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Southern Hemisphere Caytoniales: vegetative and reproductive remains from the Lonco Trapial Formation (Lower Jurassic), Patagonia

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Macrofossil impressions of caytonian leaves and micro- and megasporangiate organs from the Early Jurassic Taquetrén locality in Patagonia, Argentina, are described based on more than 300 hand specimens. Leaves of the organ-genus *Sagenopteris* are described using both discrete and continuous features allowing us to erect the species *Sagenopteris trapialensis* sp. nov. Associated microsporangiate organs of *Caytonanthus* type are the first recorded for South America and are characterized by a unique combination of architecture, size and type of dehiscence. Two specimens, one resembling an isolated *Caytonia* cupule, and the other a *Caytonia* axis, are also described. The availability of a collection with numerous specimens has proven to be an important tool in order to fully understand the intraspecific morphological plasticity of the studied species. The striking morphological resemblance of both vegetative and reproductive organ-genera with their Northern Hemisphere counterparts suggests that they were part of the same lineage, which was widely distributed during the Jurassic. Well-defined whole-plant concepts are still needed to advance the goal of deciphering the internal relationships of caytonian plants in particular, and their relationships with other groups of seed-plants in general, and thorough macro-morphological characterization of the organs that compose them, as we present here, may be of valuable use in achieving it.

Keywords: Caytoniales; Jurassic; Caytonia; Sagenopteris; Patagonia

Introduction

‘Mesozoic pteridosperms’ have figured prominently in discussions concerning the origin of flowering plants since the first part of the twentieth century (Thomas 1921, 1925; Gaussen 1946; Hill & Crane 1982; Frohlich 2002; Doyle 2006). The group is composed by four main orders (Taylor *et al.* 2006): Peltaspermales (Carboniferous–Triassic), Corystospermales (Permian–Triassic/Jurassic?), Petriellales (Triassic) and Caytoniales (Triassic–Cretaceous). However, the ‘Mesozoic pteridosperms’ seem to be polyphyletic as a whole, while the internal monophyly of each group remains uncertain, since each is usually coded as a single terminal in most phylogenetic analyses (Doyle 2006; Hilton & Bateman 2006; Rothwell & Stockey 2016).

Caytoniales are known from impressions and compressions (Harris 1964) and at its inception they comprised three organ-genera (i.e. *Sagenopteris* Presl in Sternberg, *Caytonanthus* Harris, *Caytonia* Thomas; Thomas 1925; Harris 1933). Their remains have been known since Nilsson (1820) first illustrated and described succinctly a *Sagenopteris* leaflet, whereas *Caytonanthus*-like fossils were initially regarded as

‘unknown leaves’ (Philips 1829) and as ginkgoalean catkins afterwards (Nathorst 1880; Seward & Gowan 1900). On the other hand, *Caytonia* fossils were initially described as ‘fruit-like bodies’ by Thomas (1912), who integrated these organ-genera into a compact group, based on their reiterated occurrence in the same fossiliferous beds, their shared cuticular features and the presence of certain organs in close association with the others (Thomas 1925).

Sagenopteris leaves are compound, with four lanceolate leaflets located at the apex of a petiole (Halle 1910; Harris 1940a, 1964). *Caytonanthus* pollen-bearing organs have slender axes with opposite to subopposite synangiate branches, with four elliptic and partially fused pollen sacs filled with bisaccate pollen (Thomas 1925; Harris 1937, 1941). *Caytonia* also features slender axes with an opposite to subopposite arrangement, in this case of recurved fleshy capsules or ‘cupules’ with numerous small seeds (Thomas 1925; Harris 1940b). The passage of time has only reinforced Thomas’ grouping of *Sagenopteris*–*Caytonanthus*–*Caytonia*, and the association of these three organ-genera still represents the strongest hypothesis for a Caytonian plant concept (Harris 1932, 1933, 1940a, b, 1941, 1960, 1964; Reymanowna

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1973; Krassilov 1977; Rees 1993). Nevertheless, little is known concerning their anatomy, the type of organic connections between the different organs, and the habit and complete organography of the plant.

The phylogenetic position of Caytoniales in the seed plant tree of life is still a matter of debate (Nixon *et al.* 1994; Rothwell *et al.* 2009; Doyle 2013). Initially they were regarded as members of a primitive angiosperm clade, based on the presence of seeds totally enclosed by fleshy cupules (Thomas 1921, 1925). However, a gymnospermous affiliation was suggested instead after further studies of available and freshly collected material (Harris 1933, 1964). Phylogenetic analyses recovered the clade as the sister group of flowering plants (Doyle & Donoghue 1986, 1987; Doyle 2012); nested within a pteridosperm clade not related to angiosperms (Nixon *et al.* 1994; Rothwell *et al.* 2009); and even nested within conifers (Nixon 2010). Additionally, the small number of detailed morphological studies of the group since the late 1960s, the absence of specimens showing organic connections between their major organs, and the sparse information available about their internal anatomy and general habit, has had a direct impact on obscuring numerous physiological, ecological and palaeobiological characteristics of the group, which are better known in other groups of Mesozoic pteridosperms (e.g. Petriellales; Bomfleur *et al.* 2014).

Caytoniales were geographically widespread in the Northern Hemisphere (NH), having their heyday during the Jurassic (Harris 1964; Taylor & Taylor 2009; Pattemore *et al.* 2015). The largest amount of knowledge concerning the reproductive organs of the group derives from the study of fossils from the Middle Jurassic plant-bearing beds of Yorkshire, UK (Thomas 1925; Harris 1940a,b, 1941, 1964, 1971). Specimens from Poland helped to elucidate anatomical details of *Caytonia* cupules (Reymanowna 1973, 1974), and the study of Hungarian fossils provided a second type of caytonian cupule (i.e. *Reymanownaea* Barbacka & Boka; Barbacka & Boka 2000a). In contrast, Jurassic occurrences of caytonian reproductive organs from Gondwana are exceedingly rare, adding up to a few *Caytonanthus* specimens in total (Rees & Cleal 2004; Prakash & Das 2017). In this context, the South American record of Caytoniales has been mostly suggested by Jurassic specimens of *Sagenopteris* (Bonetti 1963; Herbst 1964a, b, 1965, 1966a, b; Baldoni 1981; Baldoni & Olivero 1983; Spalletti *et al.* 2007; Morel *et al.* 2013), and it is still uncertain if whether those vegetative remains belonged to some type of ‘Caytonia plant’ or if they were part of a different natural group.

In the present contribution we describe novel findings of Caytoniales from the Early Jurassic of Taquetrén,

Patagonia, Argentina including more than 300 hand specimens of vegetative and reproductive organs. The vegetative remains correspond to *Sagenopteris* leaves, with a plethora of specimens in various ontogenetic and preservational states of complete leaves and, most commonly, isolated leaflets. The reproductive organs consist of the microsporangiate organ *Caytonanthus*, disarticulated as isolated synangia, or attached to main axes, and the possible presence of isolated *Caytonia* cupules and their naked main axes. The thorough study of this large fossil collection will be pivotal in order to understand the morphological variation that these plants managed to achieve, and also leads us to suggest that Jurassic caytonian whole-plants from Gondwana were from the same lineage as the NH ones.

Material and methods

Geological setting

The studied material was collected on field trips from 2004–2015 at two localities of the Cañadón Asfalto Basin, ‘Taquetrén A’ and ‘Taquetrén B’, at equivalent stratigraphic plant horizons 3.5 km apart, near the town of Paso del Sapo, north-west Chubut Province, Argentina (Fig. 1). The former locality was initially reported during the 1960s and its palaeofloristic elements were first described by Bonetti (1963), while ‘Taquetrén B’ was discovered in 2008, with some of its fossil plant content first described by Escapa (2009). Subsequent studies have increased the floral diversity of the Taquetrén area, which now includes equisetaleans, several fern families (Osmundaceae, Dipteridaceae, Gleicheniaceae), seedferns (caytonian and *Archangeliskya furcata* [Halle] Herbst), bennettitaleans (at least three foliage species + *Willamsonia* sp.) and conifers (Araucariaceae, Cupressaceae and Cheirolepidiaceae), adding at least 20 taxa (Herbst & Anzótegui 1968; Escapa *et al.* 2008; Escapa 2009; Escapa & Leslie 2017). Even though the plant content does not differ between the two localities, the local abundance of each plant group does vary between them, with conifers and bennettitaleans occurring in similar numbers to ferns at ‘Taquetrén A’, whereas ‘Taquetrén B’ has a clear dominance of filicalean and caytonian elements.

