

RECONSTRUCTION AND PHYLOGENETIC SIGNIFICANCE OF A NEW *EQUISETUM* LINNAEUS SPECIES FROM THE LOWER JURASSIC OF CERRO BAYO (CHUBUT PROVINCE, ARGENTINA)

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Abstract. We describe *Equisetum dimorphum* sp. nov. from the Lower Jurassic of Chubut Province, Patagonia, Argentina. This new species is based on fertile and vegetative remains preserved as impressions of stems, leaves, strobili, transversal sections of the stems showing their anatomy, and terminal pagoda-like structures. The fine-grained sedimentary matrix also preserved detailed impressions of epidermal features. The morphological characters allow a whole-plant reconstruction and assignment to *Equisetum*. *Equisetum dimorphum* sp. nov. shows a mosaic of morphological characters that are commonly present in other Mesozoic forms and representatives of the two extant *Equisetum* subgenera, e.g., sunken stomata and a blunt strobilus apex. Compared to other well-known Mesozoic equisetalean taxa, *Equisetum dimorphum* sp. nov. appears to be most closely related to a group of Jurassic *Equisetum*-like plants including *Equisetum laterale* Phillips and *Equisetites ferganensis* Seward. Additional evidence for the morphological stasis of the fertile and vegetative organs of extant horsetails is supplied with this new material, adding further support to the hypothesis that the extant horsetails are a successful group that has undergone only little morphological changeover time and that has been present, nearly worldwide, since Jurassic times.

Key words. Equisetales. *Equisetum*. Systematic. Jurassic. Patagonia.

Resumen. RECONSTRUCCIÓN E IMPLICANCIAS FILOGENÉTICAS DE UNA NUEVA ESPECIE DE *EQUISETUM* LINNAEUS DEL JURASICO INFERIOR DE CERRO BAYO (PROVINCIA DEL CHUBUT, ARGENTINA). En el presente trabajo se describe *Equisetum dimorphum* sp. nov., una nueva equisetale del Jurásico Inferior de la Provincia del Chubut, Patagonia, Argentina. Esta nueva especie está basada tanto en restos vegetativos como fértiles, preservados como impresiones y moldes de ejes, hojas, estróbilos, secciones transversales de los ejes mostrando su anatomía y estructuras terminales de tipo "pagoda". El grano fino del sedimento ayudó a preservar también impresiones detalladas de caracteres epidérmicos. Los caracteres morfológicos preservados permiten la reconstrucción de la planta y su asignación a *Equisetum*. La relación de *E. dimorphum* sp. nov. con otras equisetales del Mesozoico es discutida. *Equisetum dimorphum* sp. nov. muestra un mosaico de caracteres morfológicos que comúnmente se encuentran presentes en distintos representantes de los dos subgéneros de *Equisetum*, e.g., estomas hundidos y un ápice estrobilar romo. En comparación con otros taxones bien conocidos de equisetales del Mesozoico, *Equisetum dimorphum* sp. nov. parece estar más cercanamente emparentado con un grupo de plantas de tipo *Equisetum* del Jurásico, que incluye a *Equisetum laterale* Phillips y *Equisetites ferganensis* Seward. Se aporta evidencia adicional acerca del estasis morfológico de los órganos fértiles y vegetativos de *Equisetum* actuales, añadiendo de esta manera mayor sustento a la hipótesis que sugiere que *Equisetum* es un género exitoso que no ha cambiado mucho morfológicamente a través del tiempo y que ha tenido una distribución prácticamente global desde el Jurásico.

Palabras clave. Equisetales. *Equisetum*. Sistemática. Jurásico. Patagonia.

EQUISETALEANS are a group of plants with a worldwide distribution since Paleozoic times (see Boureau, 1964). Their origins are traceable to the Late Devonian with the Archaeocalamitaceae (Taylor *et al.*, 2009), showing a major diversification in the Pennsylvanian (Bierhorst, 1971). By the end of the Paleozoic this diversity was dramatically reduced (Behrensmeyer *et al.*, 1992; Stewart and Rothwell, 1993)

and in the Jurassic there were only a reduced number of equisetalean plants, of which only one lineage survived through the Cenozoic up to the present days (Des Marais *et al.*, 2003).

The genus *Equisetum* Linnaeus 1753, which includes 15 species according to the most widely accepted taxonomic treatment (Hauke, 1963, 1978), is the single extant repre-

sentative of the equisetalean clade. *Equisetum* has a nearly worldwide distribution, with Australia, Antarctica, New Zealand and several South Pacific islands being the only regions without natural populations of the genus (Hauke, 1963). Fossil representatives of *Equisetum* have been variously suggested to occur in deposits as old as the Jurassic (Gould, 1968), with some Mesozoic species being practically indistinguishable from their extant counterparts in either anatomy nor morphology (Channing *et al.*, 2011).

Recent phylogenetic analyses of extant species using both molecular and morphological data support the position of *Equisetum* as part of the Moniliformopses clade, a lineage first instituted by Kenrick and Crane (1997) based on the analysis of stelar patterns of fossil species. Within this group, *Equisetum* was suggested as sister group of the marattioid ferns (Pryer *et al.*, 2001, 2004). Subsequent studies placed *Equisetum* as the sister group of the Ophioglossidae+Psilotidae clade (Karol *et al.*, 2010; Grewe *et al.*, 2013; Christenhusz and Chase, 2014), which had been previously suggested on the basis of ultrastructural features of their spores (Grauvogel-Stamm and Lugardon, 2009). On the other hand, phylogenetic analyses also including extinct equisetaleans suggest that the genus *Equisetum* is not contained within the ferns (Rothwell, 1999). Rather, those studies resolve Equisetales as the sister group to zygopterids+cladoxylopsids, a view that is less at odds with traditional phylogenetic reconstructions for the overall pattern of euphyllophyte evolution (Rothwell and Nixon, 2006).

Another question that remains unresolved concerning the origins and evolution of modern *Equisetum* is to which clade of fossil sphenopsids they are most closely related; and, as a consequence, whether the characteristically peltate sporangiophores appeared just once in the evolutionary history of these plants. The traditional view is that the peltate sporangiophores of *Equisetum* are homologous to those of the calamitaleans, and that those are, in turn, homologous to the cruciate sporangiophores of the archaecalamiteans (Good, 1975). An alternative view is that peltate sporangiophores appeared independently, once in the lineage that gave rise to calamitalean plants, and a second time in the lineage that gave rise to modern equisetaleans including *Equisetum* (Cúneo and Escapa, 2006). The latter hypothesis is based on Angaran and Gondwanan

fossils with non-strobilar arrangements of sporangiophores that are virtually identical to those seen in certain teratologies of extant horsetails (Tschudy, 1939; Naugolnykh, 2004).

Living species of *Equisetum* have been traditionally grouped into two subgenera: *Equisetum* and *Hippochaete*. This division is supported by numerous morphological characters, such as: (1) stomatal position and ornamentation, (2) branching pattern, (3) chromosome size, (4) strobilus apex, (5) stem dimorphism, (6) antheridial morphology, (7) lamellae type, (8) endodermis type, (9) cell wall texture of root hairs and (10) free leaf tips persistence (Milde, 1867; Hauke, 1963, 1978; Page, 1972a,b; Duckett, 1979; Emons, 1986). Molecular phylogenetic analyses recovered the monophyly of the *Hippochaete* clade, but not that of the *Equisetum* clade (Des Marais *et al.*, 2003; Guillon, 2004, 2007) due largely to the inconsistent placement of *Equisetum bogotense* Kunth, 1815 in different studies (see Guillon, 2007 and references therein).

The date for the diversification of the *Equisetum* crown group remains controversial. It has been estimated, using molecular data, to have occurred in the Cenozoic (Des Marais *et al.*, 2003). In contrast it also has been estimated as 136 Ma. (Early Cretaceous) from the fossil record (Stanich *et al.*, 2009) and possibly extending far back into the Jurassic, since nearly all synapomorphies that define the crown group *Equisetum* already occur in the anatomically preserved *Equisetum thermale* Channing, Zamuner, Edwards and Guido, 2011 from the Jurassic of Argentina (see Channing *et al.*, 2011). Nonetheless, a phylogenetic analysis including both living and fossil representatives of the genus is required in order to confirm the position of fossil *Equisetum* species as part of the crown group, and therefore, the diversification minimum age for that group.

A great number of equisetalean remains have been found in Mesozoic rocks of Gondwana, the vast majority of them have been assigned to the genera *Neocalamites* Halle, 1908, *Equisetites* Sternberg, 1833 or *Equisetum* (see Villar de Seoane, 2005; Channing *et al.*, 2011; Bomfleur *et al.*, 2013). Differences between the latter two genera have been extensively discussed (*e.g.*, Harris, 1961; Gould, 1968; Stanich *et al.*, 2009), and many of their representatives have been suggested to belong to the same evolutionary lineage leading to the extant horsetails (Boureau, 1964; Gould, 1968).

