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SPECIAL ISSUE—ROTHWELL CELEBRATION

RELICTUAL *LEPIDOPTERIS* (PELTASPERMALES) FROM THE EARLY JURASSIC CAÑADÓN ASFALTO FORMATION, PATAGONIA, ARGENTINA

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Premise of research. Numerous leaf remains of pteridosperms occur at a new locality of the Early Jurassic Cañadón Asfalto Formation, in Patagonia, Argentina. Fossils consist of adpressions with superb cuticular preservation and are herein assigned to *Lepidopteris* (Peltaspermaceae).

Methodology. Fossils were studied using normal light, epifluorescence, and scanning electron microscopy. The cuticles of 25 specimens were chemically prepared following standard methods. The remains were described in detail and compared with other pteridosperm genera and *Lepidopteris* species.

Pivotal results. We erect *Lepidopteris scassoi* sp. nov. Elgorriaga, Escapa et Cúneo, based on its novel combination of characters. Among other features, *L. scassoi* has a bipinnate-tripinnatifid architecture, smooth rachis, 1–3 pairs of intercalary pinnules, and entire to deeply lobed pinnules with pinnate venation. Fronds are amphistomatic with a 0.5–0.7 : 1 adaxial to abaxial ratio; stomata occur scattered on rachides and pinnules and have a ring of usually seven subsidiary cells with papillae oriented toward the stomatal pit; and the guard cells are sunken. A single solid papilla is usually present on epidermal cells of pinnules and pinnae. Structures resembling isolated *Peltaspermum* disks, with similar stomata as *L. scassoi*, were found in the same locality.

Conclusions. We interpret *L. scassoi* and other members of its lineage as fast-growing, long-lived shrubby to herbaceous plants that thrived in waterside environments. *Lepidopteris scassoi* represents the youngest occurrence of the genus by more than 20 Myr. *Lepidopteris* and *Dicroidium* lineages, dominant in Southern Hemisphere Triassic ecosystems, show a similar overall pattern of origination (Late Permian), diversification (late Early-Middle Triassic), and decline (Late Triassic), with relict occurrences during the Early Jurassic. The systematic affiliation of a considerable number of Mesozoic pteridosperm records remains contentious, and future efforts should be oriented toward a better understanding of the position of each group on the gymnosperm tree of life.

Keywords: Peltaspermales, *Lepidopteris*, Jurassic, Mesozoic, Patagonia, gymnosperms, Triassic-Jurassic extinction.

Introduction

The pteridosperms are a polyphyletic group of extinct seed plants of crucial relevance for the comprehension of the overall pattern of gymnosperm phylogeny and evolution (Doyle and Donoghue 1992; Rothwell and Serbet 1994; Hilton and Bateman 2006; Rothwell and Stockey 2016). Typical Paleozoic groups such as Callistophytales (Rothwell 1980, 1981), Lyginopteridales (Arnold 1939; Tomescu et al. 2001; Taylor et al. 2009), Glossopteridales (Pigg and Taylor 1993; McLoughlin 2011), and Medullosales (Taylor et al. 2009; Cleal and Shute 2012) are arguably better understood in terms of morphology, anatomy, and ecology than most of those groups typical for the Mesozoic (e.g., Peltaspermales, Umkomasiales, and Caytoniales; Stewart and Rothwell 1993; Taylor et al. 2006; Taylor and Taylor 2009).

One of the largest groups of pteridosperms is Peltaspermales, ranging from the Late Carboniferous to Late Triassic (Harris 1932; Thomas 1933; Townrow 1960; Kerp 1988; Barbacka 1991; Kerp et al. 2001; Bomfleur et al. 2011). Peltasperms were present on Northern Hemisphere floras during the late Paleozoic (Kerp 1982, 1988; Kerp et al. 2001; Karasev 2007; Naugolnykh 2008; Naugolnykh and Oskolski 2010; Zhang et al. 2012) and widely distributed worldwide during the early Mesozoic (Antevs 1914; Harris 1931; Townrow 1960; Zamuner et al. 1999; Retallack 2002; Anderson and Anderson 2003; Vavrek et al. 2007; Bomfleur and Kerp 2010; Kustatscher et al. 2013; He et al. 2017).

Peltaspermales traditionally comprises various associations of fossil genera of different organs that represent distinct natural plants (e.g., *Lepidopteris-Antevsia-Peltaspermum* plants,

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Compsopteris-Peltaspermopsis plants, *Dejerseya-Townrovia-Matatiella* plants; Townrow 1960; Bomfleur et al. 2011; Bukhman et al. 2015). Phylogenetic analyses, however, recovered some of these plants as more closely related to Umkomasiales than to the remaining peltasperms (Doyle 2006; Hilton and Bateman 2006), suggesting that perhaps neither group as currently defined is natural.

Within Peltaspermales, the Peltaspermaceae family was established based on three distinct fossil genera: the seed-bearing *Peltaspermum* Harris, the polliniferous *Antevsia* Harris, and *Lepidopteris* Schimper type of leaves (Thomas 1933; Townrow 1960). The family's circumscription has enlarged over time and now also contains a broad variety of additional genera including widely different forms such as *Peltaspermopsis* Gomankov, *Meyenopteris* Poort et Kerp, and *Scytophyllum* Bornemann, among others (Gomankov and Meyen 1986; Poort and Kerp 1990; Zamuner and Artabe 1990; DiMichele et al. 2005; Kustatscher 2006).

The *Lepidopteris-Antevsia-Peltaspermum* assemblage ranges from the Permian to the Upper Triassic (Antevs 1914; Townrow 1960; Naugolnykh and Kerp 1996). *Lepidopteris* fronds are chiefly characterized by having a bipinnate to tripinnate architecture, rachides commonly covered by blister-like swellings or lumps, intercalary pinnules attached directly to the rachis ("Zwischenfiedern"), and monocyclic stomatal apparati with sunken guard cells and subsidiary cells with strong cutin lappets overarching the stomatal pit (Townrow 1956, 1960). Peltaspermaceans were considered one of the few large groups that became extinct at the Triassic-Jurassic mass extinction (Cascales-Miñana and Diez 2012), and its youngest species, *Lepidopteris ottonis*, has been used as a Rhaetian marker for several European, Greenlandic, and American localities (Harris 1931, 1937; Vavrek et al. 2007; Pacyna 2014).

Here, we present leaf remains of Peltapermales preserved as impressions and compressions from the Lower Jurassic of Chubut, Argentina. The abundant and well-preserved plants allowed a detailed macro- and micromorphological characterization of the fossils, which leads us to erect a new species, *Lepidopteris scassoi*. Impression fossils reveal the overall frond architecture, whereas cuticle-bearing compression specimens provided important diagnostic epidermal details that confirm the assignation to the genus. Based on the paleoenvironments in which they are often found and the fronds' macro- and micromorphological features, we suggest that *L. scassoi*—like most *Lepidopteris*-bearing plants—had a herbaceous to small shrubby habit and fast growth rate and lived in close vicinity to water bodies, being adapted to cope with fluctuating water tables. *Lepidopteris scassoi* represents the youngest confirmed peltaspermacean found to date by ca. 20 Myr (Bomfleur et al. 2018). Together with similar putative Jurassic *Dicroidium* occurrences, our finds suggest that Patagonia and Antarctica served as final refugia for lineages that once dominated Southern Hemisphere Triassic floras.

Material and Methods

Geological Setting

The Cañadón Asfalto Formation of the homonymous basin (Figari et al. 2015) yields one of the richest Gondwanan vertebrate faunas from the Early Jurassic, including dinosaurs, turtles, amphibians, fish, and mammals (see Escapa et al. 2008 and references therein), whereas the invertebrate fauna is mainly composed of spinicaudatans, ostracods, and bivalves (Tasch and Volkheimer 1970; Monferran et al. 2013, 2016).

Plant fossils from the Cañadón Asfalto Formation were first brought to light by Frengüelli (1949*a*, 1949*b*), who recorded equisetaleans, ferns, possible pteridosperms, conifers, and ginkgoalean or czekanowskialean foliage. However, as Frengüelli did not provide descriptions or illustrations of the fossils, the whereabouts of the collections are unknown and the exact localities where the fossils were collected remain uncertain. Escapa (2009) collected and described plant remains from this formation on the Frenguelli Site (a new locality named in honor of Joaquin Frengüelli but not the same described above), located in the Cañadón Lahuinco some 15 km south of Cerro Condor school village, and recorded equisetaleans, ferns of uncertain affinity, and abundant remains of araucariacean and cupressacean conifers.

The present plants were collected from two stratigraphically coeval localities from the basal portion of the Cañadón Asfalto Formation, Pomelo, and A12, located few kilometers southeast from Cerro Condor school village, Chubut Province, Argentina. A12 fossil plants are preserved as impressions, whereas Pomelo fossils are exquisitely preserved as compressions (with a single occurrence of permineralized wood; Bodnar et al. 2013). At both localities, plant adpressions occur in dark gray to yellowish finely laminated mudstones with periodic intercalations of sandstones and tuff (Cabaleri et al. 2010; Figari et al. 2015). The mudstones usually contain numerous large spinicaudatan remains (up to 7 mm long). The taphoflora has scarce equisetalean and filicalean remains, being particularly rich in conifers and pteridosperms, with moderate occurrences of cycadophytes and possible ginkgoaleans (Sender et al. 2016). The alternation of mudstones and sandstones is interpreted as repeated expansion and contraction cycles of the ancient paleolake (Figari et al. 2015), whereas the abundance of spinicaudatans in contrast to the absence of fish or any other vertebrates suggests stressing conditions (Gallego et al 2011).

