



Tempskya in the Valanginian of South America (Mulichinco Formation, Neuquén Basin, Argentina) — Systematics, palaeoclimatology and palaeoecology



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ABSTRACT

New specimens of the tree fern *Tempskya* are described from the Mulichinco Formation (Valanginian), Neuquén Basin, Argentina. *Tempskya* is a genus for permineralized false fern trunks. This extinct genus had a wide distribution during the Early Cretaceous. However, records from the Southern Hemisphere are scarce and restricted to the late Early Cretaceous in Argentina and Australia. The Patagonian specimens here described from the Valanginian represent the oldest record of this genus. The presence of this fossil fern implies humid and warm climatic conditions during the deposition of the Mulichinco Formation in the Early Cretaceous. The new specimens show petioles, leaf remains, sporangia and spores. On the basis of these new features, a new systematic position for *Tempskya* is suggested.

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1. Introduction

The tree growth habit is a type of convergent evolution in land plants. The development of the tree habit in ferns differs from other groups of plants in that they do not have a great increase in cortex tissues (e.g. lycopsids) or secondary tissues (e.g. lignophytes). Most of the tree-ferns (e.g., Psaroniaceae, Osmundaceae, Guaiaceae, Cyatheaceae and Dicksoniaceae) have a monacaulous stem with a crown of large compound leaves, and reach an arborescent growth habit by an armour of leaf scars and a mantle of adventitious roots, which support the stems and leaves (Morgan, 1959; Herbst, 1981; Large and Braggins, 2004).

The genus *Tempskya* Corda emend. Kidston et Gwynne-Vaughan, 1911 represents a particular extinct lineage of tree ferns that lived during the Cretaceous. Although *Tempskya* also has a tree-like growth habit, it is characterized by many solenostelic stems with a small dichotomous branching system, surrounded by a compact mantle of roots, which together form a false trunk. This is a rare condition in most ferns, except for some Zygopteridales (Corda, 1845; Sahni, 1929; Andrews and Kern, 1947; Galtier and Hueber, 2001).

This genus has an interesting history. The first record of *Tempskya* was described as *Endogenites erosa* by Stokes and Webb (1824). These

authors reported these fossils as monocot forms (palms). Later, similar materials were described by Cotta as *Porosus marginatus*; Cotta suggested that these fossils corresponded to portions of a large fern stem, a different idea from what Stokes and Webb had reported (Cotta, 1832).

In 1845, Corda described and published four specimens of petrified permineralized fern trunks related to “Marattiales” as a new *Tempskya* genus from several localities in Bohemia (Corda, 1845). In 1911, Kidston and Gwynne-Vaughan described a new species from Russia (*Tempskya rossica*) and emended the Corda’s generic diagnosis. However, Corda did not designate a type species. For this reason, Read and Brown (1937), in their study of the North-American *Tempskya* species, proposed *T. rossica* Kidston et Gwynne-Vaughan as the type, based on the good preservation of the fossils and the detailed descriptions available. Kidston and Gwynne-Vaughan noted that Corda’s species were very imperfectly known and had, to their knowledge, not been carefully investigated since Corda’s publication. On the other hand, Clifford and Dettmann (2005) indicated that *Tempskya pulchra* Corda has priority and that the specimen depicted by Corda (plate 58, 1–5) is the type specimen (E 5358, National Museum, Prague). Furthermore, Read and Brown (1937) suggested the erection of “a temporary Tempskyaceae family”. However, they did not give a family diagnosis, a description or a reference to a previously published diagnosis. Therefore, the name Tempskyaceae is not validly published and to be regarded as a nomen nudum (Arts. 38.11 to 38.14, and 46.5 in ICN; McNeill et al., 2012). A diagnosis of the family Tempskyaceae Read et

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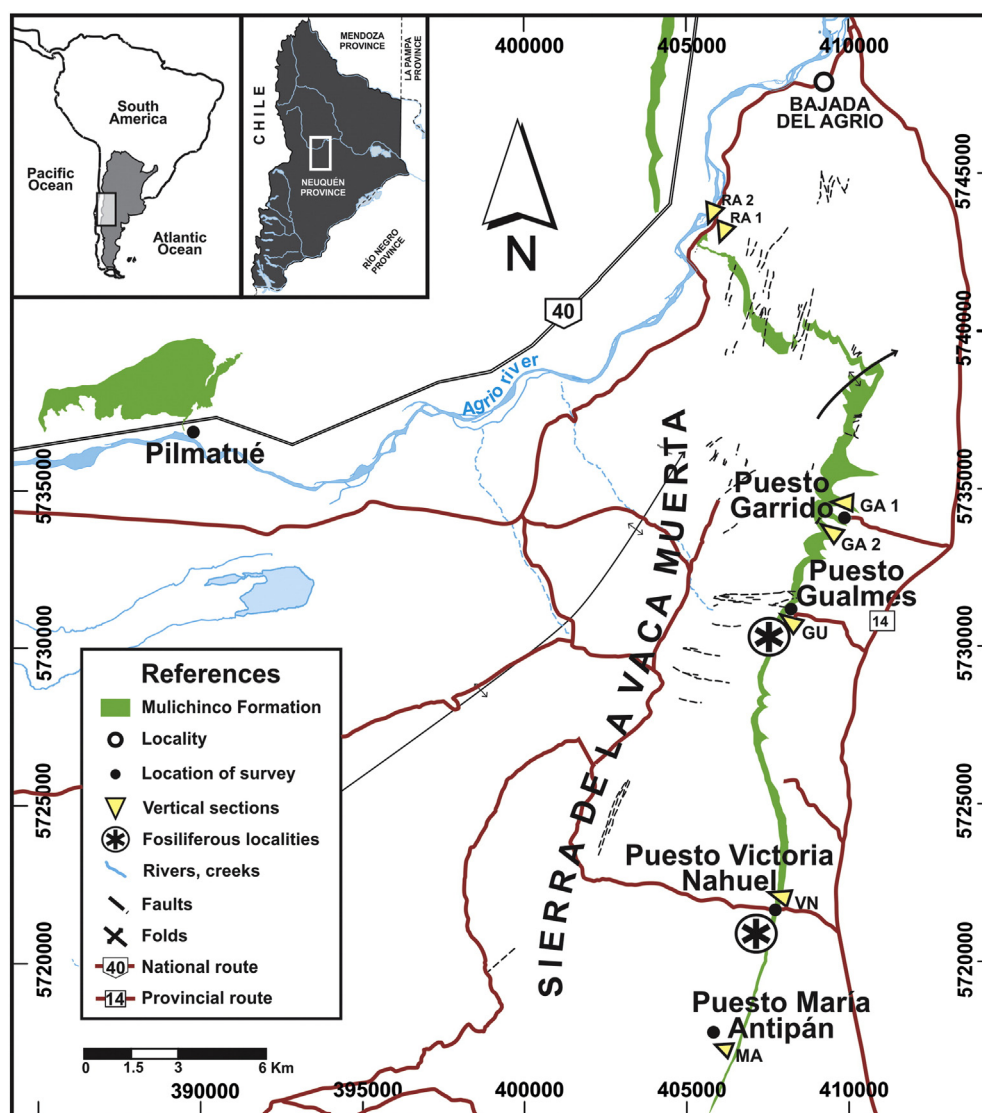


Fig. 1. Location map of the fossiliferous localities.

Brown ex L.C.A. Martínez is given here (see [Systematic Palaeobotany](#) section).

Since the first descriptions by [Corda \(1845\)](#) and [Kidston and Gwynne-Vaughan \(1911\)](#), many species of *Tempskya* have been described from the Northern Hemisphere (e.g., [Seward, 1924](#); [Read and Brown, 1937](#); [Andrews, 1943](#); [Andrews and Kern, 1947](#); [Arnold, 1958](#); [Ash et al., 1976](#); [Barale, and Viera, 1989](#); [Tidwell and Hebbert, 1992](#); [Tidwell et al., 2010](#)). The recent reports of *Tempskya* from South America ([Tidwell and Wright, 2003](#)) and Australia ([Clifford and Dettmann, 2005](#)) indicate a worldwide distribution of this genus during the Cretaceous.

The genus *Tempskya* is characterized by its particular growth structure, the “false trunk”, which enables a longitudinal growth, giving an appearance of a tree fern. Its false trunks produced fronds, which probably spread out to several directions. At present, there are no living plants with this type of growth architecture and ecological strategies.

The relations between *Tempskya* and other Filicales are somewhat uncertain, because little is known about their leaves and reproductive structures. The new specimens of *Tempskya dernbachii* Tidwell et Wright *emend.* Martínez, from the Mulichinco Formation (Valanginian), with preserved reproductive structures, show a set of new features that

contribute to the understanding of the relations between *Tempskya* and other fern genera.

Finally, the earliest records of *Tempskya* found in the Mulichinco Formation might suggest an early origin of this genus in Gondwana. The occurrence of *Tempskya* in the Mulichinco Formation provides information on the palaeoecology and the climate at the time of the deposition of this formation.

2. Geological setting

The Neuquén Basin is located in west-central Argentina (between 32°S and 40°S), on the eastern side of the Andean mountain chain. This basin constitutes a depression of the crust, which developed during the latest Triassic and contains a continuous Mesozoic infill that is at least 7000 m thick. The vertical development of the succession is important because it preserves the evolutionary history of the depocenter in a nearly continuous fashion. The basin fill was deposited in three main tectonic stages: a synrift phase (Late Triassic–Early Jurassic), a postrift/back-arc phase (Early Jurassic–Early Cretaceous), and a foreland phase (Late Cretaceous–Cenozoic) ([Legarreta and Uliana, 1991](#); [Howell et al., 2005](#)).