In this contribution we describe a new equisetalean plant from the Lower Jurassic of Argentina, preserved as impressions and casts. The large number of organs (e.g., axes, leaf whorls, nodal diaphragms, strobili), the fine epidermal

details, and organic attachments allowed an almost complete reconstruction of the aerial parts of the plant, providing important information about its paleobiological features and the evolution of ancient *Equisetum* representatives.

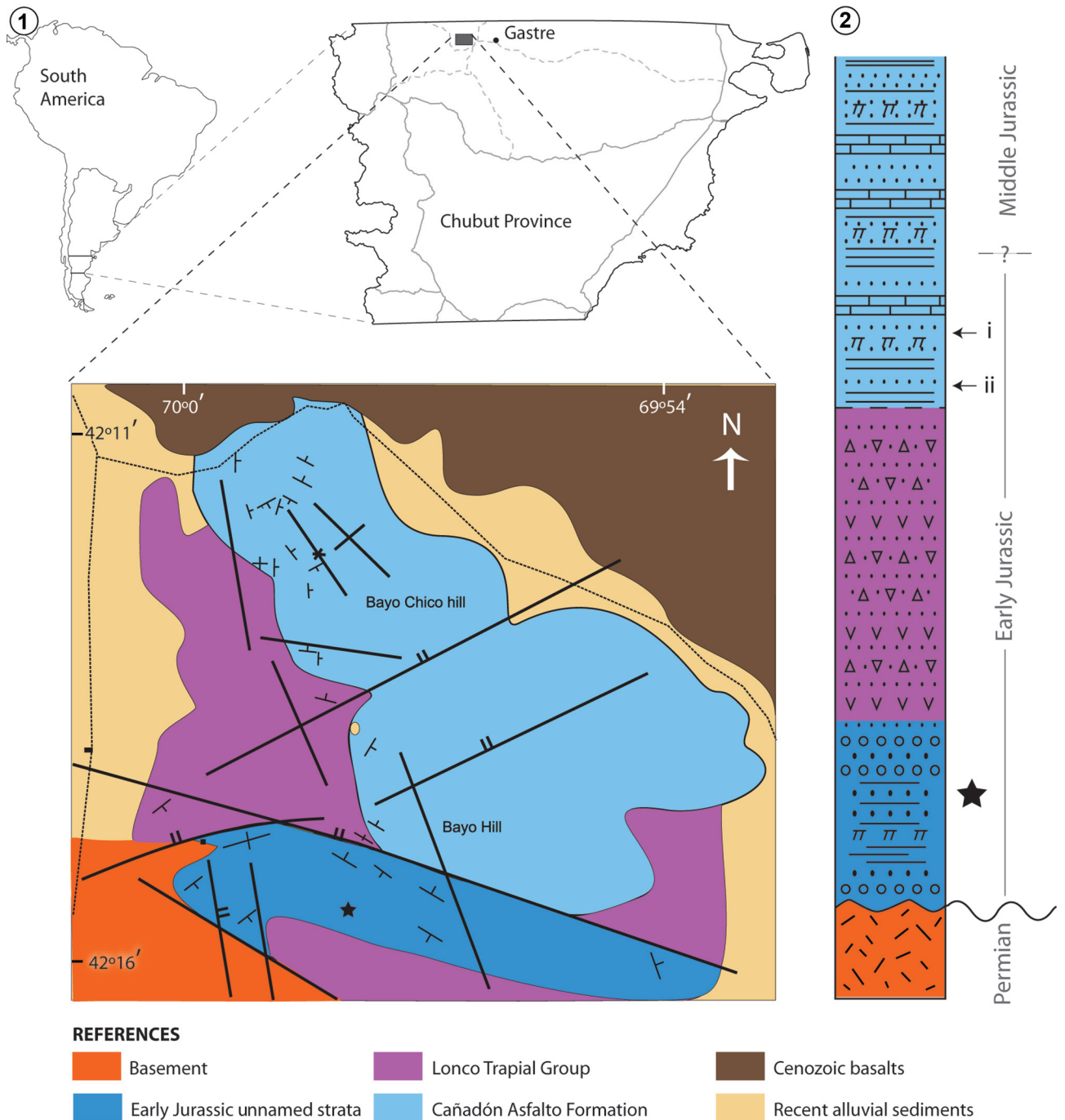


Figure 1. 1. Location and geology of the *Equisetum dimorphum* sp. nov. fossil localities; 2. Simplified stratigraphic section showing the main lithostratigraphic units cropping out in the Cerro Bayo area. Radioisotopic dates on the Cañadón Asfalto Formation are indicated: (i) 177.37 ± 0.12 Ma; (ii) 176.15 ± 0.12 (see Cúneo *et al.*, 2013). The star indicates the fossiliferous beds.

Institutional abbreviations. MPEF-Pb, Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina, paleobotanical collection.

MATERIALS AND METHODS

The material was collected at the Cerro Bayo locality near Gastre, northwest Chubut Province, Argentina (Fig. 1.1). Fossiliferous horizons at this locality belong to an unnamed unit of fluvial deposits, stratigraphically equivalent to the Las Leoneras Formation in the Las Leoneras and Zaino canyons further south, that are overlain by a succession of agglomerates and lava flows (Lonco Trapial Formation) and lacustrine deposits (Cañadón Asfalto Formation) (Fig. 1.2). Recent radiometric dating of ash layers from the Cañadón Asfalto Fm. and Las Leoneras Fm. have yielded U-Pb (CA-TIMS method) zircon average ages of 177.4 ± 0.1 Ma (early Toarcian) and 188.9 ± 0.1 Ma respectively, suggesting an Early Jurassic (most likely Pliensbachian) age for the plant-bearing beds of the unnamed unit underlying the Lonco Trapial Formation (Cúneo *et al.*, 2013). The taxonomic composition of the plant-fossil assemblages with abundant *Goeppertella* Oishi and Yamasita, 1936, *Dictyophyllum* Lindley and Hutton, 1834, and *Sagenopteris* Presl in Sternberg emend Rees, 1993 (see Escapa *et al.*, 2008a) provides further support for an Early Jurassic age assignment (see Escapa *et al.*, 2008b; Escapa and Cúneo, 2012).

The majority of the specimens described here were collected from a single plant-bearing bed at a site informally named *Equisetum* site (GPS coordinates are available upon request to the authors). The plant-fossil assemblage of this bed is strongly dominated by *Equisetum*, with only few subordinate occurrences of the conifer *Austrohamia minuta* Escapa *et al.* 2008b also the dipteridaceous ferns *Dictyophyllum* and *Goeppertella* and the osmundaceous ferns *Osmundopsis rafaellii* and *Todites cacereii* Escapa and Cúneo, 2012. Additional *Equisetum* specimens were collected from another plant-bearing bed at a site in close proximity. In addition to *Equisetum* the assemblage of this second bed contains *Dictyophyllum*, *Goeppertella*, the marattiaceous fern *Marattiopsis patagonica*, various seed-fern taxa and subordinate occurrences of *Austrohamia minuta* and the two osmundaceous ferns mentioned above (Escapa, 2009; Escapa *et al.*, 2014).

Most of the studied material (*i.e.*, that from the “*Equisetum* site”) occurs in light-gray to pale yellowish orange, partially silicified mudstones, and consists of vegetative stems, foliar whorls, nodal diaphragms, stem apices, and strobili preserved in the form of impressions, molds, and casts. Owing to the fine-grained matrix and presumably early cementation with silica, many impressions and casts preserve a very fine relief of epidermal and other fine-structural details. Organic remains are generally not preserved, but some specimens are stained in reddish-brown colours probably due to precipitation of iron oxides. The material from the other plant-bearing bed is overall similar in preservation, but occurs in dark-gray mudstones and does not show preserved of fine-structural details.

Macroscopic images were taken with a Canon (EOS 7D) camera under halogen lighting projected at different angles. Cellular and other fine-structural details were analysed and photographed using a Nikon SMZ1000 stereoscope microscope with an attached digital camera. Image stacking technique was performed using Adobe Photoshop CS6 in order to obtain one well-focused composite image from several individual images captured at successive focal planes (Bercovici *et al.*, 2009).

SYSTEMATIC PALEONTOLOGY

Order EUISETALES *sensu* Boureau, 1964

Family EUISETACEAE *sensu* Good, 1975

Genus *Equisetum* Linnaeus, 1753

Type species. *Equisetum fluviatile* Linnaeus, 1753.

Section and subgenus indet.

Equisetum dimorphum sp. nov.

Figures 2–8

Derivation of name. The specific epithet (*gr. dimorphos*= having two forms) is chosen in reference to the distinctly different morphology of apical leaf whorls of fertile stems; it furthermore appropriately describes the two different preservational aspects of the nodal region.