Based on a combination of high-precision radioisotopic dating with litho- and biostratigraphic evidence, it is estimated that the deposition of the Cañadón Asfalto Formation occurred during the Toarcian (late Early Jurassic, ca. 179–177 Ma; Cúneo et al. 2013). Both Pomelo and A12 are located at the base of the Cañadón Asfalto Formation, being of probable Toarcian age (Cúneo et al. 2013). Pomelo can be subdivided in two distinct assemblages based on lithology and fossil remain content, that is, Pomelo A is dominated by *Brachyphyllum*-type conifer remains preserved in light-colored shales, whereas Pomelo B is dominated by pteridosperm fronds and spinicaudatan remains that occur in thicker, dark-colored shales.

Preparation and Illustration of Fossils

The fossils were studied with a Nikon SMZ1000 stereoscopic microscope and a Nikon Eclipse 80i fluorescence microscope. Fluorescence microscopy proved particularly useful for nondestructive in situ analysis of partially fragmented plants that would disintegrate during chemical treatment. The A12 plants wwere further prepared with air scribes to remove attached sediment particles. In addition, 25 selected specimens from Pomelo were either manually or chemically extracted from the rock matrix and treated via standard protocols for chemical preparation of cuticles for transmitted light microscopy using hydrofluoric acid (Kerp 1990); certain cuticles were subsequently treated with Schulze's reagent using successively increasing concentrations of nitric acid (starting with 20%) and a few crystals of potassium chlorate for several hours to 3 d in order to bleach them and help to separate the lower leaf side from the upper side. Afterward, they were treated with potassium hydroxide for a few minutes. A few cuticle fragments obtained by the aforementioned chemical treatment were analyzed using scanning electron microscopy; they were attached to a regular microscopy slide with double-sided tape and analyzed using a JEOL JSM-6460 without any type of coating at the facilities of Aluar S. A., Puerto Madryn, Chubut, Argentina.

The images were captured with a Nikon DS-Fi3 camera attached to the fluorescence microscope and a Canon Eos 7D digital camera equipped with a Canon EF-S 60-mm macro lens. Postprocessing of the images was performed with Adobe Lightroom 5 and Adobe Photoshop CS6. Panoramic merging of photographs, as well as a focus stacking technique, was performed with Adobe Photoshop CS6 to obtain detailed and well-focused images. The studied specimens are deposited in the collections of the Museo Paleontologico Egidio Feruglio.

Systematic Paleobotany

Order—Peltaspermales

Family—Peltaspermaceae

*Genus—*Lepidopteris *Schimp. 1869 emend. Townrow 1956*

*Type Species—*Lepidopteris stuttgardiensis *(Jaeger) Schimp. 1869*

Lepidopteris scassoi *sp. nov. (Figs. 1–7)*

Diagnosis. Fronds bipinnate to tripinnatifid, lanceolate, with the larger pinnae occurring below the midpoint of the frond. Main rachis bearing 1–3 pairs of intercalary pinnules with entire to undulate margins between adjacent pinnae. Pinnae opposite to subopposite, linear, lanceolate, to narrow triangular, imparipinnate inserted at obtuse to right angles in the basal frond portion and increasingly acute angles toward the frond apex. Pinnules opposite to subopposite, with a decurrent fully attached base and obtuse apex. Pinnules inserted at subacute to acute angles, with entire to deeply dissected margins and basalmost lobes usually inserted to the pinnae rachis. Venation catadromous and pinnate with a prominent midvein; secondary veins opposite to subopposite, emerging at acute angles reaching the margins or lobes; third-rank veins rare, mostly near the margins. Fronds amphistomatic, with stomata more abundant on the lower leaf surface (0.5–0.7 : 1 adaxial/abaxial ratio). Stomata randomly oriented, monocyclic, with a ring of 4–9—usually 7—trapezoidal subsidiary cells bearing strong hollow papillae oriented toward, and partially occluding, the stomatal pit (papillae usually absent on rachides). Guard cells sunken, weakly cutinized. Ordinary epidermal cells straight walled, papillate, and polygonal isodiametric on pinnule lamina to more or less longitudinally elongate above rachis or pinnule midvein. Rachis mostly smooth, without macroscopic scales or lumps but with irregular epidermal pattern. Stomata on main rachis scarce, with subsidiary cells being commonly nonpapillate and not forming a ring.

Derivation of name. The species is dedicated to the Argentinian geologist Roberto Scasso for his continued work on numerous Patagonian localities in general and on the Cañadón Asfalto Basin in particular.

Holotype hic designatus. MPEF-Pb 10378 (fig. 1*A*).

Additional material. MPEF-Pb 3840, 3841, 3847, 3848, 3850, 3851, 3853, 3854, 3858–3861, 3863, 3869, 3870, 3873, 3939, 3941, 3944, 3946–3948, 10200–10297, 10299–10302, 10304–10309, 10311, 10313–10323, 10325–10377, 10379–10405, 10407–10410, 10412–10420, 10422–10427, 10429–10433, 10435–10478.

Type locality, stratigraphy, and age. Pomelo locality in Chubut Province, Patagonia, Argentina. Cañadón Asfalto Formation, Toarcian (Early Jurassic).

Description

Macromorphology. The fronds are lanceolate, up to 190 mm long, with short basal and apical pinnae and long medial ones (figs. 1, 2*A*, 2*B*). The main rachis is smooth to finely striated at low magnifications (fig. 1*A*, 1*B*), up to 3.4 mm wide on largest specimens ($\bar{x} = 2.47$, $n = 15$). Large fronds may be tripinnate at basal regions, bearing pinnules with entire margins (fig. 1), transitioning to a bipinnate arrangement toward the center, with deeply dissected pinnules resulting in up to nine lobes. Toward the apex of those fronds, the pinnules have entire to slightly undulating margins (fig. 1*A*, 1*B*). Average to small fronds are typically bipinnate, with basal and medial pinnules having undulate to lobed margins, whereas apical pinnules have mostly straight margins (figs. 1*A*, 1*B*, 2*C*, 2*D*).

One to three subopposite pairs of intercalary pinnules with entire to undulating margins are directly inserted into the main rachis between two adjacent pinnae (fig. 2*E*–2*H*). Fronds have up to 20 pairs of opposite to subopposite pinnae with an imparipinnate arrangement (figs. 1*A*, 1*B*, 3*A*, 3*B*). The pinnae are long, lanceolate, straight, and up to 60 mm × 22 mm ($\bar{x} = 34 \times 14$, $n = 22$; fig. 1)—the large ones being slightly curved toward the base of the frond (fig. 3*A*). Attachment angles decrease from up to >90° at the base of the frond (fig. 2*A*, 2*B*) to about 60° in the center of the frond to about 45° near the apex (figs. 1*A*, 1*B*, 3*A*, 3*C*). Pinnae bases are decurrent to confluent, in which case the main rachis appears to bear a narrow laminar wing (fig. 3*B*).

The pinnules have an opposite to subopposite arrangement (figs. 1, 3*B*), emerge at angles of 45°–75°, and measure up to 13 mm × 4.6 mm, with average pinnules being 8 mm × 3.2 mm; they are typically 2–2.5 times longer than wide. Pinnule apexes are obtuse to subacute and bases noncontracted to slightly expanded (fig. 3*B*, 3*C*); margins are straight to deeply lobed (fig. 3*D*–3*F*). Basiscopic lobes are commonly larger than acroscopic ones, with the second or third one usually being the longest (figs. 3*B*, 3*C*, 4*A*, 4*B*), giving the lobed pinnules a narrow-lanceolate outline. Pinnules are strongly decurrent, with their first lobe usually partially inserted into the pinnae rachis (figs. 3*E*, 3*F*, 4*A*, 4*B*).

