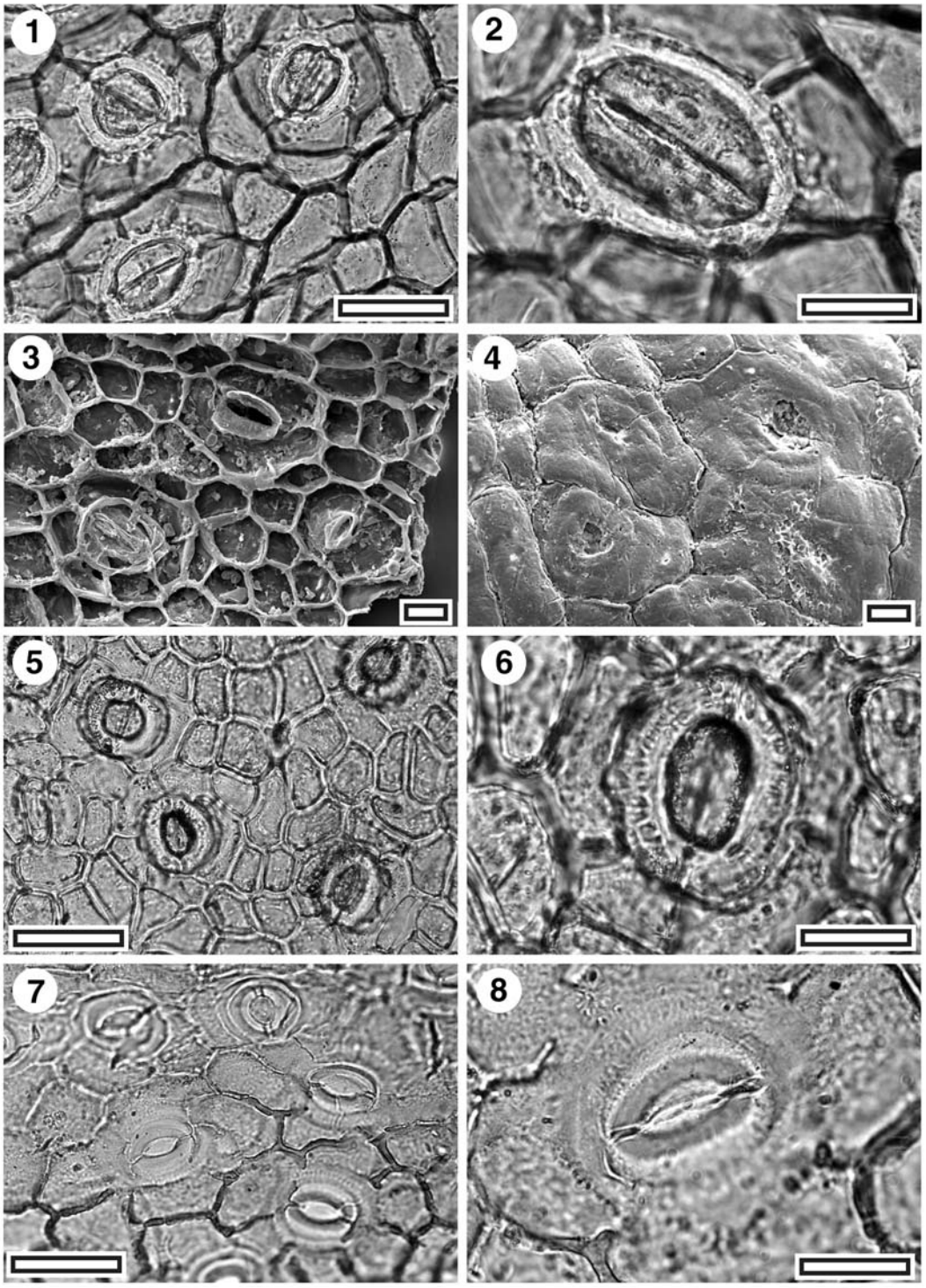

Figure 38. CUT-Z-JEE, CUT-Z-Z-JED, and CUT-Z-Z-JBH, **1.** CUT-Z-JEE. TLM view showing four stomatal complexes (SB0738, scale-bar = 50 µm); **2.** CUT-Z-JEE. TLM detail of a single stomatal complex (SB0738, scale-bar = 20 µm); **3.** CUT-Z-JEE. SEM view of inner cuticular surface showing three stomatal complexes (S-1681, x600, scale-bar = 20 µm); **4.** CUT-Z-JEE. SEM view of outer cuticular surface showing three stomatal complexes (S-1681, x600, scale-bar = 20 µm); **5.** CUT-Z-JED. TLM view showing four stomatal complexes and to right of centre) a trichome insertion scar (SB0724, scale-bar = 50 µm); **6.** CUT-Z-JED. TLM detail of a single stomatal complex (SB0724, scale-bar = 20 µm); **7.** CUT-Z-JBH. TLM view showing several stomatal complexes (SB0337, scale-bar = 50 µm); **8.** CUT-Z-JBH. TLM detail of a single stomatal complex (SB0337, scale-bar = 20 µm).

circular; Slightly pinched at the poles, extending from within the outer edge of stoma, thinner than normal epidermal cells but somewhat granular, and surrounded by a prominent ring of thin (not granular) cuticle, pore slit-like.

Epidermal cells. Epidermal cell flanges clearly visible using TLM (very thick), normal cells isodiametric-elongate, typically similar size to stomata, anticlinal walls straight, unbuttressed, unornamented.

Indumentum. Glabrous.

Distinguishing features. Mostly large staurocytic-cyclocytic stomatal complexes.

CUT-Z-JED
Figure 38.5-38.6

Reference specimen and locality: SB0724, R-24.

Referred specimens and occurrence: SL5302, R-105.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, anomocytic, size range unimodal. Subsidiary cells (5–6) isodiametric, periclinal walls same thickness as normal epidermal cells, unornamented. Guard cell pair outline elliptical to circular, length 33–45 µm (medium-large). Outer stomatal ledge sub circular, extending from outer edge of stoma, thicker than normal epidermal cells, pore elliptical - sub circular.

Epidermal cells. Epidermal cell flanges clearly visible using TLM (very thick), normal cells isodiametric, typically slightly smaller than the stomata, anticlinal walls straight, unbuttressed, unornamented.

Indumentum. With trichome insertion scars. Trichome scars common (trichomes deciduous), inserted between epidermal cells, diameter much smaller than normal epidermal cell. Epidermal cells around trichome scar modified slightly into radially elongate foot-cells (6–7), with no distinct thickening of walls.

Distinguishing features. Prominent outer stomatal ledges, and isodiametric epidermal cells, trichome insertion scars with a diameter much smaller than epidermal cells.

CUT-Z-JBH
Figure 38.7-38.8

Reference specimen and locality: SB0337, R-74.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, stomata evenly spread, isolated, randomly oriented, construction unclear, size range unimodal. Subsidiary cell periclinal walls same thickness as normal epidermal cells, unornamented. Guard cell pair outline elliptical, outlined by an indistinct anticlinal wall, length 25–35 µm (medium), with prominent T-piece thickenings at polar ends, same thickness as normal epidermal cells, Outer stomatal ledge extending from outer edge of stoma, pore elliptical.

Indumentum. Glabrous.

Epidermal cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate, approximately the same size as the stomata, anticlinal walls curved, unbuttressed, unornamented.

Distinguishing features. Bland morphology which has prominent T-piece thickenings of the stomata and lack of any distinct stomatal construction.