Cheirolepidiacean foliage and pollen from Cretaceous high-latitudes of southeastern Australia[☆]

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ABSTRACT

Cheirolepidiaceae leaves and pollen are recorded from Valanginian–Albian strata of southeastern Australia that were deposited at high-latitudes under cool, moist climates in contrast to the semi-arid or coastal habitats preferred by many northern Gondwanan and Laurasian representatives of this group. Leaves of this family are characterized by thick cuticles and cyclocytic stomata with randomly oriented apertures, arranged in scattered or longitudinal rows or bands. Stomata are deeply sunken and surrounded by four to six subsidiary cells that bear one or two ranks of prominent overarching papillae, which may constrict the mouth of the pit. Three new taxa (*Otwayia denticulata* Tosolini, Cheirolepidiaceae cuticle sp. A and sp. B) are distinguished based on cuticular features, adding to several previously documented cheirolepid conifers in the Early Cretaceous of eastern Australia. Cheirolepidiaceae foliage is preserved predominantly in fluvial floodbasin settings and is interpreted to be derived from small trees occupying disturbed or low-nutrient sites. The foliage is associated with *Classopollis/Corollina* pollen and roots characterized by prominent mycorrhizal nodules. A Cenomanian *Classopollis* type recognised from Bathurst Island, Northern Australia, is recorded for the first time from the Early Cretaceous Eumeralla Formation, Otway Basin. *Classopollis* locally is rare in Valanginian–Barremian strata of Boola Boola, Gippsland, but constitutes up to 14% of the palynomorph assemblage in Albian strata. This indicates that the family was locally abundant in cool southern high-latitude climates of the Mesozoic, contrary to previous reports of its rarity in this region.

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1. Introduction

The extinct conifer family Cheirolepidiaceae has not previously been considered a major constituent of Early Cretaceous floras of southeastern Australia (Fig. 1), or other parts of Gondwana (Dettmann, 1994; Cantrill and Poole, 2005; Quattrocchio et al., 2011). However, in lower palaeolatitudes of the mid-Mesozoic, the family was represented by a diversity unparalleled in any other conifer family (Alvin, 1982; Watson, 1988). Fossil remains of this family first appear in the Late Triassic of western North America (Ash, 1973; Watson, 1988; Axsmith et al., 2004a). In Gondwana, the distinctive pollen of this family (attributed to *Classopollis* or *Corollina*) has been recorded from the Mesozoic of Antarctica (Late Cretaceous, Askin, 1992), South America (Jurassic,

Volkheimer et al., 2008; Cretaceous e.g. Perez Loinaze et al., 2012), Africa (Jurassic–Cretaceous, Msaky, 2011; Cretaceous, Gomez et al., 2002a; Bamford, 2004) and Australia (Late Triassic to Cretaceous, Helby et al., 1987). However, in contrast to this widespread distribution of pollen, macrofossils attributed to this family from southern high-latitudes are equivocal and sparse (Villar de Seoane, 1998) or not preserved in some major floras (Cantrill and Falcon Lang, 2001; Cantrill and Poole, 2002, 2005). In most areas, the family disappeared at the Cretaceous–Paleogene (K–Pg) boundary (van der Ham et al., 2003) but recent studies suggest that some representatives survived locally and briefly flourished at high palaeolatitudes (Argentina) in the aftermath of the end-Cretaceous biotic crisis (Barreda et al., 2012). This persistence of typical Mesozoic conifers into the Paleogene is consistent with the survival of relictual populations of other gymnosperms beyond the K–Pg transition at various high-latitude sites (Carpenter and Hill, 1999; McLoughlin et al., 2008; Cúneo et al., 2010; McLoughlin et al., 2011).

Cheirolepidiaceae has a complex nomenclatural history (Watson, 1988) and has alternatively been named Cheirolepidaceae (Takhtajan, 1963; Paclt, 2011) and Hirmeriaceae (Maheshwari, 2005). Two

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Fig. 1. Map of the Gippsland and Otway basins, southeastern Australia, showing the study sites, with simplified stratigraphic sections indicating sampling levels. Symbols indicate sites where Cheirolepidiacean pollen and plant foliage and/or cuticle was found.

main groups of Cheirolepidiaceae are generally recognized based on differences in their shoot morphology: the so-called frenelopsids and non-frenelopsids. Frenelopsids have predominantly a whorled phyllotaxis and the representative genera (e.g., *Frenelopsis* and *Pseudofrenelopsis*) are found mainly in Laurasia (Alvin et al., 1981; Alvin, 1982; Francis, 1983; Watson, 1988; Clement-Westerhof and van Konijnenburg-van Cittert, 1991; Zhou, 1995; Guignard et al., 1998; Watson and Alvin, 1999; Daviero et al., 2001; Gomez et al., 2002b; Axsmith, 2006; Yang et al., 2006; Mendes et al., 2010; Bartiromo et al., 2012), but a few are also known from Gondwana (Watson, 1983; Kunzmann et al., 2006; Sucerquia et al., 2008). The non-frenelopsids have leaves borne in a spiral arrangement and include representatives of genera such as *Brachyphyllum* (Watson, 1988; Du et al., 2013) and *Watsoniocladius* (Srinivasan, 1995) from Laurasia, and *Tomaxellia* and *Tarphyderma* (Archangelsky, 1963, 1966, 1968; Archangelsky and Taylor, 1986, 1991; Villar de Seoane, 1998; Kunzmann et al., 2006) from Gondwana. Microsporangiate and ovuliferous cones attached to shoots or associated with leaves of both groups (Alvin et al., 1978, 1994; Kvaček, 2000; Axsmith et al., 2004b; Rothwell et al., 2007; del Fuego et al., 2008; Escapa et al., 2012, 2013), contain *Classopollis* pollen (synonyms: *Corollina*, *Circulina*, *Gliscopollis*; Traverse, 2004). The distinctive spherical pollen with a ring-like germinal groove is the most diagnostic character of the family (Taylor and Alvin, 1984; Watson, 1988).

Pole (2000) first recognized cheirolepidiacean foliage and leafy shoots in Australia based on awl-shaped leaves bearing cuticles with diagnostic strongly sunken stomata and prominently papillate subsidiary cells from the Eromanga Basin, northeastern Australia. Pole (2000) assigned this material to *Otwayia*, a non-frenelopsid cheirolepid. The southeastern Australian Otway and Gippsland basins host the richest Cretaceous floras in Australia and have been well documented for over a century (e.g. Seward, 1904; Medwell, 1954a,b; Douglas, 1969, 1973; Drinnan and Chambers, 1986; Cantrill, 1991, 1992; McLoughlin et al., 2002). These floras of Valanginian–Albian age incorporate a broad array of equisetaleans, lycophytes, ferns, bennettitaleans, conifers, ginkgoaleans, early angiosperms and other seed plants. Awl-leaved conifers have been reported from several assemblages in these basins but the affinities of such fossils have remained equivocal. Awl-leaved conifer foliage is particularly abundant in Albian strata at two Otway Basin localities known as Racecourse Steps and Devils Kitchen (see Douglas, 1969 for locality details). The dominant small conifer leaves at these sites were originally assigned to the morphotaxon *Geinitzia tetragona* Cantrill and Douglas, 1988 but were transferred to *Otwayia* by Pole (2000), who inferred their cheirolepidiacean affinities.

Classopollis pollen is abundant in Lower Cretaceous strata of the Eromanga Basin (Burger, 1993) and is present, though generally considered to be less common, in southeastern Australian basins (Dettmann,

1992). In the Australian succession, *Classopollis* reaches greatest abundance in the Early Jurassic (Helby et al., 1987), becoming rare later in that period but increasing again in the mid-Cretaceous (Douglas, 1985).

Cheirolepidiacean ecology can only be inferred from fossil remains. The family probably included plants with a range of habits (small shrubs to trees; Watson, 1988; Axsmith, 2006). Early studies from Laurasia highlighted their diminutive leaves, strong stomatal protection and common association with sediments of semi-arid or coastal environments, or to areas subject to repeated volcanic ash fall, in inferring that these xeromorphic plants were adapted to dry, saline or disturbed habitats (Vakhrameev, 1970; Watson, 1977; Upchurch and Doyle, 1981; Alvin, 1982; Francis, 1983, 1984; Archangelsky and Taylor, 1986; Watson, 1988). More recent studies indicate that the plants occupied a wider variety of environments (Gomez et al., 2002b; Mendes et al., 2010) but their full environmental tolerances remain poorly constrained. The distinctive pollen assigned to *Classopollis* is more characteristic of low-latitude megathermal–mesothermal palynoprovinces than higher latitude (temperate) settings during the Cretaceous (Alvin, 1982; Dettmann, 1992).

