

DISPERSED LEAF CUTICLE FROM THE EARLY MIOCENE OF SOUTHERN NEW ZEALAND

Mike Pole

ABSTRACT

This paper describes 115 parataxa of dispersed leaf fossil cuticle from 120 samples from the Early Miocene of Central Otago (the fluvial-lacustrine Manuherikia Group) and Southland (the coastal deltaic East Southland Group), New Zealand. The modern affinities include Argophyllaceae (Argophyllum), Atherospermataceae, Casuarinaceae (Gymnostoma), Cunoniaceae-Elaeocarpaceae, Ericaceae, Gnetaceae, Grisseliniaceae (Grisellinia), Meliaceae, Menispermaceae, Monimiaceae (Hedycarya), Myrsinaceae, Proteaceae (incl. Lomatia and Placospermum), Santalaceae (Notothixos), Sapindaceae, Strasburgeriaceae (Strasburgeria), and Winteraceae. The records of Argophyllaceae, Menispermaceae, Placospermum and Notothixos are the first of these families and genera for New Zealand. For the Argophyllaceae and Notothixos at least, these are the first known fossil records. With the exception of Cunoniaceae-Elaeocarpaceae, Ericaceae, Grisseliniaceae, Myrsinaceae, and Winteraceae, which occur in the south of New Zealand today, the fossils indicate a more southerly range extension in the Early Miocene than today. This evidence of extended range along with a previously published high diversity of Lauraceae and conifers is probably the result of warmer conditions despite the fossil localities lying at about 50°S in the Early Miocene - about 5 degrees further south than today. Argophyllum and Strasburgeria are evidence of a biogeographical link with New Caledonia, where they are now restricted. The plants were components of rainforest vegetation growing in microthermal to mesothermal temperatures.

Mike Pole. Queensland Herbarium, Brisbane Botanic Gardens Mt Coot-tha, Mt Coot-tha Rd, Toowong QLD 4066, Australia murihiku@yahoo.com

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INTRODUCTION

The Miocene covers a period of extraordinary global climate change, extending though for example, the early Middle Miocene Climate Optimum (Flower and Kennett 1994; Shevenell et al. 2004; although Böhme et al. 2007 identify a German optimum slightly earlier) and the profound drop in tem-

PE Article Number: 11.3.15A Copyright: Palaeontological Association October 2008 Submission: 12 January 2008. Acceptance: 10 September 2008 perature which rapidly followed (Miller et al. 1991; Zachos et al. 2001). During the optimum rainforest was widespread and thermophilic plant species grew poleward of their current extent. The succeeding temperature drop saw rainforest retreat and its replacement with deciduous forest while

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Figure 1. Location Maps. Upper map shows the extent of the Manuherikia Group schematically as a grey circle. Blue Lake is the location of sample numbers prefixed with "BL-", Grey Lake is the location of sample numbers prefixed with "GL-", Mata Creek is the location of samples prefixed with "Mata-", Harliwichs Pit is the location of sample numbers prefixed with "Harliwich-". Lower map shows the position of all drill-cores in South-land (the location of sample numbers prefixed with "Sthd-") from which fossils were obtained. For precise locations of all samples, see Appendix 1 and 2.

some deciduous forest became scrubland or grassland (Flower and Kennett 1994).

Southern New Zealand has proven to be an important source of Early Miocene plant fossils.

The fluvial-lacustrine Manuherikia Group of Central Otago (Douglas 1986) lay to the north of the coastal fluvial –deltaic East Southland Group (Isaac and Lindqvist 1990). Extensive palynologi-

cal studies have been carried out in both areas (e.g. Pocknall and Mildenhall 1984; Mildenhall and Pocknall 1989). Leaf and fruit impressions found in the Manuherikia Group include Eucalyptus (Pole 1993a), Allocasuarina (Campbell and Holden 1984) and a legume (Pole 1992). They demonstrate the variety of vegetation types which existed in the Early Miocene and from which significant climate change can be inferred (Pole 2003). Palynological studies also indicate the importance of burning during part of the deposition of the Manuherikia Group (Mildenhall 1989; Pole and Douglas 1998). Along with the vegetation there was a fauna which is becoming increasingly well-known (Feldman and Pole 1994; McDowall and Pole 1997; Pole et al. 2003; Worthy et al 2006, 2007). Earlier work on plant macrofossils focussed on impressions (see Pole 1993b and references therein) although the pioneering investigations of Holden (1987) documented the presence of leaf cuticle in the East Southland Group. More recently dispersed cuticle has been central to research in the field (Pole 1997, 1998a, 2007a, 2007b) and has resulted in the discovery of two cycads (Hill and Pole 1994, Pole 2007b), 16 conifers (Pole 2007b), and 11 Proteaceae (Pole 1998a) and 25 Lauraceae (Pole 2007a) and 17 monocots or possible monocots (Pole 2007c). The identification of these taxa may help quantify aspects of the warmer global climate at a time when New Zealand was further south than it is today. For instance the southern limit of the Lauraceae family lies within New Zealand today, where only four species of broad-leaved Lauraceae are present (Allan 1982; Wright 1984). However, in the Early Miocene 25 species are known (Pole 2007a). In the debate over the importance of long distance dispersal in the origin of New Zealand's flora (Knapp et al. 2005; McGlone 2005; Pole 1994; Winkworth et al. 2002) genetic data provided by extant plants seems to be strongly favouring the dispersal option, but good plant fossil evidence is still needed to date nodes on phylogenetic trees and to demonstrate where extinction has entirely eliminated taxa from major biogeographic regions. Basic description of cuticle morphologies will also prove useful for stratigraphic purposes. While previous papers have documented the more diverse taxonomic groups (see previous discussion) and a further paper documents the presence of families currently endemic to New Caledonia, the aim of this paper is to complete the documentation of the dispersed fossil leaf cuticle morphologies currently known from the Manuherikia and East Southland

Groups. To this end it has no taxonomic focus, and includes a large proportion of taxonomic unknowns but is a necessary step prior to a synthesis of the vegetation.

METHODS

Fossil-cuticle bearing samples of carbonaceous mud were made in 120 locations in the Manuherikia and East Southland Groups (Fig. 1). Sample numbers prefixed by "BL-" and "GL-" come from the St Bathans Paleovalley, those prefixed with "Mata-" come from Mata Creek and prefixed with "Harliwich-" come from Harliwich's Coal Pit, those prefixed with "Sthd-" come from the East Southland Group. Most Manuherikia Group samples were about 300g of sediment, with about half of that being processed. Seven samples were more intensively sampled by repeat visits as they have more abundant and intact angiosperm fossils. These samples are BL-30, GL-01, GL-02, GL-32, H41/f038, BL-32, Mata-01 where up to one or two kilos were processed. Samples from the East Southland Group come from drillcore and were limited by the diameter of the drill core (c. 50 mm) and the desire to preserve the integrity of the core as much as possible. Sample size was about 50 g and the amount of sediment prepared was about half of that.

For the St Bathans Paleovalley samples a simple stratigraphic column is inappropriate as the sampled units are lensoid and widely-spread. However, a grid-reference and notes will allow relocation of the sample site. These details can be found in Appendix 1 and 2.

The samples were disaggregated by covering with hot water and adding 40 % hydrogen peroxide, fines were then removed by sieving through a 1 mm mesh. What remained was typically a "hash" of cuticle fragments, typically around 1 - 10 mm across. Cuticle could then be purified with further hydrogen peroxide treatment (which removes opaque cellular material) and hydrofluoric acid to remove silicates. It was then stained using either safranin or crystal violet. This concentrate was then scanned in a Petri dish under binocular microscope and individual cuticle fragments were isolated and mounted on microscope slides using thymol glycerine jelly for Transmitted Light Microscopy (TLM). When sufficient additional material was present, also mounted on stubs for scanning electron microscopy (SEM) using double-sided tape, and coated with platinum. Catalogue numbers for material mounted on microscope slides are prefixed with "SB" or "SL" and SEM stubs are prefixed with "S-".

The task of distinguishing taxa was an iterative process that has taken over 15 years. This work mainly used TLM and enlarged TLM photographs were employed which could be laid side by side to facilitate comparison. SEM observation was useful to interpret the three-dimensional structure and view very fine details. However, for pragmatic purposes this study focuses on distinguishing characters which can be viewed under TLM.

As a general observation, it is relatively simple to study one sample and separate out distinct taxa. However, as more and more samples are added, perhaps with slightly differing degrees of preservation, staining, environmental differences, etc, the issue of taxon distinction becomes critical. As more samples are studied, typically many 'provisional' taxa are merged with one another. The issue then becomes one of finding similarities rather than differences. The benefits of a large sample-base being that a more realistic concept of taxa emerges. However, it is certain that a few taxa distinguished here are likely to cover more than one "real" species, and thus the final number will be an underestimate. Where there may be some issues of distinction; these are addressed under the subheading "Distinguishing features".

In this work, cuticle morphologies are described as parataxa. Each parataxon is prefixed by "CUT-", then a letter. This is a purely pragmatic subdivision of the cuticle taxa into large groups. For instance, "L" includes Lauraceae, "M" the Myrtaceae, and "P" for Proteaceae. Most parataxa described in this report were given a "Z" as they are the large group "left over" once the more immediately identifiable groups had been dealt with. Finally, each parataxon gets a unique string of three letters. This is meant as a flexible system to deal with the disparate and poorly hierarchical morphologies of cuticle fragments. The intention is that parataxa are equivalent to species. For each parataxon a reference specimen and sample is nominated, which are equivalent to the holotype and type locality of a Linnean species. A single specimen is also nominated from each other sample that the taxon is recorded from. For examples of this methodology see Pole (2007a).

Standard epidermal terminology is used to describe the cuticle taxa and is based on authors such as Baranova (1987, 1992), Stace (1965); 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. The inadvisability of constructing a terminology with a mixture of purely morphological terms as well as terms based on developmental processes have been discussed by these authors. However, there are occasions where some evidence of developmental process is obvious in cuticular fragments (for instance where one cell has been divided in two by a new wall) and need to be indicated. For these instances I have used terms (heliocyctic and tangenticytic) from Timonin (1995). More recently Carpenter (2005) has introduced several terms which incorporate developmental considerations. He did not discuss these terms in the context of several previous authors (for instance Timonin 1995) but some of them are also clearly applicable to the fossils described here and so they are listed alongside Timonin's. The reader should be aware that what appear to be fundamentally different terms describing stomatal complex structure may result from the subjectivity involved in deciding what is and isn't a subsidiary cell.

To clarify some further terms; OSL = outer stomatal ledge. By "outer stomatal ledge thickness" here is meant the combined thickness of ledges and any underlying cuticle as seen under TLM view. By "giant stomatal complexes" is meant any distinctly different population of complexes, either in terms of size, or by obviously increased development of subsidiary cells around them. "Networking" is used to describe the situation where contact or subsidiary cells are shared between stomatal complexes (Pole 1998b). When stomata are known to be on one leaf surface only the distribution is assumed to be hypostomatic. In all other cases the distribution with respect to leaf surfaces is unknown. Stomatal size classes follow Wilkinson (1979). "Texture" refers to a pattern on the outer or inner surfaces of cuticle, such as "granular" which is of much smaller dimensions than normal epidermal cells. Ornamentation refers to a pattern on the outer cuticular surface, such as ridging, which is comparable to the size of normal epidermal cells. It does not include papillae or scales.

Taxonomic identification into the Linnean system is based on morphological characters which have been detailed in the published literature as well as a large cuticle reference collection developed by the author. To date this collection includes around 4000 species in about 1500 genera and 285 families of mostly rainforest taxa from around the world. In this paper cuticle preparations of **Table 1**. Taxonomic summary of families and genera identified in this study and their present distribution (Family distributions from Watson and Dallwitz, 1992 onwards, genera from the Global Biodiversity Information Facility, http://us.mirror.gbif.org).

Family	Genus and current distribution		
Argophyllaceae	Argophyllum. Australia, New Caledonia.		
Atherospermataceae	South America to Australasia. Restricted to northern parts of New Zealand.		
Casuarinaceae	<i>Gymnostoma</i> . Througout Malesia, New Guinea, New Caledonia and highly restricted in Australia to northeast Queensland, absent in New Zealand.		
Cunoniaceae-Elaeocarpaceae	Widespread in New Zealand and from Southeast Asia, to Australia, Central and South America and (Cunoniaceae) South Africa.		
Ericaceae	Cosmopolitan		
Gnetaceae	Closest to extant <i>Gnetum</i> although the fossil is regarded as an extinct genus. <i>Gnetum</i> occurs from Amazonia, tropical west Africa, and tropical Asia from Bombay to Fiji (absent in New Caledonia and New Zealand).		
Grisseliniaceae	Grisellinia. South America and widespread in New Zealand.		
Meliaceae	Pantropical to subtropical and warm. To latitude 41° 30' S in New Zealand.		
Menispermaceae	Pantropical and warm. The family is absent from New Zealand today although it does occur in Australia to about 37 °S. The fossil localities are further south than any living occurrence today.		
Monimiaceae	Hedycarya. Australia, New Guinea, New Caledonia, widespread in New Zealand.		
Myrsinaceae	Comparable with Ardisia although other genera are not yet ruled out. Ardisia is pantropical to subtropical, but is absent from New Zealand.		
Proteaceae	Incl. Lomatia and Placospermum The family is present in the northern half of New Zealand. Placospermum is an Australian endemic, Lomatia is found in Australia and South America.		
Santalaceae	Notothixos. Ceylon, Myanmar, Philippines, Malesia, Australia.		
Sapindaceae	Temperate to tropical. Not extending to the far south of New Zealand.		
Strasburgeriaceae	Strasburgeria. New Caledonian endemic.		
Winteraceae	Distinct from extant New Zealand <i>Pseudowintera</i> . Malaysia, Pacific, Australia, New Zealand, Central and South America. <i>Pseudowintera</i> is widespread in New Zealand.		

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; "OTA" of specimens in the Botany Department Herbarium, University of Otago, Dunedin) and material in the author's own reference herbarium is prefixed with "OPH". All material is stored in the Queensland Herbarium, Toowong.

RESULTS AND DISCUSSION

One hundred and fifteen morphologies of cuticle parataxa were distinguished in the 120 samples (Appendix 3). Fifty eight taxa have been placed into extant families, and eight into extant genera. The remainder have not been identified, or have less certain, and only suggested affinities. The species-level biodiversity represented here makes a substantial contribution to that predicted from the diversity of one family in the fossil record, the Lauraceae. Based on the current relationship between the number of Lauraceae species and total tree diversity for rainforest sites in Australia, the 25 Lauraceae taxa known from the Manuherikia and East Southland Groups suggest at least 100 tree species grew with them, and probably at least 120 (Pole 2007a).

Some of the families described as fossils in this study occur in the extant flora of New Zealand, but others represent the first known occurrence of the family in New Zealand, and as such, add to another dimension of biodiversity. Among the unidentified taxa there are also likely to be totally extinct genera represented, but these will need more information, for instance evaluation of the corresponding whole leaf architecture.

A brief discussion of the significance of the identified taxa (Summarised in Table 1) follows and the detailed descriptions are relegated to Appendix 3. A fuller synthesis will await publication of some further taxa and will be integrated with more detailed stratigraphy and sedimentology.

Evidence for the presence of Gnetales in New Zealand is not new – palynological works have reported the pollen *Ephedripites notensis* Cookson (1957) for many years (e.g. Couper 1960). This pollen type has been said to have affinities with extant *Ephedra*, an arid-land plant of North America. Its presence in an obviously wet-environment

is something of an anomaly, and the likelihood is that the family identification is correct, but that it represents some other, extinct genus. The presence of cuticle with similarities (but distinct from) *Gnetum* reinforces the view. The cuticle morphology is also present in the Late Eocene of the Waikato Coal Measures (Pole unpublished) and a similar parataxon is in the Early Eocene of Tasmania (Pole 2007d). It may represent a plant lineage which continued through the putative Oligocene drowning of New Zealand (Cooper and Cooper 1995), or it may represent long-distance dispersal. In this context it is of interest that DNA evidence has suggested that *Gnetum* has dispersed globally within the Neogene (Won and Renner 2006).

The Winteraceae are represented in New Zealand today by three species in the genus Pseudowintera (Allan 1982). The cuticle record suggests that other genera of the family were present in the Miocene (there is no Miocene cuticle record of Pseudowintera). The inference of higher generic diversity at this time supports the conclusions of the palynological record (Pocknall and Mildenhall 1984; Raine et al. 2006) where Harrisipollenites annulatus Mildenhall & Crosbie (1979) is regarded as representing Zygogynum, a New Caledonian genus, and Pseudowinterapollis couperi Krutzsch (1970) is consistent with Drimys, Pseudowintera and Tasmannia and P. cranwelliae (Stover and Partridge 1973) represents Tasmannia. Today the family is a prominent component of rainforests in the cool southern Hemisphere as well as New Caledonia.

The Atherospermataceae and Monimiaceae are also important families in cooler Southern Hemisphere rainforests and both are in the current New Zealand flora (*Hedycarya* in the Monimiaceae and *Laurelia* in the Atherospermataceae). Little is known of their prehistory; the long-ranging pollen type *Liliacidites variegatus* Couper (1953) may represent Atherospermataceae, though it may also be produced by the Lilliaceae (Raine et al. 2006), but fossil wood has been reported from Antarctica, but cannot be related to any single extant genus (Poole and Francis 1999).

The Proteaceae has two genera in the extant flora of New Zealand, *Knightia*, and *Toronia*, both members of the warmer rainforests. The cuticle evidence supports the palynological evidence that the Proteaceae were much more diverse in New Zealand. The identification of *Placospermum* in this study adds another genus to the New Zealand record and those known from the Miocene (Pole 1998a). Today a diverse component of Proteaceae is a feature of the wet, mesothermal rainforests of northern Australia (Webb and Tracey 1981).

The Menispermaceae represent a new addition to the New Zealand record. They are a family dominated by climbers or creepers, mostly tropical, reaching as far south as Victoria in Australia. Added to the *Rhipogonum* already known (Pole 1993c) this identification allows the inference of a second climber in the Manuherikia Group based on macrofossil evidence.

The genus *Notothixos* is a new addition to the New Zealand record and is the first fossil record of the genus, and perhaps of the Viscaceae. *Notothixos* is a mistletoe and occurs today from Ceylon to Malesia and down the east coast of Australia to Victoria (Barlow 1983).

Strasburgeria (Strasburgeriaceae) is currently endemic to New Caledonia, but has been identified with the pollen *Bluffopollis scabratus* (Couper) Pocknall & Mildenhall (1984), which is present throughout the Tertiary of New Zealand (Jarzen and Pocknall 1993) and is a common and widespread component in many of the samples studied here (pers. obs.). This is the first fossil record of the cuticle.

Griselinia is the only genus in the Griseliniaceae, which is found today in both New Zealand and South America. This is the first fossil record of the genus.

The Meliaceae and Sapindaceae both have a single rainforest species in New Zealand today; *Dysoxylon* and *Alectryon* respectively. In the Sapindaceae there is also *Dodonaea*, a shrub of more open vegetation. The cuticle evidence confirms the palynological evidence for these families in the Neogene, but like the pollen, is not helpful to generic identification. Although Couper (1960) identified pollen of *Dysoxylum* in the Cenozoic, neither the genus nor the Meliaceae is included in Raine et al. (2006). The fossil pollen may not be distinguishable from that of many other genera of Meliaceae (e.g. Mildenhall 1980).

The Cunoniaceae-Elaeocarpaceae are prominent components of the extant New Zealand flora as the genera *Elaeocarpus* and *Weinamnnia*. Miocene Elaeocarpaceae leaf impressions were described by Pole (1993; which on the basis of their basic shape, domatia, and spinose attachments on the teeth, I am now certain are *Elaeocarpus*). The Myrsinaceae is present in New Zealand today as the widespread genus *Myrsine* and also the highly restricted *Elingamita* (Allan 1982). A compression fossil of the Mysinaceae was described by Pole (1996) from the Miocene Foulden Hills Diatomite (and based on the vein architecture, I am now certain that this is an *Ardisia*).

The Manuherikia Group would have lain at about 50°S in the Early Miocene (Lawver and Gahagan 2003), about 5° further south than its present position. The latitude of the East Southland Group, like today, would have been only a degree or two higher than the Manuherikia Group. Both of these areas lie southwards of the southern limit of several plant families represented by the cuticle (Table 1), and therefore indicate a more southerly range extension than found today. This likely refects warmer conditions, consistent with other fossil (Hornibrook 1992) and isotopic evidence (Shackleton and Kennett 1975). Judged on the present distribution of these taxa, temperatures were in the microthermal to mesothermal range (sensu Nix 1982) and the vegetation was rainforest (sensu Bowman 2000).

CONCLUSION

A diverse range of leaf cuticle is present in a wide range of localities in the Early Miocene of southern New Zealand, ranging from the inland to coastal sites. The taxa described include families still present in New Zealand today, as well as some which are now locally extinct, and some which are now restricted to New Caledonia. A large proportion cannot yet be placed into the Linnean hierarchy with any confidence, but will be useful in stratigraphic and fine-scale differentiation of vegetation and habitat types, as well as providing useful information on biodiversity and climate. In this way cuticle parataxa will compliment the palynological record as additional taxa to help refine relative ages and distinguish assemblages.

The fossils also have implications for biogeography. The new family and generic records provide interesting range-extensions to be explained. In particular they add to the growing evidence of a link between New Zealand's past vegetation and the extant vegetation of New Caledonia. They also add to the established knowledge of a warmer than present Early Miocene, and will help elucidate the specific details of this climate.

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APPENDIX 1. DETAILS FOR ST BATHANS PALEOVALLEY, MATA CREEK AND HARLIWICH'S PIT SAMPLES (ALL MANUHERIKIA GROUP

Sample	Grid reference	Stratigraphic notes
AFW-18	H41/6006 8493	Uncertain precise relationship
AFW-23	H41/6003 8490	Uncertain precise relationship
BL-01	H41/5799 8824	c. 6 m below BL-02
BL-02	H41/5799 8824	c. 6 m above BL-01
BL-03	H41/5799 8824	c. 6 m below BL-01
BL-04	H41/5796 8827	c. 7 m above BL-02
BL-05	H41/5796 8827	c. 6 m above BL-04
BL-06	H41/5796 8829	c. 10 m above BL-05
BL-07	H41/5796 8842	possibly equivalent to BL-30
BL-08	2257934 5588425	c. 15 m above BL-07
BL-09	H41/5791 8843	c. 20 m above BL-08
BL-10	H41/5776 8866	c. 23 m above BL-30
BL-11	H41/5777 8865	c. 2.5 m above BL-10
BL-12	H41/5778 8864	c. 7 m above BL-10
BL-13	H41/5778 8862	c. 9 m above BL-10
BL-14	H41/5787 8861	c. 6 m below BL-15
BL-15	H41/5782 8865	c. 6 m below BL-33
BL-16	H41/5779 8872	c. 6 m below BL-14, possibly equivalent to BL-30
BL-17	H41/5778 8878	c. 15-20 m below BI-16
BL-18	H41/5780 8877	c. 2 m above BL-17
BL-19	2257596 5588825	10 cm above BL-21
BL-20	2257596 5588825	c. 2 m below BL-26
BL-21	2257596 5588825	c. 2 m below BL-26
BL-22	2257550 5588771	c. 3 m above BL-26
BL-23	2257550 5588771	c. 7 m above BL-22
BL-24	2257562 5588748	c. 3 m above BL-23
BL-25	2257603 5588745	possibly equivalent to BL-24
BL-26	H41/5764 8881	c. 10 m below BL-27
BL-27	H41/5781 8876	c. 10 m below BL-28
BL-28	H41/5781 8870	probably 1-2 m lower than BL-25
BL-29	H41/5764 8881	c. 10 m below BL-27
BL-30	H41/5795 8831	(H41/f045) c. 10 m above BL-06
BL-31	H41/5800 8823	(H41/f048) possibly equivalent to BL-04
BL-32	H41/5800 8823	(H41/f072) possibly equivalent to BL-05
BL-33	2257911 5588447	(H41/f073) Uncertain precise relationship

Sample	Grid reference	Stratigraphic notes	
GL-01	2259089 5590115	estimated 40 m above basement	
GL-02	2259079 5590201	approximately equivalent to GL-01	
GL-03	H41/5905 9040	c. 10 m above GL-01	
GL-04	H41/5898 9040	c. 5 m above GL-01	
GL-05	H41/5942 8955	probably equivalent to GL-12	
GL-07	2259326 5589510	broadly equivalent to GL-05, est. 60 m above basement	
GL-08	2259326 5589510	50 cm above GL-07	
GL-09	2259326 5589510	c. 10 m above GL-08	
GL-10	2259326 5589510	c. 13 m above GL-09	
GL-11	H41/5933 8953	c. 4 m above GL-10	
GL-12	2259420 5589504	10-14 m above GL-11	
GL-13	2259453 5589724	10-14 m above GL-12	
GL-14	2259258 5589617	40 cm above GL-14	
GL-15	2259258 5589617	c. 1 m above GL-16	
GL-16	2259258 5589617	c. 9 m above GL-19	
GL-17	H41/5917 8968	c. 1 m above GL-18, approx equivalent to GL-19	
GL-18	H41/5917 8968	broadly equivalent to GL-20	
GL-19	H41/5917 8968	approximately equivalent to GL-17	
GL-20	H41/5914 8970	Estimated c. 40 m above basement	
GL-21	H41/5890 9001	c. 3 m above basement	
GL-22	2258994 5589951	approximately equivalent to GL-30	
GL-23	2258994 5589951	c. 1 m above GL-22	
GL-24	2259039 5589957	c. 5 m above GL-23	
GL-25	2259082 5589965	c. 10 m above GL-24	
GL-26	2259082 5590032	c. 2 m below GL-1	
GL-27	H41/5909 8999	c. 4 m below GL-26	
GL-28	H41/5917 8990	probably equivalent to GL-27	
GL-29	2259266 5589801	broadly equivalent to GL-05	
GL-30	2258940 5590041	c. 10 m above basement	
GL-31	2258940 5590041	directly overlying GL-30	
GL-32	2258940 5590041	directly overlying GL-31	
Harliwich-3	G43 211193	Mud within about 2 m above the top of the McPherson coal seam above the high wall of Harliwich's Coal Mine, Roxburgh	
Mata-01	2259921 5585353	(H41/f053) Uncertain precise relationship	
Mata-03	2260009 5585216	(H41/f074) Uncertain precise relationship	
Mata-06	H41/6000 8514	(H41/f077) Uncertain precise relationship	
Mata-18	H41/6006 8493	One of four closely-spaced carbonaceous layers in the left bank of Mata Ck. Mata-18 is the second one downstream.	
Mata-23	H41/6003 8490	Carbonaceous mud on right bank of Mata Ck.	

APPENDIX 2. DETAILS FOR GORE LIGNITE MEASURES, EAST SOUTHLAND GROUP SAMPLES

Sample	Drill Hole	Depth	Grid reference
Sthd-002	d.1024	118.45 m	2186734 5439866
Sthd-004	d.1026	27.62 m	2179606 5441890
Sthd-010	d.1027	168.02 m	2181460 5441941
Sthd-011	d.1027	174.42 m	2181460 5441941
Sthd-012	d.1027	207.25 m	2181460 5441941
Sthd-016	d.1051	4.96 m	2182300 5439100
Sthd-017	d.1051	84.36 m	2182300 5439100
Sthd-018	d.1051	86.00 m	2182300 5439100
Sthd-019	d.1051	86.42 m	2182300 5439100
Sthd-020	d.1051	92.62 m	2182300 5439100
Sthd-022	d.1051	94.41 m	2182300 5439100
Sthd-024	d.1051	105.09 m	2182300 5439100
Sthd-026	d.1051	151.95 m	2182300 5439100
Sthd-027	d.1052	4.80 m	2184396 5438625
Sthd-029	d.1052	9.78m	2184396 5438625
Sthd-030	d.1052	20.21 m	2184396 5438625
Sthd-032	d.1052	49.52 m	2184396 5438625
Sthd-033	d.1052	70.75 m	2184396 5438625
Sthd-034	d.1057	92.84 m	2179645 5439947
Sthd-040	d.1102	35.15 m	2177520 5427926
Sthd-041	d.1102	55.80 m	2177520 5427926
Sthd-043	d.1102	58.00 m	2177520 5427926
Sthd-044	d.1102	58.15 m	2177520 5427926
Sthd-045	d.1102	58.40 m	2177520 5427926
Sthd-046	d.1102	59.80 m	2177520 5427926
Sthd-047	d.1102	60.00 m	2177520 5427926
Sthd-051	d.1105	88.95 m	2183637 5427618
Sthd-054	d.1106	74.35 m	2185817 5427315
Sthd-055	d.1107	3.75 m	2187857 5427096
Sthd-056	d.1108	120.75 m	2173129 5428234
Sthd-058	d.1109	48.50 m	2170584 5428226
Sthd-059	d.1109	200.85 m	2170584 5428226
Sthd-060	d.1109	201.00 m	2170584 5428226
Sthd-067	d.1115	102.29 m	2192600 5450900
Sthd-068	d.1121	102.30 m	2170600 5422800

Sample	Drill Hole	Depth	Grid reference
Sthd-069	d.1121	150.70 m	2170600 5422800
Sthd-072	d.1124	115.45 m	2176557 5419776
Sthd-073	d.1124	157.8 or 160.3 m	2176557 5419776
Sthd-074	d.1124	c. 158.30 m	2176557 5419776
Sthd-076	d.1141	15.10 m	2163781 5408891
Sthd-078	d.1143	56.33 m	2166000 5305600
Sthd-086	d.1246	38.35 m	2188861 5435907
Sthd-087	d.1246	95.13 m	2188861 5435907
Sthd-088	d.1294	80.35 m	2163219 5411606
Sthd-089	d.1295	37.50 m	2164509 5410216
Sthd-090	d.1295	41.50 m	2164509 5410216
Sthd-091	d.1296	30.10 m	2165620 5408988
Sthd-094	d.1298	21.52 m	2162214 5407900
Sthd-095	d.1299	14.35 m	2158369 5407117
Sthd-097	d.1299	51.62 m	2158369 5407117
Sthd-098	d.1299	54.30 m	2158369 5407117
Sthd-099	d.1299	73.10 m	2158369 5407117
Sthd-100	d.1324	22.30 m	2186533 5451035
Sthd-102	d.1324	28.22 m	2186533 5451035
Sthd-106	d.1324	86.75 m	2186533 5451035
Sthd-107	d.1324	88.18 m	2186533 5451035
Sthd-108	d.1324	89.44 m	2186533 5451035
Sthd-109	d.1324	115.79 m	2186533 5451035
Sthd-110	d.1324	124.75 m	2186533 5451035
Sthd-111	d.1324	143.25 m	2186533 5451035

In this publication identified fossil cuticle taxa are presented in order following the Angiosperm Phylogeny Group (APG 2003):

Gnetales

Gnetaceae

Canellales

Winteraceae

Laurales Atherospermataceae

Monimiaceae

Proteales

Proteaceae

Ranunculales

Menispermaceae Santalales

Santalaceae

Fagales

Casuarinaceae

Oxalidales

Cunoniaceae-Elaeocarpaceae

Sapindales Meliaceae

Sapindaceae

Ericales

Myrsinaceae

Apiales

Griseliniaceae

Asterales

Argophyllaceae

The following key is a general guide for how the cuticle in this work has been allocated to families.

Key to families

- 1. Plant remains found as three-dimensional, foursided articles. Stomatal complexes oriented at right angles to long axis (The cuticle is very delicate and difficult to prepare.) *Gymnostoma*
- 1. Remains found as dispersed cuticle and typically as sheets.2.
- Raised, thick, peg-like attachment scars of deciduous trichomes common and ridges of cuticle commonly partially projecting over OSL. Argophyllaceae
- 2. Peg-like attachment scars absent, or OSL not obscured by ridges of cuticle. 3.
- 3. Stomatal complexes brachyparacytic 4.
- 3. Stomatal complexes not brachyparacytic 8.

