Memoirs of Museum Victoria 74: 81–91 (2016) Published 2016

ISSN 1447-2546 (Print) 1447-2554 (On-line)
http://museumvictoria.com.au/about/books-and-journals/journals/memoirs-of-museum-victoria/

Morphological variation of stratigraphically important species in the genus *Pilosisporites* Delcourt & Sprumont, 1955 in the Gippsland Basin, southeastern Australia

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Abstract

Seegets-Villiers, D.E. and Wagstaff, B.E. 2016. Morphological variation of stratigraphically important species in the genus *Pilosisporites* Delcourt & Sprumont, 1955 in the Gippsland Basin, southeastern Australia. *Memoirs of Museum Victoria* 74: 81–91.

Three hundred and ninety eight mudstone samples of Early Cretaceous age from the onshore part of the Gippsland Basin in southeastern Australia were used to ascertain the morphological variation in three species of spores in the genus *Pilosisporites*. In Australia all species of *Pilosisporites* are biostratigraphically useful and this study confirms that in the Gippsland Basin the ranges of *Pilosisporites notensis*, *Pilosisporites parvispinosus* and *Pilosisporites grandis* are as defined by some previous authors. Morphological variations of these three taxa from the published descriptions are discussed. In the case of *P. grandis* and *P. parvispinosus* the main variation was in the size of specimens, however *P. notensis* showed sculpture variations in regard to element size, type and distribution. Two distinct types of this species were defined with only one occurring in the youngest part of the section. Modern fern species can exhibit similar spore sculpture and size variations as a result of polyploidy. This could possibly be the cause of the variations in all three species of *Pilosisporites* and also their short-lived, in geological terms, species ranges.

Keywords palynology, Early Cretaceous, Gippsland Basin, *Pilosisporites*, palynostratigraphy.

Introduction

In Australia all four species in the Early Cretaceous spore genus *Pilosisporites* Delcourt and Sprumont, 1955 are biostratigraphically important. The endemic Western Australian species *Pilosisporites ingramii* Backhouse, 1988 is the oldest representative of the genus in Australia and ranges through the Berriasian *Biretisporites enneabbaensis* Zone in that state (Backhouse, 1988). The remaining species *Pilososporites notensis* Cookson and Dettmann, 1958 *Pilosisporites parvispinosus* Dettmann, 1963 and *Pilosisporites grandis* Dettmann, 1963 have first and last appearance datums that play critical roles in defining spore-pollen zones in eastern Australia. Originally, the endemic Western Australian species, later defined as *P. ingramii* (Backhouse, 1988), was identified as *P. notensis* (Backhouse, 1978). The confusion over what constituted the species *P. notensis* led to Morgan's (1980) conclusion that the species had a climate-controlled migration across the continent. As such *P. notensis* was regarded as exhibiting different ranges in the east and west of the continent (Morgan, 1980; Helby et al., 1987). However, the recognition of *P. ingramii* as a separate species, endemic to Western Australia (Backhouse, 1988) meant that such discussion became irrelevant and Partridge (2006) set in place the biostratigraphic usefulness of all four Australian species.

Two species of *Pilosisporites*, *P. notensis and P. parvispinosus*, first described from Australia, have subsequently been recorded in Early Cretaceous strata in other continents. Pestchevitskaya (2007) used the first appearance of *P. parvispinosus* as a biostratigraphically important datum in the late Berriasian in Siberia, and *P. notensis* just above the early/late Hauterivian boundary and at the base of the Barremian in different regions in Siberia (Pestchevitskaya, 2007, 2008). In the Athgarh Basin in eastern India both *P. notensis* and *P.* cf. *P. notensis* were recorded (Goswami et al., 2008), whereas in the Rajmahal Basin further north Tiwari and Tipathi (1995) noted the absence of *P. notensis* and *P. parvispinosus* from the Lower Cretaceous sections as being of interest. Zhang et al. (2008) listed *P. notensis* in the Lower Cretaceous of northeast China. The type species of the genus, *Pilosisporites trichopapillosus* has never been recorded in Australia but has been recorded globally in North and South America, Europe, Africa and Asia (Alroy, 2014).

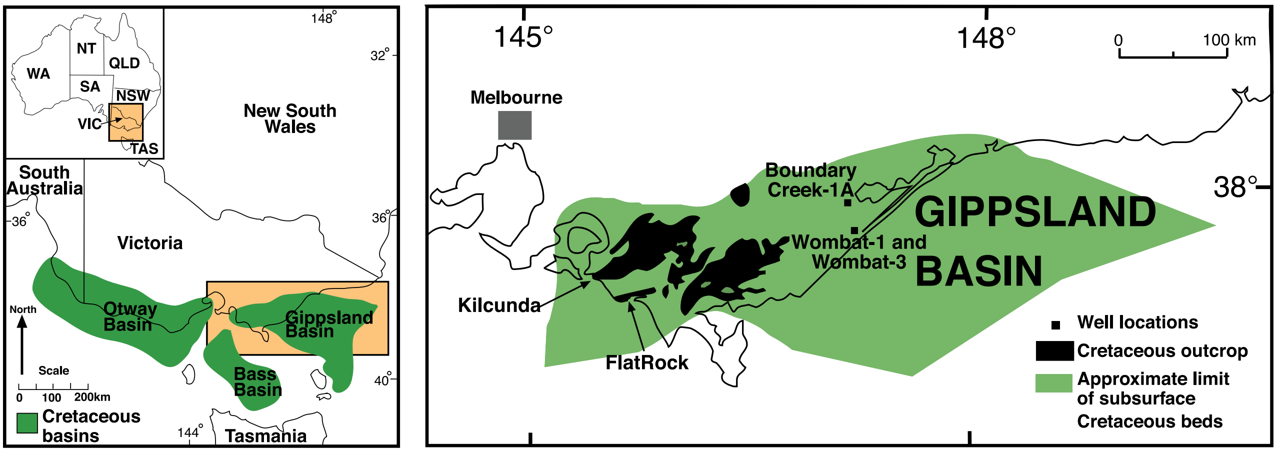

Figure 1. Gippsland Basin map showing the distribution of exposed and subsurface Cretaceous sediments and the locations of petroleum exploration wells mentioned in text (redrawn from Douglas 1988 and Tosolini *et al*., 1999).

