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### A new marattiaceous fern from the Lower Jurassic of Patagonia (Argentina): the renaissance of Marattiopsis

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## A new marattiaceous fern from the Lower Jurassic of Patagonia (Argentina): the renaissance of *Marattiopsis*

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We here describe *Marattiopsis patagonica* sp. nov. (Marattiaceae) based on vegetative and fertile foliage impressions from the Lower Jurassic of Chubut Province, Patagonia, Argentina. The new species exhibits a unique combination of vegetative and reproductive features, including a prominent basal auricle; finely undulate, denticulate, to serrulate pinnule margins; interstitial fibres (*venuli recurrentes*) alternating with regular veins; submarginal position and distinctive relative length of synangia (about 12–20% of the pinnule width); and relatively small number of sporangia pairs per synangium (usually 14 or 16). The new species is assigned to the morphogenus *Marattiopsis*, since it shows no characters that would allow an unambiguous placement in any of the modern genera, *Marattia* s.s., *Ptisana*, or *Eupodium*. The newly established paraphyly of the *Marattia* s.l. species has a profound impact on the classification of fossil species. In this context, we provide a brief assessment of the significance of the fossil *Marattiopsis* for phylogenetic and biogeographical interpretations. It appears that essentially modern marattioid ferns, including *Marattiopsis*, which are commonly considered to be typical elements of tropical areas of the northern hemisphere during the Mesozoic, may have left an important but largely ignored fossil record in subtropical Gondwana.

**Keywords:** Marattiaceae; *Marattia*; *Ptisana*; Jurassic; Patagonia

### Introduction

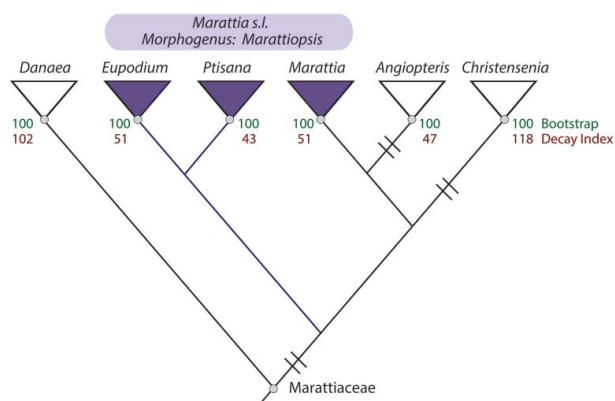
Marattiales is an ancient group of eusporangiate ferns (e.g. Delevoryas *et al.* 1992; Yang *et al.* 2008). Historically, most authors considered the modern Marattiales to include a single family, Marattiaceae Kaulfuss, with four genera, including *Marattia* O. Swartz, *Christensenia* Maxon, *Danaea* J. E. Smith and *Angiopteris* G. F. Hoffmann (see Rolleri *et al.* 2003; Smith *et al.* 2006; Murdock 2008a), although other authors recognized several individual families and additional genera (e.g. Pichi Sermolli 1977). Recent phylogenetic analyses have yielded conflicting results regarding relationships amongst Marattiales and other groups within the Euphyllophyta (e.g. Pryer *et al.* 2001, 2004; Rothwell & Nixon 2006; Schneider *et al.* 2009).

As traditionally defined, the type genus *Marattia* has been the most morphologically diverse and widespread genus, with about 20 palaeotropical species distributed in Africa, Asia and Australasia, and about 10 neotropical species in Central and South America (see Rolleri *et al.* 2003). Based on molecular and morphological data, however, it

has recently been suggested that *Marattia* s.l. should be separated into three genera (Murdock 2008a) (Fig. 1): *Marattia* s.s., which is restricted to the Neotropics and Hawaii; *Eupodium* J. Smith with Neotropical distribution; and *Ptisana* Murdock including the Palaeotropical Kingdom species (Murdock 2008b, Christenhusz *et al.* 2011). This division has been considered as tentative (Christenhusz 2010), since additional data on *Marattia* s.l. and *Angiopteris* species are necessary to verify the monophyly of the proposed genera. Furthermore, separation of *Eupodium* and *Ptisana* remains somewhat ambiguous (Fig. 1) since they are resolved as sister genera (Murdock 2008b). Despite these taxonomic issues, this new classification of *Marattia* s.l. species into at least two different lineages warrants a critical re-evaluation of the fossil record of *Marattia*-like foliage.

Marattioid ferns are considered to have one of the most extensive fossil records of any modern fern lineage (e.g. Tidwell & Ash 1994); it dates back to the late Palaeozoic and is particularly rich and diverse in the earlier Mesozoic (Seward 1922), but surprisingly scarce in the Cenozoic (Collinson 2001). Foliage that is superficially

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**Figure 1.** Phylogenetic relationships of extant Marattiaceae (modified from Murdock 2008a). Taxa previously grouped in genus *Marattia* (indicated in purple shading) and which overlap with the fossil morphogenus *Marattiopsis* forming a polyphyletic assemblage. Original support values for the clades are included.

similar to modern *Marattia* first appears in the Upper Triassic and Lower Jurassic. In particular, the fossil record of *Marattia*-like fronds has been referred either to *Marattia* or the fossil morphogenus *Marattiopsis* (Harris 1961). More recently, several authors have argued about the preferential use of *Marattia* over *Marattiopsis* (e.g. Kilpper 1964; Van Konijnenburg-van Cittert 1975; Li & Wu 1982; Hill *et al.* 1985; Schweitzer *et al.* 1997; Wang 1999; Yang *et al.* 2008), as the fossils are similar to extant *Marattia* in almost all the morphological features. However, in light of the new *Marattia s.l.* phylogenetic status, the use of *Marattiopsis* has been proposed for *Marattia sensu lato* fossil species (Bomfleur *et al.* 2013).

Likewise, the Mesozoic record of *Marattia*-like ferns, which has been mostly restricted to the northern hemisphere (e.g. Wang 1999; Yang *et al.* 2008) with species from Asia, Greenland and Europe (e.g. Harris 1961; Van Konijnenburg-van Cittert 1975; Schweitzer *et al.* 1997; Wang 1999; Yang *et al.* 2008), also includes several findings from the southern hemisphere, especially from Triassic and Lower Jurassic localities in Argentina (e.g. Arrondo & Petriella 1980; Baldoni 1987; Morel *et al.* 1999; Artabe *et al.* 2005).

In the present contribution we describe new material from the Lower Jurassic of Cerro Bayo, Chubut Province (Argentina) and discuss other records of *Marattia*-like fossils from the southern hemisphere and the phylogenetic meaning and novel relevance of *Marattiopsis*.

