

A new vesselless angiosperm stem with a cambial variant from the Upper Cretaceous of Antarctica

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We sectioned a permineralized stem preserved in marine calcareous concretions from the Campanian (Upper Cretaceous) of James Ross Island, Antarctic Peninsula using the cellulose-acetate peel technique. The material is a slender stem displaying a combination of characters such as: (i) absence of vessels and axial parenchyma, (ii) presence of a cambial variant which produces axial vascular elements in segments (AVES pattern), and (iii) elongated upright ray cells. This character combination allows us to assign this fossil to family Chloranthaceae and to relate it to an extant genus *Sarcandra*. Consequently we describe *Sarcandraxylon sanjosense* gen. et sp. nov., representing the first vegetative fossil of Chloranthaceae—a basal angiosperm family with a fossil record extending back into the Early Cretaceous and dominated by pollen grains and a limited number of reproductive mesofossils. Besides doubtfully assigned leaves, there are no reported Cretaceous macrofossils of Chloranthaceae, which hinders our understanding of the overall pattern of morphological evolution for the family. The new fossil constitutes the first fossil occurrence of the *Sarcandra* clade in high latitudes of Western Gondwana. The particular wood anatomy and small diameter suggest a new plant habit (sub-shrub) for the physiognomy of the Cretaceous Antarctic floras.

Key words: Angiospermae, Chloranthales, Chloranthaceae, cambial variant, Campanian, Antarctica, James Ross Island.

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Introduction

Chloranthaceae is a basal angiosperm family with a fossil record extending back into the Early Cretaceous, with a record dominated by pollen grains and a limited number of reproductive mesofossils. Besides doubtfully assigned leaves, there are no reported Cretaceous macrofossils of Chloranthaceae, what hinders our understanding of the overall pattern of morphological evolution for the family.

The phylogenetic position of Chloranthaceae among the basal angiosperm lineages is still unresolved. This family has received considerable attention because of its primitive morphology (i.e., monosulcate pollen, lack of vessels, tracheid-vessel transitional elements, scalariform vessel perforations, small flowers often without a perianth), which suggests a close relationship with Piperales, Magnoliales, Laurales, or Trochodendrales (Burger 1977; Cronquist 1981; Walker and Walker 1984; Verdcourt 1985; Endress 1986, 1987; Carlquist

1992a; Todzia 1993). Recent molecular analyses placed Chloranthales in a basal polytomy with the magnoliid and eudicots/monocots/Ceratophyllaceae clades (APG IV 2016).

Although the Chloranthaceae has a disjunct tropical distribution with four extant genera, it has a global pollen record since the Early Cretaceous (Couper 1958; Hughes and McDougall 1994; Eklund et al. 2004; Zhang et al. 2011) which highlights that the family had a long history, and the extant restricted distribution represents a relict of a much broader one in the past (Eklund et al. 2004). Besides the presence of *Clavatipollenites* and *Asteropollis* pollen-types, the fossil record of the family is based mostly of reproductive organs mostly from the Northern Hemisphere.

The oldest evidence of Chloranthaceae from Antarctica comes from pollen grains of *Clavatipollenites hughesii* Couper, 1958 from the lower to middle Albian and extends through the Late Cretaceous (Dettman and Thomson 1987; Dettman 1989; Askin 1994). Beside the pollen record, only

putative chloranthaceous leaves were identified from the Albian of the Alexander Island (Cantrill and Nichols 1996).

Despite its important role in the early diversification of angiosperms, little is known about the evolution of morphology and anatomy in Chloranthaceae because of the sparse fossil record. Therefore, our understanding about the secondary growth and anatomical characters is poor, making the whole plant reconstructions hardly possible.

In this work, we describe a new permineralized stem from the Santa Marta Formation (Santonian–Campanian) in the James Ross Island (Antarctic Peninsula), which represents the first Chloranthaceae vegetative fossil from the Southern Hemisphere. This stem displays a combination of characters reminiscent of the extant *Sarcandra*, and sheds a new light on the morphological diversification of the family during the Late Cretaceous.

Institutional abbreviations.—IAA-Pb, Paleontological and Geological Collection of the Argentine Antarctic Institute, Buenos Aires, Argentina.

Other abbreviations.—AVES, axial vascular elements in segments.

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in Plant Fossil Names Registry (PFNR) (<https://www.plantfossilnames.org>).

Geological setting

The Santa Marta Formation corresponds to the basal unit of the Marambio Group in the James Ross Basin (Elliot 1988; Del Valle et al. 1992), and is divided into two members: the lower Alpha Member and the upper Beta Member (Olivero et al. 1986; Olivero 2012). The studied fossil plant was found at the locality informally named as “Sítio Feliz” by Iglesias (2016), near the San José Pass (Nývlt and Šerák 2009) between the Monolithic Lake and Santa Marta Cove (Fig. 1). This locality corresponds to the upper part of the Beta Member, in the upper section of the N Sedimentary Sequence (Olivero and Medina 2000). The sedimentology of the Santa Marta Formation at the fossiliferous section consists of an alternation of thick bioturbated packages of fine-grained, well-sorted sandstone, silty very fine grained sandstone, and mudstone beds, with abundant plant debris and large tree trunks. Fossil leaves, wood, and marine macrofauna were found in calcareous concretions from a single thick fossiliferous layer. The exceptional fossil preservation in its massive and chaotic structure may be due to a rapid burial event in anoxic environment (Iglesias 2016).