Morphological variations exhibited by the illustrated holotypes of the four Australian species of *Pilosisporites* (Backhouse, 1988; Dettmann, 1963; Cookson and Dettmann, 1958) are distinctive and should not present any difficulty in identifying the spores. However, extensive studies on lower Cretaceous surface and subsurface sedimentary successions in the Gippsland Basin in Victoria have shown that the eastern Australian species of *Pilosisporites*, i.e. *P. notensis*, *P. parvispinosus,* and *P. grandis*, all exhibit morphological variations that are not included in the original descriptions.

Study location, lithology and age

All samples used in this study were from the Lower Cretaceous Strzelecki Group in the Gippsland Basin, Victoria, Australia (fig. 1). This basin was formed during the Early Cretaceous as a result of rifting between Australia and Antarctica (Duddy, 2003), with an approximately NW to SE basin axis (Willcox et al., 1992). Continuous separation, accompanied by progressive subsidence, resulted in the accumulation of vast sedimentary successions, the sediment source of which was contemporaneous volcanism from the active volcanic arc of the Tasman Rise (Bryan et al., 1997). The rift valley floor was a vast floodplain crossed by massive westward flowing (O'Sullivan et al., 2000) primarily braided river systems (Vickers-Rich et al., 1997) with subordinate lacustrine conditions (Dettmann, 1986; Waldman, 1971). The resultant lithologies are dominated by sandstone, mudstone and to a lesser extent conglomerate and coals (Wagstaff and McEwen Mason, 1989). Coastal outcrop sections of these rocks were used for the oldest part of the Early Cretaceous (*Foraminisporis wonthaggiensis*-lowest *Cyclosporites hughesii* zones/ Hauterivian-early Aptian age) and samples from exploration wells provided the lowest part (upper *Crybelosporites striatus* to *Coptospora paradoxa* zones/Albian age). The wells used in this study form part of Lakes Oil N.L. tight gas exploration program in the onshore Gippsland Basin, Victoria, Australia. Wombat-1 (Lat 38°21'15"S Long 147°09'32"E) and Wombat-3 (Lat 38°21'33"S Long 147°08'57"E) wells are located in the Wombat Gas field and the shallow (total depth 366 m) Boundary Creek-1A sidetrack bore (Lat 38°11'25"S Long 147°07'54"E). Due to lack of outcrop and core there is a gap in the section examined between the upper part of the *C. hughesii* and the lower part of the *C. striatus* zones therefore encompassing most of the Aptian.

Materials and methods

Core, cuttings and outcrop samples used had been collected over a period of 30 years by the authors of this study to undertake a range of different research objectives including palynostratigraphic dating, assessing vegetation abundance changes through time and environmental interpretation. This resulted in a total data set of 398 samples.

Samples used. At most of the outcrop localities only low-resolution sampling had been carried out for the exposed succession (a maximum of two or four samples) focusing on mudstone beds. Two outcrop sites included in this study however, involved high-resolution sampling. At the Flat Rocks (Lat 38°39'39"S Long 145°40'52"E) vertebrate fossil locality (fig. 1) near Inverloch, rock platform and cliffs had been sampled to provide 70 samples through the stratigraphic section. At Kilcunda (Lat 38°33'04"S Long 145°28'13"E) 38 samples had been taken at regular intervals through the mudstones in a cliff section (fig. 1). One hundred and nineteen samples were used from the Boundary Creek-1A sidetrack core between 203.03–366.5 m. Forty-four samples were from Wombat-1 between 1485–1971 m. They included eight unwashed cuttings samples and 36 samples from washed cuttings. Fifty-four washed cuttings samples were examined in the section in Wombat-3 between 1386–2169 m. This study also involved the re-examination of the type specimens of *P. parvispinosus*, *P. notensis* and *P. grandis.*

Table 1 Summary of the processing and mounting mediums used for all samples in this study.

Location/Well	**Number of samples**	**Hydrochloric acid**	**Hydrofluoric acid**	**Oxidation**	**Heavy liquid separation**	**Sieving**	**Mounting medium**
Western coastal outcrop (San Remo to Black Head)	14	√	√	Nitric acid	Zinc bromide	10μm	acrylic resin
	19	√	√	Schulze solution	Zinc bromide	none	acrylic resin
Kilcunda cliff	38	√	√	Schulze solution	Zinc bromide	none	silicone oil
Eastern coastal outcrop (Harmers Haven to Inverloch)	23	√	√	Nitric acid	Zinc bromide	10μm	acrylic resin
	17	√	√	Schulze solution	Zinc bromide	none	acrylic resin
Flat Rocks	31	√	√	Schulze solution	Sodium polytungstate	10μm	glycerine jelly
	39	√	√	Nitric acid	Zinc bromide	10μm	acrylic resin
Wombat-1	44	√	√	Nitric acid	Zinc bromide	10μm	acrylic resin
Wombat-3	54	√	√	Nitric acid	Zinc bromide	10μm	acrylic resin
Boundary Creek-1A	24	√	√	Nitric acid	Zinc bromide	10μm	acrylic resin
	95	√	√	Schulze solution	Zinc bromide	none	acrylic resin