## Material and methods

Vegetative and fertile impressions of marattioid ferns were collected at the ‘Cerro Bayo’ locality (Chubut Province, Argentina). Plant horizons at this locality belong to an unnamed unit of fluvially reworked, volcanoclastic deposits, which are succeeded by agglomerates and lavas

of the Lonco Trapial Formation and by lacustrine deposits of the Cañadón Asfalto Formation (Fig. 2). Recent radiometric datings of ash layers from the Cañadón Asfalto Fm have yielded U-Pb zircon mean ages of  $176.15 \pm 0.1$  Ma and  $177.37 \pm 0.1$  Ma (Cúneo *et al.* 2013), indicating an Early Jurassic age (most likely Pliensbachian) for the underlying plant-bearing beds. This age assignment agrees well with the composition of the plant-fossil assemblage, which contains taxa considered typical of Early Jurassic floras of Patagonia (Escapa *et al.* 2008a, b; Escapa & Cúneo 2012), including *Goeppertella*, *Dictyophyllum* and *Sagenopteris* (see Escapa *et al.* 2008b).

Specimens were collected at two nearby sites (GPS coordinates are available upon request to the authors) and include vegetative and fertile pinnules preserved as impressions and external moulds, some of them preserving impressions of epidermal details in their vascular traces. The material occurs in fine-grained, partially silicified sediments as part of a taphocoenosis dominated by conifers and ferns (Escapa *et al.* 2008a; Escapa & Cúneo 2012). The conifers are mostly represented by the cupressaceous *Austrohamia minuta* (Escapa *et al.* 2008a), whereas ferns are represented by Osmundaceae (*Todites cacerei* and *Osmundopsis rafaelii*; Escapa & Cúneo 2012), Dipteridaceae (*Dictyophyllum* and *Goeppertella*), putative Dicksoniaceae, and the marattioid ferns described here. In addition, seed ferns (e.g. Caytoniales) and equisetaleans complete the floral spectrum.

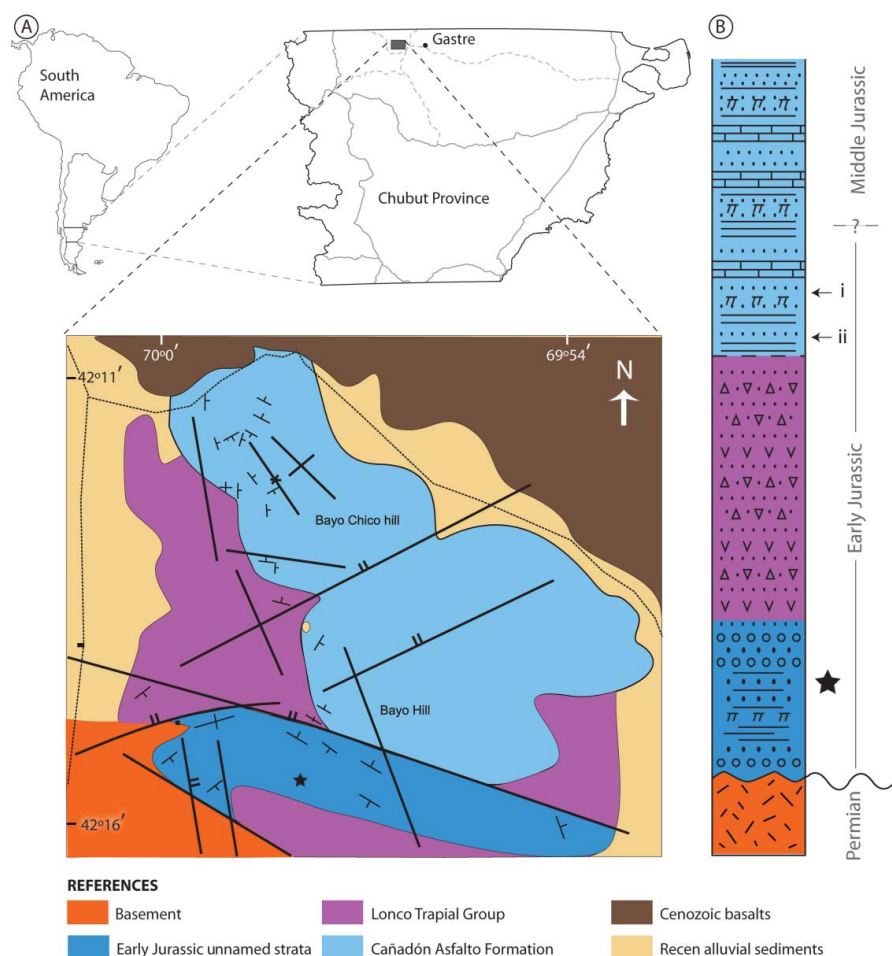
Most fertile specimens are preserved as moulds, making examination and illustration of reproductive details difficult (Fig. 3). We therefore prepared silicone rubber casts (see Watson & Alvin 1976) to study the external features of those specimens, which revealed previously unknown details in the morphology of synangia (e.g. fully sessile condition).

All specimens are deposited at the Museo Paleontológico Egidio Feruglio Palaeobotanical Collection in Trelew, Argentina (hereafter **MPEF-Pb**). Fine details of the compression/impression specimens were studied using a Zeiss MC80DX stereoscope microscope with an attached Nikon digital camera. Silicone moulds were coated with magnesium oxide (MgO) sublimate to enhance details, and studied and photographed under oblique lighting.

## Systematic palaeontology

Order **Marattiales** Link, 1833  
 Family **Marattiaceae** Kaulfuss, 1824  
 Genus *Marattiopsis* Schimper, 1869  
*Marattiopsis patagonica* sp. nov.  
 (Figs 4–7)

**Diagnosis.** Pinnules linear to oblong-lanceolate, generally <20 mm wide, tapering gradually towards apex; base with a pronounced basiscopic auricle; margins finely



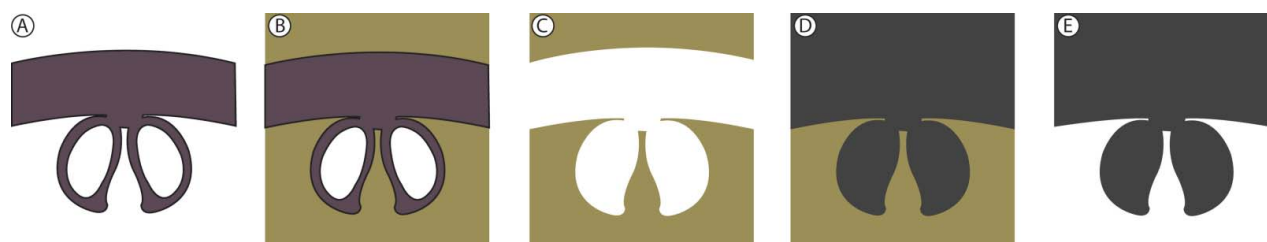
**Figure 2.** A, location and geology of the *Marattiopsis patagonica* fossil localities (indicated by star). B, simplified stratigraphical section showing the main lithostratigraphical units cropping out in the Cerro Bayo area. Radioisotopic dates on the Cañadón Asfalto Formation are indicated: (i)  $177.37 \pm 0.12$  Ma; (ii)  $176.15 \pm 0.12$  (see Cúneo *et al.* 2013).

undulate, denticulate, to serrulate. Lateral veins commonly forking immediately at or near the midrib; vein density generally between 8 and 16 in central pinnule portion; venation in basal auricle basiscopic, fan-shaped, with simple or once-forked veins. Interstitial fibres delicate, alternating with regular veins. Synangia submarginal, sessile, each occupying about 12–20% of the

pinnule width, containing about 8 to 20 (usually 14 or 16) opposite pairs of laterally fused, erect sporangia.