2. Geological setting

Palaeomagnetic data indicate that southeastern Australia was situated at high latitudes (c. 70–85°S) during the Early Cretaceous (Fig. 1). Sedimentary successions of this age in the Gippsland, Bass and Otway basins, Victoria, incorporate important reference sections for several of the Australian Cretaceous palynostratigraphic (Helby et al., 1987; Morgan et al., 1995; Wagstaff et al., 2012) and phytostatigraphic zones (Douglas, 1969; Cantrill and Webb, 1987; Tosolini et al., 2002; Fig. 2). Sedimentation began contemporaneously in these basins during the latest Jurassic to Hauterivian in association with initial rifting between Australia and Antarctica (Lowry, 1988; Featherstone et al., 1991). Deposition of the Tyers Conglomerate (Gippsland Basin; Tosolini et al., 1999), and Casterton Formation and Crayfish Subgroup (Otway Basin; Duddy, 2003) occurred during this initial phase of extension. Lower Cretaceous strata distributed in outcrop and in the subsurface across the Mornington Peninsula basement ridge demonstrate that sedimentation was

continuous between these basins from an early stage (Edwards and Baker, 1943; Douglas, 1969; Mallett and Holdgate, 1985), and the nature of the stratigraphic successions and distribution of unconformities indicate that these basins share very similar Cretaceous–Cenozoic tectonic and depositional histories (Lowry and Longley, 1991; K.A. Hill et al., 1995; Duddy, 2003; Fig. 2). During the ?Barremian–Albian, continued extension and a major influx of volcanogenic sediments from the east caused crustal loading and subsidence accommodating deposition of the plant-fossil-rich Eumeralla Formation in the Otway Basin and upper Strzelecki Group (the informal ‘Wonthaggi formation’) in the Gippsland Basin (K.A. Hill et al., 1995; Bryan et al., 1997). Younger Cretaceous and Cenozoic, predominantly marine deposits, blanket these plant-rich strata throughout most of the Otway and Gippsland basins such that Early Cretaceous strata are exposed in only a few areas (Fig. 1).

The pre-Barremian units are represented by diverse facies associations characteristic of alluvial fan to braided fluvial (alluvial valley) deposits (Tosolini et al., 1999). The post-Barremian deposits are dominated by thick volcanoclastic sandstone sheets with westerly palaeocurrent indices deposited in braided fluvial channels. Unconformities at the top of both the Otway and Strzelecki groups correspond to a Cenomanian depositional hiatus (Norvick et al., 2001) linked to the opening of the Southern Ocean (Gleadow and Duddy, 1981; K.A. Hill et al., 1995; Duddy, 2003; Green et al., 2004). A second phase of rapid subsidence during the Turonian to early Campanian has been attributed to rifting (northeast–southwest extension) between Australia and the Zealandia block (Veevers et al., 1991; K.C. Hill et al., 1995; Norvick et al., 2001) and accommodated deposition of the overlying Upper Cretaceous Golden Beach Group (Gippsland Basin) and Sherbrook Group (Otway Basin). These Upper Cretaceous strata are in turn mostly covered by a thick veneer of younger (Cenozoic) deposits.

3. Materials and methods

Macrofossils were systematically collected from key coastal cliff, stream and road cutting exposures of Lower Cretaceous strata in both the Gippsland and Otway basins (Tosolini, 2001). Sections were selected where previous palynological studies had provided some biostratigraphic

Fig. 2. Stratigraphy of the Otway–Gippsland Basin. (Stages and geochronology after Gradstein et al., 2012; megafloral zones after Douglas, 1969; Cantrill and Webb, 1987; spore/pollen zones after Partridge, 2006; megaspore zones after Tosolini et al., 2002; Otway and Gippsland basin stratigraphy after Smith, 1988; Perincek and Cockshell, 1995; Tosolini et al., 1999).

controls on the deposits (see Dettmann, 1963, 1986; Wagstaff and McEwen Mason, 1989; Wagstaff et al., 1997; Ferguson et al., 1999), and where past studies had indicated palaeontologically productive successions (Douglas, 1969, 1973). The authors collected most specimens but additional material held by Museum Victoria and the Geological Survey of Victoria (mostly collected in the 1960s by Dr J. Douglas) was also examined. All specimens illustrated in this study are now housed in the palaeobotanical collections of Museum Victoria and their registration numbers are prefixed 'MVP'.

Macrofossils were prepared using the standard *dégagement* technique of Faison-Demaret et al. (1999). Cuticle was obtained from macrofossils by degausing a portion of a leaf with a scalpel and removing adhering sediment by immersion of the fragment in 48% hydrofluoric acid for 24 h at room-temperature. Leaf fragments were then immersed in 60% HNO₃ or 10–30% CrO₃ for periods of 10 min to 4 h to dissolve the coalified mesophyll tissues. In some cases, the leaf fragments were soaked in a catalyst (NaOH) for a few minutes to a few hours before treatment with acid to assist removal of coally residues. The remaining cuticle was then rinsed in distilled water and mounted under a coverslip on a microscope slide for transmitted light microscopy or placed on an aluminium stub and coated in gold for scanning electron microscopy (Philips field emission gun SEM). Additional leaf cuticles were obtained by bulk maceration of 100–200 g sediment samples following the method of Wellman and Axe (1999). Measurements of mesofossils were obtained from SEM images rather than from specimens mounted in glycerine jelly.

Palynological samples from Eagles Nest (Gippsland coast) and Paradise Creek were collected in 1991 and processed by Laola Pty Ltd. (no longer operational) in Western Australia using standard processing techniques involving acid digestion (HCl, HF), heavy liquid separation, oxidation and sieving at 10 µm. The samples from Devils Kitchen, Racecourse Steps and Moonlight Head were collected in 2011 and processed by Global Geolab in Canada using acid digestion (HCl, HF), heavy liquid separation and oxidation using Schulze solution. No sieving step was undertaken in the latter samples because it was felt that this processing step might have contributed to the lack of widely recorded angiosperms (which have small pollen) in Lower Cretaceous strata in Victoria (Wagstaff et al., 2012). *Classopollis* specimens were recorded by scanning two entire slides for each sample at ×200 magnification; each *Classopollis* grain encountered was then examined at high power ×1000.

4. Systematic palaeobotany

4.1. Macrofossils and dispersed cuticle

Family Cheirolepidiaceae Takhtajan, 1963

Genus *Otwayia* Pole, 2000

Type species: *Otwayia tetragona* (Cantrill and Douglas) Pole, 2000; Eumeralla Formation; Albian; Otway Basin, Victoria, Australia.

Otwayia tetragona (Cantrill and Douglas) Pole, 2000 (Figs. 3A, C; 4A–M)

1988 *Geinitzia tetragona* Cantrill and Douglas, p. 263, Figs. 12, 13.

2000 *Otwayia tetragona* Pole, p. 177, Fig. 18.

Material examined: Twenty specimens examined (see Tosolini, 2001). Museum Victoria specimen numbers: macrofossils MVP210476 and MVP210478; mesofossils on SEM stubs MVP210411, MVP210419–MVP210430, MVP210434–MVP210436 inclusive.

Description: Leafy twigs, isolated leaves and cuticle fragments. Leaves are awl-shaped, keeled, entire-margined, up to 1.5 mm long with a maximum width of 1 mm (Fig. 3A, C). Leaves are unequally amphistomatic. Stomatal complexes are cyclocytic, with 4–6 subsidiary cells. Stomatal apertures are randomly oriented with respect to the leaf axis, and are strongly protected by papillae (Fig. 4A, B, D, H, J–M). Rectangular epidermal cells are oriented longitudinally and average 58 µm long by 20 µm wide (Fig. 4B, C, E, G). Epidermal cells are non-papillate or slightly inflated (Fig. 4I), as opposed to slightly papillate as described by Cantrill and Douglas (1988).

Comments: Leaves recovered in this study are smaller than those recorded from the Otway Basin by Cantrill and Douglas (1988) or the Eromanga Basin by Pole (2000). Material originally assigned to this species by Cantrill and Douglas (1988) was derived from the Racecourse Steps and Devils Kitchen localities (Otway Basin), but identical leaves and cuticle fragments were recorded from several additional Albian localities in this study. Cantrill and Douglas (1988) originally suggested a taxodiaceous (= cupressaceous) affinity for these remains, based on comparison of dimorphic foliage, leaf shape and stomatal features with extant taxa. Stomatal bands with papillate epidermal cells occur in some other conifer families (e.g., Cupressaceae (Taxodiaceae)—*Elatides* (Harris, 1979); Podocarpaceae/Cupressaceae—*Bellarinea richardsii*; Nagalingum et al., 2005), leading Cantrill and Douglas (1988) to place these leaves in *Geinitzia* (a genus recently reassigned

Fig. 3. Middle to upper Albian Cheirolepidiaceae. A: *Otwayia tetragona* (Cantrill and Douglas) Pole, 2000, MVP210476, Loc. Devils Kitchen (DK), Otway Coast. B: *Otwayia hermata* Tosolini and McLoughlin (McLoughlin et al., 2002), MVP210297, Loc. Rintouls Creek (RC) 17D, Gippsland; C: Leafy twigs of *Otwayia tetragona* (Cantrill and Douglas) Pole, 2000, MVP210478, Loc. Racecourse Steps (RS) Otway Coast. D: *Otwayia denticulata*, twig with appressed awl-shaped leaves, MVP210453, Loc. Smythes Creek (SC3), Otway Coast. Scale bar = 10 mm for all specimens.

