

LAURACEAE MACROFOSSILS AND DISPERSED CUTICLE FROM THE MIOCENE OF SOUTHERN NEW ZEALAND

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ABSTRACT

Twenty-five species of Lauraceae cuticle are described from 120 fossil-bearing samples from two Early Miocene basins in southern New Zealand; the St Bathans Paleovalley of the Manuherikia Group, and the Gore Lignite Measures of the East Southland Group. The genera *Endiandra* and *Cryptocarya* are identified, which are no longer in the extant flora of New Zealand, and *Beilschmiedia* and *Litsea* which are in the extant flora. In the St Bathans Paleovalley it is likely that at least 22 species were growing as part of a single broader community. The presence of Lauraceae at this latitude in New Zealand and their high diversity clearly implies warmer temperatures than currently exist at lowland locations at that latitude today, which lie to the south of the existing limit of the family.

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INTRODUCTION

The Lauraceae has been regarded as a component of New Zealand plant fossil assemblages at least since Holden's (1982) work on the Early Miocene of Murchison. Pole described Lauraceae leaves from the Manuherikia Group (1993a) and from the Foulden Hills Diatomite (Pole 1996), also of Early Miocene. In the case of Holden, and for some of Pole's work, these were impression fossils, and the criteria that authors have used to identify leaf impressions as Lauraceae are generally poorly defined (although I think in Holden's case, correct). For instance, entire-margined leaves with an acrodromous development of venation (sensu Pole 1991), particularly if the higher order venation is strong and percurrent, have often been placed in the family. While this kind of leaf architecture can be found in other families, the cuticle has a distinctive structure (e.g., Bandulska 1925; Pal 1978; Avita and Inamdar 1981; Hill 1986; Bakker et al. 1992), and if it is preserved, not only can it help confirm the family identification, but it opens up the possibility of identification to generic level. Small fragments of cuticle mean that Lauraceae may be

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identified even without knowledge of the leaf architecture.

Cuticular preservation has shown that Lauraceae are an almost ubiquitous component of dispersed cuticle assemblages in New Zealand extending back to at least the Late Cretaceous (Pole 1993a and unpublished data). As now, Lauraceae seem to have been a common component of most rainforests. They also have relatively robust cuticle - if cuticle is preserved at all in a fossil assemblage, it is likely to include Lauraceae. Lauraceae are an excellent example of the macrofossil record complimenting the palynological record, as the pollen has thin exine, or has extremely limited production, so are essentially invisible palynologically (Erdtman 1952; Macphail 1980). Generic names applied to impressions of Lauraceae-like leaves must be suspect, as identification of extant material from leaf morphology alone is difficult, if not impossible (e.g., Hyland 1989). With the addition of cuticular information, identification of fossils to the Lauraceae has become routine. Hill (1986) noted that extant Australasian Lauraceae cuticle has a distinctive structure whereby the guard cells are typically overarched by a pair of subsidiary cells (a paracytic structure), and a cuticularised flange develops between the two cell types. This structure uniquely distinguishes Lauraceae from all other genera in the Laurales. However, as pointed out by Upchurch and Dilcher (1990), one other family includes species with this structure-the Myristicaceae. They also stated that Myristicaceae possess trichome bases that are distinct from those in Laurales. Based on my own cuticle reference collection covering about 4000 species in more than 1500 genera and 280 families, I can confirm this. Myristicaceae have multi-celled trichome bases, a morphology that shares some similarity to Proteaceae and Platanaceae (e.g., Carpenter et al. 2005). My reference collection and all published illustrations (e.g., Hill 1986; Christophel and Rowett 1996; Christophel et al. 1996; Vadala and Greenwood 2001) agree that extant Lauraceae have simple, poral trichome bases.

While identification of well-preserved fossils to family level is routine, identification to generic level is challenging. Workers who have identified fossils as Lauraceae with the aid of cuticle have generally described them using broad organ-genera, such as *Laurophyllum* Goepp. (e.g., Weyland and Kilpper 1963; Kvacek and Bužek 1966; Hill 1986; Kvacek 1988; Conran and Christophel 1998). In a few European cases they have been placed into extant genera (for example; Ferguson 1974; Bžek et al. 1996; Uzunova and Stojanova 1999). However, Christophel and Rowett (1996) and Christophel et al. (1996) have demonstrated that Australian Lauraceae genera can be distinguished based on cuticular morphology. This information has since been applied to Australian Lauraceae fossils (Vadala and Greenwood 2001). The purpose of this paper is to document the range of Early Miocene Lauraceae, and Lauraceae-like, cuticle morphology from two regions in southern New Zealand, the Manuherikia Group, and the Gore Lignite Measures.

MATERIALS AND METHODS

This study is based on 120 samples from two separate sedimentary basins in southern New Zealand (Figure 1). In central South Island, the sedimentology of the fluvial-lacustrine Manuherikia Group has been documented by Douglas (1986), and a range of associated plants and animal life was summarised by Pole et al. (2003). The oldest Manuherikia Group sediments are those of the St Bathans Member. These sediments accumulated within a braided river environment in broad valleys incised into a basement terrane of schist and greywacke (Douglas 1986). The St Bathans Member is overlain by meandering stream sediments and lake margin sediments of the Fiddlers and Kawarau Members, and finally by open lake sediments of the Bannockburn Formation.The Bannockburn Formation represents a single "Lake Manuherikia," which extended over 5600 square kilometers. It was eventually filled in by gravels of the Maori Bottom or Maniatoto Group in the Late Miocene-Pliocene as movement across the Australian-Pacific plate became more compressive (Douglas 1986; Youngson et al. 1998; Sutherland 1999).

The 58 samples studied here come from outcrops of the St Bathans Member, in the old goldsluicing areas of Blue Lake (sample numbers prefixed with "BL"), Grey Lake, about 2 km to the northeast (sample numbers prefixed with "GL"), and the bed of Mata Creek, about 3.5 km to the southeast of St Bathans (sample numbers prefixed with "Mata"). The fossils come from lenses of carbonaceous mud separated by quartzose gravels and probably all lay within a "St Bathans Paleovalley," which had been incised into the greywacke basement rock (Douglas 1986). The palynology of the St Bathans Member indicates an Early Miocene age (Mildenhall 1989; Mildenhall and Pocknall 1989), although perhaps an extension into the Oli-



Figure 1. Locality map. The upper map shows the main localities within the Manuherikia Group. The lower map shows the position of the drill holes in the Gore Lignite Measures.

gocene cannot be ruled out. Grid references to all samples are given in Appendix 1. Eight-digit grid references preceded by H41 (the map number) were estimated from field observations and are based on the New Zealand 1:50 000 Topographic Map 260 series. Fourteen-digit references were made with a Garmin Geko 301 GPS unit and are full coordinates in terms of the New Zealand metric map grid (UTM zone 59). A realistic accuracy for these figures would be around 10-15 horizontal metres. The stratigraphy within the St Bathans Member is complicated by the usual channeling in a fluvial environment and is the subject of ongoing research. At this stage brief comments are given which show the relative stratigraphic difference between nearby samples, or their estimated height above basement rock. Where available, New Zealand Geological Society Fossil Record numbers are given in brackets in the Stratigraphy column of the Appendix.

Further to the south, the lithostratigraphy of the Gore Lignite Measures has been documented by Isaac and Lindqvist (1990), who interpreted the unit as a large coastal delta and possibly represented the drainage point for the Manuherikia Group. The fossils have been obtained from a range of drill cores drilled as part of lignite exploration. The coal measures overlie and are intercalated with marine sediments. The associated marine invertebrates have facilitated their dating, which includes latest Oligocene and Early Miocene (Pocknall and Mildenhall 1984). The 62 samples studied here (prefixed by "Sthd-") all come from levels dated as Early Miocene. The location of all samples is given in Appendix 2. The drillcore number follows Isaac and Lindqvist (1990), and the location coordinates are taken directly from that publication (which should be consulted for the individual accuracy of these figures which varies from the nearest 0.1 of a metre to the nearest hundred metres). Sample depth is measured down from the top of the core.

Most St Bathans Member samples consisted of about 300 g with about half of that amount being prepared. However, 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 and up to one or two kilos from them will have been processed. The size of Gore Lignite Measure samples was significantly smaller than those from the St Bathans Member as they were limited by the diameter of the drill core (c. 50 mm) and the need to preserve the integrity of the core for future research. Sample size was about 50 g, and the amount of sediment prepared was about half of that.

Sediment samples were broken down using boiling water and hydrogen peroxide, sieving, and removal of silicates with hydrofluoric acid. Intact specimens of mummified leaves are removed at this point (if more clearing is needed, they may be again placed in hydrogen peroxide) and mounted within sheets of plastic using thymol glycerine jelly. Clean cuticle is prepared by warming for several hours in aqueous chromium trioxide, washing, then staining with Crystal violet, and finally mounting on glass slides with thymol glycerine jelly for transmitted light microscopy (TLM). Where sufficient additional material existed, it was mounted on SEM (scanning electron microscope) stubs with doublesided cellotape and coating with platinum. For the sake of brevity, with one exception, only the stomatal (abaxial) surfaces are illustrated.

In addition, at a few localities in the St Bathans Paleovalley intact leaves could be collected adhering to slabs of mudstone, or even gathered as they fell out when mudstone blocks were split. These specimens were also cleaned in hydrofluoric acid and gently cleared in weak hydrogen peroxide solution until the venation was visible. They were then mounted between sheets of clear plastic using glycerine jelly.

As discussed above, extant Australasian Lauraceae cuticle has a distinctive structure whereby the guard cells are typically overarched by a pair of subsidiary cells (a paracytic structure), and a cuticularised flange develops between the two cell types (Hill 1986). Trichome bases, when present, are simple and poral. If fossil cuticle has this structure, it is assumed here to be Lauraceae. However, in some taxa the guard cells are not below the subsidiary cells, but adjacent, for example Endiandra (see Christophel and Rowett 1996, Plate 2C). There are extant taxa that have a somewhat similar structure and might be confused with Lauraceae in the fossil record, for example, Hedycarya (Monimiaceae). Four of the fossil taxa described below are glabrous, so their trichome bases structure is unknown. This is not unusual amongst extant Lauraceae (at least on small fragments), and the small possibility that a few of the taxa described here do not belong in the Lauraceae would not seriously effect the conclusions of this paper.

