Lepidopteris callipteroides, an earliest Triassic seed fern of the Sydney Basin, southeastern Australia

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Earliest Triassic shales in the Coal Cliff Sandstone, Caley Formation, Widden Brook Conglomerate and Dooralong Shale (all basal Narrabeen Group) of the Sydney Basin contain a low diversity fossil flora that survived the greatest mass extinction of all time at the Permian-Triassic boundary. Only one species of seed fern is known from this flora and its affinities were unclear until discovery of its reproductive organs and complete large leaves. An ovuliferous reproductive organ, *Peltaspermum townrovii* sp. nov., can be attributed to the same plant as the leaves because of their identical stomatal apparatus, which is cyclocytic with papillae overhanging the stomatal pit. Polleniferous organs, *Permotheca helbyi* sp. nov., may have belonged to the same plant, but are only linked by evidence of association on the same bedding plane yielding no other gymnosperms. Pollen masses found within the polleniferous organ include grains identified as *Falcisporites australis* (de Jersey) Stevens (1981) when found dispersed. The leaves of this plant have long been enigmatic and attributed to *'Thinnfeldia' callipteroides* or *'Dicroidium' callipteroides*; however, these genera had very different cuticular structure. Reassessment of the frond architecture of this plant, based on a large, near-complete specimen together with information from cuticles and ovuliferous organs, allows reassignment to *Lepidopteris callipteroides* (Carpentier) comb. nov. The remarkable cuticle thickness, small stomatal size and low stomatal index of these leaves reflect a time of unusually high atmospheric concentrations of carbon dioxide. This plant was an invader of the Sydney Basin from northern Gondwana, spreading southward during the post-apocalyptic earliest Triassic greenhouse.

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PROBLEMATIC LEAVES in the fossil flora of the Sydney Basin have been referred to *'Thinnfeldia' callipteroides* (Townrow 1966) and *'Dicroidium' callipteroides* (White 1984, 1986). Uncertainty concerning the taxonomic affiliation of this common fossil has been unfortunate because of its prominence as the nominate species of a biostratigraphic zone and a plant fossil association identified widely in the Gondwana supercontinent (Retallack 1977, 1978). The fossil leaves are abundant in the earliest Triassic flora of the Coal Cliff Sandstone, Widden Brook Conglomerate, Caley Formation, and Dooralong Shale, throughout the Sydney Basin and into the Gunnedah Basin (Retallack 1980, 1999). This plant was a survivor of the most profound mass extinction in the history of life at the Permian-Triassic boundary (Retallack 1999, Looy 2000, Wang 2000).

These fossil leaves are most similar to European Permian *Lepidopteris martinsii,* which is now known to include forms with terminal dichotomous forking of the rachis like that diagnostic of *Dicroidium* (Poort & Kerp 1990). The papillate and cyclocytic stomatal apparatus of the Sydney leaves is similar to that of *Lepidopteris* and *Ginkgo*, and quite unlike that of *'Thinnfeldia'* (now included in *Pachypteris* by Doludenko 1971, and in *Komlopteris* by Barbacka 1994) or *Dicroidium* (Anderson & Anderson 1983). The taxonomic affinities of this

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enigmatic seed fern are also apparent from its reproductive structures. The plant producing leaves of *Lepidopteris callipteroides* (Carpentier) comb. nov. also produced ovuliferous organs of *Peltaspermum townrovii* sp. nov., and probably also polleniferous organs of *Permotheca helbyi* sp. nov., and pollen of *Falcisporites australis* (de Jersey) Stevens (1981). This fossil was thus a peltasperm seed fern, and the first of these equatorial and northern hemisphere seed ferns known to have extended its range into southern Gondwana.

The cuticle of *Lepidopteris callipteroides* is unusually thick and has unusually small and sparse stomates, and the southward migration of this seed fern from northern Gondwanan ancestors was at a time of unusually warm and wet palaeoclimate (Retallack 1999). Counts of the stomatal index of *L. callipteroides* and of other species of peltasperm seed ferns are here used to quantify this postapocalyptic carbon dioxide greenhouse, by calibration with similar studies on living and fossil *Ginkgo* (McElwain & Chaloner 1996, Beerling *et al.* 1998, McElwain *et al.* 1999).

Localities and biostratigraphic zone

Lepidopteris callipteroides is locally common in the fossil flora of the basal Narrabeen Group at many localities in the Sydney and Gunnedah Basins (Fig. 1). It is well represented in collections of the Australian Museum (AMF-, including specimens formerly at the University of New England UNEF-) and the former Mining Museum of the NSW Geological Survey (MMF- now curated by the NSW Department of Mineral Resources at Lidcombe, Sydney). Many specimens came from collieries of the southern coalfield in roof shales of the basal Coal Cliff Sandstone immediately above the latest Permian Bulli Coal (Etheridge 1893, 1903; Dun 1908, 1911; Townrow 1967, 1966; Retallack 1980, 1995, 1996, 1997a, 1999; White 1986). The following species and specimens are representative of this flora: the seed fern *Lepidopteris callipteroides* (Carpentier) comb. nov. (AMF27431 from Bellambi Colliery; AMF59519 from Bulli, AMF51730, 51731 from north Coalcliff, MMF18161 from the Birthday Shaft near Balmain, AMF53796 from Nattai Colliery; AMF45262-6 from Burragorang Valley); seed fern ovulate organ *Peltaspermum townrovii* sp. nov. (AMF45266 from Burragorang Valley, AMF118237-40 from Oakdale Colliery); seed fern pollen organ *Permotheca helbyi* sp. nov. (AMF118242 from Oakdale Colliery); conifers *Voltziopsis africana* Seward, 1934 (AMF22426 from Bulli, AMF53797 from South Bulli Colliery) and an undescribed taxon with foliage broadly similar to *Podozamites* (MMF3084, AMF22426 from Bulli); horsetail *Schizoneura gondwanensis* Feistmantel, 1876 (AMF35729, 35761 from Bulli Colliery, AMF21243, 21231 from Birthday Shaft); marattialean or osmundalean fern *Cladophlebis carnei* Holmes & Ash, 1979 (AMF27432 from Bellambi Colliery, AMF11036 from Birthday Shaft); undescribed coniopterid fern (AMF27432 from Bellambi Colliery); quillwort *Isoetes beestonii* Retallack, 1997a (AMF58791, 60882 from Bellambi Colliery; MMF16456 from Kemira Colliery, MMF25687 from Bulli, MMF18155 from Birthday Shaft); and the problematic *Ginkgophytopsis* (AMF27432 from Bellambi Colliery, '*Rhipidopsis*' of Dun 1911 from the Birthday Shaft near Balmain). Other fossils from this assemblage in the southern coalfield include freshwater bivalves, an orthopteran insect wing, and tracks of insects and dicynodont therapsids (Retallack 1996).

In the western coalfield comparable fossil plants are found in the Beauchamps Falls Shale of the Caley Formation, and include *Lepidopteris callipteroides* (Carpentier) comb. nov (MMF13715 from Victoria Pass), and *Voltziopsis wolganensis* Townrow, 1967 (AMF48168 from Constance Gorge near Newnes).

This earliest Triassic plant assemblage has also been collected from the basal Widden Brook Conglomerate in the southeastern Gunnedah Basin (Fig. 1): where it includes the seed fern *Lepidopteris callipteroides* (Carpentier) comb. nov. (AMF91440, MMF13691, 13701, 13698 from Coxs Gap), the conifer *Voltziopsis wolganensis* Townrow, 1967 (MMF13666-7 from Coxs Gap),

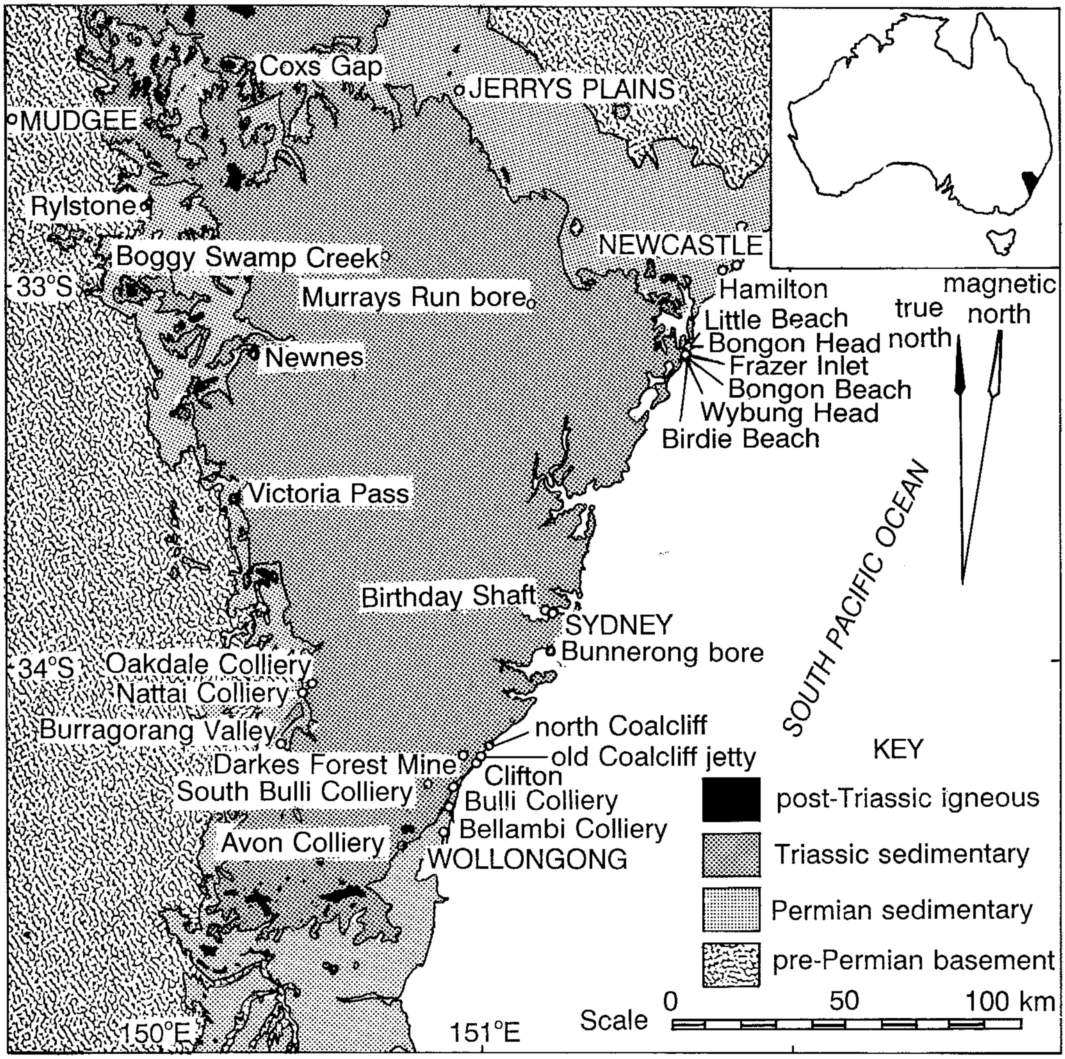


Fig. 1. Fossil localities in the Sydney Basin for earliest Triassic fossil floras characterized by *Lepidopteris callipteroides* (Carpentier) comb nov., and other significant Permian-Triassic boundary localities (after Retallack 1999).

large winged seeds (MMF13644 from Coxs Gap), ferns *Merianopteris* sp. (AMF91457 from Coxs Gap) and *Cladophlebis carnei* Holmes & Ash, 1979 (AMF91461, MMF13651 from Coxs Gap), the quillwort *Isoetes beestonii* Retallack, 1997a (MMF13643-6, 13648-52, 13666, AMF91460 from Coxs Gap; AMF39862 from Rylstone), and the horsetails *Paracalamites australis* Rigby, 1969 (AMF91447 from Coxs Gap) and *Schizoneura gondwanensis* Feistmantel, 1876 (MMF13661, 13653-4 from Coxs Gap).

