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MONOCOT MACROFOSSILS FROM THE MIOCENE OF SOUTHERN NEW ZEALAND

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ABSTRACT

Monocot cuticle is an uncommon component of dispersed cuticle samples in the New Zealand Miocene, a fact most likely due to its generally fragile nature. Nevertheless, 120 fossiliferous samples from two regions, the interior Manuherikia Basin in Central Otago, and the paleo-coastal delta of the Southland Coalfield, have produced 17 morphological types of cuticle, 15 of which are clearly monocot. These are described as parataxa and are regarded as including *Astelia*, Arecaceae, *Rhipogonum*, Pandanaceae, and *Typhaceae*. Most of the fossils remain unidentified, but are probably semi-aquatic swamp plants. Six forms of fossil *Typha* seeds are also illustrated.

KEY WORDS: Early Miocene, cuticle, biodiversity, stomata, monocot

INTRODUCTION

New Zealand's Miocene sediments have provided a small number of monocot macrofossils. One of the earliest to be described was a palm frond, *Seaforthia zeelandica* (von Ettingshausen 1887, 1891). This probably came from the same locality (near Cromwell) from which Pole (1993a) described palm fronds, fruits, and flowers and redescribed *S. zealandica* as *Phoenicites zeelandica*. *Phoenicites* is a morphogenus, the usage of which was clarified by Read and Hickey (1972) to apply to one of the limited range of palm frond shapes. As such, it is not a genus in any comparable way to extant genera, and I would no longer use the concept. *Phoenicites zeelandica* has small differences from New Zealand's single extant species of palm, *Rhopalostylis sapida*, which is the most southerly palm in the world (Wardle 1991). Impressions of the distinctive net-veined monocot, *Rhipogonum*, were also described from the same region (Pole 1993b), and *Rhipogonum* leaves with cuticle were later documented from the Miocene of the Foulden Hills Diatomite near Middlemarch (Pole 1996). Holden's (1982) *Cinnamomum miocenicum* from Murchison, and Oliver's (1936) *Coriaria latepetiolata* from Dunedin are likely to also be *Rhipogonum*. Fossil "coconuts" from the far north of the North Island were identified as *Cocos* by Berry (1926), but have since been suggested to have a closer relationship with *Parajubaea* (Endt and Hayward 1997).

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These fossils are 'macrofossils'-in the classic sense that they are apparent to the naked eye on the bedding surfaces of splitting sediment, or in the case of the 'coconuts', can be picked from the sediment or even, in the case of the fossil "coconuts" can be picked up from strand lines on the present beach. But another collecting rationale, in the appropriate sediments, involves searching for leaf cuticle, the resistant material which covers the leaf epidermis and which preserves an impression of the epidermal cell morphology. Although fragments of cuticle can be large (as large as the original leaf), the essential features can only be observed with a microscope.

Stebbins and Khush (1961) were probably the first to present a broad review of extant monocot cuticle but by far the greatest contribution has been that of Tomlinson (1960, 1961, 1965, 1969, 1971, 1974, 1982), who included descriptions of epidermal features as part of his broader treatment of the monocots. Dahlgren and Clifford (1982) included a useful comparative treatment of monocot stomatal construction. Typical monocot epidermis can be recognised primarily by having rows of longitudinally oriented stomatal complexes (although Butterfass 1987, included some monocots in his list of plants with transversely oriented stomata) and epidermal cells, a result of the typically parallel-veined leaves. The stomatal complex morphology, in the sense that they typically have a pair of distinct polar and lateral subsidiary cells, overlaps that of many conifers, although the topography and other details are quite different. For instance, in conifers the guard cells are typically embedded below overarching subsidiary cells, and the ends of the guard cells are often partially surrounded by distinct 'polar extensions'. Like other angiosperms, monocots have outer stomatal ledges, projecting from the guard cells, which are absent in conifers. Conifer cuticle is mostly much more robust, and tends to be preserved as recognizable leaves (often small and single-veined). Dunn et al. (1965) also pointed out that monocot stomatal complexes within a leaf are of equal size, or at least do not fall into distinct size classes, which they often do in non-monocot angiosperms. The epidermis of the reticulate-veined monocots is distinct from typical monocots, because the stomata and epidermal cells are not arranged in rows. Identification of taxa in this group relies on direct comparison of the fossils with an extant species.

Over some 15 years of research on Miocene cuticle in southern New Zealand, some small and typically rare fragments of monocot cuticle have been found, as well as some seeds. The purpose of this paper is to describe the cuticle and seed types as a basis for further studies of past biodiversity, ecology, and biogeography.

MATERIALS AND METHODS

Fossils were collected from two geological basins of which the sedimentary fill is now represented by two stratigraphic groups (Figure 1). The Manuherikia Group (MG) is an extensive (>5600 km^2) deposit of Miocene fluvial (Dunstan Formation) to lacustrine (Bannockburn Formation) basin fill in Central Otago, southern N.Z. The stratigraphy and sedimentology has been detailed by Douglas (1986), the palynology by Mildenhall (1989) and Mildenhall and Pocknall (1989), who dated the Group as Early-Late Miocene, and the macropaleobotany by Pole (1993c and references therein). The sediments which yield dispersed cuticle come from outcrops in the oldest unit, the incised valley fill of the St Bathans Member (sample numbers prefixed with "BL" and "GL").

The second geological unit is the Gore Lignite Measures, of the East Southland Group, which accumulated on a coastal delta (Isaac and Lindqvist 1990). Palynology of this unit has been detailed by Pocknall (1982) and Pocknall and Mildenhall (1984). Samples were taken from drill core housed in the Crown Minerals Dunedin core library (sample number prefixed with "Sthd"). Full sample details for both basins are provided in Pole (2007) including precise grid references for the MG samples and drill core depths for the East Southland Group. Detailed stratigraphic sections of the East Southland Group are present in Isaac and Lindqvist (1990). Precise stratigraphic relationships within the St Bathans Member, where there is complex fluvial channel cross-cutting, are still being resolved and cannot be shown on a simple section. Stratigraphic details at that resolution are not relevant at this stage. The only additional sample here is Bannockburn-1, which is the only sample found in the Bannockburn region, which has good cuticular preservation. It was collected at F41 087626 (grid reference based on the New Zealand 1:50 000 Topographic Map 260 series). The outcrop has since been covered over by lake-shore development after the completion of the Clyde Hydroelectric scheme.

Cuticle preparation followed a standard method whereby sediment was disaggregated by covering with hot water and adding some 40% hydrogen peroxide. The organic fraction was removed by sieving and cuticle further cleaned by

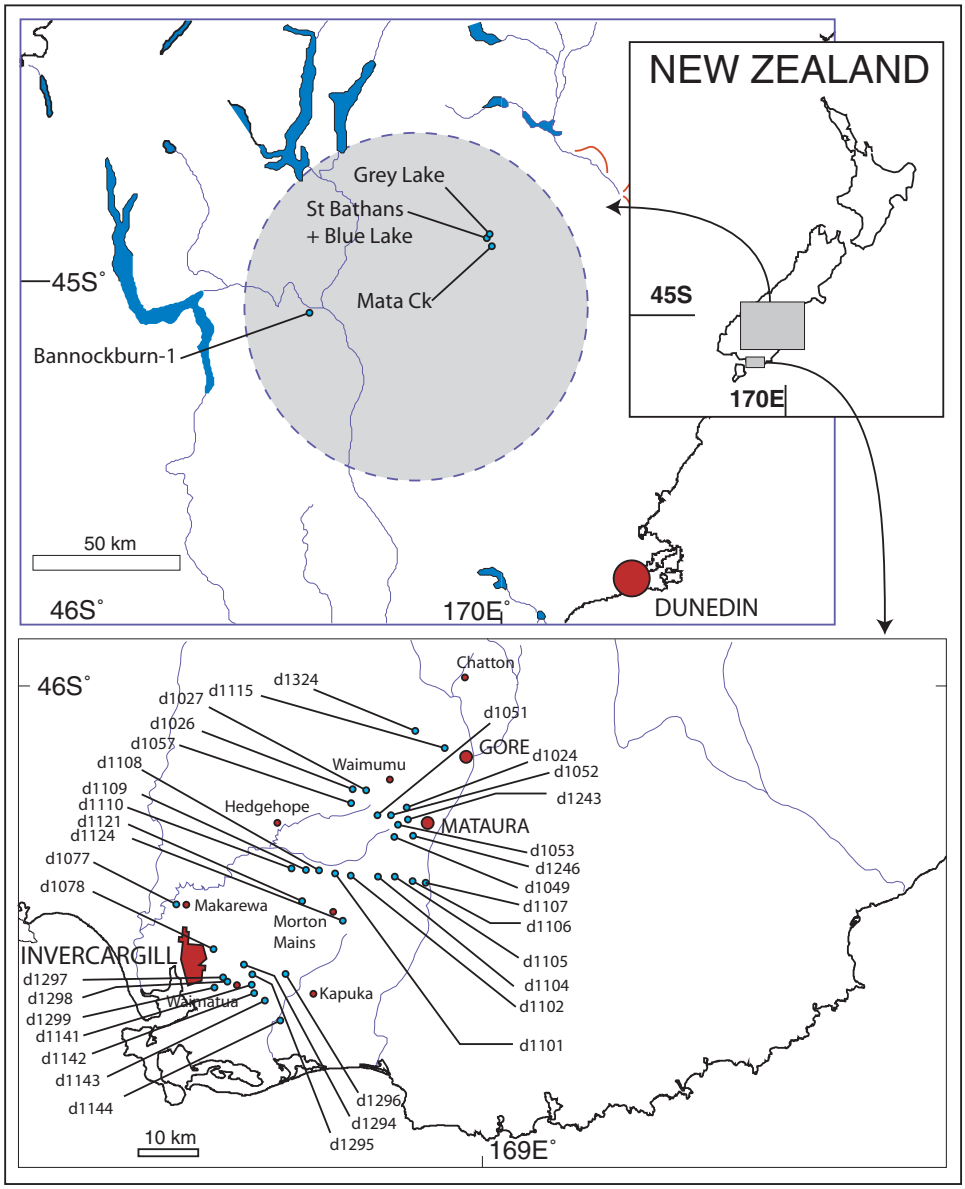

Figure 1. Locality maps. The upper map shows the position of Blue Lake (the location of sample numbers prefixed with "BL-", Grey Lake (the location of sample numbers prefixed with "GL-"), and Bannockburn-1. The grey circle is a schematic indication of the extent of the Manuherikia Group. The lower map shows the position of all drill-cores in Southland (the location of sample numbers prefixed with "Sthd-") from which fossils were obtained. For precise locations of all samples, see Pole (2007)..

immersion for several hours in warm aqueous chromium trioxide. After washing a staining in Crystal Violet or Safranin, cuticle fragments were mounted on microscope slides (specimen numbers prefixed with "SB" or "SL") in Thymol Glycerine Jelly for Transmitted Light Microscopy (TLM), or on aluminium stubs (specimen numbers prefixed with "S-") with double-sided tape and coated with platinum for Scanning Electron Microscopy (SEM). Material is lodged in the State Herbarium of Queensland.

