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First Bignoniaceae liana from the Miocene of South America and its evolutionary significance

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Abstract

Premise: Two Bignoniaceae stems with the distinctive anatomy of a liana are described from the Miocene of South America. They are the first fossil evidence of climbing habit in Bignoniaceae.

Methods: The fossil lianas are siliceous permineralizations. Transverse, tangential, and radial thin sections of the woods were prepared for study using standard petrographic techniques and observed under both light and scanning electron microscopy.

Results: The stems consist of wood and presumably bark (peripheral tissues). They exhibit phloem wedges, a cambial variant associated with the climbing habit in Bignoniaceae. The wood is diffuse-porous; solitary and in radial multiples vessels; alternated intervessel pitting; ray-vessel pitting with distinct borders; simple perforation plates; rays 1–3 seriate, composed of procumbent cells or body ray cells procumbent with one or two-row of upright or square marginal cells; fibers septate and non-septate, with simple to minutely bordered pits; axial parenchyma scanty paratracheal, vasicentric, septate; perforated ray cells; prismatic crystals in rays, and rays and fibers irregularly storied. The fossil stems are related to extant *Dolichandra unguis-cati* (L.) Miers.

Conclusions: The fossils represent a new taxon, *Dolichandra pacei* sp. nov., which confirms the presence of a neotropical Bignoniaceae liana from the Miocene and provides the first and oldest evidence of the climbing habit in the family. Paleobotanical studies in the Mariño Formation, with the record of Bignoniaceae and Verbenaceae, and phylogenetic and biogeographical studies have great importance to understand plant evolution and diversification in South American Andes.

KEYWORDS

Bignonieae, cambial variants, Cenozoic, dry forest, fossil record, neotropics, paleobiogeography, paleoecology, Precordillera, vascular structures

A liana is a plant whose structural support does not come entirely from its tissues, whose original rooting position was in the soil or a surface close to the soil, and whose climbing effort may take its foliage and reproductive organs into the tree canopies (Burnham, 2009; Cabanillas and Hurrell, 2012; Sperotto et al., 2020). Most lianas have an unusual vascular structure (Carlquist, 1991; Mabberley, 1997; Fischer et al., 2004) and characteristics such as variant secondary growth, that favor the climbing habit and increase the flexibility of the stem (Angyalossy et al., 2015).

Bignoniaceae are a pantropical family with ca. 100 genera and 800 species, mainly distributed in the neotropics (Stevens, 2001; Fischer et al., 2004). They are an important component of neotropical forests, with lesser contributions to African, Malagasy, and Southeast Asian tropical forests (Lohmann and Ulloa, 2007; Olmstead et al., 2009). Most Bignoniaceae are trees or lianas, but some are shrubs or, rarely, herbs (Fischer et al., 2004). Bignoniaceae belong to the order Lamiales (APG IV, 2016) and are currently subdivided into nine well-supported clades: the tribes Bignonieae, Jacarandae, Tourrettieae, Tecomeae, Oroxyleae, and Catalpae, the *Tabebuia* alliance, the paleotropical clade, and the genus *Delostoma* (Olmstead et al., 2009; Olmstead, 2013; Pace and Angyalossy, 2013).

The tribe Bignonieae is a large and morphologically diverse clade. It is the largest group of lianas in the neotropics (Gentry, 1991; Lohmann, 2006; Pace et al., 2009) and contains ca. 380 species, nearly half of the species in the

family (Fischer et al., 2004; Lohmann, 2006; Olmstead et al., 2009; Pace et al., 2009). This tribe consists of lianas and shrubs distributed through a variety of habitats, ranging from dry savannas to wet forests in Central America, Amazonia, the Atlantic forests of eastern Brazil, and the open dry forests and savannas of Argentina, Bolivia, Brazil, and Paraguay (Lohmann, 2006; Olmstead et al., 2009; Lohmann et al., 2013).