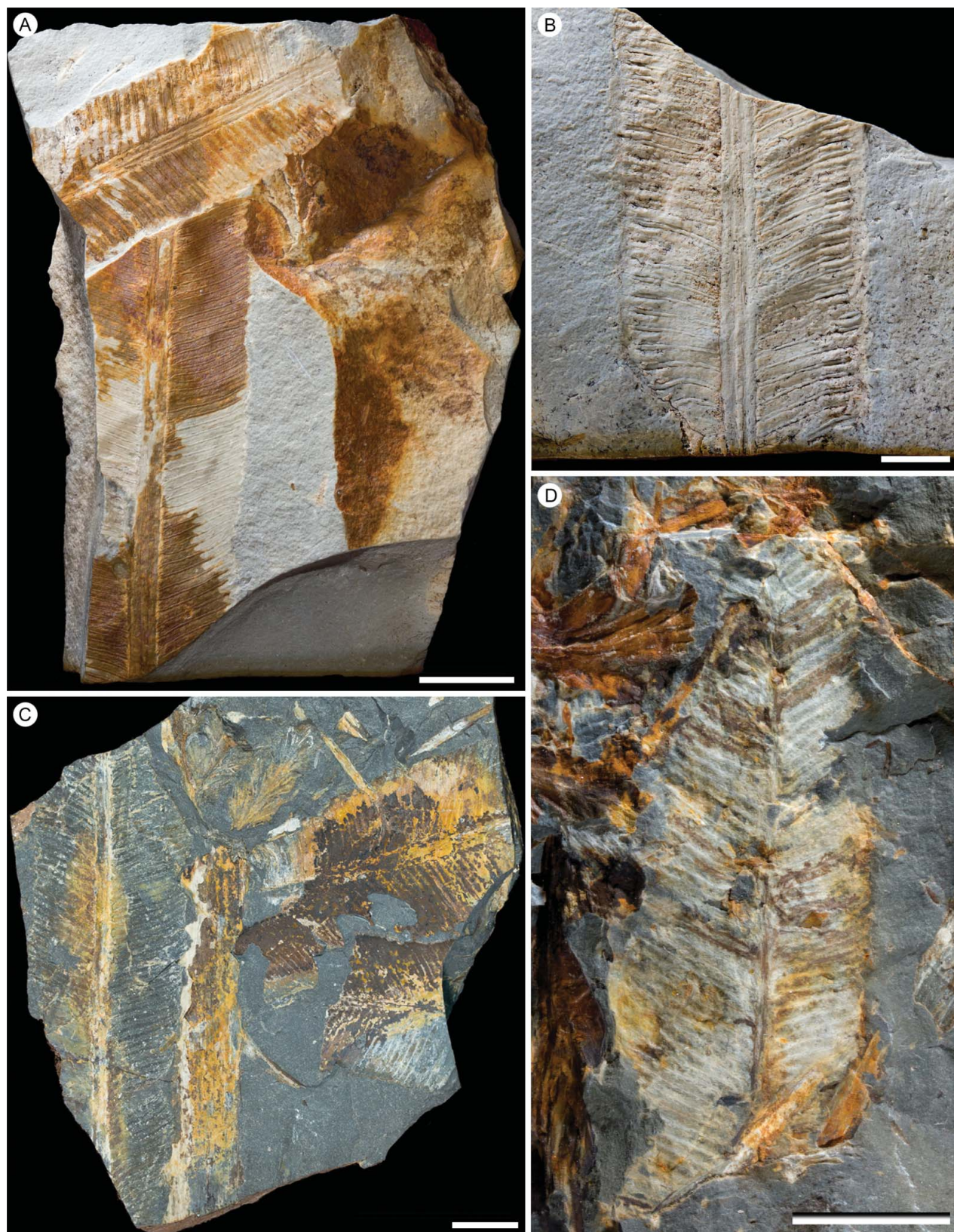
**Holotype.** MPEF-Pb 5278.

**Paratypes.** MPEF-Pb 5279 to 5316.



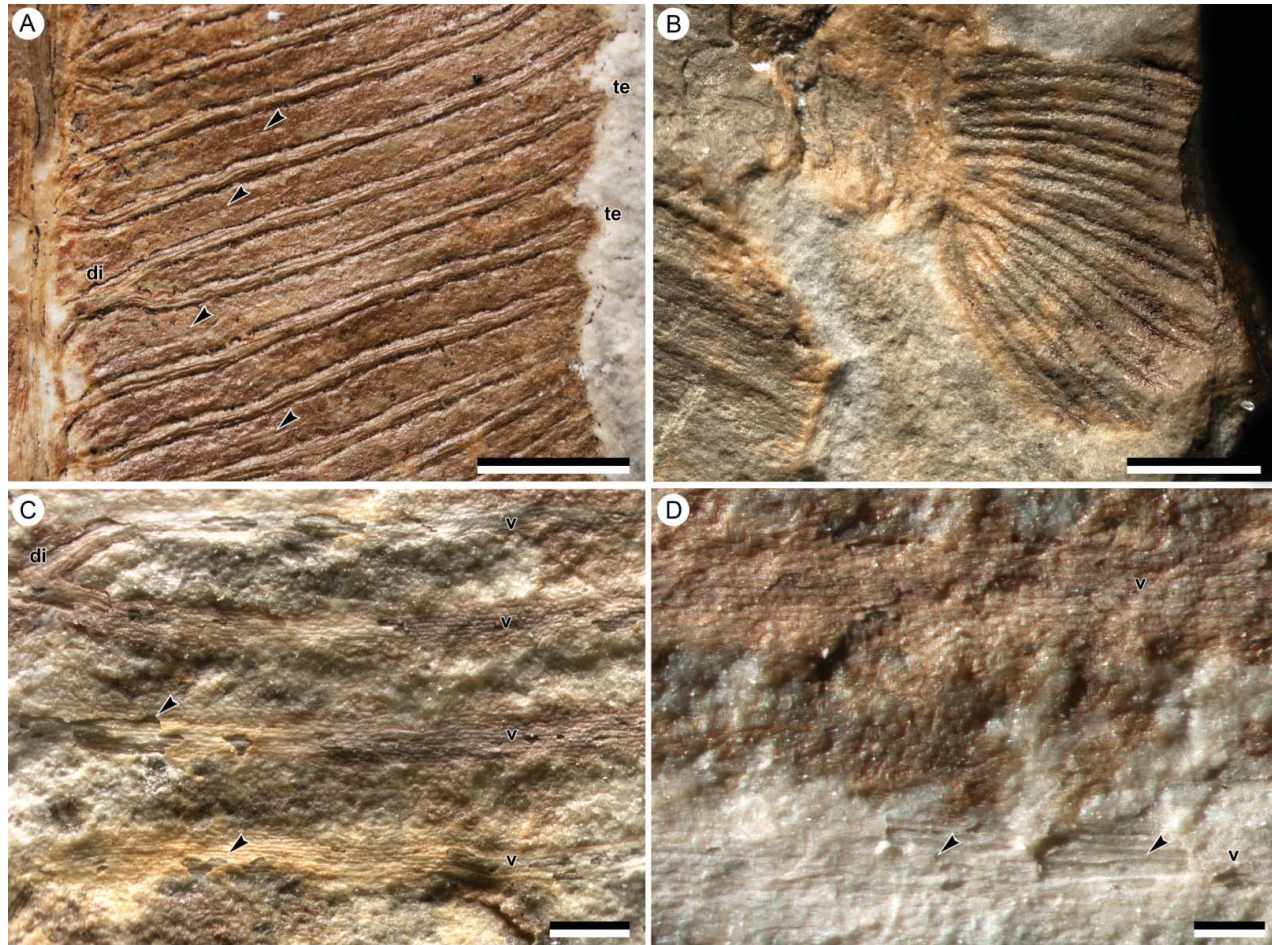
**Figure 3.** Cross section of *Marattiopsis patagonica* pinnule with adaxial synangium, showing fossil preservation and casting. A, pinnule of living plant; B, pinnule buried in sediment; C, decomposition and removal of plant material during diagenesis leaves mould of synangium in the rock; D, synangium mould filled with silicone; E, silicone cast of synangium showing original features. Plant material – brown; sediment and rock – green; silicone – grey.





