Cenozoic Cupressaceae Macrofossils From Southeastern Australia: Comparisons With Extant Genera/Species

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Submitted in fulfilment of the requirements for the degree of Doctor of Philosophy

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November, 2006

Declaration

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

R. Paull

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Acknowledgements

A child born today, or in the future, will have few reference points from which to view the 'natural' world, namely one largely unaltered by human activity. This child, despite advancing technology, is disadvantaged. In the not too distant past (some one hundred or more years ago) those interested in the evolving world were able to find and observe remote places. In the increasingly contrived environment in which today's child will grow to maturity how can it begin to imagine a pre-*Homo sapiens* world?

Abstract

Tasmanian fossil sites are rich in Cupressaceae genera and species and yet only three genera (*Athrotaxis, Diselma, Callitris*) survive there today. The general aim of this study is the identification of some new and previously undescribed Cupressaceae-related Tasmanian fossils. This is achieved by comprehensive morphological reviews of the foliage and cones (ovulate and pollen) of six extant Southern Hemisphere Cupressaceae genera (*Papuacedrus, Libocedrus, Austrocedrus, Pilgerodendron, Diselma* and *Fitzroya*). One Podocarpaceae genus (*Microcachrys*) which has foliage very similar to *Diselma* is also reviewed. Ovulate cones of one *Callitris* species are described, and compared with ovulate cones from one fossil site. Much of the data are in the form of photographic plates. Some previously described cupressaceous fossils from Tasmania and New South Wales are reassessed. Conifer regeneration, and some of the factors driving, or hampering, this are discussed. Published molecular data for some Cupressaceae genera, and some new molecular data are discussed briefly.

The fossil Cupressaceae described in this study range in age from Late Paleocene (~57 million years) to Early Miocene (~18 million years). With one exception (*Diselma*, Tasmania), the extant relatives of these fossil plants have disappeared from Australia and are variously distributed in Papua New Guinea (*Papuacedrus*), New Zealand (*Libocedrus*), New Caledonia (*Libocedrus*) and southwestern South America (*Austrocedrus, Fitzroya*). The possible reasons for the disjunct distribution of the extant genera/species are discussed, including the mechanisms involved in the final disintegration of Gondwana, and the impact these had on climatic and ecological conditions.

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Chapter 1. Introduction

Phylogenetic and fossil data suggest the conifer family Cupressaceae was more widespread and diverse in the past, and is more closely linked to fossil forms than other living conifers (Miller 1988, 1999; Farjon 2005). Extant genera (30, 135 species) generally appear to have distinct Southern (11 genera) and Northern (19 genera) Hemisphere distributions (Farjon 2001, 2005). Four of the 11 extant southern cupressaceous genera, *Athrotaxis*, *Diselma*, *Callitris* and *Actinostrobus* are found in Australia, and three of these (*Actinostrobus* is the exception) have also been found there as macrofossils (Townrow 1965; Blackburn 1985; Hill *et al.* 1993; Blackburn and Sluiter 1994; Jordan *et al.* 1995), as have species from other Southern Hemisphere genera, *Austrocedrus*, *Libocedrus*, *Papuacedrus* (Hill and Carpenter 1989) and *Fitzroya* (Hill and Whang 1996; Hill and Paull 2003). Cupressaceous genera now extinct in Australia include *Austrosequoia* (which bears a distinct resemblance to present day *Sequoia*; Peters and Christophel 1978; Hill *et al.* 1993), and possibly *Bungarbia* and *Monarophyllum* (Whang and Hill 1999; Lake Bungarby, NSW). The present day distribution of *Austrocedrus*, *Libocedrus*, *Papuacedrus*, *Fitzroya* and *Sequoia* is somewhat limited (Fig. 1). *Austrocedrus* is only found in the southern Andes (Chile and Argentina), *Libocedrus* is restricted to southern New Caledonia and New Zealand, and *Papuacedrus* grows in mountainous regions of New Guinea and nearby islands. *Fitzroya* is found in southern Chile, and *Sequoia* only grows in a narrow belt along the western coast of the USA (Farjon 1998, 2001).

● *Papuacedrus*
● *Libocedrus*
● *Austrocedrus,*
   Pilgerodendron, Fitzroya
● *Diselma*
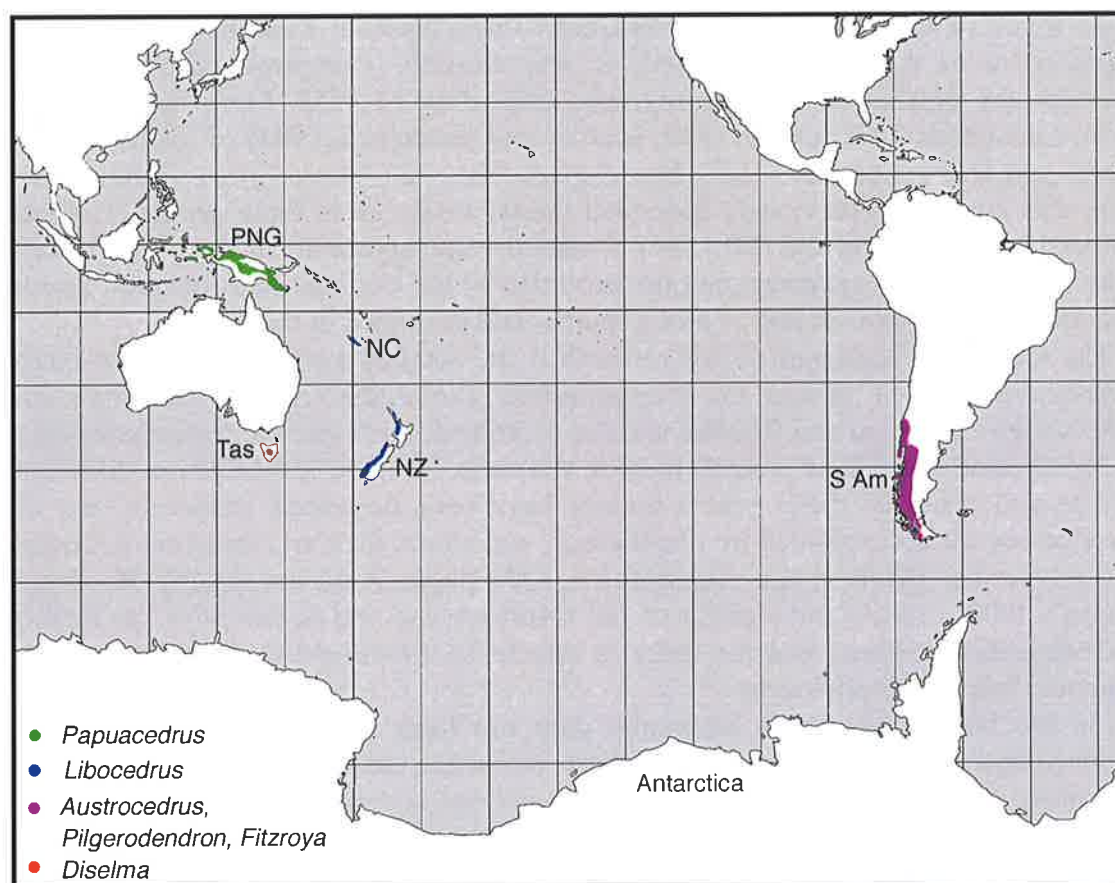
Fig. 1 Map showing the present distribution of extant genera

There is a wealth of mummified Cupressaceae related material (ovulate cones and foliage) at many Tasmanian sites, but much of this has been undocumented. The foliage is highly diverse, very fragmentary, and often consists of only a few leaves. It rarely exhibits branching. Ovulate cones are generally in poor condition and have very little, or no attached foliage.

The main aim of this thesis is the identification of some mid-Late Cenozoic fossil cupressaceous genera and species from Tasmania. This is achieved by comparisons with nearest living relatives (genera/species).

The identification of fossils via comparisons with extant genera/species can be problematic. Relationships between fossil and extant taxa are relatively easy to establish if the fossil foliage has attached reproductive structures. Unfortunately, such finds are relatively rare. In the absence of ovuliferous cones (pollen cones are rarely found), highly diverse and fragmentary foliage can be difficult to assign to a genus *and* species. When only a few specimens are found, the taxonomic information they provide may be very limited and, unless their resemblance to living plant material is unquestionable (i.e. their characters are fully consistent with a chosen extant genus and possibly species), it may be impossible to assign them to living genera (and species; Collinson 1986). The possibility that they may represent extinct genera/species should always be considered. McIver and Basinger (1989) have suggested that the structure of the female cone should form the basis of Cupressaceae classification (at the generic level) and that in the absence of ovulate cones, fossil foliage should be assigned to organ genera.

As much of the Tasmanian cupressaceous fossil material examined in this study appeared to be *Libocedrus*-related, it was initially compared with published descriptions, illustrations and photographs (including Li 1953; Florin and Boutelje 1954; Laubenfels 1972; Offler 1984; McIver and Aulenback 1994) of ovulate cones, leaves and leaf cuticle, of *Libocedrus*, *Papuacedrus* and *Austrocedrus*. Comparisons were also made with previously described fossils attributed to these genera (Hill and Carpenter 1989; Whang and Hill 1999). It soon became apparent that if the fossils were to be of any value in understanding the evolution of the Cupressaceae, material should be collected from herbaria and/or living sources and examined in detail.

The most significant part of this research is the detailed examination of the extant *Libocedrus*-related genera i.e. *Papuacedrus*, *Libocedrus*, *Pilgerodendron* and *Austrocedrus*. *Fitzroya* and *Diselma* are also examined. Photographic plates (consisting of digital camera and SEM images) provide templates for fossil identification. Although foliage and cones of these genera/species have been described elsewhere, not all descriptions are accompanied by illustrations, and where they are, these are generally few in number (McIver and Aulenback's 1994 paper is an exception). However, Farjon's (2005) recent monograph of the Cupressaceae and *Sciadopitys* has largely addressed this problem, and the order in which the *Libocedrus*-related material is presented follows his phylogeny.

In the last decade or so molecular data has been increasingly used to refine relationships within plant families. Where molecular and morphological data are combined, confidence in the results of these analyses is enhanced. As molecular data form only a minor part of this review it is hoped that the illustrated descriptions of the extant genera/species given below will prove beneficial to molecular workers (the photographs supplementing Farjon's (2005) beautiful detailed drawings). To allow direct comparisons between photographic plates, the foliage and ovulate cone

photographs for each genus and species are generally at the same scale, and cuticular photographs are presented at the same orientation.

This project did not set out to be, nor is it, a definitive study. As anatomical features were absent in the fossils, these were not examined in the extant material. The order in which the extant *Libocedrus*-related genera is documented follows that of Farjon (2005). It includes *Pilgerodendron* (although macrofossils of this genus have not been found in Australia as fossils), which has foliage unlike that of the other three genera (its leaves are homomorphic and may occasionally be in whorls of 3 rather than decussate), but very similar ovulate cones. *Widdringtonia* cones and foliage were examined in some detail but were considered very unlike the fossil material and are not included here. While the North American and East Asian genus *Chamaecyparis* has foliage relatively similar to the fossils, the leaves usually contain distinct, or relatively distinct glands (not present in any of the fossil specimens), and the cones are quite dissimilar, so it too is absent from this review.

The secondary aim of this study is to document the modification of leaf and cone morphology of the aforementioned genera/species over time and link this to climatic variation.

The ecological and climatic conditions under which the extant comparative genera/species grow is examined in some detail. This provides important background information to speculate on the conditions in which the fossil plants grew. Size (leaves and ovulate cones) and stomatal distribution are two other obvious climate indicators. Possible reasons as to why most fossils are much smaller than their related living genera/species is discussed.

The present distribution of Southern Hemisphere Cuppressaceae is the result of 80 My of continental reorganization, associated with the final stages of the disaggregation of Gondwana. In southeastern Australia, the general trend to drier climates led to the disappearance of *Papuacedrus*, *Libocedrus*, *Austrocedrus* and *Fitzroya*. The reasons as to why their present distribution is disjunct (vicariance or long distance dispersal) is investigated.

Methods
Extant material

Specimens

As all the genera to be examined in this section occur outside Australia, herbaria were the source of most material. Additional living material was collected in Tasmania.

Herbaria sources: –

1) Australian National Herbarium, Canberra, (herbarium specimens were photographed at the herbarium with a Canon EOS D30 digital camera. Small samples were removed for cuticle preparation and for mounting on scanning electron microscope (SEM) stubs.

2) School of Earth and Environmental Sciences Herbarium, University of Adelaide, South Australia.

3) Dame Ella Campbell Herbarium, Massey University New Zealand (small samples only).

4) Museum of New Zealand, Te Papa Tongarewa (small samples only).

5) Personal collection of R. Carpenter.

Ovulate and pollen cones of *Libocedrus* were particularly difficult to obtain from the various herbaria. In many cases the material available was less than perfect, or immature, and in some cases only one ovulate cone was available for examination. Farjon (2005) suggested that the paucity of cones in herbaria may be due to the low reproductive tendency of some genera (especially New Caledonian *Libocedrus*). No pollen cones were found in the fossilized material, so it had not been the original intention to include these in the extant descriptions. None were collected from the Australian National Herbarium, and few samples were available from other herbaria. In the absence of material for examination, a very brief description, taken from published literature, is included in the species description. Some living material was collected later (see below).

Living material from Tasmania: –

1) Royal Tasmanian Botanical Gardens (Hobart)
2) Tasmanian Arboretum (Devonport)

The Tasmanian specimens were cultivated and young, but were useful in providing some information lacking in herbarium samples, including ovulate and pollen cones. Leafy twigs and cones were photographed, and vouchers were made. They were then placed between sheets of newspaper, and dried in a press. These are stored in the School of Earth and Environmental Sciences Herbarium, University of Adelaide, South Australia.

Specimen preparation
Many preparation procedures were similar for extant and fossil specimens so, to avoid repetition, these are collectively dealt with here.
Fossils

Fossil specimens were removed from sedimentary blocks by macerating in 5 % H_2O_2 or, by placing in alcohol in an ultrasonic bath and loosening the plant remains by periodic (half hourly) agitation. The most intact foliage and cone samples were selected for close examination, and extraneous silicious matter was removed by soaking in 35% hydrofluoric acid (HF) for one or two days (or until clean). Specimens were rinsed several times in distilled water and brushed clean with a fine paintbrush. Leaves, leaf

fragments, and cones were assessed, and some were selected for close scrutiny. The remainder were placed in glass vials, in 80% ethanol, and stored.

Cuticles, herbarium specimens

Dried leaves were soaked overnight in 5 ml 100% ethanol, 5 ml 10% H_2O_2 and 5 ml water before gently heating (30-35 °C) in a 10-20% H_2O_2 solution (in test tubes in a waterbath) until most organic matter oxidized. Despite their small size, it often took days to weeks to clean many leaves. Throughout the cleaning process nearly all specimens required periodic brushing (with a fine paintbrush) to loosen adhering tissue and facilitate cleaning. The H_2O_2 solution was renewed after each brushing. For the more difficult samples, warm 10% aqueous chromium trioxide was used to remove the remaining organic matter. The cleaned cuticles were rinsed, neutralized in 2% ammonia for 1 min, rinsed again then stained in 1% crystal violet.

Cuticles, fossil specimens

Leaves were soaked in a warm 10% aqueous chromium trioxide solution to remove organic matter. Complete cleaning was achieved by gentle heating in 5% aqueous hydrogen peroxide for several hours (in many instances the cuticles were degraded before preparation, so the resulting samples were relatively poor). The remaining cuticle was rinsed in distilled water, neutralised in 2% ammonia for 1 min, rinsed again, brushed clean, and then stained in 1% crystal violet.

Cuticular material for light microscopy was mounted on glass slides in phenol glycerine jelly. Cuticle, vegetative, and reproductive specimens for scanning electron microscopy (SEM) were placed on double-sided carbon tape on aluminium stubs, air dried, and gold or gold-carbon coated prior to SEM scanning.

Prepared specimens are stored at the North Terrace campus of the School of Earth and Environmental Sciences, Adelaide, South Australia.

Photography

Living specimens were photographed in the field with a Pentax Optio digital camera. Herbarium, fossil and living specimens were photographed, either in various herbaria or in the laboratory, with a Canon EOS S30 digital camera. An Olympus DP11 digital camera attached to a Zeiss Stemi 2000-C dissecting microscope was used for close up photography. A Philips XL20 scanning electron microscope operated at 10 kV was used for most SEM samples, the others (some fossil and some extant ovulate cones) were photographed with a Phillips XL30 scanning electron microscope operated at 3 kV. A Leica MZ15 FA was also used to photograph some ovulate cones. An Olympus DP11 digital camera attached to a Zeiss Axioskop microscope was used for light microscopy.

Terminology

Bilaterally flattened lateral leaves - lower, adnate section

ventral surface

dorsal surface

ventral surface

facial leaf

central keel

bifacially flattened lateral leaves
upper half free,
lower half adnate

dorsal surface

adaxial surface
facial leaf

lateral leaf
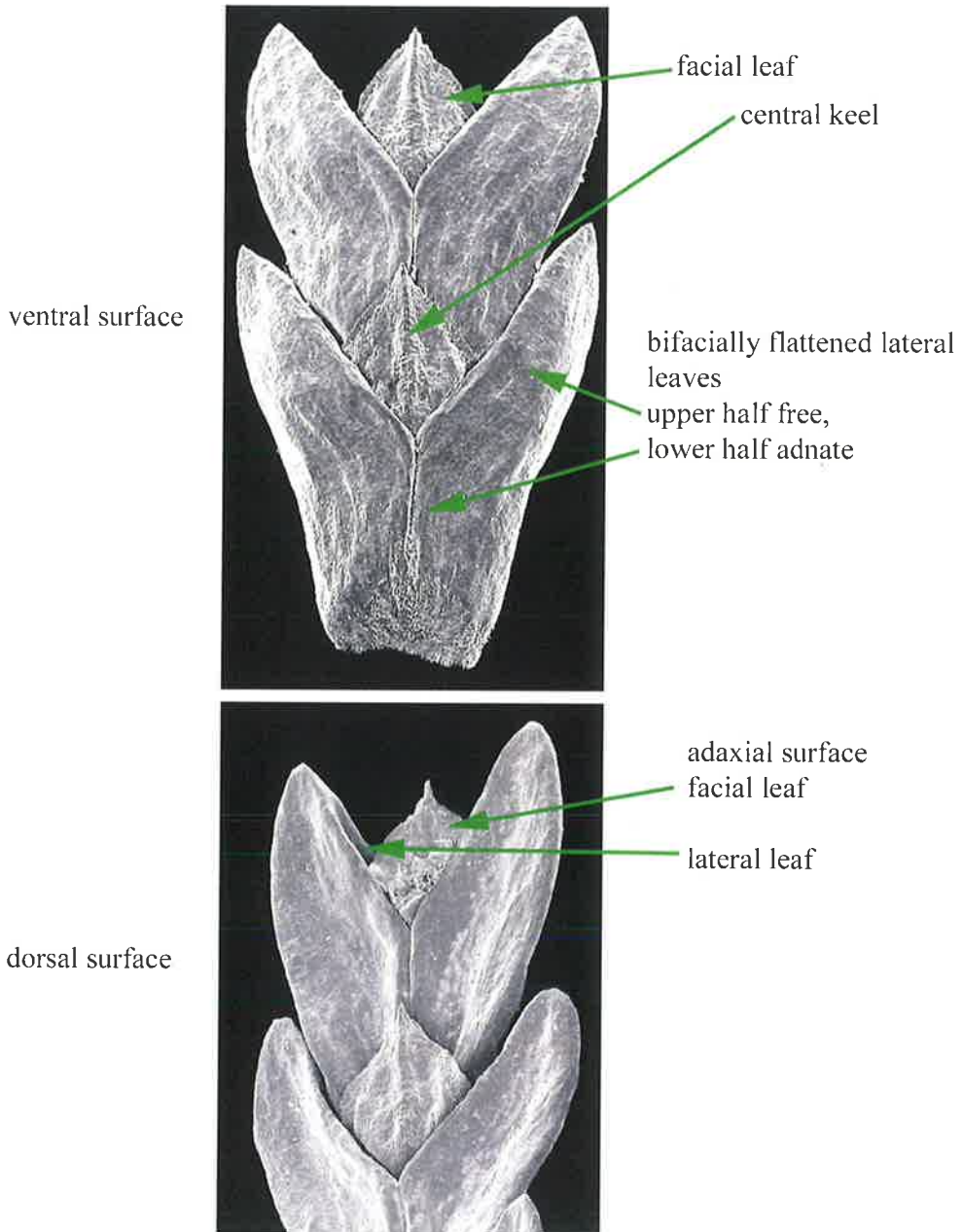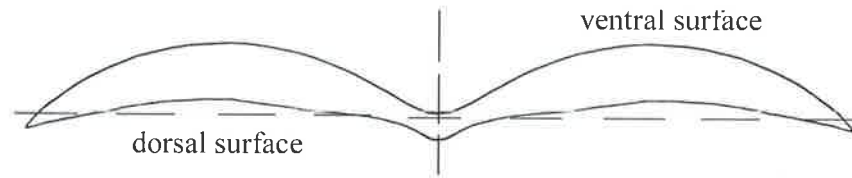
Fig. 2 Foliage terminology. Drawing and SEM photographs illustrating the terminology used in the text to describe the three leaf surfaces

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Foliage

Unlike conifer foliage, most angiosperm leaves are flattened and are positioned on twigs such that the surface facing the stem – the upper (adaxial or ventral surface) is exposed to the sun. The under (abaxial or dorsal) surface is shaded.

The Cupressaceae genera in this section have scale-like, dorsally-keeled leaves that are decussately arranged along the twigs. The lateral leaves are generally larger than the facial leaves and are bilaterally (dorso-ventrally) flattened, which means that half their surface is sun exposed, and half shaded. Florin and Boutelje (1954) called the sun exposed surface upperside and the shaded surface underside but, as this is technically incorrect, the terminology used here will be ventral (sun exposed), and dorsal (shaded). The lateral leaves are adnate towards the base for at least a quarter of their length, with the upper portion free. The term adaxial applies to the surface of the leaf facing the stem. For facial leaves this term is straightforward. For lateral leaves it applies only to the upper, free part of the leaf (Fig. 2).

Ovulate cones

In most publications concerned with conifer evolution and classification (e.g. Florin 1951, 1954; Rothwell 1982) the more complex morphology of ovulate cones has taken precedence over leaf morphology (Miller 1988, 1999). Until relatively recently the generally accepted view has been that all extant coniferous cones are compound structures comprised of a reduced branch system made up of ovuliferous scales and sterile appendages each of which are subtended by, or fused to, a bract, and that the ovules develop on the adaxial surface of the ovuliferous scale (e.g. Florin 1951, 1954). However, Tomlinson *et al* (1993) and Tomlinson and Takaso (2002) have shown that the structure and morphology of Cupressaceae seed cones is not like those of other conifer families. They are simple structures in which the ovules are not fused to, or supported by, a scale but are erect and borne either in the axil of the bract or on the cone apex. Florin's (1954) 'ovuliferous scales' are fertile bracts. Between the genera there is considerable variation in cone structure and morphology (Miller 1999; Farjon and Ortiz Garcia 2005). Cones consisting of two pairs of decussate scales is probably the ancestral condition (McIver and Basinger 1987, 1990; McIver 1992; Tomlinson *et al*. 1993; McIver and Aulenback 1994).

The terminology used by Tomlinson *et al*. (1992) to describe cone development in *L. plumosa* is used as a guide for the descriptions that follow. To avoid confusion, a summary of their paper is given here, rather than in the discussion at the end of this section.

The ovulate cones of *L. plumosa* are simple structures, initiated in late summer, before pollination occurs. Early development begins with the successive elongation of six to seven pairs of bracts at the tip of short lateral vegetative branches. These have the same decussate imbricate arrangement as the vegetative shoots below, and are only distinguishable from the leaves by their length. Elongation of the bracts continues through the winter, and ovule development is initiated. There are four ovules, two on the adaxial surface of each of the ultimate bracts. Almost coincident with the appearance of the ovules, a small primordium (which later becomes the ligule) appears in the centre, and towards the base, of each of the ultimate bracts. It protrudes slightly between the ovules (Fig. 3). In the centre of the penultimate bracts, similar primordia develop. Following pollination (in the spring), all primordia expand by intercalary growth. The base of the primordia grows down to the base of the bract, which begins expanding by intercalary growth, and pushes the 'ligule' upwards. Similar, and rapid expansion (upwards and outwards) from the primordia apex pushes the bract into a

horizontal position, giving it the appearance of an abaxial outgrowth on the ligule. A short columella (column) may also develop in the cone apex (Fig. 3). As the purpose of the ligules is to protect developing ovules, the ultimate 'scales' become the largest, but these remain imbricate within the penultimate pair until the late stages of maturity. Papillae develop on the margins of the ligules. These intertwine where the scale margins meet, to totally enclose the ovules (Farjon and Ortiz Garcia 2005).

Libocedrus, *Papuacedrus*, *Austrocedrus* and *Pilgerodendron*, all develop ligulate protuberances following pollination. When these mature they become valvate and totally enclose the seeds.
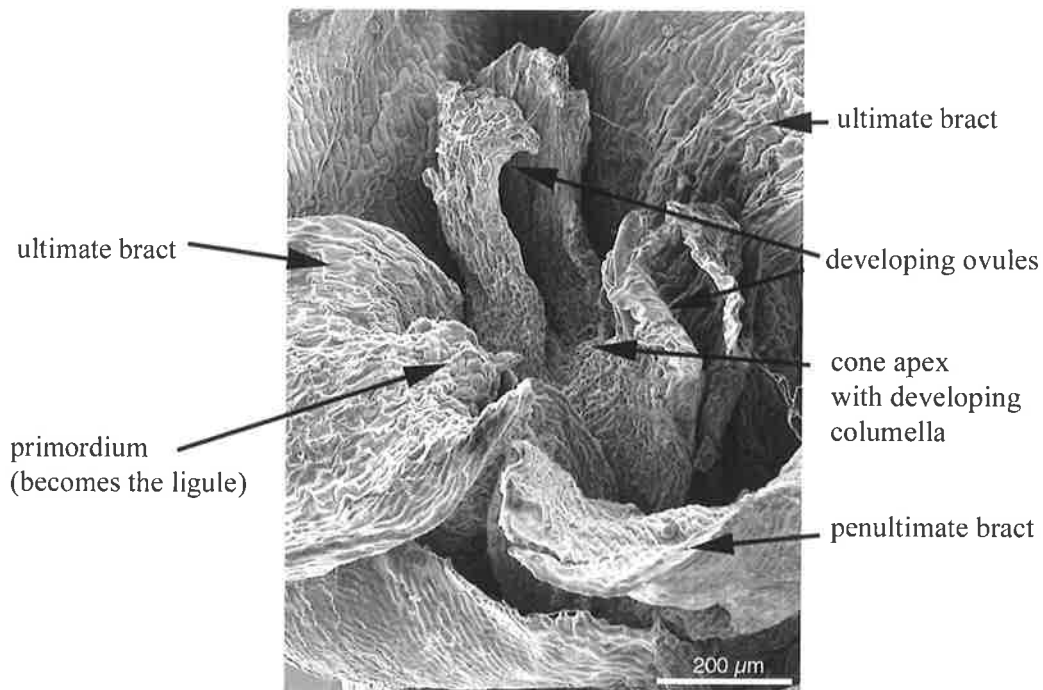
Fig. 3 Early ovulate cone development
Immature cone, *Austrocedus chilensis*

Calcium oxalate crystals

In calcium rich soils, many higher plant families synthesize calcium and oxalic acid, and produce highly insoluble crystalline salts of calcium and oxalic acid (Webb 1999; Franceschi and Nakata 2005). The function of these crystals varies between plant families, and it seems the trait for crystal production is an ancient one, evolving many times to help regulate bulk calcium in tissues and organs. Genetic and environmental factors determine the number, shape and size of crystals. They are common in the cell walls of gymnosperms (Franceschi and Nakata 2005).

In the genera/species examined they are most prevalent on exposed surfaces (very rare on protected surfaces). Here their purpose may be to protect the plant from mechanical damage. They are least frequent in *Papuacedrus*. They are most apparent in the New Caledonian *Libocedrus* species, which often grow in exposed conditions, and may also have to cope heavily mineralised soils.

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<u>Stomatal arrangement</u>
The stomatal apparatus of each genus/species is haplocheilic.

Note: With small non-robust fossil leaves (and often extant comparative material) cuticle preparations are difficult, and rarely are the resultant samples free of extraneous matter. The ornamentation of guard cells is thus highly variable and may be of dubious value as a distinguishing character.

Thesis outline

An introductory chapter indicates the aims of the thesis and provides background information. It includes source details for the samples, preparatory methods and terminology, and also discusses problems encountered when dealing fossil and herbarium specimens.

The thesis is in five parts (Parts 1-V)

Part I has four chapters that review the morphology of extant *Libocedrus*-related genera and species. These and titled *Papuacedrus*, *Libocedrus*, *Pilgerodendron*, *Austrocedrus*. The details of the relevant specimens are included in each chapter.

Part II - provides a detailed look at the cone (ovulate and pollen) morphology of *Fitzroya* for comparison with fossil cones and foliage from one of the fossil sites.

Part III is in two sections, **A** and **B**

> **Section A** - reviews previously described cupressaceous fossils
> **Section B -** describes new cupressaceous fossils

Part IV - reviews the morphology of *Diselma archeri,* and the Podocarpaceae monomorphic genus, *Microcachrys*. Some small leaved fossils from two Tasmanian sites are described.

Part V is in three sections, **A, B** and **C**

> **Section A** – discusses the Late Palaeozoic and Cenozoic breakup of Gondwana, and some of the dynamics associated with continental movement. Some of the factors that have driven climate change during the Cenozoic are examined.
> **Section B** – The past and present distribution of the cupressaceous genera discussed in earlier chapters is put into perspective.
> **Section C** – Concluding remarks

Some extant southern hemisphere Cupressaceae revisited

Part I. *Libocedrus* related genera

Introduction

Much of the fossil foliage described in this thesis consists of scale-like (Laubenfels 1953, type III conifer leaf), decussate and dimorphic leaves, quite similar to extant *Libocedrus*, *Papuacedrus* and *Austrocedrus*. These three genera have rather similar cone and leaf morphology and were once all classified as *Libocedrus*. Changes to the classification of the genus *Libocedrus* from 1847 to 2005 have been well documented by Li (1953) and Farjon (2005). For simplicity, the brief classification summary that follows does not include the Northern Hemisphere species/genera (which have 3-5 pairs of ovulate cone scales) that were added to the genus (Torrey 1853; Kurz 1873; Koch 1873; Bentham and Hooker 1880; Pilger 1926; Florin 1931a) and later removed by Li (1953).

Libocedrus was created by Endlicher (1847, see Farjon 2005) to encompass three variously named species collected by others in South America (2 species), and New Zealand (1 species) from 1824 - 1844. Common to each of these species were seed cones with two pairs of decussate scales. Endlicher's species were *L. doniana* (Hook.) Endl. (New Zealand, now *L. plumosa*, (D. Don) Sarg.), *L. tetragona* (Hook.) Endl. (southern South America, now *Pilgerodendron uviferum* [D. Don] Florin), and *L. chilensis* (D Don) Endl. (southern South America, now *Austrocedrus chilensis* (D. Don) Pic. Serm. & Bizzarri). Other 19th century additions to the genus were *L. bidwillii* Hook. F. (New Zealand; Hooker 1864), *L. austrocaledonica* Brongn. & Gris. (New Caledonia; Brongniart and Grisebach 1871) and *L. papuana* F. Muell. (New Guinea: Mueller 1889; now *Papuacedrus papuana* (F. Muell) H. L. Li). In the 20th century two New Guinea species, *L torricellensis* Schlecter 1914) and *L. arfakensis* Gibbs (Gibbs 1917), and two New Caledonia species *L. chevalieri* J. Buchholz (New Caledonia; Buchholz 1949) and *L. yateensis* Guillaumin (New Caledonia; Guillaumin 1949) were also described. Florin (1930) removed *L tetragona* (renamed *L. uvifera* by Pilger (1926)) from *Libocedrus* and placed it in the monotypic genus *Pilgerodendron*.

When Li (1953) reclassified *Libocedrus*, he suggested it should include *L. bidwillii*, *L. plumosa* (New Zealand), *L. austro-caledonica*, *L. chevalieri*, *L. yateensis* (New Caledonia) and *L. chilensis* (southern South America). He excluded the *Libocedrus* species from New Guinea (he considered their pollen cones and foliage distinctive), and proposed a new genus, *Papuacedrus* Li, to encompass what he saw as three species: 1) *Papuacedrus papuana* (F. Muell.), 2) *Papuacedrus torricellensis* (Schlechter) and 3) *Papuacedrus arfakensis* (Gibbs). Laubenfels (1988) thought Li's (1953) character differences too slight to support the separation of *Papuacedrus* from *Libocedrus*. However, as the wood anatomy (Boutelje 1955) and stomatal characteristics (Florin and Boutelje 1954), of *Papuacedrus* are somewhat dissimilar to those of *Libocedrus*, and the microsporophyll arrangement remains ambiguous (normally decussate [Farjon 2005] versus spirally arranged [Lauterbach 1914; Gibbs 1917; van Royen 1979]), *Papuacedrus* is maintained as a separate genus by Farjon (2005). Although the combined molecular (*matK* and *rbcL*) and non-molecular data of Gadek *et al.* (2000) suggest *Papuacedrus* could be sister group to all Southern Hemisphere Cupressaceae genera, this placement is not robust (i.e. has less than 90% bootstrap support). Farjon's

(2005) combined morphological and anatomical data place *Papuacedrus* close to *Pilgerodendron*, but still within the Southern Hemisphere *Libocedrus* clade.

Somewhat minor differences in leaf cuticle and cone characteristics led Florin and Boutelje (1954) to erect the new genus *Austrocedrus* to accommodate *L. chilensis*. Doweld (2001, published in Russian, see Farjon 2005 p. 438) has proposed that the cones and foliage of the New Caledonian species can be distinguished from the New Zealand species and suggested a new genus, *Stegocedrus*, for the New Caledonian species. This genus is not recognised here.

Chapter 2. *Papuacedrus*

Introduction

Until Li's (1953) reclassification of *Libocedrus* in 1953, three *Libocedrus* species had been described from New Guinea. These were (see Li 1953), *Libocedrus papuana* F. Muell. in Trans. Roy. Soc. Vict. N. S. 1(1): 32 (1889), also called *Thuja papuana* Voss in Mitt. Deutsch. Dendr. Ges. 1907 (16): 88. (1908); *Libocedrus torricellensis* Schlechter ex Lauterbach in Bot. Jahrd. **50**: 53 *f. 2, II-N*. 1913, and *Libocedrus arfakensis* Gibbs, Phytogeogr. & Fl. Arfak Mts. **84**.*f. 6, a-b*. 1917. Li (1953) noted that the ovulate and pollen cones of the New Guinea species were somewhat different from other *Libocedrus* species (the ovulate cones were less woody, the 'bract' projection was placed lower on the scale, and the arrangement of pollen cone microsporophylls was spiral rather than decussate (a finding, as yet, unconfirmed [Farjon 2005]), and erected a new genus, *Papuacedrus*. He named 3 species:- 1. *Papuacedrus papuana* (F. Muell.) comb. nov. (northern and southern New Guinea and the Moluccas); *Papuacedrus torricellensis* (Schlechter) comb. nov. (Torricelli Mountains, New Guinea) and *Papuacedrus arfakensis* (Gibbs) comb. nov. (Arfak Mountains, New Guinea). Although Laubenfels (1988) considered Li's (1953) character differences too insignificant to support the separation of *Papuacedrus* from *Libocedrus*, molecular data support the separation (Gadek *et. al.* 2000).

Offler (1984) encountered problems with the labelling of *Papuacedrus* herbarium material she evaluated, and was unable to find a 'constant character' to distinguish the foliage of the three species. Florin and Boutelje (1954) thought them closely related. Van Royen (1979) suggested that phenotypic plasticity accounts for *Papuacedrus* foliage variability and recognised only one species. Farjon (2005) found many discrepancies in the labelling of *P. arfakensis* and *P. torricellensis* specimens he examined (for the section on *Papuacedrus* in his 'Monograph of Cupressaceae and *Sciadopitys*'), and suggested that they are incorrectly identified in many collections. As there is some overlap of range of each of these species, he thought the geographic locations from which they were collected had influenced their original naming, e.g. a tendency to call specimens found in western New Guinea, Indonesia and the Moluccas *Papuacedrus arfakensis*. He considered that the mature foliage of specimens labelled *P.* (or *L.*) *arfakensis* and *P.* (or *L*). *torricellensis* are indistinguishable, and dissimilarities in their transitional foliage to be insignificant. Like Laubenfels (1988) he recognised one *Papuacedrus* species, *Papuacedrus papuana* (F. Muell.) HL Li. J. Arnold Arbor. 34: 24. 1953, and two varieties, *Papuacedrus papuana* (F. Muell.) HL Li var. *arfakensis* (Gibbs) RJ Johns, Curtis's Bot. Mag. 12 (2): 70. 1995, and *Papuacedrus papuana* (F. Muell.) HL Li var. *torricellensis*.

Evaluating the highly variable foliage of *Papuacedrus* from herbarium specimens proved to be problematic. Offler's (1984) descriptive approach was that mature foliage is small leaved, and transitional foliage larger, and more flattened. In this current study, none of the specimens examined contained both foliage types. Confusingly, all the foliage from trees under 25 m was broad leaved. This poses a number of questions. What is 'transitional' foliage? Does 'transitional' apply only to leaves of young trees? Was the broad leaved foliage from relatively tall trees taken from low lying branches, i.e. are they shade, or young growth, leaves? What role does altitude play in leaf size?

For the purpose of the descriptions that follow, mature foliage was deemed to be small leaves from trees greater than 28 m (*P. papuana* only). The leaves of *P. arfakensis* and *P. torricellenis* specimens are relatively large and flattened and, as the heights of most of the trees from which they were taken are unknown, are treated as

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transitional foliage. Where it is considered appropriate, figure captions include tree height and altitude.

Fourteen of the 20 specimens examined were from the National Herbarium, Canberra Australia. These were collected between 1954 and 1976 and labelled *Papuacedrus*. In 1999 most of these were relabelled *Libocedrus*, probably in response to Lemmens *et al.'s* (1995) publication (cited in Farjon 2005, p. 432) in which they are referred to as *Libocedrus*. Six specimens were from the herbarium collection of the University of Adelaide, and three of these were poorly labelled. Mueller's (1889) original description of *L. papuana* did not include mature foliage or ovulate cones (see Farjon 2005). No type or lectotype specimens were sighted in this study. Where seeds or pollen cones were unavailable for examination a very brief description has been taken from published literature. The only illustration of *Papuacedrus* pollen (*P. papuana*) was photographed from a herbarium sheet. The descriptions of foliage and ovulate and pollen cones that follow are based on their original identifications i.e. **Papuacedrus papuana** (14 specimens), **Papuacedrus arfakensis** (or *P. papuana* var. *arfakensis*; 3 specimens), and **Papuacedrus torricellensis** (3 specimens).

Papuacedrus papuana (F. Muell.) H. L. Li J. Arnold Arbor. 34: 25 (1953).

Description: Evergreen, monoecious trees and shrubs to 25 m (Enright 1995), rarely 40-50 m (Farjon 2005).
Distribution: Northern and southern New Guinea, and the Mollucas at 1700-3000 m (Li 1953), 620-3800 m (Farjon 2005).
Ecology: Occurs across a broad altitudinal range from upper lowland forests to subalpine shrubberies, but most abundant from ~1500 m to the tree line, in cloud forest conditions (Farjon 2005). Tolerant of a wide range of conditions, including steep stony slopes, exposed areas, basic soils and water-logged peats. Able to regenerate in the shade (Enright 1995).

Systematics
Order Coniferales
Family Cupressaceae
Genus *Papuacedrus* H. L. Li J. Arnold Arbor. 34: 25 (1953).
Papuacedrus papuana (F. Muell.) H. L. Li J. Arnold Arbor. 34: 25 (1953).

Foliage and leaves: *Seedlings* – very young seedlings single stemmed. Leaves slightly drooping, monomorphic, decussate, narrowly elongate (~0.8-1.1 cm), lanceolate, bifacially flattened, with acute bases, entire margins (Figs 1a; 2a). A pronounced central vein is ribbed and convex on the dorsal surface (Fig. 2b, d), concave on the ventral surface. Somewhat older seedlings have lateral branchlets with thin leaved transitional foliage (Fig. 1b). On juvenile (older seedlings) elongate leaves are replaced by transitional foliage (Fig. 1c). *Transitional foliage* (taken here to be broader foliage from juvenile to 28 m trees) - generally in flattened sprays, and with opposite branchlets in a single plane. Leaves thin, larger than adult, decussate, highly dimorphic, flattened, with inwardly curved apices (Figs 4a-d; 5a-e). Dorsal leaf surfaces are frequently waxy (Figs 4c; 5b, c [2]). Lateral leaves - bilaterally flattened, and much larger than facial leaves, imbricate, but not on very young trees (Fig. 4a), and young shoots (Fig. 5e [1, 2]), elongate to oblong, and connate for almost three quarters of their length, with the free apical section keeled. Leaf bases often slightly papillate. Ventral surfaces convex (Fig. 5c [1]), dorsal surfaces concave (Fig. 5c [2]), margins entire. On

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main axes leaves are subfalcate, with the upper carinate section often at right angles to the twig (Fig. 5a [1, 4], e [3]). The margins of these leaves are frequently revolute, and where this occurs the adaxial surface is convex (Fig. 5d, e [3]). At the apex of terminal branchlets leaves are smaller, narrower than those below, and curve inward to almost meet at their apices (Fig. 5a [2]). On terminal shoots the foliage is not flattened, and lateral and facial leaves are long, decurrent, similar in length, and closely overlapping. The leaves may appear to be whorled, rather than decussate (Fig. 5a [3]). Facial leaves – very small, broadly triangular, cuspidate (Fig. 2g). The broad sections of these leaves are tiny, and barely cover the base of the lateral leaves above. A narrow, elongate basal extension is fused to the lateral leaf pair below, and extends almost to their base. On the ventral surface, this feature appears as a long, narrow central depression (Fig. 2f), on the dorsal surface as a central ridge (Fig. 2h). It is more pronounced between the lateral leaves on main axes (Figs 1c; 5e [3]). *Adult foliage* - generally in semi-flattened sprays with opposite branchlets (Fig. 7a, c). Leaves small, scale-like, decussate, mostly dimorphic, thick and less flattened than transitional leaves (Fig. 7a-d). On ultimate branchlets leaves may be almost monomorphic (Fig. 7b, c) with lateral leaves only slightly flattened, facial leaves even less so. Facial leaves are slightly broader than the laterals, and both leaf types have convex dorsal and ventral surfaces. Leaves on fertile shoots smaller than on sterile foliage.

    Stomatal distribution: *Young seedlings* - on dorsal (abaxial) surface in discontinuous rows on either side of the central vein, and roughly parallel with, but not extending to, the leaf margin (Fig. 2b), fewer in number on ventral surfaces. *Transitional foliage* ventral surface - rare on lateral leaves and, where present, usually at the base, but may be in short rows elsewhere (Fig. 6b). On facial leaves, on either side of the central keel, in the lower narrower section of the leaf, where overlying leaves afford protection (Fig. 6c, d). Dorsal surface, lateral leaves - closely packed, and in discontinuous rows generally parallel to the leaf margin, with bands of epidermal cells between (Figs 2h; 5e [1&2], 6a). On laterals on main axes the size and frequency of intervening epidermal cells may increase (Fig. 5a [1&4], b). Facial leaves, on either side of the central keel (Fig. 6a). On main axes stomata extend downwards on the inwardly turned section where the facial leaf is fused to the laterals on either side (Fig. 7c). Adaxial surface, lateral and facial leaves - generally in several discontinuous rows on either side of the leaf centre (Fig. 6b). *Adult leaves* ventral surface - on lateral leaves rare, and usually at the base. On facial leaves on either side of the centre, and largely covered by the overlying lateral leaves. Dorsal surfaces, lateral leaves - on main axes in a slightly sunken groove under the free section of the leaf (Fig. 7g), but in the adnate section in discontinuous rows, parallel to, and closest to, the leaf margin, and separated by bands of epidermal cells. On ultimate branchlets, in central grooves in the lower third of the leaf (Fig. 7e). On facial leaves, clustered towards the base on either side of the centre, and largely hidden by overlying laterals (Fig. 7e). Adaxial surface, lateral and facial leaves - in short rows on either side of the centre of the leaf (Fig. 7f, g).

    Cuticle description: Seedlings with very thin cuticles (Fig. 2e). Juvenile transitional leaves very similar to older transitional foliage but with very thin cuticles (Fig. 3a-h), and slightly lobed Florin rings (Fig. 3b, d). Epidermal cells contain calcium oxalate crystals (Fig. 2d). The cuticles of transitional and adult leaves are similar and are described collectively. Inner surface. Stomatal guard cells generally elongate, and surrounded by 4-6, fine-grained, indented subsidiary cells. The latter form a conspicuous groove around the guard cells, which is distinctly bridged by their anticlinal cell walls (Fig. 8a, c). The anticlinal cell walls of the subsidiary cells are thick and slightly coarser-grained than the periclinal walls. Epidermal cells not associated

with stomata are generally elongate, irregular in shape, coarse-grained, and are clearly distinguishable from subsidiary cells. The anticlinal walls of these cells are thick and coarse-grained (Fig. 8h). Epidermal cells on exposed surfaces (i.e. those not covered by overlying leaves) may contain numerous small calcium oxalate crystals (Fig. 8i, j). These seem to be most frequent on the apices of ventral facial leaves, but are also variously present on facial and lateral leaf apices on dorsal and ventral surfaces. They are rarely associated with stomatal areas. Outer surface - Florin rings high ridged and variously lobed (obvious – barely perceptible; Fig. 8b, d, e). Associated with the Florin rings are small round papillae of variable number (few to many). Epidermal cells have indented cell walls and, frequently contain small holes or papillae indicating calcium oxalate crystals. These are more frequent on leaf apices (Fig. 8g).

Ovulate cones: Terminal to subterminal on very short branchlets. Highly variable in size and shape (Fig. 9a-e), and ~9-18 mm long when mature. Young cones - in very early development, the cone consists of 4-5 broadly triangular bracts all, except the ultimate, with acute apices (Fig. 10l). In immature cones, penultimate scales are highly rugose, and have acute apices (Fig. 10j). Mature cones - four decussate bract-scale pairs. Ultimate scales - large ovoid-oblong, and broadest at, or just below, the spiny bract projection (Fig. 10d). Scale margins papillate, and on the axial surface papillae may extend downwards forming a rough v-shape (Fig. 10a, b). On mature cones the scale apex is obtuse, and often thickened. On broadly gaping scales the apex may be outwardly recurved, giving the impression of an outward projection just below the scale apex (Fig. 10g, h). This recurvation occurs along the plane of the v formed by the papillae on the adaxial surface. The projecting tips of the bracts emerge in the centre of the lower third to centre of the scale (Fig. 10d). These are short ~2 mm, and ~1-1.5 mm wide, recurved, and often have a blunt apex (Fig. 10i). The broad basal extension of the bract has large cells, and a highly undulate, robust, bulging surface (Fig. 10e). Penultimate scales - elongate, smaller and narrower than the ultimate pair (Fig. 10e), wider at the base, widest at the bract projection, and with papillate margins. Scale apices initially acute, but may curve downwards and outwards above a thick band of papillae just below the apex, and appear blunt with an acute outward projection (Fig. 10e, f). Bract projections on these scales are slightly longer and broader than those of the ultimate scales, and have acute recurved tips (Fig. 10e). The adaxial surface of these bracts may have scattered stomata. The broad, basal extension of the bract is recessed, rather than bulging, and rugose (Fig. 10e). Subtending the cone are 2-3 small, short broad, triangular shaped, decussate bracts, with acute apices. These become progressively (but only slightly) larger towards the cone (Fig. 10k). No columella present in mature cones (Fig. 10m).

Ovules: not illustrated. 4, erect, 2 in the axil of each ultimate bract. Seeds, 2-4 per cone with 2 membranous wings (Fig. 10k, j), very unequal in size and shape (Farjon 2005).

Pollen cones: Pollen cones terminal on very short branchlets, solitary. Microsporophylls 8-12 pairs, similar in size, broadly triangular, decussate, and with acute to slightly rounded apices (Fig. 11).

Specimens examined

45004, National Herbarium, Canberra, Australia. Collected 2/1957, GFB McVeagh NGF 7582, Manki-Edie Creek spur, near Bulolo PNG. Tree 25 m at ~2460 m, a straggly second story tree.

102076, National Herbarium, Canberra, Australia. Collected 1959. LJ Brass 29687, Kaindi, Morobe District. Tree 15 m at 2150 m, sterile, occasional in *Nothofagus* forest.

105268/9, National Herbarium, Canberra, Australia. Collected 9/1961, PJ Darbyshire 418, Torricelli Mts. Lumi sub-district, Sepic District. Tree ~20 m, at ~2000 m, in tall forest.

108114.1, National Herbarium, Canberra, Australia. Collected 8/1961. R Schodde 2042, western slope Mt Giluwe above Klareg, Southern Highlands District, Papua. Tree ~40 m at ~3500 m, in high montane cloud forest.

146101.1, National Herbarium, Canberra, Australia. Collected 8/1964, RD Hoogland 9493, Mannasat, Cromwell Mountains, Huon Peninsula, Morobe District. Seedlings collected beneath adult tree in coniferous forest adjacent to tree fern grassland.

152404, National Herbarium, Canberra, Australia. Collected 2/1960, J Cavanaugh NGF 3335, Chimbu TNG.

193329, National Herbarium, Canberra, Australia. Collected 8/1966, D Frodin NGF 28292, track from Lae to Mt Ambua, Tari. Southern Highlands, PNG. Tree ~28 m at 3550-3750 m, occasional trees on ridge in mixed montane forest.

198385, National Herbarium, Canberra, Australia. Collected 9/1963, JJ Havel & A Kairo NGF 17237, Upper Watut, Wau Sub-district. Morobe District. Large tree ~39 m, at ~2000 m, dominant in montane rain forest – associated with *Casuarina, Engelhardtia, Xanthostemon, Halfordia*.

202315, National Herbarium, Canberra, Australia. Collected 7/1966, W Vink 17101, northern slope Mt Kerewa, Tari sub-district Southern Highlands, PNG. Young 2.5 m tree, at 3120 m, in fire-induced shrubbery with climbing bamboo.

229911, National Herbarium, Canberra, Australia. Collected 12/1971, G Hope ANU 10911, East Otomono River, Carstensz Mts West Irian. Spreading tree to 15 m, occasionally codominant trees in upper montane forest.

359920, National Herbarium, Canberra, Australia. Collected 5/1976, P van Royen 10914, Central Province Mt Victoria area, at the base of the 'Rock Pile'. Tree 8-15 m, at 3810 m, sterile, occasional in *Nothofagus* forest in shrubbery with *Drimys* and *Descaspermum*.

E/1194, Herbarium Collection, The University of Adelaide, South Australia. HA 154771, near Wabag, W Highlands. At ~3000 m, in lower montane rainforest with *Lithocarpus*.

E/0943, Herbarium Collection, The University of Adelaide, South Australia. Large foliage, no details.

E/0944, Herbarium Collection, The University of Adelaide, South Australia. Small foliage, no details.
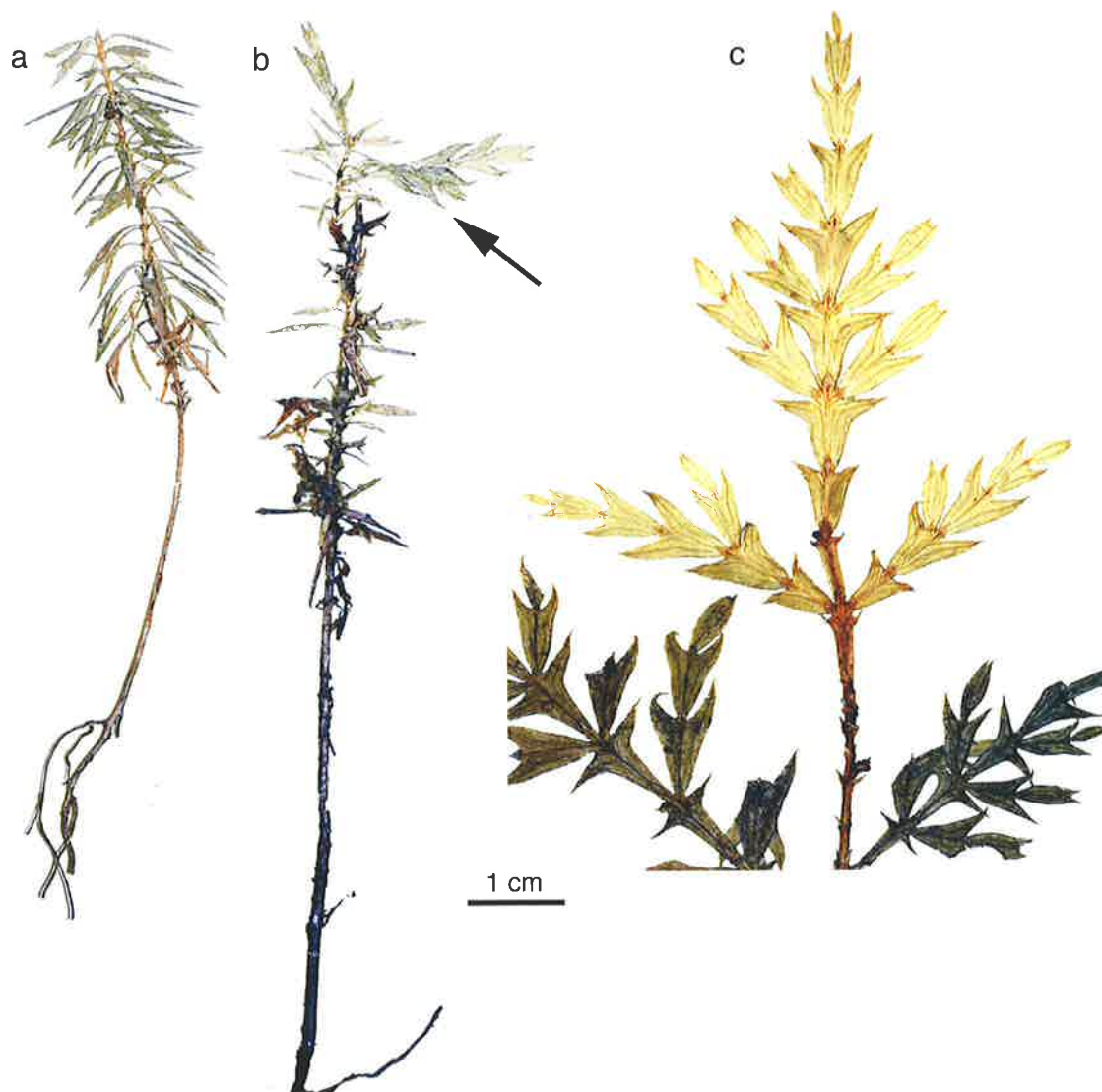
Fig. 1a-c *Papuacedrus papuana* seedlings showing variation in leaves with seedling age.

All specimens collected from beneath the same adult tree (specimen 145102 at ~3000 m, Mannasat, Cromwell Mountains, Huon Peninsula; Morobe District PNG - tree in coniferous forest along treefern grassland). Photographed from herbarium sheets.

    a. Young seedling. Leaves monomorphic, elongate, lanceolate and drooping.

    b. Slightly older seedling with lateral branchlets. These have flattened, highly dimorphic transitional leaves (arrow).

    c. Part of an older seedling with transitional foliage only. Branchlets opposite. Leaves flattened, laterals much larger than facial leaves. Facial leaves tiny, and barely covering the base of the lateral leaves.

Fig. 2a-h *Papuacedrus papuana* seedling and juvenile transitional foliage
Specimen 145102.

    a. Elongate leaf from seedling in Fig. **1a.** Dorsal surface. Stomata in discontinuous rows from leaf base to apex, and separated by bands of epidermal cells, Stomata also on ventral leaf surface, with a similar distribution but fewer (not illustrated).

    b. Middle section of a. Leaf margins entire. Central vein pronounced (arrow), and outwardly ribbed (scale 500 μm).

    c. Dorsal surface showing high ridged, lobed stomata close to the leaf margin (far right), and papillae (arrow; scale 50 μm).

    d. Detail **b**. Dorsal surface. Small nodules in epidermal cells contain calcium oxalate crystals (left arrow). Central ribbed vein (right arrow; scale 50 μm).

    e. Internal cuticle dorsal surface. Cuticle very thin. Subsidiary cells shared by adjacent guard cell. Epidermal cells away from stomatal areas with small calcium oxalate crystals (scale 50 μm).

    f. Convex ventral surface, transitional leaf. Lateral leaf margins entire. Stomata rare. Facial leaf exceedingly small in comparison to lateral leaves, with an elongate apex that extends concavely downwards (arrow) to the base of the lateral leaves (scale 500 μm).

    g. Detail facial leaf, dorsal surface. Facial leaf with frilled margin, and not overlapped by laterals below, but continuous with them. Stomata absent from upper half of facial leaf, but in small groups close to the top of the flanking lateral leaves (arrows; scale 50 μm).

    h. Slightly concave dorsal leaf surface. Stomata closely packed, and in discontinuous rows across most of the leaf. Arrow indicating the raised and convex centre of the leaf complex where the internal margin of the lateral leaves abuts the narrow descending section of the facial leaf (scale 1 mm).
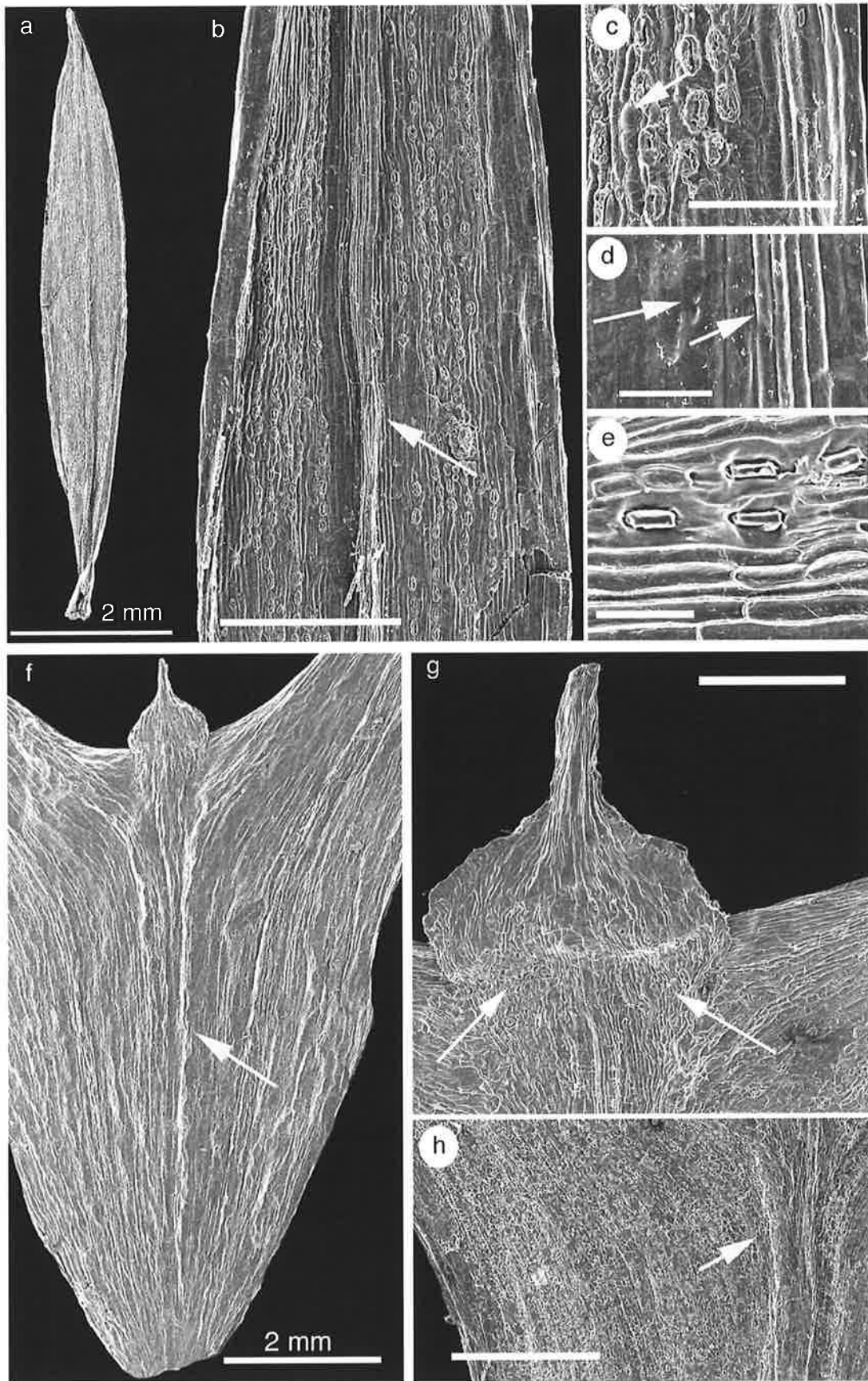
Fig. 2a-h *Papuacedrus papuana* seedling and juvenile transitional foliage

Fig. 3a-g *Papuacedrus papuana* juvenile transitional foliage cuticle
Specimen 145102

  a. Inner surface, thin cuticle. Guard cells elongate. Subsidiary cells 5, with indentations and fine-grained surface texture. Conspicuous groove around the guard cells. Epidermal cells slightly more coarse-grained. Anticlinal cell walls thin, discontinuous (scale 20 μm).
  b. Outer surface, facial leaf. Stomata with high ridged and slightly lobed Florin rings. Small round papillae associated with stomata (scale 50 μm).
  c. Inner surface. Subsidiary cells 4-6, and shared by adjacent guard cells (scale 50 μm).
  d. Outer surface, seedling leaf (Fig. **2b**). Stomata with high ridged Florin rings, in rows, and roughly parallel with the leaf margin (scale 100 μm).
  e. Inner surface. Rows of stomata separated by bands of epidermal cells (scale 100 μm).
  f. Inner surface. Stomatal rows discontinuous, and separated by wide bands of epidermal cells (scale 200 μm).
  g. Inner surface. Moderately coarse-grained, elongate epidermal cells with thin anticlinal cell walls (scale 50 μm).
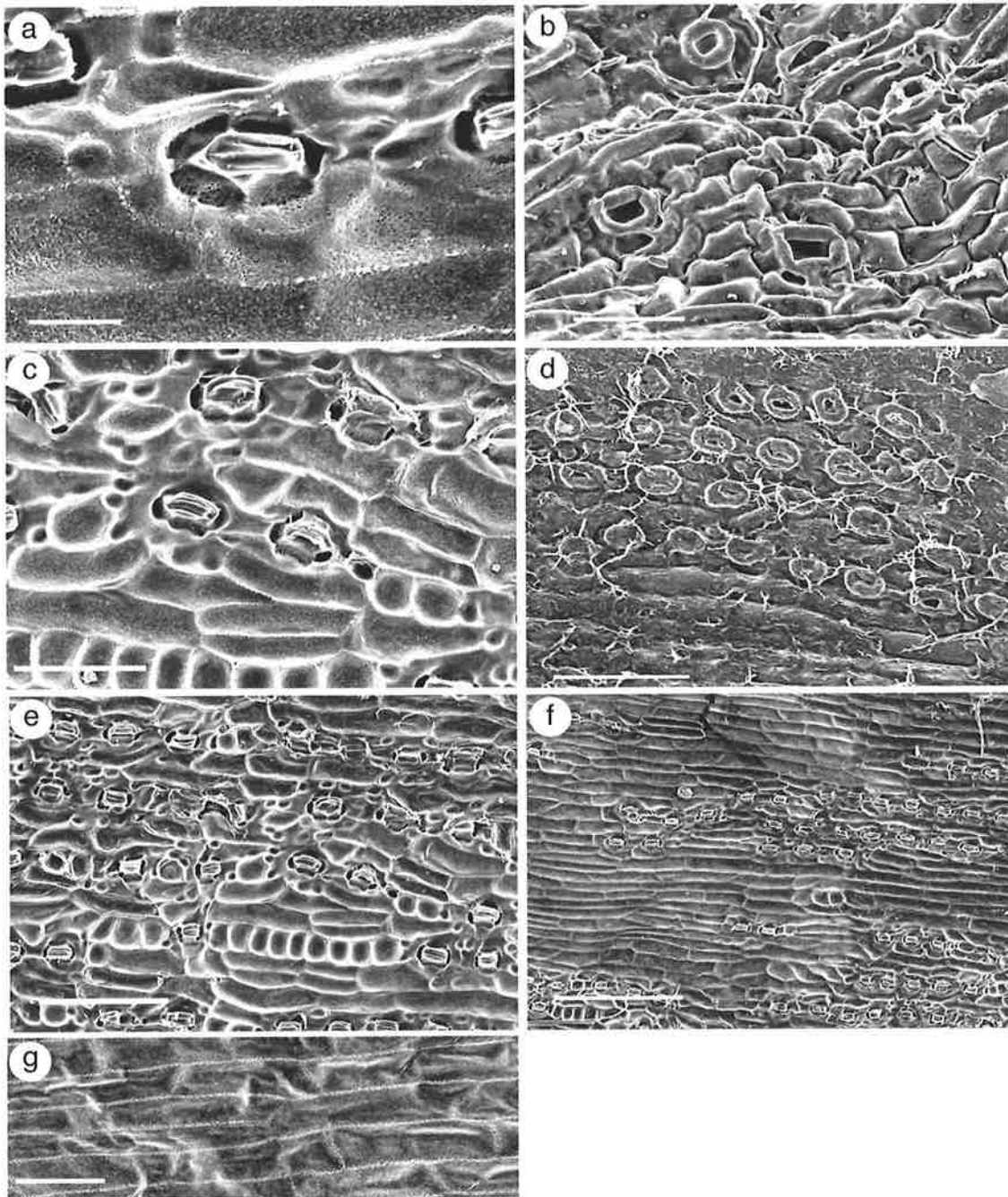
Fig. 3a-g *Papuacedrus papuana* juvenile/transitional foliage cuticle

Fig. 4a-d *Papuacedrus papuana* transitional foliage branchlets showing foliage variability with height (age)

Photographed from herbarium sheets.

    a. Young tree ~2.5 m. Highly waxy, dorsal surface. Leaves decussate, not imbricate, in flattened sprays on short branchlets. Short young terminal shoot (upper right) not flattened and with facial and lateral leaves similar in length (specimen 202315).

    b. Sterile 15 m tree. Slightly convex ventral surface. Highly dimorphic leaves on short, opposite branchlets. Lateral leaves elongate, lanceolate and generally imbricate, except on the main axis where branching occurs (specimen 102076).

    c. 15 m spreading tree. Young branching shoots. Dorsal surface (left) with concave, highly waxy, lateral leaves. Ventral surface (right) with convex leaves. Lateral leaves imbricate, except on the main axis (specimen 229911).

    d. Tree 25 m. Ventral surface. Leading shoot with short, flattened and opposite branchlets in the lower half. Leaves here slightly convex and highly dimorphic. In the upper half younger shoots are less flattened and lateral leaves are only slightly larger than facial (specimen 45004).
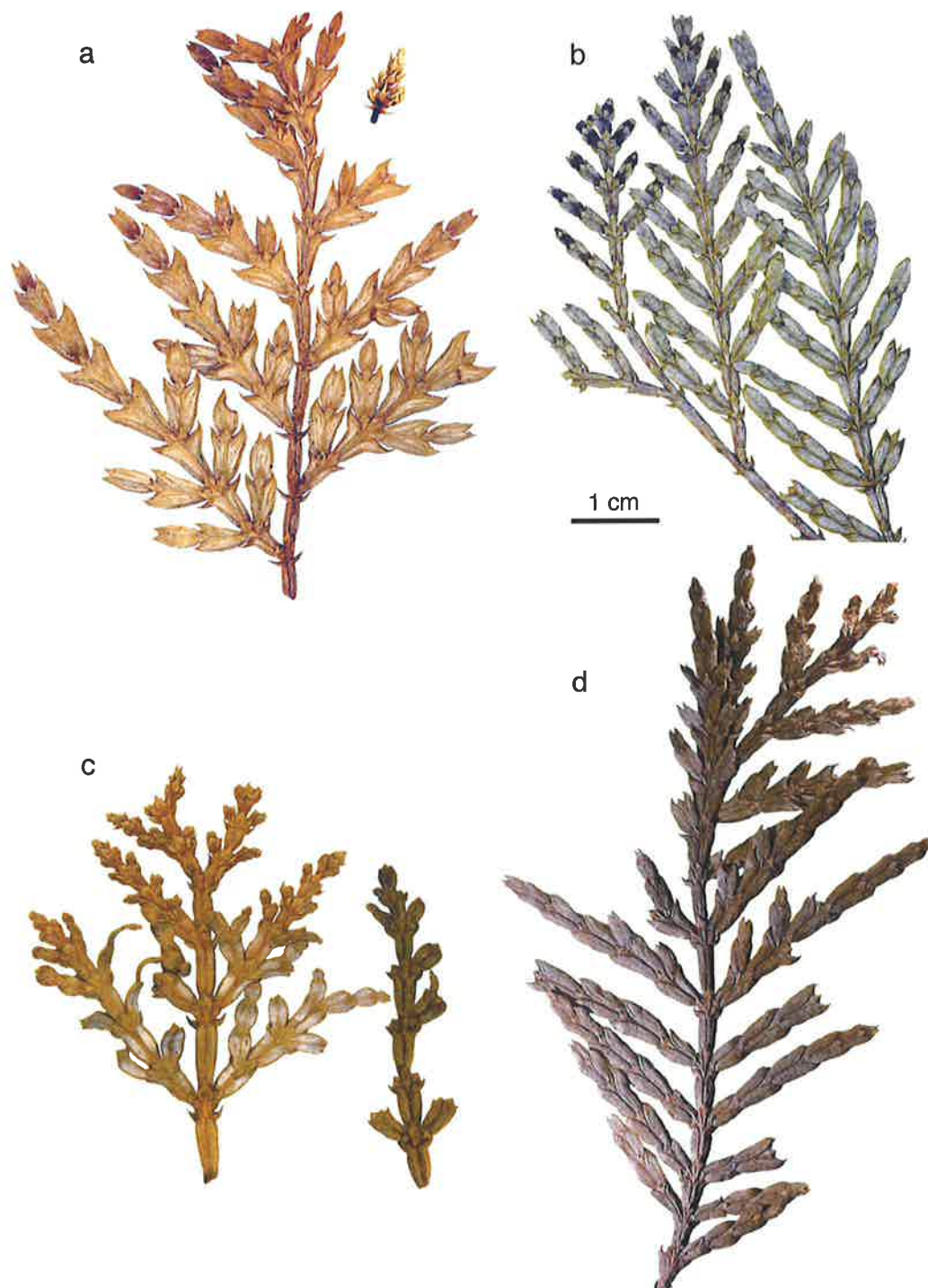
a

b

1 cm

c

d

Fig. 4a-d *Papuacedrus papuana* transitional foliage branchlets showing foliage variability with height (age)

Fig. 5a-e *Papuacedrus papuana* morphological variation in transitional foliage

    a. Variable foliage from a 2.5 m young tree (see Fig. 4a). (1) Flattened branching foliage. Free sections of lower lateral leaves almost at right angles to the lower (fused) section. Lateral leaves slightly concave, and with waxy stomata (white areas) unevenly distributed in the central section of the leaves. (2) Ventral surface, terminal lateral leaves. Leaves convex, almost touching at apices, and without stomata. (3) Young, branching shoot with monomorphic, non-flattened leaves. (4) Dorsal surface, as for a, but smaller foliage (specimen 202315).

    b. Close up of a (4) showing facial leaves continuous with lateral leaves (the latter not overlapping the facials). Note the waxy stomata and well defined central ridge (scale 500 µm).

    c. 40 m tree (1) Dorsal surface young shoot. Leaves almost monomorphic, imbricate, and rounded in appearance, with broad facial leaves overlapping the lateral pair above. (2) Ventral surface, young shoot, leaves not flattened. Lateral and facial leaves almost monomorphic with lateral leaves overlapping facial leaves (specimen 108114.1)

    d. Close up c (2), ventral surface. Stomata rare on exposed surfaces. Facial leaf with well defined central ridge (scale 500 µm).

    e. 20 m tree. (1) Dorsal surface waxy, slightly concave, and almost covered in stomata. Lateral leaves imbricate. (2) Terminal shoot with rounded lateral leaves. Stomata separated by bands of epidermal cells (3) Ventral surface. Lower lateral leaves on main axis. Upper free part of these leaves at right angles to the twig, carinate and with acute apices. Surface convex with no stomata visible. Lower part of facial leaf on main axis long, narrow, and forming a groove that extends to base of lateral leaves below. This feature is less obvious on lateral branches (specimen 105269).
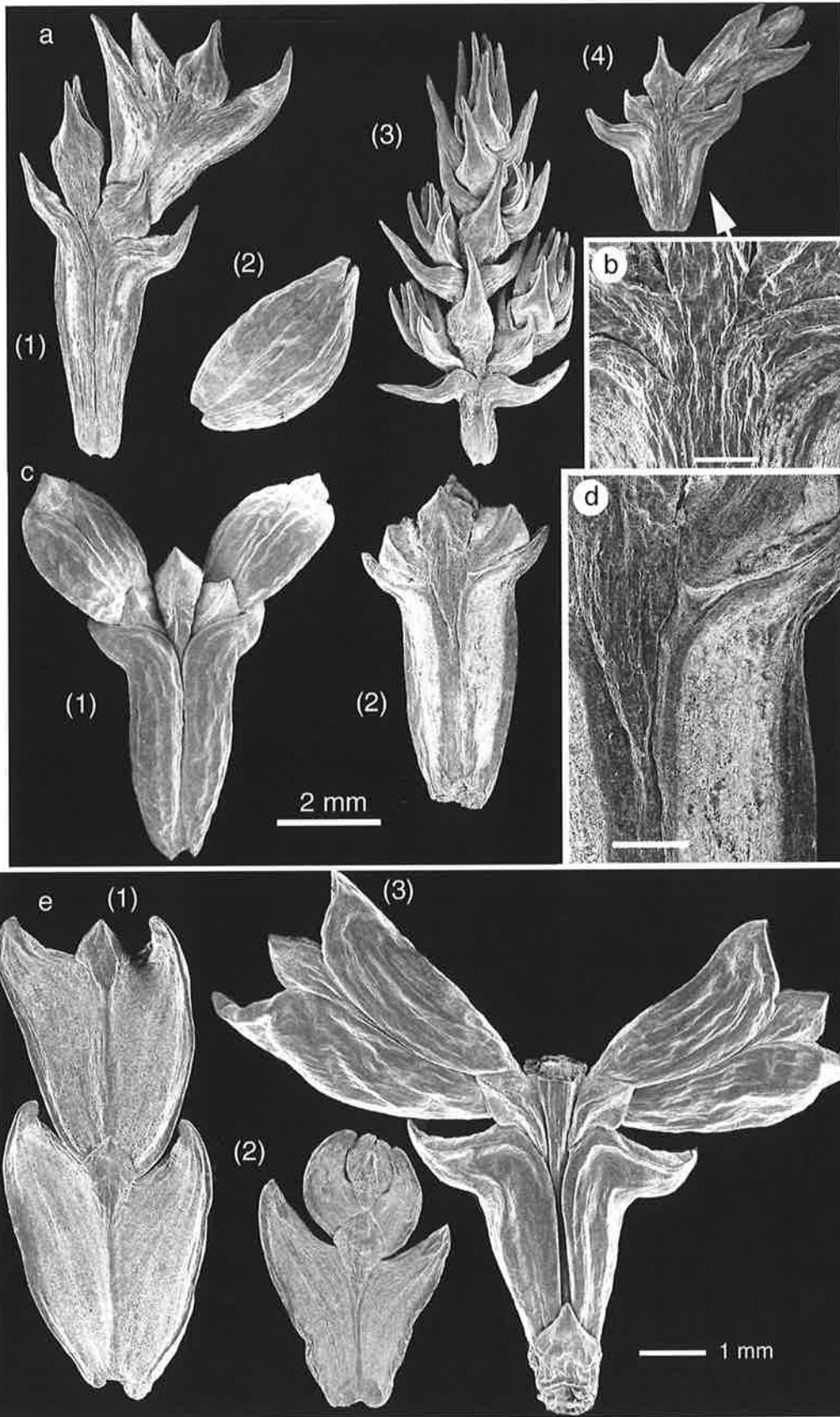
Fig. 5a-e *Papuacedrus papuana* morphological variation in transitional foliage
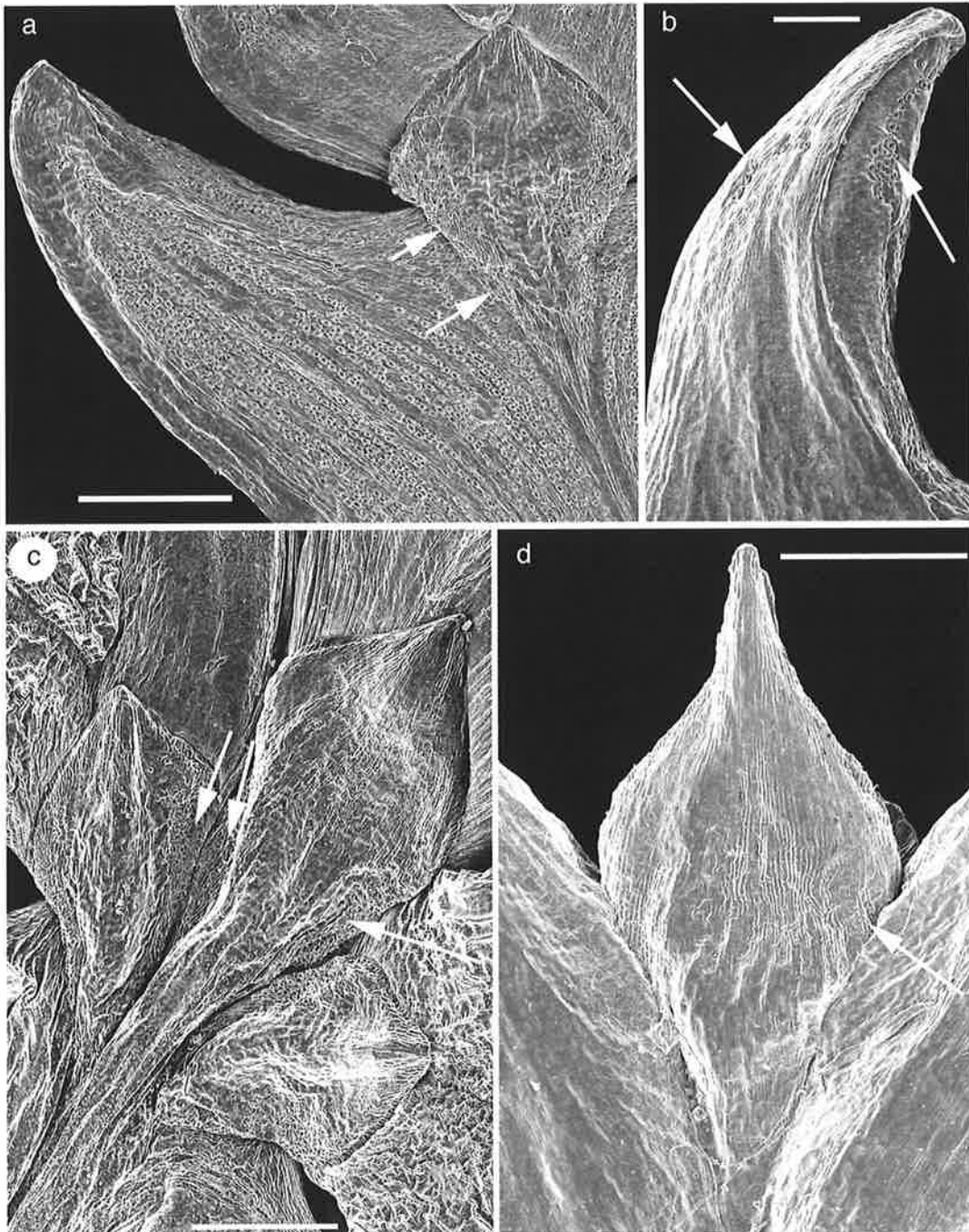
Fig. 6a-d *Papuacedrus papuana* stomatal distribution, transitional foliage

    a. Dorsal surface. Stomata on lateral leaves in rows parallel to the leaf margin, and with bands of epidermal cells between (scale 500 μm; specimen 105269).

    b. Ventral surface. Lateral leaf with a few stomata (left arrow). Adaxial surface with stomata in 1 or more rows on either side of the leaf centre (right arrow; scale 200 μm; specimen 105269).

    c. Ventral surface, young shoot. Lateral leaves astomatic, Stomata on facial leaves on either of the leaf (arrows; scale 500 μm; specimen 105269).

    d. Ventral surface. Lateral leaves astomatic. Facial leaves with a few stomata on either side of the leaf centre (arrow, scale 500 μm; specimen 202315).

Fig. 7a-g *Papuacedrus papuana* adult foliage

With the exception of c, all photographs are from specimen 108114.1, a 40 m tree from ~3500 m, Southern Highlands, PNG.

    a. Small adult foliage. Branching on ultimate branchlets opposite.

    b. Detail of young terminal shoots from **a**. The shoot on the leaf a fertile branchlet. Lateral and facial leaves on terminal shoots almost similar in size and slightly convex on dorsal and ventral surfaces.

    c. Adult foliage, 28 m tree from 3550-3750 m, Southern Highlands, PNG. Facial and lateral leaves similar in size on all branches and branchlets.

    d. Branching shoot. Lateral leaves only partially flattened bilaterally. Facial and lateral leaves similar in size.

    e. Dorsal surface. Stomata on lateral leaves in small grooves towards the base of the leaf (white arrows). Stomata of facial leaves almost covered by the overlying laterals (black arrow; scale 500 μm).

    f. Adaxial surface, ventral facial leaf. Stomata generally parallel to leaf centre. On the ventral surface (arrow) many barely visible small holes mark the presence of calcium oxalate crystals in epidermal cells (scale 200 μm).

    g. Dorsal surface. Stomata extend from the base of the lateral leaf (not shown) to a groove beneath the free section of the leaf (lowest arrow). Stomata on the adaxial surface of this leaf (right arrow) aligned with, but not present in, the centre of the leaf. Facial leaf with revolute margin and bulging adaxial surface (upper arrow; scale 500 μm).
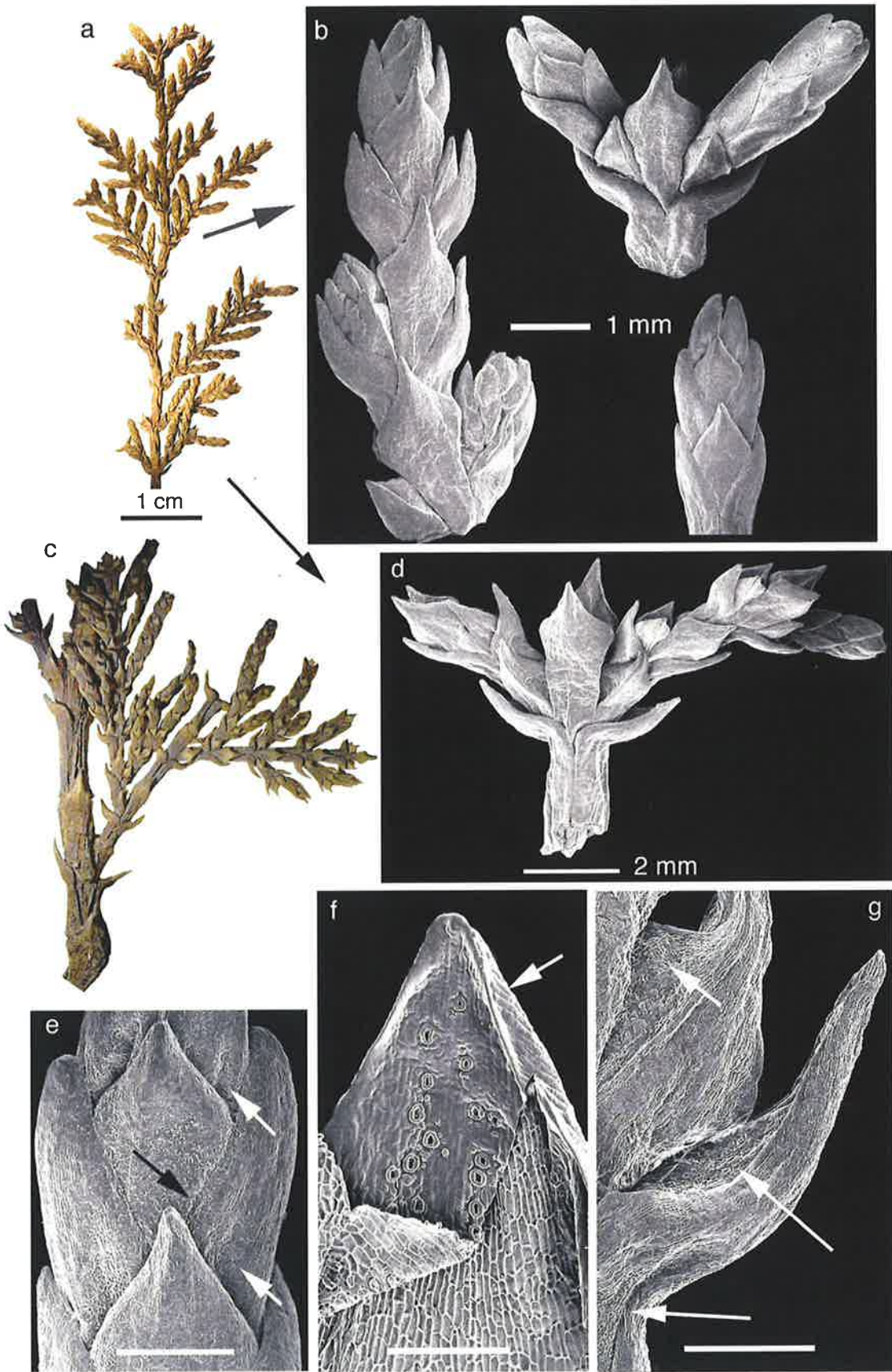
Fig. 7a-g *Papuacedrus papuana* adult foliage

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Fig. 8a-j *Papuacedrus papuana* adult and transitional leaf cuticle SEM/LM

a. Inner surface stomata, adult leaf. Elongate guard cells. Subsidiary cells 5-6, indented, with fine-grained surface texture. These fold down around the guard cells to form a conspicuous groove broken by the anticlinal cell walls. Epidermal cells coarse-grained and clearly distinguishable from subsidiary cells. Anticlinal cell walls of subsidiary cells relatively thick and moderately coarse-grained (scale 20 μm; specimen 108114.1).

b. Outer surface, cleaned cuticle, adult leaf. High ridged and lobed Florin rings surrounded by small round papillae (scale 20 μm; specimen 108114.1).

c. Inner surface, transitional leaf. Subsidiary cells 4-6, and shared by adjacent guard cells (scale 50 μm; specimen 201315).

d. Outer surface, transitional leaf, cleaned cuticle. Stomata with slightly lobed Florin rings, and surrounded by small round papillae (scale 50 μm; specimen 202315).

e. Outer surface, transitional leaf. High ridged, lobed Florin rings covered in wax (scale 50 μm; specimen 229911).

f. Inner surface, transitional leaf. Stomata similarly oriented to each other, in discontinuous rows, and separated by broad bands of coarse-grained epidermal cells (scale 200 μm; specimen 201315).

g. Lateral leaf apex, ventral surface, adult leaf. Epidermal cells with small holes or nodules indicating the presence of calcium oxalate crystals in the cell wall (scale 50 μm; specimen 108114.1).

h. Inner surface, adult leaf. Elongate and irregularly shaped epidermal cells. Periclinal walls coarse-grained, anticlinal walls thick, coarse-grained and slightly broader at the base (scale 20 μm; specimen 108114.1).

i. LM, transitional leaf. Epidermal cells with numerous small calcium oxalate crystals (scale 100 μm; specimen 229911).

j. Inner surface, adult leaf. Coarse-grained epidermal cells with numerous small calcium oxalate-containing nodules (scale 20 μm; specimen 108114.1).
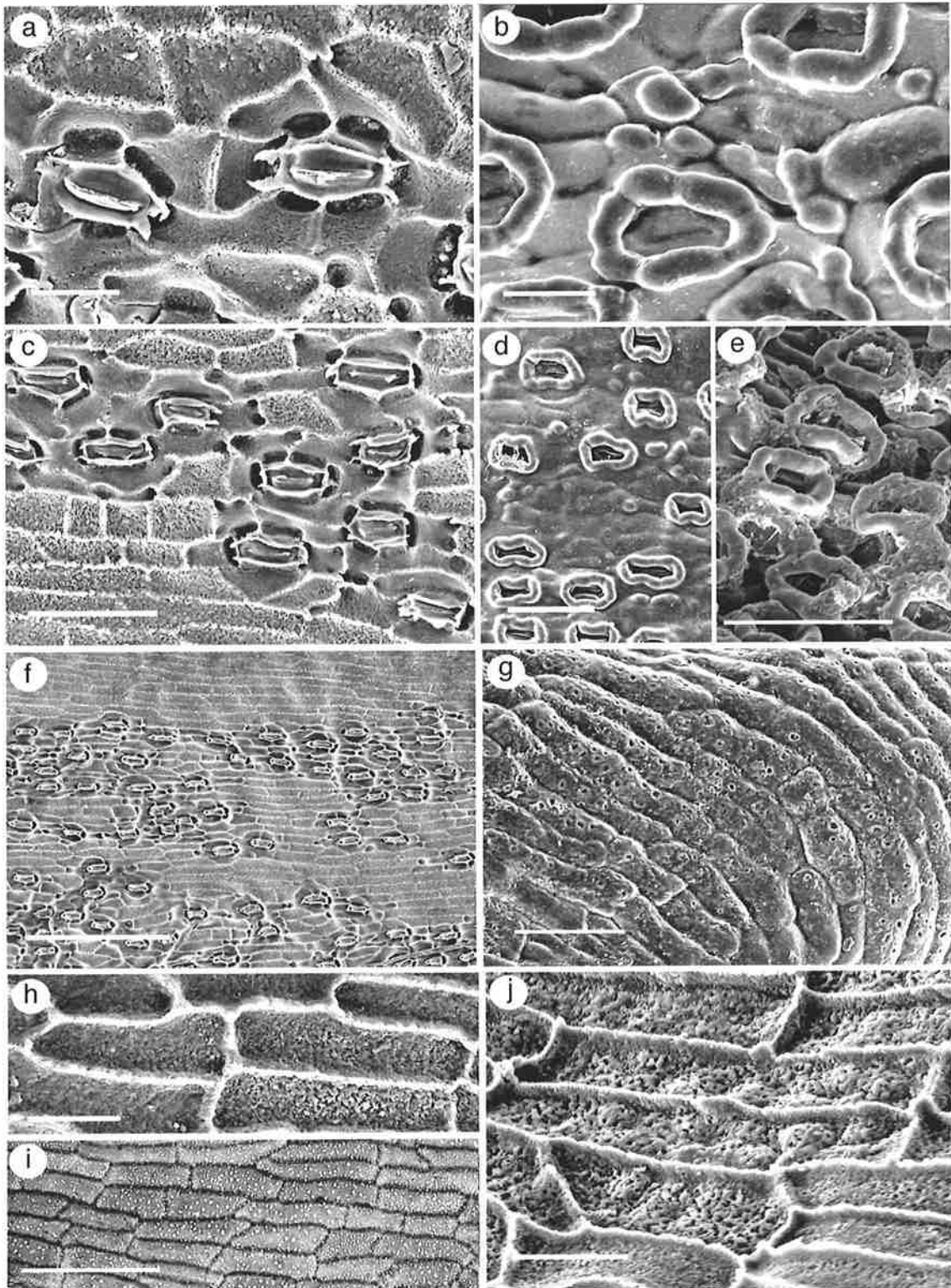
Fig. 8a-j *Papuacedrus papuana* adult and transitional leaf cuticle SEM/LM

Fig. 9a-d *Papuacedrus papuana* ovulate cones

Note variation in cone size and leaf morphology on short shoots. Photographed from herbarium sheets.

a. Comparatively small cones on short, unflattened shoots. The shoots above the cones are not flattened, and have lateral and facial leaves of similar in size. These appear to be in a whorled rather than decussate arrangement (specimen 193329, 28 m tree at ~3550-3750 m, Southern Highlands, PNG).

b. Branchlet with short, flattened fertile shoots with 5 immature (or possibly aborted cones), and one mature cone (specimen 198385, 40 m tree at ~2000 m, Upper Watat, PNG).

c. Clusters of large cones on short shoots. The small foliage on this specimen is only semi flattened (specimen 108114.1, 40 m tree at ~3500 m, Southern Highlands, PNG.).

d. Four cones (from the same specimen) showing the diversity in size and shape. When the cone scales are widely gaping the apices of both scale pairs may fold downwards and outwards (green arrow: specimen E/1944).

e. Detail of 2 large mature cones from c. Bract on lower bract-scale complex elongate and not spreading to the margins of the scale.
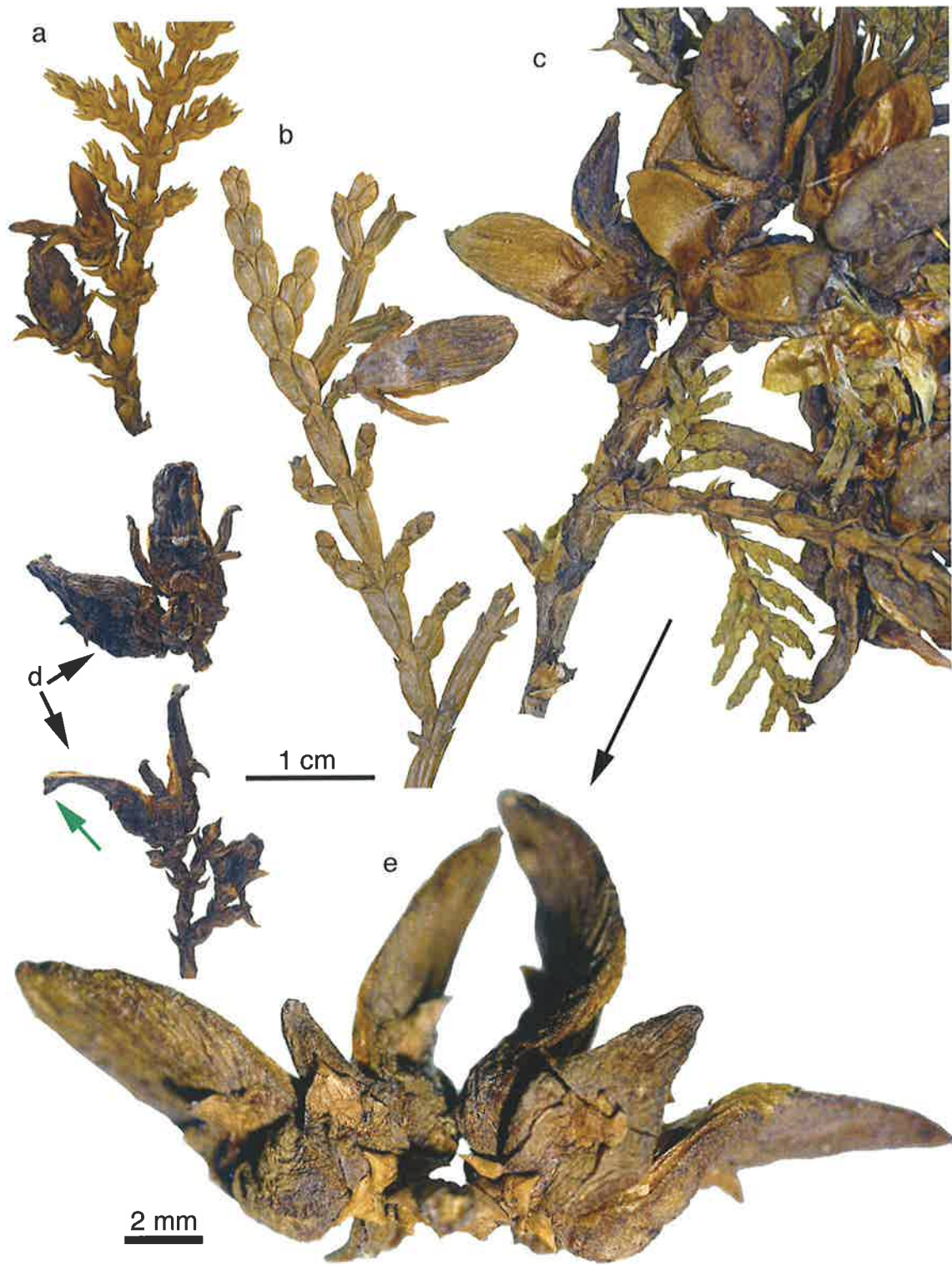
Fig. 9a-d *Papuacedrus papuana* various ovulate cones

Fig. 10a–m *Papuacedrus papuana* ovulate cones
Figs **a, c, d, h** all 2mm.

a. Large mature, gaping cone, composite photo (see LM Fig. **9e**). Ultimate scales much larger than penultimate, with slightly rugose adaxial surfaces, and papillate margins. The papillae also extend downwards in a v-shape (arrow; specimen 108114.1)

b. Detail of the scale apex, **a**. Papillae on the margins of the scale but also descending downwards into the scale from the asymmetrical apex (scale 1 mm; specimen 108114.1).

c. Side view, much smaller immature cone. Ultimate and penultimate scales only partially developed (specimen 193329).

d. Submature - mature, flattened cone on short stem. Ultimate scales broadest just below the bract projection (the apices of this cone appear to have been broken off). Penultimate scales narrow and gaping. Scale apex outwardly recurved (arrow; specimen E/0944).

e. Side view, **d**. Lower section of the ultimate bract highly undulating, and bulging outwards (arrow). Spiny section of the bract in the centre of the scale, and projecting outwards. Penultimate bract-scale complex narrow, with spiny bract projection in the lower third of the scale. The broader, lower section of this bract recurves inward. All abaxial scale surfaces rugose.

f. Detail, **d**. Adaxial surface, penultimate ultimate scale. Apex of scale outwardly recurved above a dense band of papillae (scale 500 μm).

g. Detail, **h**. Outwardly recurved apex of ultimate scale (scale 500 μm).

h. Mature and gaping (broken) cone. Ultimate scales with outwardly recurved apices (specimen E/0944).

i. Detail, **a**. Short recurved ultimate bract projection (scale 1 mm).

j. Close up of immature cone, **c**. Ultimate scale apices acute, adaxial surface rugose. Bract covering the lower abaxial half of the scale, with bract projection in the centre of the scale.

k. Detail of bracts 1–3. Subtending bracts 1 & 2 broadly triangular and with acute apices. All bracts inwardly curved towards the base (scale 1 mm; specimen E/0944).

l. Cone initiation. Ultimate bract elongate, other bracts broadly triangular, centrally keeled, outwardly curved in the upper half, and with acute apices (scale 500 μm; specimen E/0944).

m. Detail, **j**. Immature seed with membranous wings. No columella apparent in the centre of the cone (lower right; scale 500 μm).
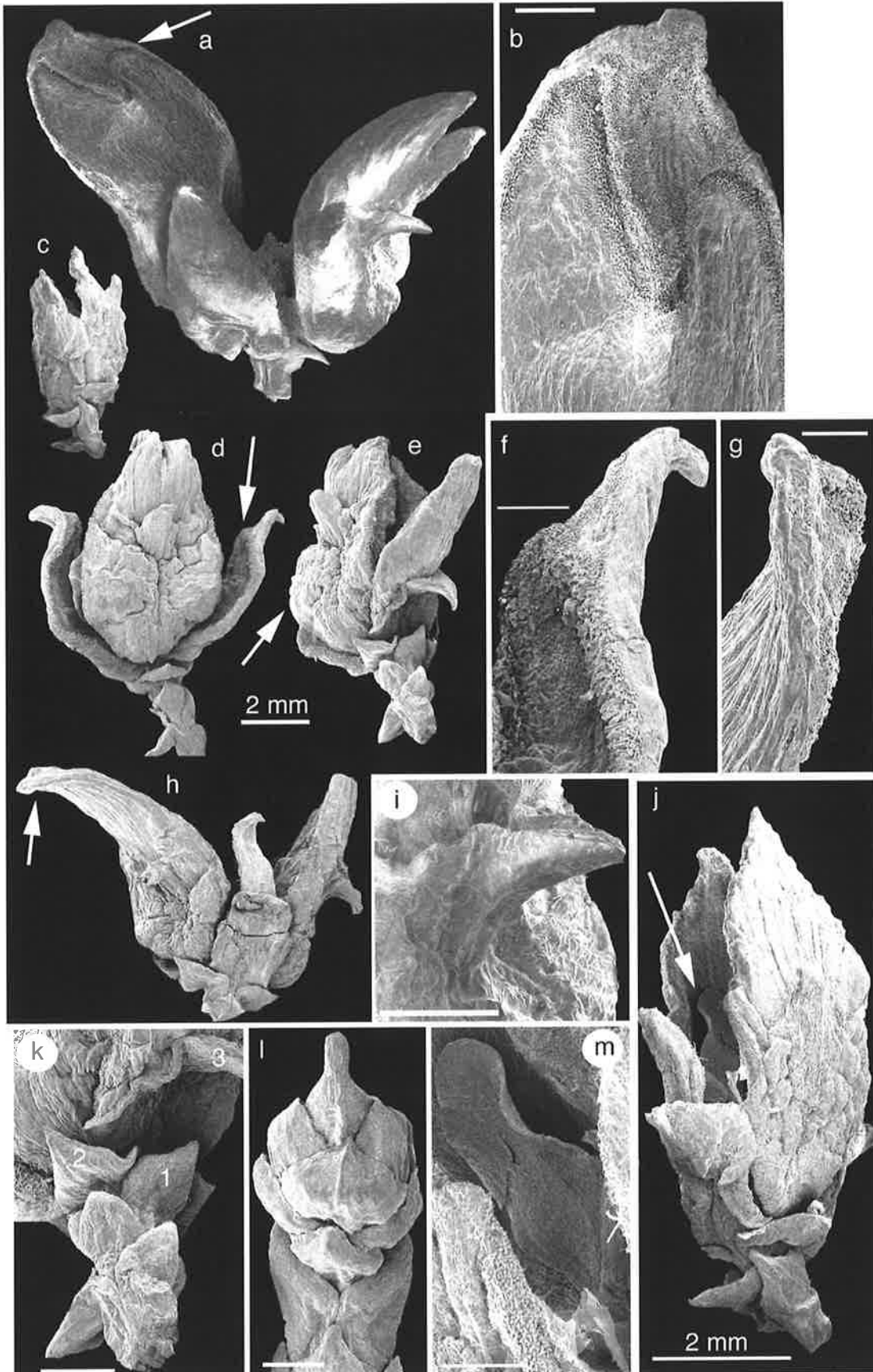
Fig. 10a-m *Papuacedrus papuana* ovulate cones
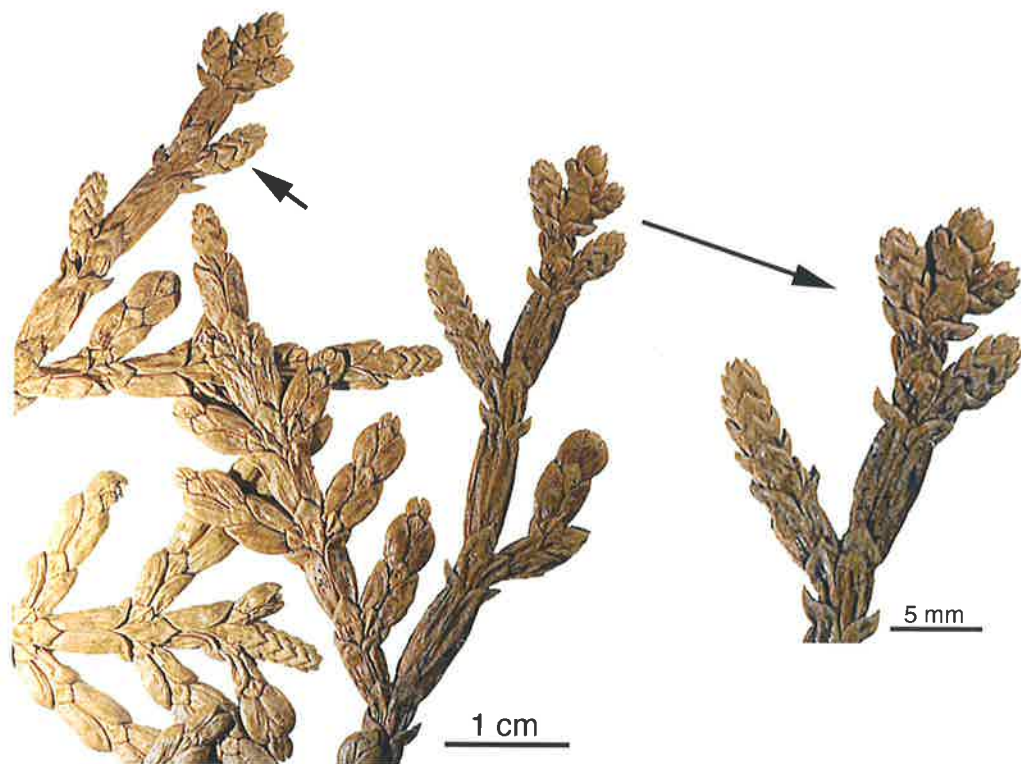
Fig. 11 *Papuacedrus papuana* pollen cones.
Specimen 198385 (photographed from herbarium sheet)
Pollen cones terminal on very short flattened ultimate branchlets, solitary. Microsporophylls broadly triangular, decussate, 8-12 similarly sized pairs, with acute to slightly rounded apices.