Geological studies interpreted the Santa Marta Formation as facies of delta slopes and channel complexes of a progradational deepwater delta system in a marine shelf (Scasso et al. 1991; Olivero 2012). During its deposition, the sediments were delivered to deltaic systems by major rivers flowing to the east-southeast, being the main clastic source

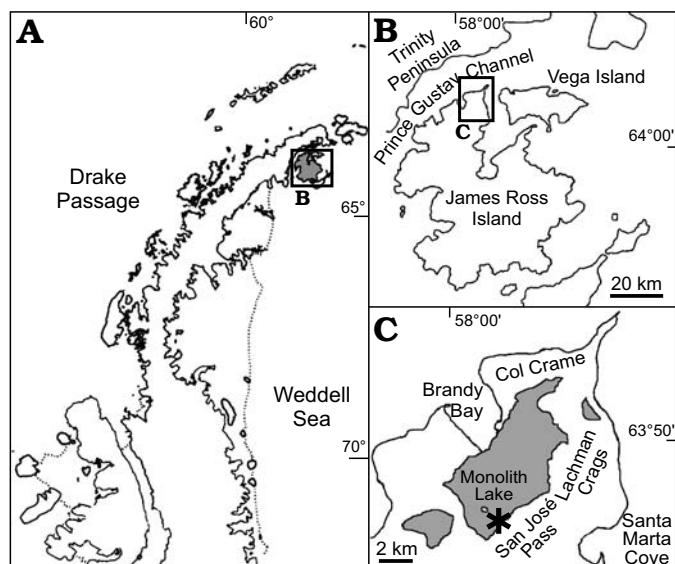


Fig. 1. A. Location of the new fossil locality in Antarctic Peninsula, James Ross Island (gray). B. Map of James Ross Island at the northern Antarctic Peninsula. C. Map with the Santa Marta Formation outcrops (area shaded in gray) at the northern James Ross Island, showing location of the new fossil locality (asterisk). Modified from Olivero 2012 and Carvalho et al. 2013.

and preserved continental biota, drained by deltaic currents (Olivero et al. 2008). Geological and paleontological studies suggested that leaves and trunks were transported from western continental areas of the Antarctic Peninsula (Scasso et al. 1991).

Earlier contributions indicated that the Santa Marta Formation would have been deposited during the Santonian–Campanian interval on the basis of mollusk, foraminifer, and palynomorph associations (e.g., Crame 1983; Dettman and Thomson 1987; Keating 1992; Olivero 2012; Carvalho et al. 2013; Florisbal et al. 2013). Strontium isotopes ($^{87}\text{Sr}/^{86}\text{Sr}$ ratio ~0.70745) analyses, indicated a late Coniacian–late Campanian age at the Santa Marta Formation (McArthur et al. 2000). Based on the stratigraphy, and according to the presence of the ammonoid association 5 (kossmatisch-eratid ammonoids: *Natalites* cf. *morenoi* Riccardi, 1983 and *Natalites taylori* Spath, 1953) of Olivero (1992), the fossiliferous level from which the studied stem occurred would correspond to the early–middle Campanian (~83–77 Ma).

Palaeobotanical background

Palaeobotanical research from the Santa Marta Formation consists of several studies on permineralized woods (e.g., Poole and Francis 1999, 2000; Poole et al. 2000a, b; Poole and Gottwald 2001; Cantrill and Poole 2005; Pujana et al. 2017, 2018), pollen grains (e.g., Dettmann and Thomson 1987; Keating 1992; Barreda et al. 2019), and leaf compressions (e.g., Hayes 1999; Hayes et al. 2006; Kvacek and Sakala 2011; Iglesias 2016). Previous studies about the floral assemblages from this formation, suggested a mixed canopy

forest with an increasing dominance of eudicots, although magnoliids (e.g., Cunoniaceae, Nothofagaceae, Laurales) and conifers (*Araucariaceae* and *Podocarpaceae*) were still frequent; that would developed in a back-arc basin of an emergent volcanic arc (Elliot 1988).

Particularly, from the upper part of the Beta Member, Iglesias (2016) described the first Campanian compression flora for Antarctica; composed of cycads (*Zamiaceae*), conifers (*Araucaria*, *Araucarites*, *Brachyphyllum*, and *Pagiophyllum*), several ferns (including *Pteridaceae* and ?*Schizaeaceae*), and angiosperms (including ?*Cunoniaceae* and *Lauraceae*). At the same locality, a new type of fossil preservation has been found, which consists of permineralized plant remains inside carbonate concretions, comprising vegetative and reproductive organs with three-dimensional organic connections. The complete flora has been described in the Ph.D. thesis of the senior author (MLP) who reported several leaves, seeds, wood, and twigs. The results have been only partially published yet (Pipo and Iglesias 2017; Pipo et al. 2018, 2019).

The calcified fossils contain also crystals of frambooidal pyrite, interpreted as a proxy of anaerobic oxidation of methane by a consortium of archaea that reduce the dissolved sulfates and induce the precipitation of carbonates and iron sulphide (Hinrichs and Boetius 2002). Although the fossil angiosperm stem from this study is fragmentary, nevertheless it retained the original shape and the almost intact anatomy with good preservation of both xylem and bark. Nonetheless the pyritization poses a problem in more detailed studies of tracheid wall characters (e.g., pits, cross-fields, wall thickenings) at light microscopy or SEM.

Material and methods

Fossil preparation.—Anatomical sections (transverse, tangential, and radial) were obtained from the calcareous concretion using the cellulose-acetate peel technique (Joy et al. 1956), in this case using hydrochloric acid (5–10%). The peels were mounted using Trabasil® NR2 mounting medium on glass slides (Noetinger et al. 2017) and studied with Olympus CH30, Olympus BX50 epifluorescence microscope (long pass green filter) from the INIBIOMA sede Salmonicultura, Argentina; a compound microscope Nikon SMZ800 from the INIBIOMA; and a FEI Nova Nano SEM-230 from the Servicio de Microscopía, Centro Atómico Bariloche (CNEA), San Carlos de Bariloche, Argentina. Photographs were taken with a Leica DMC2900 and Nikon Digital Sight DS-Fi1 digital cameras. For SEM observation, a fragment of the stem was isolated from the sample rock using Dremel®4000 rotary tool equipped with a diamond wheel, mounted in an aluminum SEM stub, and platinum/palladium coated.

The plant material is deposited in the Repositorio de colecciones paleontológicas y geológicas del Instituto Antártico Argentino, Ciudad Autónoma de Buenos Aires, Argentina.

Description and systematic treatment.—For the description of the wood anatomy we used IAWA List of Microscopic Features for Hardwood Identification (IAWA Committee 1989). A minimum of 30 measurements of each character were made, except for protoxylem cells that only 18 measurements could be taken. For systematic APG IV (2016) was followed; and for wood comparisons the InsideWood database (2004-onward; <http://insidewood.lib.ncsu.edu/search>) and the database of Japanese woods in the Forestry and Forest Products Research Institute web page (<http://db.ffpri.affrc.go.jp/WoodDB/JWDB-E/home.php> accessed in 2019) were used.