Sample processing. Thirty-one samples from the Flat Rocks site and all the samples (38) from Kilcunda were processed by the authors in the laboratory of the School of Geography and Environmental Science at Monash University. Morgan Palaeo Associates processed the remaining 39 samples from the Flat Rocks site. Laola Pty. Ltd. (subsequently Core Laboratories Australia Pty. Ltd.) in Western Australia processed 37 outcrop samples, the remainder being processed by Global Geolab in Calgary, Canada. Core Laboratories Australia Pty. Ltd. in Western Australia processed all samples from Wombat-1 and Wombat-3 plus 24 samples from Boundary Creek-1A sidetrack bore. Global Geolab in Calgary Canada processing all other samples from this bore. Table 1 summarises the chemical and physical processing of all samples. Although the slides were initially examined and counted on a range of microscopes the work for this paper was undertaken on a Zeiss Axioscope A1 microscope in the School of Earth Sciences at the University of Melbourne and all photographs were taken on a Jentopik ProgRes CT3 camera using ProgRes Mac CapturePro 2.7 software. All illustrated specimens and the type slides are housed in the palaeontological collection of Museum Victoria and have registered numbers in the collection (prefixed "P").

The authors acknowledge that the different mounting mediums may have an effect on the size of the fossils. Faegri and Iverson (1975) considered the effects on pollen grains mounted in glycerine jelly, indicating that the grains had a tendency to swell in the medium. They (Faegri and Iverson, 1975) noted that this is more serious for large grains rather than small ones. However, Faegri and Iverson (1975) also noted that in silicone oil the size of the pollen grain does not change with storage. Sluyter (1997) investigated the effects of using silicone oil, glycerine jelly and acrylic resin on pollen grain size and determined conversion factors to account for the increase of grain sizes in the latter two mounting mediums. Sluyter (1997) also determined that glycerine jelly progressively increases the size of the grains and that measurements should be made immediately after grain mounting. However, there is no discussion anywhere in the literature on either the processing or the mounting medium altering the sculptural elements or their distribution on spores. As stated by Large and Braggins (1990), exine morphology is relatively unaffected by the various chemical treatments. Table 1 summarises the processing and mounting media used in this study.

Results

Biostratigraphic outcomes. Due to the size of the Australian continent, spore-pollen biostratigraphic schemes were initially developed that related to the present day geographical location of the basins studied and the palynologists involved. This resulted in distinctive spore-pollen biostratigraphies for the Early Cretaceous in Western Australia (Backhouse, 1978, 1988; Balme, 1957, 1964), northeastern Australia (Burger 1973, 1986; Norvick and Burger, 1975) and southeastern Australia (Dettmann, 1986; Dettmann and Douglas, 1976; Dettmann and Playford, 1969; Morgan et al., 1995). Although the stratigraphic distribution of many key taxa is the same Australia-wide, the ranges of many other species that are biostratigraphically useful, as noted by Morgan et al. (1995), vary. The pan-Australian Mesozoic palynostratigraphy published by Helby et al. (1987), and its latest update by Partridge (2006), acknowledged some of these range variations, but did not utilise others. Also, of importance for this study is the fact that the order of stratigraphic occurrences of some taxa in Partridge (2006) varies when compared to the most recent biostratigraphic scheme of Dettmann (1986) for Victoria. Recently, Wagstaff et al. (2012) defined subzones of the *Coptospora paradoxa* Zone, the youngest zone in this study.

In this study, the coastal outcrop sections examined encompassed the *Foraminisporis wonthaggiensis* Zone to just above the base of the overlying *Cyclosporites hughesii* Zone of Helby et al. (1987). The first appearance of the indicator of the base of this zone, i.e. *Foraminisporis asymmetricus* and/or the first appearance of the angiosperm species *Clavatipollenites hughesii* (this study), marks the top of the coastal section. The wells examined encompass a section that starts with the upper part of the *Crybelosporites striatus* Zone and almost reaches the top of the overlying *Coptospora paradoxa* Zone. Although this study does not cover the entire Lower Cretaceous in the Gippsland Basin, due to lack of continuous stratigraphic section, enough section has been examined to allow some conclusions to be drawn in relation to the spore-pollen ranges and the biostratigraphic usefulness of taxa. This study confirms the order of first appearances of *P. notensis* and *P. parvispinosus* in the Gippsland Basin as indicated by Dettmann (1986) and *P. grandis* as shown in Dettmann and Douglas (1976). Using the zones of Helby et al. (1987), *P. notensis* first appears at the base of the *Foraminisporis wonthaggiensis* Zone, and *Pilosisporites parvispinosus* first appears within this zone. The first appearance of *P. grandis* defines the base of the *P. grandis* Subzone (Wagstaff et al., 2012) of the *Coptospora paradoxa* Zone while both *P. notensis* and *P. parvispinosus* become extinct, in the Gippsland Basin, just above this event. This study has confirmed that the order of first and last occurrences up section is as shown in figure 2, and as such rejects some of the suggestions of Partridge (2006) for the Gippsland Basin.

Taxonomic outcomes. The diagnosis of *P. grandis* and *P. parvispinosus* basically conform to those of Dettmann (1963), except for minor variations as discussed below. However, *P. notensis* shows a range of sculptural variations (size, type, distribution of sculptural elements) in which the holotype is only representative of one morphological variant. It is enigmatic as to why these variations have not been described before as a close inspection of the type slide P17611 as used by Cookson and Dettmann (1958) revealed that some of these variations were present on specimens that occur in this slide, but were not included in the original description. Also, an examination of the descriptions and the photo plates in the literature suggests that previous workers had encountered this variation, as evidenced by published images representing these different types.

The species of *Pilosisporites* are discussed in geochronologic order from oldest to youngest.

Genus *Pilosisporites* Delcourt and Sprumont, 1955

TYPE SPECIES (by original designation): *Pilosisporites trichopapillosus* (Thiergart, 1949) Delcourt and Sprumont, 1955 (Early Cretaceous, Germany).