- 4. Stomatal complexes with clearly visible guard cells, which are distinctly elongate, almost rectangular guard cells, outer stomatal ledges and separating walls between guard cells absent. Gnetales
- 4. Stomatal complexes with guard cells often partially obscured by an outer stomatal ledge, separating walls between guard cells present, guard cells irregular or rounded. 5.
- 5. Epidermis distinctly granular. Winteraceae
- 5. Epidermis not distinctly granular. 6.
- 6. Cuticle glabrous. Monimiaceae
- 6. Trichomes or trichome attachment sites present 7.
- 7. Multicelluar trichome attachment sites present (trichomes deciduous). Proteaceae
- 7. Persistent branching trichomes present. Santalaceae
- 8. Stomatal complexes anisocytic, ornamented by prominent ridging. Myrsinaceae
- 8. Stomatal complexes not anisocytic. 9.
- 9. Stomatal complexes with clear subsidiary cells. 10.
- Stomatal complexes with no clear subsidiary cells (anomocytic, although there may be occasional divisions of contact cells). Stomatal complexes with prominent outer stomatal ledges. Strasburgeriacae
- 10. Stomatal complexes with a distinctive outer stomatal rim, which is typically ovate, of equal breadth around the stoma, and under TLM appears thicker than any other area of cuticle. Atherospermataceae
- 10. No distinct outer stomatal rim as above. 11. 11. Distinctive form of massively-thickened trichome attachment scars (probably poral) present. Menispermaceae
- 11. No massively-thickened trichome attachment scars as above. 12.
- 12. Stomatal complexes typically aligned. Ericaceae
- 12. Stomatal complexes randomly oriented 13.
- 13. Stomata size large (and with prominent outer stomatal ledges). Grisselinaeaceae
- 13. Stomata size medium 14.

- 14. Subsidiary cell flanges end abruptly at or overlap the outline of the guard cells. Sapindaceae.
- 14. Subsidiary cell flanges do not end abruptly or overlap the outline of the stomata 14.
- 15. Outer stomatal ledges so thin and smooth that they leave an unobstructed view of classic 'paired kidney' stomata. giant stomata (hydathodes), simple trichome attachment scars, and cork-warts may be present. Elaeocarpaceae – Cunoniaceae.
- 15. Margin of the guard cell pair is indistinct, while the outer stomatal ledge is well-defined but narrow, covering just the inner part of the guard cells. The contact zone between guard cells and subsidiary cells is often covered by very thin cuticle which leads to the appearance under TLM of the outer stomatal ledge seeming to 'float'. The pattern of subsidiary cells is often complex, the result of tangential cell division. Meliaceae

This leaves a large group of taxa which could not be identified at all, or identified with reasonable confidence. To deal with this remainder they were grouped using morphological characters, but without any implication that they were taxonomically related. The morphological groups are segregated in this order (i.e. it is to be read sequentially as a dichotomising key):

- Group 1. Papillae present
- Group 2. Stomatal complexes generally aligned
- Group 3. Epidermal cells highly sinuous
- Group 4. Stomatal complexes surrounded by a prominent, broad peristomatal ring
- Group 5. Persistent trichomes present
- Group 6. Stomatal complexes paracytic
- Group 7. Stomatal complexes anisocytic
- Group 8. Multi cellular trichome attachment scars present
- Group 9. Fine surface ridging or striae around stomatal complexes
- Group 10. Stomatal complexes in islands
- Group 11. Outer stomatal ledges prominent or unusually shaped
- Group 12. Epidermal cells sinuous and stomatal complexes highly networked
- Group 13. Stomatal complexes typically having two rings of narrow subsidiary cells

- Group 14. Stomatal complexes prominently cyclocytic (developmentally tangeticytic) with prominent outer stomatal ledges
- Group 15. Stomatal complexes anomocytic
- Group 16. Cuticle either non-stomatiferous or stomatal complexes very inconspicuous.

DESCRIPTIONS

Gnetalaceae Lindley 1834 CUT-Z-ADE Figure 2.1-2.4

Reference Specimen and locality: SL0093, BL-08.

Referred specimens and occurrence: SL1309, BL-32; SB0841, GL-02; SL1740, Sthd-017; SL2434, Sthd-033; SL2076, Sthd-113.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, tetracytic (sometimes brachyparacytic), developmentally tangenticytic or stephanocytic bicylic, with distinct lateral subsidiary cells parallel to the stomatal axis and polar cells at right angles to the axis and which may 'enclose' the lateral cells. Sometimes subsidiary cells are modified by a tangential division, giving two lateral and two polar cells, size range unimodal. Subsidiary cells (4-6) typically elongate, or wedge-like, periclinal walls thicker than over normal epidermal cells, smooth, unornamented. Guard cell pair outline distinctly elongate, often with flattened poles, like a rounded rectangle, outlined by a well-defined anticlinal wall, length 27-37 m (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 possibly absent, with the visible cuticle lying directly over the guard cells, thinner than normal epidermal cells (often broken away), and with a narrowly elliptic pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over major veins more isodiametric shape than normal epidermal cells), distinctly larger than the stomata, anticlinal walls straight to curved, unbuttressed, smoothly textured, unornamented.

Indumentum. Glabrous.

Distinguishing features. Distinguished by the elongate guard cell pair with no division at the polar ends, lack of outer stomatal ledges and subsidiary cells which include both typically paracytic forms as well as polar forms which have formed by tangential cut-off.



Figure 2. 1-8. Fossil and extant Gnetales. 1. CUT-Z-ADE, TLM view showing stomatal complexes (SL0093, scale-bar = 50 μ m); 2. CUT-Z-ADE, TLM detail of single stomatal complex (SL0093, scale-bar = 20 μ m). Note the distinctive elongate shape of the guard cell pair, with no sign of separating walls, and no sign of an outer stomatal ledge; 3. CUT-Z-ADE, SEM view of outer cuticular surface showing a single stomatal complex (S-1125, scale-bar = 20 μ m); 4. CUT-Z-ADE, SEM view of inner cuticular surface showing a single stomatal complex (S-1125, scale-bar = 10 μ m); 5. Extant *Gnetum microcarpum*, TLM view showing stomatal complexes (AQ142225, scale-bar = 50 μ m); 6. Extant *G. gnemon*, TLM detail of single stomatal complex (AQ142229, scale-bar = 20 μ m); 7. Extant *G. tenuifolium*, TLM detail of single stomatal complex (AQ142229, scale-bar = 20 μ m); 8. Extant *G. latifolium*, TLM detail of single stomatal complex (AQ142207, scale-bar = 20 μ m).

Identification. On the basis of its highly distinctive stomatal complexes, this taxon is regarded as an extinct taxon in the Gnetaceae. Extant Gnetum species (for comparison G. microcarpum (Earl) Blume, G. gnemon L., G. tenuifolium Ridley, and G. latifolium Blume are illustrated; Figs 2.5-2.8), have uniquely-shaped stomata which are almost rounded rectangles. There is no clear division between the two guard cells and an outer stomatal ledge appears to be absent (the cuticle that is present lies directly over the guard cells). CUT-Z-ADE is distinct from Gnetum because it has distinct polar subsidiary cells, which are essentially absent in Gnetum. For further discussion see Pole (2007d) where CUT-Z-GDB from the Early Eocene of Tasmania is also regarded as Gnetalean. The clearly related cuticle of the Tasmanian specimens differs in the walls of the epidermal cells being distinctly wavy.

Comments. *Gnetum* has no fossil record, but Won and Renner (2006) have used genetics to infer that the major divergences amongst the extant clades of the genus date from the Late Oligocene.

Magnoliopsida Cronquist 1981 Winteraceae Lindley 1830

Family identification: All extant Winteraceae genera are characterized by large paracytic stomata and a highly granular or ornamented cuticle (Bongers 1973).

Key to Winteraceae

- 1. Cuticle ornamented with closely-spaced, thick (5-10 m) discontinuous ridges. CUT-Z-FJF
- 1. Cuticle unornamented. 2.
- Cuticle moderately granular (outline of outer stomatal ledge clearly visible under TLM) CUT-Z-FFD
- 2. Cuticle strongly granular (plugging and obscuring stomatal outline under TLM). CUT-Z-FJH

CUT-Z-FFD

Figure 3.1-3.2

Reference Specimen and locality: SL3140, GL-01.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, brachyparacytic, size range unimodal. Subsidiary cells elongate, periclinal walls of same thickness as normal epidermal cells, unornamented. Guard cell pair outline difficult or impossible to see in TLM view (obscured by outer stomatal ledge), but obviously elliptical, length 45–53 m (large), at same level as subsidiary cells. Outer stomatal ledge elliptical, thicker than normal epidermal cells, extending over centre of stoma, with a broad, elliptical pore, plugged with cuticular material.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, with moderately granular texture, unornamented.

Indumentum. Glabrous.

Identification. Winteraceae based on large paracytic stomata and moderately coarse cuticle. Compare with illustrations of extant Winteraceae (*Belliolum haplopus* (B. L. Burtt) A.C. Sm., *B. burttianum* A. C. Smith (1985), *Exospermum stipitatum* (Baillon) van Tieghem (1900) ex Morot, *Zygogynum balansae* Tiegh.; Figs 4.1-4.4).

CUT-Z-FJF

Figure 3.3-3.6

Reference Specimen and locality: SL2538, GL-02.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, brachyparacytic, size range unimodal. Subsidiary cells with periclinal walls of same thickness as normal epidermal cells, smooth, ornamented with thick ridges generally parallel to the stomatal axis on either side of the stoma, and at right angles to it at either end. Guard cell pair outline difficult or impossible to see in TLM view (obscured by surface ornamentation), at same level as subsidiary cells, length 38–40 m (large). Outer stomatal ledge elliptical, thinner than normal epidermal cells, extending over whole stoma, with a narrowly elliptic pore, plugged with cuticular matter.

Epidermal Cells. Epidermal cell flanges not clearly visible under TLM because of surface thickenings, normal cells elongate (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, smoothly textured ornamented with closely-spaced, thick (5-10 m) discontinuous ridges.

Indumentum. Glabrous.

Distinguishing features. Distinguished from CUT-Z-FJH by the ornamentation of massive cuticular ridges.

Identification. Winteraceae based on large paracytic stomata and highly ornamented cuticle. Com-



Figure 3. 1-8. Fossil Winteraceae: CUT-Z-FFD, CUT-Z-FJF, and CUT-Z-FJH. 1. CUT-Z-FFD. TLM view showing stomatal complexes (SL3140, scale-bar = 50 μ m); 2. CUT-Z-FFD. TLM detail of single stomatal complex (SL3140, scalebar = 20 μ m). The outer stomatal ledge is complex and may involve overlapping ledges; 3. CUT-Z-FJF. TLM view showing stomatal complexes (SL2538, scale-bar = 50 μ m). Note the ornamentation of massive ridges; 4. CUT-Z-FJF. TLM detail of single stomatal complex (SL2538, scale-bar = 20 μ m); 5. CUT-Z-FJF. SEM view of outer cuticular surface showing massive ridging obscuring stomatal complexes (S-1197, scale-bar = 20 μ m); 6. CUT-Z-FJF. SEM view of outer cuticular surface showing a single stomatal complex (S-1197, scale-bar = 20 μ m); 7. CUT-Z-FJH. TLM view showing stomatal complexes (SL2185, scale-bar = 50 μ m). Note the dark material plugging the stomatal apertures; 8. CUT-Z-FJH. TLM detail of single stomatal complex (SL2185, scale-bar = 20 μ m). Note the highly granular texture.



Figure 4. 1-4. Extant Winteraceae. Note the highly granular texture in each example. 1. *Belliolum haplopus*, TLM detail of single stomatal complex (AQ117672, scale-bar = $20 \ \mu m$); 2. *B. burttianum*, TLM detail of single stomatal complex (AQ463392, scale-bar = $20 \ \mu m$); 3. *Exospermum stipitatum*, TLM detail of single stomatal complex (AQ391245, scale-bar = $20 \ \mu m$); 4. *Zygogynum balansae*, TLM detail of single stomatal complex (AQ391241, scale-bar = $20 \ \mu m$).

pare with illustrations of extant Winteraceae (Figs 4.1-4.4).

CUT-Z-FJH Figure 3.7-3.8

Reference Specimen and locality: SL2185, GL-10.

Referred specimens and occurrence: SL3163, BL-33.

Stomatal complexes. Stomatal stomatal complexes evenly spread, isolated, randomly oriented, brachyparacytic, size range unimodal. Subsidiary cells with periclinal walls of same thickness as normal epidermal cells, texture granular, unornamented. Guard cell pair outline ovate, outer margin obscured under TLM by surface ornamentation, at same level as subsidiary cells, length 35–45 m (large). Outer stomatal ledge elliptical, thicker than normal epidermal cells, extending over whole stoma with a narrowly elliptic pore, plugged with cuticular material.

Epidermal Cells. Epidermal cell flanges somewhat diffuse, normal cells highly variable from isodiamet-

ric to elongate (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, texture strongly granular, unornamented.

Indumentum. Glabrous.

Distinguishing features. Distinguished from CUT-Z-FJF and CUT-Z-FFD the strongly granular periclinal epidermal cell walls.

Identification. Winteraceae based on large brachyparacytic stomata and highly granular cuticle. Compare with illustrations of extant Winteraceae (Figs 4.1-4.4).

Atherospermataceae Brown 1814

Family identification: Based on the reference collection the Atherospermataceae have a distinctive outer stomatal rim, which is typically ovate, of equal breadth around the stoma, and under TLM appears thicker than any other area of cuticle (*Doryphora sassafras* Endlicher (1841), *D. sassafras, Laurelia novae-zealandiae* Cunningham (1838), *L. novae-zealandiae*, *D. aromatica* (



Figure 5. 1-6. Extant Atherospermataceae. 1. *Doryphora sassafras*, TLM view showing stomatal complexes and a massively-thickened trichome attachment scar (AQ217598, scale-bar = 50 μ m); 2. *D. sassafras*, TLM view showing two stomatal complexes (AQ217598, scale-bar = 20 μ m). Note the distinctive outer stomatal rim; 3. *Laurelia novae-zealandiae*, TLM view showing stomatal complexes and a massively-thickened trichome attachment scar (OPH7027, scale-bar = 50 μ m); 4. *L. novae-zealandiae*, TLM detail of single stomatal complex (OPH7027, scale-bar = 20 μ m). Note the distinctive outer stomatal rim; 5. *D. aromatica*, TLM view showing stomatal complexes (AQ607275, scale-bar = 50 μ m); 6. *D. aromatica*, TLM detail of single stomatal complex (AQ607275, scale-bar = 20 μ m). Note the distinctive outer stomatal rim; 6. *D. aromatica*, TLM detail of single stomatal complex (AQ607275, scale-bar = 20 μ m). Note the distinctive outer stomatal rim; 7. *D. aromatica*, TLM view showing stomatal complexes (AQ607275, scale-bar = 50 μ m); 6. *D. aromatica*, TLM detail of single stomatal complex (AQ607275, scale-bar = 20 μ m). Note the distinctive outer stomatal rim; 7. *D. aromatica*, TLM view showing stomatal complexes (AQ607275, scale-bar = 50 μ m); 7. *D. aromatica*, TLM detail of single stomatal complex (AQ607275, scale-bar = 20 μ m). Note the distinctive outer stomatal rim; 7. *D. aromatica*, TLM view showing stomatal complexes (AQ607275, scale-bar = 50 μ m). Note the distinctive outer stomatal rim; 7.

F.M.Bailey) Smith (1958), are illustrated as extant examples; Figs 5.1-5.6 and see also Barrera and Meza (1992) for the Chilean *Laurelia* and *Laureliopsis*). This feature immediately distinguishes the family from the Monimiaceae, within which it has sometimes been included. Furthermore, there is often a ring of subsidiary cells, and often with massively-thickened trichome attachment scars. Prominent periclinal rims have been shown on *Doryphora* (Metcalfe (1987).

Key to Atherospermataceae

- 1. Cuticle glabrous. CUT-Z-CEF
- 1. Trichome attachment scars present. 2.
- 2. Ornamented by cuticular ridges. CUT-Z-CFA
- 2. Unornamented. 3.



Figure 6. 1-4. Fossil Atherospermataceae: CUT-Z-CEF. 1. TLM view showing two stomatal complexes (SL0100, scale-bar = 50 μ m); 2. TLM detail of single stomatal complex (SL0100, scale-bar = 20 μ m). Note the distinctive outer stomatal rim; 3. SEM view of inner cuticular surface showing a single stomatal complex (S-1112, scale-bar = 20 μ m); 4. SEM view of outer cuticular surface showing a single stomatal complex with prominent outer stomatal ledges (S-1112, scale-bar = 20 μ m).

- 3. Massively thickened trichome attachment sites present. CUT-Z-CFC
- 3. Massively thickened trichome attachment sites absent. 4.
- 4. Epidermal cells distinctly smaller than the stomata. CUT-Z-ECG
- 4. Epidermal cells of roughly similar size to the stomata 5.
- 5. Epidermal cell anticlinal walls markedly sinuous, slightly buttressed, CUT-Z- CGB
- 5. Epidermal cell anticlinal walls not sinuous or buttressed, CUT-Z-JIF

CUT-Z-CEF Figure 6

Reference Specimen and locality: SL0100, BL-08.

Referred specimens and occurrence: SL2409, BL-32; SB1392, BL-33; SL3136, GL-02.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, actinocytic, or staurocytic, size range unimodal, (some stomatal complexes have more subsidiary cell development, but they are no larger than normal stomatal complexes). Subsidiary cells (4–5) irregularly shaped, but often elongate radially to the stoma, periclinal walls thicker than over normal epidermal cells, smooth, unornamented. Guard cell pair outline distinctly circular, length c. 34 m (medium), at same level as subsidiary cells (exposed on surface), with prominent T-piece thickenings at polar ends. Outer stomatal ledge subcircular, thicker than normal epidermal cells, extending over centre to inner edge of stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells elongate (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, smoothly textured, unornamented.

Indumentum. Glabrous.

Distinguishing features. Distinguished from CUT-Z-CFC by being glabrous and from CUT-Z-EHI by the subsidiary cells being level with the other epidermal cells.



Figure 7. 1-8. Fossil Atherospermataceae: CUT-Z-CFA. 1. TLM view showing stomatal complexes and a massivelythickened trichome attachment scar (SB1373, scale-bar = 50 μ m); 2. TLM detail of single stomatal complex (SB1373, scale-bar = 20 μ m). Note the distinctive outer stomatal rim; 3. TLM view showing stomatal complexes (SL2960, scalebar = 50 μ m); 4. TLM detail of single stomatal complex (SL2960, scale-bar = 20 μ m). Note the distinctive outer stomatal rim; 5. TLM view showing stomatal complexes (SL0304, scale-bar = 50 μ m); 6. TLM detail of single stomatal complex (SL0304, scale-bar = 20 μ m). Note the distinctive outer stomatal rim; 7. SEM view of outer cuticular surface showing a single stomatal complex with prominent outer stomatal ledges surrounded by a discontinuous rim (S-1096, scale-bar = 20 μ m); 8. SEM view of inner cuticular surface showing a single stomatal complex. Note granular texture of subsidiary cell periclinal walls compared with epidermal cells (S-1096, scale-bar = 20 μ m).



Figure 8. 1-8. Fossil Atherospermataceae: CUT-Z-CFC, and CUT-Z-CGB. 1. CUT-Z-CFC, TLM view showing stomatal complexes and a massively-thickened trichome attachment scar (SL0066, scale-bar = 50 μ m); 2. CUT-Z-CFC, TLM detail of single stomatal complex (SL0066, scale-bar = 20 μ m); 3. CUT-Z-CFC, SEM view of outer cuticular surface showing stomatal complexes with prominent outer stomatal ledges (S-1108, scale-bar = 20 μ m); 4. CUT-Z-CFC, SEM view of inner cuticular surface showing a single stomatal complex (S-1108, scale-bar = 20 μ m); 5. CUT-Z-CGB, TLM view showing stomatal complexes and a massively-thickened trichome attachment scar (SL0088, scale-bar = 50 μ m); 6. CUT-Z-CGB, TLM detail of single stomatal complex (SL0088, scale-bar = 20 μ m). Note the distinctive outer stomatal rim; 7. CUT-Z-CGB, SEM view of inner cuticular surface showing a single stomatal complex (S-1111, scalebar = 20 μ m); 8. CUT-Z-CGB, SEM view of outer cuticular surface showing a single stomatal complex (S-1111, scalebar = 20 μ m).

CUT-Z-CFA Figure 7

Reference Specimen and locality: SB1373, BL-32.

Referred specimens and occurrence: SL0289, BL-01; SL3064, BL-26; SL3151, GL-01; SL2543, GL-02; SL2682, GL-04; SL2130, GL-08; SL2157, GL-09; SL2919, GL-22; SL4799, GL-23; SL2960, GL-25.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, cyclocytic, with all some, or none of the subsidiary cells having been modified by a tangential division, size range unimodal. Subsidiary cells (4-6) typically elongate, or wedge-like, often including distinct polar cells (at right angles to the stomatal axis) which may 'enclose' the lateral cells, periclinal walls of same thickness as normal epidermal cells, smooth, ornamented with one or two peristomatal ridges and there may be varying degrees of ridges which tend to flow around the stoma. Guard cell pair outline ovate, outlined by a well-defined anticlinal wall, length 27-45 m (large to medium), at same level as subsidiary cells (exposed on surface), with prominent T-piece thickenings at polar ends. Outer stomatal ledge sub circular, thicker than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over major veins more elongate), distinctly smaller than the stomata, anticlinal walls curved to wavy, unbuttressed, smoothly textured, ornamented throughout with short ridges or just in the area of the stomatal complexes.

Indumentum. Scars of deciduous trichomes sparse, scattered over venal and non-venal regions, inserted between (8–13, hard to count) epidermal cells modified by tangential divisions to form a sub-circular zone of foot cells with massive wall thickening, scar diameter much smaller than normal epidermal cell.

CUT-Z-CFC

Figure 8.1-8.4

Reference Specimen and locality: SL0066, Mata-18.

Referred specimens and occurrence: SL0370, Mata-03.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, cyclocytic, with all some, or none of the subsidiary cells having been modified by a tangential division (developmentally tangenticytic or incomplete stephanocytic bicyclic), development size range unimodal. Subsidiary cells (5-6) irregularlyshaped, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, outer margin obscured under TLM by surface ornamentation, at same level as subsidiary cells, length 23-25 m (medium). Outer stomatal ledge sub circular, circumscribed by a ring of very thin cuticle, the ledge itself thicker than normal epidermal cells, extending over centre of stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over veins not distinguished by shape), distinctly smaller than the stomata, anticlinal walls straight, unbuttressed, smoothly textured, unornamented.

Indumentum. Attachment scars of deciduous trichomes common, diameter similar or larger in size than a normal epidermal cell. Epidermal cells around trichome attachment scar (4–11) modified with massive thickening to form a rim and radiating walls.

Distinguishing features. Distinguished from CUT-Z-CEF by having massively thickened trichome attachment sites and from CUT-Z-EHI by the subsidiary cells being level with the other epidermal cells.

CUT-Z-CGB

Figure 8.5-8.8

Reference Specimen and locality: SL0088, BL-08.

Referred specimens and occurrence: SL0239, BL-04; SL3281, BL-05; SL3193, BL-32; SL1258, BL-33; SL1173, GL-01; SL2882, GL-20; SL3214, Sthd-158.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, cyclocytic, size range unimodal. Subsidiary cells (6–7) irregularly-shaped, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline ovate, outlined by a welldefined anticlinal wall, at same level as subsidiary cells, length 30–45 m (medium). Outer stomatal ledge sub circular, thicker than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over major veins more elongate), approximately the same size as



Figure 9. 1-8. Fossil Atherospermataceae: CUT-Z-JIF and CUT-Z-ECG. 1. CUT-Z-JIF, TLM view showing stomatal complexes and a massively-thickened trichome attachment scar (SB0851, scale-bar = 50 μ m); 2. CUT-Z-JIF, TLM detail of single stomatal complex (SB0851, scale-bar = 20 μ m); 3. CUT-Z-JIF, SEM view of outer cuticular surface showing stomatal complexes and (just left of centre) a trichome attachment scar (S-319, scale-bar = 0.1 mm); 4. CUT-Z-JIF, SEM view of inner cuticular surface showing a single stomatal complex (S-319, scale-bar = 10 μ m); 5. CUT-Z-ECG, TLM view showing stomatal complexes (SL1954, scale-bar = 50 μ m); 6. CUT-Z-ECG, TLM detail of single stomatal complex (S-1073, scale-bar = 20 μ m); 7. CUT-Z-ECG, SEM view of inner cuticular surface showing a single stomatal complex (S-1073, scale-bar = 20 μ m); 8. CUT-Z-ECG, SEM view of outer cuticular surface showing a single stomatal complex (S-1073, scale-bar = 10 μ m).

the stomata, anticlinal walls markedly sinuous, slightly buttressed, smoothly textured, unornamented.

Indumentum. Attachment scars of deciduous trichomes common, inserted between (5–7) epidermal cells modified into radially elongate foot cells, scar poral diameter much smaller than a normal epidermal cell.

Distinguishing features. Distinguished from CUT-Z-CFC by the sinuous and slightly buttressed walls.

CUT-Z-JIF

Figure 9.1-9.4

Reference Specimen and locality: SB0851, Mata-03.

Referred specimens and occurrence: SL1354, BL-05; SL3166, BL-33; SL2210, GL-12; SL1060, Mata-01.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, anomocytic or with occasional thin subsidiary cells produced by tangential divisions (developmentally incomplete stephanocytic bicyclic), size range unimodal. Contact cells (4-6) irregularly-shaped, periclinal walls thicker than over normal epidermal cells, smooth, ornamentation sometimes a single discontinuous ridge around the outer stomatal ledge (periclinal wall thickness near this rim is much thinner than over epidermal cells). Guard cell pair outline circular, or ovate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 37-45 m (large), with prominent polar rods. Outer stomatal ledge sub circular, much thicker than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over both major and fine venation more elongate), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, smoothly textured, unornamented.

Indumentum. Attachment scars of deciduous trichomes common, scattered over venal and nonvenal regions, inserted between (5–7) epidermal cells modified by massive wall thickening to form a rim with radiating walls, scar diameter much smaller than a normal epidermal cell.

Distinctive features. Comparable to CUT-Z-CGB but without the buttressed and sinuous epidermal cell walls.

CUT-Z-ECG

Figure 9.5-9.8

Reference Specimen and locality: SL1954, Sthd-051.

Referred specimens and occurrence: SL3042, BL-22; SL1563, Sthd-004; SL1730, Sthd-017; SL1716, Sthd-018; SL1706, Sthd-019; SL1776, Sthd-022; SL1779, Sthd-030; SL1937, Sthd-059; SL1894, Sthd-073; SL1906, Sthd-074; SL1833, Sthd-095.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, laterocyclic, all some, or none of the subsidiary cells may have been modified by a tangential division (developmentally incomplete stephanocytic bicyclic), size range unimodal (but with wide range of stomatal size). Subsidiary cells (7-8) irregularly-shaped, periclinal walls thicker than over normal epidermal cells, smooth, unornamented. Guard cell pair outline ovate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 38-43 m (large), with prominent Tpiece thickenings at polar ends. Outer stomatal ledge sub circular, thicker than normal epidermal cells, extending over most of the stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over major veins vaguely or inconsistently more elongate), approximately the same size as the stomata, anticlinal walls straight, unbuttressed, smoothly textured, unornamented.

Indumentum. Attachment scars of deciduous trichomes common, probably restricted to regions over veins (unclear), inserted between epidermal cells modified only slightly, forming a thickened rim, scar diameter similar in size to a normal epidermal cell.

Distinguishing features. Differing from the other taxa in the group in having very thick outer stomatal ledges, and stomatal complexes with clear evidence of tangential divisions, and epidermal cells distinctly smaller than the stomata.

Monimiaceae Jussieu 1809

Key to Monimiaceae

- 1. Unornamented. CUT-Z-DDG
- 1. Ornamented with ridges. 2.
- 2. Ornamented with widely-spaced short ridges, outer stomatal ledge narrow. CUT-Z-DDH



Figure 10. 1-8. Fossil and extant Monimiaceae. 1. CUT-Z-DDG, TLM view showing stomatal complexes (SB1388, scale-bar = 50 μ m); 2. CUT-Z-DDG, TLM detail of single stomatal complex (SB1388, scale-bar = 20 μ m); 3. CUT-Z-DDG, SEM view of inner cuticular surface showing two stomatal complexes (S-0327, scale-bar = 10 μ m); 4. CUT-Z-DDG, SEM view of outer cuticular surface showing several stomatal complexes (S-0327, scale-bar = 0.05 mm); 5. Extant *Hedycarya arborea*, TLM view showing stomatal complexes (OPH2624, scale-bar = 50 μ m); 6. Extant *H. arborea*, TLM detail of single stomatal complex (OPH2624, scale-bar = 20 μ m); 7. Extant *H. dorstenioides*, TLM view showing stomatal complexes (AQ063921, scale-bar = 50 μ m); 8. Extant *H. dorstenioides*, TLM detail of single stomatal complex (AQ063921, scale-bar = 20 μ m).



Figure 11. 1-8. Fossil and extant Monimiaceae: CUT-Z-DDH and CUT-Z-JIJ. 1. CUT-Z-DDH, TLM view showing stomatal complexes (SB1351, scale-bar = 50 μ m); 2. CUT-Z-DDH, TLM detail of single stomatal complex (SB1351, scale-bar = 20 μ m). Note the highly granular texture; 3. CUT-Z-DDH, SEM view of inner cuticular surface showing a single stomatal complex. Note highly granular texture (S-1227, scale-bar = 20 μ m); 4. CUT-Z-DDH, SEM view of outer cuticular surface showing distinctly narrow outer stomatal ledges (S-1227, scale-bar = 10 μ m); 5. Extant *Hedycarya angustifolia*, TLM view (AQ063593, scale-bar = 50 μ m); 6. Extant *H. angustifolia*, TLM view (AQ063593, scale-bar = 20 μ m); 7. CUT-Z-JIJ, TLM view showing two stomatal complexes (SB1329, scale-bar = 50 μ m); 8. CUT-Z-JIJ, TLM detail of single stomatal complex (SB1329, scale-bar = 20 μ m).

2. Ornamented with prominent, closely-spaced long ridges, outer stomatal ledge prominent. CUT-Z-JIJ

CUT-Z-DDG (*Hedycarya*) Figure 10.1-10.4

Reference Specimen and locality: SB1388, BL-33.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, brachyparacytic or amphibrachyparacytic, size range unimodal. Subsidiary cells typically elongate, tangential to the guard cells, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline elongate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 20– 25 m (medium). Outer stomatal ledge elliptical, same thickness as normal epidermal cells, extending over inner edge of stoma, with a narrowly elliptic pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over veins not distinguished by shape), distinctly larger than the stomata, anticlinal walls curved to wavy, unbuttressed, inner surfaces slightly granular, outer surfaces smooth and undulose, unornamented (though may have some faint ridging).

Indumentum. Glabrous.

Identification. The similarity to extant *Hedycarya arborea* Forster, J. R., and Forster, G. (1776) and *H. dorstenoides* A. Gray (1866) (Figs 10.5-10.8) is taken to indicate the genus.

CUT-Z-DDH (*Hedycarya* sp.) Figure 11.1-11.4

Reference Specimen and locality: SB1351, BL-32.

Referred specimens and occurrence: SL2105, GL-07; SL2145, GL-08.

CUT-L-DDH, SL1193, GL-02; SL2927, GL-22; SL3293, Mata-03.

Stomatal complexes. Stomatal stomatal complexes evenly spread, isolated, randomly oriented, brachyparacytic, size range unimodal. Subsidiary cells with periclinal walls thinner than that over normal epidermal cells, granular, unornamented normally, or with short ridges perpendicular to the stomatal axis. Guard cell pair outline elongate, not outlined by a clear anticlinal wall, at same level as subsidiary cells (exposed on surface), length 25–30 m (medium). Outer stomatal ledge narrow-elliptical, thinner than normal epidermal cells, extending over inner edge of stoma.

Epidermal Cells. Epidermal cell flanges somewhat diffuse, normal cells highly variable from isodiametric to elongate (cells over veins not distinguished by shape), distinctly larger than the stomata, anticlinal walls straight, unbuttressed, inner surface texture granular, outer surface mostly very smooth but with some ornamentation of short ridges perpendicular or parallel to some stomata.

Indumentum. Glabrous.

Distinguishing features. Distinguished by the rectangular outline of the stomatal complexes, the granular texture of the epidermal periclinal walls, the ridges of cuticle running at right angles to the stomatal pore on some stomatal complexes, and the obscure contact between guard cells and subsidiary cells. CUT-Z-JIJ differs by having distinct and broad outer stomatal ledges.