We apply the term “typical cambial activity” when the cambium is formed by one continuous ring of cambial cells (i.e., radial and fusiform initials) that produces both continued secondary xylem centripetally and phloem centrifugally. Every other cambial activity different from the previous is called as “cambial variant” (Carlquist 2001a). In the description of cambial variants, the terminology of Angyalossy et al. (2014) is used.

Systematic palaeobotany

Order Chloranthales Martius, 1835

Family Chloranthaceae Robert Brown ex Sims, 1820 nomen conservandus

Genus *Sarcandraxylon* nov.

PFNR: PFN001016.

Etymology: Combination of *Sarcandra*, a extant Chloranthaceae genus, and wood ending greek; in reference its similarity of stem anatomy.

Type species: *Sarcandraxylon sanjosense* sp. nov.; see below.

Diagnosis.—Stem has wide, circular and parenchymatous pith. The primary vascular system is formed by one cycle of collateral vascular bundles, with endarch protoxylem. Secondary vascular system developed by a cambial variant resulting in segments of vascular tissue separated by wide interfascicular multiseriate parenchyma rays. Secondary xylem is vesselless without axial parenchyma.

Stratigraphic and geographic range.—Upper Beta Member, Santa Marta Formation, Marambio Group, James Ross Basin at San Jose Pass, northern James Ross Island, Antarctic Peninsula, early-middle Campanian (~83–77 Ma), Late Cretaceous.

Sarcandraxylon sanjosense sp. nov.

PFNR: PFN001017.

Etymology: From the San José pass (James Ross Island), a nearest locality where the fossil was found.

Holotype: IAA-Pb 621, a stem 3 mm long and 5 mm wide in a rock sample mounted on SEM stub; six cellulose-acetate peels mounted in glass slides (three in transverse section; and three in tangential section).

Type locality: San Jose Pass (equivalent to CF cite from Iglesias 2016), northern James Ross Island, Antarctic Peninsula (63°54'14" S; 57°54'40" W; Fig. 1).