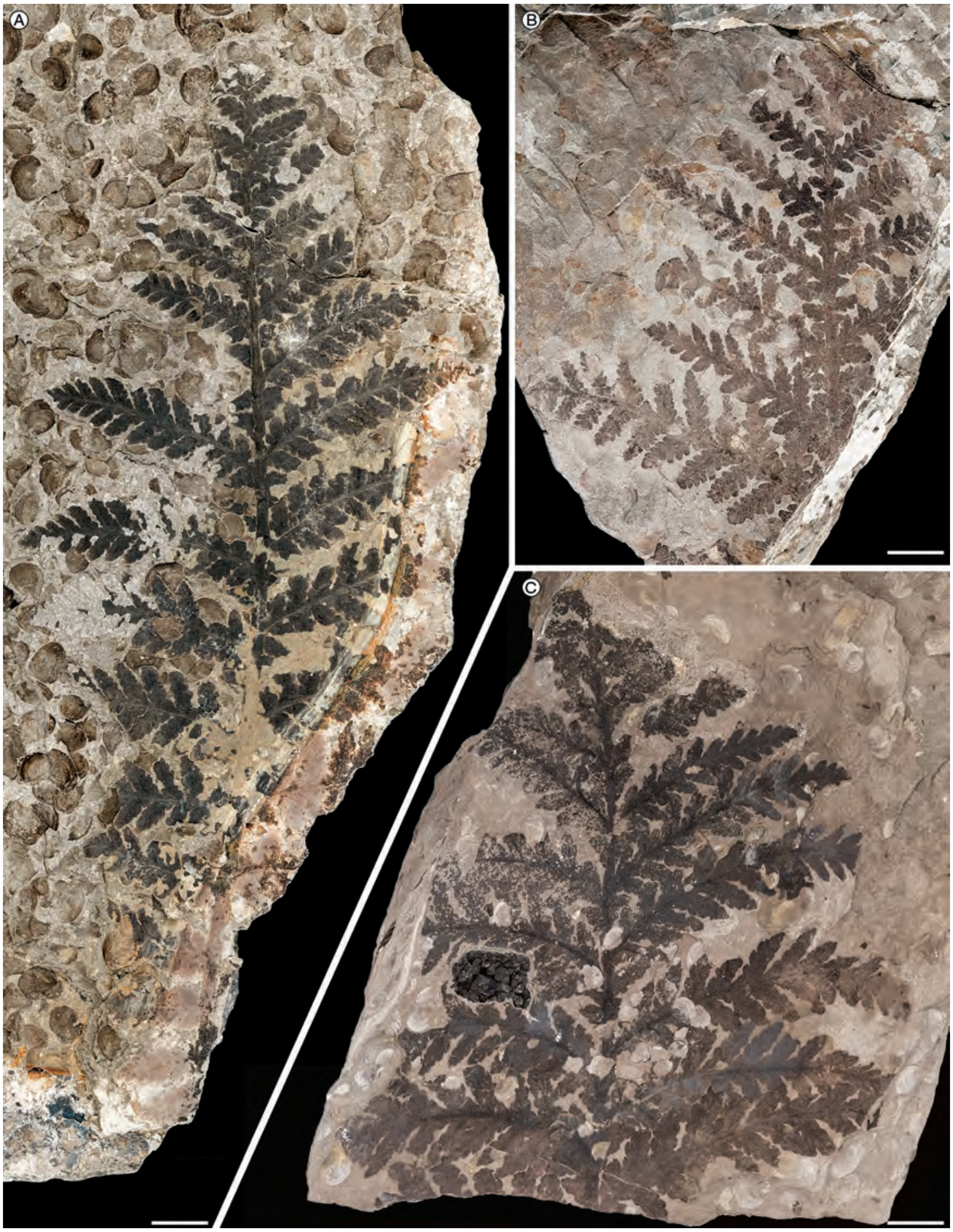

Fig. 1 *Lepidopteris scassoi* sp. nov. from the Early Jurassic Cañadón Asfalto Formation of Chubut Province, Argentina; general aspect of the frond. *A*, Nearly complete frond of moderate size; note the smooth main rachis and bipinnate to tripinnatifid architecture (MPEF-Pb 10378a, holotype). *B*, Fragmentary frond with an almost tripinnate architecture; note the deep lobes of the pinnules of the lowermost pinnae (MPEF-Pb 3940a). *C*, Large fragmentary frond with a bipinnate architecture and lobed pinnules (MPEF-Pb 3844a). Scale bars: 10 mm.

Veins are inconspicuous and do not project notably from the leaf surface. The venation is catadromous and pinnate with at least three ranks (fig. 4). First-rank veins (pinnule midveins) depart from the subtending pinna rachis at a steep angle of ca. 15°–30° and immediately curve away from the midrib to run straight toward the pinnule apex at an angle of about 55°–70° (fig. 4*A*, 4*B*). Second-rank veins emerge at ca. 20°–30°, curve away from the pinnule midvein, and

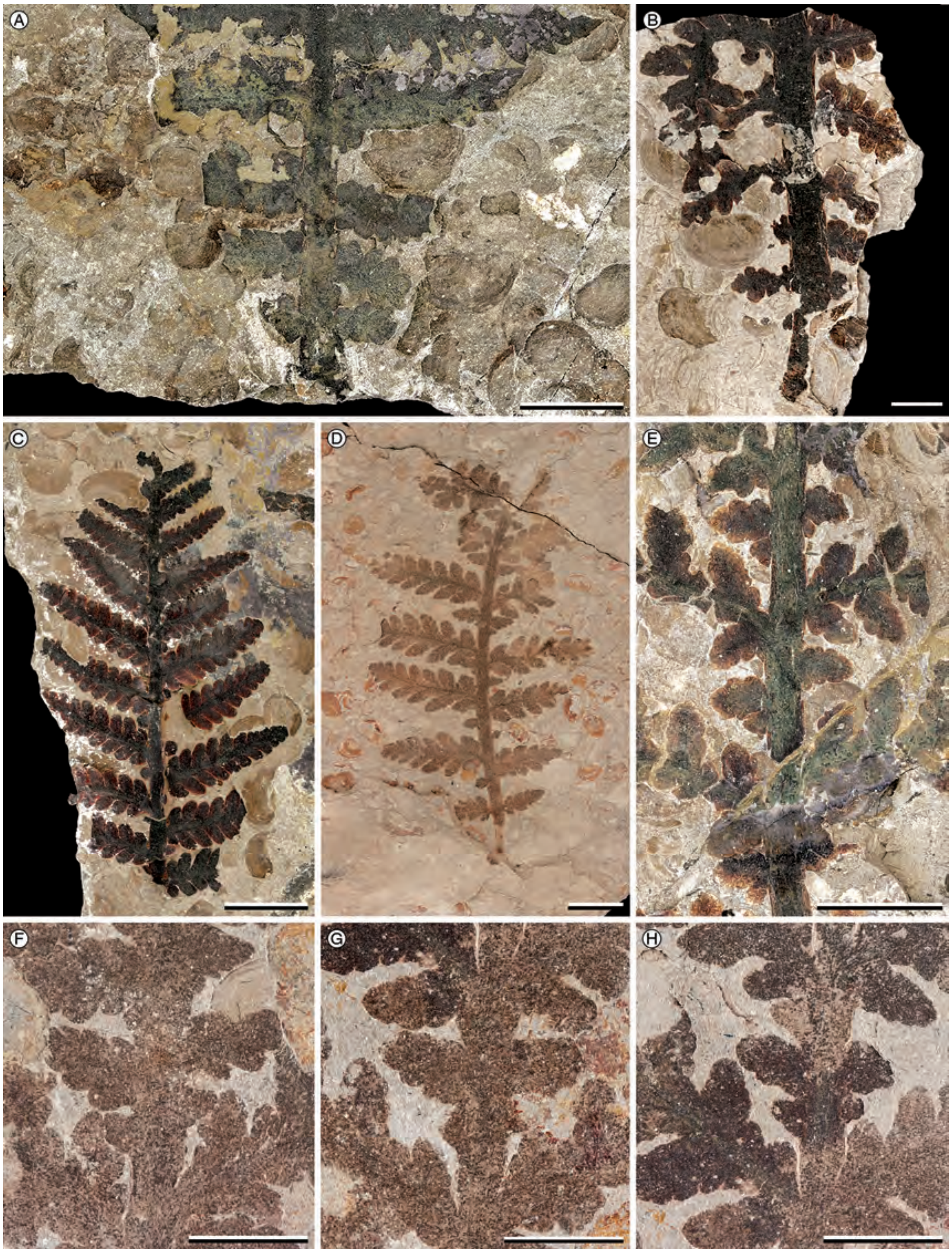

Fig. 2 *Lepidopteris scassoi* sp. nov. from the Early Jurassic Cañadón Asfalto Formation of Chubut Province, Argentina; basal and apical frond features and details of intercalary pinnules. *A*, *B*, Basal region of two fronds featuring small pinnae emerging at slightly obtuse to right angles (MPEF-Pb 3852a and 10428a). *C*, Small undeveloped frond with bipinnate architecture and pinnules with entire margins; note the acute emergence angle of the pinnae (MPEF-Pb 10310). *D*, Fragment of a frond with increasingly larger pinnae bearing pinnules with slightly undulate margins (MPEF-Pb 3945a). *E*, Detail of the central region of a frond showing longitudinally striated rachis and intercalary pinnules with lobed margins (MPEF-Pb 10411). *F–H*, Details from bottom to top of the frond showing the transition from deeply lobed to slightly undulated margins of the intercalary pinnules (MPEF-Pb 3940a). Scale bars: *A*, *C–E* = 10 mm; *B*, *F–H* = 5 mm.

