

# An Early Jurassic conifer-dominated assemblage of the Clarence-Moreton Basin, eastern Australia

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Master Thesis  
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**Abstract:** During the early Mesozoic two mass-extinction events profoundly reshaped the world's biota. The first of these took place at the end of the Triassic and affected both marine organisms and terrestrial floras. The second occurred as an oceanic anoxic event during the early Toarcian. Although the Late Triassic floral assemblages of Australia have been the focus of many studies, there have been few investigations of the recovery succession of the following Jurassic period. This study investigates an Early Jurassic terrestrial fossil assemblage from the Inverleigh quarry, Clarence-Moreton Basin, eastern Australia, deposited between these events. The Inverleigh sediments belong to the Marburg Subgroup, an entirely non-marine succession characterised by a low diversity flora. The assemblage is overwhelmingly dominated by a single conifer taxon, *Allocladus helgei* sp. nov, but ferns and possible lycophytes occur in low numbers. The macroflora is supplemented by an array of dispersed cuticle fragments with well preserved stomata and charcoalfied wood. Other mesofossils include five megaspore species, here described under open nomenclature. Additionally, a small assemblage of clitellate annelid cocoons was recovered from the organic residues.

The palaeoenvironment is interpreted as waterlogged or frequently inundated floodplain based on the dominant fine-grained lithology and the presence in the fossil assemblage of many free-sporing ferns and isoetaleans, which are dependent on moisture for reproduction. The frequent exposure to flooding would have imposed environmental stresses on the plants growing at the site. This resulted in a low diversity plant community, dominated by species adapted to moist, high-latitude conditions.

**Keywords:** Australia, Jurassic, Marburg Subgroup, conifers, palaeoenvironment.

# En tidig-jurassisk barrträds dominerad association från Clarence-Moreton bassängen, östra Australien

IDA-MARIA JANSSON

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**Sammanfattning:** Under den tidigare delen av mesozoikum inträffade två massutdöende som i stor utsträckning kom att påverka jordens ekosystem. Det första inträffade i slutet av trias och påverkade både marina organismer och terrestrisk biota. Det andra mesozoiska utdöendet skedde under tidig toarcian i samband med ett anoxiskt event. Trots att den Australienska sen triassiska floran behandlats i ett flertal studier har lite arbete ägnats åt den tidig jurassiska återhämtningssuccessionen. Detta arbete behandlar en tidig jurassisk terrestrisk fossil association från Inverleigh brottet, Clarence-Moreton bassängen, östra Australien. Inverleigh sedimenten tillhör en fullständigt terrestrisk succession vilken karaktäriseras av en lågdivers flora. Macrofloran domineras av en enda art av barrträd, *Allocladus helgei* sp. Nov. Floran innehåller dessutom ormbunkar och möjliga lummerväxter i mindre omfattning. Växtmaterialet inkluderar även fragment av kutikula med välbevarade stomata samt förkolnat trä. Bland mesofossilerna återfinns även en rik och välbevarad megaspor association tillhörande fem arter vilka har beskrivits under öppen nomenklatur. Vidare har en mindre samling av hela och fragmenterade maskägg återfunnits i det organiska materialet.

Paleomiljön har baserat på litologi samt flora tolkats som ett flodplan, med meandrande kanaler, utsatt för återkommande översvämningar. Detta överensstämmer väl med förekomsten av ormbunkar och lummer, vilka är beroende av väta för sin reproduktion. De återkommande översvämningar som växterna utsattes för utgjorde en stressfaktor som begränsade deras överlevnadsförmåga. Detta resulterade i en lågdivers flora, dominerad av arter vilka anpassat sig till de rådande förhållandena i området.

**Nyckelord:** Australien, Jura, Marburg Subgroup, barrträd, palaeomiljö.

# 1. Introduction

During the early Mesozoic two mass-extinction events profoundly reshaped the world's biota. The first of these, at the end of the Triassic, affected marine organisms, terrestrial animals, such as tetrapods, and terrestrial floras (McElwain et al. 1999). Even though the event represents one of the five most severe extinction-events in Earth's history the cause of this crisis is still highly debated (Beerling & Berner 2002). Terrestrial plants were one of the most severely affected groups (McElwain et al. 1999), North American palaeobotanical studies reveal a loss of 60% of species whereas the megafloreal turnover in the North Atlantic region was as high as > 95% (Beerling & Berner 2002). In Australia these notable floristic changes can be seen as an overall decrease in diversity (Balme et al. 1995). As a result, the initial Early Jurassic flora consisted of merely 20-25 known macrofossil species (Balme et al. 1995). In Gondwanan sediments, including Australia, this mass-extinction is clearly detectable in the fossil record by the demise of *Dicroidium*, the dominant corystosperm, and associated taxa. The Early Jurassic was characterised by the rise of new dominant conifers and bennettitalean groups (Hill et al. 1966). This floristic turnover represented a major punctuation in the evolution of the gymnosperms. These dramatic changes, of composition and distribution of global vegetation, in the Early Jurassic resulted in a flora that for the first time contained elements with affinities to modern plants (Willis & McElwain 2002).

The second major perturbation occurred as an oceanic anoxic event during the Early Toarcian (~184 Ma) and is marked by worldwide deposition of organic black shales (McElwain et al. 2005). The Toarcian oceanic anoxic event is characterised by a sharp nega-

tive carbon isotope excursion, probably due to destabilisation of continental-margin methane gas hydrates (Beerling et al. 2002). The Toarcian event had a total duration of approximately ~160 kyr and studies of marine and terrestrial carbon reservoirs suggest a release of approximately 5000 Gt C from the sedimentary methane hydrate reservoir, which in turn resulted in increased global temperatures (Beerling et al. 2002). The triggering mechanism behind the destabilization, and hence release, of the sedimentary hydrates is uncertain. However, mechanisms such as rapid decrease in pressure, deep-water warming, change in thermohaline circulation, volcanic CO<sub>2</sub> emissions and increased global temperatures have been suggested (Beerling et al. 2002). According to Beerling et al. (2002) a decrease in pressure is excluded as a possible cause of the Toarcian event as it took place during an eustatic sea level rise. However, the Toarcian oceanic anoxic event is concordant with the eruption of the Ferrar-Karoo continental flood basalt (Beerling et al. 2002), therefore a possible cause could be global warming, due to a release of CO<sub>2</sub> to the atmosphere. This in turn would have led to an increase in bottom-water temperatures and subsequently a destabilization in the sediment pile as the temperature gradient realigned (Beerling et al. 2002).

The Early Jurassic was characterised by a mild climate. Polar ice caps of any significance were lacking (Brakel et al. 1995) and plant productivity and diversity was greatest in middle latitudes (Rees et al. 2000). The Jurassic flora had a cosmopolitan disposition, an aspect probably facilitated both by broad land connections between most of the major landmasses (Fig. 1) and equable global temperatures (McLoughlin et al. 2002). The vegetation at low latitudes was pre-

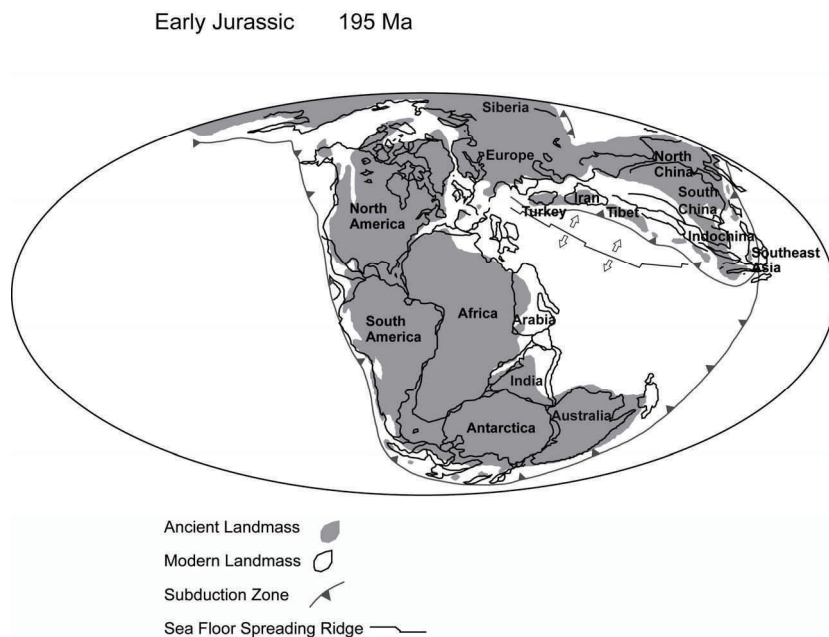


Fig. 1. Palaeomap showing the distribution of the continents during the Early Jurassic (modified from <http://www.scotese.com>).

dominately xeromorphic and characterised by small-leaved conifers and cycadophytes, whereas the vegetation at the poles was dominated by large-leaved conifers and ginkgophytes (Rees et al. 2000, Willis & McElwain 2002). Throughout the period, global warming and increased precipitation caused a shift towards more extensive, conifer-dominated, wetlands. During this period the Australian continent was mainly located in high mid-latitudes (Brakel et al. 1995) and terrestrial sedimentary environments predominated (Fig. 2), with only minor deposition of marine sediments in the northwest of the continent (Brakel et al. 1995).

This study focuses on sediments exposed in the Inverleigh quarry assigned to the Lower Jurassic Koukandowie Formation, situated in the Clarence-Moreton Basin, eastern Australia. These sediments were deposited between the Triassic-Jurassic mass-extinction

event and the Toarcian oceanic anoxic event, hence the fossil assemblages provide insights into the nature of the flora between two major phases of biotic turnover. Although the Late Triassic floral assemblages of Australia have been the focus of many studies, there have been few investigations of the post-extinction recovery successions of the following Jurassic period. The aim of this study is to systematically describe and classify the Inverleigh plant assemblage, including macro- and mesofossils, representing a key Early Jurassic locality in the Clarence-Moreton Basin. The project will also include the learning of processing and preparation methods used for plant macro- and mesofossils. The fossils and the host unit will further be studied in context of sedimentology, in order to reconstruct the palaeoenvironment. Finally, some economical aspects of Australian coal deposits will be discussed.

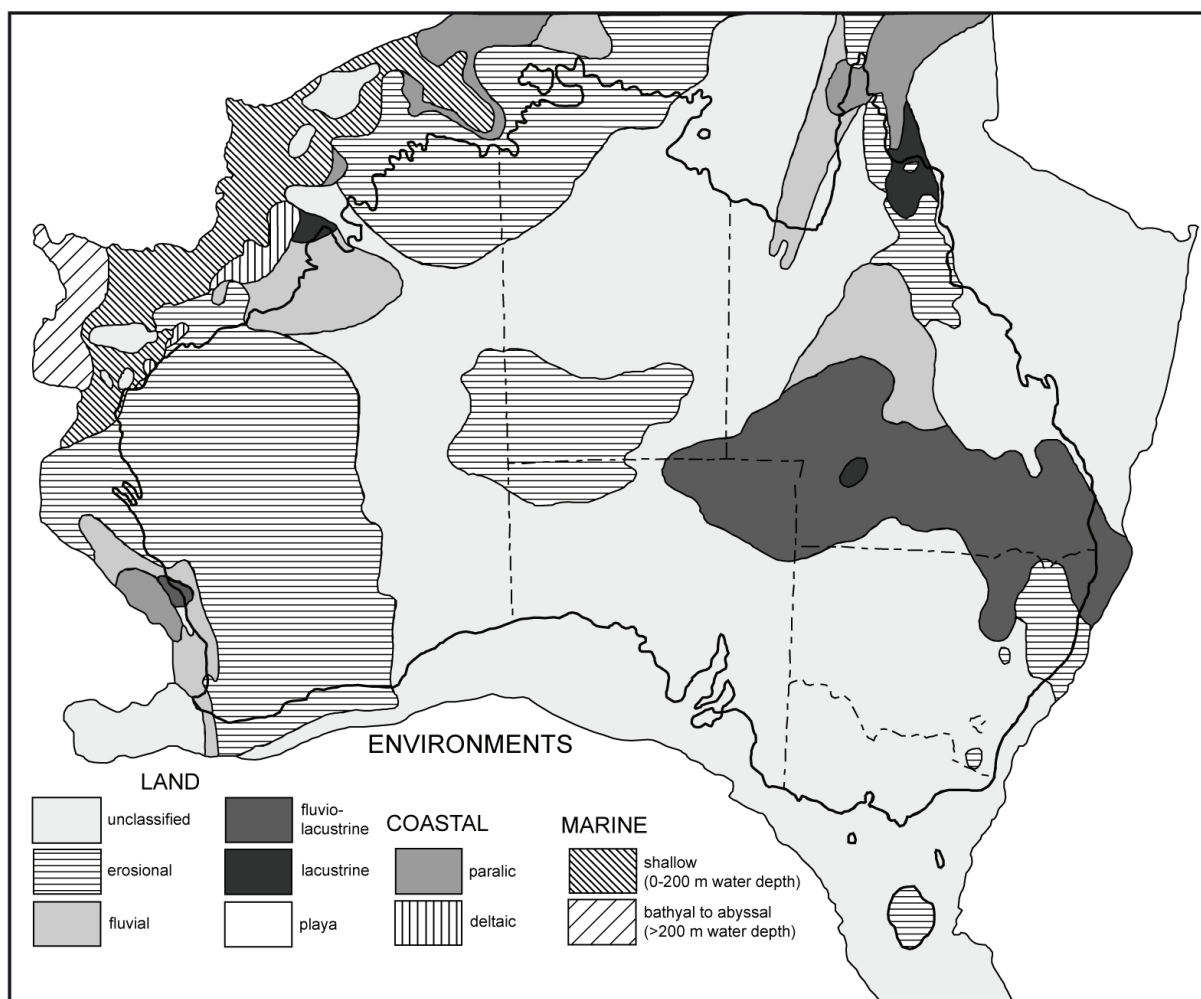


Fig. 2. Jurassic palaeogeography of Australia (modified from Brakel et al. 1995).