The stem anatomy of species of Bignonieae is one of the most diagnostic features (Pace et al., 2015) because of the presence of cambial variants (unusual cambial activity) in all the genera (Pace et al., 2009). Bignonieae differ from all other clades by a variant secondary growth and a typically lianoid wood anatomy (Pace et al., 2015). The shape and distribution of the cambial variants represent a synapormorphy in the tribe and can vary from having four to multiple of four phloem wedges (Pace and Angyalossy, 2013; Pace et al., 2011, 2015). The fossil record of Bignonieae is poorly known. Putative Bignonieae fossil leaves and pollen were found in the Eocene–Miocene of Central and South America (Berry, 1922, 1925; Chaney and Sanborn, 1933; Graham, 1985). However, the taxonomic affinities and age of these fossils need to be revised.

Here, we describe two fossil stems with the distinctive anatomy of a liana, which represents the first fossil evidence of the climbing habit in the Bignoniaceae. The materials were collected from the Mariño Formation (early Miocene) at the Potrerillos locality, at the south-southwestern extent of the Precordillera in Mendoza Province, central-western Argentina. These fossils are recognized as a new taxon, and we evaluate their evolutionary, biogeographic, and ecological significance.

MATERIALS AND METHODS

Material

The specimens include the fossil woods and several microscope slides and are inventoried as IANIGLA-PB 313 and IANIGLA-PB 835 in the Paleobotanical Collection of the paleontological repository of the Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, CCT-CONICET-Mendoza in Mendoza, Argentina. They were collected from levels of the middle Member of the Mariño Formation that crops out at Potrerillos about 70 km southwest of Mendoza in central-western Argentina. IANIGLA-PB 313 consists of a small fragment 2 cm long and 1.5 cm in diameter. IANIGLA-PB 835 consists of a fragment 2.85 cm long and 1.10 cm in diameter. A preliminary report on these specimens was presented by Franco et al. (2018).

Fossil preparation and identification

The fossil woods were permineralized by silica, and well-preserved anatomical features of the secondary xylem are visible. Transverse, tangential, and radial thin sections of the woods were prepared using standard petrographic techniques (Hass and Rowe, 1999), examined with a Nikon Eclipse E200 light microscope (Tokyo, Japan) at 40×, 100×, 400×, and 1000× magnifications, and photographed with a Nikon Coolpix S4 digital camera (Tokyo, Japan). For scanning electron microscopy (SEM), 1-cm^3 blocks of wood were cut and mounted on SEM stubs without coating and then observed in a low vacuum using an SEM PHENOM PRO (Eindhoven, Netherlands) at the Laboratory (EMLAB) Dr. Domingo S. Liotta, CICYTTP (CONICET-Prov. Entre Ríos-UADER), Diamante, Entre Ríos, Argentina.

The anatomical terms used in the descriptions and the measurements follow the recommendations of the IAWA List of Microscopic Features for Hardwood Identification (IAWA Committee, 1989). Measurements were taken using ImageJ ver. 1.45 s (Rasband, 2012), with a minimum of 25 repetitions per specimen. The average value is cited first, followed by minimum and maximum values in parentheses.

The fossil was taxonomically identified using the Inside-Wood website (InsideWood, 2004 onward) and classical descriptions of extant and fossil plants (Carlquist, 1985, 1991; León, 2007, 2009; Burham, 2009; Pace et al., 2009, 2015; Angyalossy et al., 2012). The anatomical characters used for InsideWood database searches are followed by their numerical code between parentheses (all searches with 0 allowed mismatching) (Wheeler et al., 2020). The systematic assignment is based on the classification of APG IV (2016). The bibliographic lists made by Gregory (1994) and Gregory et al. (2009) were used.