Arriving at a practical conclusion to distinguish fragments of Lauraceae cuticle and consistently grouping them in over 120 samples has been the single most difficult job in this overall project (mostly due to subtle differences in morphology, such as the density of trichome bases preservation, and degree of staining). It is likely that some taxa distinguished here may include several closely related forms. As a result, overall diversity is likely to be underestimated. A key to the fossil cuticle is given as Appendix 3, and all descriptive taxonomy is given as Appendix 4. To keep morphological similar taxa together, the taxa are presented in the same order as found in the key. Leaf architecture and epidermal terminology follows Dilcher (1974); Hickey (1973); Hill (1986); and Pole (1991).

The taxonomic method I have adopted is to give each recognisable cuticle morphology and leaf morphology a parataxon code. As these parataxa are not Latin binomials they are entirely outside of the ICBN. The ICBN recognizes 'morphotaxa', but as these are Latin binomials, the term is not used here. My concept of parataxa is that they are essentially species for purposes of biodiversity, but nomenclatural they are like Linnaean species without the genus.

I name dispersed Lauraceae cuticle taxa with the prefix "CUT-L-" followed by a unique string of

three letters (see Carpenter and Pole 1995; Pole 1996, 1998, for examples of cuticle parataxon use). This gives some flexibility to a situation where there is little obvious hierarchy. Following Pole (1993b, and references therein) Manuherikia Group leaf parataxa are given the prefix "MANU-". For parataxa a reference specimen and reference locality is nominated, equivalent to holotype and type locality. A single "referred specimen" is also nominated from each of the other samples in which the taxon occurs.

Having separate parataxa for leaves and cuticle recognises that leaves (as impressions with only gross morphology and vein architecture) and cuticle (as dispersed fragments) are commonly encountered separately in the geological record. I reject the common paleobotanical practice of developing a system of Linnaean binomials for these fragments which overtly look comparable to 'true' Linnaean taxa and yet in many cases seem to be little more than a restatement of the family to which the fragment belongs (For instance *Laurophyllum*. I have used these in the past, but will no longer do so). In the few cases where identification with a Linnaean genus is possible, the Linnaean name is applied in addition to the parataxon code.

The prefixes "OU," "SB," and "SL" refer to specimens mounted on glass slides or between sheets of plastic. Scanning Electron Microscope stubs are prefixed with "S-". All material is housed in the Centre for Marine Studies, University of Queensland, except those prefixed by "OU," which are housed in the Geology Museum of the Otago University.

RESULTS

Twenty-five species of Lauraceae have been recognized in this study. For three of these species the leaf morphology is known, but the rest are known only as fragments of dispersed cuticle. Most species are very distinct, but several of them have a generalised morphology, which may include subtly different species, therefore this number is likely to be a minimum. Based on the criteria in Christophel and Rowett (1996) four genera of Lauraceae were identified; *Beilschmedia* (with buttressed epidermal cells), *Cryptocarya* (stomatal complexes with broad, prominent scales), *Endiandra* (with two distinct, semi parallel scales in the stomatal complexes), and *Litsea* (with papillate epidermal cells).

Ninety percent of all St Bathans samples had some Lauraceae cuticle, and those without Lauraceae tended to be low diversity samples dominated by the conifer Retrophyllum and the Myrtaceae taxon CUT-M-DID (probably a Syzygium, Pole unpublished). Although not quantified, Lauraceae cuticle, fragments of leaves, or intact leaves, were clearly dominant in most samples. Twenty-two Lauraceae taxa are present in the Paleovalley, with the highest number of Lauraceae in a single sample being 10 (BL-32). Among samples in which the family is present, the average number of Lauraceae taxa is three. Research in progress suggests that, with rare exceptions, the St Bathans Paleovalley assemblages probably come from a single broad community. That is, the 22 species would have been found growing contemporaneously over an area of a few square kilometers of the valley floor. As present-day communities with Lauraceae near their cold limits only have one or two species of the family, the diversity of Lauraceae in the St Bathans Paleovalley clearly indicates temperatures were well above the minimum limit for the family.

In Southland, 53% of fossiliferous samples had Lauraceae. Twelve taxa were present overall and the maximum number in one sample was four (Sthd-54). It is harder to generalise about fossiliferous samples that did not contain Lauraceae in Southland. Certainly some of them were simply samples of very low diversity.

Nine species (36%) are found in both the St Bathans Paleovalley and Southland, but only one of these (CUT-L-DFI) is among the most widespread taxa in either basin (Figure 2). That is, both areas had a distinctly different suite of dominant Lauraceae. This may be due to the major edaphic differences between the basins – the gravel dominated St Bathans Paleovalley, and the peat and clay-rich delta of the Southland coal measures. It is possible that what are perceived to be widespread, generalist species at the local level, may in fact be edaphic specialists, widespread only in the specific environments which typify each basin.

DISCUSSION

The fossil record clearly includes additional genera, to the two which exist in New Zealand today, *Beilschmiedia* and *Litsea*. The identification of *Endiandra* is the first record in New Zealand. The case for *Cryptocarya* is confirmed, though this was fairly clear from the impressions of Holden (1982). The great diversity of the remaining cuticle suggests other genera were almost certainly present, perhaps ones now globally extinct. Conversely, neither of the two extant New Zealand genera is unequivocally present as fossils. Notable



Figure 2. The number of samples that Lauraceae taxa have been recorded in (restricted to those found in more than five samples in either area).

too, is that one extant genus in Australia with distinctive cuticle, *Cinnamomum*, has not been found as fossils in these deposits, and also some of the more distinctive species groups found today in Australia (for example the *Endiandra jonesii* group, Christophel and Rowett 1996).

The current mean annual temperature for St Bathans (about 550 m above sea level) is in the order of 8 C (recording station at Ranfurly, 40 km to the east; this and following temperatures courtesy of Department of Geography, University of Otago, and NIWA, online). However, this depressed temperature reflects the mountainous and continental situation and a more realistic comparison with the low-lying topography of the Early Miocene would be coastal stations at equivalent latitudes. For instance, Oamaru Airport has a mean annual temperature of 10.6 C. In Southland, Invercargill Airport has a mean annual temperature of 9.7 C. Given the similar temperatures that Lauraceae extend to on tropical mountains, it is likely to be winter minima which are limiting Lauraceae in southern New Zealand today. Given the high diversity of the fossils, it seems clear that mean annual temperatures at the fossil localities were warmer than what they are now (southern New Zealand was at higher latitudes in the early Miocene, around 50-51 S; Lawver and Gahagan 2003). In broad terms, annual temperatures were probably similar to the rainforests of southeastern Queensland today, around 12-18 C (Hijmans et. al 2005). The presence of Lauraceae places a lower limit on

warmth and usually is an indication of moist conditions. For instance the southern limit in New Zealand today is just south of Cook Straight, at about 42 S (Wardle 1991), where mean annual temperatures are about 12 C (Department of Geography, University of Otago, and NIWA, online). The altitudinal limit of Beilschmiedia tawa at 41S is about 1500 m (Wardle 1964). In Australia the southern limit of broad-leaved Lauraceae is the northern edge of Bass Straight at around 39 S (Cameron 1987; Helman 1987; Mills 1987; the leafless Cassytha is present in Tasmania) at about 14.5 C (Hijmans et. al 2005). In South Africa Lauraceae extend along the wettest fringe to the southernmost part of the country (Palgrave 1995) and in South America to about 40-41S and about 11C MAT (for example, species lists in Fraver et al. 1999; Veblen et al. 1979). In more tropical latitudes the altitudinal limits may reach cooler mean annual temperatures. For instance, the upper limit of Lauraceae on Mt Emei, China, is at about 8 C (Tang and Ohsawa 1997, 1999) and on Mt Kerinci, Sumatra (Ohsawa et al. 1985). Species diversity drops towards these southern boundaries and although only one or two species exist in these regions (for instance only three species occur in all of New Zealand today), they may dominate the biomass. In tropical rainforests Lauraceae tend to be much less prominent as biomass is shared amongst many more families.

Lauraceae are typically components of a rainforest, and in Australia, with the exception of Cassytha, they are absent from vegetation with a firebased ecology. In warmer areas as rainfall decreases, but fire remains absent, dry rainforests persist, but beyond some moisture limit, broadleaved Lauraceae disappear. For instance, they are absent from the dry rainforest at Forty Mile Scrub, north Queensland, where mean annual temperature is about 23 C and mean annual rainfall is about 800 mm, but about 80% of this falls within a four-month period (Fensham 1996). More uncommonly, Lauraceae may be prominent in drier regions, for example in the sclerophyllous vegetation of Chile (Ramirez et al. 2004). The presence of a high diversity of Lauraceae most likely indicates wet, fire-free conditions. All the St Bathans samples considered here come from a stratigraphic level below indications of significant dry periods and below the evidence of widespread fire in the Manuherikia Group (Pole and Douglas 1998; Pole 2003).

Lauraceae diversity may also be a good proxy for biodiversity. In the rainforests of Australia the

proportion of Lauraceae species shows a highly statistically significant positive relationship to total tree species within any given vegetation sample (Figure 3, y = 4.1703x + 36.169, $R^2 = 0.2681$, no apparent pattern in the residuals; based on plot data accumulated by Floyd 1990; Tracey 1982; and unpublished data by D.W. Butler and W. Macdonald stored in the Queensland Herbarium, Brisbane). Why this should be so is an interesting question about how vegetation communities are assembled and is something for future research, but the diversity relationship suggests a way in which total tree diversity for the source vegetation of a fossil assemblage can be estimated. The 10 Lauraceae species in sample BL-32 suggest a total tree diversity of at least 45 trees in the source or pool community. While it is not statistically valid to extend this relationship beyond the range of data, increasing the sample areas of modern vegetation would obtain a higher number of Lauraceae, but this would simply mean incorporating the smaller areas which have been used in Figure 3. The proportion of Lauraceae to trees would remain. Simple 'eye-balling' of the relationship suggests that the total number of Lauraceae species in the St Bathans Paleovalley (22) indicates a minimum number of tree species in the valley in the order of about 120. Even the possibility that one or two of these taxa are not Lauraceae, still results in a high estimation of tree biodiversity. Some support for this estimate comes from work in progress (Pole 1997 and unpublished) that has distinguished over 170 taxa of broad-leaved dicotyledons (mostly from dispersed cuticle) from the St Bathans Paleovalley. This figure can be placed in the context of about 550 trees, shrubs, and climbers in New Zealand today, about 132 of which qualify as trees (Eagle 1978). This estimate of very high local Early Miocene diversity is in line with that suggested by palynological research. Mildenhall and Pocknall (1989) reported that over 90 pollen and spore species were present in a single sample from drill 2071, near Roxburgh, most of which are likely to have been growing in the local area.