## 2. Geological Setting and Stratigraphy

The specimens described in this study were collected from the Inverleigh quarry, intermittently used for siltstone extraction, for brick-making. The locality is situated in the northwestern part of the Clarence-Moreton Basin, which extends from southeastern Queensland to northern New South Wales, Australia (Fig. 3). The basin has been subject to geological in-

km<sup>2</sup> (Goscombe & Coxhead 1995). The initial deposits consisted of extensive quartzose sandstones (Day et al. 1974). Towards the end of the Triassic deposition became more widespread as a result of eustatic changes and regional sagging (Goscombe & Coxhead 1995). The basin is bounded by pre-Permian basement metamorphics and granites and the majority of the sedi-

ments deposited in the basin have been derived from erosion of surrounding basement rocks (Goscombe & Coxhead 1995). Resulting in framework compositions dominated by quartz with lesser proportions of feldspar and lithic fragments (Exon et al. 1974). The sedimentary sequence of the basin can be subdivided into three groups, namely the Woogaroo Subgroup, the Marburg Subgroup and finally the post-Bundamba Group (Wells & O'Brien 1994). The collected samples belong to the Marburg Subgroup, an entirely non-marine succession which predominantly consists of mature quartzose sandstones and shales (Cranfield et al. 1975, Wells & O'Brien 1984, O'Brien & Wells 1994). The Marburg Subgroup is extensively distributed in the basin (Wells & O'Brien 1994) and was deposited by streams flowing generally in a northerly direction (Wells & O'Brien 1984). The sandstones are in general relatively fine-grained, thick-bedded and erosion-resistant (Exon et al. 1974). The Marburg Subgroup is further divided into two major sequences, the basal Gatton Sandstone and the overlying Koukandowie Formation (Fig. 4), which generally is 500 m and 250 m thick respectively (Wells & O'Brien 1994, Goscombe & Coxhead 1995). The former consists mainly of stacked channel sands, whereas the latter constitutes a mixture of sandstones, siltstones and shale units (Wells & O'Brien 1994, Willis 1994). Although previous mapping has not differentiated the Marburg Subgroup into its constituent formations in the northwestern part of the basin, the studied samples are attributed to the Koukandowie Formation based on lithological criteria. In central and eastern

parts of the basin the Koukandowie Formation has been subdivided into the Ma Ma Creek Member and the Heifer Creek Sandstone Member (Wells & O'Brien 1994). The Ma Ma Creek Member, which constitutes the base of the Koukandowie Formation, consists mainly of thin sandstone bodies, mudstones and siltstones (Wells & O'Brien 1984, Willis 1994). The overlying Heifer Creek Sandstone Member is characterised by thick-bedded, coarse to very coarse grained, quartzose sandstone, and granule conglomerate (Willis 1994). The studied samples derive from

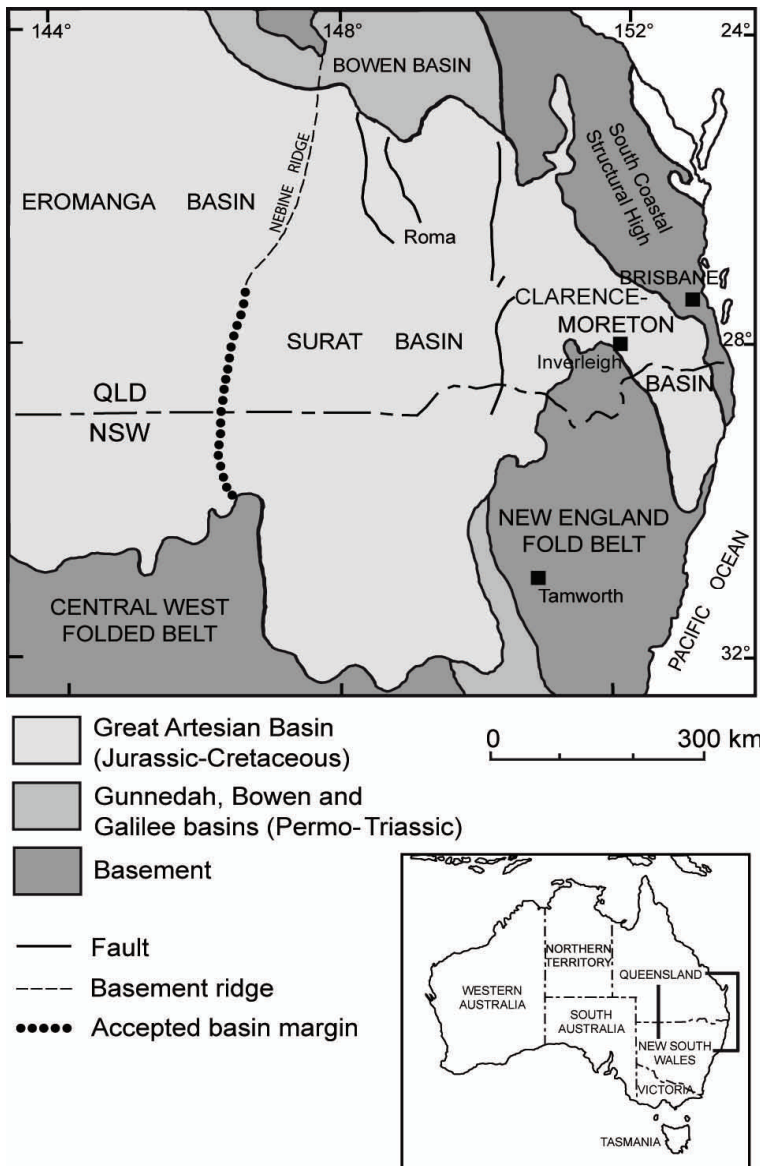


Fig. 3. Regional setting of the Clarence-Moreton Basin (modified from Exon & Burger 1981).

vestigations since the beginning of the 19th century in Queensland and the mid-19th century in New South Wales (Wells & O'Brien 1994). The Clarence-Moreton Basin is a Mesozoic intracratonic basin which overlies mid- to late Palaeozoic rocks (O'Brien et al. 1994). The basin began to develop during the Late Triassic (Day et al. 1983) and covers an area of approximately 43 000



sediments lithologically consistent with the Ma Ma Creek Member. In the area of the Inverleigh quarry the thickness of the Marburg Subgroup has been estimated at about 350 m (Wells & O'Brien 1994).

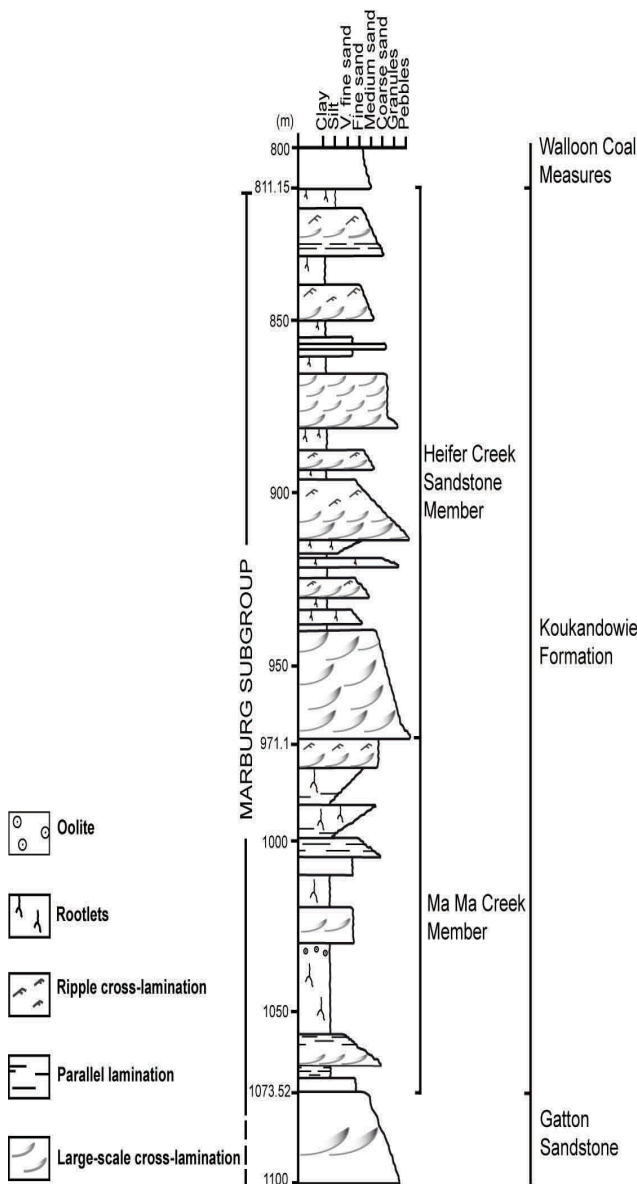


Fig. 4. Generalised graphic log of the Koukandowie Formation, showing the Ma Ma Creek Member (modified from Wells & O'Brien 1994).

### 3. Plant physiology

Vascular land plants had evolved at least by the Middle to Late Silurian and were initially composed of simple stems that were leafless or had only reduced spine-like appendages (Willis & McElwain 2002, Beerling 2005, Harrison et al. 2005). During this early period of terrestrialization, vegetation was restricted to waterlogged environments (Bateman et al. 1998). In order for the vegetation to endure the hostile terrestrial conditions, several structural modifications were required. These included; mechanical support, protection against desic-

cation, efficient water and nutrient transport as well as effective reproduction (Willis & McElwain 2002). The earliest land plants were dependent on turgor pressure to maintain a vertical position (Bateman et al. 1998). However, this constituted a substantial restriction both on plant-height and the plant's ability to support appendages (Bateman et al. 1998). Subsequently, more complex and effective systems for water uptake evolved, which in turn led to less environmentally constrained vegetation (Bateman et al. 1998). In order to further restrict water loss, plants became increasingly cutinized (Bateman et al. 1998). The cuticle is a non-cellular waxy layer that covers the surface of higher plants (Kerp & Krings 1999), and starts to appear in the fossil record from the latest Ordovician (McElwain & Chaloner 1996). The cuticle's main function is to provide protection (Willis & McElwain 2002) and restrict the plant's water loss due to transpiration (McElwain & Chaloner 1996). The cuticle consists of oxidation-resistant, fatty acid polyesters, and therefore the preservation potential for cuticle fragments is high (McElwain & Chaloner 1996). Cuticle features are typically unique for different species and can, consequently, be used for taxonomic studies (Kerp & Krings 1999, Willis & McElwain 2002). Plants developed secondary xylem in the Middle Devonian, this had effects on both water conductance, as well as canopy formation and mechanical support and was probably linked to the extra water required to supply megaphyllous leaves (Bateman et al. 1998).

As the first land plants were leafless they had to photosynthesize from their axes (Willis & McElwain 2002), and leaves did not appear until 40-50 Myr after the first vascular plants had evolved (Willis & McElwain 2002, Osborne et al. 2004, Beerling 2005). The main function of leaves is to capture sunlight, necessary for photosynthesis, and allow plant-transpiration (Clewley et al. 2001). The advent of leaves coincided with a dramatic drop in atmospheric CO<sub>2</sub> concentration, which also corresponded to a marked rise in stomatal density (Beerling 2005). This rise is significant for the evolution of leaves as the stomata constituted a way for the plant to avoid lethal overheating (Beerling 2005). Broad multi-veined leaves first developed among the progymnosperms (Clewley et al. 2001), but leaves in general evolved on at least two independent occasions (Beerling 2005). This resulted in microphylls (lycophytes, clubmosses, spikemosses and quillworts) and megaphylls in euphyllophytes (Beerling 2005). Gymnosperms, together with ferns and angiosperms belong to the second group, and are therefore classified as megaphylls (Beerling 2005, Harrison et al. 2005). However, leaves defined as "megaphylls" are also classified in an ecological sense as microphyllous or megaphyllous based on their surface area (Raunkiar 1934). Microphyllous leaves are generally minute and broadly connected to the stem whereas megaphyllous leaves are attached to the stem by a petiole (Willis & McElwain 2002). The surface of the leaf furthest from the growing apex of

the branch is known as the abaxial side, whereas the upper side (closest to the branch apex) is known as the adaxial side (Watanabe & Okada 2003). The leaf area is divided into different sections, including veinal regions that typically have elongated, rectangular, epidermal cells and interveinal areas that show epidermal cells and stomata (Upchurch 1995).

The first stomata in terrestrial land plants appeared more than 400 million years ago (Hetherington & Woodward 2003), in the beginning of the Devonian (McElwain & Chaloner 1996). The function of the stomata is to control the plant's uptake of carbon dioxide and loss of water due to transpiration (McElwain & Chaloner 1995, McElwain & Chaloner 1996). Two different types of stomatal morphologies exist (Hetherington & Woodward 2003). The first is the graminaceous stomata (Fig. 5.B), which is typical for grass. The second type, which is elliptical in shape (Fig. 5.A), is characteristic for all other types of plants (Meidner & Mansfield 1968, Hetherington & Woodward 2003).

The stomatal aperture is surrounded by two guard cells, which by opening and closing, controls the up-

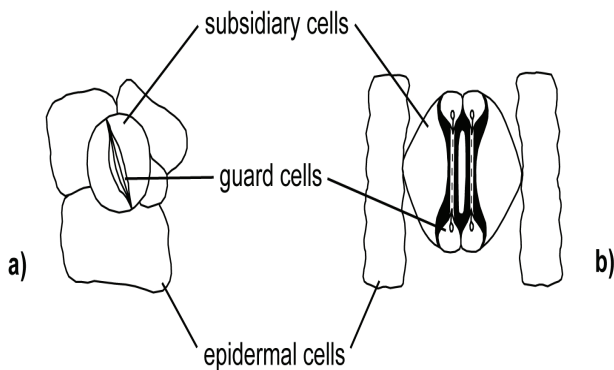


Fig. 5. Stomatal morphology (modified from Meidner & Mansfield 1968). A. Elliptical stomata. B. Graminaceous stomata.

take of carbon dioxide and loss of water (Hetherington & Woodward 2003). The aperture and guard cells are encircled by one or two additional rings of subsidiary cells. Collectively, the guard cells and the subsidiary cells constitute a stomatal complex (Upchurch 1995). Depending on environmental conditions, but also on species, stomata range from 10 to 80  $\mu\text{m}$  in length, densities varying between 5 and 1,000 per  $\text{mm}^2$  of epidermis (Hetherington & Woodward 2003). Stomata are distributed in three main patterns over the leaf surfaces (Meidner & Mansfield 1968, McElwain & Chaloner 1996):

1. Hypostomatous, stomates are restricted to the abaxial surface of the leaf.
2. Hyperstomatous, stomata limited to the adaxial side of the leaf.
3. Amphistomatous, stomata shown on both leaf surfaces.

Morphological differences can occur between stomates on the adaxial and the abaxial side, as in some cases the adaxial stomata feature hairs, horns and other surface appendages, whereas the abaxial stomata do not generally show the same degree of modification (Aston 1978). These morphological differences have been interpreted as protection, as the upper surface of most leaves usually is more exposed than the abaxial side (Aston 1978).