Cuticle morphologies are described as parataxa. They are given a non-hierarchical parataxon code. For pragmatism this consists of the prefix 'CUT-Mo-' (for "cuticle-monocot") followed by a string of three letters. These letters have no meaning, but together with the prefix, form a unique text string. For previous use of parataxa

for fossil cuticles, see Carpenter and Pole (1995), Pole (1996, 1998, 2007). For each parataxon, a 'reference specimen' is nominated. Specimens are stored in the Queensland State Herbarium. The "typical" monocot parataxa—those with aligned stomata—are distinguished on the basis of a key (Appendix) and to keep morphological similar types together, they are described in the general order of the key. *Rhipogonum* is the exception, being one of the 'net-veined' monocots, which is identifiable by direct comparison with the distinctive cuticle of extant species. It is described first.

Cuticle identification was based on the published guides listed above as well as the author's reference collection of extant monocot cuticle (specimens prefixed with "OPH"). This has been prepared from the collections of the Queensland Herbarium (AQ) and the Allan Herbarium (CHR). The numbers of the parent herbarium specimens are given to allow relocation of the specimen from which the cuticle fragment was prepared. Cuticle preparation initially followed the same aqueous chromium trioxide method as for fossils, but more recently has switched to boiling in a 6:1 mixture of hydrogen peroxide and glacial acetic acid. This was found to give better results for the relatively fragile monocot cuticle. The reference collection currently includes over 230 species of monocot, mainly Arecaceae. The cuticle of a range of common extant New Zealand monocots is shown in Figure 2.

The taxonomic details are presented in the Appendix.

RESULTS

Monocot cuticle was found in 35 out of the 121 samples investigated. Seventeen types of fossil cuticle are distinguished in this paper. For two of these, CUT-Mo-EII and CUT-Mo-FEH, monocot affinities are not certain, but are presented here for convenience. For convenient reference the cuticle of the most common New Zealand monocot is illustrated. An interesting observation is that *Cordyline*, *Phormium*, *Rhopalostylis,* which are all prominent components of the vegetation in various parts of New Zealand today, have not yet been located in the fossil cuticle record. The identifiable fossil monocot cuticle includes *Astelia*, Pandanaceae, *Rhipogonum*, and *Typha* (also present as seeds). The identification of *Rhipogonum* is important because it is one of the few fossils that can be identified as a climber (the only other one in the MG is an unknown genus of the Menispermaceae).

The relatively few specimens reported here certainly represent what would have been a more prominent monocot presence in the vegetation. Most extant monocots have such delicate cuticle that it is difficult to prepare it in the laboratory, and hence would be unlikely to survive both burial and the procedure to obtain dispersed fossil cuticle. The cuticle fragments described here are therefore unusual—the tougher fragments of the tougher species. *Typha* seeds are abundant in BL-31; unfortunately this locality was a small lens of mudstone which seems to have been destroyed during removal of an adjacent pine tree by the Department of Conservation. This is a notably low-richness locality, which is the type locality for the conifer *Retrophyllum vulcanense* (Pole 1992). The cuticle fraction is almost entirely *Retrophyllum*, as well as an extinct, unidentified dicotyledonous leaf, and the *Typha* seeds. This suggests open, marshy conditions, and is consistent with *R. vulcanense* being a conifer which favoured standing water or swampy conditions (Hope and Pask's 1998 illustration of extant *Retrophyllum* growing partially submerged in the Plaine des Lacs in New Caledonia may be a reasonable modern analogy).

Only seven out of 58 samples (12%) in the St Bathans Paleovalley have monocot cuticle, the most in one sample is GL-01 with three taxa. In Southland 22 out of 62 samples (36%) have monocot cuticle, with five taxa occurring in one sample (Sthd-163) and four in another (Sthd-055). In my opinion this is not related to any difference in alteration of the sediments between the two basins, which may have preferentially destroyed the more delicate monocot cuticle. In some cases it may be due to fluvial reworking in the St Bathans Paleovalley, which was unlikely to have been a factor in Southland. However, it may be due to a greater prominence of monocots in the vegetation in Southland. In sample Sthd-163, which has the highest monocot richness, there are no other cuticle taxa. This suggests a particular monocot-dominated habitat, probably a particular swamp or wetland habitat. The sample with the second-highest richness of monocots (Sthd-055) had the highest richness of taxa (12) in all the Southland samples. Hence, its high number of monocots may be partly a function of simply being a rich assemblage.

Although identification of these specimens is generally frustrating, they add to the documented biodiversity of the Miocene in New Zealand. Even as unidentified taxa they will help distinguish

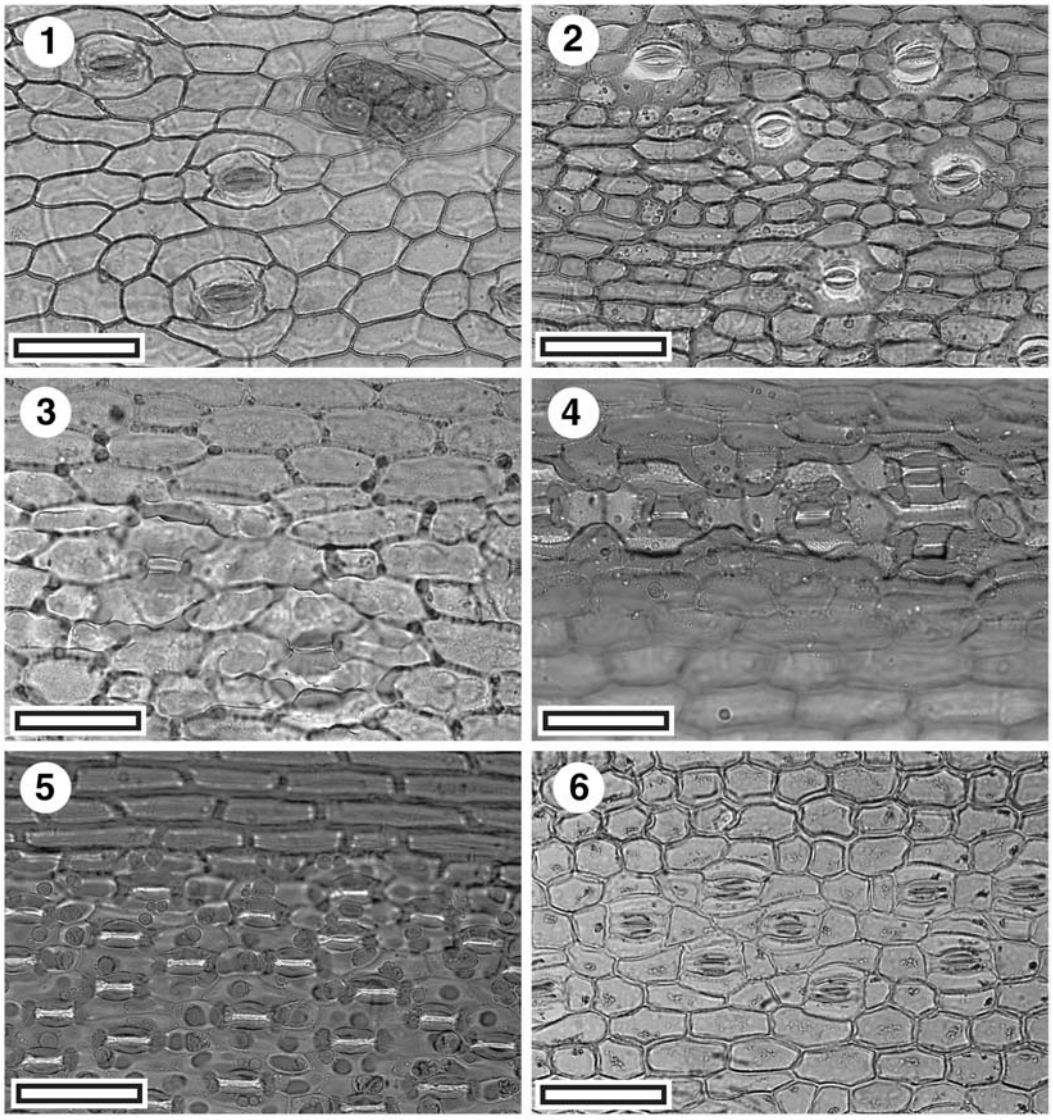

Figure 2. Extant New Zealand monocots. **1.** *Rhopalostylis sapida*, TLM view of stomatal complexes, and (upper right) compound gland (OPH2638, scale bar = 50 µm); **2.** *Freycinetia banksii*, TLM view of stomatal complexes (OPH7429, scale bar = 50 µm, CHR218519); **3.** *Cordyline australis*, TLM view of stomatal complexes (OPH7433, scale bar = 50 µm, CHR509649); **4.** *Phormium cookianum*, TLM view of stomatal complexes. Note complexes are sunken in narrow grooves (OPH7425, scale bar = 50 µm, CHR228076A); **5.** *Phormium tenax*, TLM view of stomatal complexes. Note the highly networked nature of the complexes (OPH7427, scale bar = 50 µm, CHR261417); **6.** *Typha orientalis*, TLM view of stomatal complexes (OPH7430, scale bar = 50 µm).

assemblages stratigraphically and perhaps ecologically.

CONCLUSION

These fossils add to the known Miocene biodiversity of New Zealand. They complement the macrofossil and palynological record for monocots, and indicate that extinct Pandanaceae and Arecaceae were present in the Miocene. It is notable that apart from *Rhipogonum*, the prominent extant monocots of New Zealand have not yet been found in Early Miocene deposits. This may reflect some sort of taphonomic bias, although *Phormium tenax* cuticle is present in Rangitawa Valley and cuticle very similar to CUT-Mo-EFE is at Hamilton's Gap, both being mid-Pleistocene deposits in the North Island.

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APPENDIX 1. KEY TO MONOCOT CUTICLE WITH ALIGNED STOMATES

1. Stomatal complexes not visible under TLM 2.
1. Stomatal complexes clearly visible under TLM 4.

2. Papillae or glandular trichomes present 3.
2. No papillae or glandular trichomes present CUT-Mo-EFG.

3. Glandular trichomes appear in pairs amongst normal epidermal cells CUT-Mo-EFE.
3. All cells papillate CUT-Mo-EFH.

4. Epidermal cells not in clear files CUT-Mo-FEH.
4. Epidermal cells in clear files 5.

5. Papillae present 6.
5. Papillae absent 12.

6. Papillae small and essentially restricted to the epidermal cells CUT-Mo-FJC.
6. Papillae large and found on (but not necessarily limited to) the subsidiary cells 7.