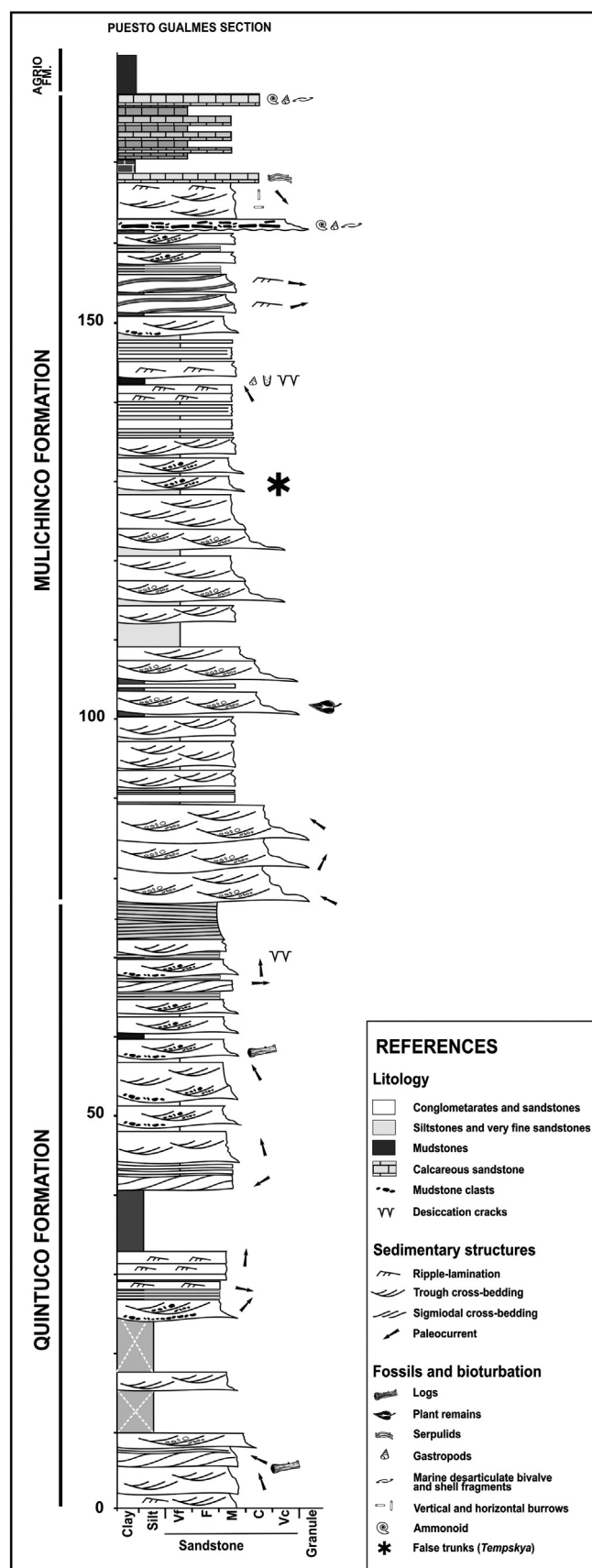


Fig. 2. Sedimentological log in Puesto Gualmes locality.

The outcrops of the Mulichinco Formation are exposed from the North to the centre of the Neuquén province, and are wedged out towards the south of the province (Schwarz, 2003; Schwarz et al., 2011). This formation has an important record of ammonites, on the basis of which the Mulichinco Formation was initially dated as Valanginian (Weaver, 1931; Groeber, 1946). The age of the Mulichinco Formation is supported by modern stratigraphic schemes based on ammonoid faunas (Aguirre-Urreta and Rawson, 1997, 1999a, 1999b; Aguirre-Urreta, 1998; Schwarz, 2003) in which the unit comprises the upper portion of the *Lissonia riveroi* Biozone and the totality of the *Olcostephanus atherstoni* Biozone (Schwarz and Howell, 2005). The Mulichinco Formation thus extends from the upper lower to the lower middle Valanginian (Aguirre-Urreta et al., 2005).

This formation was deposited immediately after an abrupt relative sea-level fall (Gulisano et al., 1984), which was associated with a regional tectonic rise (Vergani et al., 1995; Schwarz et al., 2006). Therefore, a lowstand wedge developed, characterized by a sedimentary infill with rapid lateral and vertical facies changes (Schwarz, 2003; Schwarz and Howell, 2005; Schwarz et al., 2011). As a result, this unit comprises a wide variety of sedimentary environments, ranging from gravelly fluvial systems to distal-shelf marine systems. In the southern region of the Mulichinco Formation (Sierra de la Vaca Muerta), Schwarz (2003) defined, the cuspidal section with mudstone dominated with subordinate sandstones. These deposits contain remains of vascular plants, gastropods and ostracods, and they have been interpreted on the whole as a bay or embayment (Schwarz, 2003; Schwarz et al., 2011).

The fossil studied in this article comes from the Sierra de la Vaca Muerta, located in the southern area of the Neuquén Basin (Fig. 1). In this place, outcrops of the Mulichinco Formation and their ammonite content have been reported by several authors (Weaver, 1931; Gulisano et al., 1984; Legarreta and Gulisano, 1989; Zavala, 2000; Leanza and Hugo, 2001; Leanza, 2009; Schwarz et al., 2011). The Mulichinco Formation consists of a 50–150 m thick succession of conglomeratic sandstones, sandstones, mudstones, claystones, and skeletal calcareous sandstones. It is characterized by a general upward-fining trend from fully continental strata at the base to marginal marine deposits at the top (Olivo et al., 2012). The terrestrial interval contains a variety of fluvial channel deposits with a diverse plant fossil content. *Tempskya* false trunks occur at the base of channel sandstone bodies (Fig. 2).

3. Materials and methods

The present descriptions of specimens of *Tempskya* are based on observations of many specimens of false trunks collected from the Mulichinco Formation, in three localities of the Neuquén Province, Argentina (Fig. 1). In the Puesto Gualmes locality (Plate I, 1) false trunks of *Tempskya dernbachii* and remains of *Equisetites* sp. occur in specific fossiliferous levels (Fig. 2, Plate I, 2, 3), but in two other localities, Pilmatué and Puesto Victoria Nahuel (Martínez et al., 2012), the fossil remains are dispersed and could not be associated to fossiliferous levels (Fig. 1).

Complete sedimentological logs were made for the entire Mulichinco Formation. Many fossiliferous levels were identified; three of them contain fossil plants, i.e. wood and leaf remains and false trunks. The specimens of *Tempskya* come from the upper section of this formation (Fig. 2).

The false trunks of *Tempskya* were cut and polished. Microscopic slides of the cross sections (CS) and longitudinal sections (LS) of the false trunks were made for light microscopic studies (LM) and fluorescence microscopy (FM). Cell dimensions are based on at least 25 measurements, and the numbers between parentheses indicate the minimum and maximum values.

The fossils and thin sections (MOZ–Pb) are deposited in the Paleontological Collections of Museo Provincial de Ciencias Naturales Profesor Dr. Juan A. Olsacher (Zapala, Neuquén province).

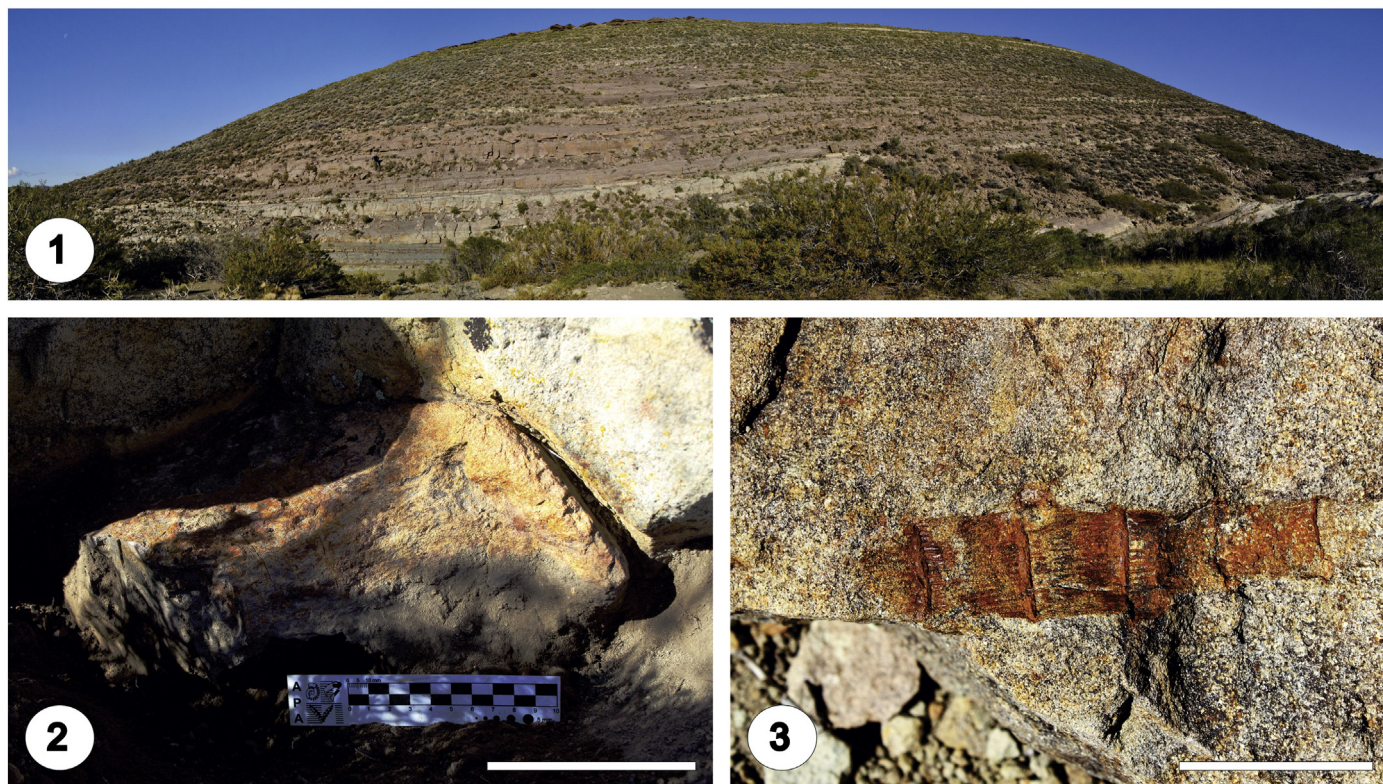


Plate I. Puesto Gualmes locality and fossil remains.

1. General view of channel sandstone bodies of Mulichinco Formation in Puesto Gualmes locality, where the specimens of *Tempskya* were collected in situ.
2. Lateral view of false trunk in situ of *Tempskya dernbachii* (MOZ–Pb 07) in sandstones of Mulichinco Formation. Scale bar = 10 cm
3. Impression of *Equisetites* sp. (MOZ–Pb 08) from the same levels of *Tempskya dernbachii*. Scale bar = 3 cm.

Thin sections: MOZ–Pb07a, MOZ–Pb 07b, MOZ–Pb 07c, MOZ–Pb 07d, MOZ–Pb 07e, MOZ–Pb 07f, MOZ–Pb 57a, MOZ–Pb 57b, and MOZ–Pb 57c.

Localities: Puesto Gualmes (Neuquén province, Argentina) – MOZ–Pb 07, MOZ–Pb 57. Puesto Victoria Nahuel (Neuquén province, Argentina) – MOZ–Pb 56.

Stratigraphic horizon: Mulichinco Formation (Valanginian) – Lower Cretaceous.

3.1. Systematic palaeobotany

Cyatheales Frank

Family **Tempskyaceae** Read et Brown ex L.C.A. Martínez

Type Genus: *Tempskya* Corda emend. Kidston et Gwynne-Vaughan, 1911

Type Species: *Tempskya pulchra* Corda, 1845

Diagnosis. Arborescent ferns with false trunks composed of a three-dimensional network of stems embedded in a matrix of adventitious roots without any particular arrangement, together forming a solid and compact trunk. Stems amphiphloic solenosteles, with a parenchymatous and/or sclerenchymatous pith, an inner endodermis, inner phloem, xylem, outer phloem, outer endodermis, parenchymatous cortex and an epidermis with hairs. Petioles with a single V- or U-shaped vascular strand. Roots adventitious, diarch, with an inner sclerenchymatous and an outer parenchymatous cortex; some roots with outer aerenchyma chambers. Leptosporangiate; sporangia in sori, with an elongated stalk and a vertical annulus; spores trilete.