Stomatal density (SD) is an expression for the total number of stomatal apertures in a specific area of the leaf (Poole & Kürschner 1999). However, as the number of stomatal apertures is constant once the guard cells have formed, the value of the stomatal density will fall as the leaf continues to expand (Chen et al. 2001). Therefore, as the stomatal density is sensitive to the state of maturity of the leaf, it is more reliable to use the values of stomatal index (SI) for climatic interpretation (Beerling 1999, Chen et al. 2001, Retallack 2001). Stomatal index is the stomatal frequency expressed as the ratio of stomata to epidermal cells (Greenwood et al. 2003). However, only the stomatal density will be used in this study as the assemblage will not be compared to others, in order to determine climatic variations.

### 3.1. Conifers

The Carboniferous *Swillingtonia denticulata* is the earliest known conifer from the fossil record (Willis & McElwain 2002). Conifer diversity increased throughout the Permian and during the Triassic the group underwent a major radiation, which resulted in the rise of the dominant conifer families (Willis & McElwain 2002).

According to Pole (2000) there are numerous criteria that allow differentiation of conifers from other plant groups in fossil assemblages. These criteria include characteristics such as single and parallel veins, equal cuticle thickness over the epidermal cells, haplocheilic stomatal structure with less than three adjacent lateral subsidiary cells and sunken guard cells over-arched by the surrounding cells (Pole 2000). Furthermore, most conifer leaves have their stomatal apertures arranged in rows (Pole 2000). This arrangement, with stomata in longitudinal files, is a consequence of both epidermal cells and stomata being initiated at the base of the needle and developing henceforth into regular files (Kouwenberg et al. 2003). Additionally, as cuticle features and stomatal arrangement are typically unique for different conifer families, genera and species, they constitute an important taxonomic tool (Kerp & Krings 1999, Willis & McElwain 2002). Extant conifers further possess characteristics such as pyramidal growth form, small simple leaves, and mature stems that are mainly composed of secondary wood (Willis & McElwain 2002). Also, the majority of conifers are evergreen (Eyre 1968).

### 3.2. Ferns

Ferns dates back to the Early Carboniferous, and in many cases these early species show a significant resemblance to extant forms (Willis & McElwain 2002). Ferns are free-sporing pteridophytes that are characterised by well-differentiated stems and large complex leaves that were derived from modified branching systems (Stewart & Rothwell 1993). Sporangia typically occur in clusters called sori and are either attached to the tips, or the margins, of the pinnules or to the abaxial surface of the leaves (Stewart & Rothwell 1993). The majority of ferns are homosporous, meaning that they only produce one kind of spores (Playford & Dettmann 1996). Ferns features alternating gametophyte and sporophyte phases (Fig. 6) during their life cycles (Playford & Dettmann 1996). The spores germinate to gametophytes, which subsequently develop male and female sex organs which in turn produce spermatozoids and eggs (Playford & Dettmann 1996). The egg is thereafter fertilized by a spermatozoid, a process dependent upon the presence of water, and subsequently develops into a sporophyte (Playford & Dettmann 1996).

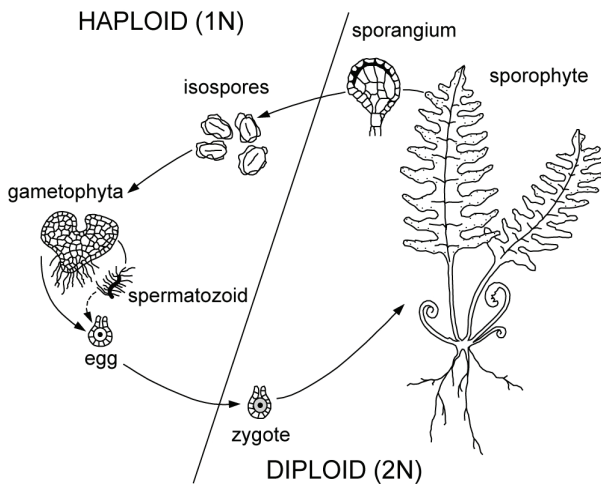


Fig. 6. Lifecycle of a homosporous fern (modified from Playford & Dettmann 1996).

### 3.3. Lycopids

Small herbaceous lycophytes are among the earliest recognizable land plant macrofossils and they constituted a prominent component of the Early Devonian flora (Bateman et al. 1998). *Baragwanathia longifolia*, from the Late Silurian, is the earliest known lycophyte species in the fossil record (Willis & McElwain 2002). During the Devonian several major lycopsid clades evolved, including the three extant families Lycopodiaceae, Selaginellaceae and Isoetaceae, which are all herbaceous plants characterised by microphylls and adaxial sporangia (Stewart & Rothwell 1993, Bateman et al. 1998, Willis & McElwain 2002). All extant lycopids are herbaceous or pseudoherbaceous, but tree-forms are known from the fossil record (Bateman et al.

1998). Isoetaceae constitutes the closest related living group to the considerably more diverse lycopsids of the late Palaeozoic (Bateman et al. 1998). Lycopsids are heterosporous (Fig. 7), which means that the plant produces both microspores and megaspores (Playford & Dettmann 1996). Megaspores, which are the lycopsid's female reproductive units, germinate to produce a female gametophyte. As in the ferns, fertilization is dependent upon the presence of water (Playford & Dettmann 1996).

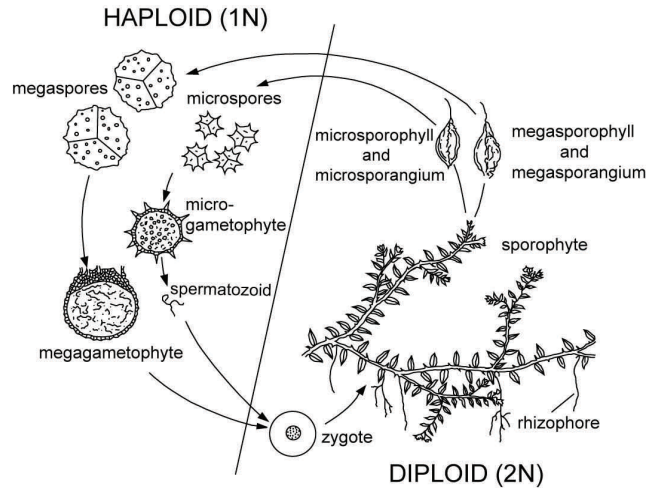


Fig. 7. Lifecycle of a heterosporous lycophyte (modified from Playford & Dettmann 1996).

### 3.4. Mesofossils

The term "mesofossils" is generally used for fossils between ~ 200 µm and 5 mm in diameter and so constitutes material that is possible to see by the eye but not to identify without the aid of a microscope (Collinson 1999).

Megaspores are known from the fossil record since the Early Devonian and are typically found in mesofossil assemblages (Willis & McElwain 2002). Megaspores are regularly between 150 µm and 400 µm in diameter (Willis & McElwain 2002). The term is used for describing larger spores produced by heterosporous plants that germinate to produce the megagametophyte (Sweet 1979). It has been suggested that heterosporous plants could constitute the precursor of seed producing plants (Playford & Dettmann 1996). The form of a megaspore is a result of its relationship to the other members of the tetrad in which it developed (Playford & Dettmann 1996). The most common forms of tetrads (Fig. 8) are termed tetrahedral and tetragonal (Playford & Dettmann 1996). Trilete megaspores with three radiating germinal slits are produced in tetrahedral arrangements (Playford & Dettmann 1996). These spores constitute the basic sporotype and first appeared in the Silurian (Traverse 1988). Monolete megaspores, with a single germinal slit, are produced in tetragonal arrangements (Playford & Dettmann 1996). Megaspores are not as widely dispersed

as isospores and microspores and they are usually produced in lesser quantities (Playford & Dettmann 1996).

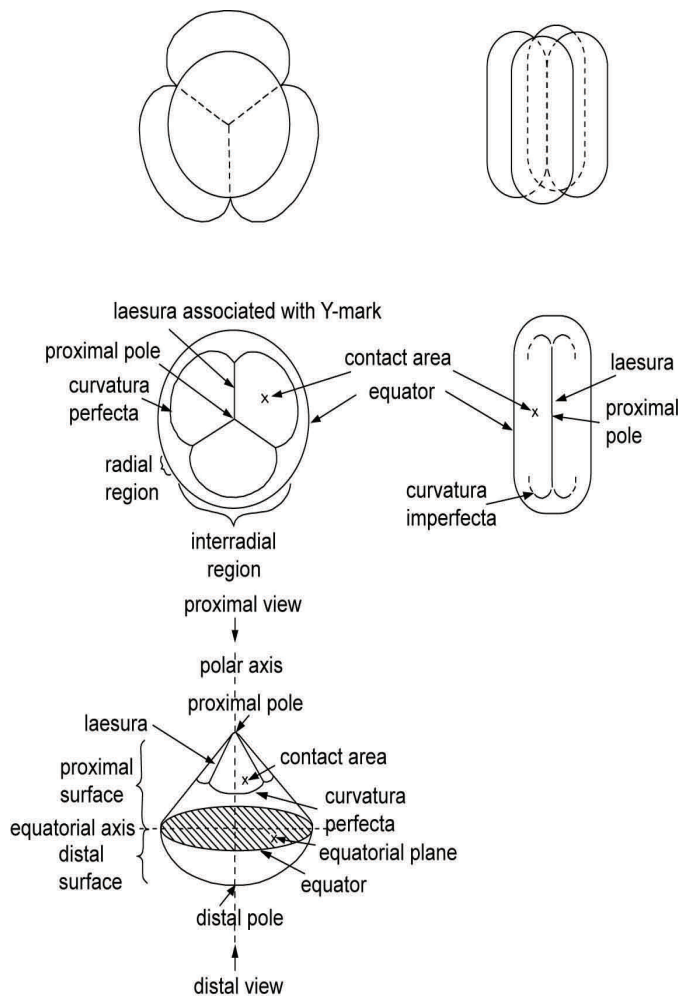


Fig. 8. Tetrad associations. To the left; tetrahedral tetrad, to the right; tetragonal tetrad (modified from Playford & Dettmann 1996).

## 4. Material and Methods

Initial material for this project was collected by Dr. Stephen McLoughlin in 2004, and additional samples were collected by the author in April 2006. Further macrofossil specimens from the same locality is held in the collections of the Queensland Museum, Brisbane. The sampled material consists of light grey, fine sandstones and siltstones. Some parts of the surface of the samples had, due to oxidation, changed to a dusky yellow tone. The samples incorporated parts of lignitized wood and well-preserved shoots with complete and fragmentary leaves. Fossils are preserved as compressions/impressions.

### 4.1. Macrofossils

The samples containing the macrofossils were first carefully numbered. Then, in order to expose the fossils as much as possible, matrix was removed with a

scalpel under a light microscope. The samples were then photographed with a Nikon CoolPix 4500, and illustrations were compiled in Adobe Photoshop 7.0. Finally, the general morphology of the fossils was described and the different components of the plant fossils were measured. Length and width of both shoots and leaves were noted, together with other macromorphological characters such as leaf insertion angles.

#### 4.1.1. Cuticle preparation

In order to release the organic material from the enclosing matrix, samples were placed in plastic beakers in 75% hydrofluoric acid (HF), for about five to eight days. The samples selected for maceration were relatively large (up to 10 × 10 cm), this in order to obtain the most complete and undamaged material. To prevent damage to the fossils, the residue was stirred cautiously during the maceration process and sharp tools were avoided in order to secure as many complete cuticle specimens as possible. After maceration was completed, the residue was washed with distilled water and sieved through a 160 µm mesh. The cuticle samples were then poured into a petri dish and sorted under a light microscope, some of the material was subsequently selected and mounted on SEM stubs. The specimens were coated with gold prior to being examined under a S-3400N Scanning Electron Microscope. To ensure that specimens could be relocated later, sketches of their positions on the SEM stubs were made.

Additional studies of the cuticle material were undertaken using both a light microscope and an OLYMPUS BX41 epifluorescence microscope. Before light microscope studies could be performed, the cuticles had to be treated further to disintegrate the coalified mesophyll tissues (coalified cellular remains trapped between the upper and lower cuticle). This was initially done by placing the material in beakers to which Schulze's solution was added. The solution was then heated for about five minutes and a few drops of NaOH were added in order to accelerate the process. This indeed left the cuticle fragments free from coalified tissues, but the method was not satisfactory as it resulted in badly cracked cuticle specimens. An alternative solution, hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>), proved to be a more appropriate method as it provided a milder maceration. In this case, the leaves were left in the solution for several days on low heat and thereafter rinsed with water and stained with safranin red. The cuticles were then mounted on slides beneath cover slips, in either glycerine or glycerine jelly, and sealed with nail polish. The material was subsequently studied under a light microscope and photographs were taken with an Olympus C55 digital camera. For the epifluorescence microscopy, material both treated in additional disintegrating solutions and only treated in the initial maceration was studied.

## 4.2. Mesofossils

Mesofossils were extracted by bulk dissolution in 75% HF. The residues were then sieved through a 160 µm mesh. The material obtained from the residues was searched through using a light microscope. The mesofossils were subsequently mounted on SEM stubs and their positions were noted. The objects were subsequently studied in a S-3400N Scanning Electron Microscope and the photographs were compiled in Adobe Photoshop 7.0.

### 4.2.1. Megaspores

The macerated material was carefully scanned under a light microscope and all megaspores found were collected. This also included broken specimens, as the structure of the spore wall is of taxonomic significance (Koppellhus & Batten 1992). Several specimens were then mounted on SEM stubs. For obtaining the information necessary for description and taxonomic classification of the megaspores, SEM constitutes one of the most important tools (Collinson 1999). The standard of morphological analysis of megaspores has improved significantly due to improvement and further utilisation of SEM to study them (Batten 1987).

In order to facilitate observation and comparison, specific groups of specimens with similar morphology were placed together. Sketches were then made of the stubs, this to ensure that specimens could be relocated. During the SEM session specimens were assigned different numbers and their orientation was noted. Additional material was mounted in glycerine jelly and glycerine and studied under a light microscope and an epifluorescence microscope. The second approach, however, proved to be of no value as no significant features were observable. Normal transmitted light microscopy did provide useful information on the architecture of the megaspores and was, therefore, used as a supplement to the data obtained from the SEM.

## 5. Results

The macrofossil assemblage in the studied samples is overwhelmingly dominated by well-preserved conifers, which all belong to one taxon. The material includes several complete shoots with attached leaves as well as dispersed leaves and sparse cones. The samples also contain sparse foliage of ferns together with some poorly preserved linear foliage, interpreted as lycophyte microphylls. The cuticle fragments encountered in the macerated material are generally well preserved with both epidermal cells and stomata clearly visible. The organic residue also contains megaspores. Preparation and careful search of the macerated material yielded more than 500 complete and damaged specimens of megaspores, belonging to five different taxa. The mesofossil residue also contains a range of other fragmentary plant remains together with annelid egg cases. Leaf morphological terminology has been adopted from Dilcher (1974).