SUMMARY

Lauraceae were an almost ubiquitous component of vegetation in the fluvial environment of the Early Miocene of the St Bathans Paleovalley and the deltaic Gore Coal Measures of southern New Zealand. Twenty-five species are recognised here, far higher than the three species which exist in the northern parts of New Zealand today. The genera recognised include *Beilschmiedia*, *Cryptocarya*,



Figure 3. The total number of tree species in vegetation samples of Australian rainforest compared with the number of Lauraceae species (based on plot data accumulated by Floyd 1990; Tracey 1982; and unpublished data by D.W. Butler and W. Macdonald stored in the Queensland Herbarium, Brisbane).

Endiandra, and *Litsea*. Several unidentified taxa do not resemble any known extant taxa and may well represent extinct genera. Both regions had a distinctive suite of dominant Lauraceae taxa, with only a little overlap.

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REFERENCES

- Avita, S., and Inamdar, J.A. 1981. Stomatal complex in Lauraceae: structure and ontogeny. Acta Botanica Indica, 9:50-56.
- Bakker, M.E., Gerritsen, A.F., and van der Schaaf, P.J. 1992. Leaf anatomy of *Cinnamonum schaeffer* (lauraceae) with special reference to oil and mucilage cell. *Blumea*, 37:1-30.
- Bandulska, H. 1925. On the cuticles of some fossil and recent Lauraceae. *Journal of the Linnean Society, Botany*, 47:383-425.

- Bžek, C., Holý, F., and Kvaek, Z. 1996. Early Miocene flora of the Cyprus shale (Western Bohemia). Acta Musei Nationalis Pragae, Series B Historia Naturalis, 52:1-72.
- Cameron, D.G. 1987. Temperate rainforests of East Gippsland, p. 33-46. In Werren, G. and Kershaw, A.P. (eds.) The rainforest legacy. Australian national rainforests study. Vol. 1. Australian Government Publishing Service, Canberra.
- Carpenter, R.J., and Pole, M.S. 1995. Eocene plant fossils from the Lefroy and Cowan paleodrainages, western Australia. *Australian Systematic Botany* 8:1107-1154.
- Carpenter, R.J., Hill, R.S., and Jordan, G.J. 2005. Leaf cuticular morphology links Platanaceae and Proteaceae. *International Journal of Plant Science*, 166:843-855.
- Christophel, D.C., and Rowett, A.I. 1996. Leaf and cuticle atlas of Australian leafy Lauraceae. *Flora of Australia Supplementary Series Number 6*. Canberra, Australian Biological Resources Study.
- Christophel, D.C., Kerrigan, R., and Rowett, A.I. 1996. The use of cuticular features in the taxonomy of the Lauraceae. *Annals of the Missouri Botanical Garden*, 83:419-432.
- Conran, J.G., and Christophel, D.C. 1998. A new species of triplinerved *Laurophyllum* from the Eocene of Nerriga, New South Wales. *Alcheringa*, 22:343-348.

- Department of Geography, University of Otago, and NIWA. New Zealand Climate Summaries. From "Summaries of Climatological Observations to 1980," New Zealand Meteorological Service [online] [cited 27 March 2006]. Available at: http://www.geography.otago.ac.nz/nzclimate/tableselectnew.php3.
- Dilcher, D.L. 1974. Approaches to the identification of angiosperm leaf remains. *The Botanical Review*, 40:1-157.
- Douglas, B.J. 1986. Lignite resources of Central Otago. New Zealand Energy Research and Development Committee Publication, P104.
- Eagle, A. 1978. 100 Trees of New Zealand: Botanical Paintings and Notes. Collins, Auckland.
- Erdtman, G. 1952. Pollen Morphology and Plant Taxonomy: Angiosperms. Almqvist and Wiksell, Stockholm.
- Fensham, R.J. 1996. The floristics and structure of dry rainforest at Forty Mile Scrub National Park, north Queensland. *Cunninghamia*, 4:483-495.
- Ferguson, D.K. 1974. On the taxonomy of Recent and fossil species of *Laurus* (Lauraceae). *Botanical Journal of the Linnean Society*, 68:572-605.
- Floyd, A.G. 1990. Australian rainforests in New South Wales. Surrey Beatty and Sons in association with National Parks and Wildlife Service of New South Wales, Chipping Norton, N.S.W.
- Fraver, S., Gonzalez, M.E., Silla, F., Lara, A., and Gardner, M. 1999. Composition and structure of remnant *Fitzroya cupressoides* forests of southern Chile's Central Depression. *Journal of the Torrey Botanical Society*, 126:49-57.
- Helman, C. 1987. Rainforest in southern New South Wales. p. 47-70. In Werren, G. and Kershaw, A.P. (eds.) The rainforest legacy. Australian national rainforests study. Vol. 1. Australian Government Publishing Service, Canberra.
- Hickey, L.J. 1973. Classification of the architecture of dicotyledonous leaves. *American Journal of Botany*, 60:17-33.
- Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones and A. Jarvis, 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology, 25: 1965-1978
- Hill, R.S. 1986. Lauraceous leaves from the Eocene of Nerriga, New South Wales. *Alcheringa*, 10:327-351.
- Holden, A.M. 1982. Fossil Lauraceae and Proteaceae from the Longford Formation, Murchison, New Zealand. Journal of the Royal Society of New Zealand, 12:79-80.
- Hyland, B.P.M. 1989. A revision of Lauraceae in Australia (excluding *Cassytha*). *Australian Systematic Botany*, 2:135-367.
- Isaac, M.J. and Lindqvist, J.K. 1990. Geology and lignite resources of the East Southland Group, New Zealand. New Zealand Geological Survey Bulletin n.s., 101:1-202.
- Kvacek, Z. 1988. The Lauraceae of the European Paleogene, based on leaf cuticles. *Courier Forschungsinstitut Senckenberg*, 107:345-354.

- Kvacek, Z. and Bužek, C. 1966. Einige insteressante Lauraceen und Symplocaceen des nordbohemischen Tartiars. Vestnik Usredniho Ustav Geologickeho, 41:291-294.
- Lawver, L.A. and Gahagan, L.M. 2003. Evolution of Cenozoic seaways in the circum-Antarctic region. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 198:11-37.
- Macphail, M.K. 1980. Fossil and modern *Beilschmiedia* (Lauraceae) pollen in New Zealand. *New Zealand Journal of Botany*, 18:453-457.
- Mildenhall, D.C. 1989. Summary of the age and paleoecology of the Miocene Manuherikia Group, Central Otago, New Zealand. *Journal of the Royal Society of New Zealand*, 19:19-29.
- Mildenhall, D.C. and Pocknall, D.T. 1989. Miocene-Pleistocene spores and pollen from Central Otago, South Island, New Zealand. *New Zealand Geological Survey Palaeontological Bulletin*, 59:1-128.
- Ohsawa, M., Nainggolan, P., Tanaka, M., and Anwar, C. 1985. Altitudinal zonation of forest vegetation on Mount Kerinci, Sumatra: with comparisons to zonation in the temperate region of East Asia. *Journal of Tropical Ecology*, 1:193-216.Mills, K. 1987. The distribution, character and conservation status of the rainforests of the Illawarra district, New South Wales, p. 71-94. In Werren, G. and Kershaw, A.P. (eds.) *The rainforest legacy. Australian national rainforests study. Vol.* 1. Australian Government Publishing Service, Canberra.
- Pal, S. 1978. Epidermal studies in some Indian Lauraceae and their taxonomic significance. *Acta Botanica Indica*, 6:68-73.
- Palgrave, K.C. 1995. *Trees of Southern Africa*. Struik Publishers, Cape Town.
- Pocknall, D.T. and Mildenhall, D.C. 1984. Late Oligocene -Early Miocene spores and pollen from Southland, New Zealand. New Zealand Geological Survey Paleontological Bulletin, 51:1-66.
- Pole, M.S. 1991. A modified terminology for angiosperm leaf architecture. *Journal of the Royal Society of New Zealand*, 21:297-312.
- Pole, M.S. 1993a. Early Miocene flora of the Manuherikia Group, New Zealand. 6. Lauraceae. *Journal* of the Royal Society of New Zealand, 23:303-312.
- Pole, M.S. 1993b. Early Miocene flora of the Manuherikia Group, New Zealand. 10. Paleoecology and stratigraphy. *Journal of the Royal Society of New Zealand*, 23:393-426.
- Pole, M.S. 1996. Plant macrofossils from the Foulden Hills Diatomite (Miocene), Central Otago, New Zealand. *Journal of the Royal Society of New Zealand*, 26:1-39.
- Pole, M.S. 1997. Miocene conifers from the Manuherikia Group, New Zealand. *Journal of the Royal Society of New Zealand*, 27:355-370.
- Pole, M.S. 1998. The Proteaceae Record in New Zealand. *Australian Systematic Botany* 11: 343-372.

- Pole, M.S. 2003. New Zealand climate in the Neogene and implications for global atmospheric circulation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 193:69-84.
- Pole, M.S. and Douglas, B.J. 1998. A quantitative palynostratigraphy of the Miocene Manuherikia Group, New Zealand. *Journal of the Royal Society of New Zealand*, 28:405-420.
- Pole, M.S., Douglas, B.J., Mason, G. 2003. The terrestrial Miocene biota of southern New Zealand. *Journal* of the Royal Society of New Zealand, 33:415-426.
- Ramirez, C., San Martin, C., San Martin, J., and Villasenor, R. 2004. Phytosociological comparisons of Belloto (*Beilschmiedia*, Lauraceae) forests in central Chile, *Bosque*, 25:69-85.
- Sutherland, R. 1999. Cenozoic bending of New Zealand basement terranes and Alpine Fault displacement: a brief review. *New Zealand Journal of Geology and Geophysics*, 42:295-301.
- Tang, C.Q. and Ohsawa, M. 1997. Zonal transition of evergreen, deciduous, and coniferous forests along the altitudinal gradient on a humid subtropical mountain, Mt Emei, Sichuan, China. *Plant Ecology*, 133:63-78.
- Tang, C.Q. and Ohsawa, M. 1999. Altitudinal distribution of evergreen broad-leaved trees and their leaf-size pattern on a humid subtropical mountain, Mt. Emei, Sichuan, China. *Plant Ecology*, 145:221-233.
- Tracey, J.G. 1982. The Vegetation of the Humid Tropical Region of North Queensland. CSIRO, Melbourne.