Remark. The family Tempskyaceae was erected by Read and Brown (1937) in order to include the genus *Tempskya*. However, the name Tempskyaceae was not validly published as there was no Latin description or diagnosis nor a reference to either (ICN Art. 38.11). Many subsequent authors have used the family name Tempskyaceae.

Therefore, a diagnosis for the Tempskyaceae is given to validate this family name.

Tempskya dernbachii Tidwell and Wright, 2003 emend. L.C.A. Martínez.

Emended diagnosis. False trunks, stems generally oriented towards the outer surface of the false trunk (radially symmetrical), some randomly oriented; individual stems dorsiventral, leaves two-ranked; dichotomizing; solenostelic; internodes short to medium, generally showing one, commonly two, three or more leaf traces in cross section; epidermal cells elongated with long epidermal hairs; cortex double-layered, outer cortex, composed of large, thick-walled parenchymatous cells; inner cortex, homogenous, small, parenchymatous cells; xylem consists of tracheids without parenchyma; inner and outer phloem, with a thin pericycle and an endodermis; pith double-zoned, cells of the outer zone small, parenchymatous; cells of the inner zone large, also parenchymatous. Petioles with a vascular simple bundle, concentric and a leaf trace with a single U- or V-shaped vascular strand. Adventitious roots, diarch, usually vertically oriented; some roots with aerenchymatic chambers in the outer cortex. Sporangia clustered in sori; spores trilete, psilate, with straight leaurae and a thin labrum.

Note: The specific diagnosis is emended in order to include features of the petioles, sori, sporangia, spores, and the presence of aerenchyma in the roots.

4. Description

Most *Tempskya* specimens are small fragments; however, there are some specimens that reach a length of 0.25 m, with a diameter of 0.14 m; the rest being only up to 0.20 m (Plate I, 2). The false trunks are permineralized, not branched and generally flattened, and consist of a three-dimensional network of stems within a matrix of roots,

without any particular arrangement, forming a solid and compact trunk (Plate II, 1, 2). In one specimen (MOZ–Pb 57), petioles, fronds, and sporangia with spores were found as well

4.1. Stems

The stems are circular to oval in cross section, commonly radially symmetrical, and more or less aligned axially (Plate II, 2). Stems are solenostelic, dorsiventral, and radially oriented in the false trunks. The stems consist of an epidermis, a cortex, an outer endodermis, outer phloem, xylem, inner phloem, an inner endodermis and a pith. The stems have a mean diameter of 0.52 (0.28–0.76) mm (Plate II, 3, 4).

The epidermis is composed of a single layer of cells. The epidermal cells are rounded in a cross section, and elongated in a longitudinal section (Plate II, 5, 6). Each epidermal cell bears a multicellular hair (Plate II, 7).

In cross section, the cortex is composed of parenchymatous isodiametric cells with thick walls, and is differentiated into two zones: the outer zone with large cells (mean diameter of 29 μm (12–42)), and the inner zone with small cells (diameter of 20 μm (8–28)) (Plate II, 3 and, Plate III, 1). In longitudinal section, the cortex cells are elongated, with an average length of 267 (160–417) μm (Plate III, 2, 3).

In cross section, the outer endodermis is visible as a single layer of cells, and underlying cortex and the outer phloem (Plate III, 4). Adventitious roots originate as small protuberances on the pericycle of the stem (Plate III, 5). The outer phloem has 5 (3–6) cell wide; the cells are circular with a mean diameter of 12 (8–18) μm . The xylem cylinder is 6 (5–8) cells in wide; the tracheids are isodiametric and polyhedral (Plate III, 1, 4, 7). The protoxylem cells are from mesarch to exarch closer to the outer margin, with a mean diameter of 13 (8–22) μm . The metaxylem cells are larger, with a mean diameter of 25 (10–44) μm and show scalariform thickenings in longitudinal section (Plate III, 6). The xylem is bordered by the inner phloem that is 6 (5–7) cell wide (Plate III, 7); phloem cells have a mean diameter of 16 (12–24) μm .

In cross section, the inner endodermis is a layer of thick cells enclosing the pith (Plate III, 4, 7). The pith is a solid cylinder of isodiametric parenchyma cells with thick walls. The cells have a mean diameter of 22 (8–36) μm . The pith is differentiated into two zones: the outer pith consists of small parenchyma cells and the inner pith of large parenchyma cells (Plate III, 1, 4, 7).

4.2. Petiole

The leaf traces depart from the stem to form the petiole vasculature. In cross section, the petioles have a mean diameter of 1.7 (1.4–2.2) mm, the leaf traces begin as a little bulge of stele (Plate II, 3). The vascular tissue and the parenchyma of the pith bulge outward. The parenchyma of the pith fills the centre of the gap. As the gap expands outward, it becomes somewhat V-shaped (Plate IV, 1). The V-shaped traces with associated tissues form the petiole bases.

The petioles are interspersed between stems and roots. Many adventitious roots encircle the petioles (Plate IV, 2, 3). In cross section, the shape of the petioles varies from oval to rhomboidal in outline, with a thick cuticle cover over the single-layered epidermis (Plate IV, 2, 3). The cortex is differentiated into two layers. The outer layer consists of 6–9 thick-walled parenchyma cells. The inner layer consists of 5–12 thick-walled sclerenchymatous cells. The endodermis is a unicellular layer of isodiametric cells, containing dark substances. The pericycle is one or two cell thick, composed of thick-walled cells (Plate IV, 2–4). The vascular bundle is simple, with a single leaf trace; the vascular strand is V- or U-shaped, with free margins slightly curving inwards. The phloem of thin-walled angular cells surrounds the xylem. The xylem is 1–2 cell thick, with oval tracheids, and usually eight protoxylem points in the petiolar stele (Plate IV, 4).

4.3. Fronds and sporangia

Some foliage portions, sporangia and spores were found in the false trunks (Plates V, and VI). The leaf remains are represented by a cross section of the very thin lamina; individual epidermal and mesophyll cells are difficult to observe (Plate V, 1). Usually, most of the sporangia are broken and interspersed among the stems and roots. However, in one sample, the abaxial side of the foliar blade bears many sporangia. These are clustered, and arranged over a vascular bundle (vein?), and grouped into sori (Plate V, 1). The sporangia display an elongate stalk, a conspicuous vertical incomplete annulus and are thin-walled (leptosporangiate) (Plate V, and Plate VI, 2–7).

4.4. Spores

The sporangia contain many spores (Plate VI, 8). The spores are trilete, triangular in polar view, with rounded corners and concave sides; in equatorial view, they are plane-hemispheric to convex-hemispheric, with an equatorial diameter of 23 μm and a polar diameter of 8 μm (Plate VI, 8–9). The leaures are straight with a thin labrum and extend from two-third to almost the entire distance to the equator. The spore wall is thick, psilate and lacks a perispore (Plate VI, 8–10). The spores can be assigned to the genus *Cyathidites* Couper, 1953.

4.5. Roots

In a cross section, the roots are circular, with a mean diameter of 680 (530–880) μm . They consist of epidermis, cortex, endodermis, pericycle, phloem and xylem (Plate VII, 1–3). The roots have a single layer of epidermal cells bearing multicellular hairs (Plate VII, 2). The cortex is differentiated into three layers: the outer, the middle and the inner cortex. The outer cortex has thin-walled cells and wheel-shaped aerenchymatous chambers (sensu Jung et al., 2008) (Plate VII, 1–3). The middle cortex consists of compact layers of thin-walled cells. The inner cortex is composed of thick-walled cells (Plate VII, 1–3). The endodermis encircles the pericycle and the vascular bundle. The pericycle is one or two very thin-walled cells wide (Plate VII, 3). The phloem is formed by a narrow band of 1–3 thin-walled cells surrounding the xylem. The xylem is exarch (diarch); the tracheids are situated in a cross-shaped area, with the protoxylem poles at the ends of the long axis, and two or three large tracheids forming the shorter axis (Plate VII, 3). In longitudinal section, the tracheids of the metaxylem show scalariform thickenings. Some roots are excellently preserved, with a root cap and an apical meristem, visible as an apical tetrahedral cell (Plate VII, 4).

4.6. Animal activity and fungal spores

Many stems, petioles and roots show tunnels and galleries bored by animals into the different tissues of *Tempskya*. The tunnels occur in the vascular tissue and between the vascular tissue and the cortex (Plate III, 2–3). They are circular, oval to irregular in outline, and generally filled with numerous loosely packed faecal pellets. The pellets are oval, with a mean diameter of 30 μm and a length of 60 μm . All pellets have similar form and size. Hence, we believe that one type of animal was feeding upon these plant structures.

5. Discussion

The new specimens of *Tempskya dernbachii* from the Mulichinco Formation allow us to give new and detailed anatomical descriptions of the species, adding information on its petioles, leaves, sporangia and spores. Moreover, this new information contributes towards a better understanding of its systematic position and the palaeoecology. Finally, the new finds expand the stratigraphic range of this extinct taxon.

5.1. Systematical approach

The *Tempskyaceae* are a family that is only known from the Cretaceous, and probably represents taxa that have been grouped in the second radiation of the filicaleans (Rothwell and Stockey, 2008). Although many *Tempskya* stems have been found, the records of their foliage and/or reproductive structures are scarce and poorly known. Therefore, the *Tempskyaceae* were suggested to be related to many families of living ferns (Cyatheales, Gleicheniales, Marattiaceae, Polypodiales and Schizaeales) based on a diverse set of features (Schenk, 1871; Boodle, 1895; Seward, 1924; Read and Brown, 1937; Andrews and Kern, 1947).

The fossils herein described include remains of foliage, sporangia and spores. Although they are not strictly in organic connection with stems and petioles, their frequency and abundance and the absence of other taxa in the permineralized false-trunks strongly suggest that the sporangium remains belong to the *Tempskya dernbachii*. The new data on these organs allow a new systematic approach and a proposal of the family *Tempskyaceae*.

5.1.1. Relationship with the *Leptosporangiate ferns*

The sporangia and spores found in this fossil show many features which can help us understand the relation between *Tempskya* and living ferns. The sporangia present in *Tempskya* are “leptosporangia” and allow the inclusion of *Tempskya* in the “Leptosporangiate ferns” (sensu Rothwell, 1996, 1999; Pryer et al., 1995, 2001).

There are seven orders of “Leptosporangiate ferns”: Osmundales, Hymenophyllales, Gleicheniales, Schizaeales, Salviniaceae, Cyatheales and Polypodiales (Smith et al., 2006, 2008). Sporangia with a vertical annulus and 1-to-3-cells-thick long sporangia stalks occur in the Polypodiales and in some members of the Cyatheales (Smith et al., 2006). These features are seen in the fossils studied here (Plate VI, 1–7). Furthermore, it is interesting to notice the presence of a vertical annulus, which has also been mentioned for other species of *Tempskya* (Andrews and Kern, 1947; Tidwell and Hebert, 1992; Clifford and Dettmann, 2005).

