Equisetum thermale sp. nov. (Equisetales) from the Jurassic San Agustín hot spring deposit, Patagonia: Anatomy, paleoecology, and inferred paleoecophysiology¹

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- Premise of the study: Dated molecular phylogenies suggest a Cenozoic origin for the crown group of Equisetum. but compression fossil equisetaleans that are morphologically indistinguishable from extant Equisetum and recently discovered anatomically preserved examples strongly suggest an earlier Mesozoic initial diversification.
- *Methods*: In situ samples of *Equisetum thermale* sp. nov. from the Upper Jurassic San Agustín hot spring deposit were collected and studied with the use of polished blocks, thin sections, and light microscopy.
- *Key results: Equisetum thermale* exhibits all the morphological and anatomical characteristics of the extant crown group *Equisetum*. It shows a mixture of features present in the two extant subgenera, e.g., superficial stomata typical of subgenus *Equisetum* allied with infrequently ramifying stems typical of subgenus *Hippochaete*. This appears to ally *E. thermale* with the least derived extant species in the genus *Equisetum bogotense* (sister species to the two subgenera). Its association of hydromorphic and xeromorphic characters allowed it to grow as an emergent aquatic in physically and chemically stressed geothermally influenced wetlands, where it formed dense monospecific stands. *Equisetum thermale*, because it is preserved in situ with intact anatomy, provides clear paleoecological, biological, plus inferred paleoecophysiological evidence of adaptations known in extant species.
- *Conclusions*: As the earliest unequivocal member of the genus, *E. thermale* supports the hypothesis of a Mesozoic origin. Its inferred tolerance of a similar range of stresses (e.g., high salinity, alkalinity, and heavy metal concentrations) to that seen in extant *Equisetum* suggests early evolution and subsequent maintenance of ecophysiological innovations in the genus.

Key words: Equisetites; Equisetum; fossil; geothermal wetland; hot spring; Late Jurassic; paleoecophysiology; silica.

The phylogeny and evolutionary history of the genus Equisetum L. has attracted considerable recent attention from both neobotanists and paleobotanists. Molecular phylogenetic studies of the extant members of the genus have placed it as a sister group to the ferns and have resolved interspecific relations (e.g., Pryer et al., 2001, 2004; Des Marais et al., 2003; Guillon, 2004, 2007), but some systematic analyses of euphyllophytes resolve equisetophytes as sister to lignophytes (Rothwell, 1999). Molecular dating of the resulting phylogenies has suggested that the probable divergence of the extant crown group of the genus was 64.8 ± 12.7 million years ago in the Paleogene (Des Marais et al., 2003). The fossil record suggests that species morphologically (and to a degree anatomically) of modern aspect appeared in the Mesozoic, and it is likely that the extant clade originated from one of these Mesozoic lineages. In a recent paper documenting two such plants,

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Stanich et al. (2009) provided evidence that all the characteristic synapomorphies of living *Equisetum* had evolved by the Lower Cretaceous (136 Ma), and they hypothesized that the extant crown group probably originated much earlier in the Mesozoic. The data substantiating their claim were based on evidence from at least two fossil species. The authors considered that the most stringent approach to determining minimum clade ages from the fossil record would come from a single fossil species that displayed all the diagnostic characters of the crown group but that chances of finding such a plant are slight, thus preventing this level of rigor.

The discovery of the San Agustín hot spring flora (Guido et al., 2010) in the Deseado Massif, southern Patagonia, Argentina, that contains a new species, Equisetum thermale Channing et al. sp. nov., allows, for the first time, reconstruction of nearcomplete plants of Late Jurassic age with excellent anatomical preservation. Our description is based on various organs (aerial stems, foliar sheaths, rhizomes, and roots) that occur in organic connection plus unconnected strobili and spores probably belonging to the same species. This contrasts with fossils common in many coeval assemblages that are morphologically similar to Equisetum but with little preserved anatomy. In addition, the fossilization of the San Agustín plants by siliceous fluids, as they grew in the vicinity of hot springs, allows not only reconstruction of their habitats but, by analogy with the physical and chemical conditions of modern hot spring systems, consideration of their paleoecology and paleoecophysiology.

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MATERIALS AND METHODS

The material comprises specimens of aerial stems, foliar sheaths, roots, and rhizomes and less common branches, apices, and strobili. All are preserved within blocks of chert, which were cut, lapped and polished, and thin-sectioned. Observations and photomicroscopy were conducted with Leica (Wetzlar, Germany) MZ16 and DMRX microscopes combined with Leica DCF480 and DCF490 digital cameras. Measurements of anatomical features were made with the use of Leica IM1000 and JMicroVision (http://www.jmicrovision.com/) image analysis software. For general morphological and anatomical description and comparisons, we use the terminology and characters as detailed by Hauke (1963, 1978); for ornamentation we use the terminology proposed by Page (1972).

Locality, geologic setting and age-The San Agustín hot spring complex occurs in the northwest area of the Deseado Massif, Santa Cruz province, Argentine Patagonia (Guido et al., 2010). Here, Late Jurassic volcanism, extension, and a high thermal gradient produced hydrothermal mineralization including epithermal deposits (e.g., Schalamuk et al., 1997) and their surface expression, hot spring deposits (e.g., Channing et al., 2007; Guido and Campbell, 2009; Guido et al., 2010). Hot spring sinters and cherts at San Agustín (Figs. 1-7) occur as part of the Bahía Laura Group (Middle to Upper Jurassic), within an area of extensive La Matilde Formation (Upper Jurassic) lacustrine sediments (>30 km²). These filled fault-related Jurassic valleys within a terrain composed dominantly of Chon Aike Formation ignimbrites. Siliceous sinter deposits developed above faults with geothermal fluid up-flow (Guido et al., 2010). Thus, the San Agustín deposit represents a laterally extensive and nearintact geothermal landscape in which hot spring and "normal" terrestrial/lacustrine deposits are exposed side by side. Excellent exposure allows a rare opportunity for observations of original lateral and vertical relations among the various hot spring subfacies present. It also enables the recognition of paleoflow directions from hot spring vent areas, across sinter aprons to geothermal wetlands, and from there into either peripheral terrestrial or lacustrine clastic depositional environments (Guido et al., 2010).

SYSTEMATICS

Division—Tracheophyta Sinnott, 1935 ex Cavalier-Smith, 1998

Subdivision—Euphyllophytina Kenrick and Crane, 1997

Class—Equisetopsida Agardh, 1825

Order—Equisetales Dumortier, 1829 *Family*—Equisetaceae *sensu* Good, 1975

Genus—Equisetaceae sensu Good,

Species—Équisetum thermale Channing, Zamuner, Edwards et Guido sp. nov., Figs. 1-7, 10-53.

Specific diagnosis—Rhizomatous, perennial plants with short and narrow, articulated, infrequently ramified, monomorphic, aerial shoots with alternating surface furrows and simple convex ridges. Shoot segments consisting of diaphragms and leaf-sheaths at nodes and narrow pith canal at internodes. Shoots with up to 12 ridges, furrows, carinal canals, vallecular canals, and leaf segments. Superficial stomata arranged in vertical files and irregular horizontal bands within stem furrows. Subsidiary cell inner periclinal wall thickened with radiating and sometimes bifurcated striations. Double-layered palisade parenchyma below epidermis, except at nodes and within leaf-sheath. Regions of deep-seated, angular collenchyma radially aligned with stem ridges occasionally fuse to form cylinder; continuous internal and external endodermes. Trichomes developed on leaf adaxial surface of rhizome buds.

Note: This diagnosis highlights in *Equisetum thermale* a novel combination of the characters that delimit the two extant subgenera of *Equisetum (Hippochaete* and *Equisetum)* plus the limited number of characters that are unique to the species.