## 5.1. Systematic palaeontology

### PLANT MACROFOSSILS

Kingdom PLANTAE  
Phylum CONIFEROPHYTA  
Class CONIFEROPSIDA  
Family Uncertain

*Allocladus* Townrow 1967

*Type species:* *Allocladus* Townrow 1967, Jurassic, New South Wales, Australia.

*Diagnosis:* Conifer shoots, leaves close set and spirally arranged. Leaves more or less triangular, 2-8 mm long, with angular margin showing scarious projections. Stomata set in two zones, scattered or showing a weak tendency to be in rows (Townrow 1967).

*Allocladus helgei* sp. nov. (Plate 1, figs. A-G)

*Holotype:* Queensland University of Technology, Brisbane, Australia.

*Etymology, helgei* - In honour and memory of Helge Jansson.

*Diagnosis:* Coniferous shoots reaching a maximum length of 91 mm, bearing spirally arranged leaves with insertion angles at approximately 40° to 50°. Leaf shape is narrowly ovate to lanceolate and tips are acuminate; maximum leaf length is 11 mm. Leaf margins are denticulate with two orders of multicellular denticles.

*Description:* The dimensions of the different specimens vary substantially due to incomplete preservation, but the maximum shoot length is approximately 91 mm. The holotype, which is the broadest specimen at 22 mm, has a total length of 82 mm. Leaves are spirally arranged and typically depart from the stem at angles of 40°-50°. In a few cases the insertion angle is as high as 70°. The leaf tip is incurved by up to 20°. The largest detached leaf within the matrix has a length of 11 mm, and other large specimens have lengths of around 10 and 9 mm. The holotype has notably large, compressed, basal leaves with a length of 13 mm, but leaf length decreases distally. The maximum width of the leaves is 5 mm; the widest point being at approximately one third of the leaf length, measured from the base of the leaf. The mean value of the leaf length is about 8.5 mm and the width approximately 3.3 mm (Appendix 2). The leaves are narrowly ovate to lanceolate in shape and leaf tip is acuminate. When viewed under the light microscope it is evident that leaves bear two different types of apical spines, the first one as previously described and a second, less common type, which has a hooked tip. The terminal spine has an average length of 0.7 mm.

Broad areas of notably elongate cells can be seen all along the leaf margins. These are locally aggregated into narrow spines forming a denticulate margin (Plate 2, figs. A-D). These denticles are composed of multiple parallel cells and are usually acute and somewhat hooked in shape. The largest denticles are located at about one half of the leaf length, thereafter they become gradually reduced in size towards the apex. The maximum length is 375  $\mu\text{m}$  and the average length is 230  $\mu\text{m}$ . The denticle maximum width is approximately 200  $\mu\text{m}$ , whereas the mean value is 128  $\mu\text{m}$ . Denticles are uniformly spaced along the leaf margin in most cases and are separated from each other by about 240  $\mu\text{m}$ . However, in some specimens, denticles seem to be distributed in pairs. Between the major denticles, so called micro-denticles are present (Plate 2, fig. C). These consist of minute spines that are triangular in shape. The micro-denticles occur regularly in groups of two or three.

Stomata are only visible on one side of the leaves; however it is uncertain whether this represents the abaxial or adaxial surface. As trees are predominately hypostomatous (Parkhurst 1978, Shugart 1998), it could be expected that the stomata of the Inverleigh conifer would be situated on the abaxial side. This surface of the leaf is better protected than the upper surface in most plants (Aston 1978). However, in the case of the conifer from the Inverleigh assemblage, the adaxial surface is more strongly protected due to the moderately high insertion angles and incurved apices of the leaves. Hence stomates may have been better protected on the adaxial side of these leaves, making the plant hyperstomatous. The number of stomatal complexes on the leaf surface is significant, with a stomatal density of approximately 12 complexes per 0.25  $\text{mm}^2$ . However, their distribution over the leaf surface is restricted to two distinct areas. These regions are bounded by areas of elongated epidermal cells along the leaf margin and are separated by a central row of rectangular epidermal cells representing a vein region. The marginal epidermal cells have an average length of 75  $\mu\text{m}$  and a width of approximately 16  $\mu\text{m}$ , whereas the epidermal cells in the vein region are about 60  $\mu\text{m}$  long and 30  $\mu\text{m}$  wide. The epidermal cells that are situated in the interveinal regions between the stomatal rows (Plate 2, fig. F) are generally more equidimensional in shape than the other epidermal cells. On average they measure 60  $\mu\text{m}$  long and 30  $\mu\text{m}$  wide. Epidermal cells that are situated in the interveinal region, between stomatas (Plate 2, fig. F), are typically shorter and measure on average 40  $\mu\text{m}$  long and 45  $\mu\text{m}$  wide. These cells are characterised by being somewhat more rounded in outline than the other epidermal cells. Stomatal complexes occur in short irregular rows, with up to seven complexes, and the apertures are orientated parallel, oblique and transverse to the line of the stomatal files. The complexes are somewhat sunken and slightly oval to circular in shape, and typically measure close to 60  $\mu\text{m}$  long and 40-50  $\mu\text{m}$  wide. The stomatal aperture and guard cells

are surrounded by a narrow ring of four to six subsidiary cells. The stomatal complex is, therefore, classified as cyclocytic (Upchurch 1995, Prabhakar 2004). The subsidiary cells have a typical width of 10-20  $\mu\text{m}$  and they have the same colour as the surrounding epidermal cells, hence the leaf cuticle-thickness is essentially uniform (Retallack 2001). Inside the aperture, lie the deeply sunken approximately 10  $\mu\text{m}$  elliptical to reniform guard cells. Stomata frequently appear as round, open holes as the guard cells commonly have detached. When viewed in SEM, stomates are hardly visible, probably due to waxy plugs that fill the aperture.

#### *Comparison and remarks:*

In order to clarify the family affinities of the specimens collected from the Inverleigh quarry, the material was compared with an extensive reference collection of gymnosperm cuticle placed at the author's disposal by Doctor Mike Pole, at The University of Queensland. The reference collections consist of several hundred slides of cuticular material prepared from leaves of a broad spectrum of species within each of the established conifer families. The pertinent characteristics of these families are outlined in Appendix 1 for comparison to the Inverleigh conifer. When comparing the cuticle of the conifer obtained from the Inverleigh quarry with the reference collection it is apparent that the Inverleigh species exhibits some unusual cuticle features that do not match closely with any of the established families. Furthermore, the study of the cuticular reference collection reveals that no single morphological character can be used to consistently differentiate representatives of the different families. Rather, a suite of characters must be used for confident attribution of a species to a particular family.

The Inverleigh conifer is most dissimilar to the families of Taxaceae/Cephalotaxaceae and Pinaceae in that these groups possess needle-like leaves. Furthermore, the stomatal arrangement differs, as these families are characterised by regularly arranged and oriented stomates. Also, both Taxaceae/Cephalotaxaceae and Pinaceae are predominantly distributed in the Northern Hemisphere. The family Cheirolepidaceae are characterised by very small leaves and by papillae, a feature that the Inverleigh conifer lacks. The foliar morphology rules out the Inverleigh conifers being attributed to the Cupressaceae, as members of the family typically display scale-like whorled leaves. A Taxodiaceae affinity is also unlikely as these commonly have a larger number of subsidiary cells. Furthermore, members of this family may also possess papillae. The remaining families Araucariaceae and Podocarpaceae, were the two dominant conifer families of swamps and forest mires in the Southern Hemisphere during the Mesozoic (Stockey 1989, Greb et al. 2006). Of these, a podocarpacean affinity is not as likely as an araucariacean, as the former typically have their stomatal complexes arranged into notably regimented files. Also, podocarp stomata display two

prominent polar and two lateral subsidiary cells. Araucariaceae have short files of stomates, of four to six subsidiary cells, similar to the arrangement in the Inverleigh conifer. Furthermore, they display characteristics such as variably orientated apertures and waxy plugs. However, no araucarians with toothed margins are known. Also, no typical araucarian cone scales have been found in the Inverleigh assemblage and the associated cone type that has been encountered is a loose structure that does not resemble araucarian cones. Therefore, even though some characteristics match, the Inverleigh material can not be assigned unequivocally to any family.

The assemblages closest in age and geographic proximity to the Inverleigh flora derive from the Walloon Coal Measures (Middle Jurassic) of the Clarence-Moreton Basin and the neighbouring Surat Basin. Conifers are well represented in the Walloon flora and much of the foliage has thick cuticle (Gould 1980). The flora is dominated by the families Podocarpaceae and Araucariaceae (McLoughlin & Drinnan 1995), represented by leafy shoots, cone scales and pollen cones (Gould 1980). Podocarps include *Mataia podocarpoides* Townrow 1967 and possibly *Elatocladus planus* Seward 1918 (Gould 1980). The araucarians are represented by *Araucaria crassa* Townrow 1967, *Allocladus rajmahalense* Townrow 1967, *Al. cribbii* Townrow 1967, *Al. heterophyllus* Townrow 1969 and *Pagiophyllum feistmantelii* Halle 1913 (Gould 1980). Of these, the taxa most similar to the material found in the Inverleigh quarry are those belonging to *Allocladus*. However, the leaves of *Allocladus rajmahalense* are orbiculate in shape, the apex is close to obtuse in outline and they show no denticles (Townrow 1967). The leaves belonging to *Allocladus cribbii* are almost oblate in shape and the apex is markedly rounded. Furthermore, no marginal denticles can be seen (Townrow 1967). *Allocladus heterophyllus* also differs from the Inverleigh conifers as its leaf shape is oblong and denticles are absent (Townrow 1969). The Inverleigh conifer shows closest resemblance to some other Gondwanan conifers, such as *Allocladus milneanus* and *Otwayia hermata*.

*Allocladus milneanus* (Tenison Woods) has been found in the Early to Middle Jurassic Talbragar assemblage of New South Wales (described by Townrow 1967 and White 1981). This species strongly resembles the Inverleigh specimens (characteristics are outlined in Appendix 3 for comparison). Similarities include features such as leaf distribution, spiral arrangement around the stem, and leaf shape (White 1981). Furthermore, leaves are about 8 mm long and 3 mm wide at their widest (Townrow 1967). Leaf margins display denticles and stomata are distributed in two zones over the leaf surface. However, *Allocladus milneanus* differs from the Inverleigh specimens in some important aspects. Firstly, it is strictly dicyclic, meaning that there are two rings of subsidiary cells encircling the guard cells (Prabhakar 2004). Furthermore, leaf insertion angles differ by at least 10° and stomata

are arranged in groups of two to five complexes instead of in short rows (Townrow 1967). Moreover, the number of subsidiary cells of *Allocladus milneanus* varies from three to six, whereas four to six characterize the Inverleigh conifer. Also, the stomatal complexes of *Allocladus milneanus* are deeply sunken, Townrow (1967) even described it like a pit. Unlike the Inverleigh conifer, the outer edges of the stomatal complexes of *Allocladus milneanus* are overhung by encircling cells. The denticle's length and distribution pattern (Fig. 9) also differs from that of the Inverleigh conifer.



Fig. 9. *Allocladus milneanus*, denticle distribution along leaf margin (modified from Townrow 1967).  $\times 10$

*Otwayia hermata* Tosolini & McLoughlin 2002 have somewhat smaller twigs reaching approximately 32 mm long (McLoughlin et al. 2002). Leaves are spirally arranged but small and appressed. The leaves are incurved and oval to lanceolate in shape. The apex is acute and formed by elongate epidermal cells resembling the Inverleigh conifer. However, the former differs in having a strong abaxial keel on the leaves (McLoughlin et al. 2002). The leaves of *O. hermata* are amphistomatic and the stomates are cyclocytic, sunken and surrounded by four to six subsidiary cells. Unlike the Inverleigh conifer, *O. hermata* bear papillae that cover the stomatal pit (McLoughlin et al. 2002). The Bohemian Cretaceous conifer, *Brachyphyllum squamosum* displays similarities such as a

serrate margin. *Brachyphyllum squamosum* shoots are spirally arranged with partially overlapping leaves (Němejc & Kvaček 1975). Leaves are described as triangular in shape, with an indistinctly marked central vein, attached by a broad base and are approximately 8 mm long and 4 mm broad (Němejc & Kvaček 1975). Similarly to the Inverleigh specimens, stomata is not arranged into distinguished rows. However, *Brachyphyllum squamosum* differs as most stomatal complexes are transversally orientated. Further more, epidermal cells show a somewhat undulating outline not seen in the Inverleigh specimen. *Brachyphyllum squamosum* leaves do show a denticulate margin, but it differs from the Inverleigh conifers as denticles are much more closely set and of regular length.

Although only one detached cone type has been obtained from the Inverleigh material no connection has been identified and the Inverleigh conifer has been assigned to the genus *Allocladus*, based upon numerous key features. However, it possesses several characteristic features not seen in any other species. Hence it has been assigned as a new species.

Kingdom PLANTAE  
Phylum POLYPODIOPHYTA  
Class POLYPODIIDA  
Order OSMUNDALES  
Family OSMUNDACEAE

*Cladophlebis* Brongniart 1849

*Type species: Cladophlebis albertsii* (Dunker) Brongniart 1849; Cretaceous (Wealden?), Germany.

*Cladophlebis* sp. (Plate 3, figs. A,B)

*Description:* The preserved frond fragments are bipinnate with a maximum length of 43 mm. The rachis is relatively slender; with an approximate width of 0.3 mm. Pinnules are uniformly distributed along the frond, sub-opposite to alternate with moderately close spacing. Pinnules are inserted on the rachis at approximately 80-90°. Pinnules are lanceolate and slightly incurved towards the stem. Pinnule bases are attached to the stem by their whole length. The apex is acute to rounded in outline and margins are entire. The largest attached pinnule has a maximum length of 14 mm and a maximum width of approximately 5 mm, the widest point being at the base.

*Comparison and remarks:* *Cladophlebis* foliage may be affiliated with a range of fern families, however, most examples are linked to the Osmundaceae (McLoughlin et al. 2002). No more than two incomplete specimens have been encountered in the collected material from the Inverleigh quarry. The description is based solely upon these specimens and the preservational state makes cuticular analysis impossible.

INCERTAE SEDIS

*Sphenopteris* (Brongniart) Sternberg 1825

*Type species: Sphenopteris elegans* (Brongniart) Sternberg 1825; Carboniferous, Silesia.

*Sphenopteris* sp. (Plate 3, figs. C,E)

*Diagnosis:* Incomplete fronds that reaches a maximum length of 36 mm, bearing closely set pinnules with insertion angles at approximately 40°-50°. Pinnules are elongated and narrowly ovate in shape. Base is obtuse cuneate and apex acute. Pinnules are up to 11 mm long and 3.5 mm wide.