**Figure 4.** *Marattiopsis patagonica* Escapa *et al.* from the Early Jurassic of Patagonia, Argentina. **A**, MPEF-Pb 5278, fragments of fertile (at top, oblique) and vegetative pinnules (vertical); vegetative pinnule shows denticulate margin. **B**, MPEF-Pb 5279, fragment of fertile pinnule with prominent midrib and submarginal synangia associated with distal portions of lateral veins. **C**, MPEF-Pb 5310, vegetative pinnule fragments; note midrib and lateral veins. **D**, MPEF-Pb 5314, incomplete vegetative pinnule fragments showing midrib, lateral veins; note the gradual width reduction towards the apex. Scale bars: A, C, D = 10 mm; B = 5 mm.





**Figure 5.** *Marattiopsis patagonica* Escapa *et al.* from the Early Jurassic of Patagonia, Argentina. **A**, MPEF-Pb 5278, vegetative pinnule showing midvein, lateral veins (v), venuli recurrentes (arrows), and marginal teeth (te). Note that one of the lateral veins is basally dichotomized (di). **B**, MPEF-Pb 5297, fragment of pinnule base showing venation pattern of basal auricle. **C**, MPEF-Pb 5314, detail of lateral veins (v) showing preservation of epidermal cells; arrows indicate regions where detached pieces of epidermis reveal the conducting strand; note vein dichotomy (di). **D**, MPEF-Pb 5314, detail of epidermal cell impressions and conducting cells (arrows) of veins (v) beneath the epidermis. Scale bars: A, B = 2 mm; C = 0.5 mm; D = 0.2 mm.

**Derivation of name.** The specific epithet *patagonica* is chosen to indicate the geographical occurrence of the type material.

**Material.** Thirty hand specimens with a total of 82 dispersed pinnule fragments from a site informally referred to as ‘*Marattiopsis* level’; additional six hand specimens containing 10 pinnule fragments were collected from a nearby site that we informally refer to as ‘*Caytonia* level’. GPS coordinates and detailed locality descriptions are deposited at the Museo Paleontológico Egidio Feruglio (Trelew, Chubut, Argentina), and are available upon request.

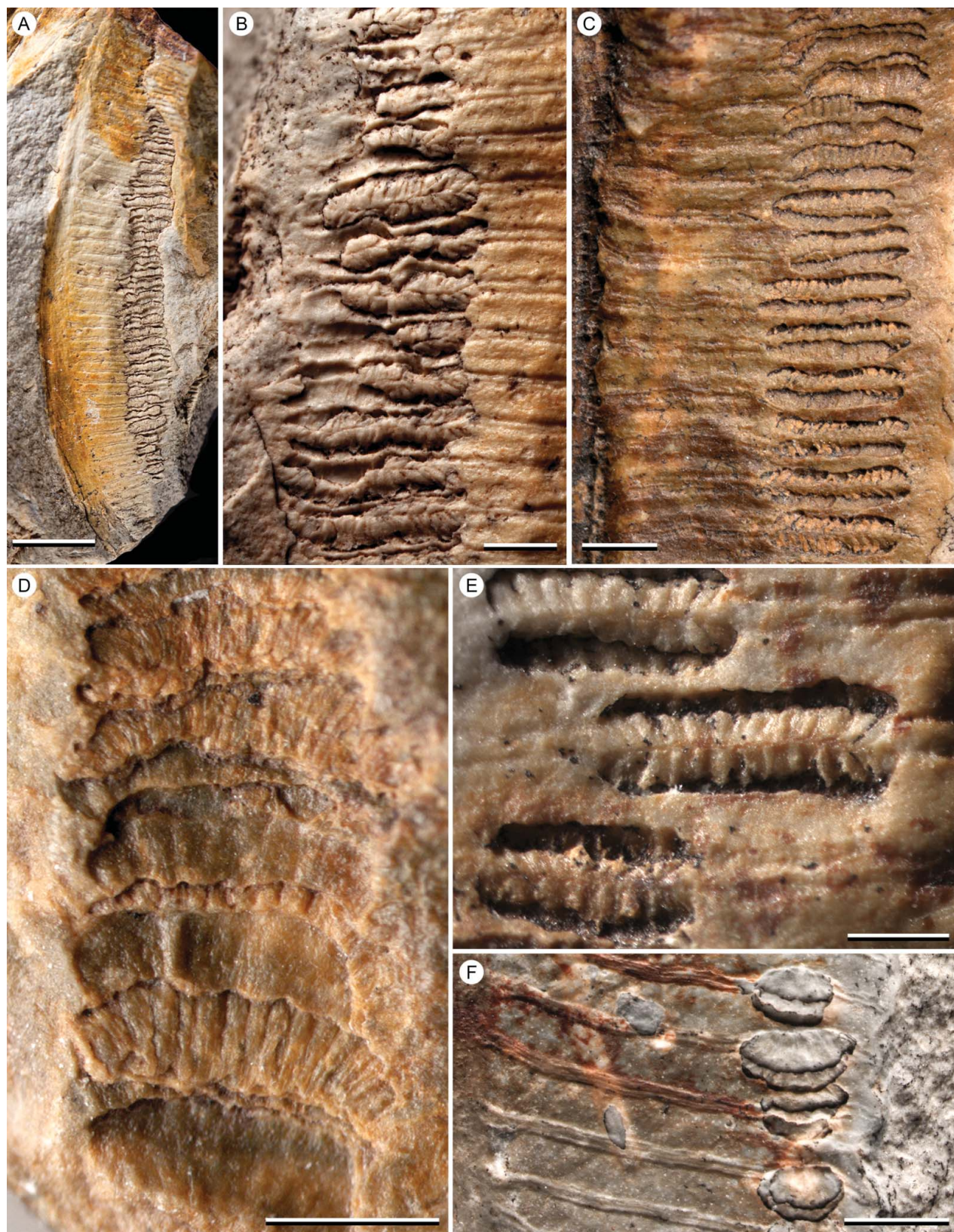
**Type locality.** Cerro Bayo locality, NW Chubut Province, Argentina.