Holotype—Plant preserved in longitudinal section (Fig. 5) in part and counterpart of permineralized slab MPM-PB 2029,

housed at Museo Padre Jesús Molina, Río Gallegos City, Santa Cruz Province.

Collecting locality—San Agustín Farm, Santa Cruz province, Argentina (70°21'31.67"W; 47°39'10.88"S).

Stratigraphic position and age—Bahía Laura Group, Middle to Upper Jurassic, Callovian to Tithonian.

Etymology—The specific epithet *thermale* refers to the hot spring habitat in which the species lived and was preserved.

RESULTS

The articulated shoot system of the plant comprises aerial stems and underground rhizomes with the same fundamental siphonostelic construction. The leaves, attached at the nodes of aerial stems and some rhizomes, with their number equivalent to that of the ridges on the internode surface, are united for parts of their length into a sheath. Branching is infrequent but when present is strongly ascending (i.e., orthotropic) and asymmetrical, with one lateral branch at each node. Roots arise from nodes on the rhizomes and bases of aerial stems. Strobili have not yet been discovered attached to aerial stems, but monomorphism is suggested because all stems found in the chert have the same overall anatomy and morphology. General morphology of *Equisetum thermale* is reconstructed in Appendix S1 (see Supplemental Data online at http://www.amjbot.org/cgi/content/full/ajb.1000211/DC1).

Description of aerial stems—Slender stems are organized into characteristic nodes and internodes (Figs. 5, 10, 14, 15) 0.7–4 mm (\overline{x} = 1.65 mm, n = 215) in diameter and up to 10 cm long. Aerial shoots, perpendicular to an underground rhizome, are almost uniform in size, ascending, ribbed, and polygonal in transverse section (TS). Stems have 6-12 convex (as opposed to biangular) ridges (commonly 8) (Figs. 11-13). Internodes are variable in length from 1–10 mm ($\overline{x} = 4$ mm, n = 20). Internode lengths decrease near the stem base (Figs. 5, 15) and apex (Fig. 14) to approximately 0.1 mm. Stems have an internodal circular central pith canal (Figs. 11, 20) 200-550 µm in diameter ($\overline{x} = 400 \ \mu m$, n = 41), which is ~15–35% of the diameter of the stem. The pith canal is surrounded by isodiametric polygonal cells with thick, unpitted walls that lack intercellular spaces. In the absence of evidence of wall chemistry, we cannot determine whether such cells are parenchymatous or sclerenchymatous. Partially embedded in this tissue is a ring of vascular bundles (Figs. 11, 20, 21) equal in number to, and radially aligned with, the external stem ridges. Collenchyma, which occurs on the same radius, comprises triangular or tangentially elongated rhomboidal shaped areas (seen in TS in Fig. 11 and in longitudinal section [LS] in Fig. 19) up to 7 layers deep. These tissues may fuse laterally to form a cylinder. Some cells may have angular thickenings, though others are relatively thinwalled (Fig. 11). Both cell types are better preserved than surrounding cortical parenchyma. Beneath the epidermis is a double-layered palisade parenchyma (Fig. 19) comprising radially elongated cells lacking abundant intercellular spaces. Hypodermal cells appear to have slightly thickened outer periclinal walls (Figs. 11, 12). The remaining cortex is mainly parenchymatous; cells are generally thin walled, round in outline in TS, and elongated in LS. Those lining vallecular canals are thick walled on the sides adjacent to the lacunae. Vallecular canals alternate with external ridges. They range in size from 110-250 μm radially and 300-450 μm tangentially, and their cross section

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Figs. 1–9. Field images, chert block macrotextures, and extant and fossil Icelandic *Equisetum*. **1**. Vertical section through supra-apron pool deposit with abundant vertically aligned and monotypic stand of *Equisetum* stems (arrowed). **2**. Bedding parallel section through supra-apron pool chert with closely spaced transverse sections of stems. Stem cut at approximates level of node (arrowed and inset box) has distinctive "cartwheel" appearance. **3**. External morphology of leaf sheath; leaf tips obscured by chert matrix. **4**. Vertical section of cut block with alternation between dark root horizon and lighter chert formed above the sediment surface. Vugs with white to clear centripetal chalcedony and quartz bands represent intrastem porosity filling. Stems (arrowed) show node-internode construction and central vascular cylinder. **5**. Close-up of stem (illustrated bottom right of 4). Basal two nodes are closely spaced, while third internode is elongated. Closely adpressed leaves are visible at second node, and dark colored area at third node represents the

ranges from ovate to triangular (Fig. 12). Vallecular canals are restricted to internodal regions. The epidermis is uniseriate and thickly (~5-7 µm) cutinized (Figs. 23-25, 30, 31). In paradermal sections, cells of ridges are vertically rectangular and arranged in vertical and almost horizontal files (Figs. 23, 24). In furrows, cells are vertically rectangular to square and are arranged in vertical files that are interrupted by stomata (Figs. 23, 24). Anticlinal cell walls in both sites are straight when sectioned near the inner edge of the epidermis (Figs. 23, 24) but are tessellate when sectioned near the outer surface (Figs. 23, 32). In TS, epidermal cells decrease in size from the ridges to the centers of furrows (Figs. 11, 35). External periclinal walls have a convex surface and an ornament of a single mamilla per cell (Fig. 25). Superficial (nonsunken) stomata form irregular horizontal bands that cross furrows (Figs. 23, 24). They also are organized into vertical files with occasional paired stomata (Figs. 23, 24). In TS, the stomatal complexes comprise a pair of external subsidiary cells (cover cells) that completely overarch the guard cells (Figs. 27, 28). Subsidiary cells are thick walled and cutinized. Silica encrusts their external surfaces (Fig. 27). Internal periclinal walls have radial striations (ribs and furrows) that sometimes bifurcate (Fig. 29). Subsidiary cells are 40-50 μm long and 12–15 μm wide; the aperture is 6–7 μm wide (Figs. 23–25, 27–29). The outer surfaces of the subsidiary cells may have isolate pilulae but more commonly have a massive silica covering. The external surfaces of the subsidiary cells are ~30 µm below the peaks of adjacent epidermal cell mamillae, giving the impression of sunken stoma, though the cover cells and guard cells form part of the epidermal cell layer. Guard cells are of a similar size and shape to subsidiary cells (in paradermal view) but with thinner and more translucent, unornamented walls.

The peaks of mamillae commonly have dome-shaped silica pilulae \sim 5–7 µm wide (Fig. 30). In the furrows, silica is deposited on the apices of mamillae. Fusion between adjacent epidermal cells forms silica bars that traverse furrows parallel to the bands of stomata (Figs. 23, 24). Occasionally the bars anastomose around stoma. Mamillae and silica encrustation of epidermal cells create a distinctive saw-blade–like appearance when stems are viewed in LS (Figs. 10, 23–25, 33) and are most highly developed on sections exposed above leaf sheaths. Areas within sheaths have a more subdued topography. Silica deposition appears in general to be greater in the distal regions of stems and internodes. Basal nodes and rhizomes lack or have reduced silica.

The siphonostelic vascular cylinder has discrete bundles, variable in number depending on the diameter and relative position within the stem. Basal nodes have up to 12 bundles, decreasing to six in the apical regions. Each bundle possesses a distinct carinal canal opposite the ridges of the stem (Figs. 11, 20, 48). Xylem is mesarch with annular, helical, and scalariform tracheids (Fig. 22). The carinal canal, which is generally elliptical in TS, has a radial length ~80–140 μ m and a width of 50–70 μ m (Figs. 11, 20, 48). Each canal generally has 2–4 (exceptionally 7–9) protoxylem tracheids scattered around its border. Tracheid diameter (TS) ranges between 8 and 24 μ m (Figs. 22, 48).