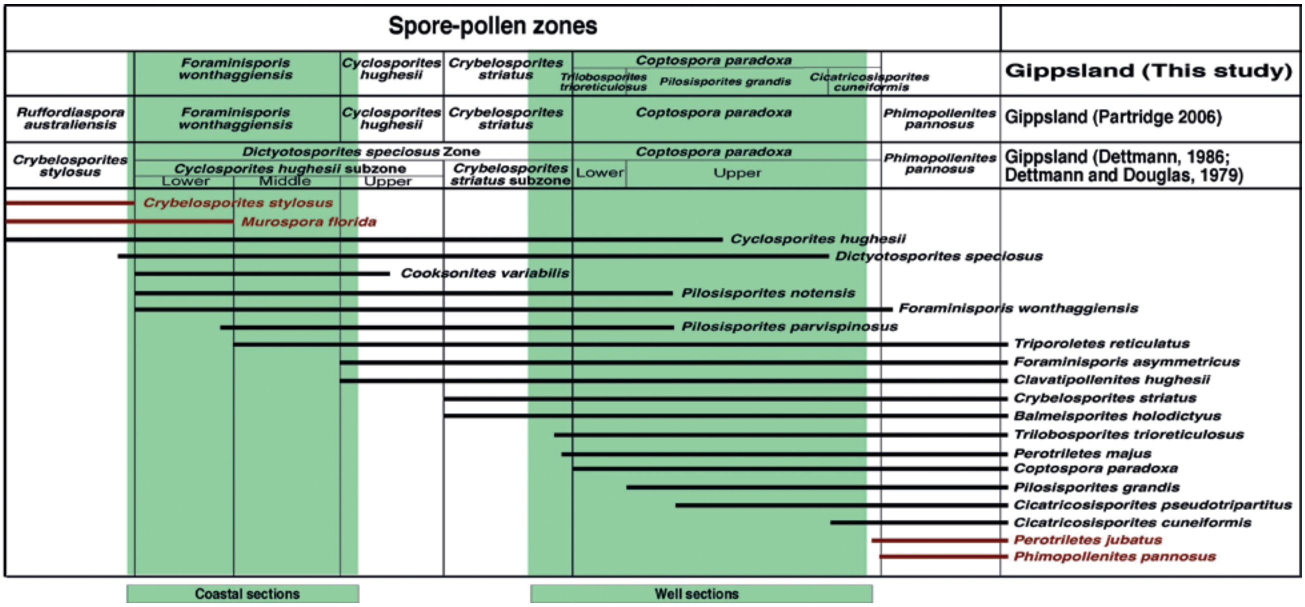

Figure 2. Spore-pollen zones and age indicator species in the Gippsland Basin. Green shaded areas represent the stratigraphy recorded in this study, with the ranges of taxa encountered shown in black and the ranges of taxa not recorded shown in brown. Some ranges are inferred from previous work of Dettmann (1986) and Dettmann and Douglas (1979).