7. Papillae mostly restricted to the subsidiary cells CUT-Mo-FFJ.
7. Papillae common on epidermal and subsidiary cells 8.

8. Papillae on subsidiary cells overarch stomatal pore 9.
8. Papillae on subsidiary cells not overarching stomatal pore 10.

9. Papillae smooth and discrete CUT-Mo-FJE.
9. Papillae slightly rough and compound CUT-Mo-AAI.

10. Stomatal complexes distinctly straight-sided CUT-Mo-EFI.
10. Stomatal complexes with curved or oblique sides 11.

11. Papillae high and distinct CUT-Mo-EIA.
11. Papillae low and indistinct CUT-Mo-FEG.

12. Stomatal complexes in well-defined zones 13.
12. Stomatal complexes not in clear zones 14.

13. Stomatal complexes in broad zones separated by narrow non-stomatal zones CUT-Mo-EHB.
13. Stomatal complexes in narrow zones, closely spaced CUT-Mo-EFF.

14. Stomata typically elliptical, without prominent arching lateral subsidiary cells CUT-Mo-FFA.
14. Stomata typically broad, irregularly circular, with prominent arching lateral subsidiary cells 15.

15. Stomatal complexes uncommon, epidermal cells isodiametric or shorter than broad CUT-Mo-EII.
15. Stomatal complexes uncommon, epidermal cells rectangular CUT-Mo-FEF.

CUT-Mo-EEI (*Rhipogonum* sp.)
Figure 3.1-3.4

Reference specimen: SL5435, Bannockburn-1.

Referred specimens and occurrence: SL1709, Sthd-019; SL2035, Sthd-046.

Description. Epidermis not divided into costal and intercostal zones (stomata evenly spread). Stomatal complex construction apparently paracytic, although subsidiary cells not clearly staining more than normal epidermal cells**,** not in rows**,** randomly oriented, stomata circular**,** but not clearly outlined, diameter 14-23 µm (medium). Outer stomatal ledge cuticle markedly thicker than normal epidermal cells, broad in centre and narrowing distinctly toward the ends**,** with slit-like, elongate aperture. Subsidiary cells each with a single arching ridge of cuticle (Figure 3.3), following the guard cells, but not meeting at the poles. Epidermal cells clearly visible under TLM**,** isodiametric**,** sinuous**,** slightly buttressed**,** glabrous**,** not papillate.

Identification: Pole (1993b) described Early Miocene leaf impressions from Bannockburn that were indistinguishable from the extant New Zealand *Rhipogonum scandens* and therefore identified them as the living species. Later, leaves with similar architecture were found with cuticle at the Early Miocene locality of Foulden Hills (Pole

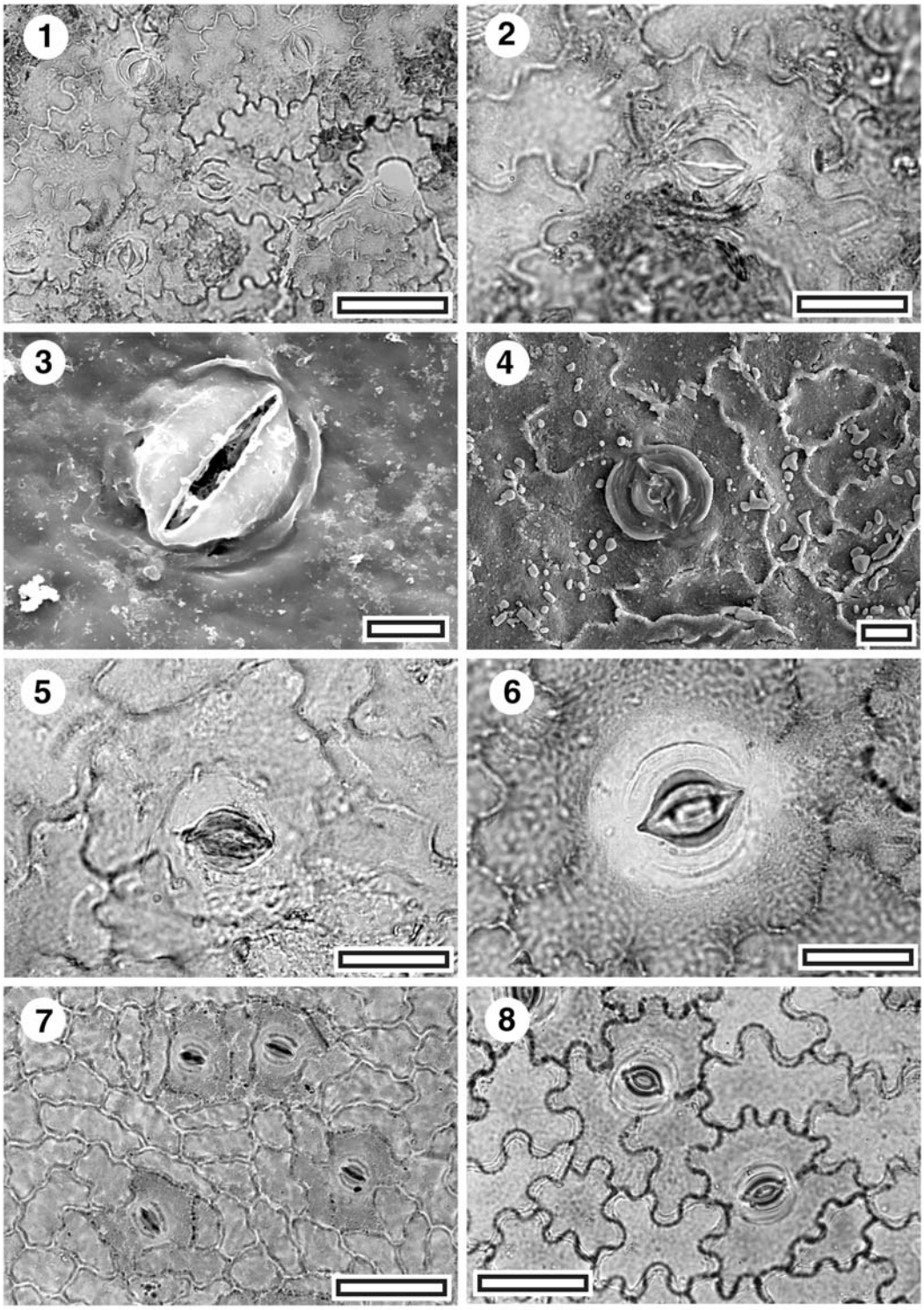

Figure 3. CUT-Mo-EEI, and extant *Smilax* and *Rhipogonum*. **1.** CUT-Z-EEI, TLM view of stomatal complex (SL5435, scale bar = 50 μm); **2.** CUT-Z-EEI, TLM detail of stomatal complex (SL5435, scale bar = 20 μm); **3.** CUT-Z-EEI, outer SEM view of a single stoma. Note pinched appearance of outer stomatal ledge, and arching ridges of cuticle (S-1049, scale bar = 10 μm); **4.** CUT-Z-EEI, inner SEM view of a single stoma (S-1709, scale bar = 10 μm); **5.** CUT-Z-EEI, TLM view of single stomatal complex (SL2035, scale bar = 20 μm); **6.** TLM of extant *Rhipogonum scandens* (OPH2631, scale bar = 20 μm); **7.** TLM of extant *Smilax australis* (AQ037802, scale bar = 50 μm); **8.** TLM of extant *Rhipogonum* album (AQ330750, scale bar = 50 μm).

1996). The cuticle details confirmed the identification (but note that figures 11c, d in Pole 1996 inadvertently lack captions. They are of extant *Rhipogonum scandens*).

The specimens in this study are dispersed cuticle only, and without the benefit of leaf architectural a broader range of possibilities must be considered for identification. The Rhipogonaceae and Smilacaceae are two of the "net-veined" monocots (Inamdar et al. 1983) and as such, they do not have stomata and epidermal cells arranged in rows like parallel-veined monocots. However, they both have similar epidermal features which makes them clearly recognisable, although hard to tell from one another. Both have paracytic stomatal complexes where the subsidiary cells are generally slightly thicker than normal epidermal cells, of uneven size, and with an irregular outer wall, and the epidermal cells are highly sinuous. The dispersed fossil material clearly fits this basic morphology.

Based on the species available in the extant reference collection (seven species of *Rhipogonum* and nine of *Smilax*), in general, *Smilax* species tend to have thin, or poorly defined epidermal cell anticlinal walls, and poorly defined margins to generally elliptical stomata which are 20-35 µm in greatest diameter (medium-sized). In contrast, *Rhipogonum* tend to have much stronger or clearly defined epidermal cell anticlinal walls, and well-defined margins to generally circular stomata, which are 28-43 µm in diameter (from medium to large) (see Figure 3.7-3.8). The new fossil is consistent with *Rhipogonum*, although there are subtle, but consistent differences with the *R. scandens* (Figure 3.5). In the fossil, the pair of ridge-arcs flanking the stomata are more prominent, and the stomata are slightly smaller. Without leaf architectural details it is inadvisable to place the dispersed cuticle fragment into an extant species. Very similar cuticle is also present in the Early Eocene of Regatta Point, Tasmania.

CUT-Mo-EFG
Figure 4.1-4.2

Reference specimen: SL1969, Sthd-055.

Referred specimens and occurrence: SL1673, Sthd-034; SL1812, Sthd-100.

Description. Epidermis not divided into costal and intercostal zones (stomata evenly spread). Stomatal complex construction unclear**,** in distinct rows**,** longitudinally oriented. Polar subsidiary cells chained (details indistinct). Subsidiary cells with periclinal walls of same thickness as those of normal epidermal cells**,** not papillate. Outer stomatal ledge cuticle same thickness as normal epidermal cells. Epidermal cell walls not clearly visible under TLM (cuticle very thin)**,** but probably straight-walled**,** unbuttressed**,** glabrous**,** not papillate.

CUT-Mo-EFE (*Astelia* sp.)
Figure 5.3-5.6

Reference specimen: SL1683, Sthd-033.

Referred specimens and occurrence: SL2624, BL-07; SL1567, Sthd-004; SL1726, Sthd-017; SL1668, Sthd-034; SL2071, Sthd-047; SL1918, Sthd-056; SL1882, Sthd-073; SL1911, Sthd-074; SL1830, Sthd-095; SL1646, Sthd-102; SL1626, Sthd-107; SL1600, Sthd-108.

Description. Epidermis not divided into costal and intercostal zones. Stomatal complex construction not known. Hirsute, with paired, short, possible uniseriate persistent glandular trichomes. Other epidermal cells clearly visible under TLM (but cuticle thin) in rows**,** irregularly shaped**,** straight-walled**,** unbuttressed**,** glabrous**,** non-papillate.

Identification. The very distinctive paired glandular trichomes appear to be characteristic of *Astelia* (Figure 2.7-2.8). No stomatiferous fossil cuticle has been found, perhaps because it was much thinner than the other surface and therefore does not survive processing. CUT-Mo-EFE is also present at Hamilton's Gap, a mid-Pleistocene deposit in the North Island.