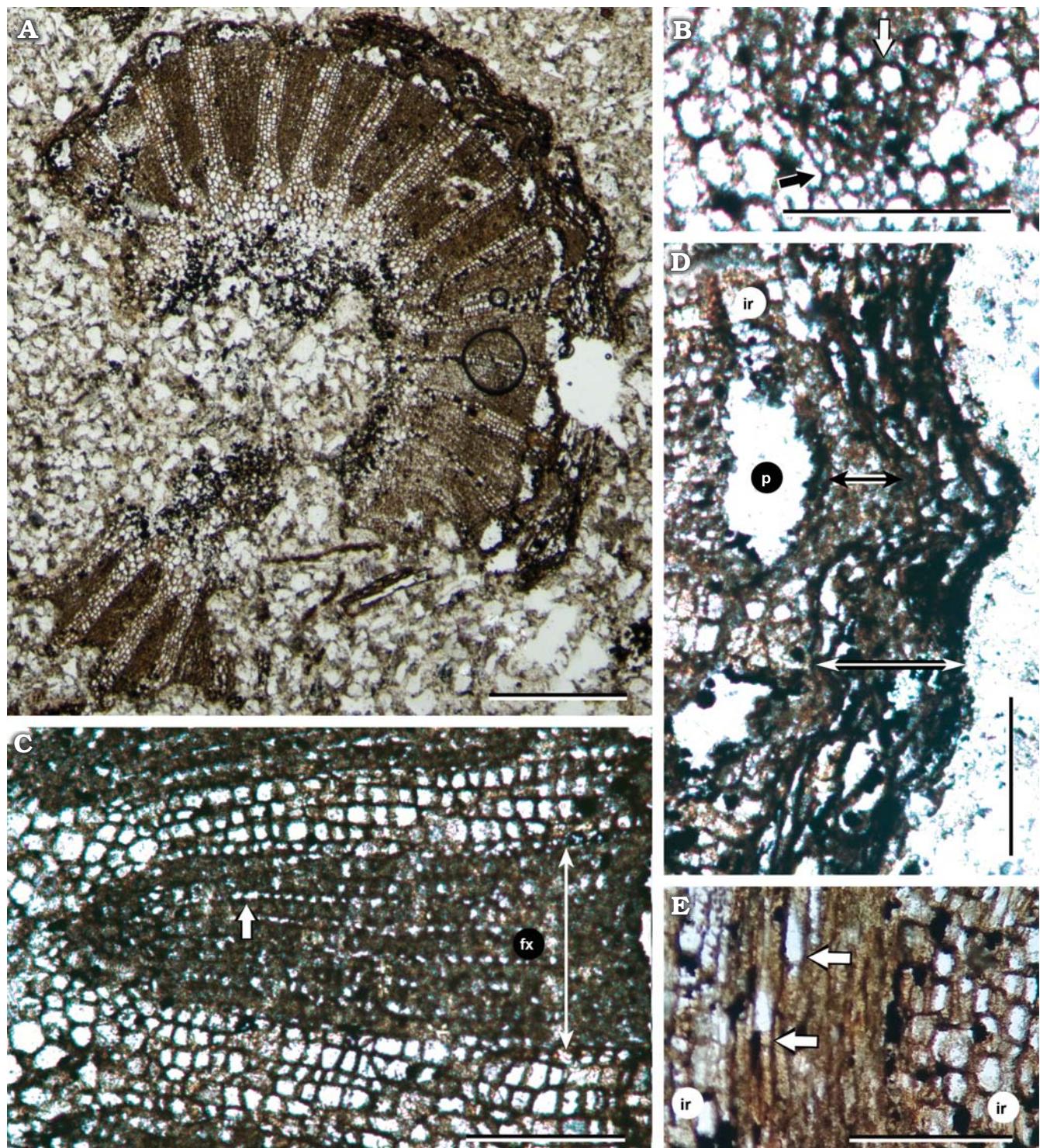


Fig. 2. Light micrographs of the stem of chloranthacean angiosperm *Sarcandraxylon sanjosense* gen. et sp. nov. (IAA-Pb 621), San José Pass, Antarctica, early–middle Campanian. A. Transverse section of the complete stem with pith, secondary xylem, phloem, and bark. B. Protoxylem (black arrow) and metaxylem (white arrow) in a vascular bundle. C. Secondary xylem in transverse section, pith in the left (white arrow), two interfascicular rays and fascicular secondary xylem (fx) intercalated. White arrow pointing uniseriate fascicular ray. D. Detail of bark and secondary phloem. Note phloem with AVES pattern as well. Phloem cells not preserved (p) and phloem fibers cap (black double head arrow) separated by interfascicular rays (ir). Bark (white double head arrow) with a continued thickened layer, forming shallow ribs. E. Tangential section of the stem, arrows pointing fascicular uniseriate rays; at both sides interfascicular rays (ir). Scale bars: 50 µm; except A, 1 mm.

Type horizon: Early–middle Campanian (~83–77 Ma), Late Cretaceous, Upper Beta Member, Santa Marta Formation, Marambio Group, James Ross Basin.

Diagnosis.—Secondary vascular cylinder with interfascicular rays and axial elements in segments. Homocellular and heterogenous interfascicular rays consisting of square

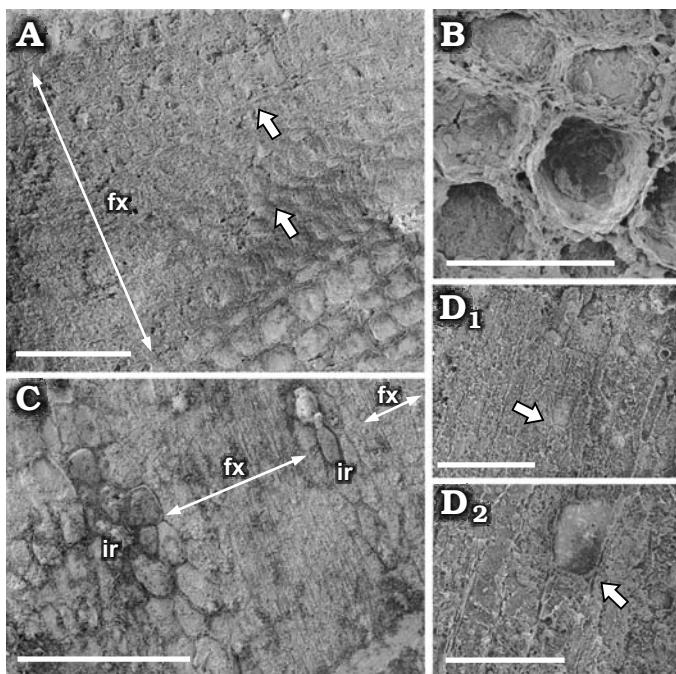


Fig. 3. SEM images of the secondary xylem of the chloranthacean angiosperm *Sarcandraxylon sanjosense* gen. et sp. nov. (IAA-Pb 621), San José Pass, Antarctica, early–middle Campanian. A. Transverse section of the stem, showing one vascular bundle in the middle, pith toward the right, white arrows pointing uniseriate fascicular rays. B. Parenchymatic cells of an interfascicular ray in transverse section showing the main shape and piritization of the cell walls. C. Secondary xylem in longitudinal tangential section, showing fascicular xylem (fx) and interfascicular rays (ir). D. Longitudinal section of fascicular xylem; D₁, showing tracheids and a two cells tall uniseriate ray (white arrow) with elongate upright cells; D₂, detail showing cell walls partially replaced with framboidal pyrite (white arrow). Scale bars: A, D, 100 µm; B, 40 µm; C, 200 µm; E, 50 µm.

and procumbent parenchyma cells. The secondary xylem segments contain tracheids and uniseriate homocellular and homogeneous rays with elongated upright cells. Growth rings are indistinct. Secondary phloem with fibers arranged in caps. Bark composed by dead cells of secondary phloem and cork cells which are accumulated in a multilayered rhytidome.

Description.—The slender stem is 5 mm in diameter, circular in transverse section (Fig. 2A). Although its periphery is not completely preserved, the whole shape remains almost intact. The central circular pith is 1.87 mm in diameter. It is composed of large isodiametric parenchyma cells (40–70 µm; mean 50.36 µm). The primary vascular system is formed by one cycle of collateral vascular bundles, only 19 could be counted due to preservation (although may reach almost 30 in the whole), with endarch protoxylem (cell sizes 2.5–5 µm), and metaxylem cells size 5–7.5 µm (mean diameter 5.92 µm) (Fig. 2B). The secondary vascular cylinder is radially dissected, due to a cambial variant derived from one vascular cambium with differential activity, in which the interfascicular cambium only produces ray parenchyma cells resulting in axial vascular elements in segments (AVES pattern). The secondary xylem lacks vessels, and is composed

by tracheids (cellular diameters range 12.5–25 µm; mean diameter 17.9 µm) and uniseriate homocellular and homogeneous rays. These fascicular rays are two cells high and composed of elongated upright parenchyma cells (Figs. 2C, E, 3A, C, D). Growth rings and axial parenchyma are absent. The radial thickness of xylem segments is up to 202.5 µm. The interfascicular rays are broad (67 µm), multiseriate (5–6, up to 8 cells wide), homocellular, and heterogenous; consisting of square and procumbent parenchyma cells (5–10 µm; mean 7.33 µm) (Fig. 3B). The secondary phloem is arranged in half-moon shaped bundles and wide interfascicular rays (Fig. 2D). Phloem cells are poorly preserved; only some collapsed cells were identified, leaving a large central gap from the center to the base of bundles. Caps of phloem fibers are present externally in the bundles, with a mean size of 26.25 µm per 68.75 µm. The fibers are hard to measure because they are small and poorly preserved. The bark is composed by dead cells of secondary phloem, and cork cells which are accumulated in a multilayered rhytidome (mean bark growth 50 µm). It has a sinuous shape, with external shallow valleys in the interfascicular areas of phloem, and pronounced ribs over the phloem fiber caps (Fig. 2D).