*Description:* At least bipinnate foliar fragments with a maximum length of 36 mm and a width of approximately 10 mm. The rachis is comparatively thick (approximately 1 mm). Pinnules are narrowly ovate, closely spaced and typically depart from the rachis at angles of 40°-50°. The pinnules become gradually smaller towards the apex of the fronds. Pinnule attachment is contracted or normal acute. In the later case the base appears to be symmetrical and obtuse cuneate in shape. The apex is possibly serrated, acute to rounded and shows no tendency of either incurving or recurving. The largest attached pinnae have a length of 11 mm and a width of 3.5 mm; the widest point being at approximately half way from the base to the tip.

*Comparison and remarks:* Three incomplete specimens are available in the collection and description is based upon these. Measurements of length and width are based on the largest available fragments. As specimens are preserved as incomplete films of coalified matter they can not be used for cuticular analysis.

INCERTAE SEDIS (Plate 3, fig. F)

Indeterminate fern foliage

*Description:* A single, incomplete, specimen present in the fossil collection measures 30 mm long and 14 mm wide. Only the rachis and one side of the lamina have been preserved. Therefore, the width of a complete specimen is estimated to be close to 30 mm. The rachis is relatively thick (approximately 1.5 mm wide). Pinnules are moderately spaced and typically depart from the rachis at angles of 60°. They are attached to the rachis along the entire length of their base. The pinnules are oblong and the apex is rounded. The largest attached pinnule is 15 mm long and has a maximum width of 5 mm; the widest point being at the middle. Pinnules also display a faint, but straight, central vein.

*Comparison and remarks:* The description is based



solely upon fragments of one specimen encountered in the Inverleigh material. The specimen is preserved as an incomplete coal film and can not be used in cuticular analysis. The specimen resembles *Cladophlebis* sp., however it displays prominent veins and pinnules are more oblong in shape.

INCERTAE SEDIS (Plate 3, figs. G,H)

Indeterminate minute fern foliage

*Description:* Two minute fronds are available, measuring 5 and 8 mm long respectively, widths are approximately 2 mm. Leaves are about 1-1.5 mm long and width is about 0.7 mm. The foliage of the larger specimen is lanceolate with an acute apex. The apex of the smaller specimen is somewhat more rounded in shape.

*Comparison and remarks:* Two specimens have been found in the Inverleigh assemblage. Both are preserved as thin coal films, and hence cuticular analysis is impossible. This form is distinguished by its diminutive size but it is possible that the fossils represent distal pinnae fragments of one of the other fern species.

Phylum LYCOPHYTA  
Class LYCOPSIDA  
Order ISOETALES  
Family ISOETACEAE

*Isoetes* Linnaeus 1753

*Type species:* *Isoetes lacustris* Linnaeus; extant.

*Isoetes* sp. (Plate 3, fig. D)

*Description:* Needle-like fragments measuring several centimetres long and approximately 0.5 mm in width. The leaves are entire, pointed, and may possess a single central vein.

*Comparison and remarks:* This species is represented by numerous dispersed plant fragments occurring throughout the samples obtained from the Inverleigh quarry. Fragments are preserved as thin coal films and it is, therefore, not possible to obtain cuticular details. The shape of the leaves resembles that of fossil isoetalean lycophytes. Isoetalean leaves (microphylls) are usually not large, complex or branching (Dilcher 2001) and are commonly dispersed after plant death. An isoetalean affinity is also supported by the abundance of co-preserved megaspores throughout the deposits.

## ANIMAL FOSSILS

Kingdom ANIMALIA  
Phylum ANNELIDA  
Class EUCLITELLATA

*Burejospermum* Krassilov emend Manum, Bose and Sawyer 1991

*Type species.* *Burejospermum crassitestum* Krassilov 1972; Cretaceous, Russia

*Burejospermum* sp. (Plate 4, figs. A-C)

*Description:* Two complete specimens and three fragments have been encountered in the Inverleigh material, these are orange to golden in colour. The largest intact specimen is 9 mm long and 6.5 mm wide, whereas the smaller specimen measures 7 mm long and 4 mm wide. The objects are ovoid and consist of a more robust inner layer covered by a thin, three-dimensional, irregular fibrous network.

In addition, acid-resistant, smooth fragments in the shape of a meshwork have been encountered in the macerated material. The fragments are lustrous, and orange to golden in colour. The most complete specimen is double folded, 1700  $\mu\text{m}$  long and 1150  $\mu\text{m}$  wide. Filaments vary considerably in size, with diameters of 15-60  $\mu\text{m}$ . Areolae are irregular rectangular to oval in shape, with regularly rounded inner edges. The size of the areolae is mainly consistent with maximum dimensions of 55-60  $\mu\text{m}$ . Furthermore, a circular object measuring about 1.75 mm has also been encountered in the macerated material. The specimen is golden in colour and shows no marked surface ornamentation.

*Comparison and remarks:* *Burejospermum* constitutes a sac-like, netted, waxy fabric and belongs to the informal group hapsidarch mesofossils (Manum et al. 1991). Hapsidarchs represent fossils that appear as compressed sacs or barrels and possess netted fabric (Manum et al. 1991). Four principal morphologies can be recognised among the hapsidarchs, of which *Burejospermum* and *Dictyothylakos* have been the objects of most studies (Manum et al. 1991). Both *Burejospermum* and *Dictyothylakos* are sac-like in shape and consist of network structures. They both show a substantial resemblance to each other and they are almost invariably associated with each other (Manum 1996). However, *Burejospermum* differs from *Dictyothylakos* as the network is supported by a solid membrane (Manum 1996). *Burejospermum* is also considerably larger, as the sacs can measure up to 15-22 mm across, whereas *Dictyothylakos* rarely exceeds five mm (Manum 1996). The affinities of both *Dic-*

*tyothylakos* and *Burejospermum* have been the topic of much debate. The variety of interpretations of *Dicthyothylakos* is more extensive than for *Burejospermum*, and these range from algal remains to the inner wall of a mesosporangium (Hueber 1982, McLoughlin et al. 2002). Additionally, *Burejospermum* has been interpreted as seed coats, ginkgoalean seeds and insect cocoons (Manum et al. 1991). However, Manum (1996) rejected a plant origin and they have lately been ascribed a zoological affinity. Manum (1996) interpreted these bodies to represent degraded egg cases of leeches (*Hirudinea*) or earthworm (*Oligochaeta*) cocoons. Leeches and earthworms are both segmented, soft bodied animals that are distinguished by the clitellum (Fig. 10). The clitellum constitutes a highly specialised organ, which contains glands used for copulation and formation of egg-cases or cocoons (Manum 1996). The cocoon forms around the clitellum and consists of a dense inner layer, the alytine, which supports a fibrous outer layer, the hapsine (Manum et al. 1991, Manum 1996). The hapsine develops first by secretion from one type of gland, thereafter the alytine forms by another type of gland (Manum 1996). Before the animals withdraw and seal the cocoon, eggs and a food reserve are deposited (Manum 1996). Mesozoic and Cenozoic cocoons assigned to clitellates, are characterised by a well developed hapsine which makes it possible to

recognise even small fragments (Manum 1996).

The two complete specimens that were encountered during the preparation of the material were indeed initially interpreted as seeds. However, the irregular surface structures of both the objects, a feature that is even more prominent on macrophotography (after fuming the specimens with salmiak), raised uncertainties about their identification as seeds. After viewing the material in macrophotography's it became apparent that the objects were not seeds. This conclusion is based on the fact that the objects are acellular and that they lack seed characteristics such as a micropyle and chalaza (Manum 1996). Instead the fossils have been interpreted as egg cases. Considering the object's shape and size, and the fact that they consist of a continuous inner layer, they have been assigned to *Burejospermum*. The acid-resistant, mesh-work fragments have also been assigned to the same taxon as the hapsine of *Burejospermum* is characterised by being well developed (Manum et al. 1991). As for the third type of object, it has been interpreted as a detached operculum. As it has withstood maceration and it consist of a robust layer, that bears no areolae or other architectural elements, it has also been assigned to *Burejospermum*.

*Distribution:* Reports of *Burejospermum* mesh fragments are comparatively rare and they have only been reported from palynological and cuticle studies (Manum 1996). Fragments were first recorded by Michael (1936) and since then fragments have been encountered in deposits ranging from the Late Triassic to Paleocene, mostly in coal and plant litter beds (Manum et al. 1991, Manum 1996). However, the records from the Late Triassic are quite diverse so it is most likely that they occurred earlier. They are sporadic elements in the macerated Inverleigh samples and these records appear to be the first identification of such remains from the Early Jurassic (Manum et al. 1991).

### MEGASPORES

The mesofossils described below are listed alphabetically and under informal nomenclature as no natural classification scheme yet exists for dispersed lycophytic megaspores and the generic affinity of some specimens in the Inverleigh assemblage is unclear. Spore morphological terminology has been adopted from Kremp (1965), Traverse (1988) and Playford & Dettmann (1996). All measurements are made from wet samples (dimensions may reduce by 20% upon desiccation). All measurements were made at spores that were studied in proximal view. These megaspores appear to be the first Australian megaspores reported from the Early Jurassic (Kovach & Batten 1989, Batten & Kovach 1990).

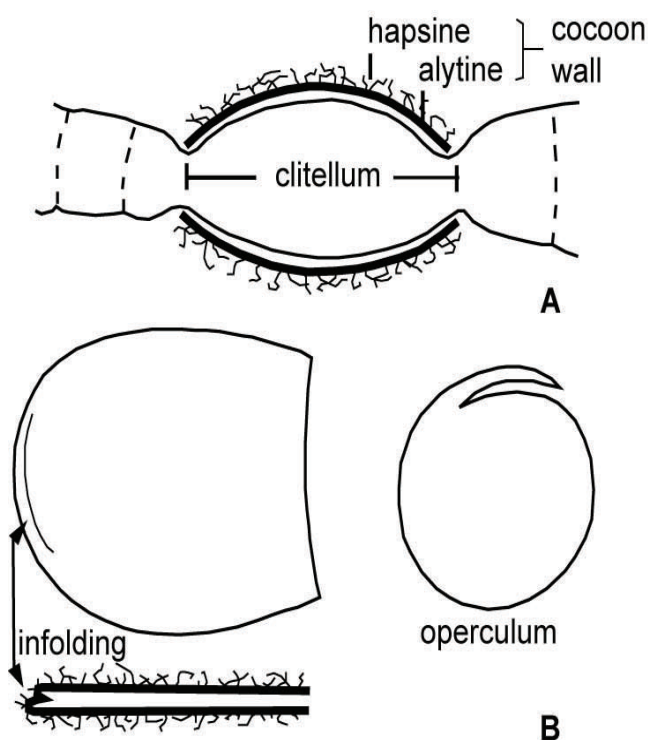


Fig. 10. A: Cocoon formation around clitellum. B: fossil compressed cocoon and operculum in surface view and section (modified from Manum 1996).

Kingdom PLANTAE  
Phylum LYCOPHYTA

***Minerisporites*** Potonié 1956

*Type species: Minerisporites (Selaginellites) mirabilis* (Miner) Potonié 1956; Paleocene, Montana.

***Minerisporites*** sp. (Plate 5, figs. A,B. Plate 6, figs. A-C)

*Description:* Somewhat pyramidal megaspores with a convexly subtriangular amb. The equatorial diameter of the megaspores is in the range 235-335 µm. Labrae are weakly developed with an average width of 10 µm. Labrae are straight to slightly sinuous and the labrae crest is undulating. Labrae usually extend beyond the equator, and then connect with a limited zona, an auricle. Auricles rarely exceed 50 µm in length. The interradiation regions, either lack a fully developed zona, or only display a denticulate fringe. The proximal side of the megaspore forms a low pyramid and contact areas are slightly sunken. The surface ornamentation is weakly granulate to reticulate.

*Remarks:* These megaspores are attributable to *Minerisporites*, which represents hemispherical, trilete, zonate megaspores with a roughly circular amb, straight to slightly sinuous labrae, and more or less reticulate ornamentation (Batten & Koppelhus 1993). The megaspores resembles *Minerisporites* sp. cf. *M. patagonicus* described by Archangelsky & Villar de Seoane (1989). However, the Inverleigh megaspore displays a wider and somewhat more sinuous labrae.

*Distribution:* This type of megaspore is by far the most abundant species obtained from the macerated material from the Inverleigh quarry.

***Paxillitriletes*** Hall & Nicholson 1973 emend Batten & Koppelhus 1993

*Type species: Paxillitriletes (Thomsonia) reticulatus* (Mädler) Hall & Nicholson 1973; Berriasian, Germany.

***Paxillitriletes*** sp. (Plate 5, figs. C,D. Plate 6, figs. D-F)

*Description:* A trilete megaspore with an equatorial diameter of 325-365 µm and convexly subtriangular amb. The trilete mark is somewhat hard to distinguish due to a 125 µm wide zone of notably prominent capilli that flank the labrae. Labrae extend to the zona, which has a maximum width of 100-125 µm. The surface ornamentation is prominent and rugulate to reticulate.

*Comparison and remarks:* The megaspores show close resemblance in size and morphology to mem-

bers of the genus *Paxillitriletes*. This genus incorporates hemispherical, zonate megaspores with a row of prominent ornamental projections flanking the laesurae on both sides. Ornamentation is reticulate to scabrate and capilli are prominent. The megaspores resembles *Paxillitriletes rintoulensis*, with its distinguished surface ornamentation. However, the capilli of *P. rintoulensis* is not as strongly developed.

*Distribution:* The mesofossil assemblage contain several megaspores of this type. They are mostly preserved in equatorial view and they are easily distinguishable in this state, even in low magnification, owing to their pronounced radial extensions of the zona and prominent capilli on the proximal surface.

***Megaspore type 3*** (Plate 5, figs. E,F. Plate 6, figs. G,H)

*Description:* Roughly spherical megaspores with a circular amb. The megaspores are laevigate and do not display a well-defined trilete mark or zona. The equatorial diameter ranges between 210-240 µm.

*Distribution:* Only a few complete megaspores have been obtained, together with sparse damaged specimens. The laevigate nature of this megaspore suggests affinities with *Trileites* (Erdtmann) Potonié 1956 or *Banksisporites* Dettmann emend Banerji, Kumaran & Maheshwari 1978 but the lack of diagnostic characters prevents confident assignation.

***Megaspore type 4*** (Plate 5, fig. G)

*Description:* Trilete megaspore with a triangular amb., reaching an equatorial diameter of 300 µm. Labrae are straight and weakly developed with a somewhat undulating ridge. The labrae extend beyond the equator and to the edge of the cingulum. The cingulum has a maximum width of 90 µm and its edge is vaguely denticulate. The cingulum and contact areas have a uniform elevation. Surface ornamentation is granulate.