Identification. The similarity to extant *Hedycarya angustifolia* A. Cunningham (1838) (AQ063593) is taken to indicate the genus (Figs 11.5-11.6).

CUT-Z-JIJ

Figure 11.7-11.8

Reference Specimen and locality: SB1329, BL-32.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, brachyparacytic, size range unimodal. Subsidiary cells with periclinal walls of same thickness as normal epidermal cells, granular, ornamented with ridges projecting at right angles to the stomatal axis. Guard cell pair outline circular, or ovate, not outlined by a clear anticlinal wall, at same level as subsidiary cells (exposed on surface), length 26–30 m (medium). Outer stomatal ledge elliptical, thicker than normal epidermal cells, extending over whole stoma, with a narrowly elliptic pore.

Epidermal Cells. Epidermal cell flanges not clearly visible under TLM because of surface thickenings, normal cells elongate, cells over veins not distinguished by shape, anticlinal walls probably wavy, unbuttressed, inner surfaces coarsely granular, outer surfaces ornamented with bands of prominent, irregular ridges parallel to the stomata and radiating from trichomes.

Indumentum. Glabrous.

Distinguishing features. Distinguished by the brachyparacytic stomatal complexes with broad and distinct outer stomatal ledges in combination with highly granular cuticle. Specimen SL2647, which



Figure 12. 1-8. Fossil Proteaceae: CUT-P-EDA (*Placospermum* sp.) and CUT-P- EFB (*Lomatia* sp.). 1. CUT-P-EDA, TLM view showing aligned stomatal complexes (SL1867, scale-bar = 100 μ m); 2. CUT-P-EDA, TLM detail of a single stomatal complex (SL1867, scale-bar = 20 μ m). Note very narrow outer stomatal ledge; 3. CUT-P-EDA, SEM view of outer cuticular surface showing a single stomatal complex (S-1037, scale-bar = 20 μ m); 4. CUT-P-EDA, SEM view of inner cuticular surface showing a single stomatal complex (S-1037, scale-bar = 20 μ m); 5. CUT-P-EFB, TLM view showing stomatal complexes (SL1828, scale-bar = 50 μ m); 6. CUT-P- EFB, TLM detail of single stomatal complex (SL1828, scale-bar = 20 μ m); 7. CUT-P- EFB, SEM view of inner cuticular surface showing two stomatal complexes. Note finely granular texture (S-1106, scale-bar = 20 μ m); 8. CUT-P- EFB, SEM view of outer cuticular surface showing two stomatal complexes is to stomatal ledges, and striae over the subsidiary cells (S-1106, scale-bar = 20 μ m).

lacks the strong surficial ornamental of ridges found in the Reference Specimen, is included in this taxon. It comes from the same sample and agrees in the other major characters. CUT-Z-DDH differs in not having the broad outer stomatal ledges and narrow, slit-like stomatal apertures.

Proteaceae Jussieu 1789

Family identification: The majority of Proteaceae have brachyparacytic stomatal complexes. They often have trichome scars associated with one to several epidermal cells (Lange 1978; Carpenter 1994).

Key to Proteaceae

- 1. Stomatal complexes aligned. 2.
- 1. Stomatal complexes randomly oriented. 3.
- 2. Outer stomatal ledge narrowly elliptic, epidermal cell anticlinal walls markedly sinuous, but-tressed. CUT-P-EDA
- 2. Outer stomatal ledge subcircular, epidermal cell anticlinal walls straight, unbuttressed. CUT-P-FEE
- 3. Cuticle glabrous. CUT-P-EFB
- 3. Attachment scars of trichomes present. 4.
- 4. Trichome attachment scar with a thickened rim, subsidiary cells ornamented with many fine ridges. CUT-P-EHA
- Trichome attachment scar thickened into a raised platform, subsidiary cells ornamented with 2-3 ridges. CUT-P-EHJ

CUT-P-EDA (*Placospermum* sp.) Figure 12.1-12.4

Reference Specimen and locality: SL1867, Sthd-089.

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic, stomatal complexes evenly spread, isolated, aligned more or less parallel to long axis of leaf, brachyparacytic, size range unimodal. Subsidiary cells elongate parallel to stomatal axis, with periclinal walls thinner than that over normal epidermal cells, smooth, unornamented. Guard cell pair outline narrow and elongate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface). Outer stomatal ledge narrowly elliptic, ridgelike, much thinner than normal epidermal cells (often broken away), extending over inner edge of stoma, with a narrowly elliptic pore. Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over veins not distinguished by shape), approximately the same size as the stomata; anticlinal walls markedly sinuous; buttressed; smoothly textured, unornamented.

Indumentum. Glabrous.

Non-stomatal surface. Epidermal cells highly variable from isodiametric to elongate; sinuous; cells over veins not distinguished; trichomes absent.

Identification. There are no multicelled trichome attachment scars which would make a stronger case for identification as Proteaceae. However, the morphology is comparable with *Placospermum coriaceum* (White and Francis 1924) (the sole member of the genus, and which also lacks or has very rare trichome attachment scars) in its generally aligned stomatal complexes, a strikingly distinctive elongate stomatal pore (cf. Carpenter 1994, figs 5-7) and sinuous epidermal cell walls. There are obvious differences in that the epidermal cells of the fossil are also buttressed, and the stomatal complexes of the extant species are often linked by large epidermal cells. The fossil is suggested to be an extinct *Placospermum*.

CUT-P-EFB (*Lomatia* sp.) Figure 12.5-12.8

Reference Specimen and locality: SL1828, Sthd-095.

Referred specimens and occurrence: SL1556, Sthd-004; SL1766, Sthd-011; SL1843, Sthd-086.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, brachyparacytic, size range unimodal. Subsidiary cells isodiametric, periclinal walls of same thickness as normal epidermal cells, smooth, ornamented with 3–4 ridges parallel with the stomatal axis, and slightly longer than the stoma. Guard cell pair outline circular, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 18–23 m (medium), with prominent Tpiece thickenings at polar ends. Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over whole stoma, with a broad elliptical or sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls sinuous, slightly buttressed, inner surfaces slightly granular,



Figure 13. 1-8. Fossil Proteaceae: CUT-P-EHA and CUT-P-EHJ. 1. CUT-P-EHA, TLM view showing stomatal complexes and (upper left) a multi-cellular trichome attachment scar. Note how epidermal cells are partially obscuring parts of some stomatal complexes (SL1680, scale-bar = $50 \mu m$); 2. CUT-P-EHA, TLM detail of single stomatal complex (SL1680, scale-bar = $20 \mu m$); 3. CUT-P-EHA, SEM view of inner cuticular surface showing a single stomatal complex (S-1056, scale-bar = $20 \mu m$); 4. CUT-P-EHA, SEM view of outer cuticular surface showing a single stomatal complex with striae over the subsidiary cells (S-1056, scale-bar = $20 \mu m$); 5. CUT-P-EHJ, TLM view showing stomatal complexes and multi-cellular trichome attachment scars (SL1682, scale-bar = $50 \mu m$); 6. CUT-P-EHJ, TLM detail of single stomatal complex and two multi-cellular trichome attachment scars (SL1682, scale-bar = $20 \mu m$); 7. CUT-P-EHJ, SEM view of inner cuticular surface showing stomatal complexes and (top right) a trichome attachment scars (S-1057, scale-bar = $20 \mu m$); 8. CUT-P-EHJ, SEM view of outer cuticular surface showing stomatal complexes and (upper left) a trichome attachment scar (S-1057, scale-bar = $20 \mu m$); 8. CUT-P-EHJ, SEM view of outer cuticular surface showing stomatal complexes and (upper left) a trichome attachment scar (S-1057, scale-bar = $20 \mu m$); 8.

outer surfaces smooth and undulose, unornamented.

Indumentum. Glabrous.

Identification. There are no multicelled trichome attachment scars which would make a stronger case for identification as Proteaceae. In addition, the subsidiary cells are rather large, while in most extant Proteaceae they are relatively narrow. However, there is a general similarity with some extant species, such as *Lomatia fraxinifolia* F. Muell. ex Bentham (1870) (cf. Carpenter 1994, figs 65-66) in which trichome attachment scars may also be rare or absent.

CUT-P-EHA Figure 13.1-13.4

Reference Specimen and locality: SL1680, Sthd-033.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, brachyparacytic, size range unimodal. Subsidiary cells isodiametric, periclinal walls of same thickness as normal epidermal cells, ornamented with many fine ridges parallel with the stoma. Guard cell pair outline ovate, not outlined by a clear anticlinal wall, at same level as subsidiary cells (exposed on surface although sometimes partially obscured by adjacent epidermal cells), length 30–37 m (medium), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge sub circular, thinner than normal epidermal cells, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls straight, unbuttressed, smoothly textured, unornamented.

Indumentum. Attachment scars of deciduous trichomes common, scattered over venal and nonvenal regions, inserted over several (2–5) modified epidermal cells selectively thickened to form a thickened rim, with a prominent central pore. Scar diameter similar in size to a normal epidermal cell.

Identification. General morphology suggests the taxon has affinities with Tribe Macadamieae

of Weston and Barker (2006) (see illustrations in Carpenter 1994). The surface ridging restricted to the subsidiary cells is similar to *Carnarvonia* although the morphology of the trichome scar is different (in *Carnarvonia* they are associated with

mostly 1-2 epidermal cells and lack the central pore).

CUT-P-EHJ

Figure 13.5-13.8

Reference Specimen and locality: SL1682, Sthd-033.

Referred specimens and occurrence: SL0291, BL-01; SL2433, Sthd-051; SL2420, Sthd-078; SL2022, Sthd-087; SL1651, Sthd-110; SL3298.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, brachyparacytic, size range unimodal. Subsidiary cells isodiametric, periclinal walls of same thickness as normal epidermal cells, smooth, ornamented with 3–4 ridges parallel with, and on either side of the stoma. Guard cell pair outline ovate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 20–22 m (medium). Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with an elliptical pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls markedly sinuous, unbuttressed, inner surfaces smooth, outer surfaces smooth and irregularly ridged with bands of irregular ridges parallel to stomatal complexes and radiating from trichomes.

Indumentum. Attachment scars of deciduous trichomes common, inserted over several (3–4) epidermal cells modified to form a thick, raised circular platform, on top of which sits a smooth, thick hollow collar, scattered over venal and non-venal regions but slightly more common over veins. Pairs of scars may be joined by a narrow extension of the platform. Scar diameter similar in size to a normal epidermal cell.

Identification. General morphology suggests the taxon has affinities with Tribe Macadamieae

of Weston and Barker (2006) (Carpenter 1994). The surface ridging, more prominent on the subsidiary cells and the morphology of the trichome scars is similar to *Sleumerodendron*, *Hicksbeachia* and *Turrillia vitensis* (Turrill) A.C. Smith (1985) (or *Kermadecia vitensis* Turrill 1915).

CUT-P-FEE Figure 14

Reference Specimen and locality: SL3221, Sthd-166.



Figure 14. 1-4. Fossil Proteaceae: CUT-P-FEE. 1. TLM view showing stomatal complexes and a trichome attachment scar over a single basal cell at upper left (SL3221, scale-bar = 50 μ m); 2. TLM detail of single stomatal complex. Note the characteristic round outline and strong polar rod thickenings (SL3221, scale-bar = 20 μ m); 3. SEM view of outer cuticular surface showing a single stomatal complex with prominent outer stomatal ledges (S-1363, scale-bar = 10 μ m); 4. SEM view of inner cuticular surface showing two stomatal complexes (S-1363, scale-bar = 10 μ m).

Stomatal complexes. Stomatal complexes in areoles, isolated, generally aligned, brachyparacytic, size range unimodal. Subsidiary cells narrow, periclinal walls of same thickness as normal epidermal cells, unornamented. Guard cell pair outline difficult or impossible to see in TLM view, outer margin obscured under TLM by surface ornamentation, at same level as subsidiary cells, length 28–35 m (medium), with strong polar rod thickenings. Outer stomatal ledge prominent, circular to sub circular, thicker than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls straight, unbuttressed, smoothly textured, unornamented.

Indumentum. Attachment scars of deciduous trichomes common, but not noted over veins. positioned over 1–2 epidermal cells modified to form an irregular platform (by thickening of the periclinal walls) which contains the trichome scar. Scar diameter similar in size to a normal epidermal cell. Identification. Identification with the Proteaceae seems clear, although further identification is uncertain. The generally aligned stomata and trichome attachment scars over only 1-2 epidermal cells are the most important characters and suggest affinities lie with Tribe Embothrieae of Weston and Barker (2006).

Menispermaceae Jussieu 1789

Family identification: Based on the reference collection the Menispermanceae typically have distinct robust and very densely staining trichome attachment scars, although some species are glabrous. They also tend to have both guard and subsidiary cells with cuticle thinner than that over normal epidermal cells. Hill (1989) described a fossil genus of the family, *Menispermaphyllum*, although it is unclear how this genus differs from some extant genera, for instance the *Legnephora* with which it was compared. Hill compared the cuticle of his Eocene *M*, *tomentosum* with extant *L*. *moorei* (F.Muell.) Miers 1867, but the papillate cuticle of *L. moorei* in his fig. 2E looks nothing like any *L. moorei* specimen prepared for this database


Figure 15. 1-8. Fossil and extant Menispermaceae. 1. CUT-Z-FCA, TLM view showing stomatal complexes (with cuticle over guard cell and subsidiary cells thinner than over normal epidermal cells) and very densely staining trichome attachment scars (SL2877, scale-bar = 50 μ m); 2. CUT-Z-FCA, TLM view showing two stomatal complexes. Note the ovate outline and each has a distinct lateral subsidiary cell on the left hand side (SL2877, scale-bar = 20 μ m); 3. CUT-Z-FCA, SEM view of inner cuticular surface showing two stomatal complexes (S-1384, scale-bar = 10 μ m); 4. CUT-Z-FCA, SEM view of outer cuticular surface showing a single stomatal complex (S-1384, scale-bar = 10 μ m); 5. CUT-Z-FEC, TLM view showing stomatal complexes (the lower of a pair is arrowed) and densely staining trichome attachment scars. Note the cuticle over guard cell and subsidiary cells is thinner than over normal epidermal cells (SB1321, scale-bar = 50 μ m); 6. CUT-Z-FEC, TLM detail of single stomatal complexes (with cuticle over guard cell and subsidiary cells thinner than over normal epidermal cells) and densely staining trichome attachment scars (AQ568296, scale-bar = 50 μ m); 8. Extant *P. australis*, TLM view showing two stomatal complexes. Note the distinct lateral subsidiary cells on the left of the left hand complex, and lower side of the right hand complex (AQ568296, scale-bar = 20 μ m):



Figure 16. 1-8. Fossil and extant *Notothixos* sp. (Viscaceae). 1. CUT-Z-FGJ, TLM view showing stomatal complexes and branching trichomes (SL1202, scale-bar = 50 μ m); 2. CUT-Z-FGJ, TLM detail of single stomatal complex (SL1202, scale-bar = 20 μ m); 3. CUT-Z-FGJ, TLM detail of single stomatal complex (SL1202, scale-bar = 20 μ m); 4. CUT-Z-FGJ, SEM view of inner cuticular surface showing a single stomatal complex. Note W-shaped depressions at either end of guard cell cuticle which reflect where the guard cells turned sharply outwards (S-1379, scale-bar = 10 μ m); 5. CUT-Z-FGJ, SEM view of outer cuticular surface showing a depressed stomatal complex in the centre. The outer stomatal ledges do not project above the surrounding epidermal cells. Branched trichomes are to right and below. (S-1205, scale-bar = 20 μ m); 6. CUT-Z-FGJ, SEM view of outer cuticular surface showing many branched trichomes (S-1205, scale-bar = 100 μ m); 7. Extant *Notothixos subaureus*, SEM view of inner surface showing a single stomatal complex (AQ609212, scale-bar = 10 μ m); 8. Extant *N. subaureus*, SEM view of outer surface showing branched trichomes and a rare instance of unobscured stomatal complexes (AQ609212, scale-bar = 20 μ m). (which are not papillate), nor any other Menispermaceae in the database.

Key to Menispermaceae

- Epidermal cell anticlinal walls curved to wavy, cuticle over stomatal complexes much thinner than normal epidermal cells (often broken away). CUT-Z-FCA
- 1. Epidermal cell anticlinal walls sinuous, cuticle over stomatal complexes thinner than normal epidermal cells. CUT-Z-FEC

CUT-Z-FCA Figure 15.1-15.4

Reference Specimen and locality: SL2877, GL-20.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, cyclocytic, size range unimodal. Subsidiary cells (5–6) irregularly shaped, but often with apparently distinct elongate lateral or polar cells, periclinal walls thinner than normal epidermal cells, smooth, unornamented. Guard cell pair outline ovate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 20–23 m (medium), some wall development between guard cells, and sometimes development of T-piece thickenings at the poles. Outer stomatal ledge sub circular, much thinner than normal epidermal cells (often broken away), extending over whole stoma, with an elliptical pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, smoothly textured, unornamented.

Distinguishing features. The most distinct character is the massively-thickened trichome attachment scar.Indumentum. Bases of thick (densely staining), probably poral (with a very narrow pore) trichomes common, scattered over venal and nonvenal regions, the bases persist, but in all cases the trichome has broken off near base, perhaps along a predefined zone of weakness, scar diameter similar in size to a normal epidermal cell. Epidermal cells around trichome attachment scar modified into (6–9) radially elongate foot cells, with no distinct thickening of walls.

Identification. Broadly comparable with extant *Pleiogyne australis* Endlicher (1843) with respect to darkly staining trichome attachment scars, ovate shape of stoma, thin cuticle over guard and subsid-

iary cells, and the scattered presence of elongate lateral subsidiary cells (Figs 15.5-15.6).

CUT-Z-FEC

Figure 15.5-15.6

Reference Specimen and locality: SB1321, BL-32.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, anisocytic, size range unimodal. Subsidiary cells (3–4) isodiametric, with periclinal walls thinner than normal epidermal cells, granular, unornamented. Guard cell pair outline ovate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 22–23 m (medium). Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with an elliptical pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells elongate (cells over veins not distinguished by shape), distinctly larger than the stomata, anticlinal walls sinuous and sometimes rather sharply so, unbuttressed, texture granular, unornamented.

Indumentum. Bases of thick (densely staining), probably poral (with a very narrow pore) trichomes common, scattered over venal and non-venal regions (but slightly more common over veins), the bases persist, but in all cases the trichome has broken off near base, perhaps along a predefined zone of weakness, base diameter similar in size to a normal epidermal cell. Epidermal cells around trichome attachment scar (4–6) unmodified.

Identification. Compare with extant *Pleiogyne australis* (Figs 15.7-15.8) in terms of very thick trichome attachment scars, shape of stoma, thin guard and subsidiary cell cuticle. However, it does not have the occasional elongate subsidiary cells.

> Santalaceae Brown 1814 CUT-Z-FGJ (*Notothixos* sp.) Figure 16.1-16.6

Reference Specimen and locality: SL1202, GL-01.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, brachyparacytic, size range unimodal (but with wide range of stomatal size). Subsidiary cells length 32–40 m (large), or (medium), periclinal walls thinner than normal epidermal cells. Guard cell pair very narrow, poles sharply reflexed outwards, overarched by the subsidiary cells (not exposed on the surface).



Figure 17. 1-4. Fossil *Gymnostoma* sp. 1. TLM view of stomatal rows. Note brachyparacytic stomatal complexes oriented perpendicular to the long axis of the article (SL2427, scale-bar = 50 μ m); 2. SEM view of outer cuticular surface showing stomatal complexes (S-1058, scale-bar = 20 μ m); 3. SEM view of inner cuticular surface showing stomatal complexes (S-1058, scale-bar = 20 μ m); 4. SEM view of article showing node with whorl of reduced leaves (arrowed) (S-1023, scale-bar = 200 μ m).

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

Indumentum. Hirsute, densely covered with stellate trichomes, inserted over, or the outgrowth of, a single modified epidermal cell, similar in size to a normal epidermal cell.

Distinguishing features. Distinguished by the unique combination of brachyparacytic stomatal complexes (a pair of narrow guard cells flanked by a broad subsidiary cell on either side) and stellate/ multibranched trichomes.

Identification. The basic stomatal morphology is comparable with the Lauraceae. However, the stellate trichomes indicate it clearly belongs to *Notothixos* (Viscaceae), a mistletoe (see Barlow 1983 for more details on the trichomes). It may be compared closely with extant *N. subaureus* Oliver (1863) (Fig. 16.7-16.8).

Casuarinaceae Brown 1814 *Gymnostoma* Johnson 1980 *Gymnostoma* sp. Figure 17.1-17.4

Reference specimen and locality: SL2427, Sthd-055.

Referred specimens and occurrence: SL3232, GL-30; SL2705, Sthd-046; SL2702, Sthd-047, SL2703, Sthd-094; SL2706, Sthd-097; SL2704, Sthd-099.

Description. Branchlets with four-sided articles, approximately square in cross-section, with four highly reduced leaves in a whorl at each junction. Leaves with acute apices, sharp sinuses, margin entire, length c. 400 m, width c. 200 m. Stomatal complexes in two compact zones within a shallow furrow on each side of the article, 4-7 files per zone, complexes brachyparacytic, oriented perpendicular to the long axis of the branchlet, length c 20 m. Mostly with 1-2 epidermal cells between each stomatal complex in a file. Glabrous. Epidermal cells isodiametric, walls distinctly thickened



Figure 18. 1-6. Fossil and extant *Strasburgeria* (Strasburgeriaceae). 1. CUT-Z-FFH, TLM view showing two stomatal complexes (SL3224, scale-bar = 50 μ m); 2. CUT-Z-FFH, TLM detail of single stomatal complex (SL3224, scale-bar = 20 μ m); 3. CUT-Z-FFH, SEM view of inner cuticular surface showing two stomatal complexes (S-1362, scale-bar = 20 μ m); 4. CUT-Z-FFH, SEM view of outer cuticular surface showing a single stomatal complex with prominent outer stomatal ledges (S-1362, scale-bar = 10 μ m); 5. Extant *Strasburgeria robusta*, TLM view showing a group of networked stomatal complexes (AQ391571, scale-bar = 50 μ m). The details are partially hindered by cutinisation around the internal walls of the epidermal cells; 6. Extant *S. robusta*, TLM view showing a single stomate (AQ391571, scale-bar = 20 μ m).

compared with the thinner cells of the stomatal zones.

Identification. Clearly belongs to the Casuarinaceae on the basis of gross morphology of article branchlets with highly reduced leaves in whorls, and transversely oreiented stomata essentially restricted to the articles (terminology follows Scriven and Hill 1995). The identification as *Gym*- nostoma is based on the four-sided articles and relatively surficial stomatal complexes (Scriven and Hill 1995). The stomatal length of c. 20 m also supports *Gymnostoma*, as Scriven and Hill noted that stomatal length in *Casuarina* and *Allocasuarina* was usually more than 35 m. Based on Scriven and Hill's summary, the shape and thickness of the epidermal cells is unusual for *Gymnostoma*.

Strasburgeriaceae Solereder 1908 CUT-Z-FFH (*Strasburgeria* sp.) Figure 18.1-18.4

Reference Specimen and locality: SL3224, Sthd-166.

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic; stomatal complexes evenly spread, mostly isolated although sometimes networked, possibly slightly aligned with one another, anomocytic (although there are 4–6 contact cells, and sometimes there have been tangential divisions around a few stomata which produce what could be called subsidiary cells), size range unimodal. Guard cell pair outline ovate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 50–53 m (large), with prominent T-piece thickenings at polar ends. Outer stomatal ledge sub circular, much thicker than normal epidermal cells, extending over whole stoma, with an elliptical pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls straight, or curved to wavy, unbuttressed, smoothly textured, unornamented.

Indumentum. Attachment scars of deciduous trichomes sparse, scattered over venal and nonvenal regions, inserted between (6–7) epidermal cells modified only slightly, with a thickened rim. Fine ridges of cuticle radiate out from the trichome attachment scars, scar diameter much smaller than a normal epidermal cell.

Distinguishing features. Distinguished by the strong thickening over the guard cells and the anomocytic stomatal complexes.

Identification: The large size and general form of the stoma, the epidermal cells, and the anomocytic stomatal construction find a good match with extant New Caledonian *Strasburgeria robusta* (Vieill. ex Panch. and Sebert) Guillaumin (1942) (Figs 18.5-18.6) The differences include scattered trichome attachment scars on the fossil, which the extant species appears to lack, and while stomata are common in this species and frequently networked, their density is much lower in the fossil although networking is still apparent. The modern specimen also shows much cuticularisation of the stomatal chamber which is absent on the fossil. The differences would be consistent with a different species of *Strasburgeria*. The genus has been recorded as pollen from the Gore Lignite Measures (Jarzen and Pocknall 1993).

Cunoniaceae (Brown 1814) Elaeocarpaceae (de Candolle 1816)

Family identification: The guard cells of almost all Elaeocarpaceae - Cunoniaceae appear essentially 'naked' under TLM. The outer stomatal ledges are so thin and smooth that they leave an unobstructed view of classic 'paired kidney' stomata. The typical narrow and darkly-staining ring around the stomatal pore may be an inner ledge, or a thickened rim of the outer stomatal ledges. There is often a distinct notch at either pole of the guard cell pair. These characters are a good first step in suspecting Elaeocarpaceae – Cunoniaceae. Pole (1996) wrote "Presently, no cuticular characters are recognised which can separate these two, unrelated families" (DNA work has since shown them, to be sister taxa). Carpenter et al. (2004) identified an Australian fossil ("Weinmannia sp. 1") based on "areolar cyclocytic stomata with 5 or 6 subsidiary cells, hydathodes, numerous small, trichome base pores along veins that are surrounded by usually 7 or 8 radially modified cells, and occasional large diameter cavities presumably left by detached trichomes". They noted "This combination of characters is only known in Weinmannia (Barnes et al. 2001)". Barnes et al's study was restricted to Cunoniaceae, so it was not possible to make this distinction, and unfortunately, this combination is also found in the Elaeocarpaceae. The author's reference collection contains 140 species of Elaeocarpus, of which 23 have hydathodes or lenticels (following Roth 1989) among which include E. altisectus Schlechter (1916), E grandis von Mueller (1861), E. kaniensis Schlechter (1916), and E. sericopetalus von Mueller (1868). The "large diameter cavities" are a feature of many species in both families. In some instances they may have had a trichome in their centre, in others it appears to have been a giant stomata, but in others the cavity appears primary. The number of subsidiary cells is more variable. The other characters are very widespread and variable throughout the two families (Even the "Weinmannia sp. 1" described by Carpenter et al. (2004) shows several stomata with 4, whereas the extant W. paitensis Schlechter (1916) illustrates has at least one stomata with 3 subsidiary cells). It is still my opinion that differentiation of the two families on cuticular characters alone is not possible (although may be for a few genera). The following 20 fossil taxa display a broad syndrome of characters that suggest Elaeocarpaceae-



Figure 19. 1-8. Fossil Cunoniaceae-Elaeocarpaceae: CUT-Z-AJC, and CUT-Z-CEB. 1. CUT-Z-AJC, TLM view showing stomatal complexes (SB1343, scale-bar = 50 μ m); 2. CUT-Z-AJC, TLM view showing two stomatal complexes (SB1343, scale-bar = 20 μ m); 3. CUT-Z-AJC, TLM view showing TLM view showing stomatal complexes and a cork wart (SB1343, scale-bar = 50 μ m); 4. CUT-Z-AJC, TLM view showing stomatal complexes and a cork wart (SB1343, scale-bar = 50 μ m); 5. CUT-Z-AJC, SEM view of inner cuticular surface showing a single stomatal complex (S-1126, scale-bar = 20 μ m); 6. CUT-Z-AJC, SEM view of outer cuticular surface showing stomatal complexes (S-1126, scale-bar = 20 μ m); 7. CUT-Z-CEB, TLM view showing stomatal complexes and a cork wart (SL0235, scale-bar = 50 μ m); 8. CUT-Z-CEB, TLM detail of single stomatal complex (SL0235, scale-bar = 20 μ m).

Cunoniaceae. In my opinion, the stomatal form described above, along with giant stomata (hydathodes), simple trichome attachment scars, and corkwarts, are highly likely to indicate Elaeocarpaceae –Cunoniaceae. A variety of subsidiary cell arrangements are possible.

Key to Cunoniaceae-Elaeocarpaceae

- 1. Cuticle glabrous. 2.
- 1. Attachment scars of trichomes present. 5.
- 2. Epidermal cell anticlinal walls sinuous. CUT-Z-ADF
- 2. Epidermal cell anticlinal walls straight, curved or wavy. 3.
- 3. Lenticels or glands absent. 4.
- 3. Lenticels or glands present. 9.
- Stomatal complexes anomocytic, size range bimodal, 'giant stomatal complexes' present. CUT-Z-FBG
- 4. Stomatal complexes cyclocytic (developmentally tangenticytic) 'giant stomatal complexes' absent. CUT-Z-EFA
- 5. Epidermal cell anticlinal walls sinuous. 6.
- 5. Epidermal cell anticlinal walls straight, curved or wavy. 12.
- 6. Bases of the trichomes are persistent, and balloon-out from the insertion hole. CUT-Z-ACC
- 6. Trichomes purely deciduous. 7.
- Epidermal cell flanges clearly visible around stomatal complexes but become unclear further away. CUT-Z-CBI
- 7. Epidermal cell flanges clearly visible everywhere. 8.
- Subsidiary cell periclinal walls thicker than normal epidermal cells, outer stomatal ledge thin. CUT-Z-FBE
- 8. Subsidiary cell periclinal walls same thickness as normal epidermal cells, outer stomatal ledge distinct. CUT-Z-CFJ
- 9. Stomatal complexes evenly spread. CUT-Z-CEB
- 9. Stomatal complexes clustered in areoles. 10.
- 10. Subsidiary cell periclinal walls same thickness as normal epidermal cells. CUT-Z-AJC
- 10. Subsidiary cell periclinal walls thicker than normal epidermal cells. 11.
- 11. Subsidiary cells elongate and tangential to stoma. CUT-Z-CAI

- 11. Subsidiary cells narrow to isodiametric. CUT-Z-FAJ
- 12. Epidermal cell anticlinal walls sinuous. CUT-Z-AJJ
- 12 Epidermal cell anticlinal walls straight, curved or wavy. 13.
- 13. Epidermal cell periclinal walls thicker than normal epidermal cells. CUT-Z-FCJ
- 13. Epidermal cell periclinal walls same thickness as normal epidermal cells. 14.
- 14. Trichome attachment sites massively thickened CUT-Z-FAA
- 14. Trichome attachment sites not massively thickened. 15.
- 15. Trichomes inserted over several cells. CUT-Z-FBC
- 15. Trichomes inserted between several cells. 16.
- 16. Foot cells around trichome attachment site with a distinctly circular outer margin, and thickened periclinal walls. CUT-Z-EDG
- 16. Foot cells around trichome attachment site without a distinctly circular outer margin, and without thickened periclinal walls. 17.
- 17. Cuticle ornamented with flowing fine ridges. CUT-Z-EDJ
- 17. Cuticle unornamented. 18.
- 18. Trichome attachment sites distinctly frilled. CUT-Z-CCE
- 18. Trichome attachment sites not frilled. 19.
- 19. Stoma typically distinctly subcircular. CUT-Z-EGA
- 19. Stoma typically distinctly broader than long. CUT-Z-CDJ

CUT-Z-AJC

Figure 19.1-19.6

Reference Specimen and locality: SB1343, BL-32.