Stratigraphic and geographic range.—Type locality and horizon only.

Discussion

Systematic affiliation.—The stem of the new Antarctic taxon possesses a very distinctive anatomical combination of character states. The absence of vessels in the xylem is one of the unique features of the general gymnosperm and some basal angiosperm woods. However, among them, only few have cambial variants as the new Antarctic taxon in this study. Among gymnosperms, the groups that present both cambial variants and vesselless wood, are cycads (Greguss 1968) and some orders of seed ferns as Medullosales, Corystospermales, Pentoxylales, Hermanophytale (Arnold 1962; Bose et al. 1985; Tidwell and Ash 1990; Tidwell 2002; Bodnar 2012; Bodnar and Coturel 2012). Cycad stem anatomy does not resemble that of the new taxon, since cycads are characterized by the presence of mucilage canals in pith, rays, and bark; medullary bundles; also they possess fascicular multiseriate wood rays and cambial variants that produce different vascular patterns than AVES (e.g., successive cambia; Greguss 1968; Cantrill 2000; Martínez et al. 2012).

Seed ferns, on the other hand, developed a broad diversity of cambial variants, such as successive cambia, differential cambial activity, multiple cambia, remnant activity of the cambium, and centripetal cambium (Bodnar 2012, and references therein). Among them only two orders present similar AVES pattern as the one found in the new taxa here described: Hermanophytale and Umkomasiales (=Corystospermales). However, in Hermanophytale the interfascicular rays are heterocellular, including parenchyma,

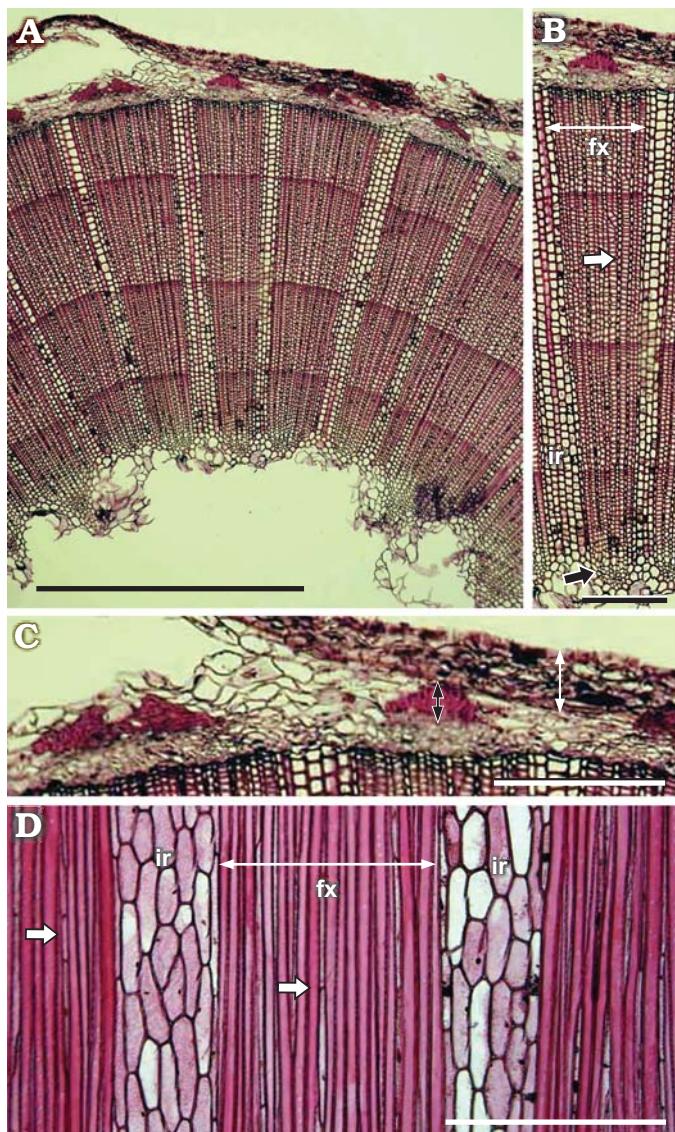


Fig. 4. Light micrographs of the stem of extant chloranthacean angiosperm *Sarcandra glabra* (Thunberg, 1794) Nakai, 1930. Images taken from the database of Japanese woods of the Forestry and Forest Products Research Institute (<http://db.ffpri.affrc.go.jp/WoodDB/JWDB-E/home.php>; accessed in 2019). **A.** Transverse section of the stem, pith almost entirely missing, secondary xylem with growth rings, secondary phloem and bark. **B.** Secondary xylem in transverse section, two interfascicular rays (ir) and fascicular secondary xylem (fx) intercalated. White arrow pointing uniseriate fascicular ray. Black arrow pointing protostele. **C.** Detail of bark and secondary phloem. Note phloem with AVES pattern as well. Phloem cells preserved and phloem fibers cap (black double headed arrow) separated by interfascicular rays. Bark (white double headed arrow) with a continued thickened layer. **D.** Tangential section of the stem, arrows pointing fascicular uniseriate rays in fascicular xylem (fx). Interfascicular rays (ir) intercalated. Scale bars 50 µm, except A, 1 mm.

fibers, and vascular traces (Arnold 1962; Tidwell and Ash 1990; Tidwell 2002). Within the Umkomiasiales, the genera *Kykloxyylon*, *Cuneumxylon*, *Tranquiloxylon*, and *Rhexoxyylon* show a stem anatomy with xylem wedges separated by wide interfascicular rays (Artabe and Brea 2003; Decombeix et al. 2014); but in the first three genera these rays are not

connected to the pith (Herbst and Lutz 1995; Artabe and Brea 2003) differing from *Sarcandraxylon* gen. nov. In *Rhexoxyylon* the secondary growth is far more complex, with two vascular systems (i.e., medullary and cylindrical) and frequently presence of successive cambia (Bodnar 2008, and references therein). Furthermore, in the Umkomiasiales, the interfascicular rays contrast with the homocellular rays of the new Antarctic taxon, since they are composed of a variety of cell types (parenchyma, sclereids, idioblasts), and abundant secretory cavities (Bodnar 2008).