The diameter of the stems was measured to estimate original diameters (Dest), using the formula proposed by Philippe et al. (2009): $D = 2r = 4a/\pi \sim 1.27a$, where a is the major axis radius. The vulnerability index (V) was calculated as $V =$ vessel diameter/vessel frequency, using the equations developed by Carlquis (1977). Also, the taxon-independent approach (TIA) was used (Martínez-Cabrera et al., 2014) to infer paleoclimate data. The distribution map of Dolichandra unguis-cati was made with QGIS desktop 3.14.0 software (QGIS Development Team, 2021). Primary point-of-occurrence data were obtained from the Global Biodiversity Information Facility (GBIF.org, 2020; Copenhagen, Denmark), using the MOBOT Institution data, Missouri Botanical Garden, St. Louis, Missouri, United States. Some points of occurrence were also obtained from Fonseca et al. (2017).

GEOLOGICAL SETTING

The Mariño Formation (Biondi, 1936, nom. subst. in Rolleri and Criado Roque, 1970) is a clastic continental sequence that reaches 1900 m thick. It crops out extensively in the northern sector of Mendoza Province. This formation is subdivided into three members: the lower Conglomerados Violáceos, the middle Areniscas Entrecruzadas, and the upper Estratos de Mariño or Serie del Higueral (Chiotti, 1946;

see also Yrigoyen, 1993). The lower and upper members correspond to fluvial and alluvial sediments deposited in arid and semiarid conditions, while the middle member is predominantly composed of eolian sediments (Yrigoyen, 1993; Irigoyen, 2000, 2002; Cerdeño et al., 2006, 2018; and references therein).

The age of the Mariño Formation has been controversial but mostly attributed to the late Oligocene or early Miocene (e.g., Yrigoyen, 1993; and a summary in Cerdeño et al., 2006). The first absolute dating was provided by Irigoyen et al. (2000, 2002), who established an age of 12.03 ± 0.45 million years (Myr) for the upper part of the Mariño Formation and proposed a range from 15.7 to 12 Myr for the entire deposition. However, mammal fossils recovered from the middle member of the formation in both Divisadero Largo and Potrerillos localities (see below), support an early Miocene age for the fossiliferous levels (Cerdeño et al., 2006, 2018; Cerdeño, 2007; Cerdeño and Vucetich, 2007). This age has been recently supported by zircon U-Pb dates of 17.58 Myr and 17.96 Myr for the middle member of the Mariño Formation (Buelow et al., 2018).

Near Mendoza city, the Mariño Formation crops out in two main areas: Divisadero Largo (inside a Natural Reserve) and Cacheuta-Potrerillos (Figure 1), which have provided both mollusk and mammal remains. From the south of Cerro Cacheuta, Rusconi (1949) firstly described freshwater bivalves as *Corbicula elchaensis* Rusconi; later, a litoptern mammal was mentioned by Yrigoyen (1993) and recently revised by Villafañe et al. (2012), but its origin is uncertain. Aside from these findings, Sepúlveda (1999) described some palynomorphs from the Mariño Formation cropping out at the north of the province, near the boundary with San Juan Province, in the Salagasta area. Research during the last 15 years has provided new mammal fossils in both Divisadero Largo and Potrerillos (Cerdeño et al., 2006, 2018; Cerdeño, 2007; Cerdeño and Vucetich, 2007), which have allowed assigning a late early Miocene age (Santacrucian South American Land Mammal Age [SALMA]) to the middle Member of the Mariño Formation.

The first fossil woods described from the Mariño Formation were *Rhaphithamnoxylon artabeae* Franco, Brea et Zavattieri (Verbenaceae), and two other unidentified dicot woods retained under open nomenclature (Franco et al., 2015). These remains were found in Potrerillos during the prospecting works in 2001 related to the construction of the Potrerillos dam. The fossil herein studied was recovered in 2017 in the same Potrerillos locality, at 32°57′32.7″S, 69°09′36.1″W, on the northern side of the dam, where a Mesotheriidae (Mammalia, Notoungulata) was also found (Cerdeño et al., 2018). The exposed section in this place is composed of 250 m of continuous and homoclinal sediments with eolian and fluvial facies associations that reveal two paleoenvironments; the stratigraphic profile and the geological data are detailed in Cerdeño et al. (2018); plant remains come from fluvial facies overlying the dune field where the mesotheriid was found.