Fig. 4. A–M: *Otwayia tetragona* (Cantrill and Douglas) Pole, 2000. N: *Otwayia hermata* Tosolini and McLoughlin (after McLoughlin et al., 2002). A: Laterally compressed leaf showing non-stomatiferous abaxial surface (left) and prominent band of stomata on adaxial surface (right), MVP210433p, Loc. RS4a. B: Enlargement of external leaf surface (from Fig. 4A). C: Enlargement of elongate abaxial epidermal cells (from Fig. 4A). D: Enlargement of stomatiferous band (from Fig. 4A). E: Interior of cuticle showing rectangular epidermal cells, MVP210433o, Loc. RS4a. F: Leaf fragment torn open to show interior surface of cuticle, MVP210433q, Loc. RS4a. G: Enlargement of stomatiferous band (from Fig. 4F). H: Enlargement of stomatiferous band showing irregularly oriented stomatal apertures, MVP210433o, Loc. RS4a. I: External surface of cuticle showing slightly inflated epidermal cells, MVP210432z, Loc. RS4a. J: Interior of stoma with guard cell platforms removed showing four subsidiary cells and over-arching papillae, MVP210433o, Loc. RS4a. K: Exterior of stoma showing strongly over-arching papillae, MVP210434r, Loc. DK4. L: Charcoalified awl-shaped leaf, MVP210441e, Loc. DK17. M: Enlargement of papillate stomata scattered near base of leaf (from Fig. 4L). N: Stomate of *Otwayia hermata* for comparison. Exterior of adaxial surface showing stomatal pit occluded by papillae from subsidiary cells raised to form a Florin ring, MVP210321b, Loc. RC17C. Scale bar = 500 μ m for A, B, F, L; 200 μ m for G; 100 μ m for C–E, H, M; 20 μ m for I, J; 10 μ m for K, N.

to an extinct conifer family Geinitziaceae; Kunzmann, 2010). The species was reassigned to *Otwayia* by Pole (2000), who described additional material from mid-Cretaceous strata of the Eromanga Basin, northeastern Australia. He considered the genus to have cheirolepidiacean affinities based on his “Cheirolepidiaceae placement rule 1” whereby “if subsidiary cells or encircling cells are papillate and subsidiary or encircling cell papillae project laterally across stomatal pore, then family is Cheirolepidiaceae” (Pole, 2000, p. 197). Further, leaf dimorphism occurs in the Cheirolepidiaceae (e.g. *Tomaxellia biforme*) of South America (Archangelsky, 1968). The unique combination of small and commonly appressed awl-shaped leaves, cyclocytic

stomatal complexes borne mostly on the adaxial surface in bands, strongly sunken stomata with overarching papillae, and association with *Classopollis* in the sediments, reinforces the assignment to Cheirolepidiaceae.

Distribution: *O. tetragona* occurs in Aptian to Albian strata of the Eumeralla Formation in the Otway Basin. It is a common to abundant component of mesofossil assemblages from: Castle Cove sites CC1h, CC2a, CC2d, CC30, CC32, CC33, and CC35; Moonlight Head site MHR; Racecourse Steps sites ?RS2p, RS2y, and RS2ci; and Devils Kitchen sites DK2, DK4, DK7b and DK7c (Fig. 1). The only other records of this species are from the Albian–Cenomanian Mackunda and Winton

formations of the Eromanga Basin in northeastern Australia, although those specimens differ slightly in having less regularly oriented stomata that are not in clear rows on the adaxial surface (Pole, 2000).

Otwayia hermata Tosolini and McLoughlin (in McLoughlin et al., 2002) (Fig. 4N)

Material examined: Fifteen specimens examined (see McLoughlin et al., 2002). Museum Victoria specimen numbers: macrofossils MVP210295–MVP210298; mesofossils on SEM stubs MVP210292, MVP210318–MVP210322, MVP210371–MVP210372, inclusive.

Diagnosis and type details: Provided by McLoughlin et al. (2002); the main characters are summarized here in Table 1 for comparative purposes.

Comments: McLoughlin et al. (2002) described the details of this Hauterivian–Barremian species from the Tyers Subgroup, Gippsland Basin. No additional samples have been found from younger sediments of the Gippsland or Otway basins. The cuticular features, such as strongly elongate apical cells of leaves, robust papillation of regular epidermal cells, randomly oriented stomatal apertures, a Florin ring incorporating 4–6 strongly papillate subsidiary cells overarched the sunken stomata in a cyclocytic arrangement (Fig. 4N), suggest that this species is a member of the Cheirolepidiaceae (Watson, 1988; Pole, 2000). Spirally arranged, small, awl-shaped leaves with thick cuticle and stomata arranged in bands are typical of the non-frenelopsid cheirolepids (Watson, 1988; del Fuego et al., 2008). No fertile material is associated with these leaves. *Classopollis* pollen is co-preserved in the sediments (Dettmann, 1963; this study), evidence that the representatives of Cheirolepidiaceae are present in the riparian vegetation. No other leaf fossils from these strata have features characteristic of this family

Otwayia hermata differs from *Otwayia tetragona* (Cantrill and Douglas) Pole, 2000 by its shorter and broader papillae on subsidiary cells. It is also somewhat similar in features, such as leaf shape, stomatal orientation, strongly sunken stomata and heavily papillated subsidiary cells raised to form a Florin ring, to *Pagiophyllum currii* Harris (1979) from the Yorkshire Jurassic and *Pseudofrenelopsis parceramosa* (Fontaine) Watson, 1974 (see Table 1) from the English Wealden (Watson, 1977; Alvin, 1982). However, more prominent papillae on the abaxial surface and the fringe of elongate apical cells, distinguish the Victorian species. The foliar variation from basally appressed and imbricate on a branch to apically spreading, has similarities to, but is less pronounced than in *Tomaxellia Archangelsky*, 1963, which has distinct heterophylly, a character not recognized in other South American Early Cretaceous conifers (Kunzmann et al., 2006).

Distribution: Recorded from numerous Valanginian–Hauterivian assemblages in the Boola Boola Forest area (see Appendix I, p. 40 and Fig. 5 in McLoughlin et al., 2002); Tyers River Subgroup; Gippsland Basin.

Otwayia denticulata Tosolini sp. nov. (Figs. 3D, 5A–M)

Holotype: MVP210406c (Museum Victoria).

Material examined: Nine specimens examined (all apart from the holotype are paratypes: see Tosolini, 2001). Museum Victoria specimen numbers: macrofossil MVP210453; mesofossils on SEM stubs MVP210390–MVP210397, inclusive.

Type locality, formation and age: Moonlight Head (1j), Eumeralla Formation, Otway Group; Albian.

Etymology: Named after the denticulate margin and fringe on the acuminate apex that distinguishes this species from other entire-margined *Otwayia* species.

Diagnosis: Leaves triangular or ovate (awl-like or claw-like); prominently keeled on the abaxial surface. Leaf margin denticulate or entire with a denticulate fringe on the acuminate apex. Leaves epistomatic. Epidermal cells inflated but lacking distinct papillae. Stomata arranged in two bands in an inverted V-shaped array. Stomata strongly sunken and protected by up to seven overarched papillae.

Description: Only a single macrofossil and rare dispersed leaves are available; the shoot phyllotaxy is spiral. The awl-like or claw-like leaves reach 3 mm long and 1.2 mm wide at the base (Fig. 5A, C–E, G, I). They

have an acuminate tip and typically a denticulate margin formed by extended epidermal cells (Fig. 5E, G, H). The basal attachment is broad (i.e., the leaf base is typically expanded with a broad scar) and slightly decurrent. Epidermal cells are inflated but lack distinct papillae. They are rectangular on the abaxial side but square on the adaxial side, particularly near the apex. Venation is unclear but the presence of a prominent abaxial keel suggests a single midvein and this is supported by the presence of a single stomata-free band along the centre of the leaf. Leaves are epistomatic, hence stomata were further protected by foliar imbrication. We refer readers to the figure of the macrofossil, which shows this imbrication (Fig. 3D). Stomata are arranged in two bands approximately 100 µm from the margins and extending from the base almost to the apex of the leaf in an inverted V-shaped array. One to two stomata form rows within the bands. Stomatal orientation appears random and pore shape is slit-like as it is obscured by overarched papillae. Strongly sunken stomata are protected by up to seven over-arching, robust, short, broad, blunt, and rounded papillae on 4 to 7 subsidiary cells (Fig. 5B, F, J, K).

Comments: *Otwayia denticulata* is very similar to *O. tetragona* (Table 1) but the former has leaves with distinct marginal denticles, expanded bases, cuticle that is epistomatic, less stomata per stomatal zone (1–2 rather than 2–5), lack of a Florin ring, shorter and broader, blunt papillae on the subsidiary cells and have more inflated, rectangular epidermal cells. The close similarity to *O. tetragona*, and especially its diminutive, awl-shaped, acuminate leaves, with heavily papillate protection of sunken stomata, suggests that *O. denticulata* is also a cheirolepidiacean conifer (Watson, 1988; Pole, 2000).

Similarities also exist between *O. denticulata* and *O. hermata*, from the Valanginian–Barremian of the Gippsland Basin, southeastern Australia (Table 1). Characters that differ include a triangular or ovate leaf shape, a denticulate margin and apex, an acuminate tip, random stomatal distribution that is epistomatic, lack of a Florin ring and lack of papillae on epidermal cells. *Otwayia denticulata* can be distinguished from *Otwayia cudgeloides* described from the Cenomanian of the Eromanga Basin, northern Australia, by its awl-like leaves with a prominent keel, denticulate margin, varied number of subsidiary cells (4–7) with short, broad, rounded papillae, and inflated, rectangular to square epidermal cells, compared to the long papillae on subsidiary cells and sharp conate papillae on epidermal cells in *O. cudgeloides* (Pole, 2000).

Distribution: This species is restricted to Aptian and Albian strata of the Otway Basin, with a distribution similar to that of *O. tetragona*, although markedly less abundant. *O. denticulata* was recorded from the following sites: Smythes Creek, SC3; Castle Cove, CC2l; Moonlight Head, MHj, MHk; Racecourse Steps, RS4a; and Devils Kitchen, DK2 (Fig. 1).