*Distribution:* Only one single specimen has been found in the collected material.

***Megaspore type 5*** (Plate 5, fig. H)

*Description:* Trilete spore with a convexly subtriangular amb. Equatorial diameter reaches 350 µm. Labrae are not very prominent and the ridge are weakly denticulate. The labrae extend beyond the equator. The zona is mostly developed in the radial areas and has a smooth outline. Surface ornamentation is granulate to laevigate.

*Distribution:* One specimen has been found in the macerated material. It differs from megaspore sp. 4 by the lack of a denticulate fringe on the zona.

## 6. Discussion

The results from this study show that the Inverleigh assemblage constituted a low diversity flora dominated by one conifer species. This conifer has been assigned to the genus *Allocladus*. However, it exhibits features so significant that it has been referred to a new species, namely *Allocladus helgei*.

### 6.1. Age of the biota

The Early Jurassic and Early Cretaceous floras of Australia differ little from each other and are generally similar to the *Ptilophyllum* flora of India, which also has a comparable time range (Gould 1980).

The Marburg Subgroup, to which the specimens of this study belong, conformably overlies the Ripley Road Sandstone that has previously been regarded as wholly Upper Triassic (Exon et al. 1974). However, a palynological study of sediments from the Ripley Road Sandstone has showed that they range into the lowermost Jurassic (Exon et al. 1974). The Marburg Subgroup constitutes an entirely non-marine succession largely composed of extensive fine-grained and thick-bedded sandstones. This is consistent with the fact that the Early Jurassic was marked by extensive fluvial sedimentation in the Clarence-Moreton Basin (Day et al. 1983). Nonetheless, Whitehouse (1955) suggested an Upper Triassic age for the Marburg Subgroup, an interpretation based on the identification of a jawbone fragment. However, this is an uncertain dating method as it is based solely on an incomplete specimen of uncertain identity. Later palynological studies have shown that the formation is Lower Jurassic in age (Exon et al. 1974), which means that the jawbone fragment may be reworked, misidentified, or that the animal had a longer range than previously thought. The most recent palynological investigations of the succession by Burger (1994) indicates that the lower parts of the Koukandowie Fm (Ma Ma Creek Member equivalents) across the basin are referable to his Assemblage D, J2 and J3 palynozones. He correlated these with the Pliensbachian to early Aalenian chronostratigraphic stages, the formation is apparently diachronous across the basin. However, the palynological samples obtained from this unit in the nearest boreholes (GSQ19-22R) to the Inverleigh quarry are assigned to Burger's (1994) Assemblage D. This is equivalent to Pliensbachian to earliest Toarcian age, and hence this is considered the most likely age for the Inverleigh assemblage.

### 6.2. Comparisons to other Mesozoic macrofloras

According to Gould (1980) no major floristic changes took place during the Jurassic. Studies of different fossil macrofloras from Australia support the conclusion that the period was characterised by floras with a cosmopolitan disposition (McLoughlin et al. 2002).

The southern extension of the Surat Basin in New South Wales contains the Early to Middle Jurassic

Merrygoen Ironstone Member which hosts the well-studied Talbragar fossil assemblage. This flora is primarily dominated by conifers and seed-ferns (White 1981). The flora contains numerous members of the conifer families *Podocarpaceae* and *Araucariaceae* (White 1981) whereas the Inverleigh flora contains just a single conifer. Different fern types, such as members of the family Dicksoniaceae, can also be found in the Talbragar flora (White 1981). The Talbragar assemblage is significantly more diverse than the Inverleigh flora, suggesting that the former assemblage contains plant remains derived from a broader range of environments. However, the similar quality of preservation of the assemblages suggests that the Talbragar plants were not extensively transported. The Inverleigh assemblage may, therefore, represent a more specialized floodbasin mire flora.

The Walloon Coal Measures of the Surat and Clarence-Moreton basins consist of Middle Jurassic sandstones, coals, siltstones and mudstones (McLoughlin & Drinnan 1995). The rich flora of these deposits has been described by authors such as Gould (1980) and comprises liverworts, lycopods, equisetaleans, ferns, seed-ferns, possible pentoxylaleans, and conifers. As the assemblage contains abundant, and relatively complete, remains of delicate plants such as ferns and equisetaleans, lacustrine and paludal environments have been suggested for the plant-bearing beds, a theory, which is further enhanced by the fine grained sediments (McLoughlin & Drinnan 1995). Massive conifer-like trunks, which exhibit prominent growth rings, have also been found within the deposit (Gould 1980) indicating strongly seasonal growth conditions. The Walloon assemblages are considerably more diverse than the one seen in the Inverleigh quarry and may represent a broader range of depositional environments and local ecosystems.

The Tyers River Subgroup is an Early Cretaceous unit in the Gippsland Basin of southeastern Australia. It contains gravely to sandy channel deposits and siltstones. The palaeoenvironment have been interpreted as an alluvial valley setting (McLoughlin et al. 2002). Six major fossil associations have been recognized within the Subgroup (McLoughlin et al. 2002). The assemblages contain three different families of, generally very small leafed, conifers species (McLoughlin et al. 2002). Seed-ferns are the most abundant group and fern foliage and liverworts constitute a subsidiary component of the biota (McLoughlin et al. 2002). Clitellate egg cases have been found in the sediments and representation of lycophytic megaspores is generally low in the biofacies (McLoughlin et al. 2002). The Tyers River Subgroup floral assemblage differs from the Inverleigh biota as it is more diverse, something which may reflect a broader range of depositional environments. Furthermore, the dominance of seed-ferns in the Tyers River Subgroup compared to the assemblage found in the Inverleigh quarry may indicate a cooler, moister, higher latitude setting (McLoughlin et al. 2002).

### 6.3. Palaeoclimatic setting/ Palaeoenvironment

The palaeoclimates of the Early Jurassic can broadly be deduced by using different climatic parameters. Plants, as well as animals, are directly affected by climatic conditions and respond to it in terms of morphology, abundance, diversity and distribution in an ecosystem (McLoughlin et al. 2002). Amongst fossils, terrestrial plants constitute one of the most responsive indicators of changes in atmospheric conditions. High-resolution investigation of floral recovery patterns can distinguish events of short duration from the more long term changes (Vajda & McLoughlin 2006). This includes parameters such as humidity, insolation and temperature (McLoughlin et al. 2002). Fossil plants could also be used as indicators when establishing information about the substrate, such as ground moisture and fertility levels (McLoughlin et al. 2002).

The climatic conditions that prevailed in Australia, and particularly the study area, during the Early Jurassic were largely a function of its position at middle to high palaeolatitudes, between 40°-60° (Willis & McElwain 2002). This position, coupled with globally warm conditions in the Mesozoic, meant that Australia probably fell within the warm temperate vegetation biome (Rees et al. 2000, Willis & McElwain 2002, Greb et al. 2006). This resulted in a generally high diversity flora, dominated by ferns, sphenopsids and macrophyllous seed-ferns and conifers. The presence of widespread Jurassic coal deposits in Australia indicates a humid climate for the time period (Johnson 1995). Although representing negative data, another aspect that supports the interpretation of the climate as humid is the absence of evaporites in Jurassic sediments of Australia (Hallam 1984).

For the Inverleigh assemblage, the occurrence of ferns and isoetales is a good indicator of a humid climate, as both these groups require moisture for reproduction (Hallam 1984). This study of the conifer specimens shows that they possess no papillae either on the epidermal or the subsidiary cells, a feature that otherwise would have supported an arid environment. Furthermore, the leaves show no preserved trichomes or attachment points for trichomes, a feature that is also considered to be an adaptation to dry conditions (Upchurch 1995).

The non-marine character of the Marburg Subgroup is supported by the dominance of plant remains and the occurrence of *Burejospermum* sp., as both leeches and earthworms are almost exclusively fresh water or terrestrial organisms (Manum et al. 1991). The depositional environment of the Ma Ma Creek Sandstone Member has been interpreted as a floodplain with meandering channels which featured elements such as swamps and at one stage a large lake (Wells & O'Brien 1984). Free-sporing ferns and isoetales are typical of moist substrates as they are dependent upon moisture for gametophyte exchange (Stewart & Rothwell 1993). Most spore-producing

plants are subaerial or aquatic inhabitants of the terrestrial realm (Playford & Dettmann 1996) and isoetalean plants are likely to have grown in or near standing water, or on low-lying land liable to frequent flooding (Baldoni & Batten 1997). The preservational potential of spores is very dependent upon the chemical and physical characteristics of the depositional environment and particularly important is anaerobic conditions (Playford & Dettmann 1996). Taking the preservation state of the megaspores into account, taphonomic sorting can be excluded as the reason for the low diversity of the Inverleigh assemblage. Restrictive environmental conditions appears to be a more probable cause for the low diversity of the assemblage. Further, the floral composition suggests a waterlogged or commonly flooded environment as a plausible depositional environment. Frequent exposure to flooding would have constituted a stress factor for the plants growing at the site and hence restricted their ability to survive (Grime 1988). As natural selection leads to specialisation this would have resulted in a plant community dominated by species that became adapted to the specific conditions at the site (Parkhurst & Loucks 1972). This is supported by both the low diversity of the Inverleigh assemblage and by the fact that where stress is the major determinant the dominant phenology is likely to be that of the evergreen plant (Al-Mufti et al. 1977).

### 6.4. Reconstruction of vegetation

The plants identified in the Inverleigh quarry can be divided into two broad groups; the spore-bearing herbaceous plants and the pollen/seed-bearing woody plants. The first group includes ferns and isoetales whereas the second group is represented by conifers. The fossil assemblage primarily consists of well-preserved conifer macrofossils, but samples also contain sparse foliage of ferns and some foliage fragments that have been interpreted as poorly preserved lycopods. The fossil remains also contain several types of megaspores. The total assemblage suggests a parent flora containing about four or five genera of vascular plants.

The abundance, as well as the preservation state of the macrofossils from the Inverleigh quarry indicates deposition at or near the growth site (Sweet 1979). The mesofossil assemblages also support proximal deposition as they consist of high numbers of well-preserved megaspores belonging to a few species. In contrast, a diverse population would have been indicative of transportation (Sweet 1979). Hence more distal deposits are typically associated with high numbers and diversity of megaspores (Sweet 1979). As the transportation potential for cuticle and spores differs, discrepancies between palynofloras and cuticle floras must be considered (Upchurch 1995). However, the considerably large size of megaspores greatly reduces their potential for long-distance transport (Hall & Peake 1968, Batten & Koppelhus 1993), and therefore a high congruence between the preserved assemblages and the

parent flora could be expected. Furthermore, the numerous root-rich horizons in the host sediments suggest a mostly autochthonous flood basin flora.

The stature of the *Allocladus* species found in the Inverleigh assemblage is so far unknown but the fossil site contains abundant log impressions that locally reaches up to 30 cm in diameter. This suggests that the conifer could have reached a considerable height. According to Grime (1988), vegetation that develops in a certain place at a particular time, is not only influenced by stress or disturbance (physical damage to the vegetation) but also by competition. This means the attempt of different species to capture the same unit of resource (Grime 1988). A high stature of the Inverleigh conifer, especially in combination with a dense growth form, would have affected the surrounding flora in terms of competition (Grime 1988). Ground vegetation would have been captured in the shaded zone, beneath the conifers. This in turn would have restricted their photosynthetic production and hence, the survival rate would have been low (Grime 1988). Production would be further restricted as the competition for light would have drained the struggling plants reserves of carbon and energy (Grime 1988). The low diversity of the Inverleigh flora could, therefore, be due to competitive exclusion as the conifers would have monopolized the environment by attaining a large size and subjected smaller species to forms of stress by shading, depletion of soil mineral nutrients and deposition of litter (Al-Mufti et al. 1977). This is supported by the fact that the major component of the plant biomass is usually the species with the largest life-form (Al-Mufti et al. 1977), and the conifers of the Inverleigh community undoubtedly constitute the dominant species of the assemblage. Therefore, they could have affected the surrounding vegetation in a way that only stress adapted species, like ferns, were able to survive. The low diversity can then be explained by the fact that relatively few species are adapted for shade tolerance (Denslow 1980). According to Lenssen et al. (2003), species are often limited not only by one stress factor but multiple factors that operate simultaneously. Therefore, the combination of water-logging and species competition could have resulted in the low diversity flora seen in the Inverleigh assemblage. In fact, field studies of modern vegetation show that water level mainly determines which species can occur, whereas access to light is the controlling factor when it comes to which species that actually will be present (Lenssen et al. 2003).

### 6.5. Economical aspects

The major part of Australia's Mesozoic coal measures were developed in fluvial swamps formed in low-lying floodplain areas (Balme et al. 1995). Australia's main Jurassic coals are the Lower to Middle Jurassic Catamarra Coal Measures of the Perth Basin, Western Australia, and the Middle Jurassic Walloon Coal Measures of the Surat and Clarence-Moreton basins, eastern Australia. Minor coal deposits also occur throughout

the remainder of the Jurassic non-marine succession.

The mild and humid climate that existed during the Jurassic, combined with steady slow subsidence over wide areas of eastern Australia, generated widespread fluvio-lacustrine deposits characterised by coal swamps (Brakel et al. 1995). These deposits are common but tend to be of lesser extent and lower quality than the very extensive Permian coals of Australia (Brakel et al. 1995). However, it appears that Jurassic and younger coal-bearing strata in Australia have a better potential to generate oil than older strata (McLoughlin et al. 2002). This is due to an increase in resin- and wax-rich components of post-Triassic plants, primarily conifers (McLoughlin et al. 2002). Some Jurassic coal measures contain coal seams of sufficient thickness to be of economic importance. For example the Walloon Coal Measures of the Clarence-Moreton Basin are currently exploited commercially at several mines (Brakel et al. 1995). The economically significant Walloon Coal Measures (Staines 1964) immediately overlie the Marburg Subgroup and contain a similar palaeoflora. In recent years, coal-seam gas (methane) has become an important exploration target in the Jurassic sequences of eastern Australia (Scott & Crosdale 1999). The best gas yields come from thick coals that are rich in woody tissues (McLoughlin pers. comm. 2006). Understanding the distribution of plant types in Jurassic mire systems could, therefore, be important for maximizing gas yield from the Jurassic coals.