**Type stratum and age.** An unnamed sedimentary unit that is conformably overlain by the late Early to early

Middle Jurassic volcanic rocks of the Lonco Trapial Group.

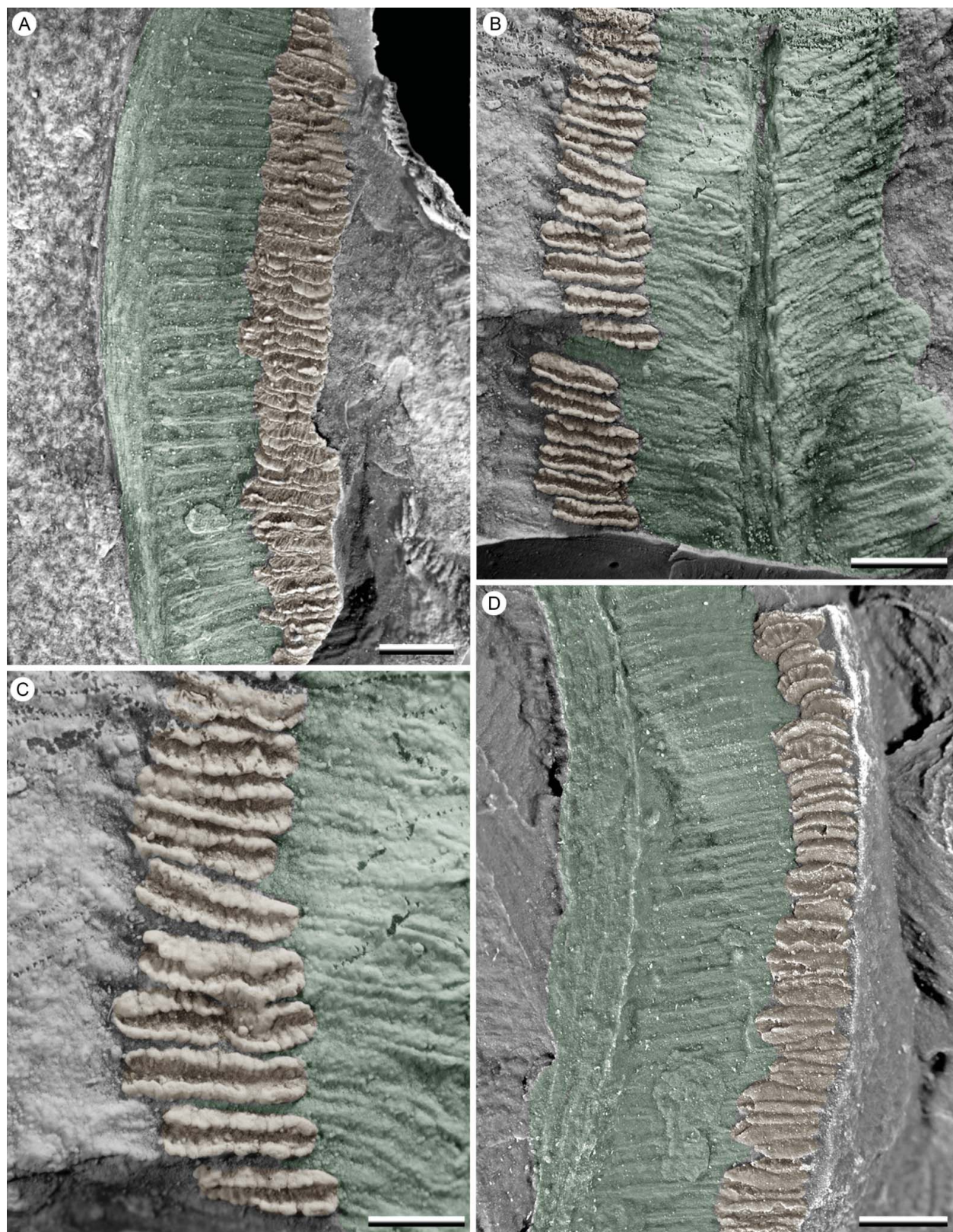
**Description.** The specimens are represented by linear to oblong-lanceolate pinnules, exceeding 80 mm in length, and usually 12–15 mm (rarely up to 27 mm) wide (Fig. 4A–D), which gradually taper towards the apical portion (Fig. 4D). Pinnule bases have a pronounced basiscopic auricle (Fig. 5B). The pinna/pinnule margin is finely undulate, denticulate, to serrulate (Figs 4A, 5A), with blunt or slightly pointed teeth up to 1 mm long (Fig. 5A), symmetrical or acroscopically curving. There is a prominent pinnule midrib with a straight trajectory, and that generally occupies *c.* 8–12% of the pinnule width (i.e. 1–2 mm, rarely up to 2.5 mm wide) (Fig. 4A–D). The lateral veins emerge free from the midrib at *c.* 45° angles, but immediately curve basiscopically (Fig. 5A), traversing the lamina at angles of *c.* 70–90° (Fig. 4A–D); they are generally straight or curving acroscopically near the margin,





**Figure 6.** *Marattiopsis patagonica* Escapa *et al.* from the Early Jurassic of Patagonia, Argentina. **A**, MPEF-Pb 5302, abaxial view of fertile pinnule showing midrib, lateral veins and synangia. **B**, detail of A; synangia showing fused sporangia. **C**, MPEF-Pb 5284, lateral veins and submarginal synangia. **D**, MPEF-Pb 5296, compressed synangia showing internal and external morphology of the valves. **E**, MPEF-Pb 5297, detail of synangial receptacles and sporangial bases. **F**, MPEF-Pb 5305, compressed synangia showing external morphology of the valves. Scale bars: A = 5 mm; B–D = 1 mm; E = 0.5 mm; F = 2 mm.