CUT-Mo-EFH
Figure 5.1-5.4

Reference specimen: SL1968, Sthd-055.

Description. Epidermis not divided into costal and intercostal zones (stomata evenly spread). Stomatal complex construction unclear. Subsidiary cells with periclinal walls of same thickness as those of normal epidermal cells; papillate, papillae not overarching stomatal pore. Outer stomatal ledge not visible. Epidermal cell walls not clearly visible under TLM, but cells obviously in rows; straight-walled; unbuttressed; glabrous; papillate; each cell with a single smooth papillae.

CUT-Mo-FEH
Figure 4.5-4.8

Reference specimen: SL3238, Sthd-163.

Description. Epidermis not divided into costal and intercostal zones (stomata evenly spread). Stomatal complex construction tricyclic**,** encyclocytic with 5-7 subsidiary cells**,** outline circular**,** not in

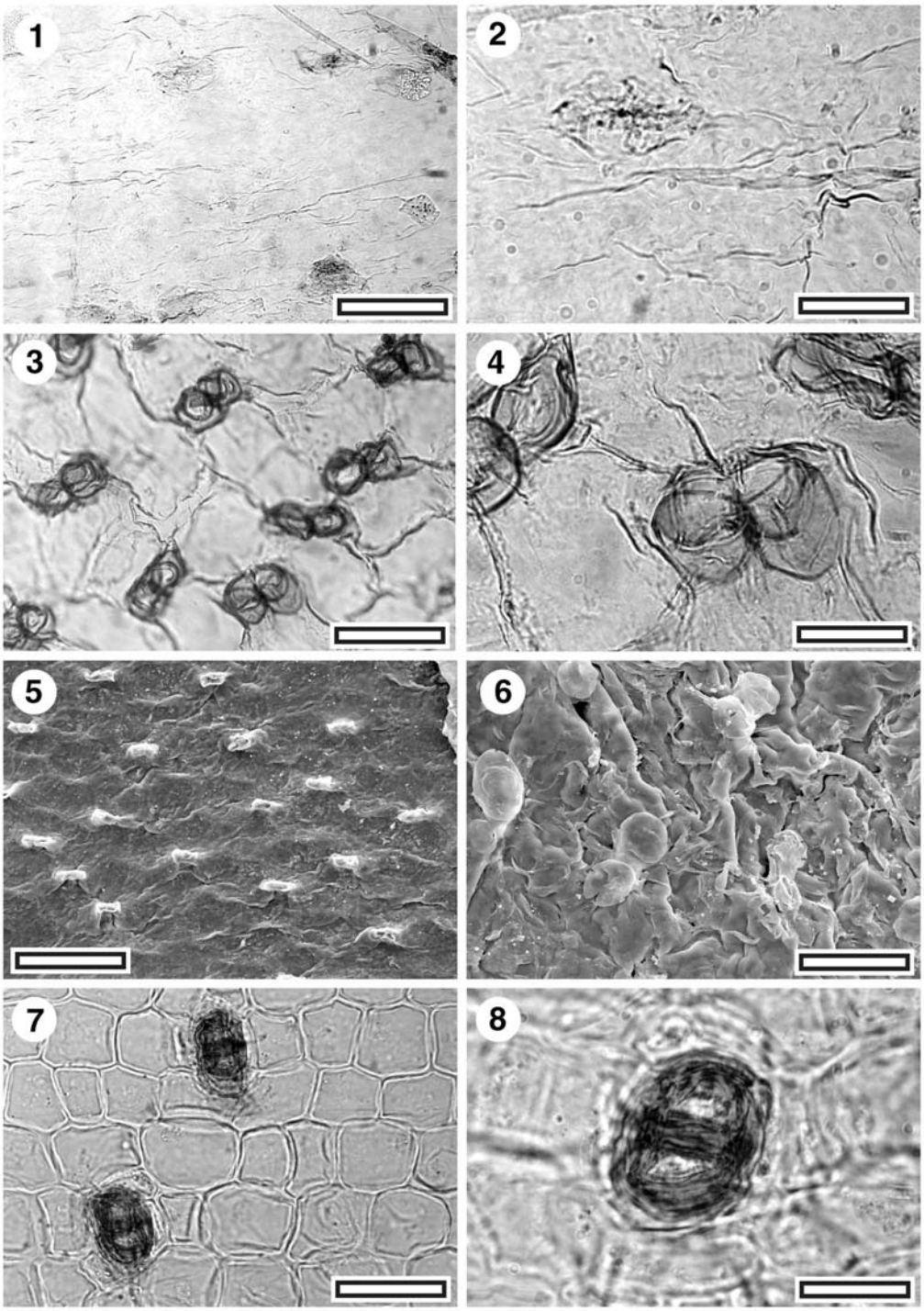

Figure 4. CUT-Mo-EFG and CUT-Mo-EFE and *Astelia papuana* (Cuticle morphologies are described as parataxa. They are given a non-hierarchical parataxon code. For pragmatism this consists of the prefix 'CUT-Mo-' (for "cuticle-monocot") followed by a string of three letters. These letters have no meaning, but together with the prefix, form a unique text string). **1.** CUT-Mo-EFG, TLM view of stomatal complexes. Note extremely thin cuticle (SL1969, scale bar = 50 µm); **2.** CUT-Mo-EFG, TLM view of single stomatal complex at upper left (SL1969, scale bar = 20 µm); **3.** CUT-Mo-EFE, TLM view of pairs of glandular trichomes which may mark the position of stomatal complexes (SL1683, scale bar = 50 µm); **4.** CUT-Mo-EFE, TLM detail of a pair of glandular trichomes (SL1683, scale bar = 20 µm); **5.** CUT-Mo-EFE, outer SEM view of pairs of glandular trichomes (S-1054, scale bar = 100 m); **6.** CUT-Mo-EFE, outer SEM view showing several pairs of glandular trichomes (S-1054, scale bar = 50 µm); **7.** Extant *Astelia papuana* (AQ053799, scale bar = 50 µm); **8.** Extant *A. papuana* (AQ053799, scale bar = 20 µm).

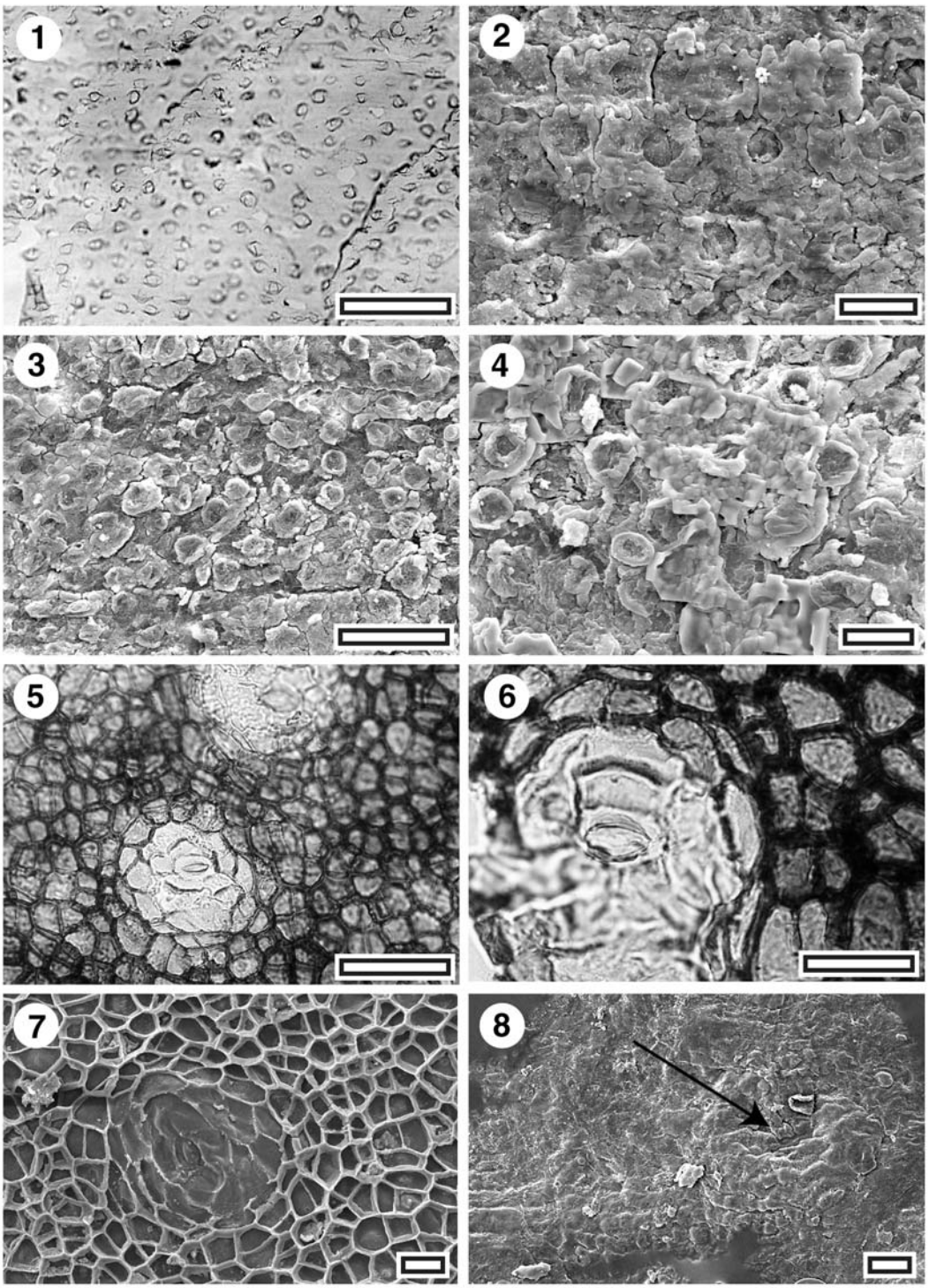

Figure 5. CUT-Mo-EFH and CUT-Mo-FEH. **1.** CUT-Mo-EFH, TLM view of rows of papillae (SL1968, scale bar = 50 µm); **2.** CUT-Mo-EFH, Outer SEM view of cuticle (S-1059, scale bar = 20 µm); **3.** CUT-Mo-EFH, inner SEM view of cuticle (S-1059, scale bar = 50 µm); **4.** CUT-Mo-EFH, inner SEM view of cuticle (S-1059, scale bar = 20 µm); **5.** CUT-Mo-FEH, TLM view of two stomatal complexes. Note lack of any row structure and complex stomatal construction (SL3238, scale bar = 50 µm); **6.** CUT-Mo-FEH, TLM detail of stomatal complex (SL3238, scale bar = 20 µm); **7.** CUT-Mo-FEH, inner SEM view of a single stomatal complex (S-1360, scale bar = 20 µm); **8.** CUT-Mo-FEH, Outer SEM view of a single stomatal pore (arrow) (S-1360, scale bar = 50 µm).

rows, longitudinally oriented. Polar subsidiary cells widely spaced. Subsidiary cells with periclinal walls thinner than those of normal epidermal cells, not papillate. Outer stomatal ledge cuticle thinner than normal epidermal cells, with elongate aperture. Epidermal cells clearly visible under TLM, not in clear rows (but some in short, irregular files), isodiametric, straight-walled, unbuttressed, glabrous, not papillate.