5.1.2. Comparisons with the *Polypodiales*

Several families grouped into the Polypodiales share some features with the fossil studied here, such as sporangia clustered in sori, sporangium and spore types, solenostelic stems, petioles with a single V-shaped vascular strand (Tryon and Tryon, 1982; Smith et al., 2006, 2008).

The sporangia with a vertical annulus in our fossil material resemble those found in the Polypodiales. Spores with trilete apertures are characteristic of all basal fern families (e.g., Ophioglossaceae, Dicksoniaceae, and Cyatheaceae). However, this feature is also common in some families of the Polypodiales such as Lindsaeaceae, Saccolomataceae, Dennstaedtiaceae, Pteridaceae and Polypodiaceae (Tryon and Tryon, 1982; Kubitzky, 1990; Tryon and Lugardon, 1990; Smith et al., 2006, 2008).

Among the basal members of the Polypodiales, the Saccolomataceae have features which distinguish them from *Tempskya*, such as scales on the stem, a half-conical indusium, and the unusually delicate tetrahedral-globose ridged spores (Tryon and Tryon, 1982; Kubitzky, 1990).

The Lindsaeaceae are another basal family of Polypodiales. Their roots have a sclerenchymatous outer cortex combined with a six-cell-wide innermost cortical layer (except *Lonchitis* L. and *Cystodium* Smith), and sori with indusium (Kubitzky, 1990; Schneider and Kenrick, 2001; Smith et al., 2006). These features have not been observed in our fossils.

The Dennstaedtiaceae share some features with *Tempskya*. However, this family clearly differs from *Tempskya* in their growth habit and in the presence of indusium. Although some genera of Dennstaedtiaceae often have solenostelic stems (*Dennstaedtia* Bernhardt, *Hypolepis* Bernhardt, *Leptolepis* Prantl, *Microlepis* Presl, *Paesia* Saint-Hilaire, *Pteridium* Gleditsch ex Scopoli) and/or vascular petiole traces with a gutter-shaped vascular strand (adaxial open end) (*Hypolepis*, *Microlepis*, *Dennstaedtia*), they are distinguished from *Tempskya* in having several vascular bundles arranged in a horseshoe-like pattern (*Monachosorum* Kunze, *Pteridium*), sori with indusia (*Dennstaedtia*, *Leptolepis*, *Microlepis*, *Oenotrichia* Copeland), and trilete or monolete spores [*Blotiella* Tryon, *Hypolepis*, *Histiopteris* (Agardh) Smith, *Paesia*] – usually with a well-developed perispore of two or three layers, often with some rodlets (Kubitzky, 1990; Tryon and Lugardon, 1990; Smith et al., 2006).

The Pteridaceae are a diverse family, whose members are generally terrestrial, rupestral or small aquatic plants, with protostelic, solenostelic or dictyostele stems, bearing scales, or – less often – only hairs, petioles with one to four or several bundles (*Ceratopteris* Brongniart), marginal or intramarginal sori, lacking a true indusium, and forming short to long soral lines; the spores are globose or tetrahedral, trilete, and variously ornamented (Kubitzky, 1990; Smith et al., 2006). The Pteridaceae have been formally subdivided into a family or a subfamily rank; the following clades have been recognized: (1) Parkeriaceae, or Parkerioideae; (2) Adiantaceae; (3) Cryptogrammaceae; (4) Sinopteridaceae, or Cheilantheaceae; and (5) Pteridaceae s.s., or Pteridoideae (Schuettpelz et al., 2007; Smith et al., 2008).

The Parkeriaceae clade (*Acrostichum* L. and *Ceratopteris* Brongniart) are the only aquatic members of the Pteridaceae (Schuettpelz et al., 2007). However, they have protostele to dictyostelic stems, with two to many vascular bundles in the petiole, and tetrahedral to globose spores, with prominent or papillate to tuberculate ridges (Kubitzky, 1990; Tryon and Lugardon, 1990).

In the Adiantaceae clade, about 12 genera are grouped (Schuettpelz et al., 2007). Some taxa are protostelic (*Monogramma* Commerson ex Schkuhr, and *Hecistopteris* Smith), whereas *Ananthacorus* Underwood et Maxon ex Maxon, *Anetium* Splitgerber, *Antrophyum* Kaulfuss, *Haplopteris* Presl, *Polytaenium* Desvaux, *Radiovittaria* Desvaux, *Rheopteris* Alston, *Scoliosorus* Moore, and *Vittaria* Smith have

Plate II. *Tempskya dernbachii*. All LM.

1. CS. General view. Scale bar = 2 cm.
2. CS. Stems and roots (detail). Scale bar = 7 mm.
3. CS. General view, stem with developing an adventitious root (arrow). Pith (p), xylem (x), inner cortex (ic), and outer cortex (oc); MOZ–Pb 07a. Scale bar = 500 µm.
4. CS. General view, stem with two foliar traces (arrows). Pith (p), xylem (x), and cortex (c); MOZ–Pb 07d. Scale bar = 500 µm.
5. and 6. CS. Epidermis and hairs (arrows); MOZ–Pb 07a. Scale bar = 100 µm.
7. LS. Epidermal hairs (detail). MOZ–Pb 07a. Scale bar = 100 µm.

Plate III. *Tempskya dernbachii*. 1–3, 5, 6 with LM and 4, 7 with FM. (see on page 8)

1. CS. Stem anatomy. Outer cortex (oc), inner cortex (ic), outer phloem (op), xylem (x), inner phloem (ip), and pith (p); MOZ–Pb 07a. Scale bar = 100 µm.
2. LS. Stem, with hairs (h), epidermis cells (e), outer cortex (oc), inner cortex (ic), and galleries with faecal pellets (g); MOZ–Pb 07b. Scale bar = 200 µm.
3. LS. Cells of outer cortex (oc) and galleries (g) with faecal pellets (detail); MOZ–Pb 07b. Scale bar = 100 µm.
4. CS. Stem with FM. Note the fluorescence in the inner, outer endodermis and xylem cell walls. Inner cortex (ic), outer endodermis (oe), outer phloem (op), xylem (x), inner phloem (ip), inner endodermis (ie), and pith (p); MOZ–Pb 07a. Scale bar = 100 µm.
5. CS. Stem with a lateral root initiation from the pericycle; MOZ–Pb 07a. Scale bar = 100 µm.
6. LS. Tracheids of metaxylem with scalariform thickening. MOZ–Pb 07c. Scale bar = 50 µm.
7. CS. Detail of stem with FM. Xylem (x), inner phloem (ip), inner endodermis (ie), and pith (p). MOZ–Pb 07a. Scale bar = 100 µm.