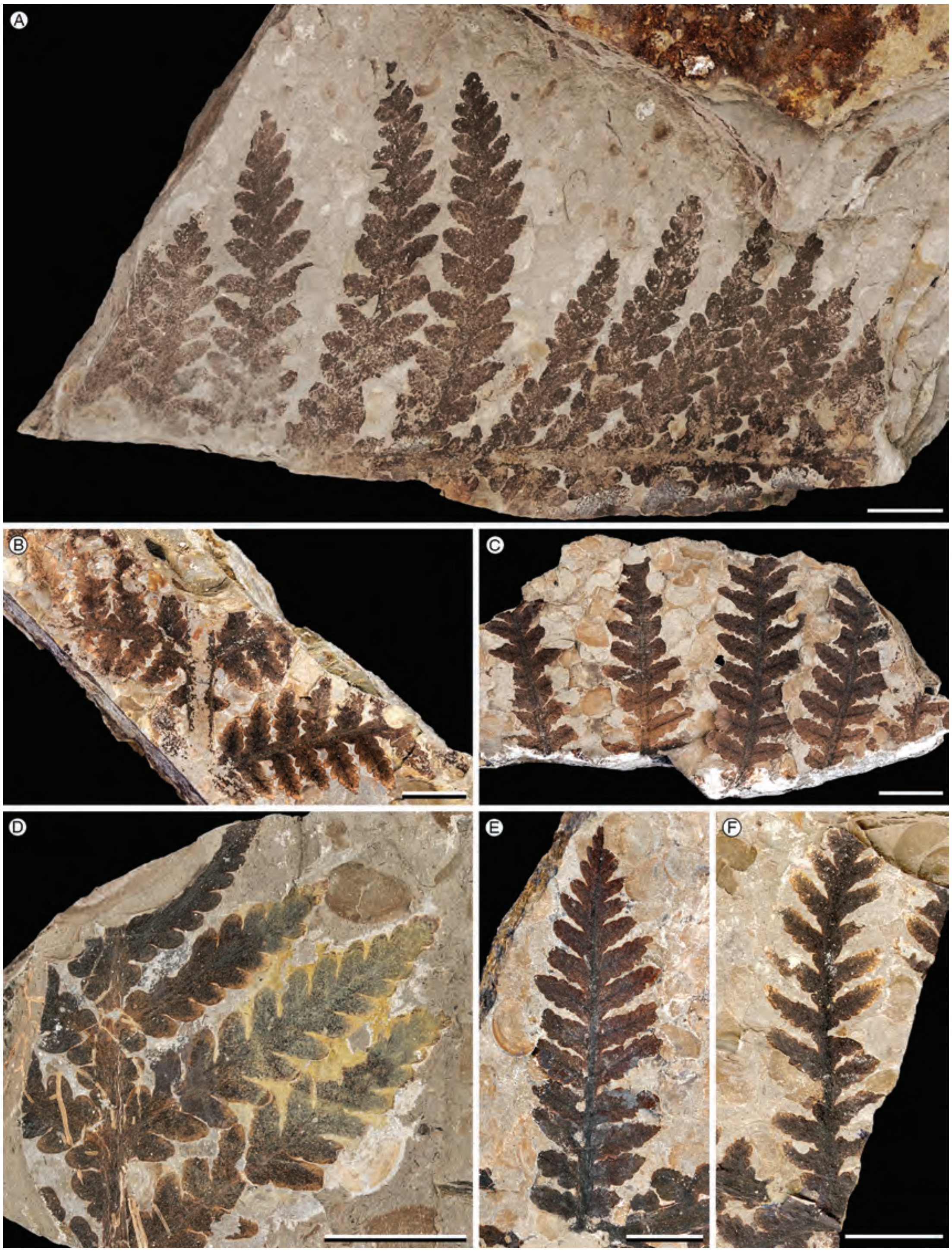

Fig. 3 *Lepidopteris scassoi* sp. nov. from the Early Jurassic Cañadón Asfalto Formation of Chubut Province, Argentina; details of pinnae and pinnules. *A*, Large frond; note the varying orientations and emergence angles of pinnae (MPEF-Pb 3852a). *B*, Fragmentary frond illustrating subopposite arrangement of pinnae (MPEF-Pb 10303a). *C*, Fragmentary pinnae; note the obtuse to subacute apex, broad base, and lobed margin of the pinnules (MPEF-Pb 10324). *D*, Fragmentary frond; note the imparipinnate pinnae and the entire to undulate margin of the pinnules (MPEF-Pb 10406a). *E*, *F*, Isolated pinnae; note the decurrent pinnule bases and the first lobe inserted directly on the pinnae rachis (MPEF-Pb 10421 and 10298). Scale bars: 10 mm.

run straight toward the pinnule margins or lobes at 37°–45° angles (fig. 4*C*, 4*D*). Third-rank veins are scarce and faint; most of them emerge in close succession near the apex of the lobes or the pinnule margin (fig. 4). Petiole, frond rachis, and pinna rachides are typically smooth, without lumps or scales, but occasionally bear longitudinal folds on the main rachis.

Micromorphology. The cuticle is brittle and usually detaches from the rock easily with the aid of dissecting needles (figs. 4–6). The adaxial cuticle is thicker and usually better preserved than the abaxial one, which is often partially degraded (fig. 5*A*–5*C*), being better preserved at the margins of pinnules (fig. 5*B*). Ordinary epidermal cells of pinnules are approximately polygonal and isodiametric, up to 45 μm large, with abaxial cells slightly smaller than those from the adaxial side (fig. 5*D*, 5*E*). The cells of both surfaces normally bear a central solid papilla up to 8 μm in diameter (fig. 5*D*, 5*E*) and have straight anticlinal walls with irregular thickenings (fig. 5*F*, 5*G*).

Epidermis cells of the rachides are longitudinally elongated, with cells in proximal rachis portions being less elongate and without papillae and those in more distant rachis portions longer (up to 90 μm × 30 μm) and bearing a small central papilla (fig. 6*A*–6*C*). Cells above first- and second-rank veins are arranged in rows up to 16 cells wide on the former and seven cells wide on the latter, measuring up to 75 μm × 25 μm, and usually bearing a small central papilla (fig. 6*D*). The veins decrease their width from proximal to distal regions and have their major axes longitudinally elongated. Trichome bases are absent, but holes, cell overgrowths, and disruptions are typical of the adaxial epidermis of both rachides and pinnules (fig. 6*E*–6*G*) and occur less frequently on abaxial surfaces. These features may derive from small subepidermal swellings, which are typical for other species of the genus and give them a scaly or blistered appearance.

Randomly oriented stomata occur on both surfaces (fig. 5*A*, 5*B*), with an adaxial/abaxial ratio of 0.5–0.7 : 1, and with average-sized individual pinnules bearing up to ca. 2400 stomata. On the abaxial side, stomata occur on both costal and intercostal areas, with a stomatal density of ca. 65 mm^2 (figs. 5*B*, 6*C*), whereas on the adaxial side they are more numerous over intercostal areas, with a density of ca. 40 mm^2 (fig. 6*D*–6*F*). The stomatal apparatus is monocyclic and has 4–9 ($\bar{x} = 7$) trapezoidal subsidiary cells (fig. 7) that are usually smaller than ordinary epidermal cells; stomatal pits of the abaxial surface are slightly smaller than those of the adaxial surface. Subsidiary cells normally have a strongly cutinized papilla oriented toward the stomatal pit (fig. 7*A*–7*D*), with proximal anticlinal walls strongly thickened, whereas the radial anticlinal walls are moderately thickened (fig. 7*E*–7*H*). The size of the papillae from the pinnules ranges from very large and almost completely occluding the stomatal pit (fig. 7*D*, 7*M*–7*O*) to nearly nonexistent (fig. 7*I*, 7*J*), with individual pinnae usually showing both extremes of development; individual papillae are 15 μm × 15 μm in average size. The guard cells are reniform, sunken, and partially covered by the subsidiary cells, up to 28 μm × 6 μm (fig. 7*E*–7*H*). They are weakly cutinized and possess a thickened internal ledge and no radial striae. Stomata are rare on the main rachis and differ from those on the remaining frond portions in lacking papillae and in being less isodiametric but rather distorted with uneven subsidiary cell sizes (fig. 7*K*, 7*L*).

Comparisons. Based on the characteristic combination of nonbifurcate, bi- to tripinnatifid frond architecture, presence of characteristic intercalary pinnules, and diagnostic epidermal details (including monocyclic stomata with a ring of strongly papillate subsidiary cells), the new plants can readily be assignable to the genus *Lepidopteris* (table 1). Several fragmentary structures with a circular outline, scalloped margins, and radial spokes (fig. 8*A*) that we consider relevant to the generic and familial assignation of Pomelo leaves were found associated with *L. scassoi*. Albeit fragmentary and isolated, these structures resemble the seed-bearing peltate disks that characterize *Peltaspermum*, the ovulate organ of peltasperms from the *Lepidopteris* lineage. These structures feature stomata with a ring of 6–8 trapezoid subsidiary cells lacking prominent papillae (fig. 8*B*, 8*C*), shared features with the stomata *Peltaspermum* (Harris 1932; Townrow 1960). We were not able to further prepare the cuticles because of their poor preservation; the numerous cracks on its surface suggest that if chemically treated, the structure will likely disperse in numerous small fragments almost impossible to reconstruct. It should be noted that these structures also resemble isolated microsporophylls of the polliniferous organ *Pteroma* (Harris 1964).

Most *Lepidopteris* species show broad morphological variability, with the extreme morphologies of certain species intergrading with those of others (table 2; Townrow 1960, 1966). Additionally, even individual fronds may show a high degree of variability, particularly in their micromorphological features. As an example, there are regions often lacking well-developed epidermal and subsidiary papillae, whereas others show highly developed papillae almost completely occluding the stomatal pore. In this regard, fossil species based on poorly preserved plants or only few specimens are most likely inadequately characterized and do not accurately encompass their intraspecific variability. We therefore opted to compare *L. scassoi* only with the best characterized *Lepidopteris* species (table 2). Among those species, *L. scassoi* shares most features with *L. stormbergensis* and *L. madagascariensis* from Gondwana and *L. ottonis* from Laurasia (table 2).

Lepidopteris stormbergensis from the Middle and Upper Triassic of Africa, South America, and Australia (Townrow 1960; Gnaedinger and Herbst 1998; Holmes and Anderson 2005) has a similar frond architecture and pinnule morphologies. Compared with other *Lepidopteris* species, *L. stormbergensis* has rather few lumps and blisters, with certain individuals having none at all, as in most fronds of *L. scassoi*. *Lepidopteris stormbergensis* differs mainly from *L. scassoi* in being overall considerably larger, in typically bearing more or less well-developed blisters on the rachis, and in having an even density of stomata on both surfaces.

Another species remarkably similar to *Lepidopteris scassoi* is *L. ottonis* from the Late Triassic of the Northern Hemisphere (Antevs 1914; Harris 1932; Lundblad 1950; Barbacka 1991). It is the youngest species of the genus prior to this record and is used as a Rhaetian marker in several localities (e.g., Scoresby Sound, Axel Heiberg Island, Tatra Mountains; Harris 1937; Vavrek et al. 2007; Pacyna 2014). Features that differ between *L. scassoi* and *L. ottonis* include the invariable presence of numerous large lumps on the rachis of the latter, the number of subsidiary cells of the stomatal apparatuses,

Fig. 4 *Lepidopteris scassoi* sp. nov. from the Early Jurassic Cañadón Asfalto Formatino of Chubut Province, Argentina; detached cuticles under transmitted light. *A*, Large fragment of a pinna showing the venation pattern; note the small vascularized lobes in between pinnules (MPEF-Pb 10467). *B*, Pinna fragment with four lobed pinnules; note acute emergence angle and gradual tapering of the pinnule midrib (MPEF-Pb 10468). *C*, Small basal fragment of a pinna with a reduced basal pinnule; note second-order veins terminating before pinna margin (MPEF-Pb 10461). *D*, Detail of a pinnule from *A*; note the repeated dichotomies of second-order veins in the lobe apexes (MPEF-Pb 10467). Scale bars: *A*–*C* = 2 mm; *D* = 1 mm.

and the overall dimensions of the fronds and pinnules (table 2). *Lepidopteris ottonis*, as *L. scassoi*, has more stomata on its lower surface, but the stomatal ratio of the European species appears to be quite larger than 1 : 2 (Antevs 1914).