The plant-bearing sediments at both localities are placed at the base of the Lonco Trapial Formation, which has an estimated thickness of 500–800 m (Nakayama 1973; Figari *et al.* 2015). The volcano-sedimentary sequence is dominated by volcanic agglomerates, breccias and basaltic lavas, occasionally alternating with tuffaceous rocks associated with mudstones and fine-grained

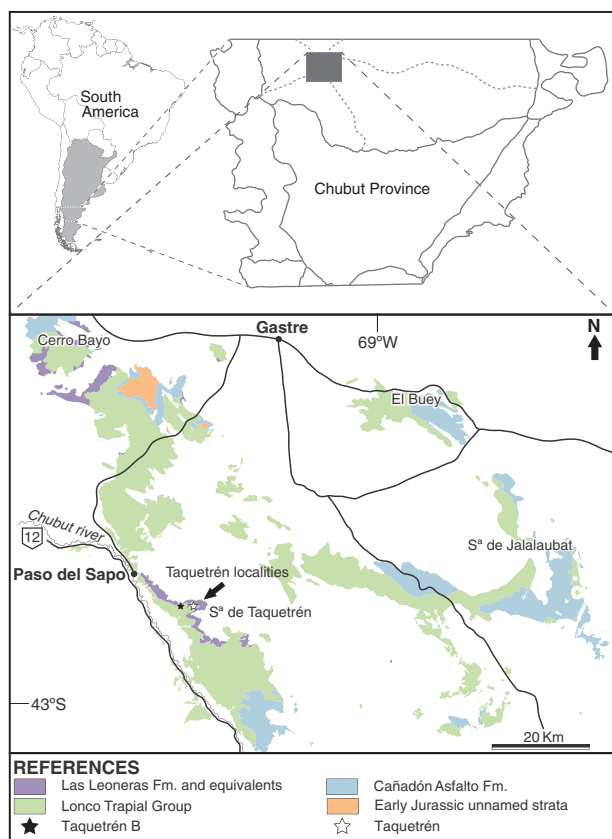


Figure 1. Geographical location of the Taquetrén A (black star) and Taquetrén B (white star) localities, Chubut Province, Argentina. Modified from Cúneo *et al.* (2013).

sandstones that reflect episodes of relative calmness, in which the plant material was incorporated into probably lacustrine settings, alternating with episodes of intense volcanism (Figari *et al.* 2015). The Lonco Trapial fossil beds occur just a few metres above the contact with the underlying Las Leoneras Formation, while the Cañadón Asfalto Formation overlays the Lonco Trapial Formation (Nakayama 1973; Cúneo *et al.* 2013; Figari *et al.* 2015).

The estimated age of the Taquetrén flora has fluctuated over the years from the Early Jurassic up to the Early Cretaceous (Baldoni 1981; Rees & Cleal 2004; Escapa *et al.* 2008) based on floristic comparisons with other localities in Argentina (e.g. Bajo de los Baguales; Menéndez 1956; Volkheimer 1969; Stipanovic & Bonetti 1970) and the Antarctic Peninsula (e.g. Hope Bay and Botany Bay, Antarctica: Gee 1989; Rees & Cleal 2004; Escapa *et al.* 2008). An Early Jurassic age was proposed based on the presence of an association of taxa (e.g. *Goeppertella* Oishi & Yamasita, *Clathropteris* Brongniart, and *Sagenopteris*; Escapa *et al.* 2008), which characterizes localities in south-west Gondwana (Herbst 1964a, 1966b; Arrondo & Petriella 1980, 1982;

Rees & Cleal 2004 and references therein). More recently, a detailed chronostratigraphic framework was developed for the Cañadón Asfalto Basin based on high precision U-Pb dating (Cúneo *et al.* 2013), corroborating an Early Jurassic age for the Taquetrén flora. According to this framework, the top of Las Leoneras Formation is dated at *c.* 189 Ma, while the base of Cañadón Asfalto Formation is dated at *c.* 178 Ma, thus bracketing the age of the Lonco Trapial Formation between them (Pliensbachian–early Toarcian; Cúneo *et al.* 2013). This has been recently confirmed by an additional U-Pb date from within the Lonco Trapial Formation of 180.318 ± 0.074 Ma. (Ramezzani, pers. comm.).

Fossil preparation and illustration

When required, mechanical preparation of the fossils was performed with air scribes at the mechanical preparation laboratory of the Museo Paleontológico Egidio Feruglio.

Fossils were photographed with a Canon EOS 7D digital camera equipped with a Canon EF-S 60 mm macro lens. In addition to the macro lens, extension tubes were also used for higher magnification photographs. An image stacking technique was performed using Adobe Photoshop CS6 in order to obtain a single, well-focused image. For this purpose, we merged several photographs captured at slightly different focal planes. The resulting images were checked and edited when necessary due to the presence of artefacts related to the stacking process (e.g. blurry edges). Schematic illustrations were performed with Adobe Illustrator CS6.

The nomenclature of Melville (1976) was used for the description of vein anastomoses. All of the studied fossil samples are deposited at the Museo Paleontológico Egidio Feruglio Palaeobotanical Collection, Trelew, Argentina (hereafter MPEF-Pb).

Systematic palaeontology

Class **Gymnospermopsida** Stewart & Rothwell, 1993

Order **Caytoniales** Gothan, 1932

Family **Caytoniaceae** Thomas, 1925

Genus ***Sagenopteris*** Presl in Sternberg emend.

Harris, 1964

Sagenopteris trapialensis sp. nov.

(Figs 2–4, 6A–C)

1963 *Sagenopteris nilssoniana* (Brongniart) Ward; Bonetti 30, pl. 4, figs 1–6.

1964a *Sagenopteris* cf. *rhoifolia* Presl; Herbst 230, pl. 1–2, figs 3, 12.

1965 *Sagenopteris* cf. *rhoifolia* Presl; Herbst 46, pl. 2, 4, figs 13, 30.

1968 *Sagenopteris rhoifolia* Presl; Herbst & Anzotegui 187, pl. 1, fig. G.

Type species. *Sagenopteris acuminata* Presl, 1838.

Diagnosis. Compound petiolate leaves bearing four leaflets, up to 58 mm long and 18 mm wide, with an average length/width (L/W) ratio of 2.5:1. The central pair of leaflets is nearly symmetrical, elliptic to obovate, emerging at 20–45°; the lateral pair is smaller, asymmetrical, oblong to ovate, with an emergence angle of 75–90°. Both types of leaflets have rounded apices, straight to slightly undulate margins, occasionally with up to two lateral lobes. Petioles slender, with straight margins gently tapering upwards. Leaflets with a strong midrib, visible up to three- to four-fifths of leaflet length. Secondary veins emerging from midrib at *c.* 9–19°, dichotomizing and anastomosing frequently forming obliquely oriented areolae with a L/W ratio of 8.5–11:1. Leaflets with anastomoses of *Z*, *X*, *H* and compound types, dichotomies simple. Bud- and scale-like leaves small, the former having a broad petiole with curved margins, clasping base and leaflets with diffuse venation; scale-like leaves with tapering upwards petioles with a broad base.

Derivation of name. The specific epithet refers to the Lonco Trapial Formation. Lonco Trapial means ‘cougar’s head’ in the Mapuche language.

Holotype. MPEF-Pb 2713a, b (Taquetren B).

Paratypes. MPEF-Pb 1864, 2034 (Taquetren A) and MPEF-Pb 2854, 2855, 2877, 6608, 6623, 9506–9508, 9510–9512, 9514–9518, 9541 (Taquetren B).

Additional material. MPEF-Pb 1864–1866, 1868, 1870, 1878, 1880, 1882, 1884, 1888, 1890, 1891, 1898–1900, 1907, 1909, 2034, 2066–2074, 2076, 2085, 2087, 2090, 2096–2099, 2145, 2152, 2156, 2157, 2159, 2161, 2162, 2167, 2168, 2172, 2174, 2410, 2412, 2413, 2423, 2424 (Taquetren A). MPEF-Pb 2713, 2831–2837, 2840, 2843, 2847, 2849, 2853–2855, 2862, 2864, 2865, 2870, 2871, 2873, 2875–2879, 2881, 2882, 2888, 2890, 2891, 6608, 6609, 6611, 6612, 6614, 6618, 6619, 6623, 6626, 6631, 9501–9649 (Taquetren B).

Type locality, stratigraphy and age. Taquetren A and Taquetren B localities, Chubut Province, Patagonia, Argentina. Lonco Trapial Formation, Pliensbachian–Toarcian, Early Jurassic.

Description and comparisons

General morphology. The leaves are petiolate and compound, measuring up to 80 mm long. Each leaf usually bears four leaflets on the same plane, measuring up to 58 × 18 mm (\bar{x} = 19.5 × 7.2, *N* = 141; Fig. 2A–C). The lamina of the two, elliptic to obovate, central leaflets is nearly symmetric, with a slight basiscopic expansion. The lateral leaflets are markedly asymmetrical, having an oblong to obovate lamina basiscopically expanded (Fig. 2D). The leaflets have entire margins and obtuse to rarely subacute apices (Fig. 2B–G); less commonly the leaflet margins are slightly undulated or may even develop up to two lobes or clefts (Fig. 2A–G). The length/width ratio of the leaflets is 1.3–3.8:1 (\bar{x} = 2.47:1, *N* = 136). The central pair of leaflets emerge at 75–90° from the petiole apex, while laterals emerge at 20–45° (Fig. 2A–F). The mean apex angle of the leaflets is 83°, while the basal angle is 65° on average.