RESULTS

Systematics

Order

Lamiales Bromhead

Family

Bignoniaceae Jussieu

Tribe

Bignonieae Dumort

Genus

Dolichandra Cham.

FIGURE 1 Location and general view of the Potrerillos locality, Mendoza Province, Argentina

Type species

Dolichandra cynanchoides Cham.

Species

Dolichandra pacei sp. nov.

Holotype

IANIGLA-PB 313 (Paleobotanical Collection, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales)

Paratype

IANIGLA-PB 835 (Paleobotanical Collection, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales)

Etymology

The specific epithet is dedicated to Marcelo R. Pace, Ph.D., for his important studies on the evolution of climbing plants, especially Bignoniaceae.

Horizon and locality

Potrerillos locality (northern margin of the Potrerillos dam), Mendoza Province, Argentina. Middle Member of the Mariño Formation, Santacrucian SALMA, early Miocene

Specific diagnosis

Stem with cambial variant dominated by furrowed xylem, with multiple-dissected phloem wedges. Wood diffuse-porous; vessels solitary, in radial multiples 2–3 (or more), vessel elements numerous (>20 per mm^2) and narrow; small, bordered and alternated intervessel pitting; parenchyma and ray-vessel pitting with distinct borders and similar to intervessel pits; simple perforation plates; rays 1–3 seriate, composed of procumbent cells or body ray cells procumbent with one or two rows of upright or square marginal cells; fibers septate and non-septate, with simple to minutely bordered pits; axial parenchyma scanty paratracheal, vasicentric, with 3–4 cells per strand as seen in tangential section; the presence of perforated ray cells and prismatic crystals in ray. Rays and fibers are irregularly storied.

Description

The stems consist of secondary wood and presumably bark. The pith is not preserved and the bark, with no structurally preserved anatomy, could be periderm (Figures 2A, B, 3A). The fossil wood has unusual arrangements of secondary xylem and phloem. The secondary phloem appears in wedges that separate the secondary xylem. The cambium is probably disjunct, with portions in the interior of the phloem wedges (variant phloem) and portions between them in the inter-wedges (regular phloem) (Figures 2A, B, 3A).

The secondary xylem has growth ring boundaries indistinct or absent (Figures 2A, B, 3A). The wood is diffuse-porous (Figure 3A). The vessel groupings are solitary (67%), radial multiple of two (16%), three (5%), four (4%) and more (1%), and in clusters (7%) (Figure 3A, D). Solitary vessel outlines are oval to circular (Figure 3D). The mean tangential diameter of vessel lumina is 60 (35–102) μm, and the mean radial diameter of vessel lumina is 60 (20–81) μm. Tyloses are common, and gums and other deposits are present in vessels (Figure 3A, D). The mean vessel element length is 360 (187–550) μm. Vessel frequency is, on average, 35 (20–50) per mm^2. Perforation plates are simple (Figure 3J). Intervessel pits are alternate arranged, bordered, with an average diameter of 5 (4–8) μm (Figure 4C). Vessel-ray parenchyma pits are with distinct borders and similar to intervessel pits in size and shape throughout the ray cell (Figure 4E). Fibers are polygonal to rounded in outline, poorly preserved, making it difficult to distinguish the wall from the lumen (Figure 3E), with simple to minutely bordered pits (Figure 4B), septate (Figure 4A, F) and non-septate (Figure 4B), and in radially oriented files (Figure 3D). The mean fiber diameter is 11 (8–14) μm; the mean fiber wall thickness is 5 (3–7) μm. Axial parenchyma is scanty paratracheal, vasicentric (Figure 3D), septate (3–4 cells per parenchyma strand; Figure 4A, F). Rays are mainly biseriate (67%), also uniseriate (30%), and less common triseriate (8%) (Figures 3B, F, H, 4B). All ray cells are procumbent or body ray cells are procumbent with one or two rows of upright or square marginal cells (Figures 3C, G, 4D). Rays are 318 (120–700) μm in height and 41 (20–60) μm in width; 11 (4–22) cells high, linear. There are 7 (6–10) rays per linear millimeter. Perforated ray cells are present (Figures 3H, 4A). Prismatic crystals are present in rays. Cambial variants present and are dominated by furrowed xylem, with multiple-dissected phloem wedges that interrupt the xylem (Figures 2A, B, 3A, I). A tendency of storied rays and fibers is observed (Figures 3B, 4F).