Lepidopteris madagascariensis Carpentier is an Early Triassic species originally described as being from Africa (Townrow 1966), which was later also found in South America and Australia (Baldoni 1972; Retallack 1983; Holmes and Anderson 2005). This species also superficially resembles *L. scassoi* (table 2), but it has a bipinnate architecture with pinnules having entire to slightly undulate margins, in addition to a very lumpy main rachis. It also differs from *L. scassoi* by having a similar number of stomata on both surfaces and by having fewer subsidiary cells on the stomatal apparatuses (table 2).

Discussion

Considerations on Ecology and Life History

The presence of epidermal features such as a thick cuticle, amphistomacy, papillate epidermal cells, sunken guard cells, and/or papillate subsidiary cells seems to be correlated with specific climatic and environmental parameters endured by extant plants (Parkhurst 1978; Mott et al. 1982; Mott and Michaelson 1991; Fahmy 1997; Weyers and Lawsom 1997). Accordingly, presence or absence of those traits on fossil leaves have been widely used in the characterization of ancient climates and environments (Hill 1998; Axsmith and Jacobs 2005; Haworth and McElwain 2008). However, according to more recent studies, the presence or absence of some of those features may not show strong or even significant correlations with the climatic and environmental parameters that were initially associated with them (Jordan et al. 2008; McElwain and Steinthorsdottir 2017 and references therein). For example, a widely used epidermal feature to interpret ancient dry environments, such as the presence of sunken stomatal pits partially occluded by the papillae of subsidiary cells (as those of *Lepidopteris*), can be beneficial in both dry and wet climates (Haworth and McElwain 2008; Jordan et al. 2008).

Lepidopteris scassoi and all other species of the genus have amphistomatic leaves (table 2), suggestive of open vegetation or high light intensity environments (Mott et al. 1982; Jordan et al. 2014; Bucher et al. 2017). However, this feature may be more strongly related to life history, since a coarse study based on plants of 94 angiosperm families suggests that amphistomatic plants with a stomatal ratio between 0.5 and 1 are more common on annual, biennial, and perennial herbaceous and small shrubby plants with high growth rates, rather than large shrubs or trees (Muir 2015).

Taking into account that (1) *Lepidopteris* species typically have a leaf stomatal ratio between 0.5 and 1 (except *L. langlohensis*; table 2), which may suggest an herbaceous habit and high light environments; (2) any evidence for large woody stems associated with *Lepidopteris* is lacking, suggesting that perhaps they were small shrubby or herbaceous plants; (3) all *Lepidopteris* species lack protruding veins and seem to have rather fleshy fronds covered by a thick cuticle, being adapted to cope with desiccation periods; (4) *Lepidopteris* fronds seem to have an abscission surface at the base of the main rachis (Townrow 1960), suggestive of a life strategy involving periodic shedding of leaves, common on long-lived plants; and (5) *Lepidopteris* leaves are common elements in fluviolacustrine deposits (Harris 1932; Townrow 1960; Retallack 1977; Retallack and Dilcher 1988; Anderson and Anderson 1989; this study), we consider that there is a reasonable possibility that *Lepidopteris-Peltaspermum-Antevsia* plants were fast-growing perennial herbs or small shrubs with limited wood development that lived in waterside environments and were adapted to fluctuating water tables. A partially similar hypothesis was previously advanced by Retallack and Dilcher (1988). We slightly favor a small shrubby habit compared with an herbaceous one due to the extreme rarity of gymnospermous herbs (but see Grauvogel-Stamm 1978; Rothwell et al. 2000).

We are aware of the limitations of this hypothesis and therefore suggest it should be taken with caution, especially since the studies that correlate stomatal features with life history and environments are largely based on angiospermous plants (Parkhurst 1978; Mott 1982; Jordan et al. 2008, 2014; Muir 2015; Bucher et al. 2017). Additional evidence, such as that provided by the study of the other species present in fossil assemblages where *Lepidopteris* occur, information concerning local taphonomic conditions, anatomical details of the mesophyll of *Lepidopteris*, and a better understanding of its phylogenetical history and relationships, will be of great aid in order to test hypotheses concerning these autopaleoecological aspects.

Relationships between Peltasperms and Umkomasiaceans (Corystosperms)

The line dividing Mesozoic peltasperms from umkomasiaceans seems to be thinner than originally thought (Thomas 1933), since most phylogenetic analyses including species from both groups recover very close and sometimes unresolved relationships between them (Doyle 2006, 2008; Hilton and Bateman 2006; Rothwell and Stockey 2016; Coiro et al 2018). Each group has at least one Mesozoic-typical association of plant organs that most likely represent a natural whole plant (i.e., *Dicroidium-Pteruchus-Umkomasia* for the umkomasiaceans and *Lepidopteris-Antevsia-Peltaspermum* for peltasperms), and, in addition to numerous isolated genera, they also have other less characteristic plant-organ associations (e.g., *Pachypteris-Pteroma*, *Komlopteris-Sacculotheca*, *Dejerseya-Townrovia-Matatiella*; Harris 1964; Bomfleur et al. 2011; Barbacka and Boka 2014). However, some of those less characteristic associations, and some isolated leaf genera, are arguably insufficiently known, and their proposed affinities with either umkomasiaceans or peltasperms are contentious, as illustrated below.

Pachydermophyllum is a genus established to accommodate plants from the Jurassic of Yorkshire, United Kingdom, which were initially described as *Thinnfeldia* (Thomas 1913, 1915) but later found to have several differences with that genus (Thomas and Bose 1955). *Pachydermophyllum* leaves are coriaceous and simple pinnate; their pinnae are lanceolate and bear a midrib out of which simple or forked secondary veins emerge. The leaves are weakly amphistomatic, and their stomatal apparatuses are composed by sunken guard cells surrounded by a ring of subsidiaries bearing papillae overarching

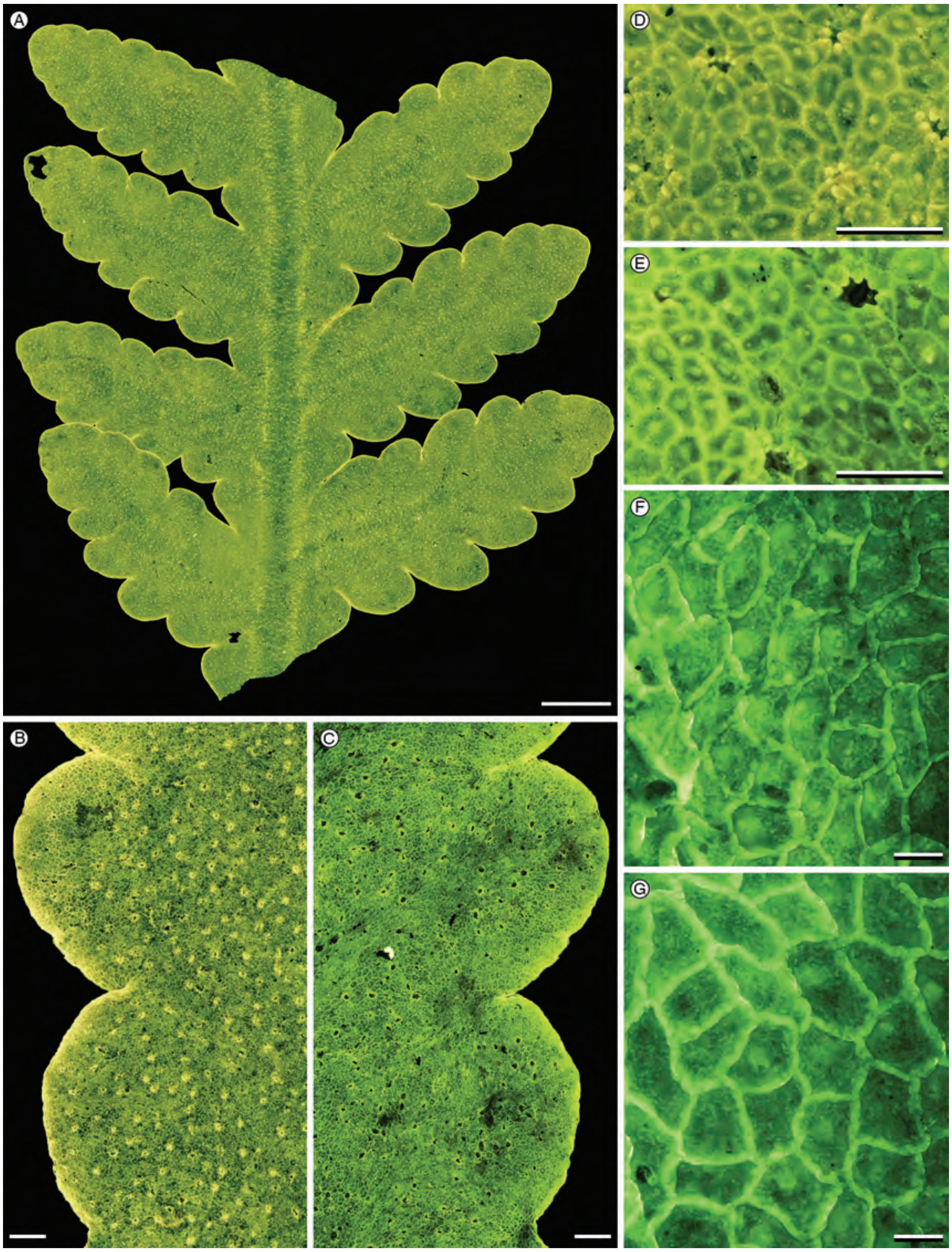

Fig. 5 *Lepidopteris scassoi* sp. nov. from the Early Jurassic Cañadón Asfalto Formation of Chubut Province, Argentina; cuticles under epifluorescence microscopy. *A*, External view of lower cuticle; note the numerous stomata on the pinna rachis and the differentiation into costal and intercostal regions (MPEF-Pb 10467). *B*, External view of lower cuticle of a pinnule; note the better preservation of the cells near the margins and the distribution of stomata over most of the surface (MPEF-Pb 10469). *C*, External view of the upper cuticle (on the other side of *B*); note the good preservation and the few stomata occurring above second-order veins (MPEF-Pb 10469). *D*, External view of the lower cuticle of an intercostal region; note the polygonal outline of ordinary cells and the solid central papillae (MPEF-Pb 10469). *E*, External view of the upper cuticle on an intercostal region; note papillae and slightly larger cell size compared to *D* (MPEF-Pb 10469). *F*, Internal view of the lower cuticle of an intercostal region; note the shape of the cells and the anticlinal walls (MPEF-Pb 10464). *G*, Internal view of the adaxial surface of an intercostal region; note the irregular thickenings of the anticlinal walls (MPEF-Pb 10464). Scale bars: *A* = 2 mm; *B*–*C* = 200 μm; *D*–*G* = 100 μm.