Petioles are up to 27 mm long and 3.78 mm wide (\bar{x} = 6.6 × 2.27 mm, *N* = 50; Fig. 2B, C); they have straight margins, and a base that gently tapers towards the point of leaflet attachment. Their base is usually straight and occasionally clasping. In cross-section the base of the petiole is trapezoid to elliptic, with an elliptical scar of 0.6–0.8 mm occupying its central portion (Figs 2C, 6A), probably corresponding to vascular tissues. An isolated branch found on the same rock slabs as *Sagenopteris* leaves has a matching trapezoid scar with a similar organization of the putatively vascular tissues (Figs 2H, I, 6B). Both petioles and leaflets show a clean abscission surface, the latter often occurring detached from petioles.

Small bud- and scale-like leaves are also found associated with average-sized leaves; the former are characterized by having very short and broad petioles with curved margins and a clasping base, bearing four minute leaflets with a L/W ratio of 1.2–1.7:1 and an obscure venation pattern (Fig. 3A–C). Scale-like leaves have petioles with a wide base that tapers upwards, a less obscure venation pattern than bud-like leaves, and leaflets with a 1.35–2:1 L/W ratio (Fig. 3D, E).

Regardless of leaf size, four leaflets occur at the top of the petiole, with the central pair always being larger than the lateral pair (Fig. 3).

Venation. One of the most prominent features in leaflets is the presence of a strong midrib up to 1.2 mm in width (\bar{x} = 0.62 mm, *N* = 56), running straight to slightly curved from the leaflet base, decreasing in width with successive emergences of a secondary veins, and being often indiscernible from second order veins around three- to four-fifths of the leaflet length (Fig. 4A–D). The midrib of the lateral leaflets is eccentric, located nearer the distal margin; whereas the midrib of the

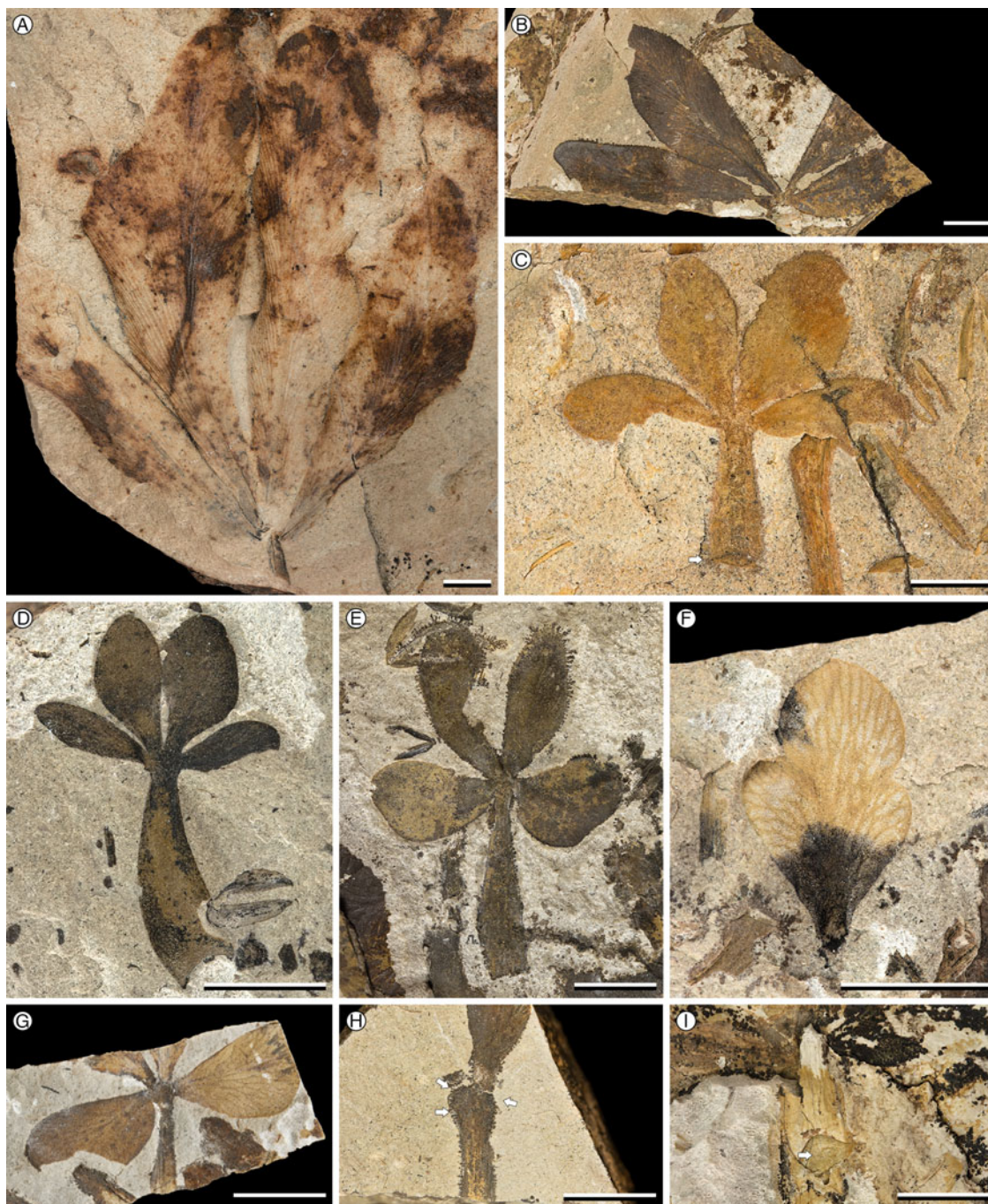


Figure 2. *Sagenopteris trapialensis* Elgorriaga *et al.* general morphology. **A**, MPEF-Pb 2034, large leaf with four articulated leaflets with slightly undulate margins. **B**, MPEF-Pb 9514, fragmented leaf with four leaflets. **C**, MPEF-Pb 2855, leaf with four leaflets and a tapering upwards petiole, note the basal trapezoid scar (arrow). **D**, MPEF-Pb 9507a, leaf with slightly expanded petiole with a clasping base. **E**, MPEF-Pb 9506a, leaf showing the asymmetry of the lateral pair and symmetry of the central pair of leaflets. **F**, MPEF-Pb 2713b, leaflet with two lateral lobes. **G**, MPEF-Pb 9541, fragmented leaf with slender petiole and faint impressions of venation network. **H**, MPEF-Pb 9517, fragmented leaf with attachment scars of three leaflets (arrows). **I**, MPEF-Pb 1864b, branch fragment with leaf attachment scar and possibly vascular supply (arrow). Scale bars: A–I = 5 mm.

central leaflets is located at its centre. Due to the aforementioned features it is possible to distinguish between central and lateral leaflets when they occur isolated.

The secondary veins are 0.09–0.32 mm wide (\bar{x} = 0.19 mm, $N=35$), emerge at a steep angle of 9–19° (Fig. 4E–G), curve basipetally towards the margins of the lamina and end freely at *c.* 80° basally and up to *c.*



Figure 3. *Sagenopteris trapialensis* Elgorriaga *et al.* small leaves. **A–C**, MPEF-Pb 9510, 9506b and 6623a, leaf buds with four minute leaflets, having short and broad petioles with curved margins and a clasping base. **D–F**, MPEF-Pb 9518, 6623a and 9508, three small leaves with an expanded petiole base tapering upwards, and four increasingly developed leaflets; note the almost horizontal emergence of the lateral leaflets. **G–I**, MPEF-Pb 2854, 9511 and 2877a, four small leaves with impressions of the venation network and a slender petiole, note the angle of emergence of the leaflets, the asymmetry of the lateral pair of leaflets, and the nearly symmetrical outline of the central pair of leaflets. Scale bars: A–I = 3 mm.

10° apically (Fig. 4A–C). They fork and anastomose irregularly.