**Figure 7.** *Marattiopsis patagonica* Escapa *et al.* from the Early Jurassic of Patagonia, Argentina. Silicone casts of pinnules. **A**, MPEF-Pb 5302, abaxial view of fertile pinnule showing midrib, lateral veins and synangia. **B**, MPEF-Pb 5295, abaxial view of fertile pinnule showing midrib, lateral veins and synangia. **C**, MPEF-Pb 5295, abaxial view of fragmentary fertile pinnule showing midrib, lateral veins and synangia. **D**, MPEF-Pb 5302, valvate synangia showing external and internal morphology of the valves. Scale bars: A–C = 2 mm; D = 1 mm.



commonly forking immediately at or near the midrib (Figs 4A, 5A, D), rarely forking one or more further times close to the margin. Secondary veins are evenly spaced in middle and outer lamina portions, usually with a density between 8 and 16, most commonly 9 to 12 veins per centimetre. The venation pattern in the basal auricle is more or less fan-shaped (Fig. 5B), with the basalmost, recurved veins forking once upon entering the lamina. Interstitial fibres (*venuli recurrentes*) always present but inconspicuous, alternating with regular veins (Fig. 5A). Cellular patterns were observed on vegetative pinnules exceptionally preserved (Figs 4D, 5C, D), in that were not possible to determinate if they correspond to the hypophyll or the epiphyll. Epidermal cells are mostly polygonal or subpolygonal in the areas between veins (Fig. 5C, D). Epidermal cells on lateral veins are elongated, parallel to the main vein axis, with a ratio of 2:1–3:1. Longitudinal cut tracheids are seen on regions where the secondary vein epidermis is broken (Fig. 5C, D).

Fertile and vegetative pinnules are similar in general morphology (shape, outline, size), but with each secondary vein bearing one submarginal synangium (Figs 4A, B, 6A). The synangia are sessile (or slightly raised), bilaterally symmetrical, linear to elongate spindle-shaped in surface view, with a length of about 12–20% of the pinnule width (i.e. *c.* 1.5–3 mm long) and a width of *c.* 0.5 mm. They stand erect, ovate to narrow triangular in transverse section (i.e. projecting prominently from the lamina surface), appearing loculate-bivalvate with a distal longitudinal slit (Fig. 7A–D), and containing 8 to 20 (usually 14 or 16) opposite pairs of laterally fused, erect sporangia (Fig. 6B–F). External surfaces of valves are smooth (Fig. 7B, C). These sporangia are elongate ovoidal in shape, *c.* 500–750  $\mu\text{m}$  long and *c.* 100–150  $\mu\text{m}$  in diameter, occurring basally disposed on a linear receptacle (Fig. 6B–E).

**Comparison and remarks.** About 15 well-known species of *Marattiopsis* (including a few that were initially described under the name *Marattia*) are currently recognized (see Yang *et al.* 2008): *Marattiopsis aganzhenensis* (Yang *et al.*, 2008) Escapa *et al.*, comb. nov. [Basionym: *Marattia aganzhenensis* Yang *et al.*, 2008]; *Marattiopsis anglica* Thomas, 1913; *Marattiopsis angustifolia* Prynada, 1938; *Marattiopsis antiqua* (Chen *et al.*, 1979) Escapa *et al.*, comb. nov. [Basionym: *Marattia antiqua* Chen *et al.*, 1979]; *Marattiopsis asiatica* Kawasaki, 1939; *Marattiopsis barnardii* (Schweitzer *et al.*, 1997) Escapa *et al.*, comb. nov. [Basionym: *Marattia barnardii* Schweitzer *et al.*, 1997]; *Marattiopsis crenulata* Lundblad, 1950; *Marattiopsis curvinervis* (Lorch, 1967) Escapa *et al.*, comb. nov. [Basionym: *Marattia curvinervis* Lorch, 1967]; *Marattiopsis hoerensis* (Schimper, 1869) Schimper, 1874; *Marattiopsis intermedia* (Münster, 1836) Weber, 1968; *Marattiopsis litangensis* (Yang, 1978) Escapa *et al.*, comb. nov.

[Basionym: *Marattia litangensis* Yang, 1978]; *Marattiopsis macrocarpa* (Oldham & Morris 1863) Seward & Sahni, 1920; *Marattiopsis muensteri* (Goeppert, 1841) Schimper, 1869; *Marattiopsis orientalis* Chow & Yeh in Sze *et al.*, 1963; *Marattiopsis paucicostata* (Li *et al.* 1976) Escapa *et al.*, comb. nov. [Basionym: *Marattia paucicostata* Li *et al.* 1976].

Some previous authors have questioned the diagnostic significance of the few macromorphological characters that the rather simple leaf morphology of extant *Marattia s.l.* and the fossil *Marattiopsis* present, and proposed to accommodate fossil representatives of the genus in rather broadly defined morphospecies (e.g. Kilpper 1964; Herbst 1964). There is, however, good evidence to suggest that the combination of seemingly minute morphological differences (e.g. pinnule margins, ratio of synangium length to pinnule width, synangium position, or number of sporangial pairs), can provide valuable criteria for species delimitation in both fossil and extant representatives of the genus (see e.g. Kawasaki 1939; Hill & Camus 1986; Schweitzer *et al.* 1997; Wang 1999; Christenhusz 2007; Yang *et al.* 2008). In addition, detailed morphological comparisons are now even more relevant in order to determine a more precise taxonomic affinity within *Marattia sensu lato* (i.e. *Marattia s.s.*, *Eupodium* and *Ptisana*).

*Marattiopsis patagonica* sp. nov. shows a unique combination of vegetative and reproductive features that readily distinguishes it from all previously described species (see Yang *et al.* 2008, table 1): (1) a basal auricle with simple or only once-forked veins; (2) finely undulate, denticulate, or serrulate margins; (3) fine interstitial fibres (*venuli recurrentes*) that alternate with regular veins; (4) submarginal position and the distinctive relative length of synangia (*c.* 12–20% of pinnule width); and (5) the comparatively few pairs of sporangia per synangium (usually 14 or 16).

*Marattiopsis muensteri* differs in having symmetrical, round pinnule bases and entire margins (Kimura & Tsujii 1980). *Marattiopsis asiatica* has a considerably larger number of sporangia pairs per synangium (25 to 40), and its synangia are terminal, i.e. they extend right to the pinnule margin (Kimura & Tsujii 1980; Yang *et al.* 2008). The recently described *Marattiopsis anghanensis* differs in having an entire margin and in lacking *venuli recurrentes* (Yang *et al.* 2008). *Marattiopsis barnardii* lacks *venuli recurrentes* and has considerably longer synangia (20–30% of pinnule width). *Marattiopsis hoerensis* is significantly larger, has longer synangia (20–30% of pinnule width), and the *venuli recurrentes* are very prominent (sometimes thicker and more conspicuous than the actual veins; Yang *et al.* 2008). *Marattiopsis anglica* also lacks *venuli recurrentes* and has an entire margin, while its synangia length represent a higher percentage relative to pinnule width (Van Konijnenburg-van Cittert 1975). *Marattiopsis intermedia* has entire margins and a greater number of sporangial pairs per synangium. Finally,

*Marattiopsis curvinervis* has a much higher vein density, whereas *Marattiopsis crenulata* bears synangia that are only about half as wide in relation to pinnule width compared to those of *Marattiopsis patagonica*.