Papuacedrus papuana (F. Muell.) H. L. Li var. *arfarkensis* (Gibbs) R. J. Johns, Curtis's Bot. Mag. 2 (2): 70 (1995)

Distribution: Found in the Arfak Mountains of Irian Jaya (western New Guinea: Li 1953), the Moluccas (Enright 1995), and Indonesia (Farjon 2005).
Ecology: Grows in forests and on ridges from 2300-2600 m (Li 1953), and overlaps the range of *P. torricellensis* (*P. papuana* var. *papuana*; Farjon 2005).

The foliage and cones of *P. arfakensis* and *P. papuana* (and *P. torricellensis*) are considered indistinguishable and separate descriptions for *P. arfakensis* are not given here. Photographic plates and figure captions (Figs 12-16) are included to illustrate these similarities. The pollen cones of *P. arfakensis* are larger than those of *P. papuana* (Farjon 2005). None were available for comparison.

The foliage from the three species that are examined is described as transitional. The leaf cuticle from these specimens is quite thin, and is more suggestive of transitional than adult foliage. The height (age) of trees from which 2 specimens were collected is unknown.

Specimens examined:
119313, National Herbarium, Canberra, Australia. Collected 10/1958, C Kalkman BW 6374, Neentjapaki Mountains, Kebar Valley, West New Guinea. Tree ~16 m at ~1090 m, in primary forest.
152400, National Herbarium, Canberra, Australia. Collected 2/1954, C Versteegh BW 254, Res. Manokwari. Anggigita Lake, at 2000 m.
E/1196, Herbarium Collection, The University of Adelaide, South Australia. HA368049, N. Moluccas, Bacan Island, Gunung Sibela near Waiaua. Sterile conifer on steep hillside at 1050 m.
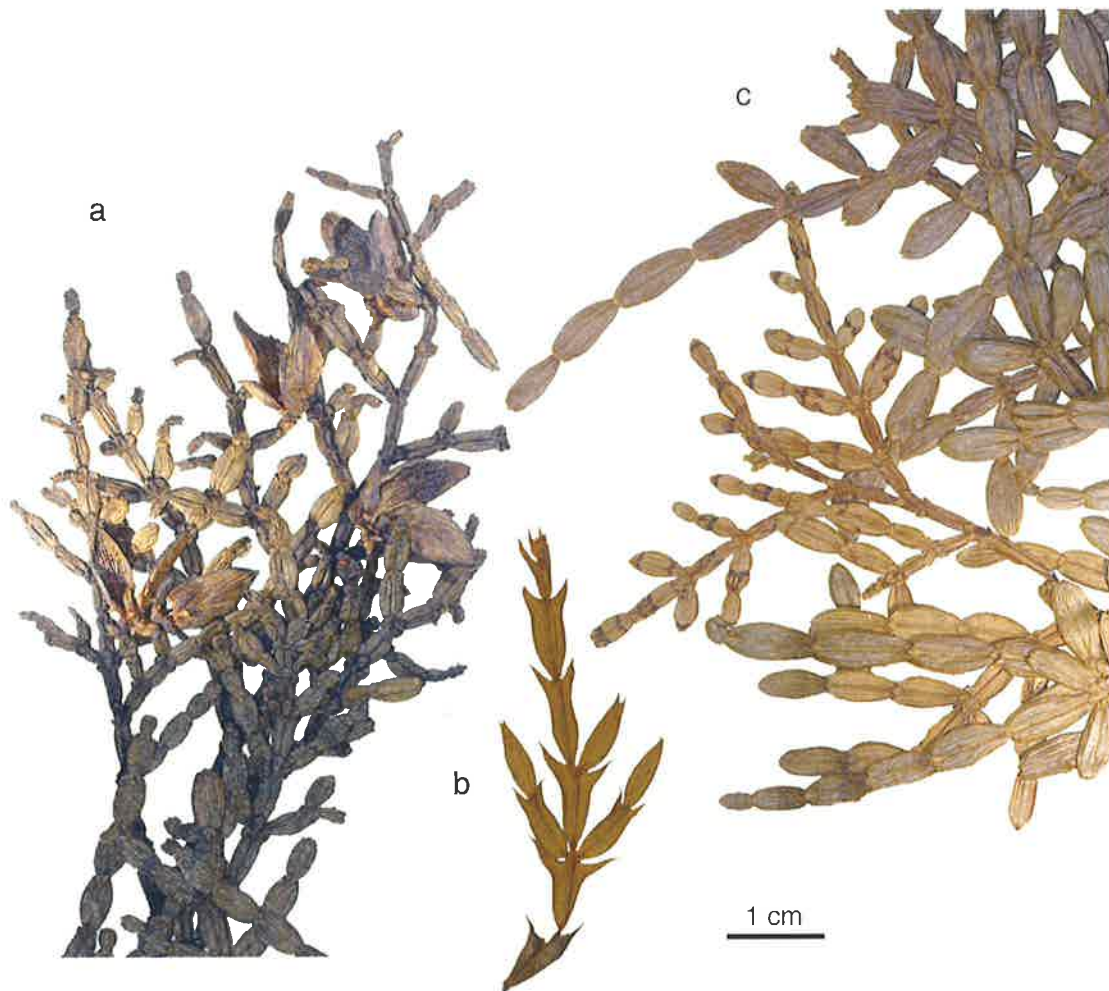
Fig. 12a-c *Papuacedrus papuana* var. *arfakensis* foliage

    a. Ventral surface, fertile foliage. Branchlets opposite, short and with very immature and mature ovulate cones. Leaves highly dimorphic, lateral leaves much larger, and bilaterally flattened (specimen 152400 from 2000 m, height unknown, West New Guinea). Photographed from herbarium sheet.

    b. Dorsal surface, transitional foliage. Branchlets opposite. Highly dimorphic leaves. Lateral leaves not imbricate. Terminal lateral leaves inwardly curved. This foliage looks quite different to the other two specimens (specimen E/1196 from ~1050 m, N. Moluccas).

    c. Ventral surface, two foliage types. 1) Small leaves, with elongate narrow laterals on main axes, and smaller young terminal shoots. 2) Larger leaves, highly dimorphic, with flattened, imbricate and elongate laterals (specimen 119313 from ~1090 m, 16 m tree, West New Guinea). Photographed from herbarium sheet.

Fig. 13a-h *Papuacedrus papuana* var. *arfakensis* foliage detail
Specimens **a-e** 152400; **f-h** 19313

a. (1)-(3) Dorsal surface, different sized foliage. Leaves highly dimorphic. Laterals elongate, lanceolate, imbricate.

b. Detail of **a** (1). On lateral leaves - leaf surface very slightly sunken. Stomata in discontinuous, often short, rows that are generally parallel with, but not reaching, the leaf margin. Stomatal rows separated by broad bands of epidermal cells. Leaf margins entire, but revolute towards the apex and producing bulging of the adaxial surface. Facial leaf – small, triangular in shape, with a slightly frilled margin. Stomata largely hidden by overlying lateral leaves (arrow). A narrow elongation of the facial leaf extends downwards between the lateral leaves (scale 1 mm).

c. Base of lateral leaves slightly papillate. The area overlain by the facial leaf is astomatic (scale 500 μm).

d. Facial leaf, adaxial surface. Stomata in short scattered rows more or less parallel with the centre of the leaf (scale 200 μm).

e. Dorsal surface, lateral leaves. Margins adjoining, and slightly revolute (scale 200 μm).

f. (1) Dorsal surface. Waxy, slightly sunken surface with numerous stomata on lateral leaves. (2) Ventral surface very slightly convex, and astomatic.

g. Dorsal surface detail, lateral and facial leaf. Lateral leaf margin revolute. Facial leaf with a few scattered stomata (lower left). Facial and lateral leaf with calcium oxalate nodules (barely visible) near their apices (but not on the adaxial surface; scale 200 μm).

h. Ventral surface, base of lateral leaves. Astomatic (scale 500 μm).
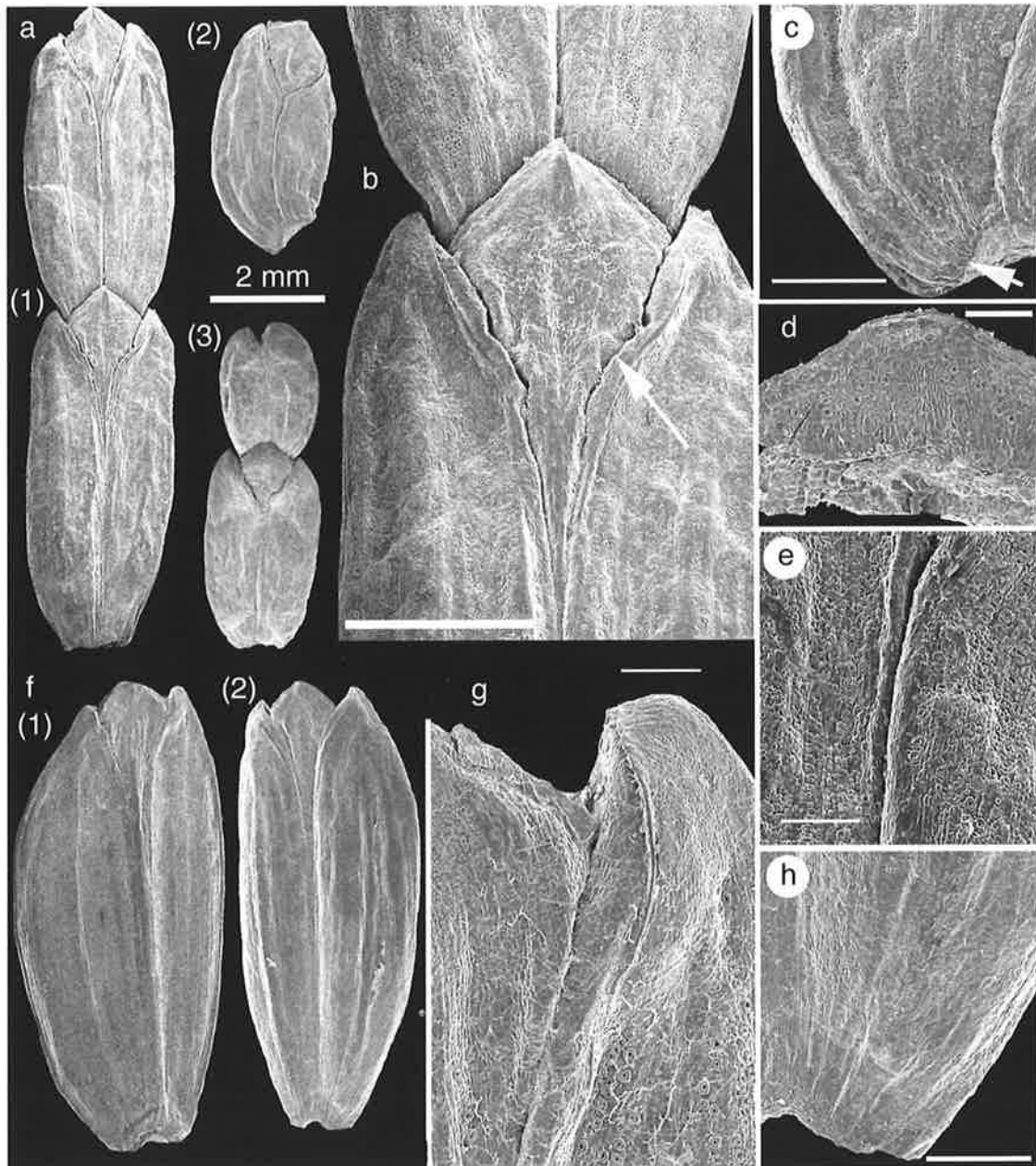
Fig. 13a-h *Papuacedrus papuana* var. *arfakensis* foliage detail

Fig. 14a-h *Papuacedrus papuana* var. *arfakensis* leaf cuticle

a. SEM inner surface stomata, transitional leaf. Guard cells slightly elongate. Subsidiary cells 4-5, with round indentations at their extremities, and fine-grained in texture. Subsidiary cells also forming a conspicuous groove around the guard cells. This groove is broken by the anticlinal cell walls. Epidermal cells coarse-grained (scale 25 μm; specimen 119313).

b. SEM outer, very waxy, surface, with epiphyllous fungi. Stomata closely packed. Florin rings, high ridged, slightly lobed, and surrounded by small round papillae (arrow; scale 20 μm; specimen 119313).

c. SEM inner surface. Stomata randomly oriented. Some sharing of subsidiary cells by adjacent guard cells (scale 50 μm; specimen 119313).

d. SEM outer surface, lateral leaf. Closely packed stomata surrounded by numerous round papillae. Florin rings lobed (scale 200 μm; specimen 152400).

e. LM. Stomata in short discontinuous rows. Guard cells mostly with the same orientation, and separated by broad bands of elongate to isodiametric epidermal cells (scale 200 μm; specimen 152400).

f. LM. Lobed stomata surrounded by frequent round papillae (arrows; scale 100 μm; specimen 119313).

g. SEM dorsal surface, lateral leaf. Adnate section raised and without stomata (arrow; scale 500 μm; specimen 119313).

h. SEM inner surface. Epidermal cells elongate, and coarse-grained in texture (scale 100 μm; specimen 119313).

i. SEM inner ventral surface, facial leaf apex. Epidermal cells with nodules containing calcium oxalate crystals (scale 10 μm; specimen 119313).
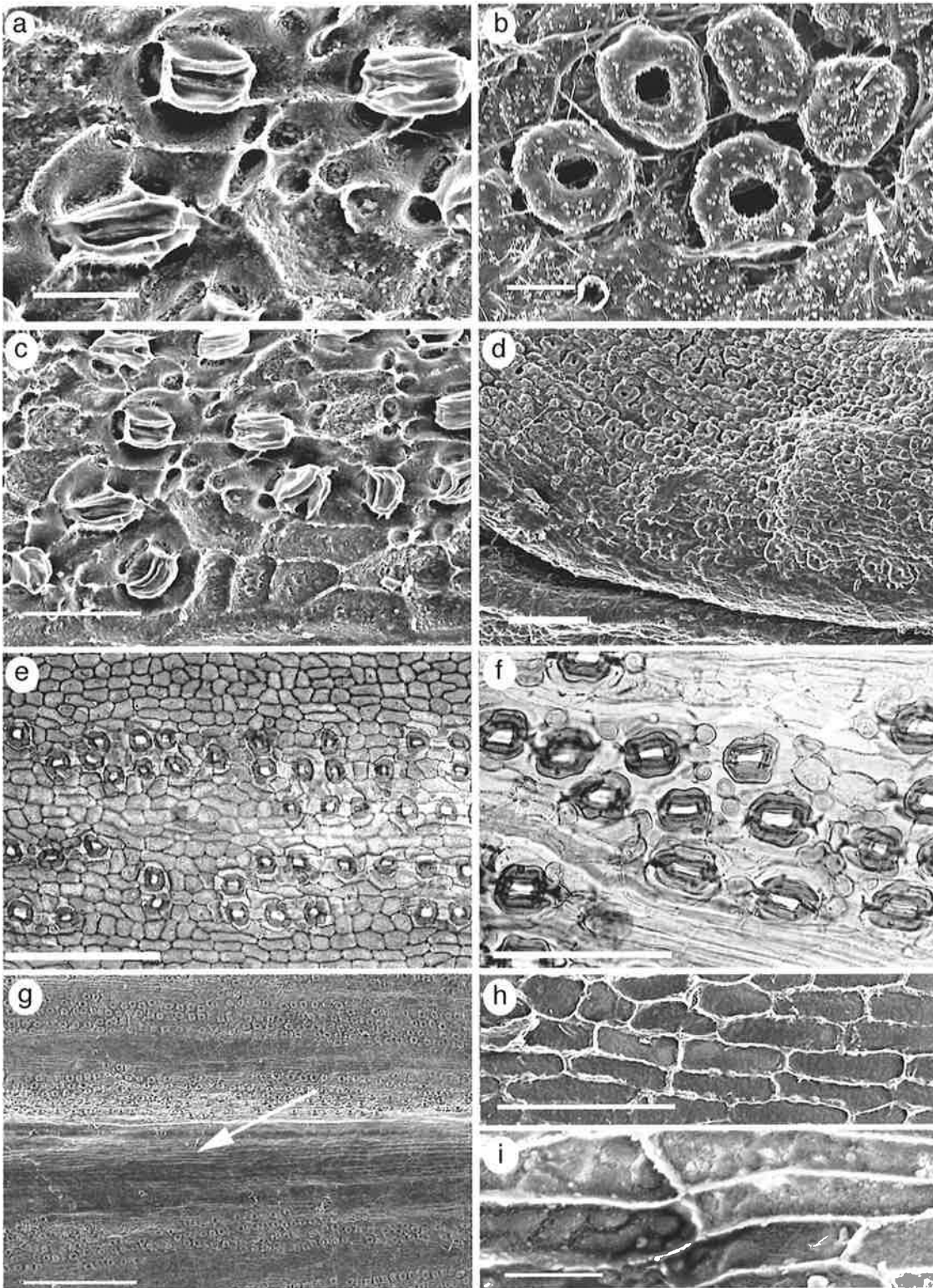
Fig. 14a-h *Papuacedrus papuana* var. *arfakensis* leaf cuticle

45

Fig. 15a-h *Papuacedrus papuana* var. *arfakensis* ovulate cone
Specimen 152400

    a. The same cone viewed from two angles. Left view - penultimate bract-scale complex elongate, narrow, with spiny bract projection towards the base of the scale. Bract projection on ultimate scale recessed. Lower section of the bract highly undulating, and bulging outwards. Adaxial and abaxial scale surfaces rugose. Right view - cone on short stem. Ultimate scales elongate, broad. Broad at the base. Apex appears acute from this angle.

    b. Base of cone in **a**. Very short shoot with 2 facial and 1 lateral decussate leaf pairs (scale 1 mm).

    c. Outwardly curved short bract projection, ultimate scale. Area beneath the projection highly undulating and bulging outwards (scale 1 mm).

    d. Bract projection ultimate scale. Stomata on the abaxial surface of the bract and immediately below (scale 200 μm).

    e. Adaxial surface, penultimate ultimate scale. Scale apex recurving outwards above a dense band of papillae near the top of the scale. From this view, the recurved section appears to be a projection just below the scale apex. Internal scale surface rugose (scale 500 μm).

    f. Papillate margins of penultimate (lower) and ultimate scales (scale 200 μm).

    g. Detail, external surface of penultimate scale (scale 50 μm).

    h. Lower bract surface, ultimate scale. Large epidermal cells and highly ridged surface (scale 200 μm).

    i. Detail, **d**. Stomata and papillae beneath ultimate bract projection (scale 100 μm).
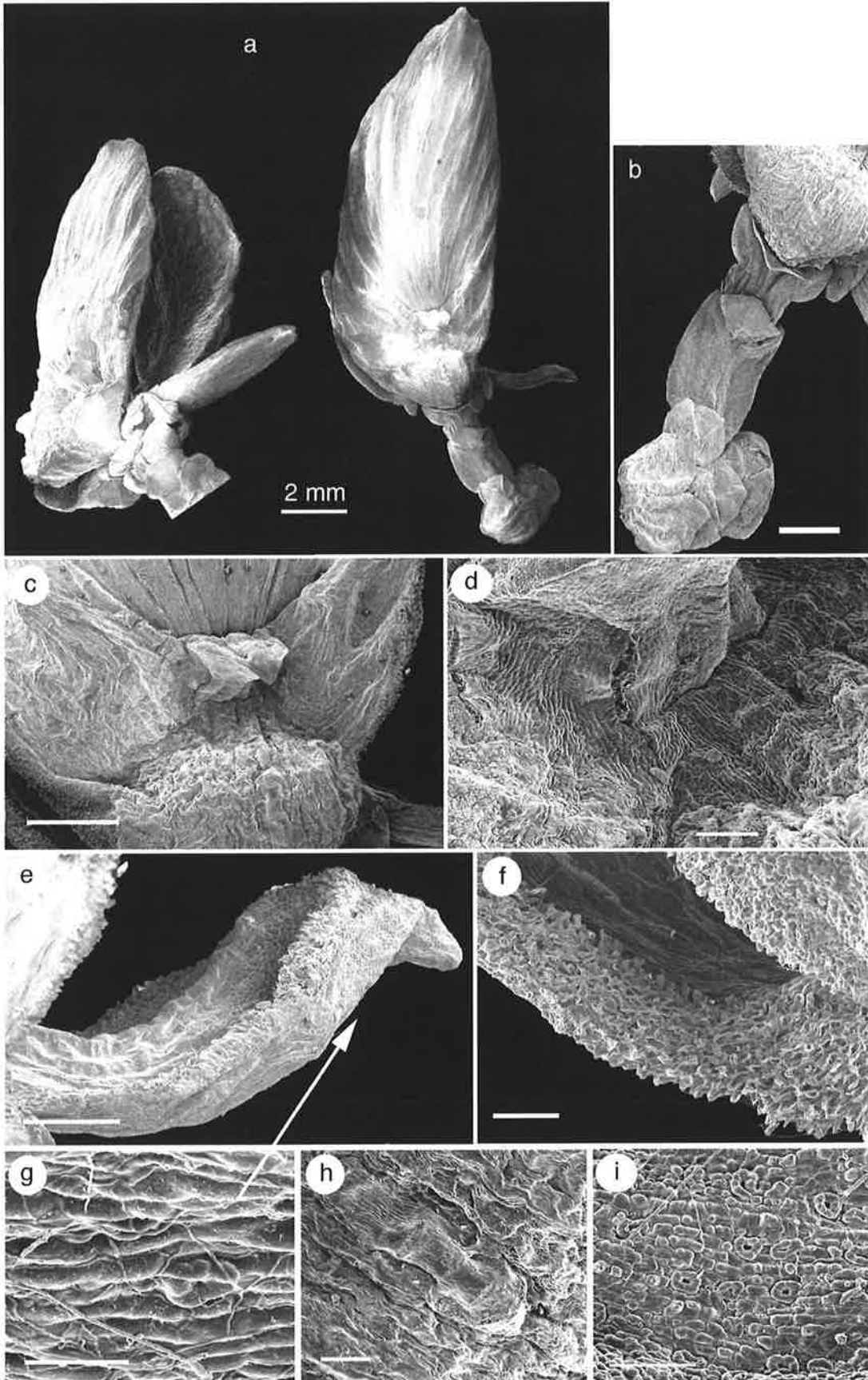
Fig. 15a-h *Papuacedrus papuana* var. *arfakensis* ovulate cone

Fig. 16a-h *Papuacedrus papuana* var. *arfakensis* immature ovulate cones
Specimen 152400

    a. LM showing a variety of ovulate cones – immature to mature.
    b. SEM. Two immature cones on short stems.
    c. Close up of **b**, right cone. Ultimate scale tightly closed, bract comparatively large and recurved (detail of outer bract surface in **g**).
    d. Close up of left cone, **b**. Immature cone, ultimate bracts larger than scales, with stomata at the base of penultimate bract (arrow).
    e. Papillate margin tightly enclosing the 2 ultimate scales (scale 200 µm).
    f. Detail of papillae in **e** (scale 50 µm).
    g. Outer bract surface, covered with many small papillae (scale 50 µm).
    h. Detail of stomata at base of bract (arrow in **d**; scale 100 µm).
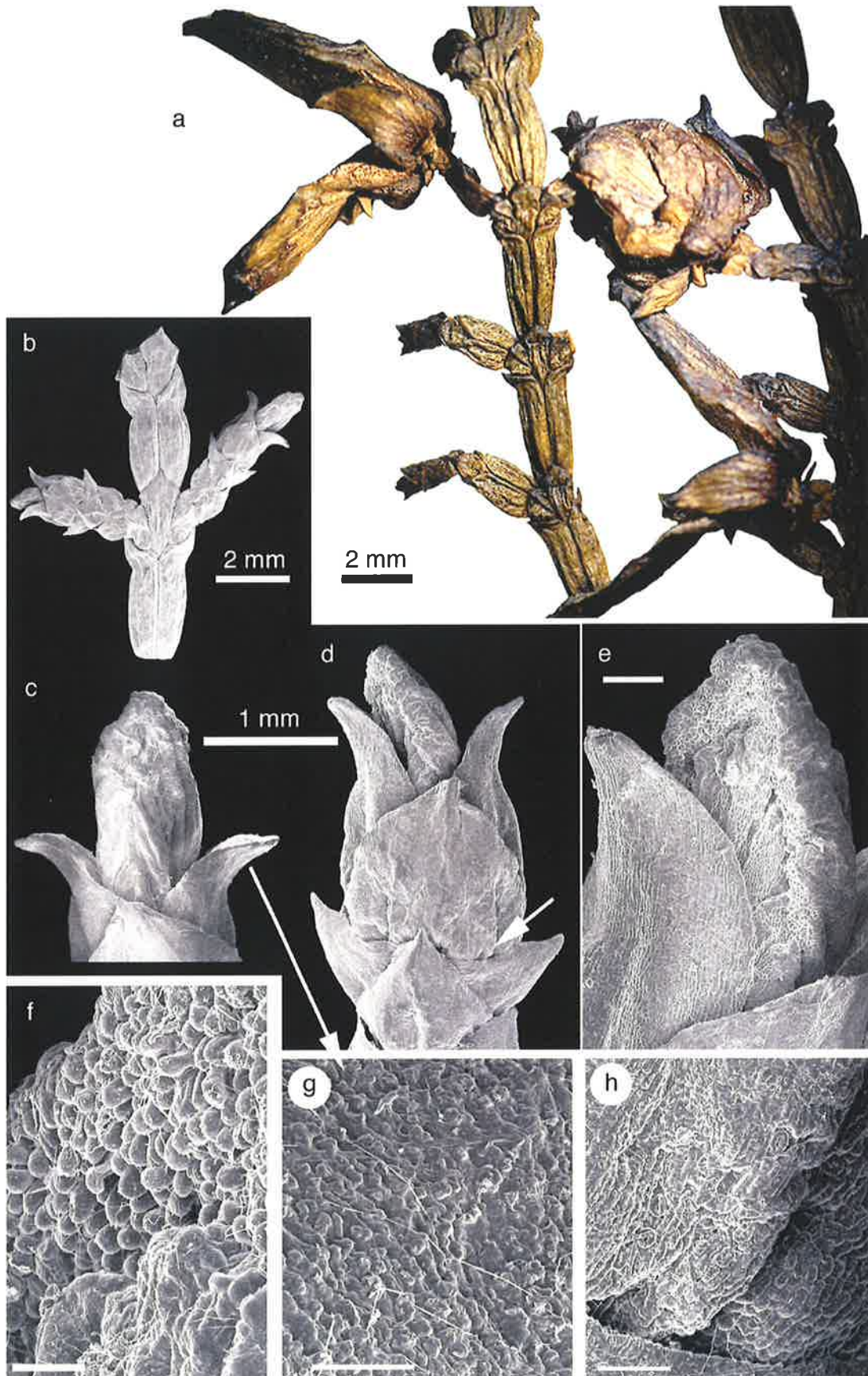
Fig. 16a-h *Papuacedrus papuana* var. *arfakensis* immature ovulate cones

Papuacedrus torricellensis (Schlechter) comb. nov. (Li 1953)
(Figs 17–19)
Libocedrus torricellensis Schltr. Ex Lauterb., Bot. Jahrb. Sys. 50: 52, f. 2. (1914)
Papuacedrus papuana (F. Muell.) H. L. Li var. **papuana**

Distribution: The Torricelli Mountains, New Guinea (Li 1953).
Ecology: Grows between 900-1000 m (Li 1953), and overlaps the range of *P. papuana* var. *arfakensis* (Farjon 2005).

The foliage and cones of *P. torricellensis* are similar to those of *P. arfakensis* and *P. papuana* and, to avoid repetition, separate descriptions for *P. torricellensis* are not given here. Photographic plates and figure captions (Figs 17-19) are included to illustrate the similarities between the three. No pollen cones were available for comparison.

Foliage: The adult leaves of *P. torricellensis* are dimorphic, with facial leaves much smaller than laterals. Ventral surfaces, lateral leaves - either convex or flattened. Dorsal surfaces concave. Florin and Boutelje (1954) suggested that the leaves of *P. torricellensis* are slightly shorter than those of *P. arfakensis*.

Specimens examined
154075, National Herbarium, Canberra, Australia. Collected 9/1963. P van Royen NGF 18250, Confluent of Warapuri and Warrangga Rivers, Wahgi-Jimmy Divide. N of Nondugl Minj sub-district, Eastern Highlands District, TNG, Tree ~35 m at ~2500 m, solitary tree with immature fruits, in grassland near Warrangga River.
E/3775, Herbarium Collection, The University of Adelaide, South Australia. Collected 8/1984, BJ Wallace 1018/84. Near Bulola, Gurni Road, NG
E/0892, Herbarium Collection, The University of Adelaide, South Australia. Minj sub-district Jimmy Divide NG, at ~2800 m.

Fig. 17a-c *Papuacedrus torricellensis* various foliage

a. (1) LM fertile foliage with ovulate cones. Branchlets opposite and short (consisting of ~6-8 decussate, highly dimorphic, imbricate and flattened leaf pairs. Lateral leaves on branchlets loosely imbricate, but imbricate and elongate for ~three quarters of their length on main axes. (2) LM young shoots (3) Close up of (1; ventral surface) showing small cones on relatively short shoots. (4) SEM dorsal surface - generally covered with discontinuous rows of waxy stomata separated by bands of epidermal cells (specimen 154075; scale 2 mm).

b. (1) Mature foliage with short opposite branchlets. Lateral leaves not imbricate, those on main axis more elongate than on branchlets. (2) SEM dorsal leaf surface. Lateral leaves concave, and separated by a well-defined central ridge. Apices inwardly curved (3) SEM ventral leaf surface. Leaves convex. Well-defined groove between lateral leaves. (4) SEM ventral surface branching shoot. Lateral leaves on main axis inwardly curved towards the apex, non-branching facial leaf elongate (specimen E/0892).

c. (1) Mature foliage with short opposite branchlets, ventral (left) and dorsal (right) surfaces. Leaves decussate, highly dimorphic, imbricate, lateral leaves convex on ventral surface, concave on dorsal surface. (2) SEM ventral surface - section of a main (branching) shoot. Facial leaf on main axis elongate. Lateral leaves separated by a deep groove. (3) SEM ventral, convex leaf surface with facial leaf removed. The facial leaf extends almost to the base of the lateral leaves. Lateral leaves not touching. (4) SEM dorsal surface. Leaves concave, with lateral leaves with dense white bands of waxy stomata. Facial leaf extending down between the lateral leaves, and with numerous stomata bounding the lateral leaves (specimen E/3775).
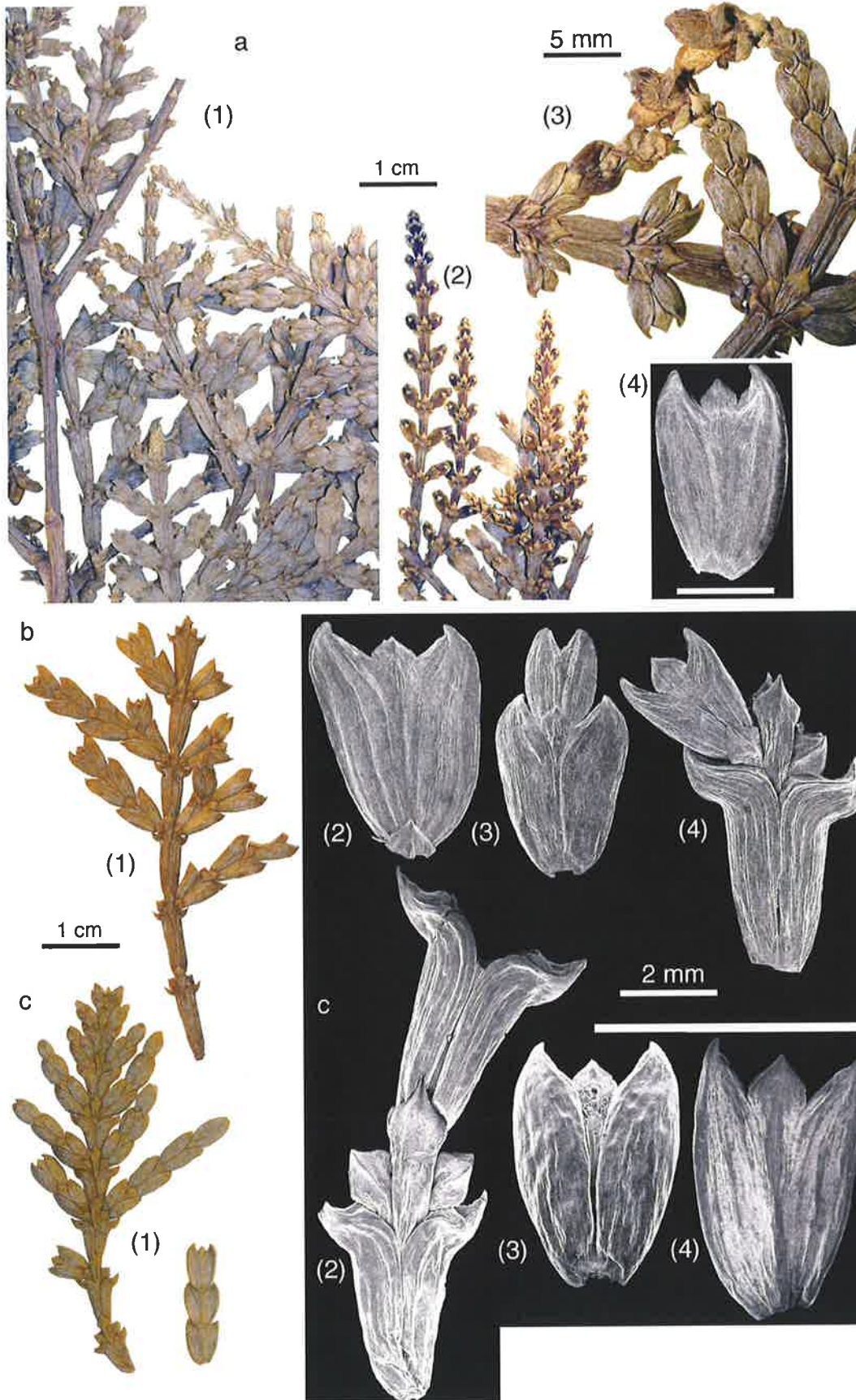
Fig. 17a-c *Papuacedrus torricellensis* various foliage

Fig. 18a-h *Papuacedrus torricellensis* cuticle SEM

a. Inner surface, stomatal complex. Thin cuticle. Stoma with elongate guard cells surrounded by a deep groove. This is broken by the anticlinal walls of the subsidiary cells (scale 20 μm; specimen E/3375).

b. Outer surface. Florin rings high ridged, slightly lobed and surrounded by round papillae (scale 20 μm; E/0892).

c. Inner surface. Stomata in discontinuous rows, and separated by bands of epidermal cells. Subsidiary cells often shared by adjacent guard cells, fine-grained and with less robust anticlinal cell walls than adjacent epidermal cells (scale 50 μm; E/0892).

d. Outer surface, lateral leaf apex. Leaf margin entire, stomata on adaxial surface. Ventral surface with numerous small papillae (scale 100 μm; E/3375).

e. Inner surface. Epidermal cells adjacent to the stoma coarse-grained, those further removed with large nodules containing calcium oxalate crystals (scale 20 μm; E/0892).

f. Outer surface. Epidermal cells convex, with indented walls, and containing numerous holes or small nodules (scale 20 μm; E/0892).

g. Inner surface. Epidermal cells elongate, coarse-grained. Anticlinal cell walls irregularly thick, and broader at the base (scale 20 μm; E/0892).

h. Inner surface. Coarse-grained epidermal cells with calcium oxalate nodules. Anticlinal cell walls broad at the base, coarse-grained (scale 20 μm; E/3375).
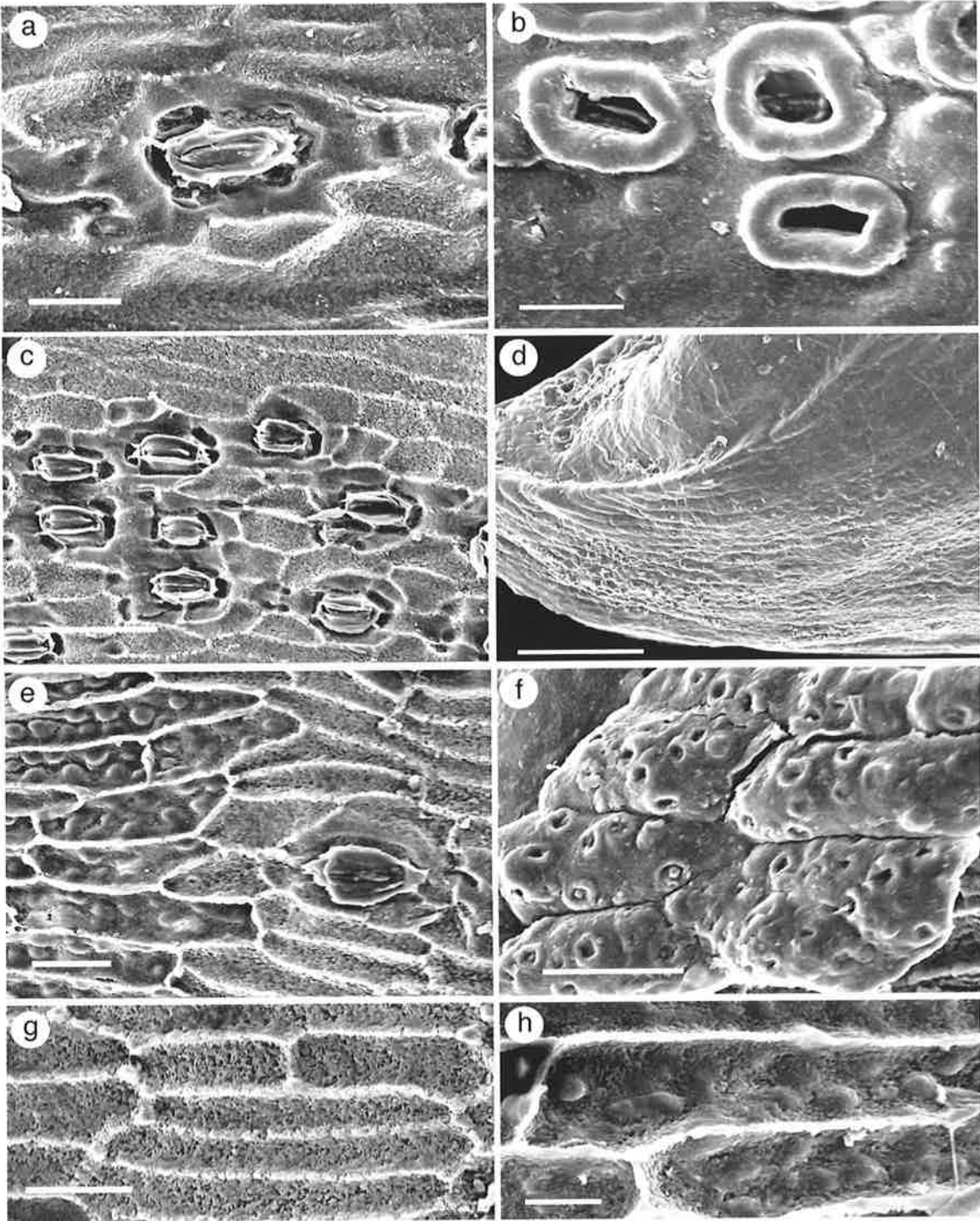
Fig. 18a-h *Papuacedrus torricellensis* cuticle SEM

Fig. 19a-f *Papuacedrus torricellensis* small immature ovulate cone
Specimen 154075

a. Cone in early developmental stage (indent shows comparative size with all other illustrated *Papuacedrus* cones). Scales gaping (this probably occurred after drying of herbarium material).

b. Two broadly triangular, non-flattened bract pairs (1, 2) with slightly frilled margins subtend the cone. Foliage beneath these 2 bracts is flattened. Bracts 3 & 4 are part of the penultimate (3) and ultimate (4) bract-scale complexes.

c. Ultimate scales with highly papillate margins. Ultimate bracts at this stage of development comparatively large and outwardly recurved (scale 500 μm).

d. Penultimate bract-scale. Bract broadly triangular, recurved and with an acute apex. Scale small, poorly developed, and with a highly papillate margin (scale 200 μm).

e. Inner surface, immature cone. Developing seeds (black arrows), and columella (white arrow; scale 200 μm).

f. Papillate margin, ultimate scale (scale 100 μm).

g. Detail abaxial surface bract 2 (as indicated in b). Apex wedge shaped (scale 200 μm).

h. Stomata on bract 2 (arrow; scale 100 μm).
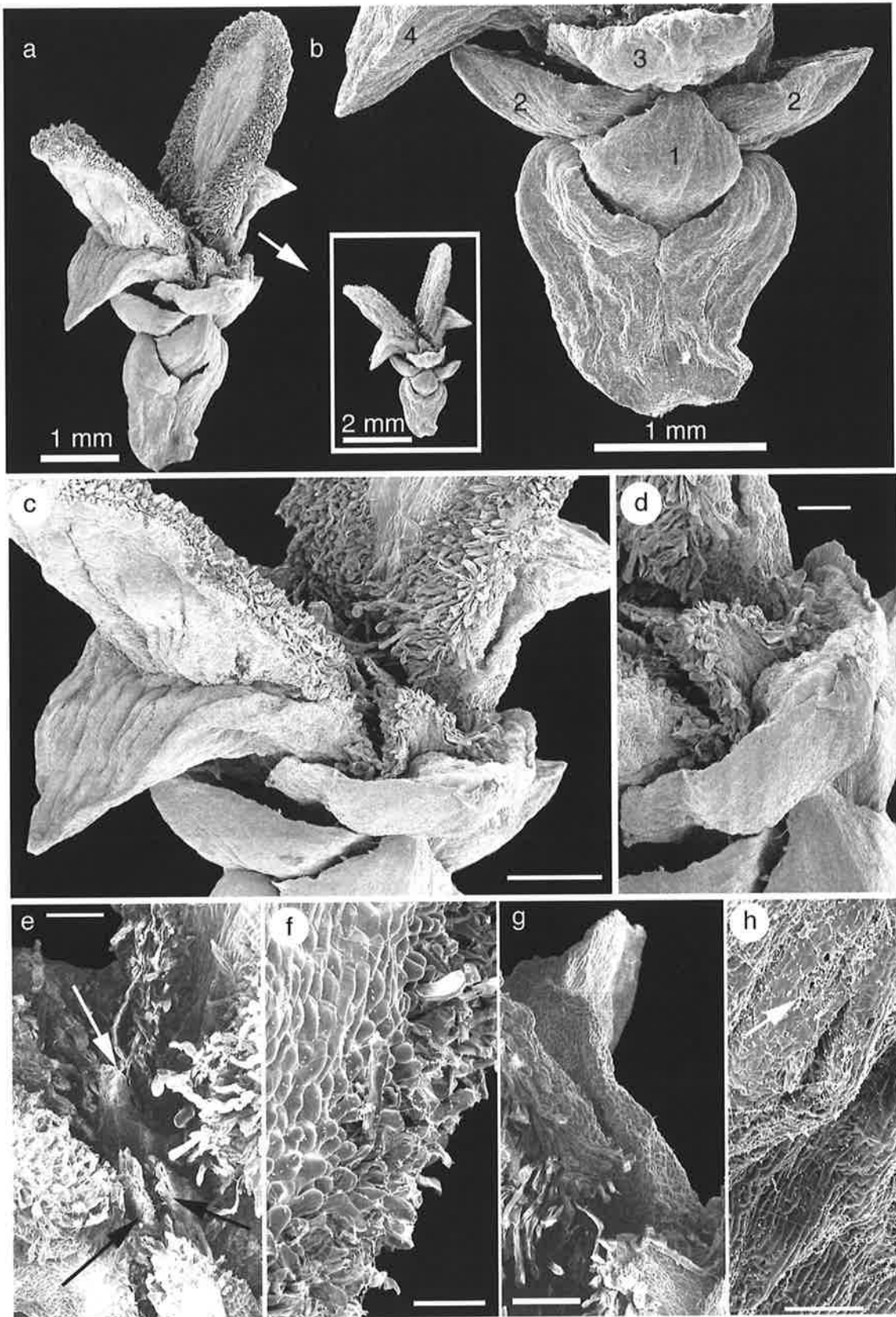
Fig. 19a-f *Papuacedrus torricellensis* small immature ovulate cone

Discussion

The foliage and ovulate cones of *Papuacedrus* is highly variable only one detailed description has been given. As others have found (Florin and Bouelje 1954; Van Royen 1979; Offler 1984), there is no clear distinction between Li's (1953) three *Papuacedrus* species. The numerous photographic plates in this section have been included to demonstrate how difficult it is to distinguish between *Papuacedrus* species/or varieties. Without having seen *Papuacedrus* growing in its natural environment, and in the absence (in most cases) of sufficient information included with herbarium specimens, it is difficult to tell what type of foliage one is examining. If it has broad, large leaves, are these 'transitional', or merely shade foliage that was collected because it was easier to reach? The cuticles of transitional foliage examined tended to be thin, which could indicate young, or shade foliage (or both). On the basis of the material that was examined it would appear, as Van Royen (1979) suggested, that there is only one species. The variation seen in *Papuacedrus* is possibly phenotypic.

Unlike the findings of Florin and Boutelje (1954) who suggested that the Florin rings of *Papuacedrus* are entire, and that papillae are rare (or absent; Farjon *et al.* 2004), the SEM photographs illustrate that the Florin rings are variously lobed, and that a significant number of small, mostly round papillae are associated with them. The internal cuticle of *Papuacedrus* is (as Florin and Boutelje 1954 suggested) distinctive, and can be used to distinguish the genus from the other genera described in this section. It was, however, of no value in distinguishing between the 3 *Papuacedrus* species/or varieties examined.

Pollen cones were not examined in any detail and none were photographed by SEM. However, the LM photo (taken from a herbarium sheet) suggests the arrangement of the microsporophylls is decussate, not spiral as Li (1953) suggested.

A final photographic plate is included here to illustrate some features common to the 3 *Papuacedrus* species examined.

Fig. 20a-i Features shared by *P. papuana*, *P. arfakensis* and *P. papuana*
a. Arrows indicating the facial leaf extending downwards between the two lateral leaves (scale 1 mm; specimen 152400, *P. papuana* var. *afakensis*).
b. Cuticle preparation, arrows indicating the extension of the facial leaf to the base of the laterals (scale 1 mm; specimen 108114.1, *P. papuana*).
c. As for **b**. (scale 1 mm; specimen 119313, *P. papuana* var. *arfakensis*).
d. As for **b**. (scale 1 mm; specimen E/0892, *P. papuana* var. *torricellensis*).
e. Facial leaf, mature foliage. Stomata roughly parallel to the leaf margin (arrow) but not in the centre of the leaf (scale 500 μm; specimen 229911, *P. papuana*).
f. LM lateral and facial co-joined leaves. Ventral leaf surface (V) with only a few scattered stomata at the base (white arrow). Dorsal leaf surface (D) with numerous stomata. Adaxial surface (A). Facial and lateral leaves with frequent stomata (scale 1 mm; specimen 108114.1, *P. papuana*).
g. LM lobed and largely elongate stomata surrounded by papillae (arrow; scale 100 μm; specimen 108114.1, *P. papuana*).
h. As for **g**. (arrow; scale 100 μm; specimen 119313, *P. papuana* var. *arfakensis*).
i. As for **g**. (arrow; scale 100 μm; specimen E/0892, *P. papuana* var. *torricellensis*).
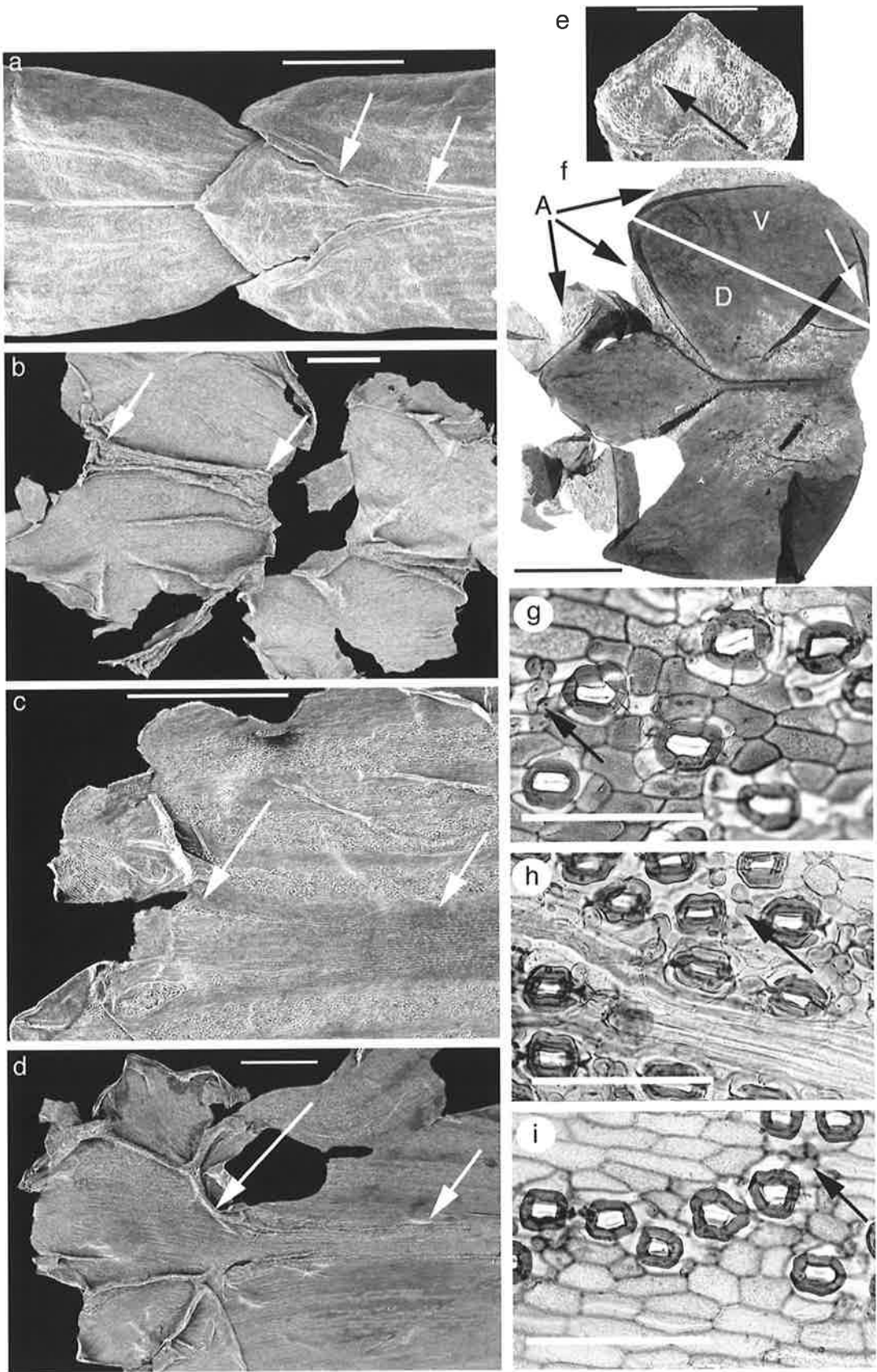
Fig. 20a-i Features shared by *P. papuana*, *P. arfakensis* and *P. papuana*

Papuacedrus: – distinguishing features

Foliage
- Transitional leaves larger than adult, and highly variable in size and shape.
- Terminal leaves of young shoots on transitional and adult foliage monomorphic, non-flattened, and appearing whorled rather than decussately arranged (more apparent on transitional foliage).
- Main axes – lateral leaves often highly flattened, large and fused for more than half their length. Free section of these leaves almost at right angles to the stem. Facial leaves extending down between the laterals, giving the appearance of an elongate groove on the ventral surface, a ridge on the dorsal surface.
- Main axes, adult foliage – lateral and facial leaves often similar in size.

Stomata
- Dorsal surface, lateral leaves, stomata grouped in discontinuous longitudinal rows across the leaf, and separated by bands of epidermal cells.
- Subsidiary cells with anticlinal cell walls thinner than those of adjacent epidermal cells (more apparent in transitional leaves).
- Guard cells surrounded by a distinctive, broken groove formed by the subsidiary cells.
- Indentations in the subsidiary cells (and some adjacent cells) only at cell corners.
- Florin rings on the outer cuticular surface high ridged and slightly lobed.
- Papillae associated with Florin rings of similar shape (round) and size.

Ovulate cones
- Ovulate cones born on very short shoots.
- Immature cones - bracts below cones short and broadly triangular (rather than elongate – see *Libocedrus* chapter).
- Mature cones – thinly woody, highly variable in size and shape.
- Apices of both scale pairs often outwardly curved above a dense band of papillae.
- Non-projecting (lower) section of bract on ultimate scales highly undulating, and bulging outwards.
- Bract projections on scales, short, relatively broad and often with a blunt apex.
- Bract projection on ultimate scales short, broad, recessed.
- Non projecting (lower) section of bract on penultimate scales, incurved.

Pollen cones
- Pollen cones borne on very short terminal shoots. Microsporophylls appear to be decussately arranged

Chapter 3. *Libocedrus*

All *Libocedrus* species have highly variable foliage with scale-like adult leaves that are dorso-ventrally flattened against the twig. The lateral leaves are larger than the facial and generally imbricate (Li 1953). Juvenile leaves are larger and more spreading (Dallimore *et al.* 1967) and the transitional foliage is larger than the adult. Ovulate (seed) cones are terminal at the end of branchlets and consist of 2 decussate bract-scale pairs, the upper bract-scale pair larger than the lower. The cone is subtended by 2-5 decussate infertile bracts.

Ovulate and pollen cones are rare on mature plants and thus are not often found in herbarium collections (Farjon 2005). For this study, at least one female cone was obtained for all species, but unfortunately some of these were immature. Some ovulate cones had intact seeds but, in cases where there was only one cone to examine, details of the seeds and internal cone morphology could not be undertaken without destroying the cone. Few herbarium specimens included male cones. Where material was sparse, or absent, brief descriptions have been taken from other publications. Some cones (female and male) were collected from young cultivated specimens growing in Tasmania.

New Zealand - 2 species

Libocedrus bidwillii Hook. f., Handb. New Zealand Fl. 1: 257. (1864)

Description: Tall, evergreen, monoecious trees (21 – 28 m), often conical, with thin scaly bark and numerous long, spreading or ascending branches.
Distribution: North and South Islands from latitude 36° 50' to 46° 30'S (Hinds and Reid 1957). Northernmost trees (North Island) restricted to mountain tops (Clayton-Green 1977). In the South Island from sea level to 1200 m (Hinds and Reid 1957; Allan 1961).
Ecology: Long-lived (600-1000 years) canopy or co-dominant trees. Most widespread on wet organic rich soils (Ogden and Stewart 1995) in humid mixed (conifer/angiosperm) rainforests, but also present in cool, wet and foggy montane and subalpine forests (Cockayne 1928 in Veblen and Stewart 1982), and superhumid, high rainfall (1200–8000 mm yr^{-1}) boggy conditions (Johnson *et al.* 1977). Seedling recruitment is intermittent, occurring only after small or large-scale disturbance (gale force winds, volcanism, fires, landslips - Clayton-Greene 1977; Veblen and Stewart 1982; Norton 1983).

Systematics
Order Coniferales
Family Cupressaceae
Genus *Libocedrus* Endl., Syn. Conif.: 42 (1847)
Libocedrus bidwillii Hook. f., Handb. New Zealand Fl. 1: 257. (1864)

Foliage and leaves: branchlets sub-opposite to alternate, and arising in the same plane (Fig. 1a-c). On mature foliage axillary branchlets arise on all sides of the stem (Fig. 1c). *Juvenile foliage* - highly dimorphic leaves in flattened sprays and lateral leaves much larger than facial, linear, and not imbricate, facial leaves not overlapping (Fig. 1a). Lateral and facial leaves with acute apices, lateral leaves slightly curved, facial leaves on dorsal and ventral surfaces outwardly keeled (Fig. 2a). Lateral leaves

entire margined (Fig. 2a, b), facial leaf margin frilled (Fig. 2b, c). Lateral leaves 3–5.5 mm x 1–1.3 mm, facial leaves 1. 6- ~2 mm x <1 mm. *Transitional foliage* - broad and flattened on lower branchlets with lateral leaves larger than facial. On ultimate branchlets foliage quadrangular (tetragonous) with imbricate, similar sized leaves (Fig. 1b). *Adult foliage* - tetragonous, with imbricate, almost monomorphic, convex leaves on ultimate branchlets (Figs 1c, 3a). Lateral leaves entire margined, facial only slightly frilled (Fig. 3c). Lateral leaves ~2.2 mm long, and basally fused for one third to half their length. Facial leaves 1.5-2 x ~0.9 mm. Facial leaves reaching to and overlapping the facial leaf pair above (Fig. 3a). All leaf apices acute. On young, cultivated trees bearing fertile cones (see Fig. 6a), leaves on sterile branchlets and leading branches, are monomorphic, and appear almost quadrangular in arrangement.

Stomatal distribution, juvenile foliage: Ventral surface - rare on lateral leaves and randomly scattered (Fig. 2a). On facial leaves confined to grooves (on both sides of the central keel) in the lower third of the leaf and largely obscured (protected) by the lateral leaf pair below (Fig. 2d). Dorsal surface - on lateral leaves densely packed and in discontinuous rows that are generally confined to slightly sunken light-coloured grooves. The latter are closer to the leaf margin than the centre of the leaf, and extend from the upper fifth of the leaf to its base (Fig. 2a). On facial leaves confined to poorly defined rows in the lower half of the leaf, some exposed, the others covered by the lateral leaf pair below (Fig. 2b). *Adult foliage*: Ventral surface – generally infrequent on lateral leaves and randomly distributed. Stomata near the base protected by the overlapping facial leaf below. Stomata on facial leaf confined to either side of the keeled centre and largely obscured by the lateral leaf pair below (Fig. 3d). Dorsal surface - on lateral leaves in discontinuous rows, mostly in an exposed central groove. On facial leaves in the lower half of the leaf in small grooves on either side of the leaf centre (Fig. 3c). Abaxial surface, lateral and facial (dorsal and ventral) leaves (juvenile to adult) – in discontinuous rows, close to the leaf margin and extending from the base to just below the leaf apex but less frequent in the basal third of the leaf (Figs 2c, 3b).

Cuticle description (all leaf morphologies): Inner surface - guard cells surrounded by 4-5 relatively smooth, generally elongate, subsidiary (epidermal) cells, some of which may be shared by adjacent guard cells (Fig. 4f). The subsidiary cells fold sharply downwards where they abut the guard cells, forming a discontinuous indentation around them (the lobed Florin rings on the outer surface). Further indentations occur within these cells, often close to the anticlinal walls (Figs 4a, c, e; 5a, c). These may be round or elongate in shape (Fig. 4c). The periclinal cell wall bulges slightly upwards. The anticlinal walls of the subsidiary cells are broad at the base and, on their outer edges fold outwards. Epidermal cells abutting the stomatal complexes elongate and irregular in shape, and have very coarse-grained periclinal cell walls. (Figs 4c, e, f; 5e, f). Those further removed are larger, more elongate, and contain calcium oxalate nodules with relatively smooth surfaces (Figs 4f, h; 5c, e, f). The anticlinal walls of these cells are thick and acute with coarse-grained bases and moderately fine-grained apices (Fig. 4h). Outer surface - stomata have elongate, high ridged, distinctly lobed Florin rings and may have waxy plugs. Stomata surrounded by numerous papillae (that correspond with the indentations on the internal surface; Figs 4b, d; 5b, d). Epidermal cells well-defined, and with very small nodules (Fig. 4d) or holes (Fig. 4g) that mark the position of calcium oxalate crystals. Outside the stomatal areas calcium oxalate crystals occur in most epidermal cells. Exceptions are the keeled areas of both leaf types and protected areas.

Ovulate cones: 6-~10 mm long (Fig. 6a-d). Terminal on very short branchlets (Fig. 6a). Decussate leaves on these branchlets somewhat rounded in appearance, and either

monomorphic (Fig. 31a), or almost monomorphic, with facial leaves only slightly shorter than lateral (Fig. 6f). Cone subtended by 2-3 pairs of infertile bracts (Fig. 6c 1-3) with frilled margins and adaxial stomata (Fig. 6j, k). In the centre of the ultimate bract-scale complexes, the bract narrows to a spiny projection that extends to (or almost to) the scale apex. Bract projections are outwardly curved but have slightly incurved apices. The base of the projection is rugose and bulges outwards. Bract bases also rugose and bulging. Scale margins highly papillate (Fig. 6e, h). Adaxial and abaxial scale surfaces highly ridged (Fig. 6g). Bracts on the penultimate scale pair larger than the scale, and enclosing it. Bract projection extending beyond the scale apex (Fig. 6i). Lower sections of bracts with an outward bulge (Fig. 6b).

Ovules: four, associated only with the ultimate bract (two per bract), seeds 2-4, flattened and with acute apices (Fig. 6d). A columella separates the seeds from each scale (Fig. 6e).

Pollen cones: (Fig. 7a-d) Terminal on branchlets. Microsporophylls: 4-8 decussate pairs, keeled, slightly rugose, ovate, with acute apices and broadly elongate tapering towards the base. Margins frilled. The lower third of the microsporophyll has a distinct broad central bulge (Fig. 7a, b). Cone subtended by 2-3 broadly triangular decussate bract pairs, the largest immediately beneath the cone. Bract margins with well developed frills (Fig. 7c). On either side of the bract, and towards the base there are small grooves containing stomata (Fig. 7d). Epidermal cells of microsporophylls and bracts contain calcium oxalate crystals (see Fig. 7c).

Specimens examined

MPN 003353, Dame Ella Campbell Herbarium, Massey University NZ. Collected 4/1957, AO Taylor, Egmont Ecological Region and District, New Plymouth. Mt Egmont, North Island, NZ. Tree 6 m at 912 m, in Podocarp forest. Cultivated "Kawaka", growing on basic andesite.

MPN 003356, Dame Ella Campbell Herbarium, Massey University NZ. Collected 9/1959, MR McDowall, Sounds-Wellington Ecological Region, Wellington Ecological District, Wellington, Wilton's Bush, North Island NZ. Cultivated vegetation growing on greywacke (edaphic habitat).

WELT SP037987, Museum of New Zealand, Te Papa Tongarewa, NZ. Collected 12/1933, ME Heine, NE side Mount Egmont. Juvenile at ~1250 m. Habitat - Kamaki Forest.

WELT SP037980, Museum of New Zealand, Te Papa Tongarewa, NZ. Collected 3/1931. WRB Oliver, NE side, Mount Egmont. Adult at ~1250 m, in forest.

E/1954, Herbarium Collection, The University of Adelaide, South Australia. Collected 1/1989. G Jordan & R Carpenter. Monkey Puzzle Gorge, South Island, NZ. Juvenile.

E/2263, Herbarium Collection, The University of Adelaide, South Australia. Collected 1/1989, G Jordan & R Carpenter, Arthur's Pass, South Island, NZ. Adult.

E/NZ/020, Herbarium Collection, The University of Adelaide, South Australia. Collected 12/1983, Upper Taipo River from Julian Hut to 7 Mile Creek adjoining Arthur's Pass National Park. Tree ~30 at ~800 m, in mixed podocarp broad leaf forest.

Culivated specimen 001487, Tasmanian Arboretum, Devonport, Tasmania, Australia. Collected 11/2004, R Paull. Young tree ~2 m.
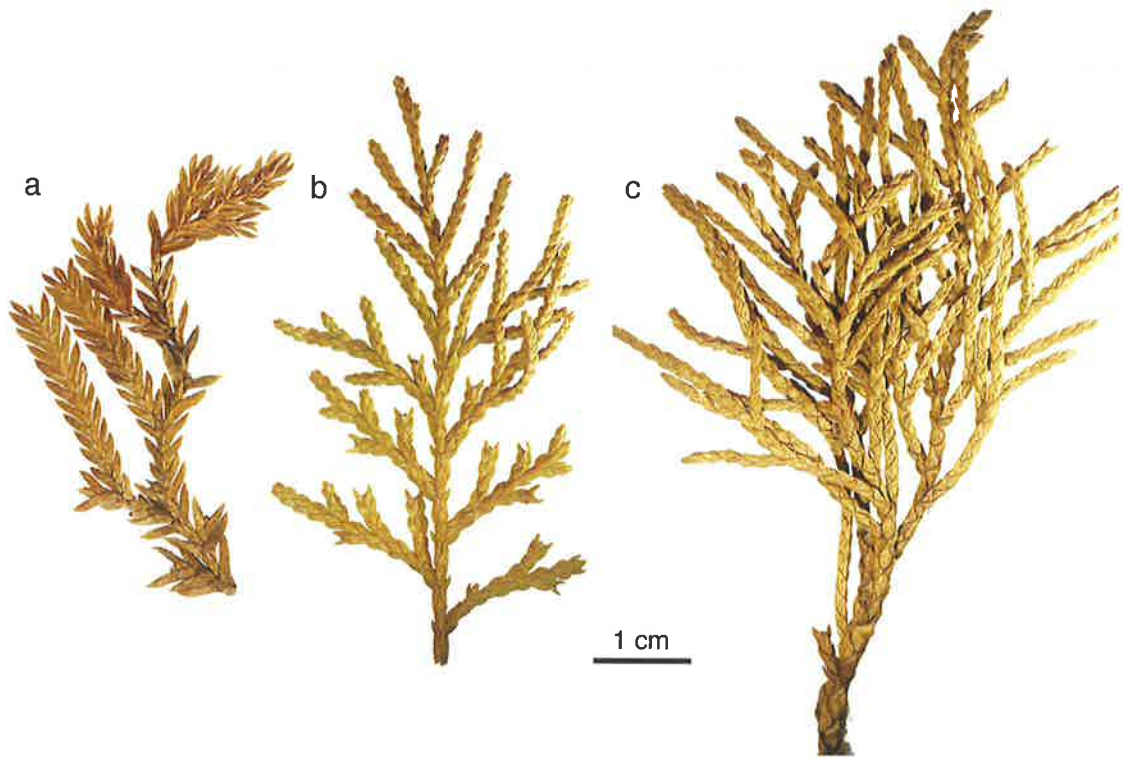
Fig. 1a-c *Libocedrus bidwillii* branchlets showing leaf arrangement
  a. Seedling (50 cm). Highly dimorphic leaves in flattened sprays (specimen SP037987, from 1200 m Mt Egmont, North Island NZ).
  b. Cultivated young tree ~2.5 m. Lower branchlets with broad, flattened transitional leaves with lateral leaves larger than facial. Ultimate branchlets quadrangular (tetragonous) with imbricate, similar sized leaves (specimen 001487 Tasmanian Arboretum, Tasmania).
  c. Adult tree. Axillary branchlets arising on all sides of the stem. Leaves on ultimate branchlets imbricate, almost monomorphic and quadrangular in appearance (specimen from Arthur's Pass, North Island NZ).
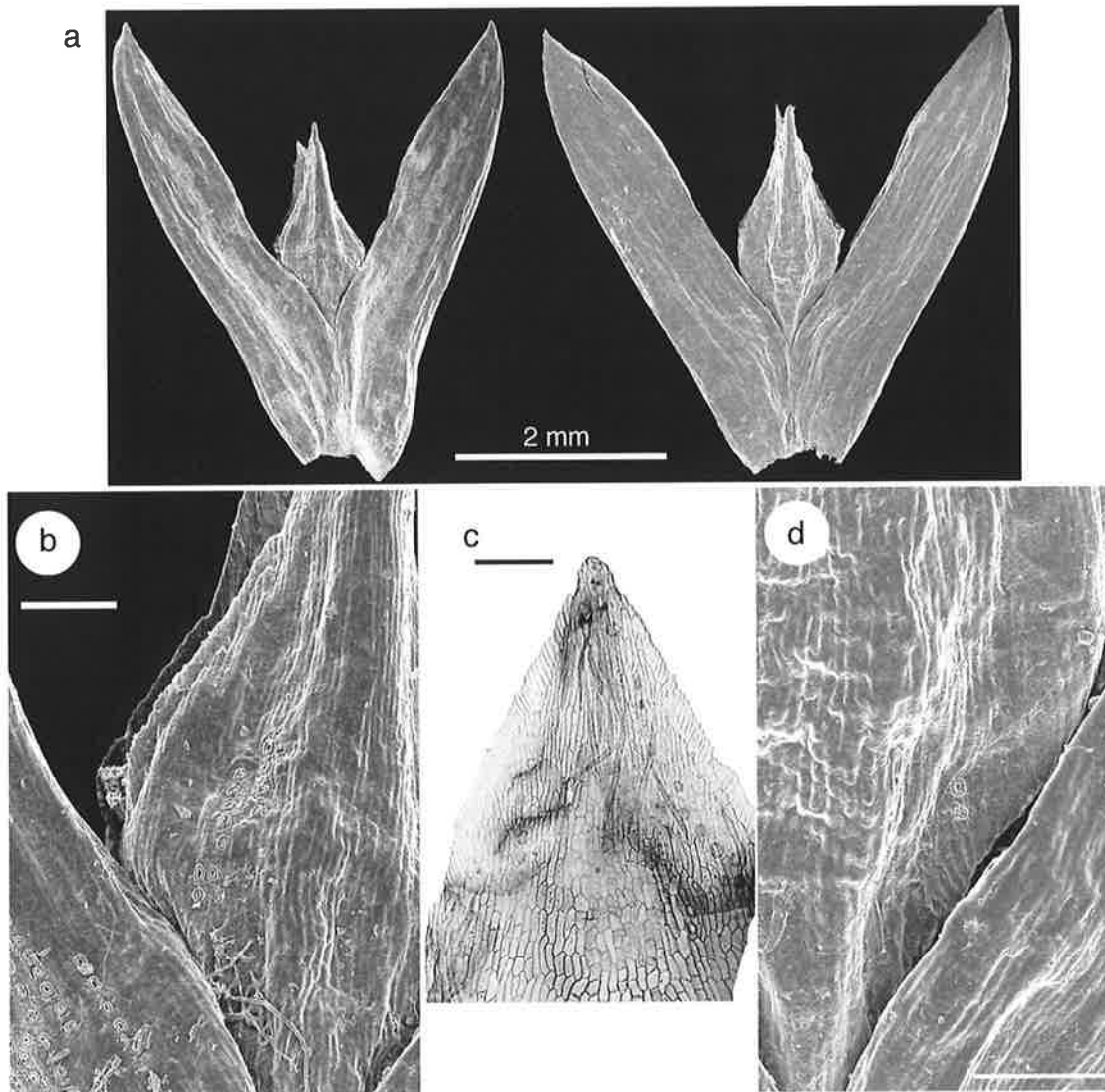
Fig. 2a-d *Libocedrus bidwilli* SEM/LM juvenile
Specimen WELT SP037987

  a. SEM dorsal (left) and ventral (right) bilaterally flattened leaf surfaces. Lateral dorsal leaves with stomata largely confined to slight central grooves. Lateral ventral leaves with rare, scattered stomata (not illustrated).

  b. SEM dorsal surface. Lateral leaves entire margined. Facial leaves with marginal frill and stomata confined to the lower two thirds of the leaf and in small bands on either side of the outwardly keeled leaf centre (scale 200 μm).

  c. LM facial leaf abaxial surface showing stomata in rows parallel to the leaf margin in the upper third to half of the leaf (scale 250 μm).

  d. Ventral surface facial leaf. Stomata largely protected by the lateral leaves below, and only a few exposed (scale 200 μm).
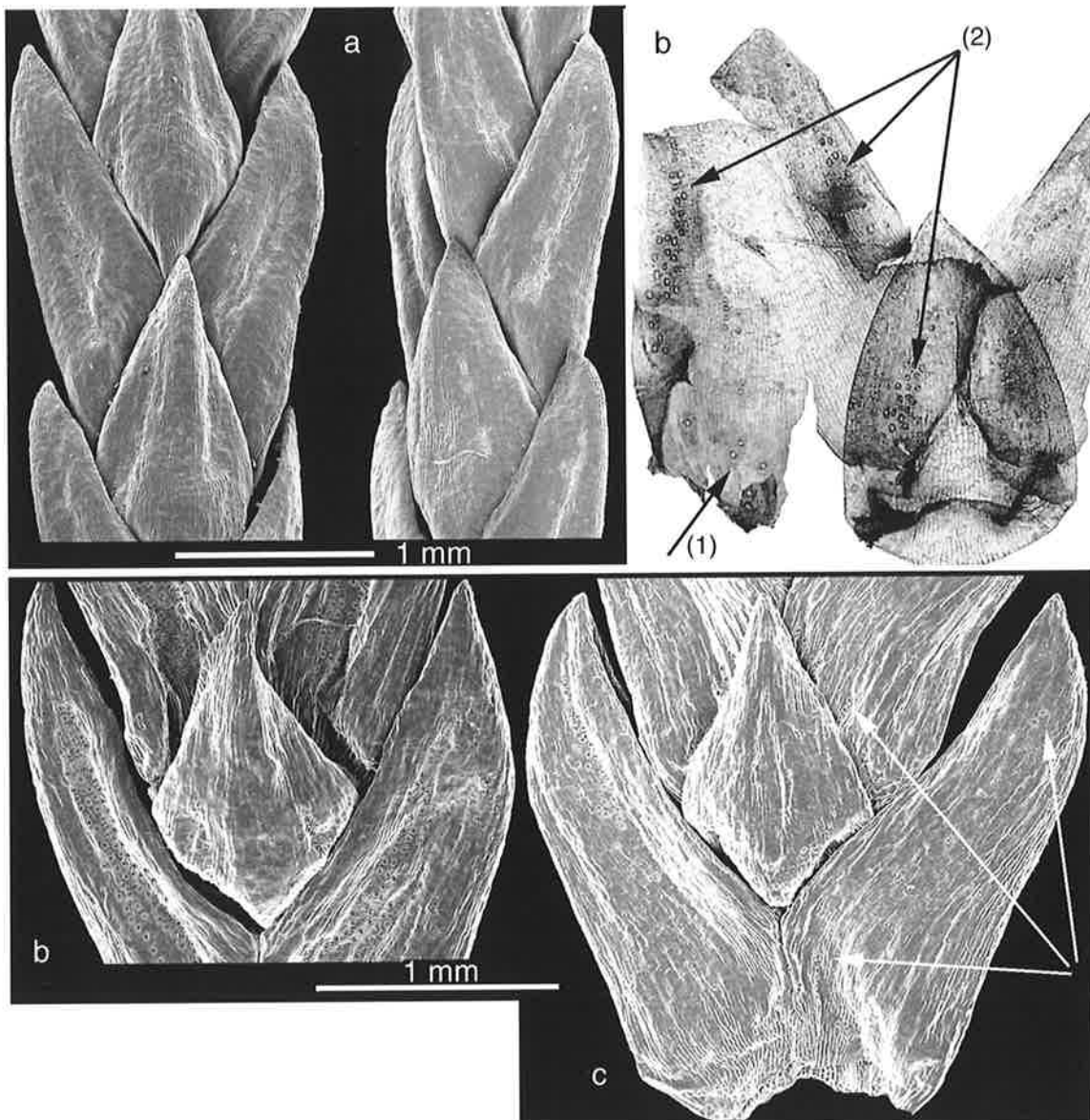
Fig. 3a-d *Libocedrus bidwilli* SEM/LM adult foliage

a. SEM dorsal (left) and ventral (right) leaf surfaces. Lateral and facial leaves imbricate, and somewhat thickened (not flattened). Stomata, dorsal surface: on lateral leaves mostly in a central groove, on facial leaves in small grooves on either side of the leaf centre and only in the lower half of the leaf. Stomata, ventral surface: scattered and less numerous (specimen 37980).

b. LM Arrow (1) indicates the position of stomata on the ventral lateral leaf surface (in intact foliage these are covered by the facial leaf). Arrows (2) indicate the position of stomata on the abaxial surfaces of lateral and facial leaves (same scale as **a**; specimen 37980).

c. Dorsal surface: stomata on lateral and facial leaves in well defined grooves. Lateral leaves entire margined, facial leaves slightly frilled (specimen 195412).

d. Ventral surface: lateral leaves with scattered stomata (arrows). Facial leaf stomata on either side of the keeled centre and largely obscured by the lateral leaf pair below (same scale as **c**; specimen 195412).

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Fig. 4a-h *Libocedrus bidwilli* juvenile leaf cuticle

Specimen 37987

a. SEM inner surface stoma: guard cells surrounded by 4 relatively elongate subsidiary (epidermal) cells. Towards the outer edges of these cells there are elongate indentations. The latter fold sharply downwards where they abut the guard cells and form a discontinuous indentation around them. Periclinal walls of subsidiary cells slightly convex, anticlinal cell walls smooth, and folding outwards at the outer cell edges. Epidermal cells very coarse-grained, elongate and irregular in shape, with thick, smooth anticlinal walls (scale 20 μm).

b. SEM outer surface stomata. Florin rings high ridged and slightly lobed. Waxy stomatal plug and fungal hyphae. Stomata surrounded by papillae (scale 20 μm).

c. SEM inner surface stomata: indentations in subsidiary cells round-elongate, relatively frequent, and scattered throughout the cell (scale 20 μm).

d. SEM outer dorsal surface showing stomata surrounded by numerous papillae. Epidermal cells (foreground) relatively smooth but with very small nodules. The latter indicate the presence of calcium oxalate crystals in the walls of the cells (scale 50 μm).

e. SEM inner dorsal surface showing rows of closely packed stomata (scale 50 μm).

f. LM showing stomata surrounded by papillate subsidiary cells. Epidermal cells immediately adjacent to the stomatal bands are coarse-grained in texture. Those further removed (foreground) are elongate and contain calcium oxalate crystals (scale 20 μm).

g. SEM outer surface showing well defined epidermal cells. Holes indicate areas where calcium oxalate crystals have dissolved (scale 20 μm).

h. SEM inner surface epidermal cells; periclinal cell walls coarse-grained in texture. Surface of calcium oxalate crystal nodules in these cells relatively smooth in texture. Texture of anticlinal cell walls coarse-grained at the base but finer-grained towards the apex (scale 20 μm).

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Fig. 4a–h *Libocedrus bidwilii* juvenile leaf cuticle
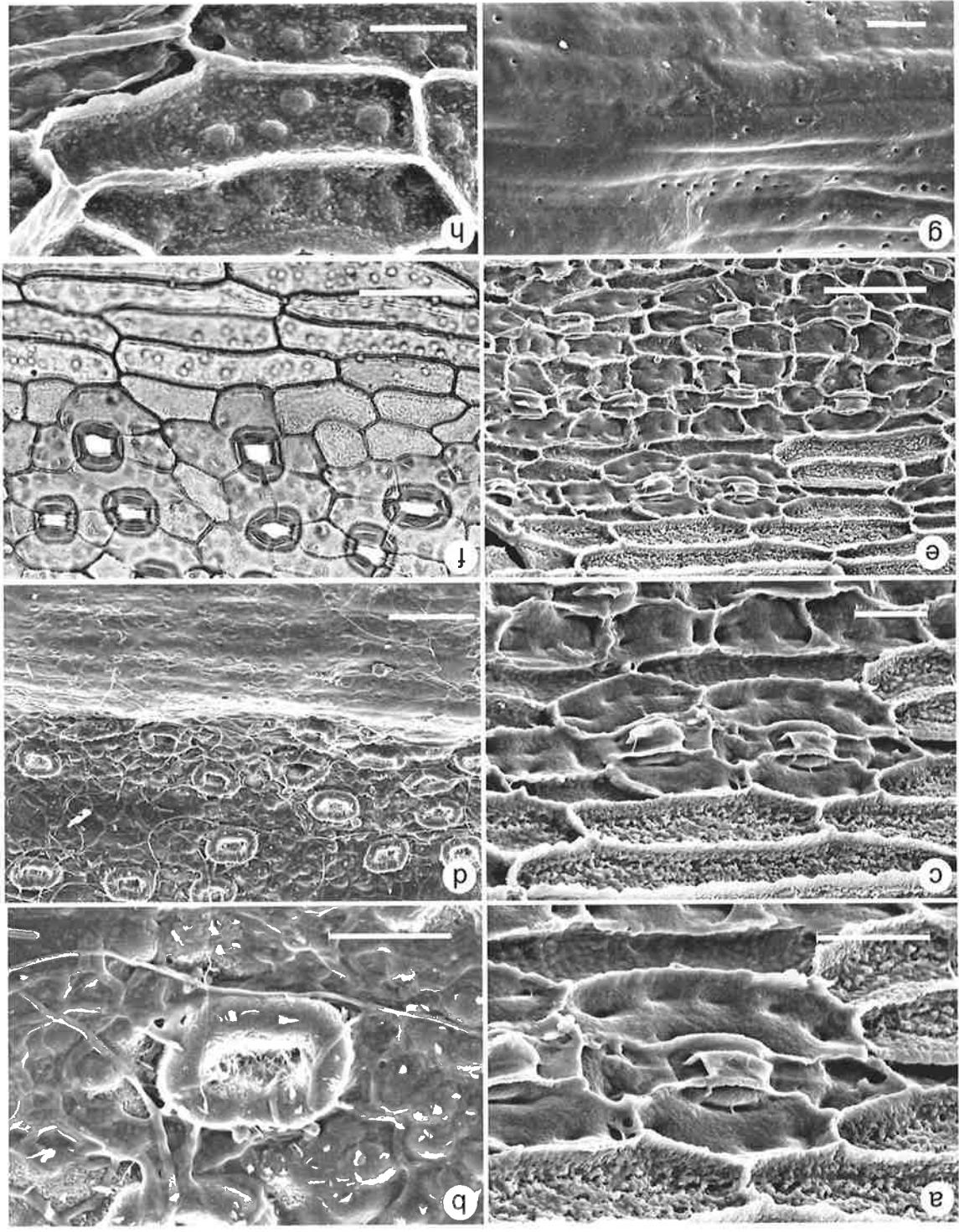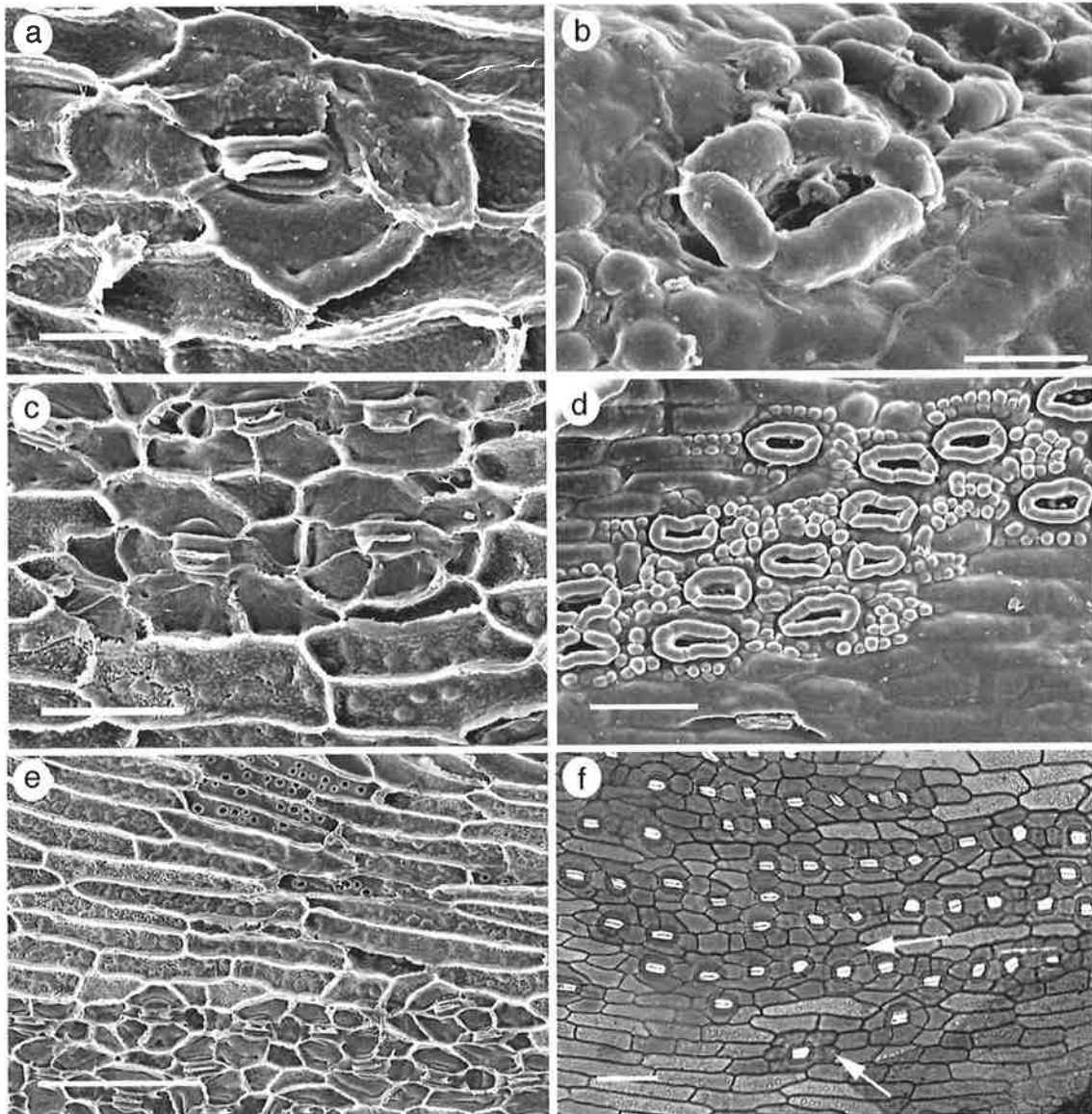
Fig. 5a-f *Libocedrus bidwilli* adult leaf cuticle

    a. SEM inner surface stomata: guard cells with 4 elongate subsidiary cells. The latter have a relatively smooth texture, and contain indentations close to the outer cell walls. They fold sharply downwards where they abut the guard cells forming a discontinuous indentation around them (scale 20 μm; specimen 37980).

    b. SEM stomata, outer surface. Florin rings elongate, highly ridged and distinctly lobed (scale 10 μm; specimen 37980).

    c. SEM inner surface. Subsidiary cells 4-6. Surrounding epidermal cells coarse-grained and with calcium oxalate crystals (scale 50 μm; specimen 003353).

    d. SEM outer surface dorsal leaf, fertile female shoot, showing stomata surrounded by papillae. Epidermal cell walls clearly visible (scale 50 μm; specimen 003353).

    e. SEM inner surface. Stomata in closely packed discontinuous rows, texture of epidermal cells close to subsidiary cells coarse-grained. Those further away elongate, with large calcium oxalate crystals (scale 100 μm; specimen E/1954).

    f. LM. Lobed stomata surrounded by papillate (arrows) subsidiary cells. Epidermal cells as for **e** (scale 50 μm; specimen E/195412).

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Fig. 6a-k *Libocedrus bidwilli* ovulate cones

Except for **a**, all illustrated specimens from MPN 003353, **b-d** 2 mm

    a. Young tree ~2 m. Two ovulate cones, terminal on short branchlets. Sterile foliage on branchlets and leading shoots monomorphic, and almost quadrangular in arrangement (specimen 001487, Tasmanian Arboretum).

    b. SEM showing columella in centre of cone (see 6e). Bracts with outward central bulge (arrows).

    c. Cone subtended by 3 infertile bracts (numbered 1-3). Lower fertile bract (4) enclosing the much smaller scale. Ultimate fertile bracts (5, only 1 shown) shorter than the scale, and with acute apices. Bract extends to the margin of the scale.

    d. Cone with flattened seed (arrow).

    e. Internal scale surface – columella (upper arrow). Lower arrow indicating position of dehisced seed (scale 1 mm).

    f. Fertile shoot foliage, dorsal (left) and ventral (right) surfaces showing the similarity in size of lateral and facial leaves and rounded, rather than flattened leaves (scale 1 mm).

    g. Ultimate bract scale pair showing ribbed internal scale surface and papillate margin (scale 500 μm).

    h. Detail, papillate margin, ultimate scale (scale 200 μm).

    i. Penultimate bract-scale pair. Bract enclosing the highly papillate scale (scale 200 μm).

    j. Infertile bract immediately beneath the cone showing frilled margin and abaxial stomata (arrow; scale 500 μm).

    k. Detail (**j**; scale 100 μm).
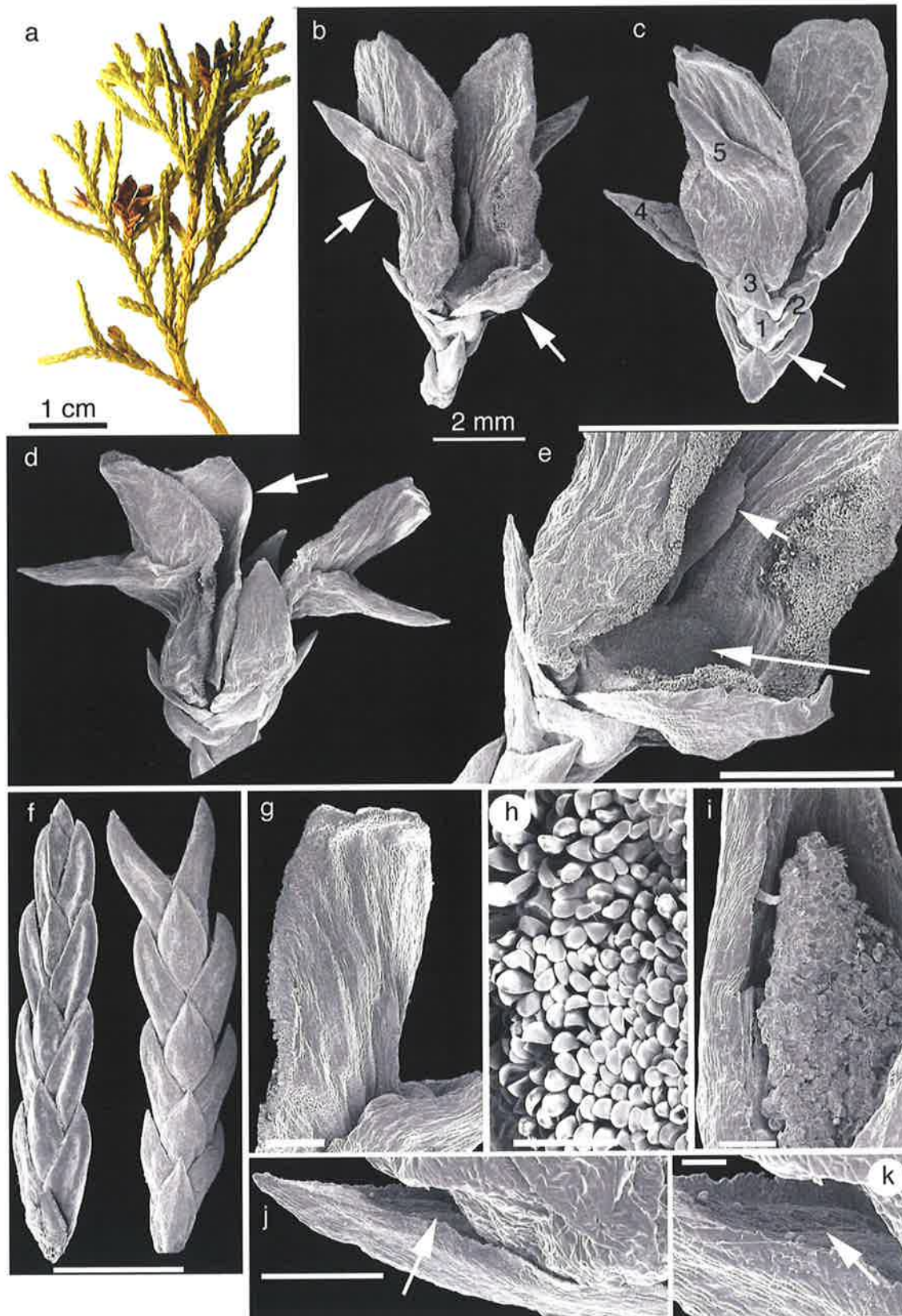
Fig. 6a-k *Libocedrus bidwilli* ovulate cones
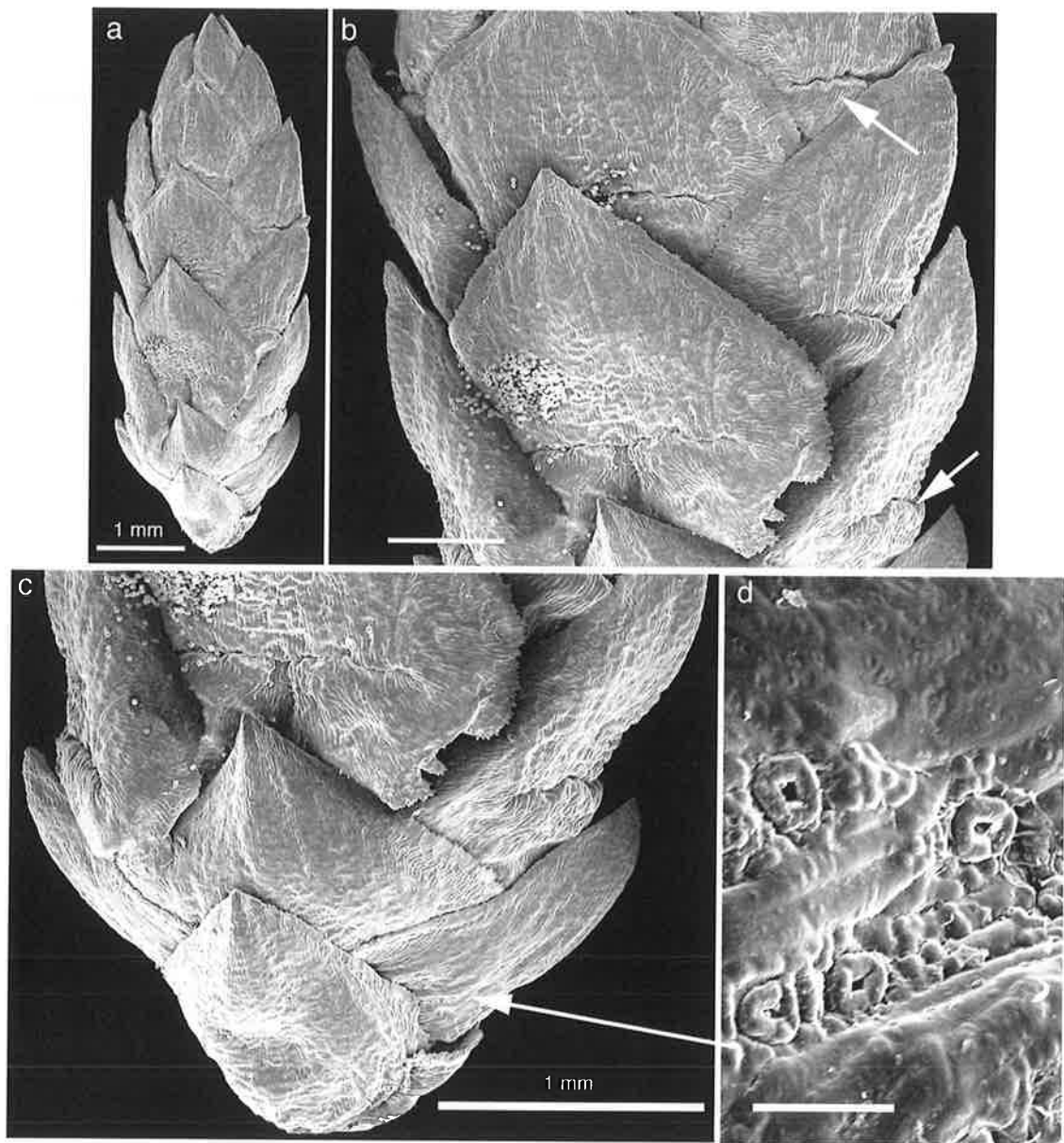
Fig. 7a-d *Libocedrus bidwilli* pollen cone

Specimen 3356

a. Pollen cone with 8 decussate microsporophyll pairs. Microsporophylls broadly elongate, keeled. Cone subtended by 3 decussate bract pairs.

b. Microsporophylls slightly rugose, broadly elongate but tapering towards the base. Apices acute, margins highly frilled. Lower third of the microsporophyll with a distinct upwardly curved, bulge (arrows). Pollen grains roughly spherical (scale 500 μm).

c. Cone subtended by 3 bracts, the two closest to the cone more elongate than the third, and broad. Bract margins with well developed frill.

d. Stomata near the base of the bract (arrow indicating position; scale 50 μm).