Metaxylem tracheids occur laterally at either side of the vascular bundle as wedge-shaped groups of ~4–7 (exceptionally 8– 12) cells that partially enclose the phloem (Fig. 48). Endodermal layers (with Casparian strips) occur both on the outside and inside of the ring of vascular bundles (Figs. 47, 48). At nodes, the vascular tissue forms a complete ring, and the pith is totally filled with parenchyma with a low volume of intercellular space (Fig. 21). Cell size increases toward the center (Fig. 21). The vascular tissue forms omega-shaped bundles that fuse laterally (Fig. 21). Alternation of bundles and emission of foliar traces produce the characteristic trifurcation present in *Equisetum* in the vascular transition between adjacent internodes (Fig. 34).

Branch traces emerge at an angle of 90° from the main vascular cylinder (Figs. 16–18) and thence to the periphery of the stem. Branch internodes are hollow. The bases of branches have numerous short internodes and nodes with leaf whorls, with the first internode shorter than the subtending sheath (Figs. 16–18). Branch diameter increases rapidly at each successive node, showing an active epidogenetic growth.

Nodes are not swollen. Stem diameter increases only slightly in the areas of whorls (Fig. 10). The latter comprise up to 12 distally directed, adpressed, single-veined, basally fused, scale leaves (Figs. 11, 13, 35, 36). Leaf number at each node is equal to the number of stem ridges and vascular bundles. Leaf disposition alternates from node to node so that the leaf always lies within the furrow of the succeeding stem internode. Leaves are 3-5 mm long, slender, lanceolate, ribbed, and connate (Figs. 3, 10, 13, 35), with the distal end single, free, acute, and smooth (Fig. 37). They are wide rhomboidal (or wide ellipsoidal when free) in cross section and have one terete vascular bundle situated below the adaxial surface (Figs. 13, 35, 36). Ground tissue is parenchymatous (Figs. 35, 36). Leaves are bifacial with weakly developed abaxial palisade (Figs. 10, 11, 35, 36). This is absent when the leaf is free (Figs. 13, 36). The abaxial epidermis, especially in the basal, fused region, has large cells with a thick cuticle and dense silica deposits. The adaxial surface has thin and uniformly sized cells that are only lightly silicified (Figs. 11, 13, 33, 35-37). Abaxial epidermal cells (Figs. 11, 13, 35, 36) increase in size from the leaf margin (minimum diameter ~13 μ m) toward the midrib (maximum diameter ~45 μ m). A file of superficial stomata and subsidiary cells occurs on each side of the midrib (Figs. 35, 36, 28). Cuticle thickness and the differences in size and shape between cells of the epidermis and mesophyll are reduced in the upper part of the leaf (Fig. 37). Sheaths are divided into segments by furrowed commissures (Figs. 3, 11, 35). Furrows are underlain by tangentially elongated, thickened cells (Figs. 26, 35). Vegetative apices possessing leaves are rare. The bud-like apex (Fig. 15) has approximately 3–5 whorls of long, slender leaves arising from closely spaced nodes up to 0.8 mm long. The combination of leaf characteristics suggests that leaves, including their tips, are persistent.

Description of rhizome and roots—The creeping rhizomes (Figs. 38–40) have a similar node/internode construction to aerial stems but are less strongly ribbed and subcircular in TS. They have fewer and less well-developed leaf whorls (except at

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nodal diaphragm; longitudinal ribs visible within the stem represent vascular bundles. Possible rhizome is preserved at base of stem. **6.** Section through block of geothermally influenced wetland chert with rare, elliptical fern stipes (arrows) and abundant remains of *Equisetum*. **7.** Section through cut block of geothermally influenced wetland chert. Woody conifer branch with well-preserved lignified tissues (left) is surrounded by variably preserved *Equisetum* stems. **8.** *Equisetum* sp. growing adjacent to an alkali-chloride hot spring vent on Iceland. **9.** Holocene sinter block from Iceland containing abundant fragments of silicified *Equisetum* stem.



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the tips). One to three (exceptionally 7–9) layers of thick-walled, sclerenchyma-like cells occur below the epidermis (Fig. 40). Vallecular canals are larger than in the aerial stems. The cuticle is thinner and lacks sculptured silica deposits (Fig. 40). The same rhizome produces a number of adjacent aerial stems. Rhizome buds comprise pointed groups of superposed leaf sheaths with over-arching free leaves (Fig. 38). Bud adaxial leaf surfaces have rows of unicellular trichomes (Fig. 39). Abaxial surfaces have two longitudinal files of stomata.

Roots occur very abundantly and often are densely matted (Fig. 41). They are up to ~400 μ m in diameter (range 120–390 μm , $\bar{x} = 230 \mu m$, n = 40) and possess a small, central bundle exhibiting exarch xylem (Figs. 41-44). Approximately 2-4 tracheids occur within the protoxylem and 3--4 larger tracheids in the metaxylem; tracheids are annular and helical (Fig. 42). Vascular tissue is surrounded by a conspicuous pericycle and endodermis with Casparian strips (Figs. 43, 44). The inner cortex is aerenchymatous. The external cortex is parenchymatous but infrequently preserved (Figs. 42, 43). The root epidermis has large, relatively thick-walled cells (Figs. 45, 46). Commonly, roots develop from the basal region of erect stems and the bases of nodes of the rhizomes. Roots always branch at 90° angles. The smaller roots commonly have unicellular, thin-walled, unbranched, 300- to 450-µm-long root hairs. Each root hair is an extension of the central part of a cuboidal epidermal cell (Figs. 45, 46). Epidermal cells associated with the root-hair-bearing cells are longer than wide (Figs. 45, 46). Lateral roots form from basal regions of some stems, occurring up to 8 nodes above subtending rhizomes. Subterranean storage tubers are absent.

Description of associated reproductive structures-Although we investigated broad areas of hot spring environment dominated by Equisetaceae and recorded many thousands of examples of vegetative axes preserved in an environment where permineralization of the most delicate parenchymatous plant tissues is common, we have not discovered substantial numbers of strobili. We have identified six bractless, fragmentary strobili, plus a few isolated sporangiophores (Figs. 49-52). Of the six strobili, five are orientated as oblique sections relative to cut block surfaces (e.g., Fig. 51) and one as an LS (Fig. 49). All samples occur in close association with E. thermale stems, the only sphenophyte recorded in the deposit. The LS has a poorly preserved central axis (Fig. 49) with a general construction similar to E. thermale, though none of the plant's diagnostic anatomical characters are visible. Sporangiophore stalks are arranged approximately at right angles to the main axis in whorls (Fig. 49, arrows).

DISCUSSION

Equisetum thermale possesses all the general vegetative features that define the family Equisetaceae, including herbaceous, jointed, aerial, and subterranean stems, with numerous wiry roots, and very thin leaves with a single vein borne in whorls and joined in a sheath (e.g., Stanich et al., 2009). Growth in the plant was exclusively primary, and it has vascular anastomosis typical of the family (e.g., Stewart and Rothwell, 1993). The strobili conform in organization to those of Equisetaceae in that they lack subtending bracts between sporangiophores. Features that differentiate the Equisetaceae from other sphenophytes are tabulated in Stanich et al. (2009, Table 1).

Comparisons with anatomically preserved equisetalean fossils including Equisetites and Equisetum—A few Mesozoic and Cenozoic taxa are described from anatomically preserved plants that exhibit characters closely related with Equisetaceae and *Equisetum*.