## Discussion

### The renaissance of *Marattiopsis*

In cases where a fossil seems to match perfectly with a living organism in all observable characters, palaeobotanists face the question of whether or not to use a name that was established for an extant genus or even species (see Stewart & Rothwell 1993; Taylor *et al.* 2009). This is particularly relevant when integrated phylogenetic analyses including fossil and extant terminals are not available. Historically, many earlier authors chose to create new, but similar-sounding taxon names in such instances to indicate the similarity with extant taxa. This is the case for the name *Marattiopsis*, which was established for fern fossils with vegetative and reproductive features similar to those of living Marattiaceae (Schimper 1869). However, because the fossils seemed to agree so closely with the living genus *Marattia* in all aspects, many authors have since argued for a preferential use of the name *Marattia* over *Marattiopsis* (Harris 1961; Van Konijnenburg-van Cittert 1975; Wang 1999; Wang *et al.* 2001; Yang *et al.* 2008). Previously Halle (1921, p. 2) commented that “if ever a natural genus, founded both on habit and on soral characters, can be distinguished in a fossil state, this is one.” As a result, the use of the name *Marattiopsis* has been largely abandoned, and most fossil species have since been assigned to the genus *Marattia*.

However, detailed phylogenetic analyses of the living marattioid ferns have recently shown that the genus *Marattia*, as traditionally defined, is paraphyletic (Murdock 2008a). The bulk of the more than 30 living species of *Marattia* s.l. was therefore split up and distributed amongst three morphologically and geographically distinct genera: (1) *Eupodium* J. Smith (Neotropics), characterized by prominently stalked synangia; (2) *Ptisana* Murdock (Palaeotropics), characterized by smooth sporangial apertures, distinct sutures at pinnule bases, and absence of *venuli recurrentes*; and (3) *Marattia* Swartz emend. Murdock (Neotropics and Hawaii), characterized by distinctly labiate sporangial apertures and occasional, weakly developed *venuli recurrentes*. This new concept has a profound impact on the taxonomic treatment of *Marattia*-like fossils. Important diagnostic characters for the extant genera, including the stalked synangia and labiate sporangial apertures, are difficult to discern in fossil material. Moreover, although most fossil species appear to agree most closely with the circumscription of the extant genus *Ptisana* (e.g. in presumably having sutures at pinnule bases, resulting in the common occurrence of

detached pinnules), many fossils show more or less distinct *venuli recurrentes*, which are present in extant *Marattia* s.s. (and occur more typically in *Angiopteris*). Hence, the revised classification and phylogeny of extant marattioid ferns has made it necessary to re-institute the name *Marattiopsis* for the identification of fossil representatives (Bomfleur *et al.* 2013).

### Systematic significance of *Marattiopsis*

Most Triassic and Jurassic species of *Marattiopsis* are superficially similar, and are distinguished on the basis of fine morphological details, e.g. pinnule margins, vein density, ratio of synangium length to pinnule width, or number of sporangia (e.g. Yang *et al.* 2008). Compared to living genera, most species are most similar to *Ptisana* in overall aspect (Murdock 2008a): the synangia are sessile, marginal or submarginal, and prominently elongated; the sporangial apertures are not labiate; pinnules are large and elongate, with entire or only slightly crenulate, serrulate, or denticulate margins; and the typical preservation of isolated pinnules is likely a result of fragmentation at pinna-base sutures, a feature typical of *Ptisana*. The only major difference between most *Marattiopsis* fossils and extant *Ptisana* is that the fossils occasionally show *venuli recurrentes*, which today are found only in *Marattia* s.s. and – more commonly – in *Angiopteris* (Murdock 2008a). The only well-established fossil species from Mesozoic deposits that differs significantly from the above-described morphological group is *Marattiopsis macrocarpa* (including *M. reversa* of Sharma, 1969) from the Jurassic of India. This species is commonly preserved in the form of penultimate frond fragments with small, short, rather pectopterid pinnules, each bearing short, submarginal to medial synangia (e.g. Seward & Sahni 1920; Bose & Sah 1968; Sharma 1969, 1972). These features are quite unlike those of other *Marattiopsis* species and of extant *Ptisana*, and are altogether much more reminiscent of the living *Marattia* s.s. (Fig. 4). An overall similar morphology occurs also in the *Neuropteridium*-type foliage of some Palaeozoic representatives of modern Marattiaceae (e.g. *Qasimia* Hill *et al.* 1985).

### *Marattiopsis* in the southern hemisphere

Compared to the widespread occurrence of *Marattiopsis* across the northern hemisphere during the Mesozoic, there have been surprisingly few reports from coeval strata of Gondwana. Apart from *Marattiopsis patagonica* described herein, perhaps the best-documented records are those of *Marattiopsis macrocarpa* (including *M. reversa*) from the Lower Jurassic of India (Seward & Sahni 1920; Bose & Sah 1968; Sharma 1969, 1971, 1972) and of *Marattiopsis* remains – commonly assigned to *M. muensteri* – from the Upper Triassic Paso Flores



Formation (Morel *et al.* 1999) and the Lower Jurassic Nestares and El Freno formations, Argentina (e.g. Herbst 1964; Arrondo & Petriella 1980; Baldoni 1987; Morel *et al.* 2013; Artabe *et al.* 2005). To our knowledge, the only other reliable identification of *Marattiopsis* is from the Upper Triassic Moolayember Formation at Cracow, Queensland (Jones 1948; see also Playford *et al.* 1982).