## 7. Conclusions

The results obtained from the description of the assemblage from the Clarence-Moreton Basin led to the following conclusions:

1. The Early Jurassic sediments from the Inverleigh quarry contain a well-preserved fossil assemblage, characterized by a low diversity flora. The macroflora includes conifers, ferns and lycophytes. Additionally, mesofossils include five species of megaspores and hapsidarchs.
2. The assemblage is dominated by one conifer taxon, which has been assigned to a new species, *Allocladus helgei*. Furthermore, five new megaspore taxa have been described under open nomenclature.
3. The climate has been interpreted as humid due to the presence of ferns and isoetaleans, as these require moisture for reproduction. This is supported by the fact that the conifer lack typical drought adaptations, such as papillae, trichomes or attachment points for trichomes.
4. The abundance and the good preservational state of the macrofossils from the Inverleigh quarry indicates deposition at or near the growth site. The low diversity and abundance of well-preserved megaspores also support an autochthonous assemblage.

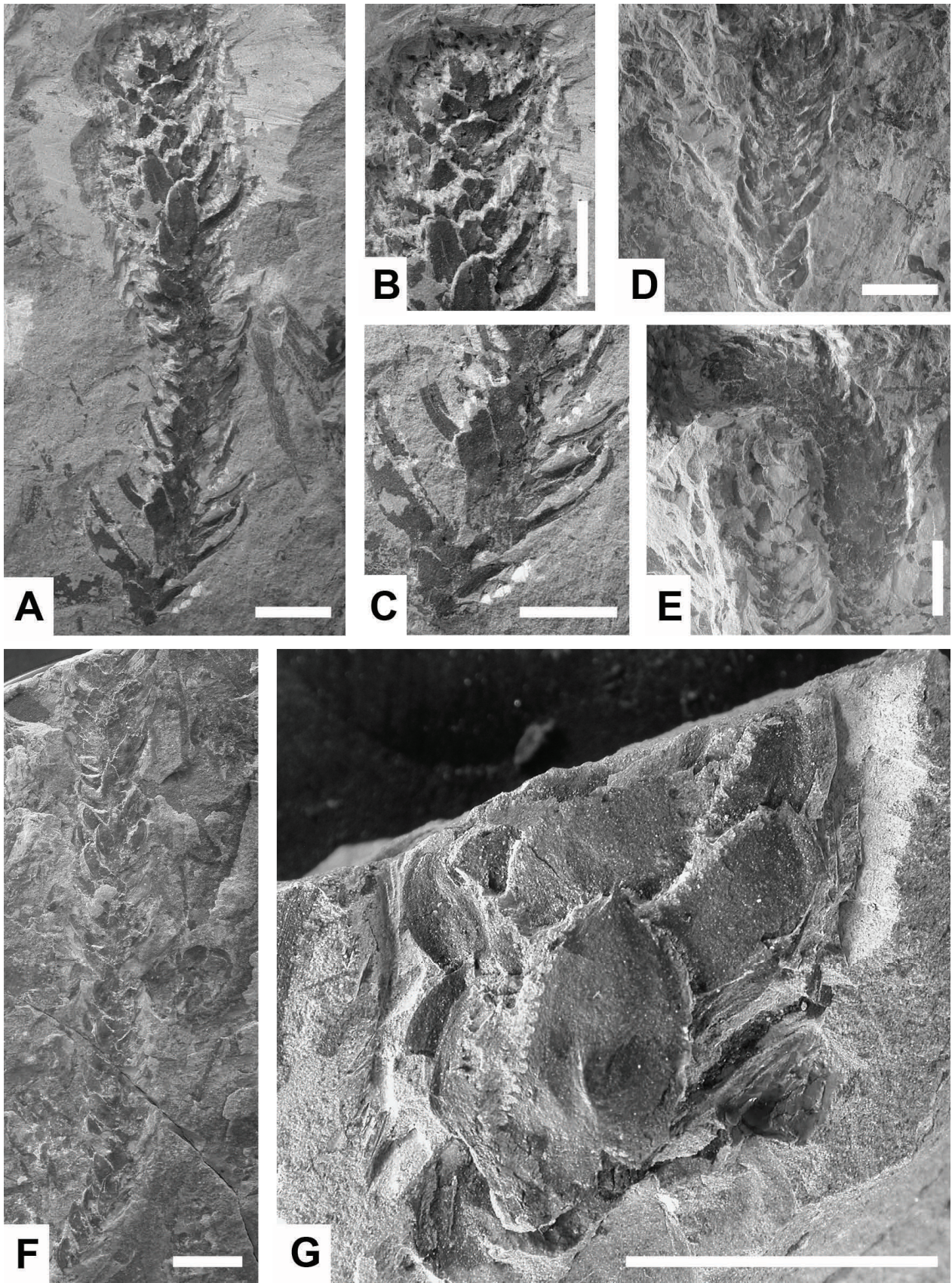
5. The palaeoenvironment is here interpreted as waterlogged or frequently flooded based on lithology and floral composition. The low diversity can be ascribed to stress, in the form of waterlogging, and competition. The ground vegetation has been subdued by competitive exclusion as the high stature conifers monopolized the environment.
6. Natural selection leads to plant communities dominated by species adapted to the specific conditions at the site. The dominance of *Allocladus helgei* is hence a result of its adaptive ability.

## 8. Suggestion for further studies

It would be of interest to investigate possible changes in the floral assemblage in response to the Toarcian anoxic event. This would require sampling of a series of assemblages stratigraphically higher in the succession. Further it would be desirable to investigate if the event could be detected as a change in stomatal density, which might reflect global atmospheric changes. Further investigations of the megaspores might also reveal useful biogeographical or biostratigraphic applications of this little-studied component of the fossil biota.

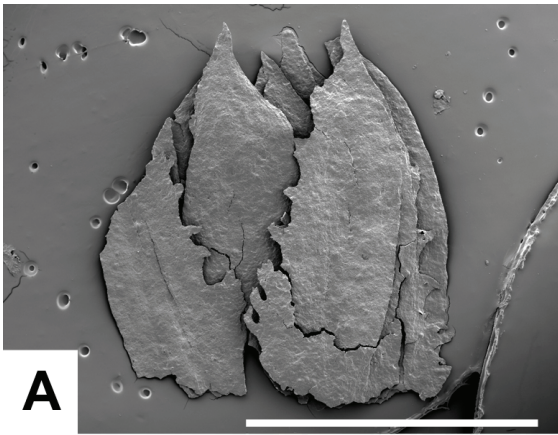
## 9. Acknowledgements

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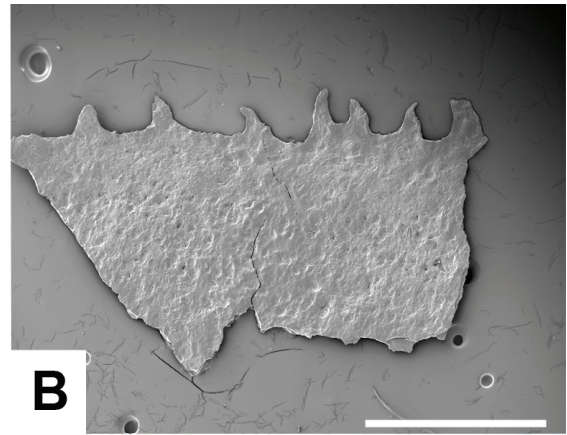


**Plate 1** - *Allocladus helgei*. Shoots and parts of shoots (macrophotographs) . A-C: holotype. Scale bar = 10 mm.

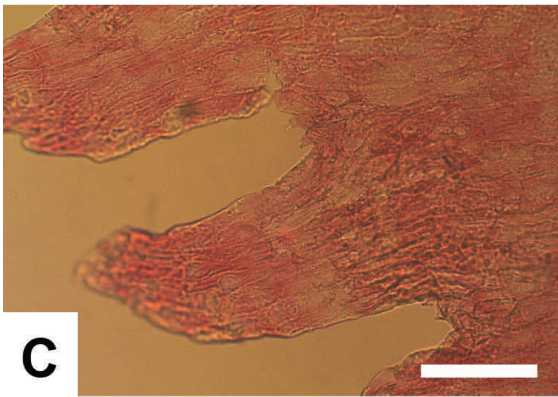




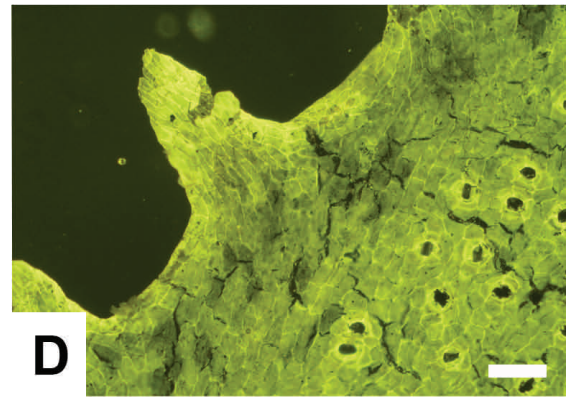
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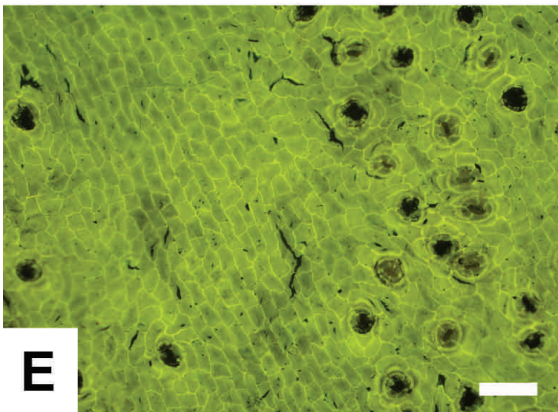
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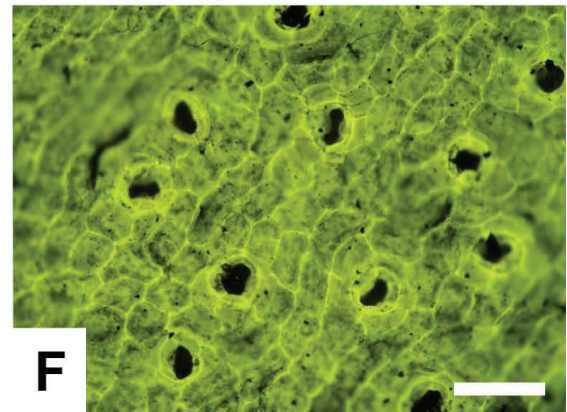
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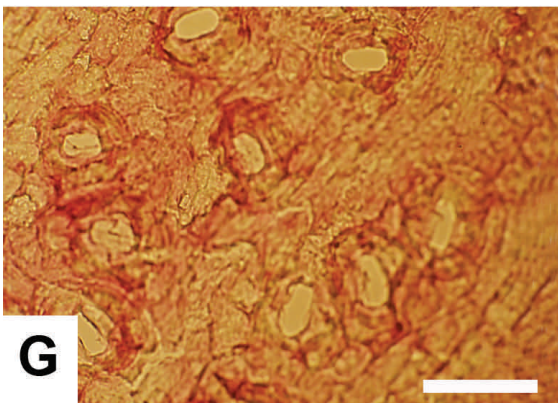
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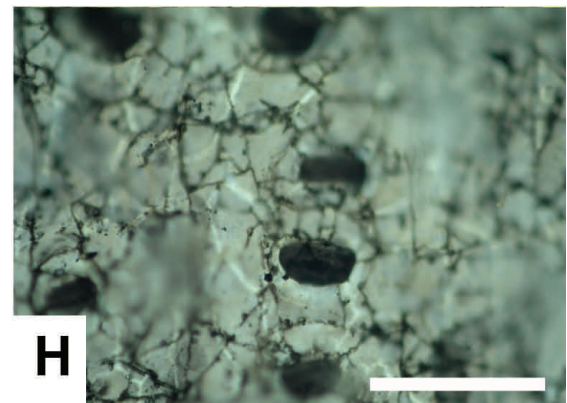
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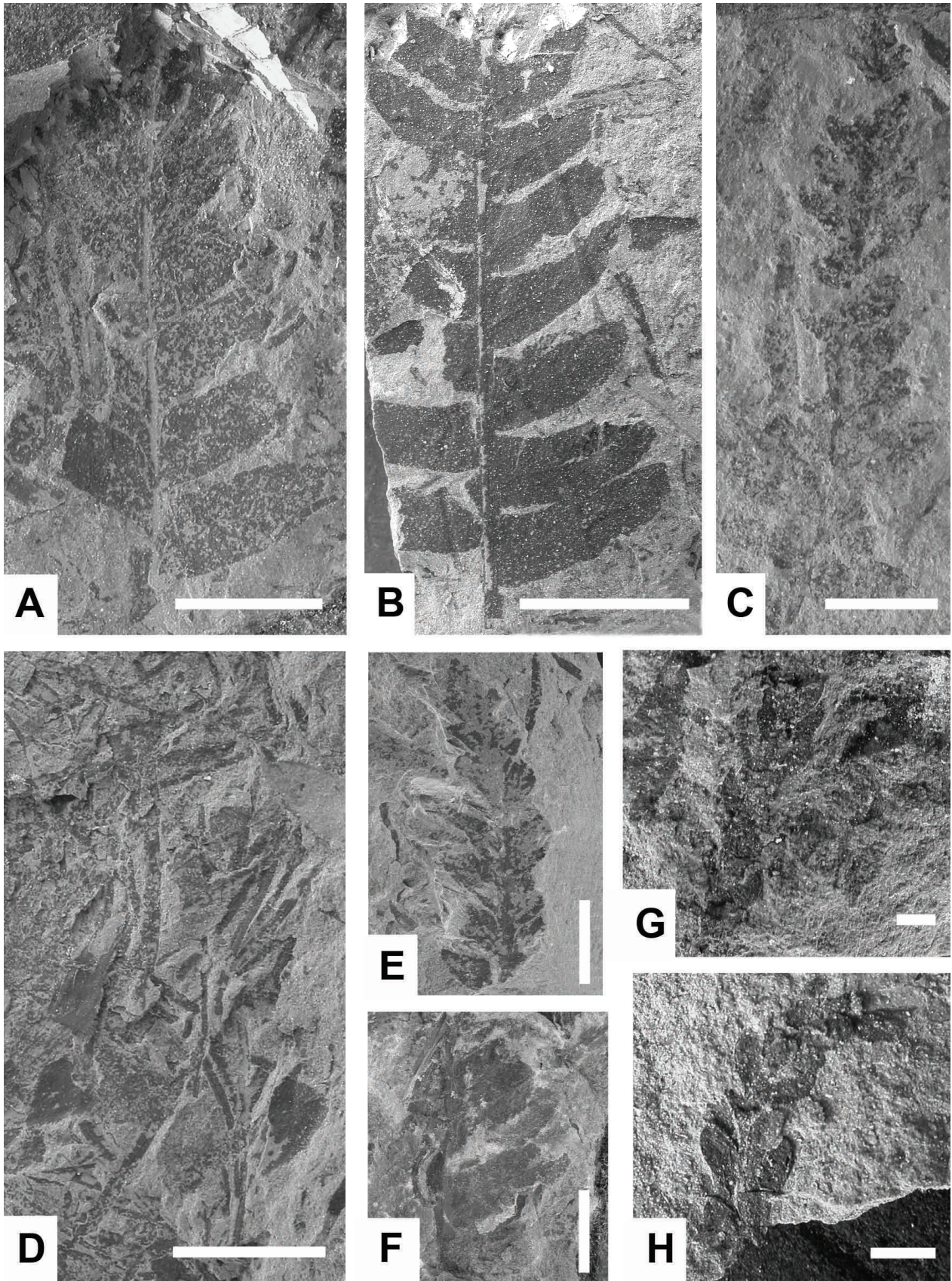