CUT-Mo-FJC
Figure 6.1-6.2

Reference specimen: SL2419, Sthd-078.

Description. Epidermis divided into costal and intercostal zones (stomata concentrated in zones at least 10 stomatal complexes wide). Stomatal complex construction dicyclic, paratetracytic, typically with four subsidiary cells, outline elongate, in distinct rows, longitudinally oriented. Polar subsidiary cells well-spaced along files (nearest neighbour typically in adjacent file). Subsidiary cells with periclinal walls thinner than those of normal epidermal cells, partially papillate (each subsidiary cell has 0-1 papillae). Outer stomatal ledge cuticle thinner than normal epidermal cells, with slit-like aperture. Epidermal cells clearly visible under TLM, in rows, isodiametric or wider than long, straight-walled, unbuttressed, glabrous, papillate, each cell with 1-3 papillae (very small and round to large and irregular). Epidermal cells of costal zones distinctly more elongate than intercostal cells.

Identification. The outer stomatal ledge shape and thin periclinal walls on the subsidiary cells suggest *Typha*, but as no extant *Typha* are known to have papillae, the identity of CUT-Mo-FJC remains uncertain.

CUT-Mo-FFJ
Figure 6.3-6.6

Reference specimen: SL3239, Sthd-163.

Description. Epidermis divided into costal and intercostal zones (stomata concentrated in zones). Stomatal zones about 4-6 stomatal complexes wide. Stomatal complex construction dicyclic, paratetracytic, typically with four subsidiary cells, outline irregular - polar subsidiary cells project beyond margin of lateral subsidiary cells. Stomatal complexes in overlapping rows, longitudinally oriented. Polar subsidiary cells well-spaced along files (nearest neighbour typically in adjacent file). Subsidiary cells with periclinal walls thinner than those of normal epidermal cells, papillate, papillae not overarching stomatal pore. (Each subsidiary cell has 1-4 papillae). Outer stomatal ledge cuticle thicker than normal epidermal cells, with slit-like aperture, tapering toward the ends. Epidermal cells clearly visible under TLM, in rows, irregularly shaped, straight-walled, unbuttressed, glabrous, essentially not papillate, but some epidermal cells within stomatal zones, and close to stomata, have papillae, each cell with 1-3 papillae (subdued). Epidermal cells of costal zones slightly elongate.

Identification. Possibly Pandanaceae. Compare with illustrations in Tomlinson (1965) and Kam (1971).

CUT-Mo-FJE
Figure 7.1-7.2

Reference specimen: SL2524, BL-05.

Referred specimens and occurrence: SL2424, Sthd-055.

Description. Epidermis not divided into costal and intercostal zones (stomata evenly spread). Stomatal complex construction monocyclic, paratetracytic, typically with 4 subsidiary cells, outline irregular - polar subsidiary cells project beyond margin of lateral subsidiary cells. Stomatal complexes in distinct rows, densely packed, with no epidermal cell files in stomatal zone, longitudinally oriented. Polar subsidiary cells well-spaced along files (nearest neighbour typically in adjacent file). Subsidiary cells with periclinal walls of same thickness as those of normal epidermal cells, papillate, papillae thick, expanding to partially obscure the stomatal pore (each subsidiary cell has a single papillae, except when the cell is networked, in which case there is a papillae per networked stomatal complex). Outer stomatal ledge cuticle same thickness as normal epidermal cells, with rectangular aperture (with bowed sides defined by edges off papillae). Epidermal cells clearly visible under TLM, in rows, isodiametric, straight-walled, unbuttressed, glabrous; papillate, each cell with 1-2, thick, smooth papillae.

Identification. Possibly Pandanaceae. Compare with illustrations in Tomlinson (1965) and Kam (1971).

CUT-Mo-AAI
Figure 7.3-7.4

Reference specimen: SB1354, BL-32

Referred specimens and occurrence: SL0106, BL-08; SB0875, GL-01; SL3242, Sthd-163.

Description. Epidermis divided into costal and intercostal zones (stomata concentrated in zones).

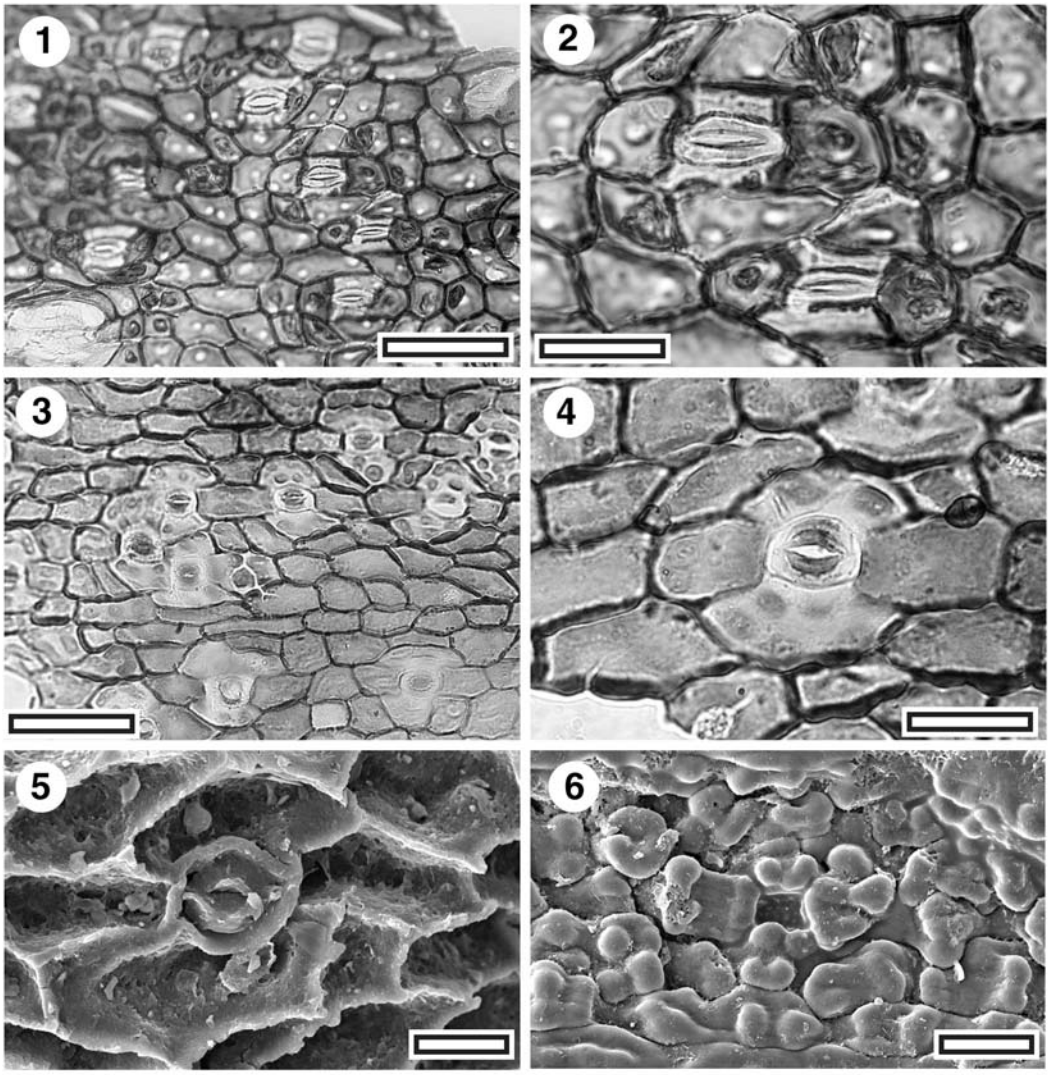

Figure 6. CUT-Mo-FJC and CUT-Mo-FFJ. **1.** CUT-Mo-FJC, TLM view of stomatal complexes. Note relatively small and sharply defined papillae (SL2419, scale bar = 50 µm); **2.** CUT-Mo-FJC, TLM detail of two stomatal complexes. Note distinctively narrow stomatal and relatively small and sharply defined papillae (SL2419, scale bar = 20 µm); **3.** CUT-Mo-FFJ, TLM view of stomatal complexes. Note papillae generally confined to subsidiary cells (SL3239, scale bar = 50 µm); **4.** CUT-Mo-FFJ, TLM detail of stomatal complex (SL3239, scale bar = 20 µm); **5.** CUT-Mo-FFJ, inner SEM detail of a single stomatal complex (S-1361, scale bar = 10 µm); **6.** CUT-Mo-FFJ, outer SEM view of at least two stomatal complexes (S-1361, scale bar = 10 µm).

Stomatal zones 2-3 stomatal complexes wide**.** Stomatal complex construction unclear**,** paratetracytic, typically with four subsidiary cells**,** outline unclear**,** not in rows**,** longitudinally oriented. Subsidiary cells with periclinal walls of same thickness as those of normal epidermal cells**,** papillate, papillae expanding to partially obscure the stomatal pore (each subsidiary cell has an indeterminate number of subdued and fused papillae). Outer stomatal ledge cuticle same thickness as normal epidermal cells**,** with slit-like aperture. Epidermal cells clearly visible under TLM**,** in rows**,** elongate**,** straight-walled, markedly hexagonal and with slightly thickened polar anticlinal walls**,** unbuttressed**,** glabrous**.** Intercostal epidermal cells papillate, each cell has up to five papillae, which are usually fused into a single multi-headed unit, or sometimes as isolated or various fused units. Epidermal cells of costal zones distinctly more elongate than intercostal cells**,** not papillate.