Diagnosis. Stems unbranched, externally smooth, and internally hollow except at the nodes. Complex nodal septa, with external diaphragm portion circular, flat, bearing pitted

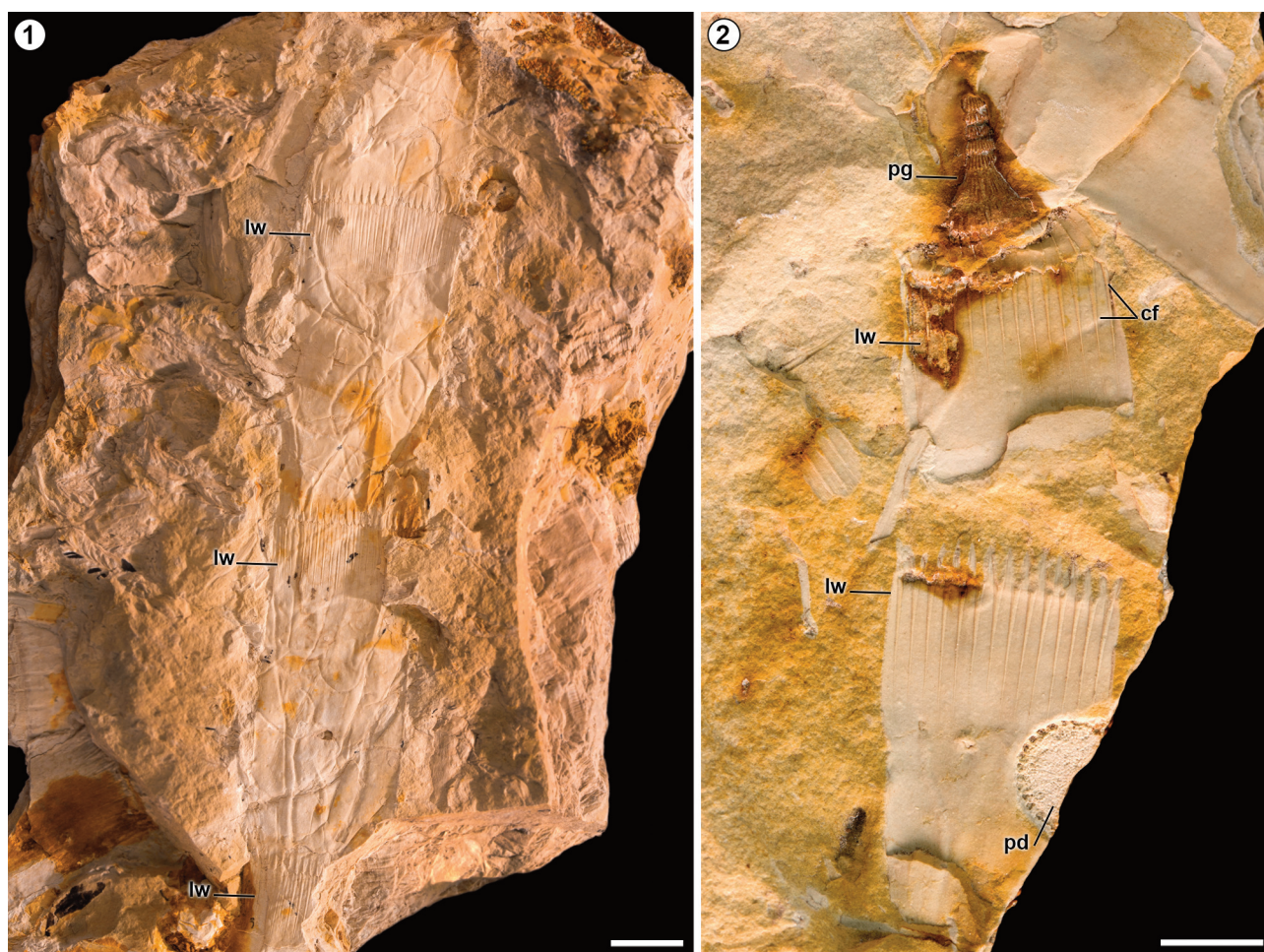


Figure 2. *Equisetum dimorphum* sp. nov. from the Lower Jurassic of Chubut Province, Argentina. **1**, MPEF-Pb 6472; **2**, MPEF-Pb 5931. Abbreviations: cf, commissural furrows; lw, leaf whorls; pd, pitted diaphragm; pg, pagoda structure. Scale bars 1= 10 mm; 2= 5 mm.

microrelief in a vague radial arrangement, surrounded by an internal ring of carinal canals and an external ring of vallecular canals; internal diaphragm part with robust tissues forming an upwardly convex structure resembling a cart-wheel, with a central hub, radiating spokes, and a thin peripheral rim of scalloped appearance; polygonal cells with thickened walls occur at the hub and the spokes. Nodal leaf whorls consisting of a fused basal sheath and free, lanceolate, usually spreading, distal leaf tips; sheath portion comprising usually 75–80% of the total leaf-length, with bicarinate commissural furrows composed of a sunken central region with large, transversely oriented cells bounded by oblique flanks with obliquely oriented cells. Number of leaves, vallecular canals, and spokes usually between 12 and 42. Stem apices commonly terminating in pagoda-like structures.

Internodal epidermal cells are square to rectangular, in longitudinal rows; stomata usually sunken and distributed in broad bands. Strobili single, terminal, cylindrical to oblong, with whorls of densely arranged sporangiophores bearing penta- or hexagonal distal shields with a central umbo and abaxial sporangia; strobili subtended by heteromorphic leaf whorls with their tips at least three to four times longer than those of regular leaf whorls.

Holotype. MPEF-Pb 5894a,b.

Paratypes. MPEF-Pb 5879–5893, 5895–5940, 6472–6479.

Additional material. MPEF-Pb 2684–2685, 2705 and 2712.

Geographic occurrence. Cerro Bayo area, NW Chubut Province, Argentina.

Stratigraphic occurrence. Unnamed beds conformably overlain by the Early Jurassic (early Pliensbachian to early Toarcian) volcanics of the Lonco Trapiel Formation.

Description

Stems. Aerial stems are unbranched, cylindrical, and uniformly wide (*i.e.*, not swollen at the node level) of up to 23 mm in compressions and with a diameter of up to 18 mm in transverse stem sections. Internodes are up to 38 mm long (Fig. 2.1) and show a smooth external surface without lon-

gitudinal ridges or furrows (Fig. 2.2). The nodes are indistinct, and show a gradual transition from internode to leaf-sheath surface. Epidermal cells on the internodes are square to rectangular in shape, about 40–90 μm long and 30–50 μm wide, and uniformly arranged in parallel, straight, longitudinal rows (Fig. 3.3–4).