Secondary vein anastomoses are assigned to the types illustrated by Melville (1976). *H* (eta) type occurs when

two secondary veins running parallel to each other slightly diverge in their paths and become close, reaching a point in which a small perpendicular connecting vein occurs between them; afterwards each vein resumes

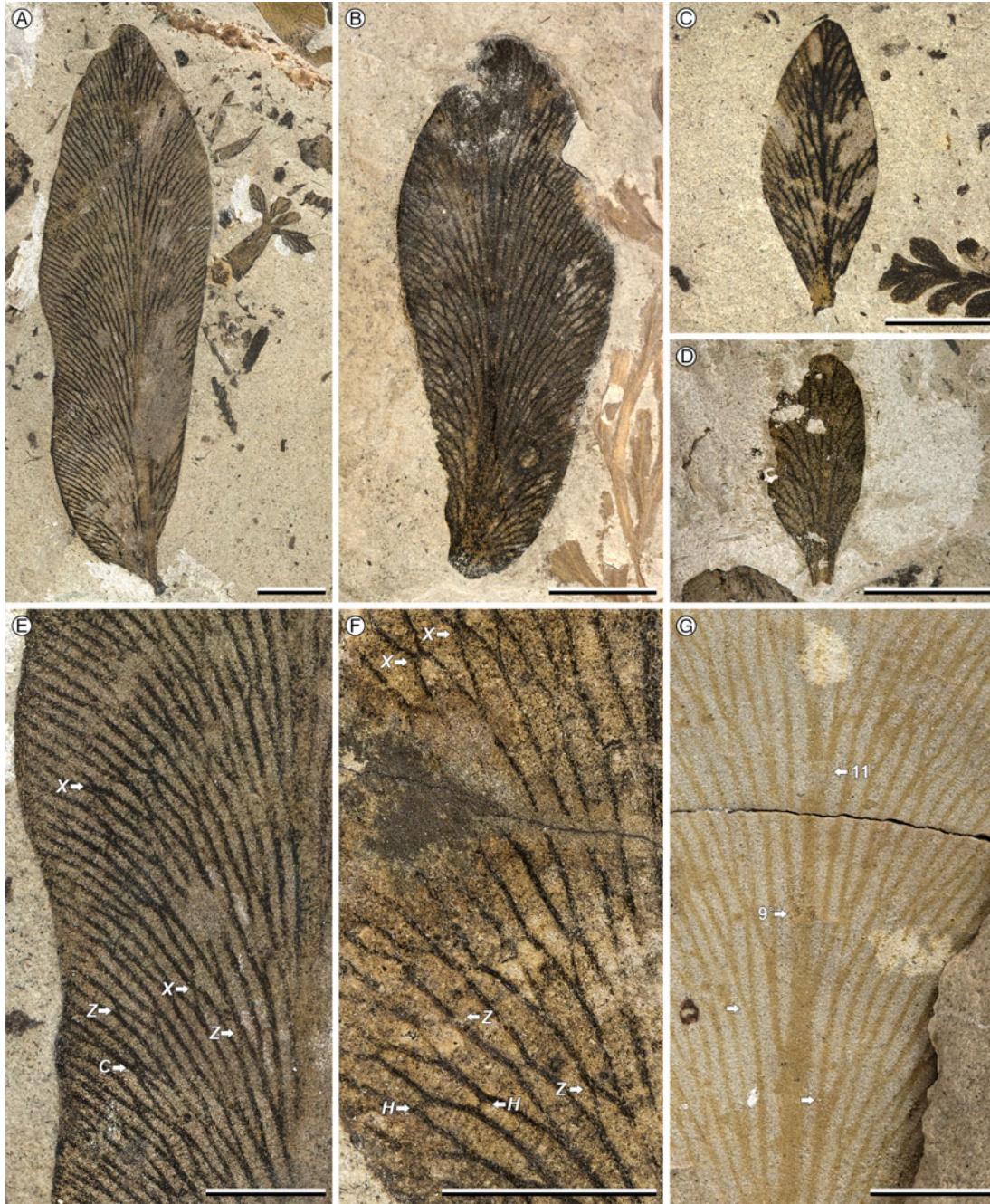


Figure 4. *Sagenopteris trapialensis* Elgorriaga *et al.* isolated leaflets showing venation. **A**, MPEF-Pb 2713a, large isolated lateral leaflet besides a small complete leaf. Note the anastomosing venation network and the faint impressions of the midrib. **B**, MPEF-Pb 9515b, isolated lateral leaflet showing the overall pattern of venation. **C**, **D**, MPEF-Pb 9512a and 2713a, small central leaflets with a prominent midrib at the base. Note the obliquely elongated rhomboidal vein meshes. **E**, close-up of (A) showing different types of vein junctions. **F**, MPEF-Pb 6608b, leaflet showing different types of junctions and elongated meshes. **G**, MPEF-Pb 2713b, close-up showing the midrib, the steep angle of emergence of the secondary veins and the simple vein dichotomies. Notes: Z = zeta type, X = chi type, C = compound type, H = eta type. Scale bars: A–D = 5 mm, E–G = 3 mm.

its original course (Fig. 4F). Z (zeta) type of anastomosis occurs when two veins run parallel to each other and an oblique junction occurs between them, a product of a dichotomy in one of them (Fig. 4E, F). In the X

(chi) type of anastomosis two veins diverge from their normal paths, converge and then resume their original courses (Fig. 4E, F). Triple junctions in which two resulting veins emerge are rare (Fig. 4E).

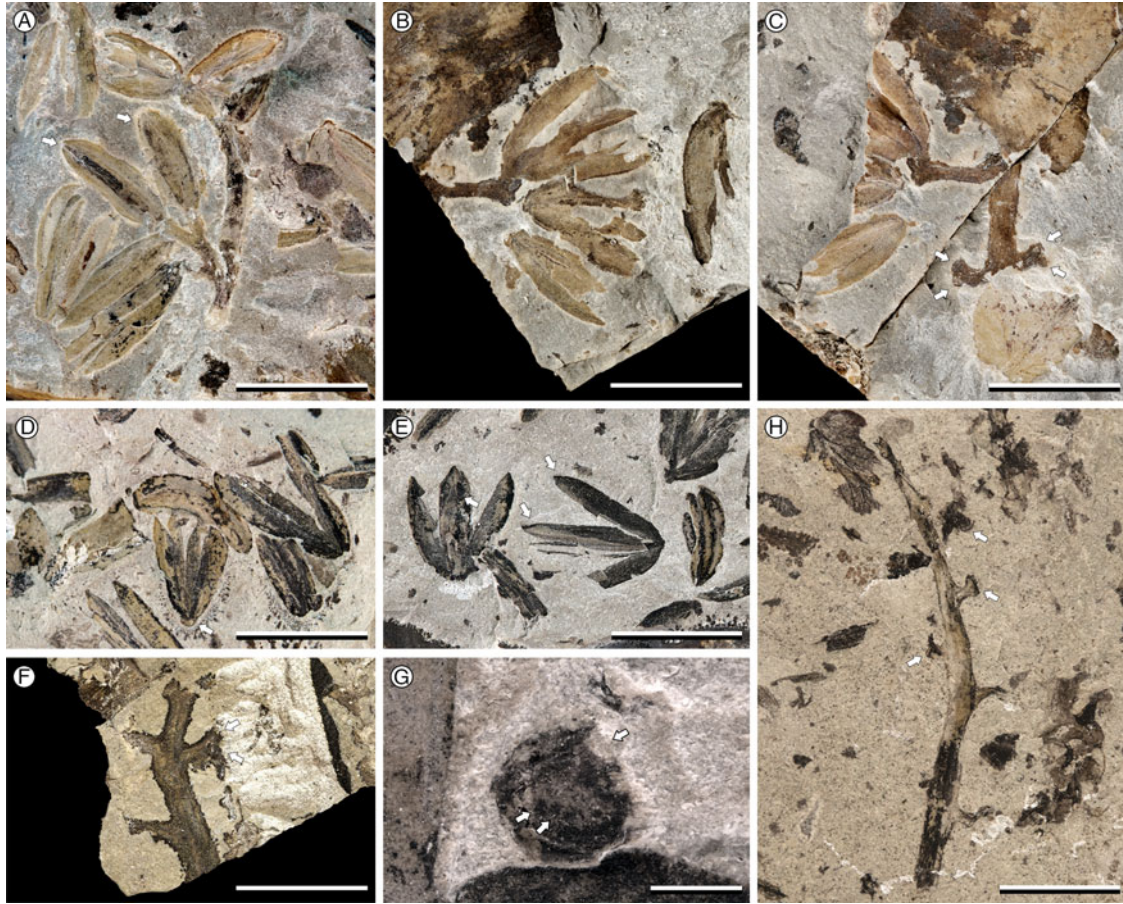


Figure 5. *Caytonanthus* sp. and *Caytonia* sp. **A**, MPEF-Pb 2877a, articulated specimen with three branching orders, note the fused synangia (arrows). **B**, MPEF-Pb 9668b, long branch with short synangia bearing branchlets. **C**, MPEF-Pb 9668a, branch figured on **B** attached to an axis also bearing two pairs of short subopposite branchlets (arrows). **D**, MPEF-Pb 2843, isolated synangia, note basal elliptic scar of one of them (arrow). **E**, MPEF-Pb 2852a, isolated synangia with ensiform pollen sacs, note the acute apex and dorsal keel (arrows). **F**, 9661b, probable naked axis of *Caytonanthus* sp., note the subopposite arrangement of branches and terminal branchlets (arrows). **G**, MPEF-Pb 2877a, *Caytonia* sp. isolated cupule, note the possible impressions of seeds and the pedicel attachment scar (arrows). **H**, MPEF-Pb 9660a, probable naked axis of *Caytonia* sp. with alternate pedicels and possible fragmented cupule (arrow). Scale bars: A–G = 5mm, H = 1 mm.