In the basal Dooralong Shale of the sea cliffs of the northeast Sydney Basin there is a comparable assemblage of plants including *Lepidopteris callipteroides* (Carpentier) comb. nov. (AMF26114 from Hamilton near Newcastle, AMF78318 from Frazer Park beach in Frazer National Park).

This low diversity (13 spp.) floral biozone can now be called the *Lepidopteris callipteroides* Oppelzone, and its seed-fern-dominated community the Lepidopteretum callipteroidium fossil plant association (Retallack 1977). Other recognizable fossil plant associations in the biozone are the conifer-dominated Voltziopsetum, and monodominant meadows of quillworts, or Isoetetum (Retallack 1997a, 1999). The *L. callipteroides* flora succeeds the *Glossopteris* flora abruptly, in the roof shales of the basal Coal Cliff Sandstone, immediately above the last thick coal seam (Retallack 1980, 1995). It was replaced by the *Dicroidium zuberi* Oppelzone in the Stanwell Park Claystone, from which Townrow (1966) recorded a mixed flora of *Lepidopteris callipteroides, L. madagascariensis* and *Dicroidium* sp. The *L. callipteroides* zone can be recognized also in bed 4 of the Sakamena Group in Madagascar (Carpentier 1935). Fragmentary leaves referred to *Lepidopteris* also have been reported from a comparable stratigraphic level in the Flagstone Bench Formation of East Antarctica (McLoughlin *et al.* 1997) and the Panchet and Kamthi Formations of India (Bose *et al.* 1975, Bose & Banerji 1976, Banerji & Bose 1977, Nandi 1992, Pal & Ghosh 1997).

Geological age

An age near the Permian-Triassic boundary for *Lepidopteris callipteroides* in bed 4 of the Sakamena Group in Madagascar (Carpentier 1935) is suggested by stratigraphic position between ammonoids of the Late Permian *Cyclolobus* and Early Triassic *Gyronites* zones (Anderson & Anderson 1983). A similar indication of age comes from palynology, because the *L. callipteroides* zone corresponds to the palynological zone of *Protohaploxypinus microcorpus*, which can be recognized throughout Australia, including marine ammonoid-bearing sequences of Western Australia (Foster *et al.* 1998). Unusual abundance of fungal spores and hyphae in the *P. microcorpus* zone of the Sydney-Bowen Basin and many other localities worldwide has been widely taken as evidence of an earliest Triassic age, but fungal spores are also common in the latest Permian (Visscher *et al.* 1996, Foster *et al.* 1998, Looy 2000) and some of these remains may be zygnematalean algae rather than fungi (Krassilov & Afonin 1999). High precision dating of tuffs across the likely global stratotype Permian-Triassic boundary in marine sequences of China gives a boundary age of 251 ± 0.3 Ma (Bowring *et al.* 1998), comparable with dating of Siberian Trap lavas at 250 ± 0.4 Ma (Renne *et al.* 1995). SHRIMP zircon dating of tuffs in the Bowen, Gunnedah and Sydney Basins of New South Wales indicates a comparable age for the *L. callipteroides* zone, but troubling anomalies remain (Foster *et al.* 1998). The most compelling evidence for age of the *L. callipteroides* and *P. microcorpus* zones is that their strata include a dramatic excursion in carbon isotopic composition ($\delta^{13}C$) ratios in kerogen and carbonate, an excursion noted also at the Permian-Triassic boundary in numerous marine sequences (Baud *et al.* 1989, Holser *et al.* 1991, Wang *et al.* 1994), and in non-marine rocks of Australia (Morante *et al.* 1994, Morante, 1996), South Africa (MacLeod *et al.* 2000), India (Ghosh *et al.* 1998) and Antarctica (Krull & Retallack 2000). Arguments that this isotopic shift represents a change from dominantly woody to dominantly herbaceous vegetation (Foster *et al.* 1998) cannot account for the magnitude of the isotopic excursion, nor for isotopic values so low that they can only come from biogenic methane outbursts (Krull *et al.* 2000, Krull & Retallack 2000). Thus the Permian-Triassic boundary in the Sydney Basin is at the contact between the Illawarra, Newcastle and other Coal Measures with *Glossopteris* and overlying fluvial deposits of the basal Narrabeen Group with *Lepidopteris callipteroides* (Retallack 1995, 1999). Ironically, this was the traditionally recognized Permian-Triassic boundary in Australia (David 1950), until the 1970s when long distance palynological correlations with the Salt Range of Pakistan encouraged the view that the boundary was significantly higher in the sequence, at the top of the *P. microcorpus* zone (Retallack 1980). Carbon isotopic study of the Salt Range (Baud *et al.* 1989) confirms that pollen comparable with those of the *P. microcorpus* zone in Pakistan are above the earliest Triassic carbon isotopic excursion. *Lepidopteris callipteroides* and its few

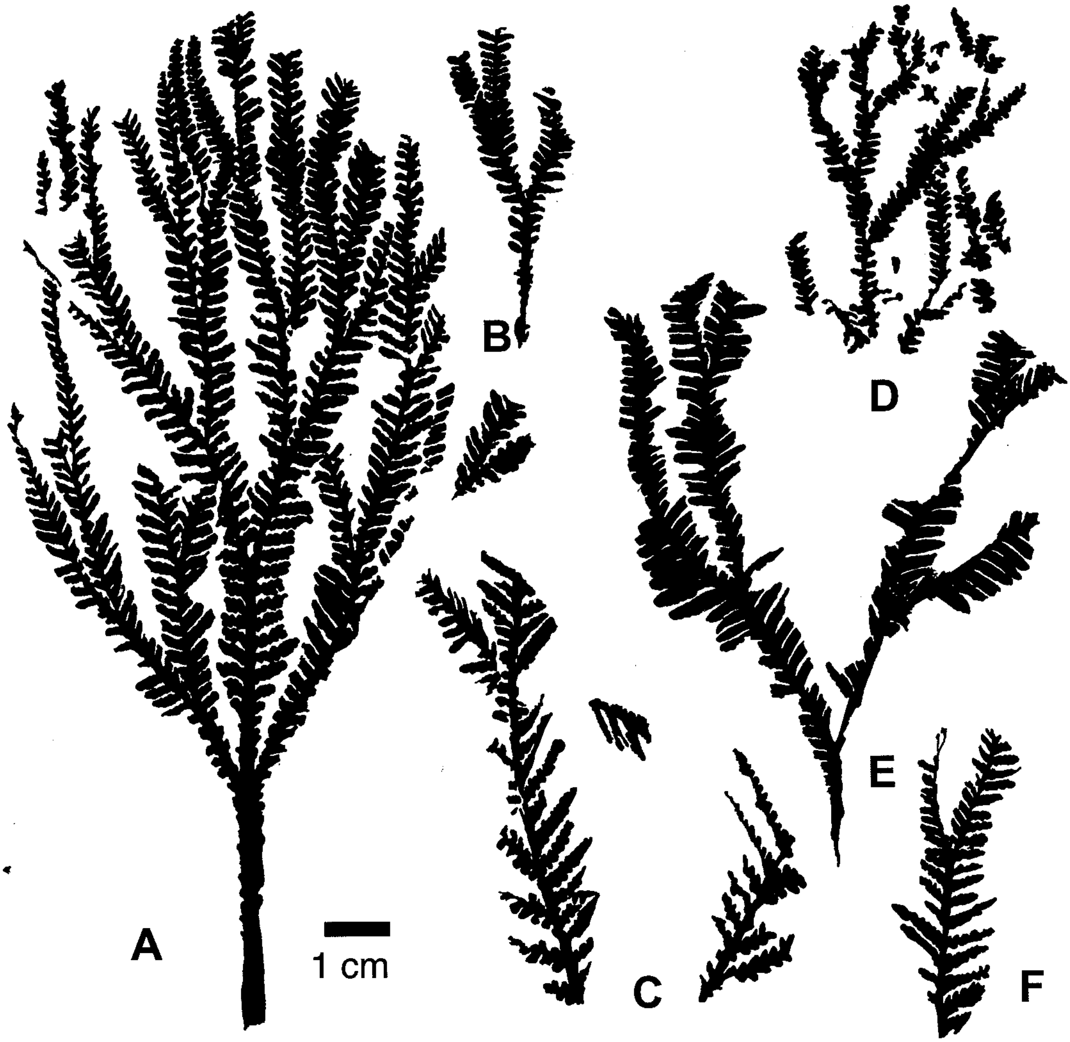


Fig. 2A-F. Variation in frond architecture of *Lepidopteris callipteroides* (Carpentier) comb. nov. from Bulli (A), Coxs Gap (D) and Oakdale Colliery (B, C, E-F), all to same scale. A, AMF59519; B, AMF118243; C, AMF118244; D, AMF91440; E, AMF78319 (formerly UNEF14738); F, AMF78319 (formerly UNEF14738).

associated species were thus the immediate survivors of the Permian-Triassic life crisis (Retallack 1995).

Frond architecture

The leaves of *Lepidopteris callipteroides* are large, complex and polymorphic (Fig. 2). There is substantial natural variation in pinnule size and shape, intergrading in such a way as to suggest a single variable species, as has been demonstrated for several other seed ferns (Meyen 1982, 1987). The complex architecture of these fronds is demonstrated by a large near-complete specimen (Fig. 2A), illustrated in color by White (1984, 1986), which reveals that different parts of the same frond are bipinnate, pinnatifid and dichotomizing. The primary rachis includes unipinnate pinnae as well as two pairs of pinnately arranged secondary rachides, also with unipinnate pinnae. These four rachides then dichotomize three times out toward the margin.