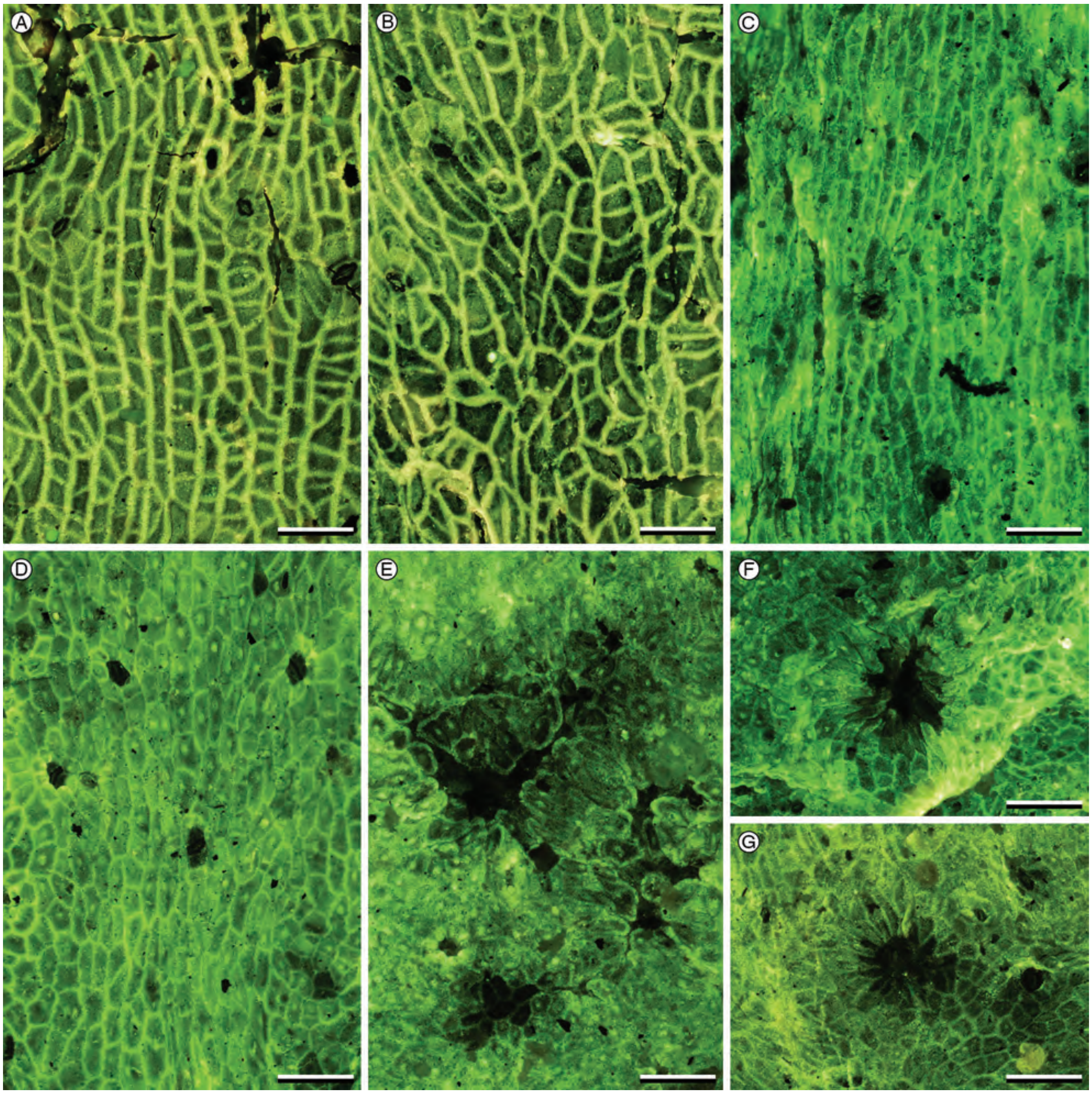

Fig. 6 *Lepidopteris scassoi* sp. nov. from the Early Jurassic Cañadón Asfalto Formation of Chubut Province, Argentina; cuticular details of main rachis, pinnule midvein, and possible subepidermal swellings under epifluorescence microscopy. *A–C*, Cellular pattern of main rachis at basal, medial, and apical regions, respectively; note the columns of cells with straight lateral walls and the papillae at apical regions (MPEF-Pb 10378a). *D*, Midvein region of a pinnule; note the longitudinally elongated cells (MPEF-Pb 10469). *E–G*, Cellular irregularities and disruptions of normal epidermal pattern and possible subepidermal swellings; note the radial arrangement of cells at *F* and *G* (MPEF-Pb 10428a, 10378a, and 10428a). Scale bars: 100 μm.

the stomatal pit. Harris (1964) transferred the Yorkshire leaves to *Pachypteris*, stating that most of the generic features separating *Pachydermophyllum* from *Pachypteris* (e.g., *Pachypteris* is bipinnate, mostly hypostomatic, and with flat subsidiary cells, whereas *Pachydermophyllum* is simple pinnate, weakly amphistomatic, and with subsidiary cells often bearing papillae oriented toward the stomatal pit; Harris 1964, 1983) were not consistent enough to merit a new genus. However, most authors have followed Thomas and Bose, and nowadays *Pachydermophyllum* has several species with a moderate presence in the Southern Hemisphere and few occurrences in the Northern Hemisphere (Retallack 1977, 1981). As noted in "Systematic Paleobotany," certain macromorphological features, but especially the aforementioned epidermal features of *Pachydermophyllum*