Cheirolepidiaceae cuticle sp. A (Fig. 6A–G)

Material examined: Two specimens examined (see Tosolini, 2001). Museum Victoria specimen number: mesofossils on SEM stub MVP210435, letters n, o.

Description: This form is represented only by cuticle fragments up to 500 µm long and 300 µm wide. The cuticle bears distinct, broad, stomatiferous bands and intervening non-stomatiferous bands (Fig. 6A, E, F). All epidermal cells are strongly inflated and within stomatal bands they are irregularly polygonal with straight or slightly beaded walls (Fig. 6A, C, F). However, within inter-stomatal bands the epidermal cells are elongate-rectangular, with thick, strongly buttressed walls, giving a highly sinuous appearance (Fig. 6D). Stomatal complexes are cyclocytic, measuring 50 µm in diameter; they occur scattered within the stomatiferous bands, are sunken, and their apertures are irregularly oriented (the majority appear oblique or perpendicular to the leaf axis). The stomatal pits are heavily protected and obscured by four or five (rarely six) over-arching, blunt, papillae (Fig. 6B, G). A Florin ring is not developed.

Comments: The papillate protection of the stomata and strongly inflated epidermal cells suggest cheirolepidiacean affinities but further details are lacking to provide confident generic assignment. Although

Table 1Comparison between Australasian species of Cheirolepidiaceae based on cuticular morphology; all are of Cretaceous age (after [Cantrill and Douglas, 1988](#); [Pole, 2000](#); [McLoughlin et al., 2002](#); [Pole and Philippe, 2010](#); this paper.).

Characters	<i>Otwayia tetragona</i>	<i>Otwayia cudgeloides</i>	<i>Otwayia hermata</i>	<i>Otwayia denticulata</i>	<i>Otwayia</i> sp. (NZ)	Cheirolepid. cuticle type A	Cheirolepid. cuticle type B	Eromanga cheirolepid sp. A (Pole, 2000)	Eromanga cheirolepid sp. B (Pole, 2000)
Branching	Spiral	Unknown, probably spiral	Spiral	Spiral	Unknown	Unknown	Unknown	Unknown	Unknown
Leaf shape	Bilaterally flattened, some small leaves tetragonal, or bifacially flattened; lanceolate to awl shaped	Two forms: falcate and bilaterally flattened	Lanceolate or awl-shaped leaves; prominent abaxial keel	Triangular or ovate (awl-like or flattened claw-like) leaves, prominent keel	Bilaterally flattened	Unknown	Unknown	Unknown, probably linear-falcate; bifacially flattened	Flattened, probably linear
Leaf maximum length	near apex 7 mm	3.5 mm	6 mm	3 mm	Broken, >6 mm	Fragments up to 500 µm	<4 mm	Unknown	Unknown
Leaf maximum width	3 mm	1 mm	1 mm	1.2 mm	2.3 mm	Fragments up to 300 µm	<4 mm	3 mm	3 mm
Leaf apex	Acuminate to acute; pungent or mucronate	Acuminate	Rounded or hooked, acute	Denticulate fringe on acuminate tip	Awl-like	Unknown	Unknown	Unknown	Unknown
Leaf base	Decurrent lacking constriction	Unknown	Decurrent and broad	Typically expanded with a broad scar, slightly decurrent	Unknown	Unknown	Unknown	Unknown	Unknown
Stomatal distribution on leaf	Amphistomatic (unequally) abaxial zone restricted to near base	Epistomatic	Amphistomatic (unequally) abaxial surface less well-defined	Epistomatic	Epistomatic	Unknown	Unknown	Amphistomatic	Hypostomatic or epistomatic
Stomatal arrangement	Two bands	Two zones	Discontinuous and irregular rows within two bands	Two zones in inverted V	Scattered, possibly in two zones	Distinct, broad stomatiferous bands, possibly in two zones	Irregular	No zones, discontinuous rows	Single zone
Stomatal rows within bands	2–5 stomatal rows in each band	1–3? (from photo)	1–3 (rarely 4)	1–2	1–3 stomata in each of two zones	Possibly up to 5	Unknown	1	Up to 13
Stomatal Orientation	Random	Random	Transverse or oblique from internal view	Appear random	General longitudinal alignment or oblique	Random	Random	Random	Random
Stomatal pore shape	Elliptical	Obscured by overarching papillae			Subcircular		Subrounded, overarching papillae	Slit like due to overarching papillae	Subcircular

Subsidiary cell number, arrangement	Dicyclic, encycloctytic, 4–6 subsidiary cells	5?	Obscured by overarching papillae Cycloctytic, 4–6 subsidiary cells	Slit-like as obscured by overarching papillae 4–7	4–5? (from photo)	Slit like internally and externally due to overarching papillae 4–5	Encycloctytic; 4–6	Dicyclic, encycloctytic,	Dicyclic, encycloctytic, typically 4–5 subsidiary cells Absent? (from photo)
Florin ring	Present? Cuticle thicker over subsidiary cells than over other cells (Pole, 2000)	Absent or degraded	Present, 5 µm high	Absent?	Massively thickened rims	Absent?	Absent	Absent	
Subsidiary cell papillae	Elongate, narrow and tapered, almost completely covering stomatal pore	Long	Short, broad and blunt, up to 11 µm long cover the stomatal pit.	Short, broad and blunt, circular in section, up to 10 µm long cover the stomatal pit.	Partially fused at base, very short, not extending over stomatal pore	Long, broad and blunt, circular in section, up to 20 µm long	Outer papillae are long, flattened, up to 45 µm long	Massive papillae across pore from encircling cells	Two per subsidiary, circular in section, broad and low, unconnected
Papillae in stomatal crypt	No	No	No	No	No	No	Flattened, reaching 20 µm long in throat of stomatal crypt Strongly sunken	No	No
Guard cells	Sunken with polar extensions; orientated longitudinally or slightly obliquely	Sunken? (from photo)	Sunken within a stomatal pit	Strongly sunken	35–40 µm	Strongly sunken		Sunken? (from photo)	Sunken? (from photo)
Epidermal cell size and shape	Square to rectangular; 15–25 µm wide by 40–90 µm long	Polygonal, more or less isodiametric	Equidimensional, squat-shaped, 35 µm in diameter	Rectangular on abaxial side, square on adaxial side particularly near apex	Elongate, rectangular	Irregularly polygonal within stomatal bands, elongate, rectangular elsewhere	Polygonal but indistinct	Isodiametric, polygonal, L/W <2.0 (maximum 3.4); flanges smooth,	Elongate, rectangular on adaxial surface, abaxial surface more polygonal
Epidermal cell papillae	Non-papillate to slightly papillate	Sharp, conate papillae	Papillate (up to 5 µm high) on adaxial side, less papillate to smooth on abaxial side	Inflated, but no distinct papillae	Nonpapillate	Strongly inflated	Glabrous	Glabrous	Glabrous
Epidermal cell walls	Beaded thickenings, (slightly sinuous), straight, unbuttressed	Straight, unbuttressed	Straight, unbuttressed	Straight, unbuttressed	Straight, blunt endwalls	Straight or slightly beaded in stomatal bands, unbuttressed	Beaded thickenings, (slightly sinuous), unbuttressed	Straight, unbuttressed	Straight, unbuttressed
Associated organs	Slender axes and mycorrhizal roots	None	Slender axes	Slender axes	None	None	None	None	None
Occurrence (formations)	Eumerella Formation, Otway Group; Allaru, Mackunda and Winton formations	Allaru, Mackunda and Winton formations	Rintouls Creek Formation, Tyers River Subgroup, Strzelecki Group	Eumerella Formation, Otway Group	Tupuangi Formation	Eumerella Formation, Otway Group	Eumerella Formation, Otway Group	Allaru, Mackunda and Winton formations	Allaru, Mackunda and Winton formations
Age range	Aptian–Albian	Albian–Cenomanian	Neocomian	Aptian–Albian	Albian–Santonian	Aptian–Albian	Aptian–Albian	Albian–Cenomanian	Albian–Cenomanian

Fig. 5. *Otwayia denticulata*. A: Exterior of adaxial surface showing two bands of stomata, as delineated by white lines, MVP210406c, Loc. MH1j. B: Enlargement of file of papillate stomata (from Fig. 5A). C: Awl-shaped leaf compressed laterally showing a band of stomata on adaxial surface, as delineated by white lines, MVP210406d, Loc. MH1j. D: Adaxial surface of leaf with acuminate apex, MVP210408b, Loc. MH1j. E: Adaxial surface of leaf with denticulate margin, MVP210408e, Loc. MH1j. F: Enlargement of leaf apex showing short spine formed by elongate epidermal cells (from Fig. 5C). G: Enlargement of distal part of leaf showing adaxial stomatal band (from Fig. 5C). H: Enlargement of adaxial stomatal file, stomatal pores are indicated by two arrows on the left, papillae obscure the two pores indicated by arrows on the right (from Fig. 5C). I: Enlargement of denticulate leaf margin (from Fig. 5D). J: Interior of adaxial cuticle showing large stomata with papillate protection, MVP210411aj, Loc. MH1r. K: Enlargement of papillate stoma (from Fig. 5J). L: Lateral view of awl-shaped leaf, MVP210404t, Loc. MH1j. M: Enlargement of leaf apex showing elongate epidermal cells forming a denticulate fringe (from Fig. 5L). Scale bar = 1 mm for C; 500 μ m for A; 200 μ m for D, G, E, L; 100 μ m for B, F, I, J, M; 50 μ m for H; 20 μ m for K.