Libocedrus plumosa (D. Don) Sargent, Silva N. Amer. 10: 134. (1896)

Description: Tall (30-35 m) monoecious trees with thin scaly bark and numerous long spreading or ascending branches.
Distribution: North and South Islands, from latitude 35°S to >38°S, from sea level to 600m. North Island distribution is to the northwest and centre of the island. Not found in the south of the North Island. In the South Island restricted to the Nelson District (northwest corner; Ogden and Stewart 1995; Farjon 2005).
Ecology: A canopy tree in species-rich evergreen forests, growing in warm lowland and hilly regions with abundant rainfall, mild winters and warm summers (Farjon 2005).

Systematics
Order Coniferales
Family Cupressaceae
Genus *Libocedrus* Endl., Syn. Conif.: 42 (1847)

Libocedrus plumosa (D. Don) Sargent, Silva N. Amer. 10: 134. (1896)

Foliage and leaves: branchlets sub-opposite to alternate (Fig. 8a-c) and, on juvenile and transitional foliage, arising in one plane (Figs 8a, b; 14). *Juvenile and transitional foliage* with dimorphic leaves in flattened sprays. Lateral leaves much larger than facial, outwardly keeled, fused for ~half their length, loosely imbricate and with acute apices (Figs 8a; 9a). Facial leaves small with frilled margins, not overlapping and only covering ~half the lateral leaf pair above (Fig. 9b). Lateral leaves 2.5-~5 mm x 1.1-1.8 mm, facial 1- ~2 mm x <1 mm. Leaves on dorsal surface slightly concave in appearance (Fig. 9a). *Adult foliage* with dimorphic leaves. Lateral leaves with entire margins, acute apices, papillate bases (Fig. 10d, e, f), and fused for around half their length. Facial leaves rhombic with frilled margins and not overlapping the facial pair above (Fig. 10b, c, d). Leaves on older trees may be almost monomorphic and imbricate, and convex on dorsal and ventral surfaces, with facial leaves slightly overlapping the facial pair above (Figs 8c; 10a).
Stomatal distribution, all foliage types: Ventral surface - on lateral leaves few and scattered (Figs 9a, 10b). On facial leaves on either side of the central keel. Also on the lower third to half of the facial leaves (where they are protected by the overlying lateral leaf pair below; Fig. 9a). Dorsal surface - on lateral leaves in densely packed discontinuous rows that are generally in a broad, slightly sunken groove extending from near the apex to the base. Stomata on facial leaves have the same distribution as those on the ventral surface. Adaxial surface, lateral and facial (dorsal and ventral) leaves (all leaf types) - in discontinuous rows, close to the leaf margin and extending from the base, and meeting just below the leaf apex (Figs 9c; 10g, h).
Cuticle description (all leaf morphologies): Inner surface - elongate stomatal guard cells surrounded by 4-5 relatively smooth, generally elongate, subsidiary cells (Figs 11a; 12a), some of which may be shared by adjacent guard cells (Figs 11c; 12c). Where they abut the guard cells the subsidiary cells fold sharply downwards forming a discontinuous groove. Subsidiary cells contain other indentations, mostly at the cell margins. These are generally elongate in shape (Fig. 12a). Outer anticlinal walls of the subsidiary cell fold outwards (away from the guard cells). Texture of all epidermal cells very coarse-grained with acute, thick, and coarse-grained anticlinal walls (Fig. 12h). Those abutting the stomatal complexes are generally irregularly elongate (Figs 11c, e; 12c, e) and may contain indentations (Fig. 11c). Most epidermal cells (those not directly

associated with stomata) are larger and more elongate and contain calcium oxalate crystals within their cell walls. These are nodular or papillate in appearance (Figs 11f; 12f), with relatively fine-grained surfaces (Fig. 12h). In areas protected by overlying leaves (leaf bases), the adaxial surfaces of lateral leaves, the adaxial surface of dorsal facial leaves, or the keeled areas of lateral and facial leaves (e.g. Fig. 12g), epidermal cells contain either no, or very few, calcium oxalate crystals. Outer surface - stomata have high ridged and lobed Florin rings with peripheral grooves (Figs 11d, f; 12b, d), and may be covered in waxy spicules (Fig. 11b). Numerous papillae (frequently round in shape) are associated with the stomata (Figs 11d, f; 12b, d). Epidermal cells have indented margins and contain small nodules or holes (Figs 11d; 12d) marking the position of calcium oxalate crystals in the cell wall.

Ovulate cones: 10-18 mm long. Terminal on short branchlets (Figs 13a; 14; 32b). Ultimate bract-scale complexes long and broad, penultimate complexes shorter and narrow. Both scale pairs with rugose adaxial and abaxial surfaces and papillate margins (Fig. 13b, f). Spiny bract projections on the ultimate bract-scale pair elongate (<5 mm), and extending outwards from the central upper third of the scale, almost at right angles to it. The bract projection is broadly triangular and wedge shaped at the base, and tapers to a narrow recurved apex. The apex of the bract reaches (or extends beyond; Farjon 2005) the scale apex. The section of the bract beneath the projection is finely rugose. On the penultimate bract-scale complexes the bracts are larger than the scales. The latter appear insignificant, and enclosed within the bract. The projecting sections of these bracts are robust, similar in appearance to the ultimate pair, and extend beyond the apex of the scale (Fig. 13a, d, e). Subtending the cone are 3-5 decussate infertile bracts. The bracts furthest from the cone are short and squat. Those closer to the cone progressively elongate, broaden and flatten. All bracts are outwardly keeled with indentations towards the base (Fig. 13c), have marginal frills (Fig. 13g), and no stomata on their abaxial surface. The bract pair closest to the cone may exhibit intercalary growth (Fig. 13g, h). At the apex of mature cones is a small narrow columella ~2mm long (Fig. 13d, e).

Ovules: not illustrated, 4 in the axil of the ultimate bracts. Seeds 2-4 with two very unequal sized wings (Farjon 2005).

Pollen cones: not illustrated. Terminal on short branchlets, with 4-6 decussate microsporophyll pairs. Microsporophylls ovoid in shape, with entire margins (Farjon 2005).

Specimens examined

MPN 002367, Dame Ella Campbell Herbarium, Massey University NZ. Collected 7/1938, BEG Molesworth, North Island NZ. Auckland Ecological Region Waitakere Ecological District, Cascades, Kauri Park. Juvenile.

MPN 002367, Dame Ella Campbell Herbarium, Massey University NZ. Collected 7/1938, BEG Molesworth, North Island NZ. Auckland Ecological Region Waitakere Ecological District, Cascades, Kauri Park. Adult

MPN 13317, Dame Ella Campbell Herbarium, Massey University NZ. Collected 1/1936, ED Campbell, North Island NZ. Coromandel Ecological Region, Great Barrier Island. Altitude unknown.

WELT SP035478, Museum of New Zealand, Te Papa Tongarewa. Collected 12/1945. Mt Burnett, Nelson, South Island NZ. Altitude unknown.

WELT SP037974, Museum of New Zealand, Te Papa Tongarewa. Collected 3/1925. Waitakerei Hills, Auckland, North Island NZ. Juvenile.

E/1124, Herbarium Collection, The University of Adelaide, South Australia. Collected 6/1987, A Watt. Young tree in cultivation, Victoria, Australia.

E/1162, Herbarium Collection, The University of Adelaide, South Australia. Collected at Melbourne Botanical Gardens, Victoria, Australia.

Cultivated specimen, Tasmanian Arboretum, Devonport, Tasmania. Collected 11/2005, R Paull, young tree ~2.5 m.
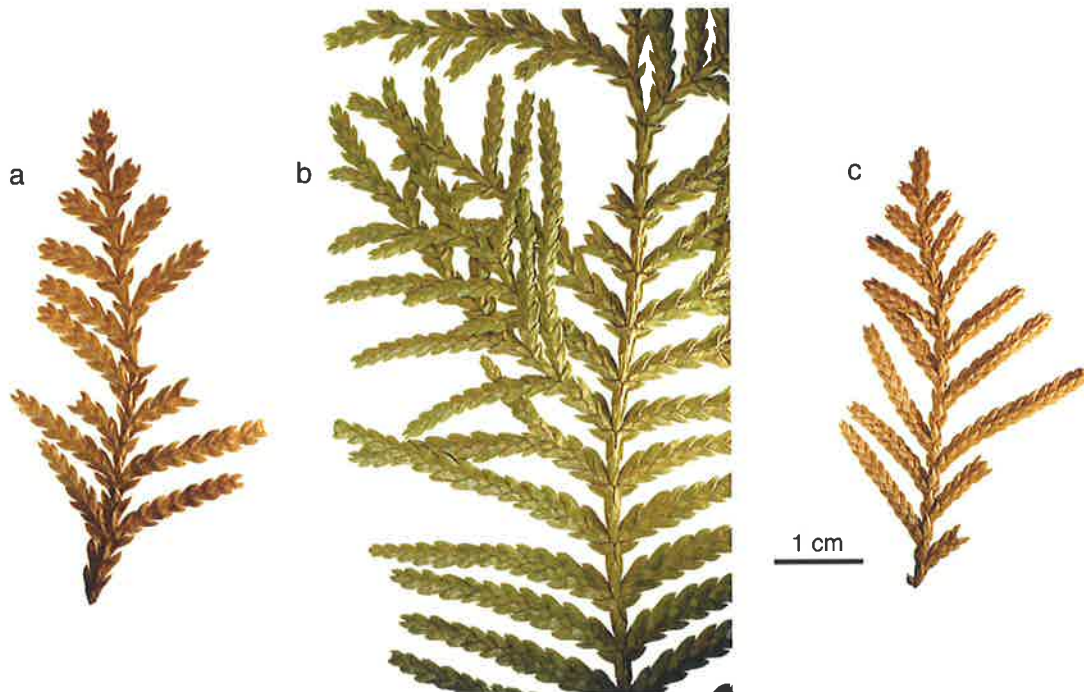
Fig. 8a-c *Libocedrus plumosa*

    a. Juvenile foliage. Leaves on young trees in flattened sprays, dimorphic, lateral leaves much larger than facial and loosely imbricate (Specimen MPN 002367, Kauri Park, North Island).

    b. Juvenile to transitional foliage, flattened spray. Lower branchlets opposite, arising in one plane, longer than ultimate branchlets with larger leaves and laterals larger than facial leaves. Upper branchlets sub-opposite to alternate. Lateral and facial leaves imbricate. Lateral leaves only slightly larger. (Cultivated specimen, Tasmanian Arboretum, Devonport, Tasmania).

    c. Adult foliage. Flattened, with smaller, almost monomorphic imbricate leaves on the ultimate branchlets of older trees (Specimen WELT SP035478, Mt Burnett, Nelson, South Island).
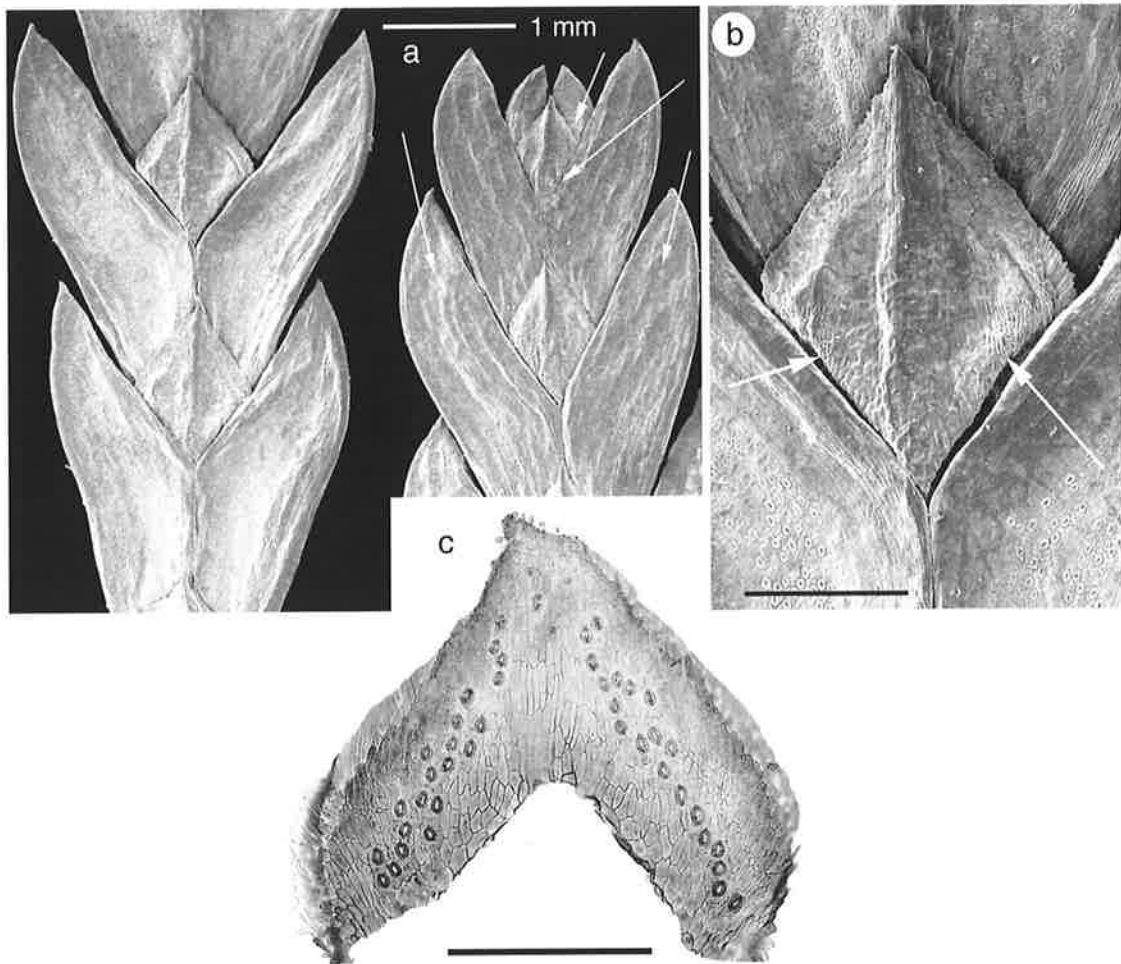
Fig. 9a-c *Libocedrus plumosa* SEM/LM juvenile foliage detail
Specimen 002367

a. SEM dorsal (left) and ventral (right) leaf surfaces. Lateral and facial leaves bilaterally flattened and with acute apices. Lateral leaves keeled, with entire margins. Facial leaves not overlapping and covering only half the lateral leaf pair above. Dorsal surface concave, lateral leaves; stomata densely packed and generally confined to a broad, slightly sunken groove extending from near the apex to the base. Ventral surface: Leaves slightly convex. Lateral leaves with few, scattered stomata (arrows). Stomata on facial leaves largely obscured by overlapping laterals.

b. SEM ventral leaf surface. Lateral leaves entire margined, facial leaves with a moderate frill. Arrows indicating facial leaf stomata (scale 500 μm).

c. LM facial leaf internal surface showing stomatal distribution and frilled leaf margin (scale 500 μm).

Fig. 10a-h *Libocedrus plumosa* SEM adult foliage detail

a. Dorsal leaf surface. Lateral and facial leaves dorsally keeled and flattened with facials not much smaller than laterals. Apex of facial leaves touching the facial leaf above. Stomata largely confined to a light coloured central and slightly sunken groove. Stomata on facial leaves towards the base, and largely covered by lateral leaf pair below (scale as for **c**; specimen 35478).

b. Ventral leaf surface. Stomata on lateral leaves infrequent and, when present, confined to small grooves in the upper part of the leaf (none apparent on this specimen; scale as for **c**; specimen 13317).

c. Dorsal leaf surface (same specimen as **b**). Note how **b** and **c** vary in shape/size from **a**, and that (unlike **a**) facial leaves cover only half the laterals above.

d. Papillae on lateral leaf bases (scale 500 μm).

e. Close up of **d,** leaf base papillae (scale 50 μm).

f. Basal section of facial leaf showing frilled margin and papillae (scale 100 μm; specimen 002367).

g. Inner surface facial leaf showing stomata parallel to leaf margin and frilled margin in lower third of leaf (scale 200 μm; specimen 35478).

h. Inner surface lateral leaf showing stomata parallel to the margin. Margin entire (scale 200 μm; specimen 35478).
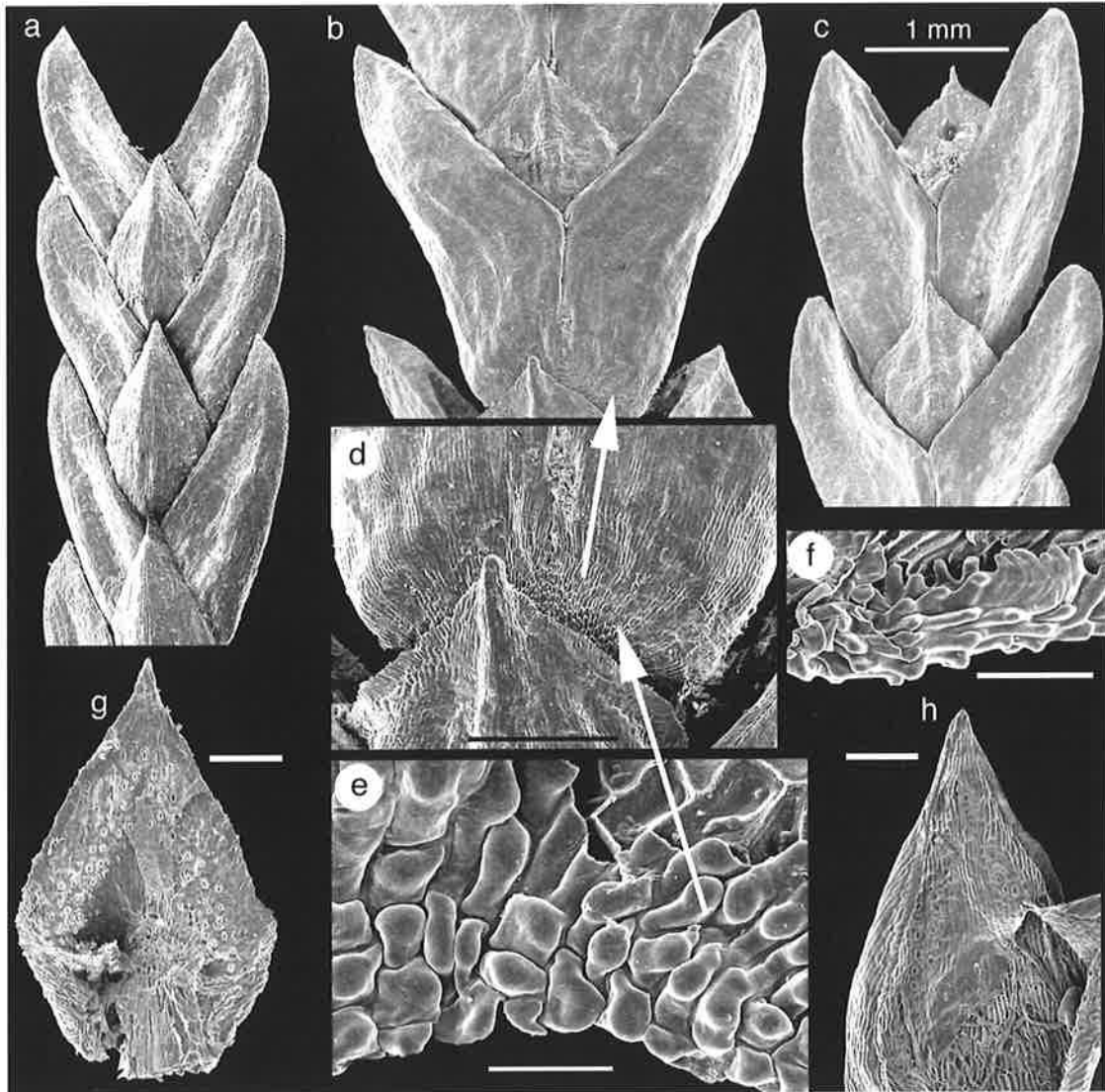
Fig. 10a-h *Libocedrus plumosa* SEM adult foliage detail

Fig. 11a-f *Libocedrus plumosa* juvenile leaf cuticle

    a. SEM inner surface, elongate guard cells with 5 relatively smooth subsidiary cells. Subsidiary cells with elongate indentations, most frequently towards the edge of the cell, and folding downwards around the guard cells. Outer edges of the subsidiary cells fold outwards. Epidermal cells elongate, very coarse-grained, with acute thick, anticlinal walls (scale 20 μm; specimen 002367).

    b. SEM waxy (natural) outer surface. Florin rings high ridged and lobed (scale 20 μm; specimen 002367).

    c. SEM inner surface, guard cells sharing adjacent subsidiary cells (scale 50 μm; specimen 002367).

    d. SEM outer (cleaned) surface showing papillae in association with the stomata. Epidermal cells (foreground) clearly delineated and containing very small nodules (scale 50 μm; specimen 37974).

    e. SEM inner surface (as for **a.** and **c.**), discontinuous rows of stomata surrounded by coarse-grained epidermal cells (scale 50 μm; specimen 002367).

    f. LM - lobed stomata surrounded by papillae (arrows). Relatively smooth-grained subsidiary cells. The epidermal cells not associated with stomatal rows coarse-grained, and with nodules containing calcium oxalate crystals (scale 50 μm; specimen 002367).
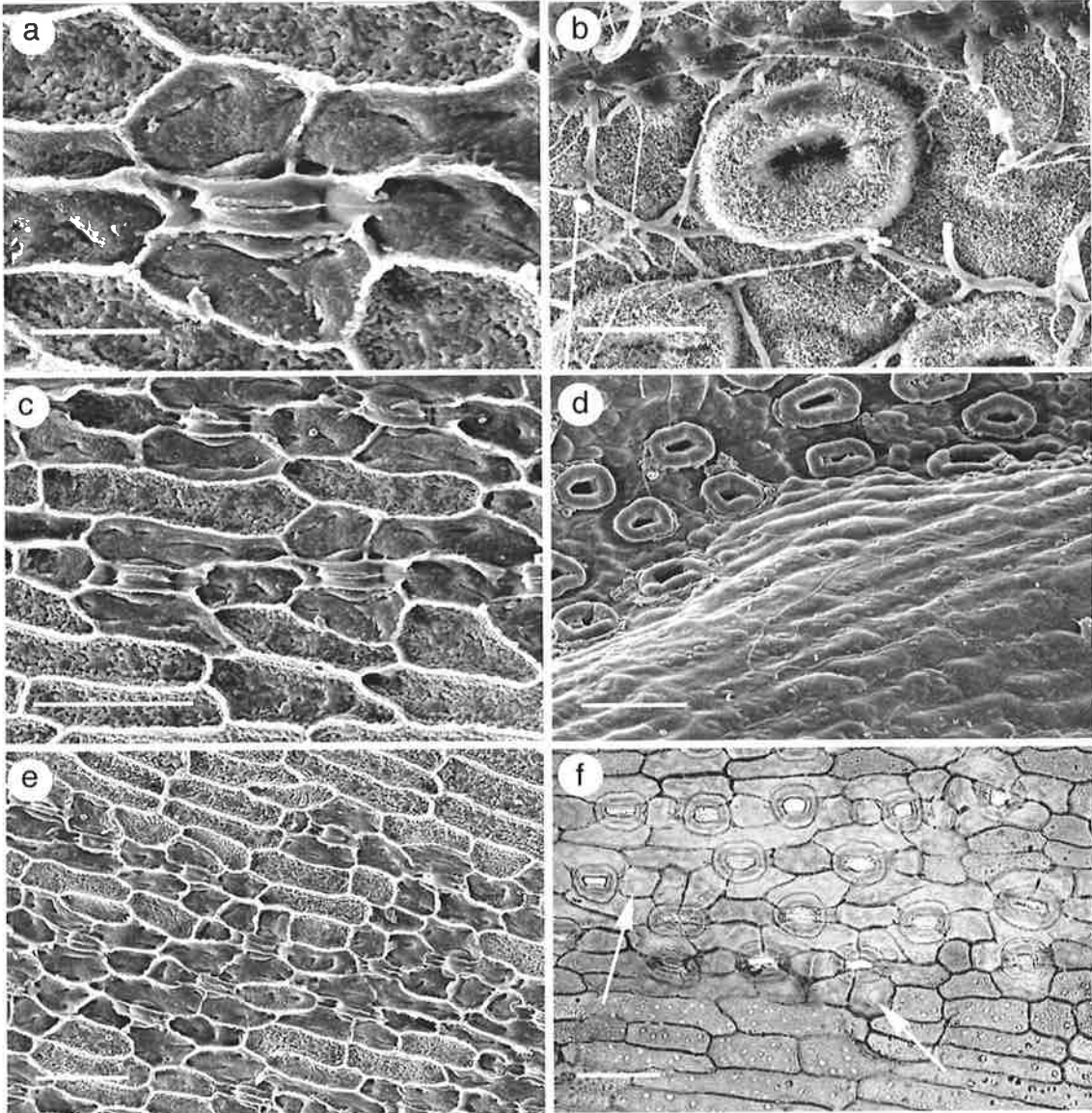
Fig. 11a-f *Libocedrus plumosa* juvenile leaf cuticle

Fig. 12a-h *Libocedrus plumosa* adult leaf cuticle

a. SEM inner surface, elongate stomata with 4 relatively smooth-grained and indented (arrows) subsidiary cells (scale 20 μm; specimen 13317).

b. SEM outer surface. High ridged, lobed and striated Florin rings with peripheral grooves, surrounded by numerous round shaped papillae (scale 20 μm; specimen 13317).

c. SEM inner surface. Stomata with 5-6 subsidiary cells. Some polar cells shared by adjacent stomata. Anticlinal cell walls thick and relatively coarse-grained. Epidermal cells elongate, coarse-grained and containing calcium oxalate crystals (arrow; scale 20 μm; specimen 35478).

d. SEM outer surface lateral leaf. Stomata parallel to the margin. Epidermal cells with indented walls and small nodules or holes (arrow; scale 50 um; specimen 35478).

e. SEM inner lateral surface showing stomata in rows. Note the sharing of subsidiary cells between stomata. The indentations in the walls of the subsidiary cells are often elongate (scale 50 μm; specimen 35478).

f. LM - stomata in discontinuous rows, epidermal cells elongate and most with crystalline nodules (scale 100 μm; specimen 35478).

g. SEM inner ventral lateral leaf surface close to the central keel. Elongate very coarse-grained epidermal cells with thick coarse-grained anticlinal walls (scale 50 μm; specimen 35478).

h. SEM coarse-grained epidermal cells with large calcium oxalate crystals. Surfaces of the latter are comparatively smooth (scale 20 μm; specimen 35478).
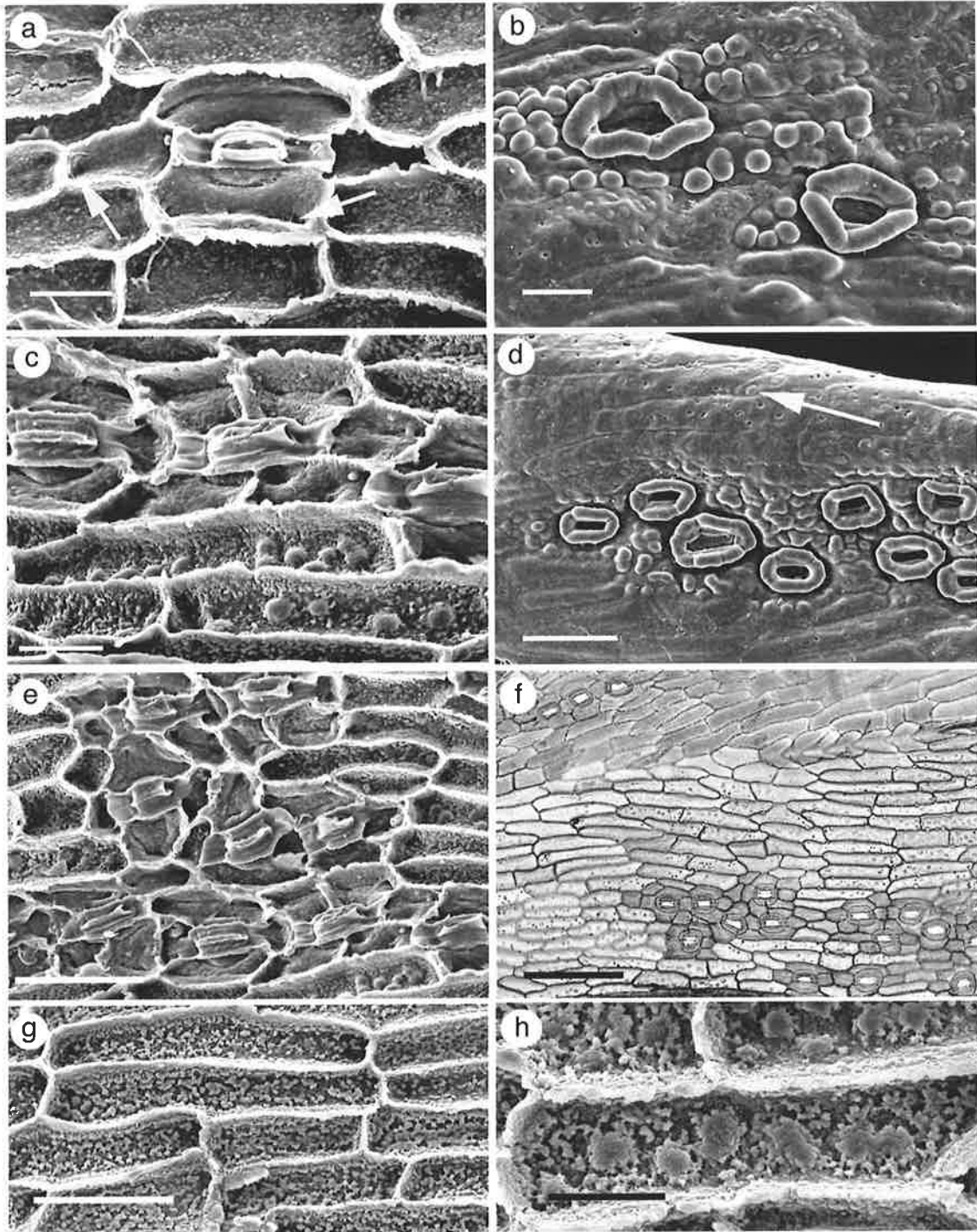
Fig. 12a-h *Libocedrus plumosa* adult leaf cuticle
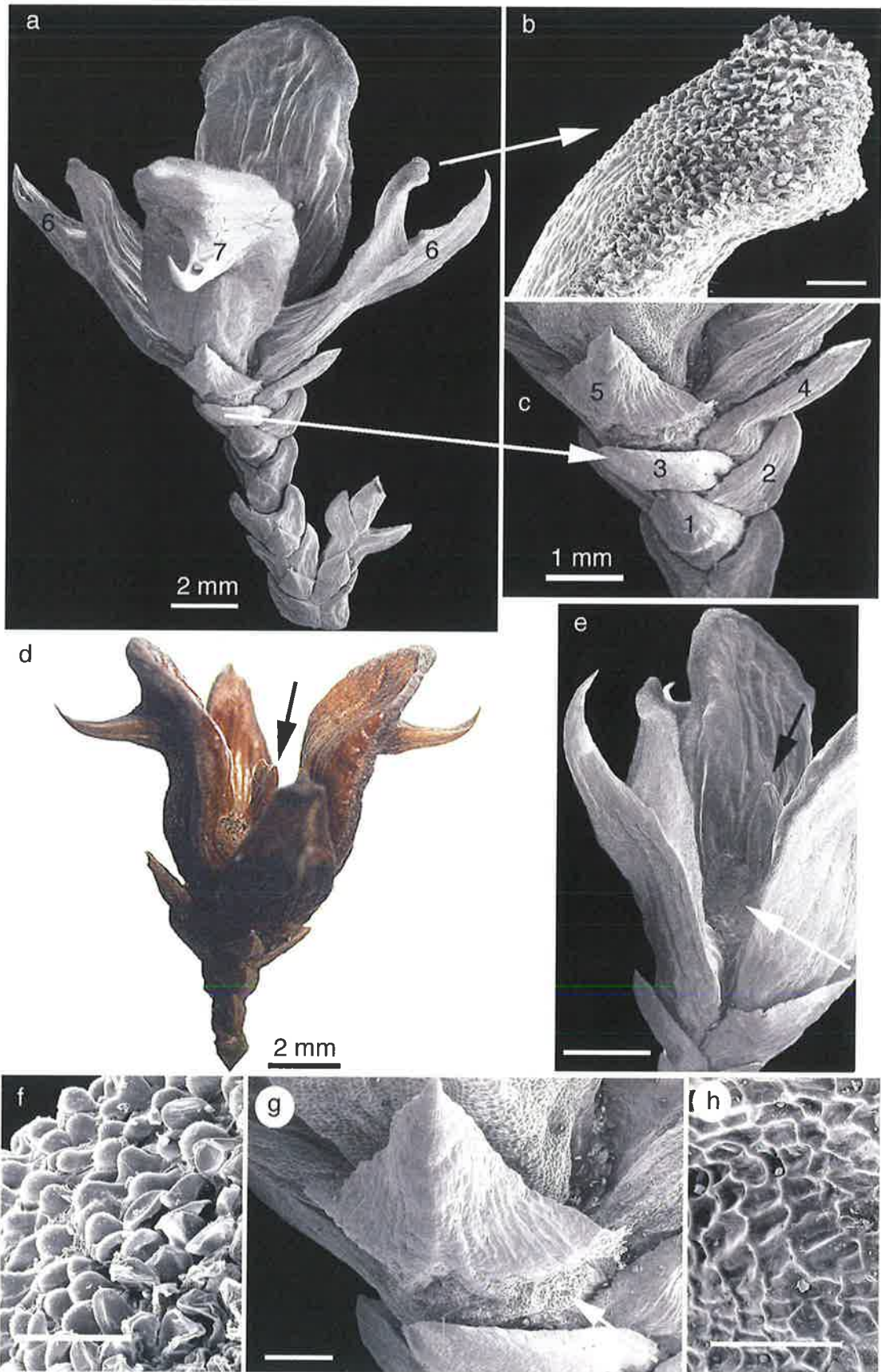
Fig. 13a-h *Libocedrus plumosa* mature female cone

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Fig. 13a-h *Libocedrus plumosa* mature female cone

Collected at the Tasmanian Arboretum, Devonport Tasmania

- **a.** SEM mature cone. The spiny section of the uppermost bracts (6, 7) is outwardly curved, broad at the base and narrowly acute at the tip.
- **b.** Papillate scale margins, penultimate scale (scale 200 μm).
- **c.** Cone subtended by 5 decussate bract pairs, each outwardly keeled but indented towards the base.
- **d.** LM, arrow indicating the narrow, central columella.
- **e.** Penultimate bract (left) larger than the scale and extending beyond it. White arrow indicating dehisced seed surface. Black arrow indicating columella (scale 2 mm).
- **f.** Detail, papillate margin ultimate scale (100 μm).
- **g.** Bract immediately subtending the ultimate bract-scale pair undergoing intercalary growth at the base. Bract with marginal frill (scale 500 μm).
- **h.** Detail of meristematic area in **g** (scale 200 μm).

Fig. 14 *Libocedrus plumosa* ovulate cone on young tree

Collected at the Tasmanian Arboretum, Devonport

Mature cone on young ~2.5 m tree. Foliage frondose, with branchlets arising in the same plane, leaves almost monomorphic (laterals larger) and somewhat flattened.

New Caledonia - 3 species

The climate of New Caledonia is subtropical to tropical, and the main island is divided by a central mountain range. Rainfall across the range is very variable. East of the range the island is relatively wet, the west is much drier (Rigg *et al.* 2002). Around one third of the island's soils (mostly in the south) are iron rich (oxides and hydroxides), and overlie ultramafic rocks. These soils are acidic, nutrient poor, have low water holding capacity, and may have toxic levels of heavy metals (Read *et al.* 2006).

New Caledonian *Libocedrus* are generally found in association with ultramafic soils. *Libocedrus austrocaledonica* is the most widespread species, *L. chevalieri* is endangered (Jaffré *et al.* 1998; Bradford and Jaffré 2004).

Libocedrus austrocaledonica Brongniart & Grisebach. Bull. Soc. Bot. France 18: 140 (1871)
Description: Shrubs or small monoecious trees (2-5 m), mostly multi stemmed, with rough scaly bark. Branches relatively few in number (Laubenfels 1972; Farjon 2005).
Distribution: Eastern slopes of mountains including Mount Humboldt from 700–1300 m (Laubenfels 1972), most often above 1000 m (Jaffré 1995).
Habitat: Understory shrubs growing in strongly humic and very acid ultramafic (often skeletal) soils. Frequently found on exposed ridges, in high altitude, conifer and pteridophyte rich, dense, evergreen. wet forests (3200 mm annual rainfall: Jaffré 1995).

Systematics
Order Coniferales
Family Cupressaceae
Genus *Libocedrus* Endl., Syn. Conif.: 42 (1847)
Libocedrus austrocaledonica Brongniart & Gris Bull. Soc. Bot. France 18: 140 (1871)

Foliage and leaves: Foliage frond like. Ultimate branchlets opposite, arising in the same plane, similar in size and becoming shorter towards the frond apex (Fig. 15a). *Transitional foliage* with highly dimorphic leaves in flattened sprays. Lateral leaves much larger than facial. Facial leaves small, with apices reaching only the lower third of the lateral leaf pair above (Fig. 15a). *Adult foliage* (Fig. 15c) - lateral leaves larger than facial, fused for about one third of their length, imbricate on terminal branchlets (Fig. 16a, b; but less so on older foliage), with convex ventral surfaces, concave dorsal surfaces (Fig. 16c; juvenile leaves also Fig. 15b), and a marginal frill in the lower half of the leaf (Fig. 16d, e, f). Facial leaves small, with bluntly acute apices, outwardly keeled on ventral and dorsal surfaces, broadly flattened on the dorsal surface and with a well developed marginal frill (Fig. 16g). Facial leaves on young shoots very small, not overlapping, and often only reaching the lower half of the fused lateral leaf pair above (Fig. 16a). On older foliage facial leaves are larger and apices extend to reach the facial leaf pair above (Fig. 16c).
Stomatal distribution, transitional and adult foliage: Ventral surface - rare on exposed lateral leaf surfaces. On facial leaves in grooves on either side of the central keel, and mostly obscured by the lateral leaf pair above (Fig. 16e, h) Dorsal surface - on lateral leaves in discontinuous rows roughly parallel to the leaf margin, in well defined, light-coloured, sunken grooves. On facial leaves on either side of the central keel and largely obscured by the lateral leaf pair above (Fig. 16d). Adaxial surfaces, lateral and facial (dorsal and ventral leaves) in short discontinuous rows parallel to the leaf margin, from near the leaf apex to close to the base (Fig. 16f).

Cuticle description: Inner dorsal surface - guard cells elongate, and surrounded by 4-5 subsidiary cells. The latter are elongate, finely coarse-grained in texture, and often shared by one or more adjacent guard cells. Subsidiary cells fold down around the guard cells, forming a discontinuous groove around them (Fig. 17a, g). Stomata in closely packed, discontinuous rows roughly parallel to the leaf margin (Fig. 17e, f). Epidermal cells surrounding the stomatal areas elongate, coarse-grained in texture and containing calcium oxalate crystals. Anticlinal cell walls acute, and coarse-grained in appearance (Fig. 17f, h). Inner adaxial surface - stomata less frequent. In protected areas e.g. close to the leaf base, epidermal cells are finely coarse-grained and lack calcium oxalate crystals (Fig. 17c). Outer surface - stomata have high ridged and lobed Florin rings with peripheral grooves (Fig. 18b, d). The lobed surface of the Florin rings may contain small nodules (Fig. 17b). Numerous, often round, but also irregularly shaped papillae are associated with the stomata. Epidermal cells have indented margins, and contain small nodules or holes (that indicate the presence of calcium oxalate crystals in their external cell walls; Fig. 17d).

Ovulate cones: (Only 2 cones were available for examination. Both were immature, and one was broken). 10-12 mm long (Laubenfels 1972). Terminal on flattened branchlets (Fig. 18). In developing cones, elongation of bracts appears to occur more rapidly than scale development (Fig. 18). Subtending the cone are 3 non-fertile, decussate bracts that become progressively elongate towards the bract-scale pairs (Fig. 19a). The margins of these bracts, and the leaves beneath are frilled (Figs 19b; 20c). Ultimate scales broad, ovate-lanceolate, slightly broader in the upper third, and with bluntly acute apices. Penultimate scales much smaller, narrow (Laubenfels 1972: Farjon 2005). All scales with papillate margins, and large epidermal cells (Figs 19c, d; 20b). Abaxial and adaxial scale surfaces slightly rugose (Farjon 2005). In developing cones, elongation of bracts appears to occur more rapidly than scale development (Figs 18b; 19a; 20a). Bract projections elongate, spike-like, triangular in cross section, and extending upwards from the centre of the scale to some distance beyond it. Bract apices inwardly turned (Fig. 19a). Epidermal cells in the bract projections elongate, much smaller than those of the scale (Fig. 19d), and containing calcium oxalate crystals (Fig. 20b). Beneath the bract projection the ultimate bract is rugose (Fig. 20a). Bracts of penultimate scales only slightly shorter than those of the ultimate.

Ovules: not illustrated as no cones were dissected in this study, but most likely 4, 2 in the sub-axillae of each of the ultimate bracts. Farjon (2005) suggests 1-2 in the sub-axillae of ultimate bracts, and 1-2 slightly-flattened and winged seeds with wings unequal in size and shape.

Pollen cones: not illustrated, terminal on flattened branchlets. Microsporophylls 8-24 decussate pairs, largely triangular in shape (Laubenfels 1972), weakly keeled (Farjon 2005).

Specimens examined

00504523, National Herbarium, Canberra, Australia. 33847, Povila, Poindimie. 5 m tree at 600 m (in schist/serpentine contact zone).

00504526, National Herbarium, Canberra, Australia. Collected 11/1947, MJ Bernier 11, Montagne des Sources. Small tree ~3 m at ~1000 m.

5859 IRD, Institut de recherché pour le développement, Nouméa, New Caledonia. Collected 12/1984, JM Veillion 5859, Montagne des Sources. 1000 m.

Cultivated seedling ~20 cm, Royal Tasmanian Botanical Garden, Hobart, Tasmania, Australia. Collected 11/2004, R Paull.
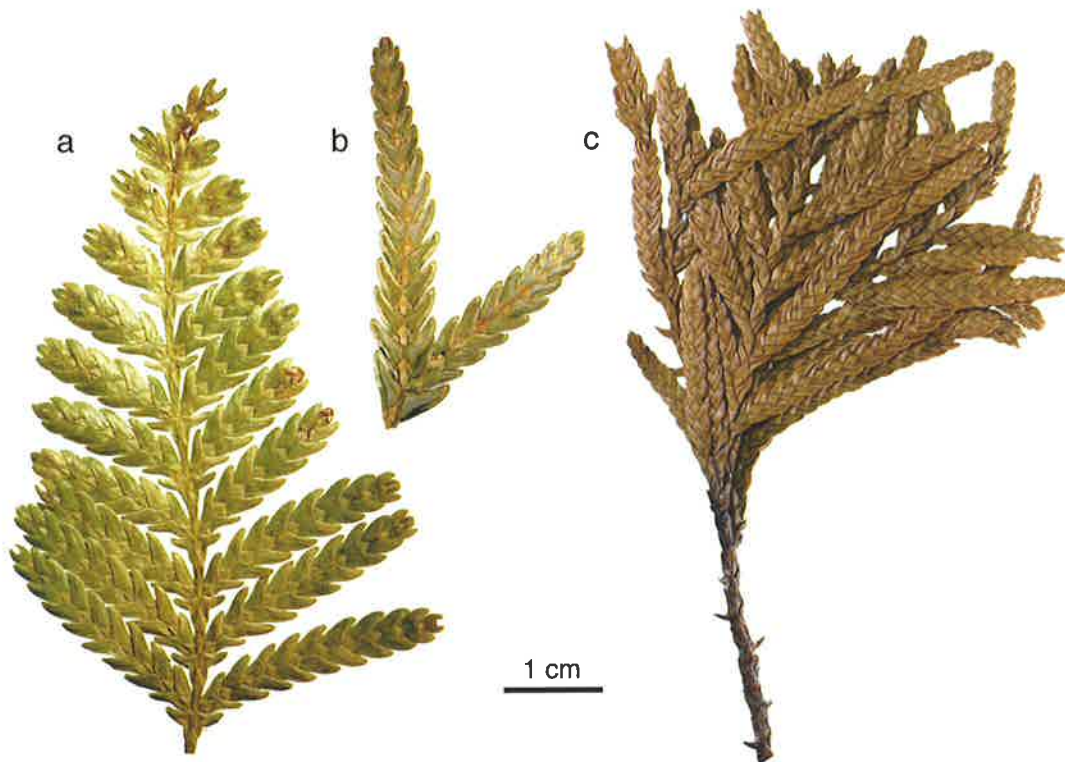
Fig. 15a-c *Libocedrus austrocaledonica* branchlets showing leaf arrangement

    a. Juvenile/transitional foliage frond, ventral surface, ultimate branchlets. Branchlets arising in the same plane. Leaves flattened, highly dimorphic, lateral leaves much larger than facial leaves. The latter barely visible with apex reaching only the lower third of the lateral leaf pair above. All leaf surfaces convex. Branchlets opposite, similar in size and becoming shorter towards the end of the frond (specimen ~20 cm, from RTBG, Tasmania).

    b. Dorsal surface, same foliage frond as **a**, but from branchlets lower in the frond. Note: lateral leaves in the lower half of the branchlet not imbricate. Central surface, lateral leaves, concave. Centre of facial leaves raised with a concave grove on either side.

    c. Young adult 5 m tree. Branchlets arising in the same plane. Leaves imbricate, lateral leaves thickened and larger than facial leaves. Facial leaves overlapping each other (specimen 00504523 Australian National Herbarium, Poindmie ~600 m).

Fig. 16a-h *Libocedrus austrocaledonica* SEM/LM adult foliage

    a. SEM dorsal leaf surface, shoot tip. Lateral and facial leaves convex. Lateral leaves outwardly keeled, imbricate. Facial leaves dorsally keeled, and not overlapping the facial pair above. No stomata on lateral leaves (scale 500 µm; specimen 5859).

    b. SEM dorsal leaf surface. Lateral and facial leaves flattened. Facial leaves dorsally keeled and broadly flattened. Stomata on either side of the keel, and mostly obscured by the lateral leaf pair above. Stomata on lateral leaves densely packed and in well defined and light coloured sunken grooves with well-defined, rounded margins (specimen 5859).

    c. SEM dorsal surface. Leaves more lanceolate in appearance. Stomata on lateral leaves in sunken central grooves. Facial leaf apices extending to reach the facial leaf pair above (specimen 504523).

    d. SEM dorsal surface close up. Note: - 1) arrow indicating the position of stomata on the facial leaf 2), clearly defined stomatal groove on the lateral leaf (right), 3) the waxy surface of the lower left lateral leaf, 4) frilled lower margin of the lateral leaves and, 5) highly frilled facial leaf margin (scale 500 µm; specimen 504526).

    e. SEM ventral surface. Arrow indicating stomata on facial leaves (specimen 504526).

    f. LM lateral leaf showing stomatal distribution on dorsal (left hand side) and adaxial (right hand side) surfaces. Arrow indicates the slightly frilled leaf margin (scale 500 µm; specimen 504523).

    g. SEM ventral surface. Lateral leaf margin frilled (left), facial leaf margin with well developed frill (right; scale 100 µm; specimen 504523).

    h. SEM ventral leaf surface. Close up of stomata (arrow) on **e** (specimen 504526; scale 100 µm).
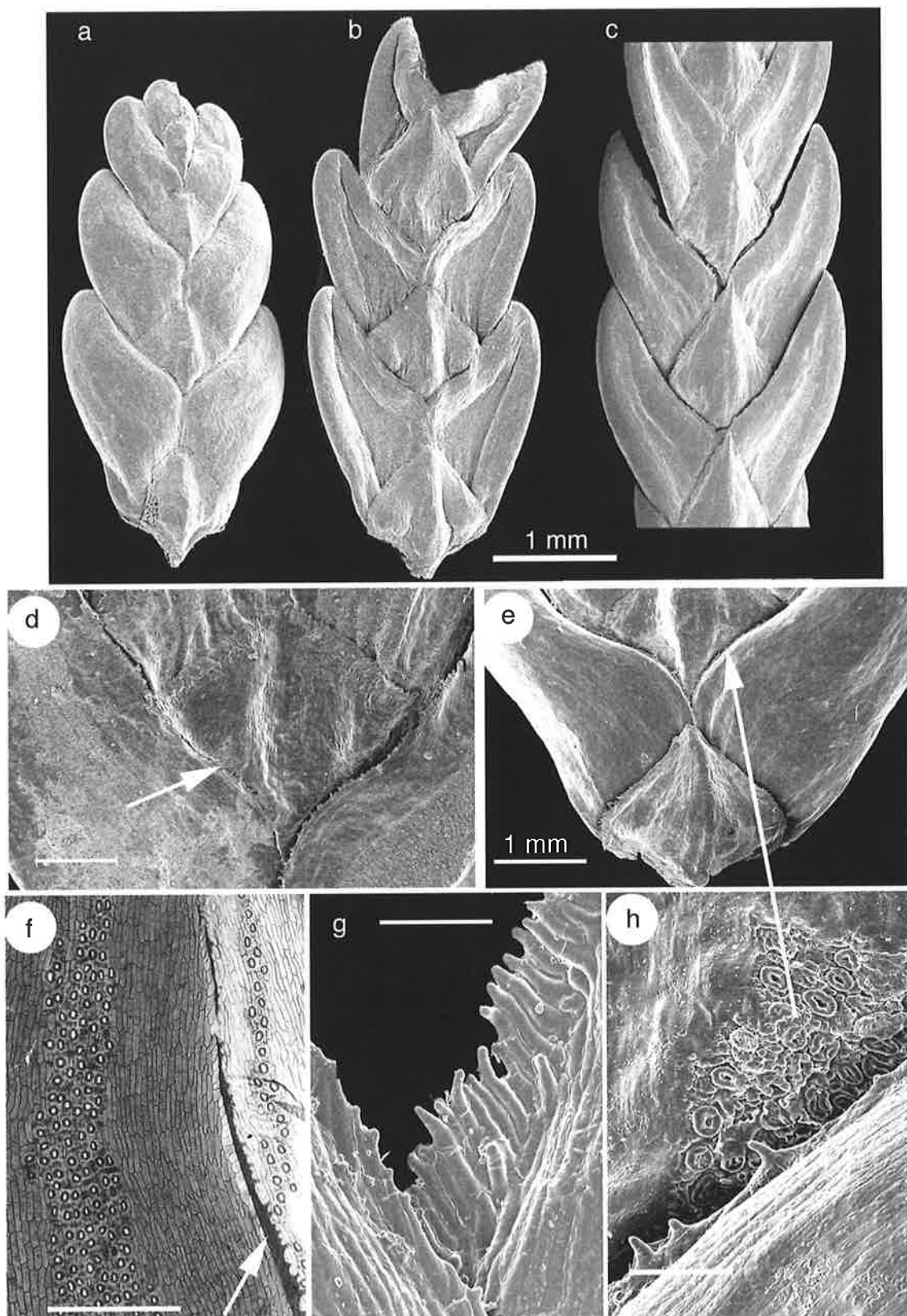
Fig. 16a-h *Libocedrus austrocaledonica* SEM/LM adult foliage

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Fig. 17a-h *Libocedrus austrocaledonica* adult leaf cuticle

a. SEM inner surface stomata. Guard cells share subsidiary cells. Subsidiary cells with slightly coarse-grained texture, forming a groove around the guard cells Indentations in subsidiary cells correspond with papillae on the outer surface (scale 20 μm; specimen 504526).

b. SEM outer surface stomata. High ridged, lobed Florin rings with small nodules (arrow). Florin rings with a peripheral groove. Numerous round, and some irregularly shaped, papillae associated with stomata (scale 50 μm; specimen 5859).

c. SEM lateral leaf internal adaxial surface. Stomata few, and in discontinuous rows. Epidermal cells coarse-grained and without calcium oxalate crystals (scale 50 μm; specimen 504526).

d. SEM outer leaf surface. Closely packed, lobed stomata surrounded by papillae (upper right). Epidermal cells (foreground) clearly delineated and with numerous small nodules (scale 50 μm; specimen 5859).

e. SEM inner surface showing numerous closely packed stomata (scale 100 μm; specimen 504526).

f. LM stomata closely packed, and in discontinuous rows roughly oriented to the leaf margin. Stomatal groove surrounded by elongate epidermal cells containing calcium oxalate crystals (scale 500 μm; specimen 504526).

g. SEM inner surface – subsidiary cells form a deep, discontinuous groove around the guard cells (scale 20 μm; specimen 5859).

h. SEM inner ventral surface, coarse-grained, elongate epidermal cells with large calcium oxalate crystals (scale 20 μm; specimen 504526).

Fig. 17a-h *Libocedrus austrocaledonica* adult leaf cuticle

95
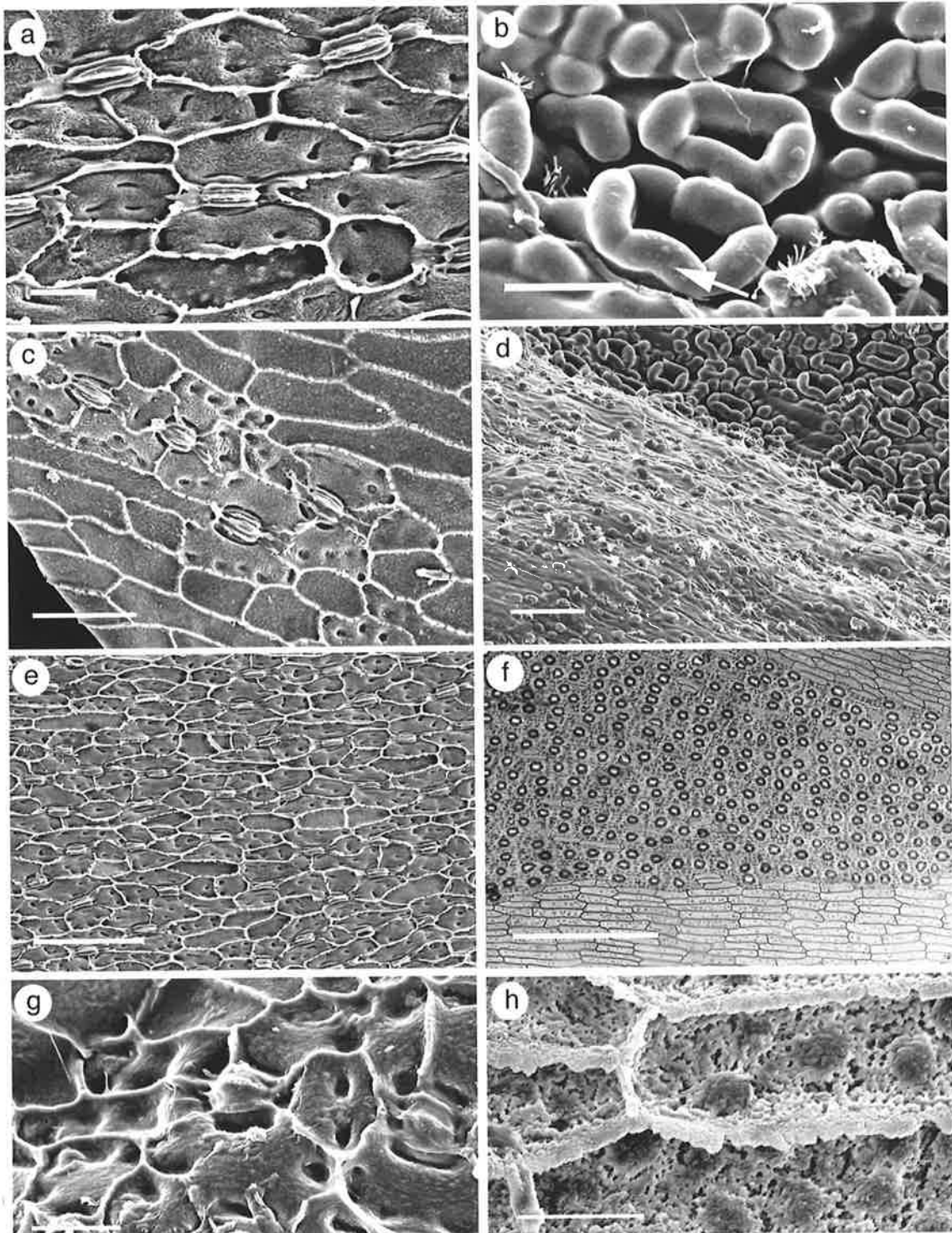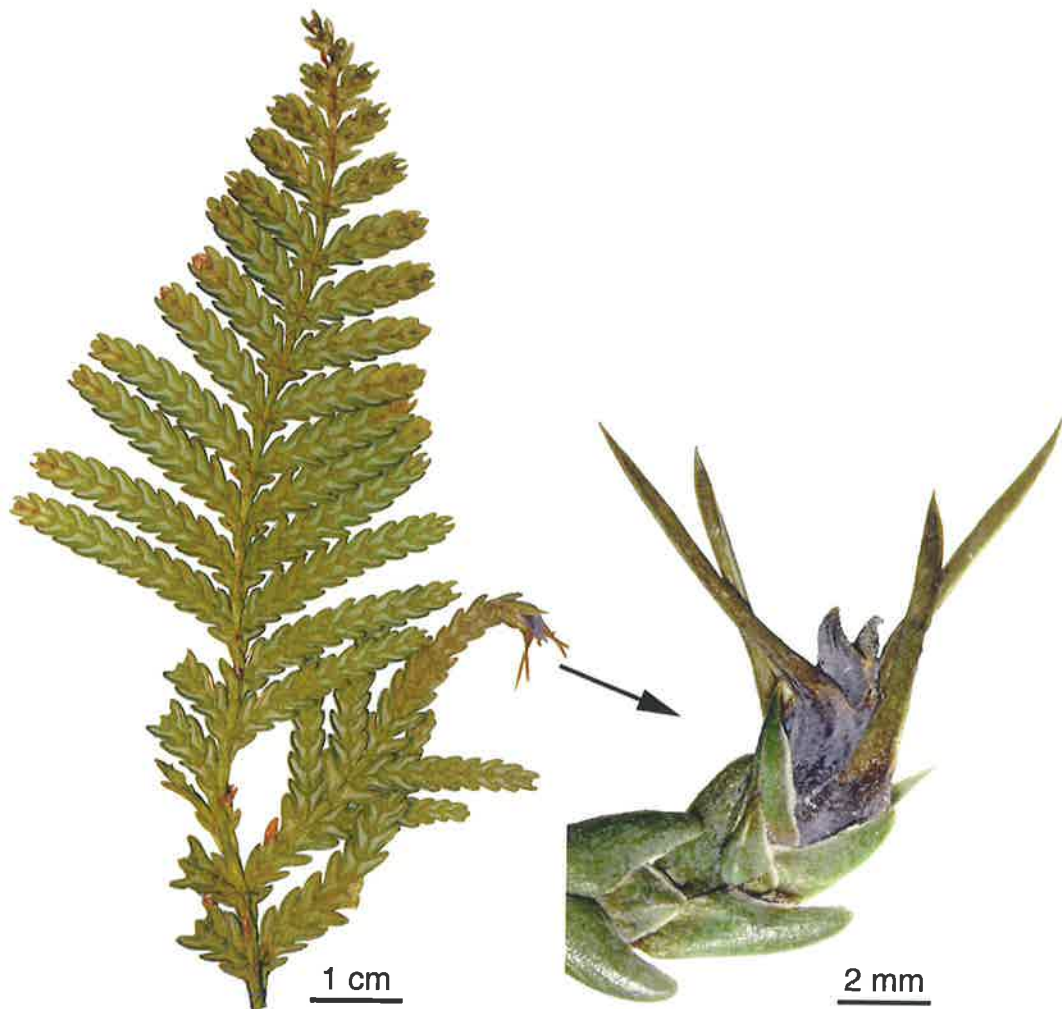
Fig. 18 *Libocedrus austrocaledonica* ovulate cone LM

Frond like foliage from very young specimen (~20 cm) collected at RTBG, Hobart, Tasmania. Dorsal surface. Branchlets opposite. Single immature, and flattened ovulate cone (arrow indicating cone detail), terminal on branchlet, solitary.

Ultimate and penultimate bracts elongate, ultimate scales small, penultimate scales very small and not visible on this photograph.
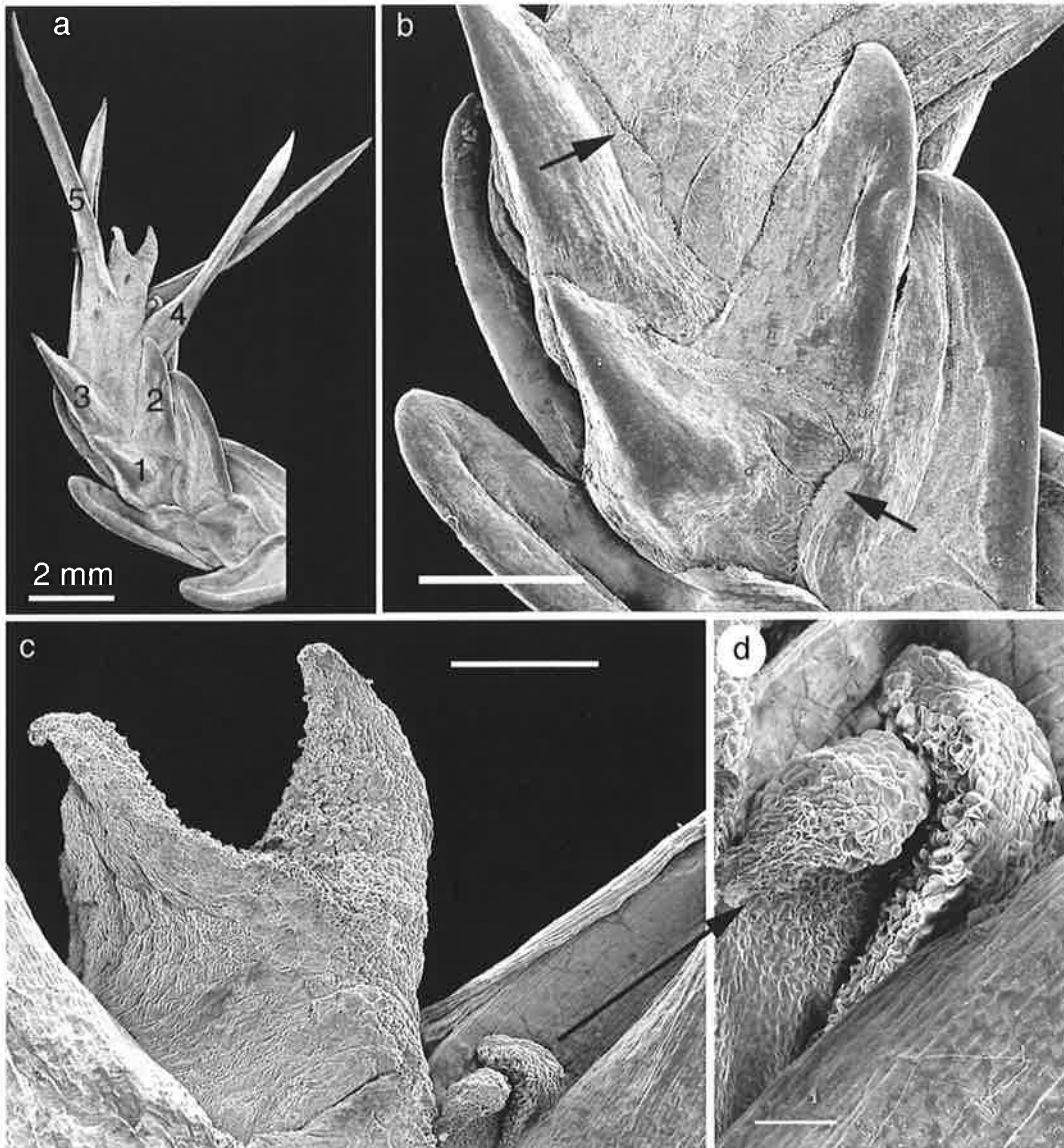
Fig. 19a-d SEM *Libocedrus austrocaledonica* immature ovulate cone
SEM of same specimen in Fig. 17.

    a. Immature cone with narrow, elongate, spike-like bracts (4-5), and poorly developed scales. Cone subtended by 3 non-fertile, decussate bract pairs (1-3). Apices of facial bracts (1&3) more acute than the lateral pair (2). Flattened appearance of cone due to pressing for preservation.

    b. Bracts subtending the cone keeled, less flattened than leaves beneath. Bracts (upper arrow) and leaves (lower arrow) with frilled margins (scale 1 mm).

    c. Inner surface of ultimate scales highly papillate. Scale cells large and irregular in shape, epidermal cells of bract projection small, elongate (scale 500 μm).

    d. Detail of developing penultimate scale. Large irregular cells. Bract projection cells much smaller (scale 100 μm).
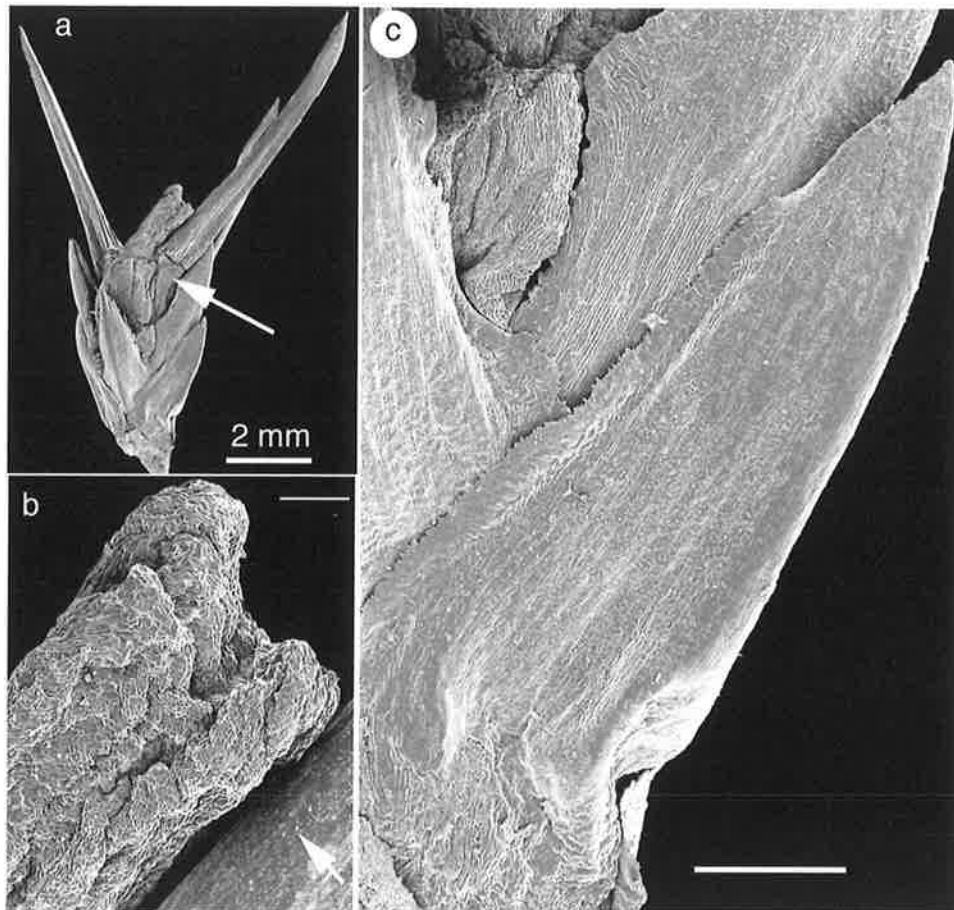
Fig. 20a-c *Libocedrus austrocaledonica* ovulate cone

    a. Sub-mature and broken cone, with missing penultimate bract projection. Base of ultimate bract slightly rugose (arrow).

    b. Ultimate scales sub-mature. Epidermal cells large, surface highly rugose. Bract projection with calcium oxalate crystals (arrow; scale 200 μm).

    c. Bracts subtending the cone with frilled margins. Epidermal cells elongate, and containing calcium oxalate crystals (scale 500 μm).

Libocedrus chevalieri J. Buchholz. Bull. Mus. Hist. Nat. (Paris), sér. 2, 21: 283 (1949)

Description: Small trees or shrubs 2-5 m. Monoecious, mostly multi-stemmed with rough brown bark. Numerous ascending branches creating an often bush-like appearance (Laubenfels 1972; Jaffré 1995; Farjon 2005).
Distribution: Found only on the summits of Mt Humboldt and Mt. Kouakoué from 1450-1600 m (Laubenfels 1972; Jaffré 1995) and Poindimié in the north (from 650 m; Farjon 2005).
Habitat: Small gregarious populations growing in very acidic, humic and often skeletal (poor) soils, in relatively cool, often windswept, cloudy sites where rainfall is high (Laubenfels 1972; Jaffré 1995; Farjon 2005).

Systematics
Order Coniferales
Family Cupressaceae
Genus *Libocedrus* Endl., Syn. Conif.: 42 (1847)
Libocedrus chevalieri J. Buchholz. Bull. Mus. Hist. Nat. (Paris), sér. 2, 21: 283 (1949)

Foliage and leaves: Foliage frond like. Ultimate branchlets alternate, in the same plane – sub-opposite, similar in length, but becoming shorter towards the end (Fig. 21a). The alternate arrangement of branchlets may result in twisting of the stem (Fig. 21b). *Juvenile/Transitional foliage* larger (Fig. 22c, d) than adult (Fig. 22a, b), with decussate, slightly dimorphic, imbricate and flattened leaves. Lateral leaves slightly larger (3-5 mm long) than facial. *Adult foliage* less flattened than transitional, and almost monomorphic on ultimate branchlets. Lateral leaves slightly larger (2.5-3 mm long) than facial, convex on dorsal and ventral surfaces, outwardly keeled, apically recurved, and fused for about one third of their length. Leaf margins entire at the apex, but mostly frilled (Fig. 22e). The bases of lateral leaves are slightly papillate (Fig. 22g). Facial leaves reaching to or overlapping the facial pair above, triangular in shape, outwardly keeled, with acute apices, and well developed marginal frills (Fig. 22a, b).
Stomatal distribution, transitional and adult foliage: Dorsal and ventral surfaces, lateral and facial adult leaves - in small deep grooves on either side of the central keel, in the lower third of the leaf. These grooves and are largely concealed by the leaf pair below, and are smaller on the ventral surface (Fig. 22a, b). On transitional foliage the stomatal grooves are longer and broader (Fig. 22c, d). Adaxial surfaces, lateral and facial (dorsal and ventral) - leaves in rows parallel to the leaf margin, extending from the base to close to the apex (Fig. 22g).
Cuticle description: Inner dorsal surface - guard cells elongate and surrounded by 4-5 relatively fine-grained subsidiary cells that may be shared by one or more adjacent guard cells. Subsidiary cells relatively fine-grained, folding down around the guard cells to form a discontinuous groove, and with indentations (mostly round in shape, and generally close to the outer cell margin; Fig. 23a, c). Epidermal cells in areas protected by overlying leaves are moderately coarse-grained in texture and have relatively thin, broad-based, short, and moderately coarse-grained anticlinal cell walls. They do not contain calcium oxalate crystals. Most other epidermal cells (keeled areas are exceptions) contain frequent (Fig. 23e), and often large, calcium oxalate crystals. The anticlinal walls of these cells are thick, coarse-grained and erect (Fig. 23h). Outer surface - stomatal areas are often waxy (Fig. 22h). Florin rings are high ridged, distinctly lobed, and may be surrounded by a peripheral ring. The Florin rings may contain small nodules. The stomata are surrounded by many round, and some

irregularly-shaped papillae (Fig. 23b, c). Where stomata are not protected, the epidermal cells abutting stomatal grooves contain small-medium sized nodules or holes (Fig. 23d, f). All epidermal cells have indented margins.

Ovulate cones: 10-12 mm (Laubenfels 1972), 10-16 mm long (Farjon 2005). Terminal on branchlets. Ultimate scales broad, widest at the bract projection, narrower at the base. Penultimate scales smaller. Both scale pairs with long spiny bract projections (6-8 mm long, Farjon 2005), that extend beyond the scale and are inwardly curved towards the tip (Fig. 24a). Epidermal cells in these projections are elongate, and contain calcium oxalate crystals (Fig. 24b). The lower section of the ultimate bracts is highly rugose (Fig. 24c; immature cone), and has large irregularly-shaped cells. The bracts of the penultimate scales are much larger, and more conspicuous than the scale. Penultimate and ultimate bracts of similar size. The cone is subtended by 4-5 non-fertile decussate bracts that increase in size towards the cone (the longest bract immediately beneath the ultimate bract-scale pair). These bracts have frilled lower margins and Calcium oxalate nodules in their epidermal cells (Fig. 24d).

Ovules: No cones were dissected in this study, but most likely 4, 2 in the sub-axillae of each of the ultimate bracts. Farjon (2005) suggests 1-2, with 1-2, slightly flattened seeds. Seeds with unequal sized membranous wings (Laubenfels 1972).

Pollen cones: not illustrated. Terminal on branchlets. Microsporophylls 8-12 decussate pairs, weakly keeled (Farjon 2005).

Specimens examined

16 IRD, Institut de recherché pour le développement, Nouméa, New Caledonia. Collected 1955, Chevalier 16, Mt Kouakoué at 800-1500 m.

E/1241, Herbarium Collection, The University of Adelaide, South Australia. Collected McPherson 3094, New Caledonia.

Cultivated seedling >50 cm, Royal Tasmanian Botanical Garden, Hobart, Tasmania, Australia. Collected 11/2004, R Paull.
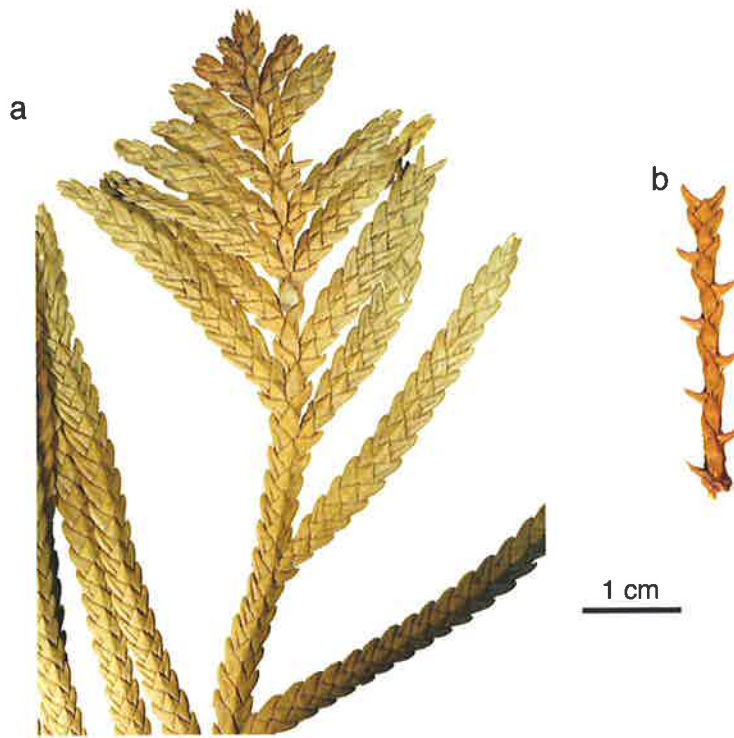
Fig. 21a-b *Libocedrus chevalieri* branchlet and stem showing leaf arrangement
Both specimens from a cultivated seedling ~40 cm RTBG, Hobart, Tasmania

- a. Juvenile/transitional frond-like foliage with alternate - sub-opposite branchlets, all arising in the same plane. Lateral and facial leaves highly keeled, imbricate and similar in size with facial leaves slightly shorter and broader at the base.
- b. Juvenile twig showing twisting due to the alternate configuration of (missing) branchlets.

Fig. 22a-h *Libocedrus chevalieri* SEM/LM adult and juvenile/transitional foliage
Adult specimen 16 IRC, juvenile specimen RTBG Tasmania.

a. SEM adult leaf, dorsal surface. Lateral and facial leaves imbricate, apically recurved. Lateral leaves only slightly larger than facial leaves. Stomata on lateral and facial leaves towards the base of the leaf and in well defined, highly sunken grooves.

b. SEM adult leaf, ventral surface. Very similar to the dorsal surface but with slightly smaller and more concealed stomatal grooves.

c. LM juvenile/transitional leaf, dorsal surface. Leaves larger, flatter than adult leaves. Stomatal grooves extend almost to the leaf apex.

d. LM juvenile/transitional leaf, ventral surface. Facial leaves with acute apices. Lateral leaf apices recurved. Lateral and facial leaves with well developed marginal frills. Stomata fewer than on dorsal surface.

e. SEM adult leaf, dorsal surface. Stomata on lateral and facial leaves in distinct grooves. Facial and lateral leaves with frilled margins (well developed on facial leaves).

f. SEM adult leaf, ventral surface. Very similar to dorsal surface but with slightly smaller stomatal grooves.

g. SEM adult facial leaf, adaxial surface. Stomata extend from the base of the leaf to the apex and are parallel to the leaf margin. Marginal frill best developed towards the base.

h. SEM adult dorsal surface, lateral leaf, well developed groove containing closely packed stomata surrounded by papillae (scale 200 µm).

Fig. 22a-h *Libocedrus chevalieri* SEM/LM adult and juvenile foliage

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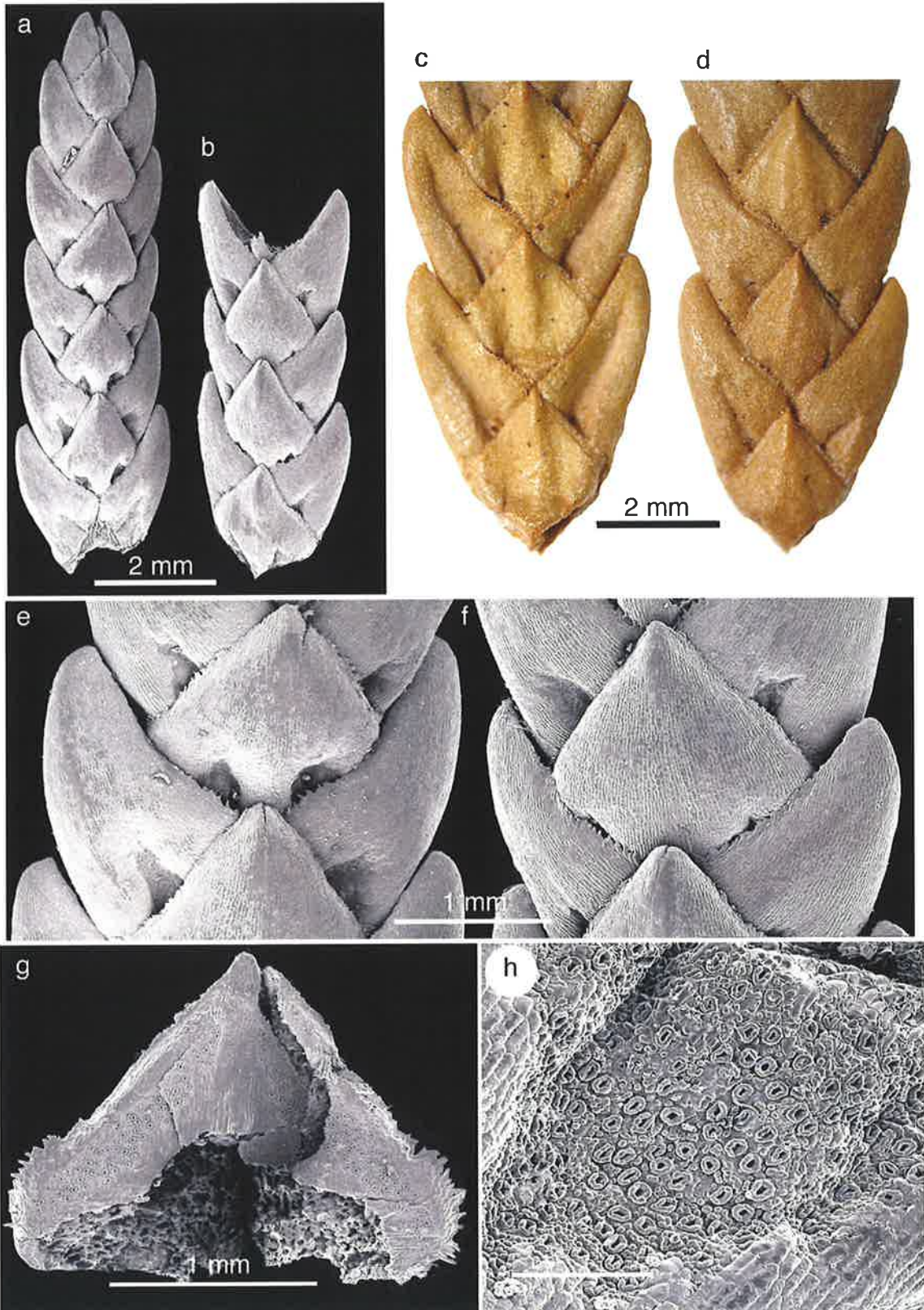
Fig. 23a-h *Libocedrus chevalieri* SEM/LM leaf cuticle
Specimen 16 IRD

a. SEM inner surface stomata. Subsidiary cells relatively fine-grained and with indentations (scale 20 μm).

b. SEM outer (cleaned) surface. Densely packed stomata, with lobed, high ridged Florin rings, some with small nodules (arrow), and peripheral grooves. Stomata surrounded by round, and irregularly shaped papillae (scale 20 μm).

c. SEM internal surface. Subsidiary cells shared by adjacent stomata (scale 20 μm).

d. SEM outer (exposed) leaf surface. Closely packed lobed stomata surrounded by papillae (upper right). Clearly delineated epidermal cells (foreground) with crystalline nodules or holes (scale 100 μm).

e. LM. Stomata on the adaxial leaf surface oriented almost parallel to the frilled leaf margin (black arrow). Epidermal cells on this surface without crystalline nodules. Epidermal cells on the ventral surface (white arrow) with nodules (scale 250 μm).

f. SEM facial leaf, ventral surface. Epidermal cells elongate, with indented margins, and containing nodules or holes (arrow indicating similar nodules on LM photo **e**; scale 20 μm).

g. LM lower lateral leaf surface. Slightly papillate base (arrow; scale 500 μm).

h. SEM ventral surface, inner cuticle. Coarse-grained epidermal cells with crystalline nodules. Anticlinal cell walls acute, coarse-grained (scale 200 μm).

i. SEM adaxial leaf surface. Moderately coarse-grained epidermal cells. Anticlinal cell walls moderately coarse-grained, short, broad at the base, and without crystalline nodules (scale 200 μm).
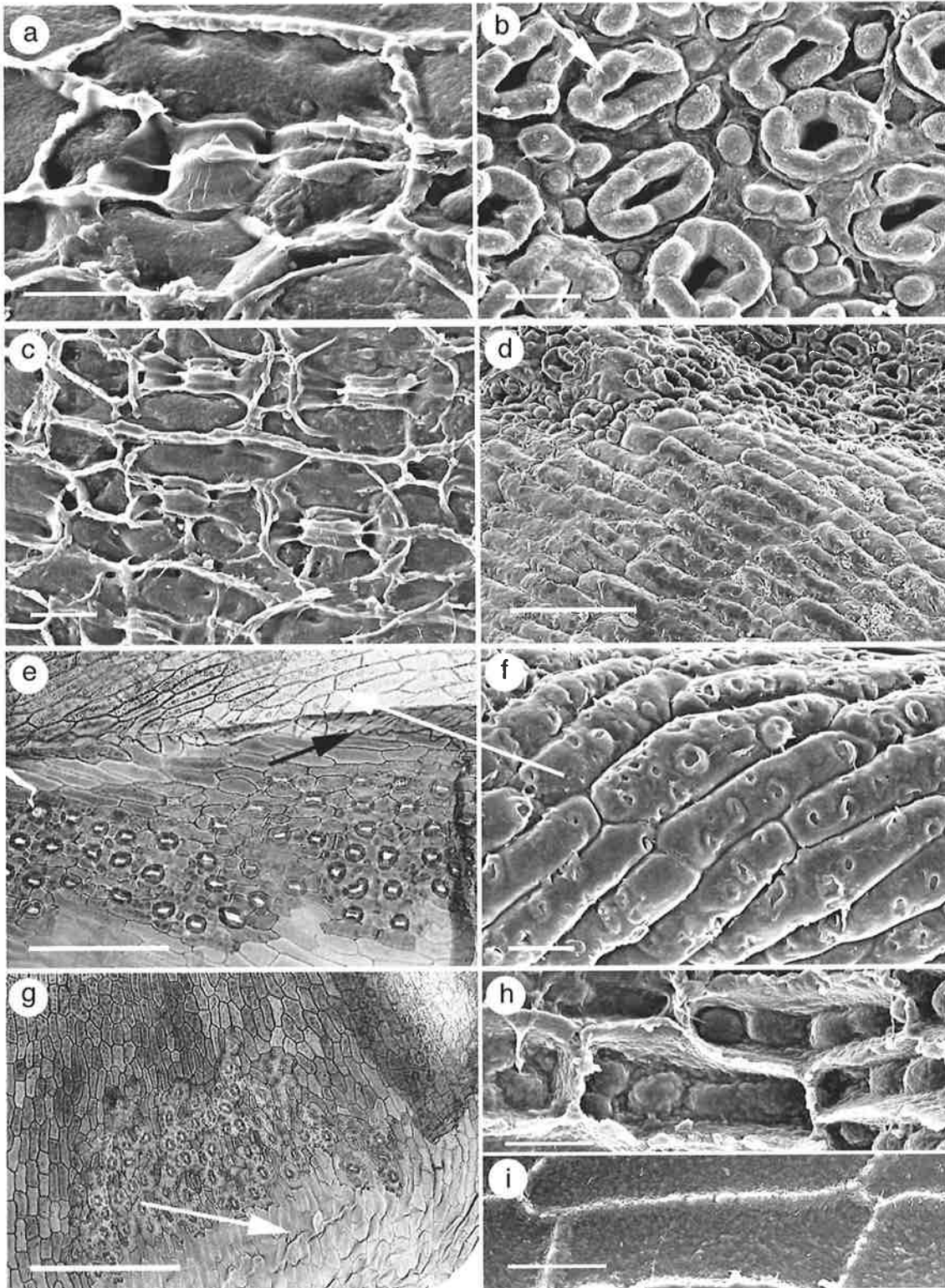
Fig. 23a-i *Libocedrus chevalieri* SEM/LM leaf cuticle
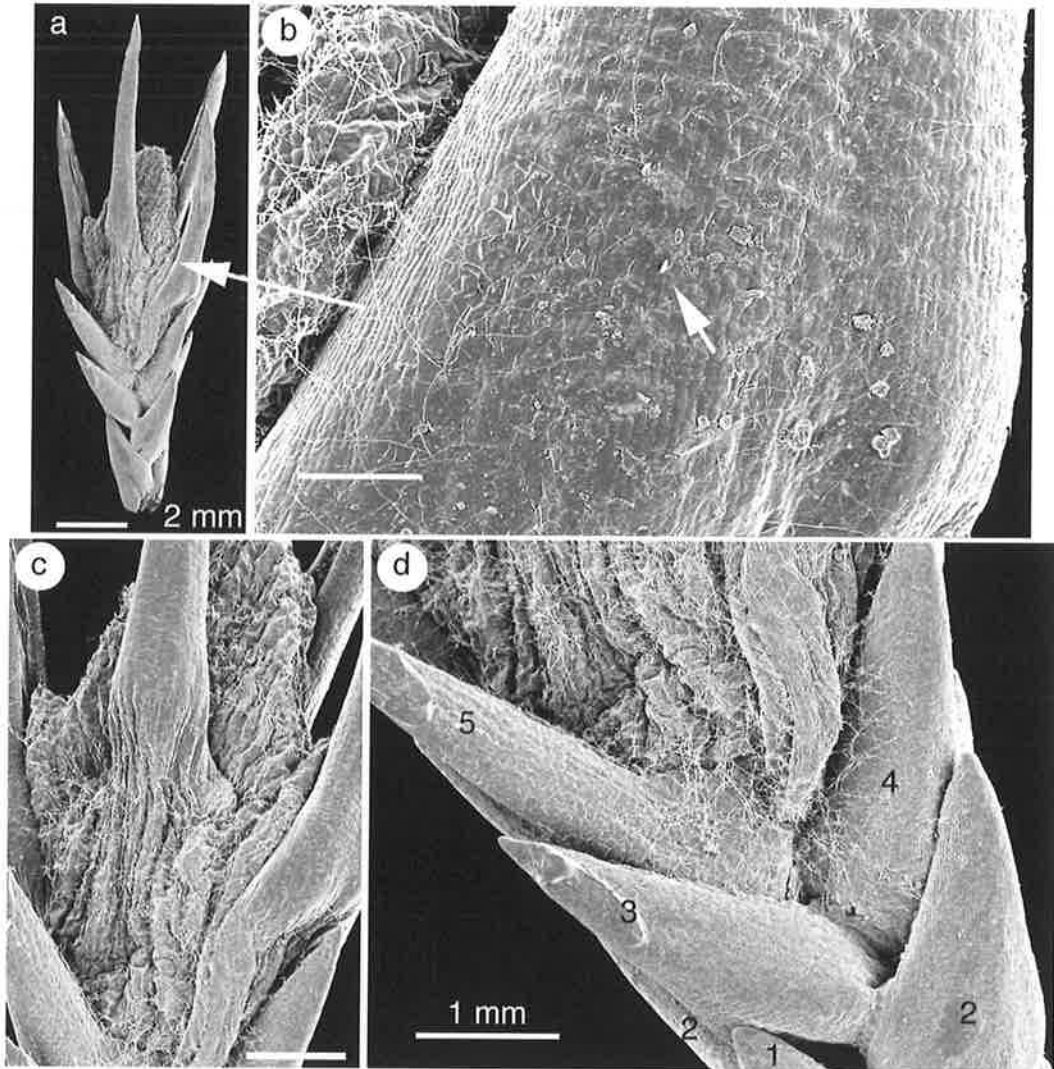
Fig. 24a-d *Libocedrus chevalieri* immature female cone SEM
Specimen 16 IRD

- **a.** Upper scale pair almost fully developed with spiny bract projection arising from the centre of the scale. Penultimate bract scale pair with small scale and elongate, spike-like bract.
- **b.** Close up of a. Left - developing scale with large irregularly shaped epidermal cells. Right - bract of penultimate bract-scale pair. Epidermal cells elongate, regularly arranged and with nodules containing calcium oxalate crystals (arrow; scale 200 μm).
- **c.** Outer scale surface highly undulate. Scale margins indistinctly papillate. Below the spiny bract extension, the ultimate bract is highly rugose, and extends across to the scale margin and down to the base of the cone (scale 1 mm).
- **d.** Five elongate non-fertile bracts subtend the cone, increasing in size from 1-5. They have frilled margins, and elongate epidermal cells containing calcium oxalate crystals.

Note: Farjon (2005) suggests that *Libocedrus chevalieri* cones differ from those of the other New Caledonian species in that the lower cone scale pair is only slightly smaller than the upper (Farjon 2005). This difference is not apparent in this immature specimen.

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Libocedrus yateensis Guillaumin, Bull. Mus. His. Nat. (Paris), sér. 2, 21: 457 (1949)

Description: Shrubs or trees 2-12 m. Monoecious and multi stemmed, with rough scaly brown-red bark. Spreading or ascending branches (Laubenfels 1972; Jaffré 1995); Farjon 2005).
Distribution: Narrow, low altitude distribution (170-180 m), along the terraces of the Bleue-Yaté and Ouinne Rivers (in the south; Laubenfels 1972), and at Polivia (150-600 m, to the north; Farjon 2005).
Habitat: Small populations or individuals in lowland tropical areas.

Systematics
Order Coniferales
Family Cupressaceae
Genus *Libocedrus* Endl., Syn. Conif.: 42 (1847)
Libocedrus yateensis Guillaumin, Bull. Mus. His. Nat. (Paris), sér. 2, 21: 457 (1949)

Foliage and leaves: Foliage frond like. Ultimate branchlets alternate to sub-opposite, in the same plane, dissimilar in length, and shorter at the frond tip. Where branchlets are alternately arranged there is some twisting of the stem (Fig. 25a). *Juvenile/transitional foliage* flattened, and much larger (Fig. 26a, b) than adult (Fig. 26c-e). Leaves decussate and highly dimorphic. Lateral leaves much larger than facial, elongate, highly flattened, ventral surface slightly convex, apically recurved, not imbricate, with very acute apices, well developed marginal frills in the lower half of the leaf, and fused for about one fifth of their length. Facial leaves small, flattened, centrally keeled, apically recurved, with well-developed marginal frills, and highly acute apices that do not overlap the facial pair above. *Adult foliage* flattened, and highly dimorphic. Fertile foliage less flattened, lateral leaves only slightly longer than facial, and lateral and facial leaves with bluntly acute apices (Fig. 26e). Lateral leaves larger than facial, slightly fused towards the base, ventral surface convex and decurrent in younger foliage (Fig. 26c), dorsal surface concave (Fig. 25d). The lower leaf margin is frilled (Fig. 27c, d, g). Facial leaves outwardly keeled and somewhat rounded in appearance, with frilled margins (Fig. 27h), and leaf apices that reach the facial pair above (Fig. 26e).
Stomatal distribution: *Juvenile/transitional foliage*, dorsal surface - on lateral leaves closely packed and mainly in well-defined sunken, often waxy, lighter-coloured central grooves extending from the leaf base to the apex. Stomata irregularly arranged and oriented. On facial leaves in a small, slightly sunken groove on each side of the central keel, and largely covered by the lateral leaves below. Ventral surface - lateral leaves with fewer stomata, and in slightly sunken, largely central depressions rather than a distinct groove. On facial leaves close to the base and barely visible. *Adult foliage*, dorsal surface - similar to juvenile leaves (Figs 26a; 27a). Ventral surface - lateral leaves, stomata far fewer. Some at the base where overlying facial leaves provide protection (Fig. 27e, f), and others in small scattered depressions (Fig. 27b). On facial leaves on either side of the keel, close to the base (Fig. 26g). Adaxial surface, lateral and facial (dorsal and ventral) leaves - in a relatively narrow band close to, and parallel with the leaf margin, extending from leaf base almost to the apex (Figs 26f: 27e, h).
Cuticle description: Inner surface - stomatal guard cells elongate and surrounded by 4-6 (mostly 5) mostly elongate subsidiary cells that fold down around the guard cells, forming discontinuous groove. The subsidiary cells contain other indentations (round to slightly elongate in shape), most frequently close to the cell margins (Fig. 28a). The

texture of the periclinal cell walls of these cells is finely coarse-grained. Stomata are closely packed and subsidiary cells are often shared by one or more adjacent guard cells (Fig 28d, f). Most epidermal cells are very coarse-grained in texture, and contain calcium oxalate crystals (Fig. 28f, h, i). The upper surface of these crystals is relatively smooth. Epidermal cells adjacent to stomata in protected areas (leaf bases) have slightly coarse-grained periclinal and anticlinal cell walls, and do not contain calcium oxalate crystals (Fig. 28a). Many epidermal cells on adaxial leaf surfaces also lack calcium oxalate crystals (Fig. 28h). Outer surface - stomatal areas waxy (Fig. 28e). Stomata with high ridged and high-moderately lobed Florin rings which may have a peripheral groove. Numerous round, and irregularly shaped, papillae surround the stomata (Fig. 28b, c). Epidermal cells have indented margins and contain many relatively large nodules (Fig. 28g).

Ovulate cones: 9-10 mm long (Laubenfels 1972; Farjon 2005). Terminal on flattened branchlets with leaves of similar shape and size (Fig. 30a). Subtending the cone are 3-5 non-fertile decussate bracts that become progressively broader and elongate towards the cone (Figs 29d; 30c). These bracts are much less flattened than the leaves beneath, and have frilled margins (Fig. 29e). Ultimate scales elongate, longer, broader than penultimate, with bluntly acute apices (Figs 29a; 30b), and slightly rugose in the upper half of abaxial and adaxial surfaces. Penultimate scales narrow, and about half to two thirds the length of ultimate scales. All scales with papillate margins (Fig. 30c, d, f) and large epidermal cells (Fig. 30f, g). Ultimate bract projections elongate, spike-like, and extending from the centre of the scale to some distance beyond it (<7 mm in length; Figs 29a: 30b). Apices of ultimate bract projections slightly recurved. On mature cones, penultimate bract projections may be outwardly curved (Fig. 30a, b). Epidermal cells in bract projections elongate, and often containing calcium oxalate crystals (Fig. 31i). Lower section of bracts (Figs 29b; 30c, e), and the base of bract projections (Figs 29b, c; 31e) highly rugose, and with large cells. For the ultimate bracts, the base of the bract projection appears to arise in a depression in the upper section of the bract (Fig. 30e), but the length and weight of the bract projection probably pull the latter downwards and outwards (Fig. 31d). On the penultimate bract scale pair the scale may be outwardly recurved, partly obscuring the bract and the bract extension (Fig. 30b, c). At the adaxial base of the ultimate scale, on either side of a central ridge, are two areas where the surface texture varies from the rest of the scale. These (Fig. 31a, c), and indentations in the scale (Fig. 31b), mark the site of dehisced seeds. At the cone apex is a narrow columella ~1 mm long (Fig. 31a).