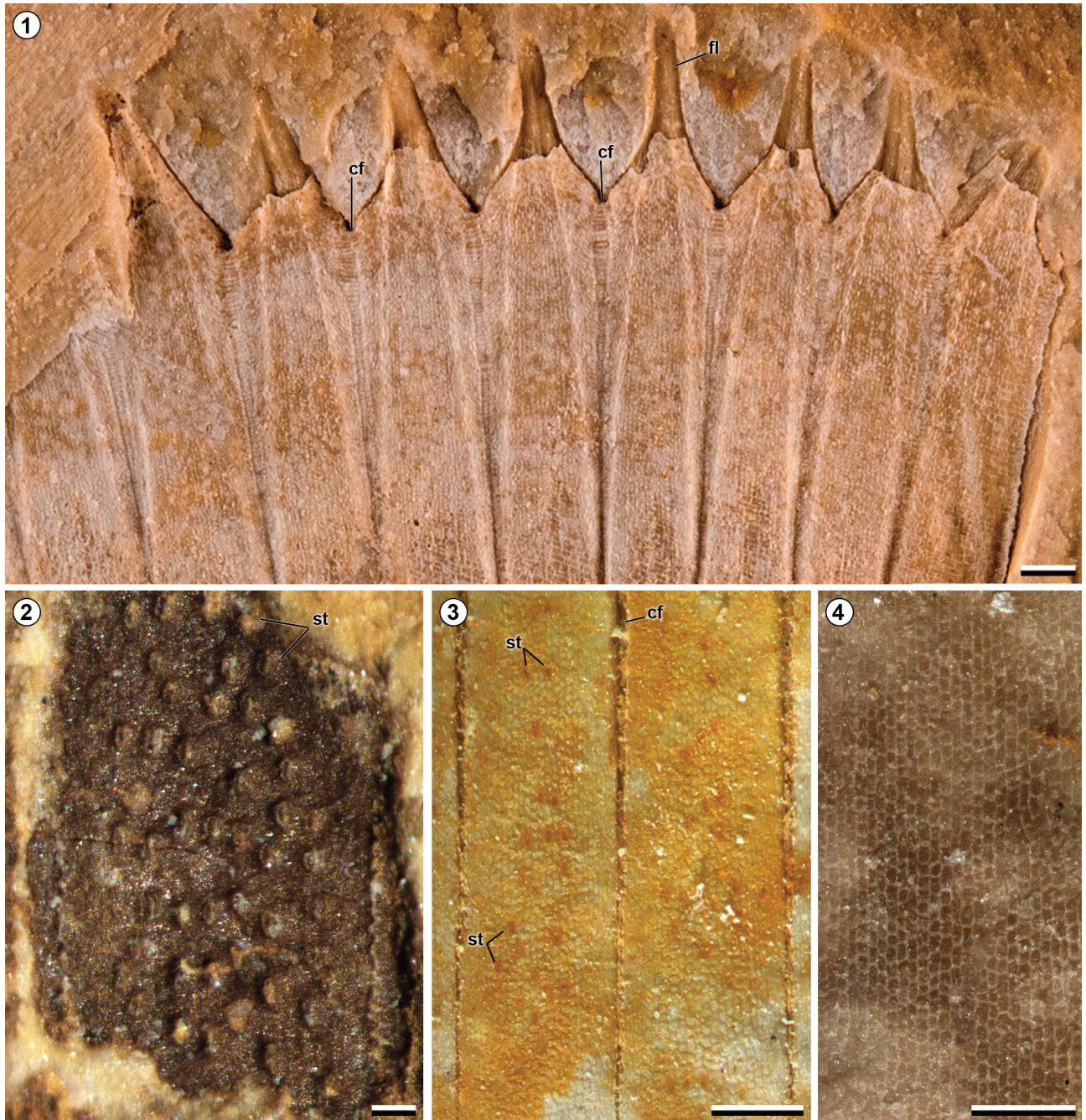


Figure 3. *Equisetum dimorphum* sp. nov. from the Lower Jurassic of Chubut Province, Argentina. 1. Epidermal details of the leaf sheath of MPEF-Pb 6473a; 2. Epidermis of MPEF-Pb 5940. 3. Lower portion of the leaf sheath of MPEF-Pb 5939; 4. Epidermis of the internode showing longitudinal columns of quadrangular to rectangular cells of MPEF-Pb 6474. Abbreviations: cf, commissural furrows; fl, free leaves; st, stomata. Scale bars 1= 0.5 mm; 2= 0.1 mm; 3-4= 0.4 mm.

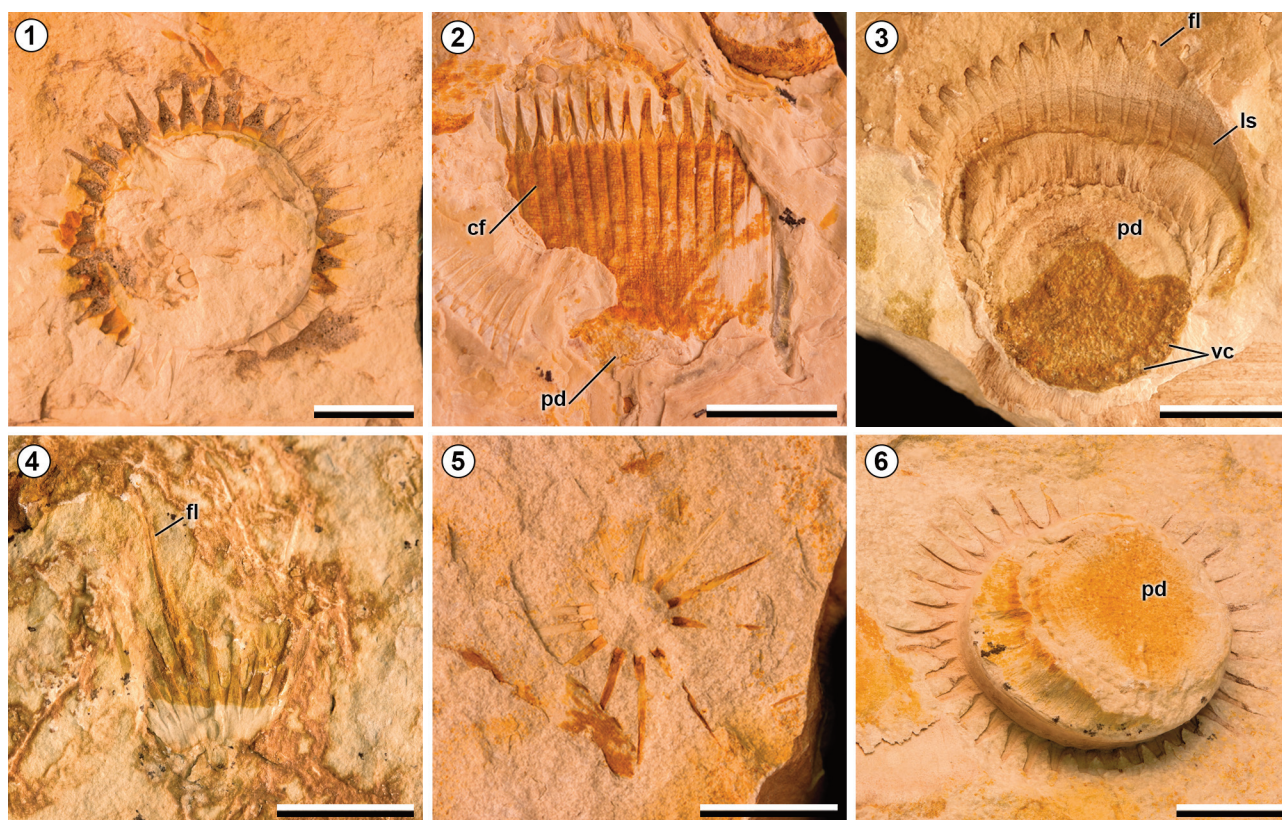


Figure 4. *Equisetum dimorphum* sp. nov. from the Lower Jurassic of Chubut Province, Argentina. 1. Leaf whorl showing spreading free leaves of MPEF-Pb 5884; 2. Lateral view of a leaf whorl showing the fused leaf sheath of MPEF-Pb 5915; 3. Leaf whorl of MPEF-Pb 5916b; 4. Leaf whorl of MPEF-Pb 5907; 5. Leaf whorl with spreading long leaves of MPEF-Pb 5895a; 6. Leaf whorl with numerous leaf tips of MPEF-Pb 5883. Abbreviations: cf, commissural furrows; fl, free leaf tips; ls, leaf sheath; pd, pitted diaphragm; vc, vallecular canals. Scale bars 1–3= 5 mm; 4, 6= 10 mm; 5= 1 cm.

The leaf whorls are composed of 12–42 (mean=32; $n=35$) basally fused, linear leaves with acute apices (Fig. 4.1–2); they are fused for about 75–80% of their total length, forming a basal sheath that is slightly expanding with respect to the node (Fig. 4.3). On the sheaths, individual leaves are separated one from another by commissural furrows that emerge approximately at the level of the node and gradually become wider and deeper towards the apex, reaching a width of 0.7 mm at the upper sheath margin. The central region of the commissural furrows consists of a longitudinal row of transversely elongated, rectangular cells, 15–30 μm long and 30–100 μm wide (Fig. 3.1). The central region is delimited on each side by an obliquely protruding flange composed of diagonally oriented cells c. 50–70 μm long and 20–40 μm wide.

The free leaf tips are usually about 1.7–3 mm long (2.4 on average; $n=35$), at apical leaf whorls of fertile stems, however, leaves are much longer, with free tips reaching up

to 20 mm in length (Fig. 4.1–6). In many occasions the free apical parts of the leaves are missing due to either taphonomic or developmental causes. In some cases, the free leaf tips show a faint central line, possibly indicating the presence of a midvein (Fig. 3.1). The lateral margins of the leaf tips are composed of a thin membrane showing diagonally oriented cells. Overall, the epidermal cellular pattern on the central to upper parts of the leaf sheaths and on the free leaf tips differs markedly from that of the stem surface and the basal leaf-sheath portions because it is composed of considerably narrower cells (only c. 15–30 μm wide).

The stomata are usually sunken and occur in broad bands on both the internodes and leaf sheaths, but are more common on the latter (Fig. 3.2). Superficial stomata may also occur scattered or arranged in short vertical rows (Fig. 3.3), but this could be a taphonomic artefact due to the compression of the stems. Each stomatal apparatus is elliptical in shape and 55–70 μm long and 35–45 μm wide. The

sunken stomata are particularly evident on impressions and casts of the leaf sheaths, where they occur in the form of elliptical lumps on an otherwise uniform, smooth surface. The

stomata are surrounded by cells that are distinctly smaller than the regular epidermal cells, and whose margins appear curved or bent to accommodate the stomatal apparatus.