some other conifer families have weakly developed papillae on subsidiary cells (e.g., some podocarps such as *Smithtonia* and *Willungia* have raised stomatal rims that may be divided into irregular lobes; Hill and Pole, 1992), Cheirolepidiaceae are noted for their strongly overarching papillae that essentially block the stomatal pore (Pole, 2000). Despite lacking complete leaves, the heavily papillate stomatal protection of Cheirolepidiaceae cuticle sp. A is similar to that of *Otwayia* species. *O. hermata* differs by its stomatal subsidiary cells being raised above the epidermal cells to form a Florin ring. *O. tetragona* has shorter papillae over the stomata, so that they do not completely block the pore, and the epidermal cells are not inflated but rather are non-papillate to slightly papillate. *O. cudgeloides* differs by having very long and sharp papillae on epidermal cells. *Eromanga cheirolepid* sp. A and sp. B of Pole (2000) both differ in having non-papillate epidermal cells and stomata in rows rather than bands. Similar to Cheirolepidiaceae cuticle sp. A, inflated epidermal cells known as “cobblestones” characterize

Frenelopsis harrisii Doludenko and Reymanowna, 1978, though two ranks of papillae occur in the stomata of the latter. *Androvettia* (Hueber and Watson, 1988), a probable cheirolepid, has stomata with much larger papillae overarching the pit (Watson, 1988).

Several of the key characters of this taxon occur in other conifer families but the combination of traits is unique. For example, *Bellarinea richardsii*, of probable podocarpacean affinity from the Early Cretaceous of the Gippsland Basin (Nagalingum et al., 2005), has weakly developed papillae surrounding the stomate, but not blocking the opening. Some Cupressaceae species have similar characters: inflated epidermal cells (e.g. *Xanthocyparis vietnamensis*; Xiang and Farjon, 2003), and papillae surrounding, but not overarching the stomatal complex, occur in both fossil and extant *Metasequoia glyptostroboides* (Leng et al., 2001) from China. Fossils *Libocedrus acutifolius* and *Libocedrus obtusifolius* from the late Paleocene of Australia (Whang and Hill, 1999) have a Florin ring that is divided into lobes, but no true papillae overarching the stomatal

Fig. 6. Aptian–Albian conifer cuticles. A–G: Cheirolepidiaceae cuticle sp. A. H, I: Cheirolepidiaceae cuticle sp. B. A: Interior of cuticle showing distinct non-stomatiferous bands of rectangular cells separating stomatiferous bands containing irregularly oriented stomata, MVP210435n, Loc. DK7b. B: Interior of stomate with ill-defined guard cells but prominent overarching papillae (from Fig. 6A). C: Interior of paratracheal stomate with well-defined guard cell ledges (from Fig. 6A). D: Sinuous-walled epidermal cells of non-stomatiferous band (from Fig. 6A). E: Exterior of stomatiferous band showing inflated epidermal cells and irregularly positioned stomata, MVP210435o, Loc. DK7b. F: Enlargement of cells in stomatiferous band (from Fig. 6E). G: Enlargement of stomate with prominent overarching papillae (from Fig. 6E). H, I: Exterior of cuticle showing stomatiferous band and details of stomatal apparatus. Stomata protected by two ranks of papillae, MVP210378e, Loc. ENG7. Scale bar = 200 μ m for A; 100 μ m for E, I; 50 μ m for F, D; 20 μ m for B, C, G, H.

pore. *Pseudotorellia linkii* Watson in Watson and Harrison, (1998), has overarching papillae on subsidiary cells but is distinctly multiveined (Watson and Harrison, 1998).

Distribution: Recorded only from bulk maceration of sediment from the Eumeralla Formation (Albian) at locality DK7b (Fig. 1).

Cheirolepidiaceae cuticle sp. B (Fig. 6H, I)

Material examined: One specimen examined (see Tosolini, 2001). Museum Victoria specimen number: mesofossil on SEM stub MVP210378, letter e.

Description: This form is represented only by cuticle fragments a few millimetres in diameter, <4 mm long and <3 mm wide. Epidermal cells on these cuticle fragments appear to have smooth periclinal walls, although preservation has flattened and damaged the cuticle. Irregularly distributed and oriented stomata occur in deeply sunken pits and are protected by papillae in two ranks (derived from two cycles of subsidiary cells: Fig. 6H, I). Each rank has four to six papillae (4–6 cells per ring). The outer papillae are up to 45 μ m long, whereas inner papillae (present in the throat of the stomatal crypt) reach only 20 μ m long. The whole stomatal complex is 80 μ m in diameter.

Comments: Since shoot phyllotaxy and leaf shape are not known, the affinities of these fragmentary cuticles cannot be definitively ascertained. However, the sunken stomata protected by two ranks of papillae strongly favours cheirolepidiacean affinities (Watson, 1988). Similar deeply sunken stomata protected by a double ring of papillae occur on some Northern Hemisphere Cheirolepidiaceae leaves (Gomez et al., 2002b), such as: *Frenelopsis*, e.g., *Frenelopsis alata* (Feistmantel) Knobloch, 1971 (Alvin, 1977; Kvaček, 2000) from the Cretaceous of Europe and U.S.A.; *Frenelopsis harrisii* Doludenko and Reymanowna, 1978 from the Cretaceous of Tajikistan (Watson, 1988); and *Frenelopsis hoheneggeri* (Ettingshausen) Schenk emend. Reymanowna and Watson,

1976, from the Cretaceous of Poland and the Czech Republic (Gomez et al., 2002b). *Frenelopsis* commonly has non-papillate Florin rings, but inner papillae protrude within the stomatal pit (Gomez et al., 2002b), except for *Frenelopsis ramosissima* (Watson, 1977; Upchurch and Doyle, 1981), which, like *Pseudofrenelopsis*, possesses overarching external papillae projecting from a Florin ring (Srinivasan, 1995) and no inner papillae. The Gippsland specimens are, therefore, more like *Frenelopsis* (Watson, 1988; Gomez et al., 2002b). Gondwanan examples of *Frenelopsis* are known from the Crato Formation of Brazil, South America, but those specimens are too poorly preserved to yield anatomical details within the stomata and the Florin ring is non-papillate (Kunzmann et al., 2006).

Distribution: This cuticle type was recorded only from the Gippsland Basin Eagles Nest locality within Aptian sediments of the 'Wonthaggi formation', Strzelecki Group (sites ENG1 and ENG7; Fig. 1).

4.2. Cheirolepidiacean pollen

The distinctive spherical pollen with a circular germinal furrow attributed to Cheirolepidiaceae has been generally assigned to *Classopollis* or *Corollina* in Australian Mesozoic palynological studies. Relatively few species of this pollen group have been distinguished as separate formal species in these studies. As stated by Reyre (1970), the assignment of a dispersed *Classopollis* grain to a definite species is always difficult and often impossible. Australian Cretaceous palynological studies have generally recognized only four species. Dettmann (1963) referred to pollen from the Early Cretaceous in southeast Australia as *Classopollis* cf. *Classopollis classoides* Pflug, 1953, whereas in northeastern Australia Burger (1980) referred to similar grains as *Classopollis* cf. *Classopollis chateauvovi* Reyre, 1970. In younger sediments from Bathurst Island,

Burger (in Norvick and Burger, 1975) also recorded *Classopollis simplex* (Danzé-Corsin and Laveine, 1963) Reiser and Williams, 1969 and illustrated an undescribed species. Most Australian consultancy reports (e.g. Harms and Bennell, 1999) have regularly recognized the species *Classopollis torosus* (Reissinger, 1950) Couper, 1958 emend. Burger, 1965. In this study, the four species of *Classopollis* recorded, one of which is probably reworked, are outlined below based on transmitted light microscopy. Materials examined are from palynological slides with Museum Victoria registration numbers MVP23599–MVP236059 inclusive.

Genus *Classopollis* (Pflug, 1953) Srivastava, 1976

Type species: *Classopollis classoides* Pflug, 1953 (original designation)

Classopollis chateaunovi Reyre, 1970 (Fig. 7C–E)

Synonymy: For full synonymy see Raine et al. (2011).

Description: Grains anisopolar, amb circular to oval, appearing to be originally spherical or ovoid, but often compressed in a polar direction. Exine 1–1.5 μm , thicker in the equatorial region and thinning towards the poles, with a sculpture of regularly distributed, small (<0.5 μm), isolated, but more often coalesced, verrucae that form an incomplete pseudoreticulum. Sculpture in the equatorial region is aligned in rows to form heavily disrupted pseudostriations. The average overall width of the equatorial band is 8 μm . Rimula is not observed. Proximal pole occasionally has a triangular area (sides of triangle up to 6 μm) in which the exine is absent. Distal pole is characterized by the presence of a circular pore 5–12.5 μm in diameter.

Grain size: Equatorial diameter 30(38)45 μm (20 specimens measured).