Ovules: not illustrated, 1-4 in the sub-axillae of ultimate bracts, erect (Farjon 2005). Seeds 1-4, slightly flattened and winged. Wings unequal in size and shape, one large and membranous (Fig. 31f. g), the other rudimentary (Fig. 31h).

Pollen cones: Terminal on flattened branchlets. Microsporophylls 8-24 decussate pairs, elongate, broadly triangular in the upper half, weakly keeled, with marginal frills, highly acute and extended apices, and crystalline nodules in their epidermal cells (Fig. 32a, b). Cone subtended by 2 decussate bract pairs, the longest immediately below the cone. These bracts have frilled margins and stomata on the adaxial surface, Epidermal cells on their outer surface contain crystalline nodules (Fig. 32c).

Specimens examined

00504524, National Herbarium, Canberra, Australia. Collected 5/1948, MJ Bernier 357, Riviére Bleue, Haute Yatè. Mixed foliage from 3-5 m trees at ~200 m.

00518751, National Herbarium, Canberra, Australia. Collected 5/1948, MJ Bernier 354[2], Riviére Bleue. Tree ~7 m at ~200 m.

34105 IRD, Institut de recherché pour le développement, Nouméa, New Caledonia. Collected 1977, Massif du Ton-Non. Collected 10/1977, HS MacKee 34105, at 650 m.

E/3783, Herbarium Collection, The University of Adelaide, South Australia. Collected 5/1948, MJ Bernier 356, Riviére Bleue, Haute Yatè.

Unnumbered sample, Collected 5/1994. R Carpenter. Riviére Bleue, Province Sud, River bank, ~2.5 m at ~150 m.

Cultivated seedling >30 cm, Royal Tasmanian Botanical Garden, Hobart, Tasmania, Australia. Collected 11/2004, R Paull.
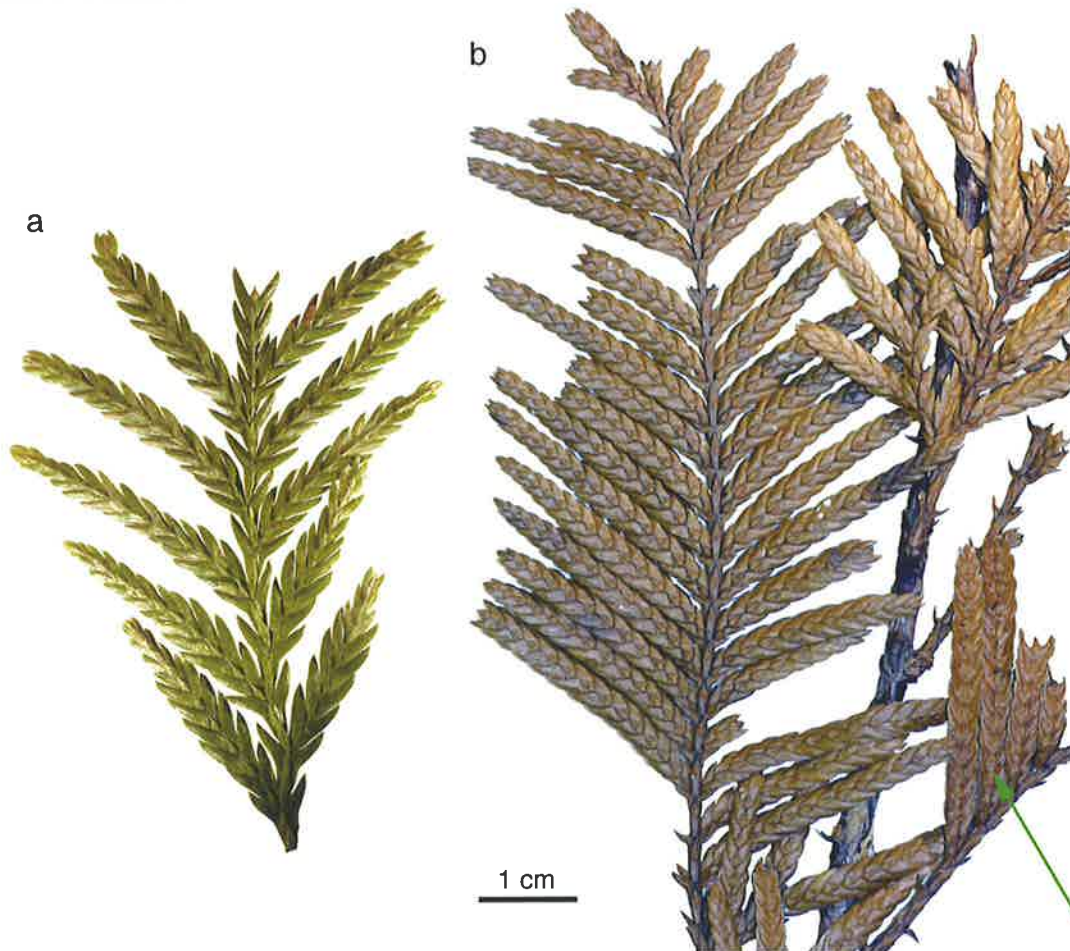
Fig. 25a-b *Libocedrus yateensis* branchlets showing leaf arrangement
a. Seedling (>30 cm) with juvenile foliage, ventral surface, Part of a frond-like foliage frond with alternate branchlets. Leaves flattened, highly dimorphic, and lanceolate with lateral leaves much larger than facial leaves. Facial leaves barely visible, centrally keeled and with apex reaching only the lower third of the lateral leaf pair above. Slight twisting of the stem when branchlets are alternate. Lateral leaf surfaces convex (cultivated specimen RTBG, Tasmania).
b. Adult foliage. Branchlets sub-opposite and different in length. Leaves on ultimate branchlets imbricate, highly dimorphic, convex on ventral surface, concave on dorsal surface (green arrow; specimen 00504524 Australian National Herbarium, Rivière Bleue ~200 m).

Fig. 26a-g *Libocedrus yateensis* juvenile and adult foliage
Note the size variation between specimens

a. LM juvenile foliage dorsal leaf surface. Lateral leaves not imbricate, elongate, highly flattened, apically recurved and with very acute apices. Lateral leaves much larger than facial leaves. Facial leaves flattened, and not overlapping the facial pair above. Stomata on dorsal and ventral surfaces of lateral leaves, but in more clearly defined grooves on the dorsal surface (specimen from RTBG, Hobart, Tasmania).

b. LM same specimen as **a**, ventral leaf surface. Stomata on lateral leaves rare, and on facials largely covered by lateral leaves below.

c. SEM smaller leaved adult foliage. Both leaf pairs flattened, imbricate and with acute apices. Lateral leaves larger than facial. Stomata on both leaf pairs in highly defined sunken grooves (specimen 504524).

d. SEM same specimen as **c**, ventral leaf surface. Lateral leaves with only few stomata. Stomata on facial leaves are towards the base and mostly obscured by the lateral leaf pair above.

e. SEM dorsal leaf surface fertile foliage. Stomata in well-defined grooves. Leaves smaller, less flattened than non-fertile foliage specimens and with less acute apices (specimen 34105).

f. SEM adaxial surface, facial leaf. Stomata in rows parallel to the leaf margin (arrow) but leaf tip without stomata. Leaf margin highly frilled in the lower half but less so towards the apex (scale 500 μm; specimen 518751).

g. SEM outer ventral surface, facial leaf. Arrow indicates position of stomata (scale 500 μm; specimen 518751).

Fig. 26a-g *Libocedrus yateensis* juvenile and adult foliage

Fig. 27a-h *Libocedrus yateensis* adult foliage SEM

a. Dorsal leaf surface. Stomata on lateral leaves densely packed and in well-defined grooves. Arrow indicating facial leaf stomata (specimen 504524).

b. Ventral surface. Stomata mostly at the base (arrow) where they are protected by the overlying facial leaf. Stomata infrequent on the exposed leaf surface, and in small pockets (upper arrow; specimen 519751).

c. Fertile shoot, dorsal surface. Lateral and facial leaves more similar in size and less flattened than other foliage. Lateral and facial leaves with well-defined facial frills (scale 500 μm; specimen 34105).

d. Close up of densely packed irregularly arranged and oriented stomata on **c.** Epidermal cells with small nodules (scale 100 μm).

e. Lateral leaf. Arrow (left) indicating stomata on ventral surface. Arrow (right) indicating narrow rows of stomata on the adaxial leaf surface, parallel to the basally frilled leaf margin (scale 500 μm; specimen 518751).

f. Close up of ventral surface stomata on **e** (scale 200 μm).

g. Dorsal leaf surface, lower facial leaf removed. Close up of lower margin frill and densely packed stomata. The latter are mostly in sunken (often waxy) grooves but occasionally randomly distributed (arrow; scale 200 μm; specimen 518751).

h. Close up of internal facial leaf surface showing stomata surrounded by papillae parallel to the frilled margin (scale 100 μm; specimen 518751).
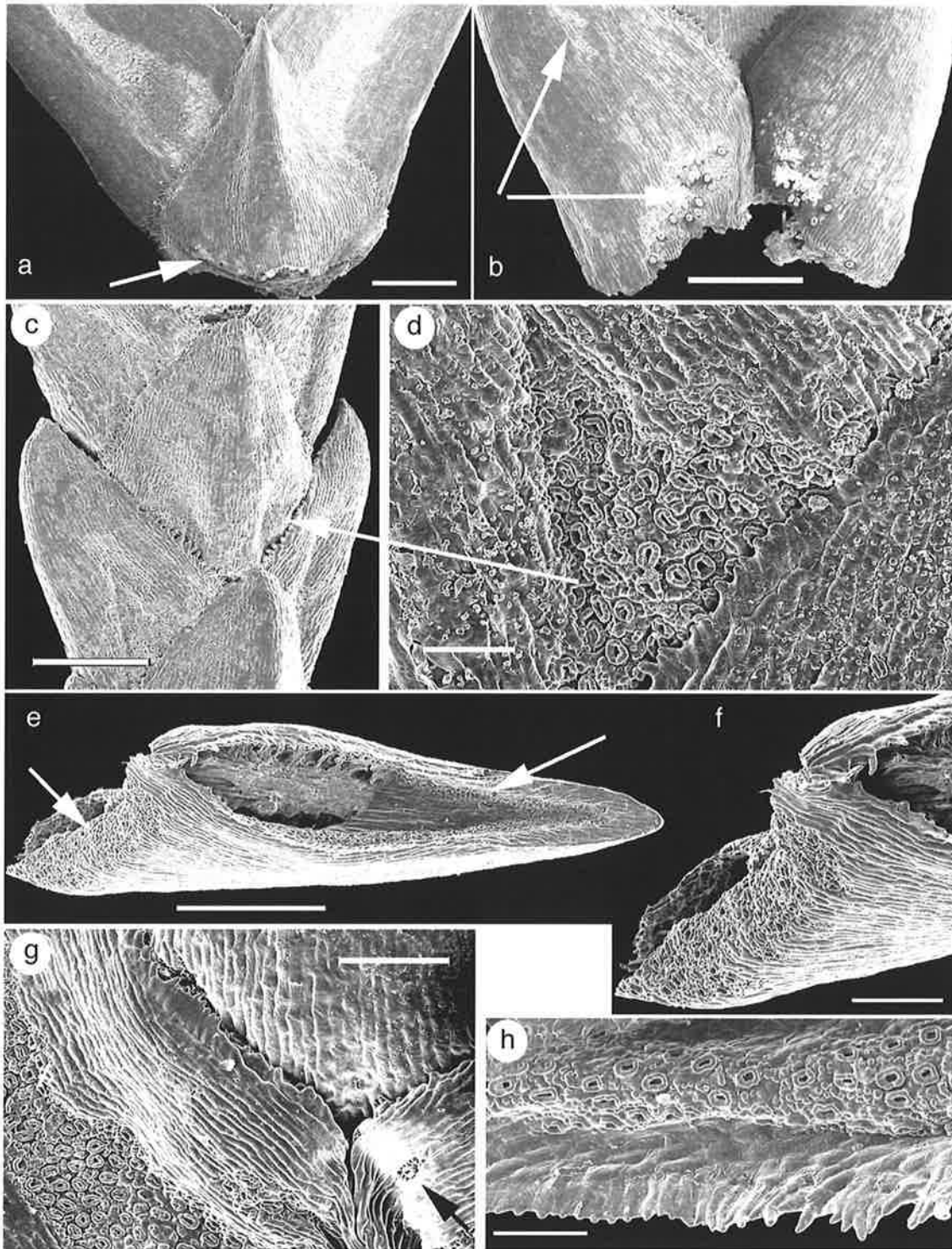
Fig. 27a-h *Libocedrus yateensis* adult foliage SEM

Fig. 28a-i *Libocedrus yateensis* SEM/LM leaf cuticle

 a. SEM internal stomata, from lateral leaf base. Guard cells elongate. Subsidiary cells 5, slightly coarse-grained and indented. A discontinuous groove around the guard cells corresponds with lobed Florin rings on the outer surface. Note: these are stomata from a protected surface. They lack the calcium oxalate nodules seen on exposed leaf surfaces - see **h** for comparison (scale 50 μm; specimen 518751).

 b. SEM outer dorsal (natural) waxy surface. High ridged and highly lobed Florin rings with peripheral groove, surrounded by round to elongate papillae (scale 50 μm; specimen 518751).

 c. SEM outer dorsal (cleaned) surface. Florin rings not so highly lobed as those in **b** (scale 50 μm; specimen 504524).

 d. SEM lateral leaf, inner dorsal surface. Stomata in rows and often sharing subsidiary cells (scale 50 μm; specimen 504524).

 e. SEM outer dorsal (natural) surface, intact leaf. Closely packed, lobed and very waxy stomata surrounded by numerous papillae. These stomata look very different from those in **c**, which have been cleared of wax during cuticle preparation. Epidermal cells (foreground) have moderately large nodules (scale 100 μm; specimen 504524).

 f. LM outer dorsal leaf surface (lateral leaf). Note the densely and often discontinuous stomatal rows, and the papillae surrounding the stomata. The elongate epidermal cells contain calcium oxalate crystals (scale 100 μm; specimen 504524)

 g. SEM lateral leaf, outer dorsal surface, showing epidermal cells with indented margins and containing large nodules (scale 100 μm; specimen 504524).

 h. LM facial leaf. The darker upper section is the ventral surface of a facial leaf. Most epidermal cells contain calcium oxalate crystals. The right arrow indicates stomata at the base of the leaf. The epidermal cells in this protected part of the leaf do not contain calcium oxalate crystals. The left arrow indicates the adaxial leaf surface. Epidermal cells here also lack calcium oxalate crystals (scale 200 μm; specimen 504524).

 i. SEM coarse-grained epidermal cells with large calcium oxalate crystals. Anticlinal cell walls coarse-grained, erect, and only slightly wider at the base (scale 10 μm; specimen 504524).
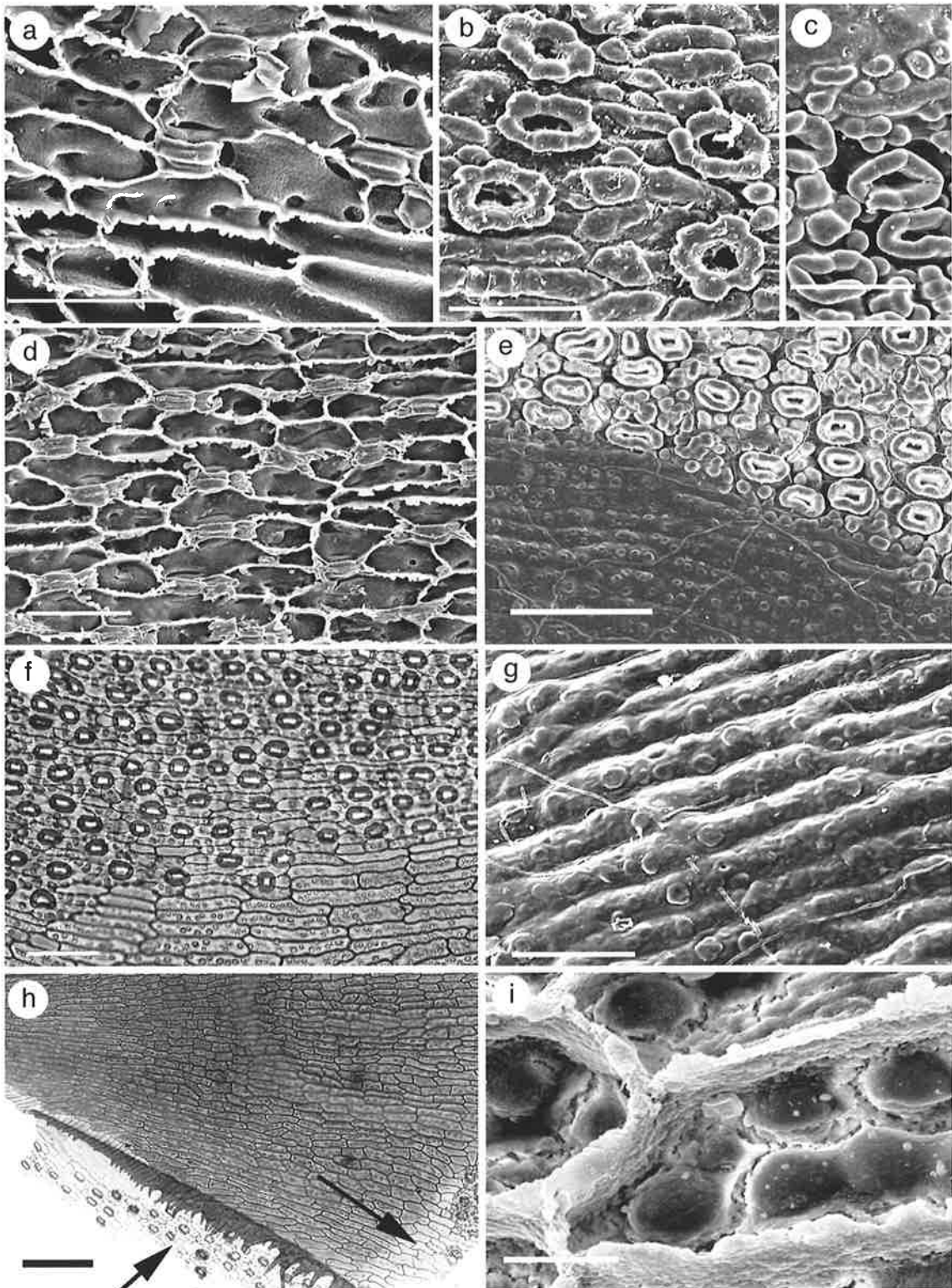
Fig. 28a-i *Libocedrus yateensis* SEM/LM leaf cuticle
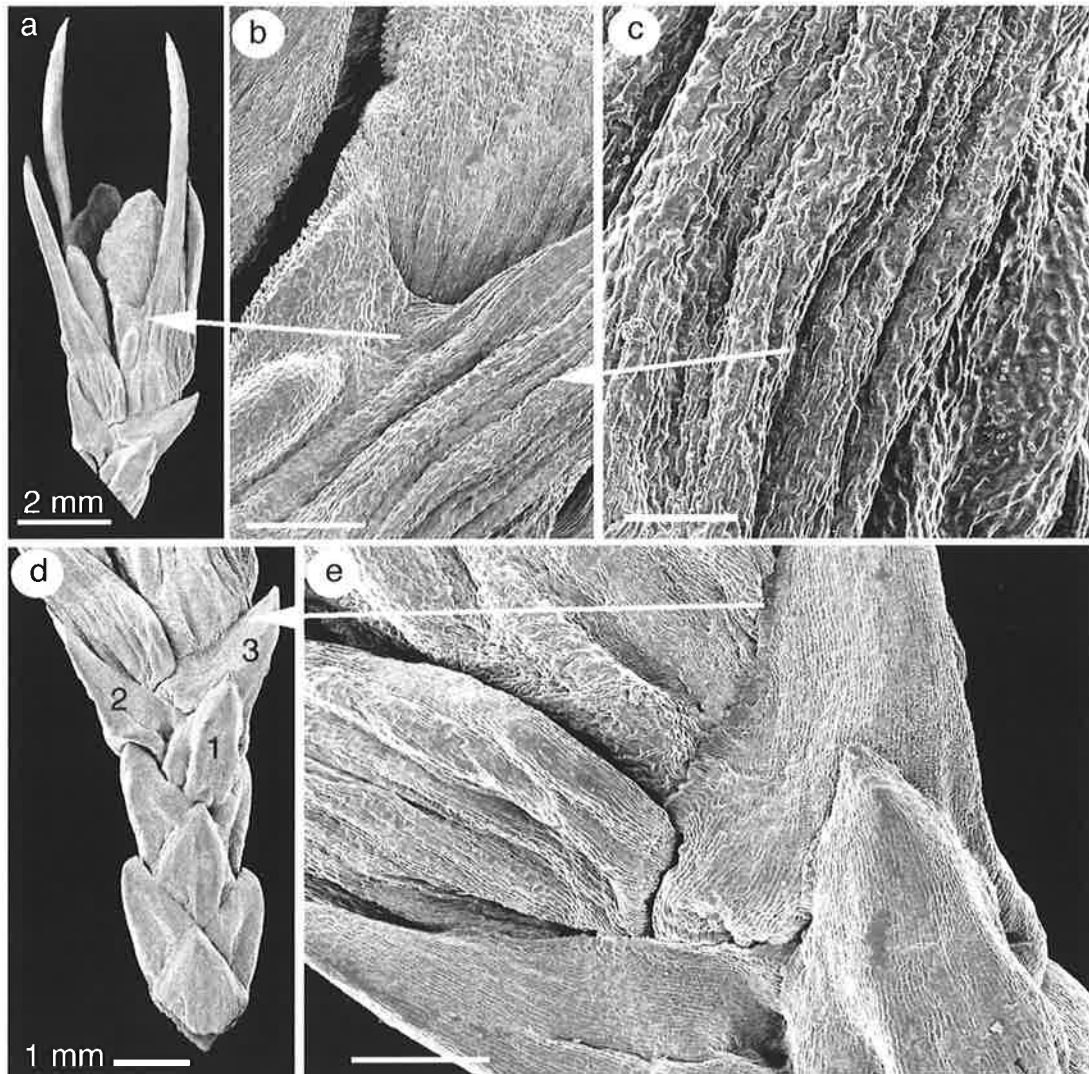
Fig. 29a-e *Libocedrus yateensis* ovulate cone SEM

    a. Sub-mature cone. Upper scale pair almost fully developed, lower scale pair less well developed. Bract projections long, spike-like, and extending upwards well beyond the scale apices (specimen 34106 IRD).

    b. Close up of **a**. Bract extending to edge of scale at the centre of the bract-scale complex. Lower section of bract highly rugose (scale 1 mm).

    c. Close up of **b**. Basal third of the upper bract showing highly undulate (rugose) surface, and large cells (scale 200 μm).

    d. Cone subtended by three non-fertile bracts. These become progressively larger and elongate towards the cone, and are less flattened than the foliage beneath.

    e. Non-fertile bracts with frilled margin (scale 500 μm).

Fig. 30a-g *Libocedrus yateensis* ovulate cone SEM

Specimens collected from a small tree ~2.5 m New Caledonia in 1994

a. Mature ovulate cone, terminal on branchlet, solitary.

b. Mature cone. The elongate spike-like bract projection (ultimate bract-scale pair) projects from the centre of the scale to beyond the scale apex and recurves slightly inwards. Penultimate bract projections elongate, recurved outwards.

c. Close up of **b**. The non-fertile bract pairs (1-5) subtending two bract-scale pairs are elongate with those immediately beneath the ultimate pair the longest (1).

d. Close up of **c**. Upper scale margin papillae (scale 50 μm).

e. Base of ultimate bract projection incurved, rugose. Below the bract projection the bract extends upwards to the margin of the scale (scale 500 μm).

f. Winged seed (arrow). Margins of the upper scale are outwardly curved and papillate (scale 500 μm).

g. Inner scale surface rugose, and with large epidermal cells (scale 200 μm).
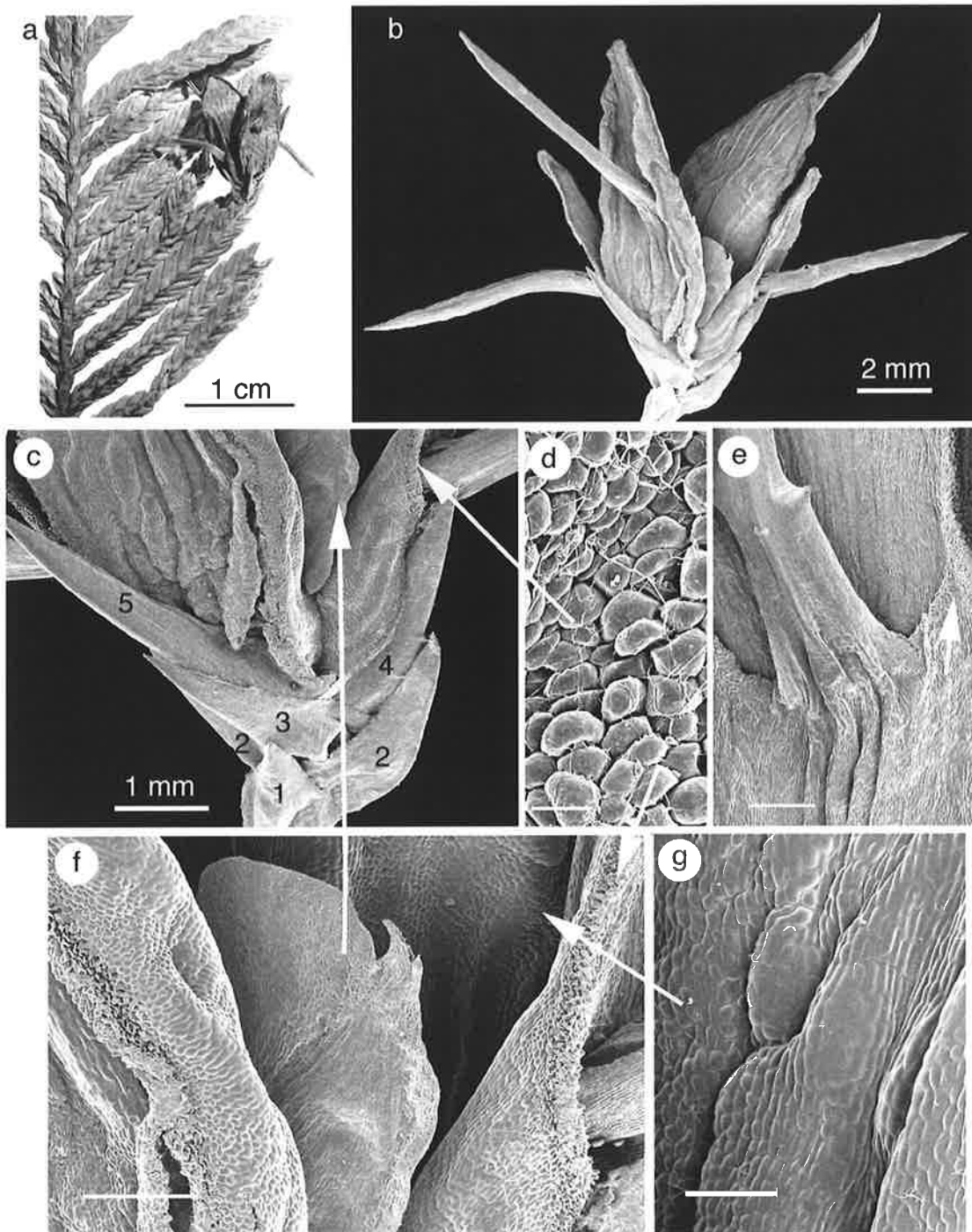
Fig. 30a-g *Libocedrus yateensis* ovulate cone SEM
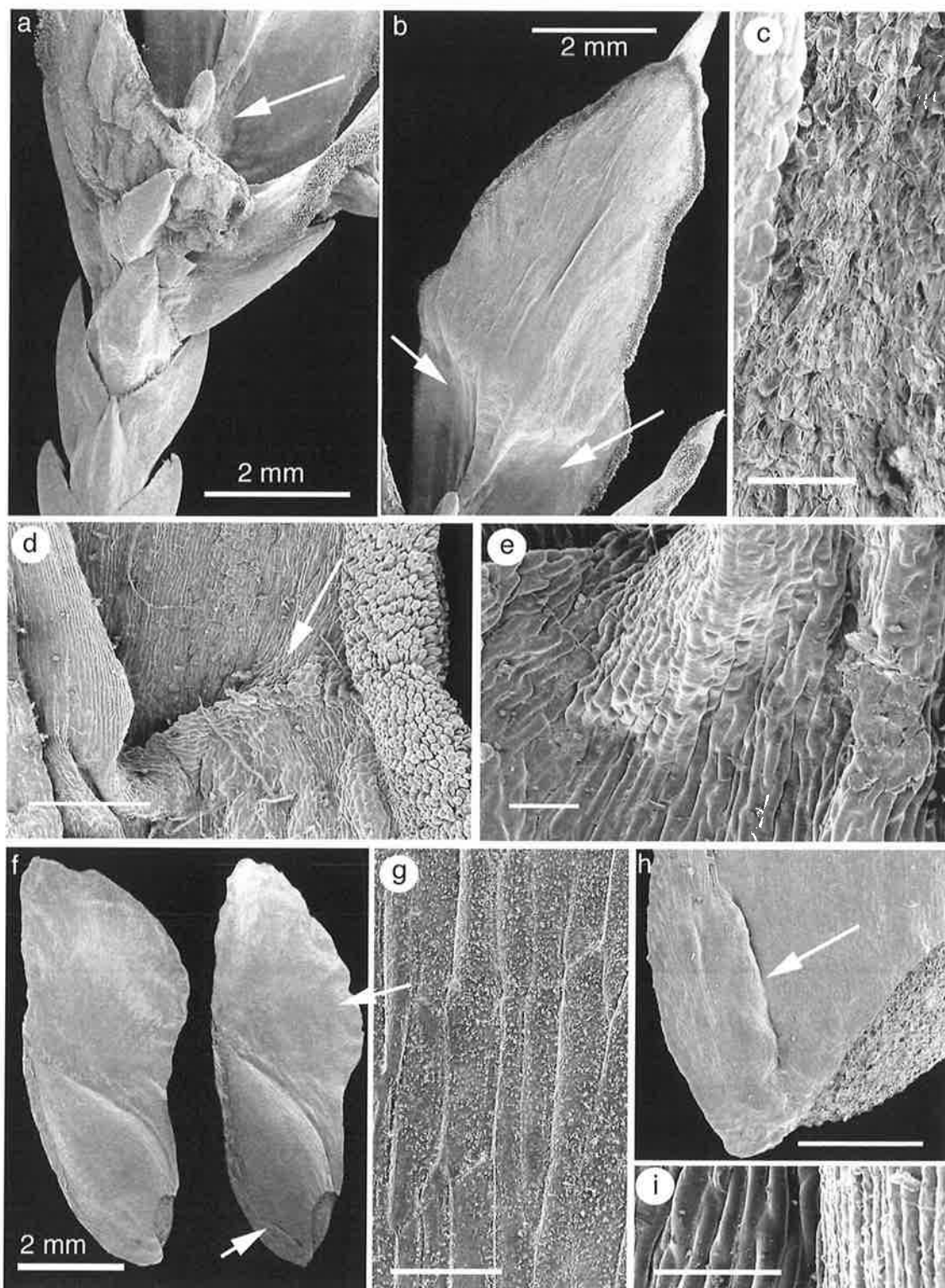
Fig. 31a-i *Libocedrus yateensis* ovulate cone and seeds SEM/LM

Fig. 31a-i *Libocedrus yateensis* ovulate cone and seeds SEM/LM

Cone collected in New Caledonia in 1994

    a. Mature cone, one ultimate scale removed to show small columella at the centre of the cone. Arrow indicating site of dehisced seed.

    b. Adaxial surface, ultimate scale. Surface slightly rugose, margin papillate. Arrows indicating 2 depressions left by dehisced seeds.

    c. Detail of seed dehiscent site, columella to the left (scale 100 μm).

    d. Detail of abaxial ultimate scale surface, spiny bract to the left, arrow indicating the lower part of the bract extending to the scale margin (scale 500 μm).

    e. Base of ultimate spiny bract. Epidermal cells large (scale 100 μm).

    f. Two of four seeds from the cone in **a** showing both surfaces. The surface of the left seed is slightly flattened, that of the right is bulging. The seeds have two wings - one large and membranous, the other barely developed (arrow).

    g. Detail of membranous wing (scale 50 μm).

    h. Detail of undeveloped wing on seed (scale 500 μm).

    i. Difference in size of cells of bract scale complex. Scale surface (left) with large elongate cells. Bract surface (right) with small elongate cells (scale 100 μm).
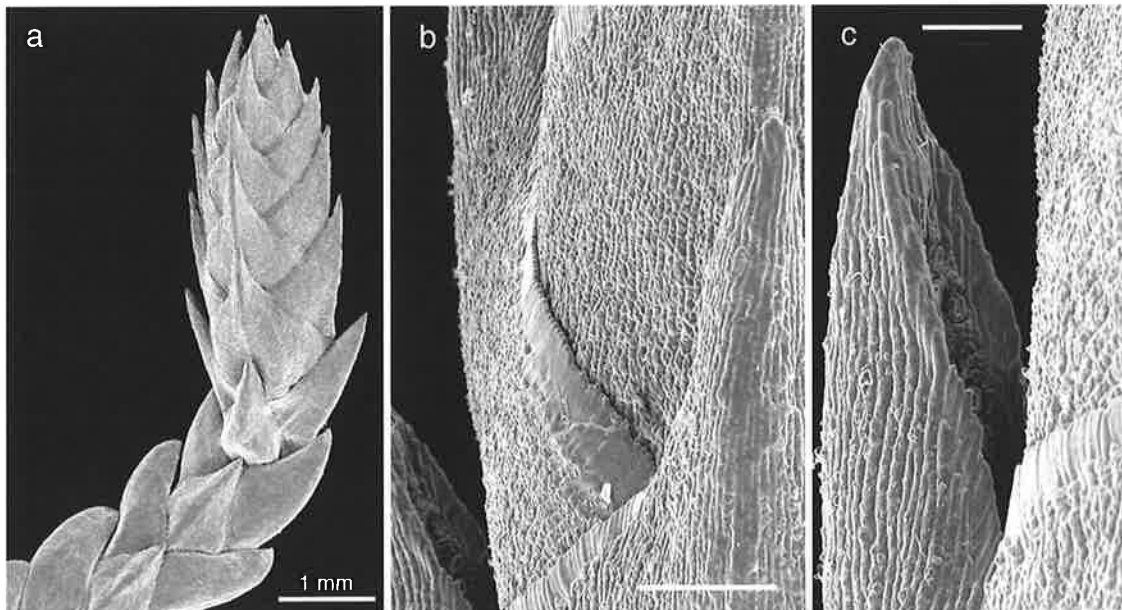
Fig. 32a-c *Libocedrus yateensis* pollen cone SEM

Specimen collected in New Caledonia

    a. Pollen cone terminal, subtended by 2 pairs of elongate, decussate bracts, the longest closest to the cone. Microsporophylls decussate, weakly keeled, and with very acute apices.

    b. Frilled margin on microsporophylls, epidermal cells with crystalline nodules (scale 200 μm).

    c. Bracts subtending the cone with frilled margins. Abaxial bract surface with crystalline nodules, adaxial bract surface with stomata (scale 100 μm).

Distinguishing features - New Zealand and New Caledonian *Libocedrus* species

New Zealand species
Foliage

Both species grow to large trees and have very similar scale-like, decussate, dimorphic leaves. There are three growth forms, juvenile, transitional and mature. Ultimate mature branchlets are sub-opposite to alternate. The leaves of *L. plumosa* are somewhat larger than *L. bidwillii*, but this could be due to the lower altitudes at which it grows. (Unfortunately no altitude details were recorded for any of the *L. plumosa* specimens examined in this study). The juvenile foliage of both species is larger than the mature, and the lateral juvenile leaves are longer. Differences between the two species are minor. These are as follows: -

Libocedrus bidwillii
- Mature branchlets may arise on all sides of the stem
- Mature leaves almost monomorphic, quadrangular in arrangement, convex on both dorsal and ventral surfaces
- Facial leaves not overlapping (juvenile foliage), overlapping or reaching facial pair above (mature foliage)
- Lateral leaf margins entire, facial leaf margins slightly frilled

Libocedrus plumosa
- Mature branchlets in one plane, foliage flattened
- Leaves on fertile branchlets almost monomorphic, less flattened, and convex on dorsal and ventral surfaces
- Facial leaves generally not overlapping (juvenile and mature foliage), but may reach the facial pair above (mature foliage)
- On juvenile foliage dorsal leaf surfaces may be slightly concave
- Lateral leaf margins mostly entire, facial leaf margins frilled
- Adult lateral leaves with papillate bases

Stomata

The stomatal distribution is similar for both species. On the ventral surface these are largely protected by overlying leaves. Stomata on the dorsal surface are closely packed and in well defined central grooves.
- Florin rings high ridged, lobed, sometimes with a peripheral groove, and associated with numerous small, and mostly round, papillae

Cuticle

The internal and external cuticular cuticles of both species are indistinguishable, but distinctive (i.e. similar to, but slightly different from the New Caledonian species; see Fig. 34a-b).
- The outer anticlinal walls of the subsidiary cells fold outwards, away from the guard cells
- The periclinal cell walls of the subsidiary cells bulge slightly upwards

Ovulate cones

The most obvious difference between the two species is the size of the cones, those of *L. plumosa* are almost twice that of *L. bidwillii*. As this size difference is still apparent when both species are growing under almost identical conditions (see Fig. 33a-b), it cannot, like the foliage, be attributed to an adaptation to growth at lower altitudes.

- Cones terminal on short branchlets with monomorphic leaves
- Penultimate bracts (including bract projection) larger than scale
- Ultimate bract projections broad based, and reaching, but rarely extending beyond, the scale

Pollen cones

Only one *L. bidwillii* cone was available for examination, so comparisons between the species were not made.

- Microsporophylls with a distinct central bulge towards the base

The photographs below (Fig. 33a-b) are of two young, similar aged, cultivated *Libocedrus* trees growing in similar conditions (climate, habitat, altitude), and clearly demonstrate some differences between the two New Zealand species.

Fig. 33a-b Comparisons, New Zealand *Libocedrus* ovulate cones, foliage
Cultivated specimens ~2-2.5 m, and less than 20 years old (Tasmanian Arboretum, Devonport; scale 1 cm, **a, b**)

    a. *Libocedrus bidwillii* fertile foliage with monomorphic leaves and almost quadrangular (tetragonous) leaf arrangement. Small ovulate cone terminal on short branchlet.

    b. *Libocedrus plumosa* fertile foliage with almost monomorphic leaves. Branchlets flattened. Large ovulate cone terminal on short branchlet with almost monomorphic leaves. Leaves on large shoots monomorphic, but on other branchlets lateral leaves larger than facial leaves

New Caledonian species
Foliage

The two high altitude species (*L. austrocaledonica* and *L. chevalieri*) grow to small trees, the other (*L. yateensis*), which is largely riparian in habit, to ~12 m. The adult (mature) foliage of *L. austrocaledonica* and *L. yateensis* is quite similar, but the leaves of *L. austrocaledonica* are more robust (thicker) than those of *L. yateensis*. Farjon (2005) suggested that environmental differences may account for this dissimilarity. The juvenile foliage of the two species is less similar. *Libocedrus chevalieri*, which is only known from three localities (Farjon 2005), differs from the other 2 species in that its dorsal and ventral leaf surfaces are both convex. In this respect it is quite similar to *L. bidwillii* (more so than *L. plumosa*) but the leaves are much larger, and the facial and lateral leaves of *L. chevalieri* are dimorphic (the facial leaves smaller than the lateral; see for comparison Figs 1a; 21a; Florin and Boutelje (1954) suggest the mature foliage of *L. chevalieri* is monomorphic), and there are more exposed stomata on the ventral surface, possibly because it grows at much lower latitudes. Laubenfels (1972) suggested it might be a relict species.

- All species have highly frilled facial leaves. The free sections of lateral leaves are frilled towards the base

Differences between the three species are as follows: -

Libocedrus austrocaledonica
- Ultimate mature branchlets opposite and similar in length
- Facial leaves small, and on young foliage barely covering half the lateral pair above. On older foliage reaching to the facial pair above
- Ventral and dorsal leaf surfaces markedly dissimilar in shape. Dorsal surface concave

Libocedrus chevalieri
- Ultimate mature branchlets alternate to sub-opposite, similar in length
- Leaves on ultimate branchlets almost monomorphic
- Dorsal and ventral leaf surfaces convex, similar in shape
- Lateral leaf bases slightly papillate

Libocedrus yateensis
- Ultimate branches alternate to sub-opposite, unequal in length
- Ventral and dorsal leaf surfaces dissimilar in shape. Dorsal surface concave, ventral surface convex

Stomata
Libocedrus austrocaledonica
- Stomata mostly in large sunken grooves on the dorsal surface (lateral and facial leaves). Groove margins very well defined

Libocedrus chevalieri
- Stomata in small, deeply sunken, grooves on dorsal and ventral leaf surfaces (smaller grooves on ventral surfaces)

Libocedrus yateensis

- Stomata mostly in large to medium sunken grooves on the dorsal surface (lateral and facial leaves). Groove margins moderately well defined
- Subsidiary cells often shared by more than one adjacent guard cell

Cuticle

The internal cuticles of *L. austrocaledonica* and *L. yateensis* are almost indistinguishable. That of *L. chevalieri* is similar to the other two New Caledonia species, but the outer anticlinal walls of the subsidiary cells are also somewhat similar to *L. bidwillii*, and *L. plumosa*. External cuticles almost identical. Papillae associated with Florin rings round to irregular in shape. Large to medium sized calcium oxalate crystals are common to all species.

Periclinal subsidiary cell walls generally flattened
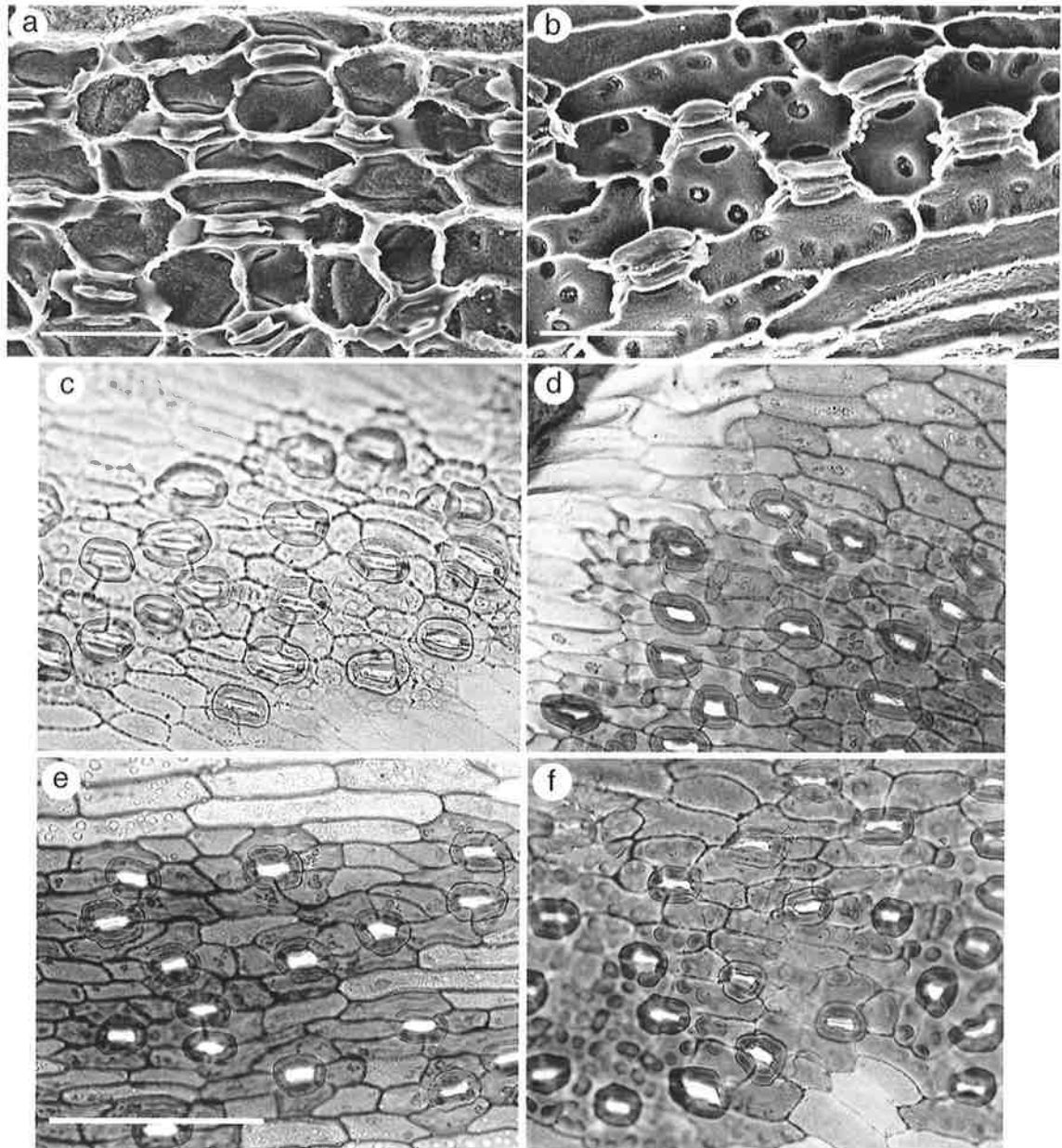
Fig. 34a-f Comparisons of New Zealand and New Caledonian cuticles
a. *L. bidwillii* E/1954 SEM, b. *L. austrocaledonica* 504524 SEM ; c. *L. bidwillii* 3353; d. *L. yateensis* 34105; e. *L. plumosa* 13317; f. *L. chevalieri* 16 (scale bar for a, b 50 μm, LM; for c-f 100 μm)

The photographs on the left are of New Zealand species, those on the right New Caledonian species. The LM photographs (c-f) are almost indistinguishable, and on this basis it would be impossible to tell the species apart. The SEM photographs (a, b) have been chosen to highlight some subtle differences. The subsidiary cells of the New Caledonian species are flatter than the New Zealand species, the anticlinal cell walls more upright, and the indentations generally more rounded in shape.

Ovulate cones

The cones of the New Caledonian species were mostly immature, or broken, so the difference in size of penultimate bracts and scales (of the three species) that Farjon (2005) and Laubenfels (1972) recorded could not be confirmed with confidence.

- Bract projections with a narrow base, elongate, spike-like, and extending well beyond the scale
- Penultimate bracts largely insignificant
- Bracts subtending the cone elongate

Fig. 35a-f Comparisons - New Zealand and New Caledonian *Libocedrus* ovulate cones
New Zealand species - a. *L. plumosa*, **b**. *L. bidwillii*, (both mature cones)
New Caledonia species - c. *L. austrocaledonica* (immature, flattened cone), **d**. *L. yateensis* (sub-mature cone), **e**. *L. yateensis* (mature cone), **f**. *L chevalieri* (immature cone)

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Pollen cones

Only one cone, *L. yateensis,* was available for examination, so comparisons between the New Caledonian species could not be made.
- Pollen cone cylindrical. Microsporophylls without an apparent central bulge

Based on photographs of only 2 cones, comparisons between the New Zealand and New Caledonian species are tenuous (to say the least), but the photographs below suggest some compelling differences.
- The *L. bidwillii* cone (Fig. 36a) is ovoid, with broad, keeled microsporophylls. The microsporophylls have acute apices and a distinct, centrally oriented, bulge towards the base. Bracts subtending the cone are broadly triangular.
- The *L. yateensis* cone (Fig. 36b) is cylindrically elongate, with weakly keeled microsporophylls. The microsporophylls have acute and extended apices, and appear to lack a central bulge. Bracts subtending the cone are lanceolate.
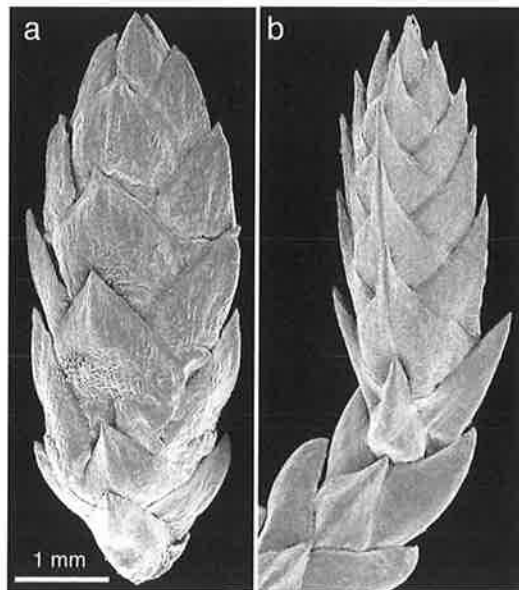
Fig. 36a-b Comparisons - New Zealand and New Caledonian *Libocedrus* pollen cones
  a. *L. bidwillii;* **b.** *L. yateensis*

Discussion

The New Zealand and New Caledonian *Libocedrus* species are dissimilar. *Libocedrus chevalieri* shares some characteristics with the two New Zealand species. Its almost monomorphic and unflattened adult foliage is somewhat similar to that of *L. bidwilli,* and, like *L. plumosa*, it has papillate lateral leaf bases. However, the cones of the New Caledonian species are quite different. Doweld (2001; in Farjon 2005), considered the New Caledonian species to be distinctive, and proposed a new genus *Stegocedrus*. Without having read his arguments for this separation his proposition is not supported here. The morphological data presented in this (current) study indicate there are dissimilarities in foliage and cones, but these are not considered significant enough to warrant a new genus.

Ecology
Reproductive strategies

Although the reproductive structures of the New Caledonian *Libocedrus* species have been described elsewhere (Laubenfels 1972; Farjon 2005), no information regarding their seedling recruitment and regeneration was found in the literature. The discussion that follows is centred on *L. bidwillii* regeneration, as this has been the subject of much debate.

As for all conifers, *L. bidwillii* seedlings need high light conditions to establish (Norton 1983), and thus they are found on the exposed margins of subalpine forests, spur crests, steep slopes, open scrub and bogs (Wardle 1978; Norton 1983). However, the most successful seedling recruitment occurs in established subalpine forests following large scale (several hectares or more), localized, disturbances that breach the forest and create high light sites (Clayton-Greene 1977; Veblen and Stewart 1982; Norton 1983). Large, infrequent, violent, ground levelling disturbances (earthquakes, volcanic eruptions, landslips, cyclonic and gale force winds, and fire) have had an impact on the structure of New Zealand forests. Many contain different sized mosaics of intermingled species of similar age (Wells *et al.* 2001). In large, old growth, evergreen forests, the angiosperm canopy is broken by long-lived (more than 600 years), broad based, and relatively widely spaced emergent gymnosperms (Ogden and Stewart 1995). The life span of the angiosperms is less than half that of the conifers and, if the forest remains undisturbed, these will all senesce, die and fall at about the same time. The opened, now largely gymnospermous, forest soon contains abundant angiosperm seedlings but few gymnosperms (Odgen *et al.* 2005). A variety of reasons have been proposed for this phenomenon, and the foci of most of these studies have been stands of old, and aging *Libocedrus bidwillii* (Wardle 1978; Veblen and Stewart 1982; Horrocks and Ogden 1994; Ogden and Stewart 1995; Rogers 1997).

Similar aged stands of large old *L. bidwillii* trees (to 700 or more years) contain many dead, yet upright trees that may have died as long as 200 years ago (Horrock and Ogden 1994) but few seedlings (Wardle 1978; Veblen and Stewart 1982; Horrocks and Ogden 1994; Ogden and Stewart 1995; Rogers 1997). Some stands contain no seedlings (Boase 1988 in Ogden and Stewart 1995), others have seedlings that have established after tree fall, but these are generally found on fallen decaying trees, and boulders (Veblen and Stewart 1982; Norton 1983; Stewart and Rose 1989), probably because at these higher surfaces, competition for light and root establishment with more vigorous angiosperm species is reduced (Clayton-Greene 1977; Stewart and Rose 1989). Seedlings in shady conditions have slow growth rates (Ogden and Stewart 1995) and have little chance of reaching maturity.

Palynological data (Horrocks and Ogden 1998, 2000) and trunk diameters (Ogden *et al.* 2005) collected across an altitudinal gradient at Mt Hauhungatahi (central North Island, New Zealand) give insight into the dynamics of New Zealand *Libocedrus* forests. Around 1800 years ago a violent tephra eruption at Lake Taupo, some 70 km south west of Hauhungatahi, flattened forests and spread pumice and volcanic ash across a large area. Subsequent fires added to the destruction (Wilmshurst and McGlone 1996). At Mt Hauhungatahi, post eruption, there was an expansion of *Libocedrus*, followed by a later decline. Punctuated regeneration followed further volcanic eruptions, fires and windthrows. Ogden *et al.'s* (2005) data indicate that (New Zealand) *Libocedrus* expands after violent disasters, and if undisturbed will live for ~700 years. In montane areas, forest gaps, created by the death of shorter-lived angiosperms, are generally too shady for *Libocedrus* seedlings and thus, over time, become dominated by angiosperms. Cold, wet and somewhat less stable subalpine areas have fewer angiosperms and thus more open canopies. Here *Libocedrus* seedling recruitment is much more successful. The relative absence of evergreen angiosperm seedlings at higher colder altitudes may be due to cavitation of their xylem vessels under free-thaw conditions (Brodribb *et al.* 2005). *Libocedrus bidwillii* leaves are resistant to freezing at temperatures −10 to −13°C (Sakai and Wardle 1978).

Few herbarium collections include ovulate cones (mature or immature; see Farjon 2005), or pollen cones, so it seemed unusual to find ovulate cones on very immature cultivated specimens (*L. austrocaledonica* ~20 cm [2 cones]; *L. bidwillii* ~2 m [numerous cones of varying size and maturity]; *L. plumosa* ~2.5 m [1 cone]). However, Clayton-Greene's (1977) study of population dynamics for *L. bidwillii* indicates that seedlings and saplings 1-1.5 m and less are reproductively mature, and suggests that this may be a strategy whereby long-lived trees colonise new habitats. In their natural environment, the age of 'seedlings' ~1 m may be 35-103 years (Norton 1983). This current study indicates that some cultivated *Libocedrus* individuals are sexually mature at ~6 years (*L. austrocaledonica*), and before 20 years (*L. bidwillii*, *L. plumosa*). Does this explain the absence of fertile material in herbarium collections? Perhaps old, tall, mature trees conserve resources by producing very few ovulate and pollen cones that are largely high in the canopy, and out of reach of collectors. If mature trees produce few fertile cones, initial regeneration rates at a levelled (disaster produced) site could be small. However, if these seedlings are reproductively mature at a very young age, a new cohort of seedlings could be generated in a relatively short time, and thus rapidly colonise the site before shading from angiosperm seedlings becomes a problem. Because the age difference between the trees is relatively small, the resultant stand would appear to be of same (similar) aged trees, and this could be interpreted as the result of a single reproductive event. (This hypothesis requires field testing to confirm or disprove). Unfortunately, the height of most herbarium New Zealand specimens (this study) was not noted on the descriptions. The *L. plumosa* cones collected by Tomlinson *et al.* (1993) for their study on *Libocedrus* cone development came from cultivated trees growing on the campus of Auckland University, but no mention is made of the size or height of these trees, nor the frequency of their cones.

Other than Clayton-Green (1977), few (Rogers 1997; Horrocks and Ogden 1998) have commented on sexual 'precociousness' in *Libocedrus*. A recent New Zealand Department of Conservation monograph notes a lack of data concerning seed production and seed viability for <u>mature</u> *L. bidwillii* trees, and recommends that if seedling recruitment is to be understood this deficit must be addressed (Peltzer *et al.* 2005). So, if *Libocedrus* species do rely on early sexual maturity to re-establish themselves over relatively large areas, this could have implications for managing

Libocedrus and associated forests. In New Zealand forests the grazing of trees by introduced herbivores is a problem. Deer appear to pose no threat to *Libocedrus* (Veblen and Stewart 1982), but possums (introduced from Australia in the late 1830's) do (Rogers and Leathwick 1997). They eat young, early summer shoots including pollen (Rogers 1997) and ovulate cones. On mature trees, the removal of growing tips results in death of the remaining foliage, as *Libocedrus* has very little ability to re-shoot from woody stems. Dieback rates following removal of young foliage are thought to be 3-4 years (Rogers 1997). Although no pollen cones were found on any of the young trees in this study, pollen cones have been observed on 15 year old cultivated trees (Rogers 1997). The ovulate cones of the two New Zealand species were gaping and had seed abscission sites, so they had to have been fertilised by pollen from the same tree.

The reproductive strategies of the New Caledonian *Libocedrus* appear to differ from those of the New Zealand species, although they too appear to be sexually mature at a very young age e.g. *L. austrocaledonica* at ~6 years in cultivation (Figs 18, 19). The means by which this small juvenile tree, which was growing in somewhat enclosed conditions under shade-cloth cover, was pollinated is unknown. None of the surrounding specimens appeared to have pollen cones. Presumably, pollen cones were produced by the seedling, or another specimen, some months before and had disappeared at the time when the ovulate cones were collected. Farjon (2005) noted that female and male cones are rare on mature *L. austrocaledonica* trees. *Libocedrus austrocaledonica* and *L. chevalleri* are small trees ~2 m that are pre-adapted to infertile, high altitude, wet conditions, and are most often found on ridges where high light and strong winds inhibit the growth of angiosperms (Jaffré 1995). The height of only one of the several herbarium specimens of these two species, which were examined in this study, is known. Material from a 3 m *L. austrocaledonica* (00504526) tree contained no fertile material, possibly because it had come from an old, senile tree. Unlike the other two species, *L. yateensis* is generally found along mountain streams, and low altitude riverbanks, either as small groves, or as individuals (Farjon 2005). Here the open canopy above the streams probably provides more light, and water is readily available. Human induced fires are now considered the greatest threat to New Caledonia's biota (Jaffré *et al.* 1998). In the last ~3500 years, clearing and burning has reduced and fragmented the original vegetation, and enhanced the growth of fire-resistant or introduced species. Practices associated with mining for rare metals also endanger the preservation of indigenous species. Although protected parks and reserves have been established to safeguard areas of highly diverse vegetation, these are considered insufficient (Jaffré *et al.* 1998).

Climate has been evoked as a cause for the decline of *Libocedrus bidwillii* in New Zealand (Holloway 1954; Wardle 1963; 1978) and cooler drier conditions may have led to periods of *Libocedrus* expansion there during the Holocene (Horrocks and Ogden 1998). However, evidence suggests that seedlings are unlikely to regenerate in stable, shady old growth forests. The disappearance of *Libocedrus* from Australia is probably the result of that continent's rapid movement into lower latitudes following the breaching of the Tasman Rise, increasing tectonic stability in the Late Miocene, and drier climates.

Chapter 4. *Austrocedrus*

Monotypic
Austrocedrus chilensis (D.Don) Pic. Serm. & Bizzarri, Webbia 32 (2): 482. (1978)

Description: Multi stemmed shrubs or conical-shaped trees 15-37 m (Veblen *et al.* 1995), mostly dioecious (Brion *et al.*1993; Castor *et al.* 1996; Rovere *et al.* 2003), with smooth young bark (older bark relatively thin; Veblen *et al.* 1995), and numerous spreading branches (Farjon 2005).
Distribution: Along two narrow corridors on either side of the Andean Cordillera, in Chile and Argentina, between 32° and 44° S, from 360-1500 m (Gobbi and Schlichter; Pastorino *et al.* 2004). Populations are discontinuous. In Chile, these are more northerly, and there are also scattered populations in coastal mountains (Dodd *et al.* 1998). The Argentinean populations are more southerly (Pastorino *et al.* 2004).
Ecology: Long-lived (400-[rarely] 1000 years), shade intolerant trees (Veblen *et al.* 1995), which grow on a variety of soil associations (La Manna and Rajchenberg 2004). Rainfall determines forest structure. Across the narrow (~50 km) Argentinean corridor in which *Austrocedrus* grows, rainfall varies from 2500 mm in the west to 600 mm in the east (Pastorino *et al.* 2004). In the wetter areas *Austrocedrus* is often found in association with the shorter-lived *Nothofagus dombeyi* (Veblen *et al.* 1995) or other *Nothofagus* species. As rainfall decreases, stands first become monotypic and compact, and then marginal forests (Pastorino *et al.* 2004). In the harsh and arid (xeric) conditions of the Patagonian steppe they form small, monotypic, stunted and more open stands (Villalba and Veblen 1997; Dodd *et al.* 1998; Dodd and Afzal-Rafii 2000), on rocky outcrops. These trees are often multi-stemmed (Pastorino *et al.* 2004). In Chile, at the northern end of its range, it grows in a Mediterranean-type climate (Relva and Veblen 1998).

Systematics
Order Coniferales
Family Cupressaceae
Genus *Austrocedrus* Florin & Boutelje, Acta Horti Berg. 17 (2): 28. (1954).
Austrocedrus chilensis (D.Don) Pic. Serm. & Bizzarri Webbia 32 (2): 482. (1978)

Foliage and leaves: dense branches, with opposite branchlets arising in the same plane. Leaves scale-like, highly dimorphic, decussate, and flattened. Lateral leaves much larger than facial, bilaterally flattened, highly variable in size and shape (Fig. 1), and basally fused for about half their length (Fig. 2a, b, f, g). Margins entire (Fig. 2h) but poorly defined, leaf bases may be slightly papillate (Fig. 2f). Facial leaves small, outwardly keeled on dorsal and ventral surfaces, and with slightly frilled margins and bluntly acute apices (Fig. 2h). On main axes, the lower halves of lateral leaves are elongate and, on the dorsal surface, appear to be fused, and the area where they abut is raised. On the ventral surface there is a long narrow groove between the 2 adjoining leaves. The upper sections of these leaves are free, variously keeled, and with bluntly acute apices (Fig. 2a). On main stems, this free section is often at a broad angle to the stem (Fig. 1).
Stomatal distribution: Amphistomatic. Dorsal and ventral surfaces, lateral leaves - longitudinally oriented, in discontinuous rows (Fig. 3f), in well-defined grooves, and roughly parallel to the leaf margins (Figs 2c, d, e, i; 3). The sun

exposed ventral surface of drooping branches may have only a few scattered stomata, but stomata are more numerous closer to the base, where they are protected by the facial leaf below. Facial leaves - confined to grooves on either side of the central keel in the lower half of the leaf (Fig. 2h). On both leaf surfaces stomata are often protected by a white, waxy coating. This is generally more conspicuous on the dorsal surface.

Cuticle description: Inner surface - stomatal guard cells elongate, and surrounded by 4-6 moderately coarse-grained subsidiary cells. Subsidiary (generally polar) cells often shared by adjacent guard cells. Polar cells often smaller, and more rounded in shape than other subsidiary cells (Fig. 4f). The periclinal walls of the subsidiary cells form a groove around the guard cells. This is intersected by anticlinal subsidiary cell walls. At the corners of the subsidiary cells are other indentations (Fig. 4a, d). Anticlinal cell walls of subsidiary cells moderately thick. Epidermal cells in non-stomatal areas are irregularly shaped, generally elongate, and more coarse-grained in texture than subsidiary cells. The anticlinal cell walls of these cells are irregularly thickened (and slightly thinner than those of the subsidiary cells), coarse-grained in texture, wider at the base and with acute apices (Fig. 4h). Epidermal cells on exposed surfaces, particularly facial leaf apices may contain small calcium oxalate nodules (Fig. 4i). Outer surface - stomata have low-moderately high ridged and lobed Florin rings (best seen on cleaned samples; Fig. 4b) that generally lack a peripheral groove. The stomatal area is covered in waxy spicules (Fig. 4e), and some stomata have waxy plugs (Fig. 4c). There are very few papillae associated with the stomata (Fig. 4e). Epidermal cells are convex, with indented margins, and often contain small holes (Fig. 4g) or nodules that mark the presence of calcium oxalate crystals in the cell walls. The latter are most frequent on, and towards, leaf apices, and do not occur in stomatal areas or near leaf bases.

Ovulate cones: ~8-12 mm long. Terminal on short branchlets (Fig. 5b) and somewhat flattened in appearance. Four decussate bract/scale pairs, the ultimate scale pair large, broad, ovoid-oblong with a rounded apex and, in the lower half, tapering to an acute base. The penultimate bract-scales much smaller, almost lanceolate, and infertile (Fig. 5c), and not extending beyond the lower tapered section of the ultimate bract-scales. Both scales with highly ridged outer surfaces and papillate margins (Fig. 5g, h). The bracts are long and broad, encompassing most of the outer scale, extending almost to the margin on the sides and close to the apex (Fig. 5g, h). The tips of the bracts on both scales are small, inwardly curved, high on the scale, close to the apex, and do not extend beyond the scale (Fig. 5a, c, g). The cones are subtended by 3-4 very small short, broad, decussate bracts that are similar size and shape (Fig. 5c, d, e) and have frilled margins.

Ovulate cone development: (Figs. 5f, i; 6a-g). Ovule initiation for *A. chilensis* is illustrated by Farjon and Ortiz Garcia (2005). Cone development is similar to that described by Tomlinson *et al.* (1993) for *L. plumosa*. On a fertile shoot, two pairs of ovules are initiated in the axillae of the ultimate bracts. Following ovule initiation a short columella forms in the cone apex, and at the base of the two uppermost bract pairs a highly papillate ligulate outgrowth is initiated (Fig. 6a, c, g). These ligules expand via intercalary growth (Fig. 6a) to envelop and protect the growing ovules (Fig. 6b). The four bracts also appear to extend at the base by intercalary growth (Figs 5f, i; 6c, e, f). Outwardly, at least, these cells are very different from the upper part of the bract and contain stomata (Fig. 6f). Subtending the cone are 3-5 short, squat bracts (Fig. 6d).

Ovules: 4, erect (Fig. 6c). Mature seeds, not illustrated, 2-4 per cone with 2 wings very unequal in size (Farjon 2005).

Pollen cones: (Fig. 7a-b): with 6–10 decussate microsporophyll decussate pairs. Terminal on short small leaved branchlets, and subtended by 1-2 small decussate bract pairs. Microsporophylls ovate, sub-peltate, outwardly keeled but with a central (somewhat indented) bulge, and with bluntly acute apices and frilled margins.

Specimens examined

E/1091, Herbarium Collection, The University of Adelaide, South Australia. Puerto Moreno, Argentina. Collection details unknown.

E/0893, Herbarium Collection, The University of Adelaide, South Australia. Chile. Collection details unknown.

E/C/01, Herbarium Collection, The University of Adelaide, South Australia. Collected 12/1998, T Brodribb, Parque Siete Tasas, Chile.

Cultivated specimen, Tasmanian Arboretum, Devonport, Tasmania, Australia. Collected 11/2004, R Paull. Small tree ~2.5 m.

E/4297, **E/4298**, **E/4299**, **E/4300**. Herbarium Collection, The University of Adelaide, South Australia. Collection details unknown.

Fig. 1 *Austrocedrus chilensis* branchlets illustrating highly diverse leaf morphology.
Ultimate branchlets most frequently opposite and arising in the same plane (E/C/01).

135
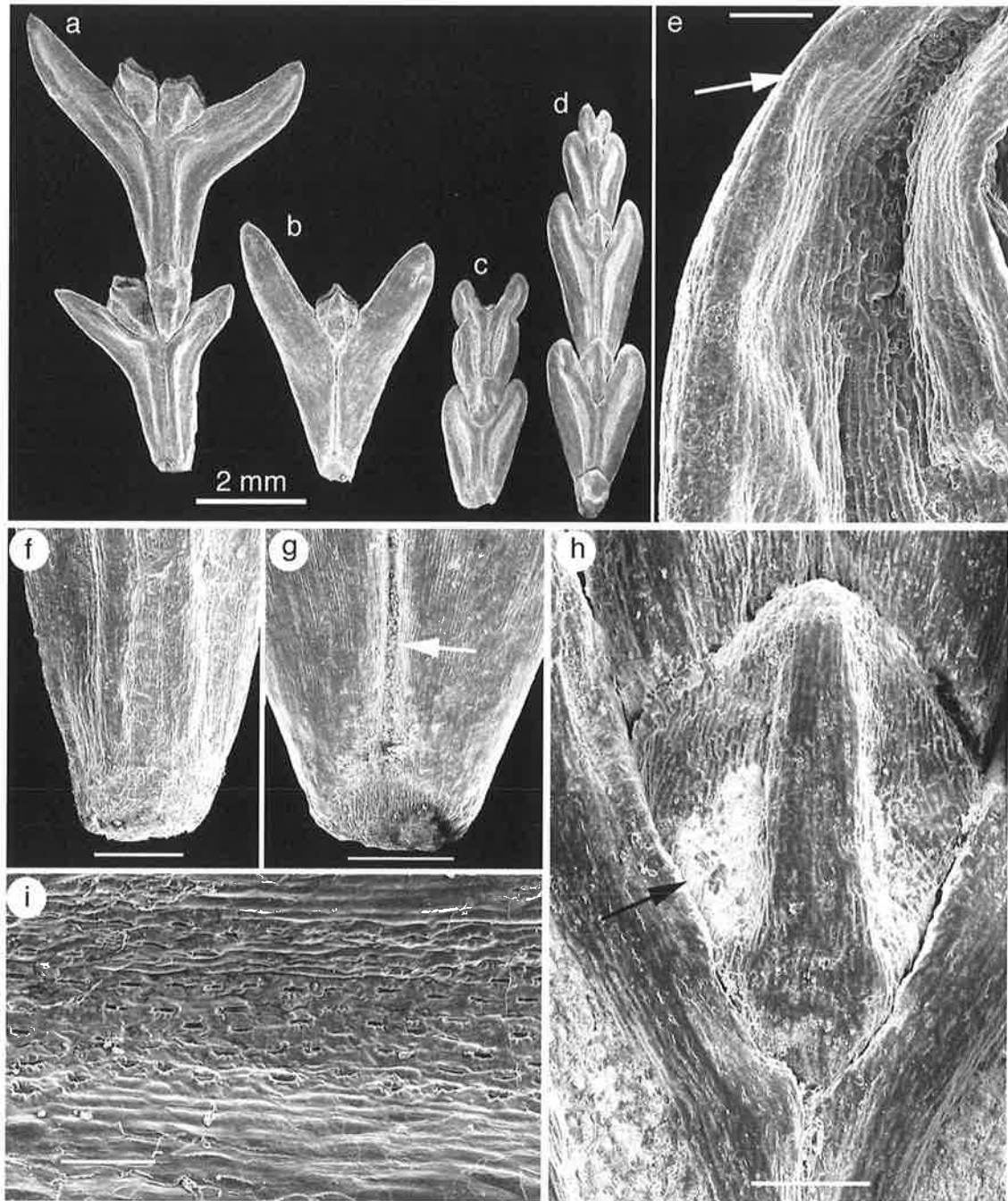
Fig. 2a-f *Austrocedrus chilensis* SEM adult foliage

Fig. 2a-f *Austrocedrus chilensis* SEM adult foliage

a. Dorsal surface, large flattened main axis foliage. Lower half of lateral leaves elongate, connate, upper free section keeled, with bluntly acute apices, Stomata in a well-defined groove in the centre of the leaf. Paired facial leaves much smaller than laterals (specimen E/C/01).

b. Ventral surface without well-defined stomatal groove (specimen E/C/01).

c. Dorsal surface, small leaved branchlet. Lateral leaves imbricate with stomata in well-defined grooves (specimen E/4299).

d. Ventral surface, leaves from same sample as c. Lateral leaves loosely imbricate, and with stomata in well-defined grooves.

e. Lateral leaf tip, ventral surface. Stomata in a well-defined groove. Epidermal cells with numerous very small holes (arrow; scale 100 μm; specimen E/4299).

f. Detail, base of a. The central area where the lateral leaves are joined is raised. Leaf bases slightly papillate (scale 500 μm).

g. Detail, base of c. Arrow indicates a long narrow groove between the adjoining lateral leaves (scale 500 μm).

h. Dorsal surface. Facial leaf outwardly keeled, with frilled margin, and rounded apex. Stomata in waxy depressions on either side of the central keel, in the lower half of the leaf. Lateral leaf margins entire (arrow; scale 200 μm; specimen E/4299).

i. Dorsal surface, cleaned lateral leaf. Stomata longitudinally oriented, in a well-defined groove, densely packed, and in discontinuous rows (scale 100 μm; specimen E/C/01).
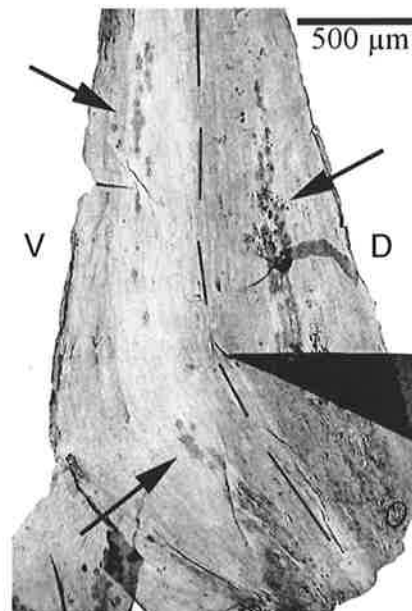
Fig. 3 *Austrocedrus chilensis* stomatal distribution, lateral leaf

Arrows indicating stomata on ventral (V) and dorsal (D) sides of a lateral leaf. (Dashed line delineating the boundary between ventral and dorsal leaf surfaces; specimen E/C/01).

Fig. 4a-i *Austrocedrus chilensis* leaf cuticle

Except where indicated specimens are from the Tasmanian Arboretum, Devonport, Tasmania

a. SEM inner surface stomata. Guard cells elongate, and surrounded by 5 elongate subsidiary cells. Subsidiary cells with indentations at the corners (scale 20 μm).

b. SEM outer surface cuticle following cleaning. Florin rings lobed and low-moderately ridged, giving the stomata a rectangular appearance (scale 20 μm).

c. SEM outer surface. Non-cleaned highly waxy cuticle from young shoots showing stomatal plugs (scale 20 μm: specimen E/4297).

d. SEM inner surface. Sharing of subsidiary cells by adjacent guard cells. Periclinal cell walls of subsidiary and epidermal cells associated with stomatal complexes finer-grained than other epidermal cells (scale 20 μm).

e. SEM outer surface. Uncleaned mature leaf, moderately waxy, moderately lobed Florin rings (scale 20 μm; specimen E/4297).

f. LM showing stomata in discontinuous rows (scale 50 μm).

g. SEM outer dorsal surface. Epidermal cells slightly convex, with indented walls, and containing numerous small holes. Florin rings low-moderately ridged, and lobed (scale 20 μm).

h. SEM ventral surface. Coarse-grained epidermal cells with irregularly and moderately thick anticlinal walls (scale 20 μm).

i. SEM inner surface. Coarse-grained epidermal cells, one with small calcium oxalate crystals (scale 10 μm).

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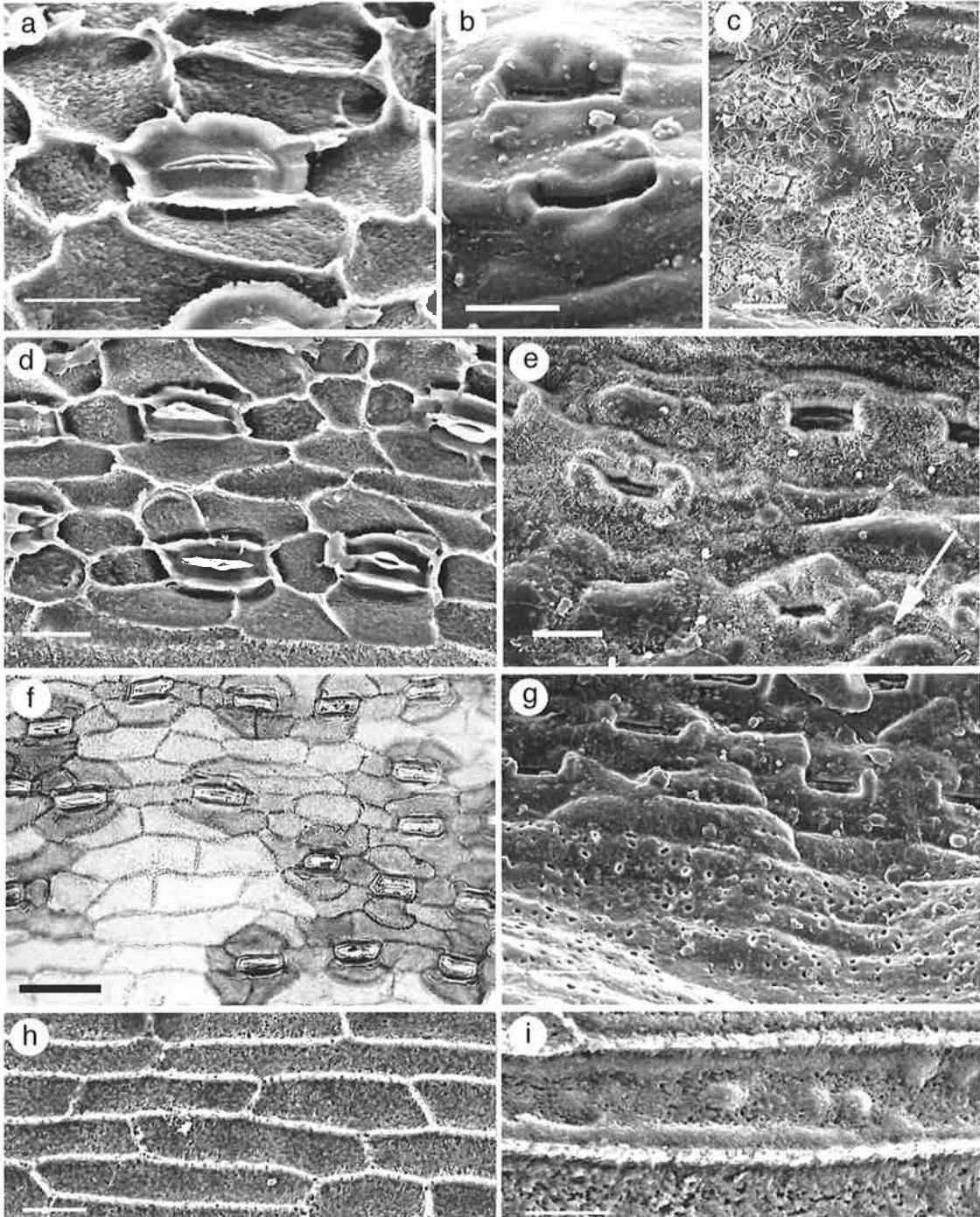
Fig. 4a-i *Austrocedrus chilensis* leaf cuticle

Fig. 5a-i *Austrocedrus chilensis* ovulate cones
Specimens from E/C/01

a. LM mature cone, scales with short bracts. Lower half of ultimate bract-scale tapering towards the base. Penultimate bract-scales not extending beyond the tapered section of the ultimate bract-scales. Bracts on penultimate scales inwardly recurved.

b. Immature cones frequent, and solitary on short shoots. Fertile foliage smaller than sterile. Two cone types - large semi-mature closed cones (above) and small immature open cones (below). All bracts on larger cones inwardly recurved.

c. Immature cone with large broad ultimate scales and small, narrowly elongate penultimate scales.

d. Very immature cone.

e. Detail of the two bract pairs subtending the cone; scale 500 um).

f. Penultimate developing scale, bract inwardly recurved (scale 500 um).

g. Detail of **c**. Side view of penultimate bract-scale showing small bract extension, and papillate scale margin (scale 500 um).

h. External surface, penultimate bract scale. Note the papillate scale margin and the width of the bract (arrows). Bract tip short, and outwardly recurved (scale 500 um).

i. Bract extending by intercalary growth at the base (scale 500 um).
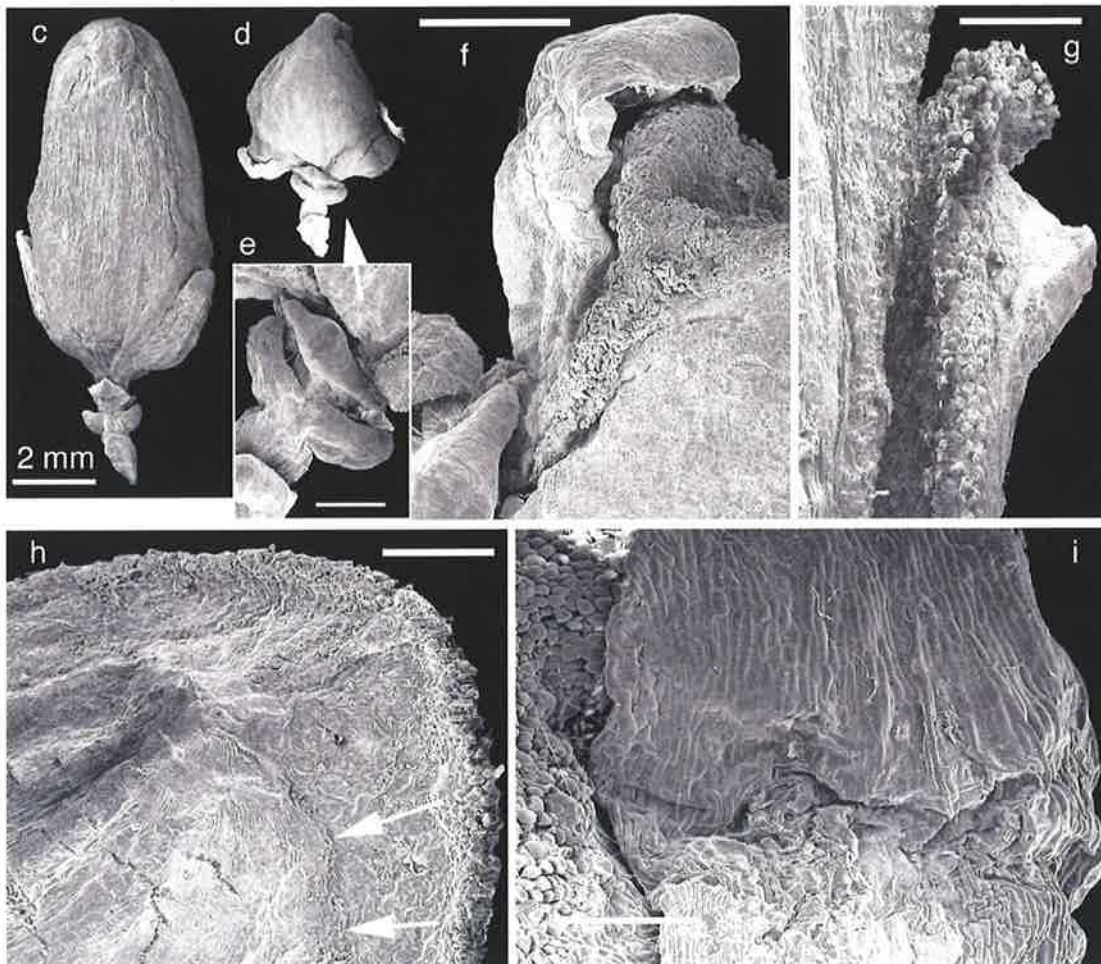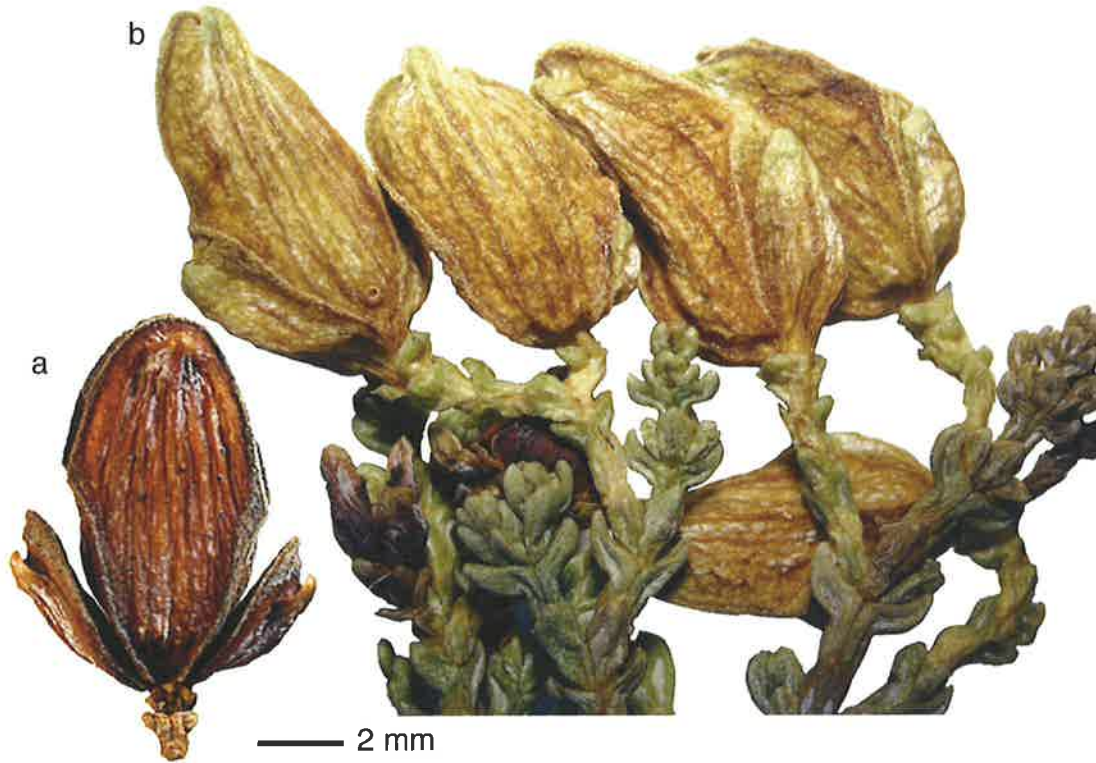
Fig. 5a-i *Austrocedrus chilensis* ovulate cones

Fig. 6a-g *Austrocedrus chilensis* ovulate cone development

Specimen from the Tasmanian Arboretum, Devonport

    a. Transverse section through young cone showing short columella (C), early papillate ligule growth (L), fertilised ovules (O), and subtending bract with frilled margins (lower right; scale 500 μm).

    b. Cone seen from above. Immature ovules enclosed by papillate ligule (scale 500 μm).

    c. Cone with short gaping bracts, four erect ovules, and poorly developed ligule (scale 500 μm).

    d. Young ovulate cone subtended by 5 short, squat bracts. Cone bracts being extended upward by intercalary growth.

    e. Detail of **d.** Bracts extending from the base via intercalary growth. Black arrow indicating a clear margin between bract and growing ligule (scale 500 μm).

    f. Detail of **e.** Non lobed stomata on the lower surface of the extending bract covered in waxy spicules (scale 500 μm).

    g. Detail of **c.** Poorly developed ligule (L) in the centre of the base of the ultimate bract. Developing ovule (O; scale 50 μm).
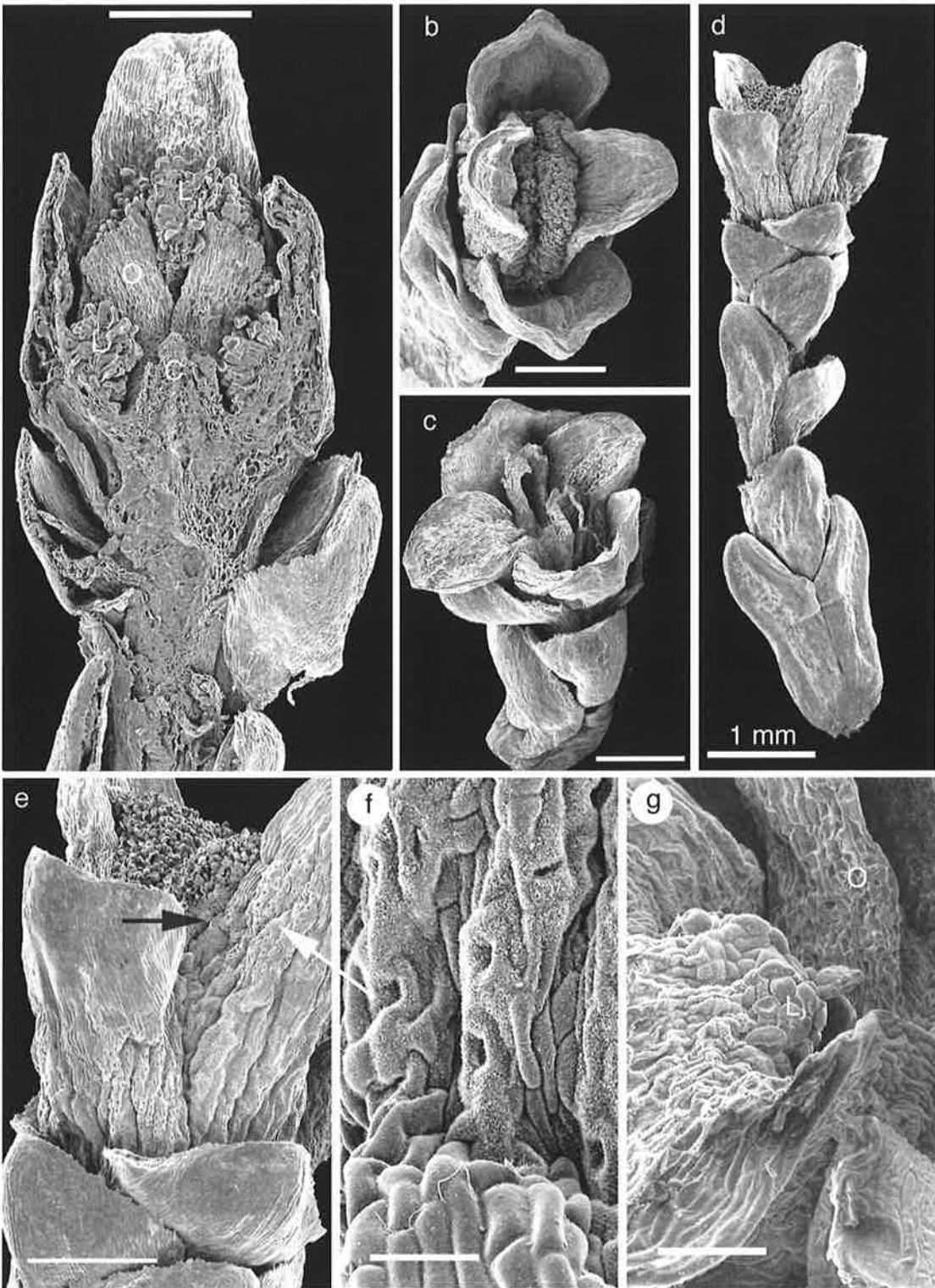
Fig. 6a-g *Austrocedrus chilensis* ovulate cone development
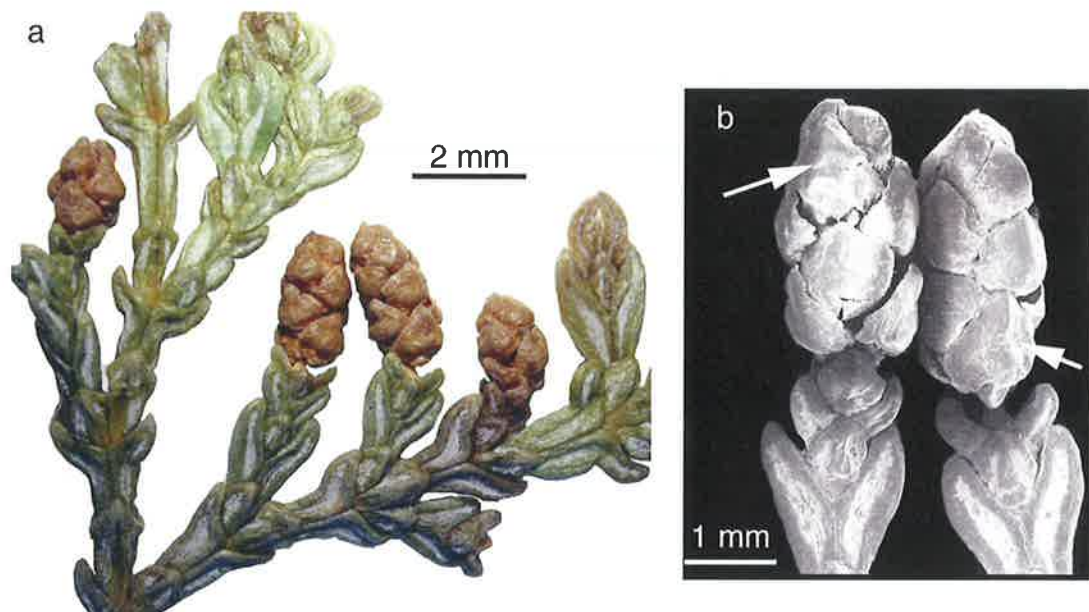
Fig. 7a-b *Austrocedrus chilensis* pollen cones
Specimen E/C/01
  a. LM. Pollen cones terminal on small leaved and short branchlets.
  b. SEM. Microsporophylls imbricate, ovate, decussately arranged, and with a central bulge (arrows). Bracts subtending the cone 1-2, decussate, short, broadly triangular.

Distinguishing features - *Austrocedrus chilensis*

- Dioecious trees

Foliage

- leaves highly dimorphic
- Main axes - lateral leaves much larger than facial. Facial leaves not extending between the lateral leaves below. Lower half to two thirds of lateral leaves elongate and fused. Combined bases of free sections often at a broad angle to the stem
- Lateral leaf margins entire and poorly defined

Stomata

- amphistomatic*
- stomata distinctive (internal cuticle most similar to *Papuacedrus*)
- stomatal areas with infrequent papillae
- Florin rings with low to medium ridges
- Few papillae associated with Florin rings

Ovulate cones

- bract projections small, squat and close to the scale apex
- penultimate bract-scale complexes about one third the size of the ultimate. Scale larger than bract

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Discussion

*The specimens examined in this study indicate that *Austrocedrus* is amphistomatic, <u>not</u>, as others have suggested, hypostomatic (Laubenfels 1953) or almost hypostomatic (Florin and Boutelje 1954). Although some lateral leaves may have few or no exposed stomata on the ventral surface, others have stomata in well-defined grooves. The dorsal and ventral surfaces (of all leaf types, early transitional to adult leaves, as illustrated by Florin and Boutelje (1954) in Plate IX; and illustrated in Fig. 1, this current study) are often almost indistinguishable. There is no evidence that stomata are confined to the dorsal surface at any growth stage. Farjon (2005) has suggested that stomata may be on both leaf surfaces if branchlets are erect. It is difficult to believe that all the material collected and used in this study came from erect branchlets, although much of it came from relatively young trees. One of the latter (from the Tasmanian Arboretum) is growing in an exposed position. The samples were taken from somewhat drooping branches, and although the ventral (sun exposed) surfaces of some lateral leaves have reduced numbers of stomata, none appear to be astomatic.

In some aspects *Austrocedrus* is similar to *Papuacedrus*. Both have highly diverse foliage of somewhat similar appearance. The stomatal apparatus of the two genera is alike, and both have relatively few indentations at the extremities of the subsidiary cells (not none as Florin and Boutelje (1954) suggested), and moderately thin cuticles. However, the ovulate cones are dissimilar. The bract protrusions on the ultimate scales of *Austrocedrus* are close to the scale apex, but for *Papuacedrus* these are in the lower half to one third of the outer scale surface (Chapter 2).

Ecology

Factors determining current Austrocedrus distribution

As elsewhere, vegetation patterns in the Andes are shaped by disturbances. In Chile, these are mainly geological: earthquakes, landslips, and volcanic ash fallout. Earthquakes also affect Argentinean forests, but in northern Patagonia, fire has been the dominant disturbance (Veblen *et al.* 1992). *Austrocedrus* has thin bark and, like *Nothofagus dombeyii*, with which it grows in wet areas, does not re-sprout after major fires (Veblen *et al.* 1995; Veblen *et al.* 1996). Anthropogenic changes to the naturally occurring (lightning induced) fire regime, have altered the structure of *Austrocedrus* forests in Argentina (Kitzberger and Veblen 1999), especially those growing in lower rainfall conditions (Kitzberger and Veblen 1999; Veblen *et al.* 1999). Burning by aboriginal hunters began ~10,000 years ago (Urretavizcaya and Defossè 2004), and peaked about 1850 (Veblen *et al.* 1999). This was largely confined to the more xeric forests, where surface fires created park-like conditions (Kitzberger and Veblen 1999). Between 1880-1910, newly arrived Europeans used massive burning to clear the wetter, mixed forests to the west, for cattle grazing (Veblen *et al.* 1992). As this practice was largely unsuccessful, intentional burning declined, and by about 1930 fires were suppressed, and areas of forest were set-aside as national parks (Veblen *et al.* 1999: Kitzberger and Veblen 1999). Since the suppression of fires, remnant patches of forest have coalesced and become denser, and what were once shrublands now also contain patches of *Austrocedrus* (Kitzberger and Veblen 1999). In the areas cleared and burnt by early settlers, forests (of same age stands) have regenerated (Kitzberger and Veblen 1999; Veblen *et al.* 1999). The frequency and effect of fires is variable. In wetter, more humid areas, fires occur less often, and usually in periods of prolonged drought, when winter-spring precipitation has been low

(Veblen *et al.* 1999). As fire suppression has increased fuel loads, when fires do occur, they can be devastating (Villalba and Veblen 1997; Pastorino and Gallo 2002; Urretavizcaya and Defossè 2004). In mesic and xeric areas fires are more frequent, but less intense, and adult trees can survive (Veblen *et al.* 1995). Stands of young trees, only a few decades old, are probably less susceptible to fire (Veblen *et al.* 1999).

In more recent times grazing of introduced herbivores (mainly cattle and deer; Villalba and Veblen 1997; Relva and Veblen 1998), even within national parks, has become a problem. *Austrocedrus* is highly palatable (Veblen *et al.* 1992), and saplings 0.5-1 m tall are frequently browsed. Although they can survive quite heavy browsing, trees become deformed, stunted and more compact, due to the loss of apical buds. Smaller seedlings appear less susceptible to damage (Relva and Veblen 1998).

For about the last 60 years many trees in wetter, low altitude areas, have been dying from a disease known locally as 'mal del ciprès'. The cause or causes of this disease are unknown, and have been attributed variously to dysfunctional root systems (Filip and Rosso 1999), including introduced root destroying pathogen(s) (Baccala *et al.* 1998; Greslebin *et al.* 2005), and to poor drainage, and/or the presence of clays close to the soil surface (La Manna and Rajchenberg 2004).

Seedling recruitment

Given the right conditions, *Austrocedrus* rapidly recolonises disturbed areas with same aged trees. In drier sites, where there is little competition from other species, all age structures can develop (Kitzberger *et al.* 2000). In dense old growth, mesic forests, seedling recruitment only occurs where tree fall, or wind throw has opened the canopy allowing light to reach the forest floor (Veblen *et al.* 1992; Gobbi and Schlichter 1998). Open areas and woodlands are often too dry for seedlings to establish, and in these settings there is often the added pressure of grazing animals (Veblen *et al.* 1995). *Austrocedrus* pollen and seeds are wind dispersed (Pastorino and Gallo 2002). The viability of pollen decreases with age (fewer grains are aborted from young trees; Aizen and Rovere 1995). Seeds may suffer serious insect predation before they are shed (Gobbi and Schlicter 1998). For *Austrocedrus* (and *N. dombeyii*) seed dispersal is only ~25 m (Kitzberger and Veblen 1999), and seed rain is highly variable from year to year (Veblen *et al.* 1995). Seeds only remain viable for about one year, so there is no permanent seed bank (Urretavizcaya and Defossè 2004). Germination occurs in the spring after a period of dormancy, during which many seeds lose viability (Urretavizcaya and Defossè 2004). Heavy *Austrocedrus* litter retards germination (Gobbi and Schlicter 1998). Successful germination requires wet, moderate to high light conditions, with water the most important factor (Gobbi and Schlichter 1998). Seedling growth can be inhibited by strong winds (Veblen *et al.* 1995). Seedling establishment and adult tree death are associated with decadal variations in climatic conditions. For the last 200 years, seedling recruitment in northern Patagonia has been most effective when prolonged years of wetter spring and summer weather have followed devastating fires. Seedlings emerge mid-spring to mid-summer, with late emerging seedlings having better survival rates. Forest expansion into drier areas is associated with these prolonged wet periods (Villaba and Veblen 1997; Veblen *et al.* 1999). In average years, survival appears to be dependent on nurse shrubs. The latter provide microsites that shade the seedlings from the afternoon sun, and have higher soil moisture (Kitzberger *et al.* 2000). High soil temperatures are not

conducive to seedling establishment especially in xeric sites, after fires (Urretavizcaya *et al.* 2006), as seedlings are prone to desiccation. In warmer, dry, years there is no seedling recruitment (Kitzberger *et al.* 2000), and trees probably conserve energy by reducing fertile foliage production. A fire occurring at this time would have disastrous consequences.