Fig. 3A-D. Leaves of *Lepidopteris callipteroides* (Carpentier) comb. nov. from Coxs Gap (A) and Oakdale Colliery (B-D). A, AMF91440; B, AMF118243; C, AMF78319 (formerly UNEF14738); D, AMF118244.

Complex fronds with a combination of unipinnate, pinnatifid and dichotomizing terminal pinnae are also found in *Rhachiphyllum retensorium* (Naugolnykh 1991, Naugolnykh & Kerp 1996), *Rhachiphyllum zeilleri* (Naugolnykh 1991, Meyen 1982), *Feonia* sp. indet. (Meyen

1982), *Madygenopteris irregularis* (Sixtel, 1959) and *Lepidopteris martinsii* (Poort & Kerp 1990). Only a single rachis dichotomy is known in *Madygenia borealis,* but complete leaves have not yet been found (Vladimirovich *et al.* 1967). A single dichotomy is typical for *Dicroidium*, as demonstrated by leaves complete to the basal abscission scar (Anderson & Anderson 1983, 1985). Leaves with multiple dichotomies, as in *L. callipteroides,* and formerly placed in '*Tetraptilon*' (Frenguelli 1950), are now regarded as hybrids or teratologies of *Dicroidium* (Anderson & Anderson 1983, 1985). All of these complex fronds, as well as *Tetraptilon* and *Dicroidium*, are distinct from *L. callipteroides* (Carpentier) comb. nov. because of their thinner leaves which are less coriaceous and show more clearly secondary veins that branch two times or more from the pinnule midrib to the margin. *Lepidopteris callipteroides* in contrast has narrow coriaceous pinnules, in which venation is difficult to see, and its secondary veins fork no more than once between midrib and margin (Fig. 4A).

Lepidopteris callipteroides has broad lumps on the rachis (Fig. 3D), as are well known in other species of *Lepidopteris*, and interpreted as secretory glands or hydathodes (Townrow 1956, 1960). *Rhachiphyllum, Madygenia* and *Madygenopteris,* on the other hand, have striated rachides, and lumps if present are small, round and discrete, like internal resin bodies, rather than the cuticular domes and flaps of *Lepidopteris.* Although *L. callipteroides* shows a mix of features found in a variety of Permian and Triassic seed fern leaves, it is most like *Lepidopteris*. The basal bipinnate and pinnatifid parts of the fronds (Fig. 3C-D) are comparable to apical leaf fragments of *Lepidopteris madagascariensis*, which is a bipinnate species of later Early Triassic rocks of the Sydney Basin (Townrow 1966).

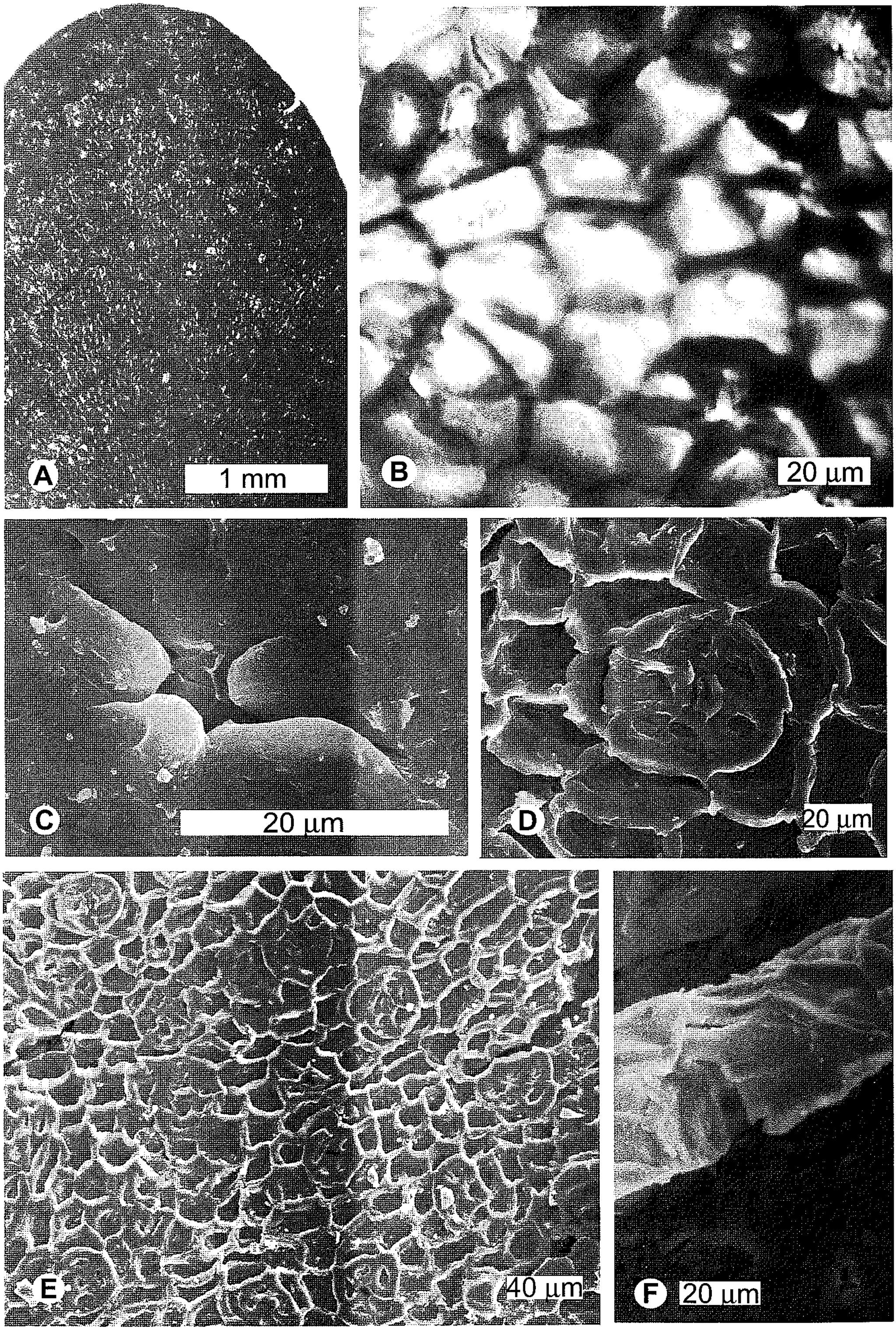
The widely-spreading *L. callipteroides* leaves are functionally comparable with leaves of Cretaceous angiosperms such as *Debeya* and *Dewalquea* (Hickey 1984), and of living umbrella trees (*Maesopis emini* and *Cecropia insignis*) or scrambling ferns (*Gleichenia dicarpa*). These living species are pioneering plants early in the ecological succession to colonize open terrane disturbed by landslides or flooding (Lind & Morrison 1974, Croat 1978, Beadle 1981). Their spreading leaf form maximizes light interception in full sunlight. Interpretation of the habitat of *L. callipteroides* as an early successional shrub of riverbanks is supported by its fossil occurrence within shales of local swales lateral to sandstone paleochannels (Retallack 1980, 1996, 1999).

Leaf cuticular anatomy

The biological affinities of *L. callipteroides* can be further constrained by examining its cuticle, which was prepared by macerating leaf fragments in Schulz's solution (Kerp & Krings 1999). The leaf is amphistomatic, with no discernible difference in stomatal density on either side of the leaf. Stomatal subsidiary cells are usually 6 in number, but range from 5 to 8, and are distinguished by a darker (because thicker) cuticle than for other epidermal cells of the cuticle, and by hollow papillae overhanging the stomatal pit (Fig. 4B-E). Such papillate-cyclocytic stomates are widespread in cycads (*Dioon*), conifers (*Torreya, Agathis, Thuja*), ginkgo (*Ginkgo*) and seed ferns (*Rhachiphyllum, Tatarina, Lepidopteris*: Florin 1931; Townrow 1956, 1960; Gomankov & Meyen, 1980, 1986; Poort & Kerp 1990).

Stomatal structure is very different in other seed ferns that have been confused with *L. callipteroides*. Although some cuticles of *Dicroidium* are papillate and cyclocytic, most *Dicroidium* and '*Tetraptilon*' stomates are non-papillate and irregularly paracytic (Townrow 1957; Anderson & Anderson 1983, 1985). '*Thinnfeldia*' has been submerged within *Pachypteris* (Doludenko 1971) and *Komlopteris* (Barbacka 1994), and both genera have cyclocytic non-papillate subsidiary cells. In stomatal structure *L. callipteroides* is most like other species of *Lepidopteris,* and the genera *Rhachiphyllum, Tatarina* and *Ginkgo.*

There has been speculation on the functional significance of stomatal pits partially occluded by large hollow papillae, as a mechanism for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E
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reducing transpiration in drought-prone soils (xeromorphic adaptation) or in soils low in nutrients (peinomorphic adaptation). By this view the taxonomic distribution of the character could be an example of convergent evolution. Kräusel (1923) addressed this issue at length and found that modern plants with such stomatal apparatus show no clear environmental preference. He concluded that this stomatal structure was an inherited character, primitive for seed ferns, conifers, ginkgos and cycads, and widespread during their initial evolutionary radiation during the Pennsylvanian and Permian. This view was confirmed by Meyen's (1982, 1987) studies of the reproductive structures of *Tatarina, Rhachiphyllum, Lepidopteris* and *Ginkgo*, which showed that these genera are more closely related than would seem likely from examination of their leaf morphology alone.

Associated ovuliferous organs

Associated with *L. callipteroides* in Oakdale Colliery are small peltate discs here referred to *Peltaspermum townrovii* sp. nov. Only one gymnosperm species is represented at this locality. In the *L. callipteroides* fossil plant zone, there is only one known seed fern (Retallack 1980). The suspicion that these are ovuliferous reproductive organs of the same plant that produced leaves of *L. callipteroides* is confirmed by preparation from one of the peltate discs of cuticle fragments with the characteristic cyclocytic, papillate stomata (Fig. 6F). Known conifer cuticles from the basal Narrabeen Group have very different, non-papillate stomates (Townrow 1967). This anatomical similarity securely links these different organs to the same ancient plant.

Some discs of *P. townrovii* have attached ovules, but no more than two were seen attached (Fig. 6G). Circular seed scars are more numerous on the disc (Fig. 6E). There may have been as many as 14 ovules per disc, one for each of the radial lobes, as in other species of *Peltaspermum* (Harris 1937). *Meyenopteris* has been proposed as a new genus for those remains formerly attributed to *Peltaspermum* in which there are fewer ovules than lobes and in which the stalk is lateral to the disc rather than peltate (Poort & Kerp 1990). The number of ovules in *Meyenopteris*, as for other peltasperms, is controversial because of demonstrable ovule dehiscence from most specimens (Meyen 1982, Retallack & Dilcher 1988).