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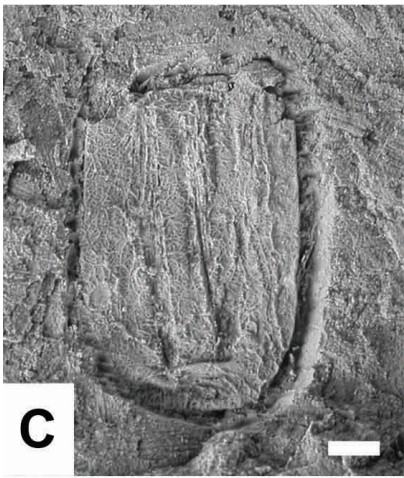
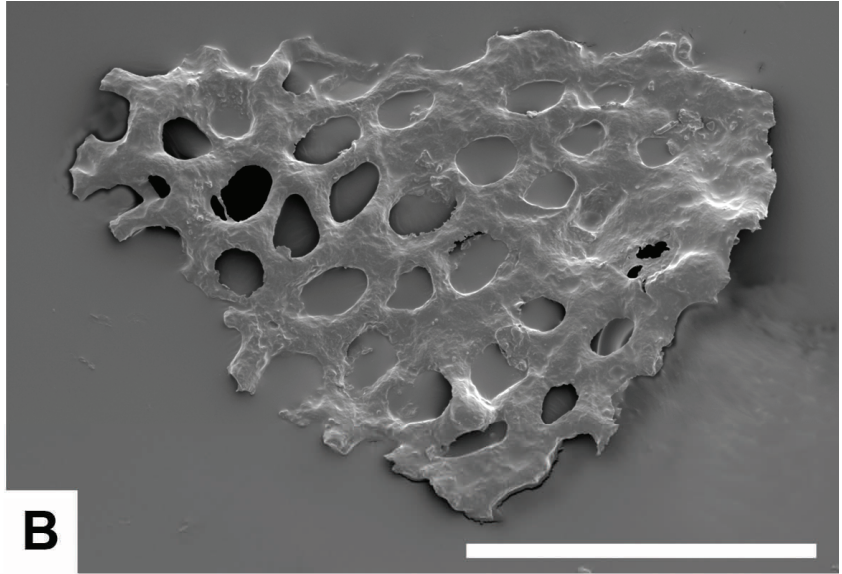


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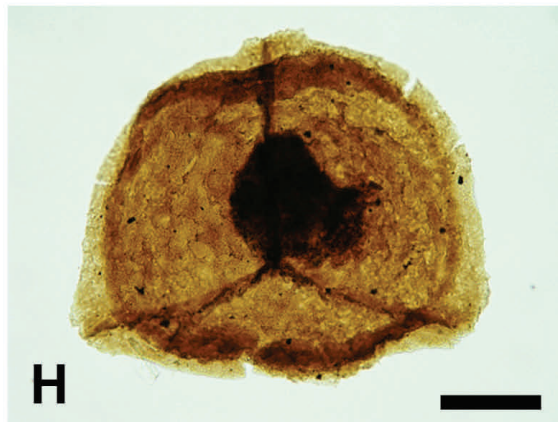
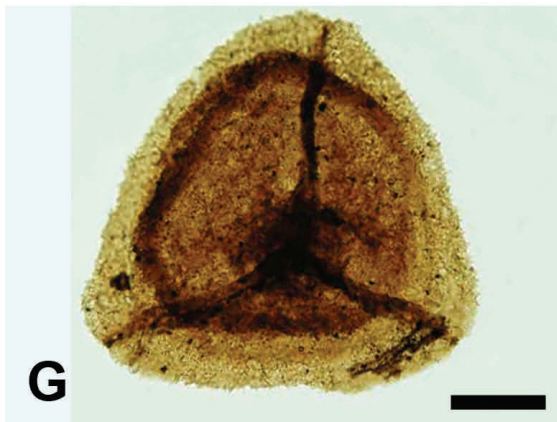
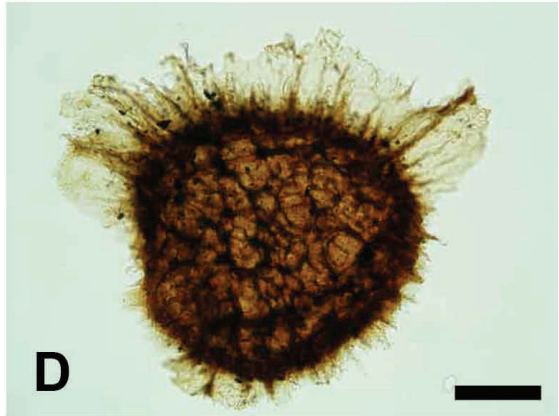
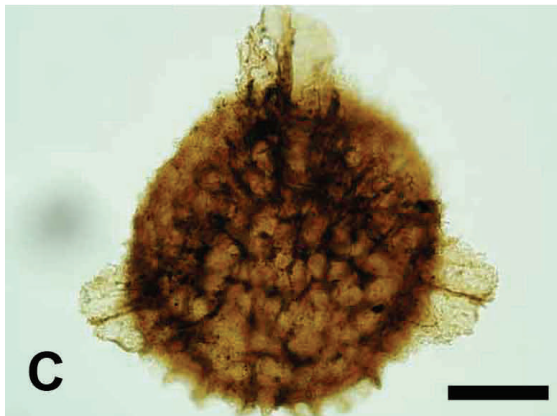
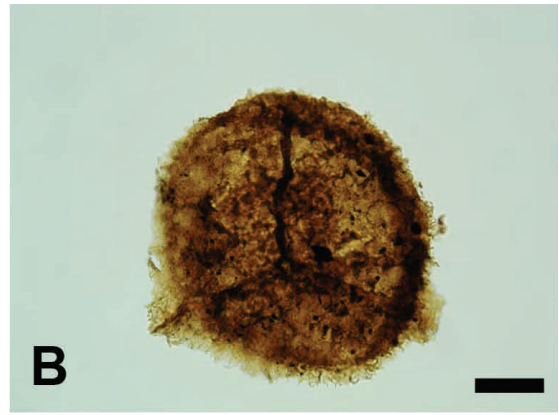
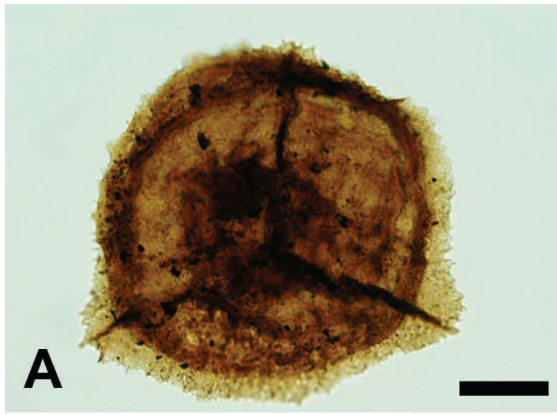
**Plate 2 - *Allocladus helgei*.** A, B: leaf cluster and leafmargin (SEM). C: denticles and micro denticles (light micrograph). D: leafmargin (epifluorescencemicrograph) . E: veinal area (epifluorescencemicrograph) . F: interveinal area (epifluorescencemicrograph) . G,H: Stomata (light micrograph, epifluorescencemicrograph) . Scale bar = 400  $\mu$ m for A; 1mm for B; 100  $\mu$ m for C-H.



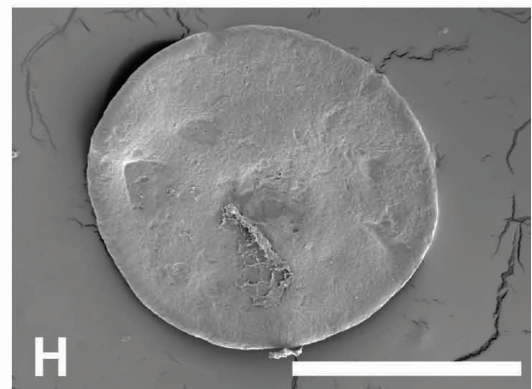
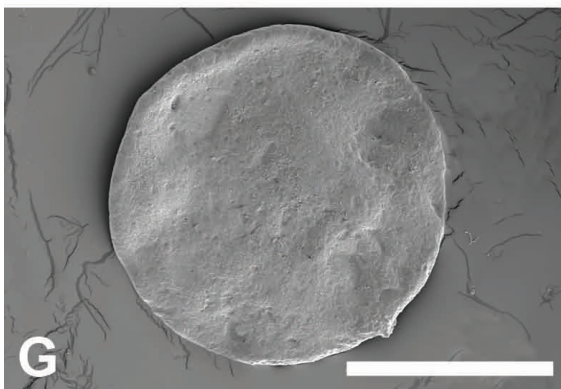
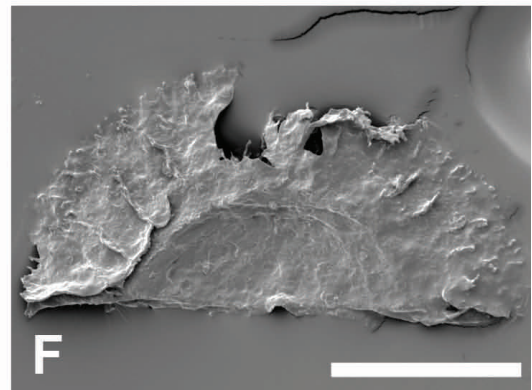
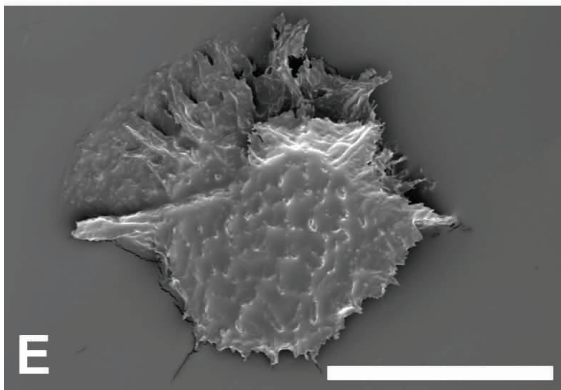
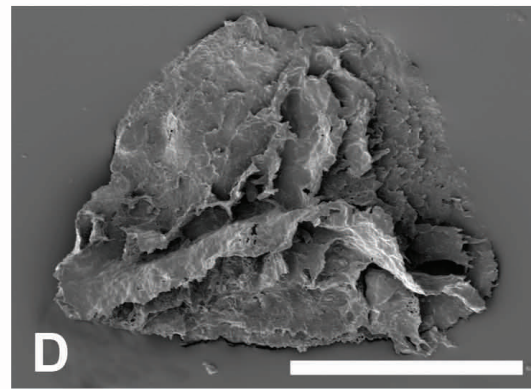
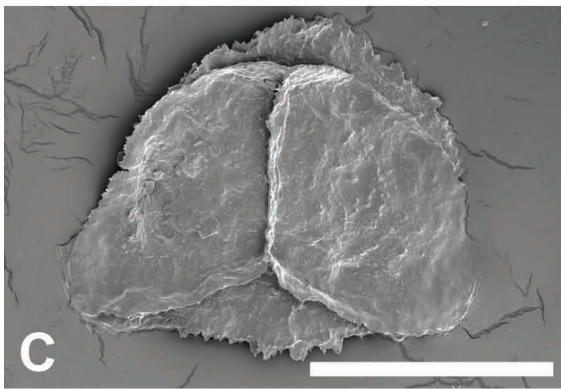
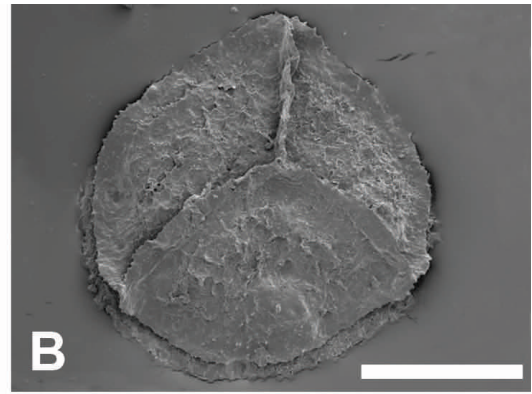
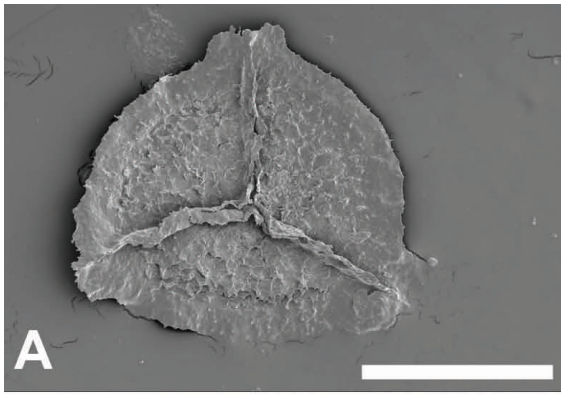
**Plate 3** - Fern foliage and lycopsids (macrophotographs). A,B: *Cladophlebis* sp. C, E: *Sphenopteris* sp. D: lycopsid fragments (microphylls). F: indeterminate fern foliage. G, H: minute fern foliage. Scale bar = 10 mm for A-F, 1mm for G,H.



**Plate 4** - *Burejospermum* sp. A,C: complete specimens, showing outer meshwork layer of hapsine (macrophotographs). B: Fragment of hapsine (SEM). Scale bar = 1 mm for A and C; 400  $\mu$ m for B.



**Plate 5** - Megaspores (light micrographs) A, B: *Minerisporites* sp. C, D: *Paxillitriletes* sp. E, F: Megaspore type 3. G: Megaspore type 4. H: Megaspore type 5. Scale bar = 100 $\mu$ m.



**Plate 6** - Megaspores (SEM). A-C: *Minerisporites* sp. D-F: *Paxillitriletes* sp. G, H: Megaspore type 3. Scale bar = 200  $\mu\text{m}$  for A, B, F; 300  $\mu\text{m}$  for C, D, E, G, H.

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