As with other long-lived trees examined in this study, *Libocedrus* (Part I, Chapter 3) and *Pilgerodendron* (Part I, Chapter 5) *Austrocedrus* is reproductively mature at a very young age. Veblen *et al.* (1995) noted that female (ovule/seed producing) trees are mature at 15-25 years, a finding confirmed by this current study. Male (pollen producing) and female trees may grow at different rates but, as there is no consistency in these growth patterns, they are considered insignificant (Rovere *et al.* 2003). The energy expenditure of female trees is probably reduced by the ability of developing cones to photosynthesise (Rovere *et al.* 2003; see also Fig. 6e, f, this chapter), as would be a reduction in the number of cones (Rovere *et al.* 2003). Seedling recruitment strategies for *Austrocedrus* differ somewhat from those of New Zealand *Libocedrus*, but it appears that, like all other genera examined in this study, precocious fertility facilitates survival.

Genetics
There is very little genetic variation in *Austrocedrus*, despite its present fragmentary distribution (Pastorino *et al.* 2004). What variation there is appears to follow a latitudinal gradient, the northern populations more variable than others. Trees growing in the harsh conditions of the steppe show the most variation (Pastorino *et al.* 2004). These authors (and Pastorino and Gallo 2002) hypothesize that during the Last Glacial Maximum ~20,000 years ago, glacial ice displaced *Austrocedrus* and it survived (with some continuity) in dry (xeric) conditions along the margins of the ice sheets. The ability of *Austrocedrus* to survive a broad range of conditions is attributed to phenotypic morphological variation (Gyenge *et al.* 2005), and climate related changes in cuticular lipids (Dodd *et al.* 1998; Dodd and Rafii 2000).

Chapter 5. *Pilgerodendron*

Monotypic
Pilgerodendron uviferum (D. Don) Florin, Svensk. Bot. Tidskr. 24: 133. (1930)
As the foliage of this genus is unflattened, the term adaxial is used to describe the leaf surface facing the stem, and abaxial, the surface facing away from the stem.

Description: Evergreen trees to 20 m, to 40 m to the north of their range (Farjon 2005), dioecious (rarely monoecious; Grosfeld and Barthélémy 2001) with grey-brown and fibrous mature bark (Farjon 2005).
Distribution: Western Chile and Argentina from ~40°S to ~55°S (Moore 1983) from 20-750 m (Farjon 2005). More northerly populations (Chile) are scattered and smaller in size (Allnutt *et al.* 2003).
Ecology: Slow growing, somewhat shade intolerant (Veblen *et al.* 1995), long lived trees to 500 years (Szeicz 1997). Found in cool climate, high rainfall conditions (>2500-4000 mm; Moore 1983; Grosfeld and Barthélémy 2001) on poorly-drained acidic soils from low to mid elevations on coastal mountains (Veblen *et al.* 1995), near mountain lakes on the eastern side of the Andes and on island mountainsides, (Farjon 1998, 2005). Often codominant with *Fitzroya cupressoides* in its northern distribution (Veblen *et al.* 1995; Allnutt *et al.* 2003). Highly valued as a timber tree, its survival is now threatened (Allnutt *et al.* 2003). Can survive light fires but appears to require large scale disturbance for regeneration.

Systematics
Order Coniferales
Family Cupressaceae
Genus *Pilgerodendron* Florin, Svensk. Bot. Tidskr. 24: 132 (1930)
Pilgerodendron uviferum (D. Don) Florin, Svensk. Bot. Tidskr. 24: 133 (1930)

Foliage and leaves: Foliage branches numerous, crowded (Figs 1, 2), branchlets sub-opposite to alternate, and arising on all sides of the stem (Figs 1a-c; 2). Leaves scale-like, generally decussate (except where there is twisting of the stem, as in young foliage; Fig. 3a 1), with paired leaves loosely joined at the base (for about one fifth of their length; Fig. 3a 4), homomorphic, imbricate (Fig. 3a 3, 4), and with entire margins. Leaves on young trees, especially fertile shoots may be loosely imbricate (Figs 2; 3a 1, 2), or imbricate and quadrangular in appearance (Figs 1b; 3a 3, 4). Adaxial leaf surface slightly convex, abaxial surface centrally keeled. Leaf apices obtuse (Fig. 3b) to bluntly acute (Fig. 3c). Leaves ranging in size from 2-5 mm x 1-1.5 mm.
Stomatal distribution: epistomatic, adaxial surface (Fig. 3 b-d). Stomata in discontinuous rows (roughly parallel to the leaf margin) extending across most of the adaxial surface (except towards the base; Fig. 4e). The stomatal area is bounded by a distinctive band of epidermal cells just within the leaf margin (Fig. 3a 3; 3b). The outer surface of this band of cells is smooth.
Cuticle description: Inner surface - stomatal guard cells surrounded by 4-6 (generally five) moderately coarse-grained, undulate, slightly convex, and generally elongate, subsidiary (epidermal) cells. The latter contain deep furrows, and polar cells are often shared by adjacent guard cells (Fig. 4 a, c). The anticlinal cell walls of the subsidiary cells are thick and moderately coarse-grained. Epidermal cells abutting the stomata are coarse grained, with thick, moderately coarse-grained anticlinal walls (Fig. 4c, g). Epidermal cells on the abaxial leaf surface are very coarse-grained and contain

nodules with calcium oxalate crystals. Epidermal cells on the adaxial leaf surface lack these nodules. The surface of these nodules is smoother than the rest of the periclinal cell wall (Fig 4h). Outer surface - Florin rings mostly absent or very poorly developed (Fig. 4b, cleaned specimen), with stomata sunken and protected by a waxy plug with wax spicules (Fig. 4d). No papillae associated with stomata. Epidermal cells on the abaxial surface with indented cell walls and containing small nodules or holes (these indicate calcium oxalate crystals in the cell wall matrix; Fig. 4f).

Ovulate cones: ~9-12 mm long. Terminal on short branchlets and comprised of 2 decussate bract-scale pairs, the ultimate pair larger (longer, broader) than the penultimate (shorter, lanceolate) pair. In the mature cone the bracts are broad at the base and extend laterally to the scale margin for around half the length of each scale (Fig. 5a, 2). The bract projections (for all 4 scales) extend outward from the centre of the abaxial scale surface. These are elongate, inwardly curved and with acute apices and, on ultimate bract-scales, do not extend beyond the scale. Bract development is best seen in immature cones (Fig. 5a, 3-5). Mature scale margins are highly papillate (arrow, Fig. 5c). The internal and external scale surfaces of both scale pairs are highly rugose.The cone is subtended by 3-4 decussate infertile bracts. On mature cones these are longer and more flattened than the older leaves beneath (Fig. 5a, 2; 5c), on immature cones they are elongate and lanceolate with acute apices (Fig 5a, 3-5). These infertile bracts have stomata on their adaxial surface (arrow, Fig. 5h). Cone development appears to be similar to that of *Libocedrus*, *Papuacedrus* and *Austrocedrus*, the 'scale' arising from the base of the last 4 bracts to envelop and protect the young fertile ovules. Papillate margins enhance ovule protection (Fig. 5f, g).

Ovules: not illustrated, 3-4 in the axil of the ultimate bracts. Seeds with two very unequal sized wings, 3-4 per cone (Farjon 2005).

Pollen cones: with 6-12 decussate microsporophyll pairs (Figs 1c; 5a). Terminal on short branchlets (Figs 1c, 2). Microsporophylls triangular in shape, rostrate, with slightly frilled margins and a central bulge (Fig. 5b).

Specimens examined

E/C/02, Herbarium Collection, The University of Adelaide, South Australia. Collected 1999. T. Brodribb, Near southern entrance Alerce Andino National Park, Chile. Trees ~3 m, growing in open swampy ground.

Cultivated specimen, Tasmanian Arboretum, Devonport, Tasmania, Australia. Collected 11/2004, R Paull. Small female tree ~3 m.

Cultivated specimen, Tasmanian Arboretum, Devonport, Tasmania, Australia. Collected 11/2004, R Paull. Small male tree ~2 m.
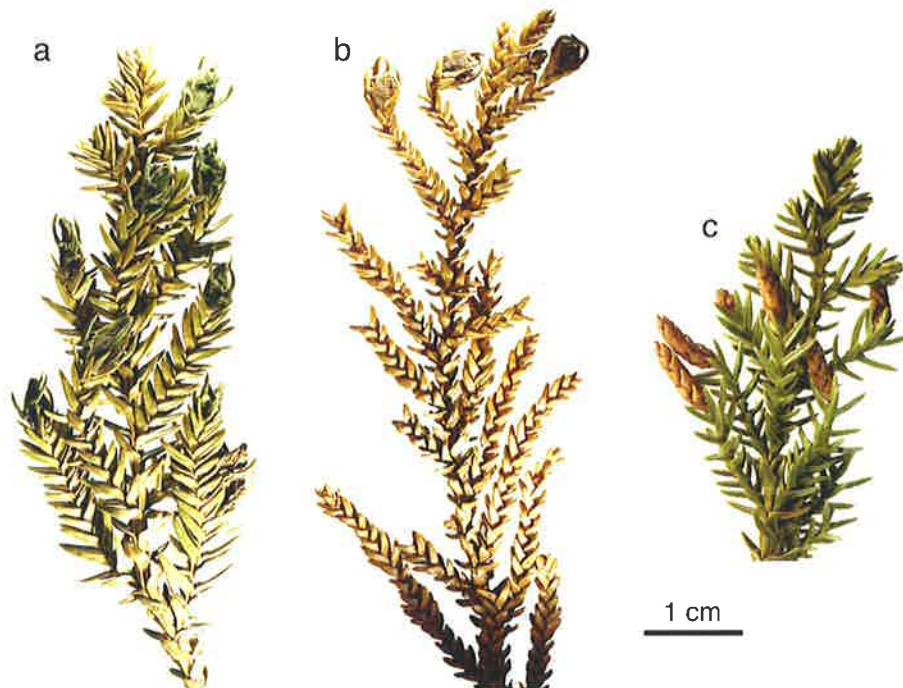
Fig. 1 a-c *Pilgerodendron uviferum* fertile branchlets showing leaf arrangement

Specimens **a**, **c**, collected at Tasmanian Arboretum, Devonport, Tasmania

- **a.** Young female tree ~2 m. Branchlets sub-opposite to alternate and arising on all sides of the stem. Leaves homomorphic, lanceolate and loosely imbricate. Ovulate cones terminal on short branchlets.
- **b.** Female tree ~3 m. Imbricate scale-like leaves, almost quadrangular in appearance (specimen E/C/02).
- **c.** Young male tree ~2 m. Leaves not imbricate, lanceolate. Pollen cones terminal on short branchlets. Branchlets arising on all sides of the stem.

Fig. 2 *Pilgerodendron uviferum* fertile male branchlets

Closely packed foliage with scale-like, homomorphic, lanceolate leaves. Pollen cones terminal on short, rigid branchlets (cultivated specimen, Tasmanian Arboretum).

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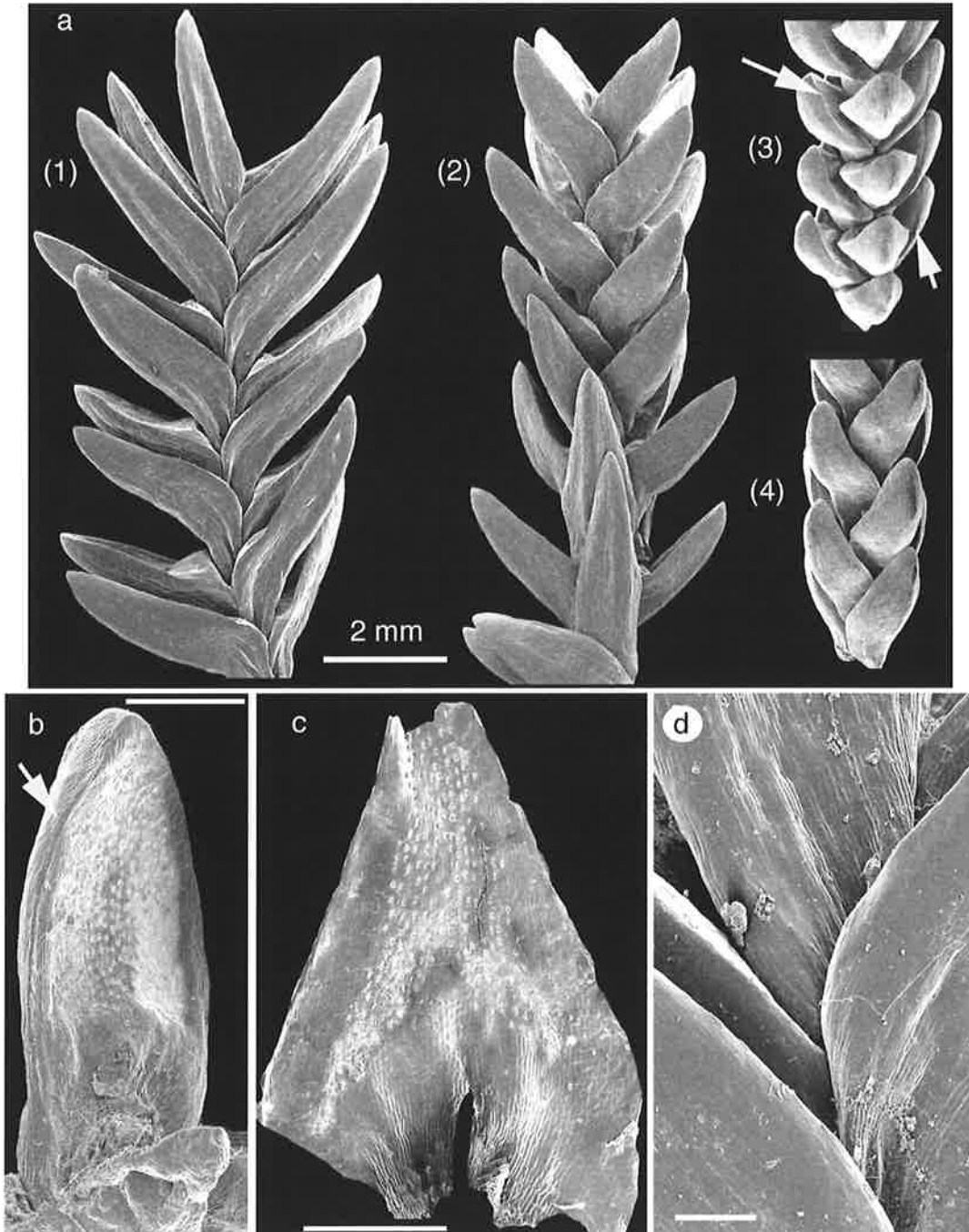
Fig. 3 a-d *Pilgerodendron uviferum* leaf arrangement
a (1-2), **b** and **d** from young fertile tree, Tasmanian Arboretum, Devonport. **a** (3-4), **c**, mature foliage (E/C/02)

- **a.** 1, 2. Fertile foliage, non-flattened leaves from young tree. Leaves almost homomorphic, lanceolate and not strictly decussate due to twisting of the stem. 3, 4. Leaves homomorphic, decussate with stomata confined to the adaxial surface (3, arrows indicating where).
- **b.** Abaxial leaf surface showing stomata covering most of the adaxial leaf surface. Stomatal area bordered by smooth surfaced epidermal cells (detail, **a**. 3; scale 500 μm).
- **c.** Cleaned leaf, adaxial surface, stomata in discontinuous rows (scale 500 μm).
- **d.** Adaxial astomatic leaf surface (scale 200 μm).

Fig. 4 a-h *Pilgerodendron uviferum* leaf cuticle SEM
Specimen E/C/02

    a. Inner surface stomata. Guard cells surrounded by 5 moderately coarse-grained, subsidiary cells with deep furrows (arrow). Periclinal walls of the subsidiary cells slightly convex (scale 20 µm).

    b. Outer surface stomata cleaned cuticle. Florin rings absent. No papillae associated with stomata (scale 20 µm).

    c. Inner surface stomata, sharing of subsidiary (most frequently polar) cells by adjacent stomata (scale 100 µm).

    d. Outer (uncleaned) surface. Stomatal area covered in wax. Stomata sunken and guard cells plugged with waxy spicules (arrows; scale 20 µm).

    e. Inner leaf surface, arrow indicating epidermal cells at the base of the adaxial surface (scale 500 µm).

    f. Outer abaxial surface. Epidermal cells with indented cell walls and small papillate nodules or holes (scale 50 µm).

    g. Inner adaxial surface, epidermal cells. Texture of periclinal cell walls coarse-grained. Anticlinal walls thick and with finer surface texture (scale 20 µm).

    h. Inner abaxial surface. Epidermal cells coarse-grained in appearance. Surface texture of calcium oxalate nodules comparatively smooth (arrow; scale 20 µm).
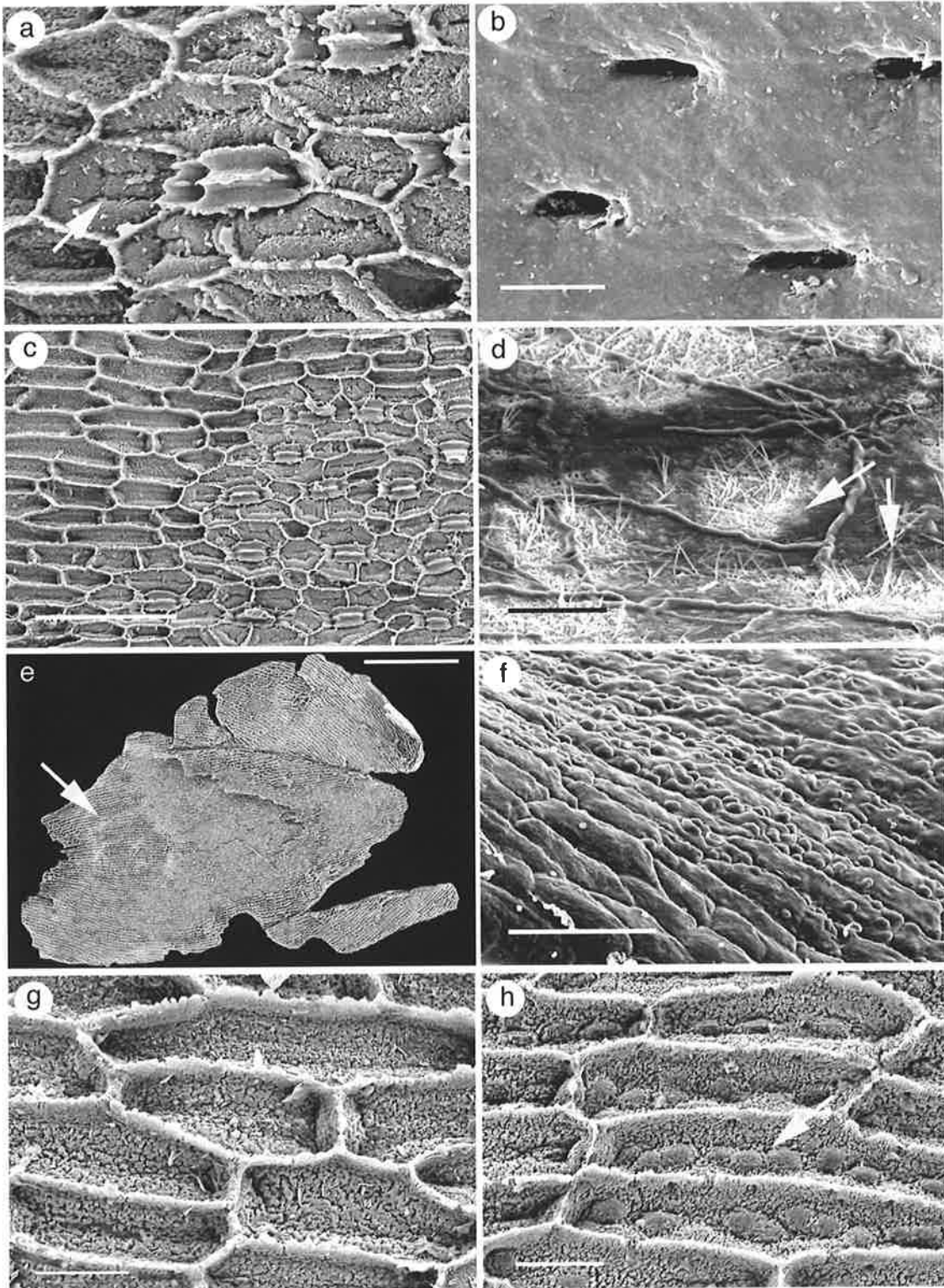
Fig. 4 a-h *Pilgerodendron uviferum* leaf cuticle SEM

Fig. 5 a-h *Pilgerodendron uviferum* pollen and ovulate cones
Specimens from the Tasmanian Arboretum

a. 1, Pollen cone from young tree with 9 pairs of decussate microsporophylls. 2, Mature, gaping, ovulate cone. Ultimate bract-scale pair larger than those below. Bracts not extending beyond the scale. 3-5, Immature cones showing progressive bract-scale development.

b. Section of pollen cone showing microsporophylls. Arrows indicating central bulge/ indentations (scale 1 mm).

c. Base of mature ovulate cone. Cone subtended by three non-fertile decussate bracts. Scale margin papillate (arrow; scale 2 mm).

d. Detail of **5a**, **5**. Elongation of the penultimate bract showing base of bract extending to the edges of the developing scale (scale 1 mm).

e. Developing bracts broad at the base. Ultimate scales closed and with papillate margins (scale 500 μm).

f. Bracts of immature scales longer than the scale (scale 500 μm).

g. Internal scale surface ridged. Margin papillate (scale 1 mm).

h. Immature cone. Arrow indicating stomata on the adaxial surface of the penultimate bract (scale 200 μm).

Fig. 5 a-h *Pilgerodendron uviferum* pollen and ovulate cones

Distinguishing features *Pilgerodendron uviferum*: -

Foliage

- Dioecious trees

- Branchlets arising on all sides of the stem
- Adult branchlets quadrangular (tetragonous)
- Leaves decussate, elongate to rounded, loosely arranged (not imbricate), and almost monomorphic

Stomata

- Stomata on adaxial surface only

Cuticle

- Subsidiary cells with deep grooves (rather than indentations)
- Subsidiary cells - periclinal walls slightly convex
- Florin rings mostly absent, but may be poorly developed
- Very few papillae associated with external stomata (Florin rings)

Ovulate cones

- Bract projections on ultimate scales of mature cones not extending beyond the scale apex

Pollen cones

- Microsporophylls with an external bulge

Discussion

Comparisons with Libocedrus and 'Libocedrus related' species

The internal leaf cuticle is somewhat similar to that of the New Zealand *Libocedrus* (more so *L. plumosa* than *L. bidwillii*) in that the subsidiary cell surface is not flat, and contains elongate grooves (although these are less well developed in *L. plumosa*). The external cuticles are quite different. The ovulate cones of *P. uviferum* and *L. plumosa* are also very similar, but those of *L. plumosa* are larger (*P. uviferum* cones are slightly larger than those of *L. bidwillii*). The base of the bract projections on *P. uviferum* ovulate cones are narrower than those of *L. plumosa*. The shape of the pollen cones of *P. uviferum* is intermediate to those of *L. bidwillii* and *L. yateensis*, but the microsporophylls are more like those of *L. bidwillii*, in that they are more broadly keeled and have a distinct central bulge. However, the microsporophylls are smaller than those of the New Zealand species (see for comparison Fig. 7a, Chapter 3), and have more microsporangia per microsporophyll (Farjon 2005). The leaves of *P. uviferum* are monomorphic. Mature leaves of *L. bidwillii* and to a lesser extent *L. plumosa* are almost, if not, monomorphic. The *matK* data of Gadek *et al.* (2000) places *P. uviferum* equally close to *L. plumosa* and *L. bidwillii*. The findings of this study suggest it is more like *L. plumosa* than *L. bidwillii*. Farjon's (2005) non-molecular data set indicate *Pilgerodendron* is more closely related to *Papuacedrus* than *Libocedrus*. The data from this study do not support this.

Most of the fertile material examined was collected from young trees (less than 20 years) growing close together, under similar conditions. As the 'precocious maturity' of *Libocedrus*-related genera and species has been discussed in the chapter dealing with *Libocedrus*, it will not be addressed here. Grosfeld and Barthèlèmy (2001) found that *Pilgerodendron* is dioecious when growing in natural conditions. It is also dioecious in cultivation (Fig. 6).

Fig. 6 Two young, fertile (male and female) *Pilgerodendron* trees at the Tasmanian Arboretum

Ecology
Present distribution

As for the two other South American Cupressaceae, *Austrocedrus* and *Fitzroya*, the present scattered distribution of *Pilgerodendron* is due to anthropogenic interference with the natural environment. The small *Pilgerodendron* populations that remain are the result of logging for timber, fires lit for land clearance, and grazing by introduced herbivores (Allnutt *et al.* 2003). Genetic diversity between these populations is high, but within populations diversity is much lower, suggesting that inbreeding is occurring (Premoli *et al.* 2001). Young seedlings will grow continuously if light and water is non-limiting (Grosfeld and Barthélémy 2004), but, although the remaining trees are now fully protected, their production of pollen or ovulate cones is poor and inconsistent from year to year (Grosfeld and Barthélémy 2001), and regeneration rates are very low (Allnutt *et al.* 2003). Although the fossil record of *Pilgerodendron* is unknown, the lineage of these trees probably extends back into the Late Cenozoic. *Pilgerodendron*, *Austrocedrus* and *Fitzroya* are dioecious and wind pollinated. The survival strategies they adapted to maximise their exposure to light *viz.* minimizing production of fertile foliage in favour of growth (girth and height) to become tall canopy trees, and the preferential colonization of disturbed, low nutrient and high altitude sites by seedlings may, unless appropriate conservation methods are put in place, soon see their demise.

Part II. *Fitzroya*

Introduction

Some fossil foliage from four of the six Tasmanian sites in this study has been attributed to *Fitzroya*. The first documentation was that of *Fitzroya tasmanensis* R. S. Hill & S. S. Whang. Aust. Sys. Bot. 9: 872 (1996) from Lea River. Fossil foliage of similar appearance from Balfour, Monpeelyata and Pioneer has also been attributed to *F. acutifolius* (Hill and Paull 2003). In the course of the current study some six-parted ovulate cones, subtended by foliage resembling *F. acutifolius*, were found in the Lea River material. The main purpose of the descriptions that follow is to compare these cones (Part III B) with fertile material from *Fitzroya cupressoides*. A brief foliage description is given, and pollen cones are also described. Extant foliage and leaf cuticle descriptions for *Fitzroya cupressoides*, *Callitris macleayana* and *Actinostrobus pyramidalis* were included in Hill and Whang (1996), and so cuticle descriptions are not included here.

Fitzroya cupressoides (Molina) I. M. Johnst., Cont. Gray Herb., n. s. 70: 91 (1924)
Monotypic

Description: Dioecious (Grosfeld and Barthelemy 2001), evergreen, long-lived (Lara and Villaba 1993), large trees to 50 m (Veblen *et al.* 1976; Allnutt *et al.* 1999), with thick, fire resistant bark (Armesto *et al.* 1995).
Distribution: Fragmented, discontinuous, temperate rainforest populations, in fairly inaccessible sites (Parker and Donoso 1993) in the southern Coastal Range of Chile, and adjacent western Argentina from 39°50'S to 42°30'S, between 100-1200 m. Extensive logging and burning have significantly reduced its range (Veblen *et al.* 1995).
Ecology: Found in low altitude bogs to the timberline. Grows in a variety of wet (2000-4000 mm annual rainfall) climatic conditions that include frosts and, in winter months, snow (Parker and Donoso 1993). Slow growing, shade intolerant, preferring poorly drained, nutrient-poor soils, where competition from other tree species is reduced (Veblen and Ashton 1982; Veblen *et al.* 1995; Lusk and Matus 2000). Wind pollinated, seeds wind dispersed (Allnutt *et al.* 1999). Also able to regenerate vegetatively (Parker and Donoso 1993; Veblen and Ashton 1982). Trees in sheltered areas are tall, and stunted where exposed (Veblen and Ashton 1982). In Chile, *Fitzroya* occurs as large infrequent trees with many other species, including *Saxegothaea conspicua* and *Caldcluvia paniculata* at low elevations. At mid elevations it is found with *Nothofagus nitida* and, at boggy sites, with *Pilgerodendron uviferum*. At high altitudes it occurs with *Nothofagus betuloides*. In Argentina it occurs with *Nothofagus dombeyi* and *Saxegothaea conspicua* at high altitudes. At sites above 1200 m (Chile and Argentina) it co-occurs with *Nothofagus pumilo* (Veblen *et al.* 1995).

Systematics
Order Coniferales
Family Cupressaceae
Genus *Fitzroya* Lindl., J. Hort. Soc. London 6: 264 (1951)
Fitzroya cupressoides (Molina) I. M. Johnst., Cont. Gray Herb., n. s. 70: 91 (1924)

Foliage and leaves: Foliage dense. Ultimate branchlets arising on all sides of the stem, short (Fig. 1b), to 4 cm, terete (Farjon 2005). Leaves persistent (to ~7 years; Lusk and Matus 2000), alternate, and in whorls, or near whorls, of three. Imbricate, and similar in size (Fig. 1a). Fertile foliage in whorls of three, not imbricate (Fig. 1b). Leaves elongate, lanceolate, broader and recurved towards the apex. Apex generally obtuse. Margins entire.

Stomatal distribution: On abaxial and adaxial surfaces in elongate bands on either side of the prominent midrib (Fig. 1a, d).

Ovulate cones: Terminal or sub-terminal on short shoots (Figs 1b, c, e; 2a). 10-12 mm in diameter to ~7 mm long. Bract-scales in two whorls of 3, the uppermost larger. Scales obovate-spathulate, highly rugose on both surfaces (Fig. 2a-c). Scale margins thick, crinkled (Figs 1h; 2d), and slightly papillate (Fig. 2h). Scales broader than bracts (e.g. Fig. 2e). Bract projections on abaxial scale surfaces, central on the upper scales, in the lower third of lower scales. Upper part of bracts broadly triangular to ovate, and outwardly keeled, with a very small, acute apex (Fig. 1g). Bracts indented towards the base (Fig. 2e). The upper section of the bracts often extending outward, away from the bract (Fig. 1h). Scale and base of bract with large cells, and indistinctly differentiated. Columella varying in number, but often 3, and alternating with the upper bract-scales, elongate (to ~3.5 mm), flattened (Fig. 2d). On the abaxial scale surface, and at the base of the bract, are frequent stomata (Fig. 2g). Subtending the cone are two whorls of broadly triangular bracts, the upper larger and subtending the uppermost bract-scales (Fig. 2b, c), the lower subtending the lower bract-scales.

Ovulate cone development: Ligulate growth is initiated at the base of bracts after the latter have broadened and expanded (Fig. 1c), and the ovules developed (Farjon and Ortiz Garcia 2005). Seeds develop rapidly, and soon extend beyond the bract-scale complexes (Fig. 1e). All bract-scales fertile. Seeds: elongate, with two broadly crescent-shaped, thin wings with undulating margins (Fig. 2f), and short micropyles (Figs 1f: 2e, f).

Pollen cones: Generally terminal, solitary (Fig. 3a). Microsporophylls 15-24, in alternate whorls of 3 (Farjon 2005), imbricate, peltate-ovate, with acute apices and tapering towards the base (Fig. 3a), margins frilled towards the apex (Fig. 3b). The abaxial surface is slightly rugose, and has a distinct central bulge in the centre or lower third of the microsporophyll (Fig. 3b, c). Microsporangia abaxial, 4-6 (Farjon 2005), small (Fig. 3b).

Specimens examined

E/C/03, Herbarium Collection, The University of Adelaide, South Australia. Collected 1999. T. Brodribb, Alerce Andino National Park. From trees ~3-4 m, growing in open swampy ground across an altitudinal gradient.

Cultivated specimen, Mt Lofty Botanic Garden, Adelaide, South Australia. Collected 10/2004. R. Paull. Small tree ~2.5 m.

Cultivated specimen, Tasmanian Arboretum, Devonport, Tasmania, Australia. Collected 11/2004, R Paull. Small tree ~1 m.

Fig. 1a-h *Fitzroya cupressoides* foliage and ovulate cones
Specimens **a-c** from Mt Lofty Botanic Gardens, **d-h** from specimen E/C/03

    a. Abaxial surface. Leaves in whorls of 3, loosely imbricate, stomata in distinct elongate, waxy bands on either side of the midrib (scale 500 μm).
    b. Foliage with ovulate cones terminal of short shoots.
    c. Immature cone. Ligulate growth at base of scale (arrow; scale 1 mm).
    d. Adaxial leaf surface. Stomata in bands on either side of the midrib (scale 200 μm).
    e. Developing cone (arrow) and immature cone (scale 1 mm).
    f. Winged seeds (arrows) with small micropyles (scale 500 μm).
    g. Small celled bract, surrounded by large cells (scale 500 μm).
    h. Mature upper scale. Abaxial and adaxial surface highly rugose. Scale margin inwardly turned, thick, crinkled, slightly papillate (scale 1 mm).
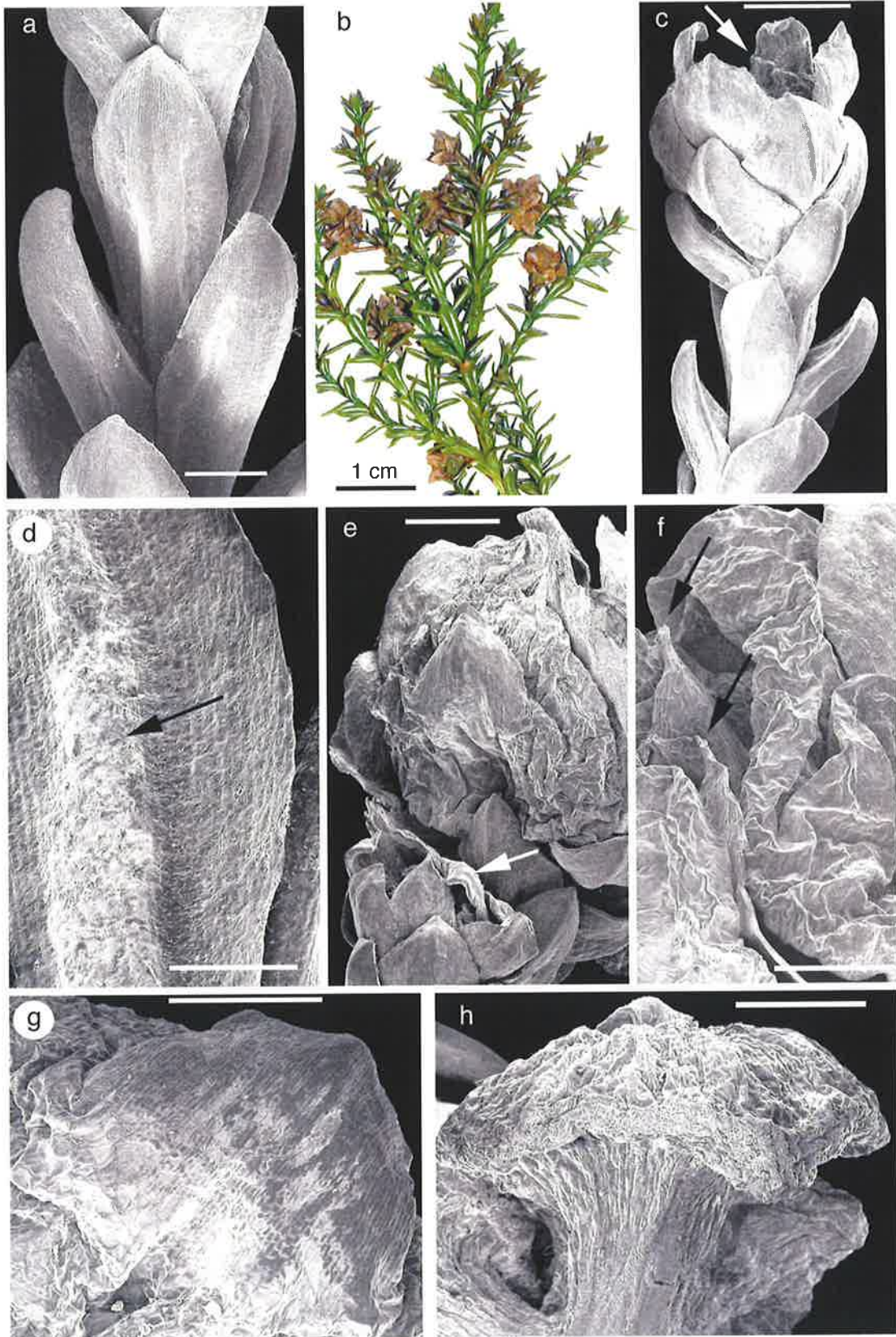
Fig. 1a-h *Fitzroya cupressoides* foliage and ovulate cones

Fig. 2a-h *Fitzroya cupressoides* ovulate cones

Specimen from E/C/03

a. Two cones. Upper immature cone terminal on a short shoot, the lower very immature cone (arrow), sub-terminal on shorter shoot.

b. Base of mature cone without seeds, showing subtending foliage in whorls of 3. Uppermost whorl, with ovate to triangular bracts and prominent abaxial midrib, subtends the upper bract-scales. Lower whorl, with smaller, similar shaped bracts, subtends the lower bract-scale whorl. Bracts on outer scales central, not extending to the scale margin, and with bluntly acute to obtuse apices.

c. Base of small cone with seeds, seen from below. Lower bract-scales not completely developed. Seeds well developed and protruding well beyond the lower bract-scales.

d. Mature cone without seeds. One columella still present, arrows indicating missing columella. Scales obovate-spathulate, highly rugose and with thickened crinkled margin.

e. Detail of **a**. Immature cone. Winged seeds with protruding micropyles (arrows). Seeds larger than scale and extending well beyond the apex of the lower scales. Abaxial scale surfaces highly rugose (scale 1 mm).

f. Elongate, flattened winged seed with small micropyle (arrow). Wings thin, broad similar in size (not obvious here), broadly crescent-shaped, and with slightly undulating margins (scale 1 mm).

g. The base of the bract and the scale are covered in stomata. One shown here (scale 20 μm).

h. Slightly papillate scale margin (scale 200 μm).
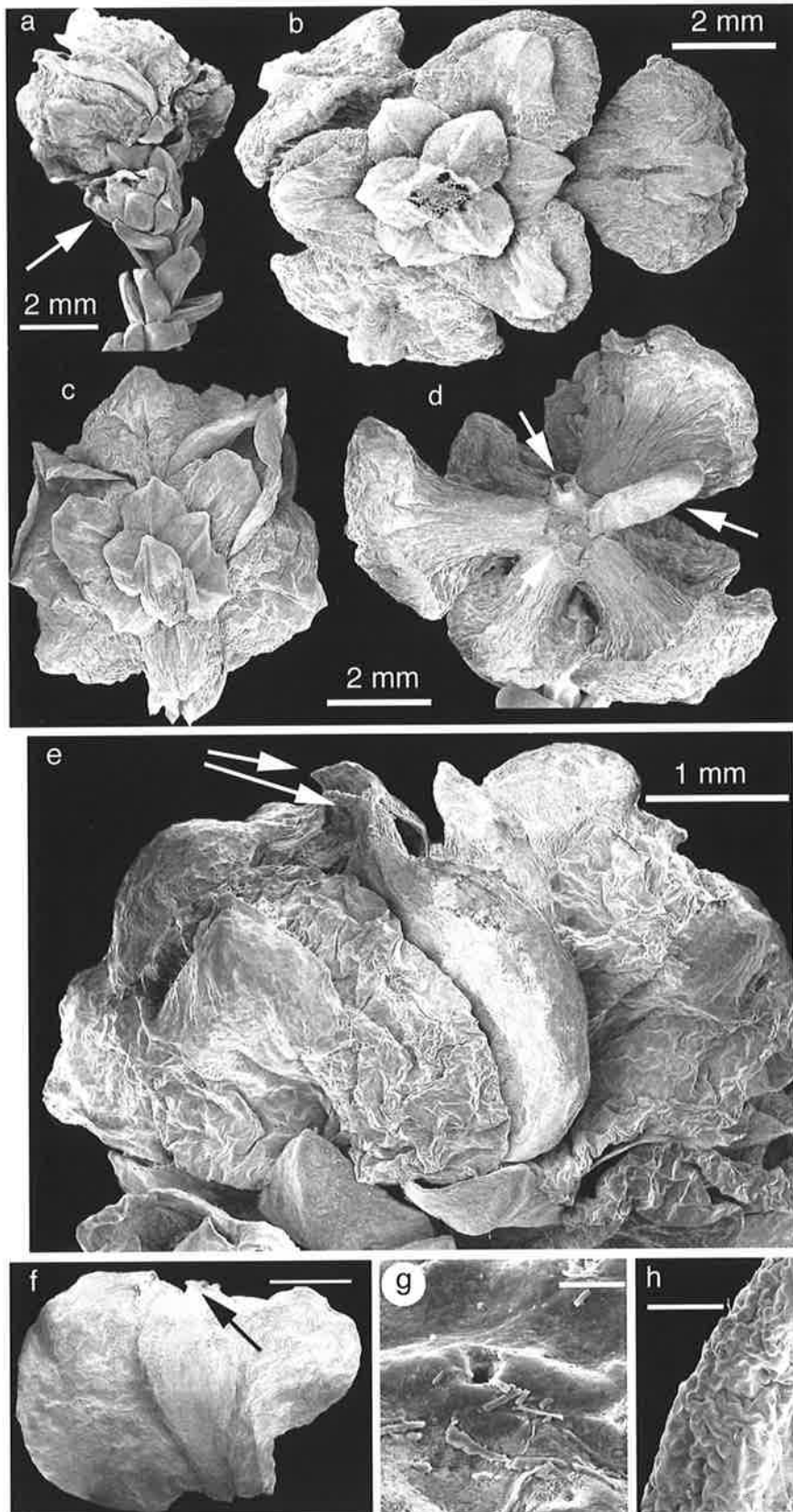
Fig. 2a-h *Fitzroya cupressoides* ovulate cones
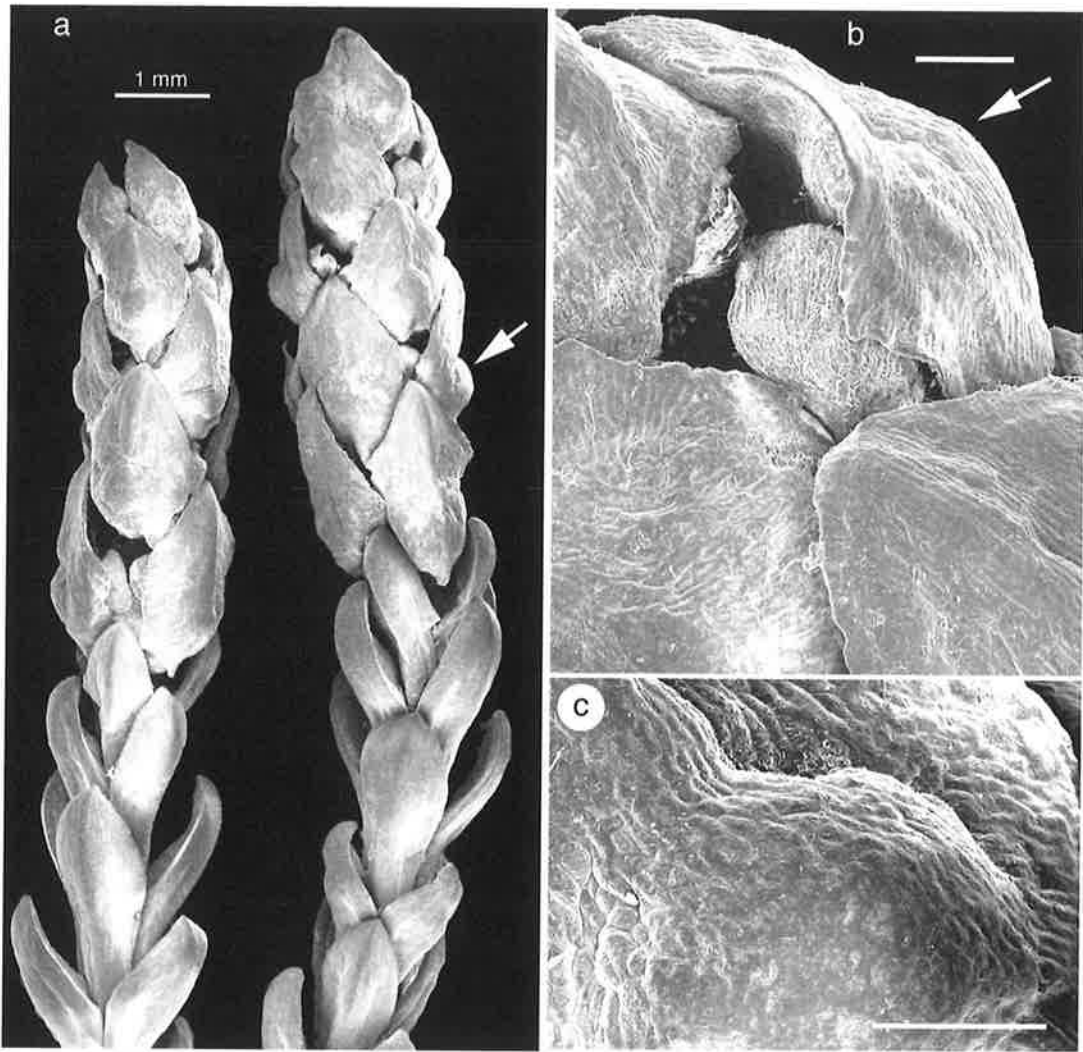
Fig. 3a-c *Fitzroya cupressoides* pollen cone
Specimen E/C/03

a. Pollen cones generally terminal, solitary. Microsporophylls in alternate whorls of 3, imbricate, peltate-ovate, with acute apices, and tapering towards the base. Lower third to half of abaxial surface with a distinct central bulge (arrow).

b. Detail of microsporophyll indicated by arrow in **a**. Microsporophyll margins slightly frilled towards the apex, abaxial surfaces slightly rugose, broadly elongate but tapering towards the base. Small microsporangium within the microsporophyll (scale 200 μm).

c. Detail of the central bulge. Very small holes indicating calcium oxalate nodules in epidermal cells (scale 200 μm).

Discussion

Ecology and dynamics of present day *Fitzroya* distribution

The distribution and decline of *Fitzroya* (and other long-lived Southern American conifers, including *Austrocedrus* and *Araucaria araucana*) was once attributed to climate change. It is now believed that this decline is largely the result of a change in frequency of naturally occurring, large-scale disturbances (earthquakes, volcanic ejecta eg ash, scoria, lava flows, fire and wind-throw), which create large clearings in established dense canopy forests, linked with climatic variability (Lara 1991 in Veblen *et al.* 1995; Donoso *et al.* 1993; Armesto *et al.* 1995). Fire and wind-throw are probably of greater importance near the Chilean coast (Armesto *et al.* 1995) than in Argentina. In closed canopy forests, small clearings, generated by tree fall, allow some *Fitzroya* reestablishment, but are more likely to be filled by shade-tolerant species (Veblen *et al.* 1981). The long life span of *Fitroya* (<3,000 years; Lara and Villaba 1993) enables it to persist in infrequently disturbed areas (Veblen *et al.* 1995). Its opportunistic establishment on high light sites creates mosaics of same age stands in established forests (Donoso *et al.* 1993).

The present highly disjunct distribution of *Fitzroya,* to sites largely inaccessible to humans (Parker and Donoso 1993), is largely due to intense logging, and burning by European settlers (from the mid-1800's) to create agricultural and grazing land (Armesto *et al.* 1995). Commercial logging was banned in 1976 (Armesto *et al.* 1995), when it was realized that *Fitzroya* was endangered. In heavily logged areas, *Fitzroya* regeneration has been impeded by repeated burning, cattle grazing (Fraver *et al.* 1999) and the absence of nearby seed producing trees (Parker and Donoso 1993). *Fitzroya* has poor seed viability (Donoso 1993 in Veblen *et al.* 1995), and most of its seeds fall in winter, when the weather is wettest (Parker and Donoso 1993). Snow cover breaks dormancy, and stratifies the seeds, aiding the likelihood of successful germination (Donoso *et al.* 1993). Seedlings are shade intolerant (Armesto *et al.* 1995) and, like most conifers, regenerate best on high light, disturbed sites (Donoso *et al.* 1993) with nutrient poor, but not barren, soils. They appear to need some soil, and moisture retaining humus, (rather than leaf litter) to survive through summer (Veblen and Ashton 1982; Silla *et al.* 2002). Rotting logs in forest gaps provide a good, relatively high light seedbed (Donoso *et al.* 1993; Parker and Dononso 1993). However, in fertile and low light sites, slow growth rates (Parker and Donoso 1993) lead to it being outgrown by angiosperms (Lusk and Matus 2000). At mid altitude sites, seedling recruitment ceases when trees on regenerated sites have grown sufficiently to close the canopy (Silla *et al.* 2002).

Fitzroya has thick bark (which may be a pre-adaptation to burning; see Armesto *et al.* 1995), and is also capable of vegetative reproduction (Veblen and Ashton 1982; Parker and Donoso 1993). It is known to sucker from the roots after light fires (Veblen and Ashton 1982), and at higher altitudes, to produce roots on ground-touching branches via layering (Parker and Donoso 1993). At lower altitudes regeneration is via seeds (Parker and Donoso 1993). The absence of young trees in southwest Argentinean forests noted by Tortorelli (1956; see Veblen and Ashton 1982) is most likely due to closed canopies and too much competition from angiosperms. Continued regeneration is best in *Fitzroya-Pilgerodendron* or *Fitzroya-Nothofagus betuloides* forests where canopies are more open (Donoso *et al.* 1993). *Fitzroya* retains its foliage for 5-6 years or more (longer than the broad leafed angiosperms with which it grows), and is thus able to maximise nutrient retention. It is also less preferable to browsers (Lusk and Matus 2000). Given the right conditions *Fitzroya* regenerates successfully (Silla *et al.* 2002). In cultivation (this study) young trees 1-2.5 m (specimens from Tasmania and

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South Australia) produce numerous pollen and ovulate cones. This probably also occurs in *Fitzroya's* natural environment.

Past *Fitzroya* distribution and dynamics

Little is known of the pre-Pleistocene macro-fossil floras of southern South America (Markgraf *et al.* 1995). A number of recent publications (c.g. Wilf *et al.* 2005; Hinojosa and Villagrán 2005; Hinojosa *et al.* 2006) have indicated that Patagonian Eocene floras were highly diverse but are more concerned with leaf physiognomy, and the implications leaf size has in determining past climates, than fossil identification (Wilf *et al.* 2005; Hinojosa and Villagrán 2005; Hinojosa *et al.* 2006), although Hinojosa *et al.* (2006) do indicate that present day Chilean floras contain trees with similar leaf morphology to Late Eocene and Early Miocene fossils. Wilf *et al.'s*. (2003) paper is more helpful, as it illustrates some of this flora and makes some tentative identifications. Earlier papers (see references in Markgraf *et al.* 1996) indicate that *Fitzroya* (also *Araucaria, Podocarpus, Weinmannia* and 3 Proteaeceae genera) was present in Paleocene-Eocene Patagonian sediments.

Romero (1986) suggests that the successive floral sequence in Patagonia for the Cenozoic is: – paratropical rain forest (Early Eocene), subtropical forest (mid-Eocene), mixed mesophytic forest (Late Eocene), to mixed hardwood forest (Oligocene), which would indicate gradual drying (and possibly cooling) over that time. Hinojosa and Villagrán's (2005) leaf physiognomy data (which concurs with that of Axelrod *et al.* 1991) indicate that the Eocene-Early Miocene was a time of mild and equable climates with a temperature range of 15-20°. Precipitation throughout this time was year round, but steadily decreased as the South American continent drifted slowly northward into lower latitudes. Romero (1986) and Hinojosa and Villagrán (2005) conclude (as Kemp [1978] suggested for southern Australian Eocene floras) that these climates have no modern analogue. The Early Eocene flora of central Chile was tropical, and unlike that of southern South America Gayó *et al.* (2005). The accelerated rise of the Andean Cordillera in the mid-Late Miocene (Gregory-Wodzicki 2000a; 2000b; Graham *et al.* 2001; Anders *et al.* 2002), and continued northward movement of the continent, into lower latitudes, altered climatic dynamics, mean annual temperatures exceeded 20°, and climates became more seasonal, with wet winters and dry summers (Hinojosa and Villagrán 2005). The flora at this time was subtropical (Hinojosa *et al.* 2006).

Present day rainforests on the southern western margin of South America are geographically isolated from other South American forests by arid and semi-arid lands (see references in Hinojosa *et al.* 2006). This probably occurred some time before the Pliocene (Hinojosa *et al.* 2006). Despite the cold, fluctuating glacial conditions of the Quaternary, many forest taxa that had grown in the warmer conditions of the Paleocene and Early Neogene are still found there, though with restricted ranges (Hinojosa et al. 2006). Quaternary pollen data suggest that the last Andean glaciation (~20,000 year ago) restricted the ranges of southern South American conifers (including *Fitzroya* and *Austrocedrus*) and that they survived in small refugia at the edge of glaciers (Pastorino and Gallo 2002; Pastorino *et al.* 2004), and at low elevations near the coast (Markgraf *et al.* 1996). Genetic data (Premoli *et al.* 2000; Allnutt *et al.* 2003) support these findings and suggest the more northern (current) populations in Argentina are due to migration from the south (Premoli *et al.* 2000). The continued presence of *Fitzroya* (and *Austrocedrus*), in western southern South America is probably due to the mediating effect of the Pacific Ocean on climate, and to intermittent geological disturbance. Should (when) cold glacial conditions return, its disjunct and often high altitude distribution make it vulnerable to extinction.

Part III A. A revision of previously described Cupressaceae related fossils

Introduction

This section reviews previously described Cupressaceae macrofossil material from one New South Wales site and three Tasmanian sites (Hill and Carpenter 1989). These are *Libocedrus acutifolius* and *L. obtusifolius* (leaves) - Lake Bungarby, NSW (Whang and Hill 1999), *Libocedrus jacksonii* (leaves) and *L. mesibovii* (ovulate cones - Little Rapid River), *Austrocedrus tasmanica* (ovulate cones) - Monpeelyata, and *Libocedrus morrisonii* and *Papuacedrus australis* (leaves) – Pioneer (Hill and Carpenter 1989). All fossils are compared with extant foliage and ovulate cones from *Papuacedrus, Libocedrus, Austrocedrus, Pilgerodendron* (Part I, Chapters 2-5). Localities and site descriptions precede each description. The fossils are reviewed in descending age, those from the oldest site (Lake Bungarby) first, those from the youngest (Pioneer) last.
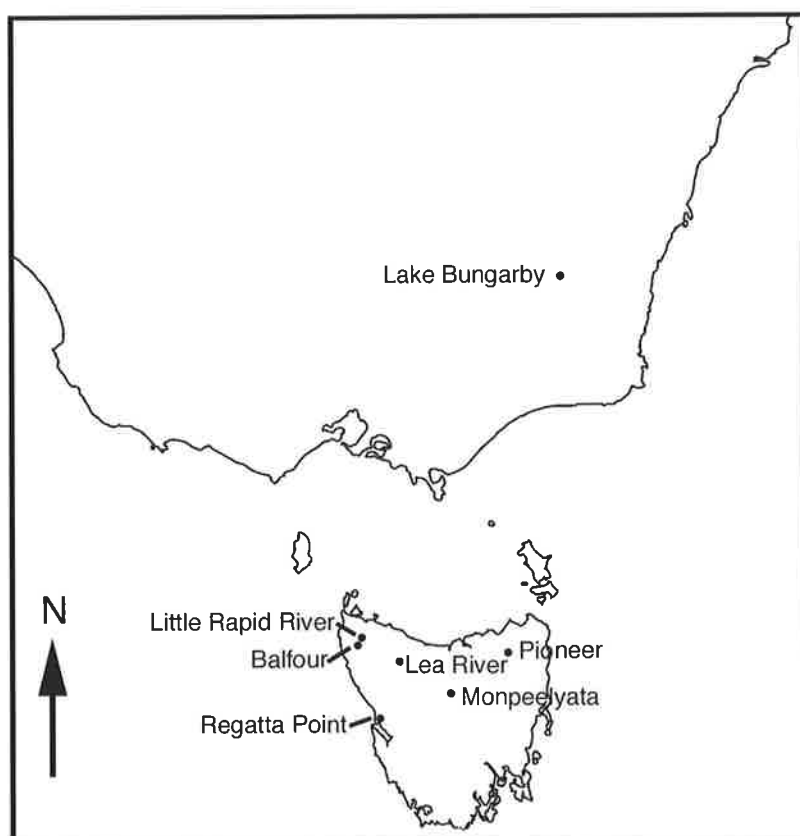
Fig. 1 Fossil localities, Tasmania and southeast New South Wales

1. Lake Bungarby, New South Wales (36°09'S, 149°08'E)

Lake Bungarby is the largest of numerous lakes that dotted the area that is now the New South Wales southern highlands in the mid-Paleocene–Early Eocene. within the lake reach a maximum thickness of ~150 m, and palynological data suggest the sediments are Late Paleocene (~58-60 Ma; Taylor *et al.* 1990). Sediments Fine-grained lacustrine sediments are interspersed with thin layers of plant debris and lignite layers.

The fossil flora (in the organic layers) is dominated by large leaved angiosperms but also contains small leaved conifers (Taylor *et al.* 1990; Pratt *et al.* 1992).

Two foliage specimens were examined from this site. They are compression fossils in a mudstone matrix. They were named *Libocedrus acutifolius* and *Libocedrus obtusifolius* by Whang and Hill (1999). Only one species is recognised and described here. Specimens were examined from black and white pre-digital photographs, and the quality of the enlarged illustrations is poor. As scale bars were absent from originally published photographs none are included here.

Foliage
Systematics
Order Coniferales
Family Cupressaceae
Genus *Libocedrus* Endl., Syn. Conif.: 42 (1847)
Libocedrus acutifolius Whang & Hill. Aust. Sys. Bot 12: 248 (1999)

Holotype: LB-217. Photographs of the specimen are stored at the School of Earth and Environmental Sciences, The University of Adelaide, South Australia.
Type locality: Lake Bungarby (36°09'S, 149°08'E)
Specimen examined LB-217

Libocedrus obtusifolius Whang & Hill. Aust. Sys. Bot 12: 248 (1999)

Holotype: LB-75. Photographs of the specimen are stored at the School of Earth and Environmental Sciences, The University of Adelaide, South Australia.
Type locality: Lake Bungarby (36°09'S, 149°08'E)
Specimen examined LB-075

Amended diagnosis
Foliage and leaves: Two foliage types, juvenile and adult. Branchlets sub-opposite to alternate. Leaves decussate, scale-like. Juvenile branchlets flattened. Juvenile leaves dimorphic, lateral leaves larger than facial, fused for around half their length, and loosely imbricate. Lateral and facial leaves with acute apices (Fig. 2b). Upper, free portion of the leaf keeled slightly inward. Facial leaves on branchlets smaller than lateral leaves. Their acute apices reach to touch the facial leaf pair above (Fig. 2d). Adult branchlets less flattened and almost quadrangular. Leaves almost monomorphic, imbricate, with facial leaves only slightly smaller than lateral (Fig. 2a).
Stomatal distribution: Scattered, and short rows, parallel to the long axis of the leaf (description taken from original paper, not apparent from photographs). Dorsal, ventral and adaxial distribution unknown.
Cuticle description: Inner surface (Fig. 3a, b) - guard cells elongate and generally surrounded by 5, mostly elongate, subsidiary cells. The latter fold down around the guard cells, forming a deep groove. This is dissected by the adaxial subsidiary cell walls. The periclinal subsidiary cell walls are slightly convex and contain indentations. The latter occur throughout the cell and are most frequent at the outer corners of adjacent cells. Anticlinal walls thick, and coarse-grained at the base. Outer surface (Fig. 3c) - Florin rings high ridged, slightly lobed and often with a peripheral groove. Numerous small, and mostly round papillae surround the Florin rings. Outer surface epidermal cells convex.
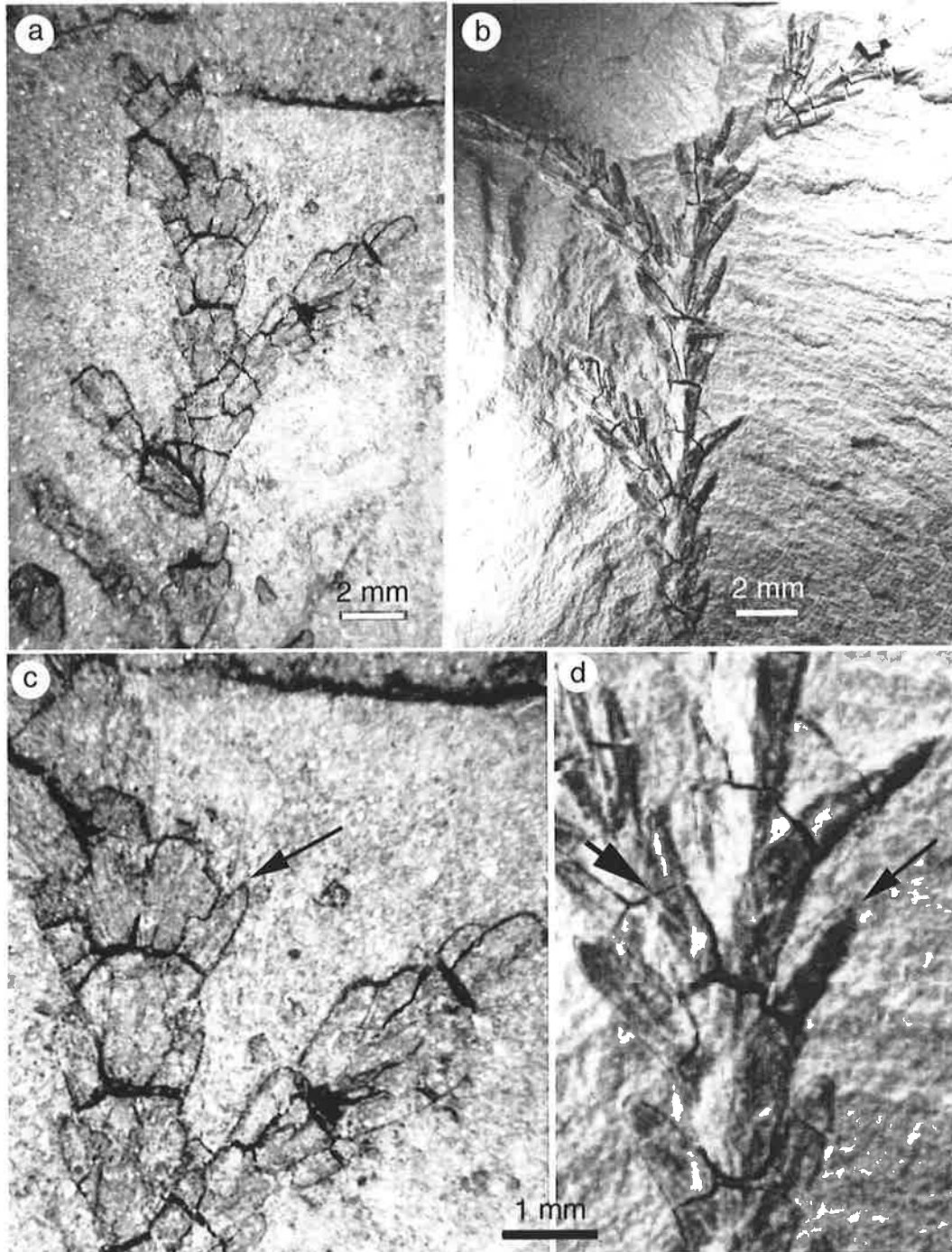
Fig. 2a-d Compression foliage, Lake Bungarby NSW

a. Degraded fossil - mature foliage (specimen LB-075 - *L. obtusifolius*).

b. Well preserved fossil – flattened foliage showing alternate to sub-opposite branching (specimen LB-217 - *L. acutifolius*).

c. Detail of a. Monomorphic leaves, some with acute apices (arrow).

d. Detail of b. Arrow illustrating the similarity of the leaf apices in this specimen with those in c. Facial leaves on branchlets smaller than lateral leaves and with apices reaching to the facial leaf pair above (left arrow).
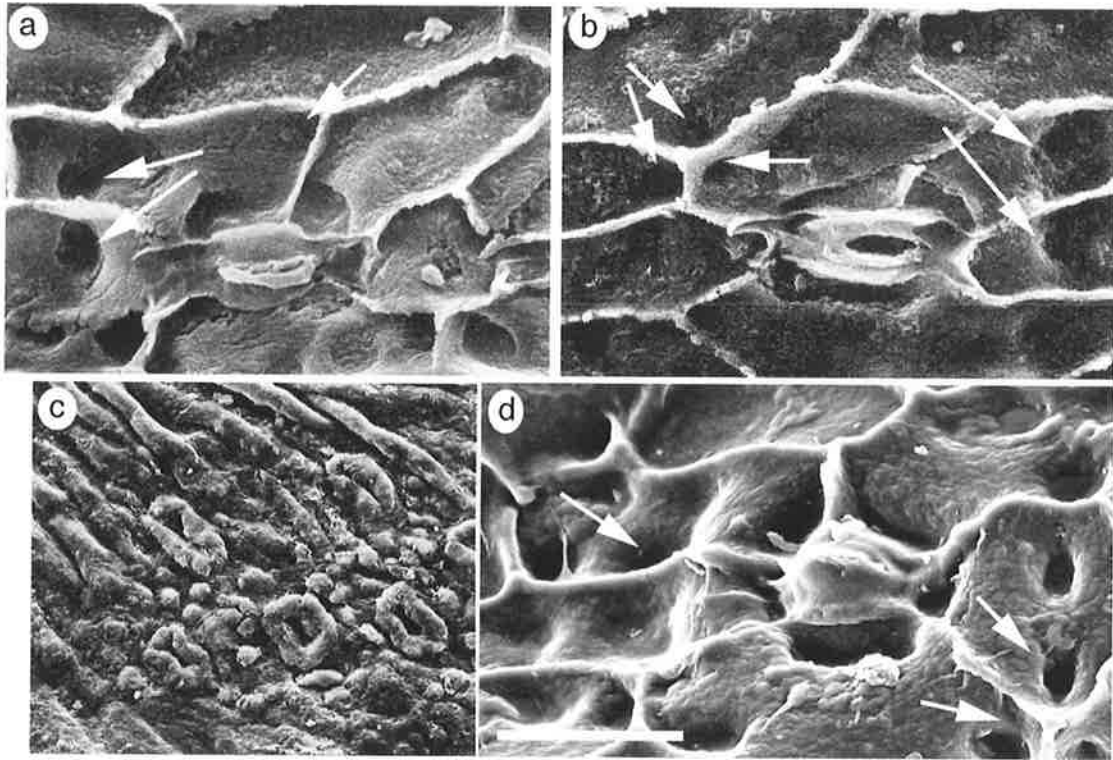
Fig. 2a-d Lake Bungarby *Libocedrus* cuticle (a-c), extant *L. austrocaledonica* (d)
The cuticle of the adult specimen is not illustrated but is identical to that of the juvenile specimen.

a. Inner cuticle from mature foliage. Guard cells elongate and surrounded by a deep groove, this is broken only by the adaxial walls of the subsidiary cells. Periclinal cell walls moderately coarse-grained and slightly convex. Five subsidiary cells with deep indentations (arrows) at the outer corners of the cells and also in the centre of the cells (scale unknown; LB-075).

b. Inner cuticle from juvenile foliage. This appears somewhat thinner than that of the mature specimen, but has the same characteristics, including the distribution of indentations in the subsidiary cells (arrows; scale unknown; specimen LB-217).

c. Outer cuticle from juvenile foliage. Florin rings slightly lobed, high ridged and with a peripheral groove. Papillae numerous, small and mostly round in shape (these correspond with the indentations on the inner cuticular surface). Stomata oriented in the same direction and in short discontinuous rows. Epidermal cells convex (scale unknown; LB-217).

d. Inner cuticle, *Libocedrus austrocaledonica*. Guard cell surrounded by a well-developed, deep groove. Periclinal cell walls moderately coarse-grained and with indentations at the corners of adjacent cells and in the centre of the cells (arrows; scale 20 μm; specimen 5859).

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Discussion

Whang and Hill (1999) suggested that these two specimens have characteristics of both *Libocedrus* and *Austrocedrus*, but opted to assign them to *Libocedrus*. This assignment is accepted as correct. However, their argument that they represent two species is not accepted. At first impression the specimens look dissimilar. One (LB-217) is flattened and well preserved (Fig. 2b), the other (LB-075) is more three dimensional but degraded and fragmentary. The internal and external cuticles of the two specimens (Fig. 3a-c) are indistinguishable (Whang and Hill [1999] failed to notice the indentations on the periclinal cells of LB-217 and yet observed papillae on the outer leaf surface), and they exhibit characteristics common to extant *Libocedrus* (see eg *L. austrocaledonica*, Fig. 3d). It is suggested that the two samples are from the same species, and that LB-217 is juvenile foliage, LB-075 mature foliage. The leaves of LB-217 are dimorphic, flattened, very loosely imbricate, and have acute apices. Those of LB-075 are more robust, almost monomorphic, and more or less quadrangularly arranged. The foliage of the two specimens, and the arrangement of the branchlets is quite similar to that of extant *L. bidwillii* (see *L. bidwillii* Fig. 2a-c, juvenile and adult foliage, Chapter 3, *Libocedrus*). Fig. 1c and 1d are been included so that the size of the Lake Bungarby specimens can be directly compared with that of all the other fossils, and also with extant species. They are most similar in size (but slightly larger) to the LRR1 *Libocedrus* (this section), and extant *L. bidwillii* (Chapter 3 *Libocedrus*). The Lake Bungarby specimens are assigned to one species, *Libocedrus acutifolius* Whang & Hill. Aust. Sys. Bot 12: 248 (1999).

The sediments at Lake Bungarby contain large leaved angiosperms (R Hill pers. com. 2006), Podocarpaceae, Araucariaceae, Casuarinaceae (Taylor *et al.* 1990), *Eucryphia* (Hill 1991) *Acmopyle* (Hill and Carpenter 1991), and *Banksieaephyllum* (Carpenter *et al.* 1994), and wood with consistently narrow growth rings (Taylor *et al.* 1990). Based on tolerances of extant descendant taxa in South American rainforests at 56°S latitude, mean annual temperatures are estimated to have been 14-20°C and rainfall between 1200-2400 mm. The altitude of the site at the time is believed to have been <400 m (Taylor *et al.* 1990). The foliage of *Libocedrus acutifolius* is remarkably similar to that of New Zealand *Libocedrus*. Its cuticles are less definitive, and bear characteristics of both New Zealand and New Caledonian species. The size of the leaves (similar to that of extant New Zealand species) suggests they were growing in conditions similar to that of today. The size of the fossil cells is not recorded and cannot be compared with those of extant *Libocedrus* species.

2. Little Rapid River, Tasmania (41°09'S, 145°14'E)

The fossiliferous sediments at this site are some 2 km south of the Little Rapid River and were exposed during road building. They represent two distinctly different sedimentary regimes, and are divided into two units (Wells and Hill 1989). Those forming the lower unit (LRR2) are dark grey, fine-grained muds interspersed with black, organic-rich layers. This <3 m unit is interpreted as having formed on a fluvial flood plain, with standing water, in which mud and plant remains were deposited during times of over-bank flooding. Between this and the upper (LRR1) unit are 20-40 cm of laterally continuous sediments. The lower section of this sequence consists of largely carbonaceous material. It is thought to represent *in situ* deposition in slightly higher lying swampy areas. It is dissected by unusually shaped channels that are in filled with sediments. The latter consist of fragments of organic material and clay at the base, overlain first by fine-grained, light coloured sediments, and then by well-sorted sands. The means by which the sediments were breached and later in filled are not understood, but may be the result of freeze-thaw associated with periglacial conditions (Hill 1995). The base of the upper ~1 m (LRR1) unit is deeply weathered. This unit consists of unlayered sands and mud, interspersed with black organic matter, and suggests a return to fluvial deposition (Hill 1995). Palynological dates indicate both units are Early Oligocene (Macphail *et al.* 1994). The site is thought to represent a low altitude forest. Recorded fossil taxa at this site include Araucariaceae, Podocarpaceae, Proteaceae, *Austrosequoia tasmanica* (Hill *et al.* 1993), *Nothofagus* (including species related to subgenera now only found in New Zealand, New Caledonia, New Guinea and South America), and *Gymnostoma*.

The fossils discussed here come from the upper LRR1 sequence.

A. Foliage
Systematics
Order Coniferales
Family Cupressaceae
Genus *Libocedrus* Endl., Syn. Conif.: 42 (1847)
Libocedrus jacksonii Hill & Carpenter Alcheringa 13: 95 (1989)

Holotype: LRR1-880, stored in the School of Earth and Environmental Sciences, The University of Adelaide, South Australia.

Type locality: Little Rapid River (41°09'S, 145°14'E)
Since the original descriptions were made some new specimens have been found in the same sediments.

Specimens examined LRR1-880, 1263, 1266, 1267, 1268, 1269, 1270, 1482, 1483, 1484, 1485, 1486, 1487, 1488, 1489, 1490, 2205.

Amended diagnosis

Foliage and leaves: Leaves decussate, scale like, highly dimorphic, imbricate. On branchlets, lateral leaves (1.5-2 mm long) and larger than facial, bilaterally flattened, fused for around one half of their length, outwardly keeled, with bluntly acute apices (Fig. 4a 1-3), and entire margins (Fig. 4c). Lateral and facial leaves on main axes larger (~3 mm) and similar in size, with facial leaves extending down between the lateral leaves (Fig. 4a 2). On the ventral surface (main axes) the lower halves of paired lateral leaves are separated by a broad groove (Fig. 4a 2). Facial leaves with a central keel, acute apices that do not extend to the base of the facial leaves above (Fig. 4d), and frilled margins (Fig. 4e).

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Stomatal distribution: Stomata closely packed, and on lateral leaf dorsal surfaces in small, clearly defined grooves in the central lower third to half of the leaf (Fig. 4b, c, f). Stomata on facial leaves in small grooves on either side of the central keel and towards the base, where they are largely concealed by the lateral leaves below (Fig. 4d, f). On ventral leaf surfaces, stomata few, towards the base, and concealed by overlapping leaves. Stomata on adaxial leaf surfaces in short rows parallel to the centre of the leaf (Figs 4e; 3c).

Cuticle description: Stomatal guard cells surrounded by a deep groove (Fig. 5g). Subsidiary cells with numerous indentations (Fig. 5a), and frequently shared by adjacent guard cells (Fig. 5h). Florin rings on outer leaf surface high ridged, highly lobed, with a peripheral groove, and surrounded by numerous round papillae (Fig. 5b, d). Epidermal cells on the inner cuticular surface coarse-grained (Fig. 5e), and on much of the outer surface, with convex surfaces and numerous holes (Fig. 5f).

Fig. 4a-f *Libocedrus jacksonii* LRR1

a. SEM. Sections of branchlets showing varying leaf morphology (1) dorsal surface, (2-3) ventral surface. Lateral leaves bifacially flattened and, except on main axes (see 2), larger than facial leaves, On main axes the facial leaves extend between the laterals (arrow). On the ventral surface, main axis lateral leaves are separated in the lower half by a broad groove (specimens LRR1-1268 (1), LRR1-2205 (2), LRR1-1269 (3)).

b. SEM. Dorsal surface, lateral leaf. Stomata closely packed and in a small central groove (arrow) at the base of the leaf (scale 200 μm; specimen LRR1-1270).

c. SEM. Dorsal surface, lateral leaf. Leaf margin entire (white arrow), stomata (black arrow) towards the base of the leaf (scale 200 μm; specimen LRR1-1270).

d. SEM. Dorsal surface, facial leaf. Facial leaf small, with an acute apex. Stomata in small grooves (arrows) on either side of the central keel (scale 200 μm; specimen LRR1-1268).

e. LM. Facial leaf with frilled margin (lower left). Stomata in the upper two thirds of the leaf in rows parallel to the leaf centre, but towards the base more closely oriented to the leaf margin (scale 0.5 mm; specimen LRR1-1267).

f. SEM. Dorsal leaf surface with arrows indicating positions of stomatal grooves (scale 200 μm; specimen LRR1-1268).

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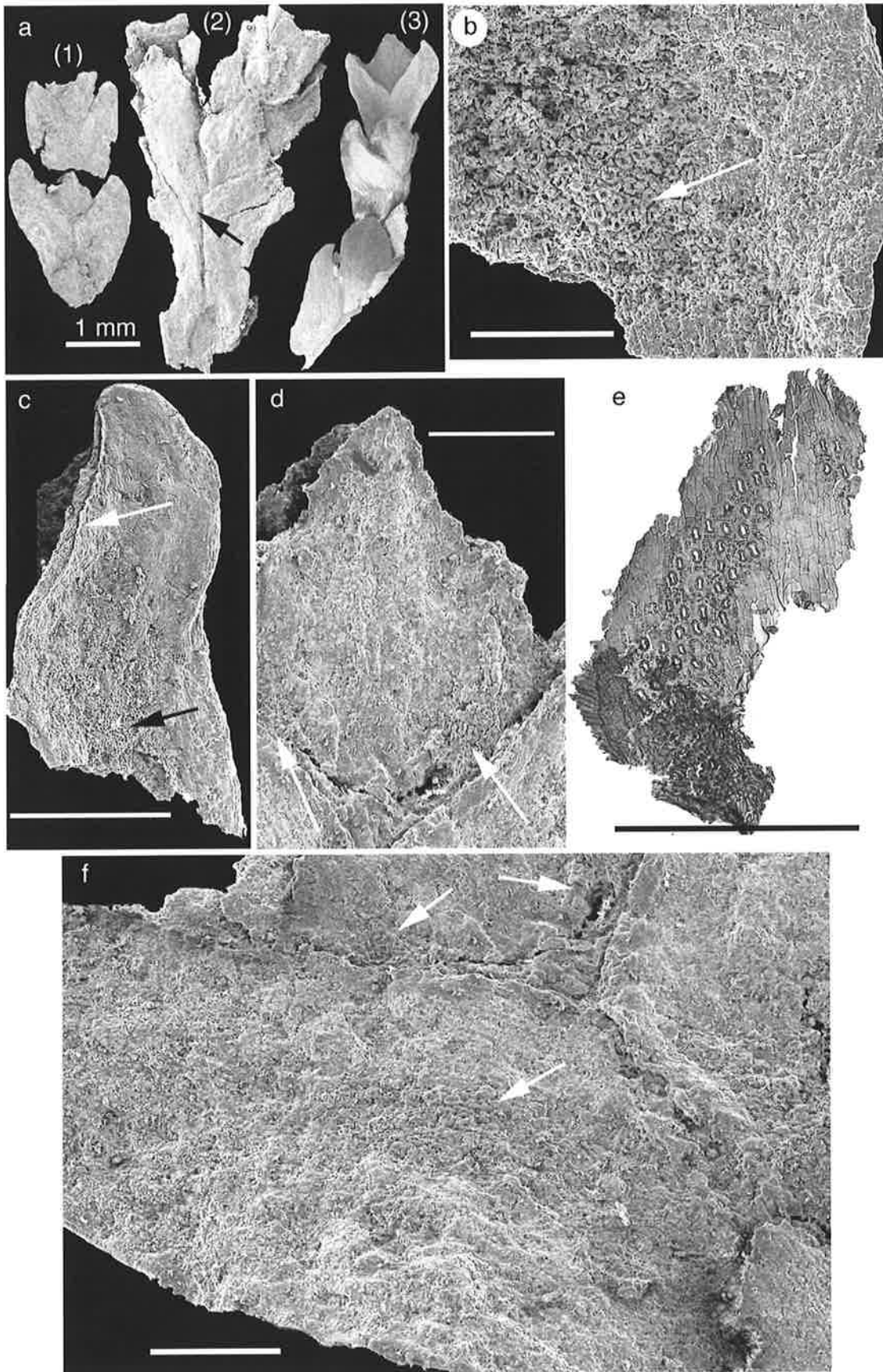
Fig. 4a-f *Libocedrus jacksonii* LRR1

Fig. 5a-g *Libocedrus jacksonii* leaf cuticle

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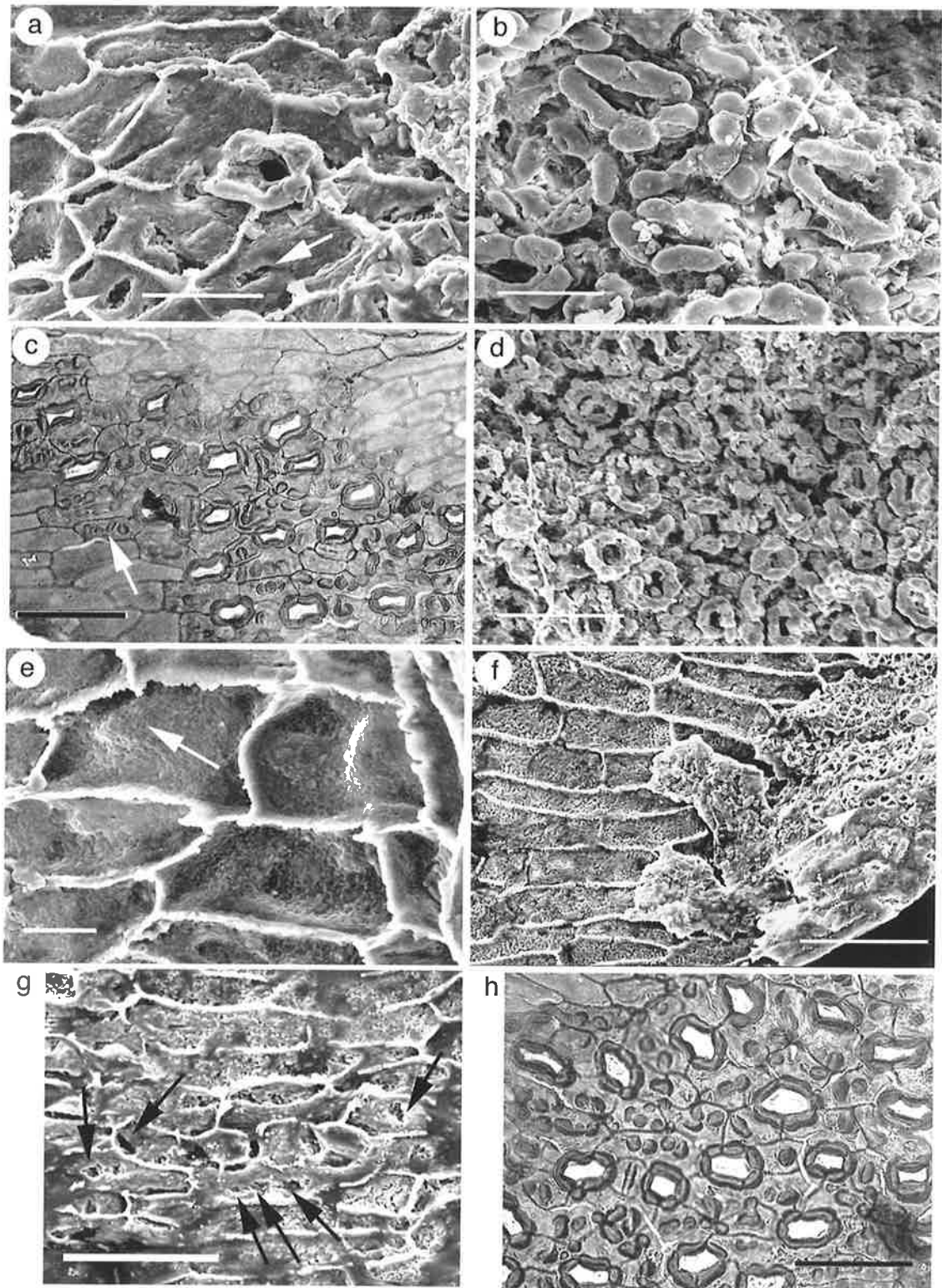
Fig. 5a-g *Libocedrus jacksonii* leaf cuticle

a. SEM, poor cuticle. Stomata monocyclic with 5 subsidiary cells. Subsidiary cells with deep indentations (arrows; scale 20 μm; specimen 1267).

b. SEM. Florin rings with numerous (~6) well-developed lobes, and surrounded by a peripheral groove. Papillae (arrows) frequent, small, and generally round in shape (scale 20 μm; specimen 1266).

c. LM. Section of facial leaf, adaxial surface. Stomata in short rows, and generally parallel to the leaf centre. Subsidiary cells with numerous papillae (arrow; scale 100 μm; specimen 1267).

d. SEM, outer dorsal surface. Numerous, closely packed stomata with highly lobed Florin rings (scale 50 μm; specimen 1270).

e. SEM. Irregularly shaped, small, coarse-grained, concave epidermal cells with relatively large nodules (arrow). Anticlinal cell walls relatively smooth grained (scale 10 μm; specimen 1267).

f. SEM. Specimen showing elongate epidermal cells. The inner cell surfaces (left) are coarse-grained. Outer epidermal cells (right) slightly convex and containing numerous small holes (arrow). Anticlinal cell walls indented (scale 50 μm; specimen 2205).

g. Poor SEM cuticle preparation, but arrows indicating indentations in the periclinal walls of subsidiary cells. Guard cells surrounded by a broad, deep groove (scale 50 μm; specimen 2205).

h. LM. Stomata closely packed and with guard cells often sharing several subsidiary cells. Subsidiary cells with numerous papillae (scale 50 μm; specimen 1267).

Discussion

The current study adds two important characters to Hill and Carpenter's (1989) original description. These are indentations in the internal periclinal cell walls of the subsidiary cells, and the distribution of stomata. The closely packed stomata, with their highly lobed Florin rings, numerous small round papillae, and indented subsidiary cells are most similar to extant New Caledonian *Libocedrus* species. The stomatal distribution (mostly on the dorsal, but also on the ventral surface), in grooves close to the bases of lateral and facial leaves, is most like that of *L. chevalieri*, but the fossil leaves appear to be more flattened than this extant species, and the apices of the facial leaves do not extend to the base of the facial leaves above. The specimens are also considerably smaller than extant *Libocedrus* species. They are considered sufficiently distinctive from extant *Libocedrus* species to warrant the new species *Libocedrus jacksonii*, to which Hill and Carpenter (1989) assigned them.

B. Ovulate cones

A single ovulate cone from Little Rapid River was described by Hill and Carpenter (1989) and named *Libocedrus mesibovii*. This specimen is re-evaluated below, and several other specimens from the site are also described and illustrated. The morphology of the cones is quite variable (Fig. 6a-d). The smaller cones are possibly immature and prematurely opened. Internal structures in these cones are thought to be undeveloped seeds, rather than columellae (see e.g. immature cones of *Austrocedrus chilensis* Fig. 6c, Chapter 4, *Austrocedrus*, and *Papuacedrus torricellensis* Fig. 19e, Chapter 2, *Papuacedrus*). The cones are considered to be Cupressaceae related. Although they have some extant *Libocedrus* characteristics, they cannot be allied with any living species. They are considered to be either an extinct, or possibly intermediate *Libocedrus* species.
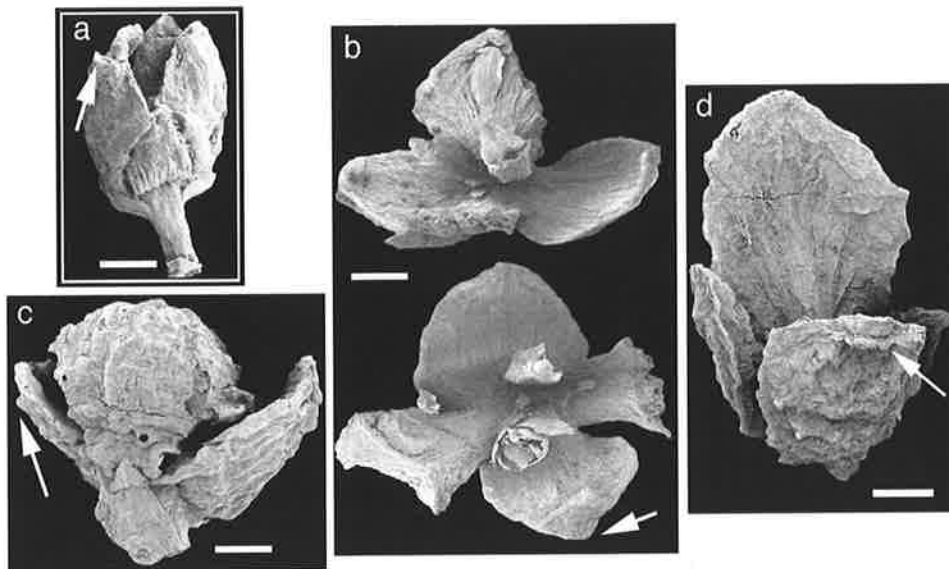
Fig. 6a-d Ovulate cones from Little Rapid River
Scale bars all 1 mm. Arrow indicate projections on the abaxial scale surface.
  a. *Libocedrus mesibovii* (Hill and Carpenter; 1989; holotype LRR1-879).
  b. Two views of specimen LRR1-2054
  c. LRR1-2890)
  d. LRR1-2892

Systematics
Order Coniferales
Family Cupressaceae
Genus *Libocedrus* Endl., Syn. Conif.: 42 (1847)
Libocedrus mesibovii Hill & Carpenter Alcheringa 13: 94 (1989)
  Holotype: LRR1-879, stored in the School of Earth and Environmental Sciences, The University of Adelaide, South Australia.
  Type locality: Little Rapid River (41°09'S, 145°14'E)
  Specimens examined LRR1-879, 2054, 2890, 2892, 5541

Amended diagnosis

Detailed descriptions of the cones take the form of figure captions (Figs 6a-d; 7a-g; 8a-f; 9a-g and 10a-b). The amended diagnosis is thus brief.

Ovulate cone: (Fig. 6a-d) Four decussate bract-scale pairs. Ultimate bract-scales larger than penultimate. Ultimate scales ovate-obovate, tapering towards the base, and with a somewhat rounded apex. Penultimate scale less tapered at the base. Bracts on the abaxial surface of both scale pairs highly rugose, and extending across the width of the scale, and almost reaching the scale apex. Bract projections on all scales close to the scale apex, and broad at the base (length unknown, but probably quite short). Scales with slightly papillate margins. Seeds possibly 4. Columella absent. Cone subtended by at least two pairs of lanceolate decussate bracts, the uppermost larger and subtending the ultimate bract-scales.

Fig. 7a-g Little Rapid River ovulate cones
With the exception of **a**, all illustrations are of LRR1-2054

    a. *Libocedrus mesibovii* (Hill and Carpenter; 1989; specimen LRR1-879). Small, possibly immature cone. Cone with 3 similar sized scales, and one damaged scale. On the abaxial scale surface there are short broad projections with acute apices. A pair of imbricate 'bracts' subtend the cone. Other bracts may also be present but are obscured by the down turned scale (scale 1 mm).

    b. LM photographs and 1 SEM photograph showing a variety of views of the same (possibly immature) cone. Numerous small holes on the abaxial cone surface (black arrows) are the result of insect damage. White arrows indicating immature seeds inside the cone. The upper bract-scale pair is slightly longer and broader than that of the lower pair

    c. The broad scale in the foreground lacks a bract projection. The bract (1) appears to have been partially removed from the scale (2). The slightly smaller penultimate bract-scale pair to the right and left of the ultimate bract-scale pair are narrower. Their bract projections are close to the scale apex. Projection tips missing (right white arrow). Lower white arrow indicating the lower part of the bract extends to the margin of the scale. The surface of this bract is highly rugose. An immature seed is visible within the cone.

    d. Arrows indicating insect damage (scale 1 mm). Inset showing possible maggot wood borer (? *Phytobia* – Nathan Schiff pers. com 2006; scale 50 μm).

    e. Detail of insect damage (scale 200 μm).

    f. Subtending foliage, decussate, fused towards the base (arrow; scale 500 μm).

    g. Detail of penultimate bract. Outer scale and bract surfaces highly rugose. Arrow indicating missing bract projection (scale 500 μm).
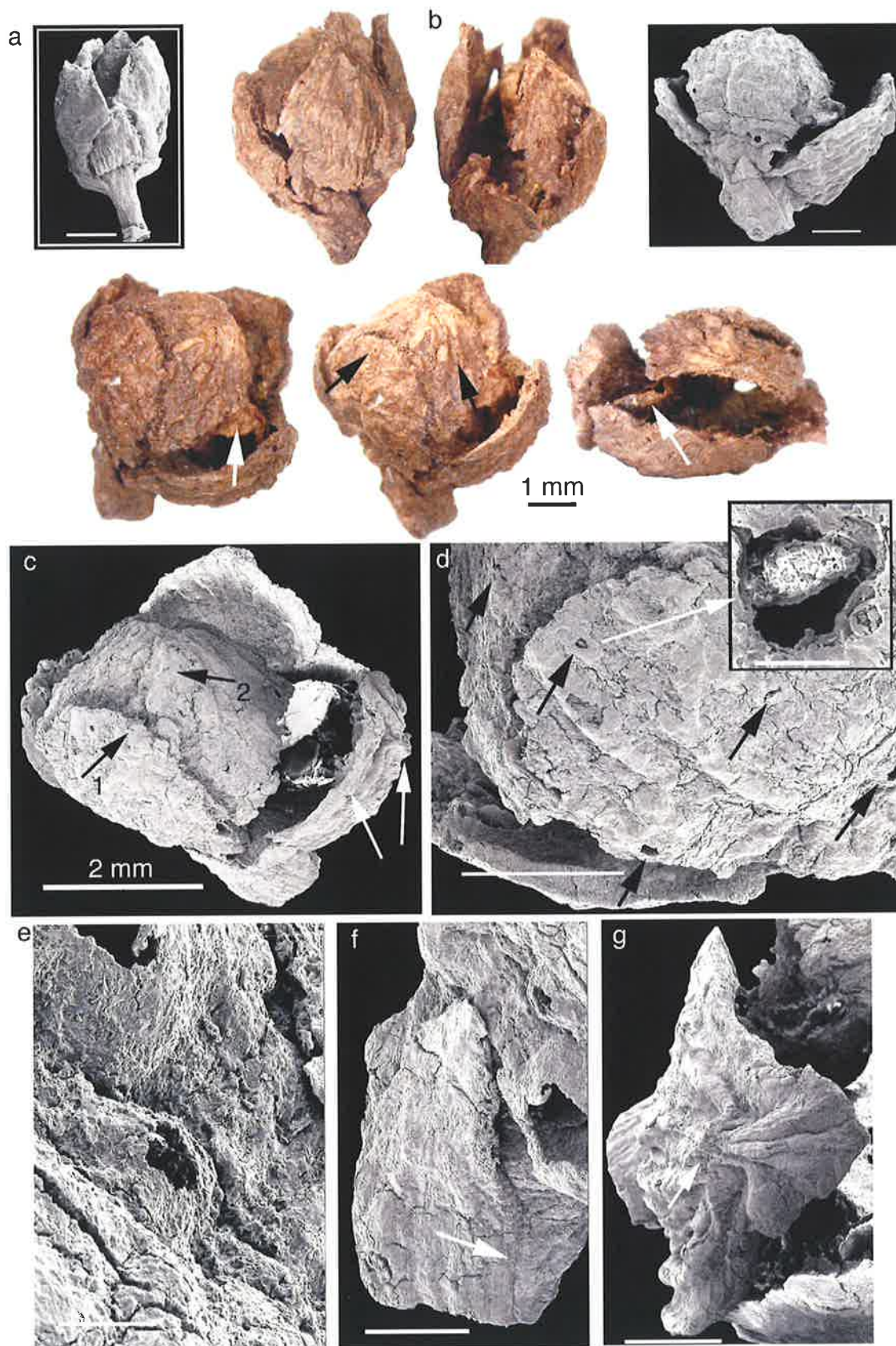
Fig. 7a-g Little Rapid River ovulate cones

Fig. 8a-f Little Rapid River ovulate cone

Specimen LRR1-2890. This is considered to be the same species as that illustrated in Fig. 7

- **a.** Two views of the same cone. Possibly immature cone, prematurely opened and revealing undeveloped seeds (these are not central to the cone and are thus not considered to be columellae)
- **b.** Detail of scale and seed (scale 1 mm).
- **c.** Detail of seed (scale 500 μm).
- **d.** Detail of seed (scale 100 μm).
- **e.** Detail of scale apex. Margin papillate (scale 200 μm).
- **f.** Detail of scale apex (scale 500 μm).
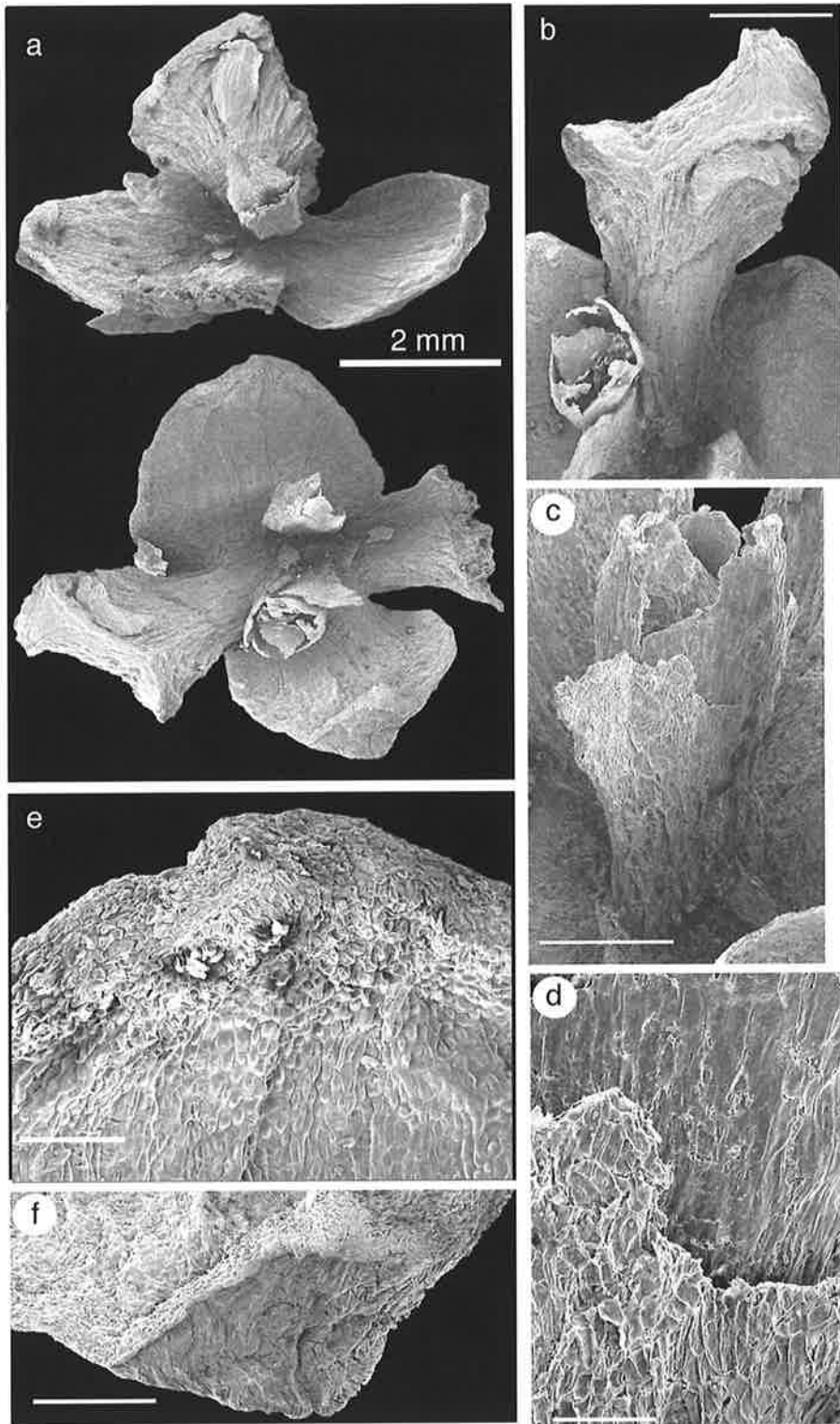
Fig. 8a-f Little Rapid River ovulate cone
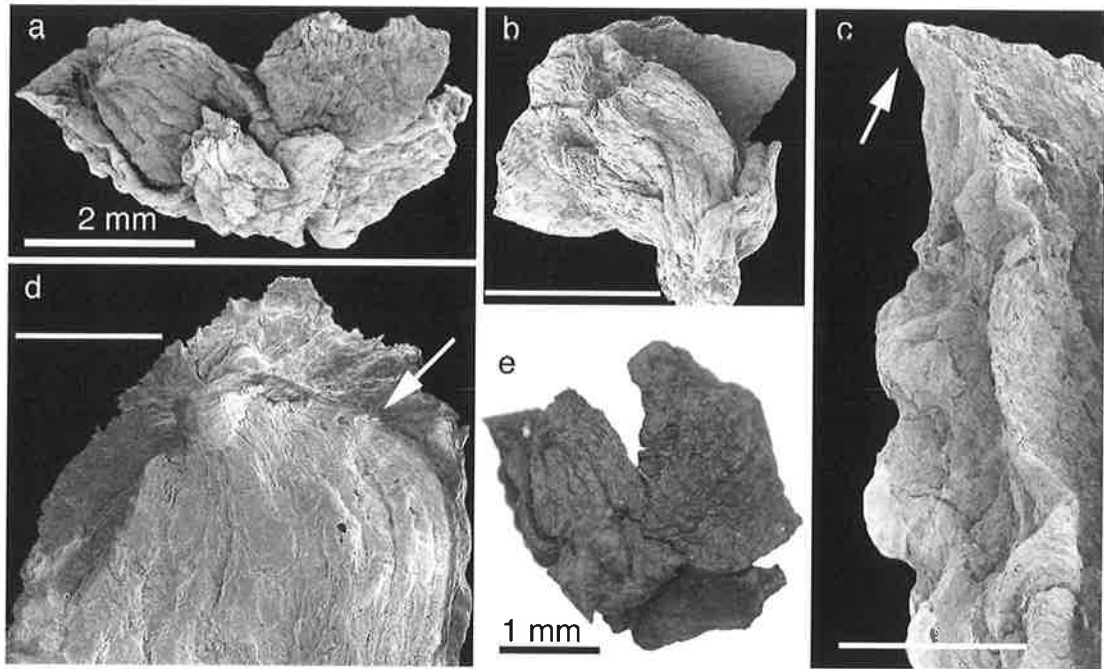
Fig. 9a-e SEM and LM LRR1 ovulate cone

Specimen LRR1-5541. (Considered to be same species as the cones in Figs 7 and 8. These illustrations demonstrate features not well seen in the other cones).

a. Small open cone subtended by large decussate, sterile bracts/leaves.

b. Detail of the subtending foliage. Bracts decussate, fused towards the base for about one third of their length, keeled in the upper free section, and with acute apices. Bracts decreasing in size away from the cone (scale 1 mm).

c. Outer bract surface very highly rugose. Bract projection? (arrow) at apex of scale (scale 500 µm; specimen 5541).

d. Bract reaching almost to the apex of the scale and extending to the scale margins. Bract projection round to wedge-shaped at the base, tip missing (scale 500 µm; specimen 5541).

e. LM base of cone (specimen 5541).
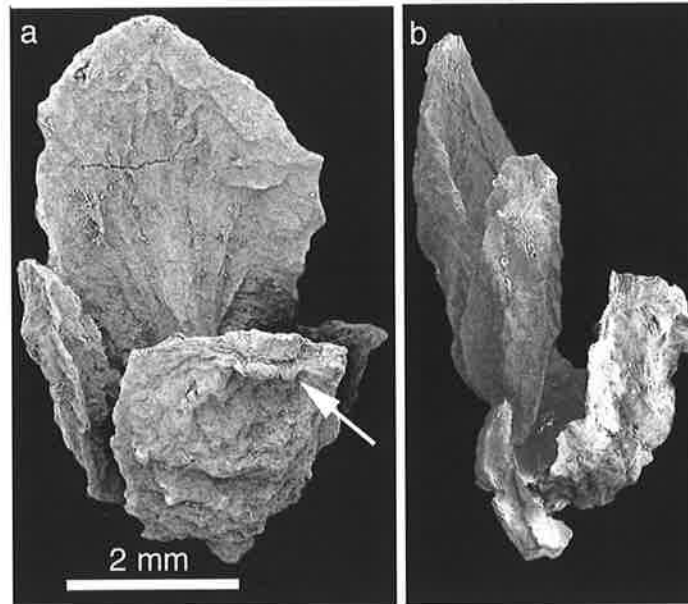
Fig. 10a-b LRR1 ovulate cone
Specimen LRR1-2892. This ovulate cone differs slightly from those illustrated above but is possibly a mature cone of the same species.

    a. Ultimate bract-scales large, broad, with rounded apices, and tapering towards the base. Internal scale surface rugose. Bract on ultimate scale highly rugose, and extending to the scale margin. Bract projection close to the scale apex, short and broad at the base.

    b. Cone seen from another angle, penultimate bract-scales narrower and slightly shorter than those of the ultimate pair. Large, elongate bracts with acute apices subtend the cone.