Within angiosperms, the AVES pattern is found in some representatives of the ANA-grade (Austrobaileyales), eumagnoliids (Piperales), Chloranthales, and certain families of the core eudicot as Apocynaceae, Asteraceae, Begoniaceae, Cucurbitaceae, Dilleniaceae, Menispermaceae, Ranunculaceae, and Vitaceae (Angyalossy et al. 2014; Trueba et al. 2015). However, the lack of vessels is an uncommon feature in angiosperms, and among all the previous groups indicated above, the only family that has representatives with both AVES pattern and vesselless wood is Chloranthaceae (see further discussions below in “Wood anatomy in an evolutionary perspective” section).

Chloranthaceae includes four extant genera (*Ascarina* J.R. Forster and G. Forster, 1777, *Chloranthus* Swartz, 1787, *Hedyosmum* Swartz, 1788, and *Sarcandra* Gardner, 1846), nonetheless only *Chloranthus* and *Sarcandra* possess the AVES pattern, and only the latter has been reported as having vesselless stems as well (Swamy and Bailey 1950).

The *Sarcandra* wood is known by having scanty axial parenchyma, and mostly composed of tracheids and transitional tracheid-vessel elements in stems (Fig. 4). It shares with the Antarctic stem the uniseriate and homogenous fascicular rays composed of elongated upright cells, but the multiseriate (4–5 cells wide) interfascicular rays are homogenous in the extant genus, composed by upright cells. *Sarcandra* has secondary phloem arranged in AVES pattern with wide interfascicular rays and phloem fibers arranged in caps (Swamy and Bailey 1950; Swamy 1953; Carlquist 1987) as in the new fossil.

Although sharing most anatomical characters with *Sarcandra* stems (Table 1), no transitional vessel elements were able to distinguish in the xylem of the Antarctic stem. Furthermore, the Antarctic specimen differs from *Sarcandra* due to the absence of distinct growth rings (even the fossil is larger than most of extant *Sarcandra* twigs), and the presence of square and procumbent parenchyma cells in the interfascicular rays. As the studied stem differs to all extant representatives of Chloranthaceae we designate it to a new genus and species.

The fossil record of Chloranthaceae.—Chloranthaceous fossils have been found on almost all continents, with a continuous record since the Early Cretaceous. The origin of the family was inferred as Barremian–Hauterivian, based on the presence of *Clavatipollenites*-type pollen (Couper 1958;

Table 1. Summary of *Sarcandraxylon sanjosense* gen. et sp. nov. wood characters compared with some basal angiosperms. TDT, tangential diameter of tracheids; + present; – absent; ? unknown; * cambial variant in *Piper betle* produce two vascular bundle cycles; ** vessels in primary xylem of stem and secondary xylem in roots. Transitional tracheids were also noted. Fascicular rays include rays in taxa that not develop AVES pattern, and taxa with AVES pattern.

Species	References	AVES pattern	Growth rings	Vessels	Imperforate tracheary elements	TDT (μm)	Pitting	Axial parenchyma	Fascicular rays	Interfascicular rays	Ray cell types	Ray dimention
<i>Amborella trichopoda</i>	Carlquist and Schneider 2001	–	+	–	+	?	scalariform	diffuse	two distinct sizes	–	upright to square cells. Procumbent cells in wider rays	multiseriate: up to 5 cells; uniseriate and biseriate
<i>Austrobaileya scandens</i>	Bailey and Swamy 1949; Carlquist 2001b	+	–	+	+ tracheids and fiber-tracheids	?	fibers: bordered pits; vessels perforation plates scalariform, pits scalariform, opposite and alternate	vasicentric	uniseriate and narrow multiseriate	wide multiseriate	upright	multiseriate: 2–3 cells wide
<i>Saururus cernuus</i>	Carlquist et al. 1995	+	–	+	+	?	fiber-tracheids with bordered pits; vessels with scalariform perforation plates	?	–	wide multiseriate	?	?
<i>Piper betle</i>	Patel and Bowles 1980; Khaing 2016	+	*	–	+ tracheids and fibers	10–15	bordered pits	+	–	wide multiseriate	upright and procumbent	?
<i>Aristolochia</i> spp.	Carlquist 1993	+	–	+	+	?	bordered pits	diffuse, diffuse in aggregates, scantily vasicentric and banded apotracheal	–	wide multiseriate	uniseriate: upright; multiseriate: upright and procumbent	?
<i>Tasmannia</i> spp.	Carlquist 1989	–	+	–	+	16–46	bordered and scalariform	scarse, diffuse, in pairs	two distinct sizes	–	uniseriate: upright; multiseriate: upright and procumbent	multiseriate: up to 4 cells wide
<i>Chloranthus</i> spp.	Carlquist 1992a	+	–	+	+ septate fiber-tracheids	mean 21	fiber-tracheids: bordered pits; vessels: scalariform perforation plate, bordered pit	–	uniseriate and biseriate	wide multiseriate	upright, prominently elongated	interfascicular multiseriate: up to 11 cells wide
<i>Sarcandra glabra</i>	see Discussion	+	+	–	**	15–20 (mean 17.5)	bordered and scalariform	–	uniseriate	wide multiseriate	uniseriate: upright elongated; multiseriate: upright	interfascicular multiseriate: up to 5 cells wide
<i>Sarcandraxylon sanjosense</i>	this paper	+	–	–	+	12.5–25 (mean 17.9)	?	–	uniseriate	wide multiseriate	uniseriate: upright elongated; multiseriate: square and procumbent	interfascicular multiseriate: 5–6, up to 8 cells wide

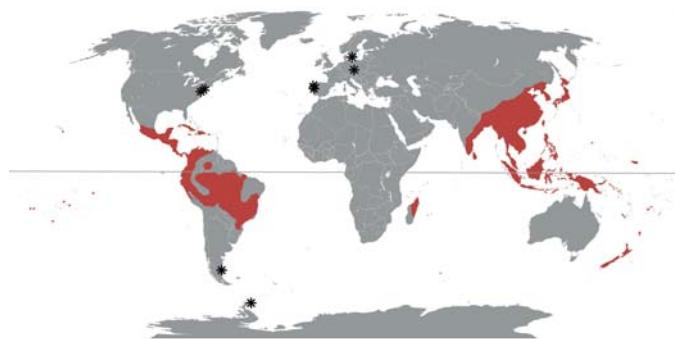


Fig. 5. World distribution of extant Chloranthaceae (red area) and sites where macro/meso fossils of the family were found (asterisks): *Couperites* (USA), *Chloranthistemon* (Sweden and USA), *Asteropollis* plant and *Canrightia* (Portugal), *Zlatkocarpus* (Czech Republic), loose anthers (Argentina), and *Sarcandraxylon* gen. nov. (Antarctic Peninsula).