The dichotomies of the secondary veins are simple (Fig. 4F, G), with daughter veins often further dividing and/or fusing, resulting in the formation of elongated meshes with an oblique orientation with respect to the midrib, up to 0.38 mm wide and 4 mm long, with a L/W ratio of 8.5–11:1. Leaflet vein density is about 1.8–3 per mm² near the midrib and margins.

Specific assignment. The vast majority of the Argentinian material belongs to *Sagenopteris rhoifolia* Presl (Bonetti 1963; Herbst 1964a, b, 1965, 1966a, b; Baldoni 1981; Baldoni & Olivero 1983; Spalletti *et al.* 2007; Morel *et al.* 2013), synonym of *Sagenopteris nilssoniana* (Brongniart) Ward (see Ward 1900). For a historical account of *S. nilssoniana* see Halle (1910). The holotype of *S. nilssoniana* from Höör, Sweden, housed at the Stockholm Natural History Museum (ID: S087455), is

a fragmentary leaflet preserving few characters, whereas other specimens from Höör show variable features. Additionally, the name *S. nilssoniana* has been broadly used, expanding its morphological range (Halle 1910; Herbst 1965; Rees 1993). As a consequence, *S. nilssoniana* has highly contrasting characters, such as: (i) acute vs rounded apices; (ii) entire vs extremely lobed margins; (iii) a midrib that reaches 50–95% of the leaflet length; (iv) secondary veins emerging from 10–60°; and (v, vi) leaflets and vein meshes dimensions usually considerably smaller in most of the Southern Hemisphere (SH) specimens compared with NH ones.

Based on their overall form and size, the Lonco Trapial fossils described here are comparable with some specimens referred to as *Sagenopteris nilssoniana* (Bonetti 1963; Herbst 1964a, 1965; Herbst & Anzotegui

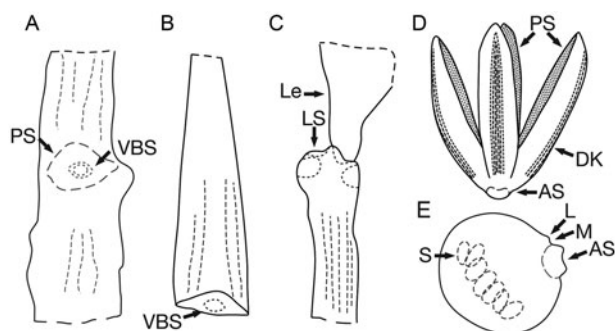


Figure 6. Line drawings of Taquetrén caytonialean organs. **A**, based on MPEF-Pb 1864b, branch with a lenticular petiole attachment scar (PS) and elliptic vascular bundle scar (VBS). **B**, based on MPEF 2855, petiole with a lenticular base and elliptic vascular bundle scar (VBS). **C**, based on MPEF 9517, leaf fragment with an attached leaflet (Le), and three leaflet attachment scars (LS). **D**, based on MPEF 2843 and 2852a, isolated *Caytonanthus* sp. synangium, note the four basally fused pollen sacs (PS), their dorsal keel (DK) and the basal attachment scar (AS). **E**, based on MPEF 2877, isolated *Caytonia* sp. cupule showing the arrangement of its seeds (S), the location of the 'lip' (L) and 'mouth' (M), and the pedicel attachment scar (AS).

1968). However, those, and the majority of reports of the species, were based on small collections, with the descriptions being based on a reduced list of features. The aforementioned issues, added to the results of the comparisons with other species (see below), lead us to assign these specimens to a new species, *Sagenopteris trapialensis* Elgorriaga, Escapa & Cuneo. It is beyond the scope of this contribution to perform a critical revision of *Sagenopteris nilssoniana*, but such a revision is necessary to truly comprehend the abundance, morphological plasticity and geographical range of this species.

Comparisons. In addition to the aforementioned comparison with *S. nilssoniana*, we compared the Taquetrén material with the most thoroughly described species worldwide (Table 1). Species heavily based on cuticular characters could not be compared due to the lack of relevant information in the studied material.

Sagenopteris hallei Harris from the Upper Triassic of Greenland is very similar in gross morphology to *S. trapialensis* (Harris 1932), but it has typically larger leaflets, longer and wider vein meshes, and secondary veins that usually reach the margin at 30°, whereas in our specimens this angle varies from 80° at the base to 10° at the apex, with a mean of 45–50°.

Sagenopteris serrata is a Rhaeto-Liassic species from Greenland and Germany (Harris 1932; Kräusel 1959), that has large leaflets, a notably contracted base, an acute apex, serrate margins and few anastomoses. These characters sharply contrast with the Taquetrén specimens.

Sagenopteris undulata Nathorst from the Rhaeto-Liassic of Scania, Sweden (Halle 1910; Lundblad 1950), has narrow and lanceolate mature leaflets with undulating to dentate margins. Due to the shared cuticular features with *S. nilssoniana*, it was suggested that they could represent extreme morphologies within the same species (Rees 1993). *Sagenopteris dentata*, from the Bjuf flora (Nathorst 1878), agrees in most of its characters with *S. undulata* and was later synonymized (Nathorst 1886).

Sagenopteris pualensis Barbacka from the Lower Jurassic of Alaska is similar in gross morphology to *S. trapialensis* (Barbacka *et al.* 2006), but it has considerably larger leaflets, vein meshes up to 8 × 1 mm, and different L/W proportions.

Sagenopteris alata Nathorst includes small bud-like leaves with broad 'winged' petioles and tiny leaflets (Nathorst 1886). Nevertheless, in his original description Nathorst (1886) cautioned that the specimens on which *S. alata* were based may be, in fact, small specimens of *S. undulata*. In this study we also describe some small leaves that could be assigned to *S. alata*, but we interpret them as small leaves of the same kind of plant that bore 'normal' type of leaves.

Sagenopteris colpodes Harris from the Middle Jurassic of Yorkshire, England, may be an aggregate of two species (Harris 1940a). It differs from *S. trapialensis* in having much larger leaflets, vein meshes usually 0.75 mm wide, and a midrib that becomes indistinguishable at a considerable distance below the apex.

Sagenopteris phillipsi (Brongniart) Presl is a well-known species of the genus, occurring at several Middle Jurassic localities of the NH (e.g. Yorkshire and Iran; Harris 1940a, 1964; Schweitzer & Kirchner 1998). Macromorphologically it differs from *S. trapialensis* in having longer leaflets, with both the lateral and central pair being nearly symmetrical, long, lanceolate, and with acute apices. Additionally, their vein meshes are larger.

Sagenopteris panda Miller & Hickey from the Lower Cretaceous rocks of the Winthrop Formation, has been thoroughly described based on macromorphology (Miller & Hickey 2010). *Sagenopteris panda* differs from *S. trapialensis* in that: (i) *S. panda* has typically larger leaflets with a L/W ratio of 4.5–5:1; (ii) their leaflets have a very low number of anastomoses; (iii) their secondary veins depart at a low angle; (iv) the vein meshes are up to 7 mm long; and (v) all leaflets have an elliptical outline.

Sagenopteris variabilis (Velenovsky) Velenovsky is a species from the Late Cretaceous of the Czech Republic known from few complete specimens (Velenovsky 1885; Kvacek 1999). Apparently it has three to five

Table 1. Comparison of *Sagenopteris trapialensis* sp. nov. with selected *Sagenopteris* species.

<i>Sagenopteris</i> species /leaflet character	Number per leaf	Dimensions	L/W ratio	Margin	Basal constriction	Apex	Vein mesh dimensions	Age	Main reference(s)
<i>S. trapialensis</i>	4	$\bar{x} = 19.5 \times 7.2$ Up to 58×18	2.6–3.2:1	Entire	No	Obtuse	4×0.38	Early Jurassic	This study
<i>S. hallei</i>	4	$\bar{x} = 40 \times 13$	c. 3.1/1	Entire	No	Obtuse	6×4	Late Triassic	Harris 1932
<i>S. serrate</i>	4	$\bar{x} = 70 \times 30$	c. 2.3:1	Serrate	Yes	Acute	?	Late Triassic	Harris 1932
<i>S. nilssoniana</i> *	4	$\bar{x} = 50 \times 14$ Up to 87×31	2.9–3.5:1	Entire to deeply lobed	No	Acute Obtuse	$? \times 0.4$	Early Jurassic	Harris 1932; Rees 1993
<i>S. pualensis</i>	4	Up to 100×35	c. 2.9:1	Entire	No	Obtuse	8×1	Early Jurassic	Barbacka <i>et al.</i> 2006
<i>S. colpodes</i>	4	Up to 200×40	2–5:1	Entire	No	Obtuse	$? \times 0.75$	Middle Jurassic	Harris 1940a; Harris 1964
<i>S. philipsi</i>	4	Up to 120×30	5–10:1	Entire	No	Acute	$? \times 0.5$	Middle Jurassic	Harris 1940a; Harris 1964
<i>S. panda</i>	4	Up to 100×20	4.5–5:1	Entire	No	Acute Obtuse	$7 \times ?$	Early Cretaceous	Miller & Hickey 2010
<i>S. variabilis</i>	3–5	Up to 70×35	c. 2.8:1	Entire	Yes	Obtuse	?	Late Cretaceous	Kvacek 1999
<i>S. microphylla</i>	4	$\bar{x} = 23 \times 11$ Up to 28×14	c. 2.1:1	Entire	No	Obtuse	$? \times 1$	Late Cretaceous	Krassilov 1979

*See Systematic palaeontology section. Characters unknown for more than 50% of species are discussed in the main text. Measurements are expressed in mm.

leaflets per leaf, with the medial pair being symmetrical and having a rather contracted base, while the lateral leaflets are asymmetrical and have a short petiole, differing from *S. trapialensis*.