Discussion

Since the single ovulate cone was described by Hill and Carpenter (1989), more specimens have been found and, unlike the original, these are intact. Unfortunately the foliage subtending all the cones is devoid of any characters (e.g. stomata) which would confirm they are linked to the *Libocedrus* foliage described in part A (this section). Although the cone illustrated in Fig. 10 is superficially similar to that described from Lea River (and assigned to *Austrocedrus*; Part II B), its bracts are highly rugose (those of *Austrocedrus* are not), and it is subtended by quite large *Libocedrus*-like foliage (*Austrocedrus* cones are subtended by very small leaves). The cones considered to be those of an extinct *Libocedrus* species, and thus retain the name given to them by Hill and Carpenter (1989) i.e. *Libocedrus mesibovii* Hill & Carpenter Alcheringa 13: 94 (1989).

3. Monpeelyata, Tasmania (42°04'S, 146°40'E, ~920 m)

At Monpeelyata a small (15 m by 1.5 m) siltstone lens was exposed when the Hydro-Electric Commission cut a canal to link Little Pine Lagoon and Lake Echo (Hill 1988). As fossiliferous sediments in the area are associated with basaltic lava flows, the lens is thought to represent sedimentation into one of many valley lakes that developed in the Midlands and Central Plateau areas of Tasmania as the result of Cenozoic volcanic activity and associated faulting. The depth of the deposit (it rests on dolerite of Jurassic age and is capped by basalt) suggests it was probably a shallow lake somewhat similar to alpine lakes in the area today (Hill 1988; 1995). At the time of deposition the altitude of the site was probably similar to that of the present (Ollier 1986; Macphail *et al.* 1991). Palynological data suggest the sediments are Early Miocene (Wells and Hill 1989). K-Ar dates for basalts in the area indicate an Early/Middle Miocene age, but the flora may be Late Oligocene (Macphail *et al.* 1991, 1994). Fossil taxa include Podocarpaceae, *Fitzroya* (Hill and Paull 2003), *Araucaria*, and two species of *Nothofagus* (Hill 1990; Scriven and Hill 1996).

A. Ovulate cones

A review - *Austrocedrus tasmanica* Hill & Carpenter Alcheringa 13: 94 (1989)
Ovulate cones from this site were assigned to the genus *Austrocedrus* by Hill and Carpenter (1989). The review below affirms this assignment. Some of the original specimens are missing, and these have been photographed from photographic plates. Other specimens are in a damaged state.

Systematics
Order Coniferales
Family Cupressaceae
Genus *Austrocedrus* Florin & Boutelje, Acta Horti Berg. 17 (2): 28. (1954)
Austrocedrus tasmanica Hill & Carpenter Alcheringa 13: 94 (1989)

Holotype: M-1942 stored in the School of Earth and Environmental Sciences, The University of Adelaide, South Australia.
Type locality: Monpeelyata (42°04'S, 146°40'E, ~920 m)
Specimens examined M-118, 1938, 1939, 1940, 1941, 1942, 1943, 1944, 1945

Amended diagnosis

Ovulate cone: Cones rather flattened in appearance. Four decussate bract-scale pairs. Bract-scale complexes of two sizes (Fig. 11a-g). Ultimate bract-scales ~25% longer than the penultimate, narrower, tapering slightly towards the base, with rounded apices, and a short bract projection close to the apex (Fig. 12a). Ultimate bract scales often recurved outwards (e.g. Fig, 11a, b, c, d, g). Bracts on ultimate scales highly rugose. Bracts on penultimate scales only slightly rugose, and not outwardly recurved (Fig. 11e, f), and with a small bract projection close to the apex. Cone subtended by relatively large leaves or bracts. The uppermost 'bracts' are the largest, and subtend the ultimate bract-scales (Fig. 12b, d).

Fig. 11a-g *Austrocedrus tasmanica* ovulate cones, Monpeelyata

Scale for all cones 1 mm

a. Four parted open ovulate cone. Bract-scale complexes of two sizes - ultimate ~25% longer than the penultimate, and narrower. Ultimate bract-scales with rounded apices, and tapering slightly towards the base. Bracts on ultimate bract-scales highly rugose, with short bract projections. Cone subtended by elongate-lanceolate decussate leaves (specimen M-1938).

b. Penultimate scale tapering at the base, with a broad apex. Short bract projection just below the scale apex (specimen M-118).

c. Same specimen as **a**. Ultimate bract-scales elongate, narrow, and highly rugose. Apices outwardly turned, and with a short, sturdy bract projection close to the apex. Penultimate scale missing. Cone subtended by elongate foliage.

d. Ultimate bract-scales subtended by large foliage (specimen M-1943).

e. Ultimate and penultimate bract-scales taper towards the base. Abaxial bract-scale surface much less rugose than that of other cones (specimen M-1945).

f. Partly opened, possibly young cone. Both scale pairs with bract projections just below the apex (similar to those of *Austrocedrus chilensis*).

g. the penultimate scales sit within the ultimate scales (specimen 1942).

h. Bracts on ultimate bract-scales highly rugose, with short bract projections. Penultimate scales almost ovate, with rounded apices and bases, bract projection not obvious on the penultimate scale. Bract surface relatively smooth by comparison with that of ultimate bract-scale (specimen M-1941).

Fig. 11a-g *Austrocedrus tasmanica* ovulate cones, Monpeelyata
Specimens - **a** M-1938, **b** M-118, **c** M-1938, **d** M-1943, **e** M-1945, **f** M-1942, **g** M-1941
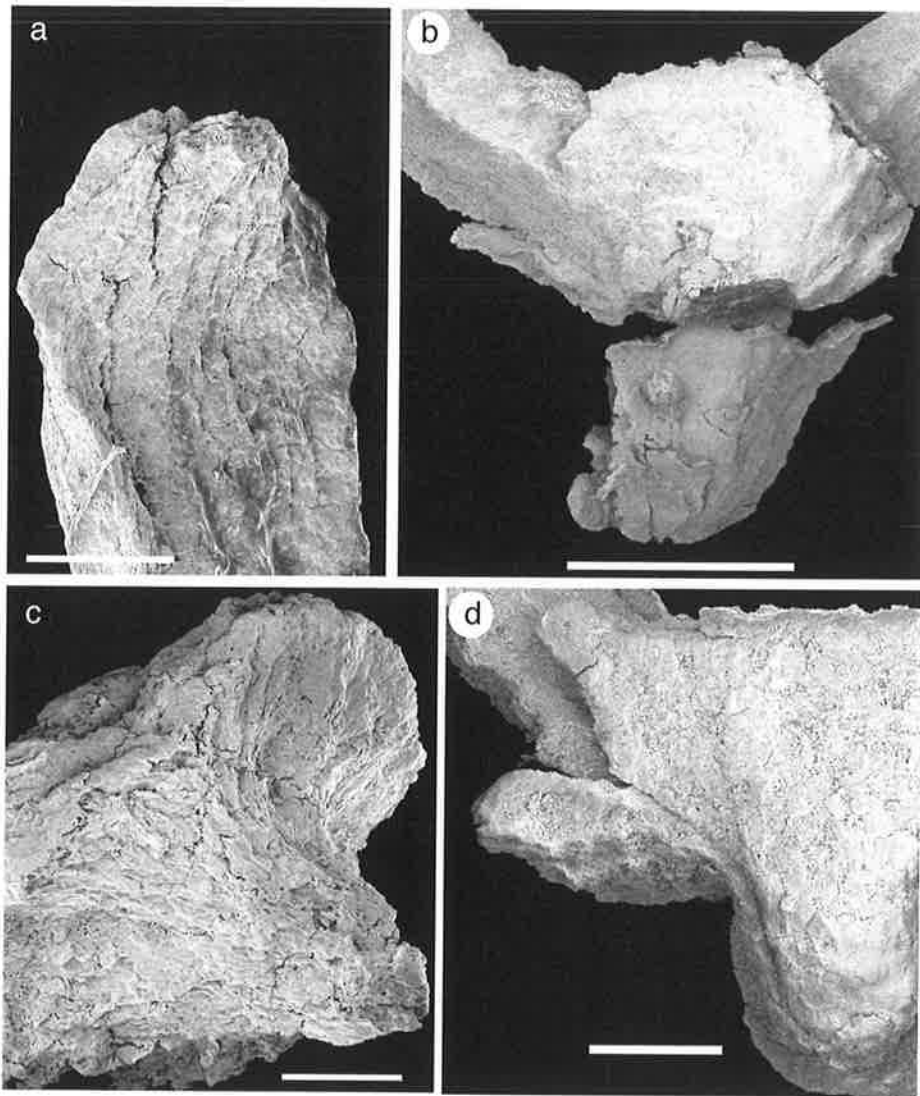
Fig. 12a-d *Austrocedrus tasmanica* cone detail

    a. Ultimate bract-scale. Highly rugose surface, Bract projection missing (specimen M-118; scale 500 um).

    b. Elongate foliage subtending the ultimate bract-scales (specimen M-1938; scale 1 mm).

    c. Bract projection wedge-shaped at the base (M-1941; scale 200 um).

    d. Elongate foliage subtending the ultimate bract-scale (specimen M-1943; scale 500 um).

Discussion

The ovulate fossil cones share many characteristics with those of extant *Austrocedrus chilensis* (in particular the placement of the bract projection close to scale apex), but the size of the foliage subtending the cones is considerably larger than those of extant *Austrocedrus* cones (Hill and Carpenter 1989). Careful scrutiny (by SEM) for features that would link these 'leaves' to *Austrocedrus* was unfruitful. Unfortunately no foliage has been found at the site that can be positively linked to *Austrocedrus*. However, Hill and Carpenter's (1989) diagnosis is accepted as correct, and the cones retain their original assignment.

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4. Pioneer, Tasmania (41°05'S, 145°14'E ~90 m)

The sediments are about 1 km to the north of Pioneer, and were exposed by tin mining. They are now covered by water. There are two sequences. The lower is ~6 m in depth and comprises horizontal, cross-bedded coarse sands and gravels, and sandy clays rich in organic matter, and is suggestive of a braided alluvial fan. The upper sequence ~34 m thick, extends to the surface, and largely consists of cross bedded coarse sands and quartz granules, interspersed with white clay and organic rich clay lenses. This is also suggestive of braided alluvial fan sedimentation. Fossil taxa at the site include *Nothofagus*, and a variety of conifers including Podocarpaceae, *Athrotaxis* (Hill *et al.* 1993), and *Fitzroya* (Hill and Paull 2003). The presence of abundant epiphyllous fungi on fossils from this site is suggestive of high rainfall conditions. K-Ar dates for nearby basalts indicate an Early/Middle Miocene age, but the fossils may be Late Oligocene (Hill and Macphail 1983; Macphail *et al.* 1994).

Hill and Carpenter (1989) described two new cupressaceous species (from two different genera) at this site. These are *Libocedrus morrisonii,* and *Papuacedrus australis.* The current review of the specimens recognises only one genus and species, *Papuacedrus australis.*

Systematics
Order Coniferales
Family Cupressaceae
Genus *Papuacedrus* H. L. Li J. Arnold Arbor. 34: 25 (1953).
Papuacedrus australis Hill & Carpenter. Alcheringa 13: 97 (1989)

Holotype: P-1168 stored in the School of Earth and Environmental Sciences, The University of Adelaide, South Australia.

Isotype: P-343 (previously *Libocedrus morrisonii* Hill & Carpenter. Alcheringa 13: 97 (1989)) stored in the School of Earth and Environmental Sciences, The University of Adelaide, South Australia.

Type locality: Pioneer, northeast Tasmania (41°05'S, 145°14'E)
Specimens examined P-343, 662, 1166, 1168

Amended diagnosis: *Foliage and leaves*: Foliage partially flattened, with alternate branching. Leaves decussate, scale-like, dimorphic. Lateral leaves on branchlets larger than facial. Lateral leaves on main axes are elongate to oblong, and connate for almost three quarters of their length. The upper carinate free section of these leaves is roughly at an angle of 80° to the twig. Facial leaves on main axes similar in size to lateral leaves. Lateral and facial leaves tapering to very acute apices. Leaf margins of facial leaves slightly frilled (not illustrated). Lateral leaf margins entire (Figs 13a; 15a, d).

Stomatal distribution: Unknown for dorsal and ventral surfaces. On adaxial surface stomata roughly aligned with the centre of the leaf, and towards the margin, but not extending to the leaf apex (Fig. 13b).

Cuticle description: Inner cuticle - guard cells elongate and surrounded by 4-6 moderately coarse-grained subsidiary cells (Fig. 13c). Where the subsidiary cells abut the guard cells a deep groove is formed. The anticlinal walls of the subsidiary cells dissect this groove. Small round indentations are found at the outer edges of the subsidiary cells. These are most frequent where cell walls abut (Fig. 15b). Epidermal cells elongate, concave, coarse-grained and containing calcium oxalate nodules (Fig. 13e). Outer cuticle - Florin rings high ridged, lobed and surrounded by small round papillae that are frequently grouped together (Figs 13d, f; 15c).

Fig. 13a-f Pioneer *Papuacedrus australis*

a. LM, elongate branching shoot with flattened foliage. Lateral leaves on leading shoot elongate in lower half to two thirds and fused towards the base. Upper, free section of lateral leaves adnate Upper free part of these leaves carinate and at about 80° to the twig. Facial leaves on the main axis similar in size to the lateral leaves, but on branchlets smaller. Lateral and facial leaves with acute apices

b. Adaxial surface, lateral leaf. Stomata roughly aligned with the centre of the leaf (specimen P-1168; scale 200 μm).

c. Inner cuticle, detail poor. Guard cells elongate and sharing subsidiary cells (specimen P-1166; scale 25 μm).

d. Outer cuticle. Florin rings high ridged, lobed and surrounded by small round papillae (arrow; specimen P-1166; scale 25 μm).

e. Internal surface. Epidermal cells coarse-grained, elongate, convex, and with numerous calcium oxalate nodules. Anticlinal cell walls thick, coarse grained (specimen P-1168; scale 10 μm).

f. Detail of **b**. Arrow indicating papillae (specimen P-1168; scale 50 μm).
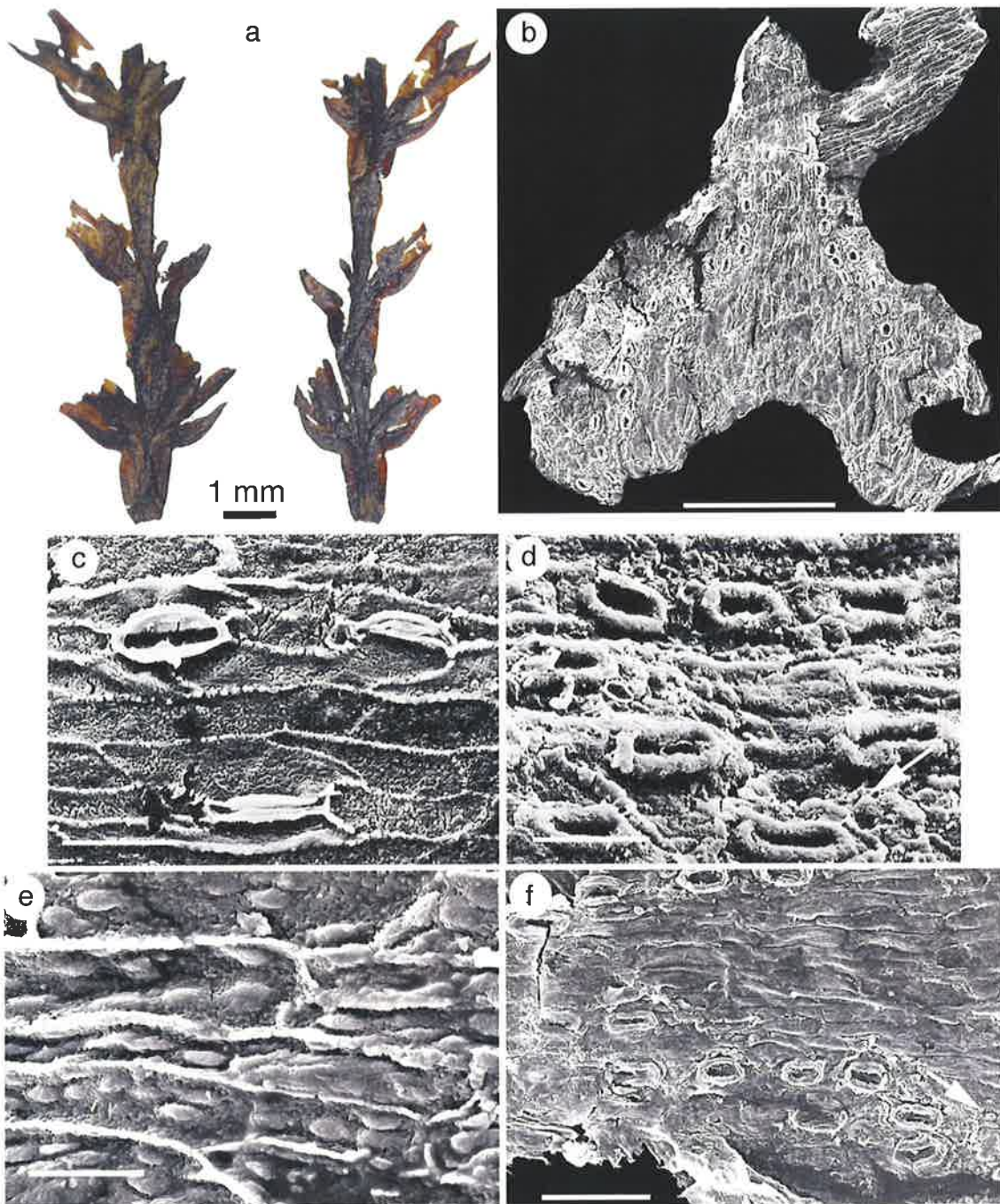
Fig. 13a-f Pioneer *Papuacedrus australis*
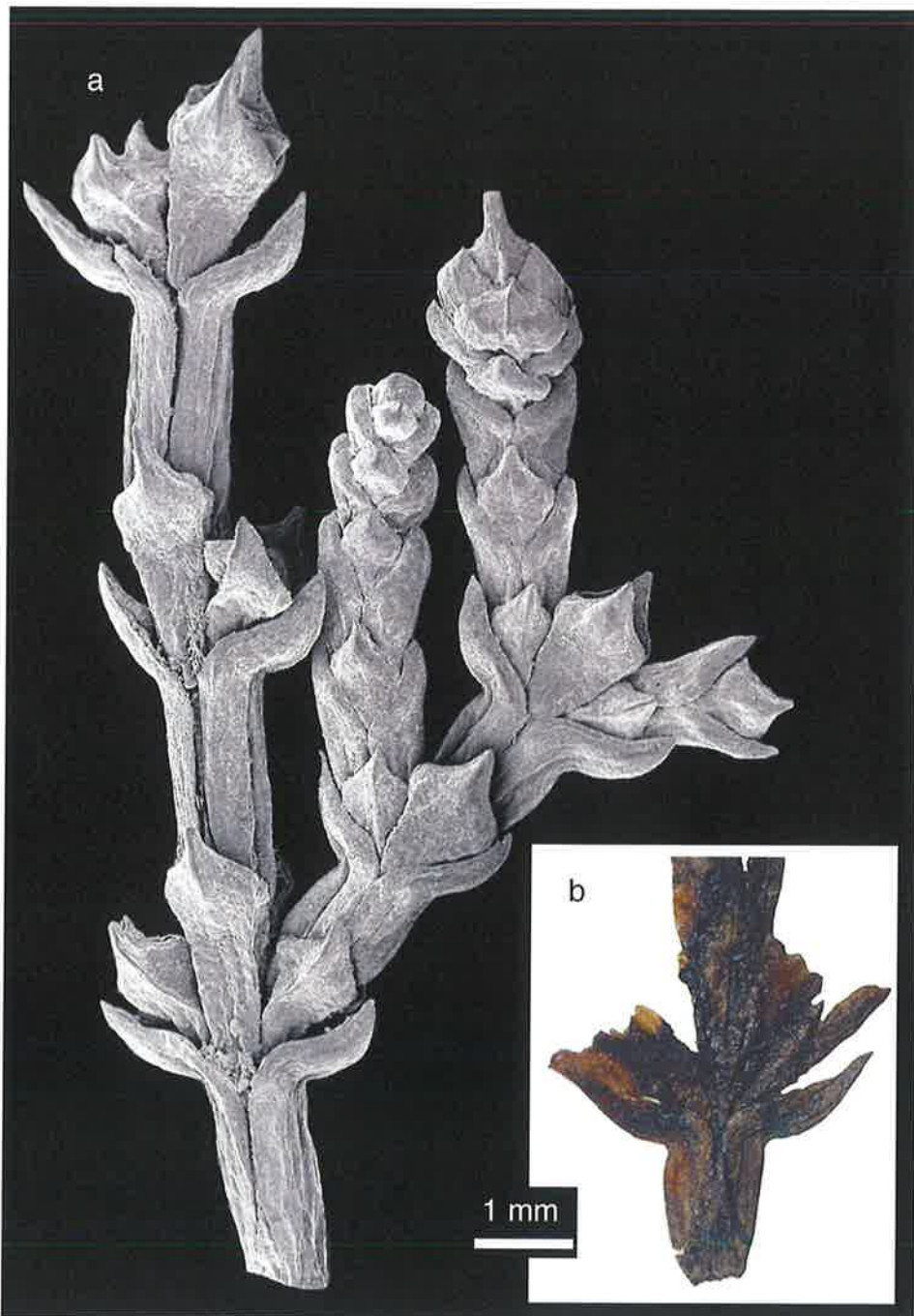
Fig. 14a-b Extant and fossil *Papuacedrus* comparison.
  a. *Papuacedrus papuana* (specimen 108114.1).
  b. *Papuacedrus australis* – fertile foliage with ovulate cones (specimen P-1168).
Leaves of extant and fossil species remarkably similar in size and shape.
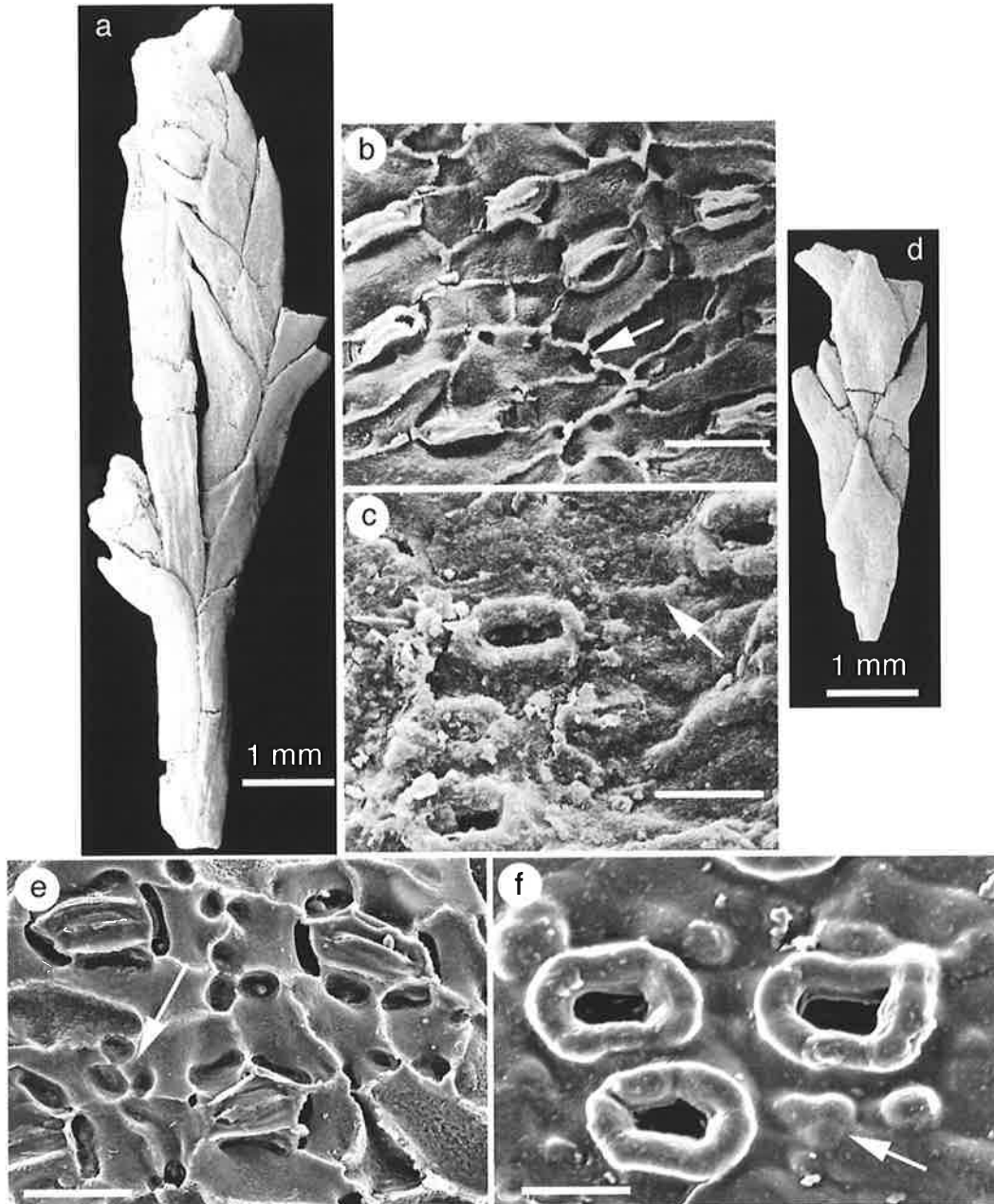
Fig. 15a-f Comparisons of *Papuacedrus australis* (previously *L. morrisonii*), foliage and cuticles (**a-d**) with extant *Papuacedrus papuana* cuticles (**e-f**).

  a. Elongate, partially flattened, branching shoot, Lateral leaves on leading shoot elongate, fused for around two thirds of their length (specimen P-343; foliage similar to that of *P. papuana* Fig.6a-d, Chapter 2, *Papuacedrus*).

  b. Inner surface cuticle. Subsidiary cells 4-6, and with indentations at the cell margins (arrow). Guard cells surrounded by a deep groove, and sharing subsidiary cells. Stomata somewhat randomly oriented (specimen P-662; scale 25 μm).

  c. Florin rings high ridged and with several lobes. Papillae adjacent to stomata, round and often in groups (specimen P-662; scale 25 μm).

  d. Lateral and facial leaves similar in size and with apices (specimen P-1152).

  e. Inner cuticular surface *Papuacedrus papuana,* Stomata larger than those of **b** (specimen P-662) but characteristics very similar. Arrow indication indentations at the corners of adjoining cells (specimen 108114.1; scale 25 μm).

  f. High ridged, lobed Florin rings. Papillae small, round, and often in groups (arrow; specimen 108114.1; scale 25 μm).

Discussion

The foliage of P-1168 (Fig. 13a) is convincingly that of *Papuacedrus* (see the comparative Fig. 14a-b). The internal cuticle illustrated by Hill and Carpenter (1989) and shown again in Fig. 13c is poor and unconvincingly that of *Papuacedrus*, but the outer cuticle characteristics (Fig. 13d) are more persuasive. Although the foliage specimens P-343 and P-1152 are somewhat similar to that of extant *Libocedrus*, they are more like that of *Papuacedrus* (see Fig 6a-d, Chapter 2, *Papuacedrus*). The cuticles illustrated by Hill and Carpenter (1989) as belonging to this foliage type (*viz. Libocedrus*, Fig. 15b, c) are more like those of *Papuacedrus* (see Fig. 15e, f). Interestingly, the *P. papuana* foliage with which one of the fossils is compared (Fig. 14a) is from a 40 m growing at ~3500 m. Although the leaves are similar in size to the fossils, the cells of the latter are about 20% smaller (see Fig 15b, c, e, f). Only one Cupressaceae genus and species is recognised at Pioneer i.e. *Papuacedrus australis* Hill & Carpenter. Alcheringa 13: 97 (1989).

Part III B. Newly described Cupressaceae related fossils

Introduction

This section describes new Cupressaceae macrofossil leaf material from three Tasmanian sites, Balfour, Lea River and Regatta Point, and ovulate cones from Lea River. The fossils are compared with extant foliage and cones from *Papuacedrus, Libocedrus, Austrocedrus,* and *Pilgerodendron* illustrated in Chapters 3-6. Localities and site descriptions precede each description. Except where indicated, site descriptions are from Hill (1995).

1. Balfour, Tasmania (41°18'S, 144°54'E, 240 m)

Few geological details have been documented so the description is brief.
Sediments were taken from a partially exposed road cutting. Palynostatigraphic data indicates they are of Oligocene-Early Miocene age (Hill *et al.* 2001). Fossil taxa include *Fitzroya* (Hill and Paull 2003).

Systematics
Order Coniferales
Family Cupressaceae
Genus *Libocedrus* Endl., Syn. Conif.: 42 (1847)
***Libocedrus balfourensis* sp. nov.**

Diagnosis. Lateral leaves larger than facial, bilaterally flattened, loosely to tightly imbricate, convex on ventral surface, concave on dorsal surface, fused for about one third their length, with entire margins, slightly papillate bases, and a well defined band of epidermal cells between the stomatal area and the margin. Facial leaves with frilled margins, and with apices reaching to the leaf pair above. Amphistomatic. Numerous closely packed stomata in well defined depressions in the central section of dorsal leaf surface, fewer on ventral surface leaves. Internal epidermal cell surface slightly coarse grained, and in exposed areas, often containing small nodules. Florin rings high ridged, lobed and surrounded by numerous, often round, papillae.

> *Holotype*: B-750 stored in the School of Earth and Environmental Sciences, The University of Adelaide, South Australia.
> *Type locality*: Balfour, Tasmania (41°18'S, 144°54'E)
> *Specimens examined* (41): B-018, 019, 020, 021, 022, 023, 024, 025, 026, 027, 111, 112, 136, 137, 138, 139, 140, 328, 329, 330, 331, 571, 572, 576, 575, 578, 579, 580, 750, 751, 752, 753, 754, 821, 832, 833, 834, 835, 836, 837, 839.
> *Etymology*: named for the site at which they were found.

> *Foliage and leaves*: Fig. 1a-h. Leaves decussate, dimorphic and flattened. Lateral leaves – 1.8-3.6 mm long, larger than facial, bifacially flattened, lanceolate, loosely to tightly imbricate, slightly concave on dorsal surface (Fig. 2a), convex on ventral surface (Fig. 2c), fused for around one quarter to one third of their length (Figs 2a, c; 3e), and with well defined entire margins, and a broad band of epidermal cells between the margin and the stomatal area (Fig. 2e), and rounded apices. Leaf bases slightly papillate (Fig. 3c). Facial leaves; slightly longer than wide, 1.2-1.8 mm long, generally not overlapping the pair above, dorsally keeled, with well-defined central ridges, frilled margins (Fig. 3b), and acute to bluntly acute inwardly curved apices. Dorsal facial leaves outwardly keeled, but more flattened than those on the ventral surface.

Stomatal distribution: Ventral surface, lateral leaves – stomata fewer than on dorsal surface, and mostly in short discontinuous rows in a slight broad depression in the central section of the leaf (Fig. 2a). Facial leaves – in small depressions on either side of the central keel, where they are largely hidden by the lateral leaves below (Fig. 2b). Dorsal surface - stomata on lateral leaves numerous, closely packed, generally aligned with the leaf margin, and largely within relatively well-defined, slightly sunken grooves extending from near the base to just below the apex. On facial leaves in slight depressions on either side of the central keel, where they are almost completely concealed by the overlying lateral leaves (Fig. 2c, d). Adaxial surface, lateral and facial leaves in discontinuous rows roughly parallel to the leaf margin, but absent from the lower central section of the leaf (Figs 2f; 3a, d).

Cuticle description: Inner surface – stomatal guard cells generally elongate, with 4-6 subsidiary cells, which may be shared by adjacent guard cells (Fig. 4a, c, e). Periclinal subsidiary cell walls relatively fine grained, frequently indented (mostly along the cell margins) and folding down sharply downwards around the guard cells, forming a discontinuous groove. Epidermal cells not directly abutting the stomatal areas are elongate, slightly coarse grained in texture, and have concave periclinal walls. Anticlinal walls are thick, regularly thickened, acute and more coarsely grained towards the base. Epidermal cells on ventral leaf surfaces, especially the tips of lateral and facial leaves contain numerous nodules or holes (Fig. 4g. i). Outer surface – Florin rings high ridged, distinctly lobed, and with a peripheral groove. Numerous round papillae are associated with the stomata (Fig. 4b, d). Epidermal cells convex, with sunken cell walls and frequently containing small holes (or nodules; Fig. 4f).
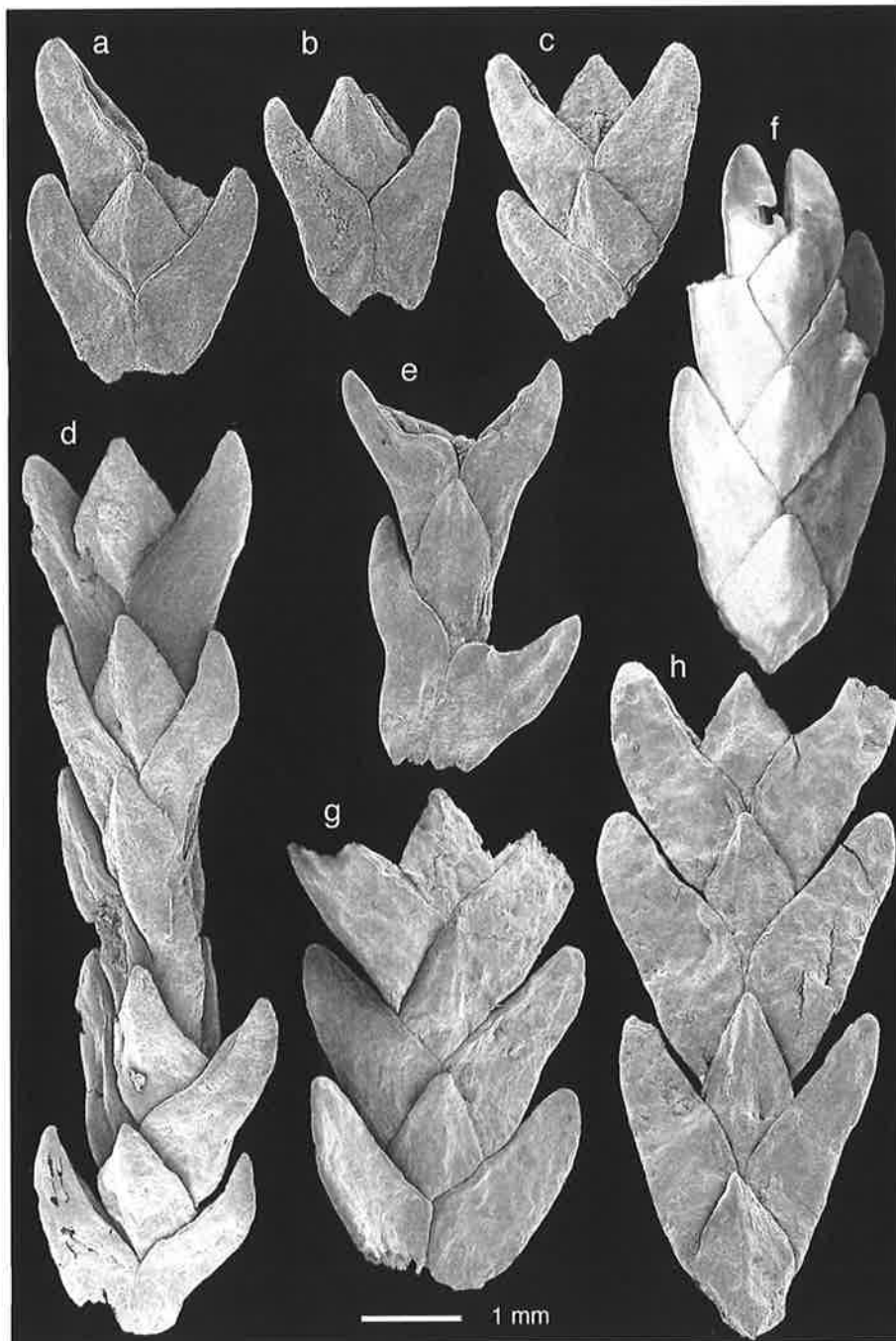
Fig. 1a-h SEM *Libocedrus balfourensis* sp. nov., Balfour, representative foliage samples

a, b, c B-136; **d**, B-571; **e**, B-111; **f**, B-112; **g**, B-832; **h**, B-750.
(**b**, **c**, **f** ventral surface, all other photographs dorsal surface)

Fig. 2a-f *Libocedrus balfourensis* sp. nov., Balfour, foliage detail

a. Ventral leaf surface. Lateral and facial leaves imbricate, slightly convex. Lateral leaves with a broad central depression, narrow towards the apex, containing discontinuous rows of stomata (right arrow). Lateral leaves fused for ~ one third of their length. Facial leaf small, with frilled margin. Stomata in small depressions on either side of the central keel towards the base (left arrow; specimen B-833).

b. Ventral surface, detail of **a**. Arrow indicating stomata on facial leaf (scale 200 μm; specimen B-833).

c. Dorsal surface. Lateral and facial leaves flattened. Lateral leaves slightly concave, and with entire margins. Stomata in well defined broad and central depressions (grooves). Stomata on facial leaves almost completely concealed by the lateral leaves below (specimen B-832).

d. Dorsal surface, detail of **c**. Arrow indicating position of stomata on facial leaf (scale 200 μm; specimen B-832).

e. Dorsal surface. Lateral leaf (below) with entire margin and stomata closely packed, and in discontinuous rows roughly parallel to the leaf margin. Between the stomata and the leaf margin is a well-defined band of epidermal cells (scale 200 μm; specimen B-111).

f. Dorsal surface, lateral leaf. Towards the leaf margin is a clearly delineated band of epidermal cells containing numerous small holes or nodules. Adaxial surface has stomata in a band roughly parallel to the leaf margin (arrow; scale 100 μm; specimen B-111).
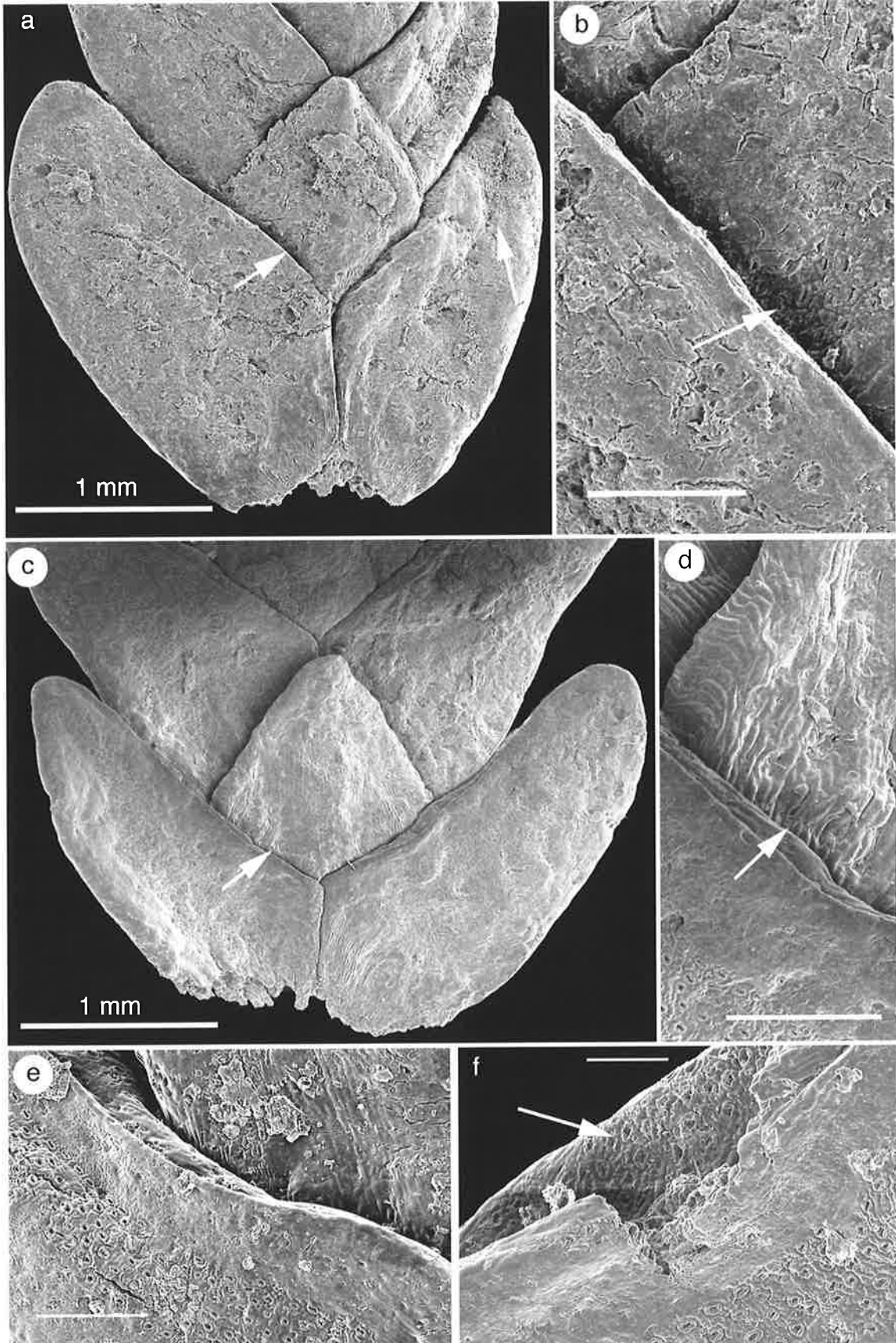
Fig. 2a-f *Libocedrus balfourensis* sp. nov., Balfour, foliage detail
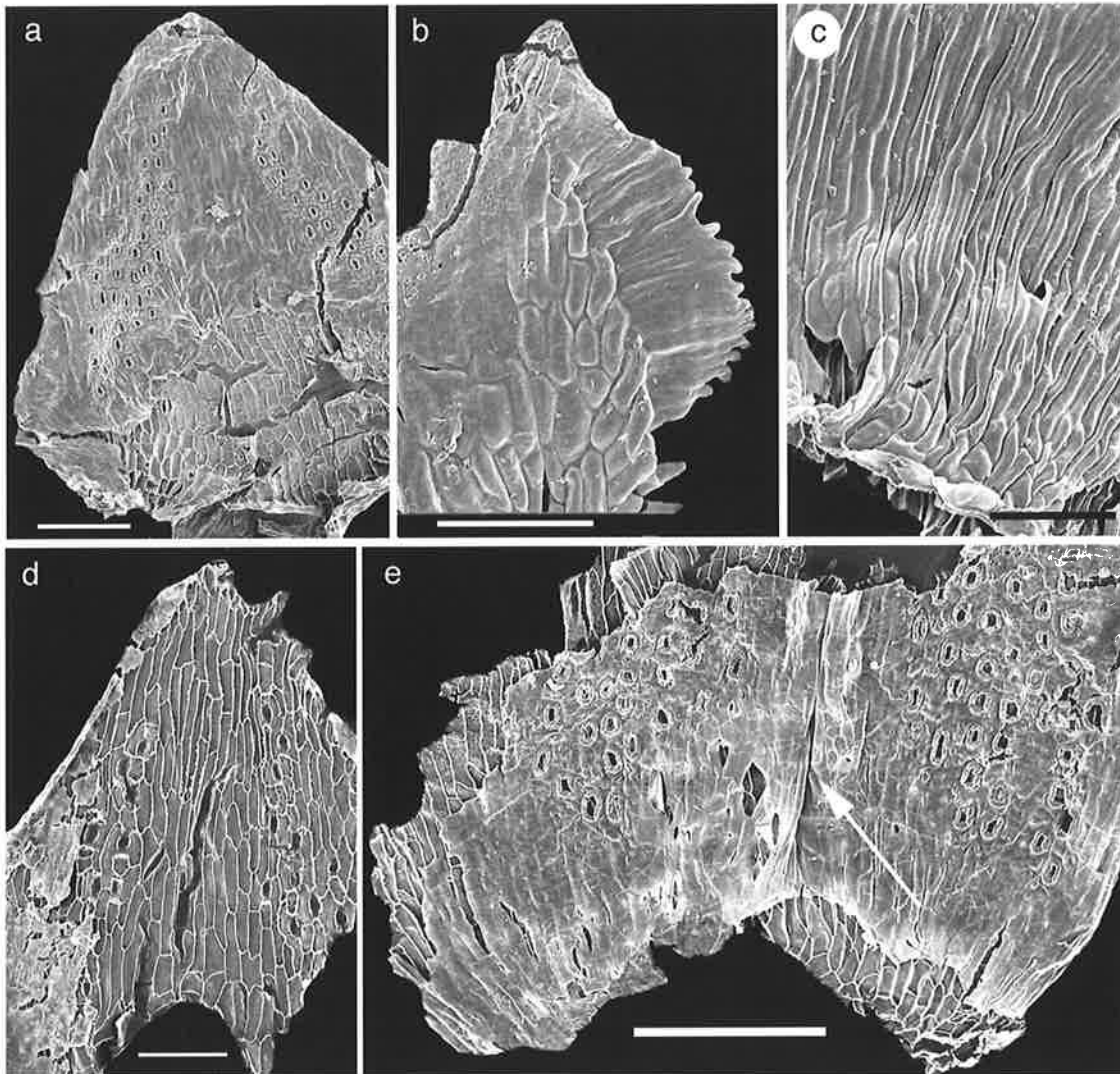
Fig. 3a-e *Libocedrus balfourensis* sp. nov., Balfour, foliage detail from cuticle preparations

    a. Facial leaf, adaxial surface. Stomata in discontinuous rows roughly parallel to the leaf margin, more frequent towards the leaf base (scale 200 μm; specimen B-137).

    b. Portion of facial leaf showing marginal frill, well defined epidermal cells and small holes (upper left; scale 100 μm; specimen B-137).

    c. Slightly papillate adaxial lateral leaf base (scale 100 μm; specimen B-137).

    d. Adaxial surface, facial leaf. Stomata roughly parallel to leaf margin. No stomata in lower central section of the leaf (scale 100 μm; specimen B-753).

    e. Dorsal surface, lateral leaf bases. Arrow indicating fused section of lateral leaves (scale 200 μm; specimen B-753).

Fig. 4a-i *Libocedrus balfourensis* **sp. Nov,** Balfour, SEM leaf cuticle

a. Inner surface. Elongate-round guard cell complex with 4-5 fine grained and indented subsidiary cells (scale 20 μm; specimen B-137).

b. Outer surface. Florin ring distinctly lobed, high ridged, and with a peripheral groove (scale 10 μm; specimen B-832).

c. Inner surface. Stomata with 4-6 fine grained subsidiary cells with frequent indentations. Guard cells surrounded by a discontinuous groove (scale 25 μm; specimen B-753).

d. Outer surface. Closely packed and lobed stomata surrounded by numerous papillae. Epidermal cells bordering the stomatal complex with frequent holes (scale 20 μm; specimen B-832).

e. Internal adaxial surface, lateral leaf. Stomata less frequent than on dorsal surface and in short discontinuous rows. Epidermal cells bordering stomatal areas with coarser-grained texture (scale 50 μm; specimen B-575).

f. Outer surface. Clearly delineated convex epidermal cells with indented walls and containing numerous small holes (scale 20 μm; specimen B-112).

g. Internal dorsal surface, cell margin. Epidermal cells with relatively coarse-grained texture, and frequent small nodules or holes (scale 20 μm; specimen B-575).

h. Internal surface. Periclinal cell walls of epidermal cells concave, and coarse-grained in appearance. Anticlinal cell walls thin, and coarse-grained towards the base (scale 20 μm; specimen B-832).

i. Internal surface, exposed section of facial leaf. Irregular cells with large holes (scale 20 μm; specimen B-839).
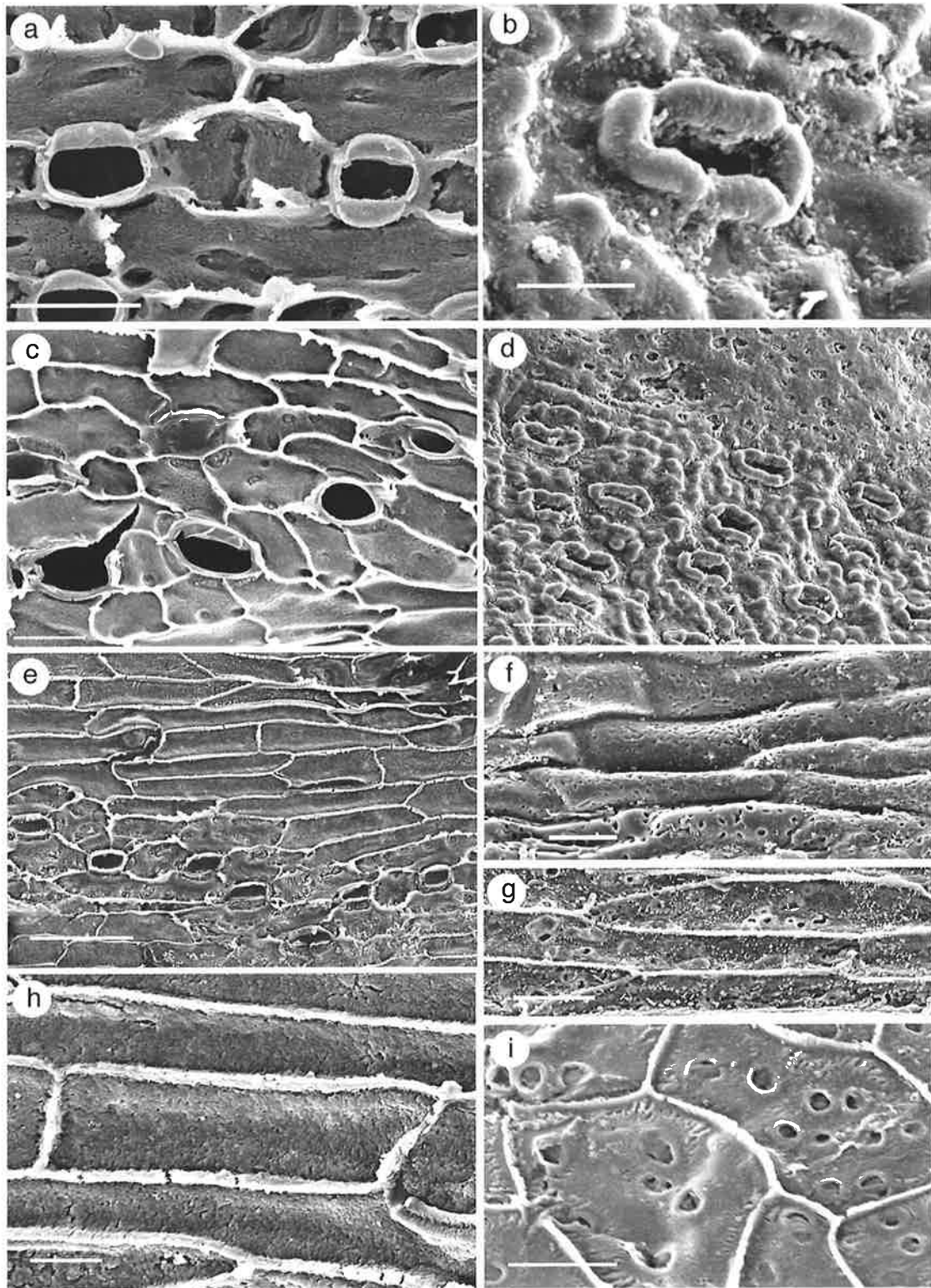
Fig. 4a-i *Libocedrus balfourensis* sp. nov., Balfour, SEM leaf cuticle

Comparison of fossil and living species

The fossil leaves share characteristics with *Libocedrus* species from New Zealand and New Caledonia, but are least like *L. bidwilli* and *L. chevalieri*. They are slightly larger than leaves from the New Zealand species, and slightly smaller than the New Caledonian species. They share several characteristics with *L. plumosa* (e.g. the lateral leaves have papillate bases and entire margins), and *L. austrocaledonica* (e.g. the broad band of epidermal cells between stomatal areas and the leaf margin, and the stomatal complex). They are assigned to the genus *Libocedrus* and, as they do not resemble a living species, are named after the site at which they were found i.e. *Libocedrus balfourensis*.

2. Lea River, Tasmania (41°30'S 145°39'E)

The site is an eroded cliff on the south side of the Lea River at ~670 m asl. Three different sedimentological phases are recognised. Toward the base of the lower, sub-horizontal unit are planar-bedded fine-grained muds containing some plant remains. Overlying these are several metres of muds interspersed with numerous sandy beds (5-10 cm thick). Above are two sand and fine-gravel cross-bedded sequences (40 and 130 cm thick respectively). The first unit consists of flat-bedded muds capped by a 20 cm leaf layer, and is suggestive of floodplain deposition The middle unit (which appears to conformably overly unit one) is mostly comprised of steeply dipping (NSEW) coarse sands and gravels interspersed with shallow channels (30-100 cm deep). They probably represent alluvial fan sedimentation, rather than a change in river direction. The base of the upper, mud-dominated, unit is undefined. The sediments in this sequence are flat bedded and contain shallow gravel-filled channels. At the top of the sequence are clay-rich muds rich in *Nothofagus* remains. These sediments suggest a return to floodplain conditions (Hill 1995). Palynological data for the site suggests the sediments are Early Oligocene (Macphail *et al.* 1994). Fossil taxa at the site include *Athrotaxis* (Hill *et al.* 1993), *Fitzroya* (Hill and Whang 1996), and *Nothofagus* (species from three subgenera; Scriven and Hill 1996).

Two Cupressaceae foliage types and two ovulate cone types are present at this site. Leaf and cone type 1 are assigned to the genus *Austrocedrus*. The discussion for these specimens follows the description of the ovulate cone.

Leaf genus/species 1

Systematics
Order Coniferales
Family Cupressaceae
Genus *Austrocedrus* Florin & Boutelje, Acta Horti Berg. 17 (2): 28. (1954)

Austrocedrus australis sp. nov.,

Diagnosis. Leaves highly dimorphic. Lateral leaves larger than facial, bifacially flattened, with entire but poorly defined margins. On main axis lateral leaves much larger than facial, elongate and fused in the lower half to two thirds, and on the ventral surface, separated by a distinct groove. Free sections of these leaves often at a broad angle to the stem. Lateral leaf bases slightly papillate. Facial leaves on main axes, descending at the base between the lateral leaves. Florin rings elongate, low to moderately ridged and slightly lobed.

Holotype: LEA-1640, stored in the School of Earth and Environmental Sciences, The University of Adelaide, South Australia.
Type locality: Lea River (41°30'S 145°39'E).
Specimens examined (50): LEA-275, 444, 445, 631, 632, 633, 634, 635, 636, 637, 638, 639, 640, 821, 822, 823, 824, 825, 826, 827, 990, 991, 1004, 1005, 1586, 1597, 1601, 1602, 1603, 1604, 1636, 1637, 1638, 1640, 3257, 3309, 3310, 3311, 3312, 3400, 3460, 3467, 3468, 3469, 3470, 3471, 3472, 3473, 5158, 5159.

The external surface of all specimens is highly degraded and lacks fine detail.

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Foliage and leaves: Leaves scale-like, decussate, flattened, and mostly highly dimorphic (Figs 5a-f; 6a-d), with branchlets arising in the same plane (Figs 5c; 6d) Lateral leaves – bifacially flattened, generally much larger than facial leaves, and highly variable in shape and length (e.g. Fig. 5c). Main axes laterals are elongate, subfalcate, and the upper carinate section is often at right angles to the stem (Fig. 5a, d). Lateral leaves on branchlets apically recurved (Fig. 6a). Leaf margins are entire, generally poorly defined, and may be revolute below the acute to bluntly acute apices (Fig. 6d). On the ventral surface paired leaves are separated by a distinct groove or depression (Fig. 5b, d). This appears as a ridge on the dorsal surface (Fig. 5f). On branchlets the leaves are generally elongate, lanceolate, and either imbricate or with inwardly curved apices (Fig. 6c), with entire margins (Fig. 7d). Some leaves less flattened (Fig. 6b). On branchlets, the groove, or ridge, separating the lateral leaves is apparent, but less well defined. Facial leaves – small, outwardly keeled on ventral and dorsal surfaces, and with slightly frilled margins (Fig. 7a, b). On main axes the leading facial leaf is usually larger and more elongate than those at the base of branchlets. The base of these leaves extends into, and is contiguous with, the boundary between the lateral leaves beneath (Figs 5b, e; 7a). Leaf apices are generally bluntly acute. Facial leaves at the base of branchlets rhomboid to triangular in shape. The bases of these leaves may be acutely elongate, and extend down for a short distance between the lateral leaves (Fig. 5e).

Stomatal distribution: Because all leaf surfaces are highly degraded this was difficult to ascertain. Adaxial surfaces, lateral and facial leaves, are somewhat better preserved and on both leaf types stomata appear to be relatively frequent, and oriented with the centre of the leaf (Fig. 7b). Stomata and in discontinuous rows (Fig. 8g, h).

Cuticle: The cuticle was difficult to prepare and it was impossible to determine where, and on what leaf type, the very small sections of cuticle came from. Inner surface – stomatal guard cells elongate and surrounded by a discontinuous groove. Subsidiary cells 4-5, and generally elongate, but often smaller and more rounded at the guard cell poles. These cells are moderately coarse grained and contain indentations. The latter are generally small, and most frequent at the corners of cells. Some larger indentations also occur, most often in the centre of smaller subsidiary cells (Fig. 8a, c). Epidermal cells immediately adjacent to some stomata are elongate, and contain large nodules (Fig. 8e). The anticlinal cell walls of all cells are relatively thick and slightly broader at the base. Epidermal cells not associated with stomatal complexes are elongate and irregular in shape, and have coarser grained periclinal walls (Fig. 8f, i). Outer surface, lateral leaves – stomata appear to be generally oriented in the same direction, in discontinuous rows (Fig. 8d, g, h) and have elongate, low (Fig. 8b) to moderately ridged, Florin rings (Fig. 8d). Adaxial surface, facial leaves – Florin rings low to moderately ridged and slightly lobed Fig. 7b). The bases of main axis lateral leaves have highly convex epidermal cells that are almost papillate in appearance (Fig. 7c).
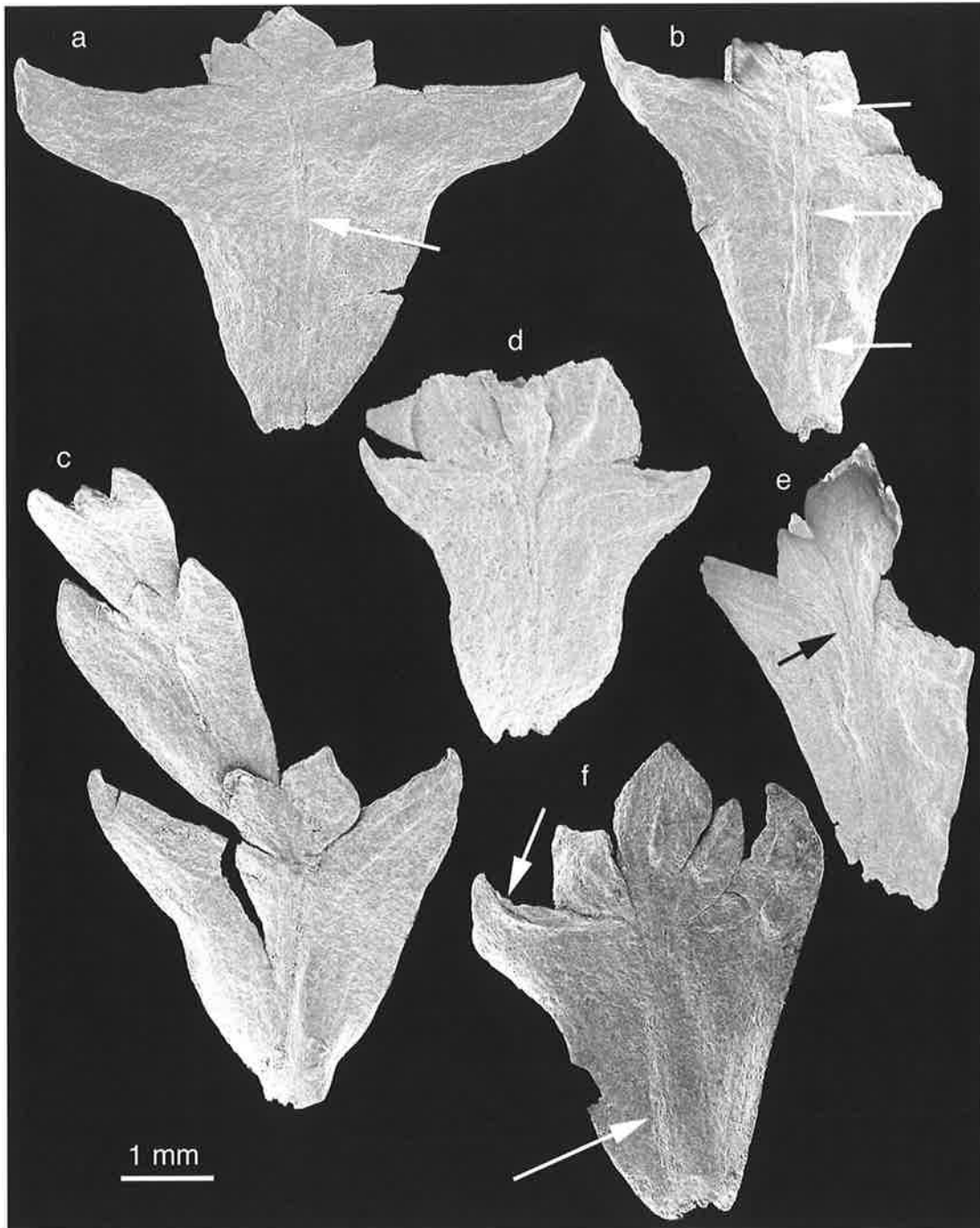
Fig. 5a-f SEM *Austrocedrus australis* sp. nov., large, main axis foliage
(figure caption p. 214)

Fig. 5a-f SEM *Austrocedrus australis* sp. nov., large, main axis foliage

a. Ventral surface, large lateral leaves, fused for ~half their length. Free half outwardly recurved and at right angles to the main axis. Central facial leaf extending downwards between the 2 lateral leaves to their base (arrow; specimen LEA-5257).

b. Lateral leaves, one with an acute, inwardly curved, apex. A distinct groove extending from the leading (missing) facial leaf separates the lateral leaf pair (arrows; specimen LEA-5251).

c. Holotype, ventral surface, large main axis leaves with smaller leaved branchlet arising in the same plane (LEA-1640).

d. Ventral surface. Lateral leaves separated by a distinct groove (specimen LEA-631).

e. Dorsal surface. Main axis facial leaf elongate and tapering to a narrow base. The base of the smaller facial leaves is acutely elongate and extends down between the lateral leaves (arrow; specimen LEA-5253).

f. Dorsal surface. Main axis facial leaf outwardly keeled, with a bluntly acute apex and tapering to a narrow elongate base. The area where the 2 lateral leaves abut is raised (lower arrow). The free margin of the lateral leaves is entire and revolute near the apex. The adaxial leaf surface bulges outwards (upper arrow; specimen LEA-3467).
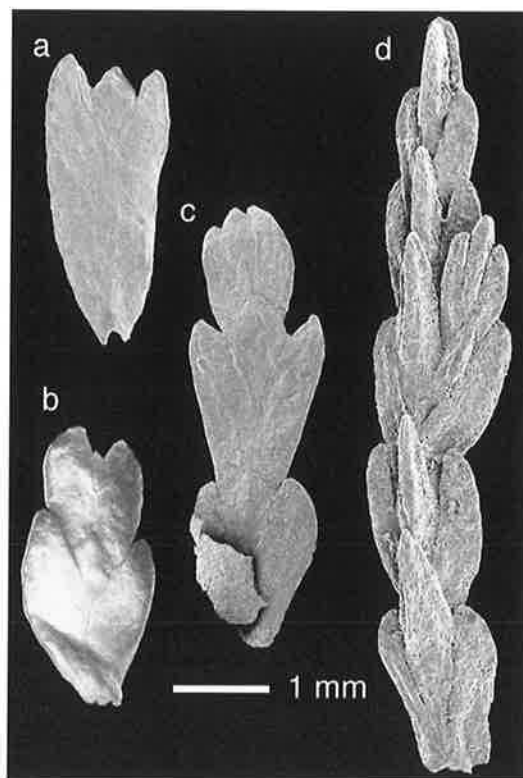
Fig. 6a-e SEM *Austrocedrus australis* sp. nov., small foliage

a. Lateral leaves elongate, lanceolate, and apically recurved (specimen LEA-5256).

b. Ventral surface, terminal leaves. Lateral and facial leaves slightly less flattened (specimen LEA-5252).

c. Terminal leaves. Facial leaves extending downwards between the laterals, and not reaching the facial pair above (specimen LEA-5255).

d. Non flattened, branching foliage (specimen LEA-750).
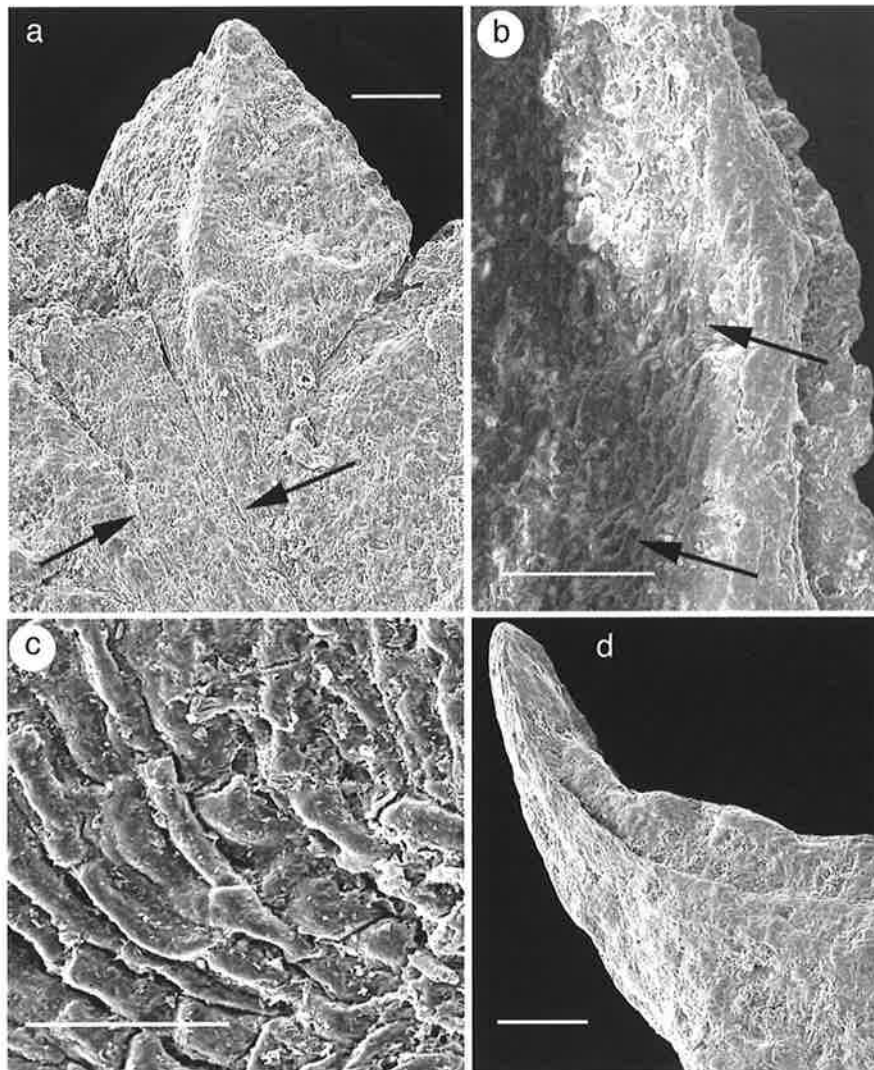
Fig. 7a-d SEM *Austrocedrus australis* sp. nov., detail, main axis leaves

    a. One of 3 facial leaves. Leaf outwardly keeled and with a frilled margin. The leading facial leaf is broken but the base can be seen to extend down between the lateral leaves (arrows; scale 200 μm; specimen LEA-5251).

    b. Adaxial surface, facial leaf. Stomata (arrows) appear to be oriented with the centre of the leaf. Florin rings low to moderately ridged and slightly lobed (scale 50 μm; specimen LEA-5253).

    c. Lateral leaf base. Epidermal cells bulging outwards and somewhat papillate in appearance (scale 50 μm; specimen LEA-5257).

    d. Inwardly turned lateral leaf apex, Leaf margin entire and revolute away from the acute apex (scale 200 μm; specimen LEA-5251).

Fig. 8a-g SEM, LM *Austrocedrus australis* sp. nov., cuticle

    a. Inner surface stomata. Elongate guard cells with four elongate and moderately coarse grained, indented subsidiary cells (arrows; scale 20 μm; specimen LEA-5250).

    b. Outer lateral leaf surface (probably dorsal surface). Surface eroded, but appears waxy. Florin rings not clearly apparent (scale 20 μm; specimen LEA-5256).

    c. Inner surface. Stomata closely packed. Guard cells surrounded by a discontinuous groove, and sharing subsidiary cells (scale 20 μm; specimen LEA-3400).

    d. Highly eroded outer leaf surface. Stomata with Florin rings, closely packed and in rows (scale 20 μm; specimen LEA-5256).

    e. Inner surface. Epidermal cells adjacent to stomatal complexes elongate, coarse grained, and containing large nodules (arrow). Anticlinal epidermal cell walls thick, acute (scale 20 μm; specimen LEA-3400).

    f. Inner surface. Epidermal cells elongate with coarse grained periclinal cell walls. Anticlinal walls thick, acute, and slightly broader at the base (scale 25 μm; specimen LEA-5250).

    g. Stomata with elongate guard cells. Epidermal cells immediately adjacent to stomatal complexes irregularly shaped (scale 50 μm; specimen LEA-3468).

    h. Stomata in discontinuous rows (scale 100 μm; specimen LEA-3468).

    i. Coarse grained, irregularly shaped epidermal cells (scale 50 μm; specimen LEA-3468).
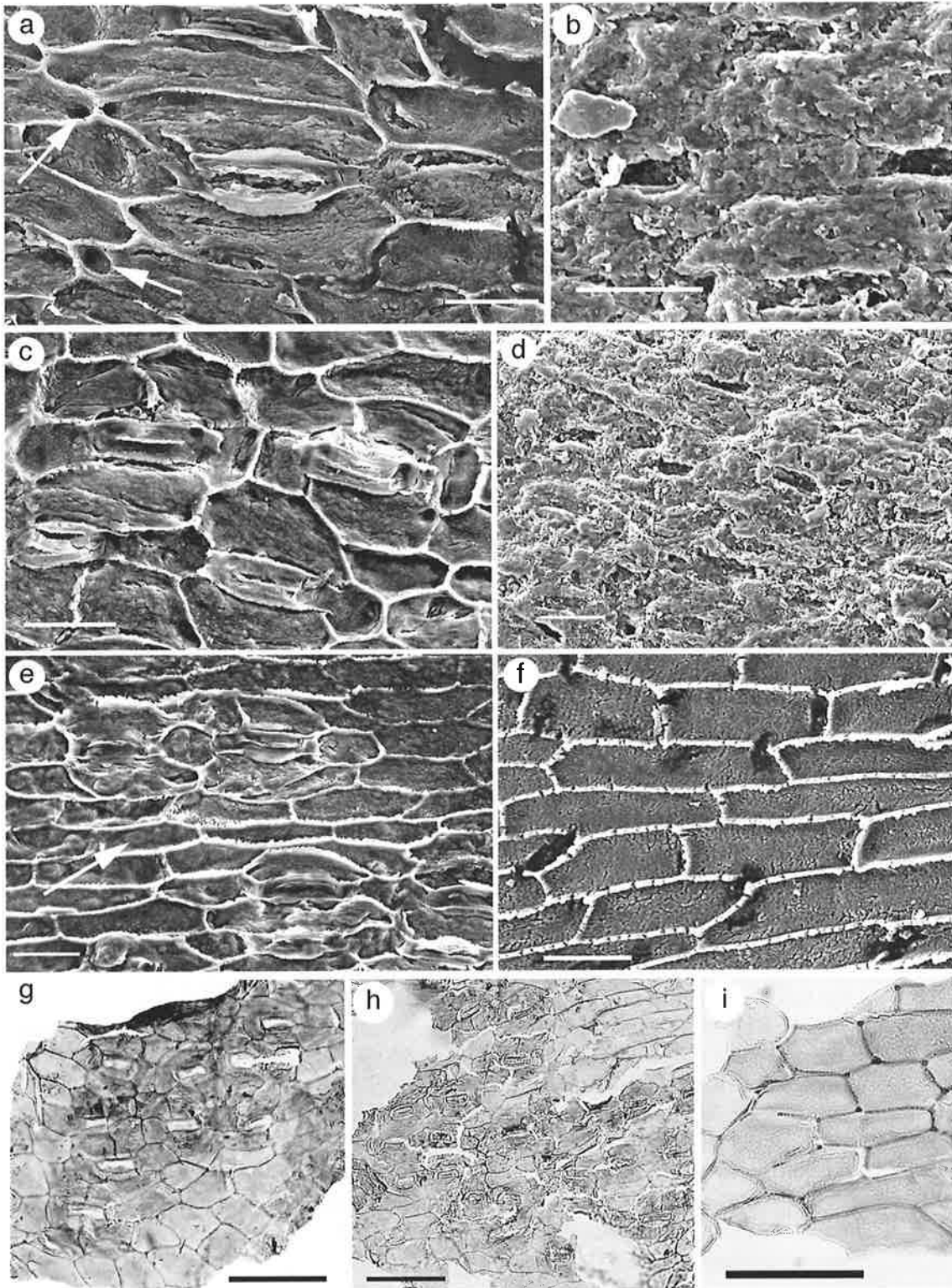
Fig. 8a-g SEM, LM *Austrocedrus australis* sp. nov., cuticle

Cone genus/species 1

Systematics
Order Coniferales
Family Cupressaceae
Genus *Austrocedrus* Florin & Boutelje, Acta Horti Berg. 17 (2): 28. (1954)

Austrocedrus australis sp. nov.,

Diagnosis. Bract projections squat, small, close to scale apex. Scales of penultimate bracts-scale complexes larger than bracts.

Holotype: LEA- 4214 stored in the School of Earth and Environmental Sciences, The University of Adelaide, South Australia.
Type locality: Lea River (41°30'S 145°39'E).
Ovulate cone specimen examined (1) LEA-4214.

Ovulate cone: (Fig. 9a-e) 5.65 mm long, and flattened in appearance. Four decussate bract/scale pairs. Ultimate scales larger, ovoid, with a rounded apex, and tapering to an acute base (Fig. 9e). Penultimate bract/scales sit within this tapered area (Fig. 9a). Adaxial surface of ultimate scale, slightly rugose. Bract projection on abaxial surface with an acute apex, and extending just beyond the scale apex (Fig. 9b). Penultimate bract/scales about two thirds the length of the ultimate pair, and broadly elongate. Abaxial scale and bract surfaces rugose. Penultimate bracts broad, about two thirds the length of the scale, with small, acute bract projections (Fig. 9c). Ultimate and penultimate scales with papillate margins (Fig. 9d). All bract-scale bases acute, and with large cells (Fig. 9e).

Fig. 9a-e SEM *Austrocedrus australis* sp. nov., ovulate cone
Holotype specimen LEA-4214
  a. Mature cone. Ultimate scales larger, broader than penultimate, and tapering towards the base to accommodate the penultimate bract-scales.
  b. Ultimate scale, adaxial surface. Bract projection small, with an acute apex, and extending just above the scale margin (scale 500 μm).
  c. Penultimate bract-scale. Abaxial scale surface highly rugose, with papillate margin. Upper scale and bract margins scalloped. Bract broad, two thirds the length of the scale. Bract projection small, central, with acute, slightly outwardly curved apex (scale 1 mm).
  d. Detail of c. Penultimate bract reaching the papillate scale margin (scale 100 μm)
  e. Bases of ultimate and penultimate bract-scales bluntly acute, and with large cells (scale 500 μm).
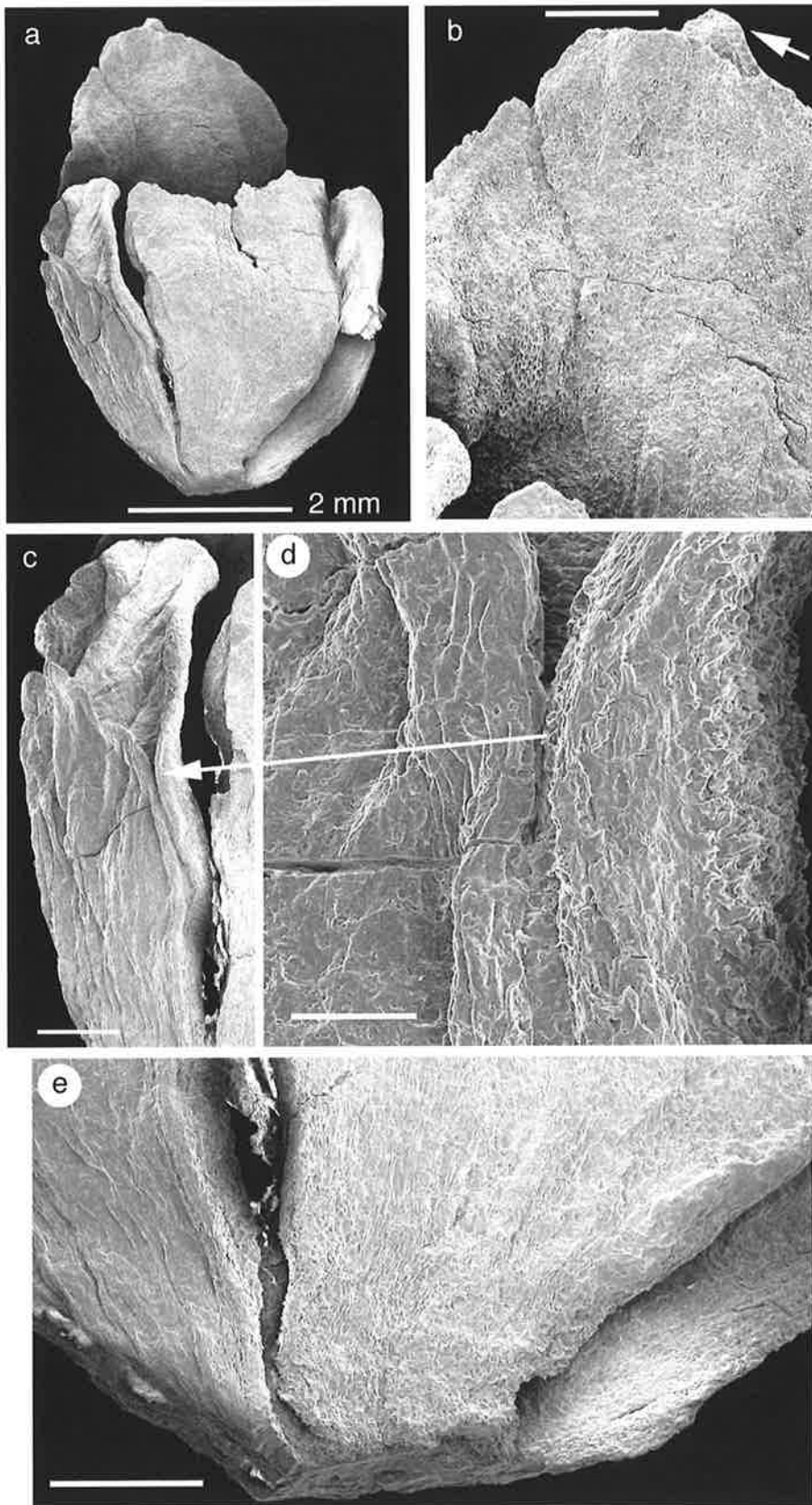
Fig. 9a-e SEM *Austrocedrus australis* sp. nov., ovulate cone

Comparison of fossil and living species (Fig. 6a-f)

Foliage: The shape of the fossil foliage is much like that of extant *Austrocedrus chilensis* (Fig. 10a, b), and (although the LM fossil cuticle is poor) has very similar stomatal complexes and epidermal cell shapes (Fig. 10e, f) and is therefore assigned to the genus *Austrocedrus*. The foliage also has similarities to *Papuacedrus*, but the external surface stomata lack the high ridged Florin rings that are characteristic of that genus. Early Eocene cupressaceous fossil leaves from Patagonia (Argentina), thought to be similar to extant *Austrocedrus* (Wilf *et al.* 2003), are also somewhat similar to the Lea River fossils.

Ovulate cone: Whilst a single cone with no attached foliage (Fig. 9d) is not a good basis for comprehensive comparison with extant cones (Fig. 9c), the shape of the scales, and the size and placement of the bract, are very similar to *Austrocedrus chilensis*.

The only major difference between *Austrocedrus chilensis* and the fossils is the small size of the latter.
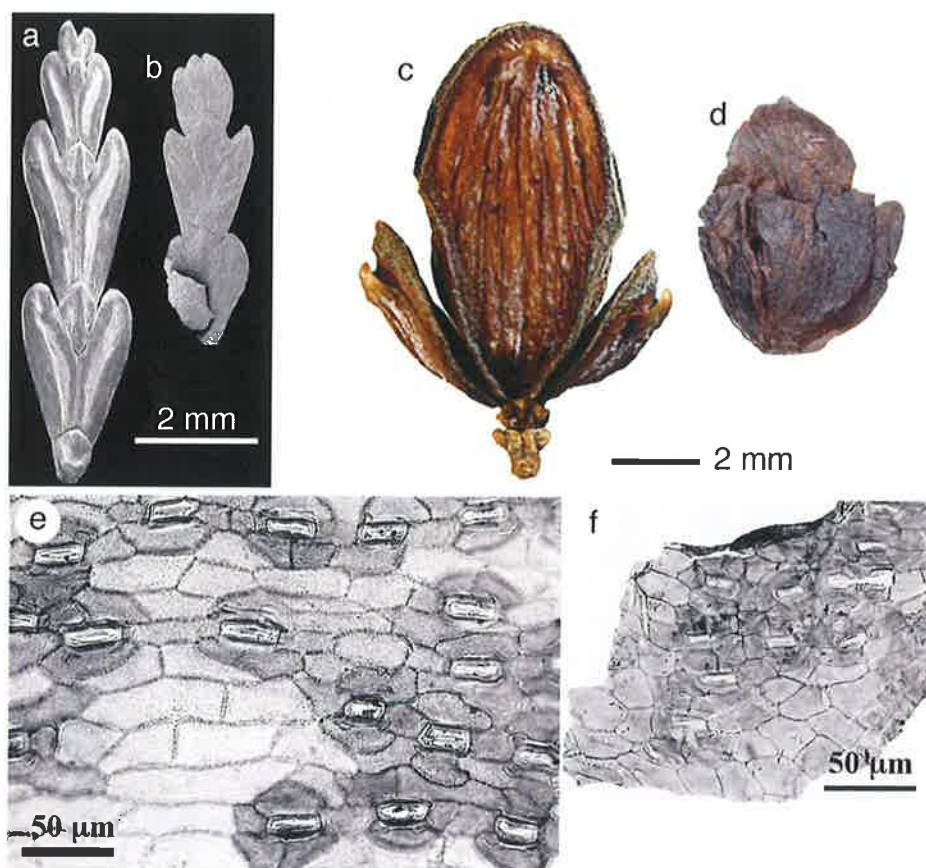
Fig. 10a-e Comparisons between *Austrocedrus australis* and *Austrocedrus chilensis*
    a. *Austrocedrus chilensis* (specimen E/C/01).
    b. *Austrocedrus australis* LEA-5525.
    c. *Austrocedrus chilensis* (specimen E/C/01).
    d. *Austrocedrus australis* LEA-4214.
    e. *Austrocedrus chilensis* cultivated specimen, Tasmanian Arboretum.
    f. *Austrocedrus australis* LEA-3468.

Systematics
Order Coniferales
Family Cupressaceae
Genus *Libocedrus* Endl., Syn. Conif.: 42 (1847)
Libocedrus leaensis sp. nov.,

Diagnosis. Fertile shoots with frequent alternate branching in the same plane. Ovulate cones terminal on short shoots, and with elongate bracts. Lateral leaves with bluntly acute apices, entire margins, fused for around half their length, and with ventral surface stomata protected by overlying facial leaves. Facial leaves with few, if any, stomata on ventral surface. External surface stomata with high ridged and lobed Florin rings.

Holotype: LEA-3693 stored in the School of Earth and Environmental Sciences, The University of Adelaide, South Australia.
    Type locality: Lea River (41°30'S 145°39'E).
    Leaf specimens examined (8): LEA-1004, 1639, 1607, 3091, 3313, 3417, 3693 5254
    Etymology: named for the place from which it was collected

Foliage and leaves: Fig. 11a-d. Leaves decussate, dimorphic. Lateral leaves – 1.3-2.1 mm long, bifacially flattened, and fused for half to two thirds their length. Free section of leaves keeled, apices bluntly acute, bases slightly papillate (Fig. 12g). Margins entire and generally well defined (Fig. 12f). Facial leaves – generally small, but may be larger on main axis shoots (Fig. 11a), 1-2.6 mm long, rhombic, with acute apices (Fig. 13a, c), often not reaching the facial pair above (Fig. 12c, d), keeled on dorsal and ventral surfaces, and with frilled margins (Fig. 13a, c). Fertile foliage – Ultimate shoots short, with alternate branching in the same plane (Fig 11a). Foliage somewhat less flattened than non fertile, and generally more compact, and lateral and facial leaves often similar in size.
    Stomatal distribution: Ventral surface, lateral leaves – none in exposed areas. A few towards the base, where they are protected by overlying facial leaves (Fig. 12f). None apparent on facial leaves. Dorsal surface distribution unknown. Adaxial surfaces, lateral and facial leaves – in short, discontinuous rows, close to, and generally oriented with the margin, that extend from near the base almost to the apex (Figs 12c; 13a, b).
    Cuticle description: No internal details known (there were too few specimens for cuticle preparation). Outer surface – Florin rings high ridged, distinctly lobed, and with a peripheral groove. Numerous round papillae are associated with the stomata (Figs 12e; 13b, d). Epidermal cells contain numerous small holes (Fig. 12g).
    Ovulate cones: Figs 11b and 12a (specimen (LEA–3693) illustrate cone initiation, *viz*. a short shoot, with elongation of ultimate, penultimate and subtending decussate bracts. This, and specimen LEA–3147 (Fig. 11a) show remarkable similarities with Tomlinson *et al.'s* (1993) Figs 7-14 showing ovulate cone initiation for *L. plumosa*.
    Pollen: Pollen grains spherical (Fig. 12d).
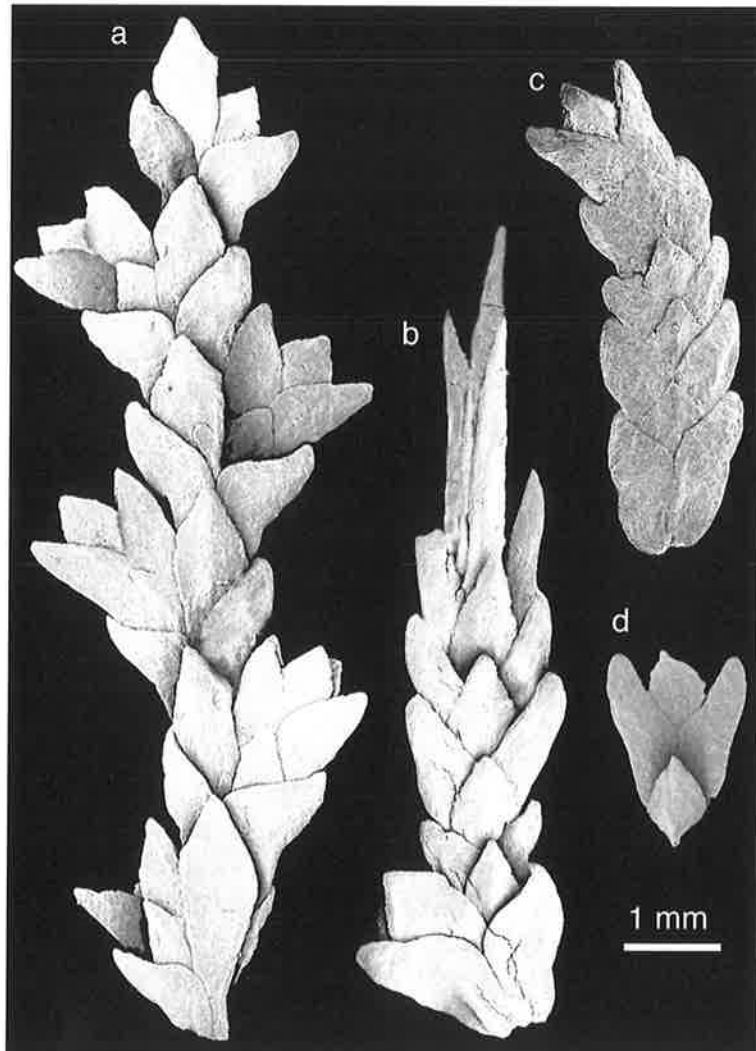
Fig. 11a-d. SEM *Libocedrus leaensis* sp. nov., foliage

    a. Highly branching, and possibly fertile branchlet. Tips of branchlets missing. Leading lowest facial leaf elongate, and larger than laterals. Branching appears to be in the same plane (specimen LEA-3417).

    b. Shoot with fertile branchlet? Ovulate cone initiation in *Libocedrus* species begins with elongation of bracts at the tips of short branchlets - in a very similar manner to that seen here (see Tomlinson *et al*. 1993; holotype LEA-3693).

    c. Ventral surface, small shoot with dimorphic decussate leaves. Lateral leaves imbricate and larger than facial leaves. Facial leaves reaching, or almost reaching the facial leave above. Leaves slightly convex (specimen LEA-1639).

    d. Ventral surface, small shoot (specimen LEA-5254).