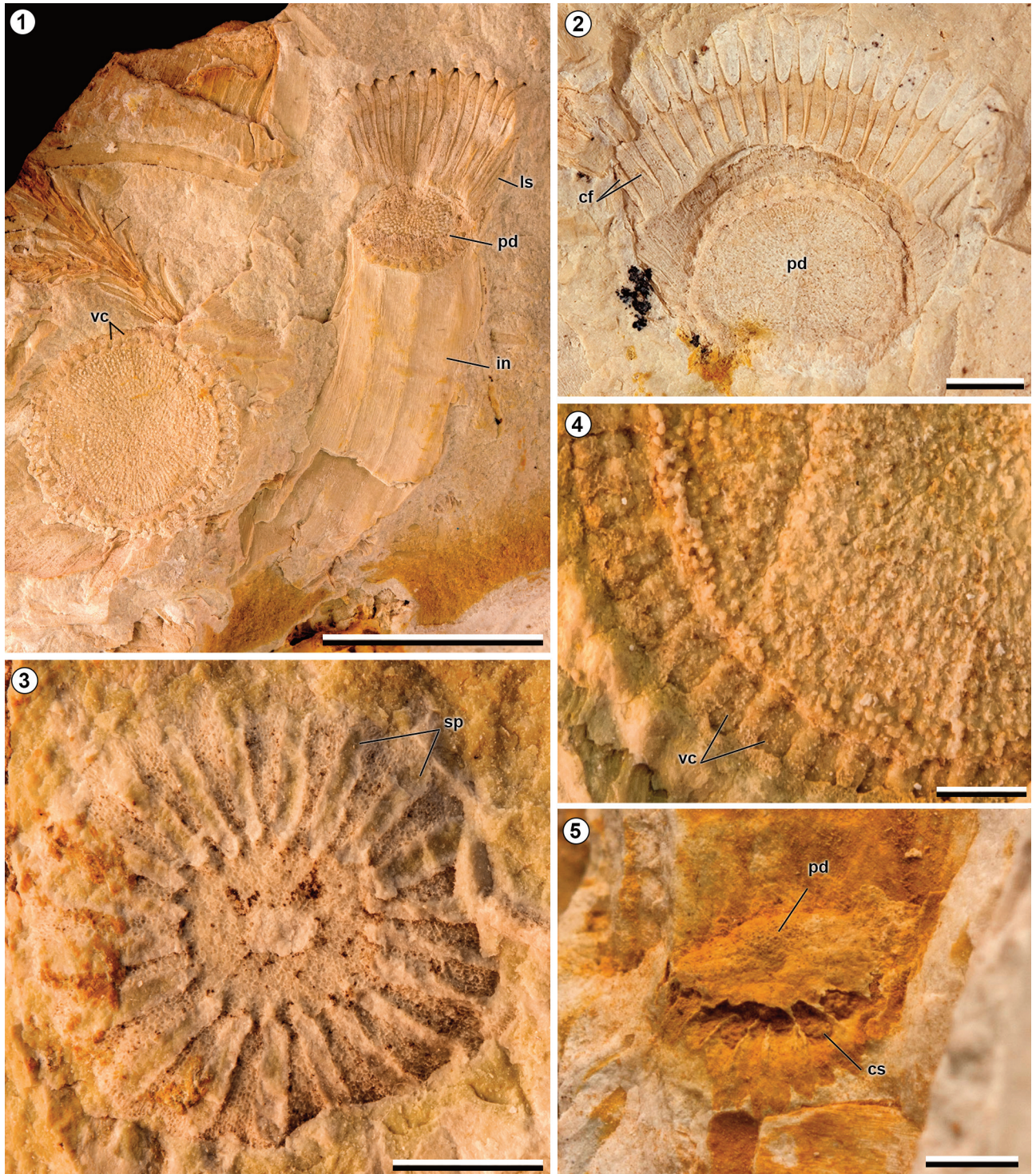


Figure 5. *Equisetum dimorphum* sp. nov. from the Lower Jurassic of Chubut Province, Argentina. 1. MPEF-Pb 5886; 2. MPEF-Pb 5906; 3. Cart-wheel structure of MPEF-Pb 6475; 4. Pitted diaphragm of MPEF-Pb 5900; 5. Transverse view of stem of MPEF-Pb 5940. Abbreviations: cf, commissural furrows; cs, cart-wheel structure; in, internode; ls, leaf sheath; pd, pitted diaphragms; sp, spokes; vc, vallicular canals. Scale bars 1= 10 mm; 2= 3 mm; 3, 5= 2 mm; 4= 1 mm.

The stems are hollow and divided at the nodes by transverse septa with a complex organization producing two distinct types of structures, both occurring commonly isolated in the sediment or -more rarely- attached to leaf sheaths or to stem sections at the node level. The more common is the former of transversal structure (pitted diaphragms= PD), which occurs in the form of flat, circular diaphragms with diameters between 2 and 13 mm (mean= 5.95 mm; n= 48). These consist of a large, flat, circular central portion with numerous, somewhat radially arranged pits (probably cast of parenchymatic cells of the pith, Fig. 5.1–2) that is surrounded by a peripheral ring with numerous regularly distributed rectangular to wedge-shaped segments (vallecular canals), at the outermost periphery these segments merge with the axis, forming a thin circular rim (Fig. 5.4). In a few cases, the central portion appears to be surrounded by an additional narrow ring of small circular lumps (partial molds of carinal canals) alternating with the position of vallecular canals in the outer ring. The second type of structure is also circular in outline, 2.3–11.5 mm (mean= 5.48; n= 30) in diameter, upwards convex, and resembles a cart-wheel (cart-wheel structure= CS) in that it consists of a small central hub, radiating spokes, and a thin peripheral rim (Fig. 5.3). The central hub is 0.5–5 mm wide and bears a small, 0.2–1 mm wide hole in its centre. The spokes are about 0.1–0.3 mm wide, and their length accounts for approximately 1/4 to 3/4 of the radius of the structure. The central hub and the spokes are composed of polygonal, more or less isodiametric cells 35–75 µm in diameter; toward the periphery of the spokes, cells appear to become increasingly radially elongated. Where the spokes merge into the peripheral rim, they dip slightly downward, giving the periphery of the whole structure a scalloped appearance.

Vegetative shoot apices are commonly terminated by a distinctive structure that resembles a tiny pagoda (Fig. 6.1). These pagoda structures are 3–7 mm tall and 0.7–3 mm wide, and consist of up to 16 tightly packed whorls of minute, reduced, inwardly-curved leaves (Fig. 6.2). Usually, the basal whorl of these structures is covered by the adhering leaf sheaths and apices of the subtending immature regular leaf whorls (Fig. 6.1).

Very rarely, stems dichotomize, with a pair of slender “daughter stems” arising from the leaf sheath of the main stem (Fig. 6.3–4).

Reproductive organs. Strobili are borne terminally and singly on the apices of fertile stems. Each strobilus is subtended by modified leaf sheaths with free leaf tips that are at least three times longer (total leaf length c. 20 mm) than those of regular leaf whorls (Fig. 7.2). Strobili are cylindrical to oblong, 12–19 mm long and 4–7 mm wide, and formed by a central axis with 7–12 whorls of sporangiophores (Fig. 7.1). The sporangiophores bear 0.6–1 mm large, penta- to hexagonal distal shields with straight margins. At the center of the shield is an umbo 0.3–0.4 mm in diameter, visible on the casts of the sporangiophores, which has the same shape as the shield (Fig. 7.4). The estimated number of sporangiophores per whorl is 8 to 10. The sporangia are preserved as impressions, oblong in shape and 0.5–0.7 mm long by 0.12–0.2 mm wide (Fig. 7.3). Spores are unknown.

Generic assignment and comparisons

Specimens from Cerro Bayo are here assigned to *Equisetum* based on numerous vegetative and reproductive features that are virtually identical to the extant representatives of the genus, i.e., stems comprising nodes and internodes, internal transverse diaphragms occurring at the nodes, absence of secondary growth, partially fused leaf whorls and strobilar reproductive organs consisting of whorled peltate sporangiophores with polygonal shields without intercalated bracts. In addition to the broad morphological characters mentioned before, the detailed preservation in *Equisetum dimorphum* sp. nov. allowed the observation of numerous epidermal features that further support the generic assignment. For instance, cellular arrangement of commissural furrows in *E. dimorphum* sp. nov. is identical to the one that is present on extant species of both modern subgenera, e.g., *Equisetum diffusum* Don, 1825, *Equisetum telmateia* Ehrhart, 1783 and *Equisetum variegatum* Schleicher, 1797 (Hauke, 1963, 1978, 1985). In the leaf whorls of living species of *Equisetum*, the central cells of the commissural region (C-cells, Hauke, 1985) acquire their particular shape beginning with cuboidal cells that undergo successive divisions to attain rectangular and ultimately tangentially elongated shapes, the divisions of the C-cells being always transverse (Hauke, 1985). Based on the morphological similarities the same developmental pattern is here inferred for the fossil species.