Sagenopteris microphylla Krassilov from the Late Cretaceous of Sakhalin, Russia (Krassilov 1978, 1979), is the youngest representative of the group. Their leaflets have a rather similar average length, but differ in width and shape, with the outer pair of leaflets having a broad, nearly rectangular outline. Additionally, the vein density and midrib width (as measured from figured specimens) are smaller in the Russian species.

Associated reproductive organs

Genus *Caytonanthus* Harris emend. Harris, 1964

Caytonanthus sp.
(Figs 5A–E, 6D)

Type species. *Caytonanthus arberi* Thomas (Harris) emend. Harris, 1964.

Material examined. MPEF-Pb 2087, 2168 (Taquetrén A). MPEF-Pb 2831, 2836, 2840, 2843, 2849, 2852, 2854, 2855, 2866, 2877, 2890, 6609, 6619, 6626, 9506, 9507, 9539, 9550, 9650, 9652–9653, 9655–9659, 9662–9700 (Taquetrén B).

Description. Numerous detached synangia and two specimens with synangia attached to branched axes were found. They feature main axes up to 1 mm wide, each of them having at least one branching order. First order branches up to 0.65 mm wide, whereas second order ones up to 0.52 mm wide (Fig. 5A–C). Each ultimate order branch usually bi- or trifurcates distally, producing short synangia bearing branchlets, each with a spatulate to rounded apex (Fig. 5A–C). The synangia are narrow, elliptic to ovate, radially symmetrical, with rounded to rarely subacute apices (Fig. 5D, E). When detached, the synangia show a circular to crescent-shaped scar at the base (Fig. 5D). Each synangium is composed of four, less often three or five, ensiform, longitudinally striated pollen sacs, with a dorsal keel and an acute apex (Figs 5A–E, 6D). The sacs measure up to 8.3 mm long and 1.3 mm wide ($\bar{x} = 5.1 \times 0.9$ mm, $N = 142$), with a L/W ratio of 6:1, and an apex angle of 35–55°. When detached (and presumably dehiscent) the pollen sacs remain fused only at their bases, being free for up to 90% of their length (Fig. 5A–E). Several naked *Caytonanthus* sp. branches were also found (Fig. 5F).

Comparisons. The delimitation of species within this genus is often difficult due to their apparent conservative macro- and micromorphology, the usually low number of specimens available to study (either complete or fragmentary), and the size overlap that occurs between species (Table 2; Harris 1941, 1964). These factors are the main reason why species delimitation has been traditionally based on measurements of pollen grains, which are often encountered in large masses. In this context, we decided to assign these specimens to *Caytonanthus* sp., precluding the creation of a new taxon or assignation to a particular morphospecies. Although pollen grains were not recovered from the Taquetrén fossils, their comparison with other species was achieved satisfactorily due to the large number of isolated synangia found and their unique features. The vast majority of hand-specimens bearing *Caytonanthus* sp. fragments also contain fragments of *Sagenopteris trapialensis* (c. 70%). Other taxa co-occurring with *Caytonanthus* sp. are ferns of *Cladophlebis*-type (29%), conifer leafy branches, *Sphenopteris*-type foliage and equisetalean remains (<1%), all taxa that are not likely to be biologically related to *Caytonanthus*-type organs. Because of the close association of *Caytonanthus* sp. with *Sagenopteris trapialensis* leaves, and the already existing hypotheses linking these types of organs (see Introduction), we consider them as different parts of the same type of plant.

All of the *Caytonanthus* species compared differ from the Taquetrén *Caytonanthus* in the degree of fusion of their pollen sacs (see Table 2). This particular feature will be explored in the Discussion.

Two fragmentary specimens of *Caytonanthus* were described by Rees (1993) from the Lower Jurassic of Botany Bay, Antarctica. Their synangia are short and broad and appear to be in large numbers per branch (which are noticeably short), differing from the Taquetrén fossils. *Caytonanthus kochii* Harris from the Lower Jurassic of Scoresby Sound, Greenland (Harris 1937, 1964), carries small pollen sacs without a dorsal keel, and its synangia have an abruptly contracted base.

Caytonanthus arberi (Thomas) Harris is the commonest species from the Jurassic of Yorkshire (Harris 1941, 1964). Contrary to the Taquetrén *Caytonanthus*, it features small synangia with acute apices emerging from short first order branches. They have a main axis with a broad base that gently tapers to the apex, bearing small pollen sacs apparently fused at both base and apex (but see Discussion), and lacking a dorsal keel. *Caytonanthus oncodes* Harris (1964), also from the Middle Jurassic of Yorkshire, differs from the Taquetrén *Caytonanthus* by having slightly shorter and broader synangia with a rounded apex.

Table 2. Comparison of *Caytonanthus* sp. from Taquetrén with selected *Caytonanthus* species.

<i>Caytonanthus</i> species/character	Synangia per ultimate branch	Length of synangia	Dehiscence pollen sacs*	Dorsal keel	Branching orders	Diameter of pollen grains (µm)	Age	Main reference
<i>Caytonanthus</i> sp. (Taquetrén)	1	$\bar{x} = 5.1$	Free	Present	>1	?	Early Jurassic	This study
<i>C. kochii</i>	1	$\bar{x} = 4.0$?	Absent	>1	30	Early Jurassic	Harris 1932
<i>Caytonanthus</i> sp. (Antarctica)	1	$\bar{x} = 3.5$	Fused	Absent	>1?	?	Jurassic	Rees 1993
<i>C. arberi</i>	1	$\bar{x} = 3.0$	Fused?*	Absent	1	22	Early Jurassic	Harris 1964
<i>C. oncodes</i>	1	$\bar{x} = 2.5$	Fused	Absent	>1	31	Middle Jurassic	Harris 1964
<i>C. tyrmensis</i>	Up to 6	3.5–5	Fused	Present	?	25	Late Jurassic	Krassilov 1977
<i>C. rewaensis</i>	Up to 5	3–4.2	Fused	Absent	1	?	Early Jurassic	Prakash & Das 2017
							Cretaceous	

Characters unknown for more than 50% of species are discussed in the main text. Measurements are expressed in mm otherwise stated. *See discussion.

Caytonanthus tyrmensis Krassilov from the Late Jurassic–Early Cretaceous of Russia (Krassilov 1977), differs from the Taquetrén fossils in having up to 6 synangia per terminal branch, which are radially disposed. The Early Cretaceous *Caytonanthus rewaensis* Prakash & Das from south Rewa, India (Prakash & Das 2017), differs by having shorter and broader synangia placed in groups of four to five per branch. Additionally, it has simple lateral branches, whereas the Taquetrén fossils has more than one branching order.

Genus *Caytonia* Thomas, 1925

Caytonia sp.

(Figs 5G, H, 6E)

Type species. *Caytonia sewardi* Thomas, 1925.

Material. MPEF-Pb 2877, 9660, 9661 (Taquetrén B).

Description. A detached circular structure with a diameter of 1.55 mm, resembling a detached *Caytonia* sp. cupule, was found along with *Sagenopteris trapialensis* and *Caytonanthus* sp. (Figs 5G, 6E). It appears to bear several elliptical bodies up to 0.3 mm long, positioned in a single row near one of the internal margins. According to their morphology, number and position, they are interpreted as possible seeds. Opposite to the putative seeds there is a small protruding structure, closely resembling the ‘lip’, and a depression similar to the ‘mouth’ of the NH *Caytonia* fossils (see Harris 1940b, fig. 1). A naked axis, 18.5×0.9 mm, with a sub-opposite arrangement of pedicels, one of them bearing a cupule-like structure, was also found (Fig. 5H).