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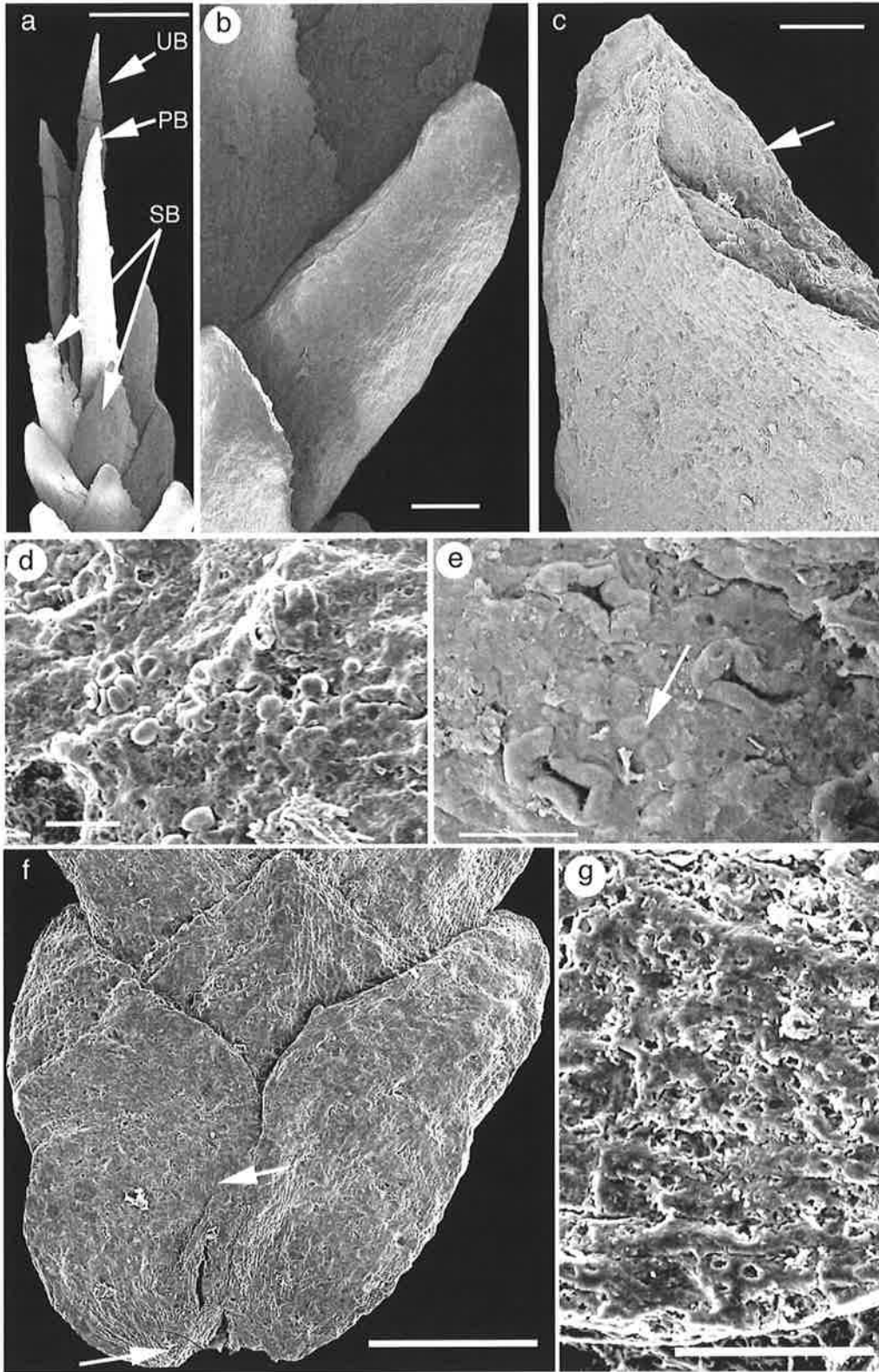
Fig. 12a-g SEM *Libocedrus leaensis* sp. nov., foliage detail
(figure caption p. 224)

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Fig. 12a-g SEM *Libocedrus leaensis* sp. nov., foliage detail

    a. Detail of elongate terminal shoots. Ultimate bract (UB), penultimate bract (PB), subtending bracts (SB) (scale 1 mm; holotype LEA-3693).

    b. Lateral leaf with entire, and slightly revolute, margin (scale 200 μm; holotype LEA-3693).

    c. Lateral leaf, adaxial stomata (arrow) not oriented with leaf margin (scale 100 μm; specimen LEA-3417).

    d. Eroded outer surface with pollen grains (scale 50 μm; specimen LEA-3417).

    e. Detail of **c.** adaxial stomata with high ridged and distinctly lobed Florin rings. Numerous small round papillae (arrow; scale 20 μm; holotype LEA-3693).

    f. Lateral leaves with entire margins. Upper arrow indicating a few scattered stomata. Lower arrow indicating papillate leaf base (scale 500 μm; specimen LEA-1639).

    g. Outer surface lateral leaf. Epidermal cell walls indented. Epidermal cells with small holes (scale 50 μm; specimen LEA-1639).
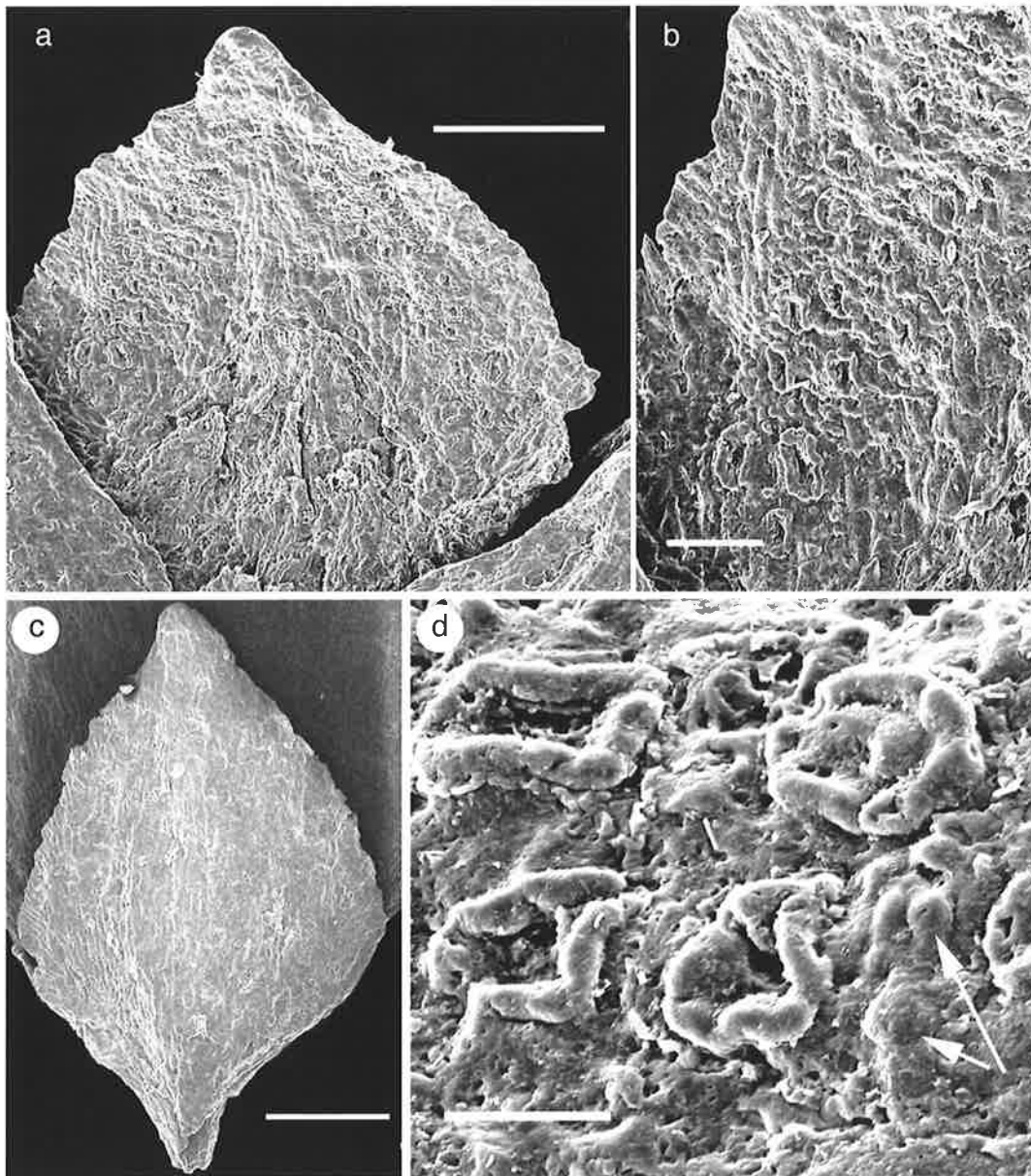
Fig. 13a-d SEM *Libocedrus leaensis* sp. nov., foliage detail
a-e holotype LEA-3693; **f, g** specimen LEA-3417.

    a. Ventral facial leaf removed to show stomatal distribution on the adaxial surface of a dorsal facial leaf (scale 200 μm).

    b. Detail of **a**. Stomata more or less oriented with the frilled margin (scale 50 μm).

    c. Dorsal facial leaf, with frilled margin. No stomata apparent (scale 200 μm).

    d. Detail of stomata **b**. Florin rings mostly elongate, highly lobed, with a peripheral ring, and surrounded by numerous small papillae (arrows). Fungal hyphae are also present (scale 20 μm).

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Discussion

Despite the paucity of fertile extant material in this study (Part 1), Tomlinson *et al.'s* (1993) excellent illustrations show how the ovulate cones of *L. plumosa* are initiated (see Chapter 1, pp. 7-8 for a summary of their work). In this current study (Part 1), only two very immature extant *Libocedrus* ovulate cone specimens (*L. austrocaledonica*) were examined. One of these (illustrated in Figs 18 and 19a, Part 1) shows a developing cone, borne on an elongate shoot. It demonstrates that elongation of the ultimate, penultimate and subtending bracts well precedes scale development. The photographs of the fertile shoots (Lea River), especially the surface detail, are poor (due to difficulties in adhering the specimens to SEM stubs), and there are no internal cuticular characters for comparison with extant *Libocedrus* related species. However, the elongate bracts of the developing cones, are unique to New Zealand and New Caledonian *Libocedrus*. The absence of stomata on the unprotected surface of lateral leaves, the slightly papillate leaf bases, and the short branchlets on which the ovulate cones are borne, suggest similarities with *L. plumosa* (New Zealand), rather than New Caledonian *Libocedrus* species. The fertile foliage is somewhat similar to fertile *Papuacedrus* foliage, but the numerous papillae in association with the Florin rings, and the elongate fertile bracts are not characteristic of *Papuacedrus*. The presence of fungal hyphae on the leaves would indicate it grew in high rainfall conditions. What is unusual is the small size of the fossils. They are about a quarter the size of extant *L. austrocaledonica* and around a third the size of *L. plumosa*. The fossil leaves are assigned to the genus *Libocedrus*.

Cone genus/species 2

These six-parted ovulate cones are subtended by foliage in whorls of three. Foliage in alternate whorls of three, believed to be closely related to, or possibly ancestral to *Callitris* is also present at Lea River (Hill *et al.* unpublished data). This foliage is illustrated in this section, but is not discussed in detail.

Systematics
Order Coniferales
Family Cupressaceae
Genus *Callitris* Vent., Decas Gen. Nov.: 10. (1808)
Callitris leaensis sp. nov.

Diagnosis. Ovulate cone six-parted. Bract-scale complexes in alternate whorls of three. Upper bract scales larger, broader than penultimate, and tapering at the base. Bract projection near the cone apex, short. Single columella. Cone subtended by similar sized leaves in alternate whorls of three.

Holotype: LEA-441, stored in the School of Earth and Environmental Sciences, The University of Adelaide, South Australia.
Type locality: Lea River (41°30'S 145°39'E).
Ovulate cone specimens examined (7) LEA-441, 442, 450, 1642, 1780, 1875, 5160
Etymology: Named for the site at which they were found.

Ovulate cones: Fig. 14a-d. 4.5–3.6 mm long, flattened in appearance, and terminal on leafy shoots. Bract-scale complexes in two alternate whorls of three. These remain incurved when open. The lower bract/scales are about two thirds the length of those above (Figs 15b, 16a, e). Upper bract-scales broadest in the upper third, with an obtuse apex, and tapering towards the base (Figs 15b; 16a, c, e). The adaxial surface of all scales highly rugose, and centrally raised (Fig 15c, d). Abaxial bract-scale surfaces may also be rugose (Figs 14c; 16c). Scale margins papillate (Fig 15d, e). Bract protuberances on lower bract-scales short, broad, extending slightly above the apex (Figs 15d; 16a, e), and outwardly curved (Fig. 15h). This probably also applies to the upper bract protuberances, but is less apparent as most are broken (Fig. 15e, g). There appears to be a single, elongate and flattened columella (Fig. 15c), with a broad apex (Fig. 15a). Bracts (or leaves) that are slightly longer and broader than the other foliage subtend the upper bract-scales (Figs 15f; 16b, d, f). All foliage is astomatic. Seeds winged (Figs 16a; 17).
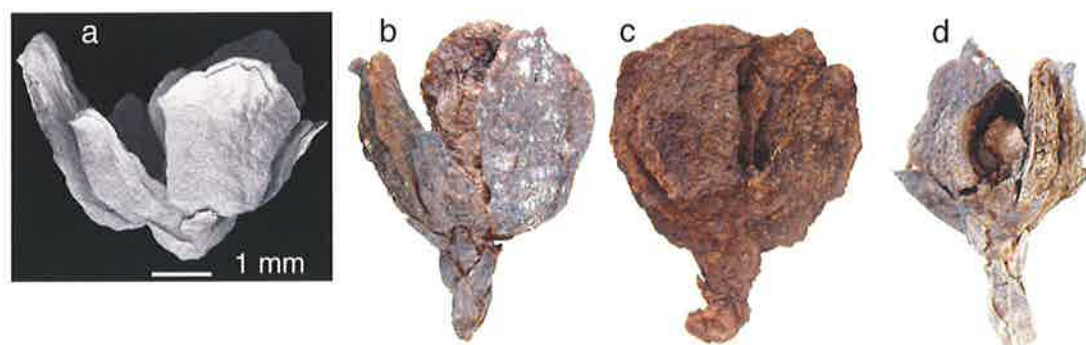
Fig. 14a-d *Callitris leaensis* sp. nov. showing size and shape variation
   a. LEA-5160, **b.** LEA-441, **c.** LEA-1780, **d.** LEA-442

Fig. 15a-i *Callitris leaensis* sp. nov. ovulate cone
Specimen LEA-5160

a. **a-c** shows the same cone from different angles. Cone with one ultimate bract removed.

b. Cone before removal of large bract-scale.

c. Cone showing a large central, and somewhat flattened, columella. The adaxial surface of the upper scales is highly rugose and, in the centre, bulges into the cone.

d. Detail of lower scale. Bract extending to the margin at the sides of the scale, and beyond it at the apex. Scale margin papillate. Adaxial scale surface rugose and centrally bulging (scale 500 μm).

e. Upper scale margin. Adaxial surface papillate. Bract projection on outer surface short, outwardly turned and not reaching the apex (scale 200 μm).

f. Astomatic leaves at base of cone (scale 500 μm).

g. Broken bract projection, upper scale (scale 500 μm).

h. Lower bract-scale. Short, broad, outwardly turned bract projection (scale 200 μm).

i. Cone shown at the same scale of extant cone illustrations (Part 1). Arrow indicating removed bract-scale.
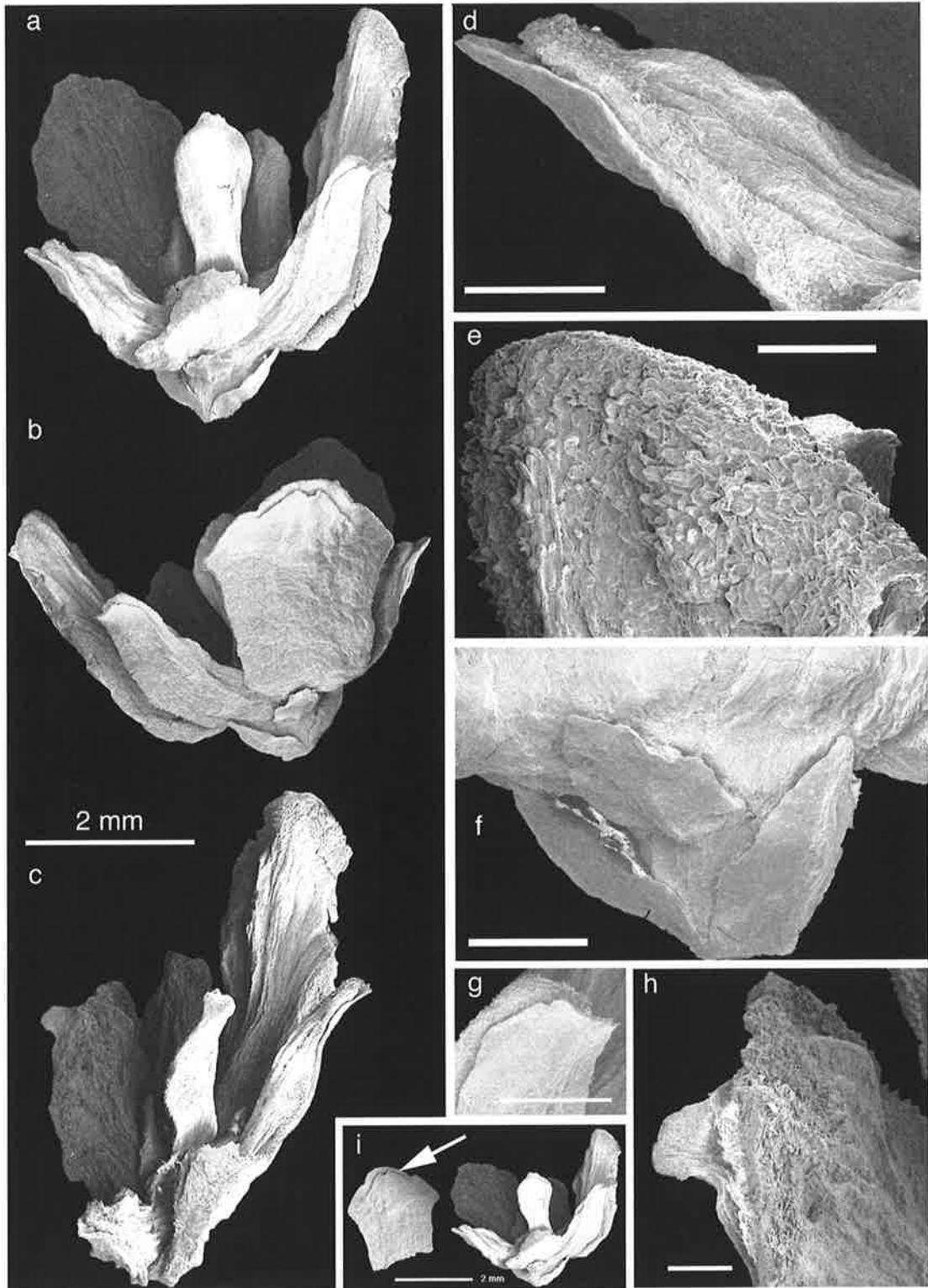
Fig. 15a-i *Callitris leaensis* sp. nov. ovulate cone

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Fig. 16a-d *Callitris leaensis* sp. nov. ovulate cone

    a. Slightly flattened cone with winged seed (black arrow). Bract protuberances short, outwardly turned and extending slightly beyond the scale apex (holotype specimen LEA-441).

    b. Detail of **a**. Leaf arrangement at cone base. Base of upper scales subtended by a bract (upper left) that is slightly longer, and wider than other foliage (scale 500 μm).

    c. Degraded cone. Arrows indicating bract protuberances on upper scales. Abaxial bract-scale surface rugose (specimen LEA-442).

    d. Detail of **b**. Leaf at base of cone (scale 200 μm).

    e. Small, probably immature cone with bract-scales inwardly curved (specimen LEA-1780).

    f. Detail of **e**. Leaf arrangement at base of cone. Arrow indicating slight overlapping of leaves (scale 500 μm).

    a. Detail of **e**. Immature seed (scale 50 μm).
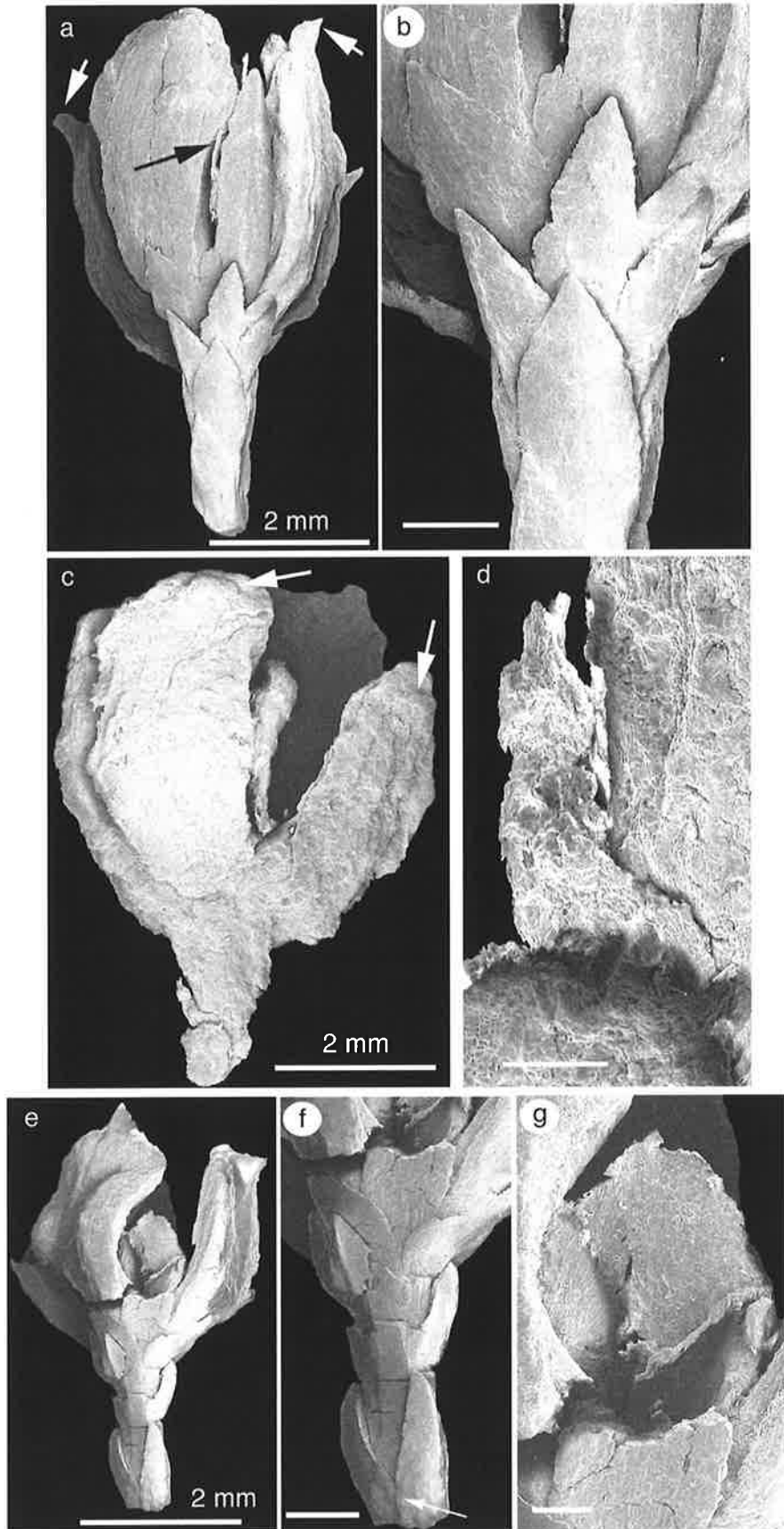
Fig. 16a-d *Callitris leaensis* sp. nov. ovulate cone

Comparison of fossil and living species

The six parted cones are in varying stages of preservation, and range from old and degraded to immature. The foliage beneath the cones tapers to an acute apex, and appears to be in whorls of 3, but is totally lacking in any other characters (especially stomata) that might help identify it, and the cones. Foliage in whorls of 3, identified as *Fitzroya* (*F. acutifolius*, Hill and Paull 2003) has been found in the Lea River sediments, and the possibility that the cones could be related to this foliage was considered. A specimen of small-leaved *F. acutifolius* and a Lea River type 2 cone are illustrated below for comparison (Fig. 17a, b). Although the size and shape of the leaves of the two specimens are very similar, the cones are quite different from extant *Fitzroya* (see illustrations in Part III B).

The Lea River sediments also contain a number of other foliage specimens (Fig. 17c) that, although they are in whorls of three, appear unlike foliage assigned to *Fitzroya*. These seem to be closely related to *Callitris* (Hill *et al*. unpublished data) but, unlike mature *Callitris* foliage, the leaves are variably fused. It seems much more likely that the cones are related to this foliage. A detailed review of other Southern Hemisphere extant Cupressaceae *viz. Callitris, Actinostrobus, Neocallitropsis* and *Widdringtonia* was considered beyond the scope of this study, and ovulate cones and foliage from only a few species were available for comparison. *Widdringtonia* cones are four-parted, and although the three extant *Actinostobus* species have foliage in whorls of three, the six bract scale complexes are similar in size, and the subtending foliage is broad leaved (Farjon 2005). *Neocallitropsis* cones have numerous bract-scales. A chance collection of *Callitris verrucosa* (possibly a hybrid with *C. glaucophylla* [see Hill KD 1998 p. 579]; growing near the roadside close to Moorie in the Darling Downs, Queensland) in late October 2006 indicates that the <u>small immature</u> cones of at least one *Callitris* species are quite similar to, but larger than, the fossil cones. These are illustrated below. Unlike the much larger and more robust mature cones, the immature cones of this extant species are subtended by small leaved foliage (Fig. 18a-e). The cones are six parted, and are comprised of three slightly shorter, narrower penultimate bract-scales, and three larger, broader ultimate bract scales that taper towards the base (as do those of the fossils). Bract extensions on mature cones are short and barely visible just below the scale apex (Fig. 18a, b). On immature cones these are more prominent (Fig. 18 d, c). Like the fossil cones (Fig. 15a) mature *C. verrucosa* cones terminate in a conical columella (Fig. 18b). Seeds (not illustrated) are 2 or 3 winged (Farjon 2005), and have a small central micropyle, similar to that of the fossils (Fig. 17b). The ovulate fossil cones are considered to be *Callitris* related and thus represent the earliest record of this genus. They are thought to be immature. Like the other Cupressaceae fossils at Lea River, they are much smaller than their extant relatives.

Discussion

The genus *Callitris* is widespread and has 19 species, 17 in Australia, 2 in New Caledonia (Hill KD 1998). These are generally adapted to relatively dry environments, and only two species, *C. macleayana* (northeastern Australian margin) and *C. sulcata* (New Caledonia) grow in relatively high rainfall conditions. These two species have spreading juvenile leaves, not unlike those attributed to *Fitzroya* (Hill and Whang 1996; Hill and Paull 2003), but these are frequently in whorls of 4 (especially those of *C. sulcata*; Farjon 2005). The presence of *Callitris*, with rainforest taxa such as *Austrocedrus, Libocedrus* (this study) and *Nothofagus* (Scriven and Hill 1996) suggests that extant *Callitris* had an adaptable rainforest ancestor.
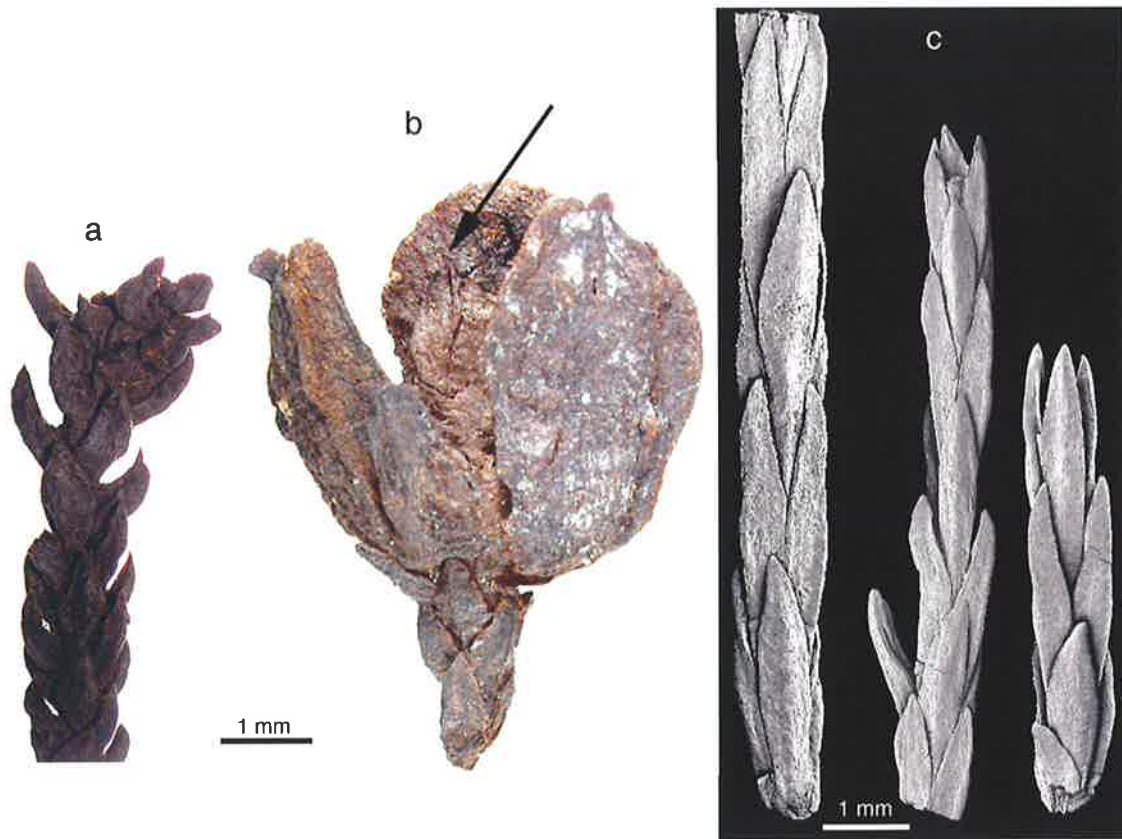
Fig. 17 *Fitzroya acutifolius* foliage, *Callitris leaensis* sp. nov. ovulate cone, and *Callitris* attributed foliage.

    a. Small-leaved *Fitzroya acutifolius* foliage in alternate whorls of 3 (specimen Lea-1883).

    b. *Callitris leaensis* sp. nov. ovulate cone, arrow indicating winged seed with possible micropyle (holotype LEA-441).

    c. Possible *Callitris* foliage. Leaves elongate, imbricate, in alternate whorls of three, and (unlike extant *Callitris*) variably fused towards the base (specimens LEA-1760, LEA-3608, LEA-3465).

Fig. 18a-e *Callitris verrucosa*, immature and mature ovulate cones

a. Mature ovulate cones terminal on short, solitary or clustered, thick shoots. Subtending leaves almost inconspicuous (arrow). Small immature cone to the left.
b. Large mature cone with central columella. Outer bract surface covered with verrucae. Adaxial scale surface highly rugose and with a prominent central ridge.
c. Two views of the same immature cone. Outer surface relatively smooth, bract extensions close to the scale apex, short, narrow and outwardly turned. Cone subtended by similar sized leaves in alternate whorls of three. Leave subtending the ultimate bracts slightly larger than other foliage.
d. Slightly larger immature cone with small verrucae on the abaxial surface.
e. Detail of foliage subtending the cone. As this is dry land species the trichomes on the abaxial surface probably aid water conservation.
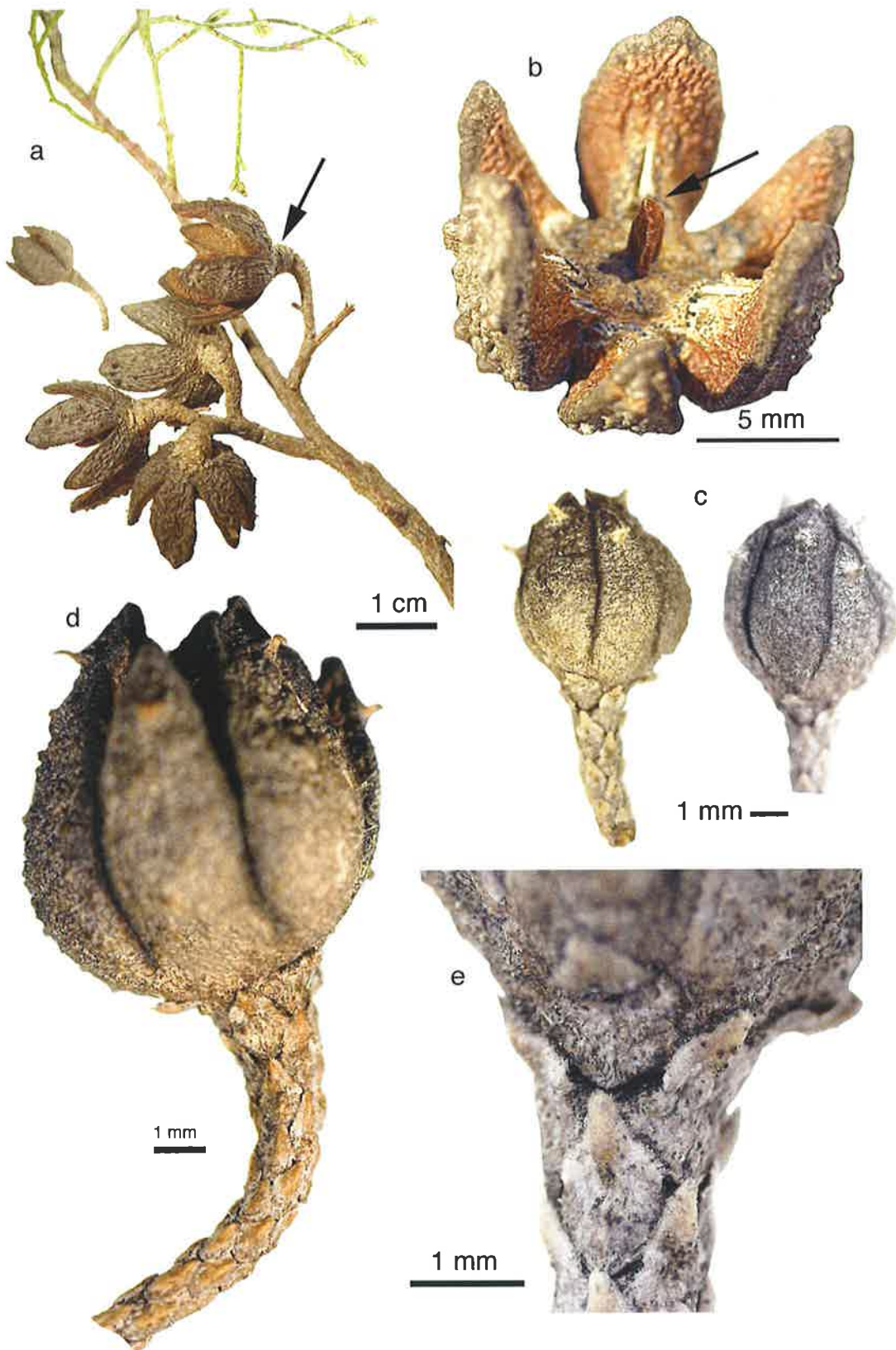
Fig. 18a-e *Callitris verrucosa*, immature and mature ovulate cones

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3. Regatta Point, Tasmania (42°09'S, 145°20'E)

Regatta Point is located northwest of the mouth of the King River, Macquarie Harbour, on the west coast of Tasmania. Fossil-bearing sediments at this site are of two ages. The oldest are late Early Eocene (palynostratigraphic data; Macphail *et al.* 1994; Macphail 2005*) and flank the SE, E, N and NW sides of the Harbour. They are possibly of widespread floodplain/lacustrine origin and consist of thin brown coal seams are overlain by Pleistocene sediments. The large age gap between the two fossiliferous horizons is suggestive of prolonged erosion, or non deposition (Macphail 2005). The younger sediments are Early Pleistocene (0.8-2.2 Ma; Macphail *et al.* 1993; Jordan 1997). The samples in this study come from blocks of the older sediments.
* Macphail's (2005) palynological report is primarily concerned with a contemporaneous site at Strahan (to the north of Regatta Point), but he considers the data from the two sites to be similar.

Systematics
Order Coniferales
Family Cupressaceae
Genus *Libocedrus* Endl., Syn. Conif.: 42 (1847)
***Libocedrus microformis* sp. nov.,**

Diagnosis. Branchlets sub-opposite–alternate, arising in the same plane. Leaves decussate, almost monomorphic. Lateral leaves slightly bifacially flattened, and with slightly papillate bases. Lateral and facial leaves imbricate, keeled, and with bluntly acute apices, and marginal frills. Facial leaves reaching, and generally overlapping, the facial pair above. Amphistomatic. Stomata close to the leaf margins, and not within clearly defined grooves. Stomata fewer on ventral leaf surfaces. Florin rings high ridged, lobed, and with associated round papillae.

Holotype: RPE-641, stored in the School of Earth and Environmental Sciences, University of Adelaide, South Australia.
Type locality: Regatta Point, Tasmania (42°09'S, 145°20'E).
Specimens examined in detail (48): RPE-65, 66, 68, 69, 71, 161, 191, 192, 193, 194, 195, 197, 198, 271, 272, 351, 352, 353, 354, 355, 461, 481, 482, 483, 522, 523, 621, 624, 641, 642, 644, 645, 661, 662, 663, 664, 645, 701, 702, 703, 704, 705, 706, 721, 722, 723, 724, 801. There are many other similar specimens from Regatta Point and these were chosen to represent the morphological variability (Fig. 1a-s).

Foliage and leaves: Fig. 19a-s. Branchlets sub-opposite to alternate, arising in the same plane. Leaves decussate, and somewhat flattened in appearance. Lateral and facial leaves imbricate and generally of similar length, but with lateral leaves sometimes slightly longer than facial leaves (e.g. Fig. 19a, i, j). Lateral and facial leaves with bluntly acute apices. Lateral leaves slightly bifacially flattened, lanceolate, 0.8-~2.2 mm long, dorso-ventrally keeled, with a weak marginal frill (Fig. 20d), and slightly fused towards the base (Fig. 20b, e). Lateral leaf bases slightly papillate (Fig. 20b). Facial leaves ovate to lanceolate, ~0.8-1.9 mm long, outwardly keeled towards the bluntly acute apex, but more flattened towards the base, and with a weakly frilled margin (Figs 20d; 21d). Facial leaves reaching to, and generally overlapping, the facial leaf pair above (Fig. 19a-s).

Stomatal distribution: Ventral surface – on lateral leaves towards the base (where they are mostly protected by the overlying facial leaves (Fig. 20b). On facial leaves in small depressions on either side of the leaf centre, but largely hidden (and protected) by the overlying lateral leaves (Fig. 20a). Dorsal surface, lateral and facial leaves – in discontinuous rows or small groups close to, and roughly parallel to, the leaf margin. These stomatal groupings extend from the base of lateral (Fig. 20e) and facial leaves for about half to two thirds the length of the leaf (Fig. 20a, d), and are not within clearly defined grooves. Adaxial surface (including dorsal and ventral facial leaves) – stomata on either side, and roughly parallel to, the centre of the leaf axis, and extending from near the base to the leaf apex (e.g. Figs 20c; 21a).

Cuticle description: Inner surface – stomatal apparatus monocyclic, guard cells elongate, and surrounded by 4-6 subsidiary cells which may be shared by adjacent guard cells (Fig. 22c, e). Where epidermal cells abut the guard cells they fold downwards, forming a discontinuous groove around them. Subsidiary cells and immediately adjacent epidermal cells are fine grained and may contain indentations. The latter are generally more frequent on the outer edges of the cell (but not close to guard cells). Anticlinal cell walls of subsidiary cells broader at the base, and folding slightly outward, away from the guard cells (Fig. 22a). When stomata are close to a leaf base, or possibly on a smaller facial leaf, the cells of the stomatal complex are smaller. The guard cells are less elongate and subsidiary cells are more frequently shared by guard cells (Fig. 22e). Epidermal cells outside stomatal complexes are elongate, irregular in shape and with moderately coarse-grained, and frequently concave, periclinal walls (Fig. 22h). Those close to stomatal complexes may contain indentations (Fig. 22g). The anticlinal cell walls (of these, and cells adjacent to stomata) are acute, moderately and evenly thickened, and coarser grained at the base. Outer surface – stomata have elongate, high ridged and distinctly lobed Florin rings (Fig. 22d) that may have a peripheral groove. Round (circular) papillae are associated with the stomata (Figs 21d; 22d). Epidermal cells are well defined, and contain numerous nodules or holes (Figs 21c; 22f). These are most apparent on the tips of lateral and facial leaves (dorsal and ventral surfaces; e.g. Fig. 21b) but are also present in other epidermal cells on ventral leaf surfaces.
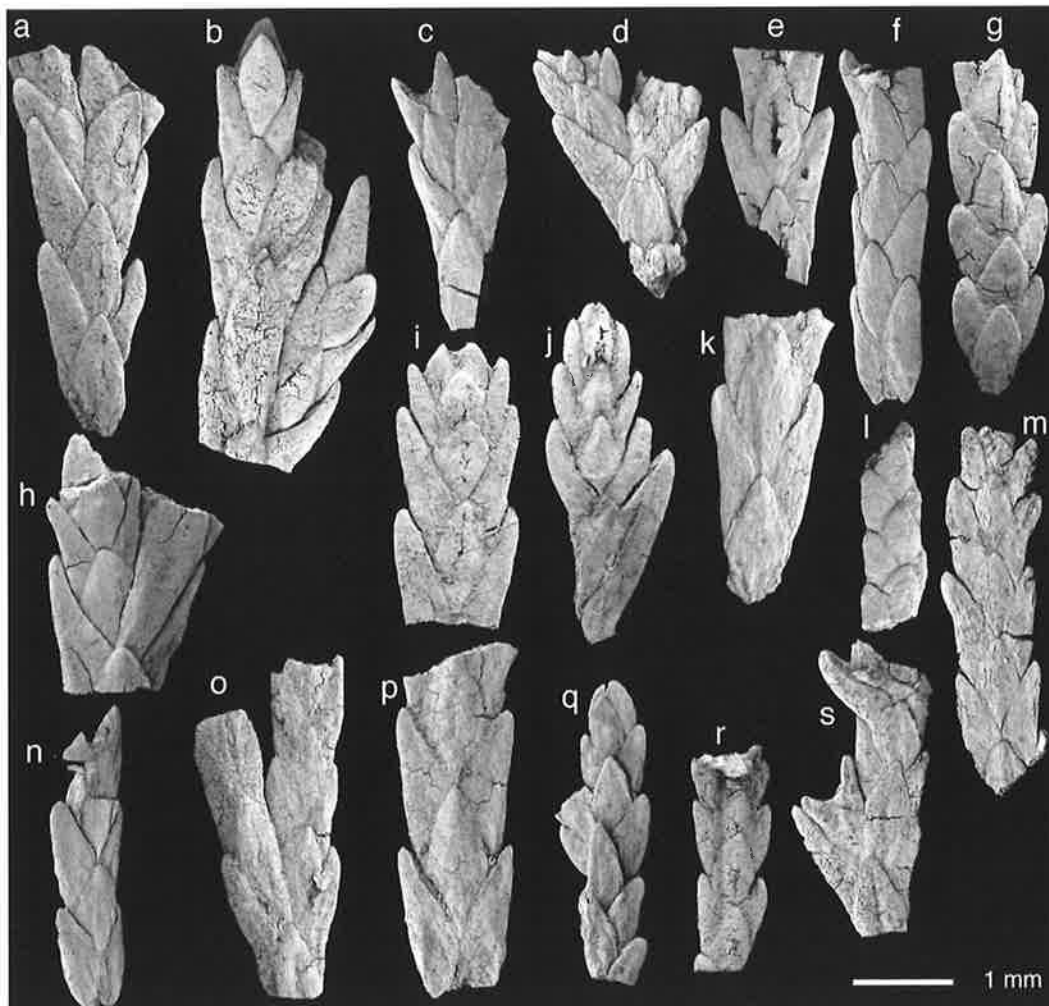
Fig. 19a-t *Libocedrus microformis* sp. nov., Regatta Point. A selection of specimens chosen to represent morphological diversity.

a. RPE-661; **b.** RPE-641 (holotype); **c.** RPE-662; **d.** RPE-705; **e.** RPE-723; **f.** RPE-701; **g.** RPE-801; **h.** RPE-706; **i.** RPE-645; **j.** RPE-642; **k.** RPE-722; **l.** RPE-644; **m.** RPE-702; **n.** RPE-703; **o.** RPE-663; **p.** RPE-664; **q.** RPE-704; **r.** RPE-721; **s.** RPE-481.

Fig. 20a-e SEM *Libocedrus microformis* sp. nov., Regatta Point, foliage detail

    a. Ventral leaf surface. Lateral and facial leaves imbricate, slightly flattened. Facial leaf broad and with stomata in small depressions on either side of the central keel towards the base (arrows; scale 200 μm; specimen RPE-722).

    b. Ventral surface. Facial leaf removed to show clusters of stomata towards the base of the lateral leaves. Lateral leaves fused (but barely) towards their slightly papillate bases (scale 200 μm; specimen RPE-701).

    c. Dorsal surface, lateral leaf. Stomata somewhat randomly distributed, more or less parallel, and close to the leaf margin, and reaching just above the lower half (white arrow) of the leaf. Stomata on adaxial surface (black arrow) randomly distributed. (scale 100 μm; specimen RPE-703).

    d. Dorsal surface. Stomata on lateral and facial leaves generally confined to small groups close to the frilled leaf margins (arrows). These stomatal areas extend for ~half to two-thirds the length of the leaf. Facial leaf broadly keeled, slightly flattened, and reaching to the facial leaf above (scale 200 μm; specimen RPE-703).

    e. Dorsal surface, base of specimen illustrated in **d**. On lateral leaves the stomata are towards the base (scale 200 μm; specimen RPE-703).
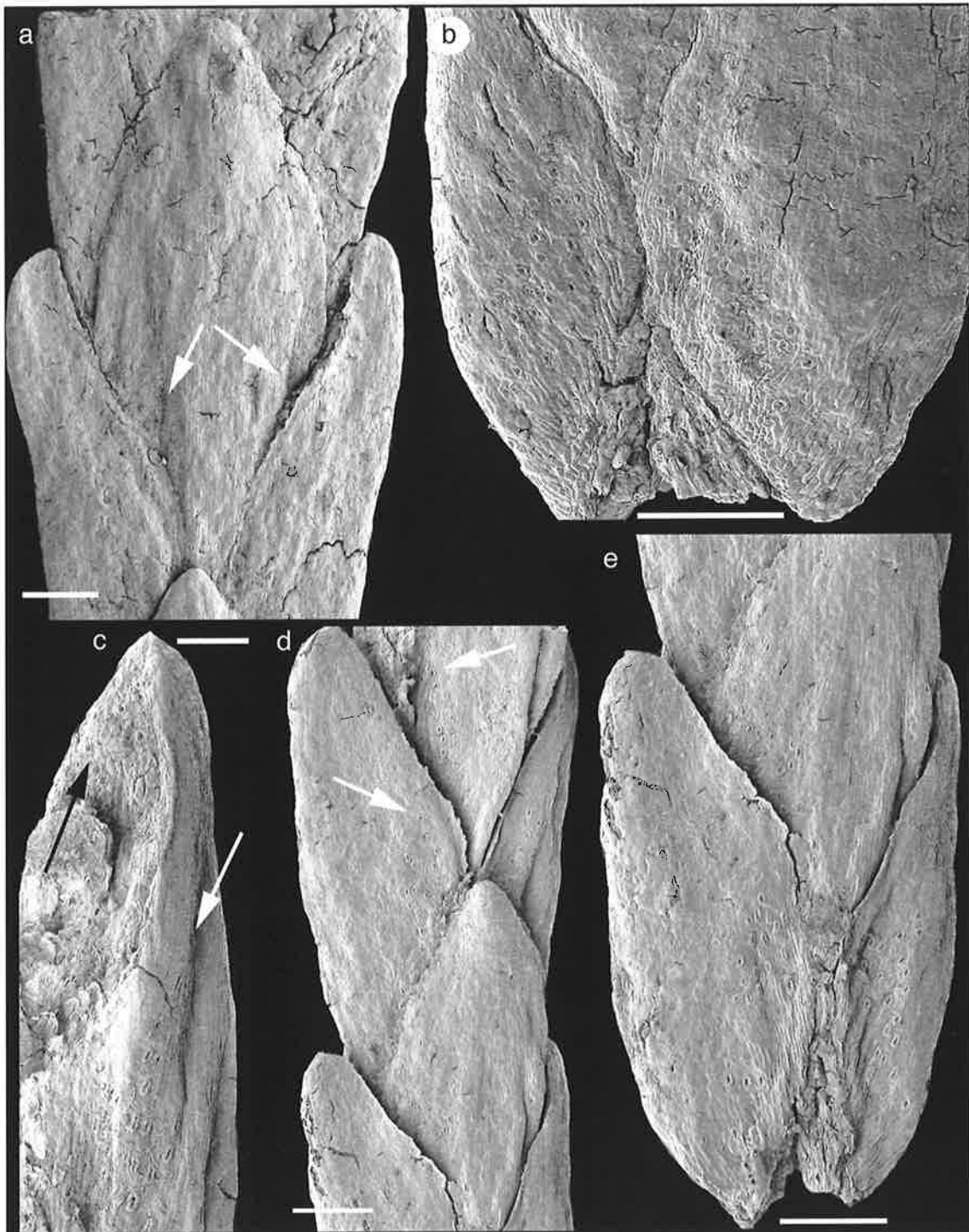
Fig. 20a-e SEM *Libocedrus microformis* sp. nov., Regatta Point, foliage detail
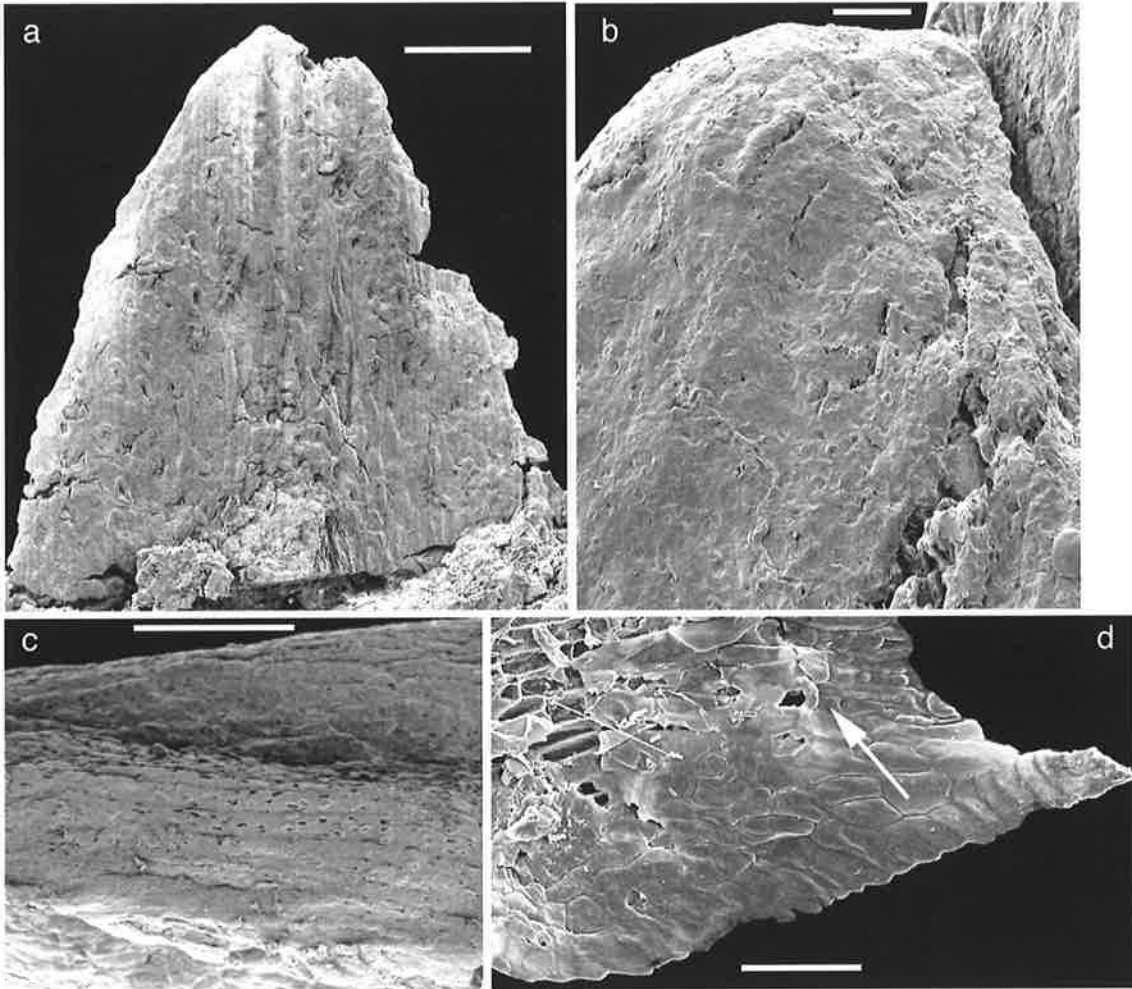
Fig. 21a-d SEM *Libocedrus microformis* sp. nov., Regatta Point, foliage detail

    a. Adaxial surface, dorsal facial leaf. Stomata randomly oriented, absent in the central third of the leaf, and roughly parallel to the leaf centre (scale 100µm; specimen RPE-706).

    b. Small nodules on the bluntly acute apex of a lateral leaf (scale 20µm; specimen RPE-702).

    c. Small nodules and holes in clearly delineated epidermal cells close to the margin of a lateral leaf (scale 50µm; specimen RPE-703).

    d. Slightly frilled facial leaf margin, adaxial surface. Arrow indicating stomata surrounded by circular papillae (scale 50µm; specimen RPE-702).

Fig. 4a-i *Libocedrus microformis* sp. nov., Regatta Point, cuticle SEM

a. Inner surface stomata. Elongate guard cells with 5 smooth-grained elongate subsidiary cells. Right arrow indicating an indentation in a subsidiary cell. Subsidiary cells fold down around the guard cells to form a discontinuous groove. Anticlinal walls of subsidiary cells fold slightly outwards, away from the guard cells. Epidermal cells adjacent to the stomata contain small nodules (left arrow; scale 20 µm; specimen RPE-482).

b. Outer surface stomata. High ridged and distinctly lobed Florin ring surrounded by round (circular) papillae (scale 20 µm; specimen RPE-461).

c. Inner surface. Stomata with 4-6 subsidiary cells, some of which are shared by adjacent guard cells. Subsidiary cells with fine-grained texture, and containing with indentations (arrows). Texture of epidermal cells more coarse (scale 20 µm; specimen RPE-482).

d. Outer surface. Florin rings and papillae (scale 20 µm; specimen RPE-482).

e. Inner surface. Stomata close to a leaf base. Here guard cells are smaller, rounder and more closely grouped. Subsidiary cells are less elongate, and more frequently shared by adjacent guard cells (scale 20 µm; specimen RPE-645).

f. Outer surface. Epidermal cells convex, with clearly defined indented walls and containing numerous holes or nodules (scale 20µm; specimen RPE-703).

g. Inner surface. Indentations in epidermal cells immediately adjacent to subsidiary cells (scale 10µm; specimen RPE-702).

h. Inner surface. Epidermal cells moderately coarse-grained in texture, concave. Anticlinal walls acute, moderately thick, relatively coarse grained in texture, coarser towards the base (scale 20µm; specimen RPE-645).

i. Inner surface. Elongate epidermal cells containing small-medium nodules (scale 20 µm; specimen RPE-482).
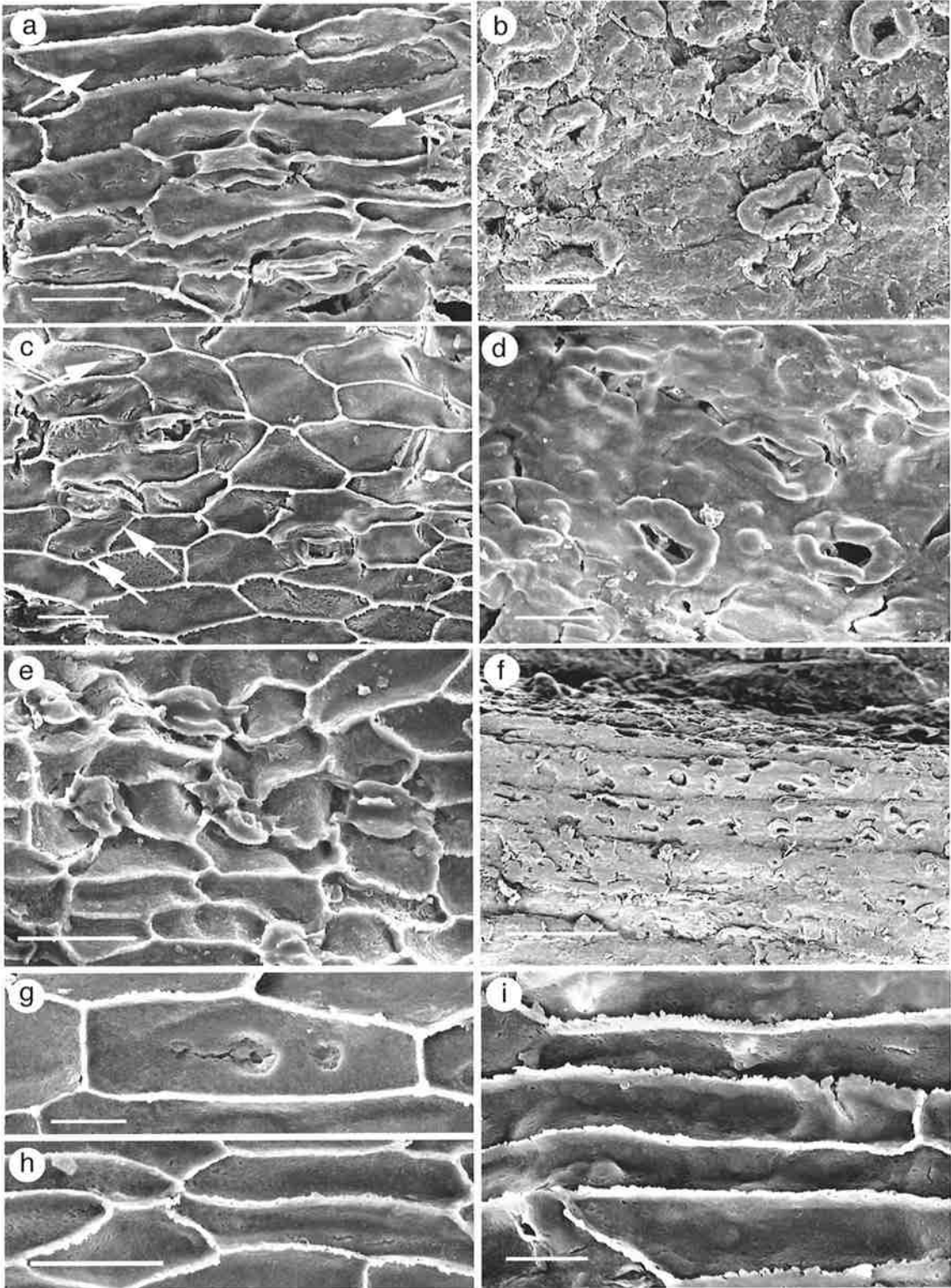
Fig. 22a-i *Libocedrus microformis* sp. nov., Regatta Point, cuticle SEM

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Comparison of fossil and living species

The Regatta Point fossil foliage is most similar to *L. bidwillii.* (see Fig. 23a-h), but differs from that species in several ways. The facial and lateral leaf apices of the fossils are less acute, and, on the dorsal surface of lateral and facial leaves, the stomata are close to the leaf margin in the lower half of the leaf, rather than in well-defined central grooves (*L. bidwillii*). The Regatta Point fossils have papillate lateral leaf bases, a characteristic of *L. plumosa*. The texture of internal epidermal cell walls of *L. microformis* is generally less coarse than those of *L. bidwillii* and *L. plumosa*. However, as the texture of some (Fig. 22c) is more obviously coarse grained, this may be due to the preservational state of the leaves, or poor cuticle preparation. The fossil leaves are characteristically very similar to those of extant *Libocedrus* and they are therefore assigned to that genus.
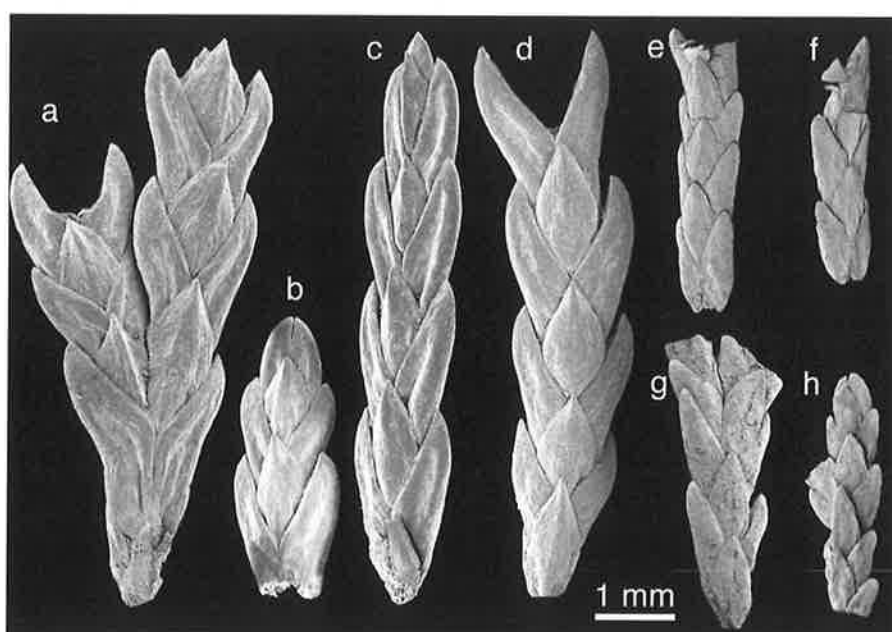
Fig. 23a-h Morphological similarities: *Libocedrus bidwillii* **(a-d) and** *Libocedrus microformis* **sp. nov., (e-h)**
a, b WELT SP37980; c, d MPN 3356; e, RPE-701; f, RPE-703; g, RPE-661; h, RPE-704.

Discussion

As Australia and Antarctica rifted apart from the west during the Cenozoic (see Chapter 9) a rotational change in plate movement initiated the formation of several large basins at the eastern end of the rift. These include the Sorrel Basin (which formed a narrow seaway between Australia and Antarctica), and the Gippsland, Otway and Bass basins (on the southern Australian margin). Macquarie Harbour (and Regatta Point) is the western extension of the Sorrel Basin. Macphail's (2005) palynological report for Regatta Point indicates that the Early Eocene flora was highly diverse, and growing close to the basin margin in warm water estuarine conditions, at ~65°S latitude. Mangroves (*Nypa*) grew at the basin edge, and a broad mix of large leaved taxa, including *Bowenia* and Lauraceae (R. Carpenter* pers, com. 2006) were present. Macphail (2005) suggests modern floristic analogues for Regatta Point are the complex multi-storied, angiosperm-dominated rainforests of New Caledonia and tropical Malesia.

The fossil leaves were variously covered with fungal hyphae (not illustrated), which suggests they were growing in wet conditions. When compared with *L. bidwillii* growing at higher altitudes ~1250 m (Fig. 5a, b) they are quite small. The predominance of large leaved angiosperm taxa at the Regatta Point site, could suggest these fossils are an oddity. Their small leaf size may be an adaptation to cope with suboptimal warm temperatures. Macphail (2005) suggests the flora at Regatta Point may indicate the early transition from warm to cooler climatic conditions.

*Ray Carpenter is currently making a comprehensive study of the flora at the Strahan site (~1 km from Regatta Point). The fossil cupressaceous taxon described above are also present at that site.

Part IV. *Diselma, Michrocachrys* and some Tasmanian fossils

Introduction

In the course of the current study two very small leaved macrofossils were found at two of the fossil sites (one specimen each at Balfour and Little Rapid River). These posed a problem. They are morphologically fairly similar to the larger leaved cupressaceous foliage from both sites, but appear to be too small to be related to them.

Diselma archeri Hook. f., Fl. Tasmania 1 (5): 353, t. 98. (1857) is a monotypic, very small leaved extant Cupressaceae genus. It is endemic to Tasmania where it grows at high altitudes (generally above 1000 m), to less than 6 m in height. *Diselma* macrofossils have been found in Early-Middle Pleistocene Tasmanian sediments. These are smaller in size than extant *Diselma,* but are morphologically similar (Jordan *et al.* 1995). *Microcachrys tetragona* is an extant prostrate shrub in the family Podocarpaceae, that sometimes co-occurs with *Diselma archeri* and has remarkably similar foliage (morphology and size). Macrofossils of *Microcachrys* have been found at two Australian sites, Morwell (Latrobe Valley, Victoria, Miocene; Blackburn 1985) and Regatta Point (western Tasmania, Early-Middle Pleistocene; Jordan 1995).

This section reviews the morphology of *Diselma archeri* and *Microcachrys tetragona,* describes the two small leaved fossils, and compares them with *D. archeri* and *M. tetragona,* and other fossils described in this study. Although extant *D. archeri* and *M. tetragona* have small fragile ovuliferous and pollen cones that are unlikely to survive taphonomic processes and thus occur as fossils, descriptions of these are included here.

Methods

Extant and fossil specimens underwent the same preparation as all other material in this study. The lengths of the Balfour and Little Rapid River leafy twigs were 1.25 cm and 0.9 cm (respectively). As there was very little material for cuticular preparation, that which was obtained was first placed on glass slides (mounted in water) and photographed with an Olympus DP11 digital camera attached to a Zeiss Axioskop microscope before mounting on SEM stubs.

Freshly collected samples of *Diselma archeri, Libocedrus bidwillii* (both from the Tasmanian Arboretum) and *Widdringtonia cedarbergensis* (Mt Lofty Botanic Gardens Adelaide) were subjected to *matK* analysis by Greg Guerin (University of Adelaide). The methods (and primers) used matched those of Gadek *et al.* (2000). Additional genbank data included *Taiwania* (outgroup), *Picea* (outgroup), *Sequoia sempervirens, Papuacedrus papuana, L. plumosa, Callitris, Actinostrobos acuminatus* and *Neocallitropsis.*

Terminology

The foliage is unflattened and the terms adaxial and abaxial are used to describe the inner and outer leaf surfaces respectively.

Diselma
Monotypic

Description: Evergreen bushy shrubs or small trees (to ~4-6 m) with numerous short branches (Farjon 2005; Fig. 1). Monoecious. Trunk often branching.

Distribution: Endemic to Tasmania. Widely distributed in high altitude (1000-1500 m) communities in the west, southwest and central plateau (Hill 1998). Also found (although rarely, see description below) at lower altitudes.

Ecology: Grows in high altitude rainforest (Kirkpatrick 1982) and wet-temperate subalpine communities, in acidic, often waterlogged soils, where precipitation is high and snow covers the ground for several months. Frosts and snow are also common throughout the year (Farjon 2005).

Systematics
Order Coniferales
Family Cupressaceae
Genus *Diselma* Hook. f., Fl. Tasmania 1 (5): 353, t. 98. (1857)
Diselma archeri Hook. f., Fl. Tasmania 1 (5): 353, t. 98. (1857)

Foliage and leaves: Foliage dense (Fig. 1). Branchlets short (to 20 mm) often rigid, non-flattened, and arising from all sides of the stem (Fig. 2a). *Juvenile leaves* -~2 x 0.5 mm, monomorphic, elongate, lanceolate, loosely arranged, and without a marginal frill (Fig. 3a, b). *Adult leaves* - small ~1.25 x~0.85 mm, decussate, scale-like, broadly trullate, thick, imbricate, connate close to the base, abaxially keeled (distally), with bluntly acute to acute apices (Fig. 4a 1-3), and frilled margins (Fig. 4f). Leaf arrangement tetragonal (Fig. 2b, 4a 2; 7c). Where *D. archeri* is found below 1000 m its leaves are more elongate (Fig. 4b, c). On main axis shoots, lateral and facial leaves larger, of similar size, with free portion of lateral leaves extending outwards beneath axial shoots (Fig. 5a).

Stomatal distribution: Amphistomatic. *Juvenile leaves* - adaxial surface few, and randomly scattered (Fig. 3c). On abaxial surface, in discontinuous rows within shallow elongate grooves, on each side of the central keel, and parallel to the leaf margin (Fig. 3b). *Adult leaves* - amphistomatic, but with few stomata on the abaxial surface. The latter are close to the leaf base (lateral and facial leaves), where they are largely concealed by overlying leaves (Figs 4c-e; 6g). On adaxial leaves roughly oriented with, and parallel to the astomatic leaf centre, and extending from the base to just below the apex (Figs 4f; 6i). On main axis, or leading shoots, outwardly turned lateral leaves may have small groups of stomata close to the top of the connate section of dorsal (Fig. 5b), and ventral surfaces.

Cuticle description: Inner surface - Stomatal complexes simple. Guard cells elongate, and surrounded by 4-6 subsidiary cells. The latter are fine-grained, frequently shared by adjacent stomata, and often have indentations in their outer extremities (Fig. 6a). These correspond with papillae on the outer surface (Fig. 6b). Where they abut the guard cells the subsidiary cells fold down, forming a groove around them. The latter is broken by the anticlinal walls of the cells. Epidermal cells irregularly shaped, often elongate, concave, and with coarse-grained periclinal cell walls (Fig. 6e). Anticlinal cell walls thick, irregularly cutinised (Fig. 6e). Outer surface - Florin rings variously (but frequently highly) lobed, high-ridged, without a peripheral groove, and on juvenile leaves, associated with well-developed elongate to rounded papillae (Fig. 6b). On adult

leaves the papillae vary in frequency but appear to be less numerous on the abaxial surface (Fig. 6c) On the abaxial surface the papillae are slightly more frequent (Fig. 4e). Epidermal cells are convex, and often contain numerous small nodules, with calcium oxalate crystals within (Fig. 7k).

Ovulate cone development: *Diselma archeri* cones differ from those of the other '*Libocedrus* related' Cupressaceae described in this study. On fertile shoots there is no ligulate growth on the adaxial base of the ultimate and penultimate terminal bracts. The ultimate (fertile) and penultimate (non-fertile) decussate 'scales' form by intercalary growth from the base of the bracts. In early development the apices of the bracts are bluntly acute (Fig. 7b). With increasing development, the bracts widen, broaden (especially the ultimate bracts), and elongate via intercalary growth from the base of the bract (Fig. 7c, e). The developing seeds rapidly dominate the structure of the cone, and are more robust than the 'scales' (Fig. 8b, e, f).

Ovulate cones: Cones terminal, solitary, on short ultimate branchlets (Figs 7a; 8a) small (Fig. 8a), less than 5 mm in diameter, non robust (Fig. 8d). Ultimate scales small, elongate, broad, obtuse. Adaxial and abaxial surfaces with large cells (Fig. 7f), rugose. Margin of adaxial apex with large papilla-like cells (Fig. 8d, g). Penultimate scales smaller than ultimate, less obtuse, and with frilled-papillate margins (Fig. 7d.)

Ovules: Ovules 4, 2 axillary to each of the 2 terminal scales (Fig. 8h). These develop around a large central columella (Fig. 8f). Seeds winged, ovoid, and large in size in comparison to the cone scales. Wings of equal size, inwardly turned (Fig. 8i). Micropyle robust, and protruding above the seed (Fig. 8 h).

Pollen cones: Pollen cones terminal on short branchlets. Microsporophylls 3-6 decussate pairs, slightly smaller than the leaves, outwardly keeled, inwardly turned (Fig. 9). Each microsporophyll with two abaxial microsporangia (Hill 1998).

Specimens examined: Herbarium specimens from Tasmanian Herbarium, Hobart.
HO444208, collected 4/1999, AC Rozefelds. At 1240 m, near ski huts, Mt Field National Park. Collected from three stunted shrubs. Common, in sub-alpine community.
HO326486, collected 9/1997, JG Jordan & T Brodribb. At 1260 m, near Lake Seal Lookout, Mt Field National Park. Seedlings aged 14 months.
HO68664, collected 11/1982, A Moscal. At 680 m, near Lea River. Rare, riparian within stream trough dominated by *Nothofagus cunninghamii* and *Phyllocladus asplenifolius*.
Other specimens examined at the herbarium, but details not recorded: HO2529, HO2682, HO326271, HO401469, HO411125, HO443363, HO513970, 121066, 122458.
Cultivated specimen, Tasmanian Arboretum, Devonport, Tasmania, collected 11/2004, R Paull, bushy shrub ~1 m (Fig. 1).

Fig. 1 *Diselma archeri* - cultivated shrub, Tasmanian Arboretum, Devonport
Foliage dense, highly branched
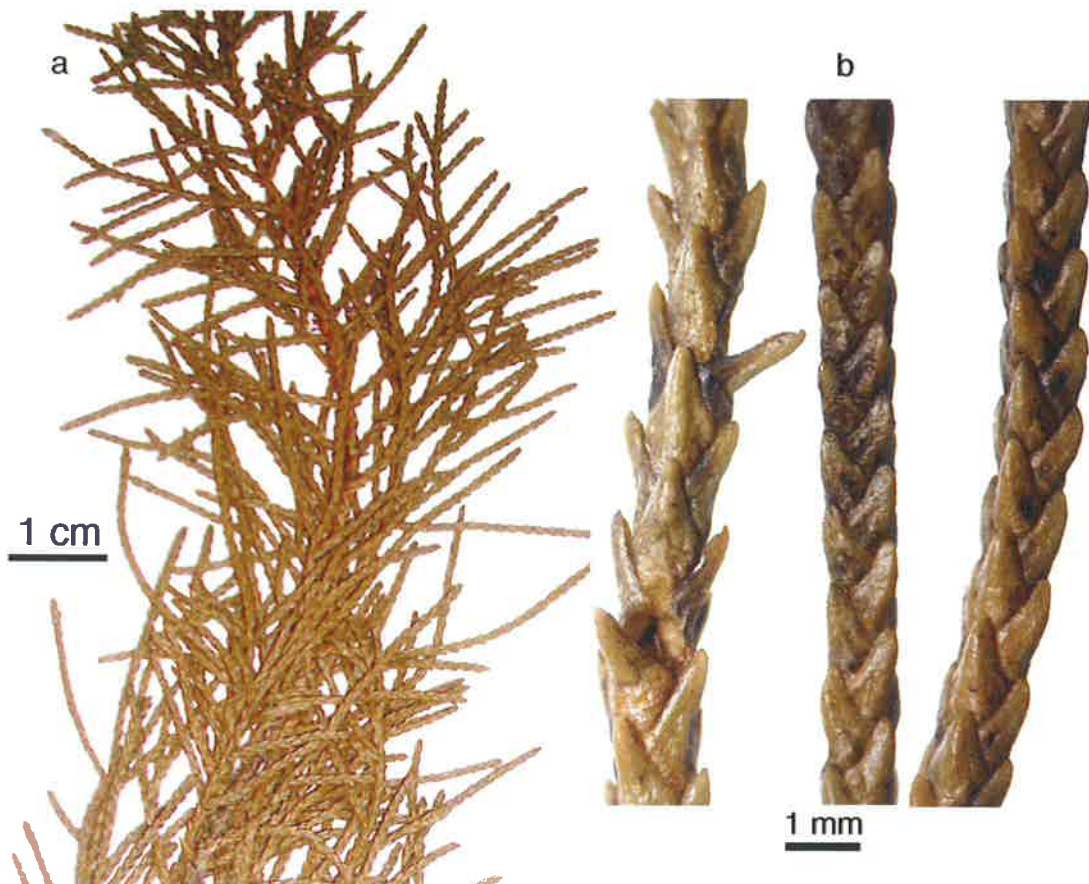
Fig. 2a-b *Diselma archeri* foliage
  a. Dense, highly branched, small leaved foliage, arising on all sides of the stem (photographed from an herbarium sheet; specimen HO513970).
  b. Foliage from the same specimen, viewed from different angles. Central branchlet squarrose (tetragonous) in appearance (specimen HO122458).

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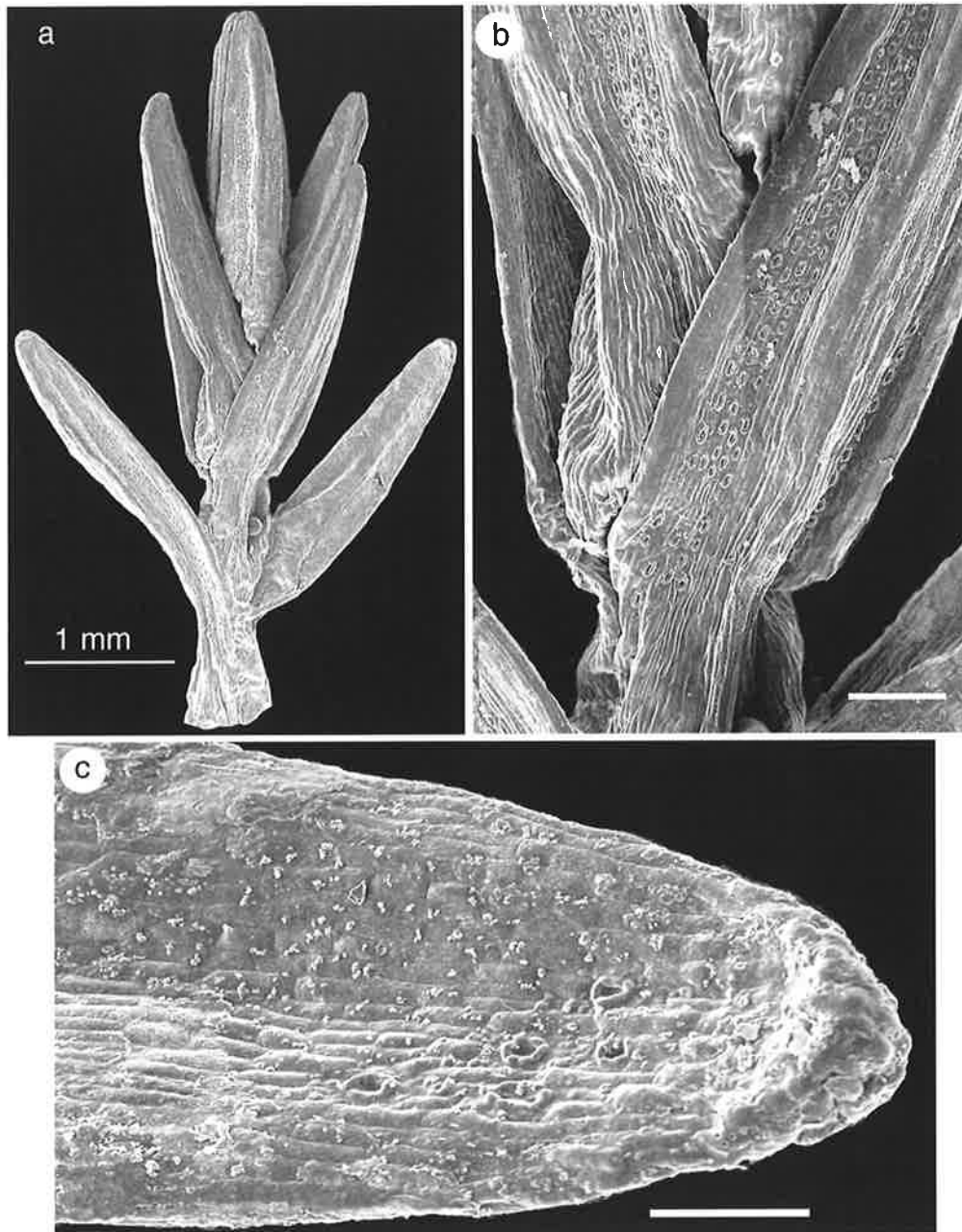
Fig. 3a-c *Diselma archeri* juvenile foliage
Specimen HO326486

    a. Terminal juvenile shoot. Leaves decussate, loosely arranged, outwardly keeled, lanceolate, with bluntly acute apices, and entire margins.

    b. Detail of **a**. Stomata on abaxial surface, and in well defined grooves on either side of the central keel (scale 200 μm).

    c. Adaxial leaf surface. Stomata very few, and randomly distributed. Numerous small calcium oxalate nodules, barely visible on this photograph, cover the surface (scale 100 μm).
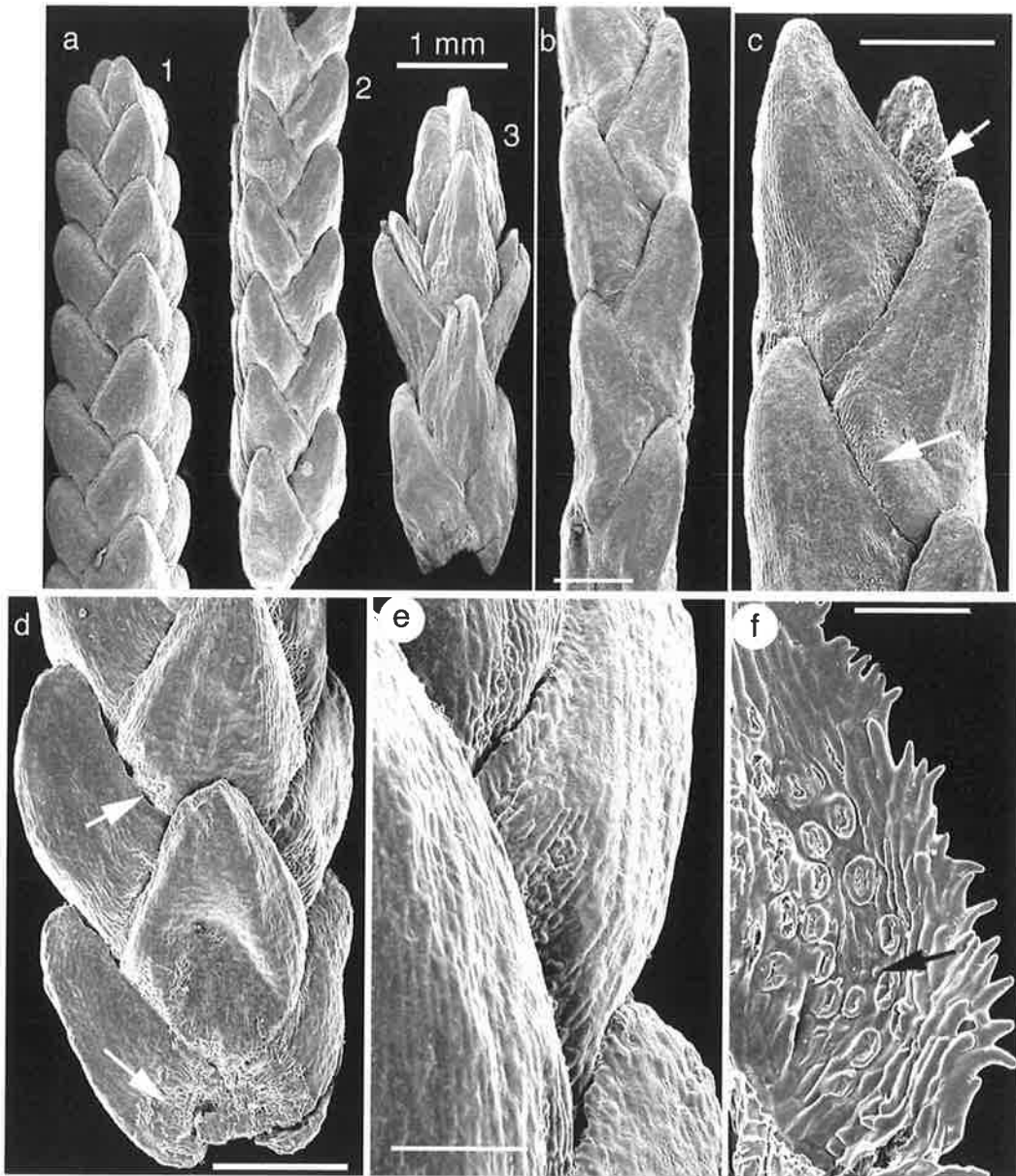
Fig. 4a-f *Diselma archeri* adult foliage SEM

a. One, 2, branchlets from a high altitude (1240 m) shrub viewed from different angles. Leaves tetragonally arranged, decussate, longer than wide, lateral and facial leaves similar in size, dorsally keeled (HO444208). 3, male reproductive foliage, with elongate leaves (specimen HO326271).

b. Vegetative branchlet growing at lower altitude (680 m). Leaves more elongate, lateral and facial leaves indistinguishable (scale 500 μm; specimen HO68664).

c. Detail of **b**. Upper arrow indicating stomata on the adaxial leaf surface. Lower arrow indicating stomata (on the abaxial surface) close to the base (scale 500 μm).

d. Stomatal distribution. On facial (upper arrow) and lateral (lower arrow) leaves, close to the base, where they are largely protected by overlying leaves (scale 500 μm; specimen HO444208).

e. Detail of **d**. Infrequent papillae associated with stomata (scale 200 μm).

f. Adaxial leaf surface. Leaf margin frilled. Stomata in discontinuous rows, with infrequent scattered papillae (arrow; scale 200 μm; specimen HO444208).

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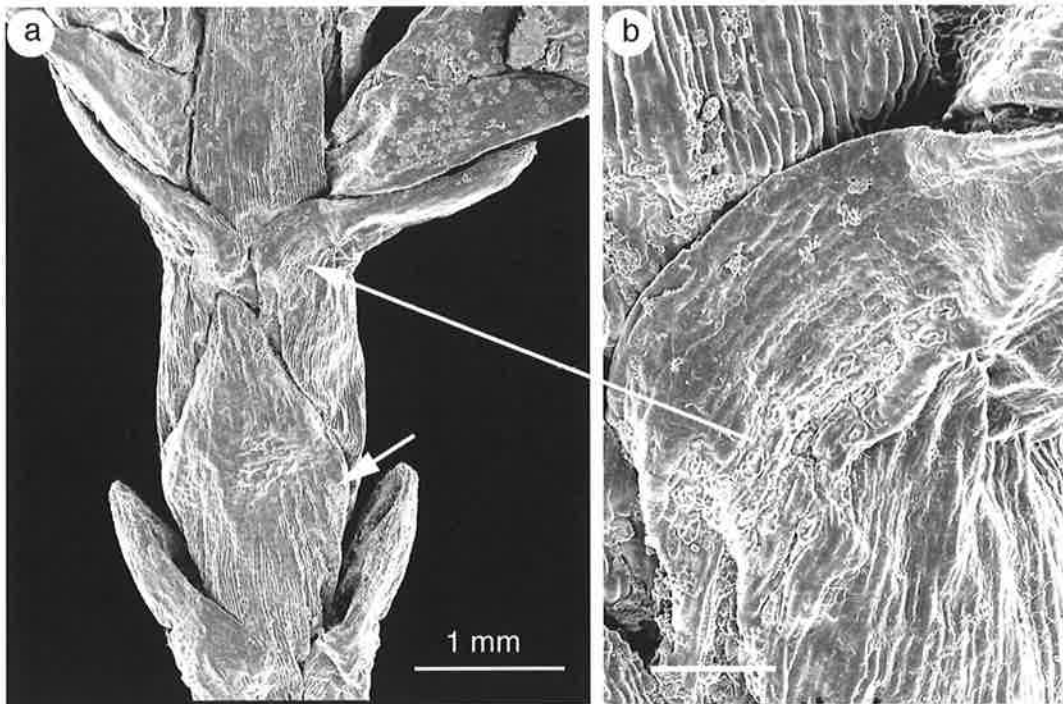
Fig. 5a-b *Diselma archeri* main axis shoot foliage SEM
Cultivated specimen from the Tasmanian Arboretum, dorsal surface.

    a. Lateral and facial leaves similar in size, and connate towards the base. Free section of lateral leaves extending outwards beneath lateral branchlets. Stomata on facial leaves confined to small areas on either side of the leaf and towards the base (lower arrow).

    b. Detail of **a**. Stomata on lateral leaves in a small group near the margin of the free section of the leaf. Epidermal cells convex (scale 200 μm).
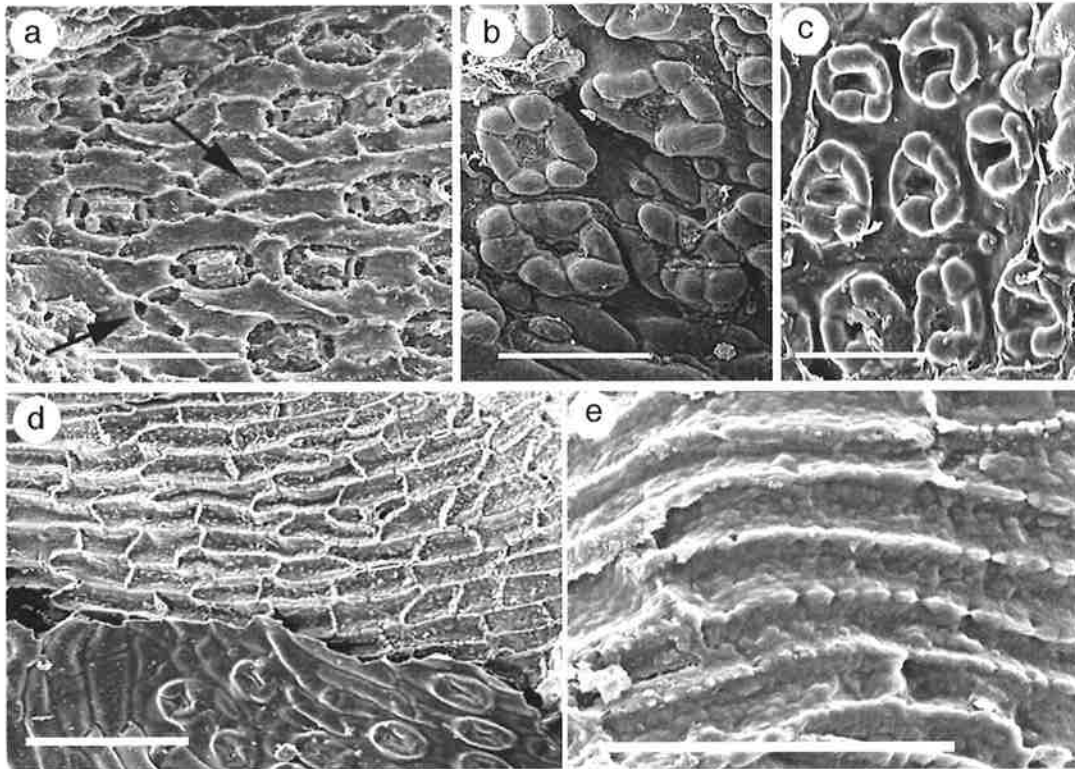
Fig. 6a-e *Diselma archeri* cuticle SEM

a. Internal surface. Guard cells elongate, and surrounded by 4-6 subsidiary cells. Subsidiary cells frequently shared by adjacent guard cells, and often with small indentations at the corners (arrows). Periclinal walls of subsidiary cells collectively form a deep, discontinuous groove around the guard cells (scale 50 μm; specimen HO444208).

b. Juvenile outer surface. High ridged and very highly lobed Florin rings with stomatal plugs. Papillae associated with stomata (scale 50 μm; specimen HO326486).

c. Adult outer adaxial surface. Cleaned cuticle. Moderate to highly ridged Florin rings. Small, relatively infrequent, round papillae associated with stomata (scale 50 μm; specimen HO444208).

d. Internal and external cuticle. Inner surface, with irregularly shaped, coarse-grained epidermal cells (scale 100 μm; specimen HO444208).

e. Elongate, coarse-grained, concave epidermal cells. Anticlinal cell walls thick, irregularly thickened (scale 50 μm; specimen HO444208).

Fig. 7a-k *Diselma archeri* ovuliferous cones - development and detail
All cones from specimen 121066

a. Ultimate branchlets with ovuliferous cones in varying stages of development. Cones terminal on short branchlets (numbers 1-3 identify cones described as **b, c, e,** below). Foliage on main axis with larger, more elongate leaves than those of the fertile branchlets. Facial and lateral leaves similar size. Foliage not in one plane - note the position of the (partially seen) branchlet at the base of the main axis.

b. Very immature cone before bract extension (scale 500 μm).

c. Immature cone. Ultimate (facial) bract becoming broad, squat, obtuse. Rapid expansion by intercalary growth just visible towards the base (arrow). Penultimate bracts slightly increasing in length (scale 500 μm).

d. Detail of **e**. Immature cone. Penultimate bract with frilled, papillate, margin. Adaxial surface highly rugose (scale 100 μm).

e. Immature cone. Ultimate and penultimate bracts broader, longer than subtending foliage (scale 500 μm).

f. Detail of **e**. Intercalary growth. Large cells at the base of the ultimate bract (scale 50 μm).

g. Developing cone with 2 decussate scale pairs. Ultimate (US) and penultimate bracts (PS) both short, and broad. Lateral leaf bases with stomata towards the base (arrows; scale 200 μm).

h. Mature seed with two broad wings and prominent protruding micropyle (scale 200 μm).

i. Adaxial surface of facial leaf (seen at the base of **a**.) Leaf margin frilled towards the base. Stomata roughly oriented with, and parallel to, the centre of the leaf, and extending from the leaf base to just below the apex. (scale 200 μm).

j. Detail of **h**. (arrow). Highly indented seed surface (scale 50 μm).

k. Lateral leaf margins slightly frilled. Numerous small nodules on the leaf surface indicate the presence of calcium oxalate crystals in the epidermal cells (scale 100 μm).
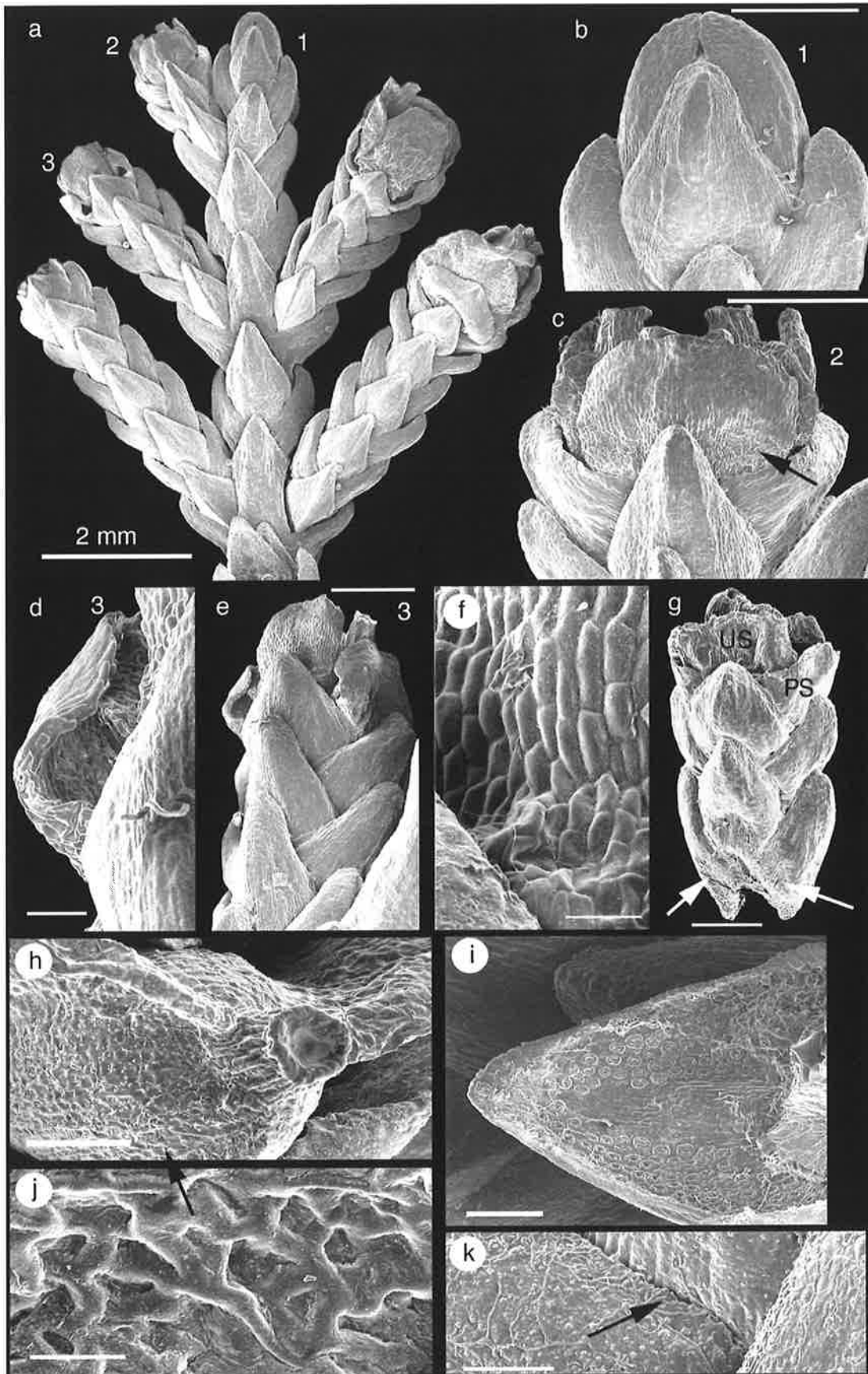
Fig. 7a-k *Diselma archeri* ovuliferous cones – development and detail

Fig. 8a-i *Diselma archeri* ovulate cones

All cones from specimen 121066

    a. Mature small cones with seeds, terminal on short, compact branchlets with decussate leaves of similar size. Arrow indicating photograph of specimen at the same dimension as other cones illustrated in this study.

    b. Scales are a relatively minor component of the mature cone. Seeds (arrows) larger, more robust (scale 500 μm).

    c. Same cone as **b**, seen from below. Non-fertile foliage, tetragonally arranged. Leaf (bract?) subtending the ultimate 'scale', slightly longer, broader than non-fertile foliage (scale 500 μm).

    d. Mature cones after seeds have been shed. Cone a very simple, non-robust structure, consisting of two decussate 'scale' pairs. Ultimate 'scale' longer (fertile), broader than sterile penultimate (scale 1 mm).

    e. Maturing cone with intact seeds (scale 1 mm).

    f. Mature cone seen from above. Ultimate 'scale' (US), penultimate 'scale' (PS), seeds (4 in total, S), relatively large central columella (C; scale 1 mm).

    g. Scale margin, with large cells, resembling papillae (scale 50 μm).

    h. Adaxial surface, broken cone. Arrow indicating scars from 2 seeds. Columella removed (scale 500 μm).

    i. Mature seed, ovoid, bulging, with two large, broad, and inwardly turned wings of equal size. Micropyle protrudes above the seed body (scale 500 μm).

Fig. 8a-i *Diselma archeri* ovulate cones

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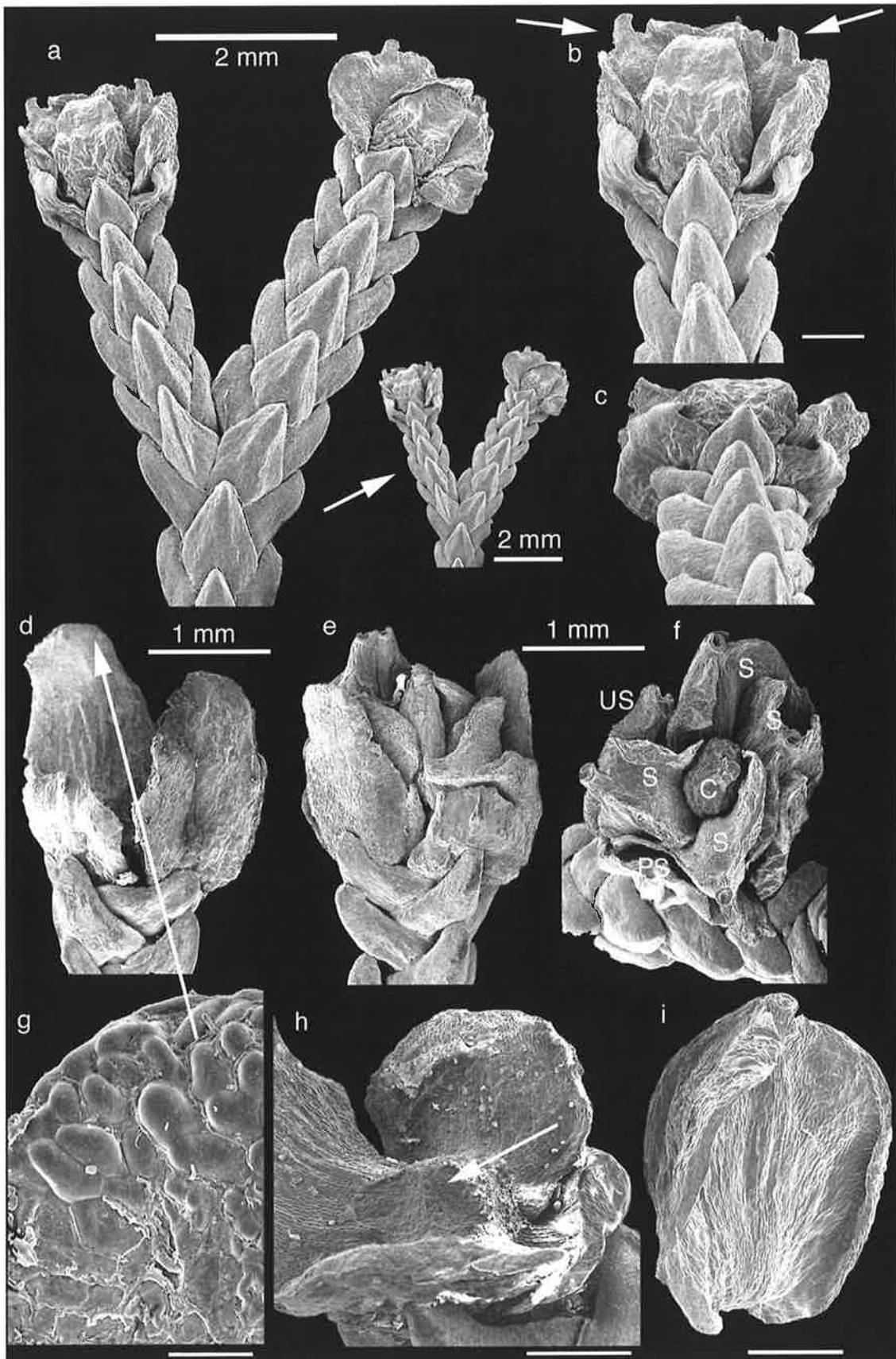
Fig. 9 *Diselma archeri* pollen cones
Specimen HO326271
Pollen cones terminal, solitary, on relatively short branchlets.