Spaciinodum collinsonii and Equisetum bryanii—Spaciinodum collinsonii Osborn and Taylor (Osborn and Taylor, 1989; Osborn et al., 2000; Ryberg et al., 2008) from the Middle Triassic of Antarctica has a few features linking it to genus Equisetum (e.g., superficial stomata and tubers), but it is placed in a separate genus. A single character (the presence of superficial stomata) was used to link the plant very tentatively to the extant subgenus Equisetum (Osborn and Taylor, 1989). The slightly

Figs. 10–15. Stem morphology and anatomy. **10.** Slightly oblique longitudinal section (LS) through center of stem. Two nodes with anatomically preserved tissue are linked by the vascular cylinder and a hollow pith canal. The leaf sheath of the first node is only slightly swollen, and leaf tips remain adpressed to the subsequent internode epidermis. The saw-blade–like ornament of the epidermis is most strongly developed in those regions of the stem exposed above the level of the fused leaf sheath. **11.** Transverse section (TS) stem at the level of the fused leaf sheath. Leaves with obvious midribs (MR) on the abaxial surface flanked by shallow furrows (F) containing files of stoma are separated by deep commissures (C). Leaves aligned with the furrow of the stem. The obvious single-layered epidermis of the stem comprises cells that increase in size from stem ridges toward furrow centers. Remnant radially elongate cells of the palisade parenchyma occur below the epidermis (white arrows), as do areas of the putative strengthening tissue (black arrows). Two dark vascular bundles with carinal canals occur toward the base of the vascular cylinder, and remnant parenchymatous cells of the pith canal. Centripetal chalcedony and quartz fill cavities within the stem. **12.** Stem (TS) at the young internode. Well-preserved double-layered palisade parenchyma cells (CP) form the margins of elliptical-circular vallecular canals. **13.** Transverse section stem at the level where leaf apices are free. Tissue decay has allowed collapse and distortion of the stem. Durable cells of the vascular cylinder persist in the stem, and tissue preservation is generally excellent in the free leaves. **14.** Longitudinal section basal region of stem with five closely spaced nodes. The stem with expands rapidly in the basal three nodes and stabilizes on the successive nodes. **15.** Longitudinal section: poorly preserved stem apex with closely spaced nodes and many leaf tips.

The best-preserved strobili are represented by associated groups of tightly packed hexagonal sporangiophores (Fig. 51). Each sporangiophore has a central stalk approximately 0.8 mm long and 0.1 mm wide (Fig. 50) that has small, radially arranged areas of helically thickened tracheids at the distal end (Fig. 52). The heads of the sporangiophores are about 1 mm in diameter, with a flat external surface, smooth cuticle, and an epidermis above a layer of parenchyma comprising cells that are elongated perpendicular to the sporangiophore surface (Figs. 50, 51). Sporangial walls are not preserved, but each sporangiophore is accompanied by aggregations of similar spores (Figs. 50-53). These are smooth, alete, thin walled, and spherical but sometimes partially collapsed or folded. Spore diameter (Fig. 53) is 26 to 40 µm, $(\bar{x} = 33 \ \mu m, n = 50)$. We have not observed apertures, haptotypic marks, or convincing elaters.

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younger species *Equisetum bryanii* Gould (Gould, 1968) from the Jurassic of Australia, based on the same character (but few anatomical data), was assigned to the genus *Equisetum* (Gould, 1968). No diagnostic anatomical features link these plants closely to *E. thermale*.

Equisetites lyellii—Equisetites lyellii Mantell emend. Allen, from the Lower Cretaceous (Purbeck and Wealden Groups) of southern England (Allen, 1941; Watson, 1983; Watson and Batten, 1990), like E. thermale, was a wintergreen plant that lacked tubers. Other similarities include the presence of slender, strongly sculptured leaves united by thick commissures until close to their toothed apex, rectangular epidermal cells with sinuous walls, and broad longitudinal bands of stomata. Stomata are oval and superficial in both species, but those of E. lyellii are also ornamented with a beaded external sculpture along the slit-like aperture and around the distal margin. Annular thickenings are present in vascular bundles in both taxa, but E. thermale additionally produces tracheids with helical and scalariform thickenings. Associated strobili in E. lyellii with circular sporangiophore heads (Watson, 1983; Watson and Batten, 1990) differ from the hexagonal morphology in E. thermale. However, both species produce alete spores. Several major features distinguish E. lyellii from E. thermale, most notably E. lyellii had (probable) dimorphic aerial shoots (see discussion in Watson and Batten, 1990), and its vegetative shoots bore radial and regular whorls of branches. Leaf sheaths of E. lyellii have large numbers of leaves (up to 26), and ridges of stems are biangulate, whereas E. thermale has low numbers of leaves and convex ridges. Additionally, the rhizomes of E. lyallii are very large (up to ~ 2 cm in diameter) as compared with those of *E. thermale* (up to ~4 mm in diameter). Anatomical differences between the two species include, within E. lyellii aerial stems, the presence of an extremely large pith (~50% of the stem diameter), relatively small vallecular canals, and an outer cortex with small, triangular bundles of sclerenchyma that are aligned radially between the vallecular canals. Two characters in E. lyellii separate the species from the remaining extinct Equisetum-like plants: the vascular bundles, constructed of up to 14 tracheids, have a crescent-shaped TS, and the vascular system produces small subsidiary vascular traces of uncertain nature. Equisetites lyellii shares features with both subgenera Equisetum and Hippochaete (Milde) Baker, but most features (e.g., large canals, numerous leaves, biangulate ridges, triangular bundles of sclerenchyma related with vallecular canals, stomata length/width ratio, and ornamented, beaded external sculpture on subsidiary cells) align the plant more closely with the latter (Hauke, 1963).

Equisetum haukeanum and E. vancouverense—Equisetum haukeanum and E. vancouverense Stanich et al. from the Lower Cretaceous, British Columbia (Stanich et al., 2009), have narrow stems with a maximum diameter of 2 mm and short internode length (available from a single stem fragment) of up to 5.7 mm. Both have low numbers of leaves and ridges (5-7). Leaves are fused in whorls and adpressed with free tips that appear persistent. Both species are infrequently branched. These morphological features are shared with those of Equisetum thermale, Equisetites minimus Falaschi et al., and *Équisetites pusillus* Villar de Seoane (discussed later). The anatomical features that these species share with E. thermale include epidermal cells in vertical files. Central pith, carinal, and vallecular canals are uniformly small. Vascular bundles are deep seated. Low numbers of protoxylem tracheids border carinal canals, but metaxylem is absent from areas bordering the phloem. Sclerenchyma is poorly and discontinuously developed. In E. haukeanum, sclerenchymatous bundles occur below the epidermis in the ridges, but in E. vancouverense, the sclerenchyma is described as occurring toward the periphery of the cortex as in E. thermale. In E. haukeanum, a well-developed palisade parenchyma appears in basal regions of the leaf sheath (their Fig. 1), and apparently thin-walled parenchymatous cells occur directly below the internodal epidermis (their Fig. 7). Major differences between the two species and E. thermale are the apparent presence of double files of stomata in E. haukeanum, and the presence of individual endodermes surrounding each vascular bundle together with biangulate and concave stem ridges in E. vancouverense. The two species are most easily associated with the extant subgenus Hippochaete because they have irregular branching, though, as with E. thermale, the plants show a mixture of characters of both subgenera (Stanich et al., 2009, Table 2).