Comments: The New Zealand fossil pollen and spore catalogue (Raine et al., 2011) retains the species *Classopollis chateaunovi* and tentatively also includes both *C. classoides* and *C. torosus* in this species. The current study rejects the inclusion of the latter two taxa based on the verrucate sculpture that forms an incomplete pseudoreticulum and the pseudostriations on the equatorial band and retains *C. chateaunovi* as a distinct species. One morphological type of *Classopollis* recorded from Valanginian to Albian strata of the Gippsland and Otway basins in this study is placed in *C. chateaunovi* (Fig. 7C–E). Reyre (1970) distinguished this species as having only vague pseudostriations and a grumous–verrucose sculpture. Specimens in this study that have this coarser type of sculpture and a very disrupted equatorial band created by aligned, commonly coalesced verrucae are placed in *C. chateaunovi* (Fig. 7C–E). The specimens of *C. chateaunovi* in this study are in general larger than those recorded by Reyre (1970).

Distribution: In this study, *C. chateaunovi* is recorded from Paradise Creek and Eagles Nest in the Gippsland Basin (Valanginian–Aptian) and Devils Kitchen, Racecourse Steps and Moonlight Head in the Otway Basin (Albian).

Classopollis simplex (Danzé-Corsin and Laveine, 1963) Reiser and Williams, 1969 (Fig. 7A–B)

Fig. 7. *Classopollis* species recorded in Lower Cretaceous strata of the Gippsland and Otway basins (this study). A–B: *Classopollis simplex*. C–E: *Classopollis chateaunovi*. F, I: *Classopollis classoides*. G–H: *Classopollis* sp. A: Devils Kitchen (Otway Coast) MVP236013, England finder reading U31(3). B: Devils Kitchen (Otway Coast) MVP236009, England finder reading G27(2). C: Eagles Nest (Gippsland coast) MVP236003, England finder reading H42(3). D: Devils Kitchen (Otway Coast) MVP236009, England finder reading Q25(0). E: Devils Kitchen (Otway Coast) MVP236009, England finder reading S31(0). F: Devils Kitchen (Otway Coast) MVP236022, England finder reading L28(4). I: Devils Kitchen (Otway Coast) MVP236006, England finder reading L41(0). G: Devils Kitchen (Otway Coast) MVP236021, England finder reading I29(1). H: Devils Kitchen (Otway Coast) Sample 1, slide 1, England finder reading V39(3). All scale bars = 10 μm .

Synonymy:

For full synonymy see [Raine et al. \(2011\)](#).

non 1975 *Classopollis simplex* (Danze-Corsin and Laveine) Reiser and Williams; Burger in Norvick and Burger, p. 142, pl. 13, Figs. 1, 2; text-Fig. 28.

Description: See [Reiser and Williams \(1969\)](#).

Comments: It is assumed that specimens in this study that conform to *Classopollis simplex* are reworked from older sediments, since this species is typical of Early Jurassic assemblages of northeastern Australia ([de Jersey, 1973](#)), the grains are in poor condition, and reworking of older palynomorphs is common in the samples.

Distribution: *C. simplex* is recorded from Eagles Nest in the Gippsland Basin (Aptian) and from Devils Kitchen, Racecourse Steps and Moonlight Head in the Otway Basin (Albian).

Classopollis classoides [Pflug, 1953](#) emend. [Pocock and Jansonius, 1961](#) (Fig. 7F, I)

Synonymy:

1994 *Classopollis classoides* [Mildenhall, 1994](#), pl. 15, Figs. 13, 14.

For full synonymy and comments regarding synonymy see [Raine et al. \(2011\)](#).

Description: Grains anisopolar, amb circular, compressed in polar direction (spherical?). Exine 1–2 μm thick in the equatorial region and thinning towards the pole, with a sculpture of regularly distributed, isomorphous, granulae. Sculpture in the equatorial region is aligned in continuous rows parallel to the equator to form continuous annular bands of overall width 5 μm . A rimula is always present. Proximal pole usually has a triangular area (sides 5–9 μm) in which the exine is absent. Distal pole is rarely characterized by the presence of a circular pore.

Grain size: Equatorial diameter 32(37.5)45 μm (14 specimens measured).

Comments: [Burger \(1966\)](#) noted the possible synonymy of *Classopollis classoides* and *C. torosus*. However, as discussed by [Peyrot et al. \(2007\)](#), the loss of the type material precludes any comparison. *C. classoides* was described by [Pocock and Jansonius \(1961\)](#) as having a granulate sculpture whereas *C. torosus* was described by [Couper \(1958\)](#) and [Burger \(1965\)](#) as having a scabrate exine, as was *C. sp. cf. C. torosus* ([Balme, 1957](#)). [Pocock and Jansonius \(1961\)](#) described continuous bands of sculpture around the equator of *C. classoides* whilst [Couper \(1958\)](#) and [Burger \(1965\)](#) suggested that *C. torosus* has forms that have continuous endostriae or features that are not continuous but are formed by discrete granules. [Peyrot et al. \(2007\)](#) attempted to distinguish the two species based on SEM, TEM and CSLM and determined that their Type B grains were related to *C. torosus*, based on a thinner scabrate exine than their Type A, which had features that resembled the description of *C. classoides* by [Pocock and Jansonius \(1961\)](#). This is in agreement with the measurements by [Reyre \(1970\)](#) who indicated that *C. classoides* has a thicker exine (1–2 μm) than *C. torosus* (0.75–1.0 μm). As this study is reliant on light microscopy *Classopollis* grains that have a granulate sculpture, continuous equatorial striae made of granulae and a consistently thicker exine (>1 μm) are placed in *C. classoides*. The equatorial diameter of the grains is, however, much larger than described by [Pocock and Jansonius \(1961\)](#).

Distribution: In this study, *C. classoides* is recorded from Moonlight Head and Devils Kitchen, Otway Basin (Albian).

Classopollis sp. (Fig. 7G–H)

Synonymy:

1975 *Classopollis* sp., Burger in Norvick and Burger, pl. 30, Fig. 4.

Description: Grains anisopolar, amb circular or angularly subcircular, exine 1 μm thick. The exine of the distal surface is broadly folded with no discernible consistency to the pattern of the folding direction in relation to the amb. Sculpture is regularly distributed, isomorphous, and consisting of minute granules and rare spines. Sculpture in the equatorial region is aligned more or less distinctly in rows parallel to the equator and closely spaced. Rimula is not observed. Proximal polar area is not differentiated. Distal pole is characterized by the presence of an area of thinned exine (1 specimen) or a poorly defined circular pore 11 μm in diameter (1 specimen).

Grain size: 32–37 μm (2 specimens measured).

Comments: This is a rare form in the assemblage from Albian strata at Devils Kitchen. Burger (in [Norvick and Burger, 1975](#)) described a *Classopollis* species that has a sculpture of minute grana and spines that are arranged in rows in the equatorial region and lacks a rimula. However, the majority of the illustrated specimens are intensely folded at right angles to the equator and it was suspected that it was a recycled element. The two specimens of this type found in this study most closely resemble the specimen shown in plate 30, Fig. 4 of Burger's (in [Norvick and Burger, 1975](#)) study, in which the grain is not so strongly folded.

Distribution: In this study, *Classopollis* sp. is recorded from Devils Kitchen, Otway Basin (Albian).

5. Discussion

5.1. Taxonomic affinities

Given the remarkable range of morphology, habit and habitat represented among the Cheirolepidiaceae ([Watson, 1988](#), p. 382), no single foliar or distributional character can definitively discriminate members of this family from those of other conifer clades. Although the leaves of cheirolepids are consistently small and awl-shaped, there is considerable variability in the phyllotaxy, epidermal ornamentation and stomatal distribution, such that several fossils of this group have been erroneously assigned to various alternative conifer families, e.g. Cupressaceae and Araucariaceae by previous workers. Fossil foliage attributed to *Pagiophyllum araucarinum* and *Pagiophyllum maculosum* ([van Konijnenburg-van Cittert, 1987](#); [Watson, 1988](#)), *Brachyphyllum crucis* ([Watson, 1988](#)), possibly *Brachyphyllum patens* ([van der Ham et al., 2003](#)), *Watsoniocladius valdensis* ([Seward](#)) [Srinivasan, 1995](#) ([Watson and Alvin, 1999](#)) and *Geinitzia* spp. ([Watson, 1988](#)) fall into this category. However, other members of these genera are confidently placed in Podocarpaceae and Araucariaceae ([Harris, 1979](#)). This diversity of form may explain why cheirolepidiacean foliage has not been widely identified in Australian fossil floras by previous workers. Where more complete plant remains have been found, Cheirolepidiaceae reveal a variety of phyllotaxy patterns from spirally arranged leaves to whorls of leaves in twos or threes ([Watson, 1988](#); [Daviero et al., 2001](#)). Similarities in branching morphology and leaf arrangement exist between *Frenelopsis* and extant Cupressaceae. In living conifers the branches always emerge from the axils of the leaves; no modern gymnosperms display branching in the internodal area as in *Frenelopsis*, rather it is only seen in some modern herbaceous angiosperms ([Daviero et al., 2001](#)).