Stomatal complexes. Stomatal complexes clustered in areoles, typically isolated though networking may occur, randomly oriented, cyclocytic, size range bimodal, with distinct 'giant stomatal complexes' present. Subsidiary cells (6–8) irregularlyshaped, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, outlined by a welldefined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 19–20 m (medium), with prominent T-piece thickenings at



Figure 20. 1-8. Fossil Cunoniaceae-Elaeocarpaceae: CUT-Z-CCE, and CUT-Z-FBG. 1. CUT-Z-CCE, TLM view showing stomatal complexes and a trichome attachment scar (SL0099, scale-bar = 50 μ m); 2. CUT-Z-CCE, TLM detail of two stomatal complexes (SL0099, scale-bar = 20 μ m); 3. CUT-Z-CCE, SEM view of inner cuticular surface showing stomatal complexes. Note granular texture (S-1110, scale-bar = 20 μ m); 4. CUT-Z-CCE, SEM view of outer cuticular surface showing stomatal complexes with simple outer stomatal ledges in an otherwise almost smooth surface (S-1110, scale-bar = 20 μ m); 5. CUT-Z-FBG, TLM view showing stomatal complexes (SB0853, scale-bar = 50 μ m); 6. CUT-Z-FBG, TLM view showing two stomatal complexes (SL0853, scale-bar = 20 μ m); 7. CUT-Z-FBG, TLM view showing stomatal complexes (SL3058, scale-bar = 50 μ m); 8. CUT-Z-FBG, TLM view showing two stomatal complexes (SL3058, scale-bar = 20 μ m); 7. CUT-Z-FBG, TLM view showing stomatal complexes (SL3058, scale-bar = 20 μ m); 7. CUT-Z-FBG, TLM view showing stomatal complexes (SL3058, scale-bar = 20 μ m); 7. CUT-Z-FBG, TLM view showing stomatal complexes (SL3058, scale-bar = 20 μ m); 8. CUT-Z-FBG, TLM view showing two stomatal complexes (SL3058, scale-bar = 20 μ m); 7. CUT-Z-FBG, TLM view showing stomatal complexes (SL3058, scale-bar = 50 μ m); 8. CUT-Z-FBG, TLM view showing two stomatal complexes (SL3058, scale-bar = 20 μ m).

polar ends. Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over both major and fine venation more elongate), approximately the same size as the stomata, anticlinal walls straight, unbuttressed, inner and outer surfaces smooth, unornamented.

Indumentum. Glabrous.

Other structures. Lenticels present, with a distinct outer zone where the periclinal walls are thicker than those of normal epidermal cells, and a central zone where they are thinner.

CUT-Z-CEB Figure 19.7-19.8

Reference Specimen and locality: SL0235, BL-04.

Referred specimens and occurrence: SL3191, BL-32.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, cyclocytic, developmentally stephanocytic bicyclic size range unimodal. Subsidiary cells (6–8) irregularlyshaped, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, outlined by a welldefined anticlinal wall, clearly separated by polar walls, at same level as subsidiary cells (exposed on surface). Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over centre of stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over veins not distinguished by shape), distinctly smaller than the stomata, anticlinal walls straight, unbuttressed, smoothly textured, unornamented.

Indumentum. Glabrous.

Other structures. Lenticels present, as large circular areas of very thinly cutinised cells (often broken away), surrounded by radiating files of normalthickness epidermal cells.

CUT-Z-CCE Figure 20.1-20.6

Reference Specimen and locality: SL0099, BL-08.

Referred specimens and occurrence: CUT-Z-CCE, SL0353, BL-05; SL3044, BL-22; SL1220, BL-30; SL3190, BL-32; SL2683, GL-04; SL2982, GL-26;

SL0384, Mata-01; SL2575, Mata-06; SL1754, Sthd-012; SL3216, Sthd-158.

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic, stomatal complexes in areoles, isolated, randomly oriented, cyclocytic, developmentally incomplete stephanocytic bicyclic, all some, or none of the subsidiary cells have been modified by a tangential division, size range bimodal, with distinct 'giant stomatal complexes' present. Subsidiary cells (4-8) irregularly-shaped, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, or ovate, outlined by a welldefined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 15-20 m (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 sub circular, thinner than normal epidermal cells, extending over whole stoma and just thickened along inner edge, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over both major and fine venation more elongate), approximately the same size as the stomata, anticlinal walls straight, or curved to wavy, unbuttressed, inner surfaces slightly granular, outer surfaces smooth, unornamented.

Indumentum. Attachment scars of deciduous trichomes sparse, restricted to regions over veins, inserted between (7–9) epidermal cells modified to form a ring of more or less isodiametric foot-cells (sometimes with a distinctly circular outer margin) and with a 'frilly' thickened rim and radial walls, scar diameter similar in size to a normal epidermal cell.

Distinguishing features. Clear and naked guard cells and distinctly frilled trichome attachment scars.

CUT-Z-FBG

Figure 20.7-20.8

Reference Specimen and locality: SL3058, BL-25.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, anomocytic, size range bimodal, with distinct 'giant stomatal complexes' present (restricted to venal regions). Subsidiary cells (5–7). Guard cell pair outline circular, or ovate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 19–27 m (medium), little polar devel-



Figure 21. 1-8. Fossil Cunoniaceae-Elaeocarpaceae: CUT-Z-ADF, CUT-Z-EDG, and CUT-Z-FCJ. 1. CUT-Z-ADF, TLM view showing stomatal complexes (SB0844, scale-bar = 50 μ m); 2. CUT-Z-ADF, TLM detail of single stomatal complex (SB0844, scale-bar = 20 μ m); 3. CUT-Z-ADF, SEM view of outer cuticular surface showing stomatal complexes with simple, raised outer stomatal ledges in an otherwise smooth surface (S-1383, scale-bar = 10 μ m); 4. CUT-Z-ADF, SEM view of inner cuticular surface showing a single stomatal complex. Note granular texture (S-1383, scale-bar = 10 μ m); 5. CUT-Z-EDG, TLM view showing stomatal complexes and a trichome attachment scar (SL2026, scale-bar = 50 μ m); 6. CUT-Z-EDG, TLM view showing stomatal complexes (SL2026, scale-bar = 20 μ m); 7. CUT-Z-FCJ, TLM view showing stomatal complexes and a giant complex at lower left (SL3085, scale-bar = 50 μ m); 8. CUT-Z-FCJ, TLM detail of single stomatal complex (SL3085, scale-bar = 20 μ m).

opment between guard cells (guard cells appear as continuous ring). Outer stomatal ledge sub circular, thinner than normal epidermal cells, with an elliptical pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over both major and fine venation more elongate), approximately the same size as the stomata, anticlinal walls straight, or curved to wavy, unbuttressed, smoothly textured, unornamented.

Indumentum. Glabrous.

CUT-Z-ADF Figure 21.1-21.4

Reference Specimen and locality: SB0844, Mata-06.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented. Subsidiary cells (5–7) typically elongate, or wedge-like, often with distinct polar cells (at right angles to the stomatal axis) which may 'enclose' the lateral cells, developmentally incomplete stephanocytic bicyclic periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 20–22 m (medium), at same level as subsidiary cells (exposed on surface). Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (unclear if cells over veins are distinguished), approximately the same size as the stomata, anticlinal walls markedly sinuous, unbuttressed, inner surface moderately granular, outer surfaces smooth, unornamented.

Indumentum. Glabrous.

Distinguishing features. OSL thin and approximates the guard cell outlines very closely, so appears almost invisible under TLM. Sinuous epidermal cells.

CUT-Z-EDG Figure 21.5-21.6

Reference Specimen and locality: SL2026, Sthd-087.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over

major veins more elongate), approximately the same size as the stomata, anticlinal walls straight. smoothly unbuttressed, textured, unornamented.Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, cyclocytic, all some, or none of the subsidiary cells may have been modified by a tangential division (developmentally stephanocytic bicyclic), size range unimodal (but with wide range of stomatal size). Subsidiary cells (6-7) irregularly-shaped, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, outlined by a well-defined anticlinal wall. length 14-20 m (small - medium), underthrust by subsidiary cells (subsidiary cell anticlinal walls bisect outline of the guard cells), with prominent Tpiece thickenings at polar ends. Outer stomatal ledge sub circular, same thickness or slightly thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Indumentum. Attachment scars of deciduous trichomes common, scattered over venal and nonvenal regions, inserted between epidermal cells modified into a distinct ring of foot cells with a distinctly circular outer margin, with thickened periclinal walls, scar diameter much larger than a normal epidermal cell.

CUT-Z-FCJ

Figure 21.7-21.8

Reference Specimen and locality: SL3085, BL-28.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, cyclocytic, size range bimodal, with distinct 'giant stomatal complexes' present (restricted to venal regions). Subsidiary cells (6-8) of varying size, curved and generally tangential to the guard cells, developmentally incomplete stephanocytic bicyclic, periclinal walls thicker than over normal epidermal cells, smooth, unornamented. Guard cell pair outline ovate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 23-38 m (medium), some wall development between guard cells, and sometimes development of T-piece thickenings at the poles. Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over centre of stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over both major and fine venation more elongate), approximately the same size as the stomata, anti-



Figure 22. 1-8. Fossil Cunoniaceae-Elaeocarpaceae: CUT-Z-ACC, CUT-Z-FAA, and CUT-Z-EGA. 1. CUT-Z-ACC, TLM view showing stomatal complexes and trichome attachment scars (upper right and lower centre) (SB1302, scale-bar = 50 μ m); 2. CUT-Z-ACC, TLM detail of single stomatal complex (SB1302, scale-bar = 20 μ m); 3. CUT-Z-ACC, SEM view of inner cuticular surface showing a single stomatal complex (S-1406, scale-bar = 10 μ m); 4. CUT-Z-ACC, SEM view of outer cuticular surface showing three stomatal complexes with simple outer stomatal ledges, but surrounded by a thin, discontinuous rim (S-1406, scale-bar = 10 μ m); 5. CUT-Z-FAA, TLM view showing stomatal complexes and a trichome attachment scar with massive thickening (SL2574, scale-bar = 50 μ m); 6. CUT-Z-FAA, TLM view showing stomatal complexes (SL1887, scale-bar = 50 μ m); 8. CUT-Z-EGA, TLM detail of single stomatal complex (SL1887, scale-bar = 20 μ m).

clinal walls straight, unbuttressed, smoothly textured, unornamented.

Indumentum. Attachment scars of deciduous trichomes sparse, restricted to regions over major veins, inserted between (6–8) epidermal cells modified into radially elongate foot cells, scar diameter much smaller than a normal epidermal cell.

CUT-Z-ACC Figure 22.1-22.4

Reference Specimen and locality: SL2660, GL-04.

Referred specimens and occurrence: SL1201, GL-01; SB1302, Mata-03.

Stomatal complexes. Stomatal stomatal complexes in areoles, isolated, randomly oriented; anomocytic; size range bimodal, with distinct 'giant stomatal complexes' present. Subsidiary cells (4–6, difficult to tell under TLM) with periclinal walls of same thickness as normal epidermal cells; smooth; unornamented. Guard cell pair outline circular; outlined by a well-defined anticlinal wall; at same level as subsidiary cells (exposed on surface), length 20–31 m (medium); with prominent T-piece thickenings at polar ends. Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM; normal cells highly variable from isodiametric to elongate (cells over veins not distinguished by shape); approximately the same size as the stomata; anticlinal walls markedly sinuous; unbuttressed; inner surfaces very finely granular, outer surfaces smooth, although ornamented with a few bands of irregular ridges parallel to stomatal complexes and radiating from trichomes.

Indumentum. Attachment scars of deciduous trichomes common; scattered over venal and nonvenal regions; inserted between (5–9) epidermal cells modified into radially elongate foot cells, with no distinct thickening of walls; scar diameter much smaller than a normal epidermal cell, but the trichome expanded abruptly above the insertion point. Trichome-bases over the midvein are distinct in having a massively-thickened rim.

Distinguishing features. This is reasonably thin cuticle, where the guard cells are raised above the general surface, and have distinct polar T-pieces. The very bases of the trichomes are persistent, and balloon-out from the insertion hole. In TLM this means the insertion hole appears surrounded by a ring, or perhaps having a circular cap to it. The reality only becomes clear when a trichome base is found which has been flattened obliquely.

CUT-Z-FAA

Figure 22.5-22.6

Reference Specimen and locality: SL2574, Mata-06.

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic, stomatal complexes in areoles, sometimes networked, randomly oriented, laterocytic, developmentally incomplete stephanocytic bicyclic, size range unimodal (but with wide range of stomatal size). Subsidiary cells (4-7) with periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline ovate, outlined by a welldefined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 20-25 m (medium), clearly separated by polar walls. Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over both major and fine venation more elongate), approximately the same size as the stomata, anticlinal walls straight, unbuttressed, smoothly textured, unornamented.

Indumentum. Attachment scars of deciduous trichomes common, scattered over venal and nonvenal regions, inserted between (6–10) epidermal cells modified by many tangential divisions and massively thickened to form a frilly rim, scar diameter smaller than a normal epidermal cell.

Distinguishing features. Distinguished from CUT-Z-EDC in having straight epidermal walls (even distal to stomatal complexes), subsidiary cells that do not staining darker than normal epidermal cells, and common trichome scars which have massively thickened poral rims.

CUT-Z-EGA Figure 22.7-22.8

Reference Specimen and locality: SL1887, Sthd-073.

Referred specimens and occurrence: SL2245, BL-14; SL2109, GL-07; SL2165, GL-09; SL1963, Sthd-054; SL1538, Sthd-067.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, anomocytic (and sometimes incompletely cyclocytic), developmentally tangenticytic, size range unimodal, (but with



Figure 23. 1-8. Fossil Cunoniaceae-Elaeocarpaceae: CUT-Z-CDJ, and CUT-Z-EDJ. 1. CUT-Z-CDJ, TLM view showing stomatal complexes (SL0279, scale-bar = 50 μ m); 2. CUT-Z-CDJ, TLM view showing stomatal complexes (SL0279, scale-bar = 20 μ m); 3. CUT-Z-CDJ, SEM view of inner cuticular surface showing a single stomatal complex (S-1221, scale-bar = 10 μ m); 4. CUT-Z-CDJ, SEM view of outer cuticular surface showing a single stomatal complex (S-1221, scale-bar = 10 μ m); 5. CUT-Z-EDJ, TLM view showing stomatal complexes (SL1902, scale-bar = 50 μ m); 6. CUT-Z-EDJ, TLM detail of single stomatal complex (SL1902, scale-bar = 20 μ m); 7. CUT-Z-EDJ, SEM view of inner cuticular surface showing two stomatal complexes (S-1370, scale-bar = 20 μ m); 8. CUT-Z-EDJ, SEM view of outer cuticular surface showing probable positions of stomatal pores, obscured by cuticular ridges (two are arrowed) (S-1370, scale-bar = 10 μ m).

wide range of stomatal size). Subsidiary cells (4–5) irregularly-shaped, (hard to count as radial flanges of subsidiary cells are not well developed), periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, not outlined by a clear anticlinal wall, at same level as subsidiary cells (exposed on surface), length 16–22 m (medium), at same level as subsidiary cells (guard cells appear as continuous ring). Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, smoothly textured, unornamented.

Indumentum. Attachment scars of deciduous trichomes common, restricted to regions over veins, inserted between epidermal cells modified by tangential divisions to form a sub-circular zone of foot cells, scar diameter similar in size to a normal epidermal cell.

CUT-Z-CDJ

Figure 23.1-23.4

Reference Specimen and locality: SL0279, BL-01.

Referred specimens and occurrence: SL0354, BL-05.

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic, stomatal complexes in areoles, isolated, randomly oriented, cyclocytic, developmentally incomplete stephanocytic bicyclic, size range bimodal, with distinct 'giant stomatal complexes' present. Subsidiary cells (5-8) irregularlyshaped, periclinal walls of same thickness as normal epidermal cells, smooth, with a narrow, disconperistomatal tinuous ridge, otherwise unornamented. Guard cell pair outline varies from broadly elliptic (wider than long), to circular, to narrowly elliptic, outlined by a well-defined anticlinal wall, length 12-18 m (small), at same level as subsidiary cells (exposed on surface), clearly separated by polar walls. Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over centre of stoma, with a broad, subcircular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over

major veins more elongate), distinctly smaller than the stomata, anticlinal walls straight, unbuttressed, inner and outer surfaces smooth, unornamented except for a few subdued ridges.

Indumentum. Scars of deciduous trichomes sparse, scattered over venal and non-venal regions but slightly more common over veins, simple, inserted between (5–8) epidermal cells modified to form a broadly thickened rim, scar diameter similar in size to a normal epidermal cell.

Distinguishing features. The presence of broadly elliptical (wider than long) stomata and the relatively broad thickening of the trichome scar are both distinctive characters.

CUT-Z-EDJ

Figure 23.5-23.8

Reference Specimen and locality: SL1902, Sthd-073.

Referred specimens and occurrence: SL1647, Sthd-109.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, cyclocytic, size range unimodal. Subsidiary cells (4–5) irregularly-shaped, with periclinal walls thicker than over normal epidermal cells, smooth, unornamented. Guard cell pair outline ovate, at same level as subsidiary cells, outer margin obscured under TLM by surface ornamentation, length 35–40 m (medium large). Outer stomatal ledge elliptical, thinner than normal epidermal cells, extending over whole stoma, with a narrowly elliptic pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, irregularly extended, normal cells isodiametric (unclear if cells over veins are distinguished), approximately the same size as the stomata, anticlinal walls straight, unbuttressed, inner surfaces smooth, outer surfaces smooth and ornamented with a flowing pattern of many fine ridges.

Indumentum. Deciduous trichome scars sparse, not clear.

CUT-Z-FBC

Figure 24.1-24.4

Reference Specimen and locality: SL3022, GL-29.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, cyclocytic, There are usually two rings of subsidiary cells, an inner with periclinal walls thinner than epidermal cells, and an outer with periclinal walls thicker than epidermal cells, developmentally stephanocytic bicy-



Figure 24. 1-8. Fossil Cunoniaceae-Elaeocarpaceae: CUT-Z-FBC, and CUT-Z-FBE. 1. CUT-Z-FBC, TLM view showing stomatal complexes (SL3022, scale-bar = 50 μ m); 2. CUT-Z-FBC, TLM detail of single stomatal complex (SL3022, scale-bar = 20 μ m); 3. CUT-Z-FBC, TLM view of a trichome attachment scar (SL3022, scale-bar = 20 μ m); 4. CUT-Z-FBC, SEM view of outer cuticular surface showing a single stomatal complex (S-1388, scale-bar = 10 μ m); 5. CUT-Z-FBE, TLM view showing stomatal complexes (SL3007, scale-bar = 50 μ m); 6. CUT-Z-FBE, TLM view showing two stomatal complexes (SL3007, scale-bar = 20 μ m); 7. CUT-Z-FBE, SEM view of inner cuticular surface showing a single stomatal complexes (S-1389, scale-bar = 10 μ m); 8. CUT-Z-FBE, SEM view of outer cuticular surface showing two stomatal complexes (S-1389, scale-bar = 10 μ m).



Figure 25. 1-8. Fossil Cunoniaceae-Elaeocarpaceae: CUT-Z-AJJ, CUT-Z-CFJ, CUT-Z-EFA, and CUT-Z-CAI. 1. CUT-Z-AJJ, TLM view showing stomatal complexes (SB1369, scale-bar = $50 \mu m$); 2. CUT-Z-AJJ, TLM detail of single stomatal complex (SB1369, scale-bar = $20 \mu m$); 3. CUT-Z-CFJ, TLM view showing stomatal complexes (SL0347, scale-bar = $50 \mu m$); 4. CUT-Z-CFJ, TLM detail of single stomatal complex (SL0347, scale-bar = $20 \mu m$); 5. CUT-Z-EFA, TLM view showing (SL1899, scale-bar = $50 \mu m$); 6. CUT-Z-EFA, TLM detail of single stomatal complex (SL1899, scale-bar = $20 \mu m$); 7. CUT-Z-CAI, TLM view showing stomatal complexes (SL3294, scale-bar = $50 \mu m$); 8. CUT-Z-CAI, TLM detail of single stomatal complex (SL3294, scale-bar = $50 \mu m$); 7. CUT-Z-CAI, TLM view showing stomatal complexes (SL3294, scale-bar = $50 \mu m$); 8. CUT-Z-CAI, TLM detail of single stomatal complex (SL3294, scale-bar = $20 \mu m$); 7. CUT-Z-CAI, TLM view showing stomatal complexes (SL3294, scale-bar = $50 \mu m$); 8. CUT-Z-CAI, TLM detail of single stomatal complex (SL3294, scale-bar = $20 \mu m$); 7. CUT-Z-CAI, TLM view showing stomatal complexes (SL3294, scale-bar = $50 \mu m$); 8. CUT-Z-CAI, TLM detail of single stomatal complex (SL3294, scale-bar = $20 \mu m$).

clic, size range unimodal (but with wide range of stomatal size). Subsidiary cells (4–7) typically elongate, or wedge-like, often with distinct polar cells (at right angles to the stomatal axis) which may 'enclose' the lateral cells, smooth, unornamented. Guard cell pair outline circular, or ovate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 30–37 m (medium), with prominent T-piece thickenings at polar ends. Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, inner and outer surfaces smooth, unornamented, but with sharp grooves over the anticlinal walls.

Indumentum. Attachment scars of deciduous trichomes common, scattered over venal and nonvenal regions, inserted between epidermal cells, with the distinctly circular and thickened base expanding over (6–7) surrounding cells and similar in size to a normal epidermal cell.

Distinguishing features. The multicellular trichome attachment scar with its central insertion point is distinctive.

CUT-Z-FBE

Figure 24.5-24.8

Reference Specimen and locality: SL3007, GL-28.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, cyclocytic, size range bimodal, with distinct 'giant stomatal complexes' present (restricted to venal regions). Subsidiary cells (5-7) irregularly-shaped, periclinal walls thicker than over normal epidermal cells, developmentally incomplete stephanocytic bicyclic, smooth, unornamented. Guard cell pair outline circular, or ovate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 22-25 m (medium), with T-piece thickenings at polar ends (often just the cross-bar of the T). Outer stomatal ledge sub circular to elliptical, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over both major and fine venation more elongate), distinctly larger than

the stomata, anticlinal walls markedly sinuous, unbuttressed, inner surfaces slightly granular, outer surfaces smooth, unornamented.

Indumentum. Attachment cars of deciduous trichomes sparse, restricted to regions over major veins, inserted between (5–7) epidermal cells modified into a distinct ring of foot cells, with thickened periclinal walls, scar diameter similar in size to a normal epidermal cell.

CUT-Z-AJJ

Figure 25.1-25.2

Reference Specimen and locality: SB1369, BL-32.

Stomatal complexes. Stomatal complexes isolated, randomly oriented, cyclocytic, all some, or none of the subsidiary cells have been modified by a tangential division, size range unimodal. Subsidiary cells (4-5) sometimes forming 2 distinct polar cells (right angles to stomatal orientation) and 2 lateral cells (parallel to stomatal orientation), developmentally incomplete stephanocytic bicyclic, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, outlined by a well-defined anticlinal wall, length 35-40 m (medium), at same level as subsidiary cells (exposed on surface), some wall development between guard cells, and sometimes development of T-piece thickenings at the poles, slightly granular. Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells elongate (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, smoothly textured, unornamented.

Indumentum. Attachment scars of deciduous trichomes sparse, restricted to regions over major veins, simple, inserted between (c. 8) epidermal cells modified into radially elongate foot cells, scar diameter much smaller than a normal epidermal cell.

Distinguishing features. Subsidiary cells having distinctly straight tangential walls and with clear polar and lateral forms. Epidermal cells highly sinuous.

CUT-Z-CFJ Figure 25.3-25.4

Reference Specimen and locality: SL0347, BL-05.



Figure 26. 1-8. Fossil Cunoniaceae-Elaeocarpaceae: CUT-Z-CBI and CUT-Z-FAJ. 1. CUT-Z-CBI, TLM view showing stomatal complexes and (lower right) a trichome attachment scar. Note how outlines of epidermal cells become obscure away from stomatal complexes (SL3049, scale-bar = 50μ m); 2. CUT-Z-CBI, TLM view showing stomatal complexes and (centre) a trichome attachment scar (SL3049, scale-bar = 50μ m); 3. CUT-Z-CBI, TLM detail of single stomatal complex with clear brachyparacytic structure (SL3049, scale-bar = 20μ m); 4. CUT-Z-CBI, TLM detail of single stomatal complex with no apparent brachyparacytic structure (SL3049, scale-bar = 20μ m); 5. CUT-Z-CBI, SEM view of inner cuticular surface showing a single stomatal complex. Note very shallow anticlinal walls of subsidiary cells, and essential absence of walls else where (S-1122, scale-bar = 20μ m); 7. CUT-Z-CBI, SEM view of outer cuticular surface showing a single stomatal complex (S-1122, scale-bar = 20μ m); 8. CUT-Z-FAJ, TLM view showing stomatal complexes. Note giant stomatal complex (lower right) (SL2106, scale-bar = 20μ m); 8. CUT-Z-FAJ, TLM view showing stomatal complexes. The narrow subsidiary cells are well-defined by their thicker periclinal walls (SL2108, scale-bar = 50μ m).

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, anomocytic, size range unimodal. Subsidiary cells (4-7) when distinct are typically elongate, or wedge-like, often with distinct polar cells (at right angles to the stomatal axis) which may 'enclose' the lateral cells, developmentally incomplete stephanocytic bicyclic, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline ovate, outlined by a well-defined anticlinal wall, length 25-30 m (medium); at same level as subsidiary cells (exposed on surface); with prominent T-piece thickenings at polar ends. Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over centre of stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM; normal cells elongate (cells over major veins more elongate); approximately the same size as the stomata; anticlinal walls markedly sinuous; unbuttressed; smoothly textured, unornamented.

Indumentum. Attachment scars of deciduous, poral trichomes sparse; restricted to regions over veins; inserted between (c. 7) epidermal cells modified into radially elongate foot cells; scar diameter much smaller than a normal epidermal cell.

CUT-Z-EFA

Figure 25.5-25.6

Reference Specimen and locality: SL1899, Sthd-073.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, cyclocytic, developmentally tangenticytic or stephanocytic bicyclic, size range unimodal. Subsidiary cells (4– 5) elongate, periclinal walls thicker than over normal epidermal cells, smooth, unornamented. Guard cell pair outline ovate, not outlined by a clear anticlinal wall, length c. 32 m (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 elliptical, much thinner than normal epidermal cells (often broken away), extending over whole stoma, with a narrowly elliptic pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls straight, or curved to wavy, unbuttressed, smoothly textured, unornamented. Indumentum. Glabrous.

CUT-Z-CAI Figure 25.7-25.8

Reference Specimen and locality: SL3294, BL-04.

Referred specimens and occurrence: SL3280, BL-05; SL2848, GL-18.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, cyclocytic, developmentally tangenticytic or stephanocytic bicyclic, size range unimodal. Subsidiary cells (5–8) isodiametric or elongate and tangential to the guard cells, periclinal walls thicker than over normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 23–28 m (medium), clearly separated by polar walls. Outer stomatal ledge sub circular, thicker than normal epidermal cells, extending over centre of stoma, with a broad, subcircular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells elongate (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, smoothly textured, unornamented.

Indumentum. Glabrous.

Other structures. Lenticels present, formed of large circular areas of very thinly cutinised cells (often broken away), surrounded by radiating files of epidermal cells with relatively thick periclinal walls.

CUT-Z-CBI Figure 26.1-26.6

Reference Specimen and locality: SL3049, BL-22.

Stomatal complexes. Stomatal complexes small clusters, isolated, randomly oriented, anomocytic, or brachyparacytic, developmentally incomplete stephanocytic bicyclic or amphibrachyparacytic, size range unimodal. Subsidiary cells (5–7 contact cells) irregularly-shaped, or typically elongate, tangential to the guard cells, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 15–25 m (medium). Outer stomatal ledge sub circular, thicker than normal epidermal cells, extending over inner edge of stoma, with a broad, sub-circular pore.



Figure 27. 1-8. Fossil and extant Meliaceae. Note the tendency to have well-defined outer stomatal ledges "floating" within a poorly–outlined stoma: 1. Extant *Dysoxylum spectabile*, TLM view (OPH2595, scale-bar = 50 μ m); 2. Extant *Reinwardtiodendron celebicum*, TLM view (AQ062423, scale-bar = 50 μ m); 3. CUT-Z-AAB, TLM view showing stomatal complexes (SB1344, scale-bar = 50 μ m); 4. CUT-Z-AAB, TLM detail of single stomatal complex (SB1344, scale-bar = 50 μ m); 5. CUT-Z-CCH, TLM view showing stomatal complexes (SL0330, scale-bar = 50 μ m); 6. CUT-Z-CCH, TLM view showing three stomatal complexes. (SL0330, scale-bar = 20 μ m); 7. CUT-Z-FFC, TLM view showing stomatal complexes (SL3009, scale-bar = 50 μ m); 8. CUT-Z-FFC, TLM detail of single stomatal complex (SL3009, scale-bar = 20 μ m).

Epidermal Cells. Epidermal cell flanges clearly visible around stomatal complexes but become unclear further away (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls sinuous, unbuttressed, inner surfaces slightly granular, outer surfaces smooth, unornamented.

Indumentum. Attachment scars of deciduous trichomes common, epidermal cells around trichome attachment scar (6–7) modified into radially elongate foot cells.

CUT-Z-FAJ Figure 26.7-26.8

Reference Specimen and locality: SL2108, GL-07.

Referred specimens and occurrence: SL2252, BL-14; SL1242, BL-32; SL2166, GL-09; SL2175, GL-10.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells elongate (cells over both major and fine venation more elongate), distinctly larger than the stomata, anticlinal walls straight, unbuttressed, smoothly textured, unornamented.Stomatal complexes. Stomatal complexes in areoles, isolated (very rarely networked), randomly oriented, cyclocytic, developmentally tangenticytic or stephanocytic bicyclic, size range bimodal, with distinct 'giant stomatal complexes' present. Subsidiary cells (4-7) with periclinal walls thicker than over normal epidermal cells, smooth, unornamented, shape varying from narrow to isodiametric. Guard cell pair outline circular, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 20-32 m (medium), with prominent T-piece thickenings at polar ends. Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Indumentum. Glabrous.

Glands. Glands present, distinguished by patches of thin cuticle (often broken away) located over veins, surrounded by relatively small epidermal cells with thickly cutinised walls.

Meliaceae Jussieu 1789

Family identification: Based on the reference collection, one Meliaceae "syndrome" that stands out is a tendency to have stomata in which the margin of the guard cell pair is indistinct, while the outer stomatal ledge is well-defined but narrow, covering just the inner part of the guard cells. The contact zone between guard cells and subsidiary cells is often covered by very thin cuticle which leads to the appearance under TLM of the outer stomatal ledge seeming to 'float'. The pattern of subsidiary cells is often complex, the result of tangential cell division (see Figs 27.1-27.2 for two examples of extant Meliaceae cuticle, *Dysoxylum spectabile* (G.Forst.) Hooker (1864) and *Reinwardtiodendron celebicum* Koorders (1898). The following five taxa are offered as likely examples of fossil Meliaceae.

Key to Meliaceae

1. Cuticle glabrous. CUT-Z-CCH

1. Trichome attachment sites present. 2.

2. Ornamented with 'flowing' pattern of many fine ridges. CUT-Z-CDD

2. Cuticle unornamented. 3.

3. Periclinal walls of epidermal cells distinctly thinner than normal epidermal cells. CUT-Z-FFC

3. Periclinal walls of epidermal cells same thickness (or sometimes slightly thicker) than normal epidermal cells. 4.

4. Subsidiary cells (4-8) typically isodiametric, anticlinal walls typically slight indistinct. CUT-Z-CDE

4. Subsidiary cells (3-5) very irregularly shaped, anticlinal walls typically distinct. CUT-Z-AAB

CUT-Z-AAB

Figure 27.3-27.4

Reference Specimen and locality: SB1344, BL-32.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, anisocytic, size range unimodal. Subsidiary cells (3–5) with periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline ovate, not outlined by a clear anticlinal wall, length 17–20 m (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 sub circular, same thickness as normal epidermal cells, with an elliptical pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells elongate (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, smoothly textured, unornamented.

Indumentum. Glabrous.



Figure 28. 1-8. Fossil Meliaceae. Note the tendency to have well-defined outer stomatal ledges "floating" within a poorly–outlined stoma: CUT-Z-CDE, and CUT-Z-CDD. 1. CUT-Z-CDE, TLM view showing stomatal complexes (SL0302, scale-bar = 50 μ m); 2. CUT-Z-CDE, TLM detail of single stomatal complex (SL0302, scale-bar = 20 μ m); 3. CUT-Z-CDE, SEM view of outer surface showing stomatal complexes in a slightly papillate surface (S-1347, AQ 441329, scale-bar = 50 μ m); 4. CUT-Z-CDE, SEM view of inner cuticular surface showing four stomatal complexes. Note clearly different texture of subsidiary cells than ordinary epidermal cells, and that by this criteria, not all subsidiary cells are in direct contact with the guard cells (S-1346, B. Hyland 8650, scale-bar = 50 μ m); 5. CUT-Z-CDD, TLM view showing stomatal complexes (SL0342, scale-bar = 50 μ m); 6. CUT-Z-CDD, TLM view showing two stomatal complexes (SL0342, scale-bar = 20 μ m); 7. CUT-Z-CDD, SEM view of inner cuticular surface showing a single stomatal complex (S-1201, scale-bar = 20 μ m); 8. CUT-Z-CDD, SEM view of outer cuticular surface showing a single stomatal complex (S-1201, scale-bar = 20 μ m); 8. CUT-Z-CDD, SEM view of outer cuticular surface showing a single stomatal complex with radiating striae (S-1201, scale-bar = 20 μ m).