DISCUSSION

Affinities with extant Bignoniaceae

Secondary phloem wedges have evolved independently in lianas of several families including Asteraceae, Apocynaceae s.l., Bignoniaceae, Convolvulaceae s.l., Celastraceae s.l., Fabaceae, Icacinaceae, Malpighiaceae, Menispermaceae, Passifloraceae, Sapindaceae, Rubiaceae (Angyalossy et al., 2012, 2015). Phloem wedges like those in the fossil are combined with secondary xylem parts and represent a synapomorphy of Bignonieae (Lohmann, 2006; Angyalossy et al., 2012; Lohmann and
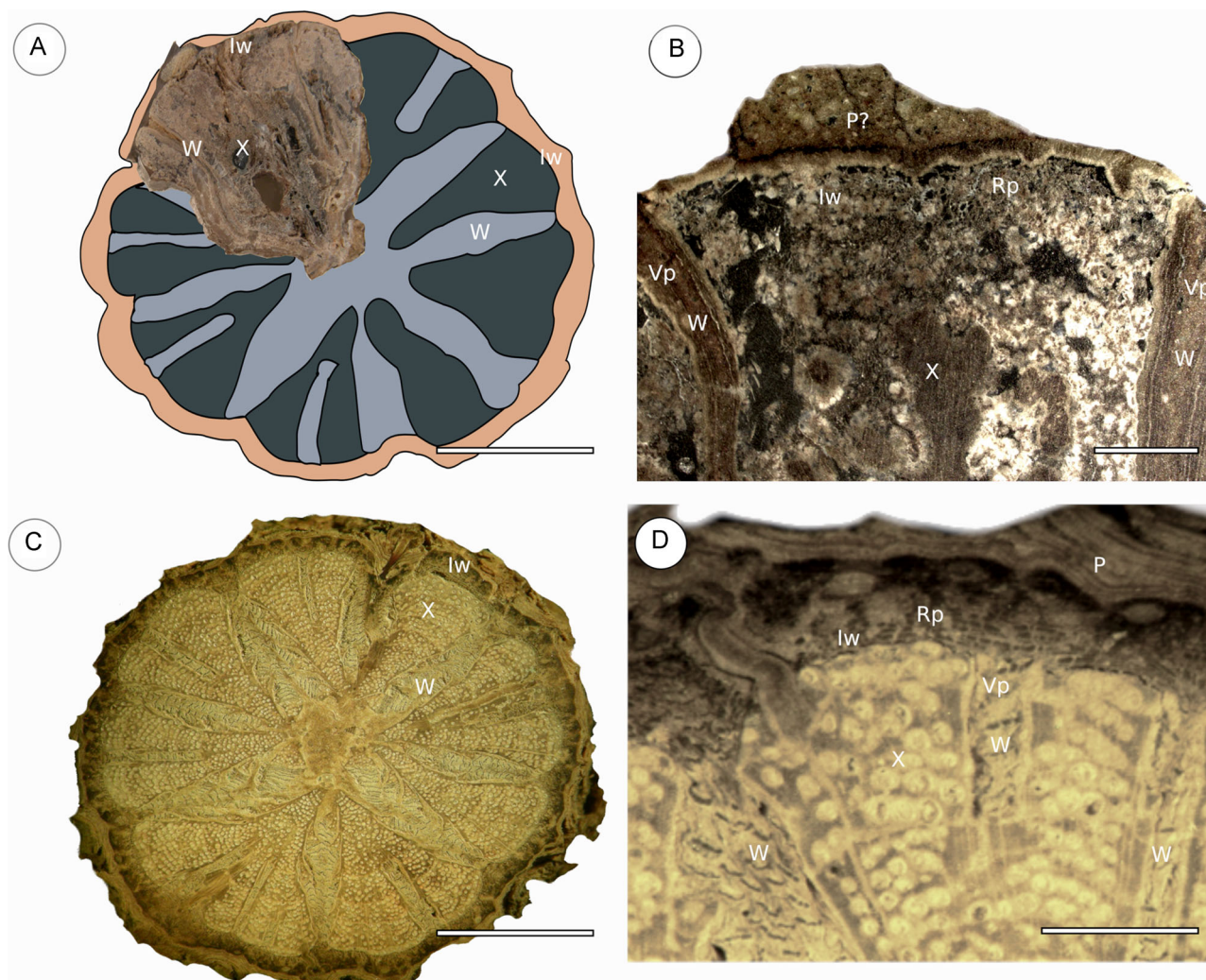
FIGURE 2 (A) *Dolichandra pacei* sp. nov., IANIGLA-PB 313, stem cross section of the fractured specimen and its reconstruction from the cross section of *Dolichandra unguis-cati* showing the cambial variant characterized by furrowed xylem with multiple-dissected phloem wedges. (B) Detail of phloem wedges with variant phloem, the interwedges with regular phloem and xylem in *Dolichandra pacei* sp. nov. The presence of a possible non-preserved periderm is indicated. (C) Stem cross section of *Dolichandra unguis-cati* showing the anatomical architecture characterized by multiple-dissected phloem wedges. (D) Detail of phloem wedges with variant phloem, the interwedges with regular phloem, and xylem in *Dolichandra unguis-cati*. Iw = interwedge, P = periderm, Rp = regular phloem, Vp = variant phloem, W = wedge, X = xylem. Scale bar: (A) = 20 mm; (B) and (D) = 2 mm; (C) = 6 mm