- Upchurch, G.R., Jr. and Dilcher, D.L. 1990. Cenomanian angiosperm leaf megafossils, Dakota Formation, Rose Creek locality, Jefferson County, southeastern Nebraska. *US Geological Survey Bulletin,* 1915: 1-52.
- Uzunova, K. and Stojanova, R. 1999. Anatomically grounded new taxonomical point of view to *Laurophyllum pseudoprinceps*-complex. *Documenta naturae*, 126:7-19.
- Vadala, A.J. and Greenwood, D.R. 2001. Australian Paleogene vegetation and. environments: evidence for palaeo-Gondwanic elements in the fossil records of Lauraceae and Proteaceae, p. 201-226. In Metcalfe, I., Smith, J.M.B., Morwood, M., and Davidson, I. (eds.), Faunal and floral migration and evolution in SE Asia-Australasia. A.A. Balkema, Lisse.
- Veblen, T.T., Ashton, D.H., and Schlegel, F.M. 1979. Tree regeneration strategies in a lowland *Nothfagus*-dominated rainforest in south-central Chile. *Journal of Biogeography*, 6:329-340.
- Wardle, P. 1964. Facets of the distribution of forest vegetation in New Zealand. *New Zealand Journal of Botany*, 2:352-366.
- Wardle, P. 1991. *Vegetation of New Zealand*. Cambridge University Press, Cambridge.
- Weyland, H. and Kilpper, K. 1963. Kritishe Untersuchungen zur Kuticularanalyse Tertiär Blätter VI. *Palaeontographica Abt*. B, 113:93-116.
- Youngson, J.H., Craw, D., Landis, C.A., and Schmitt, K.R. 1998. Redefinition and interpretation of late Miocene-Pleistocene terrestrial stratigraphy, Central Otago, New Zealand. *New Zealand Journal of Geology and Geophysics*, 41:51-68.

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	
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	

APPENDIX 1. ST BATHANS PALEOVALLEY, MANUHERIKIA GROUP SAMPLES

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	
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	

APPENDIX 2. GORE LIGNITE MEASUES, 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
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

APPENDIX 3. KEY TO DISPERSED CUTICLE OF LAURACEAE BASED ON CHARACTERS VISIBLE USING TLM

1. Epidermal cells papillate. 2.

1. Epidermal cells not papillate. 5.

2. More than one papilla per epidermal cell, or papillae lobed **CUT-L-EEH**

2. A single papilla per epidermal cell. 3.

3. Whole surface of each epidermal cell raised up as a papilla **CUT-L-DFI**

3. Discrete papilla in the middle of each epidermal cell. 4.

4. Massive thickening along stomatal pore/stomatal ledges **CUT-L-DEJ**

4. Details of stomatal ledge not visible CUT-L-ECI

5. Epidermal cell walls sinuous. 6.

5. Epidermal cell walls not sinuous. 11.

6. Massive thickening along stomatal pore/stomatal ledges **CUT-L-DEC**

6. Stomatal ledges thin, not massively thickened. 7.

7. Epidermal cells not buttressed CUT-L-DCA

7. Epidermal cells buttressed. 8.

8. Stomatal complexes distinctly rounded and surrounded by a thick wall. 9.

8. Stomatal complexes not distinctly rounded and surrounded by a wall of normal thickness. 10.

9 Cuticular scales butterfly-like, no distinct pattern of cells around complex **CUT-L-EHE**

9. Cuticular scales thin, paired epidermal cells on either side of complex **CUT-L-EEB**

10. Subsidiary cell periclinal walls distinctly thinner than normal epidermal cells, complex often broadly diamond-shaped **CUT-L-EHD**

10. Subsidiary cell periclinal walls distinctly thicker than normal epidermal cells, sometimes granular, complex often narrower than broad **CUT-L-FJD**

11. Cuticular scales clearly visible and butterfly-like. 12.

11. Cuticular scales not clearly butterfly-like, may be indistinct. 14.

12. Epidermal cell anticlinal walls not visible, periclinal walls very granular **CUT-L-FJA**

12. Epidermal cell anticlinal walls distinct, periclinal walls not granular. 13.

13. Scales smaller than the subsidiary cells CUT-L-DFA

13. Scales extending over most of subsidiary cells CUT-L-DGA

14. Scales appearing double, subsidiary cells much thinner than epidermal cells **CUT-L-DBD**

14. Cuticular scales narrow, or not visible. 15.

15. Trichomes persistent CUT-L-DCC

15. Trichomes deciduous. 16.

16. Stomatal complexes small-sized. 17.

16. Stomatal complexes medium-sized. 18.

17. Complex rounded, trichome bases with flanges not strongly thickened CUT-L-DBH

17. Complex polygonal, trichome bases with very thick flanges **CUT-L-EEF**

Subsidiary cells darker than epidermal cells.
19.

18. Subsidiary cells lighter than or same thickness as epidermal cells. 20.

19 Complex often flattened at polar ends, shows no sign of an anisocytic style of division in surrounding epidermal cells **CUT-L-EED**

19. Complexes often have a wedge-shaped outline, often shows an anisocytic style of division in surrounding epidermal cells **CUT-L-EEG**

20. Complexes polygonal CUT-L-ECB

20. Complexes rounded. 21.

21. Stomatal pore obviously granular, trichome bases sparse **CUT-L-DGD**

21. Stomatal pore not granular, trichome bases remarkably dense **CUT-L-EHG**

APPENDIX 4. DESCRIPTIVE TAXONOMY

CUT-L-EEH Fig. 4

Reference specimen and locality: SL1607, Sthd-108.

Referred specimens and occurrence: SL3179, BL-01; SL2626, BL-07; SL2258, BL-15; SL1174, GL-01; SL2674, GL-04; SL2137, GL-08; SL3286, Mata-03; SL1550, Sthd-002; SL1577, Sthd-004; SL1747, Sthd-016; SL1727, Sthd-017; SL1774, Sthd-022; SL1793, Sthd-029; SL1960, Sthd-054; SL1905, Sthd-074; SL2020, Sthd-087; SL1850, Sthd-088; SL1813, Sthd-100.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces unknown; stomatal complexes in clear areoles; isolated; randomly oriented; paracytic; outline rounded, but irregular; length 16–22 m (medium); stomatal size range bimodal, with distinct 'giant stomatal complexes' present. Subsidiary cell periclinal cuticle thinner than over normal epidermal cells, smooth, unornamented. Guard cells overarched by subsidiary cells; Stomatal pore slitlike; cuticular scales narrow; not clear. **Epidermal Cells**. Epidermal cell flanges clearly visible using TLM; cells over fine venation distinguished as 'venal' (elongated); normal epidermal cells isodiametric; walls straight; unbuttressed.

Indumentum. Outer surface smooth; unornamented; with scars of trichome bases and papillose. Papillae present over all normal epidermal cells, and some, but not all, venal cells; 1–4 papillae per cell; formed by the projection of a discrete region within the boundaries of the epidermal cell; smooth. Trichomes sparse; restricted to regions over veins; deciduous (and therefore trichome type unknown); inserted between epidermal cells; diameter generally smaller than a normal epidermal cell; epidermal cells around trichome base modified with thickened poral rim and radial walls, radially elongated as distinct foot cells (5–6); trichome bases sometimes paired.

Distinguishing features. The multi-headed papillae make CUT-L-EEH distinct from all the other Lauraceae taxa.

Identification. Not similar to any species illustrated by Christophel and Rowett (1996). No extant



Figure 4. CUT-L-EEH; (A) TLM view of stomatal complexes, SL1607, scale: 50 m; (B) TLM view of a stomatal complex (lower right) and a trichome base (centre). Note multi-headed papillae, SL1607, scale: 20 m; (C) Inner SEM view of stomatal complexes and papillate epidermal cells, S-1052, scale: 20 m; (D) Outer SEM view showing papillae and obscure stomata, S-1052, scale: 20 m.

species of Australasian Lauraceae appear to have multi-lobed papillae.

CUT-L-DFI (*Cryptocarya* sp.) Fig. 5

Reference specimen and locality: SL0242, BL-04.

Referred specimens and occurrence: SL2530, BL-05; SL2452, BL-32; SL2656, GL-04; SL2912, GL-21; SL2955, GL-25; SL3001, GL-27; SL0065, Mata-18; SL1561, Sthd-004; SL1735, Sthd-017; SL1883, Sthd-073; SL1596, Sthd-108; SL2079, Sthd-113.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic; stomatal complexes in clear areoles; isolated; randomly oriented; paracytic; outline rounded, but irregular; length 10–15 m (small); stomatal size range unimodal with a small range. Subsidiary cell periclinal cuticle thinner than over normal epidermal cells; smooth; unornamented. Guard cells overarched by subsidiary cells. Stomatal pore slit-like; cuticular scales



Figure 5. CUT-L-DFI; (A) TLM view of stomatal complexes and (upper left) a trichome base, SL0242, scale: 50 m; (B) TLM view of stomatal complexes, SL1883, scale: 50 m; (C) TLM view of stomatal complexes, clearly showing "butterfly" like scales, SL0242, scale: 20 m; (D) Inner SEM view of stomatal complex. Note distinct scales, S-1040, scale: 10 m; (E) Inner SEM view. Note scales virtually covering the subsidiary cells, S-1088, scale: 10 m; (F) Outer SEM view showing each epidermal cell which is raised up as a single papillae and clearly visible stomatal complexes, S-1088, scale: 20 m.

'butterfly-like', about two-thirds the length of the subsidiary cells.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM; cells over fine venation distinguished as 'venal' (elongated); normal epidermal cells isodiametric; walls sinuous, or curved or wavy; unbuttressed.

Indumentum. Outer surface smooth; unornamented; with scars of trichome bases and papillose. Papillae present over all epidermal cells; 1 papilla per cell; formed by the entire outer surface of the epidermal cell projecting upwards; smooth. Trichomes common; scattered over venal and nonvenal regions; deciduous (and therefore trichome type unknown); inserted between epidermal cells; diameter similar in size to a normal epidermal cell; epidermal cells around trichome base (6–9) modified with thickened poral rim and radial walls, forming a distinct ring of isodiametric foot cells.

Non-stomatal surface. Epidermal cells isodiametric; polygonal; cells over veins not distinguished. Simple trichome bases present.

Distinguishing features. The epidermal cells which are entirely raised up as papillae make CUT-L-DFI distinct from all the other Lauraceae taxa.

Identification. The distinct cuticular scales suggest *Cryptocarya*, although the broadly papillate nature of the epidermal cells is unlike any extant Australasian species (Christophel and Rowett 1996). It is probably an extinct species of *Cryptocarya*.

Reference specimen and locality: SL3147, GL-01.