Equisetum dimorphum sp. nov. is part of a rather small

and poorly understood group of *Equisetum* fossils with wheel-like nodal structures and divergent free leaf tips that appear to be typical elements of mid-Mesozoic floras worldwide. Two common and comparatively well-known

species of this complex are *Equisetum laterale* Phillips, 1829, originally described from the Middle Jurassic of Yorkshire (see also Harris, 1931, 1961; Gould, 1968), and *Equisetites ferganensis* Seward, 1907 from the Jurassic of Kazakhstan,

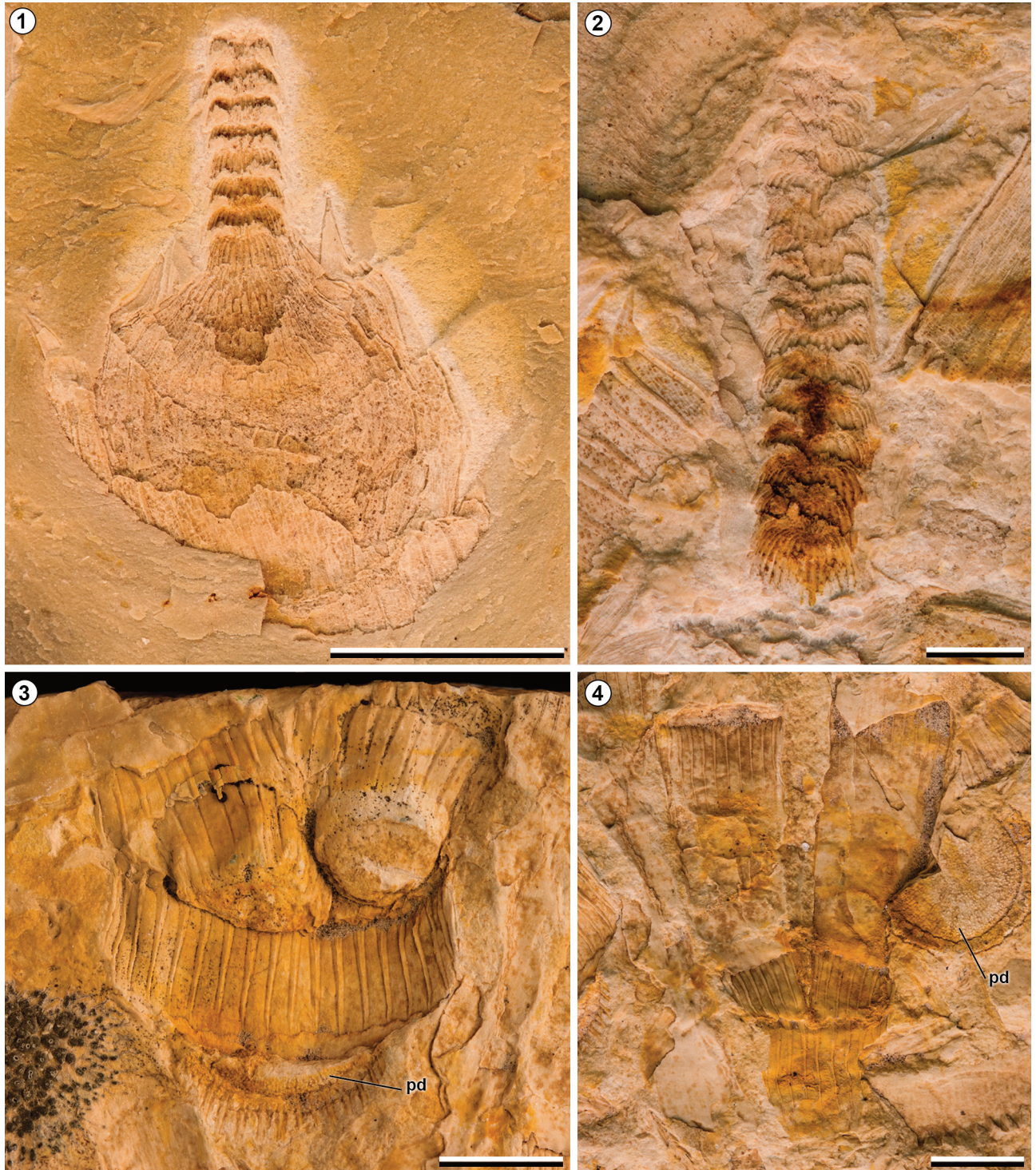


Figure 6. *Equisetum dimorphum* sp. nov. from the Lower Jurassic of Chubut Province, Argentina. 1. Pagoda structure connected to the stem, MPEF-Pb 5932; 2. Isolated long pagoda structure, MPEF-Pb 6476; 3–4. Dichotomous stems of MPEF-Pb 5930. Abbreviation: pd, pitted diaphragm. Scale bars 1= 4 mm; 2= 2 mm; 3–4= 5 mm.

Madagascar, and China (Appert, 1973; Sun *et al.*, 2010). The two species are very similar in most of their morphological

features, and are distinguished mainly by a characteristic “arcaded line” that runs perpendicular to the commissural

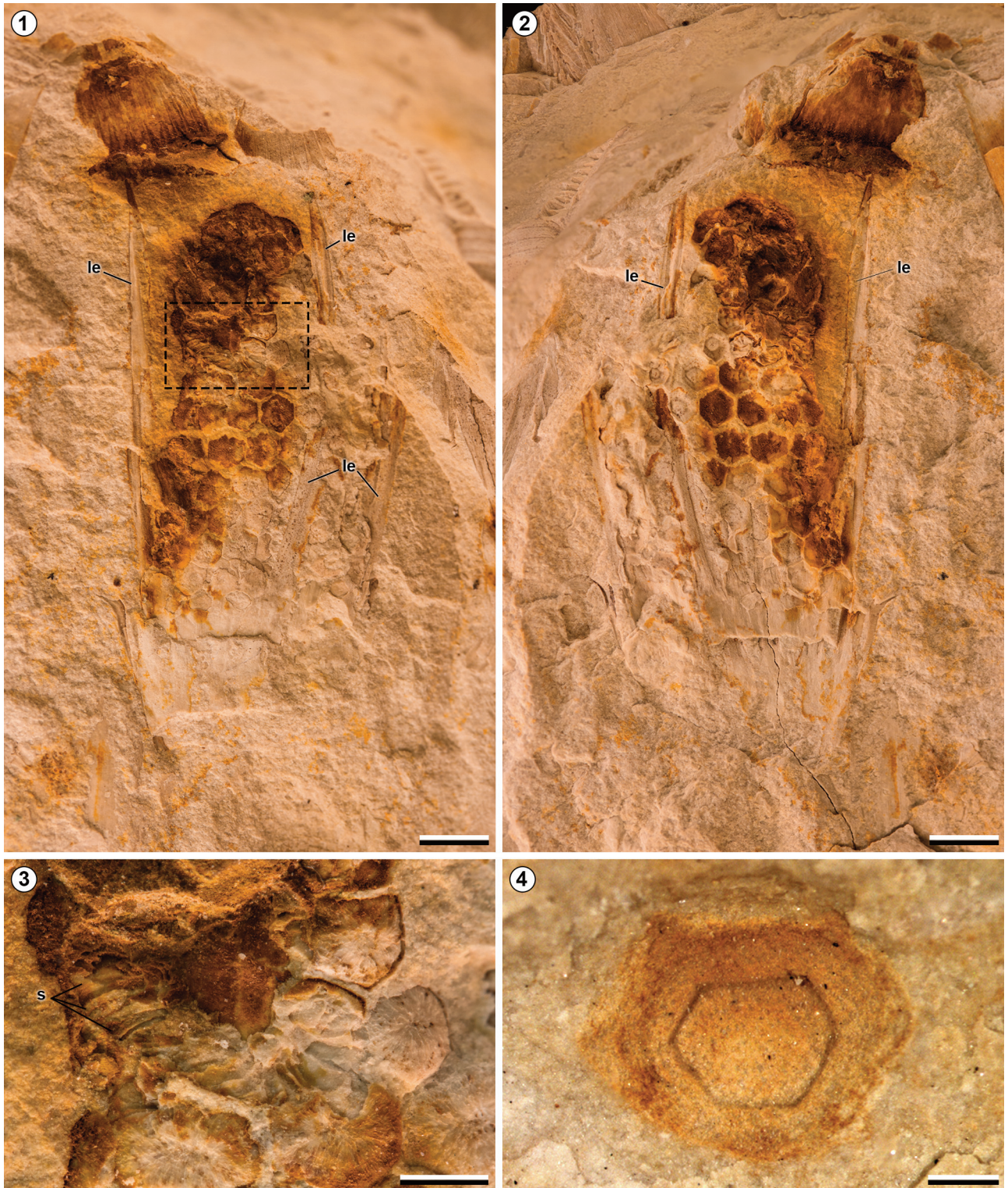


Figure 7. *Equisetum dimorphum* sp. nov. from the Lower Jurassic of Chubut Province, Argentina. 1–2. Part and counterpart of a strobilus showing the hexagonal sporangiophores and the long leaves of MPEF-Pb 5894a and MPEF-Pb 5894b; 3. Detailed inner view of 1 showing oblong sporangia of MPEF-Pb 5894a; 4. Isolated external cast of sporangiophore showing central umbo of MPEF-Pb 6477a. Abbreviations: le, leaves; s, sporangia. Scale bars 1–2= 3mm; 3= 1 mm; 4= 0.5 mm.

furrows on the leaf sheaths of *E. ferganensis* (Appert, 1973). These broad and single zigzagging lines extend around each individual leaf sheath. Based on a detailed investigation of macro- and micro-morphological features of well-preserved *E. ferganensis* material from the Upper Jurassic of Madagascar, Appert (1973) concluded that, apart from the arcaded line mentioned above, *E. laterale* and *E. ferganensis* may represent two preservational types of the same natural species.