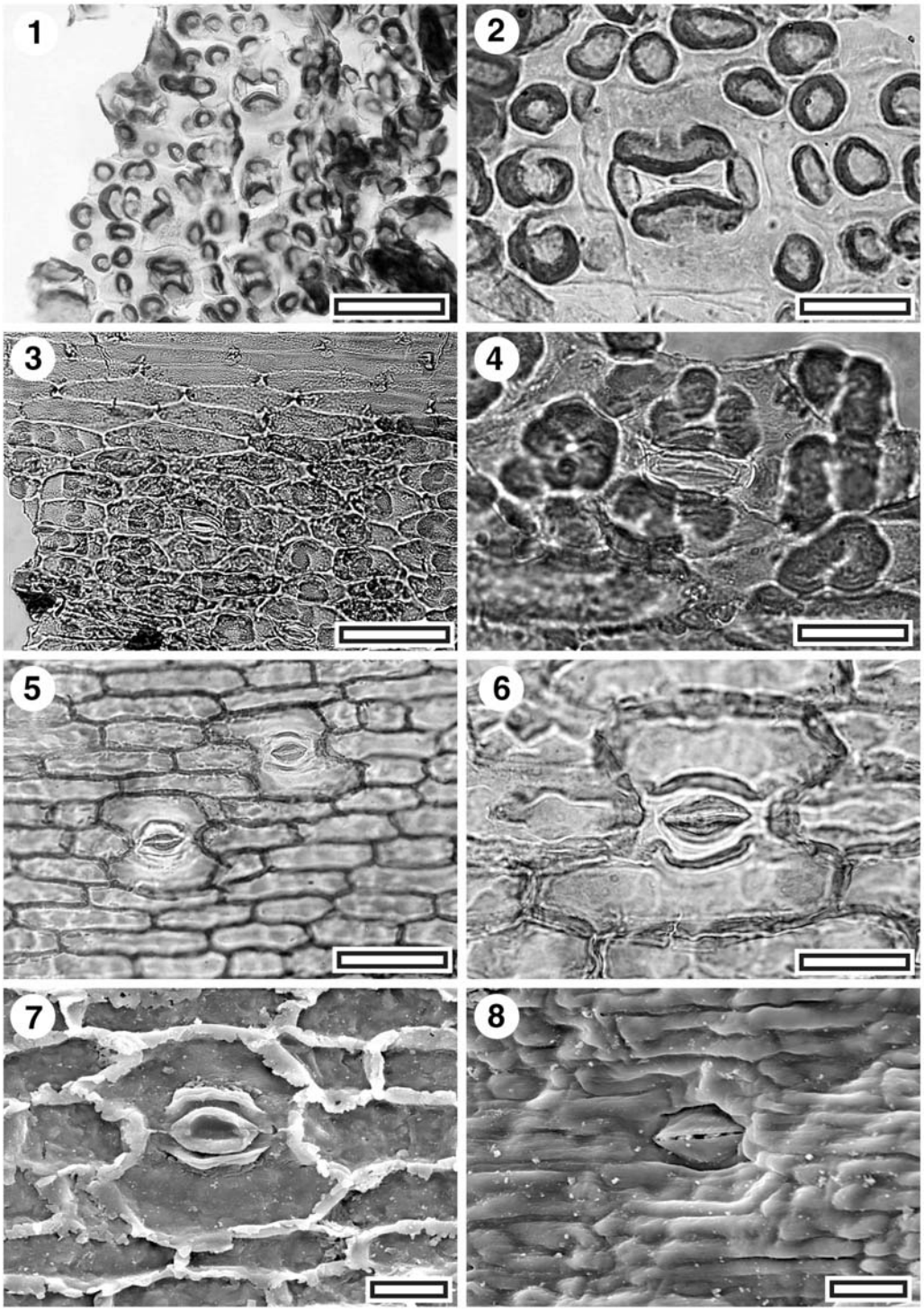

Figure 7. CUT-Mo-FJE, CUT-Mo-AAI, and CUT-Mo-EFI. **1.** CUT-Mo-FJE, TLM view of stomatal complexes (SL2524, scale bar = 50 μm); **2.** CUT-Mo-FJE, TLM detail of stomatal complex (SL2524, scale bar = 20 μm); **3.** CUT-Mo-AAI, TLM view of stomatal complexes, SB1357, scale bar = 50 μm); **4.** CUT-Mo-AAI, TLM detail of stomatal complex (SB1357, scale bar = 20 μm); **5.** CUT-Mo-EFI, TLM view of two stomatal complexes (SL1973, scale bar = 50 μm); **6.** CUT-Mo-EFI, TLM detail of stomatal complex. Note distinctive straight sides to complex and ridges of cuticle flanking the outer stomatal ledges (SL1973, scale bar = 20 μm); **7.** CUT-Mo-EFI, inner SEM detail of a single stomatal complex (S-1060, scale bar = 20 μm); **8.** CUT-Mo-EFI, outer SEM view of a single stoma. Note pinched appearance of outer stomatal ledge and slit-like aperture (S-1060, scale bar = 20 μm).

Identification. Possibly Pandanaceae. Compare with illustrations in Tomlinson (1965) and Kam (1971).

CUT-Mo-EFI
Figure 7.5-7.8

Reference specimen: SL1973, Sthd-055.

Referred specimens and occurrence: SL2041, Sthd-076; SL2073, Sthd-113.

Description. Epidermis not divided into costal and intercostal zones (stomata evenly spread). Stomatal complex construction monocyclic, paratetracytic, typically with four subsidiary cells, outline irregular, straight-sided, polar subsidiary cells project beyond margin of lateral subsidiary cells, not in rows, longitudinally oriented. Guard cells flanked on the inside by a thick ridge of cuticle. Polar subsidiary cells widely spaced. Subsidiary cells with periclinal walls thinner than those of normal epidermal cells, not papillate. Outer stomatal ledge cuticle thicker than normal epidermal cells, narrowly-elliptic, with elongate, slit-like aperture. Epidermal cells clearly visible under TLM, in rows, elongate, straight-walled, unbuttressed, glabrous, slightly papillate.

Identification. Similar cuticle is present in the Early Eocene of Tasmania, but the lateral subsidiary cells, have a more arched appearance, and the thick ridge flanking the guard cells is absent.

CUT-Mo-EIA
Figure 8.1-8.2

Reference specimen: SL2446, Sthd-068.

Referred specimens and occurrence: SL3241, Sthd-163.

Description. Epidermis not divided into costal and intercostal zones (stomata evenly spread). Stomatal complex construction dicyclic, paratetracytic, typically with 4 subsidiary cells, outline irregular - polar subsidiary cells project beyond margin of lateral subsidiary cells, not in rows. Polar subsidiary cells well-spaced along files (nearest neighbour typically in adjacent file). Separated, with one or more purely epidermal cell files within the stomatal zone, longitudinally oriented. Subsidiary cells with periclinal walls of same thickness as those of normal epidermal cells, papillate, papillae not overarching stomatal pore (each subsidiary cell has a single smooth papilla, divided into 1-5 crowns). Outer stomatal ledge cuticle same thickness as normal epidermal cells, with slit-like aperture, tapering towards ends. Epidermal cells clearly visible under TLM, in rows, isodiametric or wider than long, straight-walled, unbuttressed, glabrous, papillate, each cell has up to five papillae, which are usually fused into a single multi-headed unit, or sometimes as isolated or various fused units. Epidermal cells of costal zones distinctly more elongate than intercostal cells.

Identification. Possibly Pandanaceae. Compare with illustrations in Tomlinson (1965) and Kam (1971).

CUT-Mo-FEG
Figure 8.3-8.4

Reference specimen: SL2093, GL-07.

Description. Epidermis divided into costal and intercostal zones (stomata concentrated in zones). Stomatal zones about 10-15 stomatal complexes wide. Stomatal complex construction monocyclic and dicyclic, paratetracytic, typically with four subsidiary cells, outline irregular - polar subsidiary cells project beyond margin of lateral subsidiary cells, not in rows, longitudinally oriented. Polar subsidiary cells well-spaced along files (nearest neighbour typically in adjacent file). Subsidiary cells with periclinal walls thinner than those of normal epidermal cells, papillate, papillae not overarching stomatal pore (each subsidiary cell has an indeterminate number of subdued and fused papillae). Outer stomatal ledge cuticle thicker than normal epidermal cells, with slit-like aperture. Epidermal cells clearly visible under TLM, in rows, straight-walled, unbuttressed, glabrous, papillate, each cell has up to five papillae (smooth), which are usually fused into a single multi-headed unit, or sometimes as isolated or various fused units. Epidermal cells of costal zones distinctly more elongate than intercostal cells.

Identification. Possibly Pandanaceae. Compare with illustrations in Tomlinson (1965) and Kam (1971).

CUT-Mo-EHB
Figure 8.5-8.6

Reference specimen: SL2524, BL-05.

Referred specimens and occurrence: SL2036, Sthd-046; SL1541, Sthd-068; SL2078, Sthd-113.

Description. Epidermis not regularly divided into costal and intercostal zones (stomata essentially evenly spread). Stomatal complex construction monocyclic and dicyclic, paratetracytic, typically with four subsidiary cells, outline irregular - polar subsidiary cells project beyond margin of lateral