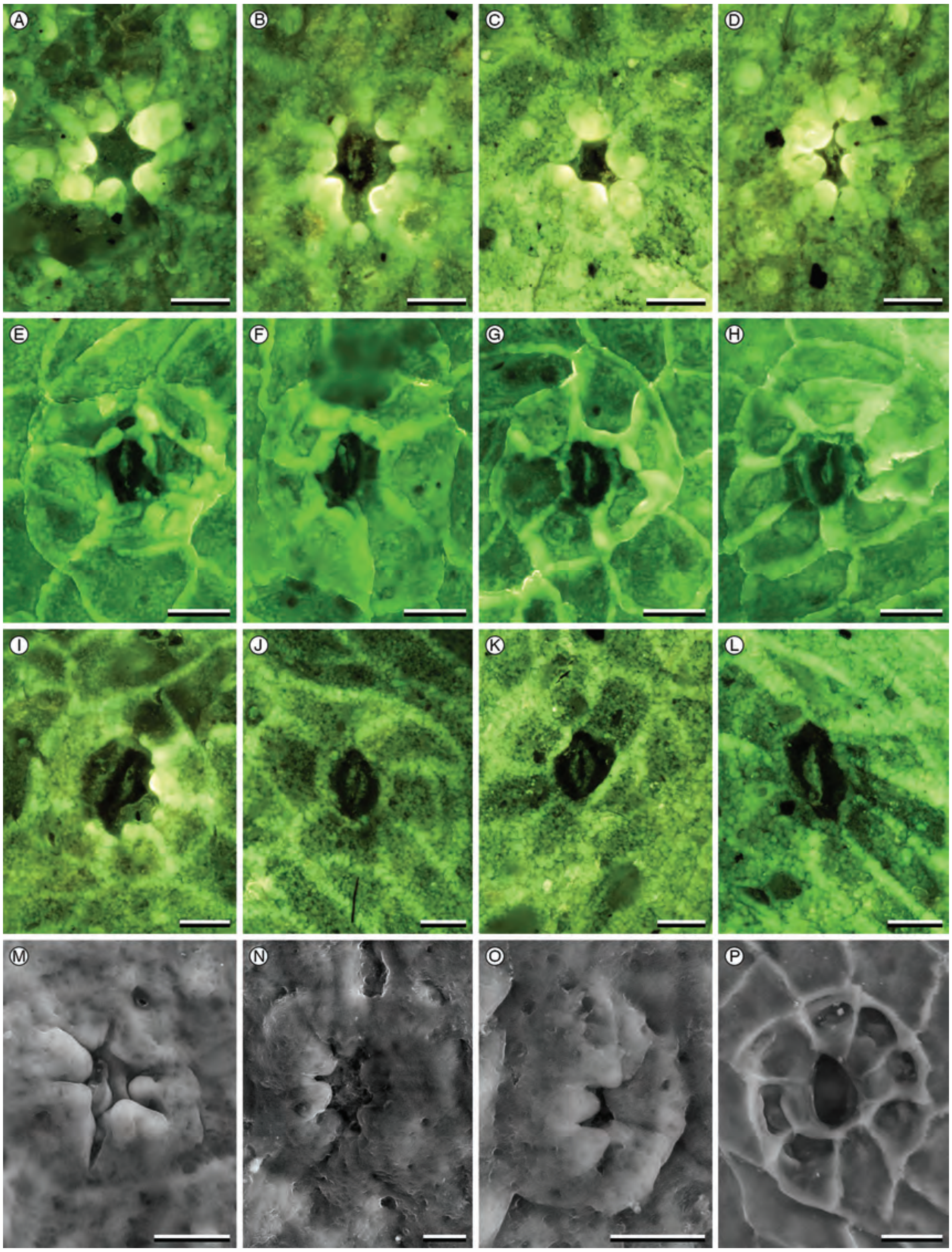

Fig. 7 *Lepidopteris scassoi* sp. nov. from the Early Jurassic Cañadón Asfalto Formation of Chubut Province, Argentina; details of stomatal complexes under epifluorescence microscopy and scanning electron microscopy. *A*, *B*, External view of the upper cuticle; note the papillae oriented toward the stomatal pit and the sunken guard cells in *B* (MPEF-Pb 10226 and 10471). *C*, *D*, External view of the lower cuticle; note the prominent papillae almost completely occluding the stomatal pit (MPEF-Pb 10428b and 10471). *E*, *F*, Internal view of the upper cuticle; note the cuticle lining of the reniform guard cells and the trapezoid subsidiary cells (MPEF-Pb 10464). *G*, *H*, Internal view of the lower cuticle; note the thickenings of the anticlinal and radial walls of the subsidiary cells (MPEF-Pb 10464). *I*, External view of a stomatal complex occurring within the pinnule lamina; note weakly developed papillae of the subsidiary cells (MPEF-Pb 10224). *J*, External view of a stomatal complex occurring within the pinnule lamina; note the lack of papillae of the subsidiary cells (MPEF-Pb 10227). *K*, External view of a stomatal complex on the rachis; note the absence of papillae and the ring-like organization of the subsidiary cells (MPEF-Pb 10428a). *L*, External view of a stomatal complex occurring on the rachis; note the absence of papillae and the irregular shape of subsidiary cells (MPEF-Pb 10378a). *M*, *N*, External view of stomatal complexes of the upper cuticle; note the guard cells on *M* and the development of the papillae of subsidiary cells (MPEF-Pb 10464 and 10455). *O*, External view of stomatal complex of the lower cuticle; note how the papillae almost close the stomatal pit (MPEF-Pb 10465). *P*, Internal view of stomatal complex; note the trapezoid shape and apparently hollow structure of the subsidiary cells (MPEF-Pb 10464). Scale bars: 20 μm.

papillosa (and other species of the genus), are particularly similar to those of *Lepidopteris* (table 1), perhaps suggesting a peltaspermalean affinity for *Pachydermophyllum*.

Pachydermophyllum papillosa from Yorkshire was associated with the polliniferous organ *Pteroma thomasii* Harris from the same locality (Harris 1964). *Pteroma* is characterized by having oval fertile heads attached to a main axis via slender stalks, and each fertile head possesses numerous embedded pollen sacs bearing bisaccate pollen grains (Harris 1964). The arrangement of *Pteroma* stalks was originally described as pinnate (Harris 1964), but they were afterward interpreted as helical (Frohlich 2002). Harris (1964) considered that the most likely affiliation for *Pteroma* was with umkomasiaceans due to the overall macromorphological resemblance with *Pteruchus* and because the in situ pollen found inside *Pteroma* pollen sacs resembled those of *Pteruchus* (Harris 1964).

The hypothesis of *P. papillosa* and *Pteroma thomasii* being parts of the same whole plant has moderate support, since the two organs were found on the same layers of a single locality and share some micromorphological features such as straight-walled cells with unsculptured surfaces and strong papillae (Harris 1964); however, as is the case for most Mesozoic seed ferns, they have not been found in organic connection. If both organs indeed represent parts of the same natural plant, then each of them suggests a different affinity for the plant as a whole—*Pachydermophyllum* with peltasperms because of the aforementioned aspects and because umkomasiacean leaves (i.e., *Dicroidium*) differ on several macro- and micromorphological features (e.g., frond morphology, venation, stomatal configuration) and *Pteroma* with umkomasiaceans. However, the relationship of the *Pachydermophyllum-Pteroma* plant with a group other than umkomasiaceans has not been really discussed.

Another supposed umkomasiacean, *Thinnfeldia* Ettingshausen, a probable synonym of *Pachypteris* (Doludenko 1974), is a common element of the European Lias, sharing several features with *Pachydermophyllum* and *Pachypteris*; it was found associated with reproductive organs described as *Pteruchus* and *Umkomasia* (Kirchner and Müller 1992), thus being affiliated with umkomasiaceans. However, due to the still uncertain affinities of *Pachypteris* and *Pachydermophyllum* with umkomasiaceans, and criticisms regarding the nature of the fossils described as *Pteruchus* and *Umkomasia* (Anderson and Anderson 2003), the latter being recently placed in the new genus *Kirchmuellia*, the affinity of *Thinnfeldia* with umkomasiaceans is also contentious. *Pachypteris*-type foliage was also associated with the ovuliferous structure *Baruligyna disticha* from the Callovian of Georgia (Krassilov and Doludenko 2004). *Baruligyna* does not resemble any umkomasiacean nor peltaspermalean ovuliferous organ and was affiliated with Cycadales instead (Krassilov and Doludenko 2004), thus suggesting that *Pachypteris*-type foliage was shared between various not closely related plant lineages.

Another superficially similar genus, *Komlopteris* Barbacka, was also initially allied with umkomasiaceans because of its micromorphological similarities with *Thinnfeldia* and *Pachypteris* (Barbacka 1994). However, due to shared stomatal features and repeated association, *Komlopteris* was later associated with *Sacculotheca* Barbacka et Boka, a complex type of cupulate organ (Barbacka and Boka 2014). Since *Sacculotheca* is hard to reconcile with other cupulate Mesozoic organs, and the affinities of the other leaf genera similar to *Komlopteris* are uncertain, the *Sacculotheca-Komlopteris* plant relationships also remain obscure.

Finally, further complicating the panorama of umkomasiaceans, the affinities of the Lower Cretaceous fossils from Mongolia, originally described by Shi et al. (2016) as *Umkomasia mongolica*, remain contentious (Rothwell and Stockey 2016; Anderson et al. 2019). Recently, Anderson et al. (2019) rejected the placement of the Mongolian fossils in *Umkomasia* and supported their placement in *Doylea*, the only genus of the Doyleales order, as previously suggested by Rothwell and Stockey (2016). But in a contemporaneous article, Shi et al. (2019) described two new species from the same locality, assigned them to *Umkomasia*, and reaffirmed their previous assignment of *U. mongolica*. However, it should be noted that they also associated *U. mongolica* with the leaf *Pseudotorellia palustris* (Shi et al. 2019), which has few similarities with most *Dicroidium*-type leaves and thus does not support an umkomasiacean nature for the Mongolian fossils (see Anderson et al. 2019), at least not with the traditional definition of the group.

Peltapermacean Diversity during the Early Mesozoic

The first records of undisputable peltaspermacean plants related to the Triassic *Lepidopteris* lineage date to the late Permian (i.e., *Lepidopteris callipteroides* and *Germaropteris martinsii*). The lineage steadily diversified during the Early Triassic and had its heyday during the Middle to Late Triassic, especially the Ladinian to Carnian interval, with up to five species (i.e., *L. africana*, *L. madagascariensis*, *L. stormbergensis*, *L. dissitipinnula*, and *L. langlohensis*) recorded from several Gondwana localities, and one species (*L. stuttgardiensis*) from Laurasia (Townrow 1956, 1960, 1965, 1966; Anderson and Anderson 1989; Kustatscher and van Konijnenburg-van Cittert 2013). *Lepidopteris* plants then underwent a gradual decline during the later Triassic, with the latest Triassic record of *L. langlohensis* from Gondwana (Bomfleur and Kerp 2010) and *L. ottonis* from Laurasia (Harris 1932; Barbacka 1991) being the hitherto youngest occurrences. Jurassic occurrences of peltasperms of the *Lepidopteris* lineage were nonexistent previous to this record. In this context, the occurrence of the relictual *L. scassoi* from the late Early Jurassic of Patagonia considerably expands the range of the genus, not only on Gondwana, but on a global scale, and suggests that *Lepidopteris* may be also present on Lower Jurassic rocks elsewhere, if not already in museum collections.

A similar pattern of diversification and decline is also seen in the *Dicroidium* plants (Umkomasiaceae; Anderson and Anderson 1983; Pattemore et al. 2015), with a peak abundance in Gondwana during the Middle and early Late Triassic (see Bomfleur and Kerp 2010), with few occurrences in the Rhaetian (Anderson and Anderson 1983), and at least three reports of possible *Dicroidium* leaves in Lower Jurassic rocks of Antarctica and Patagonia (Rees and Cleal 2004; Bomfleur et al. 2018; Coturel et al. 2018). Both the Early Jurassic Patagonian record of *Lepidopteris* and the putative Early Jurassic records of *Dicroidium* suggest that Patagonia and Antarctica served as refugia for plant lineages that were ubiquitous in Gondwanan Triassic ecosystems.