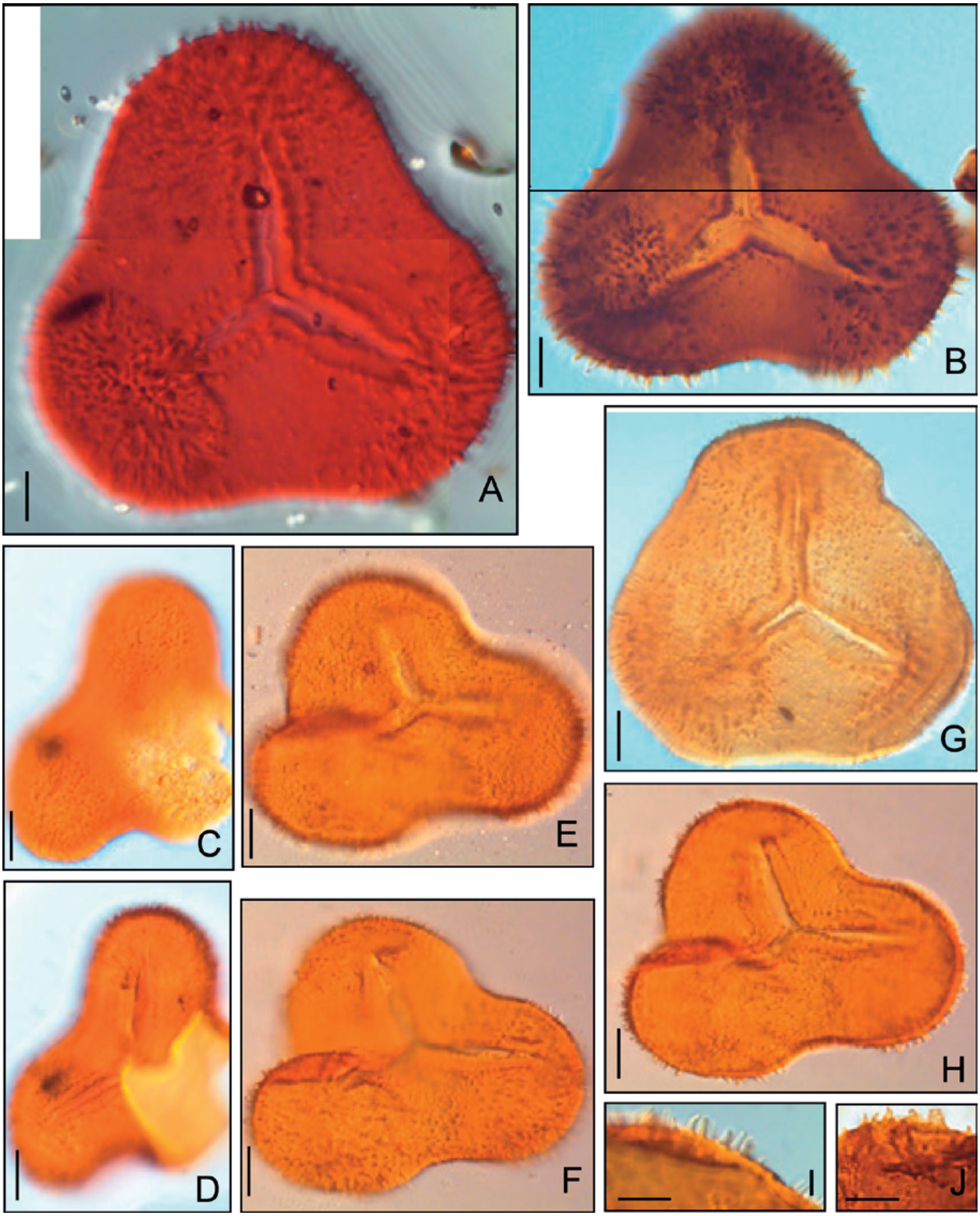

Figure 3. Scale bar Figs A–H = 10 µm; Figs I–J = 12 µm, EFR = England Finder Reference, DIC = Differential interference contrast. A *Pilosisporites notensis* Holotype Slide P1761 EFR Q37/4. Photograph taken using DIC. B *Pilosisporites notensis* Flat Rocks Slide P252131 EFR T31/1. Specimen with long apical spines. Photograph taken using DIC. C, D *Pilosisporites notensis* Wombat-3 Slide P252136 #2 EFR P28/0. E, F, H *Pilosisporites notensis* Shack Bay Slide P252135 EFR H21/1. G *Pilosisporites notensis* Flat Rocks Slide P252132 EFR H37/1 Photograph taken using DIC. I *Pilosisporites notensis* Flat Rocks Slide P252132 EFR F39/4. Sculpture predominantly spines. Photograph taken using DIC. J *Pilosisporites notensis* Flat Rocks P252133 EFR E21/1. Sculpture cones and curved spines.

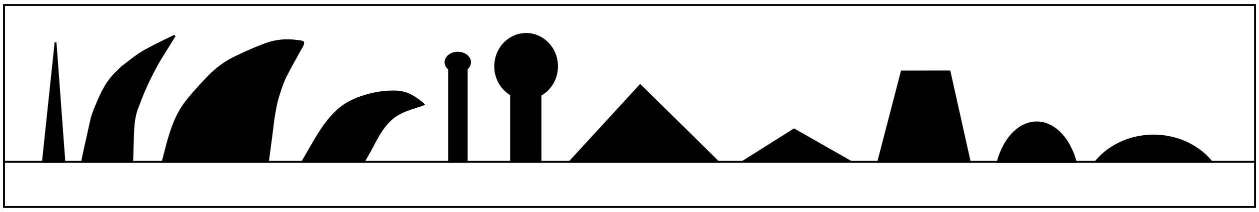

Figure 4. Range of sculptural elements recorded in *Pilosiporites notensis*.

Pilosisporites notensis Cookson and Dettmann, 1958 emend.

Figure 3 A–J

Synonymy: 1958 *Pilosisporites notensis* Cookson and Dettmann, p. 102, pl. 15, figs 1, 3

1963 *Pilosisporites notensis* Cookson and Dettmann; Dettmann, p. 37–38, pl. 4, figs 1–5; p. 33 fig 4D

1964 *Pilosisporites notensis* Cookson and Dettmann; Balme, p.74, pl. VII, fig. 10

1969 *Pilosisporites notensis* Cookson and Dettmann; Dettmann and Playford, pl. 11, fig. 2

1973 *Pilosisporites notensis* Cookson and Dettmann; Burger, pl. 2, fig. 1

1974 *Pilosisporites notensis* Cookson and Dettmann; Burger, pl. 13 fig 11

1976 *Pilosisporites notensis* Cookson and Dettmann; Norvick and Burger, pl. 18, fig 17

non 1978 *Pilosisporites notensis* Cookson and Dettmann; Backhouse, p.18, Pl. 2, fig. 1

1980 *Pilosisporites notensis* Cookson and Dettmann; Burger, p. 52, pl. 6, fig. 5

1986 *Pilosisporites notensis* Cookson and Dettmann; Dettmann, fig. 6M

1987 *Pilosisporites notensis* Cookson and Dettmann; Helby et al., fig. 20N

1988 *Pilosisporites notensis* Cookson and Dettmann; Backhouse, pl.15 fig. 2

2012 *Pilosisporites notensis* Cookson and Dettmann; Wagstaff et al., pl.II fig. 2

Emended diagnosis: Trilete spores, with strongly convex distal and almost flat proximal surface. Amb triangular with concave to nearly straight sides and broadly rounded apices. Laesurae straight, length $^2/_3$ to ¾ of spore radius, with raised, membraneous lips. Exine 1.5–3.5 μm thick, ornamented by straight-sided or curved cones and/or spines (*sensu* Punt et al., 1994) of 0.5–3.5 μm basal diameter and 1–6.5 μm height. This sculpture co-occurs with rare other sculpture types including baculae, clavae, pilae, tuberculae and verrucae (fig. 4). Sculptural elements consistently arranged along laesurae margins and either covering the entire spore surface or restricted to the apical areas. Sculpture elements of equal size and distribution on proximal and distal surface.

Size: Equatorial diameter 52 (80) 125 μm (136 specimens), polar diameter 52 (71) 91 μm (14 specimens).

Remarks and comparison: Specimens generally conform to the original descriptions (Cookson and Dettmann, 1958; Dettmann, 1963). However, observations on a large number of specimens in this study have revealed differences regarding the distribution and type of sculptural elements (figs. 3, 4). The most common morphological extreme of *P. notensis* exhibits short sculptural elements (up to 3 μm high) and base diameters of between 0.5–3 μm. This group shows sculpture distributed either over the entire spore surface as illustrated by Backhouse (1988) or mainly restricted to apical areas where they are closely packed (fig. 3G). The second morphological extreme, shows elongate sculptural elements (up to 6.5 μm), with a narrow basal diameter of as little as 1 μm. Sculptural elements are either distributed over the entire distal and proximal surface (figs. 3E, F, H) or primarily restricted to and closely packed together in the apical areas of the spore (fig. 3B) as in the original description of *P. notensis* by Cookson and Dettmann (1958) and as occurs in the holotype (fig. 3A).