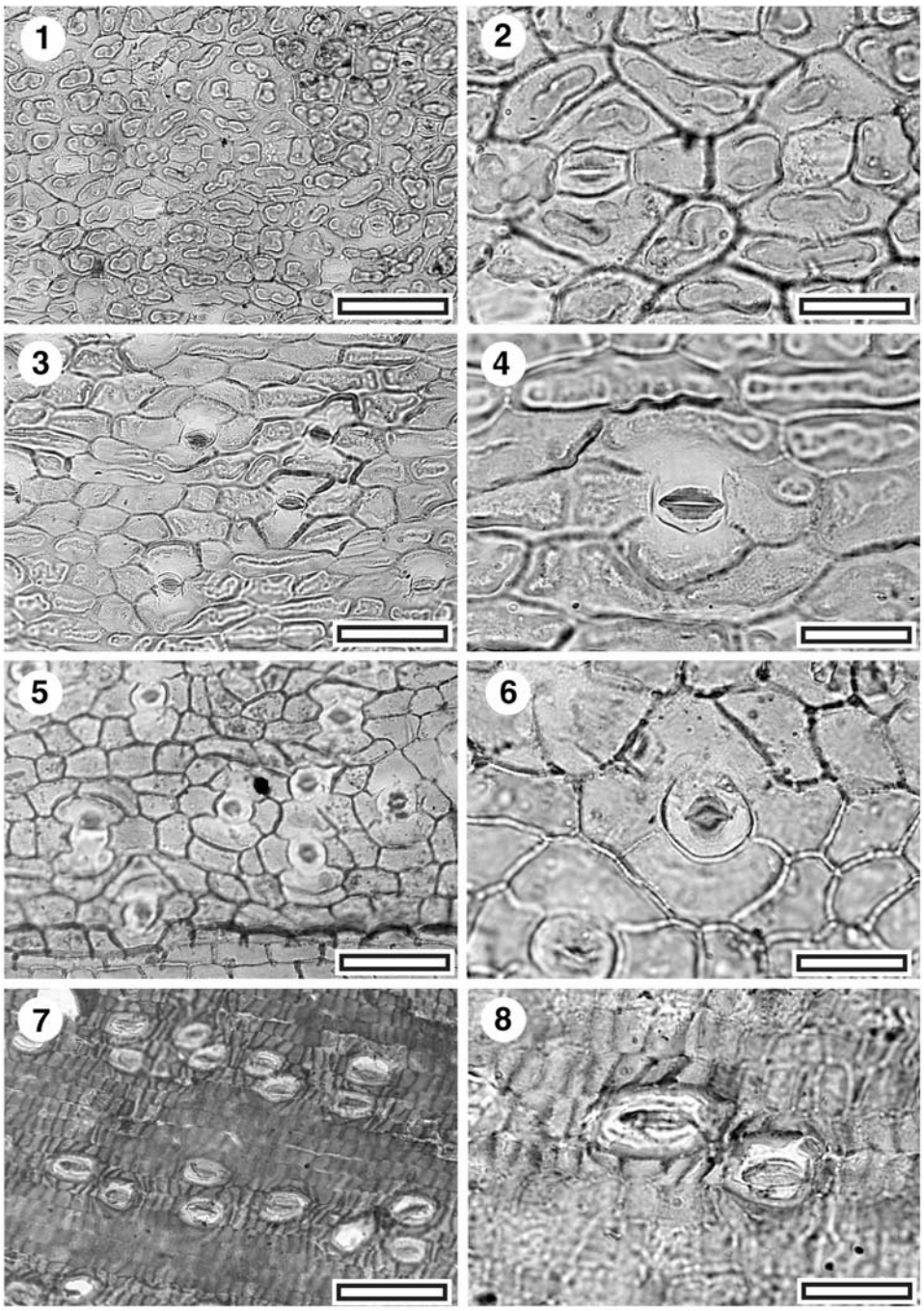

Figure 8. CUT-Mo-EIA, CUT-Mo-FEG, CUT-Mo-EHB, and CUT-Mo-EFF. **1.** CUT-Mo-EIA, TLM view of stomatal complexes (SL2446, scale bar = 50 μm); **2.** CUT-Mo-EIA, TLM detail of two stomatal complexes (SL2446, scale bar = 20 μm); **3.** CUT-Mo-FEG, TLM view of stomatal complexes. Note subdued and fused papillae (SL2093, scale bar = 50 μm); **4.** CUT-Mo-FEG, TLM detail of stomatal complex. Note subdued and fused papillae (SL2093, scale bar = 20 μm); **5.** CUT-Mo-EHB, TLM view of stomatal complexes. Note absence of any clear row structure or regular costal-intercostal distinction. Some more elongate epidermal cells are visible near the lower edge of the figure (SL1541, scale bar = 50 μm); **6.** CUT-Mo-EHB, TLM detail of stomatal complex. Note distinctive rounded outline of the stoma and the pinched ends of the stomatal aperture (SL1541, scale bar = 20 μm); **7.** CUT-Mo-EFF, TLM view of stomatal complexes (SL1785, scale bar = 50 μm); **8.** CUT-Mo-EFF, TLM detail of two stomatal complexes. Note four isodiametric lateral subsidiary cells on left complex (SL1785, scale bar = 20 μm).

subsidiary cells, in overlapping rows, separated, with one or more purely epidermal cell files within the stomatal zone, mainly longitudinally oriented, but with some slightly oblique. Polar subsidiary cells well-spaced along files (nearest neighbour typically in adjacent file). Subsidiary cells with periclinal walls of same thickness as those of normal epidermal cells, not papillate. Outer stomatal ledge cuticle thicker than normal epidermal cells, with slit-like aperture, tapering towards ends. Epidermal cells clearly visible under TLM, in rows, isodiametric or wider than long, wavy-walled, unbuttressed, glabrous, not papillate. Irregular costal zones formed of epidermal cells distinctly more elongate than normal cells.

CUT-Mo-EFF
Figure 8.7-8.8

Reference specimen: SL1785, Sthd-030.

Referred specimens and occurrence: SL1666, Sthd-034; SL1931, Sthd-058.

Description. Epidermis divided into costal and intercostal zones (stomata concentrated in zones). Stomatal zones about two stomatal complexes wide. Stomatal complex construction unclear, essentially paratetracytic, but extreme variation in number and shape of subsidiary cells (up to four lateral subsidiary cells on each side), outline elongate, in overlapping rows, separated, with one or more purely epidermal cell files within the stomatal zone, longitudinally oriented. Polar subsidiary cells well-spaced along files (nearest neighbour typically in adjacent file). Subsidiary cells with periclinal walls thicker than those of normal epidermal cells, not papillate. Outer stomatal ledge cuticle thinner than normal epidermal cells, with slit-like aperture. Epidermal cells clearly visible under TLM, in rows, isodiametric, straight-walled, unbuttressed, glabrous, not papillate. Epidermal cells of costal zones isodiametric.

CUT-Mo-FFA (*Typha* sp.)
Figure 9.1.-9.2

Reference specimen: SL3141, GL-01.

Identification. The elongate shape of the subsidiary cells with distinctive, truncate polar ends and the narrow subsidiary cells indicate *Typha,* although clearly not the common *T. orientalis* currently in New Zealand (Figures 9.3, 9.4). A further extant species, *T. domingensis* is shown for comparison. A further extant species, *T. domingensis* is shown for comparison.

Description. Epidermis not divided into clear costal and intercostal zones, although possibly in many narrow zones about two stomatal complexes wide where the stomatal complexes are widely-spaced. Stomatal complex construction dicyclic, paratetracytic, typically with four subsidiary cells, outline elongate, in overlapping rows, mainly longitudinally oriented, but with some slightly oblique. Polar subsidiary cells well-spaced along files (nearest neighbour typically in adjacent file). Subsidiary cells with periclinal walls of same thickness as those of normal epidermal cells, not papillate. Outer stomatal ledge cuticle thicker than normal epidermal cells, with elliptical aperture, flanked on each side by a thin ridge of cuticle. Epidermal cells clearly visible under TLM, in rows, isodiametric, straight-walled, unbuttressed, glabrous, not papillate. Epidermal cells of costal zones slightly elongate.

CUT-Mo-EII
Figure 10.1-10.4

Reference specimen: SL1873, Sthd-078.

Referred specimens and occurrence: SL3240, Sthd-163; SL1536, Sthd-067.

Description. Epidermis not divided into costal and intercostal zones (stomata evenly spread). Stomatal complex construction tricyclic, essentially paratetracytic, but extreme variation in number and shape of subsidiary cells, outline circular, not in rows, longitudinally oriented. Polar subsidiary cells well-spaced along files (nearest neighbour typically in adjacent file). Subsidiary cells with periclinal walls thicker than those of normal epidermal cells, not papillate. Outer stomatal ledge cuticle thicker than normal epidermal cells, aperture rounded. Epidermal cells clearly visible under TLM, in rows, normally elongate, but sometimes several contiguous cells are much shorter than broad (partially formed stomatal complexes?), wavy-walled, unbuttressed, glabrous, not distinctly papillate although outer periclinal walls bulge outwards. Often with some cutinisation of inner periclinal walls.

CUT-Mo-FEF
Figure 10.5-10.6

Reference specimen: SL3143, GL-01.

Referred specimens and occurrence: SL3168, BL-33.

Description. Epidermis not divided into costal and intercostal zones (stomata evenly spread). Stomatal complex construction tricylic and dicylic,

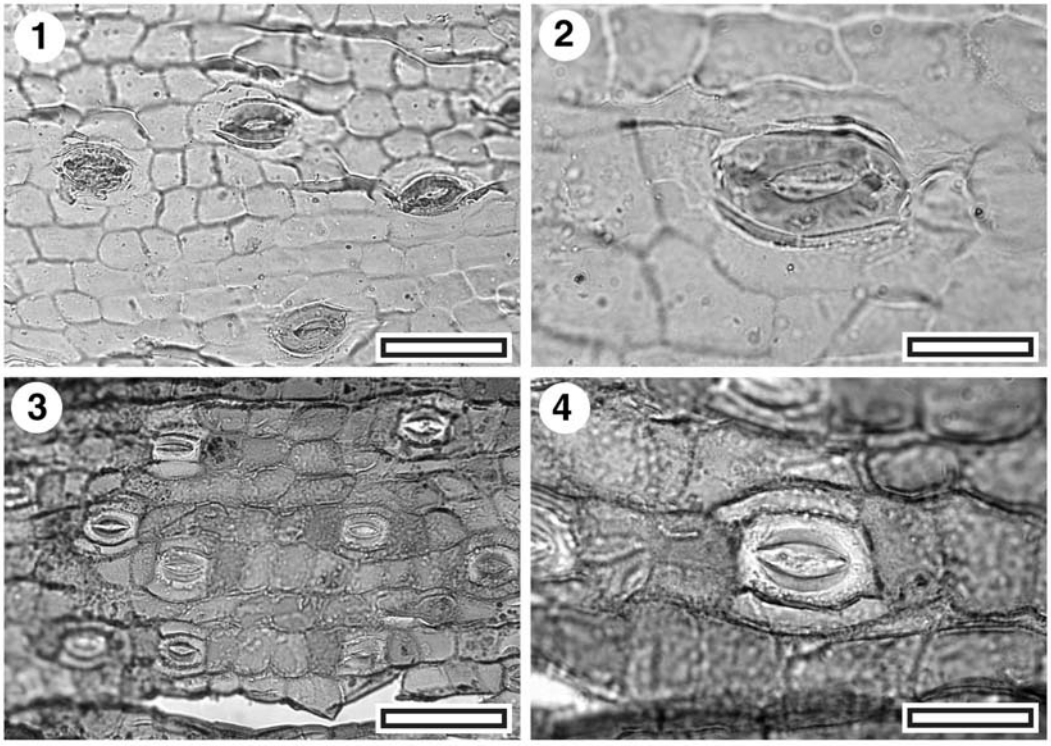

Figure 9. Fossil and extant *Typha*. **1.** CUT-Mo-FFA, TLM view of stomatal complexes (SL3141, scale bar = 50 µm); **2.** CUT-Mo-FFA, TLM detail of stomatal complex. Note ridges of cuticle closely flanking the outer stomatal ridges (SL3141, scale bar = 20 µm); **3.** extant *Typha domingensis* (AQ399599, scale bar = 50 µm); **4.** extant *T. domingensis* (AQ399599, scale bar = 20 µm).

encyclocytic with 5–7 subsidiary cells, outline circular, not in rows, obliquely oriented. Polar subsidiary cells widely spaced. Subsidiary cells with periclinal walls thicker than those of normal epidermal cells, not papillate. Outer stomatal ledge cuticle thinner than normal epidermal cells, with slit-like aperture, tapering towards ends. Epidermal cells clearly visible under TLM, in rows, irregularly shaped, typically longer than wide, straight-walled, unbuttressed, hirsute. Trichomes common, scattered over leaf, attached over epidermal cell having much thicker periclinal cuticle than normal epidermal cells, unicellular, persistent, not papillate.

Typhaceae

The bulrush (or cattail) *Typha* forms very small operculate seeds which have been described from fossil assemblages around the world (e.g., Collinson 1988). A specimen from the Miocene Yallourn Coal Measures of Victoria previously described as a moss capsule was reidentified as a *Typha* seed by Dettmann and Clifford (2000). Further discussion of the morphology of Typhaceae seeds, including the description of a new fossil genus of Typhaceae, *Typhaspermum*, was given in Dettmann and Clifford (2000).