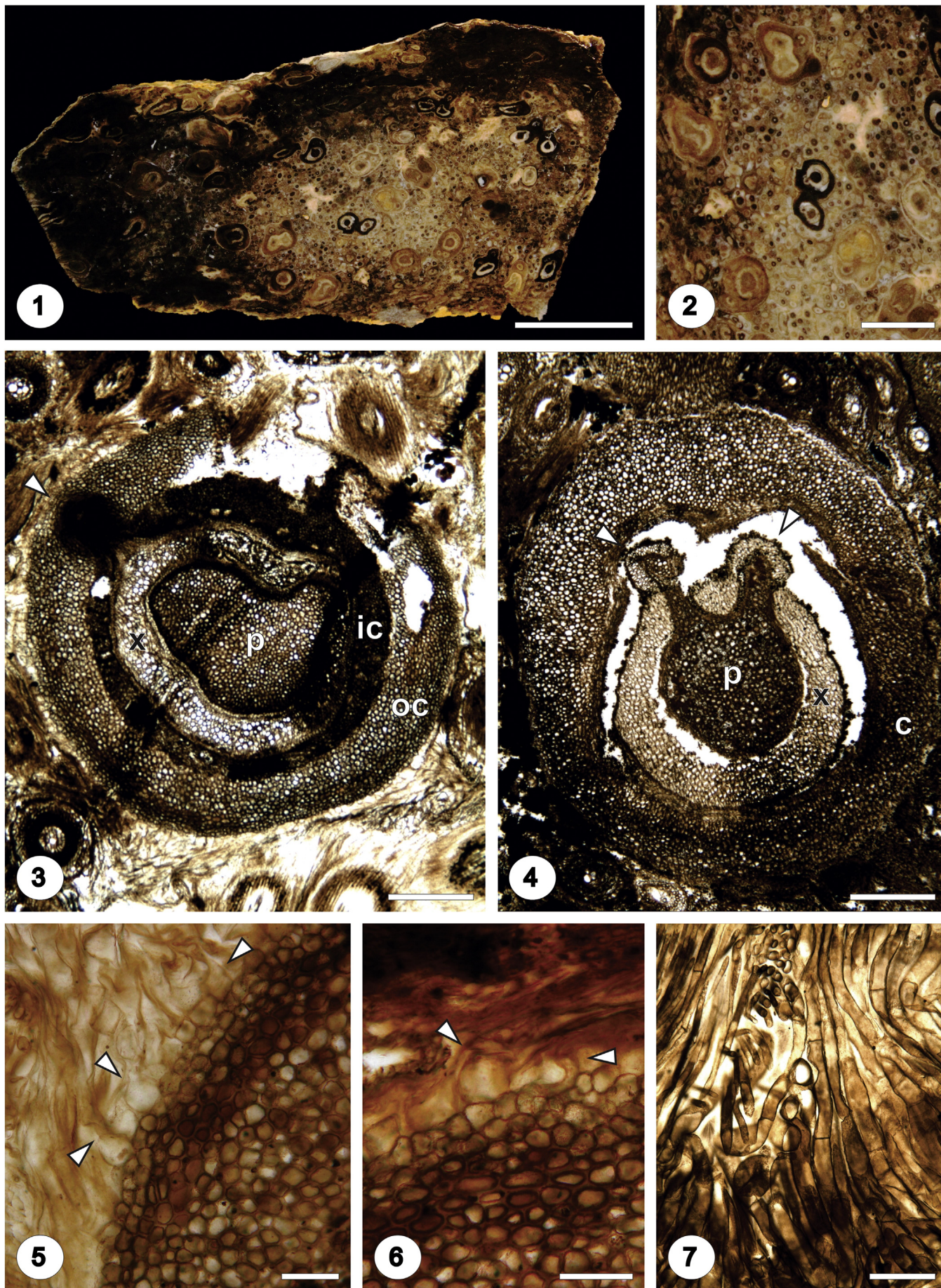


Plate II

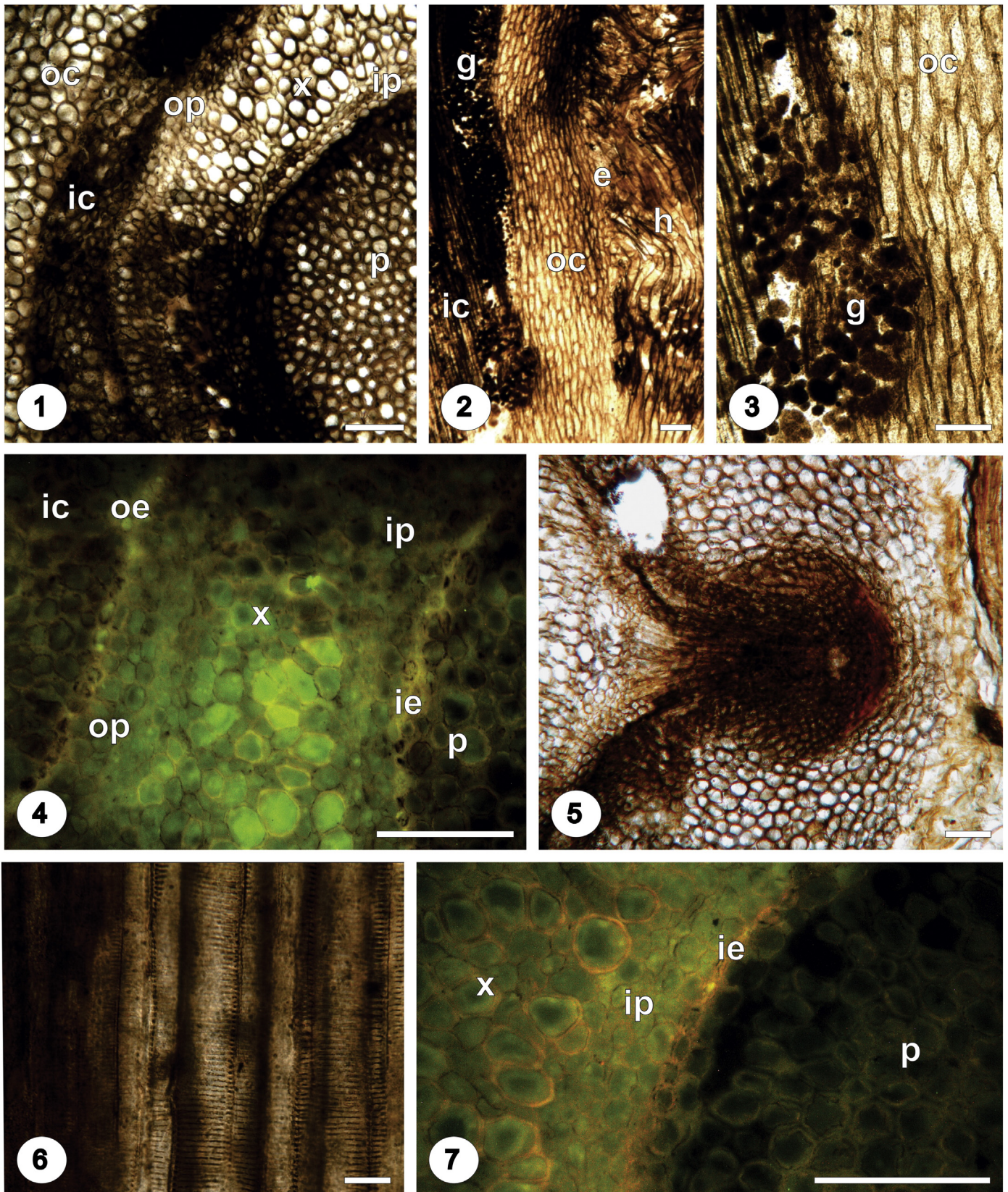


Plate III. (caption on page 6).

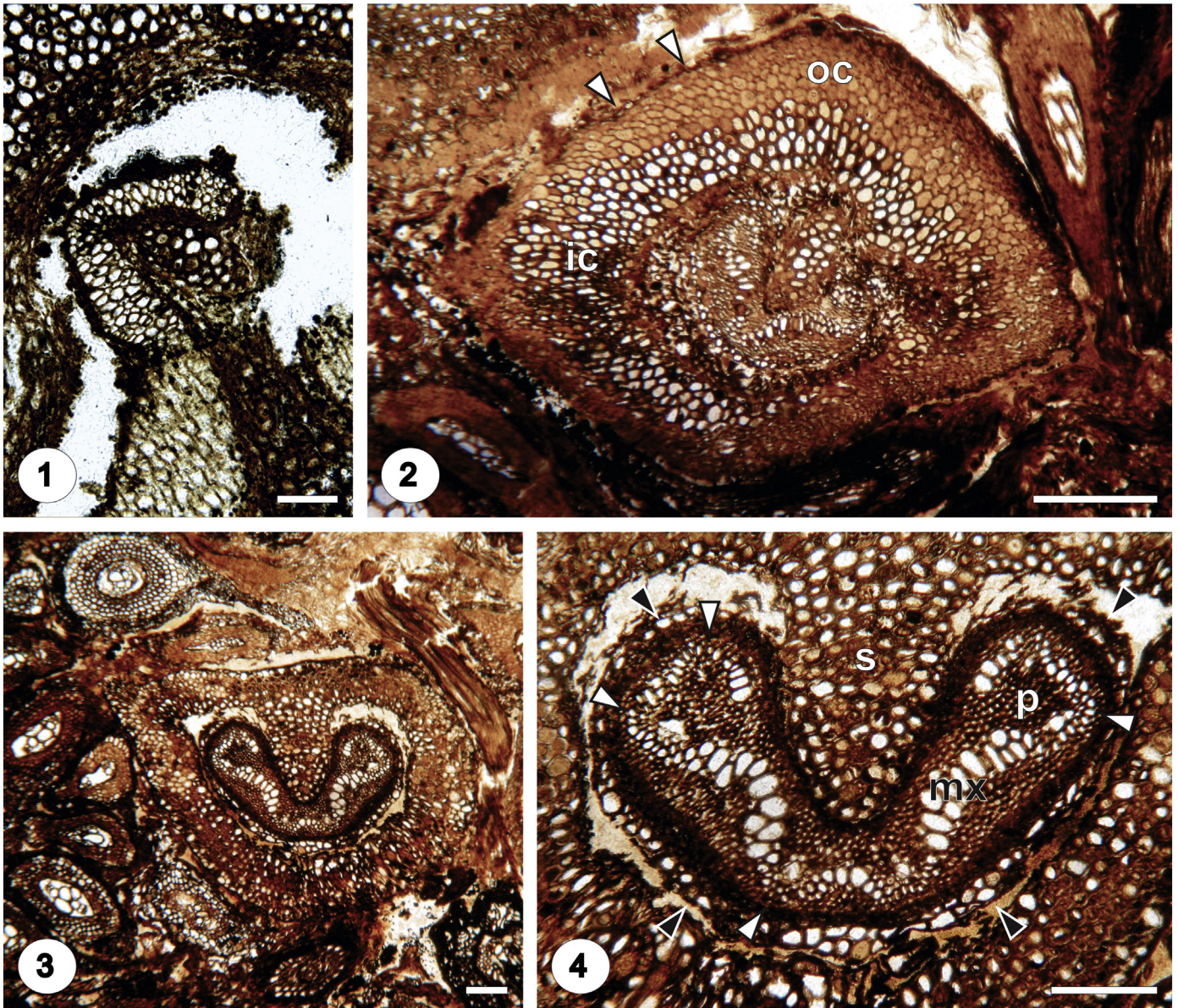


Plate IV. *Tempskya dernbachii*. All LM.

1. CS. Stem. Leaf tracer development; MOZ-Pb 07d. Scale bar 100 = μm .
2. CS. Anatomy of petiole. Epidermis (white arrows), outer cortex (oc), inner cortex (ic); MOZ-Pb 57a. Scale bar = 200 μm .
3. CS. Adventitious roots, petiole and vascular bundle; MOZ-Pb 57a. Scale bar = 200 μm .
4. CS. Vascular bundle. Pericycle (black arrows), phloem (p), protoxylem (white arrows), metaxylem (mx) and, stelar sheath (s). MOZ-Pb 57a. Scale bar = 200 μm .

solenostelic to dictyostelic stems, with smooth, monolet or trilete, spores. They differ from *Tempskya* in the presence of trichomes among the sporangia (Tryon and Tryon, 1982; Tryon and Lugardon, 1990). *Adiantum* has a solenostelic stem and one (to many) bundle(s) in the petiole. However, they have an indusium (recurved lobe), and tetrahedral-globose spores with a rugulate, or tuberculate, rarely psilate, surface (Kubitzky, 1990; Tryon and Lugardon, 1990).

The Cryptogrammaeae clade comprises three genera: *Coniogramma* Fée, *Cryptogramma* Brown, and *Llavea* Lagasca (Schuettpelz et al., 2007). These genera have a solenostelic stem and one bundle in the petiole, but with scales, and the sporangia are long with irregularly papillate, tuberculate or rugulate spores (Tryon and Tryon, 1982; Kubitzky, 1990; Tryon and Lugardon, 1990), thus being different from *Tempskya*.

The Sinopteridaceae, or Cheilantheae, comprise about 20 genera (Schuettpelz et al., 2007). The genera with solenostelic stems and one bundle (to many) in the petiole are: *Adiantopsis* Fée, *Bommeria* Fournier, *Cheilanthes* Swartz (including the genera: *Aleuritopteris* Fée,

Argyrochosma Windham, *Aspidotis* Copeland, *Cheiloplecton* Fée, *Mildella* Trevisan, and *Sinopteris* Christensen et Ching), *Doryopteris* Smith, *Hemionitis* L., *Notholaena* Brown, *Pellaea* Link, and *Trachypteris* André ex Christ (Kubitzky, 1990). However, they have tetrahedral to spheroidal, tuberculate, echinate, granulate, reticulate, papillate, cristate, rugulate or crostate spores, commonly with more or less coalescent ridges (Tryon and Tryon, 1982; Tryon and Lugardon, 1990).

The Pteridaceae s.s., or Pteridoideae clade, comprise about 17 genera and 400 species (Schuettpelz et al., 2007). Some genera (e.g., *Actiniopteris* Link, *Anogramma* Link, *Cosentinia* Todaro, *Eriosorus* Fée, *Jamesonia* Hooker et Greville, *Neurocallis* Fée, *Ochropteris* Smith, *Onychium* Kaulfuss, *Pityrogramma* Link, *Platyzoma* Brown, *Pteris* L., *Pterozonium* Fée, *Taenitis* Willdenow ex Schkuhr) have solenostelic stems and one (to many) bundle(s) in the petiole. However, this group has cingulate spores (Tryon and Lugardon, 1990).