Distinguishing features: *Diselma archeri*

- Small, shrub-like bushes

Foliage
- Juvenile and adult foliage dimorphic
- Adult leaves small, decussate, similar size and shape, imbricate, somewhat lanceolate, <u>tetragonally arranged</u>, (marginal frills generally less well developed than those of *Microcachrys*)

Stomatal distribution
- Astomatic

Outer cuticle
- Papillae associated with Florin rings

Ovulate cones
- Ovulate cones very small, simple, consisting modified bracts rather than bract-scale complexes
- Seeds larger than cone scales, and with two large, equal sized wings and prominent micropyle

Microcachrys
Monospecific

Description: Prostrate evergreen shrubs with dense branches and long branchlets.
Distribution: Endemic to Tasmania. Widely distributed in high altitude (1000-1500 m), sub-alpine communities in the west, south-west and central plateau (Hill 1998).
Ecology: Grows in wet moorlands, and on rocky ridges (Hill 1988).

Systematics
Order Coniferales
Family Podocarpaceae
Genus *Microcachrys* Hook. F., *London J. Bot.* 4: 149 (1845)
Microcachrys tetragona (Hook) Hook. F., *London J. Bot.* 4: 150 (1845)

Foliage and leaves: Adult and juvenile foliage indistinguishable (Hill 1998), and branching in several planes (Offler 1984). Leaves scale-like, decussate, slightly longer than wide (~1.25 mm x ~1 mm), imbricate, similar in size, trullate, keeled towards the apex, broad and indented towards the base, with highly frilled margins (Fig. 10b, e), and tetragonally arranged (Fig. 10a (1 &3)).

Note - the specimens illustrated by Offler (1984) indicate a broader range of leaf size/shape and differences in the degree of imbrication.

Stomatal distribution: Epistomatic. No apparent stomata on abaxial surface. On adaxial leaf surface, frequent and in discontinuous rows parallel to, and generally oriented with, the astomatic centre of the leaf. These rows extend outwards to the leaf margin, but do not reach the leaf apex (Fig. 10b).

Cuticle description: Inner surface - Stomatal complexes simple. Guard cells elongate. Subsidiary cells mostly 5, moderately coarse-grained, and generally elongate and often shared by adjacent guard cells. When polar cells are shared these are often smaller and more rounded in shape. Where the periclinal walls of the subsidiary cells abut the guard cells a broad rim is formed. This is slightly dissected by the anticlinal walls of these cells (Fig. 10c). Subsidiary cells may contain small indentations at, or near, the corners of adjacent cell walls (Fig. 10c). Periclinal walls of epidermal cells moderately coarse-grained, anticlinal cell walls irregularly thickened (Fig. 10f). Few, insignificant (not illustrated) papillae associated with Florin rings. Anticlinal walls of subsidiary and epidermal cells indented, periclinal walls convex (Fig. 10d).

Calcium oxalate crystals occur across the abaxial leaf surface, but are much more frequent at the leaf apex (Fig. 10e).

Ovulate cones: These were not looked at in any detail. Terminal, solitary, ovoid, 5-8 mm long, and consisting of more than 20 fertile broad, round to ovate, keeled 'scales' (Hill 1998) that are obtuse towards the apex but taper to a short acute tip. The scales appear to be bract derived (Fig. 11a).

Pollen cones: Terminal, solitary. 1-4 mm long. consisting of <12 microsporophylls. These are elongate, peltate, outwardly keeled and with highly frilled margins (Fig. 11b).

Specimen examined: Herbarium specimen from the Tasmanian Herbarium, Hobart. **HO502820**, Prostrate shrub, Mt Field, Tasmania.

Fig. 10a-f *Microcachrys tetragona* foliage and cuticle
Specimen HO502820

    a. (1-3) Branchlets viewed from different angles to show the tetragonal leaf arrangement.

    b. Adaxial leaf surface showing highly frilled margins and stomata in rows oriented with the centre of the leaf.

    c. Inner cuticle. Stomata in discontinuous rows, roughly oriented in the same direction, sharing subsidiary cells. Guard cells surrounded by a broad depression (scale 50 μm).

    d. Waxy outer surface. Florin rings lobed and with a moderate ridge. No papillae associated with stomata. Inset showing cleaned leaf surface. No peripheral groove around the Florin rings (both scale bars 50 μm).

    e. Abaxial surface lacks stomata. Leaf margins highly frilled (black arrow). Leaf apices with frequent calcium oxalate nodules (white arrow; scale 500 μm).

    f. Epidermal cells elongate to rectangular in shape. Anticlinal cell walls irregularly thickened (scale 50 μm).
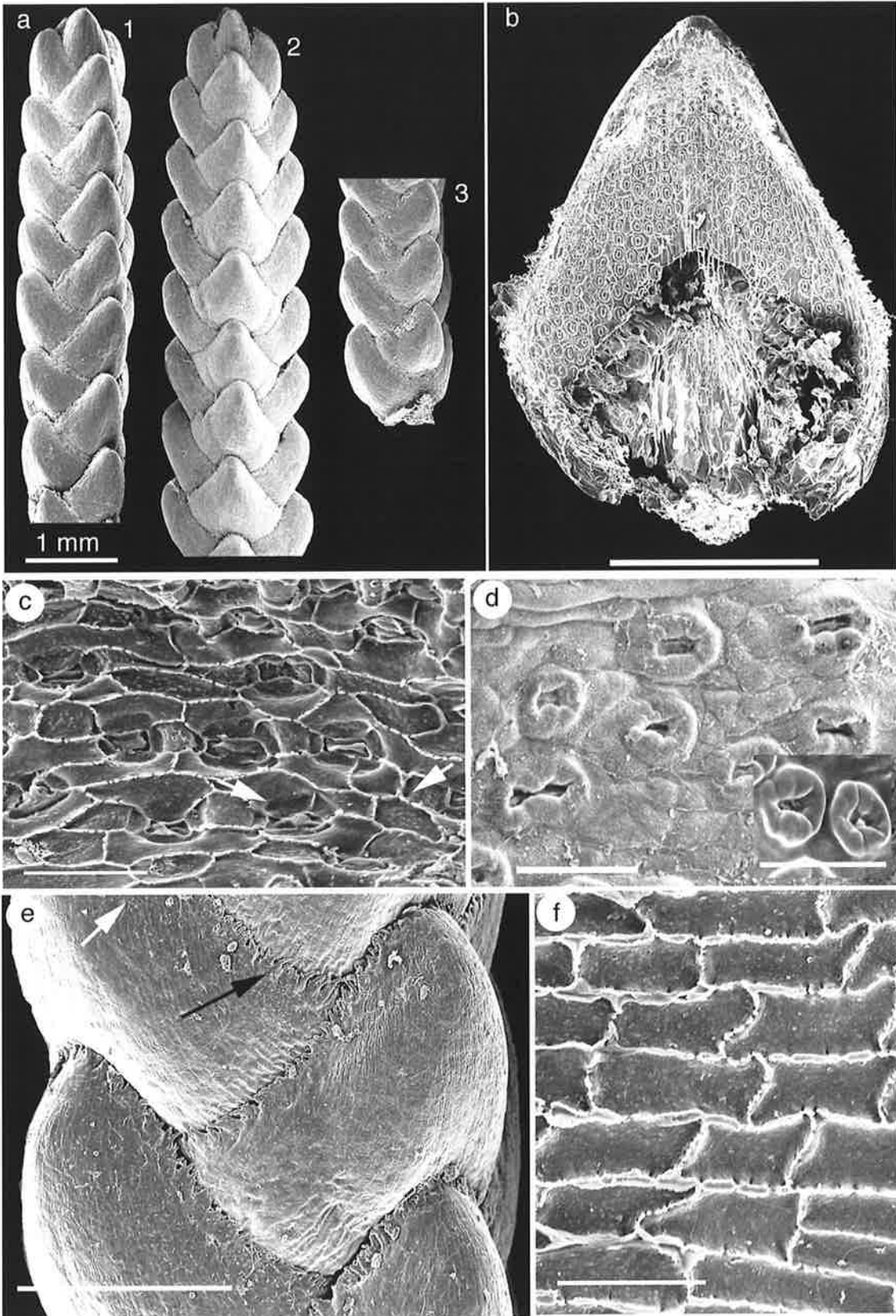
Fig. 10a-f *Microcachrys tetragona* foliage and cuticle
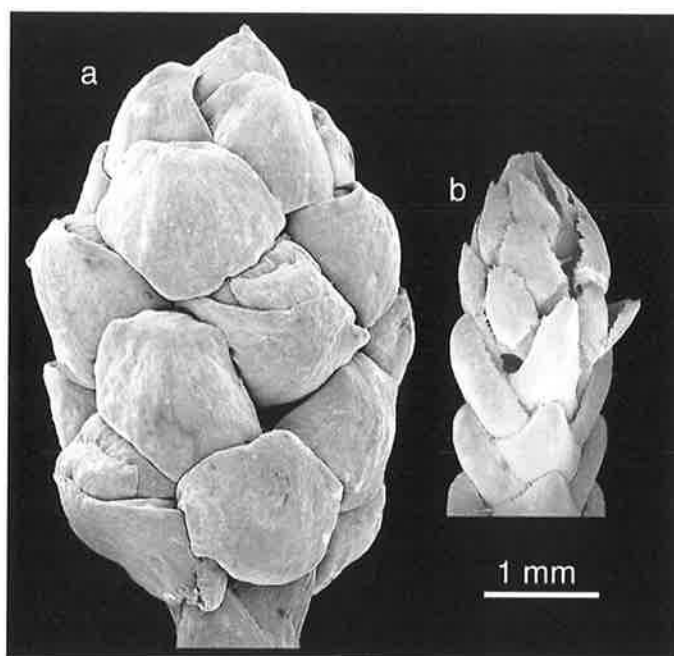
Fig. 11a-b *Microcachrys tetragona* ovulate and pollen cones
Specimen HO502820
   a.   Ovulate cone
   b.   Pollen cone

Distinguishing features - *Microcachrys tetragona* foliage

Foliage
  • Juvenile and adult foliage similar
  • Leaves similar in length and width, marginal frill well developed
Stomatal distribution
  • Epistomatic
Outer cuticle
  • Few (if any) papillae associated with Florin rings

Comparison of D. archeri and M. tetragona
The foliage of *D. archeri* and *M. tetragona* is subtly different. Oladele's (1983) SEM data indicate that the adaxial and abaxial leaf surfaces of *D. archeri* lack papillae. However, SEM photographs, this study (Figs 4e; 6b, c, d) show well-developed papillae (of varying frequency) on both leaf surfaces. The absence of papillae on the outer surface of *M. tetragona* was a criterion used by Jordan (1995) when identifying *M. tetragona* in Early Pleistocene sediments from Regatta Point. The closely imbricate leaves and apparent lack of stomata on the abaxial surface of *M. tetragona* suggest it has adapted to grow in somewhat harsher (possibly more exposed; see Hill KD 1998; and windy) climatic conditions than *D. archeri*. Close scrutiny of numerous *Diselma archeri* herbarium sheets (Tasmanian Herbarium, Hobart) showed that the leafy twigs of lower altitude shrubs are much longer than those from higher altitudes, and that their leaves are more elongate and less imbricate.

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Small leaved fossil specimens
   1. Balfour
Systematics
Order Coniferales
Family Cupressaceae
Genus *Diselma* Hook. f., Fl. Tasmania 1 (5): 353 (1857)
Diselma microfolius sp. nov.

Holotype: B 475 stored in the School of Earth and Environmental Sciences, The University of Adelaide, South Australia.
   Type locality: Balfour, Tasmania (41°18'S, 144°54'E)
   Specimen examined (41): B-475
   Etymology: named for the small size of the leaves.

Diagnosis Leaves tetragonally arranged, scale-like, decussate, elongate-lanceolate, overlapping, loosely imbricate, tapering to somewhat rounded apex. Epistomatic. Few papillae associated with stomata on adaxial outer surface.

To illustrate the tetragonal arrangement of the leaves, the 1.25 cm shoot was broken in half before attaching to the SEM stub.

Foliage and leaves: Elongate shoot (Fig. 12a) with tetragonal leaf arrangement (Fig. 12b, c). Leaves small ~0.8 x 0.5 mm, scale-like, decussate, with paired leaves almost similar size, lanceolate, loosely imbricate, barely connate at the base, with acute keeled apices that overlap at least half the length of the leaves above (Fig. 12b, c), and frilled margins (Fig. 12d, f).
   Stomatal arrangement: None on the abaxial surface. On the adaxial surface - roughly parallel and oriented to the centre of the leaf (Fig. 12d, e), in discontinuous rows, from near the leaf base to close to the apex. Centre of leaf raised and astomatic (Fig. 12e).
   Cuticle description: Internal cuticle - guard cells elongate, and with 4-5 (mostly 4) subsidiary cells that are frequently shared by adjacent guard cells. Periclinal wall texture of subsidiary cells fine-medium grained. Inner edge of subsidiary cells fold down around the guard cells forming a deep, relatively narrow, groove that is intersected by the anticlinal cell walls (Fig. 13a, c). There are often small indentations at the outer corners of these cells. Where polar subsidiary cells are shared these are often rounded in appearance. Anticlinal cell walls of subsidiary and epidermal cells irregularly thickened. Epidermal cells generally elongate and irregular in shape (Fig. 13e). External cuticle - Florin rings high ridged and slightly lobed (Fig. 13b). Irregularly shaped and non-prominent papillae surround the stomata (Fig. 13d). Epidermal cells with indented anticlinal walls and quite convex periclinal walls (Figs 12d, 13f).

Fig.12a-f SEM *Diselma microfolius* sp. nov., Balfour, foliage detail
  a. LM photo, elongate, intact shoot before placing on SEM stub.
  b. Two views of the broken shoot showing the tetragonal arrangement of the lanceolate leaves.
  c. Detail of the 2 sections of the shoot in **b**. Lanceolate, loosely imbricate leaves, barely joined at the base.
  d. Frilled leaf margin (scale 100 μm).
  e. Adaxial leaf surface. Stomata roughly parallel to, and with long axis oriented to the centre of the leaf. Stomata not reaching the leaf apex (scale 100 μm).
  f. Detail of abaxial leaf surface showing frilled margin (arrow). No stomata apparent on this surface (scale 200 μm).
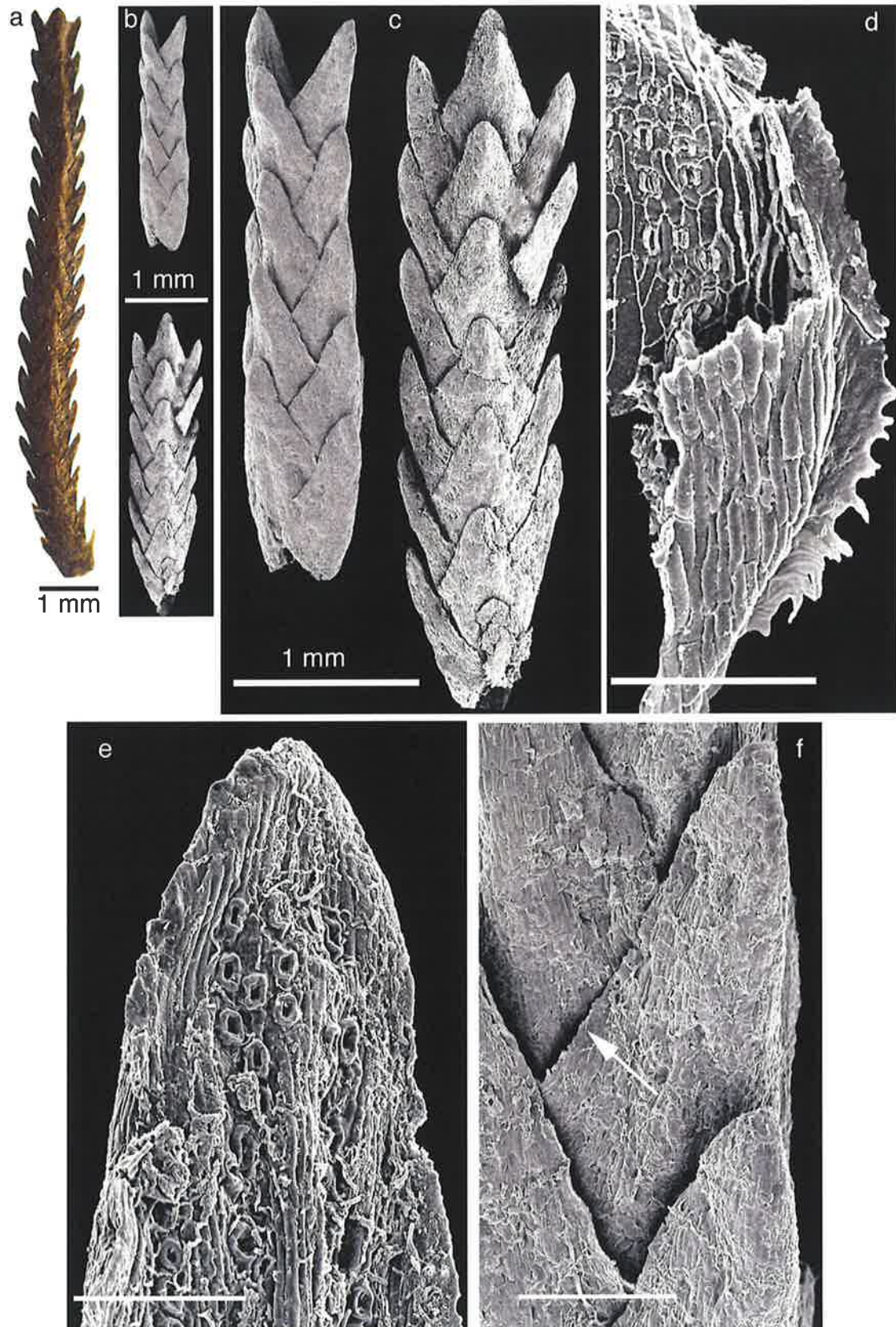
Fig.12a-f SEM *Diselma microfolius* sp. nov., Balfour, foliage detail
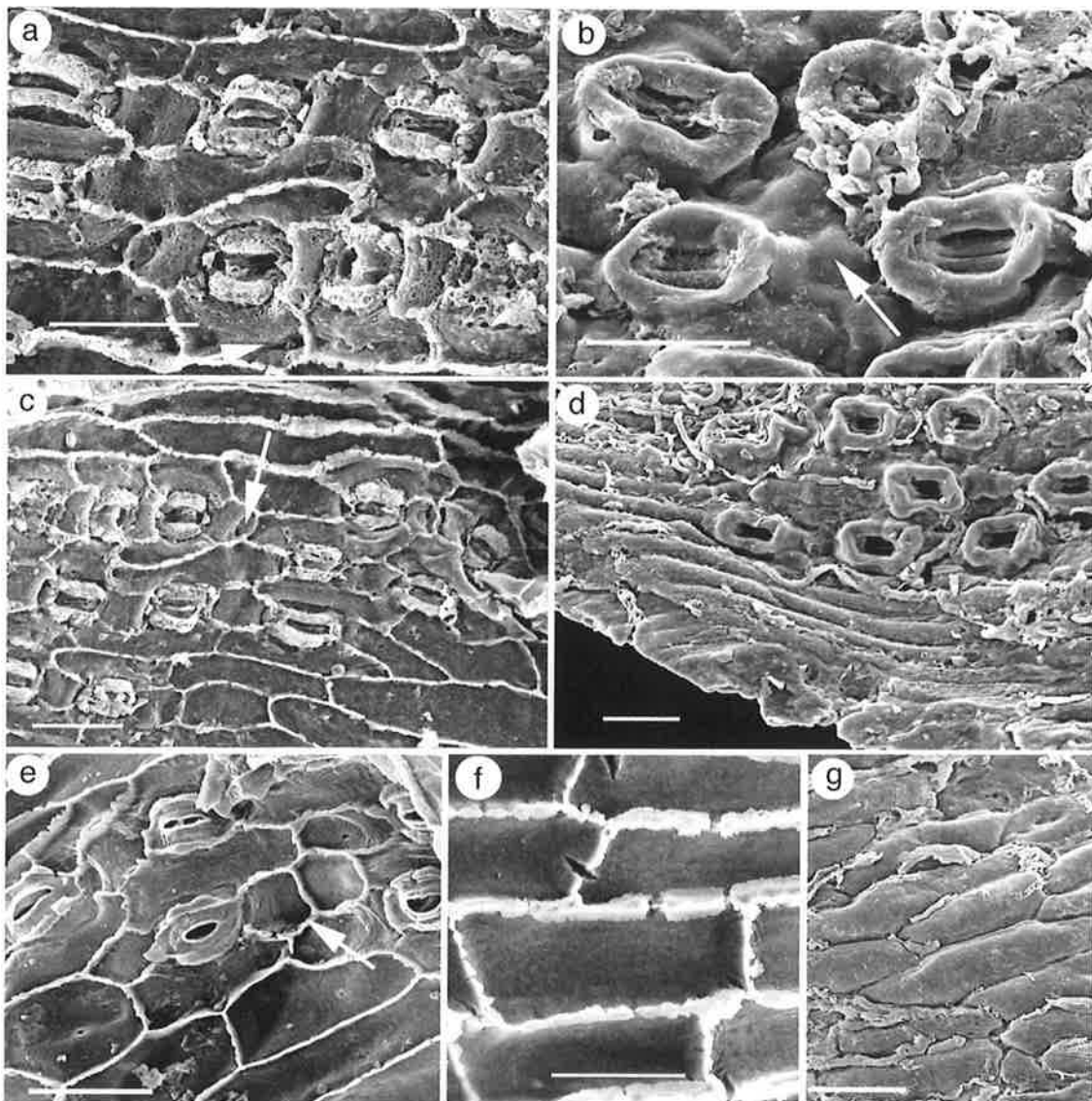
Fig. 13a-f *Diselma microfolius* sp. nov., Balfour, SEM leaf cuticle

   a. Inner adaxial surface. Elongate guard cells with 4 subsidiary cells. Subsidiary cells have indentations at their outer corners (arrow) and form a deep, narrow groove around the guard cells (scale 20 µm).

   b. Outer surface. Florin rings high ridged and slightly lobed. Papillae (arrow) not prominent (scale 20 µm).

   c. Inner adaxial surface (poor cuticle preparation) showing sharing of subsidiary cells. Arrow indicating small indentations at the corners of subsidiary cells (scale 20 µm).

   d. Outer surface. Epidermal cells convex, Florin rings elongate to slightly round (scale 20 µm).

   e. Inner surface (good cuticle preparation). Relatively smooth-grained and convex subsidiary and epidermal cells. Only minor indentations (arrow) at the outer corners of the subsidiary cells (scale 20 µm).

   f. Inner surface. Epidermal cells with irregularly thickened anticlinal cell walls. Periclinal walls concave, slightly coarse-grained (scale 20 µm).

   g. Outer surface, epidermal cells. Anticlinal walls indented, periclinal walls convex (scale 20 µm).

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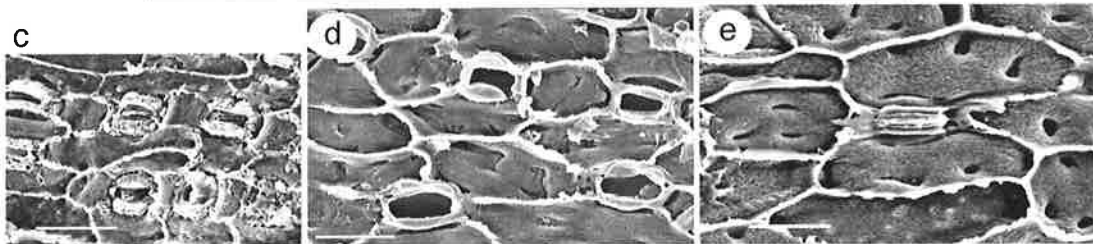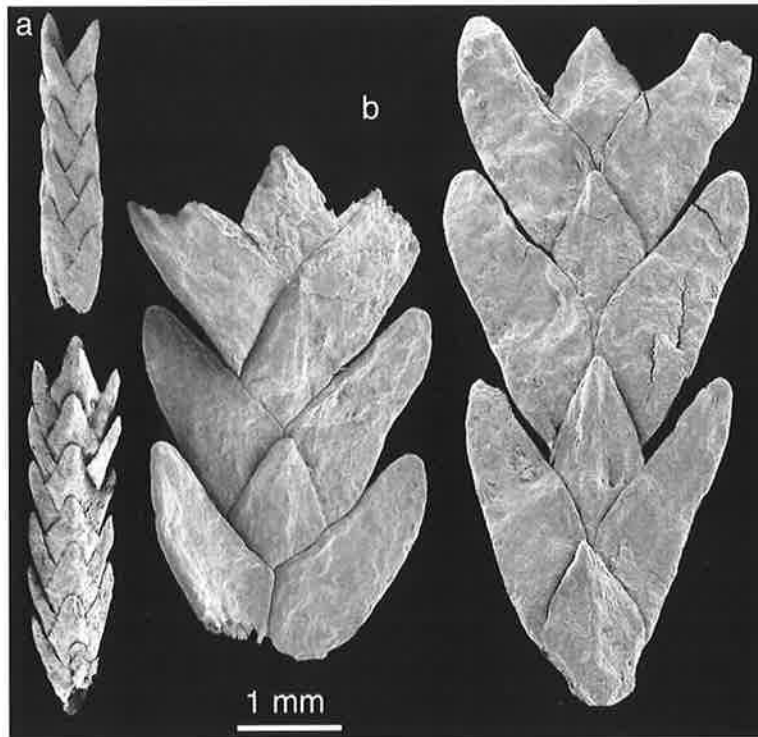
Fig. 14a-f. Comparison of *D. microfolius* with other Cupressaceae fossils from Balfour and *L. austrocaledonica*

a, Small leaved fossil (*Diselma microfolius*) **b**, large leaved fossils (*Libocedrus balfourensis* sp. nov.).

c, Small leaved fossil (B-475 *Diselma microfolius*), **d**, Large leaved fossil (B-137 *Libocedrus balfourensis* sp. nov.,), **e**, *L. austrocaledonica* 504526 (scale bars for all specimens same size - 20 μm).

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Comparison of small and large leaved Balfour fossils

The single small leaved specimen from Balfour is considerably smaller than the foliage described in Part II B and has tetragonally arranged, rather than flattened leaves (Fig. 14a-b). It could be argued that the larger leaved specimens are juvenile or transitional foliage and the small leaves adult foliage. If this were the case, one would expect to see many small leaved specimens rather than just one. This discrepancy in sample numbers could be due to several preparation factors (the specimens had already been sorted before this study was carried out.) *viz.* disintegration of small leaved samples during maceration, and/or poor sorting of fossils from sediments (this is unlikely; RS Hill pers. com. 2006), or it could be a rare element in the foliage. The review of extant *Libocedrus* related foliage in Part I (Chapters 2-5) demonstrates that (for those Cupressaceae) leaf cuticle characters are useful in distinguishing genera, but are of little value in distinguishing between species of the same genus. Comparisons of large and small leaf type cuticles (Fig. 14c-f) show them to be dissimilar. The large leaved specimens have frequent indentations in the periclinal cell walls of the subsidiary cells (Fig. 14d). On the small leaved specimen (Fig. 14c) these are generally confined to the corners of the cells. The large leaves have prominent papillae on their outer surface. On the small leaved specimen the papillae are fewer and less prominent. It seems unlikely that that the small foliage is related to the large. It is interesting to note the different cell size of the two Balfour leaf types (Fig. 14c, d), and the much larger cells of extant *L. austrocaledonica* (Fig. 14e).

2. Little Rapid River
Systematics
Order Coniferales
Family Cupressaceae
Genus *Diselma* Hook. f., Fl. Tasmania 1 (5): 353 (1857)
Diselma microfolius sp. nov.,

This specimen is similar to that of B-475 but with larger, tightly imbricate leaves that are narrower at the base

Specimen examined LRR1–3320

Etymology: named for the small size of the leaves

To illustrate the tetragonal arrangement of the leaves, the shoot was broken in half before attaching to the SEM stub.

Foliage and leaves: Non branching shoot, with tetragonal leaf arrangement (Fig. 15a, b) Leaves small, decussate, with paired leaves slightly dissimilar in size ~1 x 0.65 mm – ~0.8 x 6 mm, lanceolate in shape, with acute apices, and basally connate for ~30% of their length. Leaves imbricate, and overlapping around half the leaf pair above (Fig. 15c). Leaf margins slightly frilled (eg Fig. 15e).

Stomatal arrangement: Epistomatic. On the adaxial surface – roughly parallel and oriented to the centre of the leaf, and in discontinuous rows, from near the leaf base to close to the apex (Figs 15d, 16a).

Cuticle description: The cuticle is of poor quality. Internal cuticle - guard cells elongate, and with generally 4 subsidiary cells. Polar cells are frequently shared by adjacent guard cells. A deep groove is formed around the guard cells by the abutting edge of the periclinal walls of the subsidiary cells (Fig. 16a, c, e). The outer edges of the subsidiary cells may have small indentations at the corners (Fig. 16c). Epidermal cells generally elongate, irregular in shape, and with irregularly thickened anticlinal walls (Fig. 16c, f). External cuticle - Florin rings high ridged, slightly lobed and without a peripheral groove (Fig. 16b). Small infrequent, and irregularly shaped papillae are associated with the stomata (Fig. 16d). Epidermal cells with indented anticlinal walls and highly convex periclinal walls (Fig. 16b, d).

Fig. 15a-e SEM *Diselma microfolius* sp. nov., Little Rapid River, foliage detail

- **a.** Shoot broken into two sections to illustrate the tetragonal leaf arrangement
- **b.** Shoot illustrated at the same scale as the Balfour specimen
- **c.** Leaves imbricate and overlapping those above for about half their length. The abaxial leaf surface is astomatic (scale 200 µm).
- **d.** Adaxial leaf surface. Stomata generally parallel with the leaf axis and oriented in the same direction. Abaxial surface keeled towards the acute apex (scale 100 µm).
- **e.** Leaf margins frilled (arrow). Leaf bases basally connate for ~30% of their length. No stomata near the leaf base (scale 200 µm).
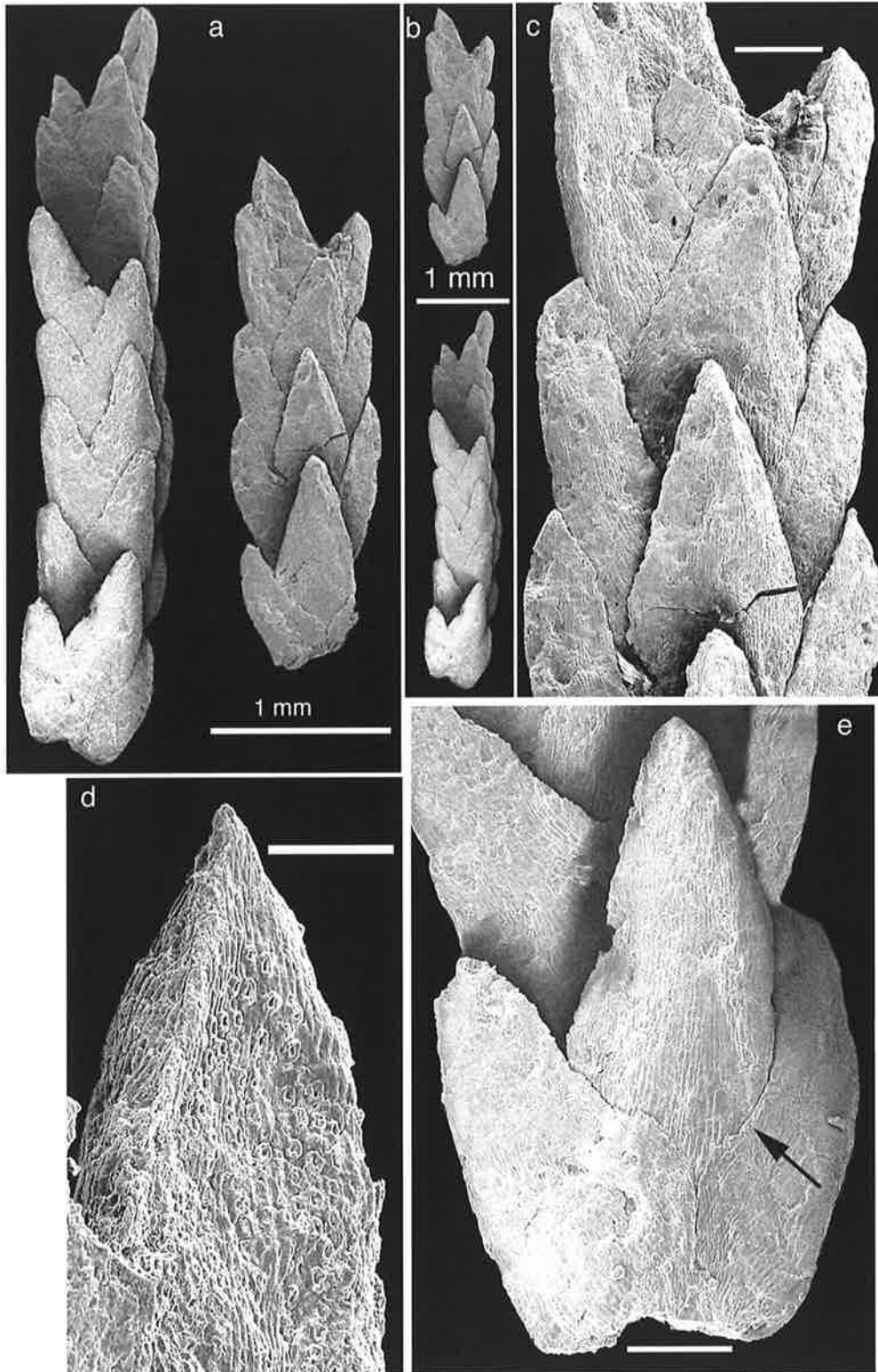
Fig. 15a-e SEM *Diselma microfolius* sp. nov., Little Rapid River, foliage detail
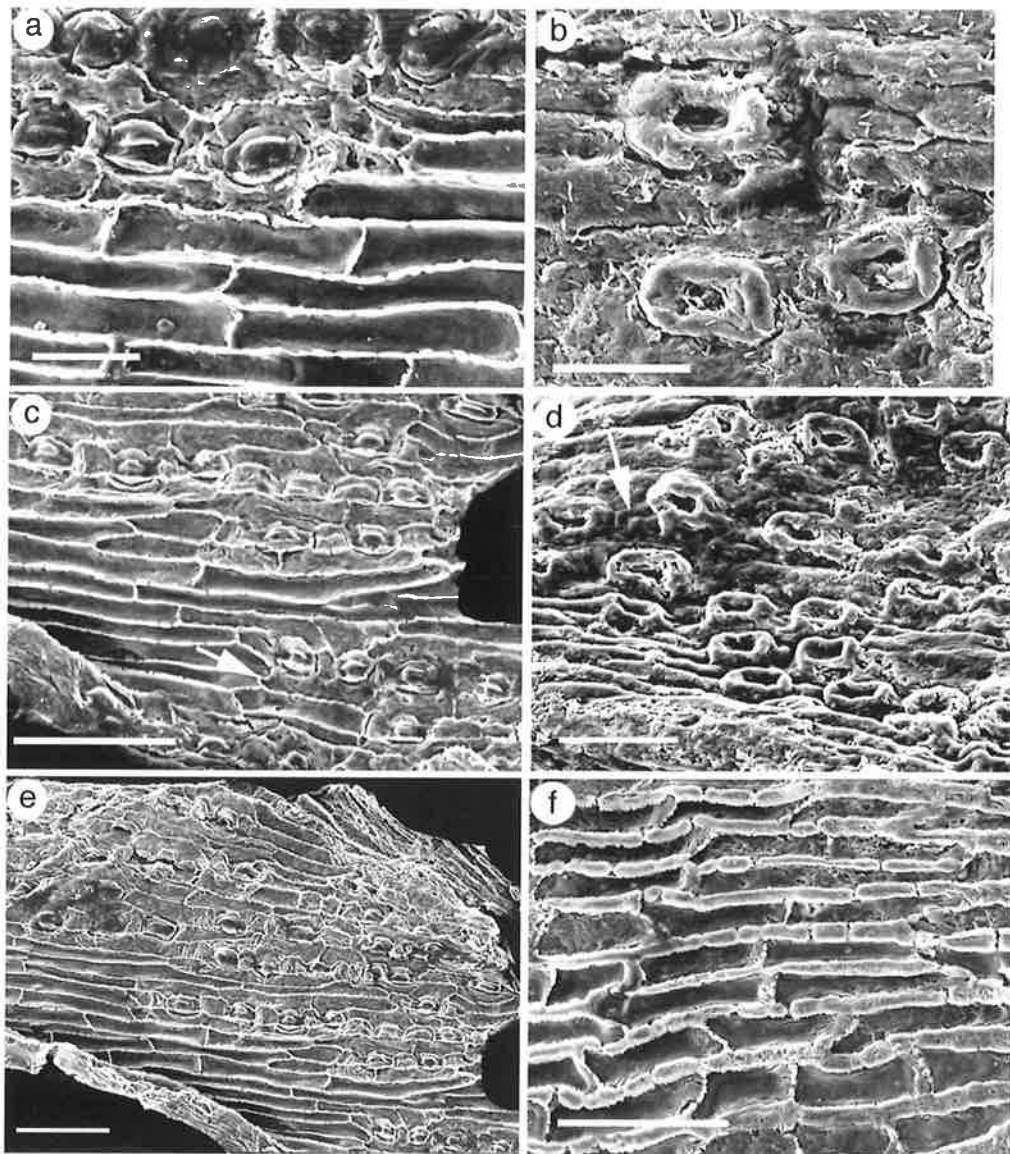
Fig. 16a-d. SEM *Diselma microfolius* sp. nov., Little Rapid River, leaf cuticle

   a. Inner surface. Guard cells surrounded by a deep groove, and sharing polar subsidiary cells (scale 20 μm).

   b. Outer surface. Florin rings high ridged and only slightly lobed. No papillae associated with the stomata. Epidermal cells convex (scale 20 μm).

   c. Stomata in distinct, discontinuous rows. Epidermal cells elongate, with concave periclinal cell walls, and irregularly thickened anticlinal cell walls (scale 50 μm).

   d. Outer leaf surface. Florin rings slightly elongate, high ridged. Small papillae (arrow) associated with the stomata (scale 20 μm).

   e. Inner surface Stomata generally oriented with the long axis of the leaf, and in discontinuous rows. Arrow indicating an indentation in the outer corner of a subsidiary cell (scale 50 μm).

   f. Inner surface. Epidermal cells with irregularly thickened anticlinal walls (scale 50 μm).

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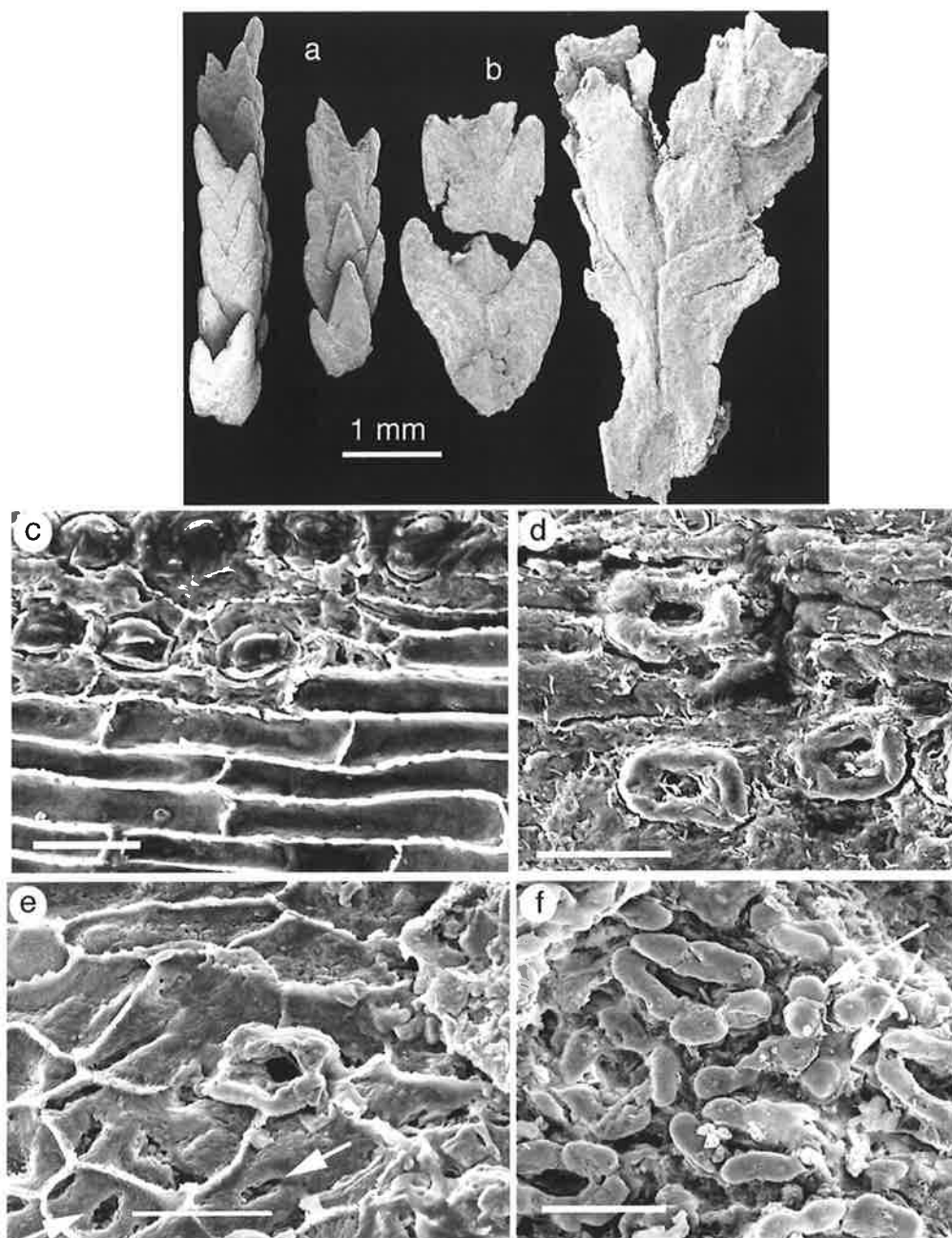
Fig. 17a-f. Comparison with other Cupressaceae fossils from Little Rapid River I

    a, c, d, Small leaved fossils (*Diselma microfolius*; scale bars for c, e, 20 μm).

    b, e, f, Large leaved fossils (*Libocedrus jacksonii*; scale bars d, 25 μm; e, 20 μm).

Comparison of small and large Little Rapid River fossils

The single small leaved specimen from Little Rapid River (LRR1-3320) is smaller than the foliage described in Part III A and attributed to *Libocedrus* (Fig 6a, b). Whilst it could represent mature foliage from the same species, this seems unlikely. In contrast to these specimens, its decussate leaves are elongate, similar in size, and have apices that overlap at least half the length of the leaves above. The subsidiary cells have relatively few indentations (not corresponding papillae on the external surface), and the Florin rings are not highly lobed and lack a peripheral groove. The stomata and cells of the small specimen are only slightly smaller than those of the larger specimens.

Fig. 18a-d Leaf comparisons - Balfour, Little Rapid River, extant *Diselma,* and *Microcachrys,* and Regatta Point
(a) B-475, (b) LRR1-3320, (c) *Diselma archeri,* (d) *Microcachrys tetragona*
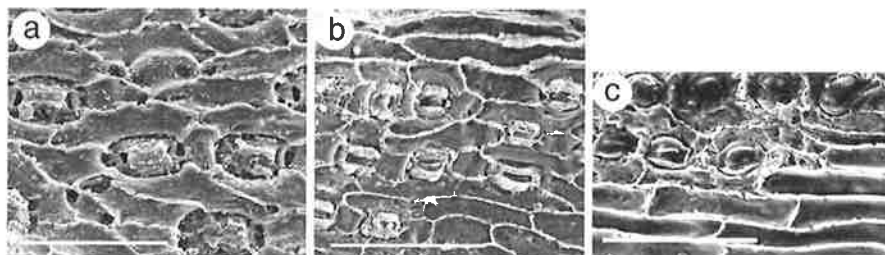
Fig. 19a-c Cuticle comparisons: - **a**, extant *Diselma archeri*; **b**, *Diselma microfolius* (Balfour); **c**, *Diselma microfolius* (Little Rapid River)

Foliage similarities - *Diselma* and *Libocedrus*

In the course of this study it became apparent that the leaves of *Diselma* and adult *L. bidwillii* and *L. plumosa* and *L. chevalieri* share a number of morphological characteristics. All have tetragonally arranged leaves, stomata on their 'adaxial' surface, and their cuticular characteristics are quite similar. The foliage of *L. bidwillii* with that of *D. archeri* is compared in Fig. 20.

Fig. 20 Comparisons - *L. bidwillii* and *D. archeri*
Each has decussate, elongate-lanceolate, monomorphic, imbricate leaves that are tetragonally arranged. Leaves of *L. bidwillii* (left) are larger, broader and less tightly imbricate than those of *D. archeri* (right).

Diselma and *Libocedrus* have very similar leaf morphology. In two of *Gadek et al.'s* (2000) Cupressaceae phylogenies (*matK*, and molecular [*matK*] plus non-molecular), *Diselma* (decussate leaves) and *Fitzroya* (leaves in whorls of three) are a sister group clustered with *Widdringtonia* (leaves spirally arranged, but decussate on small branchlets). This places *Diselma* remote from other genera with similar leaf arrangement. The possibility that the *Diselma* specimen included in their data set (GenBank - UNSW21742) had been misidentified was considered, and matK analyses were performed for 3 genera (*D. archeri*, *L. bidwillii* and *W. cedarbergensis*). The results were identical to that of Gadek *et al.* (2000).

Despite their foliage similarities, the ovulate cones of *Diselma* and *Libocedrus* are quite different. Although those of *Libocedrus* are relatively simple, those of *Diselma* are even more so, and lack the ligulate 'scale' common to *Libocedrus, Fitzroya* and *Widdringtonia*.

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Discussion

The Balfour and Little Rapid River sites are in relatively close proximity but the Little Rapid River sediments are older (Hill 2001) than those of Balfour (~5-20 million years; G. Jordan pers. com. 2004). Despite the age difference, the flora at the two sites includes *Libocedrus* (Hill and Carpenter 1989, Part III A, B, this study), at least one *Nothofagus* species (subgenus *Brassospora*; Hill 2001), and genera/species from other families, including Araucariaceae, Podocarpaceae, Lauraceae, and Casuarinaceae (*Gymnostoma*; unpublished data), none of which are now found there. This would seem to indicate the climate and conditions within which the two floras grew may have been similar, and that present day conditions are quite different to those in which the fossils grew.

The leaves of Balfour *Libocedrus* (Part III B) and *Fitzroya* (Hill and Paull 2003) fossils are similar in size to their extant relatives. The small-leaved fossil appears unrelated to the *Libocedrus* specimens. Mid Pleistocene *Diselma* (Regatta Point; Jordan *et al.* 1997) and Early Pleistocene *Microcachrys* (Regatta Point; Jordan 1995) have leaves and cuticles that are not much smaller than their extant relatives but, unlike them, grew close to sea level. Miocene *Microcachrys* (Morwell; Blackburn 1985) is of similar size to extant *M. tetragona*. The small leaved Balfour specimen (B-475) is considerably smaller than any extant *Libocedrus* and almost half the size of extant *Diselma* (Fig. 18a, c) and *Microcachrys* (Fig. 18d). It differs from the Little Rapid River specimen (LRR1-3320; Fig. 18b) in that its leaves are slightly smaller, only loosely imbricate, and are broader towards the base. The Little Rapid River specimen appears to be unrelated to the other small leaved foliage from that site. Both fossils have stomatal complexes that appear more like those of extant *Diselma* than *Libocedrus,* but are around half the size of extant *Diselma* (Fig. 19a-c). Unlike *Diselma*, neither fossil has stomata on their abaxial surface. As both have elongate-lanceolate leaves, and papillae in association with outer surface stomata, they are not considered related to *Microcachrys*.

The small sample size of the Balfour and Little Rapid River fossils (one from each site) presents a problem. Is the taxonomic information sufficient to assign the fossils to a living genus (see Collinson 1986)? The paucity of samples seems to suggest that they were a rare element in the flora at both sites. Cooler climatic conditions cannot be evoked to explain the small size of the Balfour specimen, as *Libocedrus* fossils from this site (Fig. 14b) are similar in size to their extant relatives. In contrast, the leaves of the Little Rapid River *Libocedrus* are relatively small (Fig. 17b). The two small leaved fossils are much smaller than extant *Diselma* and slightly different from each other (the latter could be explained by the different age of the two sites, and somewhat different climatic conditions). Although they, and *Diselma*, have many characteristics in common, many of these are not far removed from some extant *Libocedrus*. Neither of the two small-leaved fossils appears to be related to fossil *Libocedrus* species at Balfour and Little Rapid River. The possibility that they are relatives of Northern Hemisphere Cupressaceae (the Little Rapid River sediments also contain fossil *Austrosequoia* whose extant relatives are only found in western North America; Hill *et al.* 1993) has not been investigated, but seems unlikely. The fossils have many characteristics similar to extant *Diselma,* and to a lesser extent, *Libocedrus.* Whether either or both fossils are an extinct *Diselma,* or an unusual (also extinct) *Libocedrus* species, possibly living in marginal conditions, remains debatable. However, with so many other extant Southern Hemisphere genera present Cenozoic Tasmanian sediments the absence of *Diselma* (which is now a Tasmanian endemic) seems unusual. As most Cupressaceae pollen is remarkably similar, the pollen record does not provide enlightenment (Hill and Orchard 1999).

Interestingly, most of the fossil Cupressaceae described in this study (Part II A, B) have fewer stomata than their living relatives (e.g. the small leaved Balfour and Little Rapid River fossils only have stomata on their adaxial surfaces), and all have smaller cells and stomata. Numerous authors (including Beerling *et al.* 1998; Retallack 2001, McElwain *et al.* 2002; Kouwenberg *et al.* 2003 and) have suggested that atmospheric CO_2 levels may influence stomatal size. Although the Tasmanian fossils described in this study probably grew at times when CO_2 levels were higher than those of today, there are no carbon isotope data to confirm this. It must also be remembered that CO_2 is only one of many factors that determine cell physiology (Kürschner 2002).

Ecology

Diselma and *Microcachrys* are now restricted to 'wet subalpine shrub communities in the central plateau and mountains of west and south-west' Tasmania (Hill 1998). In the mid-Pleistocene, possibly at a time when the climate was much colder than the present, they grew at much lower altitudes (Jordan *et al.* 1997). The past ecological ranges of *Diselma* (Jordan *et al.* 1995) and *Microcachrys* (Blackburn 1985; Jordan 1995) were probably more extensive, and they appear to have grown in more diverse floristic assemblages. *Diselma* (unlike *Libocedrus;* Part I) does not appear to require catastrophic disturbances for regeneration (Jarman *et al.* 1999), but its distribution and density are affected by fire frequency and intensity (Jackson 1999). Since the arrival of humans around 40,000 years ago, the progressive use of fire to clear vegetation has modified the Tasmanian landscape (Jackson and Brown 1999). In high montane areas, mosaics of different aged communities attest that successions after fire can be slow, particularly if these occur in these areas during very dry conditions. Such fires are often so intense that all conifers (including *Diselma*), and most woody plants are destroyed. Surficial peat, and any seeds contained within it, is also often burnt. Post fire re-establishment depends on prevailing conditions and seed availability, and may take several hundred years (Jackson and Brown 1999). Perhaps *Diselma's* present relatively high altitude distribution is coincident with anthropomorphic changes to the natural fire regime. Cultivated specimens (e.g. Tasmanian Arboretum, Devonport) show it is capable of vigorous healthy growth at low altitudes. Herbarium specimens (this study) suggest that if water is abundant it occurs naturally at lower altitudes (~680 m) and may modify its leaf morphology when it does so.

The Balfour and Little Rapid River small leaved fossils probably grew in quite wet conditions as they, and other fossils from these two sites, are covered with fungal hyphae. Why they are so small remains debatable.

Part V A: Processes and factors involved in the disaggregation of Gondwana: implications for climate and plant distribution

The continents and islands mentioned in this study (Australia, Antarctica, South America, New Zealand, New Guinea, New Caledonia, and also India, Africa, and Madagascar) were once part of the super-continent Gondwana. This formed in the Late Cambrian and was originally situated at low latitudes, but had moved to high latitudes by the Ordovician-Silurian (McLoughlin 2001). Although the main concern of this study is the documentation of new fossil plant genera/species in the mid-Late Cenozoic, the pre-fragmentation configuration of Gondwana, the sequence in which the continents separated, their latitudinal movement, and the subsequent effects this disintegration had on climatic conditions have a direct bearing on understanding the evolution, and past and present distribution of Southern Hemisphere flora. The interpretation presented below is based on a diverse range of data, much of which is of marine origin.

Gondwana – mechanisms involved in breakup

The formation and disintegration of supercontinents takes about 500 million years (Wilson cycles). Why super-continents (such as Gondwana) become unstable and disintegrate has been, and is still, the subject of many tectonic theories, including either mantle plume activity, changes to the forces driving plate-boundaries, or a combination of these of these two forces (see Storey 1995; Storey and Kyle 1997). Anderson (1982) suggested that over long time periods (10^8 yr) the lithosphere beneath a supercontinent thickens, altering convection in the underlying mantle, generating heat and partial mantle melting. Thermal expansion of the mantle causes it to rise towards the surface, weakening the lithosphere and producing surface uplift (that can extend to thousands of kilometres in diameter). This surface anomaly, a 'geoid high' (Lowman and Gable 1999), gradually changes the spin axis of the earth, so that it (the uplifted area) is located at the equator Anderson (1982). Extensional deformation and regional tectonism associated with uplift would initiate continental breakup. The larger the landmass, the bigger the thermal anomaly (Phillips and Bunge 2005). Mantle plumes appear to play a role in continental disintegration Storey *et al.* 1999; Hawkesworth *et al.* 1999; Dalziel *et al.* 2000; Condie *et al.* 2001). Significant periods of volcanic activity (largely pre-Cenozoic) were associated with the breakup of Gondwana (Smith 1999). Disintegration of the supercontinent was possibly triggered by a super-plume, or several closely spaced smaller plumes ~185 Ma, in the area that included southeast Africa, southern South America, east Antarctica and the Antarctic Peninsula (these areas contain significant flood basalts of this age; Storey 1995; Storey and Kyle 1997; King 2000; Dalziel *et al.* 2000). A change in continental plate boundary forces (from compressional to extensional) may also have been important (e.g. Storey 1995), as extensional environments possibly favour plume melting (Ernst and Buchan 2003). The approximate current continental positions were reached in the Late Cenozoic. Present and past topographical features on these continents are the result of tectonic and erosional processes.

The isolation of New Zealand, New Caledonia, Australia, South America, Antarctica and New Guinea: Implications for floristic exchange

As Gondwana disintegrated new continents and oceans were created. For some time the margins of the newly formed continents were in close proximity, separated only by shallow seas. During this time continental margins would have been unstable and, as such, excellent places for floral exchange, and evolution (Dettmann 1989; Hill and Scriven 1995).

Southwest Pacific - New Zealand and New Caledonia
The geology of the linear island chains, submerged ridges and basins of the southwest Pacific is highly complex (e.g. Veevers *et al.* 1991, Gaina *et al.* 1998, McLoughlin 2001; Mortimer 2004; Schellart *et al.* 2006). The islands of New Zealand, New Caledonia, Lord Howe Rise, Norfolk Ridge and West Norfolk Ridge are underlain by continental crust (accreted terraces and plutonic suites of Palaeozoic age) that was connected to eastern Australia and east Antarctica (Lee *et al.* 2001; Mortimer 2004) until about 100 Ma. They form the continental fragment Tasmantis, which is now largely submerged. Until ~85 My ago eastern Antarctica, Australia and New Zealand, and probably New Caledonia (Specht *et al.* 1992) had a shared flora. Around ~104-94 Ma, a mantle plume beneath Marie Byrd Land (east Antarctica) and south western New Zealand produced significant uplift of Marie Byrd Land, and ~84 Ma an eroded New Zealand landmass began to rift away from Antarctica (Gaina *et al*, 1998; Storey *et al.* 1999; Sutherland 1999; Laird and Bradshaw 2004). As it did so its western margin subsided (Storey *et al.* 1999). Extension within the rift led to the formation of the Tasman Sea (and the separation of eastern Australia from New Zealand and New Caledonia), and also the South Pacific Ocean (Sutherland 1999). Sea floor spreading in the Tasman Sea ceased between 55 Ma (Storey *et al.* 1999) and 52 Ma (Gaina *et al.* 1998). The present day position of the continental fragments to the east of Australia has remained much the same since that time (Hall 2002). New Zealand is now ~2000 km from Australia (Lee *et al.* 2001).
New Zealand and New Caledonia are linked via a number of large underwater ridges and plateaus (Sutherland 1999; Chardon and Chevillotte 2006). As a result of tectonic activity and rising and falling sea levels, the size of the two landmasses has varied over time. New Caledonia may have been substantially (or totally) covered by sea in the Early Eocene (~55 Ma; Aitchison *et al.* 1995). The island's large ultramafic complexes are the result of a tectonic collision in the Late Eocene (~44 Ma; Aitchison *et al.* 1995; Fitzherbert *et al.* 2004). In the Late Oligocene, New Zealand was only about 20% of its present size (Lee *et al.* 2001), and at present only about 10% of its continental crust is above sea level (Mortimer 2004). Campbell and Landis (2003; in Waters and Craw 2005) have suggested that New Zealand was totally submerged in the Oligocene, but this remains debatable (Waters and Craw 2005). Undersea extensions of western New Zealand include the Challenger Plateau and Lord Howe Rise (Sutherland 1999). The northern part of the Lord Howe Rise may have remained relatively close to Australia until ~75 Ma (Hall 2002), possibly providing a link with New Caledonia. It subsided ~65 Ma (Lee *et al.* 2001). To New Zealand's north the underwater Norfolk Ridge forms a link with New Caledonia (Eade 1988 in Sutherland 1999; Chardon and Chevillotte 2006). At various periods of tectonic activity, sections of these ridges may have been above water, e.g. Herzer *et al.* (1997) suggest the Norfolk and Reinga Ridges were uplifted (in the Oligocene and Miocene respectively) and could have provided

links between New Zealand and New Caledonia. Until the Early Miocene (Mortimer *et al.* 1998) New Zealand and New Caledonia (and New Guinea) may have also have been linked a chain of hotspot related seamounts (or island arcs; McLoughlin 2001). However, as hot spot generated islands are usually small and only remain above sea level for relatively short periods, McLoughlin (2001) thinks they were unlikely to have provided the means for floristic interchange or dispersal. Lee *et al.* (2001) think otherwise. Lord Howe (600 km east of Australia on the Lord Howe Ridge) and Norfolk Islands (700 km south of New Caledonia on the Norfolk Ridge, and 800 km north of New Zealand; Pole 1994) are volcanic seamounts that erupted at 6.9 and ~3 Ma (McDougall *et al.* 1981). Their flora is more like that of New Caledonia and New Zealand than that of Australia (Green 1994), and Pole (2001) believes it arrived on these islands by long distance dispersal. Sanmartin and Rondquist (2004) suggest that the New Caledonian flora is more like that of New Guinea or other ocean islands than that of New Zealand, Australia and South America.

On the eastern side of New Zealand's South Island are two large, highly modified, submerged continental extensions, the Chatham Rise (east) and the Campbell Plateau (south) Cande *et al.* 2000; Sutherland 1999; Schellart *et al.* 2006). The latter was connected to Marie Byrd Land ~85 Ma (McAdoo and Laxon 1997). These areas contain small, widely spaced islands related to episodes of volcanic activity. These decrease in age (~28 My to 0.5 My) in an easterly direction, Those on the Campbell Plateau are linear and are probably due to plate reorganization (Adams 1981). The Chatham Islands may have been submerged during the Early Oligocene (Wood *et al.* 1989 in McLoughlin 2001). Michaux and Leschen (2005) suggest that the biota of the Subantarctic Islands on the Campbell Plateau is more like that of South America and Antarctica than that of the Chatham Rise.

The main islands of New Zealand were probably low lying for most of the Cenozoic (Chamberlain *et al.* 1995). At ~45 Ma new plate boundary dissected New Zealand (Storey *et al.* 1999, Sutherland 1999; Laird and Bradshaw 2004). The South Island is divided by the Alpine Fault, the western half of the Island is on the Australian Plate, the eastern half on the Pacific plate. Uplift on the fault (the Southern Alps) began ~20 Ma, but was not significant until ~5 Ma (Chamberlain *et al.* 1995; Winkworth *et al.* 2005). The ranges are now up to 50 km wide and create a massive rain shadow, with very wet conditions to the west (up to 12 m rain per year), and semi arid conditions to the east.

Antarctica and Australia

Breakup around Antarctica began ~155 Ma (Brown *et al.* 2006). Rifting of the southern margin of Australia from Antarctica began in an NW-SE direction ~83.5 (Brown *et al.* 2006) to 71 Ma (Tikku and Cande 1999) others, e.g. Wilford and Brown 1994 suggest this occurred much earlier ~130Ma). This may have been initiated by extensional forces due to ocean floor subduction beneath Eurasia to the north (Storey 1995). As rifting was not associated with excessive volcanism, and both continental margins were passive, spreading rates were initially slow (Storey 1995; Brown *et al.* 2006). Around 43 Ma spreading rates increased and, as Australia moved to lower latitudes, contact between the two continents (which had been maintained via Tasmania and the Tasman Rise) was severed when the Tasman Rise (to the south of Tasmania) subsided (the implications of this are discussed later). Rifting between the Australian mainland and Tasmania (through Bass Straight) had failed (Finlayson *et al.* 1996). The new seaway connected the Indian and Pacific Oceans (Brown *et al.* 2006). At times of low sea level the Australian mainland and Tasmania were linked via land bridges.

Palaeomagnetic data indicate that Antarctica has not always behaved as a rigid plate, and that in the mid Cenozoic West and East Antarctica moved relative to each other (McAdoo and Laxon 1997; Cande et al. 2000; Cande and Stock 2004). Displacement between east and west may have been as much as 300 km, and was associated with rotation, and episodic uplift of the Transantarctic Mountains (Cande et al. 2000).

Australia

Tectonism associated with the isolation and rifting apart of South America and Antarctica and Australia during the Late Cretaceous–Early Cenozoic initiated the collapse of the southern margin of the Australian plate and the formation of several large basins, each of which contains coals of varying thicknesses and ages. The eastern continental margin, from northern Queensland to Tasmania, is bounded by a wide (400-500 km) mountain range (Taylor 1993). Uplift of this area was largely the result of episodic volcanic activity, that probably began ~100 Ma, in response to the opening of the Tasman Sea (Wellman 1987; Quilty 1994). Some of the uplift was due to plate margin development, the rest is the result of the northward transit of the Australian plate over a stationary (or slow moving) southerly located hotspot. This created a linear chain of volcanoes that extend from northern Queensland into south-eastern South Australia (Quilty 1994). By the Early Eocene the form of the eastern margin was similar to that of today (Hall 2002). Australia and South America were linked via Antarctica until the Tasman Rise was breached.

New Guinea

New Guinea is at the northern margin of the Indo-Australian plate (RS Hill 1991). Rifting between Australia and New Guinea and the subsequent formation of the Coral Sea began ~90 Ma. The opening of the latter (to the southeast of New Guinea) was completed ~52 Ma Gaina et al. 1998), and was associated with uplift and erosion. The geology of New Guinea is highly complex, and evolutionary models and the timing of the numerous tectonic events are many and variable (Hall 2002). The southern part of the continent is autochthonous Australian continental crust and was a passive margin until the Cretaceous. The northern margin consists of accreted island arc terranes (e.g. Haddad and Watts 1999), but there is no consensus as to the number of plate/microplate boundaries involved and the times at which they were accreted (Hall 2002; Ufford and Cloos 2005). Slivers of original continental margin crust appear to have been transferred to eastern Indonesia as these terranes moved along the northern margin (Vroon et al. 1995). The first of these collisions ~35-30 Ma produced uplift of easternmost New Guinea (Ufford and Cloos 2005). The central mountain range is the result of numerous other collisions due to a change in plate motion between 12-4 Ma (Hill and Raza 1999; Ufford and Cloos 2005). Ultramafic rocks (with high levels of iron and magnesium) outcrop throughout the main range and also smaller ranges on the Papuan Peninsular. These are remnants of the old terranes and are areas of regional biotic endemism (Polhemus and Polhemus 1998; Heads 2002). Heads (2002) suggests disjunct taxa at these sites are relicts from accreted arcs. Widespread carbonate sedimentation (at the Oligocene Miocene boundary; Haddad and Watts 1999; and in the Early Miocene; Hill et al. 1993 in Hill and Raza 1999) suggests there were times when much of the continent was underwater. At times during the Quaternary, sea levels fell due to expansion of Antarctic ice sheets and Australia and New Guinea (and also Australia and Tasmania) were linked via land bridges. During these times tree lines in New Guinea were much lower (below 2200 m) than at present (3900 m; Hope 1994).

South America

During the Late Cretaceous to Early Cenozoic southern South America and Australia were connected via Antarctica. This link extended from the southern Andes, through the Scotia Arc to the Arctic Peninsula and across East Antarctica into Southern Australia, and allowed ongoing floristic interchange between Australia and South America (via Antarctica) until the Late Eocene (Sanmartin and Ronquist 2004). Pollen evidence suggests this was a temperate climate flora (Sanmartin and Ronquist 2004), dominated by *Nothofagus* (Dettmann *et al.* 1990). The opening of the Drake Passage severed the connection between South America and Antarctica. The implications of this event are discussed below. In the Late Miocene-Pliocene there was significant uplift of the central Andes (Gregory-Wodzicki 2000b).

Mid-Cenozoic cooling: a change in ocean circulation patterns or in CO_2 levels?

In the early Cenozoic the southern pole was covered by land, and the northern pole by water. These regions were warm and had low atmospheric pressure systems. As land (unlike water) is unable to maintain relatively constant temperatures, it is warmer than surrounding oceans during summer, but colder during winter (Hay *et al.* 2005). Ocean and atmospheric circulation patterns were unlike those of the present (Rack and Pittenger 1992). Global cooling in the latter half of the Cenozoic has been attributed to the isolation of Antarctica (which appears to have been located near the southern pole since the Early Cretaceous; DiVenere *et al.* 1994) following the breaching of the South Tasman Rise (south of Tasmania) and the opening the Drake Passage (between South America and Western Antarctica). The formation of Antarctic ice sheets and the cooling of previously warm ocean bottom temperatures are thought to be the direct result of the formation of the largely wind-driven Antarctic circumpolar current (ACC; e.g. Kemp 1978; Lawver and Gahagan 1998; Toggweiler and Bjornsson 1999; Livermore *et al.* 2005). As the ACC strengthened seawater in the earth's three major oceans was exchanged. This altered oceanic heat transport patterns and the transfer of heat between Southern and Northern Hemispheres (Sijp and England 2004; Eagles *et al.* 2006; Huber and Nof 2006).

The times at which the southern gateways opened (especially the Drake Passage), and the significance of the ACC in lowering global temperatures, are subjects of vigorous debate (e.g. Huber and Sloan 2001; DeConto and Pollard 2003; Barker and Thomas 2004; Livermore *et al.* 2005). It is generally agreed that initial shallow opening of the South Tasman Rise occurred ~35 Ma (e.g. Lawver and Gahagan 2003; Stickley *et al.* 2004; Pfuhl and McCave 2005). Widening and deepening of the seaway took place gradually and was completed ~30.2 Ma (Stickley *et al.* 2004; Pfuhl and McCave 2005). There is no common consensus as to when the Drake Passage first opened. Initiation dates range from ~50 Ma (Livermore *et al.* 2005; Eagles *et al.* 2006), ~41 Ma (Scher and Martin 2006) i.e. **before** the opening of the Tasman Rise, to 31 Ma (Lawver and Gahagan 2003), ~23.95 Ma (Pfuhl and McCave 2005), and ~22 Ma (Cande and Kent 1995). A deep-water passage was established by the Early Miocene (Barker and Burrell 1977; Livermore *et al.* 2005). Until a more precise date for the opening of the Drake Passage can be established, the degree to which the ACC influenced global weather patterns will remain debatable. If the ACC, and the atmospheric patterns associated with it, were not fully effective until the Early Miocene, why were there extensive Antarctic icecaps in the Early Oligocene (e.g. Pekar and DeConto 2005; Pekar *et al.* 2006)? Global oceanic heat flow is also influenced by the transport of oceanic heat between Arctic and North Atlantic Oceans. If, as Davies *et al.* (2001) suggest, a deep water connection between these two oceans was established in the Early Oligocene ~35 Ma

(rather than ~25 Ma; Schnitker 1980), this would also have attributed to global cooling at this time (Davies *et al.* 2001).

However, new data suggest that global cooling began before ocean circulation patterns changed. Recent collaborative results from a drilling program in the Arctic Ocean (Moran *et al.* 2006) indicates there was synchronous ice cover at the northern and southern poles at ~45 Ma (sea ice in the north, glaciers in the south; and also ~14.5 Ma). Waning temperatures, and ice at the poles are now being linked to changes in greenhouse gas levels (especially declining CO_2; e.g. DeConto and Pollard 2003; Barker and Thomas 2004; Huber *et al.* 2004; Huber and Nof 2006; Moran *et al.* 2006), the effects of orbital forcing (e.g. Coxall *et. al.* 2005), and albedo feedback, rather than ocean circulation patterns. Cool ocean temperatures were probably due to glaciation rather than a cause of it (Barker and Thomas 2004). During the summer the poles receive more radiation than anywhere else on earth. Summer temperatures probably determine whether, and how much, ice accumulates in these regions (Huber and Nof 2006).

Climate: past and present

Atmospheric CO_2 and other greenhouse gases are generally thought to be responsible for the change from glacial to interglacial conditions (Veizer *et al.* 2000). What controls the level of these gases is not really well understood, but it is obvious that a multitude of interacting factors drive climate change. It is beyond the scope of this study to discuss any of these in detail, but a brief look at some of the more relevant ones will help understand some of the conditions in which the fossil plants that form the focus of this study grew.

CO_2, oceans, and temperatures

Ocean temperatures are linked to atmospheric carbon, oxygen and methane levels. The CO_2 content of the entire atmosphere/ocean system is influenced by the variability of weathering rates and metamorphism of carbonate and sedimentary rocks (the source of dissolved carbon to oceans) over long time periods (10^6 to 10^7 years: Kasting *et al.* 1986). Oceans are the largest carbon cycle reservoirs. In normal marine conditions the ocean is a layered system in which the shallow, upper layer is well-mixed and remains in equilibrium with the atmosphere, whilst the deep, massive layer does not. Variations in CO_2 levels are driven by biological pumping of CO_2 to the deep ocean from surface waters, with deep water containing around three times more dissolved CO_2 than surface water (Kasting *et al.* 1986; Archer *et al.* 2004). In the deep sea most of the organic carbon produced by primary activity is re-oxidised (Margaritz *et al.* 1992). As carbon burial is greater in anoxic oceans, ocean levels are seen to determine biological cycles and other nutrients (including phosphorus; Handoh and Lenton 2003; Archer *et al.* 2004).

High atmospheric CO_2 levels affect outgoing solar radiation levels, trapping heat and warming oceans. Water evaporated from oceans is vaporised, stored and transported in the atmosphere and released, by condensation, elsewhere. Precipitation rates determine the chemical weathering rates of sedimentary rocks, and hence the amount of atmospheric CO_2 (Pierrehumbert 2002). Circulating deep ocean waters redistribute heat, salt, and nutrients (Mackensen 2004), and atmospheric circulation patterns also affect meridional heat transport. Experimental evidence suggests that when CO_2 levels are high the poles are more influenced by warming than the tropics (Pierrehumbert 2002).

Sea surface temperatures influence how much ice accumulates at the poles (Huber and Nof 2006).

Ice sheets are large topographical features that influence the albedo effect, and thus outgoing solar radiation. They are repositories of large fluctuating volumes of fresh water that grow slowly but melt relatively quickly. The growth and melting of ice sheets reorganise continental drainage, creating lakes, changing river courses etc. Melting ice releases large pulses of cold fresh water into the oceans (Clark *et al.* 1999). Nesje *et al.* (2004) have suggested that abrupt climatic change in the early-Holocene may be linked to the outbursts of fresh water into the north Atlantic and Arctic oceans). This fresh water has greater density than seawater and sinks to the bottom of the ocean. The present day Southern Ocean is a mixture of North Atlantic Deep Water and recirculated Pacific and Indian Ocean waters. The volume of NADW is dependent on sea ice coverage in the Northern Hemisphere. Nutrient depleted NADW provides heat to Antarctic waters and thus influences how much sea ice forms and regulates primary productivity (Archer *et al.* 2004). Strong winds in the tropics cause up-welling of colder waters (Clark *et al.* 1999). Changes to ocean floor bathymetry (due e.g. to mid ocean ridge volcanism or hot spot activity) affect deepwater flow patterns, and add heat and CO_2 to the oceans and atmosphere.

Methane

During the last 65 My, mean ocean temperatures have varied by more than 10° C. The highest temperatures (~12° C) were at the start of the Eocene ~55 Ma. At this time ocean surface temperatures rapidly increased (over ~10,000 years) from ~12°C to ~20°C and stayed high for ~250,000 years (Schiermeier 2003). This is thought to be due to a massive release of methane, stored as methane hydrates, from exposure of continental shelf sediments due to falling sea levels (Schiermeier 2003; Archer *et al.* 2004). (Methane is a by-product of organic carbon metabolism by marine chemoheterotrophs. Methane hydrates are crystalline solids made up of methane enclosed in water molecules, and are stable at ocean depths of 200 to 6000 m and temperatures of -8 to +14 °C; Jahren 2002. Accumulation times for methane hydrates are much longer than discharge rates; Archer *et al.* 2004). The high ocean temperatures at ~10 Ma (when the temperature remained high for around one million years) are also linked to methane release. This was followed by a gradual decrease to present day levels of ~1.5° at ~5 Ma (Archer *et al.* 2004).

When super-continents break-up new oceans and ocean ridges form. These release CO_2 and methane (CH_4) into the (initially shallow) oceans and atmosphere (Condie *et al.* 2001). How much CO_2 and CH_4 is released depends on the rate of sea floor spreading. Large volumes of CO_2 may enter the atmosphere over relatively short time scales (<50 My). If aerial or sub-aerial igneous volcanic activity is associated with early rifting, further extension of continental margins occurs, new mountain ranges form, and weathering rates increase. If the mountains contain carbon rich (carbonate or organic carbon) sedimentary strata, sediment eroded from the continents may become trapped within the rift, recycling carbon back into the ocean (Condie 2004). This influx of nutrients increases biological activity, and if other nutrients are also involved productivity is further enhanced, and burial rates of organic carbon increase. Circulation in these young basins is restricted (there is no deep water flow) and the water column is stratified, with an upper, shallow, warm oxic layer and a lower, deep, anoxic layer. Plants growing on either side of opening ridges are in close contact, separated by warm shallow seas and in CO_2 and CH_4 enhanced atmospheric conditions.

Planetary cycles and polar wander

The amount of solar radiation reaching the earth is modified by cyclical changes (Milankovitch cycles) in the earth's orbital parameters (e.g. Ruddiman *et al.* 2005). Around every 100,000 years, earth's orbit around the sun varies ~5% from elliptical to almost circular. This alters the distance between the sun and the earth and is characterised by long glacial periods interspersed with shorter warmer periods. (It is interesting to note that the present orbital parameters are reaching an unusual phase (circular orbit) in which insolation will remain almost constant for some time; Berger *et al.* 2002). The angle of the earth's poles to the sun (obliquity or axial tilt) varies from 21.5 - 24.5° about every 41,000 years. The degree of tilt determines the length of seasons in each hemisphere, and conditions are most seasonal when the tilt is greatest (Levrad and Laskar 2003). Changes in contrast between equator and pole effect water vapour transport (Broecker 1997). Around every 21,000 years earth's rotational axis changes direction (precession). This 'wobble' is due to torque effects between the non-spherical earth, the sun, moon and other planets, and determines the position of the solstices. In summer the poles receive more radiation than elsewhere on Earth.

Longer term changes in the earth's rotational axis (obliquity) other than those of Milankovitch cycles are known as true polar wander (TPW) and are due to mass anomalies either on the earth's surface, or within it (Evans 2003), such as large mantle plumes (Greff-Lefftz 2004). These anomalies are associated with the formation and disassociation of supercontinents and continental fragments may experience very rapid paleolatitudinal change (Evans 2003). Small continents and oceanic plates move at different velocities to those of large, supercontinents (Phillips and Bunge 2005: e.g. India and Australia moved rapidly northwards after they broke away from Gondwana). Greff-Lefftz (2004) suggests that between 130-60 Ma TPW rates were quite fast (~30 Km Ma^{-1}), but for the next 50 Ma were almost negligible. A rapid change in polarity at ~84 Ma (and possibly 43 Ma) is probably related changes in global plate motion (Sager and Koppers 2000). The relative volumes of water in oceans and glaciers (rising and falling sea levels; Nakada 2003, 2006; Levrad and Laskar 2003) also alter the shape of the earth. An increase in TPW rates in the last few million years is attributed to the effects of Holocene glaciation and subsequent melting (Evans 2003: Nakada 2003, 2006; Greff-Lefftz 2004).

Cenozoic global climate trends

The general global climate trend for the last 100 My has been one of progressive cooling (McGowran and Li 1998; McGowran *et al.* 2004). This has been a time of global continental fragmentation, and the formation of new mountain ranges. In the late Paleocene to early Eocene ocean surface temperatures at high latitudes were 9-16° C warmer than at present (Zachos *et al.* 1994). As the continents moved further apart, tectonic plates collided and rotated, new seaways opened and old ones closed. The equatorial circulation pattern that had dominated early Paleogene climates declined (Veblen *et al.* 1996) and the direction and intensity of ocean currents changed (Frakes 1999), and the distribution of oceanic heat changed from low latitude halothermal to high latitude thermohaline (McGowran and Li 1998). Latitudinal thermal gradients increased and this led to well-developed climatic zonation (Frakes 1999). During the Cenozoic there have been three important periods of tectonic plate reorganization in the SW Pacific and SE Asia - 45 Ma, 25 Ma and 5 Ma. Between 25 and 20 Ma major changes in plate boundaries were associated with continental uplift (Hall 2002). McGowran and Li (1998) have identified four distinct periods of warm, wet climatic conditions and high sea levels from the Latest Paleocene to the present. These are the

Paleocene to Early Eocene, the Late middle to Late Eocene, the Early to Middle Miocene, and the Early Pliocene. In Australia, these were times of coal accumulation, and prolific plant growth. Dramatic cooling followed the warm periods, ice built up at the poles, and sea levels fell. Throughout these warm and cool periods temperatures and sea levels were not static, and climates varied on a regional and local scale. During times of high sea levels low lying continental areas were submerged, when sea levels were low land bridges reconnected previously isolated areas. In warmer times temperature gradients are low, in cooler times much higher (Pierrehumbert 2002).

In the last 60 My Australia has moved some 30° to the north (Veevers *et al.* 1991; Frakes 1999). Hill and Jordan (1993) have suggested that the continent shifted from a polar light regime (low sun angles, constantly light summers and dark winters) into very different mid-latitude photoperiod conditions. (However, before the continent began its rapidly northward transit, there were probably times when the sun angle was higher; see section on polar wander). In the same time period New Zealand (and New Caledonia) has moved 20° north (from ~60° in the Paleocene to ~40° at present; Lee *et al.* 2001). South America has moved relatively little, ~10° (Markgraf *et al.* 1996) from its original Early Paleocene position (at ~65°). This relatively small latitudinal change, and the climatic impact of the rising Andean Cordillera could partly explain the why floristic evolution in south western South America is more conservative than that of Australia, New Zealand, New Caledonia and New Guinea.

Paleoclimates and fossils

Temporal data is essential for evolutionary studies (Crisci *et al.* 2006). Our knowledge of the evolving earth is largely sedimentalogically based. When sediments contain microfossils (either marine e.g. planktonic and benthic foraminifera, and/or terrestrial pollen and spores [these are compared with living taxa]) their age can be estimated. Dates obtained from marine sediments (especially deep marine) are more reliable than those from terrestrial sediments, because marine sedimentation is generally continuous. Dates from terrestrial sediments are often erroneous (Crane *et al.* 2004). If terrestrial sediments are overlain or inter-bedded by basalts a reasonably reliable date can be accomplished. In Australia most Cenozoic volcanism was confined to the eastern continental margin and Tasmania, so most Cenozoic fossil plant sites are dated palynologically. This is problematic. Pollen is most frequently identified at the family, or genus level (Martin 1997). However, some pollen forms are taxonomically difficult to resolve, and others belong to extinct taxa. Pollen production between taxa can be highly variable (those with the most pollen are not necessarily the most abundant), and various taxa (e.g. the Lauraceae; Christophel 1989; Martin 1994) produce pollen that does not survive the sedimentation process. Robust pollen grains may survive erosion processes and be redeposited in younger sediments. Palynomorphs are typically transported by wind or water and so assemblages (especially those from shallow marine sediments) tend to reflect a regional, rather than local, flora, and can tend to be biased to high pollen producers (Martin 1982). Sediments in coastal basins are relatively easy to date because pollen data can be correlated with that from marine planktonic and benthic foraminifera (biostratigraphic data; Hill *et al.* 1999; McGowran and Li 1998; McGowran *et al.* 2004). The age of sedimentary sequences are more certain when pollen, spore and macrofossil data are combined (Truswell 1993). This combination of data also produces a much better picture of the local flora (Martin 1994). However, macrofossils take much longer to process than pollen and spores, and most dates (and much of the fossil plant record) are based on palynological data. The macrofossil record is also not straight forward, because fossil preservation is biased towards leaves with

robust cuticles, which excludes many herbaceous, and possibly some deciduous plants (Nip *et al.* 1986). Isotopic (e.g. O_2, CO_2) data is also helpful in constraining dates, but is rarely collected. As pollen and plant material require wet anaerobic conditions to be preserved (lakes, bogs and swamps), the record of vegetation growing in extended dry periods is non-existent or poor (Martin 1982).

The microfossil record tells us that the earth's climate has always been highly variable (due, as discussed earlier, to a complex interaction of many, mostly cyclical, factors). Plates growing at high southern latitudes during the Paleocene and Eocene, were subjected to low insolation. The degree of tilt of the earth to the sun determined daylight length, and was variable over long time periods. In Australia there has been an increasing tendency to arid conditions since the Eocene (Martin 2006). Most of the sites in this study have been dated palynologically, and so the age of these is an approximation only. None of the sites has (as yet) a comprehensive macrofossil record.

Ecology

Plant growth and distribution are climate dependent. Variability in climate, either small scale (annually or over decades) or over much longer time periods alters plant demographics. In tropical forests diversity is best maintained by gradual climatic change and frequent environmental disturbances (Connell 1978). Many southeastern Australian Tertiary macrofossil assemblages appear to have been deposited during dramatic climatic and/or geological events (e.g. flooding in association with volcanism). As such they probably reflect a flora well adapted to regeneration and survival in highly disturbed sites.

Part V B: Vicariance or long distance dispersal for Cupressaceae genera?

The rearrangement of continents and oceans profoundly effects the distribution of plants and animals (Crisci 2001). Vicariant populations may remain the same, speciate or become extinct. Dispersal events tend to occur in certain areas and directions, and may also be followed by allopatric speciation, and result in extinction (Sanmartin and Ronquist 2004). As climatic conditions vary through time, uplifted areas (mountains and mountain ranges) provide the means whereby plant species can advance or retreat, and thus facilitate the survival of many species (G. Hewitt pers. com 2006). Higher areas also provide refuge from rising sea levels.

Extant *Libocedrus*-related genera frequently co-occur with *Nothofagus* subgenera/species and have done so since at least the Early Eocene (this study). Both generally occur in mountainous regions, and less frequently at lower altitudes where precipitation rates are high. *Nothofagus* is frequently used in evolutionary studies concerned with southern hemisphere biota (e.g. Steenis 1971; Dettmann *et al.* 1990; Hill 1992; Linder and Crisp 1995; Swenson *et al.* 2001; Crisp *et al.* 2004; Cook and Crisp 2005). It has very distinctive pollen, and fossil pollen data indicate it may have evolved in southernmost South America and the Antarctic Peninsula, during the Late Cretaceous, some 80 million years ago (Hill 1992; Hill and Dettmann 1996; Swenson *et al.* 2000). It was widespread in Antarctica, Australia, South America and New Zealand by the Early Eocene (Dettmann *et al.* 1990; McGlone *et al.* 1996; Cook and Crisp 2005), and was present in New Guinea in the Miocene (Khan 1974; and perhaps earlier). Its pollen record in New Caledonia is poor, and although this indicates it is a recent arrival there (~2 Ma; Dettmann *et al.* 1990), Swenson *et al.* (2001) suggest it has been there much longer arriving via dispersal from New Zealand. Heads (2006) refutes this, suggesting a New Guinea origin. Ancient *Nothofagus* pollen types (Dettmann *et al.* 1990) indicate that many species became extinct. In Australia and New Zealand *Nothofagus* appears to have been most widespread during the Late Oligocene to early Miocene (Hill 2001) i.e. long after tectonic separation. In the later Miocene, the general trend to cooler, drier climates led to its demise in Australia (Hill 2001). Its current distribution is attributed to vicariance and dispersal (Cook and Crisp 2005).

From both an evolutionary and biogeographic perspective the Southern Hemisphere cupressaceous macrofossil record is important. Unlike that of *Nothofagus*, cupressaceous pollen is relatively indistinctive, and of little help in determining what genera/species were present at fossil sites (see Pocknall 1981). *Libocedrus* tends to produce relatively small quantities of pollen that is often either destroyed or distorted by preservational processes and/or preparation techniques (Horrocks and Ogden 1994).

This study confirms that *Libocedrus,* similar (in morphology and size) to extant New Zealand *Libocedrus*, was growing in southeastern Australia at ~58-60 Ma (Whang and Hill 1999), after New Zealand and New Caledonia had moved away from Australia. It also indicates the genus survived in Tasmania until at least 20 Ma by modifying the size of its foliage (e.g. from very small, in late Early Eocene sub-tropical coastal conditions at Regatta Point, to not much smaller than extant New Caledonian species in warm, slightly higher altitude conditions at Balfour during the Oligocene-Early Miocene). After the late Early Eocene, some *Libocedrus* fossil species have characteristics of extant New Zealand and New Caledonian species. *Austrocedrus* (now only found in southwestern South America) was present in Tasmania in the Early Oligocene i.e., after the Tasman rise was breached. Although its foliage is very similar

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to that of extant *Austrocedrus*, its ovulate cones are somewhat less so. Both fossil foliage and cones are considerably smaller than their living relatives. *Papuacedrus* also has a long macrofossil record (Late Oligocene–Early Miocene, Tasmania, Hill and Carpenter 1989; reviewed in this study; Middle Eocene, central Australia, Alley 1996), and was growing at Pioneer, Tasmania after the seaway between Antarctica and Australia had formed. The Pioneer fossils are remarkably similar, even in size, to extant *Papuacedrus*, now found only in montane New Guinea. It is interesting that the estimated dates for all the larger leaved fossils more or less coincide with two very warm Cenozoic periods (with sea surface temperatures ~10°C; Martin 2006), believed to have been caused by high atmospheric CO_2 (possibly methane) levels, i.e. the Early Eocene and Early Miocene. Hinojosa *et al.* (2006) also indicate that present day Chilean floras contain trees with similar leaf morphology to Eocene and Early Miocene fossils. It seems then, that the much smaller-leaved fossils (with very small cells) may have been growing at times when CO_2 levels were much lower. The size of the foliage of extant cupressaceous genera, with which the fossils were compared, is probably a response to current, relatively high, CO_2 levels.

The Cenozoic Southern Hemisphere macrofossil record for *Libocedrus*-related cupressaceous taxa has been poor, and for Antarctica is nonexistent. This study shows that *Libocedrus*-related species grew in southeastern Australia from the Early Eocene to the Early Miocene. Wilf *et al.* (2003) indicate that *Austrocedrus* (or a close relative) was also growing in south-western South America during the Early Eocene. Whether *Libocedrus*-related species were present in New Zealand, New Caledonia and New Guinea during the Eocene is unknown.

Fitzroya was present in Patagonia during the Paleocene-Eocene (Markgraf *et al.* 1996). *Fitzroya* macrofossils were not discussed in any detail in this study, but the genus appears to have been present in Tasmania from the early Oligocene (Hill and Paull 2003) and, like the *Libocedrus*-related genera, it foliage has varied in size and shape over time. The fossil record of *Diselma* now extends back to the Late Oligocene-Early Miocene. Florin (1940) indicated it was also present at Vegetable Creek (Emmaville), NSW during the Early Miocene. (He believed that foliage described by Ettingshausen [1988] as *Heterocladiscos thujoides* [Figs 5-7, Plate VIII] was *Diselma*). Until now, the earliest known *Callitris* macrofossils were mid Miocene (Yallourn, southern Victoria; Blackburn and Sluiter 1994). These foliage fossils are very similar in appearance and shape to extant species. The foliage subtending the Early Oligocene (Lea River) ovulate *Callitris* cones is much smaller than that of the Yallourn fossils, and the loose foliage believed to be related to the cones is variably fused. Could it be an ancestral species to extant *Callitris*? Fig. 1 indicates the known Cupressaceae macrofossil record for the extant species described in this study.

Recent ecological data (see Part I, chapters 3-5; Part II) indicate that an important factor in the distribution of all *Libocedrus*-related genera, and *Fitzroya*, (frequently with *Nothofagus* subgenera/species) are mountainous areas prone to irregular disturbance. The origin of these genera is unknown, but they have survived for a very long time. The characteristics they developed, such as the ability to colonise infertile, toxic soils*; long-lived, scale-like leaves; the capability to regulate foliage size as climatic conditions changed; and precocious fertility etc., made them resilient. Nelson and Ladiges (2001) suggest that the distribution of many Gondwanan species was restricted. This may have been true for the Cupressaceae species mentioned above. They, and *Nothofagus*, flourished in areas most affected by continental disaggregation i.e., along coastal and inland mountain ranges, expanding and contracting their ranges as climates waxed and waned. However, macrofossils from Western (e.g. Hill and Merrifield 1993;

Macphail *et al.* 1994) and central Australia (Sluiter 1991; Macphail *et al.* 1994) indicate there were many times when *Nothofagus* had a much less confined range i.e., was widespread across much of the Australian continent. This appears to be true for some *Libocedrus*-related genera too, e.g. *Papuacedrus* extended into what is now inland South Australia (Lake Eyre) in the Middle Eocene (Alley 1996). This appears to be an unusual distribution for taxa adapted to disturbed environments. These expansionary periods are probably related to the removal of dispersal barriers by climatic amelioration i.e. a change to temperate, wet climates. Foliage resembling *Libocedrus* is present in the Kojonup (Late Eocene) sandstone flora of WA (Fig. 5, 7 p. 70; McLoughlin and Hill 1996). This flora contains *Grevillea*-like and *Banksia*-like taxa, *Gymnostoma* and a variety of angiosperms indicative of a relatively dry environment. If the foliage is that of *Libocedrus*, it indicates the genus can survive relatively dry conditions. As Australia severed its ties with Antarctica and southern South America it moved rapidly northward and climatic conditions for most of the continent became increasingly drier and more seasonal. Vicariant Cupressaceae (*Austrocedrus*, *Fitzroya*, and probably *Libocedrus* and *Papuacedrus*) either speciated, migrated northward, or became extinct. How long they remained in southeastern Australia is unknown.
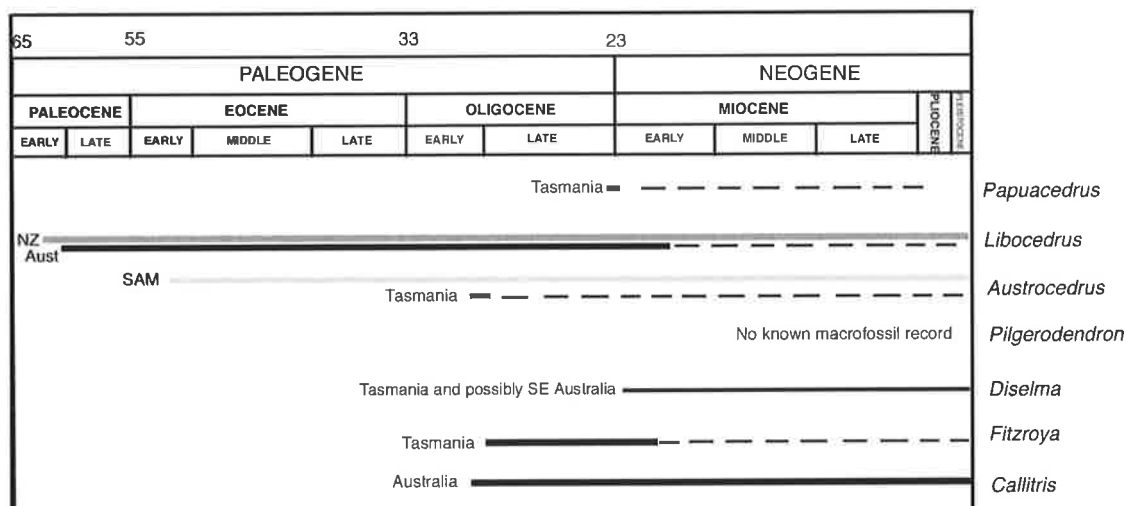
Fig. 1 Known macrofossil fossil record for extant species described in this study

Numerous authors (e.g. Hill and Jordan 1993; Swenson *et al.* 2001; Pole 2001; Cook and Crisp 2005; Knapp *et al.* 2005) suggest that *Nothofagus* was not vicariant across the Tasman sea, and that the ancestors of present day New Zealand *Nothofagus* arrived by dispersal from elsewhere. The origin of present day New Zealand *Libocedrus* is unknown, but Pole (2001) suggests the genus has had a continuous presence there since the early Late Paleocene. Whether they are descendents of a vicariant population, surviving periods of high sea levels in high land refugia, or the product of more recent dispersal events is speculative. As New Caledonia was submerged ~55 Ma (Aitchison *et al.* 1995), the origin of its current *Libocedrus* is uncertain. *Libocedrus chevalieri* (NC) and *L. bidwillii* (NZ) have similar foliage, but dissimilar ovulate cones. It seems most likely that *L. chevalieri* is descended from a *L. bidwillii*-like New Zealand ancestor via dispersal. Cook and Crisp (2005) and Heads (2006) suggest that New Caledonian *Nothofagus* originated in New Guinea and diversified elsewhere before migrating to New Caledonia. There is currently no evidence to support a New Guinea origin for New Caledonian *Libocedrus*. As is the case for *Nothofagus* (see Heads 2006), evolutionary rates for *Libocedrus* (foliage rather than reproductive structures) seem to have been

slow. At present, the macrofossil record for *Papuacedrus* is poor, and its presence outside Australia remains undocumented. Whether its current distribution is related to continental uplift ~35 Ma is uncertain, but most likely.

Calcium oxalate crystals

Calcium oxalate crystals are present in the external cell walls of the foliage of all *Libocedrus*-related genera (including the cones of some species), and also in fossil species. The size, frequency and position of these crystals is quite variable, and appears to be related to the environmental conditions in which they grow. The New Caledonian *Libocedrus* species e.g. tend to have large, frequent crystals, particularly on exposed surfaces, and the parts of leaves that are most likely to be damaged (i.e leaf apices). These species grow mostly on ultramafic derived soils, often in exposed conditions. The compartmentalization of toxic compounds has a twofold effect, that of reducing the effect of toxins, and protection from mechanical damage.

Part V C: Conclusions

Unlike many studies that briefly describe and attribute many fossil plants at a site to various unrelated genera and species, the aim of this study was to identify some southeastern Australian fossil Cupressaceae, and to look at their morphological evolution over time by comparison with extant Cupressaceae. Studies such as this are important for phylogenetic reconstructions (Crane *et al.* 2004) but are rarely done. This study was only possible because the extant genera believed to be fossils' nearest relatives are small in number, and are either monospecific, or contain few species. Three evolutionary trends are noted :-

- for at least the last 30 million years the only significant morphological change in *Libocedrus, Austrocedrus, Fitzroya,* and possibly *Diselma,* has been leaf size. This is possibly related to atmospheric CO_2 levels.
- Ovulate cone morphology (for some genera at least) has been less conservative.
- Not all fossil Cupressaceae have living relatives.

If small isolated (refugial) populations become genetically similar, rapid adverse climatic change can lead to their extinction. Were it not for human activities the range of many temperate species adapted to cool wet conditions would be much larger. The current distribution of *Libocedrus*-related genera is probably attributable to vicariance and dispersal events. How long *Libocedrus*-related genera remained in Australia is unknown. The current distribution of some cupressaceous genera is attributed to large or small scale disturbance. During the past, there appears to have been times when disturbance may have been less important.

The problem with the plant macrofossil record is that most fossil sites are happenchance, unearthed by mining, road-building activities etc. As time and labour constraints encourage macrofossil researchers to look only at the 'best' of the fossil rich horizons exposed, rather than all sedimentary sequences, their account, no matter how good, is biased towards recording those times in earth's history when climates were wet (and mostly warm). If data gathering at these sites were to include a detailed description of the sedimentary sequence, and intensive (macro- *and* microfossil) sampling down *and* across sequences it would provide a synchronous continuum that might provide evidence of significant (and more subtle) climate change. It might also indicate when taxa made their first/last appearance at the site and divulge how (and if) they adapted their morphology in order to survive. Unfortunately the likelihood of this occurring is slim. A combination of pollen and cuticle data would provide a cheaper quicker alternative for sedimentary section sampling.

If a single fossiliferous lens is found within otherwise nondescript, often sandy, sediments or coal seams it presents a dilemma. Although it may contain a wealth of macrofossils that can be given an approximate (palynological) date, it offers no evidence for how long, or how close the flora existed at (or near) the site. Similarly, allochthonous sediments (e.g. boulders; and also museum specimens etc) may contain many interesting fossils that (through their complexity, size and shape) are indicative of

growth in particular climatic conditions. However, as they cannot be correctly located in time and place, their value is diminished.

With increasing land clearance, herbarium specimens will become a valuable resource for future scientists, recording plants from areas now depauperate or denuded of natural vegetation. Plant collecting in the United States is declining (Prather *et al.* 2004a: 2004b), and probably elsewhere too. Collections from cultivated and roadside trees were invaluable for this study.

Comment

In relatively recent years, climate change has been the focus of much attention. It is generally believed, thanks largely to propagation by the popular media, that rising atmospheric CO_2 levels and 'freak' weather patterns (including temperature rise) across the globe are due to the impact of human activity since the onset of the industrial age, in particular the release of greenhouse gasses due to fossil fuel burning, and the denudation of rainforests. Over the last century there has been an enormous growth in the world's human population. Highly populous developing countries such as China and India (both with huge brown coal reserves) are rapidly joining the developed (less populous) world in search of better, technologically based lifestyles. Fossil fuel burning has, and will, increase until extraction methods and supply of this finite resource are exhausted and other non-CO_2 producing energy sources are developed. However, rising temperatures cannot be attributed to fossil fuel burning alone. As observing humans in a technological society, our tendency is to see the changes in the climate we are experiencing as 'abnormal' and only something that is happening to us in the here and now, despite scientific, historical and anecdotal evidence to the contrary.

Fossils (plant and animal) provide us with time slices of earth's evolution that tell us that its climate is dynamic, ever changing. *Homo sapiens* is perhaps the biggest of the catastrophes to befall the earth. The unchecked increase in the human population and their quest for better lifestyles (whatever the socio-economic status) is the primary issue that governments should be addressing. Rampant, unchecked clearing of native vegetation, changes and unreasonable demands on natural watercourses, in the interest of 'progress' can only lead to wholesale extinction of plants and animals, and eventually the human race. 'Highly desirable' low-lying coastal areas are transitory features best left uninhabited. 'Taming' the environment to suit human desires may work well for a time but we cannot hope to control the multitude of 'naturally occurring' factors that interact to shape the earth's landscape and climate. Temperatures are predicted to rise by 2° C or more in the next few decades. Should this occur, mountain adapted floras that have survived a multitude of different climatic regimes for more than 40 Ma, but have been reduced to small disjunct populations by human demand, will most likely become extinct.

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