The ovules were tear-shaped with elongated micropyle (Figs 6C-D), small (3x2 mm) and numerous. In ovule size *P. townrovii* was more like plants with abundant small seeds adapted to pioneering freshly exposed ground (ruderals of Grime 1979), than plants producing a few large seeds adapted to germinating under closed canopy forests (competitors of Grime 1979). In contrast, *Meyenopteris natalensis* had seeds twice as large, and probably less numerous (Townrow 1960). A wide spectrum of seed form, and presumed reproductive biology, was established among seed ferns by the Carboniferous (Retallack & Dilcher 1988),

I agree with Poort & Kerp (1990) that the reconstructed whole plant should be named for its ovuliferous organ, because ovuliferous cones and flowers are the most diagnostic parts of seed plants (Retallack & Dilcher 1988). However, this plant should be called *Peltaspermum townrovii* sp. nov., rather than combining the ovule genus and leaf epithet in the confusing manner of Poort & Kerp's (1990) infelicitous name '*Peltaspermum ottonis*', because *Peltaspermum* is defined and differentiated on the basis of ovuliferous organs, not leaves such as *Lepidopteris ottonis*. I maintain this traditional view of form taxa as defined by the International Code of Botanical Nomenclature (Greuter 1988) largely because of the likelihood that different plant organs evolved at different rates. *Peltaspermum townrovii* was

Fig. 4A-F. Cuticular anatomy of *Lepidopteris callipteroides* (Carpentier) comb. nov. leaves in plane light (A-B) and SEM (C-F). A, pinnule tip of unseparated but macerated cuticles showing indistinct venation; B, lower cuticle; C, papillae surrounting stomatal pit on outside surface of cuticle; D, inside view of stomatal cuticle; E, inside view of lower cuticle; F, outside view with stomate (below) and inside view (folded over above) of lower cuticle: all preparations of specimen AMF118243 from Oakdale Colliery. *[see page 482].*

probably the ovuliferous organ of *L. callipteroides* at two localities in the Sydney Basin, but this is not secure for other localities of *L. callipteroides* in Australia and Madagascar (Carpentier 1935), and doubtful for fragmentary remains of *Lepidopteris* leaves from India (Bose *et al.* 1975, Bose & Banerji 1976, Banerji & Bose 1977, Nandi 1992, Pal & Ghosh 1997), and Antarctica (McLoughlin *et al.* 1997). Some leaf fragments from India and Antarctica have papillate epidermal cells, and could have been a distinct species. If, on the other hand, they prove to have had ovuliferous organs identical to *P. townrovii*, the cuticular difference would be merely variation in leaves, not natural species. *Peltaspermum retensorium* has comparable peltate ovuliferous structures linked to leaves referred to *Rhachiphyllum* (Kerp 1988, Naugolnykh & Kerp 1996). Other species of *Rhachiphyllum* have ovuliferous organs referable to *Autunia*, in which the ovule-bearing head is fan-shaped rather than a disc. *Lepidopteris stormbergensis* leaves are securely linked to ovuliferous structures of *Meyenopteris natalensis*, with lateral stalks to ovulate discs (Poort & Kerp 1990). Peltate ovuliferous structures are common in association with *Lepidopteris* leaves (Harris 1935, 1937; Meyen 1982, Holmes 1982, Gomankov & Meyen 1986, Anderson & Anderson 1989).

Associated polleniferous organs

Other remains found in association with *L. callipteroides* and *P. townrovii* in Oakdale Colliery were on a single slab with many clusters of radially-arranged, cigar-shaped, pollen sacs referred here to *Permotheca helbyi* sp. nov. (Figs 5C, 6G). The pollen sacs are partly fused near the base, which can be seen as a ragged lump at the end of the stalks in parts of specimens that appear decayed (Figs 5D, 6H-I). The most coherent group of 5 clusters appear helically arranged (Figs 5C, 6H). Other clusters do not form a clear pattern, but their close proximity suggests dismembered remnants of a large and complex structure with more slender axes than the reconstruction of *Permotheca disparis* by Krassilov *et al.* (1999).

No stomatiferous cuticle was found on this polleniferous organ to link it to *Lepidopteris callipteroides* or *Peltaspermum townrovii*, but these are thought to be parts of the same plant for reasons of association and lack of other options. At the Oakdale Colliery crib room locality where *Permotheca helbyi* was found, the only other gymnospermous remains were *L. callipteroides* and *P. townrovii*. Other fossil plants here included equisetalean axes (*Paracalamites*) and unidentified coniopterid ferns. *Lepidopteris callipteroides* is the only seed fern known in the low-diversity fossil flora of the basal Narrabeen Group (Retallack 1980) and affinities with peltasperm seed ferns are most likely for other species of *Permotheca* (Gomankov & Meyen 1986, Krassilov *et al.* 1999).

A search for pollen in the pollen sacs met with limited success. No large pollen masses were found, only small clusters of up to 17 grains of poorly preserved *Falcisporites australis* (Figs 6J-K). Isolated spores of *Osmundacites wellmanii* were found on this specimen, as well as pollen grains of *Praecolpatites sinuosis*, *Vitreisporites pallidus* and *Falcisporites australis*. The palynoflora (*Protohaploxypinus microcorpus* palynozone) of the *L. callipteroides* zone includes 73 species of pollen and spores, and the following common pollen: *Falcisporites australis*, *Vitreisporites pallidus* and *Protohaploxypinus microcorpus* (Helby *et al.* 1987). *Praecolpatites* is an enigmatic form, perhaps gnetalean (Balme 1995), and probably recycled from older Permian rocks. *Vitreisporites* is best known from caytonialean seed ferns, but also has been recorded from the likely peltasperm ovule *Salpingocarpus* (Gomankov & Meyen 1986), and is broadly comparable with *Vesicaspora* found in the peltasperm pollen organ *Permotheca disparis* (Krassilov *et al.* 1999). *Protohaploxypinus* is well known from glossopterids, but also has been found in peltasperms such as *Permotheca striatifera*, and in the voltzialean conifer *Voltziopsis wolganensis* (Townrow 1967, Gomankov & Meyen 1986, Balme 1995). *Voltziopsis wolganensis* is common in the *L.*

Species	Locality	Age	Ma	N_e	N_s	N_f	SI	Reference
'A.' conferta	Crock, Germany	Autunian	295±3	1020	96	17	8.3±1.2	Barthel & Haubold 1980, Kerp & Barthel 1993; Kerp 1990, 1996
'A.' conferta	Langenthal, Germ.	Artinsk.	285±3	797	80	3	8.6±1.1	Kerp 1988, 1990, 1996
L.retensorium	Chekarda, Russia	Kungur.	275±3	807	83	4	9.8±0.9	Naugolnykh 1996; Naugolnykh & Kerp 1996; Markov & Naugolnykh 1998
'C.' sadovnikovii	Peschansk, Russia	Kazan.	268±5	1244	88	5	5.9±1.1	Meyen & Migdisova 1969
'C.'aequabilis	Pechora R., Russia	Kazan.	267±5	1341	119	7	7.3±1.4	Meyen & Migdisova 1969
'C.' sp. indet.	Pechora R., Russia	Kazan.	266±5	2210	209	6	6.4±1.7	Meyen & Migdisova 1969
'C.' lepidopteroides	Kosio River, Russia	Kazanian	265±5	596	48	5	6.6±1.3	Meyen & Migdisova 1969
L.martinsii	Aldino, Italy	Dzulfian	256±2	568	34	14	5.7±1.1	Kerp 1990, Poort & Kerp 1990
T. olferievii	Vokma River, Rus.	Tatarian	252±1	1583	133	4	7.4±1.7	Meyen 1969
T. sp. indet.	Vokma River, Rus.	Tatarian	252±1	1531	139	7	7.3±1.4	Meyen 1969
T. mira	Mulino, Russia	Tatarian	252±1	1722	124	4	6.7±0.4	Gomankov & Meyen 1986
T. conspicua	Aristovo, Russia	Tatarian	251±1	2545	169	10	6.5±1.0	Gomankov & Meyen 1980, 1986
T. pinnata	Aristovo, Russia	Tatarian	251±1	1387	88	6	6.2±0.9	Gomankov & Meyen 1980, 1986
T. olferievi	Luptyug, Russia	Tatarian	251±1	579	37	3	7.2±2.0	Gomankov & Meyen 1986
T. conspicua	Luptyug, Russia	Tatarian	251±1	744	46	4	5.3±2.4	Gomankov & Meyen 1986
L.callipteroides	Oakdale, NSW	Griesb.	249±2	1748	89	11	4.9±0.8	herein
L. sp. indet.	Tubed, India	Griesb.	247±3	622	32	5	4.9±0.9	Bose & Banerji 1976
L.madagascariensis	Narrabeen, NSW.	Spathian	243±3	>500	>15	9	6.7±3.3	Townrow 1966, herein
L. haizeri	Dzhenischke R., R.	Ladinian	231±5	671	46	2	6.4±0.4	Dobruskina 1980
L. haizeri	Khoseda-Khard, R..	Ladinian	230±5	960	79	3	7.6±0.1	Dobruskina 1980
L. remota	Dzhenischke R., R.	Ladinian	230±5	850	65	5	6.3±1.3	Dobruskina 1980
L. haizeri	Ust-Usa, Russia	Carnian	229±5	782	42	3	5.9±1.5	Dobruskina 1980
L.stormbergensis	L. Switzerland, S.A.	Carnian	229±3	4477	292	28	5.9±1.2	Anderson & Anderson 1989
''L.' africana	L. Switzerland, S.A.	Carnian	229±3	2458	170	18	6.5±1.7	Anderson & Anderson 1989
L.stormbergensis	U. Umkomaas, S.A.	Carnian	228±3	>500	-	22	7.3±2.2	Townrow 1956, 1960
'L.' africana	U. Umkomaas, S.A.	Carnian	228±3	>500	-	20	6.6±2.1	Townrow 1956, 1960
L. microcellularis	Blagoveschenka,R.	Carnian	227±5	1142	108	3	8.4±0.4	Dobruskina 1980
L. heterolateralis	Blagoveschenka,R.	Carnian	227±5	1842	148	9	7.1±1.0	Dobruskina 1980
L. stormbergensis	Cacheuta,Argentina	Carnian	224±3	597	45	5	7.0±2.2	Baldoni 1972
L. stormbergensis	Giar, India	Norian	220±5	2212	128	13	5.5±1.3	Pal 1984
cf.*L. ottonis*	Suiskiou, China	Rhaetian	204±4	1521	112	3	7.0±0.3	Sze 1953
L. ottonis	Astarte R.,Greenl.	Rhaetian	202±2	1001	62	6	6.9±2.1	Townrow 1960; Dobruskina 1980
L. ottonis	Bjuv, Sweden	Rhaetian	202±2	651	53	4	7.5±1.0	Dobruskina 1980

Table 1. Stomatal index (SI), and numbers of epidermal cells (N_e), stomates (N_s) and fragments (N_f) of *Lepidopteris*, *Tatarina* and *Rhachiphyllum* (including *'Autunia'* and *'Callipteris'*) leaf cuticles passing rarefaction analysis of Retallack (2001).

callipteroides zone (Retallack 1980), so that contamination of megafossils with pollen of this other plant is plausible. *Falcisporites* is well known from corystosperm seed ferns, but also has been found in peltasperm seed ferns such as *Permotheca vesicasporoides* (Balme 1995). Thus the mostly likely pollen grain of *P. helbyi* is *Falcisporites australis* (de Jersey) Stevens (1981).