Distinguishing features. Distinguished by having highly variable subsidiary cells (although generally on an anisocytic pattern).

CUT-Z-CCH Figure 27.5-27.6

Reference Specimen and locality: SL0330, Harliwich-3.

Stomatal complexes. Stomatal surfaces, stomatal complexes in areoles, isolated, randomly oriented, cyclocyctic, size range unimodal, (but with a wide range of stomatal size). Subsidiary cells (5–9), iso-diametric, periclinal walls thicker than over normal epidermal cells, smooth, unornamented. Guard cell pair outline ovate, outlined by a well-defined anticlinal wall, length 15–20 m (medium), at same level as subsidiary cells (exposed on surface). Outer stomatal ledge narrowly elliptical, thinner than normal epidermal cells, extending over inner edge of stomate. Pore narrowly elliptic.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric, distinctly smaller than the stomata, cells over major veins more elongate, anticlinal walls curved - wavy, unbuttressed, texture smooth, unornamented.

Indumentum. Glabrous.

Distinguishing features. Distinguished from CUT-Z-CDE and CUT-Z-EID by the absence of trichome attachment scars, by subsidiary cells which are not clearly defined, and by a simple and thin OSL.

CUT-Z-FFC

Figure 27.7-27.8

Reference Specimen and locality: SL3009, GL-28.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, actinocytic, or staurocytic, size range unimodal. Subsidiary cells (3–5) irregularly-shaped, periclinal walls thicker than over normal epidermal cells, unornamented. Guard cell pair outline difficult or impossible to see in TLM view, not outlined by a clear anticlinal wall, at same level as subsidiary cells (exposed on surface), length 15–25 m (medium). Outer stomatal ledge elliptical, thinner than normal epidermal cells, extending over whole stoma. Pore narrowly elliptic.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls curved to wavy, slightly buttressed, smoothly textured, unornamented.

Indumentum. Attachment scars of deciduous trichomes sparse, mostly over, or close to, major veins, inserted between (5–7) epidermal cells modified only slightly, with a thickened rim, scar diameter much smaller than a normal epidermal cell.

CUT-Z-CDE Figure 28.1-28.4

Reference Specimen and locality: SL0302, BL-01.

Referred specimens and occurrence: SL2281, BL-18; SL3070, BL-26; SL2131, GL-08; SL2151, GL-09; SL2197, GL-11; SL2853, GL-18; SL2894, GL-20; SL2938, GL-23; SL3099, GL-24; SL2961, GL-25; SL2984, GL-27; SL2990, GL-27.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, cyclocytic, all some, or none of the subsidiary cells may have been modified by a tangential division, size range unimodal. Subsidiary cells (4-8) irregularlyshaped, periclinal walls same thickness or sometimes thicker than over normal epidermal cells, with a slightly more granular inner surface than normal epidermal cells, unornamented. Guard cell pair outline ovate, not outlined by a clear anticlinal wall, length 23-25 m (medium), at same level as subsidiary cells (stomatal complex slightly sunken so that outer stomatal ledges are at same level as surface of epidermal cells), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge elliptical, much 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 (cells over both major and fine venation more elongate), distinctly smaller than the stomata, anticlinal walls straight, unbuttressed, inner surfaces smooth, outer surfaces irregular, slightly rough and some cells raised up in a slightly papillose manner, otherwise unornamented.

Indumentum. Attachment scars of deciduous trichomes sparse, scattered over venal and nonvenal regions but slightly more common over veins, simple, inserted between (5–8) epidermal cells modified only slightly, with a thickened rim, scar diameter much smaller than a normal epidermal cell.

Distinguishing features. Distinguished from CUT-Z-CCH by having clearly defined subsidiary cells (based on texture), prominent OSL, and stomatal complexes which are about twice as large. CUT-Z-



Figure 29. 1-8. Fossil Sapindaceae: CUT-Z-EDD and CUT-Z- FJI. 1. CUT-Z-EDD, TLM view showing stomatal complexes (SL1818, scale-bar = 50 μ m); 2. CUT-Z-EDD, TLM view showing three stomatal complexes. Note that the walls of the subsidiary cells abut or slightly bisect the outline of the guard cells (SL1818, scale-bar = 20 μ m); 3. CUT-Z-EDD, SEM view of inner cuticular surface showing two stomatal complexes. Note buttressing of epidermal cell walls (S-1036, scale-bar = 20 μ m); 4. CUT-Z-EDD, SEM view of outer cuticular surface showing two stomatal complexes. Note striae radiating from each complex (S-1036, scale-bar = 20 μ m); 5. CUT-Z- FJI, TLM view showing stomatal complexes (SL2539, scale-bar = 50 μ m); 6. CUT-Z- FJI, TLM detail of single stomatal complex (S-1393, scale-bar = 20 μ m); 7. CUT-Z- FJI, SEM view of outer cuticular surface showing a single stomatal complex (S-1393, scale-bar = 10 μ m); 8. CUT-Z- FJI, SEM view of outer cuticular surface showing stomatal complexes. Note guard cell pair are slightly sunken and the very small outer stomatal ledges do not protrude above the surrounding subsidiary cells (S-1393, scale-bar = 10 μ m).

CDE differs in having many subsidiary cells and no peristomatal ridge.

CUT-Z-CDD Figure 28.5-28.8

Reference Specimen and locality: SL0342, Mata-23.

Referred specimens and occurrence: SL3130, GL-02; SL2208, GL-12; SL2930, GL-22; SL2992, GL-27.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, cyclocytic, size range unimodal (but with wide range of stomatal size). Subsidiary cells (4–5), irregularly-shaped, difficult to count under TLM; periclinal walls thicker than over normal epidermal cells; smooth; ornamented with groups of ridges radiating from the stoma. Guard cell pair outline ovate; not outlined by a clear anticlinal wall; at same level as subsidiary cells (exposed on surface), length 20–22 m (medium). Outer stomatal ledge elliptical, thinner 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 (cells over major veins more elongate); distinctly larger than the stomata; anticlinal walls markedly sinuous; buttressed, inner surfaces smooth, outer surfaces smooth and ornamented with 'flowing' pattern of many fine ridges, areas over anticlinal walls marked by a groove flanked on either side by a ridge.

Indumentum. Attachment scars of deciduous trichomes sparse, probably restricted to regions over veins (unclear), inserted between (5–6) epidermal cells modified into a distinct ring of foot cells, with thickened periclinal walls, scar diameter much smaller than a normal epidermal cell.

Sapindaceae Jussieu 1789

Family identification: The extant Sapindaceae have a very wide range of epidermal morphology. The epidermis of the Australasian species is under review by the author and although some genera and groups of genera are distinct, there is no simple set of epidermal features which will identify the family. However, stomata which are at the small end of the medium size class, have thin-walls, and subsidiary cells with flanges which abruptly end or even overlap the outline of the stomata appear to be common and distinctive in the Sapindaceae. The following five parataxa are suggested as Sapindaceae based on broad resemblance to extant taxa.

Key to Sapindaceae

1. Epidermal cell flanges buttressed. CUT-Z-EDD

- 1. Epidermal cell flanges unbuttressed. 2.
- 2. Epidermal cell walls sinuous. CUT-Z-GDC
- 2. Epidermal cell walls straight or wavy. 3.

3. Cuticle unornamented, subsidiary cell number up to 5. CUT-Z-FJI

3. Cuticle ornamented with ridges, subsidiary cell number up to 6. 4.

4. Subsidiary cells elongate tangential to stoma, often wedge-like. CUT-Z-CEI

4. Subsidiary cells typically isodiametric, not wedge-like. CUT-Z-ABF

CUT-Z-EDD

Figure 29.1-29.4

Reference Specimen and locality: SL1818, Sthd-091.

Referred specimens and occurrence: SL2540, GL-02; SL1733, Sthd-017; SL1713, Sthd-018; SL1965, Sthd-054; SL1993, Sthd-072; SL1622, Sthd-106; SL1595, Sthd-108.

Stomatal complexes. Stomatal complexes evenly spread, sometimes networked, randomly oriented, staurocytic, developmentally tangenticytic, size range bimodal, with distinct 'giant stomatal complexes' present. Subsidiary cells (4-5) typically elongate, or wedge-like, or skewed tangentially, often forming distinct polar cells (at right angles to the stomatal axis) which may 'enclose' the lateral cells, periclinal walls thicker than over normal epidermal cells, smooth, unornamented. Guard cell pair outline ovate, not outlined by a clear anticlinal wall, at same level as subsidiary cells (stomatal complexes sunken so that outer stomatal ledges are at same level as surface of epidermal cells), length 22-30 m (medium), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over inner edge of stoma, with an elliptical pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls markedly sinuous, buttressed, inner surfaces smooth, outer surfaces smooth except ornamented with narrow bands of fine ridges joining some stomatal com-



Figure 30. Extant Sapindaceae. 1. *Cupaniopsis anacardioides*, TLM view of stomatal complexes (AQ380045, scalebar = 20 µm); 2. *Diploglottis diphyllostegia*, TLM view of stomatal complexes (AQ011960, scale-bar = 20 µm); 3. *Rhysotoechia bifoliolata*, TLM view of stomatal complexes (AQ504166, scale-bar = 50 µm); 4. *Mischocarpus stipitatus*, TLM view of stomatal complexes (AQ389174, scale-bar = 20 µm).

plexes and radiating from trichome attachment scars.

Indumentum. Scars of deciduous trichomes sparse, scattered over venal and non-venal regions but slightly more common over veins, inserted between epidermal cells modified into radially elongate foot cells, scar diameter much smaller than a normal epidermal cell.

Distinguishing features. One of a group of taxa which have relatively small stomatal complexes without a distinct rim around the guard cells, and where the flanges of the subsidiary cells sometimes project over the stomatal outline. CUT-Z-EDD is distinct in having buttressed epidermal cells and straight subsidiary cell anticlinal walls. CUT-Z-FJI differs in having unbuttressed epidermal cell walls, and curved subsidiary cell anticlinal walls. CUT-Z-ABF differs in having large diameter, hollow trichome attachment scars, which are surrounded by a ring of many foot cells, each distinctly smaller than the trichome diameter.

Identification. Suggested as Sapindaceae based on the thin-walled stomata surrounded by subsidiary cells which have prominent flanges terminating abruptly at the stomatal outline, and in some cases bisect the outline. It is compared with extant *Cupaniopsis anacardioides* (A.Rich.) Radlk. (1879) in terms of stoma shape, thin outer stomatal ledges, thickened subsidiary cell periclinal walls and flanges of the subsidiary cells which abruptly abut against the stomatal outline (Fig. 30.1). However, the subsidiary cell flanges tend not to project over the guard cell outlines and the subsidiary cells are typically elongate, which is not a feature of *C. anacardioides*.

CUT-Z-FJI

Figure 29.5-29.8

Reference Specimen and locality: SL2539, GL-02.

Referred specimens and occurrence: SL2260, BL-15; SL2270, BL-16.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, actinocytic, or staurocytic, size range unimodal. Subsidiary cells (4–5) with periclinal walls of same thickness as normal epidermal cells, smooth, unornamented.



Figure 31. 1-6. Fossil Sapindaceae: CUT-Z-ABF, CUT-Z-CEI and CUT-Z-GDC. 1. CUT-Z-ABF, TLM view showing stomatal complexes and (just to lower right of centre) a trichome attachment scar (SB1382, scale-bar = 50 μ m); 2. CUT-Z-ABF, TLM detail of single stomatal complex. Note flanges of subsidiary cells projecting over the outline of the guard cells (SB1382, scale-bar = 20 μ m); 3. CUT-Z-ABF, SEM view of inner cuticular surface showing three stomatal complexes (S-1345, NE 043791A, scale-bar = 10 μ m); 4. CUT-Z-ABF, SEM view of outer cuticular surface with a clear stomatal complex at upper right. Note short bands of striae radiating from complex (S-1345, NE 043791A, scale-bar = 20 μ m); 5. CUT-Z-CEI, TLM view showing stomatal complexes and trichome attachment scars (SL0364, scale-bar = 50 μ m); 6. CUT-Z-CEI, TLM detail of single stomatal complexes (SL1222, scale-bar = 50 μ m); 8. CUT-Z-GDC. TLM view showing stomatal complexes (SL1222, scale-bar = 50 μ m); 8. CUT-Z-GDC. TLM detail of single stomatal complexes (SL1222, scale-bar = 50 μ m); 8. CUT-Z-GDC. TLM detail of single stomatal complexes (SL1222, scale-bar = 50 μ m); 8. CUT-Z-GDC.

Guard cell pair outline ovate, not outlined by a clear anticlinal wall, at same level as subsidiary cells (stomatal complexes sunken so that outer stomatal ledges do not protrude above normal epidermal cells), length 18–20 m (medium), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with an elliptical pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells elongate (cells over both major and fine venation more elongate), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, inner and outer surfaces smooth, unornamented.

Indumentum. Scars of deciduous trichomes sparse, simple, inserted between (4–7) epidermal cells modified into a distinct ring of foot cells, with thickened periclinal walls, scar diameter much smaller than a normal epidermal cell.

Distinguishing features. One of a group of taxa which have relatively small stomatal complexes without a distinct rim around the guard cells, and where the flanges of the subsidiary cells sometimes project over the stomatal outline. CUT-Z-FJI is distinct in having unbuttressed epidermal cell walls, and curved subsidiary cell anticlinal walls. CUT-Z-EDD differs in having buttressed epidermal cells and straight subsidiary cell anticlinal walls. CUT-Z-ABF differs in having large diameter, hollow trichome attachment scars, which are surrounded by a ring of many foot cells, each distinctly smaller than the trichome diameter.

Identification. Suggested as Sapindaceae based on the thin-walled stomata surrounded by subsidiary cells which have prominent flanges which terminate abruptly at the stomatal outline, and in some cases bisect the outline. It may be compared in a very broad way with extant *Cupaniopsis anacardioides* (Fig. 30.1), although it differs in shape of the subsidiary cells (which are more elongate in the fossil) and thickness of the subsidiary cell flanges (thinner in the fossil).

CUT-Z-ABF Figure 31.1-31.4

Reference Specimen and locality: SB1382, BL-32.

Referred specimens and occurrence: SB0879, GL-01; SL2233, GL-12; SL2875, GL-20; SL3106, GL-24; SL2951, GL-25; SL2995, GL-27; SL3019, GL-29; SL1218, BL-30; SL1855, Sthd-088; SL1861, Sthd-089.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, actinocytic, size range bimodal, with distinct 'giant stomatal complexes' present. Subsidiary cells (4-6) irregularly-shaped, typically isodiametric, periclinal walls thicker than over normal epidermal cells, smooth, ornamented with 5-6 bands of fine ridges radiating from the pore. Guard cell pair outline circular, outlined by a well-defined anticlinal wall, length c. 20 m (medium), underthrust by subsidiary cells (subsidiary cell anticlinal walls bisect outline of the guard cells in TLM view), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over veins not distinguished by shape), approximately the same size as the stomata; anticlinal walls curved to wavy, unbuttressed, inner and outer surfaces smooth, unornamented.

Indumentum. Attachment scars of deciduous trichomes common, scattered over venal and nonvenal regions, inserted between (8–11) epidermal cells modified by tangential divisions to form a subcircular zone of foot cells, scar diameter similar in size to a normal epidermal cell.

Distinguishing features. One of a group of taxa which have relatively small stomatal complexes without a distinct rim around the guard cells, and where the flanges of the subsidiary cells sometimes project over the stomatal outline. CUT-Z-ABF is distinct in having large diameter, hollow trichome attachment scars, which are surrounded by a ring of many foot cells, each distinctly smaller than the trichome diameter.

Identification. Suggested as Sapindaceae based on the thin-walled stomata surrounded by subsidiary cells which have prominent flanges which terminate abruptly at the stomatal outline, and in some cases bisect the outline. It compares closely with extant *Cupaniopsis anacardioides* in terms of stoma shape, thin outer stomatal ledges, flanges of the subsidiary cells abruptly abutting against and sometimes project over the stomatal outline, and thickened subsidiary cell periclinal walls (Fig. 30.1).

CUT-Z-CEI

Figure 31.5-31.6

Reference Specimen and locality: SL0364, BL-09.

CUT-Z-GDC Figure 31.7-31.8

Reference Specimen and locality: SL1222, BL-30.

Stomatal complexes. Stomatal complexes in areoles, isolated (but very rare networking noted), randomly oriented, actinocytic, or staurocytic, size range unimodal. Subsidiary cells (4–5) isodiametric, periclinal walls thicker than over normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, or ovate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 28–32 m (medium), with prominent T-piece thickenings at polar ends. Outer stomatal ledge sub circular, much thicker than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells elongate (cells over major veins more elongate, but those over finer veins inconsistently so), approximately the same size as the stomata, anticlinal walls markedly sinuous, unbuttressed, smoothly textured, unornamented.

Indumentum. Attachment scars of deciduous trichomes common, scattered over venal and nonvenal regions, inserted between (5–7) epidermal cells modified by several tangential divisions, with a massively thickened rim, scar diameter much smaller than a normal epidermal cell.

Identification. Suggested as Sapindaceae based on broad similarity with extant species such as *Rhysotoechia bifoliolata* inn terms of stomatal and subsidiary cell shape and degree of thickening (Fig. 30.3).

Ericaceae Jussieu 1789

Family identification: The fossil record of the Epacridaceae, which is now regarded as included within the Ericaceae (Angiosperm Phylogeny Group 2003) was summarized by Jordan and Hill (1996) and leaf cuticle of some fossil and extant species was illustrated by Jordan and Hill (1995). The stomatal complexes range from cyclocytic, to paracytic to anomocytic and are generally aligned. The epidermal cells are often (not always) highly sinuous. The tree-heath *Trochocarpa* has generally aligned anomocytic stomata and highly sinuous epidermal cells. For comparison two species of extant *Trochocarpa*, *T. laurina* Brown (1814) and *T. bellendenkerensis* Domin (1930) are illustrated (Figs 32.5 -32.6).

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, cyclocytic, all some, or none of the subsidiary cells have been modified by a tangential division, size range unimodal. Subsidiary cells (5-6) typically elongate tangential to stoma, or wedge-like, often with distinct polar cells (at right angles to the stomatal axis) which may 'enclose' the lateral cells, periclinal walls thicker than over normal epidermal cells, smooth, ornamented with groups of ridges radiating from the stoma. Guard cell pair outline circular, outlined by a well-defined anticlinal wall, length 20-25 m (medium), underthrust by subsidiary cells (subsidiary cell anticlinal walls bisect outline of the guard cells). Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over centre of stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM; normal cells elongate (cells over major veins more elongate); approximately the same size as the stomata; anticlinal walls straight, unbuttressed, smoothly textured except for an irregular ridge on either side of stoma.

Indumentum. Attachment scars of deciduous trichomes common, scattered over venal and nonvenal regions, inserted between (6–10) epidermal cells modified into radially elongate foot cells, with no distinct thickening of walls, scar diameter much smaller than a normal epidermal cell.

Distinguishing features. CUT-Z-CEI can be compared with CUT-Z-ABF, CUT-Z-EDD, and CUT-Z-FJI, where the subsidiary cell flanges sometimes intersect the outline of the guard cells. However, in those cases, the guard cell outline is not rimmed, and the outer stomatal ledges are much thinner. CUT-Z-CEI has clearly rimmed guard cells, and well-developed outer stomatal ledges. The stomatal complexes also have distinctly more subsidiary cells.

Identification. Suggested as Sapindaceae based on subsidiary cells which have prominent flanges which terminate abruptly at the stomatal outline, and in some cases bisect the outline. The stomata have a more developed outer stomatal ledge than CUT-Z-EDD, CUT-Z-FJI, or CUT-Z-ABF, but may still be compared with some extant Sapindaceae, for instance *Diploglottis diphyllostegia* Mueller, F.J.H. von ex Bailey (1885), (Fig. 30.2), *Rhysotoechia bifoliolata* Radlk. (1879) (Fig. 31.3), and *Mischocarpus stipitatus* S.T. Reynolds (1985) (Fig. 30.4).



Figure 32. 1-4. Fossil and extant Ericaceae. 1. CUT-Z-ECD, TLM view showing generally stomatal complexes (SL1929, scale aligned -bar = 50 μ m); 2. CUT-Z-ECD, TLM detail of single stomatal complex (SL1929, scale-bar = 20 μ m); 3. CUT-Z-ECD, SEM view of outer cuticular surface showing (upper centre) a single stomatal complex with prominent outer stomatal ledges, and 4-5 smaller structures which are probably trichome attachment scars (S-1077, scale-bar = 20 μ m); 4. CUT-Z-ECD, SEM view of inner cuticular surface showing three stomatal complexes. Note buttressing of walls right up to the margins of the guard cells (S-1077, scale-bar = 20 μ m); 5. Extant *Trochocarpa laurina*, TLM view showing aligned stomata and highly sinuous epidermal cell walls (AQ610328, scale-bar = 50 μ m); 6. Extant *T. bellendenkerensis*, TLM view showing aligned stomata but little sinuosity of epidermal cells (AQ188409, scale-bar = 50 μ m).

CUT-Z-ECD

Figure 32.1-32.4

Reference Specimen and locality: SL1929, Sthd-058.

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic, stomatal complexes evenly spread, isolated, showing a clear trend towards alignment, cyclocytic, size range unimodal. Subsidiary cells (5–7) irregularly-shaped, difficult to count

under TLM, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline ovate, outlined by a welldefined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 20–25 m (medium), with prominent T-piece thickenings at polar ends. Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.



Figure 33. 1-8. Extant and fossil (CUT-Z-AJG, CUT-Z-CDH) Myrsinaceae. 1. Extant *Ardisia quinquegona*, TLM view showing stomatal complexes and (upper left) a trichome attachment scar (AQ433196, scale-bar = 50 μ m); 2. Extant *A. humilis*, TLM view showing stomatal complexes and (upper left) a trichome attachment scar (AQ452160, scale-bar = 50 μ m); 3. Extant *A. brevipedata*, TLM view showing stomatal complexes (AQ366276, scale-bar = 50 μ m); 4. Extant *A. bakeri*, TLM detail of single stomatal complex. OPH3334, AQ440726, scale-bar = 20 μ m); 5. CUT-Z-AJG, TLM view showing stomatal complexes and (upper left) a trichome attachment scar (SB1290, scale-bar = 50 μ m); 6. CUT-Z-AJG, TLM view showing stomatal complexes and (upper left) a trichome attachment scar (SB1290, scale-bar = 50 μ m); 6. CUT-Z-AJG, TLM detail of single stomatal complex (SB1290, scale-bar = 20 μ m); 7. CUT-Z-CDH, TLM view showing stomatal complexes and (upper left) a trichome attachment scar (SL0241, scale-bar = 50 μ m); 8. CUT-Z-CDH, TLM detail of two stomatal complexes (SL0241, scale-bar = 20 μ m).

Epidermal Cells. Epidermal cell flanges often indistinct using TLM, normal cells isodiametric (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls markedly sinuous, buttressed, inner surfaces slightly granular, outer surfaces strongly granular, unornamented.

Indumentum. Glabrous.

Glands. Possible sparse multicellular glands present.

Distinguishing features. Distinguished from CUT-M-EFJ in having stomatal complexes which are approximately twice as large. Lid cells, which are present in CUT-M-EFJ, have not been found in CUT-Z-ECD.

Myrsinaceae Brown 1814

Family identification: The typical morphology is an anisocytic stomata associated with peltate trichomes (like Myricaceae). There is often an ornamentation of fine ridging, and this is often restricted to the subsidiary cells. For comparison four species of extant *Ardisia* are illustrated; *A. quinquegona* Blume, *A. humilis* Vahl (1794), *A. brevipedata* Mueller (1868), and *A. bakeri* White (1942) (Figs 33.1-33.4).

Key to Mysinaceae

1. Cuticle unornamented. CUT-Z-AJG

1. Cuticle ornamented. 2.

2. Ornamentation consisting of a single ridge on either side of the stoma. CUT-Z-CGG

2. Ornamentation consisting of multiple ridges. 3.

3. Ornamentation of fine ridges extending all over cuticle (epidermal and subsidiary cells). 4.

3. Ornamentation of fine ridges restricted to subsidiary cells. CUT-Z-CDH

4. Stomatal complexes slightly depressed, portions of subsidiary cell cuticle extending over parts of the outer stomatal ledge. CUT-Z-EDF

4. Stomatal complexes not depressed, not obscured by subsidiary cells. CUT-Z-CGC

CUT-Z-AJG Figure 33.5-33.6

Reference Specimen and locality: SB1290, Mata-03.

Referred specimens and occurrence: SL3303, Sthd-078.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, anisocytic, heliocyctic, size range unimodal. Subsidiary cells (3–4) irregularly-shaped, periclinal walls of same thickness as normal epidermal cells, smooth, ornamented with many ridges which tend to flow around the stoma. Guard cell pair outline ovate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 22– 23 m (medium). Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over inner edge of stoma, with an elliptical pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over veins not distinguished by shape), distinctly larger than the stomata, anticlinal walls curved to wavy, unbuttressed, smoothly textured, unornamented.

Indumentum. Attachment scars of deciduous trichome common, not clearly rimmed with thicker cuticle.

Distinguishing features. Distinguished from CUT-Z-CDH by the absence of a thick rim around the trichome scars.

CUT-Z-CDH

Figure 33.7-33.8

Reference Specimen and locality: SL0241, BL-04.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, anisocytic, heliocyctic, size range unimodal. Subsidiary cells (3–4) irregularly-shaped, periclinal walls of same thickness as normal epidermal cells, smooth, ornamented with ridges concentric about the stoma. Guard cell pair outline ovate, outlined by a welldefined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 20–25 m (medium). Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over inner edge of stoma, with an elliptical pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over veins not distinguished by shape), distinctly larger than the stomata, anticlinal walls curved to wavy, unbuttressed, smoothly textured ornamented with fine ridges over subsidiary cells which flow around the stoma.

Indumentum. Attachment scars of deciduous trichomes common, restricted to regions over major veins, inserted between (5–7) epidermal cells modified into radially elongate foot cells, and with a dis-



Figure 34. 1-8. Fossil Myrsinaceae (CUT-Z-CGG, CUT-Z-CGC, and CUT-Z-EDF). 1. CUT-Z-CGG, TLM view showing three stomatal complexes (SL0097, scale-bar = 50 μ m); 2. CUT-Z-CGG, TLM detail of single stomatal complex (SL0097, scale-bar = 20 μ m); 3. CUT-Z-CGG, SEM view of inner cuticular surface showing a single stomatal complex (S-1109, scale-bar = 20 μ m); 4. CUT-Z-CGG, SEM view of outer cuticular surface showing a single stomatal complex with sunken outer stomatal ledges and a thin, discontinuous rim (S-1109, scale-bar = 20 μ m); 5. CUT-Z-CGC, TLM view showing stomatal complexes and (upper right) a trichome attachment scar (SL0324, scale-bar = 50 μ m); 6. CUT-Z-CGC, TLM detail of single stomatal complex (SL0324, scale-bar = 20 μ m); 7. CUT-Z-EDF, TLM view showing stomatal complexes and (centre left) a trichome attachment scar (SL2070, scale-bar = 50 μ m); 8. CUT-Z-EDF, TLM detail of single stomatal complex and trichome attachment scar (SL2070, scale-bar = 20 μ m);

tinct rim, scar diameter similar in size to a normal epidermal cell.

Distinguishing features. Distinguished from CUT-Z-EDF in that the stomatal complexes not depressed (so outer stomatal ledge is not obscured by portions of subsidiary cell cuticle), and both anticlinal and radial walls of foot cells are thickened. Distinguished from CUT-Z-AJG by the presence of a distinct poral rim around the trichome scar.

CUT-Z-CGG Figure 34.1-34.4

Reference Specimen and locality: SL0097, BL-08.

Referred specimens and occurrence: SB0870, BL-30; SL3171, BL-33; SL1962, Sthd-054.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, anisocytic, heliocyctic, size range unimodal. Subsidiary cells (3–4) of varying size, curved and generally tangential to the guard cells, periclinal walls thicker than over normal epidermal cells, smooth, ornamented with 1–2 ridges parallel with, and on either side of the stoma. Guard cell pair outline ovate, outer margin obscured under TLM by surface ornamentation, at same level as subsidiary cells (exposed on surface), length 20–30 m (medium). Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells elongate (cells over major veins more elongate), distinctly larger than the stomata, anticlinal walls markedly sinuous, unbuttressed, inner surfaces very finely granular, outer surfaces smooth, ornamented with an irregular ridge on either side of the stoma.

Indumentum. Glabrous.

Distinguishing features. Distinguished from other taxa with anisocytic stomatal complexes in having sinuous anticlinal walls, and ornamentation restricted to a ridge or two on either side of the stomata, and being glabrous.

CUT-Z-CGC Figure 34.5-34.6

Reference Specimen and locality: SL0324, Harli-wich-3.

Referred specimens and occurrence: SL3198, BL-32.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, anisocytic,

heliocyctic, size range unimodal. Subsidiary cells (3) irregularly-shaped, periclinal walls of same thickness as normal epidermal cells, smooth, ornamented with many ridges which tend to flow around the stoma. Guard cell pair outline ovate, outlined by a well-defined anticlinal wall, length 22–23 m (medium); at same level as subsidiary cells (exposed on surface). Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over inner edge of stoma, with an elliptical pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM; normal cells elongate (cells over veins not distinguished by shape); distinctly larger than the stomata; anticlinal walls markedly sinuous; unbuttressed; smooth, ornamented with 'flowing' pattern of many fine ridges.

Indumentum. Attachment scars of deciduous trichomes common; scattered over venal and nonvenal regions, inserted over a single epidermal cell with a strongly thickened periclinal wall and a central pore, epidermal cells around trichome attachment scar (6–7) unmodified, scar diameter similar in size to a normal epidermal cell.

Distinguishing features. Distinguished from CUT-Z-EDF and CUT-Z-CDH in having an ornamentation of fine ridges extending all over cuticle (both epidermal and subsidiary cells).

CUT-Z-EDF

Figure 34.7-34.8

Reference Specimen and locality: SL2070, Sthd-047.

Referred specimens and occurrence: SL1875, Sthd-078.

Stomatal complexes. Stomatal complexes evenly spread, isolated, possibly slightly aligned with one another, anisocytic, heliocyctic, size range unimodal. Subsidiary cells (3) of varying size, curved and generally tangential to the guard cells, periclinal walls of same thickness as normal epidermal cells, smooth, ornamented with fine ridges, often radiating laterally from guard cells, and partially obscuring them. Guard cell pair outline ovate, outer margin obscured under TLM by surface ornamentation, length 25-34 m (medium), overarched irregularly by subsidiary cells, little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over inner edge of stoma, with an elliptical pore.


Figure 35. 1-8. Fossil and extant *Grisselinia* (Grisseliniaceae). 1. CUT-Z-GBF, TLM view showing two stomatal complexes. The cuticle is very thick and stains darkly (SL4860, scale-bar = 50 μ m); 2. CUT-Z-GBF, TLM detail of single stomatal complex (SL4860, scale-bar = 20 μ m); 3. CUT-Z-GBF, SEM view of outer cuticular surface showing a single stomatal complex with prominent outer stomatal ledges which are surrounded by sharp and deep grooves (S-1582, scale-bar = 20 μ m); 4. CUT-Z-GBF, SEM view of inner cuticular surface showing a single stomatal complex (S-1582, scale-bar = 20 μ m); 5. Extant *Griselinia lucida*, TLM view showing three stomatal complexes (OTA31637, scale-bar = 50 μ m); 6. Extant *G. lucida*, TLM detail of single stomatal complex (OTA31637, scale-bar = 20 μ m); 7. Extant *G. lucida*, SEM view of outer cuticular surface showing stomatal complexes with prominent outer stomatal ledges and rims (S-1588, OTA31637, scale-bar = 20 μ m); 8. Extant *G. lucida*, SEM view of inner cuticular surface showing a single stomatal complex surface showing a single stomatal complex (S-1588, OTA31637, scale-bar = 20 μ m); 7.