Material attributed to *Otwayia* in this study was interpreted by [Cantrill and Douglas \(1988\)](#) to be of possible taxodiacean (=cupressacean) affinity. Morphological features of Cheirolepidiaceae can be easily confused with those of modern Cupressaceae. For example, *Cupressinocladius* was originally named for its similarity to members of the Cupressaceae based on characters, such as stomatal arrangement (see, e.g., examples from the Lower Purbeck of England: [Francis, 1983](#)). However, [Srinivasan \(1995\)](#) removed some species from *Cupressinocladius* to the cheirolepidiacean genus *Watsoniocladius* based on cuticular morphology as described by [Watson \(1988\)](#) and [Okubo and Kimura \(1991\)](#). Major differences between *Watsoniocladius* and extant Cupressaceae include: stomata distributed all over the abaxial surface rather than in two marginal bands; stomata surrounded by a raised ring or flat, rather than concentric papillae that form a Florin ring; papillae projecting from subsidiary cells, overarched the stomatal aperture, or papillae inside the stomatal pit—features not seen in Cupressaceae; papillae or trichomes in non-stomatal zones, compared to being restricted to the stomatal zones; inner periclinal walls of epidermal cells are smooth, rather than sculptured; and crystal cavities (calcium oxalate) are absent in *Watsoniocladius* ([Srinivasan, 1995](#)).

Cheirolepidiaceae and Cupressaceae have a range of similarities, including small, scale-like leaves, similar phyllotaxy (in some genera), sunken stomata, and small plant stature in many species.

Cheirolepidiacean phyllotaxy varies (Watson, 1988), from predominantly whorled in the frenelopsids, to opposite decussate in non-frenelopsids. Cupressaceae generally has opposite or helically inserted lanceolate, dorsiventrally flattened and univeined leaves (Ma et al., 2009), apart from a clade with whorled (e.g., in *Callitris*, *Actinostrobus* and *Fitzroya*; de Laubenfels, 1953; He et al., 2012) or opposite-decussate leaves (*Widdringtonia*, *Diselma* and *Papuacedrus*; Srinivasan, 1995; Wilf et al., 2009; He et al., 2012). Escapa et al. (2008) emphasized the need to assess vegetative and reproductive characters collectively to demonstrate confident attribution to Cupressaceae.

Opposite decussate phyllotaxy is expressed in frenelopsid cheirolepidids (Alvin and Pais, 1978; Mendes et al., 2010) but this subgroup has segmented shoots with extremely reduced leaves forming a collar around the stem, and stomata that lack a distinct Florin ring. In some cases, two to three sheathed leaves arise from the nodes of *Frenelopsis* stems (Mendes et al., 2010). Cuticular descriptions of frenelopsids (Gomez et al., 2002b) share with *Otwayia* only the strongly overarched subsidiary cell papillae in the stomatal complex. Leaves of *O. tetragona* and *O. hermata* are spirally arranged on the axis, identifying them as non-frenelopsids, according to Watson (1988).

The cuticular morphology of Cupressaceae also differs from Cheirolepidiaceae. For example, the non-frenelopsid *Watsoniocladius* was erected by Srinivasan (1995) on the basis of cuticular characters, such as: having stomata arranged mainly on the abaxial surface, the presence of a raised ring around stomata, and papillae either overarched the stomatal aperture or positioned within the pit. This differs from morphologically similar foliage attributed to *Cupressinocladius* (Cupressaceae), which is a form genus that lacks cuticle on the type specimen (Watson, 1988; Srinivasan, 1995; Watson and Alvin, 1999). However, extant examples of Cupressaceae have stomata distributed in bands with an interstomatal zone on the abaxial surface. Papillae on the subsidiary cells form a raised rim (Florin ring) around the stomate, but lack the papillae overarched the stomatal pit (Srinivasan, 1995). Recent work has highlighted distinctive cuticular characters of other fossil cupressaceous leaves, including: stomata in bands, elliptical stomatal pores, subsidiary cells that are commonly raised to form a prominent Florin ring, and epidermal cells near the stomata being commonly papillate (e.g., Kvaček et al., 2000; McIver, 2001; Ma et al., 2009; Shi et al., 2011; He et al., 2012; Serbet et al., 2013). According to Pole (2000), other differences are evident between Cupressaceae and Cheirolepidiaceae. 'Taxodiaceous' Cupressaceae have cyclocytic stomata that are not in rows, are not surrounded by a raised rim and are randomly oriented. This contrasts with Cheirolepidiaceae stomata that have subsidiary cells that are papillate, whereby papillae project laterally across the stomatal pore (Pole, 2000).

The unique combination of awl-shaped leaves, deeply sunken stomata in a variety of consistent arrangements, randomly oriented stomatal openings, each heavily protected and/or obscured by one or two ranks of papillae on subsidiary cells, commonly forming a Florin ring (though not in some *Pseudofrenelopsis*; Yang et al., 2009), appears to be a relatively robust measure for attributing foliage to Cheirolepidiaceae (Alvin, 1982; Watson, 1988; Guignard et al., 1998; Watson and Alvin, 1999; Pole, 2000; Du et al., 2013). Nonetheless, the broad architectural similarities in foliage and phyllotaxy suggest a potentially close relationship between Cheirolepidiaceae and Cupressaceae that should be evaluated by further phylogenetic analysis.

Cheirolepidiaceae may be more readily separated from Cupressaceae on reproductive architecture, whereby ovuliferous cones of the former consist of helically arranged bract scale complexes where the bract and scale are separated, in some cases with fusion occurring between two fertile bracts (each bearing two adaxially attached ovules covered by an epimatium) and sterile scales but retaining a free scale apex (del Fueyo et al., 2008; Escapa et al., 2012). Cheirolepidiaceans have flattened bilateral dwarf shoots with several scales (del Fueyo et al., 2008; Escapa et al., 2013) and one or two seeds per ovuliferous scale (Rothwell et al., 2011; Escapa et al., 2012). Unique to the Cheirolepidiaceae is the primitive

character of an inner cuticle on the dwarf shoot (Clement-Westerhof and van Konijnenburg-van Cittert, 1991), the presence of scale tissue covering but not enclosing the seed (Escapa et al., 2012), and the shedding of ovuliferous dwarf shoots from the cone when ripe, but having persistent sterile bracts (del Fueyo et al., 2008). Cupressaceae sensu lato typically have ovulate cones that are weakly lignified at maturity (Kvaček, 2000), and consist of helically arranged partially fused bract-scale complexes bearing numerous, small, flattened ovules adaxially (Yao et al., 1998; Escapa et al., 2008).

Pollen cones consist of helically arranged peltate sporophylls with pollen sacs attached abaxially on the microsporophyll in both Cupressaceae and Cheirolepidiaceae. Cupressacean microsporangiate cones are generally smaller with up to six pollen sacs per sporophyll (Rothwell et al., 2007; Escapa et al., 2008), whereas cheirolepid pollen cones may have had 2–3 pollen sacs per sporophyll, though this character is uncertain or unknown in some frenelopsids (Axsmith et al., 2004b; Axsmith and Jacobs, 2005) and non-frenelopsids (Archangelsky, 1968). However, it is its pollen morphology that most clearly separates the families: spherical pollen with a ring-like germinal groove and a complex columellate-like exine structure in Cheirolepidiaceae (Taylor and Alvin, 1984; Krassilov, 1987; Clement-Westerhof and van Konijnenburg-van Cittert, 1991) versus spherical, weakly scabrate, non-tectate pollen, with an inconspicuous germinal pore in Cupressaceae (Yao et al., 1998; Kunzmann et al., 2009).

The similar timing in appearance of both Cupressaceae (now including Taxodiaceae; Farjon, 2005) and Cheirolepidiaceae in the mid-Mesozoic of southern South America indicates co-radiation of these possibly related groups (Escapa et al., 2008, 2013) and their potential co-existence across southern Gondwana during the mid-Mesozoic. *Austrohamia* described from the Cañadón Asfalto Formation (Jurassic age), Chubut Province, Argentina, is the oldest macrofossil record of Cupressaceae from the Southern Hemisphere (Escapa et al., 2008). The oldest confident Cupressaceae macrofossils from Australia are leaves and cones of *Austrosequoia wintonensis* from the Winton Formation (Cenomanian) Eromanga Basin (Peters and Christophel, 1978; McLoughlin et al., 1995, 2010).

Confident Gondwanan records of Cheirolepidiaceae (Fig. 8) include *Tomaxellia* (Archangelsky, 1963, 1968; Kunzmann et al., 2006), *Frenelopsis* (Kunzmann et al., 2006) and *Otwayia* (Pole, 2000; McLoughlin et al., 2002). However, a range of other mid-Mesozoic austral awl- and scale-leaved conifers may belong to this family in the absence of definitive reproductive or cuticular details, including various species of *Pagiophyllum* (McLoughlin et al., 2000; McLoughlin and Pott, 2009) and *Brachyphyllum* (Baldoni, 1980; Gould, 1980; Gomez et al., 2002a,c; Rees and Cleal, 2004) and even *Araucaria*-like forms (McLoughlin, 1996; McLoughlin and Hill, 1996; McLoughlin and McNamara, 2001). Only non-frenelopsid cheirolepidids have been recorded from the Mesozoic of southern Gondwana, suggesting that this clade had a greater range of environmental tolerance, including moist climates and polar photoperiod regimes, than the mostly aridity- and salinity-adapted frenelopsids (see Subsection 5.4 Palaeoenvironmental signals).

5.2. Association with *Classopollis* pollen

Classopollis (Cheirolepidiaceae) pollen is distinguished by a clear autapomorphy—a circular germinal groove on the spherical grain. This distinctiveness, together with their greater abundance than macrofossils, endows dispersed pollen with the best means of identifying the past distribution of Cheirolepidiaceae. Cones with in situ *Classopollis* have not been recorded from Australia. However, the fossil record of dispersed pollen is extensive (Helby et al., 1987; Backhouse, 1988; Dettmann et al., 1992; Burger, 1994; Jansson et al., 2008).