The poor preservation of pollen in pollen sacs of *P. helbyi* is unsurprising because the specimens are on the same bedding plane as leaves of *L. callipteroides,* ovuliferous organs of *P. townrovii* and mature ovules. Furthermore, the locality includes fossil plants preserved in place of growth within a weakly developed paleosol (Fluvent) within the scroll bar system of a stream (Retallack 1980, 1999). If this plant was like living *Ginkgo*, cycads, conifers, or extinct seed ferns (Retallack & Dilcher 1988), several months passed between pollination and the maturation of ovules; during this time, *Ginkgo* pollen organs wither and decay on the ground.

Cuticle thickness, stomatal index and greenhouse atmospheres

The cuticle of *L. callipteroides* is exceptionally thick and requires extended preparation.

Maceration in Schultz's solution (Kerp & Krings 1999), which takes minutes or hours for most fossil plants, takes days or weeks for *L. callipteroides*. Only after dose intensification to stock solution of nitric acid do the leaves turn brown and transparent. The cuticles are about 5-10 µm thick, with internal flanges that reach down as much as 10 µm between the periclinal walls of the stomatal and epidermal cells (Fig. 4).

Such extraordinarily thick cuticle may indicate that these plants were under some kind of environmental stress. It certainly was not too dry, because analysis of palaeosol geochemistry and petrography indicates a humid earliest Triassic palaeoclimate in the Sydney Basin (Retallack 1999). Nor is there any evidence that *L. callipteroides* was a mangrove plant enduring the osmotic stress of sea water (Retallack 1980, 1996, 1999), although a case has been made that other species of *Lepidopteris* were mangroves (Krassilov 1975).

The stomatal guard cells of *L. callipteroides* are also small (24 ± 4 µm long), about a third of the length of guard cells in Permian *Rhachiphyllum* from Crock, Germany (62 ± 11 µm) and about half the length of guard cells in living *Ginkgo* (42 ± 5 µm on leaves picked in Eugene in 2000 and 45 ± 5 µm on leaves picked in East Lansing in 1988: Retallack 2001). This size difference is not immediately apparent from illustrations of cuticle, because the epidermal and subsidiary cells of *L. callipteroides* cuticles are also proportionally small.

Sparse and small stomates would have lowered transpiration and stomatal conductance of *L. callipteroides*. Stomatal density varies with partial pressures of atmospheric carbon dioxide, as well as insolation, water stress, in sun leaves rather than shade leaves, and between taxa (Kürschner *et al.* 1996, Kürschner 1997). Sun and shade leaves are suspected if there is high variance in stomatal index, as is the case for some species of *Lepidopteris* (Townrow 1960, 1966). Water stress and insolation also affect epidermal cell size (Kürschner 1997), as does variation of ploidy level within varieties of the same species (Roth & Dilcher 1979). Size-related compromising variables can be factored out by calculating stomatal index (SI), using the formula:

$$SI = 100.N_s/(N_s + N_e)$$

where N_s is the number of stomates and N_e is the number of epidermal cells in the same area of cuticle.

Stomatal index is commonly used as a palaeobarometer of atmospheric carbon dioxide concentrations (Beerling *et al.* 1998, McElwain *et al.* 1999, Retallack 2001). Studies of living plants have shown that different taxa respond differently to carbon dioxide concentrations, so the analysis presented here was done only with leaves of *Lepidopteris*, *Rhachiphyllum* and *Tatarina* known to have had peltasperm ovulate structures (Meyen 1982, 1987). Rarefaction analysis shows that at least 500 epidermal cells should be counted in order to be within the standard deviation of a count of 6000 cells (Retallack 2001), and these reliable counts are listed in Table 1. Other fossil cuticles not meeting this statistical criterium, but worthy of further attention, are listed in Table 2.

The stomatal index of *L. callipteroides* is exceptionally low, as if it lived at a time of unusually high atmospheric carbon dioxide during the earliest Triassic (Fig. 8). Other times of high carbon dioxide were during the mid-Permian (late Kazanian), Late Permian (latest Guadalupian) and Late Triassic (latest Carnian), which also have been considered times of mass extinction for both marine invertebrates (Stanley & Yang 1994) and terrestrial vertebrates (Benton 1987). Transient carbon dioxide greenhouses and plant extinctions of the late Kazanian, latest Guadalupian, latest Permian and latest Carnian each selected for *Lepidopteris* in preference to other plants (Wang 2000). However, *Lepidopteris* was a casualty of mass extinction and transient carbon dioxide greenhouse at the Triassic-Jurassic boundary (200 Ma; McElwain *et al.* 1999).

The amount of atmospheric carbon dioxide during the earliest Triassic can be estimated at 3314 ± 1097 ppmV (12 ± 4 times present atmospheric level or PAL), using a transfer function derived from stomatal index of living *Ginkgo biloba* grown in greenhouses under

Species	Locality	Age	Ma	N_e	N_s	N_f	SI	Reference
'A.' conferta	Rümmelbach, Ge.	Sakmar.	291±1	178	13	3	7.2±1.5	Kerp 1988
L. martinsi	Middridge, UK	Tatarian	258±2	379	18	4	4.8±1.4	Stoneley 1958, Townrow 1960, Poort & Kerp 1990
L. martinsi	Kimberly, UK	Tatarian	258±2	178	8	2	4.8±1.1	Stoneley 1958
L. martinsi	Cinderhill, UK	Tatarian	258±2	120	7	1	5.5	Stoneley 1958
L. martinsi	Geismar, German	Tatarian	258±2	415	30	3	6.0±0.4	Poort & Kerp 1990
L. sp. indet.	Baizovka, Russia	Tatarian	252±1	347	25	2	6.3±0.9	Gomankov & Meyen 1986
T. olferievii	Baizovka, Russia	Tatarian	252±1	400	67	2	7.9±2.7	Gomankov & Meyen 1986
T. conspicua	Baizovka, Russia	Tatarian	252±1	466	27	2	5.5±1.1	Gomankov & Meyem 1986
T. conspicua	Titovo, Russia	Tatarian	251±1	270	16	2	5.6±0.1	Gomankov & Meyen 1986
L. sp. indet.	Ledho Nala, India	Tatarian	251±2	375	26	3	6.6±1.2	Bose *et al.* 1975
L. indica	Nidpur, India	Tatarian	250±2	183	11	2	5.0±0.8	Srivastava 1974
L. sp. indet.	Kumarpur, India	Griesb.	247±3	109	6	1	5.2	Banerji & Bose 1977
L. sp. indet.	Beaver L.,Antarct.	Smithian	245±2	88	5	1	5.4	McLoughlin *et al.* 1997
L madagascariensis	Harai, India	Anisian	239±2	260	17	2	5.5±1.3	Pal 1984
L. microcellularis	Lyasov farm, R.	Ladinian	231±5	229	21	3	8.4±0.3	Dobruskina 1980
L. langlohensis	Langloh, Australia	Norian	220±5	367	22	2	4.9±1.6	Townrow 1965
L. ottonis	Gostyń, Poland	Norian	217±5	54	4	2	6.9±0.2	Marcinkiewicz & Orlowska-Zwolińska 1994
L. sp. indet.	Heilgersdorf, Germany	Rhaetian	204±4	410	30	1	6.8	Kelber & van Konijnenberg-van Cittert 1997
cf. *L. ottonis*	Höllviken, Swed.	Rhaetian	202±2	373	30	3	6.3±1.9	Lundblad 1949
L. ottonis	Bosarp, Sweden	Rhaetian	202±2	20	19	1	8.7	Lundblad 1949
L. ottonis	Rawicz, Poland	Rhaetian	202±2	361	33	2	8.1±0.4	Piwocki 1970

Table 2. Stomatal index (SI), and numbers of epidermal cells (N_e), stomates (N_s) and fragments (N_f) of *Lepidopteris, Tatarina* and *Rhachiphyllum* (including *'Autunia'* and *'Callipteris'*) leaf cuticles failing rarefaction analysis of Retallack (2001) because of inadequate materials.

different concentrations of carbon dioxide (Beerling *et al.* 1998), combined with stomatal index of herbarium specimens of *Ginkgo biloba* chosen to span post-industrial carbon dioxide increase (Retallack, 2001). This is greater than atmospheric carbon dioxide levels estimated from stomatal index for the late Kazanian (2098 ± 1166 or 7 ± 4 PAL), latest Guadalupian (2316 ± 1234 ppmV or 8 ± 4 PAL) or latest Carnian (2547 ± 1540 ppmV or 9 ± 6 PAL). The temporal coincidence of greenhouse transients and mass extinctions (Benton 1987, Stanley & Yang 1994, MacLeod *et al.* 2000), may indicate that atmospheric levels of carbon dioxide in excess of 2000 ppmV or 7 PAL are harmful to metazoan life.

Peltasperm seed ferns and the Permian-Triassic life crisis

The Permian-Triassic boundary has long been known as a major discontinuity in the history of life in the sea (Erwin 1993), and is known to have been devastating on land as well. In the Sydney Basin 97% of Late Permian species based on fossil leaves became extinct, including the former dominant *Glossopteris* (Retallack 1995). Euramerica lost many archaic walchiacean conifers (Poort *et al.* 1997, Looy 2000). Angara (modern Siberia) lost all ruflorian and voynovskyan cordaites and many seed ferns, such as *Tatarina* (Meyen 1982). China, then a series of isolated equatorial landmasses, lost many archaic lycopsids and the seed ferns *Gigantopteris* and *Gigantonoclea,* among others (Wang 1996). The crisis was especially severe among peat-forming floras, because no coals are known for the entire Early Triassic (Retallack *et al.* 1996). Extinction was also heavy among reptiles and amphibians (Benton 1987, MacLeod *et al.* 1998). Increased soil erosion and landscape instability is indicated by widespread claystone breccias of soil clasts (Retallack *et al.* 1998) and the onset of braided streams at the boundary (Retallack 1999, Retallack & Krull, 1999, Ward *et al.* 2000). Cyclostratigraphy and radiometric dating indicate that the extinctions and other environmental disruptions all occurred within 165,000 years (Bowring *et al.* 1998, Rampino *et al* 2000).