Equisetum clarnoi—*Equisetum clarnoi* Brown from the Eocene Clarno Chert of Oregon (Brown, 1975) was described from four silicified stem fragments and numerous small roots. On the basis of anatomical characters, including the presence of sunken stomata organized in single files on the margins of furrows, a double common endodermis, and irregular branching, the plant appears to be allied to extant subgenera *Hippochaete* (e.g., Brown, 1975; Stanich et al., 2009). The two latter characters of the plant are shared with *E. thermale*. Other shared characters include the presence of vallecular canals lined by thick-walled parenchyma cells and similar numbers of protoxylem tracheids lining the carinal canals and flanking the phloem in vascular bundles. Roots of *E. clarnoi*, up to 2.0 mm in diameter, with paired cuboid epidermal cells from which root hairs arise

Figs. 16–22. Stem branching, palisade parenchyma, and vascular cylinder. **16.** Poorly preserved branching stem (longitudinal section [LS]). Branch is emitted approximately at the level of the main stem node (N) at an acute, ascending angle. Leaf sheaths of first- and second-order branches (FS) are preserved. A possible third-order branch (arrow) occurs near the second-order branches base. **17.** Transverse section (TS) stem at level just below nodal diaphragm. Branch emerges through leaf sheath. **18.** Branch emission magnified. Branch trace (arrowed) is preserved within stem. Vascular cylinder in branch expands and encloses pith (P) below the first nodal diaphragm of the branch. **19.** Stem (LS) with well-developed palisade parenchyma (PP) below epidermis (E), and elongated cells of the putative strengthening tissue (S) occur outside parenchymatous cortical cells (CP). **20.** Vascular cylinder from internode region. Eight vascular bundles (e.g., VB) and inner endodermal layer (IE) enclose circular pith canal. Well-preserved bundle at top of image has small circular canal (acut (C) and wedge-shaped bundles of metaxylem tracheids that partially enclose the phloem (P). The outer endodermis (arrow) forms the inner margin of the vallecular canals (e.g., V), while cortical parenchyma with walls thickened on the surfaces facing the canal line the lateral margins. **21.** Vascular cylinder at a level of nodal diaphragm. Central pith (P) of parenchymatous cells occurs within vascular cylinder with omega-shaped vascular strands (e.g., arrowed); dot at right is a foliar trace. **22.** Poorly preserved stem vascular strands (oblique LS) with annular, helical, and scalariform tracheids.



and a central stele with exarch xylem, are strikingly similar to those of *E*. *thermale*.

Significant differences between *E. thermale* and *E. clarnoi* include, in the latter, wider stems (up to 8 mm), a much larger percentage of the stem taken up by the central pith canal, a more-completely fused leaf sheath, smaller vallecular canals, and a very prominent hypodermis with long and short, alternating radially elongated bundles of fibers.

Comparisons of Equisetum thermale with compression fossil equisetaleans including Equisetites—Compressions of Equisetum-like plants (genus Equisetites) are conspicuously present from the Upper Triassic onward. Some have well-preserved, comparable morphological features that offer opportunities to discuss relations between the genus and E. thermale. Comparisons are, however, hampered by a paucity of species in which strobili are known, most being preserved only as fragmentary segments of aerial stems, lacking detailed anatomy. This is true for most species of Equisetites known from Argentina and Gondwana (see Appendix S2), where most of the characters are restricted to size of stems, internode lengths, number of leaves and ridges, and degree of leaf fusion and leaf orientation (adpressed/spreading). However, two compression species of Equisetites, both from Santa Cruz province, E. minimus (Upper Jurassic: Falaschi et al., 2009) and E. pusillus (Lower Cretaceous: Villar de Seoane, 2005), exhibit characters more closely comparable to E. thermale and deserve special attention. Both plants are small, with observed stem heights of 10 and ~5 cm respectively, and stem diameter ranges of 0.5-1.9 and 2.7-3.0 mm, respectively. Internode lengths are short (5.5-13 and 5.0-10 mm, respectively). Both species have fused leaf whorls with adpressed leaves; free leaf lengths are in the range of 1-2.5 and 1-5 mm, respectively. Stems of both species have low numbers of leaves and stem ridges (4-6 and 12-13, respectively). Both species have attached terminal strobili with generally hexagonal sporangiophore heads. Stems of E. minimus are unbranched; those of E. pusillus may branch once. Epidermal cells of stems and leaves form vertical files in E. pusillus. In E. minimus, the stems and foliar sheath have surface micro-ornaments of transverse bars and ridges. A similar surface ornamentation was possibly present in the sheaths of E. pusillus. Both species have leaves with prominent midribs. Spores are yet to be recorded from *E. minimus*. *Equisetites pusillus* spores are spherical to subspherical, small (46–69 μ m), and alete, with an exospore that is smooth to slightly scabrate. They lack elaters. *Equisetum thermale* spores are smaller but morphologically similar, and the exospore is not sculptured. Both E. minimus and E. pusillus fertile and vegetative stems show identical general

morphology, indicating that both species are monomorphic. Many of the available characters of these two plants fall within the ranges of variation for those we have observed in *E. thermale*. Although available evidence suggests that all three species are closely related, the lack of anatomical features in the compressions and the fragmentary nature of the strobili of *E. thermale* prevent more detailed comparisons of *E. thermale* with either species.

Comparisons of Equisetum thermale with extant crown group subgenera—The anatomical features of E. thermale indicate it shares characters with both crown subgenera (see Appendix S3). Such characters most commonly fit with those of the subgenus *Hippochaete* (Hauke, 1963). *Equisetum thermale* is evergreen, monomorphic, unbranched or with irregular ascending branches, has leaf apices that are persistent, and a double endodermis. Features of E. thermale that are shared with subgenus Equisetum include highly sculptured silica deposits, convex external ridges, stomata scattered or occurring in broad bands within furrows, and the first internode of branches is shorter than the subtending sheath (Hauke, 1978). A number of features of the subgenus Equisetum are absent in E. thermale and the subgenus Hippochaete. These include tubers, deciduous aerial stems and leaf apices, regular and common branching, and a single, external common endodermis.

Other features of *E. thermale* that do not appear to have taxonomic value in distinguishing between the subgenera but do provide striking examples of structures present in extant species of *Equisetum* include stomatal complexes comprising guard cells overlain by subsidiary cells with a radial striated ornament on their inner wall (Fig. 29; cf., e.g., Hauke, 1957; Pant and Kidwai, 1968; Page, 1972; Kaufman et al., 1973), the radially elongated cells associated with the leaf sheath commissure (Fig. 26; cf., Pant and Kidwai, 1968, Fig. 3a), rhizome bud construction, and presence of trichomes on rhizome leaf adaxial surfaces (Figs. 38, 39; cf., Hauke 1987, Figs. 1–7). These features do not appear to have been previously documented in fossil *Equisetum* species.

The most obvious difference between *E. thermale* and extant species is the presence of a strongly developed and apparently continuous palisade parenchyma occurring outside, rather than below, the collenchyma bundles/layer (or sclerenchyma of some authors). However, palisade parenchyma that is either discontinuous (occurring only below furrows) or continuous (occurring below furrows and extending below collenchyma bundles) is reported from species of the subgenus *Hippochaete*, e.g., *E. giganteum* L. and *E. laevigatum* Engelm. (Brown, 1975); the relative position of the two tissues were not considered of phylogenetic significance by Hauke (1963).

Figs. 23–32. Epidermal and cuticular features. 23. Cuticle and epidermis in paradermal and longitudinal section. Area of missing tissue (star) corresponds to a stem ridge. Inset left, stomata and epidermal cells within furrow. Inset right, epidermal cells of stem ridge. 24. Stomata and transverse bars typical of stem furrows. Stomatal pores form files that are aligned with stem longitudinal axis. Stomata traverse furrow in irregular bands separated by bars formed of coalesced silica deposits on mamillae of epidermal cells, which occasionally bifurcate around stoma. 25. Longitudinal section of epidermis and cuticle from 23. Subsidiary cell external surfaces occur in positions several tens of microns below the peaks of adjacent epidermal cell mamillae, giving a sunken appearance. Knobs of silica occur on the apices of mamillae (e.g., arrows). 26. Paradermal section of leaf-sheath with transversely elongated cells of the sheath commissure (e.g., arrows). 27. Transverse section (TS) stem epidermis and stomatal complex. Guard cells (GC) are thin-walled and lay inside the overarching subsidiary cells (SC). Subsidiary cells are thickened on inner surfaces and encrusted with silica on external surfaces. 28. Transverse section epidermis and stomatal complex of leaf abaxial surface. Guard cells (GC) are thin-walled and occur below cover cells (SC). Parenchyma below stoma appears to form a substomatal cavity (SSC) and has intercellular air spaces. 29. Inner surface of subsidiary cells viewed from within stem. Upper cell has distinctive radial striations. 30. Epidermal cell mamillae with thick (silica impregnated?) cuticle and pair of merged hemispherical silica pilulae. 31. Stem epidermal cells in TS with spine-like (organic?) projections from their lateral margins. Silica impregnated cuticle of uniform thickness coats lateral and external walls. 32. Paradermal section of stem ridge with tessellate epidermal cells.