The Pteridaceae are a diverse family, which inhabit a broad range of ecological (terrestrial, epiphytic, xeric-adapted rupestral, and aquatic)

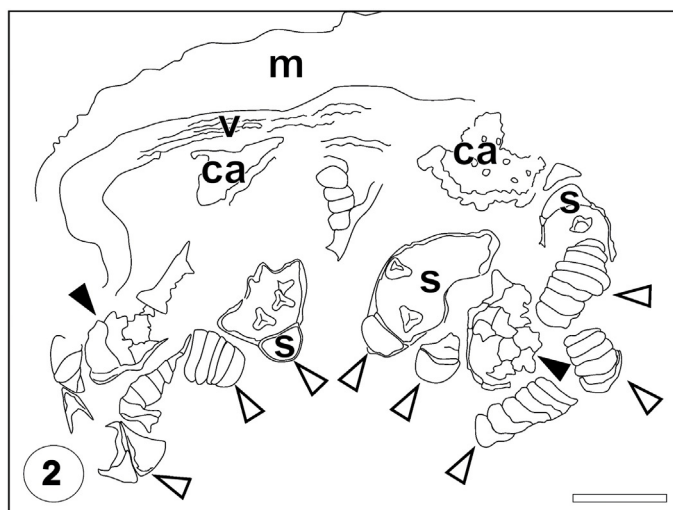
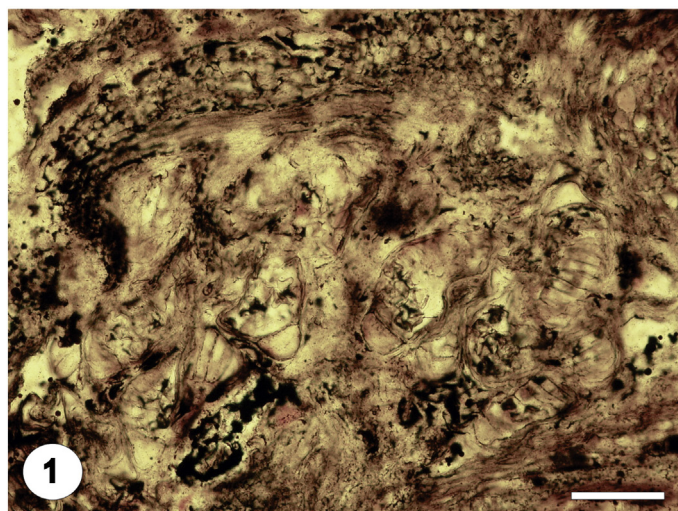


Plate V. *Tempskya dernbachii*.

1. Leaf remains, sori with sporangia and spores. LM; MOZ–Pb 57a. Scale bar = 100 μ m.
2. Sketch. Mesophyll (m), vein (v), sporangium with spores inside (s), central axis of sorus (ca), annulus cells (white arrows) and capsule cells (black arrows); MOZ–Pb 57a. Scale bar = 100 μ m.

habitats. Some clades of Pteridaceae appear to be characterized by their ecological preferences (Schuettelpelz et al., 2007). Despite the diversity of genera within the Pteridaceae, this family shows a great uniformity in their typical growth habit of herb, commonly with elongate sporangia and/or with paraphyses, and ornamented, and tetrahedral-globose, spores, being different from our *Tempskya*.

The eupolypod ferns have two large clades, resolved by molecular data, called “Eupolypods I” and “Eupolypods II” (Schuettelpelz and Pryer, 2007, 2008). These clades also have a common morphological character, i.e. the vasculature of the petiole (Schuettelpelz and Pryer, 2007, 2008). The Eupolypods I have three or more vascular bundles (with the exception of the diminutive grammitid ferns with one, and the genus *Hypodematum* Kunze with two), and the Eupolypods II have only two (with the exception of the well-nested blechnoid ferns, with three or more) (Schuettelpelz and Pryer, 2007, 2008). Other anatomical features present in the petioles of most Polypodiales are leaf traces surrounded by a circum-endodermal band (Hernández-Hernández et al., 2012). Most of the families have monolete spores (with the exception of some genera in the Polypodiaceae) (Tryon and Tryon, 1982; Tryon and Lugardon, 1990; Smith et al., 2006). The families grouped into the Eupolypods I and Eupolypods II can thus be easily distinguished from *Tempskya* by their vascular anatomy and spore morphology.

A summarized comparison with families of Polypodiales and Tempskyaceae appears in Table 1.

5.1.3. Comparisons with the Cyatheaes

The Cyatheaes (“tree ferns”) occupy a basal position within the core of the Leptosporangiate ferns. This order consists of eight families: the Thyrsopteridaceae, the Loxomataceae, the Culcitaceae, the Plagiogyriaceae, the Cibotiaceae, the Cyatheaceae, the Dicksoniaceae and the Metaxiaceae (Smith et al., 2006, 2008). Although molecular evidence indicates a close relationship between the families grouped in the Cyatheaes, this order does not have evident defining morphological characters (Pryer et al., 2001, 2004; Wikström and Pryer, 2005; Korall et al., 2006; Schuettelpelz et al., 2006; Schuettelpelz and Pryer, 2007). Nevertheless, the presence of some common features – such as creeping rhizomes – can help us distinguish them from other ferns. Some only have hairs on the stems and the lamina, whereas others have scales. Sori are abaxial or marginal, and either indusiate or exindusiate. Spores are

globose or tetrahedral-globose, each with a trilete mark (Smith et al., 2006, 2008).

In many respects, *Tempskya* resembles particular families and genera of “Tree fern clade” (Smith et al., 2006, 2008; Schuettelpelz and Pryer, 2008), such as the stem, the stele of the petiole, the stele of the root, sporangia and spores.

The Metaxiaceae is the only family of the Cyatheaes with a vertical to slightly oblique annulus in the sporangia (Tryon and Tryon, 1982; Kubitzky, 1990; Qiu et al., 1995; Smith et al., 2006). *Metaxya* Presl has a solenostelic rhizome without a sclerenchyma sheath and hairy rhizomes (Lucansky, 1974; Nishida, 1984; Qiu et al., 1995). However, *Metaxya* has paraphyses in the sporangium, and globose spores with a granulate perispore (Tryon and Tryon, 1982; Tryon and Lugardon, 1990; Qiu et al., 1995), although the stele type in *Metaxya* petioles resembles that of *Tempskya*, but differs from it having many protoxylem poles (4 to 24) in a more developed structure (Lucansky, 1974; Nishida, 1984; Qiu et al., 1995). It is interesting to notice that the Metaxiaceae are medium-sized plants with creeping rhizomes, differing from other Cyatheaes in several aspects of their shoot anatomy and spore morphology (Lucansky, 1974, 1982; Tryon and Tryon, 1982; Tryon and Lugardon, 1990; Qiu et al., 1995).

The Dicksoniaceae also have some characters that are similar to those in *Tempskya*. They are arborescent or have erect or ascending rhizomes; some are solenostelic [*Calochlaena* (Maxon) R.A. White et M.D. Turner, and *Lophosoria* Presl]. The stelar anatomy of the stems and the petioles are comparable to the fossil material described here (Lucansky, 1974; Nishida, 1984). However, the sporangium of the Dicksoniaceae is slightly oblique, with an annulus that is not interrupted by the stalk, different to those of *Tempskya* (Tryon and Tryon, 1982; Smith et al., 2006, 2008).

It is interesting to notice that the stele types of petioles and the ornamentation of the spores in some living species of *Loxoma* Cunningham (Loxomataceae) are similar to those of *Tempskya dernbachii* (Ogura, 1972; Tryon and Lugardon, 1990). Nevertheless, the Loxomataceae have sori with an urceolate indusium, sporangia with a multiserial stalk, and a subvertical and slightly oblique annulus (Tryon and Tryon, 1982; Kubitzky, 1990).

Tempskya differs from the rest of the Cyatheaes (Thyrsopteridaceae, Culcitaceae, Plagiogyriaceae, Cibotiaceae and Cyatheaceae) in several features (See Table 2).

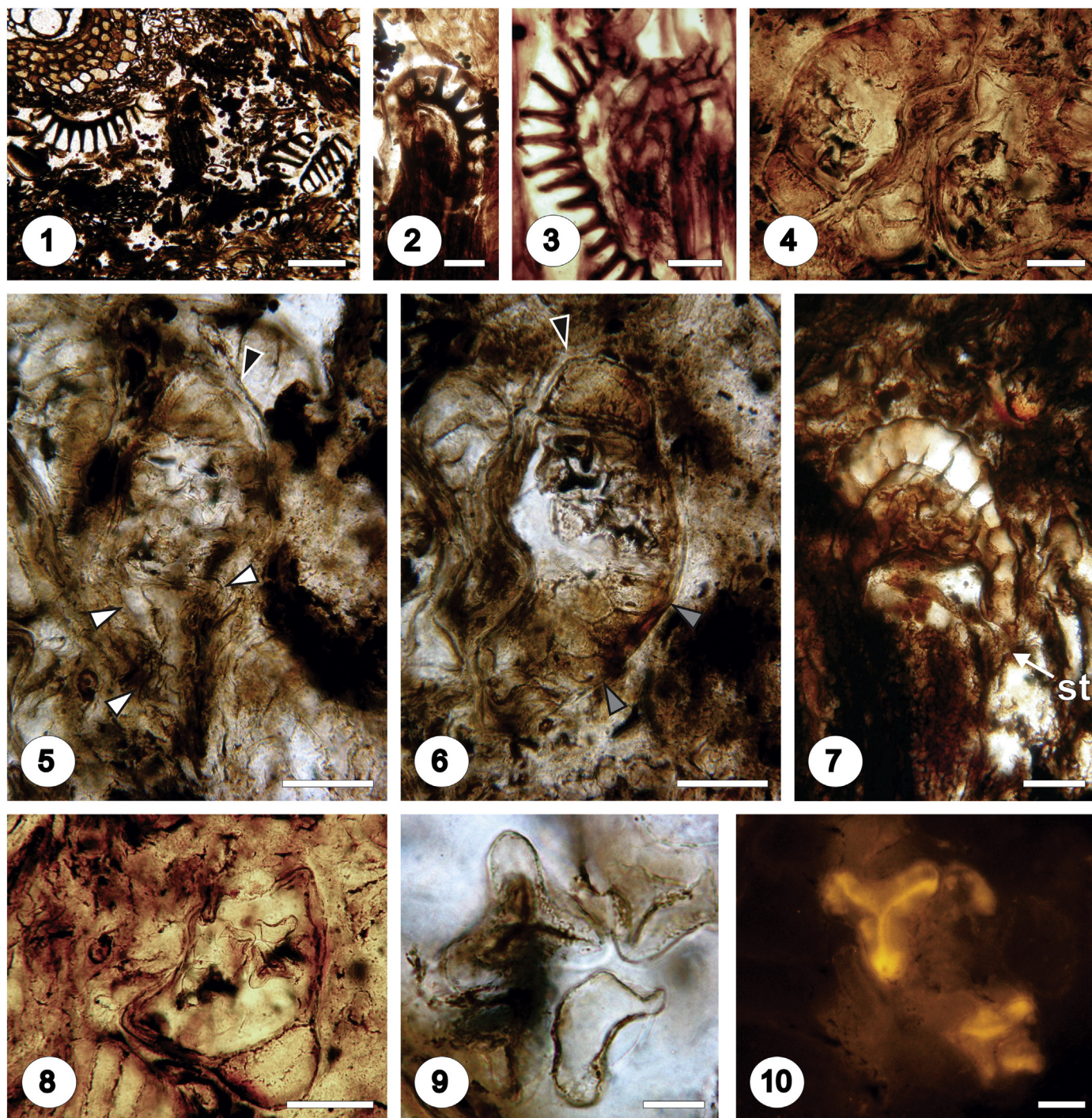


Plate VI. *Tempskya dernbachii*. Sporangia and spores. 1–9 with LM, 10 in FM.