Fungal, fern and lycopsid spores show transient high abundance at the Permian-Triassic boundary worldwide (Eshet *et al.* 1995, Visscher *et al.* 1996, Foster *et al.* 1998). Abundant fungal spores may represent a period of plant destruction and decay, followed by lycopsid and fern spores of regenerating herbaceous plants (Looy 2000, Twitchett *et al.* 2001). Stromatolites found in earliest Triassic marine and lacustrine facies may also be disaster recovery biota (Schubert & Bottjer 1992). Early Triassic plants show several indications of difficult conditions, including herbaceous habit, succulence, heterophylly, sclerophylly, recurving leaves and reduced branching (Mader 1990, Wang 2000). Early Triassic floras are low in diversity and similar worldwide, in contrast to floral provincialism of the latest Permian. Isoetalean lycopsids (*Isoetes, Tomiostrobus, Pleuromeia*), voltzialean conifers (*Voltziopsis, Voltzia*) and the seed fern *Lepidopteris* are common and widespread globally (Dobruskina 1975, Retallack 1997a, Wang 2000). It is not until the Middle Triassic that floral provinciality remerges with the *Dicroidium* flora of Gondwana, and the *Scytophyllum* flora of Eurasia (Dobruskina 1975, Retallack 1977). The *Lystrosaurus* therapsid fauna is similarly widespread and low in diversity compared with Permian therapsid faunas and Middle to Late Triassic rhynchosaur faunas (Benton 1987, Retallack 1996, MacLeod *et al.* 2000). Similarly in the sea, Early Triassic marine faunas are very low in diversity (Erwin 1993, Hallam & Wignall 1997) and there are no known Early Triassic reefs (Flügel 1994).

The extraordinarily protracted effects of the Permian-Triassic extinctions can be seen also from studies of Australian and Antarctic palaeosols (Retallack 1997b, 1999; Retallack & Krull 1999) and of their carbon isotopic composition (Morante 1996, Krull & Retallack 2000). Carbon remains isotopically light ($\delta^{13}C_{org}$ -24 ‰) through much of the Early Triassic, with very light compositions ($\delta^{13}C_{org}$ -37 to -42 ‰) at the Permian-Triassic boundary and at several stratigraphic levels above it in many sections (Magaritz *et* al 1992, Ghosh *et al.* 1998, MacLeod *et al.* 2000, Krull & Retallack 2000). Values lighter than -37‰ at the Permian-Triassic boundary are only known to be produced by methanogenic bacteria, and could have come from massive release of methane from hydrate reservoirs in high latititude continental shelves or permafrost (Krull *et al.* 2000), as envisaged for greenhouse warming during the Jurassic and Paleocene (Hesselbo *et al.* 2000). Such large release could have been facilitated by extraterrestrial bolide impact (Retallack *et al.* 1998, Tonkin 1998) or flood basalt eruptions (Renne *et al.* 1995) into large reservoirs of methane hydrates in permafrost or high-latitude marine continental shelves. Atmospheric methane would be oxidized into carbon dioxide within 2-12 years, but while it lasts, methane is 50 times more effective as a greenhouse gas than carbon dioxide (Khalil 2000). Such greenhouse warming explains the spread to high palaeolatitudes (68-70°) of earliest Triassic palaeosols (Ultisols) currently found no further south than 58° (Retallack 1997b, 1999). Calculations based on oxygen isotopic analysis of carbonate from Austria indicate a 6-11° C rise in temperature across the Permian-Triassic boundary (Holser *et al.* 1991).

At this time of crisis, *P. townrovii* (Fig.7) was the first peltasperm seed fern to extend its range southward into the Antarctic Circle of the Gondwana supercontinent, thus making this previously Laurasian and northern Gondwanan genus cosmopolitan. Its southward migration may have been due to global warming, because its likely ancestors lived primarily in former tropical regions of India, Britain, Germany and Russia (Stoneley 1958, Srivastava, 1974, Pal 1985, Naugolnykh & Kerp 1996). Associated root traces and stems in its weakly developed palaeosols (Retallack 1980, 1999) are evidence that it was a shrubby pioneering plant of open, disturbed, river-margin habitats. This ecological role is compatible with its spreading fronds and the small size of ovules attributed to this plant here. It was also a stress tolerant plant, with extraordinarily

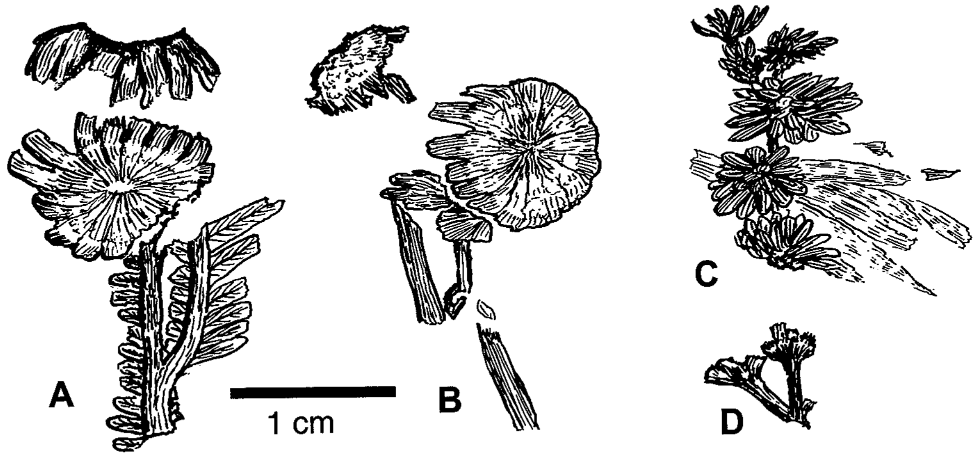


Fig. 5A-D. Reproductive structures associated with leaves of *Lepidopteris callipteroides* (Carpentier) comb. nov. from Oakdale Colliery. A-B, ovuliferous organs *Peltaspermum townrovii* sp. nov. (AM F118238 and AM F118237 respectively); C-D, polliniferous organs *Permotheca helbyi* sp. nov. (both AM F118242).

thick cuticles, narrow leaf segments, and sparse stomates, well adapted to nutrient-poor siliceous soils in which it is preserved (Retallack 1999) and to a post-apocalyptic greenhouse rich in methane and carbon dioxide (Retallack & Krull 1999, Krull *et al.* 2000, Retallack 2001). At this time of global crisis *Peltaspermum townrovii* found opportunity.

Systematic palaeontology

Lepidopteris Schimper, 1869

Type species. Lepidopteris stuttgardiensis (Jaeger, 1827) Schimper 1869 from the Schilfsandstein (Late Triassic) near Stuttgart, Germany (Townrow 1956, 1960; Dobruskina 1980).

Lepidopteris callipteroides (Carpentier 1935) comb. nov. (Figs 2-4, 7)

1935 *Dicroidium (Thinnfeldia) callipteroides* Carpentier, p. 12, pl. III, figs 1,2.
1966 *Thinnfeldia callipteroides* Carpentier; Townrow, p. 210, text-fig. 2D.
1977 *'Thinnfeldia' callipteroides* Carpentier; Retallack, p. 251.
1980 *'Thinnfeldia' callipteroides* Carpentier; Retallack, p. 407, fig. 21.6.
1984 *Dicroidium callipteroides*; White, p. 18.
1986 *Dicroidium callipteroides*; White, p. 138.
1993 *Dicroidium callipteroides*; McLoughlin, p. 616.
1995 *Dicroidium callipteroides* Carpentier; Retallack, p.77, fig. 1.

Holotype. Leaf figured by Carpentier (1935, pl. III, fig. 1). No number and repository information were given by Carpentier (1935), and my efforts to relocate this specimen have been unsuccessful.

Type locality. Bed 4, Sakamena Group (Early Triassic), near Amboriky, 5 km NNE of Ankavandra, Madagascar.

Other material. Lepidopteris callipteroides is well represented in collections of the Australian Museum (AMF-) and the former Mining Museum of the NSW Geological Survey (MMF-): basal Coal Cliff Sandstone [AM F27431 from Bellambi Colliery; AMF59519 from Bulli, AMF51730, 51730 from Coalcliff, AMF53796 from Nattai Colliery; AM F118243-46 from Oakdale Colliery; AM F45262-6 from Burragorang Valley (= Oakdale Colliery?)], Beauchamps Falls Shale of the Caley Formation (MMF13715 from Victoria Pass), basal Widden Brook Conglomerate (AM F91440, MMF13691, 13701, 13698 from Coxs Gap), basal Dooralong Shale (AM F261114 from Hamilton near Newcastle, AM F78318 from Frazer Park beach in Frazer National Park).

Emended diagnosis. *Lepidopteris* leaves with pinna rachides dichotomizing at least three times successively beyond the primary rachis to form a large (30 cm) radially spreading leaf; pinnules coriaceous, 0.5 to 30 mm long, ranging from rounded, to ovate and pinnatifid with increasing length; pinnule supplied by midrib and lateral veins which branch once toward the margin; rachides striated, with scattered, small (0.5-2 mm) raised bumps; cuticle thick (5-10 µm), amphistomatic; stomates cyclocytic, with 5-8 subsidiary cells, each with a papilla overhanging the stomatal pit.

Comparison. As its epithet implies, *L. callipteroides* is similar to '*Callipteris*' Brongniart, which was proposed for conservation (Kerp 1981), then withdrawn in favor of its senior synonym *Callipteris* Bory, a living fern (Kerp 1986). Poort & Kerp (1990) and Naugolnykh & Kerp (1996) argued that various leaf species of this genus are best referred to natural taxa such as *Autunia* or *Peltaspermum*, which are based on ovuliferous reproductive structures. They also argued that only foliage with unknown reproductive structures should be referred to *Rhachiphyllum* and other form genera (Kerp 1988, Naugolnykh 1991). In contrast, a traditional approach is taken here, in which *Lepidopteris* and *Rhachiphyllum* are used as form genera for leaves.

Lepidopteris callipteroides has narrow, coriaceous, pinnules in which the secondary veins are difficult to see and fork only once from the midrib to the margin, unlike the thinner leaves and more copiously branched venation of *Rachiphyllum, Madygenia, Madygenopteris,* and *Feonia* (Sixtel 1959, Meyen 1982, Kerp 1988). Most species of *Lepidopteris* are bipinnate or bipinnatifid (Townrow 1956, 1960; Dobruskina 1980, Pal 1985, Anderson & Anderson, 1989). Only *L. martinsii* has dichotomizing terminal rachides and a dichotomy of the main rachis (Poort & Kerp 1990), although it lacks multiple terminal dichotomies as in *L. callipteroides*. The pinnules of *L. martinsii* are also wider and more equidimensional, and its fronds shorter and narrower, than those of *L. callipteroides*.