Remarks. Regardless of the fragmentary nature of the putative cupule, we note that it is similar to a detached *Caytonia sewardi* cupule (see Harris 1940b, fig. 3H), which features numerous seeds in a single row near its margin, being part of a similarly organized organ as the naked axis found on Taquetrén. However, for the moment it is advisable to treat this record with caution.

Discussion

Species delimitation

It has been argued that without cuticular information from leaves, the recognition of *Sagenopteris* species is a troublesome issue: “The cuticles provide a valuable and perhaps the only safe specific criterion [to distinguish species]” (Harris 1940a, p. 263). However, from the >60 *Sagenopteris* species erected (Jongmans & Dijkstra 1964), several of them lack cuticular information and were characterized based on a low number of specimens

(e.g. *S. latifolia* Fontaine, *S. variabilis*. Fontaine, *S. nar-iwaensis* Huzioka. Fontaine 1889; Huzioka 1970). Similarly, many *Caytonanthus* species have been defined based on a reduced number of micromorphological characters (i.e. pollen size, presence/absence of trichomes/hairs) and the length and width of the pollen sacs (e.g. Harris 1941; Krassilov 1977).

Descriptions based on numerous specimens, even without the preservation of cuticular features, allow a detailed, complete macromorphological characterization, including information on developmental series and intra-specific variation, which could be easily mistaken for interspecific variation if a small sample was examined. Herein, we characterize the Taquetrén fossils with a suite of characters that have not been consistently used in previous studies (see Description and comparisons, above), most of them of continuous nature, such as: base and apex angle of leaflets, midrib width, secondary veins width, angle of emergence of secondary veins, length of the secondary veins before their first dichotomy, venation density (at margins and near midrib), vein mesh L/W ratio, leaflet L/W ratio, anastomoses types, base and apex angle of the pollen sacs, type of dehiscence, number of synangia per terminal branch, and pollen sac L/W ratio. In order to elucidate the value of these features to characterize species, detailed measurements of the various species of the group are still required.

Possible caytonian reproductive organs from Gondwana

We offer a brief summary of relevant occurrences of caytonian-like organs from Gondwana that have been reported since the 1980s, in addition to *Sagenopteris*, *Caytonanthus* and *Caytonia* species.

Nidianthus indicus Bhowmik & Parveen is based on isolated synangiate polliniferous organs from the Upper Triassic of Nidpur, India (Bhowmik & Parveen 2008). The synangia are tetrasporangiate, longitudinally striated and basally fused, with pollen sacs measuring $2-4 \times 1-1.5$ mm bearing bisaccate pollen. Naked axes resembling those of *Caytonanthus* were found in the same beds, but there are no articulated specimens. No *Sagenopteris* remains were found in the same locality (Bhowmik & Parveen 2008).

Kachchhia navicula Bose & Banerji, *Caytonia indica* Bose & Banerji and *Sagenopteris* cf. *colpodes* are synangiate, cupulate and foliar organ-species from the Middle–Late Jurassic flora of Kachchh, India, with a caytonian organization (Bose & Banerji 1984). However, *Caytonia indica* fossils are fragmentary, with one of its possible cupules bearing a single seed (in contrast with the numerous seeds that are found on most

Caytonia specimens), while another minute specimen shows imprints of probable seeds (Bose & Banerji 1984). The synangia of *Kachchhia* are bisporangiate instead of the usual tetrasporangiate synangia of *Caytonanthus*. Although their similarity with caytonian reproductive organs is remarkable (added to the presence of *Sagenopteris* leaves in the same beds), the bisporangiate nature of *Kachchhia* (Bose & Banerji 1984) may indicate the presence of a different lineage of caytonian compared to the one from the NH.

Caytonia cucullata McLoughlin from the Jurassic of the Clarence–Moreton Basin, Australia, was described as a megasporophyll bearing opposite to subopposite recurved and lobed cupules, each with a contracted apex (Jansson *et al.* 2008). Due to the unusual combination of characters for a caytonian plant, and to the discovery of more specimens that allowed a more detailed description, these remains were later assigned to *Knezourocarpon narangbaensis* Pattemore, a gymnosperm ovuliferous organ of uncertain affinities (Pattemore *et al.* 2014).

Poorly preserved leaf fragments showing reticulate venation and detached fruit-like bodies from Williams Point, Antarctica were assigned to *Sagenopteris* and *Caytonia*, respectively (Banerji & Lemoigne 1987). Although the fossils were very fragmented and showed little detail, the supposed Late Triassic age of the flora seemed to agree with their tentative assignation. However, as the flora is now regarded as Late Cretaceous (Chapman & Smellie 1992; Cantrill 1997), and contains numerous angiosperm remains (Rees & Smellie 1989; Poole & Cantrill 2001), the assignation of both types of fossils to Caytoniales is dubious.

Ktalenia circularis Archangelsky from the Early Cretaceous of Argentina is a megasporangiate organ-species found associated with leaves of *Rufflorinia sierra* Archangelsky, and tentatively allied with Caytoniales by its similarity with *Caytonia* (Archangelsky 1963; Taylor & Archangelsky 1985). *K. circularis* is characterized by the presence of opposite to subopposite cupules arranged along an axis, which are opposite to subopposite to bract clusters. The cupules are fleshy, ellipsoidal, with a beak-like extension at the distal end and bear one or two ovules each (Taylor & Archangelsky 1985). The associated *R. sierra* fronds are up to tripinnate, with alternate to subopposite decurrent pinnae, obliquely oriented pinnules concrescent at their base, and a lanceolate acute apex, contrasting with *Sagenopteris*-type leaves and resembling peltaspermalean or corystospermalean fronds instead. Additionally, the stomata of the various *Rufflorinia* species do not resemble any caytonian type stomata (Barbacka & Boka 2000b; Villar de Seoane 2000; Carrizo *et al.* 2014). *Ktalenia* superficially

resembles *Caytonia* in its cupular arrangement and possible presence of internal canals, but differs in cupule shape, number of seeds per cupule, seed architecture, presence of a beak-like extension, and presence of bract clusters opposite to the cupules. These dissimilarities do not support the suggested relationship of *Ktalenia* and *Ruflorinia* with Caytoniales.

Petriellaleans cupules from the Middle–Late Triassic of Antarctica and South Africa, of the *Petriellaea* Taylor, Del Fueyo & Taylor and *Kannaskoppia* Anderson & Anderson types show a slight resemblance with *Caytonia*. However, *Petriellaea* cupules bear fewer seeds per unit, lack the characteristic internal canals of *Caytonia*, are arranged in pairs compared to the single attachment of *Caytonia*, and have a dorsal shallow depression (Taylor *et al.* 1994). The reproductive axes of *Kannaskoppia* cupules are proximally forked, with each cupule splitting in three lobes at maturity, features that do not agree with *Caytonia* (Anderson & Anderson 2003). *Kannaskoppianthus* Anderson & Anderson microsporangiate organs differ greatly from *Caytonanthus*, with individual microsporangia being often small, occurring in groups of five attached to an arcuate scale, and being externally surrounded by a dehiscent operculum. Also, the microsporophylls are arranged in two rows on a bifurcate axis. Finally, *Rochipteris* Herbst type of leaves found in association with *Petriellaea*, *Kannaskoppia* and *Kannaskoppianthus* share few similarities with *Sagenopteris* type leaves, the main one being the presence of vein anastomoses of the Z and X types (Bomfleur *et al.* 2014).

Palaeobiological insights of a cosmopolitan lineage

The Caytoniales from Taquetrén represent a new source of information concerning the palaeobiology of caytonealean plants from the SH, which were scarcely accounted for in previous reports due the fragmentary nature of the fossils (Herbst 1964a, b, 1965, 1966a, b; Bose & Banerji 1984; Rees 1993; Jansson *et al.* 2008). When compared with their NH counterparts (Harris 1964; Krassilov 1977; Barbacka & Boka 2000b), an overall similar architecture, habit and organization of the different organs is easily recognizable (e.g. type of leaves and leaflets, abscission of foliar and polliniferous organs).

Sagenopteris leaves and leaflets from the NH show a clean abscission layer (Harris 1951, 1964), with the same type of layer occurring on the Taquetrén fossils (Fig. 2C, G–I). Detached leaflets and petioles are found at the Taquetrén locality in large quantities compared to complete leaves, as in most localities throughout the world (Harris 1964; Herbst 1966b; Rees 1993; Kvacek

1999), being occasionally dominant in some fossiliferous levels. The aforementioned facts suggest that these plants may have been of deciduous nature (Friis *et al.* 2011), shedding petioles and leaflets separately (Figs 2G–I, 4A–D). Deciduousness is a rare trait among modern gymnosperms (e.g. *Larix* Miller, *Pseudolarix* Gordon, *Taxodium* Rich, *Ginkgo* L.; Gower & Richards 1990; Crane 2013); however, it was also suggested for other pteridosperms (e.g. corystosperms, glossopterids: Plumstead 1958; Taylor 1996). Similarly, the *Caytonanthus* from Taquetrén also show an abscission layer like those from the NH, in this case on the base of the synangia (Figs 5D, E, 6D; Harris 1941), which seem to have been shed after dehiscence and are often found in large accumulations (Fig. 5A–F).