Equisetum dimorphum sp. nov., *E. laterale* and *E. ferganensis* are similar in the following characters: (1) smooth and unbranched stems, (2) stem and nodal-diaphragm diameters, (3) internode length, (4) presence of cart-wheel structures, (5) spreading leaves, (6) cellular organization of the epidermis at commissural furrows and internodes, (7) number of spokes of cart-wheel structures, and (8) number of leaves of *E. laterale* and *E. ferganensis* being within the range

of *E. dimorphum* sp. nov. In addition, some of the stomata present in *E. dimorphum* sp. nov. occur sunken in broad bands while others appear to be scattered flush within the epidermis (a possible taphonomic artefact) or in short vertical rows, whereas those of *E. laterale* are described as being scattered and “usually sunken” (Gould, 1968, p. 159), which, in part, agrees with the ones here described.

Nonetheless, *E. dimorphum* sp. nov. also differs from *E. laterale* and *E. ferganensis* in several aspects, including pitted diaphragms (although there is a mention of a single specimen of *E. laterale* from Antarctica showing a diaphragm with a pitted surface; Rees and Cleal, 2004); notably shorter mean length of the leaf tips of *E. dimorphum* sp. nov., usually measuring 1.7–3 mm, while those in the other two species are usually between 3–15 mm; presence of pagoda-like structures; and the presence of long subtending leaves at the base of the strobili (strobili of *E. ferganensis* are unknown). In addition, fertile specimens of *E. laterale* described from Australia (Gould, 1968) have smaller strobili than *E. dimorphum* sp. nov., while those from Antarctica have helically arranged sporangiophores (Rees and Cleal, 2004).

Equisetites patagonica (Herbst, 1965) from the Lower Jurassic of Santa Cruz was synonymized with *E. laterale* (Rees and Cleal, 2004; see also Gould, 1968). The length of the free leaf tips of the Patagonian specimens, however, is similar to that seen in *E. dimorphum* sp. nov.

Other species can also be compared with *E. dimorphum* sp. nov. on the basis of either vegetative or reproductive features. *Equisetites rajmahalensis* Oldham and Morris, 1963 from the Upper Jurassic is commonly found in the Rajmahal Formation, India (see Par and Basu, 2007). It shares characters with *E. dimorphum* sp. nov. including internode length, number of leaves, presence of pitted nodal diaphragms, and sunken stomata. However, pagoda-like structures, epidermal details, cart-wheel and reproductive structures are unknown in the Indian species.

Several equisetalean plants from the Mesozoic of Argentina were described in recent years. *Equisetites pusillus* Villar de Seoane, 2005 from the Lower Cretaceous of Santa Cruz differs from *E. dimorphum* sp. nov. in having, for instance, much smaller stems (up to 3 mm wide) with external longitudinal ridges and furrows, and in having helically arranged, rhomboidal sporangiophores. *Equisetites minimus* Falaschi, Zamuner and Foix, 2009 from the Upper

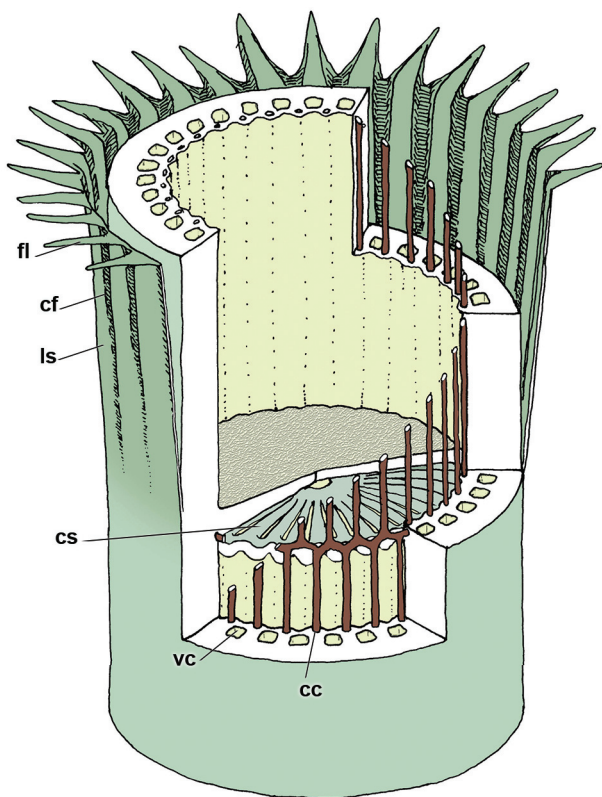


Figure 8. *Equisetum dimorphum* sp. nov. from the Lower Jurassic of Chubut Province, Argentina. Hypothetical reconstruction of the external and internal morphology of a node and partial internodes of a vegetative axis. Abbreviations: cc, carinal canals; cf, commissural furrows; cs, cart-wheel structure; fl, free leaves; ls, leaf sheath; pd, pitted diaphragm; vc, vallecular canals and vascular system (in brown).

Jurassic of Santa Cruz differs from *E. dimorphum* sp. nov. in having much smaller stems (1.3 mm in diameter) that are hexagonal in cross section, in having fewer leaves per whorl (usually 6), and in having also smaller strobili without long subtending leaves. The anatomically preserved *E. thermale* from the Middle Jurassic of Santa Cruz, Argentina (Channing *et al.*, 2011), shares with *E. dimorphum* sp. nov. the presence of superficial stomata (although, as mentioned above, this could be a taphonomic artefact), the arrangement of the epidermal cells in vertical rows, and the gross morphology of the strobili. However, numerous features also differ between the two species: stems of *E. thermale* are again considerably smaller than those of *E. dimorphum* sp. nov. (with a mean diameter of 1.65 mm), polygonal in cross section, the internodes bear 6 to 12 longitudinal ridges that are equal in number to leaves per whorl.

Finally, *Equisetum dimorphum* sp. nov. has numerous features comparable in general with extant representatives of the genus, and in particular with *Equisetum hyemale* Linnaeus, 1753, such as the unbranched stems and the very characteristic pagoda structures (Hauke, 1963).

DISCUSSION

Reconstruction of the Equisetum dimorphum sp. nov. plant

Even though the studied material is preserved in the form of impressions and casts, a type of preservation that is generally believed to provide only little paleobiological information, the large amount and the fine details identified on the specimens enables a comprehensive reconstruction of the *E. dimorphum* sp. nov. plant. Herein we will discuss certain features of *E. dimorphum* sp. nov. that we consider to be of particular significance for morphological and phylogenetic interpretations.

Plant height. *Equisetum dimorphum* sp. nov. was an unbranched plant with stems up to 18 mm in diameter. By analogy with extant species, a height of up to 2 meters can be estimated for the *E. dimorphum* sp. nov. plants. Upright stems of *E. hyemale*, with a similar height range as *E. dimorphum* sp. nov. gain their mechanical stability due to specific strengthening features, such as the presence of a double continuous layer of endodermis (Spatz and Emanns, 2004). Other features that contribute to the mechanical stability of particularly tall equisetalean stems are an outer ring

of strengthening tissue plus an inner lining of turgid parenchyma as in *Equisetum giganteum* (Spatz *et al.*, 1998), and, in species with small central cavities under low turgor pressures, a single continuous layer of endodermis (Spatz and Emanns, 2004). Unfortunately, because the internal anatomy of *E. dimorphum* sp. nov. is preserved only in the form of casts, the stability mechanism of the axes remains unknown. We hope that additional material with more complete structural details of the stems (*e.g.*, with a preserved endodermis pattern) may provide further information on this subject.

Leaf dimorphism. By far the most common foliage type associated with *Equisetum dimorphum* sp. nov. bears short free leaf tips of 1.7–3 mm length. A second foliage type, which occurs very rarely in the same rock samples as the common type, bears free leaf tips that are at least three times longer. We interpret both foliage types as being part of the same natural species. Appert (1973) and Gould (1968) also illustrated similar leaf whorls types for the species *Equisetites ferganensis* and *Equisetum laterale*, respectively, and interpreted them as part of the same natural plant. In these fossil species, however, the longer leaf type occurs more commonly. In *Equisetum dimorphum* sp. nov. the leaf whorls with long leaf tips occur at the node(s) immediately below the strobilus, as is demonstrated by a specimen in which the strobilus is organically attached to the stem (Fig. 7.1–2). In this specimen, free leaf tips are approximately the same size as the strobilus. Similar epidermal details such as cells organization and size observed in the two types of leaf tips provide further support for this hypothesis.

At present, it remains unknown whether the whorls bearing long leaves are present only on the node directly below a strobilus, or whether they occur throughout fertile stems.

Nodal anatomy and cart-wheel structures. Two different kinds of morphologically distinct structures are observed on transversal views of the node region in *Equisetum dimorphum* sp. nov.: the cart-wheel structures (CS) and the pitted diaphragms (PD). As noted previously, CS also occur in other Mesozoic equisetalean species, such as *E. laterale* (Gould, 1968; Rees and Cleal, 2004) in which they are convex upwards and possess scalloped margins. In both cases the spokes apparently played some role in the vascular system,

since their number is directly correlated with the number of leaves at the nodes, and also, as seen in *E. laterale*, because they appear to be connected to the internodal vascular bundles (Gould, 1968: pl. 1; figs. 4, 5). By contrast, PDs are flat and circular in shape and bear numerous pits that may represent pores on the diaphragms, similar to those of living *Equisetum* species (see illustrations in Barber, 1961).