Referred specimens and occurrence: SL2220, GL-12.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces unknown; stomatal complexes evenly spread; isolated; randomly oriented; paracytic; outline typically broader than long; length 25–30 m (medium); stomatal size range unimodal with a small range. Subsidiary cell periclinal cuticle not distinct in thickness from normal epidermal cells; smooth; unornamented. Guard cells overarched by subsidiary cells; Stomatal pore plugged; cuticular scales narrow, but massively thickened; full length



Figure 6. CUT-L-DEJ; (A) TLM view of stomatal complexes, SB0850, scale: 50 m; (B) TLM view of s ingle stomatal complex surrounded by papillae, SB0850, scale: 20 m; (C) Inner SEM view of stomatal complex (note the massive thickenings along the stomatal pore) and papillate epidermal cells, S-1208, scale: 20 m; (D) Outer SEM view showing large papillae and a stomatal complex which is clearly visible and has the subsidiary cells raised, S-1208, scale: 20 m.

of subsidiary cells (appearing very distinct under TLM).

Epidermal Cells. Epidermal cell flanges not clearly visible under TLM; cells over major veins distinguished as 'venal' (elongated); normal epidermal cells unclear; walls unclear; unbuttressed.

Indumentum. Outer surface smooth; unornamented; papillose. Papillae present over all epidermal cells; 1 papilla per cell; formed by the projection of a discrete region within the boundaries of the epidermal cell; smooth.

Distinguishing features. CUT-L-DEJ has discrete papillae within the bounds of the epidermal cell outline. This is similar to CUT-L-ECI but cuticle thickness/robustness is much less.

Identification. The broad, well-defined papillae are similar to four species of *Litsea* (*L. bennettii* B. Hyland, *L. breviumbellata* C.K. Allen, *L. connorsii* B.Hyland, *L. leefeana* (F. Muell.) Merr.) as illustrated by Christophel and Rowett (1996) and indicate identity with that genus.

CUT-L-ECI Fig. 7

Reference specimen and locality: SL1678, Sthd-033.

Referred specimens and occurrence: SL1763, Sthd-011; SL1610, Sthd-108.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces unknown; stomatal complexes evenly spread; isolated; randomly oriented; paracytic; outline typically broader than long; length c. 35 m (medium); stomatal size range unimodal with a small range. Subsidiary cell periclinal cuticle not distinct in thickness from normal epidermal cells; smooth; unornamented. Guard cells overarched by subsidiary cells; Stomatal pore plugged; cuticular scales narrow; not clear.

Epidermal Cells. Epidermal cell flanges not clearly visible under TLM; cells over veins not distinguished by shape; normal epidermal cells unclear; walls unclear; unbuttressed.

Indumentum. Outer surface smooth; unornamented; papillose. Papillae present over all epider-



Figure 7. CUT-L-ECI; (A) TLM view of stomatal complexes. Note prominent papillae, SL1678, scale: 50 m; (B) TLM view of s ingle stomatal complex surrounded by papillae, SL1678, scale: 20 m; (C) Inner SEM view of stomatal complex. Note massive thickening around papillae, S-1053, scale: 20 m; (D) Outer SEM view showing papillae and an obscure stomatal pore, S-1053, scale: 20 m.

mal cells; (probably) just 1 papilla per cell; formed by the projection of a discrete region within the boundaries of the epidermal cell; smooth.

Distinguishing features. CUT-L-ECI has discrete papillae within the bounds of the epidermal cell outline. This is similar to CUT-L-DEJ but cuticle thickness/robustness is much greater.

Identification. The thick-walled papillae are similar to *Cryptocarya mackinnoniana* F.Muell. and *Endiandra palmerstonii* (F.M.Bailey) C.T. White & W.D.Francis as illustrated by Christophel and Rowett (1996), but nothing else about the fossil is

convincingly similar. Its generic identity remains unclear.

Reference specimen and locality: SL0250, BL-04.

Referred specimens and occurrence: SL1278, BL-05; SL3084, BL-28; SL1311, BL-32; SL1181, GL-01; SL2657, GL-04; SL2099, GL-07; SL2134, GL-08; SL2162, GL-09; SL2215, GL-12; SL2826, GL-16; SL2841, GL-18; SL2892, GL-20; SL3103,



Figure 8. CUT-L-DEC; (A) TLM view of stomatal complexes, SL0250, scale: 100 m; (B) TLM of stomatal complex. Note massive thickening, SL0250, scale: 20 m; (C) TLM view of stomatal complexes. Note the more granular texture than the previous specimen, SL1835, scale: 50 m; (D) TLM detail of stomatal complexes, SL1835, scale: 20 m; (E) Outer SEM view. Note the highly granular surface. The stomatal complex is subdued but easily visible, S-1107, scale: 20 m; (F) Inner SEM view. Note massive thickening around stomatal pores, S-1107, scale: 20 m.

GL-24; SL2959, GL-25; SL2980, GL-26; SL2994, GL-27; SL2546, Mata-23; SL1827, Sthd-095.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic; stomatal complexes in clear areoles; isolated; randomly oriented; paracytic; outline typically broader than long; length 25– 30 m (medium); stomatal size range unimodal with a small range. Subsidiary cell periclinal cuticle not distinct in thickness from normal epidermal cells; granular; unornamented. Guard cells overarched by subsidiary cells; Stomatal pore massively thickened and with prominent T-piece thickenings at polar ends; cuticular scales narrow, but massivelythickened; full length of subsidiary cells (appearing very distinct under TLM).

Epidermal Cells. Epidermal cell flanges clearly visible using TLM; cells over major veins distinguished as 'venal' (isodiametric); normal epidermal cells highly variable from isodiametric to elongate; walls sinuous, or curved or wavy; unbuttressed to buttressed.

Indumentum. Outer surface coarsely granular; unornamented; with scars of trichome bases. Trichomes sparse; distribution not clear; deciduous (and therefore trichome type unknown); inserted between epidermal cells.

Non-stomatal surface. Epidermal cells isodiametric; polygonal; cells over veins not distinguished.

Distinguishing features. CUT-L-DEC is immediately recognisable based on its sinuous epidermal cell walls, the massive thickening around the stomatal; pores, and granular texture.

Identification. The massively thickened stomatal aperture region is quite unlike anything illustrated by Christophel and Rowett (1996) and this fossil

probably belongs to an extinct (at least locally) genus.

CUT-L-DCA Fig. 9

Reference specimen and locality: SL0414, Mata-03.

Referred specimens and occurrence: SL0232, BL-04; SB1284, BL-33; SL2954, GL-25; SL2017, Sthd-010.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces unknown; stomatal complexes in clear areoles; isolated; randomly oriented; paracytic; outline typically broader than long; length 18– 21 m (medium); stomatal size range unimodal with a small range. Subsidiary cell periclinal cuticle thinner than over normal epidermal cells; smooth; unornamented. Guard cells overarched by subsidiary cells; Stomatal pore slit-like; cuticular scales narrow.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM; cells over fine venation distinguished as 'venal' (elongated); normal epidermal cells isodiametric; walls sinuous; relatively thin, unbuttressed.

Indumentum. Outer surface smooth; unornamented; with scars of trichome bases;. Trichomes common; restricted to regions over veins; deciduous (and therefore trichome type unknown); inserted between epidermal cells; diameter similar in size to a normal epidermal cell; epidermal cells around trichome base (5–8) modified with thickened poral rim and radial walls, radially elongated as distinct foot cells.



Figure 9. CUT-L-DCA; (A) TLM view of stomatal complexes and (upper right) a trichome base, SL0414, scale: 50 m; (B) TLM of single stomatal complex, SL0414, scale: 20 m.

Distinguishing features. CUT-L-DCA is recognised by its thin, sinuous epidermal cell walls.

Identification. None of the species illustrated by Christophel and Rowett (1996) are particularly similar.

CUT-L-EHE Fig. 10

Reference specimen and locality: SL1759, Sthd-012.

Referred specimens and occurrence: SL0308, BL-01; SB1340, BL-32.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic; stomatal complexes in clear areoles; isolated; randomly oriented; paracytic; outline circular; length 15–23 m (medium); stomatal size range unimodal with a small range. Subsidiary cell periclinal cuticle thinner than over normal epidermal cells; smooth; unornamented. Guard cells overarched by subsidiary cells; Stomatal pore slit-like; cuticular scales 'butterfly-like'; about one-third the length of the subsidiary cells.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM; cells over fine venation distin-

guished as 'venal' (elongated); normal epidermal cells isodiametric; walls sinuous, or straight; slightly buttressed.

Indumentum. Outer surface smooth; unornamented; with scars of trichome bases. Trichomes sparse; distribution not clear; deciduous (and therefore trichome type unknown); inserted between epidermal cells; diameter generally smaller than a normal epidermal cell; epidermal cells around trichome base (seven) modified with thickened poral rim and radial walls, unmodified in shape.

Non-stomatal surface. Epidermal cells highly variable from isodiametric to elongate; walls slightly wavy; cells over veins distinguished by being longer and staining much darker than normal epidermal cells.

Distinguishing features. Recognisable by the very rounded outline of the stomatal complexes in combination with slightly wavy epidermal cell walls.

Identification. None of the species illustrated by Christophel and Rowett (1996) is particularly similar.



Figure 10. CUT-L-EHE; (A) TLM view of stomatal complexes, SL1759, scale: 50 m; (B) TLM of two stomatal complexes. Note small scales, SL1759, scale: 20 m; (C) Outer SEM view showing raised subsidiary cells and otherwise very subdued surface, S-1244, scale: 20 m; (D) Inner SEM view of stomatal complex, showing distinct scales, S-1244, scale: 10 m.

CUT-L-EEB

Fig. 11

Reference specimen and locality: SL1857, Sthd-088.

Referred specimens and occurrence: SL2163, GL-09; SL1786, Sthd-029; SL2027, Sthd-087.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces unknown; stomatal complexes in clear areoles; isolated; randomly oriented; paracytic; outline rounded, but irregular; length 16–21 m (medium); there often appears to be a pair of epidermal cells, one on either side of the stomatal complex, which are probably part of the complex in the broader sense; stomatal size range unimodal with a small range. Subsidiary cell periclinal cuticle not distinct in thickness from normal epidermal cells; smooth; unornamented. Guard cells overarched by subsidiary cells; Stomatal pore slit-like; cuticular scales narrow; not clear.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM; cells over fine venation distinguished as 'venal' (elongated); normal epidermal cells isodiametric; walls sinuous; buttressed.

Indumentum. Outer surface smooth; unornamented; glabrous.

Distinguishing features. Recognisable by the very rounded outline of the stomatal complexes in combination with sinuous and buttressed epidermal cell walls and also the pair of epidermal cells on either side of the stomatal complex.