Peltaspermum Harris, 1937

Type species. Peltaspermum rotula Harris, 1937 from the Fleming Fjord Formation (Late Triassic) of East Greenland (Clemmensen 1980).

Peltaspermum townrovii sp. nov. (Figs 5A-B, 6A-G, 7)

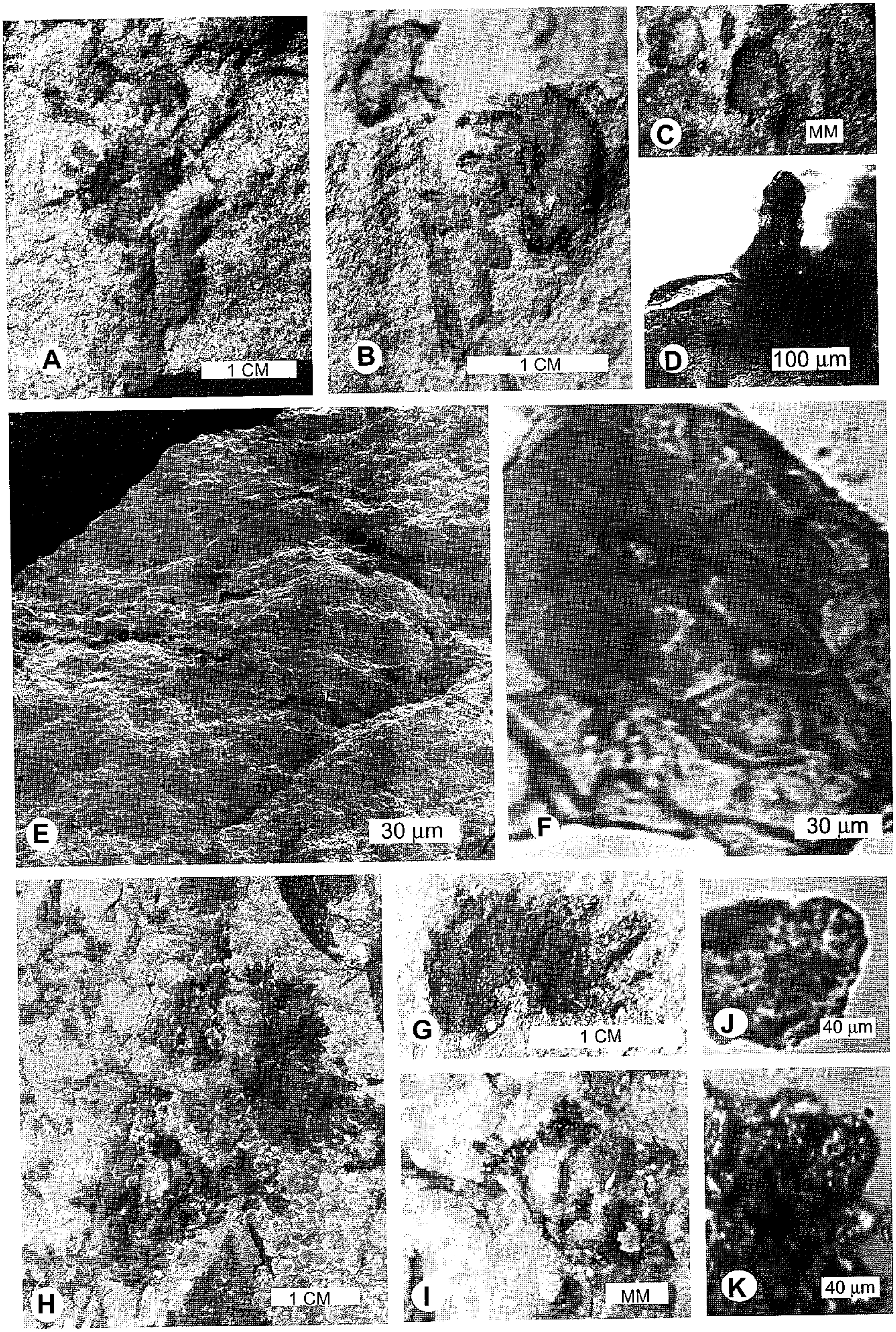
1935 diaphragme d'Equisétinée; Carpentier, p. 10, pl. IV, fig. 1.

Holotype. Two terminal stalked discs (AMF118237; Australian Museum, Sydney).

Type locality. Oakdale Colliery, an underground mine near Camden and the Burragorang Valley, N.S.W.: specifically from the crib room locality 250 m south of the entrance shaft (N 2,383, 010' E1,043,650' in mine coordinates) where the roof is a gray shale with fine root traces; Coal Cliff Sandstone; Early Triassic; collected by G.J. Retallack and R. Hall, August 16, 1974.

Other material. The type locality also yielded additional specimens of ovulate discs (AM F118239, 118242) and of isolated ovules (AM F118241a-b). Another part of the Oakdale mine roof yielding *Peltaspermum* (AMF118238a-b) is the old south locality just north of the entrance shaft (N 2,383,900' E 1,044,000' in mine coordinates), where laminated shales and sandstones immediately overlie a 20 cm thick

Fig. 6A-K. Reproductive structures associated with leaves of *Lepidopteris callipteroides* (Carpentier) comb. nov. from Oakdale Colliery. A-B, ovuliferous organ *Peltaspermum townrovii* sp. nov. (AM F118238, 118237 respectively); C, un-named associated ovules (AM F118241); D-F, preparations from *Peltaspermum townrovii* (specimen AM F118237) including micropylar beak of ovule in plane light (D), ovuliferous disc under SEM (E) and cuticle fragment from disc under plane light (F); G, *Peltaspermum townrovii* sp. nov., isolated head with two attached ovules (AM F118239); H-I, pollen organ *Permotheca helbyi* sp. nov. (all AM F118242), including fossiliferous slab (H), close-up of synangial stalks (I), and masses of pollen (J-K) *Falcisporites australis* (de Jersey) Stevens (1981). *[see page 491].*


A
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fireclay (Wybung pedotype of Retallack 1999) above the coal. Discs of *P. townrovii* in the Australian Museum (AM F45266) labelled 'Burragorang Valley' have a similar unweathered matrix and are probably from the same locality. These specimens are all from the Coal Cliff Sandstone, basal Narrabeen Group (earliest Triassic). *Peltaspermum townrovii* is probably also represented by a fossil figured as a horsetail diaphragm (by Carpentier 1935, pl. IV, fig. 1) from Bed 4 of the Sakamena Group near Amboriky, Madagascar (also Early Triassic).

Diagnosis. Peltaspermum with peltate ovuliferous discs, borne on slender stalks arranged around a stouter axis; ovuliferous discs small (7-8 mm), with 11-14 radial lobes, that extend beyond the margin as a fringe of subrectangular lappets 2 mm wide and 3 mm long; ovules ovoid in shape, 2.6x2 mm in size, with blunt micropyle.

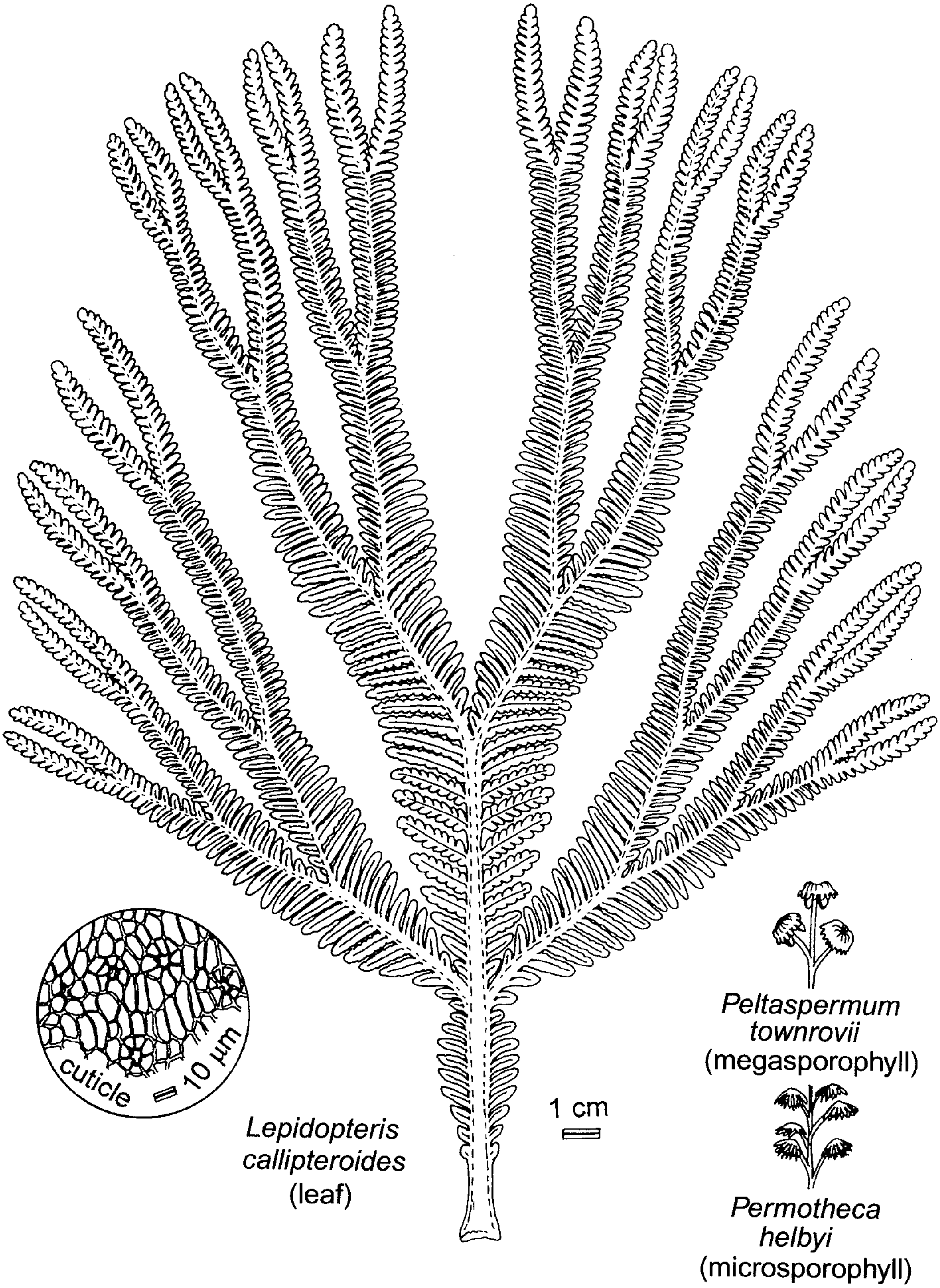
Etymology. The epithet is in honour of Dr. J. A. Townrow, who pioneered study of floras of the basal Narrabeen Group.