Classopollis is a significantly more important component of low-latitude Early Cretaceous palynofloras than araucarian and podocarp pollen, which dominate high southern palaeolatitude palynoflorassemblages (Alvin, 1982; Dettmann et al., 1992; Cantrill and Poole, 2002). Nevertheless, some cheirolepidiacean pollen (*Classopollis/Corollina*) is clearly

Fig. 8. Chart of major events in the diversification of Cheirolepidiaceae at southern high latitudes with emphasis on the Australian fossil record (Burger, 1973; Contreras et al., 2013; de Jersey, 1963; Mays, 2011; Shu et al., 2000; Vajda and McLoughlin, 2004; Vajda et al., 2001; Walkom, 1921; Warrington, 1996).

represented in high-palaeolatitude Cretaceous assemblages highlighting the penetration of cheirolepids into polar vegetation (Cantrill and Poole, 2002). Apart from a notable spike in abundance during the Hettangian (Filatoff, 1975; Burger, 1994; McLoughlin et al., in press), *Classopollis* occurs essentially as a background element in southern Australian palynomorph assemblages from the latest Triassic up to at least the Maastrichtian (Fig. 7; Helby et al., 1987; Dettmann, 1992; Turner et al., 2009). Several factors may account for the family's relatively low

abundance in the Australian Mesozoic. The plants may have been ecologically and numerically subordinate in high-latitude Gondwanan vegetation. Further, low quantities of pollen may have been produced per individual plant. In this regard, Labandeira et al. (2007) suggested that Cheirolepidiaceae may have been insect pollinated based on the enclosed nature of the ovules. Nevertheless, cheirolepids may have been more important in some high-latitude habitats than regional palynofloral surveys have suggested. In this regard, *Classopollis* is very rare (<1%) in the Valanginian–Barremian strata of Boola Boola, Gippsland, as Aptian records show ranges from 0.8% to 2.8% in Koonwarra, Gippsland (Dettmann, 1986), but *Classopollis* makes up from 3 to 14% of the Albion palynomorph assemblage at Devils Kitchen. Further, their diversity is now known to be greater than previously assumed based on the recognition of six cheirolepidiacean leaf/cuticle forms and four pollen species in the Early Cretaceous of eastern Australia (Table 1).

5.3. Association with Mycorrhizal roots

Cantrill and Douglas (1988) noted the symbiotic association of fungi and conifer roots in the form of distinct mycorrhizal nodules at the Devils Kitchen (Albian) locality in the Otway Basin. These roots were found in the same beds as abundant *O. tetragona* foliage. Since most of the *Otwayia* remains do not appear to have undergone significant transport, Cantrill and Douglas (1988) argued that these fossils belonged to the same plant. A strong relationship with mycorrhizal fungi may have enabled cheirolepids to successfully colonize disturbed or low-nutrient substrates in high-latitude alluvial valley settings. Cheirolepid remains at the Devils Kitchen site are typically preserved in sandy to silty levee and laterally adjacent floodbasin facies of a predominantly high-energy braided fluvial depositional system. The levee deposits show weak palaeosol development and contain extensive nodular root traces and clitellate egg cases that imply better aerated and less acidic conditions than intercalated strongly carbonaceous floodbasin lake and mire facies (Behrensmeyer and Hook, 1992; Tosolini and Pole, 2010).

Mycorrhizal nodules occur on many extant plants including the conifer families Podocarpaceae, Araucariaceae and Sciadopityaceae (Dickie and Holdaway, 2011). This form of fungi–conifer interaction extends back to at least the Middle Triassic (Schwendemann et al., 2011) and evidence for mycorrhizae in general extends back to the dawn of terrestrial plant communities (Remy et al., 1994). Mycorrhizae play an important role in phosphate and possibly nitrogen-fixing (Spratt, 1912; Bergersen and Costin, 1964; Becking, 1965; Mosse, 1973; Slankis, 1974), and may also act in calcium-fixing (Blum et al., 2002). Spherical nodules produced by increasing the volume of the root cortex may also be an adaptation to maximize the interaction with arbuscular mycorrhizal hyphae at the least cost to the plant (Dickie and Holdaway, 2011). Such associations convey obvious benefits for plants growing on low-nutrient substrates or occupying disturbed riparian habitats where rapid growth and opportunistic ecological strategies are advantageous (Morrison and English, 1967; Blum et al., 2002). Such mycorrhizal nodules are particularly characteristic of exposed sites with mafic rocky and episodically inundated substrates in modern tropical–subtropical areas low in phosphorous (Bergersen and Costin, 1964).

5.4. Palaeoenvironmental signals

A range of data from foliar physiognomy, the presence of abundant epiphyllous fungi, mycorrhizal root nodules, semi-aquatic ferns and lycophytes, and sedimentary features suggest that consistently moist climates prevailed during the Early Cretaceous in southeastern Australia (Dettmann et al., 1992; Tosolini, 2001). Although features such as diminutive leaf size, leaf imbrication and thick cuticles with papillate protection of stomata, evident in *Otwayia* and related dispersed cuticle, are normally linked to dry, saline or windy sites, we hypothesize that such features in

the Victorian species reflect adaptations to humid conditions, but where low-nutrient substrates and strong seasonality locally favoured plants with xeromorphic characters.

Cheirolepidids are an extinct group, hence their ecology can only be inferred from fossil remains. The family probably included plants with a considerable range of habits (small shrubs to trees), occupying a wide variety of environments (Gomez et al., 2002b; Axsmith, 2006). Based on their diminutive leaves, strong stomatal protection and association with evaporite deposits at low latitudes, cheirolepidids have been linked to arid or coastal environments by many authors (Alvin, 1982; Francis, 1983, 1984; Watson, 1988). They have also been linked to sites disturbed by high volcanic ash fall at higher palaeolatitudes (Archangelsky and Taylor, 1986). Although such foliar morphological features occur in truly arid-adapted plants, in *Otwayia*, they may have aided the reduction of resource loss through respiration and transpiration during the long period of winter darkness at high latitudes. These features may alternatively, or additionally, be a response to growth on low-nutrient soils, which have limiting effects on photosynthetic capacity and respiration rates in modern plants commonly resulting in scleromorphy (Groves, 1981; Wright et al., 2001). Recent palaeoecological evidence from Texas (Axsmith and Jacobs, 2005) and the Iberian Peninsula (Gomez et al., 2001, 2002b; Mendes et al., 2010) not only revealed succulence and other xeromorphic characters in some frenalopsids, but also highlighted the diversity of environments in which these conifers are found (Table 1, Mendes et al., 2010): ranging from freshwater, braided or meandering rivers, distal floodplains and swamps, to deltas, brackish estuaries and lagoons, with some dispersed remains even found in tidal flats, fully marine back-reef lagoons and shelf settings.

Species of *Otwayia* were present throughout the Early Cretaceous of eastern Australia and are known to have ranged as far as the eastern fringe of Zealandia (Pole and Philippe, 2010). In most cases, they retained their diminutive leaves on the parent plant (i.e., without obvious abscission scars). The fossil remains of these plants represent branched twigs of various sizes suggesting that they were not shed as discrete units akin to those of the contemporaneous podocarp or cupressacean *Bellarinea* (Nagalingum et al., 2005) and had an evergreen rather than deciduous habit. They co-existed with a flora of large conifers, several seed-ferns, and a modest range of ferns and herbaceous lycophytes (Douglas, 1969, 1973; Drinnan and Chambers, 1986; Cantrill, 1991, 1992; McLoughlin et al., 2002; Tosolini et al., 2002).

Our results and a growing body of evidence from other studies (e.g., Archangelsky, 1968; Archangelsky and Taylor, 1986; Cantrill and Poole, 2002; Escapa et al., 2012) reveal that cheirolepidids were a significant subsidiary component of the mid- to late Mesozoic austral high-latitude vegetation. They may locally have achieved positions of dominance in disturbed habitats, low nutrient substrates, and in altered vegetation after mass extinction events (Turner et al., 2009; Barreda et al., 2012).

6. Conclusions

Five species of Cheirolepidiaceae are recognized in the Early Cretaceous strata of the Gippsland and Otway basins, southeastern Australia based on foliar cuticular differences. One of these taxa and an additional three forms were also reported from the Eromanga Basin, northeastern Australia by Pole (2000). Four cheirolepid (*Classopollis*) species are recognized from the same strata hosting *Otwayia* species in the Gippsland and Otway basins, although one of these pollen types (*C. simplex*) is likely reworked. These discoveries indicate that the cheirolepidids formed an important subsidiary component of Australian high-latitude floras through the Early Cretaceous.

These conifers survived in cool humid climates in contrast to semi-arid or coastal settings of low palaeolatitudes, where cheirolepidids (especially frenalopsids) are best known. *Otwayia* species (non-frenalopsid cheirolepidids) are interpreted to have been shrubs to small

trees, i.e., of a lesser stature than araucarians and podocarps that dominated the regional vegetation (Drinnan and Chambers, 1986; Cantrill, 1991, 1992; McLoughlin et al., 2002). Their xeromorphic characters, such as diminutive leaves with papillate sunken stomata, an evergreen habit, and association with mycorrhizal root nodules suggest that the *Otwayia* lived on nutrient-poor soils of regularly disturbed braided fluvial systems, within the Australian–Antarctic rift system.

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