Typha seeds have not previously been described from New Zealand assemblages but some of the Manuherikia Group seeds clearly fit the morphology of *Typha*, for instance those from sample BL-31. They show the lid-like operculum, or where it has inferred to have detached. They appear to be essentially symmetrical about their long axis (although some may have been distorted by flattening during burial) and therefore consistent with *Typha* and not the asymmetrical *Typhaspermum*. However, there are clearly a range of species and some of the smaller forms may not represent *Typha*. Dettmann and Clifford (2000) noted that *Trithuria* has a similar basic morphology as *Typha*, but has a smooth seed wall without cell outlines. The seeds described here have visible cell outlines, although they are often not very clear. For the purposes of this paper they are all provisionally placed in *Typha*, and six seed types are distinguished but no detailed comparison is attempted.

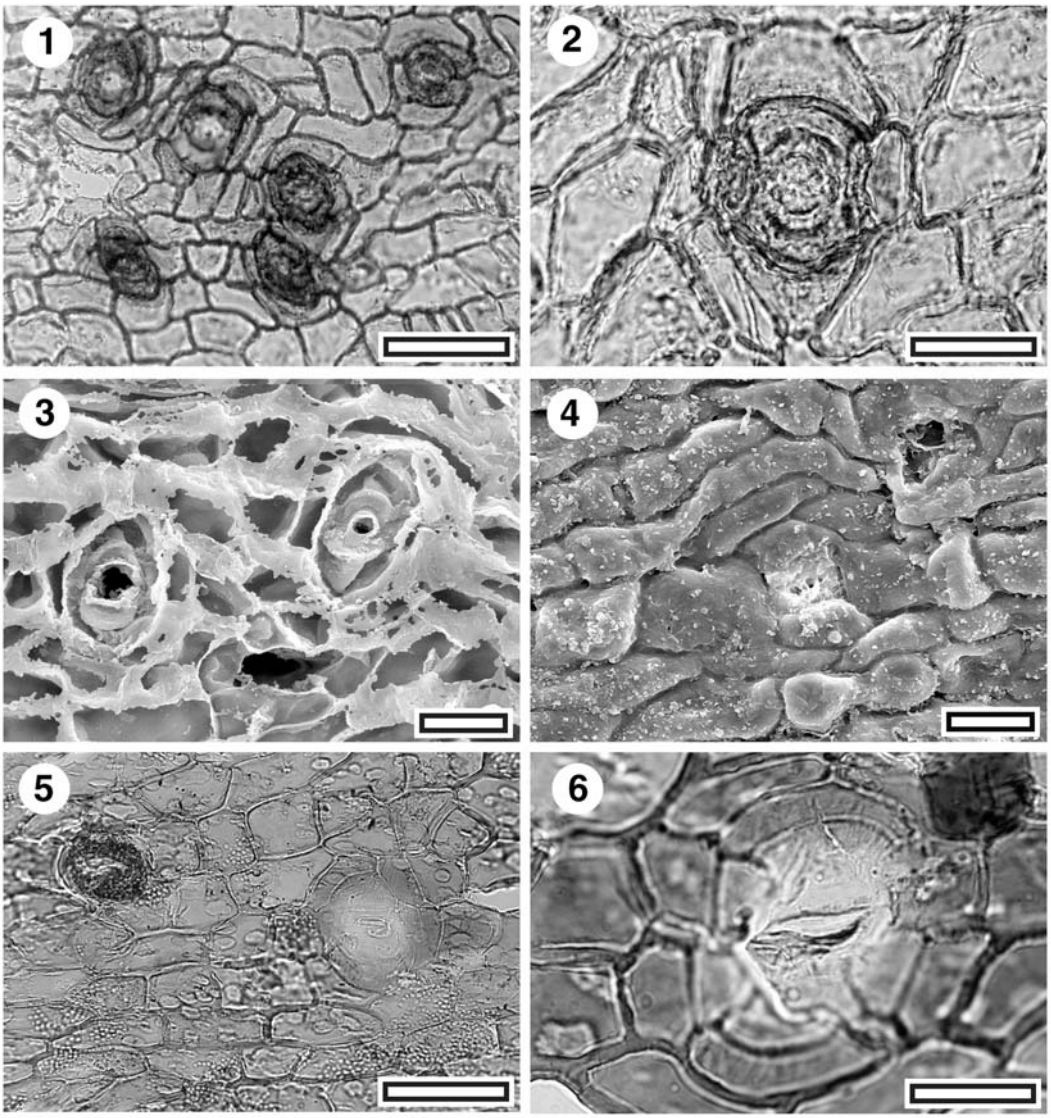

Figure 10. CUT-Mo-EII and CUT-Mo-FEF. **1.** CUT-Mo-EII, TLM view of stomatal complexes (SL1873, scale bar = 50 µm); **2.** CUT-Mo-EII, TLM detail of stomatal complex (SL1873, scale bar = 20 µm); **3.** CUT-Mo-EII, inner SEM detail of two stomatal complexes. Ragged flanges are partial cutinisation of inner periclinal walls (S-1105, scale bar = 20 µm); **4.** CUT-Mo-EII, outer SEM view of a single stomatal complex. Note how periclinal walls bulge outwards (S-1105, scale bar = 20 µm); **5.** CUT-Mo-FEF, TLM view of stomatal complexes. Note dark ring of trichome at centre left (SL3143, scale bar = 50 µm); **6.** CUT-Mo-FEF, TLM detail of stomatal complex (SL3143, scale bar = 20 µm).

Typha form A.
Figure 11.1-11.2

Specimens: SL4408, SL25219, both BL-31.

Description. Obovate, 2700-3000 m long, 1150-1550 m wide.

Typha form B.
Figure 11.3

Specimen: SL4410, BL-31.

Description. Elliptical, 1525 m long, 775 m wide.

Typha form C.
Figure 11.4

Specimen: SL1957, Sthd-054.

Description. Narrow elliptical, with almost parallel sides, 1325 m long, 350 m wide.

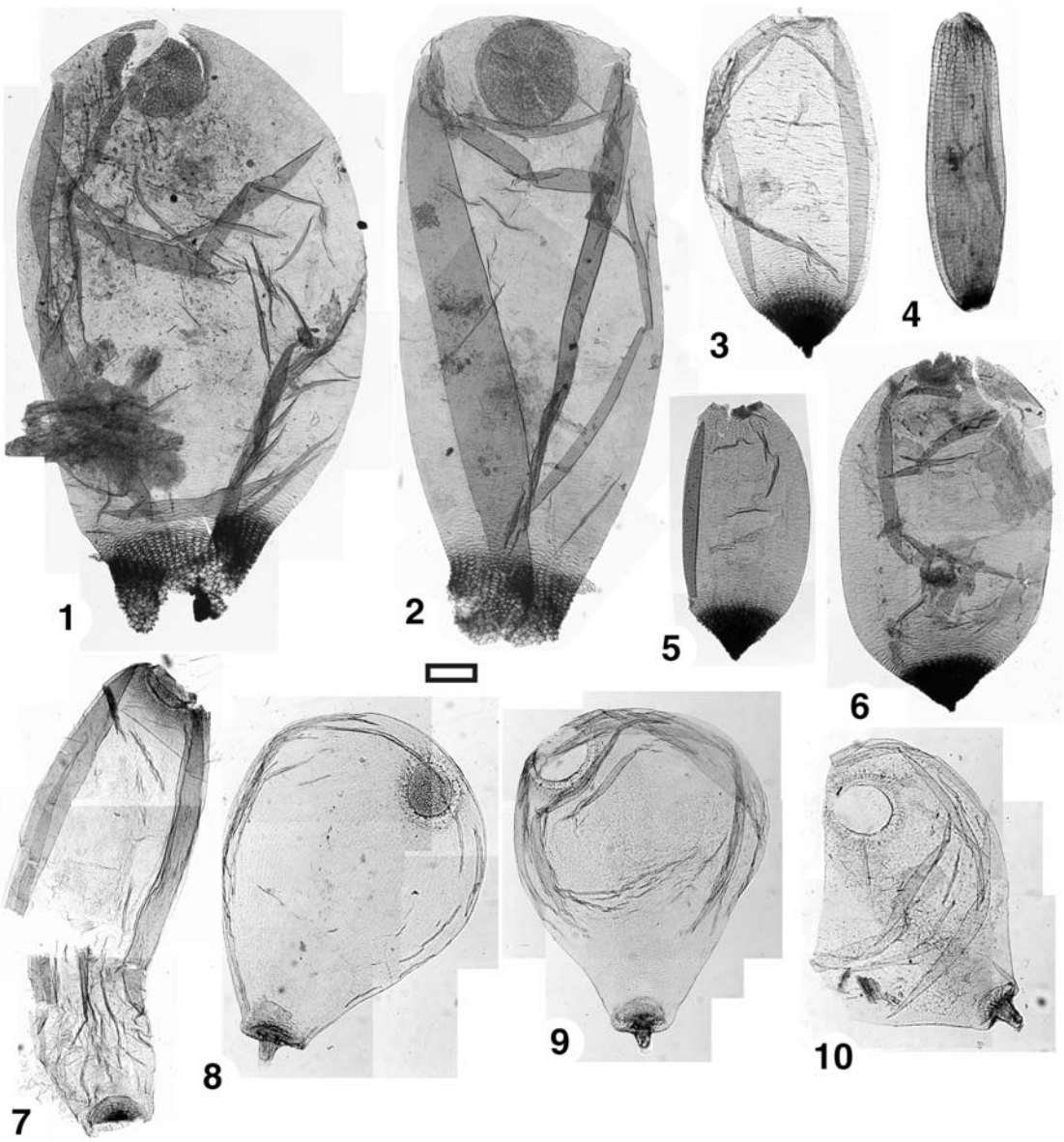

Figure 11. *Typha* seeds, TLM views of seeds mounted in glycerine jelly; scale bar = 0.2 mm. *Typha* form A: **1.** SL4408; **2.** SL2519; *Typha* form B: **3.** SL2430; *Typha* form C: **4.** SL1957; **5.** SL4407; *Typha* from D: **6.** SL4405; *Typha* form E: **7.** SL2196; *Typha* form F: **8.** SL2430; **9.** SL2429; **10.** SL2431.

Typha form D.
Figure 11.5-11.6

Specimens: SL4405, SL4407, both BL-31.

Description. Elliptical. 1600-1125 m long, 950-575 m wide.

Typha form E.
Figure 11.7

Specimen: SL2196, GL-11.

Description. Narrow, with almost parallel sides, 2125 m long, 750 m wide.

Typha form F.
Figure 11.8-11.10

Specimens: SL2429, SL2430, SL2431, all Sthd-030.

Description. Strongly obovate, 1500-1625 m long, 1125-1175 m wide.