Description. Peltaspermum townrovii may have been a large, lax, structure, but only the upper few ovuliferous heads are preserved in the available specimens. The main axis of the fructification is 2.1–1.8 mm in compressed diameter (2 specimens only), and gives rise to slender (1.5 ± 0.5 mm: mean and standard deviation) stalks some 8 mm long and spaced at intervals of 8-10 mm along the main axis. These stalks terminate in discs that are 7.8 ± 0.7 mm in diameter and have 11-14 radial lobes defined by the most prominent radial creases. Beyond the margin of the disc the lobes extend as subrectangular lappets 3.1 ± 0.6 mm long and 1.6 ± 0.3 mm wide. Only one specimen has ovules, only two of them, attached to the lower (adaxial) side of the disc (Fig. 6G). These ovules are ovoid and 1.9x2.8 and 1.7x2.2 mm in size. Twelve comparable ovules found loose on the same bedding plane (Fig. 6C) are 2.7 ± 0.5 mm long and 2.0 ± 0.3 mm wide. The ovules have an elongate micropyle (Fig 6C-D), without evident elongation or elaboration. Some ovules show one or two prominent ribs, suggestive of a triradiate sclerotesta. Sarcotesta development was minimal. It is uncertain how many ovules were borne on each head: 14 are possible, considering rounded disruptions on each of the radial lobes suggestive of scars where seeds have fallen (Fig. 6E).

Comparison. Comparable ovulate structures of peltasperms have been reviewed by Poort & Kerp (1990). *Autunia, Autuniopsis* and *Meyenopteris* all have ovulate heads that are fan-shaped, rather than umbrella-shaped as in *Peltaspermum*. *Lopandiangium* has peltate ovulate heads with more radial segments (19-24), sharper, down-turned, segment terminations and shorter, stouter stalks than in *Peltaspermum* (Naugolnykh 1991). *Peltaspermopsis* has ovuliferous heads closely aggregated into a cone-like ball, unlike the lax and elongate fructifications of *Peltaspermum*. *Nidia* (Bose & Srivastava 1973) is very similar to *Peltaspermopsis* (Gomankov & Meyen 1986), and may be a senior synonym of that genus.

Peltaspermum townrovii has smaller ovulate heads with fewer radial lobes, less marked ribbing, and shows no evidence of slightly eccentric stalk insertion seen in the Permian species *P. martinsii* from Germany and Italy (9-16 mm diameter: Poort & Kerp 1990), and *P. retensorium* from Russia (5-25 mm diameter; Naugolnykh & Kerp, 1996). *Peltaspermum incisum* from the Late Triassic of Russia (Stanislavsky 1976, Dobruskina 1980) is similar to an un-named species of *Peltaspermum* from the Late Triassic of South Africa (Anderson & Anderson 1989) and Australia (Holmes 1982) in having deep incisions of the radial lobes reaching almost to the stalk of the ovuliferous head, unlike the clearly differentiated disc with marginal lobes in *P. townrovii* sp. nov. and in *P. rotula* (Harris 1937, Townrow 1960). The

Fig. 7. Restoration of leaves and reproductive structures of the earliest Triassic seed fern, *Peltaspermum townrovii* sp. nov. (ovuliferous structures), which characterise this whole plant restoration including leaves of *Lepidopteris callipteroides* (Carpentier) comb. nov. and polleniferous organs of *Permotheca helbyi* sp. nov.*[see page 493].*


cuticle
10 µm
Lepidopteris
callipteroides
(leaf)
1 cm
Peltaspermum
townrovii
(megasporophyll)
Permotheca
helbyi
(microsporophyll)

ovuliferous disc of *P. rotula* is similar to the present specimens, but it differs in a number of points: slightly larger size (10-15 mm diameter), more seeds (10-20), more marked lateral flange, and equidimensional (rather than subrectangular) marginal lappets.

Permotheca Zalessky, 1929

Type species. Permotheca sardykensis Zalessky, 1929 from the Late Permian (Tatarian) of Kullarovo, Cisuralian Russia.

Permotheca helbyi sp. nov. (Figs 5C-D, 6H-K, 7)

Holotype. Branching system of terminal synangia (AM F118242 in the Australian Museum, Sydney), upper right specimen on slab of Fig 6G, sketched in Fig. 5C.

Type locality. Old south locality of Oakdale Colliery, as for *P. townrovii* above: Coal Cliff Sandstone; Early Triassic.

Diagnosis. Permotheca with synangia arranged on short slender stalks to a main axis; synangia of some 15-20, radially-arranged, elongate, pollen sacs, fused in the basal quarter of their length; pollen probably *Falcisporites australis* (de Jersey 1962) of Stevens (1981).

Etymology. This species is named in honour of Robin Helby, who first recognized the *Protohaploxypinus microcorpus* palynozone of the Sydney-Bowen Basins.

Description. The single known specimen is a complex, branching microsporophyll (Fig. 6G). The apical portion has synangia at the end of stalks 4-5 mm long and 1 mm wide around a stouter central axis 1.5 mm wide. Individual synangia include 15-20 pollen sacs arranged radially in a wide arc from the basal quarter of the sacs, which are fused. Synangiate fusion is indicated by partly rotted specimens (Fig. 5D, 6I) which show at the end of the stalks ragged globular masses of fused pollen sacs with diameter of 2.9 ± 0.4 mm (n = 4). The pollen sacs are cigar-shaped, 3.3 ± 0.7 mm long and up to 0.7 ± 0.1 mm wide (n = 27). Their widest point is usually about two thirds of the way out from their base. Dehiscence was by a longitudinal slit. Small pollen masses of *Falcisporites australis* (de Jersey) Stevens (1981) were found (Fig. 6J-K), together with isolated grains referable to the dispersed palynospecies *Osmundacites wellmanii, Praecolpatites sinuosis, Vitreisporites pallidus* and *Falcisporites australis* (Helby *et al.* 1987).

Comparison. Permotheca has synangia of many pollen sacs, fused at their base, but is attached to slender branching structures, unlike *Idanothekion* and *Crossotheca* which are attached to fern-like leaves (Retallack & Dilcher 1988). There is also no hint of a laminar head on which pollen sacs are attached or embedded, as in *Pteruchus, Pteroma, Townrovia, Harrisiothecium* or *Pramelreuthia* (Retallack 1981, Meyen 1982, Anderson & Anderson 1989, Ash & Litwin 1996). In this respect *Permotheca* is more like *Telangium, Telangiopsis,* and *Antevsia,* but differs in having many more pollen sacs in each cluster (Retallack & Dilcher 1988). This is also true of the pollen organs such as *Stachyopitys*, which have in addition no basal fusion of the pollen sacs (Anderson & Anderson 1989). The most similar genus to *Permotheca* is *Pteridospermostrobus* (Kerp 1988), which has pollen sacs fused for about half their length in urn-shaped clusters, rather than the splayed clusters of *Permotheca.*

Among the species of *Permotheca* recognized by Gomankov & Meyen (1986) and Krassilov *et al.* (1999), *P. sardykensis, P. striatifera* and *P. disparis* have fewer, stouter pollen sacs arranged in a more compact synangium than *P. helbyi. Permotheca disparis* also had a much thicker central axis than *P. helbyi* (Krassilov *et al.* 1999). Pollen sacs of *P. vesicasporoides* and *P.? vittatiferina* are similar to those of *P. helbyi*, but only isolated pollen sac clusters are known in *P. vesicasporoides* and only isolated pollen sacs in *P. vittatiferina*. These taxa are in part defined by their contained pollen, referable to palynogenera

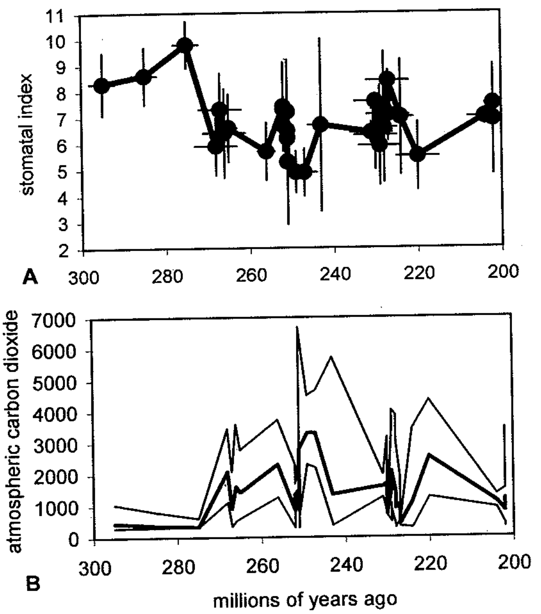


Fig. 8. A peltasperm paleobarometer of atmospheric carbon dixide levels through time (B), inferred from measurements of stomatal index of leaves of *Lepidopteris*, *Tatarina*, and *Rhachiphyllum* (A, Table 1). Stomatal index is inversely correlated with atmospheric carbon dioxide levels. Transient greenhouses of the mid-Permian, Late Permian, terminal Permian and Late Triassic all correspond to mass extinctions of land plants and verterbates (see text). Error envelopes and bars are one standard deviation.

Vesicaspora and *Vittatina,* respectively. *Vittatina* was not found in *P. helbyi,* nor in the palynoflora of the *Protohaploxypinus microcorpus* zone (Helby *et al.* 1987). Balme (1995) thought pollen from *Permotheca vesicasporoides* identified as *Vesicaspora* by Gomankov & Meyen (1986) should be referred to *Falcisporites,* but Krassilov *et al.* (1999) used both SEM and TEM studies to attribute the pollen of *Permotheca disparis* to *Vesicaspora,* albeit broadly defined. Pollen from these Russian fossils is distinct from pollen of *P. helbyi* in several features, including more inflated sacci which envelop more of the corpus. The pollen of *P. helbyi* is thus similar to that of the corystosperm microsporophyll *Pteruchus* (Balme 1995). Most species of *Pteruchus* have clearly laminate structures to which the pollen sacs are attached (Townrow 1962, Yao *et al.* 1995), but this is not true of *'Pteruchus' nidpurensis* (Srivastava, 1974) and *'Pteruchus' simmondsi* (Townrow, 1962), which should be reconsidered as possible additional species of *Permotheca.* Both species have shorter and wider pollen sacs than *P. helbyi.*

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