Figure 36. 1-4. Fossil and extant *Argophyllum* (Grossulariaceae). 1. CUT-Z-ACD, TLM view showing stomatal complexes and papillae or trichome bases (SB1366, scale-bar = 50 μ m); 2. CUT-Z-ACD, TLM detail of single stomatal complex (SB1366, scale-bar = 20 μ m). Note slight overlapping of cuticle ridge onto stomata; 3. Extant *Argophyllum nullamense*, TLM view showing several stomata interspersed with darker staining trichomes (AQ268618, scale-bar = 50 μ m); 4. Extant *A. nullamense*, TLM view showing two stomata surrounded and partially sunken below irregular ridges of cuticle and separated by dark trichomes (AQ268618, scale-bar = 20 μ m).

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, smoothly textured ornamented with 'flowing' pattern of many fine ridges.

Indumentum. Attachment scars of deciduous trichomes common, scattered over venal and nonvenal regions, inserted between epidermal cells, epidermal cells around trichome attachment scar modified into radially-elongate foot-cells (some tangential divisions result in concentric rings), with a massively thickened rim, scar diameter much smaller than a normal epidermal cell.

Distinguishing features. Distinguished from CUT-Z-CDH in that the stomatal complexes are slightly depressed, with portions of subsidiary cell cuticle extending over parts of the outer stomatal ledge. In addition, only the anticlinal walls around trichome insertion points are thickened to form a poral ring (no thickening of radial walls).

Grisseliniaceae Cunningham 1839 CUT-Z-GBF (*Grisselinia* sp.) Figure 35.1-35.4

Reference Specimen and locality: SL4860, BL-32.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, cyclocytic, developmentally tangenticytic, size range unimodal. Subsidiary cells (mostly appears to be 5, but difficult to count) of varying size, curved and generally tangential to the guard cells, periclinal walls slightly thicker than over normal epidermal cells, smooth, unornamented. Guard cell pair outline ovate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 68–83 m (large). Outer stomatal ledge elliptical, much thicker than normal epidermal cells, extending over whole stoma, surrounded by a deep, narrow groove, pore elliptical.



Figure 37. 1-8. Papillate Cuticle: CUT-Z-ABA and CUT-Z-ABC. 1. CUT-Z-ABA, TLM view showing stomatal complexes surrounded by a ring of papillate subsidiary cells. (SB1335, scale-bar = 50 μ m); 2. CUT-Z-ABA, TLM detail of single stomatal complex (SB1335, scale-bar = 20 μ m); 3. CUT-Z-ABA, SEM view of outer cuticular surface showing stomata surrounded by papillate subsidiary cells as well as papillae on some epidermal cells (S-324, scale-bar = 20 μ m); 4. CUT-Z-ABA, SEM view of inner cuticular surface showing a single stomatal complex. Note about 12 subsidiary cells (S-324, scale-bar = 10 μ m); 5. CUT-Z-ABC, TLM view showing stomatal complexes and trichome attachment scars (a large one is at lower left). The papillae are restricted to the subsidiary cells and a few other epidermal cells. Note also the position of a giant stomatal complex over a vein at centre left (SB1334, scale-bar = 50 μ m); 6. CUT-Z-ABC, TLM detail of stomatal complexes showing papillae projecting over the stomatal pore (SB1334, scale-bar = 20 μ m); 7. CUT-Z-ABC, SEM view of outer cuticular surface showing papillae almost blocking the stomatal pore (S-309, scale-bar = 10 μ m); 8. CUT-Z-ABC, SEM of inner cuticular surface showing large trichome attachment scars and smaller stomatal complexes (S-309, scale-bar = 20 μ m); 8. cut-Z-ABC, SEM of inner cuticular surface showing large trichome attachment scars and smaller stomatal complexes (S-309, scale-bar = 20 μ m).

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, with a smooth junction with the periclinal walls, normal cells isodiametric (cells over veins not distinguished by shape), distinctly smaller than the stomata, anticlinal walls straight, unbuttressed, inner and outer surfaces smooth, unornamented.

Indumentum. Glabrous.

Identification: CUT-Z-GBF is identified as *Griselinia* because of the basic similarity, especially with respect to the large stomata and prominent outer stomatal ledges (Fig. 35.5-35.8). The extant species *G. lucida* Forst.f. (1786), has peristomatal rings which are not present on the fossil.

Argophyllaceae Takhtajan 1987 CUT-Z-ACD (*Argophyllum* sp.) Figure 36.1-36.2

Reference Specimen and locality: SB1366, BL-32.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, number of subsidiary cells unclear, size range unimodal. Irregularly-shaped, periclinal walls of same thickness as normal epidermal cells, smooth, ornamented with irregular rims of cuticle, which partially project over the OSL. Guard cell pair outline circular, at same level as subsidiary cells, outer margin obscured under TLM by surface ornamentation, length c. 35 m (medium). Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over whole stoma, with an elliptical pore.

Epidermal Cells. Epidermal cell flanges not clearly visible under TLM because of surface thickenings, approximately the same size as the stomata, (cells over major veins more elongate), anticlinal walls curved to wavy, unbuttressed, ornamented with irregular, broad concentric ridges which cut irregularly across the subsidiary cells.

Indumentum. Raised, thick, peg-like attachment scars of deciduous trichomes common, scattered over venal and non-venal regions, simple, inserted between (c. 7) unmodified epidermal cells, scar diameter similar in size to a normal epidermal cell.

Distinguishing features. Distinguished by the ornamentation of irregular ridges and trichome attachment scars.

Identification. CUT-Z-ACD can be compared directly with *Argophyllum nullumense* R.T.Baker (1899) especially with respect to the thick, irregular ridges of cuticle and prominent trichome attachment scars (Fig. 36.3-36.4).

TAXA OF UNCERTAIN FAMILY

Group 1. Papillae present

Key to papillate cuticle

- 1. Cuticle hisute (trichomes persistent). 2.
- 1. Trichomes deciduous. 3.
- 2. Papillae simple and smooth. CUT-Z-ECH
- 2. Papillae peltate. CUT-Z-ABI
- 3. Stomatal complexes scattered.4.

3. Stomatal complexes in clearly defined patches. CUT-Z-ABD

4. Papillae restricted to subsidiary cells CUT-Z-ABA

4. Papillae on both subsidiary and normal epidermal cells. 5.

5. Papillae much smaller than the epidermal cell. CUT-Z-ABC

5. Papillae comparable in size to the epidermal cell. CUT-Z-ABB

CUT-Z-ABA Figure 37.1-37.4

Reference Specimen and locality: SB1335, BL-32.

Referred specimens and occurrence: SL0281, BL-01; SL0240, BL-04; SL1279, BL-05; SL0365, BL-09; SL3088, BL-28; SL3178, BL-33; SL2097, GL-07; SL2140, GL-08; SL2219, GL-12; SL2895, GL-20; SL2904, GL-21; SL2929, GL-22; SL3109, GL-24; SL2965, GL-25; SL0383, Mata-01; SB0845, Mata-06.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, laterocyclic, size range unimodal. Subsidiary cells (9–11) isodiametric, periclinal walls of same thickness as normal epidermal cells, granular. With a single papilla which projects horizontally over the stomatal pore. Unornamented. Guard cell pair outline difficult or impossible to see in TLM view, sunken below subsidiary cells and epidermal cells, outer margin obscured under TLM by surface topography, length 20–35 m (medium).

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, inner surfaces very slightly granular, outer surfaces smooth, unornamented, occasionally papillate.



Figure 38. 1-8. Papillate Cuticle: CUT-Z-ABI and CUT-Z-ECH. 1. CUT-Z-ABI, TLM view showing stomatal complexes entirely obscured by papillae and trichomes (SB1299, scale-bar = 50 μ m); 2. CUT-Z-ABI, TLM detail showing papillae (SB1299, scale-bar = 20 μ m); 3. CUT-Z-ABI, SEM view of outer cuticular surface showing papillae obscuring stomata (S-1217, scale-bar = 20 μ m); 4. CUT-Z-ABI, SEM of inner cuticular surface showing stomatal complex (upper left) (S-1217, scale-bar = 20 μ m); 5. CUT-Z-ECH, TLM view showing trichomes, papillae, and obscured stomatal complexes (SB1208, scale-bar = 50 μ m); 6. CUT-Z-ECH, TLM view showing a single stomatal complex with papillae overarching the stomatal pore (SL1208, scale-bar = 20 μ m); 7. CUT-Z-ECH, SEM view of outer cuticular surface showing papillae and trichomes (S-1209, scale-bar = 20 μ m); 8. CUT-Z-ECH, SEM view of inner cuticular surface showing (left) a single stomatal complex and (right) a trichome attachment scar (S-1209, scale-bar = 20 μ m).

Indumentum. Attachment scars of deciduous trichomes common, scattered over venal and nonvenal regions but slightly more common over veins, inserted between (7–9) epidermal cells modified only slightly, with a thickened rim. Scar diameter much smaller than a normal epidermal cell. Smooth papillae present.

Distinguishing features. Distinguished from CUT-Z-ABC in that papillae are restricted to subsidiary cells.

CUT-Z-ABC

Figure 37.5-37.8

Reference Specimen and locality: SB1334, BL-32.

Referred specimens and occurrence: SL0084, BL-08; SL1182, GL-01; SL2654, GL-04; SL2090, GL-07; SL1760, Sthd-012.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, cyclocytic, size range bimodal, with distinct 'giant stomatal complexes' present (restricted to venal regions). Subsidiary cells (6–10) isodiametric, periclinal walls of same thickness as normal epidermal cells, smooth. With a single papilla which projects horizontally over the stomatal pore. Unornamented. Guard cell pair outline difficult or impossible to see in TLM view, sunken below subsidiary cells, outer margin obscured under TLM by surface topography, length c. 20 m (medium).

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over both major and fine venation more elongate), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, inner surfaces slightly granular, outer surfaces slightly rough, unornamented.

Indumentum. Attachment scars of deciduous trichomes common, restricted to regions over veins, inserted between (6–11) epidermal cells modified into radially elongate foot cells, insertion 'peg' diameter much smaller than a normal epidermal cell, but the trichome then expands abruptly above the insertion. Papillae in patches, generally restricted to regions surrounding stomatal complexes, one papilla per cell, formed by the projection of a discrete region within the boundaries of the epidermal cell, smooth, much smaller than the epidermal cell, oriented vertically.

Distinguishing features. Distinguished from CUT-Z-ABB by the smaller papillae – much smaller than the epidermal cells, and from CUT-Z-ABA in that papillae are found on subsidiary cells and commonly also on some normal epidermal cells.

CUT-Z-ABI

Figure 38.1-38.4

Reference Specimen and locality: SB1299, Mata-03.

Referred specimens and occurrence: SL3167, BL-33.

Stomatal complexes. Stomatal complexes apparently in well-defined areoles. All details of stomata obscured under TLM by surface ornamentation and trichomes.

Epidermal Cells. Details of normal epidermal cells obscured under TLM because of surface thickenings, but cells over some veins are distinguished by being unornamented.

Indumentum. Hirsute and with dense peltate extensions of epidermal cells. Trichomes abundant, uniseriate, apparently more common over venal areas.

CUT-Z-ECH

Figure 38.5-38.8

Reference Specimen and locality: SL1208, GL-01.

Referred specimens and occurrence: SL3156, GL-01; SB1208, Mata-01.

Stomatal complexes. Stomatal complexes in areoles, isolated, number of subsidiary cells unclear because of obscuring papillae, size range bimodal, with distinct 'giant stomatal complexes' present. Subsidiary cells (4–6) isodiametric, periclinal walls of same thickness as normal epidermal cells, smooth, each with a single papilla which projects horizontally over the stomatal pore. Guard cell pair outline difficult or impossible to see in TLM view as obscured by surface topography, but appears to be sunken with respect to subsidiary and epidermal cells.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over both major and fine venation more elongate), approximately the same size as the stomata, anticlinal walls straight, unbuttressed, inner surfaces smooth, outer surfaces rough, unornamented.

Indumentum. Hirsute and papillate, trichomes common, scattered over venal and non-venal regions, simple, inserted between (6-11) unmodified or sometimes radially elongate epidermal cells, insertion peg diameter very small, but trichome base similar in size to a normal epidermal cell. The peri-



Figure 39. 1-8. Papillate Cuticle: CUT-Z-ABB and CUT-Z-ABD. 1. CUT-Z-ABB, TLM view showing stomatal complexes obscured by papillae and, at lower centre, a trichome attachment scar (SB1333, scale-bar = 50 μ m); 2. CUT-Z-ABB, TLM detail of stomatal complexes obscured by papillae (SB1333, scale-bar = 20 μ m); 3. CUT-Z-ABB, SEM view of inner cuticular surface showing stomatal complexes and a trichome attachment scar (S-338, scale-bar = 20 μ m); 4. CUT-Z-ABB, SEM view of outer cuticular surface showing a patch of stomatal complexes obscured by papillae (SB1332, scale-bar = 20 μ m); 5. CUT-Z-ABD, TLM view showing a patch of stomatal complexes obscured by papillae (SB1332, scale-bar = 50 μ m); 6. CUT-Z-ABD, TLM detail of a single stomatal complex (SB1332, scale-bar = 20 μ m); 7. CUT-Z-ABD, SEM view of outer cuticular surface showing papillae which are covering stomatal complexes (S-360, scale-bar = 0.1 mm); 8. CUT-Z-ABD, SEM view of inner cuticular surface showing a single stomatal complex. Note the very narrow guard cell pair and the coarsely granular texture of the subsidiary and epidermal cell walls (S-360, scale-bar = 10 μ m).

clinal surface of each epidermal cells projects upwards as a single smooth papilla.

Distinguishing features. Distinguished from other taxa with persistent trichomes in that the entire surface of all epidermal and subsidiary cells are raised up as papillae.

CUT-Z-ABB Figure 39.1-39.4

Reference Specimen and locality: SB1333, BL-32.

Referred specimens and occurrence: SL1277, BL-05; SL3081, BL-28; SL2141, GL-08; SL2173, GL-09; SL2180, GL-10; SL2205, GL-11; SL2218, GL-12; SL2849, GL-18; SL2890, GL-20; SL2943, GL-23; SL3101, GL-24; SL2968, GL-25; SL2975, GL-26.

Stomatal complexes. Stomatal distribution over leaf surfaces unknown, randomly oriented, actinocytic, size range bimodal, with distinct 'giant stomatal complexes' present. Subsidiary cells (4–6) isodiametric, periclinal walls of same thickness as normal epidermal cells; smooth, each with a single papilla that projects horizontally over the stomatal pore. Guard cell pair outline difficult or impossible to see in TLM view as obscured by surface topography.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM but only away from stomatal areas; anticlinal walls curved to wavy (cells over major veins more elongate); approximately the same size as the stomata; unbuttressed; inner and outer surfaces moderately granular, unornamented.

Indumentum. Scars of deciduous trichomes and papillae present. Trichome attachment scars abundant, scattered over venal and non-venal regions, inserted between (6–9) epidermal cells modified into radially elongate foot cells, scar diameter much smaller than a normal epidermal cell. Papillae in patches, generally restricted to regions surrounding stomatal complexes, with one smooth, discrete papilla per cell, comparable in size to the epidermal cel.

Distinguishing features. Distinguished from CUT-Z-ABC by the larger papillae – comparable in size to the epidermal cell.

CUT-Z-ABD Figure 39.5-39.8

Reference Specimen and locality: SB1332, Mata-03.

Referred specimens and occurrence: SL0286, BL-01; SL0238, BL-04; SL1275, BL-05; SL2697, BL-

06; SL0026, BL-07; SL0098, BL-08; SL2467, BL-09; SL2250, BL-14; SL2271, BL-16; SL2292, BL-18; SL3052, BL-24; SL3076, BL-27; SL3083, BL-28; SL3093, BL-29; SL1224, BL-30; SL2517, BL-31; SL1377, BL-32; SL2537, BL-33; SL1179, GL-01; SL1187, GL-02; SL2658, GL-04; SL2190, GL-10; SL2201, GL-11; SL2216, GL-12; SL2823, GL-16; SL2838, GL-17; SL2861, GL-18; SL2883, GL-20; SL2899, GL-21; SL2918, GL-22; SL2939, GL-23; SL3104, GL-24; SL2949, GL-25; SL2993, GL-27; SL3018, GL-29; SL1057, Mata-01; SL0334, Mata-23.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, cyclocytic, size range unimodal. Subsidiary cells (4–6) isodiametric, periclinal walls of same thickness as normal epidermal cells; with peltate scales. Unornamented. Guard cell pair outline distinctly narrow and almost rectangular, but difficult or impossible to see in TLM view; overarched by subsidiary cells, outer margin obscured under TLM by surface topography; length c. 10 m (small).

Epidermal Cells. Epidermal cell flanges clearly visible using TLM; normal cells highly variable from isodiametric to elongate (cells over both major and fine venation more elongate); distinctly larger than the stomata; anticlinal walls curved to wavy; unbuttressed; inner surfaces coarsely granular, outer surfaces smooth, ornamented with short ridges perpendicular or parallel to some stomatal complexes.

Indumentum. Attachment scars of deciduous trichomes common, restricted to regions over veins, inserted between (9–11) epidermal cells modified by tangential divisions to form a sub-circular zone of foot cells, scar diameter similar in size to a normal epidermal cell.

Distinguishing features. Distinguished by having stomatal complexes in clearly defined patches and which are entirely hidden below peltate cuticular extensions.

Group 2. Stomatal complexes generally aligned

Key to cuticle with Stomatal complexes generally aligned

1. Outer stomatal ledge elliptical, Guard cell pair outline difficult or impossible to see in TLM view. CUT-Z-AAE

1. Outer stomatal ledge sub circular, guard cell pair outline ovate. CUT-Z-CGJ



Figure 40. 1-4. Cuticle with stomatal complexes generally aligned: CUT-Z-AAE and CUT-Z-CGJ. 1. CUT-Z-AAE, TLM view showing stomatal complexes aligned generally left to right (SB1367, scale-bar = 50 μ m); 2. CUT-Z-AAE, TLM detail of single stomatal complex (SB1367, scale-bar = 20 μ m).Note the narrowly elliptic stomatal pore; 3. CUT-Z-CGJ, TLM view showing stomatal complexes aligned generally left to right (SL0352, scale-bar = 50 μ m); 4. CUT-Z-CGJ, TLM detail of single stomatal complex (SL0352, scale-bar = 20 μ m).

CUT-Z-AAE Figure 40.1-40.2

Reference Specimen and locality: SB1367, BL-32.

Referred specimens and occurrence: SL0122, BL-03.

Stomatal complexes. Stomatal complexes in areoles, isolated, showing a clear trend towards alignment, cyclocytic, size range unimodal. Subsidiary cells (5–7) irregularly-shaped, difficult to count under TLM, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline difficult or impossible to see in TLM view, not outlined by a clear anticlinal wall, at same level as subsidiary cells, length 17–21 m (medium). Outer stomatal ledge elliptical, same thickness as normal epidermal cells, extending over inner edge of stoma. Pore narrowly elliptic.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over both major and fine venation more elongate), distinctly smaller than the stomata, anticlinal walls

straight, unbuttressed, very smoothly textured, unornamented.

Indumentum. Glabrous.

CUT-Z-CGJ Figure 40.3-40.4

Reference Specimen and locality: SL0352, BL-05.

Stomatal complexes. Stomatal complexes evenly spread, isolated, with a tendency to be aligned with one another at least in patches, anomocytic, size range bimodal, with distinct 'giant stomatal complexes' present. Subsidiary cells (4–5) irregularly-shaped, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline ovate, outlined by a well-defined anticlinal wall, length 27–30 m (medium), at same level as subsidiary cells (exposed on surface), some wall development between guard cells, and sometimes development of T-piece thickenings at the poles. Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extend-



Figure 41. 1-6. Cuticle with highly sinuous epidermal cells: CUT-Z-AAC and CUT-Z-AAD. 1. CUT-Z-AAC, TLM view showing stomatal complexes (SB1345, scale-bar = 50 μ m); 2. CUT-Z-AAC, TLM detail of single stomatal complex (SB1345, scale-bar = 20 μ m); 3. CUT-Z-AAC, SEM view of inner cuticular surface showing a single stomatal complex (S-339, scale-bar = 10 μ m); 4. CUT-Z-AAC, SEM view of outer cuticular surface showing stomatal complexes with low outer stomatal ledges and slight concentric striae, in an otherwise smooth surface (S-339, scale-bar = 25 μ m); 5. CUT-Z-AAD, TLM view showing stomatal complexes (SB1291, scale-bar = 50 μ m); 6. CUT-Z-AAD, TLM detail of single stomatal complex (SB1291, scale-bar = 20 μ m).

ing over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls straight, unbuttressed, slightly rough, unornamented.

Indumentum. Glabrous.

Distinguishing features. Glabrous cuticle with virtually naked kidney-shaped guard cells.

Group 3. Epidermal cells highly sinuous

Key to cuticle with highly sinuous epidermal cells

1. Guard cell pair outline circular, clearly visible under TLM. CUT-Z-AAC

1. Guard cell pair outline ovate, but obscured by the strong outer stomatal ledge. CUT-Z-AAD

CUT-Z-AAC

Figure 41.1-41.4

Reference Specimen and locality: SB1345, BL-32.



Figure 42. 1-8. Cuticle with prominent peristomatal rings: CUT-Z-ADD, CUT-Z-EIG, and CUT-Z-FGA. 1. CUT-Z-ADD, TLM view showing three stomatal complexes (SB0843, scale-bar = 50 μ m); 2. CUT-Z-ADD, TLM detail of single stomatal complex. Note pronounced peristomatal ring (arrowed) (SB0843, scale-bar = 20 μ m); 3. CUT-Z-ADD, SEM view of inner cuticular surface showing a single stomatal complex (S-1198, scale-bar = 50 μ m); 4. CUT-Z-ADD, SEM view of outer cuticular surface showing a single stomatal complex with prominent outer stomatal ledges surrounded by a prominent rim (S-1198, scale-bar = 20 μ m); 5. CUT-Z-EIG, TLM view showing two stomatal complexes (SL1764, scale-bar = 50 μ m); 6. CUT-Z-EIG, TLM detail of single stomatal complex. Note peristomatal ring (arrowed) (SL1764, scale-bar = 20 μ m); 7. CUT-Z-FGA, TLM view showing stomatal complexes (SL2016, scale-bar = 50 μ m); 8. CUT-Z-FGA, TLM detail of single stomatal ring (arrowed) (SL2016, scale-bar = 20 μ m).

Referred specimens and occurrence: SL2597, BL-01; SL2284, BL-18; SL1183, GL-01; SL1198, GL-02; SL2675, GL-04; SL2187, GL-10; SL2200, GL-11; SL2831, GL-17; SL3012, GL-28.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, cyclocytic, size range unimodal. Subsidiary cells (8–10, difficult to count under TLM) isodiametric; periclinal walls of same thickness as normal epidermal cells; smooth; unornamented. Guard cell pair outline circular; outlined by a well-defined anticlinal wall; length 25–30 m (medium); at same level as subsidiary cells (exposed on surface); with prominent polar rods. Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM; normal cells irregular (cells over both major and fine venation elongate); approximately the same size as the stomata; anticlinal walls markedly sinuous; strongly buttressed; inner surfaces slightly granular, outer surfaces smooth, unornamented.

Indumentum. Attachment cars of deciduous trichomes sparse, restricted to regions over veins, simple, inserted between (6–9) epidermal cells modified by tangential divisions to form a sub-circular zone of foot cells, scar diameter much smaller than a normal epidermal cell.

Distinguishing features. Distinguished from CUT-Z-AAD in having very round stomatal complexes and many subsidiary cells.

CUT-Z-AAD Figure 41.5-41.6

Reference Specimen and locality: SB1291, Mata-03.

Referred specimens and occurrence: SL3295, BL-04; SL2207, GL-12; SL2842, GL-18; SL3123, Sthd-198.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, laterocyclic, or cyclocytic, developmentally tangenticytic, size range unimodal. Subsidiary cells (4–5) typically elongate tangential to the stoma, periclinal walls of same thickness as normal epidermal cells, smooth, ornamented with groups of ridges radiating from the stoma. Guard cell pair outline ovate, but obscured by the strong outer stomatal ledge, at same level as subsidiary cells (exposed on surface), length 32–38 m (medium). Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over inner edge of stoma, with an elliptical pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls markedly sinuous, strongly buttressed, smoothly textured ornamented with ridges of irregular course.

Indumentum. Attachment scars of deciduous trichomes sparse, not noted over veins, inserted between (7–8) epidermal cells modified by tangential divisions to form a sub-circular zone of foot cells, scar diameter much smaller than a normal epidermal cell.

Distinguishing features. Distinguished from CUT-Z-AAC in having ovate stomatal complexes and fewer (about 4) subsidiary cells.

Group 4. Stomatal complexes surrounded by a prominent, broad peristomatal ring

Key to cuticle with prominent peristomal ring

1. Peristomal ring margins sharply defined, epidermal cells distinctly small than stoma. CUT-Z-ADD

1. Peristomal ring margins smooth, epidermal cells of comparable size to the stoma. 2.

2. Outer stomatal ledge separated from the peristomatal rim by a narrow groove. Stoma with prominent thickenings of polar rods. CUT-Z-EIG

2. Outer stomatal ledge separated from the peristomatal rim by a broad groove. Stoma without thickenings of polar rods. CUT-Z-FGA

CUT-Z-ADD Figure 42.1-42.4

Reference Specimen and locality: SB0843, GL-02.

Referred specimens and occurrence: SL3137, GL-01.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, cyclocytic, all some, or none of the subsidiary cells have been modified by a tangential division (developmentally stephanocytic bicyclic), size range bimodal, with distinct 'giant stomatal complexes' present (separated from other stomatal complexes by a distinct stomatal-free zone). Subsidiary cells (3–5) typically elongate tangential to stoma, periclinal walls of same thickness as normal epidermal cells, granular, ornamented with a thick, sharply defined and slightly lumpy peristomatal rim. Guard cell pair outline ovate, outer margin obscured under TLM by surface topography, length c. 50 m (large). Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over whole stoma, separated from the peristomatal rim by a deep, narrow groove. Pore broad, sub-circular.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over veins not distinguished by shape), distinctly smaller than the stomata, anticlinal walls curved to wavy, unbuttressed, inner surfaces slightly granular, outer surfaces smooth, unornamented.

Indumentum. Glabrous.

Distinguishing features. Distinguished by the massive peristomatal ring.

CUT-Z-EIG Figure 42.5-42.6

Reference Specimen and locality: SL1764, Sthd-011.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, cyclocytic, developmentally tangenticytic, size range unimodal. Subsidiary cells (4–5) isodiametric, periclinal walls of same thickness as normal epidermal cells, smooth, ornamented with a thick, smooth-edged peristomatal rim. Guard cell pair outline ovate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 42–43 m (large), with prominent thickenings of polar rods. Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore, separated from the peristomatal rim by a narrow groove.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls curved to wavy, or markedly sinuous, unbuttressed, smoothly textured, unornamented.

Indumentum. Glabrous.

CUT-Z-FGA

Figure 42.7-42.8

Reference Specimen and locality: SL2016, Sthd-010.

Stomatal complexes. Stomatal complexes isolated, possibly with some general alignment although this is not clear, number of subsidiary cells unclear, size range unimodal. Periclinal walls of same thickness as normal epidermal cells, smooth, ornamented with a thick, smooth edged peristomatal rim. Guard cell pair outline difficult or impossible to see in TLM view, outer margin obscured under TLM by surface ornamentation, length 35–41 m (large-medium). Outer stomatal ledge sub circular, thicker than normal epidermal cells, extending over whole stoma, separated from peristomatal rim by a broad, shallow groove. Pore broad, sub-circular.

Epidermal Cells. Epidermal cell flanges somewhat diffuse, normal cells elongate (unclear if cells over veins are distinguished), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, slightly granular, flanges reflected on the surface by discontinuous, broad ridges, otherwise unornamented.

Indumentum. Glabrous.

Group 5. Persistent trichomes present

Key to cuticle with persistent trichomes

1. Trichome width multicellular at base. CUT-Z-ABG

- 1. Trichome width single-celled at base. 2.
- 2. Cuticle surface ornamented with ridges. 3.
- 2. Cuticle surface unornamented. 4.
- 3. Normal epidermal cells curved to wavy and unbuttressed. CUT-Z-CDC
- 3. Normal epidermal cells sinuous and buttressed. CUT-Z-FFE
- 4. Stomatal complexes not anisocytic. 5.
- 4. Stomatal complexes often anisocytic. 6.
- Stomatal complexes anomocytic (developmentally tangeticytic), Stomatal pore elliptical. CUT-Z-ACJ
- Stomatal complexes cyclocytic, developmentally stephanocytic Stomatal pore with a keyhole outline. CUT-Z-ABH
- Cuticle over the stoma so thin it often breaks away, or, under TLM view, gives impression of the outer stomatal ledge is "floating". CUT-Z-EEJ
- 6. Cuticle over the stoma typically robust, not breaking. 7.

7. Stomatal outline unclear under TLM, no T-thickenings at poles. CUT-Z-FGB

7. Stomatal outline clear under TLM, often T-thickenings at poles. CUT-Z-EDI



Figure 43. 1-8. Cuticle with persistent trichomes: CUT-Z-FGB and CUT-Z-EDI. 1. CUT-Z-FGB TLM view showing stomatal complexes and a trichome (SL1826, scale-bar = 50 μ m); 2. CUT-Z-FGB TLM detail of single stomatal complex (SL1826, scale-bar = 20 μ m); 3. CUT-Z-FGB TLM view of a trichome (SL1826, scale-bar = 50 μ m); 4. CUT-Z-FGB TLM view of a trichome (SL1826, scale-bar = 50 μ m); 5. CUT-Z-EDI. TLM view showing stomatal complexes (lower right) the remaining base of a trichome (SL2002, scale-bar = 50 μ m); 6. CUT-Z-EDI. TLM detail of single stomatal complex (SL2002, scale-bar = 20 μ m); 7. CUT-Z-EDI. SEM view of outer cuticular surface showing a single stomatal complex with prominent outer stomatal ledges. The light, granular material may be fungal growth after the specimen was mounted (S-1078, scale-bar = 10 μ m); 8. CUT-Z-EDI. SEM view of inner cuticular surface showing where two stomata have detached (S-1078, scale-bar = 50 μ m).



Figure 44. 1-8. Cuticle with persistent trichomes: CUT-Z-CDC, CUT-Z-FFE, and CUT-Z-EEJ. 1. CUT-Z-CDC, TLM view showing stomatal complexes and a trichome (SL0332, scale-bar = 50 μ m); 2. CUT-Z-CDC, TLM detail of three stomatal complexes (SL0332, scale-bar = 20 μ m); 3. CUT-Z-CDC, SEM view of outer cuticular surface showing a stomatal complex (left) partially obscured by ridges of cutin, and a broken trichome (right) (S-1104, scale-bar = 20 μ m); 4. CUT-Z-CDC, SEM view of inner cuticular surface showing a single stomatal complex. Note very granular texture (S-1104, scale-bar = 10 μ m); 5. CUT-Z-FFE, TLM view showing stomatal complexes and trichomes (SL2120, scale-bar = 50 μ m); 6. CUT-Z-FFE, TLM detail of two stomatal complexes (SL2120, scale-bar = 20 μ m); 7. CUT-Z-EEJ, TLM view showing stomatal complexes and broken trichomes (SL1778, scale-bar = 50 μ m); 8. CUT-Z-EEJ, TLM detail of single stomatal complex (SL1778, scale-bar = 20 μ m).

CUT-Z-FGB Figure 43.1-43.4

Reference Specimen and locality: SL1826, Sthd-095.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, anisocytic, size range unimodal. Subsidiary cells (3) with periclinal walls thinner than that over normal epidermal cells, smooth, ornamented with ridges concentric about the stoma. Guard cell pair outline difficult or impossible to see in TLM view, not outlined by a clear anticlinal wall, at same level as subsidiary cells (exposed on surface), length 20–22 m (medium), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge elliptical, thinner than normal epidermal cells, only extending over inner edge of stoma, with a narrowly elliptic pore.

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

Indumentum. Hirsute, trichomes common, scattered over venal and non-venal regions, uniseriate, a chain of 4-5 individual cells, inserted between radially elongate epidermal cells. Insertion diameter much smaller than a normal epidermal cell, but then the trichome base expanded abruptly above the insertion point.

Distinguishing features. Clearly distinguished by the uniseriate trichomes which are inserted over several modified epidermal cells.