The specimens of *P. notensis* with long apically distributed spines, superficially resemble *P. ingramii* Backhouse (1988) in that they possess long spines, and in some instances, a single row of small spines on the laesurae. However, the grain size in general exceeds that of *P. ingramii* and sculptural elements are in general shorter. Between each morphological end member there is a continual spectrum of distribution of sculptural elements on the amb of the spores ranging from primarily the apex with rare inter-apical occurrences, to increasing frequency of elements inter-apically to spores in which the sculpture extends over the entire surface of the amb. Sculptural element size and distribution is independent of the overall size of the grain.

Two other species of *Pilosisporites* bear a resemblance to *P. notensis*. *Pilosisporites trichopapillosus* (Thiergart) Delcourt and Sprumont, 1955 is recorded as also having sculpture variation in which the long spines were restricted to apical areas or covering the entire surface of the grain (Couper, 1958). However, there is no suggestion that there are any sculptural elements other than spines on this species (e.g. Couper, 1958; Singh, 1964; Archangelsky and Llorens, 2005). *Pilosisporites verus* (Delcourt and Sprumont) emend. Archangelsky and Llorens, 2005 has sculptural elements that include spines with broad bases and acute apices that are sometimes curved, with lesser numbers of cones, bacula, granules and mameliform processes. The sculptural elements are often concentrated at the apical areas (Singh, 1964) but the spines in *P. verus* are longer, i.e. 5.5–11 μm (Archangelsky and Llorens, 2005), than those that occur in *P. notensis*. The equatorial diameter of both these species is also within the lower end of the size of *P. notensis*.

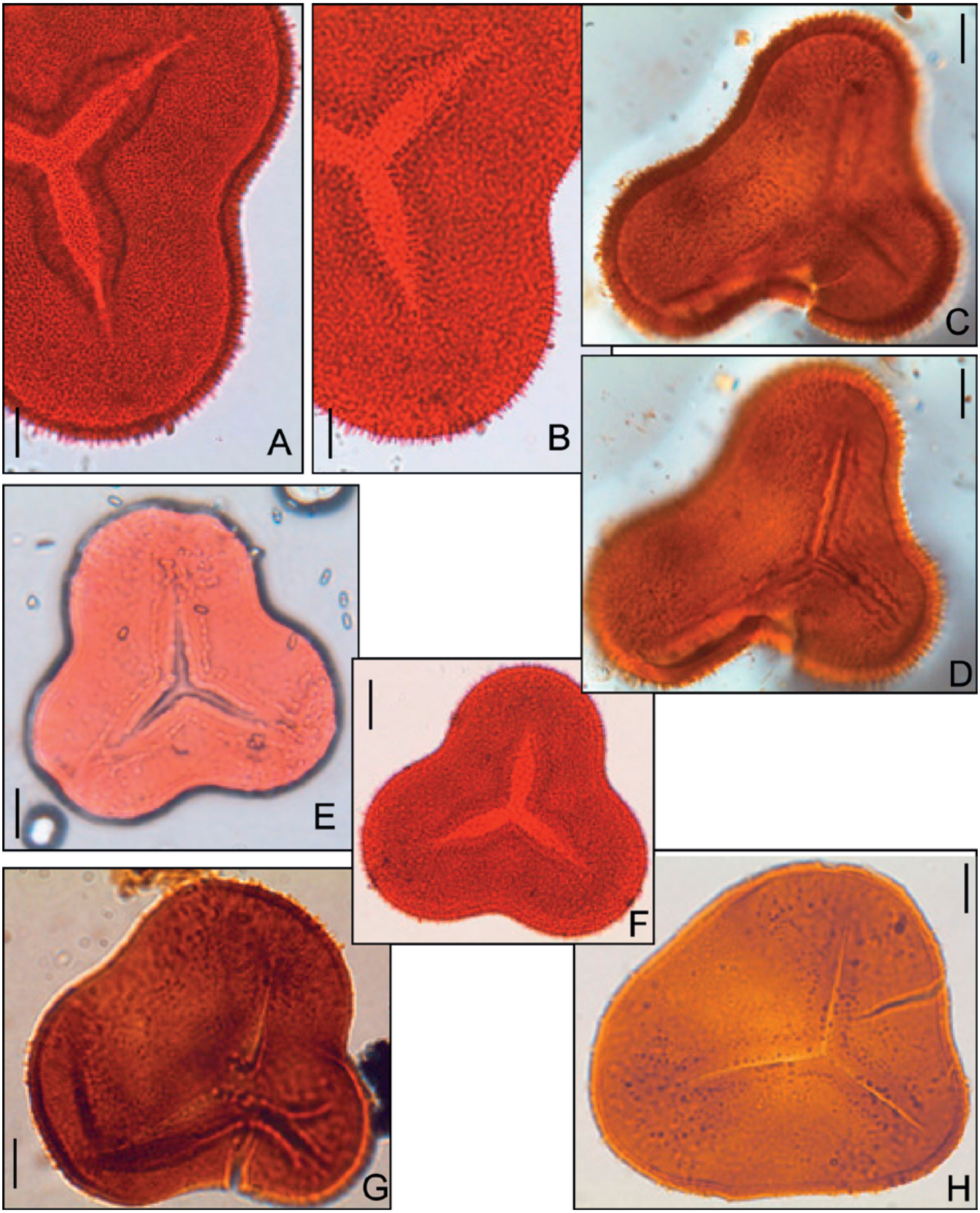

Figure 5. Scale bar Figs A–E and G–H = 10 µm; Fig. F=25 µm, EFR = England Finder Reference. A, B, F *Pilosisporites grandis* Holotype Slide P22098 EFR N20/0. C, D *Pilosisporites grandis* Boundary Creek -1A core 285.5m Slide P252137 EFR Q14/4. E *Pilosisporites parvispinosus* Holotype Slide P21997 EFR E37/3. G *Pilosisporites parvispinosus* Flat Rocks Slide P252134 EFR L41/3. H *Pilosisporites parvispinosus* Flat Rocks Slide P252134 EFR Q31/1.