We interpret both types of transversal views of the node being part of the same species mainly because of their similar size range and their presence on the same slabs, both attached to the same leaf whorls. They do not appear to represent a continuous variation of the same structure, since the CS has no continuous range in the length and number of their spokes perhaps leading to a complete reduction, and therefore to morphology similar to the PD type.

The most likely explanation for the presence of two different transversal structures in the stems of a single species is that the CS were contained within the more delicate, possibly parenchymatic tissue that is preserved in the form of the PD. One specimen that provides some support for this hypothesis shows an oblique section of a node with part of a CS partially covered by a PD (Fig. 5.5). The interpretation, originally suggested by Gould (1968, p. 160; fig. 2A–B), may be further supported by the occurrence of occasional pitted diaphragms in association with cart-wheel structures in *E. laterale* from Australia (Gould, 1968) and Antarctica (Rees and Cleal, 2004).

Pagoda structures. The pagoda structures of *Equisetum dimorphum* sp. nov. are remarkably similar to those commonly occurring on the shoot apices of extant *E. hyemale* and *Equisetum x ascendens*, a hybrid of the former species (see Schaffner, 1932; Lubienski and Jäger, 2012). In extant species, pagoda structures arise during the development of the stems, with the successive abscission of the partially fused leaves that are in contact and contained one below another in the growing stem. The free part of the leaves wither away or are torn apart from their sheath with the elongation of the succeeding internode, and thus carried upwards to the apex. In this way, the apical leaf whorl of the pagoda derives from a lower leaf sheath than the one located below, and so it is reflecting a stacking order opposite to the order that the leaf whorls were produced on the stem (Duval-Jouve, 1863; Page, 1997). It is interesting to note that when the pagoda structures are found without an or-

ganic connection to the rest of the plant, they can be easily confused with abortive strobili (Duval-Jouve, 1863).

What particular stimulus triggers the formation of these structures is unknown. Duval-Jouve (1863) stated that the pagoda structures do not appear to have a function in the plant, and therefore are rather the result of a particular type of developmental path. Nevertheless, the presence of these structures has been considered an important diagnostic character for taxonomic classification (Schaffner 1928, 1930, 1932; Hauke, 1963; Lubienski and Jäger, 2012; Jepson *et al.*, 2013), since they are known to occur only in *E. hyemale* and one of its hybrids, both of them contained within the subgenus *Hippochaete*.

There are two other fossil species, *Equisetum columnare* from the Jurassic of England (Harris, 1961, p. 19) and *Equisetites quindecimdentata* from the Triassic of Argentina (Menendez, 1958) that bear organs morphologically similar to pagoda-like structures. However, in both cases these structures were not interpreted as such, and therefore further investigation on these species is needed in order to confirm their homology with the ones in *E. hyemale* and *E. dimorphum* sp. nov.

The possibility that pagoda apices were in fact located at the tip of underground rhizomes cannot be completely discarded, but seems implausible since the acroscopic orientation of the leaf tips below the pagoda would not be possible on a growing underground rhizome because the leaves that are outwardly oriented could not maintain that orientation without bending backwards when the rhizome is horizontally growing through the ground.

Stem dichotomies. Two dichotomous stems (Fig. 6.3–4) have been found among the specimens of *E. dimorphum* sp. nov. Based on their close proximity on the same rock sample, we infer that they belonged to the same individual plant. In one of the specimens it is possible to observe that the internodal length of the first internode after the split, on each stem, is the same. Extant horsetails, including *E. hyemale*, occasionally present this abnormal character of dichotomizing stems as well (Schaffner, 1933).

Systematic considerations

Character evolution. Detailed reconstruction of *E. dimorphum* sp. nov. provides relevant information in terms of the possible early configuration, and therefore evolution, of several

morphological characters. For instance, the presence of longer leaf tips in the proximal nodes of the strobili has been also mentioned for the extant *Equisetum pratense* Ehrhart, 1784 and *Equisetum sylvaticum* Linnaeus, 1753 (Hauke, 1978). However, the difference in leaf length of reproductive and vegetative whorls in the latter is not as pronounced as it is in *E. dimorphum* sp. nov., perhaps suggesting a progressive reduction in this character that is completed in other extant species. One of the theories concerning the origin of *Equisetum* postulates the genus *Neocalamites*, which bears whorls of free long leaves, as its sister group (Stewart and Rothwell, 1993). This hypothesis clearly implies that fusion in equisetalean leaf whorls happened several times in the evolution of the group, and that the morphologically similar leaf sheaths of *Equisetum* and, for instance, the late Paleozoic to mid-Mesozoic *Phyllothea* Brongniart, 1828, would not be homologous. An alternative evolutionary scenario considers the increasing number of herbaceous equisetalean plants described from Gondwana and Angara (Naugolnykh, 2002, 2004; Escapa and Cúneo, 2005; Cúneo and Escapa, 2006) as possibly closely related to *Equisetum*. This is supported by the presence of basally fused leaves, together with numerous shared characters in their reproductive organs.

The apical pagoda-like structure, as seen in *E. hyemale* and its hybrids, which is believed to be an apomorphic character for *Equisetum*, may actually represent a plesiomorphic condition for the genus. Nonetheless, the presence of leaf whorls subtending the pagoda structure in *E. dimorphum* sp. nov. might be interpreted as a different developmental scenario, suggesting that further analyses will be necessary to confirm its homology with respect to extant species.

***Equisetum dimorphum* sp. nov. in the context of extant subgenera.** The two modern *Equisetum* subgenera –*Equisetum* and *Hippochaete*– have been historically distinguished based on numerous morphological features (Hauke, 1963, 1978; Des Marais et al., 2003). However, their morphological differentiation has been recently questioned on the basis of molecular phylogenetic inferences (Des Marais et al., 2003; Guillon, 2004, 2007). In these studies, *Equisetum bogotense*, a species classically assigned to the subgenus *Equisetum* based on morphological features, has been recovered as basal to subgenus *Hippochaete* (Guillon, 2007) or sister to both subgenera (Des Marais et al., 2003; Guillon, 2004). This would indicate that morphological character states present in *E. bogotense* and species from the *Equisetum* subgenus represent the plesiomorphic conditions in the evolution of

TABLE 1 - Morphological characters of *Equisetum* subgenera and *E. dimorphum* sp. nov. aerial stems

Character	<i>Equisetum</i>	<i>Hippochaete</i>	<i>Equisetum dimorphum</i> sp. nov.
Position of stomata	Superficial, scattered or in bands	Sunken, in single or double lines	Sunken in bands/ Superficial
Strobili	Non-apiculate	Usually apiculate	Non-apiculate
Branching pattern	In regular whorls*	Regular/Irregular/Absent	Irregular/Absent
Aerial stem dimorphism	Monomorphic/ Dimorphic/ Semi-dimorphic	Monomorphic	Dimorphic/Semi- dimorphic
Free leaf tips	Persistent	Persistent/Break off/Wither	Persistent/Break off
Pagoda structure	Absent	Present (<i>E. hyemale</i>)	Present
Habit	Annual	Perennial	?
Stem endodermis pattern	Single common external	Single common external/ Double/Surrounding each bundle	?
Micro-relief and surface sculpturing	Mamillae and pilulae very numerous	Mamillae and pilulae sparse or absent	?

* Except in *E. fluvatile* where unbranched stems are frequently found and occasionally *E. palustre*.

the genus (see Guillon, 2007). Nonetheless, the fossil record indicates that modern representatives of *Equisetum* constitute only a minute sample of its past diversity (Boureau, 1964; Stewart and Rothwell, 1993; Taylor *et al.*, 2009) and therefore conclusions on character evolution exclusively based on extant species may be poorly supported.

The specimens here described are characterized by a combination of features present in representatives of both extant *Equisetum* subgenera (see Tab. 1). Similar situations are corroborated for other Mesozoic species such as *E. thermale* (Channing *et al.*, 2011), *Equisetum haukeanum* Stanich, Rothwell and Stockey 2009 and *Equisetum vancouverense* Stanich, Rothwell and Stockey 2009. It is interesting to note that, when Mesozoic fossils are considered, several morphological features generally assumed as synapomorphies for particular living groups are better explained as plesiomorphic conditions (e.g., endodermis pattern). On these grounds, the affiliation of *E. dimorphum* sp. nov. to one of the two living subgenera is discounted.

In addition, the fact that *E. dimorphum* sp. nov. shares some distinctive anatomical characters (e.g., cart-wheel structures) with some other Jurassic species such as *E. laterale* and *E. ferganensis* –both of them present in Gondwana and Laurasia (Harris, 1961; Gould, 1968; Appert, 1973; Sun *et al.*, 2010)– might indicate the presence of an unidentified subgenus that would include several widely distributed species during the Jurassic. A comprehensive phylogenetic analysis integrating extinct and extant forms will be instrumental in order to test this hypothesis, and to identify character polarity in the representatives of the horsetail lineage.

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