Identification. The distinctive pair of epidermal cells on either side of most stomatal complexes makes this taxon distinct to any of the species illustrated by Christophel and Rowett (1996).

CUT-L-EHD Fig. 12

Reference specimen and locality: SL1953; Sthd-051.

Referred specimens and occurrence: SL0102, BL-08; SL2534, BL-33; SL2821, GL-16; SL2074, Sthd-113.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces unknown; stomatal complexes evenly spread; isolated; randomly oriented; paracytic; out-line typically broader than long; length 20–27 m



Figure 11. CUT-L-EEB; (A) TLM view of stomatal complexes, SL2125, scale: 50 m; (B) TLM of single stomatal complex, SL1857, scale: 20 m; (C) Outer SEM view showing slightly raised subsidiary cells and generally subdued surface, S-1067, scale: 20 m; (D) Inner SEM view of stomatal complex showing large scales, S-1067, scale: 20 m.

(medium); stomatal size range bimodal, with distinct 'giant stomatal complexes' present. Subsidiary cell periclinal cuticle thinner than over normal epidermal cells; smooth; unornamented. Guard cells overarched by subsidiary cells; Stomatal pore slitlike; cuticular scales double; very small.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM; cells over major veins distinguished as 'venal' (elongated); normal epidermal cells isodiametric; walls sinuous, or curved or wavy; buttressed.

Indumentum. Outer surface smooth; unornamented; glabrous, or with scars of trichome bases. Trichomes sparse; deciduous (and therefore trichome type unknown); inserted between epidermal cells; epidermal cells around trichome base (3–9) modified with massively thickened poral rim, unmodified in shape.

Distinguishing features. Distinguished by the sinuous and buttressed epidermal cells in combination with a stomatal complex which has very thin cuticle over the subsidiary cells.

Identification. The sinuous and buttressed abaxial epidermal cells are found today in *Beilschmiedia*, *Cryptocarya* and *Endiandra* (Christophel and

Rowett 1996). Not similar to any species illustrated by Christophel and Rowett (1996).

CUT-L-FJD (*Beilschmiedia* sp.) Fig. 13

Reference specimen and locality: SL2498, BL-09.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces unknown; stomatal complexes in clear areoles; isolated; randomly oriented; paracytic; outline rounded, but irregular; length 8–10 m (small); development type often appear to be epidermal cells on either side of the stomatal complexes which are probably part of the complex in the broader sense; stomatal size range unimodal with a small range. Subsidiary cell periclinal cuticle not distinct in thickness from normal epidermal cells; granular; unornamented. Guard cells overarched by subsidiary cells; Stomatal pore slit-like; cuticular scales broad; full length of subsidiary cells (appearing very distinct under TLM).

Epidermal Cells. Epidermal cell flanges clearly visible using TLM; cells over major veins distin-



Figure 12. CUT-L-EHD; (A) TLM view of stomatal complexes, SL1953, scale: 50 m; (B) TLM of two stomatal complexes. Note the very thin cuticle over the subsidiary cells, SL1953, scale: 20 m; (C) Outer SEM view showing very distinct, but sunken stomatal complexes in an otherwise featureless surface, S-1243, scale: 20 m; (D) Inner SEM view of poorly preserved stomatal complexes, S-1243, scale: 20 m.



Figure 13. CUT-L-FJD; (A) TLM view of stomatal complexes, SL2498, scale: 50 m; (B) TLM of single stomatal complex, SL2498, scale: 20 m.

guished as 'venal' (elongated); normal epidermal cells highly variable from isodiametric to elongate; walls curved or wavy; buttressed.

Indumentum. Outer surface smooth; unornamented; with scars of trichome bases. Trichomes sparse; restricted to regions over veins; deciduous (and therefore trichome type unknown); inserted between epidermal cells; diameter generally smaller than a normal epidermal cell; epidermal cells around trichome base (6–7) modified with massively thickened poral rim, radially elongated as distinct foot cells.

Distinguishing features. Distinguished by the buttressed (but not sinuous) epidermal cell walls in combination with broad scales.

CUT-L-DFA and MANU-3 (*Cryptocarya* sp.) Identification. The buttressed epidermal cells and the broadly thickened subsidiary cells indicate this taxon is likely *Beilschmiedia* (cf. *B. brunnea* B. Hyland illustrated by Christophel and Rowett 1996).

Figs. 14, 15

MANU-3

Reference specimen and locality: OU29163, F41/f235 Bannockburn.

Referred specimen and locality: SL1494, GL-01.

Note. The mummified specimens found in this study fit the description of leaf parataxon MANU-3 described in Pole (1993a) reasonably well. There may be subtle differences in leaf shape, and much



Figure 14. CUT-L-DFA and MANU-3; (A) Mummified leaf, SL1494, scale: 10 mm; (B) Detail of venation, SL1494, scale: 5 mm; (C); Mummified leaf, SL1499, scale: 10 mm (D) Mummified leaf SL1497 scale: 10 mm.

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larger leaves were typical at the reference locality. A larger collection from the St Bathans Paleovalley may eventually show a distinct but probably closely related taxon.

CUT-L-DFA

Reference specimen and locality: SL1494, GL-01.

Referred specimens and occurrence: SL1349, BL-05; SL0095, BL-08; SL2272, BL-16; SL2115, GL-07; SL2132, GL-08; SL2174, GL-09; SL2193, GL-10; SL2915, GL-21; SL2917, GL-22; SL2933, GL-23; SL2948, GL-25; SL2987, GL-27; SL3255, GL-31; SL3033, GL-32.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic; stomatal complexes in clear areoles; isolated; randomly oriented; paracytic; outline polygonal; length 18–30 m (medium); stomatal size range unimodal with a small range. Subsidiary cell periclinal cuticle not distinct in thickness from normal epidermal cells; smooth; unornamented. Guard cells overarched by subsidiary



Figure 15. CUT-L-DFA; (A) TLM view of stomatal complexes and (lower right) a trichome base, SL1494, scale: 50 m; (B) TLM detail of two stomatal complexes. Note prominent scales, SL1494, scale: 20 m; (C) TLM of adaxial surface showing distinctly darker staining venal epidermal cells, SL1494, scale: 50 m; (D)TLM of stomatal complexes, SL1499, scale: 50 m; (E) Inner SEM view of stomatal complex with distinct scales, S-1565, scale: 10 m; (F) Outer SEM view of a stomatal complex identifiable only as a patch of granular cuticle (i.e., the pore has been largely plugged), S-1565, scale: 10 m.

cells; Stomatal pore slit-like; cuticular scales 'butterfly-like'; full length of subsidiary cells (appearing very distinct under TLM).

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

Indumentum. Outer surface smooth; unornamented; glabrous.

Non-stomatal surface. Epidermal cells isodiametric; polygonal; cells over veins not distinguished. Simple trichome bases present.

Distinguishing features. CUT-L-DFA has smallmoderately sized "butterfly" shaped scales in combination with smooth and wavy-walled epidermal cells. The adaxial epidermis is very distinctive in having venal epidermal cells which stain much darker than the normal epidermal cells.

Identification. The small stomatal complexes with broad scales are broadly similar to some species of *Cryptocarya* (e.g. *C. vulgaris* B.Hyland) as illustrated by Christophel and Rowett (1996), and probably belong in that genus.

CUT-L-DGA (*Cryptocarya* sp.) Fig. 16

Reference specimen and locality: OU30306; Mata-01.

Referred specimens and occurrence: SL0303, BL-01; SL0245, BL-04; SL2632, BL-15; SL2267, BL-16; SL2285, BL-18; SL2305, BL-21; SL1310, BL-32; SL2679, GL-04; SL2117, GL-07; SL2153, GL-09; SL2181, GL-10; SL2195, GL-11; SL2212, GL-12; SL2845, GL-18.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic; stomatal complexes in clear areoles; isolated; randomly oriented; paracytic; outline rounded, but irregular; length 12–20 m (medium); stomatal size range unimodal with a small range. Subsidiary cell periclinal cuticle thicker than over normal epidermal cells; smooth; unornamented. Guard cells overarched by subsidiary cells; Stomatal pore slit-like; cuticular scales 'butterfly-like'; full length of subsidiary cells (appearing very distinct under TLM).

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

cells highly variable from isodiametric to elongate; walls curved or wavy; unbuttressed.

Indumentum. Outer surface smooth; unornamented; with scars of trichome bases. Trichomes sparse; restricted to regions over veins; deciduous (and therefore trichome type unknown); inserted between epidermal cells; diameter generally larger than a normal epidermal cell; epidermal cells around trichome base (5–7) unthickened, unmodified in shape.

Non-stomatal surface. Epidermal cells isodiametric, unbuttressed; cells over veins somewhat distinguished by being more aligned, but not elongated. Sparse trichome bases present.

Distinguishing features. CUT-L-DGA is distinguished by having large "butterfly" scales, making the subsidiary cells appear much darker under TLM than CUT-L-DFA.

Note. This cuticle was originally described by Pole (1993a) under the name *Laurophyllum longfordiensis* (Holden) Pole, which was based on a mummified leaf. Following the convention used here, the cuticle is given its own parataxon code, CUT-L-DGA.

Identification. Pole (1993a) placed mummified material, as well as impressions named as *Cryptocarya* by Holden (1982) into the organ-genus *Laurophyllum* Goeppert and gave it the leaf parataxon code MANU-1. I wrote that the cuticle key to the Australian Lauraceae Christophel and Rowett (1996) was still being developed, and that it would be prudent to retain the specimens in the more non-committal taxon until it was published. This now being the case, the case for *Cryptocarya*, as concluded by Holden (1982) based on leaf architecture is confirmed, and all material should be placed in *Cryptocarya*.

CUT-L-FJA (*Cryptocarya* sp.) Fig. 17

Reference specimen and locality: SL2125, GL-08.

Referred specimens and occurrence: SL2520, BL-31.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces unknown; stomatal complexes in clear areoles; isolated; randomly oriented; paracytic; outline circular; length 17–22 m (medium); stomatal size range unimodal with a small range.



Figure 16. CUT-L-DGA; (A) TLM view of stomatal complexes, SL0303, scale: 50 m; (B) TLM of two stomatal complexes. Note the darker areas corresponding to the broad scales, as well as darker, granulated thickenings along the stomatal pores, SL0303, scale: 20 m; (C) Inner SEM view of several stomatal complexes. Note very prominent scales, S-1116, scale: 20 m; (D) Outer SEM view, S-1116, scale: 20 m; (E) Inner SEM view of stomatal complex with large scales, S-1085, scale: 10 m; (F) Outer SEM view of a stomatal complex. Note granular thickening along the pore, S-1085, scale: 10 m.