Figs. 33–39. Stem and leaf anatomy. **33.** Enlargement of stem nodal region (longitudinal section [LS]) in Fig. 10. Abaxial epidermis of upper leaf has obvious saw-blade ornament, while abaxial surface of lower leaf, which is cut close to the plane of the line of epidermal cells in the leaf furrow, has smaller epidermal cells and reduced ornament. **34.** Moderately degraded LS of stem revealing organization of vascular bundles as they split and fuse again at the node. **35.** Leaf at level of fused sheath magnified. Abaxial surface comprises epidermal cells that increase in size from leaf margin to central rib. Stomata

Structural features of the strobili are similar to those of *Equisetum*, though details of the sporangial wall characters are absent in the fossil. Instead, masses of abundant alete spores occur in the position of sporangia. These differ from extant *Equisetum* in that they lack elaters. Most of the spores are spherical but are smaller in size (mean diameter \sim 33 µm) than those in the subgenera *Equisetum* (47–53 µm) and *Hippochaete* (48–61 µm) (Duckett, 1970). This difference and the presence of distorted and folded thin-walled spores in the fossils might indicate immaturity, but this would not account for the lack of elaters. Duckett (personal communication, 2010), having studied size ranges and germination frequencies in the extant subgenera, has observed elaters in both aborted and immature spores. Failure of preservation of elaters remains a possibility, especially because the sporangial wall is not preserved.

Reference to Appendix S3 shows that the combination of characters exhibited by *E. thermale* has many parallels in the sole surviving species of *Equisetum* from the sister group to the two extant subgenera, *E. bogotense* Kunth. However, features of this plant differ from *E. thermale* in the presence of a solid central pith, biangulate stem ridges, and an external common endodermis.

Justification for erecting a new species—From the above comparisons it is clear that *E. thermale* does not fit exactly within any extant or fossil species of *Equisetum* or within *Equisetites*. However, the set of characters we have described are considered sufficient to allow its placement in genus *Equisetum* with the epithet "thermale" signifying the hot spring deposits in which it was discovered. The Late Jurassic species *E. thermale* is the earliest known representative of the extant genus *Equisetum* that shows the main characteristics including all typical anatomical features.

Ecology and ecophysiology—Extant species of *Equisetum* have an association of xeromorphic (thick cuticle, sunken or protected stomata, and reduced leaves) and hydromorphic (air chambers and reduced vascular tissue) characters (e.g., Hauke, 1978). This allows them to colonize habitats with a range of edaphic conditions. *Equisetum* may grow in diverse habitats but predominantly occurs in wet places such as shallow ponds, marshes, wet meadows, seepage slopes, ditches, stream banks, salt flats, and moist woodlands (Hauke, 1978; Page, 1997). Some extant species may give the impression of living in xeric conditions, e.g., when growing up through sandy or gravelly substrates on roadsides or railway embankments, but even in these settings, the plant's rhizome system penetrates to saturated soils below (Hauke, 1978).

Extant *Equisetum* often colonizes stressed environments. It is commonly found in environments with high concentrations of heavy metals (e.g., Siegel et al., 1985; Barghigiani et al., 1989; Hozhina, et al., 2001; Deng et al., 2004; Chang et al., 2005; Cornara et al., 2007; Mir et al., 2007). *Equisetum* is a common member of communities associated with saline soils

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and oligohaline to saline wetlands (e.g., Williams, 1991; Boggs, 2000; Funk et al., 2004; Purdy et al., 2005; Van der Hagen et al., 2008). Equisetum species may be tolerant of high pH, alkalinity, and calcareous soils and water conditions in alkaline wetlands, fens, and lakes (e.g., Mäkelä et al., 2004; Mayes et al., 2005; Hájek et al., 2006). Equisetum is also a characteristic early pioneer species on disturbed ground (e.g., Hauke, 1963; McFarland et al., 2002; Bardgett and Walker, 2004; Geertsema and Pojar, 2007; Milner et al., 2007). Equisetum species are early colonizers of volcanic ash-fall environments (e.g., Siegel et al., 1985; Adams et al., 1987) and are among the first recorded colonizers of ash plain and newly created wetland environments associated with Mount St. Helens (e.g., Siegel and Siegel, 1982) and Japanese volcanoes (e.g., Tsuyuzaki, 1987, 1997). Equisetum also may dominate nutrient-poor environments including oligotrophic lakes (e.g., Sarvala et al., 1982).

Importantly, in the context of this paper, *Equisetum* colonizes mineral- and geothermal-spring environments (e.g., Fig. 8; Siegel et al., 1985; Barghigiani et al., 1989; Moseley, 1995; Juday, 1998). In these settings the plants grow with high levels of environmental Hg/As plus other phytotoxic elements. The ability of *Equisetum* to tolerate and uptake As, Hg, and Sb allows it to colonize soils above mineralized and altered parent rocks such that the plant has been used in bioprospecting as a guide to the presence of gold mineralization (e.g., Warren and Delavault, 1950; Brooks, 1979; Brooks et al., 1981).

A limited number of records exist of sphenophytes associated with ancient hot spring environments. Walter et al. (1998) reported sphenophytes from the Upper Devonian hot spring sinters of the Drummond Basin, Queensland, Australia. At East Kirkton, Scotland, Lower Carboniferous marsh environments around an alkaline hot spring-influenced lake provided habitat for sphenophytes (e.g., Brown et al., 1994). Equisetum clarnoi (Late Eocene, Clarno chert) inhabited similar environments (Brown, 1975). An unnamed species of Equisetum of the subgenus Hippochaete is reported from travertine deposits associated with Mio-Pliocene volcanic rocks of the Central Valley of Costa Rica (Gómez, 1978). Baron (1889) recorded Equisetum in a siliceous sinter deposit close to extinct volcanic craters, near Ambhidratrimo, Madagascar. Equisetum occurs in situ in great numbers in Holocene sinter deposits at the Geysir thermal area, Haukadalur valley, Iceland (Fig. 9).

Ecology of Equisetum thermale—The San Agustín hot spring deposit offers an excellent opportunity to explore aspects of the ecology and ecophysiology of the preserved plants. Plants at the locality were preserved in situ within environments where a combination of observations of the disposition of fossiliferous subenvironments, matrix chert fabrics, and biotic associations allow fossil distribution to be tied, via analogy drawn from observations of active thermal areas, to physical and chemical conditions experienced during plant growth (e.g., Channing and Edwards, 2004; 2009a, b).

occur in two furrows on either side of the midrib (arrows). The commissures at the leaf margin are underlain by broad U-shaped cells (e.g., C). Adaxial epidermal cells are small relative to abaxial cells. Palisade-like parenchyma of the leaf surrounds the small vascular bundle situated toward the adaxial margin of the leaf. Cells of the stem epidermis are elongated radially and in the upper corner of the image are underlain by radially elongated parenchyma of the outer palisade layer of the stem (P). **36.** Transverse section (TS) free leaf. Differences in cell size between adaxial and abaxial surfaces are less distinct as is the leaf midrib. Vascular bundle occupies a more central position within the leaf mesophyll. **37.** Longitudinal section through leaf sheath illustrating palisade parenchyma (PP), abaxial epidermal ornament, and LS of midvein (arrow). **38.** Longitudinal section of acute free leaf with unornamented adaxial surface and reduced abaxial ornamentation. **39.** Leaves of rhizome bud leaf sheath with trichomes arising from adaxial surface.