CUT-Z-EDI Figure 43.5-43.8

Reference Specimen and locality: SL2002, Sthd-072.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, anisocytic, or unevenly paracytic, size range unimodal. Subsidiary cells (2–4) irregularly-shaped, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, not outlined by a clear anticlinal wall, at same level as subsidiary cells (exposed on surface), length 22–29 m (medium), little wall development between guard cells but often with prominent Tthickenings at poles. Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls curved to wavy, buttressed, inner and outer surfaces smooth, unornamented.

Indumentum. Bases of trichomes common, probably restricted to regions over veins (unclear), persistent, but all cases the main length of the trichome has broken off irregularly just above the base, inserted between unmodified epidermal cells, basal diameter much larger than a normal epidermal cell.

CUT-Z-CDC

Figure 44.1-44.4

Reference Specimen and locality: SL0332, Mata-23.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, number of subsidiary cells unclear (difficult to count under TLM), size range bimodal, with distinct 'giant stomatal complexes' present. Subsidiary cell periclinal walls thicker than over normal epidermal cells, smooth, ornamented with many ridges which tend to flow around the stoma but also frequently cross portions of the stoma. Guard cell pair outline ovate, outer margin obscured under TLM by surface ornamentation, length 11–12 m (small), at same level as subsidiary cells (exposed on surface). Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges poorly visible under TLM and only visible away from stomatal complexes, normal cells highly variable from isodiametric to elongate (cells over major veins more elongate), anticlinal walls curved to wavy, unbuttressed; inner and outer surfaces smooth, ornamented with bands of irregular ridges parallel to stomatal complexes and radiating from trichomes.

Distinguishing features. Distinguished from other taxa with persistent trichomes in that the surface is densely ornamented with irregular ridges concentric or roughly parallel to stomatal complexes and which radiate from trichomes.Indumentum. Trichomes sparse; scattered over venal and nonvenal regions, simple, mostly broken of irregularly above the base, trichome diameter similar in size to a normal epidermal cell. Epidermal cells around



Figure 45. 1-6. Cuticle with persistent trichomes: CUT-Z-ABG and CUT-Z-ACJ. 1. CUT-Z-ABG, TLM view showing stomatal complexes and multi-cellular trichomes (SB1353, scale-bar = 50 μ m); 2. CUT-Z-ABG, TLM detail of single stomatal complex (SB1353, scale-bar = 20 μ m); 3. CUT-Z-ABG, SEM view of inner cuticular surface showing two stomatal complexes (S-1123, scale-bar = 20 μ m); 4. CUT-Z-ABG, SEM view of outer cuticular surface showing stomatal complexes and (upper right) a trichome (S-1123, scale-bar = 20 μ m); 5. CUT-Z-ACJ, TLM view showing stomatal complexes and trichomes (SB1350, scale-bar = 50 μ m); 6. CUT-Z-ACJ, TLM detail of two stomatal complexes (SB1350, scale-bar = 20 μ m); 6. CUT-Z-ACJ, TLM detail of two stomatal complexes (SB1350, scale-bar = 20 μ m).

trichome base (6–7) modified by tangential divisions to form 4–5 rings of foot cells.

CUT-Z-FFE Figure 44.5-44.6

Reference Specimen and locality: SL2120, GL-07.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, number of subsidiary cells unclear, possibly brachyparacytic, size range unimodal. Periclinal walls of same thickness as normal epidermal cells, smooth; ornamented with bands of ridges projecting at right angles to the stomatal axis. Guard cell pair outline difficult or impossible to see in TLM view because of ornamentation; not outlined by a clear anticlinal wall; at same level as subsidiary cells (exposed on surface), length 17–18 m (medium). Outer stomatal ledge elliptical, same thickness as normal epider-



Figure 46. 1-4. Cuticle with persistent trichomes: CUT-Z-ABH. 1. TLM view showing stomatal complexes and trichomes (SB1372, scale-bar = 50 μ m); 2. TLM detail of single stomatal complex. Note distinctive 'keyhole' shape to stomatal pore (SB1372, scale-bar = 20 μ m); 3. SEM view of outer cuticular surface showing stomatal complexes and trichomes (S-1091, scale-bar = 100 μ m); 4. SEM view of inner cuticular surface showing a single stomatal complex (S-1091, scale-bar = 20 μ m).

mal cells, extending over whole stoma, with a narrowly elliptic pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM; normal cells highly variable from isodiametric to elongate (cells over veins not distinguished by shape); approximately the same size as the stomata; anticlinal walls markedly sinuous; buttressed; smoothly textured, ornamented with ridges of irregular course.

Indumentum. Trichomes common; uniseriate although some may branch from the base, or are perhaps in clusters, trichome diameter similar in size to a normal epidermal cell.

CUT-Z-EEJ Figure 44.7-44.8

Reference Specimen and locality: SL1778, Sthd-030.

Referred specimens and occurrence: SL1731, Sthd-017.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, anisocytic, size range unimodal. Subsidiary cells (3–4) irregularly-shaped, (hard to count as radial flanges of subsidiary cells are not well developed), periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline ovate, not outlined by a clear anticlinal wall, at same level as subsidiary cells (exposed on surface), length 18–23 m (medium), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge elliptical, much thinner than normal epidermal cells (often broken away), extending over whole stoma. Pore narrowly elliptic.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls straight, unbuttressed, smoothly textured, unornamented.

Indumentum. Bases of trichomes common, apparently uniseriate although most broken off in the lower segment, inserted between (6-8) epidermal cells modified into radially elongate foot cells, but with no distinct thickening of walls, basal diameter similar to much larger than a normal epidermal cell.

Distinguishing features. Distinguished from other taxa with persistent trichomes in the very thin cuticle over the stoma which often breaks away, or gives impression of the outer stomatal ledge "floating" in a TLM view.

CUT-Z-ABG Figure 45.1-45.4

Reference Specimen and locality: SB1353, BL-32.

Referred specimens and occurrence: SL3131, GL-02.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, anisocytic, size range unimodal. Subsidiary cells (3–4, difficult to count under TLM) irregularly-shaped, periclinal walls of same thickness as normal epidermal cells, smooth, ornamented with ridges concentric about the stoma. Guard cell pair outline circular, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 12– 16 m (small). Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls markedly sinuous, unbuttressed, inner surface very finely granular, outer surface smooth, ornamented with ridges of irregular course.

Indumentum. Trichomes abundant, scattered over venal and non-venal regions, multicellular, unbranched, lower part of trichome formed of several elongate cells packed side by side, which then narrows to a single apical cell, base diameter equivalent to 3–6 epidermal cells.

Distinguishing features. Distinguished from other taxa with persistent trichomes in that the trichomes are multicellular.

CUT-Z-ACJ Figure 45.5-45.6

Reference Specimen and locality: SB1350, BL-32.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, anomocytic (developmentally tangeticytic), size range unimodal. Subsidiary cells (4–5) irregularly-shaped, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Outlined by a welldefined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 13–15 m (small). Outer stomatal ledge elliptical, same thickness as normal epidermal cells, extending over inner edge of stoma, with an elliptical pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over at least some veins are more elongate), approximately the same size as the stomata, anticlinal walls markedly sinuous, unbuttressed, smoothly textured, unornamented.

Indumentum. Hirsute, trichomes common, probably restricted to regions over veins (unclear), uniseriate, 3–5 cells long, the cells nearest the trichome base are sometimes about as long as they are wide, more distal cells are 5–6 times as long as wide, total length about 88–113 m, the base is a circular, non-poral cell, but the base may expand over surrounding epidermal cells, basal diameter of similar or distinctly larger size than normal epidermal cells. Epidermal cells around trichome base unmodified

CUT-Z-ABH

Figure 46.1-46.4

Reference Specimen and locality: SB1372, BL-32.

Referred specimens and occurrence: SL2101, GL-07; SL2160, GL-09.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, cyclocytic, developmentally stephanocytic bicyclic, size range unimodal (but with wide range of stomatal size). Subsidiary cells (5-7) typically elongate tangential to stoma, with periclinal walls thinner than that over normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, outer margin obscured under TLM by robustness of outer stomatal ledge, at same level as subsidiary cells (stomatal complexes sunken so that outer stomatal ledges at same level as surface of epidermal cells), length 20-28 m (medium). Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over whole stoma. Pore broad, but narrows abruptly towards the poles (a key-hole outline) and may be slightly off-set from one guard cell to the other.



Figure 47. 1-8. Cuticle with paracytic stomatal complexes: CUT-Z-CCD and CUT-Z-CFF. 1. CUT-Z-CCD, TLM view showing stomatal complexes (SL0297, scale-bar = 50 μ m); 2. CUT-Z-CCD, TLM detail of single stomatal complex (SL0297, scale-bar = 20 μ m); 3. CUT-Z-CCD, SEM view of inner cuticular surface showing two stomatal complexes. Note granular texture of subsidiary cells (S-1583, scale-bar = 10 μ m); 4. CUT-Z-CCD, SEM view of outer cuticular surface showing two stomatal complexes and irregularly raised epidermal cells (S-1583, scale-bar = 10 μ m); 5. CUT-Z-CFF, TLM view showing stomatal complexes (SL0359, scale-bar = 50 μ m); 6. CUT-Z-CFF, TLM detail of single stomatal complex (SL0359, scale-bar = 20 μ m); 7. CUT-Z-CFF, SEM view of outer cuticular surface showing a single stomatal complex and prominently raised epidermal cells (S-1232, scale-bar = 20 μ m); 8. CUT-Z-CFF, SEM view of inner cuticular surface showing a single stomatal complex (S-1232, scale-bar = 20 μ m).

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over major veins more elongate), distinctly larger than the stomata, anticlinal walls curved to wavy, unbut-tressed, inner surfaces slightly rough, outer surfaces smooth, unornamented.

Indumentum. Trichomes common, scattered over venal and non-venal regions, persistent, inserted between (6–12) epidermal cells modified into radially elongate foot cells, with no distinct thickening of walls, diameter of insertion 'peg' much smaller than a normal epidermal cell, but then the trichome expands abruptly to about the same size or larger than a typical epidermal cell.

Distinguishing features. CUT-Z-ABH is distinguished from CUT-Z-AJD in the presence of trichomes. It is distinguished from other taxa with persistent trichomes in that the subsidiary cell periclinal walls are much thinner than either normal epidermal cells or the outer stomatal ledges.

Group 6. Stomatal complexes paracytic

Key to cuticle with paracytic stomatal complexes

1. Stomatal complexes large, prominent T-piece thickening at guard cell poles, epidermal cell anticlinal walls sinuous. CUT-Z-CDD

1. Stomatal complexes medium, slight T-piece thickening at guard cell poles, epidermal cell anticlinal walls wavy to slightly sinuous. CUT-Z-CFF

CUT-Z-CCD Figure 47.1-47.4

Reference Specimen and locality: SL0297, BL-01.

Referred specimens and occurrence: SL0234, BL-04; SL3075, BL-27; SL3152, GL-01; SL4791, GL-07; SL2128, GL-08; SL2870, GL-20; SL2920, GL-22; SL2947, GL-25; SL1235, BL-32.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, brachyparacytic, size range unimodal. Subsidiary cells more or less equal to unevenly sized, typically expanding to longer than the guard cells, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline elongate, often with flattened poles, outlined by a welldefined anticlinal wall, length 38–40 m (large), at same level as subsidiary cells (exposed on surface), with very prominent T-piece thickenings at polar ends. Outer stomatal ledge sub circular, thicker than normal epidermal cells, extending over centre of stoma, with a broad, sub-circular pore. Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells elongate (cells over major veins more elongate), distinctly larger than the stomata, anticlinal walls markedly sinuous, unbuttressed, inner surfaces granular, outer surfaces smooth, unornamented.

Indumentum. Attachment scars of deciduous trichomes rare, inserted between (c. 6) epidermal cells modified by tangential divisions to form a subcircular zone of foot cells, scar diameter much smaller than a normal epidermal cell.

Distinguishing features. Distinguished by the large and unevenly sized brachyparacytic subsidiary cells.

CUT-Z-CFF

Figure 47.5-47.8

Reference Specimen and locality: SL0359, BL-05.

Referred specimens and occurrence: SL3181, BL-01; SL2541, GL-02.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, brachyparacytic, or anisocytic, size range unimodal. Subsidiary cells (2–4) sometimes forming distinct polar cells (right angles to stomatal orientation) and 2 lateral cells (parallel to stomatal orientation), periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline ovate, outlined by a well-defined anticlinal wall, length 22–30 m (medium), at same level as subsidiary cells (exposed on surface), with slight T-piece thickenings at polar ends. Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over veins not distinguished by shape), distinctly larger than the stomata, anticlinal walls wavy to slightly sinuous, unbuttressed, outer surfaces smooth, but with periclinal walls irregularly raised leaving grooves over the anticlinal walls.

Indumentum. Glabrous.

Distinguishing features. Although the typical subsidiary cell pattern of CUT-Z-CFF is brachyparacytic, the underlying stomatal pattern is probably anisocytic. A spiralling process of cell division results in two subsidiary cells of reasonably equal size and on opposite sides of the guard cells. A third subsidiary can sometimes be distinguished.



Figure 48. 1-8. Cuticle with anisocytic stomatal complexes: CUT-Z-AJH, CUT-Z-FCD, and CUT-Z-JII. 1. CUT-Z-AJH, TLM view showing stomatal complexes (SB1300, scale-bar = 50 μ m); 2. CUT-Z-AJH, TLM detail of single stomatal complex (SB1300, scale-bar = 20 μ m); 3. CUT-Z-FCD, TLM view showing stomatal complexes (SL3016, scale-bar = 50 μ m); 4. CUT-Z-FCD, TLM detail of single stomatal complex (SL3016, scale-bar = 20 μ m); 5. CUT-Z-JII, TLM view showing stomatal complexes (SB1356, scale-bar = 50 μ m); 6. CUT-Z-JII, TLM detail of single stomatal complex (SB1356, scale-bar = 20 μ m). Note the prominent polar rods; 7. CUT-Z-JII, SEM view of inner cuticular surface showing a single stomatal complex. Note lumpier texture of subsidiary cells than epidermal cells (S-1092, scale-bar = 10 μ m); 8. CUT-Z-JII, SEM view of outer cuticular surface showing a single stomatal complex with low outer stomatal ledges and flanked by short, low ridges (S-1092, scale-bar = 10 μ m).

This taxon thus differs fundamentally from truly brachyparacytic taxa.

Group 7. Stomatal complexes anisocytic

Key to cuticle with anisocytic stomatal complexes

1. Trichomes present and persistent. CUT-Z-AJH

1. Cuticle glabrous. 2.

2. Epidermal cell periclinal walls distinctly raised, leaving very narrow, deep grooves over anticlinal walls. CUT-Z-ECE

2. Epidermal cell periclinal walls not distinctly raised. 3.

3. Epidermal cell anticlinal walls sinuous, prominent polar rod thickenings. CUT-Z-JII

3. Epidermal cell anticlinal walls straight to wavy, without prominent polar rod thickenings. 4.

4. Subsidiary cells granular, stomatal complex with distinctive angular outline. CUT-Z-FFB

4. Subsidiary cells not granular, stomatal complex without a distinctive angular outline. 5.

5. Peristomatal rim present. CUT-Z-FJG

5. Peristomatal rim absent. 6.

6. Normal epidermal cells elongate, outer stomatal ledge distinctly thinner than normal epidermal cells, subsidiary cells (3–4). CUT-Z-FCD

6. Normal epidermal cells isodiametric to elongate, outer stomatal ledge slightly thinner than normal epidermal cells, subsidiary cells (4–5). CUT-Z-EIH

CUT-Z-AJH Figure 48.1-48.2

Reference Specimen and locality: SB1300, Mata-03.

Referred specimens and occurrence: SL0087, BL-08; SL1196, GL-02.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, anisocytic, heliocyctic, size range bimodal, with distinct 'giant stomatal complexes' present. Subsidiary cells (3) of varying size, curved and generally tangential to the guard cells, periclinal walls of same thickness as normal epidermal cells; smooth; unornamented. Guard cell pair outline circular; outlined by a welldefined anticlinal wall; length 13–15 m (small); at same level as subsidiary cells (exposed on surface); with prominent T-piece thickenings at polar ends. Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM; normal cells elongate (cells over major veins more elongate); distinctly larger than the stomata; anticlinal walls curved to wavy; unbuttressed; smoothly textured, unornamented.

Indumentum. Hirsute; trichome bases common; scattered over venal and non-venal regions but slightly more common over veins, persistent, but all cases broken off near base, inserted between unmodified epidermal cells, basal diameter similar in size to a normal epidermal cell.

Distinguishing features. Distinguished from CUT-Z-JII in the presence of persistent trichomes.

CUT-Z-FCD

Figure 48.3-48.4

Reference Specimen and locality: SL3016, GL-28.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, anisocytic, (this appears to be the basic state, but there are often more than the definitive three subsidiary cells), size range unimodal. Subsidiary cells (3–4) irregularlyshaped, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline ovate, outlined by a welldefined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 22–30 m (medium), with prominent T-piece thickenings at polar ends. Outer stomatal ledge sub circular, distinctly thinner than normal epidermal cells, extending over centre of stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells elongate (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, smoothly textured, unornamented.

Indumentum. Glabrous.

CUT-Z-JII

Figure 48.5-48.8

Reference Specimen and locality: SB1356, BL-32.

Stomatal complexes. Stomatal complexes in areoles, sometimes networked, randomly oriented, anisocytic, size range unimodal. Subsidiary cells (3–4) with periclinal walls of same thickness as normal epidermal cells, inner surfaces granular, unornamented. Guard cell pair outline circular, out-



Figure 49. 1-6. Cuticle with anisocytic stomatal complexes: CUT-Z-FFB and CUT-Z-FJG. 1. CUT-Z-FFB, TLM view showing stomatal complexes (SL3135, scale-bar = 50 μ m); 2. CUT-Z-FFB, TLM detail of single stomatal complex (SL3135, scale-bar = 20 μ m); 3. CUT-Z-FFB, SEM view of inner cuticular surface showing two stomatal complexes (S-1397, scale-bar = 10 μ m); 4. CUT-Z-FFB, SEM view of outer cuticular surface showing a single stomatal complex (S-1397, scale-bar = 10 μ m); 5. CUT-Z-FFB, TLM view showing stomatal complexes (SL2506, scale-bar = 50 μ m); 6. CUT-Z-FJG, TLM detail of two stomatal complexes (SL2506, scale-bar = 20 μ m); 6.

lined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 16–20 m (medium), with very prominent polar rods. Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells elongate (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls markedly sinuous, slightly buttressed, inner and outer surfaces smooth, unornamented.

Indumentum. Glabrous.

Distinguishing features. Distinguished from CUT-Z-AJH in being glabrous and having buttressed epidermal cell walls.

CUT-Z-FFB Figure 49.1-49.4

Reference Specimen and locality: SL3135, GL-02.



Figure 50. 1-6. Cuticle with anisocytic stomatal complexes: CUT-Z-ECE and CUT-Z-EIH. 1. CUT-Z-ECE, TLM view showing stomatal complexes (SL1840, scale-bar = 50 μ m); 2. CUT-Z-ECE, TLM detail of single stomatal complex (SL1840, scale-bar = 20 μ m); 3. CUT-Z-ECE, SEM view of inner cuticular surface showing stomatal complexes. Note massively thickened epidermal cell walls (S-1083, scale-bar = 20 μ m); 4. CUT-Z-ECE, SEM view of outer cuticular surface showing stomatal complexes surrounded by epidermal cells with prominently raised outer (periclinal) walls (S-1083, scale-bar = 20 μ m); 5. CUT-Z-EIH, TLM view showing stomatal complexes (SL1566, scale-bar = 50 μ m); 6. CUT-Z-EIH, TLM detail of single stomatal complex (SL1566, scale-bar = 20 μ m).

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, size range unimodal. Subsidiary cells (3–4) with periclinal walls of same thickness as normal epidermal cells, granular, unornamented, with angular outline. Guard cell pair outline elongate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (though may be slightly sunken below surface), length 22–30 m (medium). Outer stomatal ledge same thickness as normal epidermal cells, with a narrowly elliptic pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over both major and fine venation more elongate), approximately the same size as the stomata, anticlinal walls straight, unbuttressed, inner surfaces smooth, outer surfaces rough, unornamented.

Indumentum. Glabrous.

Identification. The distinctive angular outline to the stomatal complex is reminiscent of the *Oxylobium illicifolium* illustrated by Jordan (1997). This may indicate relationships with the Fabaceae.

CUT-Z-FJG Figure 49.5-49.6

Reference Specimen and locality: SL2506, BL-03.

Referred specimens and occurrence: SL2238, GL-12.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, anisocytic, heliocyctic, size range unimodal. Subsidiary cells (3–5) with periclinal walls of same thickness as normal epidermal cells, smooth, ornamented with a thick peristomatal rim. Guard cell pair outline elongate, outer margin obscured under TLM by surface topography, length 21–30 m (medium). Outer stomatal ledge elliptical, same thickness as normal epidermal cells, extending over whole stoma, with a narrowly elliptic pore.

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

Indumentum. Glabrous.

Distinguishing features. Stomatal complex is elongate with rounded ends and with a peristomatal ridge. CUT-Z-CDE differs in having many subsidiary cells and no peristomatal ridge.

Identification. The distinctive angular outline to the stomatal complex is reminiscent of the *Oxylobium ilicifolium* (Andrews) Domin illustrated by Jordan (1997). This may indicate relationships within the Fabaceae.

CUT-Z-ECE Figure 50.1-50.4

Reference Specimen and locality: SL1840, Sthd-086.

Referred specimens and occurrence: SL2686, Sthd-090.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, anisocytic, heliocyctic, size range unimodal. Subsidiary cells (3) of varying size, curved and generally tangential to the guard cells, periclinal walls of same thickness as normal epidermal cells, smooth, ornamented with a single, irregular rim. Guard cell pair outline circular, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 25–35 m (medium). Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges not clearly visible under TLM because of surface thickenings, normal cells very irregular or elongate (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls curved to wavy, very thick, unbuttressed, smoothly textured, periclinal walls raised, leaving very narrow, deep grooves over anticlinal walls.

Indumentum. Glabrous.

Distinguishing features. Distinguished from other taxa with anisocytic stomatal complexes in having anticlinal walls of epidermal and subsidiary cells reflected by strong ridges on cuticle surface. The subsidiary and epidermal cell anticlinal walls are also markedly depressed below general surface of cuticle.

CUT-Z-EIH

Figure 50.5-50.6

Reference Specimen and locality: SL1566, Sthd-004.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, anisocytic, all some, or none of the subsidiary cells may have been modified by a tangential division, size range bimodal, with distinct 'giant stomatal complexes' present (separated from other stomatal complexes by a distinct stomatal-free zone). Subsidiary cells (4-5) irregularly-shaped, difficult to count under TLM, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, not outlined by a clear anticlinal wall, at same level as subsidiary cells (exposed on surface), length 25-32 m (medium), some wall development between guard cells, and sometimes development of T-piece thickenings at the poles. Outer stomatal ledge sub circular, slightly thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric to elongate (cells over veins not distinguished by shape), anticlinal walls curved to wavy, unbuttressed, smoothly textured, unornamented.

Indumentum. Glabrous.



Figure 51. 1-8. Cuticle with multicellular trichome attachment scars: CUT-Z-ECC and CUT-Z-EID. 1. CUT-Z-ECC, TLM view showing tightly clustered stomatal complexes and a multi-cellular trichome attachment scar (SL1811, scale-bar = $50 \mu m$); 2. CUT-Z-ECC, TLM view (SL1811, scale-bar = $20 \mu m$); 3. CUT-Z-ECC, SEM view of inner cuticular surface showing a single stomatal complex (S-1366, scale-bar = $10 \mu m$); 4. CUT-Z-ECC, SEM view of outer cuticular surface showing a single stomatal complex depressed with a rough, irregular surface (S-1366, scale-bar = $10 \mu m$); 5. CUT-Z-EID, TLM view showing stomatal complexes and a multi-cellular trichome attachment scar with a thickened rim (SL1811, scale-bar = $20 \mu m$); 7. CUT-Z-EID, TLM view showing stomatal complexes and a multi-cellular trichome attachment scar with a thickened rim (SL1811, scale-bar = $20 \mu m$); 7. CUT-Z-EID, TLM view showing stomatal complexes and a multi-cellular trichome attachment scar with a thickened rim (SL1811, scale-bar = $20 \mu m$); 7. CUT-Z-EID, TLM view showing stomatal complexes and a multi-cellular trichome attachment scar with a thickened rim (SL1811, scale-bar = $20 \mu m$); 7. CUT-Z-EID, TLM view showing stomatal complexes and a thickened rim (SL1811, scale-bar = $20 \mu m$); 7. CUT-Z-EID, TLM view showing stomatal complexes and a thickened rim (SL1811, scale-bar = $20 \mu m$); 7. CUT-Z-EID, TLM view showing stomatal complexes and a thickened rim (SL1811, scale-bar = $20 \mu m$); 7. CUT-Z-EID, TLM view showing stomatal complexes and a thickened rim (SL1811, scale-bar = $20 \mu m$); 7. CUT-Z-EID, TLM view showing stomatal complexes (SL1718, scale-bar = $50 \mu m$); 8. CUT-Z-EID, TLM view showing stomatal complexes (SL1718, scale-bar = $20 \mu m$).

Group 8. Multi Cellular trichome bases present

Key to cuticle with multi-cellular trichome bases

1. Trichome attachment scar with thickened, raised rim, cells forming base of scar not thickened. CUT-Z-ECC

1. Trichome attachment scar without thickened, raised rim, cells below scar distinctly thickened. CUT-Z-EID

CUT-Z-ECC

Figure 51.1-51.6

Reference Specimen and locality: SL1811, Sthd-100.

Referred specimens and occurrence: SL1351, BL-05; SL1249, BL-32; SB1308, Mata-03; SL1751, Sthd-016; SL1704, Sthd-019; SL1871, Sthd-078; SL1527, Sthd-111.

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic, stomatal complexes tightly clustered in areoles, frequently networked, randomly oriented, anisocytic, size range bimodal, with distinct 'giant stomatal complexes' present. Subsidiary cells (3) isodiametric, periclinal walls thicker than over normal epidermal cells, smooth, ornamented with many ridges which tend to flow around the stoma. Guard cell pair outline ovate, outlined by a well-defined anticlinal wall, length 9-16 m (small), at same level as subsidiary cells (exposed on surface), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over major veins vaguely or inconsistently more elongate), approximately the same size as the stomata, anticlinal walls straight, unbuttressed, inner and outer surfaces smooth, ornamented with many fine ridges over subsidiary cells, running parallel to stomatal axis.

Indumentum. Insertion scars of deciduous trichomes abundant, scattered over venal and nonvenal regions but slightly more common over veins, inserted over several (3–7) modified epidermal cells. Scar diameter similar in size to a normal epidermal cell. Epidermal cells are selectively thickened to form a slightly raised, thickened rim, although the cells within the rim are not thickened. Distinguishing features. Distinct in having stomatal complexes with well-defined (by thickness of anticlinal walls) subsidiary cells which occur in tight clusters, within which there is some networking, and by the many and prominent trichome attachment scars which are situated over several epidermal cells.

CUT-Z-EID Figure 51.7-51.8

Reference Specimen and locality: SL1718, Sthd-018.

Referred specimens and occurrence: SL3176, BL-33.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, cyclocytic, size range unimodal. Subsidiary cells (6–8) isodiametric, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline ovate, not outlined by a clear anticlinal wall, at same level as subsidiary cells (exposed on surface), length 13–18 m (medium), or (small), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge elliptical, thinner than normal epidermal cells, extending over inner edge of stoma, with a narrowly elliptic pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over major veins vaguely or inconsistently more elongate), distinctly smaller than the stomata, anticlinal walls straight, unbuttressed, smoothly textured, unornamented.

Indumentum. Attachment scars of deciduous trichomes common, probably restricted to regions over veins (unclear), inserted over several (4–5) modified epidermal cells. Scar diameter much larger than a normal epidermal cell. Epidermal cells of the trichome attachment scar strongly thickened.

Distinguishing features. Distinguished from CUT-Z-CCH by the presence of multi-cellular trichome attachment scars.

Group 9. Fine surface ridging or striae around stomatal complexes

Key to cuticle with fine surface ridging or striae around stomatal complexes

- 1.Cuticle glabrous. 2.
- 1. Attachment scars of trichome present. 3.



Figure 52. 1-8. Cuticle with prominent ridging or striae: CUT-Z-AAF, CUT-Z-AJE, CUT-Z-EIB, and CUT-Z-JIB. 1. CUT-Z-AAF, TLM view showing stomatal complexes. Most complexes are plugged (SB1354, scale-bar = 50 μ m); 2. CUT-Z-AAF, TLM detail of single stomatal complex (SB1354, scale-bar = 20 μ m); 3. CUT-Z-AJE, TLM view showing a stomatal complex and a trichome attachment scar (SB1289, scale-bar = 50 μ m); 4. CUT-Z-AJE, TLM detail of single stomatal complex (SB1289, scale-bar = 50 μ m); 4. CUT-Z-AJE, TLM detail of single stomatal complex (SB1289, scale-bar = 20 μ m); 5. CUT-Z-EIB, TLM view showing two stomatal complexes (SL1762, scale-bar = 50 μ m); 6. CUT-Z-EIB, TLM detail of single stomatal complex (SB1364, scale-bar = 20 μ m); 7. CUT-Z-JIB, TLM view showing two stomatal complexes within a single patch of striae (SB1364, scale-bar = 50 μ m); 8. CUT-Z-JIB, TLM detail of single stomatal complex (SB1364, scale-bar = 50 μ m);



Figure 53. 1-4. Cuticle with stomatal complexes in islands: CUT-Z-EEA. 1. TLM view showing a patch of stomatal complexes on the left and a glandular structure to the right (SL1820, scale-bar = $50 \mu m$). Note granular texture over stomatal patch; 2. TLM detail of a single stomatal complex (SL1820, scale-bar = $20 \mu m$); 3. SEM view of inner cuticular surface showing a single stomatal complex (S-1066, scale-bar = $10 \mu m$); 4. SEM view of outer cuticular surface showing a single stomatal complex covered by granular cuticular material (S-1066, scale-bar = $20 \mu m$).

- 2. Surface ridging very fine, inconsistent, epidermal cells granular. CUT-Z-EIB
- 2. Surface ridging distinct, over subsidiary cells, epidermal cells not granular. CUT-Z-JIB
- 3. Ridges over subsidiary and normal epidermal cells, stomatal pores plugged. CUT-Z-AAF
- 3. Ridges restricted to subsidiary cells, stomatal pores not plugged. CUT-Z-AJE

CUT-Z-AAF Figure 52.1-52.2

Reference Specimen and locality: SB1354, BL-32.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, cyclocytic, size range unimodal. Subsidiary cells (4–6) irregularlyshaped, difficult to count under TLM, periclinal walls of same thickness as normal epidermal cells, smooth, ornamented with many ridges which tend to flow around the stoma. Guard cell pair outline ovate, at same level as subsidiary cells, outer margin obscured under TLM by surface ornamentation, length c. 20 m (medium). Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore which typically appears plugged with dark material.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over both major and fine venation more elongate), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, smoothly textured, ornamented with 'flowing' pattern of many fine ridges over subsidiary and normal epidermal cells.

Indumentum. Attachment scars of deciduous trichomes sparse, scattered over venal and nonvenal regions but slightly more common over veins, simple, inserted between (6–8) epidermal cells modified only slightly, with a thickened poral rim, scar diameter similar in size to a normal epidermal cell.

CUT-Z-AJE

Figure 52.3-52.4

Reference Specimen and locality: SB1289, Mata-03.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, number of subsidiary cells unclear, size range unimodal. Subsidiary cells irregularly-shaped, periclinal walls of same thickness as normal epidermal cells, smooth, ornamented with ridges concentric about the stoma (outline not visible under TLM). Guard cell pair outline ovate, at same level as subsidiary cells, outer margin obscured under TLM by surface ornamentation, length 29–32 m (medium), at same level as subsidiary cells (exposed on surface). Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, smoothly textured ornamented with irregular concentric ridges around subsidiary cells.

Indumentum. Attachment scars of deciduous trichomes common, scattered over venal and nonvenal regions, persistent, but all cases broken off near base, inserted between (4–7) epidermal cells modified only slightly, with a thickened rim, scar diameter much smaller than a normal epidermal cell.