Kemp 1968; Doyle 1969; Hughes and McDougall 1987; Crane 1989; Friis et al. 1999).

Eklund et al. (2004), and Doyle and Endress (2014) summarized the fossil record with affinities to the family, which comprises pollen grains of *Clavatipollenites* and *Asteropollis*. Reproductive mesofossil genera come from the Northern Hemisphere (Fig. 4) and related to the *Asteropollis* plant and *Canrightia* from the Barremian–Aptian of the Western Portuguese Basin, Portugal (Hedlund and Norris 1968; Friis and Perdersen 2011); *Chloranthistemon* from the Santonian–Campanian of the Kristianstad Basin, Sweden, and the Turonian of the Potomac Group, USA (Crane et al. 1989); *Couperites* from the Cenomanian of the Potomac Group, USA (Pedersen et al. 1991); and *Zlatkocarpus* from the Cenomanian of the Bohemian Cretaceous Basin, Czech Republic (Kvacek and Friis 2010; Doyle and Endress 2014).

In the Southern Hemisphere the chloranthoid fossil record is abundant but not as diverse as in the Northern Hemisphere; and exclusively based on pollen grains from Australia, Argentina, and Antarctica (Fig. 5). Dettman (1994) recognized the presence of *Clavatipollenites hughesii* in the Barremian to the Campanian in the Eromanga and Gippsland basins, and *Asteropollis asteoroids* (Hedlund and Norris 1968) in the early Albian from the Eromanga and Surat basins all for Southern Australia. In the Cretaceous of Patagonia the pollen record is widespread (Archangelsky et al. 2009), although showing a broader morphological spectrum thus not necessarily closely related with Chloranthaceae (Perez-Loinaze et al. 2015). The oldest record for *Clavatipollenites* is from the late Barremian–Aptian, at the Deseado Massif and Austral basins; whereas the oldest record for *Asteropollis* is from the Aptian, in the Deseado Massif, Neuquén, and San Luis basins (Archangelsky et al. 2009, and references therein). Particularly, in the early Aptian of the Deseado Massif Basin, Archangelsky and Taylor (1993) reported small dispersed anthers with *in situ* *Clavatipollenites* pollen grains, being the first record of a chloranthoid reproductive mesofossil for the whole Southern Hemisphere (Fig. 5).

In Antarctica the oldest chloranthoid pollen record was found in the early to middle Albian Kotick Point Formation,

Gustav Group, at the James Ross Island; and corresponds to *Clavatipollenites hughesii* (Dettman and Thomson 1987; Dettman 1989). The Antarctic pollen record extends through the Upper Cretaceous, with Campanian records in the Marambio Group (Santa Marta Formation) at the James Ross Island (Dettman and Thomson 1987), and in the Maastrichtian Lopez de Bertodano Formation at the Seymour Island (Askin 1994). There are putative Antarctic macrofossils, based on leaves with chloranthoid teeth, found in the early Albian at the Alexander Island (Cantrill and Nichols 1996), although diagnostic leaf characters used are disputed, due that similar teeth and main leaf venation are present in others angiosperm groups (Hickey and Wolf 1975; Doyle and Endress 2000).

The fossil genera presented above were related to different extant Chloranthaceae genera: *Clavatipollenites*, *Couperites*, and *Zlatkocarpus* to *Ascarina*; *Chloranthistemon* to *Chloranthus*; and *Asteropollis* and *Canrightia* to *Hedyosmum* (Eklund et al. 2004, and references therein). The *Pennipollis* plant (Friis et al. 2000) was cautiously assigned to Chloranthaceae, but the phylogenetic analysis of Doyle (2014) related it to Ceratophyllaceae.

In this manner, the fossil studied herein corresponds to the first record of a vegetative organ unequivocally assignable to Chloranthaceae, and the first anatomically preserved stem assignable to the family. It also agrees with pollen interpretation, which indicates the presence of the family in the Cretaceous for Antarctica. Furthermore, the similar morphology to the extant genus reveals the first occurrence of a *Sarcandra*-related taxon by the Campanian in high latitudes from Western Gondwana; other than *Ascarina* clade-relationship due to the phylogenetic relationship claimed for the *Clavatipollenites hughesii* pollen grains, for the same formation.

Wood anatomy in an evolutionary perspective.—There are two unusual characters combined in the wood anatomy of *Sarcandraxylon sanjosense* gen. et sp. nov. that make it unusual among angiosperms: the absence of vessels and the presence of AVES pattern.

Although vessels are considered to be a hallmark of flowering plants, some angiosperm groups lack them and produce wood entirely composed of tracheids. Vessels are defined by the absence of pit membranes, short length and wide diameter, interconnection of a large number of vessel elements, and by differentiated perforation plates (Frost 1930). Tracheids, on the other hand, are characterized by great length, small diameter, angularity of outline, presence of primary wall in the pit membrane, and absence of a distinct end wall (Frost 1930). The extant woody vessel-less angiosperm families are Amborellaceae, Winteraceae, Trochodendraceae, and Chloranthaceae (Fig. 6).