1. Sporangium remains. Annulus (arrows); MOZ–Pb 57a. Scale bar = 10 μ m.
- 2–7. Sporangia.
- 2 and 3. LS. Sporangia with vertical annulus; MOZ–Pb 57a. Scale bar = 50 μ m.
4. CS. Sporangia with spores inside; MOZ–Pb 57a. Scale bar = 50 μ m.
- 5, 6 and 7. Sporangium remains, with spores, annulus (black arrows), capsule cells (grey arrows), stalk (white arrows) and stomium? (st). Detail; MOZ–Pb 57a. Scale bar 50 = μ m.
8. CS. Sporangium with spores inside; MOZ–Pb 57a. Scale bar = 50 μ m.
9. Spores. Detail. MOZ–Pb 57a. Scale bar = 10 μ m.
10. Spores with MF (Detail). MOZ–Pb 57a. Scale bar = 10 μ m.

These comparisons show that *Tempskya* has a similar combination of anatomical characters, at least, with some extant families of the Cyatheales.

The differences among Tempskyaceae and the families of Cyatheales are seen in Table 2.

5.2. Stratigraphic interpretation

In the first description of *Tempskya dernbachii*, Tidwell and Wright (2003) suggested that this species came from the Rayoso Formation (Cañadón de la Zorra Fm., sensu Uliana et al., 1975) (Leanza, 2003).

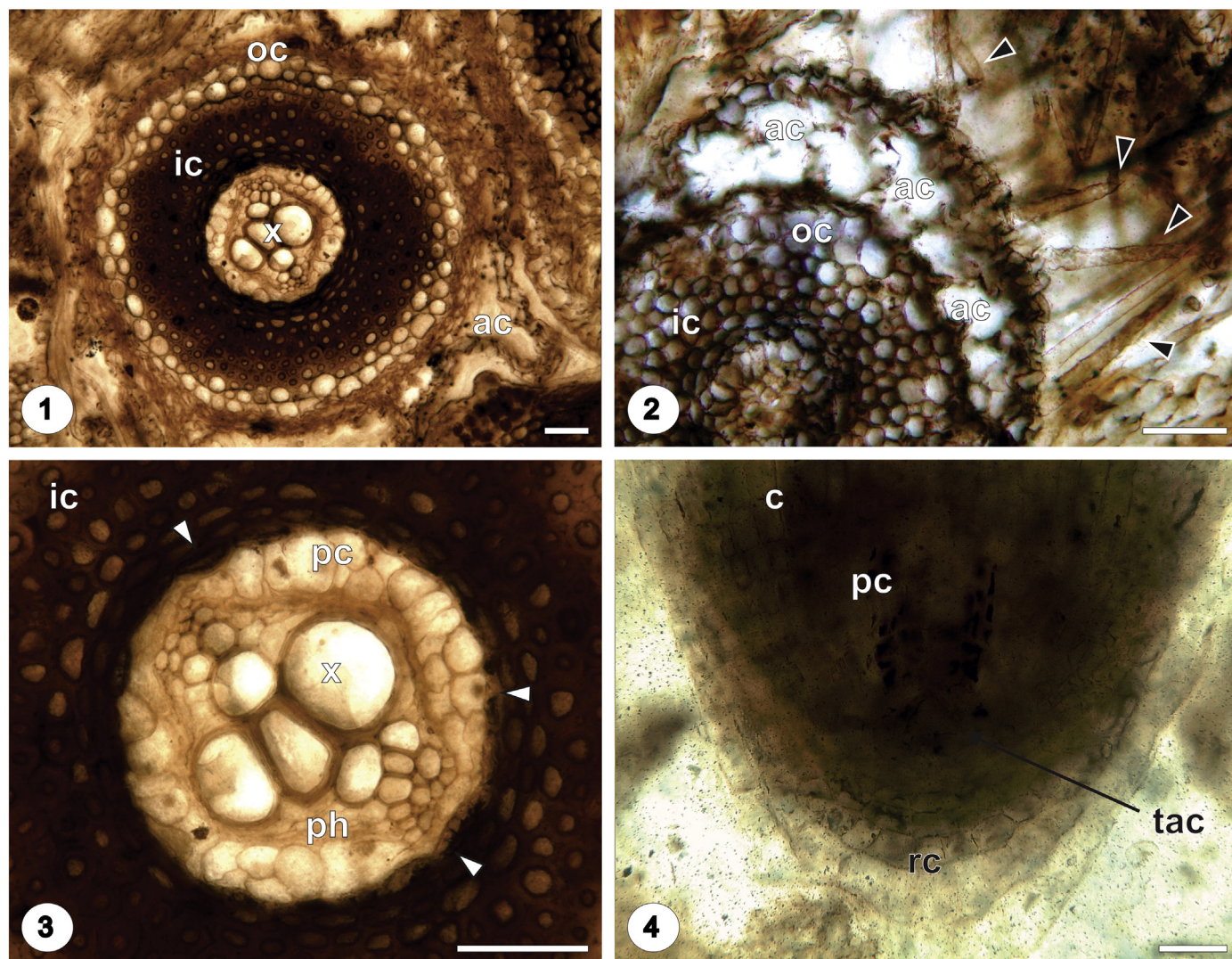


Plate VII. *Tempuskyia dernbachii*. Roots. All LM.

1. CS. Diarch root. Aerenchymatic chambers (ac), outer cortex (oc), inner cortex (ic), endodermis, pericycle, phloem, and xylem (x); MOZ-Pb 07a. Scale bar = 100 μ m.
2. CS. Root with aerenchyma (Detail). Radical hairs (black arrows), aerenchymatic chambers (ac), outer cortex (oc), and inner cortex (ic); MOZ-Pb 07a. Scale bar = 100 μ m.
3. CS. Root. Detail. Inner cortex (ic), endodermis (white arrows), endodermis (white arrows) pericycle (pc), phloem, and xylem (x); MOZ-Pb 07a. Scale bar = 100 μ m.
4. LS. Detail of root. Rootcap (rc), tetrahedral apical cell (tac), pericycle (pc) and cortex (c). MOZ-Pb 07c. Scale bar = 100 μ m.

However, the outcrops in the area indicated by these authors correspond to the Mulichinco and Agrio formations (Leanza and Hugo, 2001). The incorrect age and stratigraphic provenance suggested by Tidwell and Wright (2003) could be a mistake made during the collection, or a confusion of the Rayoso Formation (Albian) and the Mulichinco Formation. All fossil remains described here are from the Mulichinco Formation (Valanginian). Furthermore, the Rayoso Formation is predominantly continental, and marks the definitive disconnection between the Neuquén Basin and the palaeo-Pacific Ocean. The unit was interpreted as aeolian and saline playa-lake systems, with alternated humid and extreme arid climatic periods (Zavala and Ponce, 2011). This regime would not have been favourable for the development of tree-ferns; and this, reinforces the hypothesis that *T. dernbachii* could not have been collected from the Rayoso Formation, as suggested by Tidwell and Wright (2003).

The presence of many specimens of *Tempuskyia dernbachii* in different localities in the Mulichinco Formation indicates that these plants were abundant in this region during the deposition of this formation.

Tempuskyia is only recorded in Cretaceous deposits (See Table 3), with the earlier records of *Tempuskyia riojana* Barale and Viera

(1989), from La Rioja (Spain) dated as Valanginian to Hauterivian. However, the new record of *Tempuskyia* from the Mulichinco Formation shows that these ferns had an earlier distribution in the Southern Hemisphere, which might indicate that the genus originated in Gondwana.

5.3. Fossil plants assemblages and palaeoecological inferences

The fossil plant assemblages from the Mulichinco Formation provide information on the climate during the Valanginian in the Neuquén Basin. The fossil material from the Mulichinco Formation might be allochthonous. The fossils may be from a nearby source, or they may be a mixture from different sources, of which the proximal source is not necessarily the dominant vegetation. However, plant remains (e.g., leaves and stems) transported over long distances can be easily fragmented and destroyed. The well-preserved fossils of *Equisetites* sp. and the false trunks of *Tempuskyia* (Plate I, 2–3) collected from the same level in the Puesto Gualmes locality suggest little transport. *Tempuskyia* and *Equisetites* probably grew in nearby areas. The deposits associated to fossil trunks suggest moderate to low energy conditions.

Table 1
Comparisons between Tempskyaceae and some families of Polypodiales.

	Stem	Stelar type	Vascular bundles in petiole	Sori	Sporangium		
					Indusium	Annulus	Spores
Tempskyaceae	With hairs	Solenostele	Single V- or U-shaped vascular strand	Present	Absent	Vertical	Trillete. Triangular
Lindsaeaceae	With scales	Protostele with internal phloem	Single vascular bundle, adaxially grooved	Present	Present	Vertical	Trillete. Tetrahedral, infrequently monolete
Saccolomataceae	With scales	Dictyostele	Single omega-shaped vascular strand (open end adaxial)	Present	Present	Vertical	Trillete. Tetrahedral-globose ridged
Dennstaedtiaceae	With hairs	Solenostele, dictyostele	Several vascular bundles in gutter-shaped vascular strand (adaxial open end)	Present	Present or absent	Vertical	Trillete or monolete, usually with perispore
Pteridaceae s. l.	Parkeriaceae	With scales	Dictyostele	Absent	Present	Vertical	Trillete. Tetrahedral to globose
	Adiantaceae	With scales	Protostele, solenostele to dictyostele	Present	Present	Vertical	Monolete or trillete
	Cryptogrammeae	With scales	Solenostele	Present	Present or absent	Vertical	Trillete. Papillate, tuberculate or rugulate
	Sinopteridaceae or Cheilantheaceae	With scales	Solenostele	Present	Present	Vertical	Trillete. Tetrahedral to globose
Pteridaceae s.s.	Pteridaceae s.s.	With scales	Solenostele to dictyostele	Present or absent	Present	Vertical	Trillete. Tetrahedral-globose and cingulate
Polypodiaceae	With hair and scales	Dictyostele	Many U-shaped vascular bundles	Present	Absent	Vertical	Monolete or trillete

Nowadays, tree ferns inhabit humid forests in tropical lowlands and submontane environments, and subtropical, Southern Hemisphere temperate forests (Large and Braggins, 2004). This is according to the sedimentary information from those levels of the Mulichinco Formation in the Puesto Gualmes locality, where *Tempskya* was found in deposits that have been interpreted as a mixed-load fluvial system, with moderate to high sinuosity and moderate to low energy (Olivo et al., 2012), suggesting that these plants grew adjacent to rivers in humid lowlands. The occurrence of *Equisetites* is a good indicator of humid conditions or wetlands. The in situ preserved specimens of *Tempskya* from Idaho were found in growth position, in sediments deposited in a swampy environment (Andrews and Kern, 1947). The roots of *Tempskya dernbachii* and *Tempskya minor* Read et Brown have aerenchyma, a feature present in aquatic and marsh plants, which reinforces the idea of these plants growing in swamp or pond environments.

The abundance of *Tempskya* in different localities in the Mulichinco Formation suggests similar environment conditions throughout the area. However, *Tempskya* and other tree ferns are absent in other Cretaceous deposits in the Neuquén Basin, such as, the Neuquén and Malargüe groups. This condition would be related to a climate change in the Cretaceous of Neuquén Basin, from temperate/warm and humid to warm and dry (Martínez, 2010, 2012).