Subsidiary cell periclinal cuticle thinner than over normal epidermal cells; smooth; unornamented. Guard cells overarched by subsidiary cells; Stomatal pore slit-like; cuticular scales 'butterfly-like'; about two-thirds the length of the subsidiary cells.

Epidermal Cells. Epidermal cell flanges not clearly visible under TLM; cells over fine venation distinguished as 'venal' (elongated); normal epidermal cells unclear; walls curved or wavy; unbuttressed.

Indumentum. Outer surface granular; unornamented; with scars of trichome bases. Trichomes common; scattered over venal and non-venal regions; deciduous (and therefore trichome type unknown); inserted between epidermal cells; diameter similar in size to a normal epidermal cell; epidermal cells around trichome base (6–8) modified with thickened poral rim and radial walls, forming a distinct ring of isodiametric foot cells.

Distinguishing features. CUT-L-FJA looks similar to CUT-L-DFA, but is distinguished by the very granular texture of the cuticle.

Identification. The distinct scales suggest *Cryptocarya* (Christophel and Rowett 1996).



Figure 17. CUT-L-FJA; (A) TLM view of stomatal complexes, SL2125, scale: 50 m; (B) TLM of stomatal complex. Note distinct scales, SL2125, scale: 20 m; (C) Inner SEM view of stomatal complex. Note granular surface, S-1405, scale: 10 m; (D) Outer SEM view of a stomatal complex. The outline is subdued and the rest of the surface almost featureless, S-1405, scale: 10 m.

CUT-L-DBD and MANU-33 (*Endiandra* sp.) Fig. 18

MANU-33

Reference specimen and locality: SL4710, GL-01.

Description

Lamina length 42-c. 80 mm; width 10–32 mm. Shape elliptic; apex acute; base decurrent; margin entire; midrib generally straight and lamina symmetrical. Development normal. Venation externodromous. First order lateral veins relatively thin; irregularly spaced; alternate; angle of divergence obtuse; notably decurrent on midvein in lower part of lamina; straight until curving at the loops. Basal laterals not paired. Second order venation cascade. Third order venation dendritic with freely ending veinlets. No fimbrial marginal vein.

Distinguishing features. Clearly distinguished from all other Manuherikia Group leaf taxa in the irregularly spaced latera I veins and dendritic finer veins.

CUT-L-DBD

Reference specimen and locality: SL1349, BL-32.

Referred specimens and occurrence: SL2698, BL-06; SL0101, BL-08; SL2461, BL-09; SL2263, BL-16; SL3079, BL-28; SL3165, BL-33; SL1518, GL-01; SL1191, GL-02; SL0418, GL-09; SL2214, GL-12; SL2829, GL-17; SL2 47, GL-18; SL3105, GL-24; SL3014, GL-28; SL4925, Mata-01.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces unknown; stomatal complexes in clear areoles; isolated; randomly oriented; paracytic; outline typically broader than long; length 28–30 m (medium); stomatal size range unimodal with a small range. Subsidiary cell periclinal cuticle thinner than over normal epidermal cells; smooth; unornamented. Guard cells overarched by subsidiary cells; Stomatal pore slit-like; cuticular scales double; full length of subsidiary cells (appearing very distinct under TLM).

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



Figure 18. CUT-L-DBDand MANU-33; (A) Intact leaf, SL4710, scale: 10 mm; (B) Detail of venation, SL4710, scale: 5 mm; (C) Intact leaf, SL4921, scale: 10 mm; (D) Intact leaf, SL4922, scale: 10 mm; (E) Intact leaf, SL4920, scale: 10 mm; (F) TLM view of stomatal complexes, SL4710, scale: 50 m; (G) TLM of stomatal complex. Note distinct "double" scales, SL4710, scale: 20 m; (H) Outer SEM view showing distinct, but sunken stomatal complexes in an otherwise surface, S-1532, scale: 10 m; (I) Inner SEM view of stomatal complex, S-1532, scale: 10 m.

cells highly variable from isodiametric to elongate; walls curved or wavy; unbuttressed.

Indumentum. Outer surface smooth; unornamented; with scars of trichome bases. Trichomes common; scattered over venal and non-venal regions; deciduous (and therefore trichome type unknown); inserted between epidermal cells; diameter generally smaller than a normal epidermal cell; epidermal cells around trichome base (5–6) modified with massively thickened poral rim, unmodified in shape. **Distinguishing features**. CUT-L-DBD is easily distinguished by the stomatal complexes which stain lighter than the surrounding epidermal cells, and the distinctive "double" cuticular scales.

Identification. The two distinct, semi parallel scales ("scales double") strongly suggest identity with *Endiandra* (Christophel and Rowett 1996).

CUT-L-DCC Fig. 19

Reference specimen and locality: SB1307, Mata-03.

Referred specimens and occurrence: SB0881, GL-01; SL0331, Mata-23.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces unknown; stomatal complexes in clear areoles; isolated; randomly oriented; paracytic; outline rounded, but irregular; length 14–19 m (medium); stomatal size range unimodal with a small range. Subsidiary cell periclinal cuticle not distinct in thickness from normal epidermal cells; smooth; unornamented. Guard cells overarched by subsidiary cells; Stomatal pore plugged; cuticular scales narrow; full length of subsidiary cells (appearing very distinct under TLM).

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

Indumentum. Outer surface smooth; unornamented; with scars of trichome bases. Trichomes abundant; scattered over venal and non-venal regions; persistent, but all cases broken off near base; inserted between epidermal cells; diameter similar in size to a normal epidermal cell; epidermal cells around trichome base (6–8) modified with massively thickened poral rim, radially elongated as distinct foot cells.

Distinguishing features. Easily recognised by the very thick walls of epidermal cells and stomatal complexes in combination with persistent trichomes.

Identification. The overall robust construction and persistent trichome bases make this taxon distinct from any of the species illustrated by Christophel and Rowett (1996).



Figure 19. CUT-L-DCC; (A) TLM view of stomatal complexes and trichomes, SB1307, scale: 50 m; (B) TLM of stomatal complexes and (upper and lower right) two trichomes, SB1307, scale: 20 m; (C) Outer SEM view showing distinctly raised stomatal complexes, S-1103, scale: 20 m; (D) Inner SEM view of stomatal complex. Note essential absence of scales but massive thickening around stomatal pore, S-1103, scale: 10 m.

CUT-L-DBH Fig. 20

Reference specimen and locality: SB1306, Mata-03.

Referred specimens and occurrence: SL1489, BL-30; SL1761, Sthd-011.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic; stomatal complexes in clear areoles; isolated; randomly oriented; paracytic; outline rounded, but irregular; length 13–17 m (medium), or (small-medium); stomatal size range unimodal with a small range. Subsidiary cell periclinal cuticle not distinct in thickness from normal epidermal cells; smooth; unornamented. Guard cells overarched by subsidiary cells; Stomatal pore slit-like; cuticular scales very narrow; very small.

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

Indumentum. Outer surface smooth; unornamented; with scars of trichome bases. Trichomes common; restricted to regions over veins; deciduous (and therefore trichome type unknown); inserted between epidermal cells; diameter generally smaller than a normal epidermal cell; epidermal cells around trichome base (5–8) unthickened, unmodified in shape.

Non-stomatal surface. Epidermal cells isodiametric; polygonal; cells over veins not distinguished.

Distinguishing features. CUT-L-DBH has a very bland-looking epidermis under TLM. It has relatively small stomatal complexes, no differential staining, and unremarkable scales. It is essentially recognisable by this blandness.

Identification. The small, indistinct stomatal complexes are distinct from any of the species illustrated by Christophel and Rowett (1996).

CUT-L-EEF Fig. 21

Reference specimen and locality: SL1663, Sthd-040.

Referred specimens and occurrence: SL2277, BL-17; SL2291, BL-18; SL2096, GL-07; SL1298, BL-32; SL1756, Sthd-012; SL1545, Sthd-069.



Figure 20. CUT-L-DBH; (A) TLM view of stomatal complexes, SB1306, scale: 50 m; (B) TLM of stomatal complexes, SB1306, scale: 20 m; (C) Inner SEM view of stomatal complexes. Note absence of scales, S-1120, scale: 20 m.; (D) Outer SEM view showing raised outlines of epidermal cells surrounding stomatal complexes and (upper left) a trichome base, S-1120, scale: 20 m.



Figure 21. CUT-L-EEF; (A) TLM view of stomatal complexes and darker trichome bases, SL1663, scale: 50 m; (B) TLM of stomatal complexes, SL1663, scale: 20 m.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic; stomatal complexes evenly spread; isolated; randomly oriented; paracytic; outline polygonal; length 11–15 m (small); stomatal size range unimodal with a small range. Subsidiary cell periclinal cuticle thicker than over normal epidermal cells; smooth; unornamented. Guard cells overarched by subsidiary cells; Stomatal pore slit-like; cuticular scales narrow; not clear.

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

Indumentum. Outer surface smooth; unornamented; with scars of trichome bases. Trichomes common; scattered over venal and non-venal regions; deciduous (and therefore trichome type unknown); inserted between epidermal cells; diameter similar in size to a normal epidermal cell; epidermal cells around trichome base (6–7) modified with thickened poral rim and radial walls, unmodified in shape.

Non-stomatal surface. Epidermal cells isodiametric; polygonal; cells over veins not distinguished.

Distinguishing features. CUT-L-EEF is distinguished by its small, almost rectangular stomatal complexes.

Identification. The very small stomatal complexes are not similar to any of the species illustrated by Christophel and Rowett (1996).

CUT-L-EED Fig. 22

Reference specimen and locality: SL1659, Sthd-040.

Referred specimens and occurrence: SL2249, BL-14; SB0873, GL-01; SL2669, GL-04; OU30177, Mata-01; SL1562, Sthd-004; SL1748, Sthd-016; SL1729, Sthd-017; SL2005, Sthd-020; SL1958, Sthd-054; SL1884, Sthd-073; SL1621, Sthd-106; SL2443, Sthd-110.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic; stomatal complexes evenly spread; isolated; randomly oriented; paracytic; outline typically broader than long; length 28– 32 m (medium); stomatal size range unimodal with a small range. Subsidiary cell periclinal cuticle thicker than over normal epidermal cells; granular; unornamented. Guard cells overarched by subsidiary cells; Stomatal pore slit-like; cuticular scales narrow; full length of subsidiary cells (appearing very distinct under TLM).