Over the past century there has been much discussion about the evolution of secondary xylem in angiosperms, with respect to the origin of vessels (Thompson and Bailey 1916; Bailey 1944; Young 1981; Carlquist 1987) if it was

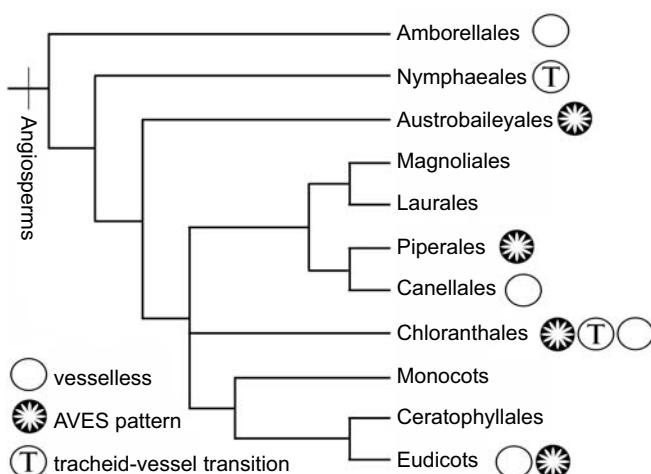


Fig. 6. Simplified phylogenetic representation (modified from APG VI 2016), with the three main atypical morphological characters discussed: presence of AVES pattern, absence of vessels, and presence of transitional tracheid-vessel elements.

primitively vesselless, in which case vessels were gained repeatedly in every group within angiosperms, or if vessels came first in the angiosperms stem-group and were lost in Amborellaceae, Winteraceae, Trochodendraceae, and Chloranthaceae. After this, a new element was found and added to the equation: the tracheid-vessel transitional elements. These tracheids show extensive pitting where the end of the cells overlap and the primary wall of the pits is partially degraded (Carlquist 1987; Takahashi 1988; Takahashi and Tamura 1990).

In the first anatomical researches of *Sarcandra* (Swamy and Bailey 1950; Swamy 1953) the secondary xylem was described as vesselless. Afterwards, Carlquist (1987) observed the presence of vessels in the secondary xylem of roots and in the primary xylem of stems, and transitional tracheid-vessel elements in the secondary xylem. Also, based on SEM studies of wide tracheary elements with scalariform patterns on end walls, Carlquist (1987) detected the presence of different amount of degradation in the pit membrane. This kind of porosity in the pit membranes was found in tracheids of several basal angiosperms as well as: *Amborella*, some representatives of Winteraceae, *Tetracentron*, *Illicium*, Schisandraceae, and in *Austrobaileya* (Carlquist 1987). Even though no transitional elements were able to distinguish in *Sarcandraxylon* gen. nov., the above discussion shows that several genera originally described as vesselless actually show transitional vessel elements, probably illustrating early stages in angiosperm vessel evolution (Carlquist and Schneider 2001, and references therein). Due to the pyritization of the cell walls in the new fossil material, we cannot refuse the total absence of transitional elements in it.

The organization of secondary vascular system found in *Sarcandraxylon sanjosense* gen. et sp. nov. is the result of a cambial variant derived from one vascular cambium with differential activity which produces axial vascular el-

ements in segments (AVES) pattern. In this cambial variant the interfascicular cambium produces only multiseriate rays and the fascicular cambium produces axial elements and, in some cases, also rays (Angyalossy et al. 2014).

This type of cambial variant is present in different groups within the flowering plants (Fig. 6), being quite well represented in basal angiosperms. The order Piperales is characterized by its presence of this cambial variant, producing one cycle of vascular bundles (Aristolochiaceae and Saururaceae) or several (Piperaceae) (Carlquist et al. 1995; Trueba et al. 2015). Within Austrobaileyales, the genus *Austrobaileya*, was described as having two kinds of rays: uniseriate and multiseriate (Bailey and Swamy 1949; Carlquist 2009), which is compatible with AVES pattern. In Chloranthales, the genera *Sarcandra* and *Chloranthus* differ from *Hedyosmum* and *Ascarina* by the presence of the cambial variant (Carlquist 1992a, b, 2009).

The AVES pattern is also present in several families within the eudicots core as: Apocynaceae, Asteraceae, Begoniaceae, Cucurbitaceae, Dilleniaceae, Menispermaceae, Ranunculaceae, and Vitaceae (Angyalossy et al. 2014). Given the variety of groups developing this cambial variant it seems that this kind of secondary growth is successful in different habitats and growth habits. For example, it is present in many groups of climbing plants. The proliferation of parenchyma is thought to be an adaptation to this growth habit, which requires flexibility at later stages of development, additionally the parenchyma provides torsional resistance to stems and, because of their latent meristematic activity, can repair stems that have become fractured or split (Spicer 2016, and references therein). The AVES pattern also occurs in some sub-shrubs (e.g., *Sarcandra*) with restricted wood production. There are not clear explanations of the anatomical benefits of this cambial variant for sub-shrub habit.

It has been proposed that early-diverging lineages of angiosperms possessed an active bifacial cambium being the reduction of secondary growth in sub-shrubs and strictly herbaceous habits a result from a reduction of cambial activity and the limitation of axial elements into the fascicular areas (Carlquist 2009; Trueba et al. 2015). At least in some seed plants, the formation of fascicular cambium precedes the interfascicular cambium (Nieminen et al. 2015); thus the delayed or decelerated activity of the interfascicular cambium could respond to heterochronic processes (Bodnar et al. 2018). The new taxon described in this study adds a new element to the flora that grew in the early-middle Campanian in the Antarctic Peninsula. The small stem diameter, the anatomical characters sharing with the extant *Sarcandra*, and the absence of growth rings, let us interpret that the new fossil genus corresponds to a sub-shrub, probably living in the understory. This discovery strengthens the hypotheses that the basal angiosperms would have presented different stages in the xylem evolution (Carlquist and Schneider 2001; Field et al. 2004) already by the Cretaceous.

Conclusions

Sarcandraxylon sanjosense gen. et sp. nov. is the first fossil of an anatomically preserved stem of Chloranthaceae. Although the presence of *Clavatipollenites hughesii* pollen in the Santa Marta Formation has already suggested the presence of this family in the Antarctic continent, that pollen species was related to the extant *Ascarina* clade. The new permineralized stem with preserved wood and bark has so similar wood anatomy to the extant genus that reveals the first occurrence of a *Sarcandra*-related taxon by the Campanian in high latitudes from Western Gondwana.

The finding of a cambial variant in a Late Cretaceous sub-shrub plant, proposes a revaluation about woodiness and cambial evolution among early angiosperms.

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