Equisetum thermale dominated two hot spring subenvironments: supra-apron pools and geothermally influenced wetlands. In both settings, inflow of hot spring water to the environment of plant growth is evident because sinter apron chert fabrics are developed vertically below and above and laterally adjacent to the plant habitat. Additionally, in each environment the persistence of plant growth can be demonstrated by the presence of stacked plant root and growth horizons.

Supra-apron pools—The best preserved supra-apron pool occurs at the Cerro Alto outcrop of Guido et al. (2010). This locality has broad areas of mid-temperature (estimated water temperature $40-55^{\circ}$ C) and low-temperature (estimated temperature less than 40° C) apron sinter (see Figs. 1 and 2 of Guido et al., 2010) that lack identifiable higher plant fossils. These deposits occur above, below, and laterally adjacent to a pool feature, which is defined by the presence of massive to mottled chert containing upright and in situ *E. thermale* (Figs. 1, 2, 4, 5). The massive pool-fill chert has a lenticular geometry and is 10–20 cm thick and 5–10 m in diameter.

Within supra-apron pools, the chert matrix is generally characterized by an opaque white color (Figs. 1, 2, 4, 5), suggesting the incorporation of relatively little amounts of degraded and dispersed organic material. In detail, vertical sections are seen to comprise 4-5 plant growth horizons represented by 3-5 cmthick alternations between relatively dense horizons with a beige-brown coloration. These contain roots and rhizomes within a litter of prostrate and partially decayed aerial stems and cleaner, whiter, more open horizons with parallel, vertically aligned, aerial stems (Fig. 5). In general, preservation in life-position of roots, rhizomes, and basal stems occurs to 4-5 cm, indicating a corresponding general water depth within pools. We have not observed any lithic clasts or ash horizons within the Equisetum-bearing chert and no true soil. This, and the presence of microbial meshworks between stems, might indicate that water entering the pool came predominantly from thermal sources from the adjacent apron. Horizontal sections through the chert bed (Fig. 2) reveal that stems were crowded together with densities of ~ 10 stems per cm².

Geothermal wetlands—At San Agustín, massive to mottled and diffusely bedded, distal apron margin cherts commonly overly silicified clastic deposits. In situ and vertically orientated *Equisetum thermale* stems and their roots and rhizomes occur commonly within the upper horizons of these outcrops. Matrix chert within this setting is generally dark and lithologically more variable than within supra-apron pools, indicating more

commonly fluctuating environmental conditions. Root horizons are extremely common. Well-preserved roots vertically and horizontally traverse an often thick litter, comprising prostrate aerial stems with variable preservation. In places, extremely thin-walled tissues are preserved intact. In others, the epidermis, delicate root hairs, and central vascular strand remain intact, while the ground tissue is degraded or absent. This contrasts with the often high level of decay of the fallen aboveground parts of the same plants. Although some fallen aerial axes have excellent preservation, many occur as cuticular/epidermal straws or fragmented cuticles. Dense carpets of in situ and inlife position Equisetum stems appear less common in the geothermal wetlands than in the supra-apron pool setting. This suggests a more patchy cover of vegetation on wetland surfaces. In many chert blocks, litter and roots appear to represent the same species. However, some blocks also contain fragments of ferns in lower horizons with monotypic Equisetum litter above (Fig. 6). Conifer cones, leafy axes, and seed scales are abundant in some chert blocks (Fig. 7) that otherwise contain only E. thermale, indicating the presence of a relatively close forested environment. Cones and leaves of pines are common components of geothermal wetland sediments in Yellowstone, where they are shed from trees growing at the periphery of, or on "dryland islands" within, the wetland complex (e.g., Channing and Edwards, 2009b).

Physical and chemical parameters in areas of Equisetum thermale growth derived from analogous active thermal areas-On the basis of observations of active hot spring and geothermally influenced wetland environments worldwide (e.g., Yellowstone, USA; Taupo, New Zealand; El Tatio, Chile; Iceland), typical physical and chemical parameters in the areas of plant growth at San Agustín would have been as follows: temperature in the range 35°C to ambient, salinity ~1.0–1.5 ppt (oligohaline), pH 7–9 and conductivity in the range 2.25–3.01 mS/cm. Major ions dissolved in the fluids include Si²⁺ (up to ~750 ppm), Na+ (up to ~550 ppm), Cl- (up to ~900 ppm), K+ (up to ~100 ppm), complex anions include SO_4^{2-} (up to ~100 ppm) and HCO_3^- (up to ~100 ppm) (e.g., Channing and Edwards, 2009a, b). Trace concentrations of ions, some of which are potentially phytotoxic, are also present, including Li⁺, Mg²⁺, Ca²⁺, F⁻, Mn²⁺, Fe²⁺, Al³⁺, B³⁺, As³⁺, Sb³⁺, Tl⁺ and Hg⁺ (e.g., Channing and Edwards, 2009a, b).

A typical extant plant living in these environments (e.g., *Eleocharis rostellata* Torr.) is a salinity- and alkalinity-tolerant emergent aquatic plant able to withstand high levels of metal and metalloid concentrations. Typically, although not exclusively,

Figs. 40–53. Roots, stem endodermis, and strobili. **40.** Part of rhizome (transverse section [TS]) with large vallecular canals separated by strands of parenchymatous cortical cells. Epidermis, which lacks silica ornament, is underlain by 2–3 layers of putative strengthening tissue. Cortical strands are radially aligned with vascular bundles (arrowed) **41.** Geothermally influenced wetland chert matrix with root horizon. **42.** Slightly oblique longitudinal section (LS) root with narrow central vascular strand. **43, 44.** Transverse section of root with central strand comprising protoxylem and metaxylem with a few larger tracheids occurring at the margin. The vascular bundle is surrounded by a pericycle, a conspicuous endodermis with Casparian strips (e.g., arrows), and two-layered cortex. **45.** External surface of root with files of elongated epidermal cells interspersed with shorter cells from which root hairs arise. **46.** Close-up of cuboidal cells with root hairs arising from central evagination. **47.** Poorly preserved vascular cylinder of stem with remnant Casparian bars of the inner (e.g., black arrows) and outer (e.g., white arrows) endodermes. Radially arranged features are remnants of the cortical cell strands forming the walls of the vallecular canals. **48.** Transverse section well-preserved stem vascular bundle. Casparian bars of the two endodermal layers occur as a semicircle in the poorly preserved cells above the bundle (e.g., white arrows) and as a line within the cells below the carinal canal (black arrows). Pholoem (P) is preserved within the area delimited by the outer edge of the carinal canal (CC) and wedge-shaped bundles of xylem. **49.** Poorly preserved LS section of strobilus with central axis and whorls of sporangiophore stalks (arrows). **50.** Sporangiophore with central stalk and in situ spores. **51.** Tightly packed hexagonal sporangiophore with four radially arranged vascular strands (arrowed). **53.** Spherical, alete spores contained in spore masses within strobilus. Dark areas within spor

such plants belong to families recognized as silicon accumulators (e.g., Hodson et al., 2005). Plants appear to favor vegetative rather than sexual reproduction, often forming monotypic stands of adjacent clones as they often do in ruderal habitats. Plants tend to be shallow rooting, in part because of the high water table but also because of difficulties involved in penetrating hard sinter substrates in apron settings (e.g., Channing and Edwards, 2009a, b; Channing et al., 2004). The dominant ecological characteristic of fossil hot spring flora since the Late Devonian is that the plants belong to families that are commonly associated with wetland conditions or damp to saturated soils (e.g., Cyperaceae in the Cenozoic [Channing and Edwards, 2009b; in progress work] and herbaceous lycopsids in the Late Devonian [e.g., Walter et al., 1998; in progress work]).