Epidermal Cells. Epidermal cell flanges clearly visible using TLM; cells over major veins vaguely or inconsistently distinguished (elongate) as 'venal'; normal epidermal cells isodiametric; walls straight; unbuttressed.

Indumentum. Outer surface smooth; unornamented; glabrous.

Glands. Possible hydathodes present, as cells with much thinner periclinal walls surrounded by 5–6 epidermal cells.

Non-stomatal surface. Epidermal cells isodiametric; polygonal; cells over veins not distinguished.



Figure 22. CUT-L-EED; (A) TLM view of stomatal complexes, SL1659, scale: 50 m; (B) TLM of two stomatal complexes, SL1659, scale: 20 m; (C) Inner SEM view of stomatal complex. Note the narrow scales, S-1042, scale: 20 m; (D) Outer SEM view of a subdued but clearly visible stomatal complex, S-1042, scale: 20 m.

Distinguishing features. CUT-L-EED is recognisable by a combination of size (stomatal complexes are relatively large), staining (the subsidiary cells stain rather darkly, but just like the surrounding epidermal cells), and texture (under TLM the periclinal walls appear flecked, although this does not have any apparent expression under SEM).

Identification. Not similar to any species illustrated by Christophel and Rowett (1996).

CUT-L-EEG Fig. 23

Reference specimen and locality: SL1903, Sthd-073.

Referred specimens and occurrence: SL1352, BL-05; SL2466, BL-09; SL0417, GL-09; SL2192, GL-10; SL2206, GL-11; SL2235, GL-12; SB1383, BL-32; SL1551, Sthd-002; SL1755, Sthd-012; SL1749, Sthd-016; SL1728, Sthd-017; SL1715, Sthd-018; SL1790, Sthd-029; SL1686, Sthd-032; SL1675, Sthd-033; SL1950, Sthd-051; SL1959, Sthd-054; SL1971, Sthd-055; SL1907, Sthd-074; SL1877, Sthd-078; SL2023, Sthd-087; SL1821, Sthd-091; SL1617, Sthd-106.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic; stomatal complexes in clear areoles; isolated; randomly oriented; paracytic; outline typically broader than long; length 14–21 m (medium); development type in many cases the stomatal complex has clearly been blocked out by a series of oblique, intersecting cell divisions which form 3–4 cells around the stomatal complexes (comparable to an anisocytic subsidiary cell arrangement); stomatal size range unimodal with a small range. Subsidiary cell periclinal cuticle thicker than over normal epidermal cells; smooth; unornamented. Guard cells overarched by subsidiary cells; Stomatal pore slit-like; cuticular scales narrow; not clear.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM; cells over fine venation distinguished as 'venal' (elongated); normal epidermal cells elongated; walls curved or wavy; unbuttressed.

Indumentum. Outer surface smooth; unornamented; with scars of trichome bases. Trichomes common; restricted to regions over veins; decidu-



Figure 23. CUT-L-EEG; (A) TLM view of stomatal complexes, SL1903, scale: 50 m; (B) TLM of stomatal complex. Note "anisocytic" arrangement of epidermal cells around the complex, SL1903, scale: 20 m; (C) Outer SEM view showing two clear trichome bases in a bumpy surface in which stomatal complexes are obscured, S-1041, x1000; (D) Inner SEM view of stomatal complex. Note absence of scales and massive thickening around pore, S-1041, scale: 10 m.

ous (and therefore trichome type unknown); inserted between epidermal cells; diameter generally smaller than a normal epidermal cell; epidermal cells around trichome base unthickened, radially elongated as distinct foot cells (5–7); trichome base expanding abruptly from insertion.

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

Distinguishing features. Easily identifiable by the pattern of epidermal cells surrounding the stomata; complexes, which appear to have been produced in an "anisocytic" pattern. In a true anisocytic pattern, subsidiary cells and the stomata are blocked out by a series of walls which leaves the stomata surrounded by there or four subsidiary cells of unequal size. In CUT-L-EEG the same process seems apparent, but with an entire stomatal complex (subsidiary cells and guard cells) being surrounded by the three or four cells. The subsidiary cells are typically stained much darker than the epidermal cells.

Identification. The distinct pattern of epidermal cells surrounding the stomatal complexes makes this taxon clearly different from any of the species illustrated by Christophel and Rowett (1996).

CUT-L-ECB (?*Beilschmiedia* sp.) Fig. 24

Reference specimen and locality: SL0339, Mata-23.

Referred specimens and occurrence: SL0283, BL-01; SL0231, BL-04; SL2470, BL-09; SL2286, BL-18; SL3045, BL-22; SL3051, BL-24; SL3061, BL-25; SL3094, BL-29; SL1488, BL-30; SL2408, BL-32; SL2533, BL-33; SL1175, GL-01; SL1189, GL-02; SL2150, GL-09; SL2242, GL-11; SL2241, GL-12; SL2828, GL-16; SL2837, GL-17; SL2846, GL-18; SL2911, GL-21; SL2974, GL-26; SL2985, GL-27; SL3008, GL-28; SL3025, GL-29; SL0412, Mata-01; OU30204, Mata-01; SB1305, Mata-03; SL1257, Mata-06.



Figure 24. CUT-L-ECB; (A) TLM view of stomatal complexes, SL0339, scale: 50 m; (B) TLM of two stomatal complexes, SL0339, scale: 20 m; (C) Inner SEM view of stomatal complexes, S-1378, scale: 10 m; (D) Outer SEM view showing clear stomatal complexes and clearly defined epidermal cells, S-1378, scale: 10 m.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic; stomatal complexes in clear areoles; isolated; randomly oriented; paracytic; outline polygonal; length 15–20 m (medium); stomatal size range unimodal with a small range. Subsidiary cell periclinal cuticle thinner than over normal epidermal cells; smooth; unornamented. Guard cells overarched by subsidiary cells; Stomatal pore slit-like; cuticular scales narrow; very small.

Epidermal Cells. Epidermal cell flanges clearly visible using TLM; cells over major veins distinguished as 'venal' (elongated); normal epidermal cells isodiametric; walls straight; unbuttressed.

Indumentum. Outer surface smooth; unornamented; with scars of trichome bases. Trichomes common; scattered over venal and non-venal regions; deciduous (and therefore trichome type unknown); inserted between epidermal cells; diameter generally smaller than a normal epidermal cell; epidermal cells around trichome base (5–6) modified with thicker periclinal walls near the trichome, forming a distinct ring of isodiametric foot cells.

Distinguishing features. Distinguished by the epidermal cells which have a polygonal outline and

are raised outwards, although not in my opinion, like papillae (cf. CUT-L-DFI). **Non-stomatal sur-face.** Epidermal cells isodiametric; polygonal; cells over veins not distinguished. Simple trichome bases present.

Identification. The polygonal outline of the stomatal complexes is distinct from any of the species illustrated by Christophel and Rowett (1996), although some species of *Beilschmiedia* (e.g. *B. collina* B.Hyland) may come closest.

Reference specimen and locality: SL0343, Mata-23.

Referred specimens and occurrence: SL2231, GL-12; SL2940, GL-23.

Description

Stomatal complexes. Stomatal distribution over leaf surfaces unknown; stomatal complexes in clear areoles; isolated; randomly oriented; paracytic; outline rounded but typically with sharp vertices; length 15–17 m (medium); stomatal size range unimodal with a small range. Subsidiary cell



Figure 25. CUT-L-DGD; (A) TLM view of stomatal complexes, SL0156, scale: 50 m; (B) TLM of stomatal complexes. Note prominent granular thickenings along stomatal pores, SL0156, scale: 20 m; (C) Inner SEM view, S-1377, scale: 10 m; (D) Outer SEM view showing three trichome bases, reasonably defined epidermal cell outline sand obscured stomatal complexes, S-1377, x600.

periclinal cuticle not distinct in thickness from normal epidermal cells; smooth; unornamented. Guard cells overarched by subsidiary cells; Stomatal pore surrounded by thickened, granular cuticle (probably plugged); cuticular scales butterflylike; not clear under TLM.

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

Indumentum. Outer surface smooth; unornamented; with scars of trichome bases. Trichomes common; scattered over venal and non-venal regions; deciduous (and therefore trichome type unknown); inserted between epidermal cells; diameter generally smaller than a normal epidermal cell; epidermal cells around trichome base (4–6) modified with thickened poral rim and radial walls, radially elongated as distinct foot cells.

Distinguishing features. Distinguished by the very prominent granular thickening along the stomatal pore, and the outline of the stomatal complex which is rounded but often with some sharp angles.

Identification. Not similar to any of the species illustrated by Christophel and Rowett (1996), although some *Endiandra* may come closest.

CUT-L-EHG Fig. 26

Reference specimen and locality: SL1966, Sthd-054.

Referred specimens and occurrence: SL0090, BL-08; SL2086, GL-07; SL2198, GL-11; SL2444, Sthd-098.

Stomatal complexes. Stomatal distribution over leaf surfaces hypostomatic; stomatal complexes in clear areoles; isolated; randomly oriented; paracytic; outline polygonal; length c. 20 m (medium); stomatal size range unimodal with a small range. Subsidiary cell periclinal cuticle thinner than over normal epidermal cells; smooth; unornamented. Guard cells overarched by subsidiary cells; Stomatal pore slit-like; cuticular scales narrow; not clear.

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



Figure 26. CUT-L-EHG; (A) TLM view of stomatal complexes and many trichome bases, SL1966, scale: 50 m; (B) TLM of stomatal complex surrounded by trichome bases, SL1966, scale: 20 m; (C) Inner SEM view of stomatal complex showing distinct scales, S-1245, scale: 20 m; (D) Outer SEM view showing bumpy surface, flattened trichomes, and generally obscured stomatal complexes, S-1245, scale: 20 m.

Indumentum. Outer surface smooth; unornamented; with scars of trichome bases and papillose. Papillae irregularly distributed; 1 papilla per cell; formed by the projection of a discrete region within the boundaries of the epidermal cell; smooth. Trichomes abundant; scattered over venal and non-venal regions; deciduous (and therefore trichome type unknown); inserted between epidermal cells; diameter similar in size to a normal epidermal cell; epidermal cells around trichome base (4–7) modified with thickened poral rim and radial walls, unmodified in shape.

Non-stomatal surface. Epidermal cells isodiametric; polygonal; cells over veins not distinguished. Simple trichome bases present.

Distinguishing features. CUT-L-EHG is distinguished by the mass of thickened trichome bases.

Identification. Not similar to any of the species illustrated by Christophel and Rowett (1996), although some *Endiandra* may come closest.