The synangia of the Taquetrén *Caytonanthus* dehiscenced across their entire length and remained fused only at the base (Figs 5A–F, 6D), contrary to all NH species, which remain fused at the base and apex even after dehiscence (Harris 1964). However, the degree of fusion of the pollen sacs of the NH *Caytonanthus* species should be interpreted with caution, since it was suggested that the pollen sacs of *C. arberi* from Yorkshire were perhaps only slightly fused, as in the Taquetrén *Caytonanthus*, or even completely free from each other (Osborn 1991). A completely free arrangement of the pollen sacs seems unlikely, since the four sacs are usually found forming distinct units when detached from main polliniferous organs, and not having a distinct petiole. In light of what is observed for the Taquetrén material, and the apparent free nature of *C. arberi*, a revision of the NH *Caytonanthus* material is necessary in order to correctly code this character state.

Bud- and scale-like leaves of *Sagenopteris* (see Description and comparisons) were previously reported from European localities (Nathorst 1886; Halle 1910; Harris 1964, 1971), but their presence in the SH was uncertain prior to the current record. It is interesting to note that the petioles of certain small to almost average-sized leaves are similar to the petioles of bud- and scale-like leaves (Fig. 3A–F), suggesting that those leaves had the potential to continue growing, at least to a small extent (Fig. 2D, E). Other small leaves have long slender petioles (Fig. 3G–I), as in average to large-sized leaves. In this context, the spectrum of leaflet size in *Sagenopteris trapialensis* includes forms that range from 1 mm to nearly 60 mm long and 0.78–18.33 mm wide, with average dimensions around 19 × 6.8 mm. The notable size difference between average-sized and the largest leaflets may be explained by the presence of a large number of very small leaves, skewing the mean towards smaller sizes. Moreover, large leaves are prone to be fragmented due to biological, biostratinomic and

Table 3. Caytonian assemblages with at least two organ-genera of the *Sagenopteris*-*Caytonanthus*-*Caytonia* suite.

Locality	Age	<i>Sagenopteris</i> species	<i>Caytonanthus</i> species	<i>Caytonia</i> species*	Main reference(s)
Bjuv, Sweden. NH	Late Triassic – Early Jurassic	<i>S. undulata</i>	?	<i>Caytonia</i> sp.	Lundblad 1948, 1950
Scoresby Sound, Greenland. NH	Early Jurassic	<i>S. nilssoniana</i>	<i>C. kochi</i>	<i>C. thomasi</i>	Harris 1932
Grojec, Poland. NH	Early Jurassic	<i>S. colpodes</i> ^a	<i>Caytonanthus</i> sp.	?	Reymanowna 1973
Mecsek Mountains, Hungary. NH	Early Jurassic	<i>S. nilssoniana</i> / <i>S. hallei</i> / <i>S. pilosa</i>	<i>Caytonanthus</i> sp.	<i>R. kvacekii</i>	Barbacka & Boka 2000a
Botany Bay, Antarctica. SH	Early Jurassic	<i>S. nilssoniana</i>	<i>Caytonanthus</i> sp.	?	Rees 1993
Taquetrén, Argentina. SH	Early Jurassic	<i>S. trapialensis</i>	<i>Caytonanthus</i> sp.	<i>Caytonia</i> sp.	This study
Yorkshire, UK. NH	Middle Jurassic	<i>S. phillipsi</i>	<i>C. arberi</i>	<i>C. nathorsti</i>	Harris 1964
Yorkshire, UK. NH	Middle Jurassic	<i>S. colpodes</i> ^a	<i>C. oncodes</i>	<i>C. sewardi</i>	Harris 1964
Yorkshire, UK. NH	Middle Jurassic	<i>S. colpodes</i> ^b	<i>Caytonanthus</i> sp.	<i>C. kendalli</i>	Harris 1964
Alborz, Iran. NH	Middle Jurassic	<i>S. phillipsi</i> / <i>S. cf. colpodes</i> ^a	?	<i>Caytonia</i> sp.	Schweitzer & Kirchner 1998
Kachchh, India. SH	Middle–Late Jurassic	<i>S. cf. colpodes</i> ^b	?	<i>C. indica</i> ^c	Bose & Banerji 1984
Tyrma River, Russia. NH	Late Jurassic–Early Cretaceous	<i>S. phillipsi</i>	<i>C. tyrmensis</i>	?	Krassilov 1977

^a*S. colpodes* small form; ^b*S. colpodes* large form; ^csee discussion; **Reymanownaea* species.

diagenetic processes or during collection (Shute & Cleal 1987; Spicer 1991).

Ten fossil assemblages from all over the world yielded at least two of the three major caytonian organ-genera (i.e. *Sagenopteris*-*Caytonanthus*-*Caytonia*; Table 3). Out of these, the assemblage from Yorkshire, UK, is the most thoroughly studied and has also provided isolated seeds, pollen and two leafy branches (Harris 1932, 1933, 1964). Only three assemblages from the SH contain more than a single caytonian organ-genus (i.e. Kachchh, Botany Bay, Taquetrén), with the record of *Caytonia indica* from India subject to the issues previously mentioned (Bose & Banerji 1984; see Discussion, above). Although the Botany Bay record already suggested the southern presence of the same caytonian lineage as the one of those in the NH, this hypothesis was based on the presence of *Sagenopteris* fossils, most of which are of doubtful assignation to the genus (see Schweitzer & Kirchner 1994), and only two *Caytonanthus* specimens (Rees & Cleal 2004). With the new palaeobiological information provided by the large number of Taquetrén caytonians, the presence of this lineage in the SH, at least since the Early Jurassic, is reinforced.

Conclusions

The caytonians from Taquetrén, Patagonia, strengthen the presence of the group in the SH, provide insights

about palaeobiological features (e.g. degree of fusion of the pollen sacs), and invite future biogeographic, phylogenetic and palaeoecological analyses of the group. The morphological plasticity of *Sagenopteris* was identified thanks to the large number of fossils collected. Thoroughly measured continuous features were employed to describe and differentiate these fossils from similar ones. In order to achieve more accurate descriptions and better specific delimitations, techniques that better capture overall shape and venation should be explored in the future (e.g. geometric morphometrics and multivariate statistics) since these kinds of methods have repeatedly showed their power to discriminate remarkably similar species of organisms with few discrete features separating them (see Cope *et al.* 2012; Milla Carmona *et al.* 2016).

The marked similarity in both reproductive and vegetative morphology of caytonians from both hemispheres suggest that they were part of a successful and widely distributed lineage. However, valuable information concerning their habit, organography, anatomy and organic connections between their major organs is still lacking. The aforementioned issues have hindered the establishment of individual caytonian whole-plant reconstructions, which are essential for performing reliable phylogenetic analyses. As a consequence, most phylogenetic studies code a generic ‘*Caytonia* plant’ with 40–70% of character states scored as unknown (Doyle 2006; Hilton & Bateman 2006; Rothwell & Stockey 2016). It is

intended that the suite of macromorphological characters used to describe the Taquetrén fossils will be used in future studies on caytoniales, in order to establish well characterized whole-plant reconstructions.

Vegetative and reproductive remains of corystosperms and probable petriellaleans, mostly preserved as impressions and compressions, are known from the Upper Triassic El Tranquilo Group of Santa Cruz Province (Petriella 1979, 1980; Herbst *et al.* 2001). *Pachypteris* Brongniart and *Archangelskya* Herbst type foliage was reported from the Early Jurassic of Chubut (Escapa 2009), but the affinity of these genera with corystosperms (Harris 1964; Rees & Cleal 1993) remains doubtful. With the addition of the caytoniales from Taquetrén to the Patagonian record, at least three out of the four main groups of Mesozoic pteridosperms (i.e. Caytoniales, Corystospermales and Petriellales) are present in Patagonia, as evidenced by both vegetative and reproductive structures, with possible records of well-preserved peltaspermales currently under study (Elgorriaga *et al.* 2016). On a global scale, several localities have provided new gymnosperm groups and taxa in the past decades, suggesting a higher diversity of gymnosperms during the Mesozoic than previously thought (e.g. Basin Creek Formation, Molteno Formation, Apple Bay locality, Falla Formation: Holmes & Anderson 2005; Anderson & Anderson 2003; Stockey & Rothwell 2009; Bomfleur *et al.* 2011).

Within this context, a thorough revision of each of the major groups of Mesozoic pteridosperms, phylogenetic analyses including gymnosperm taxa from new localities and terminals based on reliable whole plant concepts, combined with the exploration of alternative character coding schemes, will represent future steps that might prove useful in testing competing hypotheses of gymnosperm relationships and angiosperm origins.

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