Distribution (this study): Base of the *Foraminisporis wonthaggiensis* Zone to within the lower part of the *P. grandis* subzone of the *C. paradoxa* Zone. This study found that both end members co-occur in the older part of the succession with their First Appearance Datum (FAD) at the base of the *F. wonthaggiensis* Zone. However, in the uppermost part of the range of *P. notensis*, i.e. in the *C. striatus* and *C. paradoxa* zones, only the shorter spined forms occur (figs. 3C, D). *P. notensis* is never abundant or common in the upper part of its range.

Pilosisporites parvispinosus Cookson and Dettmann, 1958

Figure 5E, G, H

Synonymy 1958 *Pilosisporites notensis* Cookson and Dettmann, p. 102, pl. XV fig. 2

1963 *Pilosisporites parvispinosus* Dettmann, p. 38, pl. IV figs. 6–8; p. 33 fig 4F

1980 *Pilosisporites parvispinosus* Dettmann; Burger, p. 52, pl. 5 fig 9; pl. 6 figs 1–3

non 2012 *Pilosisporites parvispinosus* Dettmann; Lebedeva and Pestchevitskaya, pl. 1 fig. 7

2012 *Pilosisporites parvispinosus* Dettmann; Wagstaff et al., pl. II fig. 7

Diagnosis: see Dettmann (1963).

Size: Equatorial diameter 78 (85) 106 μm (11 specimens).

Remarks: Representatives of this species usually conform to the diagnosis by Dettmann (1963), but show, in rare cases, a slightly thicker exine (2–3.5 μm compared to Dettmann's (1963) 2–3 μm). The spinulate sculpture occasionally has spinules with a wider base diameter (1–2 μm) compared to Dettmann's 1 μm) and a sculpture height of (1–2.5 μm). Rarely present are longer apical sculptural elements.

Distribution (this study): Upper part of the *Foraminisporis wonthaggiensis* Zone to *Coptospora paradoxa* Zone, specifically the lower part of the *Pilosisporites grandis* subzone.

Pilosisporites grandis Dettmann, 1963

Figures 5A–D, F

Synonymy: 1963 *Pilosisporites grandis* Dettmann, pp. 38–39, pl. V, figs 1–3; p. 33 fig 4E

1969 *Pilosisporites grandis* Dettmann; Dettmann and Playford, pl.11 fig. 1

1980 *Pilosisporites grandis* Dettmann; Burger, p. 52, pl. 6, fig. 4

2012 *Pilosisporites grandis* Dettmann; Wagstaff et al., p. 69, pl. 2 fig. 2

non 2014 *Pilosisporites grandis* Dettmann; Takeshi and Vijaya, fig. 5E

Size: Equatorial diameter 85 (92) 100 µm. (4 specimens).

Remarks: As discussed in Wagstaff et al. (2012) the grains encountered in the Gippsland Basin are smaller than those originally described by Dettmann (1963) from the Great Artesian and Otway Basins. Dettmann (1963) gave the equatorial diameter of the species as 100 (117) 142 µm. The specimen illustrated by Burger (1980) from the Surat Basin (Burger, 1980, plate 6, fig. 4) is also smaller (appearing to be approximately 90 µm) than the size range given by Dettmann (1963). We accept the statement of Burger (1980) in the plate (pl. 6, fig. 4) description that the species is primarily identified by its "dense and regular distribution of spines on the exine".

*Distribution (this study)***:** *Coptospora paradoxa* Zone, specifically *Pilosisporites grandis* to *Cicatricosisporites cuneiformis* subzones.

Discussion

The genus *Pilosisporites* is unique in Australian palynology in that all four species of the genus are biostratigaphically useful. In spite of the morphological diversity of *P. notensis*, and the size variations of *P. grandis* and *P. parvispinosus*, this fact is not altered. However, this variation is, in the case of *P. notensis*, so extreme that it warrants further investigation.

Hughes (1989) made an in-depth critique of the concept of species and indicated that over time the addition of new specimens identified as a species can cause the original definition of the species to become broader causing the taxon to become an ever larger cluster with irregular limits rather than the neat concept of its generator. This is due to more specimens being examined that encompass a greater span of geologic time, geography (other localities) or both. Hughes (1989, p. 12) also stated that "From the moment of publication, it is customary for appropriate other newly discovered material to be 'identified with', or attributed to, the existing species as far as possible, because new species are in general erected with caution and even with reluctance." This leads over time to the alteration of the meaning or scope of definition of the totality of specimens included in the species under the name. This seems to be the case for *P. notensis* where an examination of the published images from across eastern Australia from different localities and different spore-pollen zones, shows a variation in morphology. However, temporal and geographic components cannot be the only reasons for the variation in the current study. The Flat Rocks and Kilcunda localities are both small stratigraphic sections that were sampled (70 and 38 respectively) with high resolution. At each locality the full range of morphological variation of *P. notensis* occurred, even in many instances in a single sample. As such, the variation cannot be attributed to geologic time or geographic differences and needs to be explained.