Equisetum thermale fits anatomically and ecologically extremely well with this model derived from observations of extant and other fossil hot spring plants. It shows clear anatomical evidence of adaptation to wetland settings, i.e., aerenchyma, that provide aeration for submerged or waterlogged roots/rhizomes capable of withstanding physiological (rather than actual) drought. It also has aerial stems with obvious xeromorphic characters including an epidermis with thick outer walls and well-developed cuticle and silica deposits. The plant does not have sunken stomata, but the subsidiary cells covering the guard cells are ~30 μ m below the peaks of silica deposits that form lateral bars across furrows. Pilulae on the walls of adjacent epidermal cells that project across the furrow and silica deposits on the subsidiary appear to further restrict the area above the stoma.

Equisetum thermale had a branching rhizome that produced extensive colonies of aerial stems. Very dense, shallow rootrhizome developed only mm to cm below sediment surfaces in geothermal wetland and supra-apron environments. We have observed numerous Equisetum thermale aerial stems in connection with underground rhizomes and apparent evidence of branching of stems and production of new aerial shoots across successive root horizons. We take the scant evidence of strobili within our samples to indicate the predominance of vegetative reproduction over sexual mechanisms. Vegetative reproduction via rhizomes, tubers (Sakamaki and Ino, 2006), and fragmentation (Hauke, 1963) is adopted by many extant species of Equisetum and their hybrids. Equisetum thermale appears to have adopted this strategy to successfully colonize and persist in stressed settings of the hot spring complex. Finally, the plant appears not to have developed subterranean storage tubers. Analogy with extant *Equisetum* of the subgenus *Hippochaete*, which lack tubers and are perennial, suggests the plant had evergreen aerial stems rather than underwent periodic dormancy.

In combination, the general characters of *E. thermale* suggest it was an emergent aquatic, tolerant of and apparently very well adapted to environmental stress. An abundance of groundwater supply and a lack of competition were key habitat requirements for the plant. As with extant plants of active thermally influenced wetlands (Channing and Edwards, 2009a, b), growth of *E. thermale* created monotypic stands that extended across broad areas of the San Agustín geothermal landscape.

Silicon uptake and biomineralization in Equisetum thermale—From the preceding notes on the ecology of the extant genus Equisetum, it is clear that many species are salinity tolerant (e.g., Williams, 1991; Boggs, 2000; Funk et al., 2004; Purdy et al., 2005; Van der Hagen et al., 2008). The alkalinity and salinity of hot spring waters suggest that *E. thermale* also was alkaliphilic and, more importantly, halophytic. The perennial stems of *E. thermale* indicate that over the life of the aerial stems, considerable volumes of water passed through the plant. This means the plant was capable of tolerating the uptake of salt and other dissolved constituents. We hypothesize that silicon uptake in *E. thermale* provided ecophysiological benefits that facilitated life in hot spring environments.

Silicon uptake is perhaps one of the most important defining characters of Equisetum. It is considered an essential element for extant Equisetum (e.g., Epstein, 1994, 1999), and their stems may have up to 25% dry weight silica (e.g., Kaufman et al., 1971). In extant Equisetum, silica deposits are associated predominantly with cells of the epidermis and the mamillae and pilulae projecting from the stem surface (e.g., Kaufman et al., 1971, 1973; Gierlinger et al., 2008). We interpret the distinctive silica deposits associated with similar locations on the stems of E. thermale, which have optical properties that differ from those of the matrix chert, as silica deposited in life by the plant. Silicon uptake in E. thermale resulted in the formation of stemencrusting deposits of opaline silica (now chalcedony or quartz) comparable to those of extant genera. In the extant species of Equisetum, silicon is considered to impart strength to cell walls and rigidity to the erect stems (e.g., Kaufman et al., 1971). Other functions may include the reduction of water loss through the epidermis and mechanical prevention of biotic stresses such as attack by pathogens and insects (e.g., Kaufman et al., 1971). Silicon uptake by E. thermale is likely to have assisted in ameliorating abiotic stresses present in the hot spring wetland habitat, as the element has been implicated in amelioration of a range of abiotic stresses across numerous plant groups (e.g., Currie and Perry, 2009; Liang et al., 2007). Notably, silicon is important in the amelioration of salinity stress (e.g., Matoh et al., 1986; Saqib et al., 2008) and increases plant tolerance to excess metal concentrations including Al, Mn, As, Fe, and Cu (Korndörfer et al., 1999; Neumann and zur Nieden, 2001; Neumann and De Figueiredo, 2002; Liang et al., 2007). Further stresses that appear to be reduced by silicon application include nutrient imbalance, drought, high and low temperature, and UV radiation (e.g., Epstein, 1999; Wang et al., 2005). Little is known of the actual mechanisms employed in stress reduction by extant Equisetum, as most studies to date have concentrated on crop plants. This hampers detailed discussions of potential mechanisms used by E. thermale. However, the fact that the plant was capable of withstanding the stresses and thus had developed tolerance mechanisms appears inescapable. As this Jurassic species shares this capability with its extant relatives, it appears that by the Late Jurassic, Equisetum plants had evolved a successful set of anatomical, ecophysiological, and reproductive adaptations that remain to this day.

Conclusions—Equisetum thermale provides key data for our understanding of the timing of the advent of the crown group Equisetum. It represents not only the first and most complete anatomically preserved Equisetum species from South America but also is one of the most ancient species for this genus. Equisetum thermale is unique among the currently available group of permineralized Equisetum-like plants such as E. clarnoi, E. vancouverense, and E. haukeanum because it is preserved in great numbers and in situ with various organs in connection. The quality of preservation of E. thermale means we have been able to observe almost all the anatomical and morphological synapomorphies established for crown group Equisetum plus features present in extant species that have not formerly been

observed in the fossil record. The level of preservation also allows us to discount the presence of significant characteristics (that in other fossils may be taphonomically removed) that would exclude a position within the genus *Equisetum*. *Equisetum thermale* thus confirms the hypothesis that *Equisetum* was established prior to the Cenozoic (Stanich et al., 2009).

Equisetum thermale combines in a single species a suite of characters that span morphology, anatomy, and ecology (with presumed ecophysiological inferences) that may be observed in extant crown group species. With its mixture of crown group characters that includes those present in both crown subgenera, and in sharing most common characters with *E. bogotense*, it seems highly probable that the plant represents one of the oldest records of the root of crown group *Equisetum*. At the very least, it records that anatomically, essentially modern *Equisetum*-like equisetaleans have a history extending back to the Late Jurassic.

The San Agustín hot spring complex and its contained biota provide an excellent snap-shot of a Mesozoic hot spring ecosystem that would not look out of place if situated alongside an active extant spring system. Ecosystem composition, functioning, and interactions with the thermal environment appear to have been remarkably stable over geological time at least from the Mesozoic to recent (Guido et al., 2010). The most commonly preserved plant, E. thermale, appears to have anatomical, ecological, and vegetative reproductive adaptations closely comparable with plants such as Eleocharis rostellata, typically preserved around active hot spring areas. Analogy with active hot spring environments allows details of the plant's ecology and ecophysiology to be discussed with some confidence. The plant behaved and interacted with its environment in ways that would be recognizable to a neobotanist. Ecologically, and therefore presumably ecophysiologically, it exhibits many close similarities to the extant genus. It was aquatic to emergent aquatic. It biomineralized considerable volumes of silica in life and was capable of withstanding a similar suite of abiotic stresses to extant forms. The plant very successfully dominated the stressed, unstable geothermal wetland settings by employing vigorous vegetative growth, with sexual reproduction taking a lesser role. The presence of extant forms of Equisetum (and Holocene fossils) associated with hot springs of the Haukadalur area of Iceland indicate that *Equisetum* had developed the suite of adaptations required to colonize hot spring-influenced settings in Late Jurassic times and has maintained them for over 150 million years.

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