CUT-Z-EIB

Figure 52.5-52.6

Reference Specimen and locality: SL1762, Sthd-011.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, number of subsidiary cells unclear, size range unimodal. Subsidiary cells irregularly-shaped, difficult to count under TLM, periclinal walls of same thickness as normal epidermal cells, granular, ornamented with ridges concentric about the stoma. Guard cell pair outline circular, not outlined by a clear anticlinal wall, at same level as subsidiary cells (exposed on surface), length c. 35 m (medium), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges poorly visible under TLM and only visible away from stomatal complexes, normal cells isodiametric (unclear if cells over veins are distinguished); anticlinal walls straight; unbuttressed; texture granular; some very fine ridging on some subsidiary cells, but generally unornamented.

Indumentum. Glabrous.

CUT-Z-JIB

Figure 52.7-52.8

Reference Specimen and locality: SB1364, BL-32.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, number of subsidiary cells unclear, size range unimodal. Subsidiary cells with periclinal walls thinner than that over normal epidermal cells, smooth, ornamented with many ridges which tend to flow around the stoma (outline not visible under TLM). Guard cell pair outline ovate, at same level as subsidiary cells, outer margin obscured under TLM by surface ornamentation, length 35–40 m (medium), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over veins not distinguished by shape), distinctly smaller than the stomata, anticlinal walls straight, unbuttressed, smoothly textured ornamented with many fine ridges over subsidiary cells, running parallel to stomatal axis.

Indumentum. Glabrous.

Group 10. Stomatal complexes in islands

Key to stomatal complexes in islands

- 1. Glandular structures or lenticels common. CUT-Z-EEA
- 1. Glandular structures or lenticels absent or indistinct. 2.
- Subsidiary cells often modified by tangential divisions, attachment scars of trichomes present. CUT-Z-EDC
- 2. Subsidiary cells not modified by tangential divisions, glabrous. CUT-Z-EIC

CUT-Z-EEA Figure 53.1-53.4

Reference Specimen and locality: SL1820, Sthd-091.

Referred specimens and occurrence: SL1268, BL-32; SL1560, Sthd-004, SL2008, Sthd-020; SL1657, Sthd-040; SL2004, Sthd-072; SL1616, Sthd-106; SL1598, Sthd-108; SL1650, Sthd-110.



Figure 54. 1-8. Cuticle with stomatal complexes in islands: CUT-Z-EDC and CUT-Z-EIC. 1. CUT-Z-EDC, TLM view showing stomatal complexes. Note the giant stomatal complex at lower left (SL1908, scale-bar = 50 μ m); 2. CUT-Z-EDC, TLM view showing stomatal complexes (SL1908, scale-bar = 100 μ m); 3. CUT-Z-EDC, TLM view showing stomatal complexes (SL1908, scale-bar = 200 μ m); 3. CUT-Z-EDC, TLM view showing stomatal complexes. The lower complex has a brachyparacytic subsidiary cell arrangement while the others are less ordered and can be termed cyclocytic (SL1908, scale-bar = 20 μ m); 4. CUT-Z-EDC, SEM view of inner cuticular surface showing stomatal complexes. Note networking and granular texture (S-1048, scale-bar = 20 μ m); 5. CUT-Z-EDC, SEM view of outer stomatal ledges and an otherwise smooth surface (S-1048, scale-bar = 20 μ m); 6. CUT-Z-EDC, SEM view of inner cuticular surface showing a trichome attachment scar (S-1048, scale-bar = 20 μ m); 7. CUT-Z-EIC, TLM view showing stomatal complexes. Note common networking (SL2438, scale-bar = 50 μ m); 8. CUT-Z-EIC, TLM view showing stomatal complexes (SL2438, scale-bar = 20 μ m);

Stomatal complexes. Stomatal complexes in areoles, crowded, randomly oriented, paracytic, or anisocytic, stomatal complexes are in groups of typically 2–3 which are located within a group of cells clearly bounded by a series of anticlinal cell walls which form a continuous loop. All cells within this group appear to have divided as part of the stomatal-forming process, size range unimodal. Subsidiary cells irregularly-shaped, periclinal walls of same thickness as normal epidermal cells, the exterior of all cells in the stomatal patch are covered with granular cuticular material. Guard cell pair outline difficult or impossible to see in TLM view, sunken below subsidiary cells, length 18–23 m (medium).

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over veins distinguished by being more regularly oriented, in flowing files. but not elongate), distinctly larger than the stomata, anticlinal walls straight, unbuttressed, inner surfaces very finely granular, outer surfaces smooth, unornamented.

Indumentum. Glabrous.

Glands. Glandular structures or lenticels common, visible as large (50–75 mu) circular holes surrounded by rings of highly, tangentially divided cells.

CUT-Z-EDC

Figure 54.1-54.6

Reference Specimen and locality: SL1908, Sthd-074.

Referred specimens and occurrence: SL2007, Sthd-020.

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic, stomatal complexes in areoles, frequently networked, randomly oriented, cyclocytic or brachyparacytic, all some, or none of the subsidiary cells may have been modified by a tangential division, developmentally stephanocytic bicyclic, size range bimodal, with distinct 'giant stomatal complexes' present (separated from other stomatal complexes by a distinct stomatal-free zone). Subsidiary cells (4-7) irregularly-shaped, periclinal walls thicker than over normal epidermal cells, inner surface granular, outer surfaces smooth, unornamented. Guard cell pair outline circular; outlined by a well-defined anticlinal wall; length 20-23 m (medium); at same level as subsidiary cells (exposed on surface); with prominent Tpiece thickenings at polar ends. Outer stomatal

ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM; normal cells isodiametric (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls curved to wavy, or markedly sinuous, unbuttressed, inner and outer surfaces smooth, unornamented.

Indumentum. Attachment scars of deciduous trichomes sparse, scattered over venal and nonvenal regions but slightly more common over veins, inserted between epidermal cells modified by tangential divisions to form a sub-circular zone of foot cells with thickened periclinal walls. Scar diameter distinctly smaller, about a third to a quarter of typical epidermal cells.

Non-stomatal surface. Epidermal cells isodiametric, polygonal, cells over major veins distinguished, trichomes present and sparse (same morphology as stomatal surface).

Glands. Multi-cell glands possibly present.

Distinguishing features. Distinguished from CUT-Z-FAA in having epidermal walls which are sinuous away from the stomatal complexes, subsidiary cells which stain darker than normal epidermal cells, uncommon trichome scars, and, when present, do not have a massively thickened poral rim.

CUT-Z-EIC Figure 54.7-54.8

Reference Specimen and locality: SL2438, Sthd-073.

Referred specimens and occurrence: SL3043, BL-22; SL3063, BL-25; SL2962, GL-25.

Stomatal complexes. Stomatal complexes in areoles, frequently networked, randomly oriented, actinocytic, or staurocytic, size range unimodal. Subsidiary cells (4–6) irregularly-shaped, periclinal walls thicker than over normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, outlined by a well-defined anticlinal wall, length 15–20 m (medium), at same level as subsidiary cells (exposed on surface), with prominent Tpiece thickenings at polar ends. Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells elongate (cells over



Figure 55. 1-6. Cuticle with unusually shaped outer stomatal ledges: CUT-Z-FBI and CUT-Z-FCB. 1. CUT-Z-FBI, TLM view showing stomatal complexes and trichome insertion scar (SL2956, scale-bar = 50 μ m); 2. CUT-Z-FBI, TLM view showing two stomatal complexes (SL2956, scale-bar = 20 μ m); 3. CUT-Z-FCB, TLM view showing stomatal complex (SL3027, scale-bar = 50 μ m); 4. CUT-Z-FCB, TLM detail of single stomatal complex (SL3027, scale-bar = 20 μ m); 5. CUT-Z-FCB, SEM view of inner cuticular surface showing a single stomatal complex. Note pronounced granular texture (S-1386, scale-bar = 10 μ m); 6. CUT-Z-FCB, SEM view of outer cuticular surface showing three stomatal complexes. Note the distinctive key-hole shape of the stomatal pore (S-1386, scale-bar = 10 μ m).

major veins vaguely or inconsistently more elongate), distinctly larger than the stomata, anticlinal walls curved to wavy, or markedly sinuous, unbuttressed, smoothly textured, unornamented.

Indumentum. Glabrous.

Distinguishing features. Distinguished from CUT-Z-CGE in having stomatal complexes which are clearly in tight clusters, subsidiary cells clearly distinguished by thick periclinal walls, and relatively smaller stomatal complexes.

Group 11. Outer stomatal ledges prominent or unusually shaped

Key to cuticle with prominent or unusually shaped outer stomatal ledges

- 1. Stomatal pore elliptical, outer stomatal ledge possibly complex. CUT-Z-FBI
- 1. Stomatal pore typical or often "key-hole" shaped, outer stomatal ledge simple. 2.



Figure 56. 1-8. Cuticle with unusual shaped outer stomatal ledges: CUT-Z-AJD and CUT-Z-FFG. 1. CUT-Z-AJD, TLM view showing stomatal complexes (SB1379, scale-bar = 50 μ m); 2. CUT-Z-AJD, TLM detail of single stomatal complex (SB1379, scale-bar = 20 μ m). Note key-hole shape to the stomatal pore; 3. CUT-Z-AJD, SEM view of inner cuticular surface showing a single stomatal complex (S-1200, scale-bar = 10 μ m); 4. CUT-Z-AJD, SEM view of outer cuticular surface showing a single stomatal complex with prominent outer stomatal ledges (S-1200, scale-bar = 10 μ m); 5. CUT-Z-FFG, TLM view showing stomatal complexes (SL2229, scale-bar = 50 μ m); 6. CUT-Z-FFG, TLM detail of single stomatal complex (SL2229, scale-bar = 20 μ m); 7. CUT-Z-FFG, SEM view of inner cuticular surface showing (near centre) a reasonably well preserved stomatal complex and (left) a poorly preserved one (S-1396, scale-bar = 10 μ m); 8. CUT-Z-FFG, SEM view of inner cuticular surface showing a single stomatal complex and (left) a poorly preserved one (S-1396, scale-bar = 10 μ m); 8. CUT-Z-FFG, SEM view of inner cuticular surface showing a single stomatal complex and (left) a poorly preserved one (S-1396, scale-bar = 10 μ m); 8. CUT-Z-FFG, SEM view of inner cuticular surface showing a single stomatal complex (S-1396, scale-bar = 10 μ m).

- 2. Outer stomatal ledge a distinctive 'lemon' shape. CUT-Z-FCB
- 2. Outer stomatal ledge not 'lemon' shaped. 3.
- Outer stomatal ledges thinner than normal epidermal cells, epidermal cell anticlinal walls straight. CUT-Z-AJD
- Outer stomatal ledges thicker than normal epidermal cells, epidermal cell anticlinal walls sinuous. CUT-Z-FFG

CUT-Z-FBI Figure 55.1-55.2

Reference Specimen and locality: SL2956, GL-25.

Referred specimens and occurrence: SL2851, GL-18.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, cyclocytic, size range unimodal. Subsidiary cells (4-6, difficult to count under TLM) with periclinal walls of same thickness as normal epidermal cells, smooth, ornamented with 3-4 ridges parallel with, and on either side of the stoma. Guard cell pair outline difficult or impossible to see in TLM view, outer margin usually obscured by subsidiary cell ornamentation projecting over the outer stomatal ledge, length 22-33 m (medium), clearly separated by polar walls. Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over whole stoma, narrowing towards poles, possibly with a complex structure (two ledges may overlap), with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over major veins more elongate), approximately the same size as the stomata; anticlinal walls markedly sinuous; buttressed; smoothly textured, unornamented.

Indumentum. Attachment scars of deciduous trichomes common; scattered over venal and nonvenal regions; inserted between (5–7) epidermal cells modified into a distinct ring of foot cells, with thickened periclinal walls; scar diameter similar in size to a normal epidermal cell.

Distinguishing features. Has a similar outer stomatal ledge as CUT-Z-FCB but differs in having sinuous and buttressed epidermal cells and trichome attachment scars.

CUT-Z-FCB

Figure 55.3-55.6

Reference Specimen and locality: SL3027, GL-29.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, size range unimodal (but with wide range of stomatal size). Subsidiary cells (4-7) irregularly-shaped, difficult to count under TLM, periclinal walls of same thickness as normal epidermal cells, inner surfaces granular, outer surfaces smooth, ornamented with 3-4 ridges parallel with, and on either side of the stoma. Guard cell pair outline difficult or impossible to see in TLM view, at same level as subsidiary cells, outer margin obscured under TLM by surface ornamentation, length 20-38 m (medium). Outer stomatal ledge a distinctive 'lemon' shape, broad in the middle, and narrowing sharply at either end, thicker than normal epidermal cells, extending over whole stoma, with a broad pore, but which narrows abruptly towards the poles (a key-hole outline).

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, inner surfaces finely granular, outer surfaces smooth, unornamented.

Indumentum. Glabrous.

Glands. Glands present, compound, composed of a cluster of cells with periclinal walls thicker than normal epidermal cells, and surrounded by a rosette of cells, 2–3 cycles broad, which otherwise look similar to normal epidermal cells.

Distinguishing features. Clearly distinguished by the lemon-shaped outer stomatal ledges, and the compound glands. Differs from CUT-Z-FBI in having straight, unbuttressed epidermal cell walls

CUT-Z-AJD

Figure 56.1-56.4

Reference Specimen and locality: SB1379, BL-32.

Referred specimens and occurrence: SL0350, BL-05; SL3041, BL-22; SL3133, GL-02; SL2144, GL-08; SL2182, GL-10; SL2213, GL-12; SL2822, GL-16; SL2998, GL-27.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, cyclocytic, size range unimodal. Subsidiary cells (6) irregularlyshaped, with periclinal walls thinner than that over normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, at same level as subsidiary cells, outer margin obscured under TLM by surface ornamentation, length 17–25 m (medium). Outer stomatal ledge sub circular, thinner than normal epidermal cells, extending over



Figure 57. 1-8. Cuticle with sinuous epidermal cells and networked stomatal complexes: CUT-Z-ADJ and CUT-Z-EGB. 1. CUT-Z-ADJ, TLM view showing stomatal complexes and trichome attachment scars (SB0860, scale-bar = 50μ m); 2. CUT-Z-ADJ, TLM detail of single stomatal complex (SB860, scale-bar = 20μ m); 3. CUT-Z-ADJ, SEM view of inner cuticular surface showing stomatal complexes. Note networking, slight buttressing and granular texture (S-1119, scale-bar = 20μ m); 4. CUT-Z-ADJ, SEM view of outer cuticular surface showing a single stomatal complexes and a trichome attachment scar (SL1955, scale-bar = 10μ m); 5. CUT-Z-EGB, TLM view showing stomatal complexes (SL1955, scale-bar = 20μ m); 7. CUT-Z-EGB, SEM view of inner cuticular surface showing a single stomatal complexes (SL1955, scale-bar = 20μ m); 7. CUT-Z-EGB, SEM view of inner cuticular surface showing a single stomatal complex (S-1368, scale-bar = 10μ m); 8. CUT-Z-EGB, SEM view of outer cuticular surface showing a single stomatal complex (S-1368, scale-bar = 10μ m); 8. CUT-Z-EGB, SEM view of outer cuticular surface showing a single stomatal complex (S-1368, scale-bar = 10μ m); 8. CUT-Z-EGB, SEM view of outer cuticular surface showing a single stomatal complex with slightly raised outer stomatal ledges in a bumpy surface (S-1368, scale-bar = 10μ m).



Figure 58. 1-4. Stomatal complexes with two rings of narrow subsidiary cells (CUT-Z-FBD) and tangentic stomatal complexes (CUT-Z-FBH). 1. CUT-Z-FBD, TLM view showing stomatal complexes (SL2946, scale-bar = 50 μ m); 2. CUT-Z-FBD, TLM detail of single stomatal complex (SL2946, scale-bar = 20 μ m). Note the two rings of very narrow subsidiary cells; 3. CUT-Z-FBH, TLM detail of two stomatal complexes (SL2108, scale-bar = 20 μ m); 4. CUT-Z-FBH, TLM view showing three stomatal complexes (SL2981, scale-bar = 20 μ m).

whole stoma, with a broad pore but which narrows abruptly towards the poles (a key-hole outline).

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over both major and fine venation more elongate), distinctly larger than the stomata, anticlinal walls straight, unbuttressed, inner surfaces finely granular, outer surfaces smooth, unornamented.

Indumentum. Glabrous.

Distinguishing features. Similar to CUT-Z-ABH, but glabrous.

CUT-Z-FFG Figure 56.5-56.8

Reference Specimen and locality: SL2229, GL-12.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, number of subsidiary cells unclear, size range unimodal. Subsidiary cells with periclinal walls of same thickness as normal epidermal cells, smooth, ornamented with ridges concentric about the stoma. Guard cell pair outline difficult or impossible to see in TLM view, not outlined by a clear anticlinal wall, at same level as subsidiary cells, length 19–23 m (medium). Outer stomatal ledge sub circular, thicker than normal epidermal cells, extending over whole stoma, with a broad pore, but which often narrows abruptly towards the poles (a "key-hole" outline).

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls markedly sinuous, slightly buttressed; smoothly textured, unornamented.

Indumentum. Glabrous.

Group 12. Epidermal cells sinuous and stomatal complexes highly networked

Key to cuticle with sinuous epidermal cells and highly networked stomatal complexes

- 1. Stomatal complexes clustered, cuticle glabrous, often with 2-3 thin ridges parallel to the long axis of stoma. CUT-Z-ADJ
- 1. Stomatal complexes not clustered, cuticle with trichome attachment scars, unornamented. CUT-Z-EGB

CUT-Z-ADJ

Figure 57.1-57.4

Reference Specimen and locality: SB1298, Mata-03.

Referred specimens and occurrence: SL1228, BL-30.

Stomatal complexes. Stomatal complexes in areoles, often networked, randomly oriented, anomocytic (3–4 contact cells), size range unimodal. Subsidiary cells with periclinal walls of same thickness as normal epidermal cells, inner surfaces finely granular, outer surfaces slightly rough, unornamented, or with 2-3 thin ridges parallel to the long axis of stoma. Guard cell pair outline ovate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 19–23 m (medium), clearly separated by polar walls. Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells elongate (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls markedly sinuous, unbuttressed, inner surfaces finely granular, outer surfaces slightly rough, unornamented.

Indumentum. Glabrous.

CUT-Z-EGB

Figure 57.5-57.8

Reference Specimen and locality: SL1955, Sthd-051.

Referred specimens and occurrence: SL2289, BL-18; SB0860, Mata-03.

Stomatal complexes. Stomatal complexes evenly spread, frequently networked, randomly oriented, anomocytic, size range unimodal. Subsidiary cells (4–6) isodiametric, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, outlined by a well-defined anticlinal wall, length 16–24 m (medium), at same level as subsidiary cells (exposed on surface), with prominent T-piece thickenings at polar ends. Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells elongate (cells over major veins vaguely or inconsistently more elongate), approximately the same size as the stomata, anticlinal walls markedly sinuous, unbuttressed, smoothly textured, unornamented.

Indumentum. Attachment scars of deciduous trichomes common, probably restricted to regions over veins (unclear), inserted between epidermal cells modified into radially elongate foot cells, scar diameter similar in size to a normal epidermal cell.

Group 13. Stomatal complexes typically having two rings of narrow subsidiary cells

CUT-Z-FBD Figure 58.1-58.2

Reference Specimen and locality: SL2946, GL-23.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, cyclocytic, There are typical two rings of markedly narrow subsidiary cells, plus the outer ring of broader and more irregular cells that the subsidiaries have been cut off from, developmentally stephanocytic brachyparacytic, size range unimodal (but with wide range of stomatal size). Subsidiary cells (4-7) with periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, or ovate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 29-30 m (medium), with prominent T-piece thickenings at polar ends. Outer stomatal ledge sub circular, much thicker than normal epidermal cells, extending over whole stoma, with an elliptical pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over both major and fine venation more elongate), approximately the same size as the stomata, anticlinal walls straight, unbuttressed, smoothly textured, unornamented.

Indumentum. Glabrous.



Figure 59. 1-8. Stomatal complexes tangeticytic: CUT-Z-AJI, CUT-Z-FCC, and CUT-Z-EHI. 1. CUT-Z-AJI, TLM view showing stomatal complexes (SL2411, scale-bar = 50 μ m); 2. CUT-Z-AJI, TLM detail of two stomatal complexes (SB1293, scale-bar = 20 μ m); 3. CUT-Z-FCC, TLM view showing stomatal complexes (SL3010, scale-bar = 50 μ m); 4. CUT-Z-FCC, TLM detail of single stomatal complex (SL3010, scale-bar = 20 μ m). Note the wedge-shaped subsidiary cells; 5. CUT-Z-FCC, TLM view showing stomatal complexes (SL2531, scale-bar = 50 μ m); 6. CUT-Z-FCC, TLM detail of single stomatal complex (SL2531, scale-bar = 50 μ m); 7. CUT-Z-EHI, TLM view showing stomatal complexes (SL1576, scale-bar = 50 μ m). Note the distinctly raised OSLs; 8. CUT-Z-EHI, TLM detail of two stomatal complexes. The tangenticytic divisions are so close to the prominent outer stomatal ledges that they are usually obscured (SL1576, scale-bar = 20 μ m).

Group 14. Stomatal complexes prominently cyclocytic (developmentally tangenticytic) with prominent outer stomatal ledges

Key to cuticle with prominently cyclocytic complexes

- 1. Trichome attachment scars present. CUT-Z-EHI
- 1. Cuticle glabrous. 2.
- 2. Guard cell outlines difficult or impossible to see under TLM, outer stomatal ledges distinct but appearing to "float" over very thin guard cell cuticle under TLM. CUT-Z-FCC
- 2. Guard cell outlines generally clearly visible, outer stomatal ledges not "floating". 3.
- 3. Periclinal walls of subsidiary cells thicker than normal epidermal cells. CUT-Z-FBH
- 3. Periclinal walls of subsidiary cells thinner than normal epidermal cells. CUT-Z-AJI

CUT-Z-FBH

Figure 58.3-58.4

Reference Specimen and locality: SL2981, GL-26.

Stomatal complexes. Stomatal complexes in areoles, isolated, randomly oriented, cyclocytic, developmentally tangenticytic, size range unimodal. Subsidiary cells (4–8) typically elongate, or wedgelike, often with distinct polar cells (at right angles to the stomatal axis) which may 'enclose' the lateral cells, periclinal walls thicker than over normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, or ovate, outlined by a welldefined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 17–19 m (medium), with prominent T-piece thickenings at polar ends. Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over whole stoma, with an elliptical pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, smoothly textured, unornamented.

Indumentum. Glabrous.

CUT-Z-AJI Figure 59.1-59.2

Reference Specimen and locality: SB1293, Mata-03.

Referred specimens and occurrence: SL2411, BL-32.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, cyclocytic, developmentally tangenticytic, size range unimodal. Subsidiary cells (4–7, difficult to count under TLM) with periclinal walls thinner than that over normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, or ovate, outlined by a well-defined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 22–27 m (medium), clearly separated by polar walls. Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over centre of stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over veins not distinguished by shape), distinctly smaller than the stomata, anticlinal walls straight, unbut-tressed, smoothly textured, unornamented.

Indumentum. Glabrous.

CUT-Z-FCC

Figure 59.3-59.6

Reference Specimen and locality: SL3010, GL-28.

Referred specimens and occurrence: SL2531, BL-05; SL2087, GL-07.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, cyclocytic, or staurocytic (there are two rings of subsidiary cells, the inner has granular periclinal walls which are thinner than normal epidermal cells, while the outer are smooth, but thicker than normal epidermal cells), developmentally tangenticytic, size range unimodal (but with wide range of stomatal size). Subsidiary cells (4-5) sometimes forming 2 distinct polar cells (at right angles to stomatal orientation) and 2 lateral cells (parallel to stomatal orientation), smooth, unornamented. Guard cell pair outline difficult or impossible to see in TLM view, not outlined by a clear anticlinal wall, at same level as subsidiary cells, length 25-30 m (medium), with prominent T-piece thickenings at polar ends. Outer stomatal ledge elliptical, thicker than normal epidermal cells, extending over whole stoma, typically appearing under TLM to "float" within the much thinner cuticle over the rest of the guard cells, with a narrowly elliptic pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over major veins more elongate), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, smoothly textured, unornamented.



Figure 60. 1-6. Stomatal complexes anomocytic: CUT-Z-ADA and CUT-Z-ECF. 1. CUT-Z-ADA, TLM view showing networked stomatal complexes (SB1285, scale-bar = 50 μ m); 2. CUT-Z-ADA, TLM detail of single stomatal complex (SB1285, scale-bar = 20 μ m). Note the distinctly circular outline of the guard cell pair; 3. CUT-Z-ECF, TLM view showing stomatal complexes (SL0062, scale-bar = 50 μ m); 4. CUT-Z-ECF, TLM detail of single stomatal complex (SL0062, scale-bar = 20 μ m). Note the lemon-shaped outline of the OSL; 5. CUT-Z-ECF, SEM view of inner cuticular surface showing a single stomatal complex (S-1051, scale-bar = 20 μ m); 6. CUT-Z-ECF, SEM view of outer cuticular surface showing a single stomatal complex (S-1051, scale-bar = 20 μ m).

Indumentum. Attachment scars of deciduous trichomes common, more common over major veins, inserted between (4–6) epidermal cells modified by tangential divisions to form a sub-circular zone of foot cells having periclinal walls much thicker than normal epidermal cells, diameter much smaller than a normal epidermal cell.

CUT-Z-EHI Figure 59.7-59.8

Reference Specimen and locality: SL1576, Sthd-004.

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic, stomatal complexes evenly spread, isolated, randomly oriented, cyclocytic, all some, or none of the subsidiary cells may have been modified by a tangential division, develop-



Figure 61. 1-8. Cuticle apparently non-stomatiferous: CUT-Z-CFE, CUT-Z-EHC, CUT-Z-EIF, and CUT-Z-JIC. 1. CUT-Z-CFE, TLM view showing possible stomatal complexes (SL0321, scale-bar = 50 μ m); 2. CUT-Z-CFE, TLM detail of possible single stomatal complex (SL0321, scale-bar = 20 μ m). Note the slight thickening around the pit; 3. CUT-Z-EHC, TLM view showing possible stomatal complexes (SL1526, scale-bar = 50 μ m); 4. CUT-Z-EHC, TLM detail of possible stomatal complexes (SL1526, scale-bar = 50 μ m); 4. CUT-Z-EHC, TLM detail of possible stomatal complexes (SL2432, scale-bar = 20 μ m). Note the very smooth, raised rim; 5. CUT-Z-EIF, TLM view showing possible stomatal complexes (SL2432, scale-bar = 50 μ m); 6. CUT-Z-EIF, TLM detail of possible single stomatal complexes obscured by papillae (SB1395, scale-bar = 50 μ m); 8. CUT-Z-JIC, TLM detail of possible stomatal complexes obscured by papillae (SB1395, scale-bar = 20 μ m).

mentally tangenticytic, size range unimodal. Subsidiary cells (5–7) irregularly-shaped, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, outlined by a well-defined anticlinal wall, length 23–30 m (medium), underthrust by subsidiary cells (subsidiary cell anticlinal walls bisect outline of the guard cells), with prominent T-piece thickenings at polar ends. Outer stomatal ledge sub circular, same thickness as normal epidermal cells, distinctly raised, extending over whole stoma, with a broad, sub-circular pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells isodiametric (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls straight, unbuttressed, smoothly textured, unornamented.

Indumentum. Glabrous.

Glands. Glands present, compound, or large circular areas of very thinly cutinised cells (often broken away), surrounded by radiating files of normalthickness epidermal cells.

Distinguishing features. Distinguished from CUT-Z-CEF and CUT-Z-CFC by having stomatal complexes which are raised well above the level of epidermal cells.

Group 15. Stomatal complexes anomocytic

Key to anomocytic cuticle

- 1. Stomatal complexes networked, attachment scars of trichomes present. CUT-Z-ADA
- 1. Stomatal complexes isolated, glabrous. CUT-Z-ECF

CUT-Z-ADA

Figure 60.1-60.2

Reference Specimen and locality: SB1285, BL-33.

Stomatal complexes. Stomatal complexes in areoles, frequently networked, randomly oriented, anomocytic, size range unimodal, (but with wide range of stomatal size). Subsidiary cells (5–6) isodiametric, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline circular, outlined by a welldefined anticlinal wall, at same level as subsidiary cells (exposed on surface), length 20–30 m (medium), little polar development between guard cells (guard cells appear as continuous ring). Outer stomatal ledge sub circular, same thickness as normal epidermal cells, extending over whole stoma, with a broad, sub-circular pore. Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells highly variable from isodiametric to elongate (cells over both major and fine venation more elongate); approximately the same size as the stomata; anticlinal walls straight; unbuttressed; smoothly textured, unornamented.

Indumentum. Attachment scars of deciduous trichomes sparse; restricted to regions over veins; simple; inserted between (4–6) epidermal cells modified by tangential divisions to form a sub-circular zone of foot cells, scar diameter much smaller than a normal epidermal cell.

Distinguishing features. Distinguished from other taxa with networked stomatal complexes in having anomocytic stomatal complexes and very thin cuticle.

CUT-Z-ECF Figure 60.3-60.6

Reference Specimen and locality: SL0360, BL-05.

Referred specimens and occurrence: SL0062, Mata-18; SL1614, Sthd-106; SL1597, Sthd-108.

Stomatal complexes. Stomatal complexes evenly spread, isolated, randomly oriented, anisocytic, or anomocytic, size range unimodal. Subsidiary cells (4–5) irregularly-shaped, periclinal walls of same thickness as normal epidermal cells, smooth, unornamented. Guard cell pair outline elliptical, not outlined by a clear anticlinal wall, at same level as subsidiary cells (exposed on surface), length 28– 38 m (medium), at same level as subsidiary cells (exposed on surface), some wall development between guard cells, and sometimes development of T-piece thickenings at the poles. Outer stomatal ledge elliptical, sometimes lemon-shaped, thinner than normal epidermal cells, extending over whole stoma, with a narrowly elliptic pore.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM, normal cells elongate (cells over veins not distinguished by shape), approximately the same size as the stomata, anticlinal walls curved to wavy, unbuttressed, smoothly textured ornamented with discontinuous ridges, which probably correspond to epidermal cell walls.

Indumentum. Glabrous.

Group 16. Cuticle either non-stomatiferous or stomatal complexes very inconspicuous.

Key to non-stomatiferous cuticle.

1. Ornamented with prominent ridges or peltate scales. CUT-Z-JIC

- 1. Unornamented. 2.
- 2. Possible stomatal complexes surrounded by a double ring of subsidiary cells. CUT-Z-EIF
- 2. Possible stomatal complexes surrounded by distinct subsidiary cells. 3.
- 3. Possible stomatal complexes not surrounded by raised rings of cuticle. CUT-Z-CFE
- 2. Possible stomatal complexes surrounded by raised rings of cuticle. CUT-Z-EHC

CUT-Z-CFE

Figure 61.1-61.2

Reference Specimen and locality: SL0321, Harliwich-3.

Description. Cuticle with polygonal depressions or pits which may contain sunken stoma. The edges of the pits show diffuse thickening. Epidermal cells irregularly shaped, but typically isodiametric, distinctly straight-walled.

CUT-Z-EHC

Figure 61.3-61.4

Reference Specimen and locality: SL1526, Sthd-111.

Referred specimens and occurrence: SL1775, Sthd-022.

Description. Cuticle with scattered highly thickened, elliptical rings of cuticle, possibly stomata or trichome attachment sites. Epidermal cells isodiametric on one surface, but more elongate and organised into loose rows on the other.

CUT-Z-EIF

Figure 61.5-61.6

Reference Specimen and locality: SL2432, Sthd-051.

Description. Possible stomatal complexes surrounded by a double ring of subsidiary cells, with cuticle thinner than that over normal epidermal cells, guard cells probably deeply sunken. Epidermal cell anticlinal walls straight, epidermal cell texture smooth, unornamented

CUT-Z-JIC

Figure 61.7-61.8

Reference Specimen and locality: SB1395, BL-33.

Description. Stomatal distribution over leaf surfaces unknown, size range difficult to observe. Ornamented with prominent ridges or peltate scales. Epidermal cell flanges not clearly visible under TLM because of surface thickenings, normal cells unclear, anticlinal walls unclear, smoothly textured, unornamented.