Dettmann (1963, 1986) suggested no modern equivalents for the Victorian *Pilosisporites* spore species, but did consider them to be produced by ferns. Variation of the spore sculpture within a species is not unknown in extant ferns. Parks et al. (2000) found that the monolete fern spore *Cystopteris fragilis* (L.) Bernhardi 1805 that occupied different microclimates and substrates in Scotland had three distinctive sculptural types: echinate, rugose and a "smooth" type that appeared to be slightly granular using SEM. The plants producing these distinctive spore types occupied different microclimates and substrates (Parks et al., 2000). Parks et al. (2000) concluded that the fern *C. fragilis* was polyploid with several populations of variants. Beck et al. (2011) indicated that ploidy level could also control the size of spores with diploids, triploids, and tetraploids of fern species in the genus *Astrolepis,* Benham and Windham 1992 having statistically different and non-overlapping spore diameter distributions. Diverse ploidy levels were also used to explain marked spore size differences in the tropical American fern genus *Stigmatopteris* Christensen 1909 (Tryon and Tryon, 1982). These morphological variations pose an interesting dilemma for palynologists as Otto and Whitten (2000) estimate that the frequency of polyploidy is particularly high in extant ferns (41.7%).

Polyploidy is the existence of genetically related taxa (Thompson and Lumaret, 1992) with three or more basic chromosome sets in their cell nuclei as opposed to the usual two (Bennet, 2004). Polyploidy is heritable (Comai, 2005) and allows homosporous ferns to create and maintain genetic variation in spite of the effects of self-fertilisation due to their monoecious gametophtye stage (Klekowski and Baker, 1966). Klekowski and Baker (1966) further suggested that polyploidy provides selective advantages to homosporous ferns allowing them to maintain, create and release genetic variability in spite of producing homozygous sporophytes. Page (2002) indicates that the entire process of polyploidy in ferns results in the creation of morphological and ecological novelty providing a rapid route for species evolution and adaption and increasing the plants' vigour. The resulting taxa have the ability to adapt to a broader range of ecological conditions compared to their parents and in an actively evolving flora in a changing environment higher ploidy derivatives more often find niches for ecological success. Comai (2005) provided evidence that polyploidy increases the diversity and plasticity of a species, and contributes to its adaptive potential in the arctic where polyploids are able to rapidly adapt to new niches and are able to efficiently invade newly deglaciated areas due to hybrid vigour. However, these polyploids are often considered to be static entities in which gene silencing results in isolated populations (Haufler, 2008). Thus, the picture for polyploids is not favourable in the long term. Their ability to establish and flourish during periods of environmental change when new niches are opened is well recognised, but polyploids face evolutionary difficulties as gene selection is inefficient due to the multiple copies and they are often evolutionary dead-ends (Arrigo and Barker, 2012).

High levels of niche variablity would be a major feature of the Early Cretaceous of the Gippsland Basin. The evolving rift between Australia and Antarctica (Duddy, 2003) and its fast flowing braided river system (Vickers-Rich et al., 1997) would have been a dynamic unstable landscape. The palaeogeographic setting of southeastern Australia was significant in that it was near or inside the Antarctic Circle (Rich and Vickers-Rich, 2000; Wagstaff et al., 2013). Therefore, in spite of the high carbon dioxide levels characteristic of the Cretaceous Greenhouse, and warm and equable global climates (Spicer and Corfield, 1992), it is suggested that in the Aptian-Albian this region would still have been cold (Gregory et al., 1989) and in winter would have experienced months of darkness.

The short biostratigraphic ranges of the species of *Pilosisporites* that occur in the Cretaceous successions in Australia suggest each species is very intolerant of climate/environmental variability. The inability of *P. ingramii* to migrate from Western Australia to the east implies high levels of endemism, as does the inability of *P. parvispinosus*, *P. notensis* and *P. grandis* to migrate into Western Australia. As the climate became drier in the Gippsland Basin (Wagstaff et al., 2013) the extinction of both *P. parvispinosus* and *P. notensis* in the Albian and the evolution of *P. grandis* just prior to this event, seems to suggest that the two former species could not cope with these changed conditions. The variation that occurs in the morphology of *P. notensis* could represent a fern species that had undergone polyploidy thus allowing it to inhabit a range of niches in an unstable braided fluvial setting. The fact that the full range of morphotypes can occur in one sample appears to indicate that the fern is occasionally abundant/diverse in a riparian setting that encompasses a range of sub-environments.

Conclusions

This study on spores in the genus *Pilosisporites* in Lower Cretaceous strata in the Gippsland Basin has three outcomes. The biostratigraphic usefulness of the three species is confirmed with the following ranges. *Pilosisporites notensis* first appears at the base of the *Foraminisporis wonthaggiensis* Zone, and *Pilosisporites parvispinosus* within the zone. The first appearance of *Pilosisporites grandis* defines the base of the *P. grandis* subzone of the *Coptospora paradoxa* Zone while both *P. notensis* and *P. parvispinosus* become extinct just above this event. Taxonomically, the descriptions of *P. grandis* and *P. parvispinosus* have extended size ranges compared to the original descriptions. *P. notensis* shows not only variation in size from the original description but also a division into shorter and longer sculptural element types, and within these, variation in the distribution of the sculpture on the amb. This study suggests that the inability of the eastern and western Australian species of *Pilosisporites* to migrate across the continent, in combination with their short geological ranges and the size and sculptural variation exhibited by the three species examined from the Gippsland Basin, may be evidence of polyploid reproductive strategies in the ferns of this genus.

Acknowledgements

We would like to thank Professor Patricia Vickers-Rich and Dr Thomas Rich who funded the majority of the research on the outcrop samples. BHP Billiton funded the research at Kilcunda. We would like to thank Lakes Oil N.L. for providing some of the samples from Wombat-3. The Department of Primary Industries allowed sampling of the wells and we would particularly like to thank Terry Smith for providing help with accessing the cuttings and core. We would like to thank David Pickering from Museum Victoria for locating and loaning us the type slides from their collection. We appreciate the comments provided by the editor and two anonymous reviewers that helped improve the text. ARC Linkage Grant LP0989203 funded the research on the well sections with industry partners Lakes Oil N.L., Nexus Energy and Geotrack International.

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