Table 1

Comparison of *Lepidopteris* Schimper with Various Mesozoic Gymnosperm Leaf Genera

Genus/character	Leaf architecture	Leaf bifurcations absent or present	Intercalary pinnules absent or present	Epidermal papillae absent or present	Distribution and organization of stomata	Papillate subsidiary cells absent or present (no.)	Guard cells sunken or shallow	Stratigraphic occurrence	Main references
Lepidopteris	Pinnate to tripinnatifid	Absent[a]	Present	Present	Amphistomatic to majority on LS monocyclic	Present (4–9)	Sunken	UPm–MJ	Townrow 1960
Dejerseya	Simple to pinnate	Absent	na	Present	Majority on LS monocyclic	Present (4–8)	Sunken	MTr–LT	Bomfleur et al. 2011
Dicroidium	Pinnate to bipinnate	Present	Absent	Absent/present	Amphistomatic to majority on LS noncyclic	Absent/present	Shallow/sunken	UPm–LTr (LJ?)	Anderson and Anderson 1983
Rintoulia	Pinnatisect to pinnate	Absent	na	Absent	Majority on LS monocyclic	Present (4–9)	Sunken	LJ–LK	McLoughlin et al. 2002
Scytophyllum	Pinnate to bipinnatifid	Absent	Absent	Absent	Majority on LS monocyclic	Present (4–10)	Sunken	LTr–UTr	Zamuner and Artabe 1990
Kurtziana	Pinnate	Absent	na	Absent	At least on LS monocyclic	Absent/present (6?)	Sunken	MTr–LJ	Petriella and Arrondo 1982
Komlopteris	Pinnate	Absent	na	Absent	Majority on LS amphicyclic	Absent (5–6)	Shallow	LJ–Eo?	Barbacka 1994
Pachydermophyllum	Pinnate	Absent	na	Present	Majority on LS monocyclic	Present (5–11)	Sunken	LTr–MJ	Harris 1964
Pachypteris	Pinnate to bipinnate	Absent	Absent/present?	Absent	Majority on LS monocyclic	Absent/present (4–7)	Sunken	UTr–LK	Harris 1964
Germaropteris	Bipinnate to tripinnate	Present?	Present	Present/absent	Majority on LS monocyclic	Present (4–8)	Sunken	UP	Kustatscher et al. 2014
Mesodescolea	Bipinnate	Absent	Absent	Absent	LS monocyclic	Absent (5–8)	Shallow	LK	Archangelsky 1963
Mesosingeria	Bipinnate	Absent	Absent	Absent	Majority on LS	Present (5–8)	Sunken	LK	Archangelsky 1963
Ruflorinia	Bipinnate to tripinnate	Absent	Absent	Absent	LS	Present (6–18)	Sunken	LK	Archangelsky 1963
Ticoa	Tripinnate	Absent	Absent	Absent	Majority on LS	Present (8–14)	Sunken	LK	Archangelsky 1963

Note: [a] Except *Lepidopteris callipteroides*; Eo = Eocene; LJ = Lower Jurassic; LK = Lower Cretaceous; LS = lower surface; LTr = Lower Triassic, MJ = Middle Jurassic; MTr = Middle Triassic; na = not applicable; UPm = Upper Permian; UTr = Upper Triassic. Question marks indicate uncertainty. See references.

Table 2

Comparison of *Lepidopteris scassoi* with Selected *Lepidopteris* Species

Lepidopteris species/character	Leaf architecture	Max. length (mm)	Rachis width (mm)	Intercalary pinnules	Pinnule insertion angles	Pinnule dimensions (mm)	Surface with most stomata (U/L)	Subsidiary cells ($\bar{x}$)	Lumps on rachis	Main reference(s)
L. scassoi	Bi-tripinnatifid	190	3–4	1–3	45–75	$\bar{x}$ = 7.9 × 3.15	Lower (>.5<.75)	4–9 (7)	Absent	This study
L. madagascariensis	Bipinnate	280	3–5	2–3	50–70	2.5–6 × 1.25–3	Both (ca. 1)	4–7 (5)	Present	Townrow 1956
L. arctica	Bipnnate	…	…	…	55–65	1.2–1.8 × .6–.9	Lower (>.5<1)	5–6	Present	Karasev 2015
L. dissitipinnula	Bipinnate	110	2–3	1–2	55–60	12 × 1–2	…	…	Absent?	Holmes and Anderson 2005
L. africana	Pinnate-bipinnate	180	4	0?	45/45	…	Both (ca. 1)	4–6	Absent?	Anderson and Anderson 1989
L. ottonis	Bi-tripinnatifid	300	3–5	1–2	…	$\bar{x}$ = 20 × 5	Lower (?)	4–6	Present	Antevs 1914; Harris 1932
L. stuttgardiensis	Bipinnatifid	250	4–6	1–4	60–75	4–20 × 3.5–6	…	?	Present	Schimper 1869
L. stormbergensis	Bi-tripinnatifid	400	5	1–3	60–90	6–25 × 3–6	Both (ca. 1)	3–8 (6)	Absent/present	Townrow 1960
L. langlohensis	Bipinnate	100	1.5–3.5	1	…	$\bar{x}$ = 3 × 2.5	Lower (<.2)	4–8 (5)	Present	Townrow 1965
L. callipteroides	Pinnate-bipinnate	300	…	0?	…	.5–30 × ?	Both (ca. 1)	5–8	Present	Retallack 2002

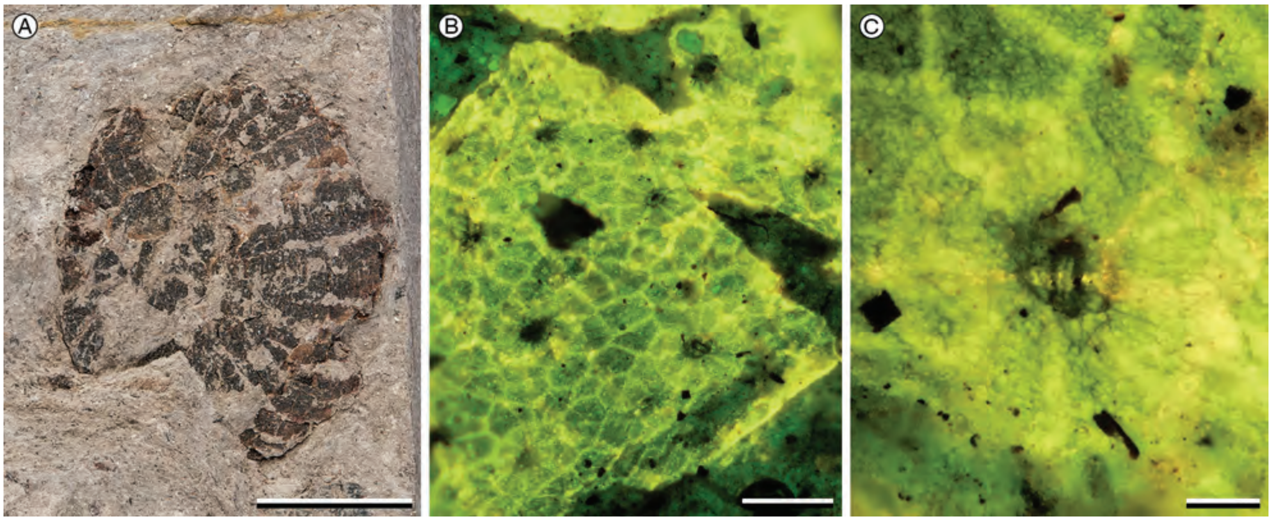

Fig. 8 Structure resembling an isolated *Peltaspermum* sp. disk from the Early Jurassic Cañadón Asfalto Formation of Chubut Province, Argentina (MPEF-Pb 10479). *A*, General aspect of an isolated disk; note the radial spokes. *B*, Cuticular details of *A* under epifluorescence microscopy; note the polygonal shape of the epidermal cells and the randomly distributed and randomly oriented stomata. *C*, Close-up of a stomatal complex; note the ring formed by the seven to eight trapezoid subsidiary cells. Scale bars: $A = 5$ mm; $B = 100$ μm; $C = 20$ μm.

Concluding Remarks and Future Directions

The remains of *Lepidopteris scassoi* sp. nov. from Pomelo considerably extends the range of the genus into the Jurassic, evidencing that at least in Patagonia some peltasperms survived the Triassic-Jurassic extinction. A study of their remains allowed a detailed macro- and micromorphological characterization and comparison with other species of the group, which in turn led us to suggest that at least *L. scassoi*, and probably most species of the genus, were long-lived fast-growing herbaceous/small shrubby plants that thrived in close proximity to water bodies such as riversides, lakes, lagoons or ponds, in some cases with fluctuating water tables.

Due to the superficial fernlike gross morphology of *Lepidopteris*, and to the now realized possibility of its occurrence in Jurassic sediments, special attention should be taken into account when studying new or museum-stored plants of Early Jurassic age, since it would not be a big surprise to find *Lepidopteris*-type foliage among these collections. The occurrence of *L. scassoi* in the Lower Jurassic of Patagonia is yet another example that adds to already numerous ones (see Bomfleur et al. 2018), supporting the hypothesis that land plant communities were less, or at least differentially, affected by the big five mass extinctions compared with both terrestrial and especially marine animal realms (McElwain and Punyasena 2007; Nowak et al. 2019).

Plant fossils have been increasingly used in phylogenetic analyses of various groups in recent years, proving to be of great aid to resolve numerous problems inherent to phylogenetic analyses that rely on living taxa only (see Rothwell et al. 2018 and references therein). However, the affinities of numerous leaf types of Mesozoic pteridosperms (e.g., *Pachidrmophyllum papillosa*, *Komlopteris nordenskioeldii*, certain specimens of *Thinnfeldia rhomboidalis*, among many others; Harris, 1964; Kirchner and Müller 1992; Barbacka and Boka 2014) still remain uncertain despite the finding of their respective reproductive structures. Their phylogenetic placement is a nontrivial one, since various representatives of their lineages have been hypothesized as the most closely related to angiosperms (Frohlich 2002; Doyle 2006; Rothwell and Stockey 2016) and play a significant role in the resolution of the gymnosperm tree of life. Thus, we are currently working to incorporate as many of these pteridosperms as possible, plus other gymnosperms with obscure affinities, into a phylogenetic framework, with the objective of shedding some light on their complex evolutionary history and complicated phylogenetic relationships with other large groups of seed-bearing plants.

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