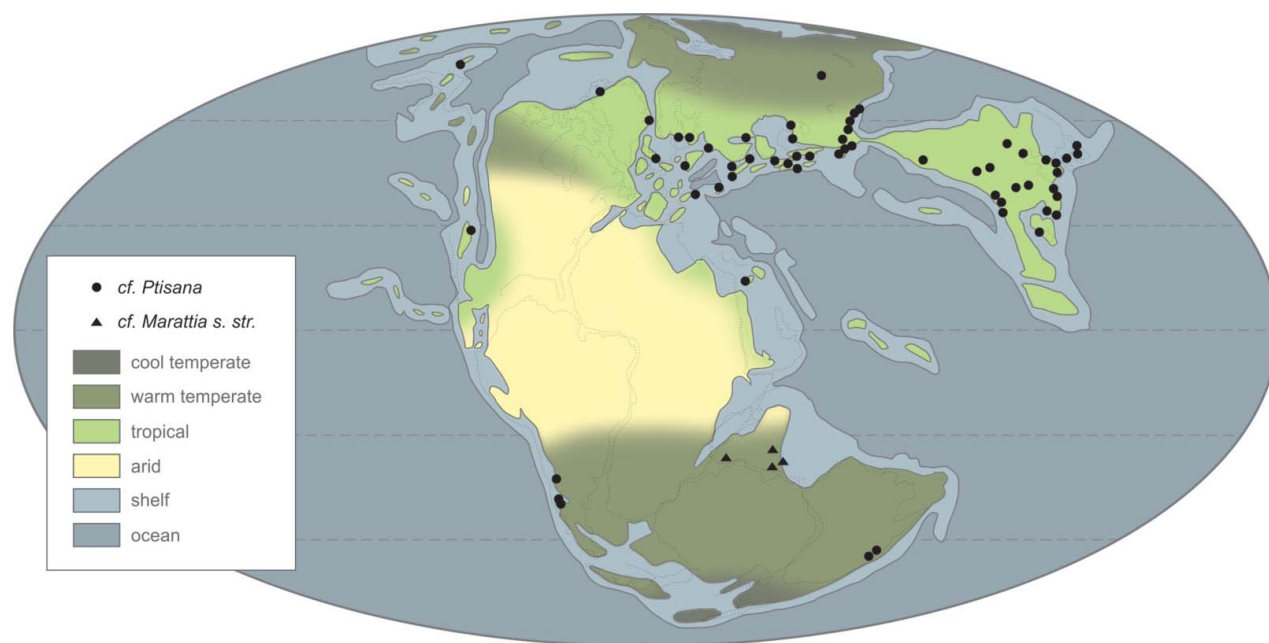
Putative additional occurrences of *Marattiopsis* in Gondwana are from Triassic deposits of the South Rewa Basin, India (Lele 1962) and from the Middle Jurassic Walloon Coal Measures of eastern Australia (Gould 1980); these specimens, however, are fragmented and poorly preserved, and may as well represent remains of other ferns (e.g. *Danaeopsis* Heer ex Schimper, *Scolopendrites* Göppert) or possibly cycad sporophylls (e.g. *Dioonitocarpidium* Rühle von Lilienstern) (see e.g. Kustatscher *et al.* 2004).

Interestingly, fossil ferns related to the order Marattiales are well known since the earliest Permian in the SW Gondwanan region (Patagonia). They were widely spread and diverse and played an important role in subtropical plant communities through the presence of tree forms (Cúneo 1996). Taxa that were referred to marattialean ferns include a number of *Asterotheca* and *Dizeugotheca* frond species (Archangelsky & de la Sota 1960; Cúneo *et al.* 2000), and trunk impressions assigned to the form genera *Caulopteris*, all of them representing impression fossils of the classic late Palaeozoic psaroniacean marattialean ferns (Taylor *et al.* 2009). The group later spread

out to most of the Gondwana continent when glacial conditions were replaced by more temperate ones from the mid Permian due to glacial retreat, excepting the Antarctic subcontinent where the group has not been recorded during the Permian. Representatives of these (asterothecae/psaroniae) early marattialean ferns probably survived the Permian/Triassic transitional event, and were also part, although highly reduced, of the Triassic floras in the same Patagonian area (Gnaedinger & Herbst 1998).

### Palaeoclimatic and phytogeographical considerations

Practically all living Marattiaceae, including *Marattia* s.s., *Ptisana* and *Eupodium*, are today restricted to tropical regions with consistently high temperatures and humidity. The palaeogeographical distribution of *Marattiopsis* indicates that the early representatives of these lineages probably flourished under similar environmental conditions. Fossils with this morphology are very common in Upper Triassic to Middle Jurassic deposits worldwide, whereas they are notably scarce in younger strata. As outlined above, the Triassic and Jurassic occurrences of *Marattiopsis* are concentrated in Central and south-eastern Europe, the Caucasus region, Central Asia, China, Korea, and Japan, documenting that the plants were distributed primarily in a broad belt fringing the northern Tethys margin (Fig. 8). This main distribution matches very well with palaeoclimate reconstructions indicating tropical,



**Figure 8.** Palaeogeographical occurrences of Triassic and Jurassic *Marattia*-like fossils. Base map modified from Golonka (2007, fig. 3); palaeoclimatic reconstruction for the Early Jurassic after the PALEOMAP Project (Scotese 2000); *Marattiopsis* occurrences (in many cases referred to as *Marattia*) compiled using the Paleobiology Database (current version: <http://fossilworks.org/cgi-bin/bridge.pl>).

megathermal and humid conditions for this region during the Triassic and Jurassic (Scotese 2000).

By contrast, occurrences outside the (para)tropical northern Tethys margin are rare. In the northern hemisphere, three isolated occurrences from California (Fontaine 1896), the northern Sinai (Lorch 1967), and the Omolon Terrane (Samylina & Yefimova 1968) all lie in island areas with inferred tropical climate; a further occurrence lies in the extensive warm–temperate climatic belt in the continental interior of Eurasia (Vladimirovich 1967). Unlike in the northern hemisphere, however, no major tropical climatic belt is thought to have developed across Gondwana, and temperatures throughout most of the southern mid- to high latitudes are supposed to have been rather warm-temperate (e.g. Scotese 2000). *Marattiopsis* is rare in the southern hemisphere, being restricted to only few occurrences in three isolated regions in present-day Patagonia (see Arrondo & Petriella 1980; Baldoni 1987; Herbst & Stipanovic 1996; Artabe *et al.* 2005; Morel *et al.* 2013), India (Seward & Sahni 1920; Bose & Sah 1968; Sharma 1969, 1971, 1972), and eastern Australia (e.g. Gould 1980). Since most of these records occur near the Panthalassan and Tethyan margins, it is possible that the local microclimates in those near-coastal regions were affected by warming ocean currents, causing favourable maritime conditions that enabled the establishment of extrazonal, typically tropical floral elements. A modern analogue may be the outlying occurrence of *Ptisana salicina* (Smith) Murdock in the maritime, subtropical climate of northern New Zealand today. In this respect, *Marattiopsis* occurrences may form a valuable indicator for refining palaeoclimatic reconstructions on a regional to local scale.

## Conclusion

*Marattiopsis patagonica* sp. nov. from the Lower Jurassic of Chubut Province shows a combination of characters comparable with respect to extant *Marattia*, *Ptisana* and *Eupodium*.

Even though detailed information on the morphology, anatomy, and systematic position of the Mesozoic *Marattiopsis* species is still lacking, it seems that an early morphological divergence in *Marattia* s.l. may already be recognizable in the occurrence of two distinct forms of *Marattiopsis* during the Jurassic, one resembling extant *Ptisana* and the other resembling extant *Marattia* s.s. This is especially interesting given the separate geographical occurrences of *Ptisana* in the Neotropics and *Marattia* s.s. in Palaeotropics today. In this context, it has only recently been suggested that the Marattiaceae are one of few plant groups that clearly demonstrate a vicariant distribution pattern (Christenhusz & Chase 2013). Further investigations must include the revision of Mesozoic *Marattiopsis* species and an integrative phylogenetic analysis, in order

to understand an evolutionary history that seems to be more complex than previously assumed.

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