5.4. Affinities of the Tempskyaceae

The genus *Tempskya* has often been regarded as being related ferns (Cyatheales, Gleicheniales, Marattiaceae, Polypodiales and Schizaeales). However, all anatomical and morphological parameters here observed indicate that the Tempskyaceae can be clearly distinguished from

Table 2
Comparisons between Tempskyaceae and families of Cyatheales.

	Stem	Stelar type	Vascular bundles in petiole	Sori	Sporangium		
					Indusium	Annulus	Spores
Tempskyaceae	With hairs	Solenostele	Single V- or U-shaped vascular strand	Present	Absent	Vertical	Trillete. Triangular
Metaxyaceae	With hairs	Solenostele	Single V- or U-shaped vascular strand	Present	Absent	Vertical to slightly oblique	Trillete. Globose, with perispore
Thyrsopteridaceae	With hairs	Solenostele	Horseshoe-shaped, corrugate vascular strand	Present	Present	Oblique	Trillete. Globose or tetrahedral
Dicksoniaceae	With hairs	Polycyclic dictyostele, or solenostele	One to many vascular bundles arranged in an horseshoe-shaped	Present	Present or absent	Oblique	Trillete. Globose or tetrahedral
Loxsomataceae	With hairs	Solenostele	Single gutter-shaped vascular strand	Present	Present	Slightly oblique	Trillete. Tetrahedral
Culcitaceae	With hairs	Solenostele	Single U-shaped vascular strand	Present	Present	Slightly oblique	Trillete. Globose-tetrahedral
Plagiogyriaceae	Without hairs or scales	Dictyostele	Single V- or U-shaped vascular strand	Present	Absent	Slightly oblique	Trillete. Tetrahedral
Cibotiaceae	With hairs	Solenostele or dictyostele	Three vascular bundles arranged in an omega-shaped	Present	Present	Slightly oblique	Trillete. Globose-tetrahedral
Cyatheaceae	With scales and hairs	Polycyclic dictyostele	Three to many vascular bundles	Present	Present or absent	Oblique	Trillete. Tetrahedral

Table 3List of species of *Tempskya* showing geographic distribution, stratigraphic horizon and period/age.

Species	Geographic distribution	Stratigraphic horizon	Period/Age
<i>Tempskya dernbachii</i> Tidwell et Wright, emend. Martínez.	Neuquén province, Argentina–South America	Mulichinco Formation	Valanginian
<i>Tempskya riojana</i> Barale and Viera (1989) (Puente-Arauzo et al., 2014)	Castilla y León and La Rioja, Spain–Europe	Enciso Group? and Pinilla de los moros Formation	Valanginian?. Upper Hauterivian–Lower Barremian
<i>Tempskya reesidei</i> Ash et Read (Ash et al., 1976)	Animas Mountains, United States–North America	Mojado Formation	Albian
<i>Tempskya zelleri</i> Ash et Read (Ash et al., 1976)	Big Hatchet Mountains, United States–North America	Mojado Formation	Albian
<i>Tempskya stichkae</i> Tidwell and Hebert (1992)	Utah, United States–North America	Cedar Mountain, Burro Canyon Formations	Albian
<i>Tempskya judithae</i> Clifford and Dettmann (2005)	Belmont Station, Australia	Winton Formation	Albian
<i>Tempskya erosa</i> (Stokes et Webb) Stopes (1915)	Potton–England–Europe	Lower Greensand Group	Lower Cretaceous
<i>Tempskya schimperi</i> Corda (1845)	Germany–Czech Republic–France–Europe	Perucér Formation	Lower Cretaceous
<i>Tempskya whitei</i> Berry (1911)	Maryland, United States–North America	Patapsco Formation	Lower Cretaceous
<i>Tempskya knowltonii</i> Seward (1924)	Montana and Utah, United States–North America	Kootenai Formation?	Lower Cretaceous
<i>Tempskya wessellii</i> Arnold (1945)	Montana, Oregon and Utah, United States–North America	Kootenai Formation	Lower Cretaceous
<i>Tempskya wyomingensis</i> Arnold (1945)	Utah, Wyoming and Colorado, United States–North America	Morrison Formation? Mowry Shale or Thermopolis Shale?	Lower Cretaceous?
<i>Tempskya superba</i> Arnold (1958)	Dawes County, Nebraska, United States–North America	Lakota Formation?	Lower Cretaceous?
<i>Tempskya readii</i> Tidwell and Hebert (1992)	Utah, United States–North America	Burro Canyon Formation	Late Early Cretaceous
<i>Tempskya jonesii</i> Tidwell and Hebert (1992)	Utah, United States–North America	Cedar Mountain, Burro Canyon, and Dakota Formations	Albian–Cenomanian
<i>Tempskya varians</i> Velenovsky (1888)	Bohemia, Czech Republic–Europe	?	Cenomanian?
<i>Tempskya iwataensis</i> Nishida (1986)	Taneichi district, Japan	Taneichi Formation	Santonian
<i>Tempskya uemurae</i> Nishida (2001)	Iwate, Japan	Taneichi Formation	Santonian
<i>Tempskya cretacea</i> Hosius and Marck (1880)	Westfalia, Germany–Europe	?	Upper Cretaceous
<i>Tempskya grandis</i> Read and Brown (1937)	Wyoming, United States–North America	Bear River Formation	Upper Cretaceous
<i>Tempskya minor</i> Read and Brown (1937)	Wyoming, United States–North America	Bear River Formation	Upper Cretaceous
<i>Tempskya rossica</i> Kidston and Gwynne-Vaughan (1912)	Mugadjar, Kazakhstan–Asia	?	Upper Cretaceous?
<i>Tempskya pulchra</i> Corda (1845)	Bohemia, Czech Republic–Europe	?	Cretaceous?

other fern families. The new features described for *Tempskya dernbachii* provide new data on the relationships of the Tempskyaceae.

The nature of the sporangia places *Tempskya dernbachii* within the “Leptosporangiate ferns” and the presence of a vertical annulus suggest a relationship to the Polypoidales and some Cyatheales. Regarding the anatomy of the petiole and morphology of the spores a relationship to the Cyatheales is most plausible. However, the lack of a clear morphological synapomorphy makes it difficult to group it together with the Cyatheales.

Among the Cyatheales, the features present in the Metaxyaceae are closer to those observed in *Tempskya* (e.g., a solenostelic rhizome without a sclerenchyma sheath and hairy rhizomes, the stelar type of the petioles and the vertical to slightly oblique annuli in the sporangia), but *Metaxya* differs from *Tempskya* in having prostrate rhizomes, paraphyses in the sporangium, and globose spores with a granulate perispore.

The Tempskyaceae thus show a combination of anatomical features that are similar to those present in some members of the Cyatheales, which are characterized by the presence of an arborescent growth habit, an amphiphloic solenostele, petioles with a single V- or U-shaped vascular strand, roots with an inner sclerenchymatous cortex, an outer parenchymatous cortex, leptosporangia with a vertical annulus, and trilete spores. However, some features, such as the arborescent growth habit, the false trunks, the aerenchyma in the roots, and the sporangia and spores, clearly distinguish the Tempskyaceae from other families of the Cyatheales.

5.5. Ecology of the Tempskyaceae

Rothwell (1987) recognized three major pulses of evolutionary radiation within leptosporangiate ferns. The Tempskyaceae evolved during the second radiation beginning in the Jurassic (Rothwell and Stockey, 2008). This is a remarkable thing to notice, because the fossil record

indicates the diversification of the Cyatheales (tree ferns) across the Jurassic and the Cretaceous (Tidwell and Ash, 1994; Pryer et al., 2004; Rothwell and Stockey, 2008; Vera, 2009, 2013; Vera and Herbst, 2015). Therefore, the arborescent growth in the Cyatheales could be a result of adaptive radiation, occupying new or vacant niches (e.g. canopy and understory in the forest). The arborescent growth in the Tempskyaceae would also have adapted in order to inhabit environments with specific ecological preferences, e.g. such as swamps, low lands and/or coastal areas, with occasional dry periods, such as those present in the Mulichinco Formation (Schwarz, 2003; Schwarz et al., 2011).

Aerenchyma roots of *Tempskya* with an exodermis and endodermis, are features commonly present in plants inhabiting swampy environments. The aerenchyma offers an internal system for the exchange of gases in submerged tissues of aquatic plants (Jung et al., 2008). The exodermis is similar in structure and function to the endodermis and regulates the transport of water and solutes from and to the root (Ma and Peterson, 2001). However, its main function is the restriction of apoplastic water loss from the roots during water low stands during in periods of drought (Enstone and Peterson, 1997; Taleisnik et al., 1999), or in plants growing in saline substrates (Taleisnik et al., 1999).

Tempskya dernbachii was probably a tree fern with small fronds, because the petioles are only up to 2.2 mm in diameter.

Probably, swampy environments or environments with coastal lagoons would have been common across the Jurassic and the Cretaceous (Krasilov, 1975; Person and Delevoryas, 1982; Cross and Phillips, 1990; Greb et al., 2006; Villar de Seoane and Archangelsky, 2008); then, these environments would have offered opportunities for the specialization and the diversification of the Tempskyaceae.

There are many records of *Tempskya* from the Aptian and the Albian, (Read and Brown, 1937; Arnold, 1958; Ash et al., 1976; Tidwell and Wright, 2003; Clifford and Dettmann, 2005), which suggests great dispersion and diversification. The dispersion of *Tempskya* could be

explained by favourable climates and environments around the world. The warmer and drier climate after the Late Cretaceous–Paleocene and the diversification of magnoliophytes might have contributed to the extinction of the *Tempskyaceae*.

6. Conclusions

The new specimens of *Tempskya dernbachii* described here, have provided new information on the systematics, age, and ecology of this family.

The anatomical characteristics present in the fossils studied here, have several features that allow us to include them in the leptosporangiate ferns, with affinities with the Cyatheaales. However, the *Tempskyaceae* have a set of particular characters in accordance with the taxonomic status of this family (e.g. false trunks, amphiphloic solenosteles, petioles with a single V- or U-shaped vascular strand, adventitious and diarch roots, leptosporangia with a vertical annulus, trilete spores), which distinguish them from other leptosporangiate ferns.

This research supports the provenience of *Tempskya dernbachii* from the Mulichinco Formation (Valanginian) by the records made in several localities (Puesto Victoria Nahuel and Pilmatué), with a detailed sedimentological study (Puesto Gualmes). Therefore, this early record suggests that *Tempskya* would have originated in South America.

The aerenchyma in roots of *Tempskya* is a feature of plants, which inhabit swampy environments. This feature added to the record of *Equisetites*, and the sedimentological studies reinforce the hypothesis about the presence of environments like swamps, low lands and coastal areas during the deposition of the Mulichinco Formation.

Finally, the climatic change and the diversification of magnoliophytes in swampy environments might have been determining factors in the extinction of the *Tempskyaceae* after the Late Cretaceous–Paleocene.

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