Taylor, 2014). Furthermore, the combination of wood anatomy characters such as scanty paratracheal to vasicentric axial parenchyma, generally tall and heterocellular rays, and septate fibers in the fossil only occur in this tribe (Carlquist 1985, 2001; Pace et al., 2015).

Within Bignoniae are six types of cambial variants based on the form and distribution of the phloem arcs/wedges: Type 1 with four broad equidistant phloem arcs derived from increased activity of variant cambial (continuous cambium); Type 2, the most common in Bignonieae, with deeply embedded phloem wedges (disjunct cambium); Type 3, with four narrow phloem arcs derived from reduced activity of variant cambia (continuous cambium); Type 4, with multiple of four phloem wedges (disjunct cambium); Type 5, with multiple dissected phloem wedges (disjunct cambium); and Type 6, with phloem wedges at the same radii (disjunct

cambium) (Figure 4 of Pace et al., 2009, 2015). The fossil stems exhibit Type 5, which is only found in the genus *Dolichandra* (Figure 2C; Pace et al., 2009, 2015). In this genus, nonlignified axial and ray parenchyma is present and proliferates during development dissecting the secondary xylem (Pace et al., 2009). The genus *Dolichandra* also has short rays (lower than 1 mm), and both axial and radial parenchyma is storied (Pace and Angyalossy, 2013).

The studied stems show a combination of features only known in *Dolichandra unguis-cati*: diffuse-porous; vessels solitary, in radial multiples 2–3 (or more), and narrow; small, bordered, and alternated intervessel pitting; parenchyma and ray-vessel pitting with distinct borders and similar to intervessel pits; simple perforation plates; rays 1–3 seriate, composed of procumbent cells or body ray cells procumbent with one or two rows of upright or square
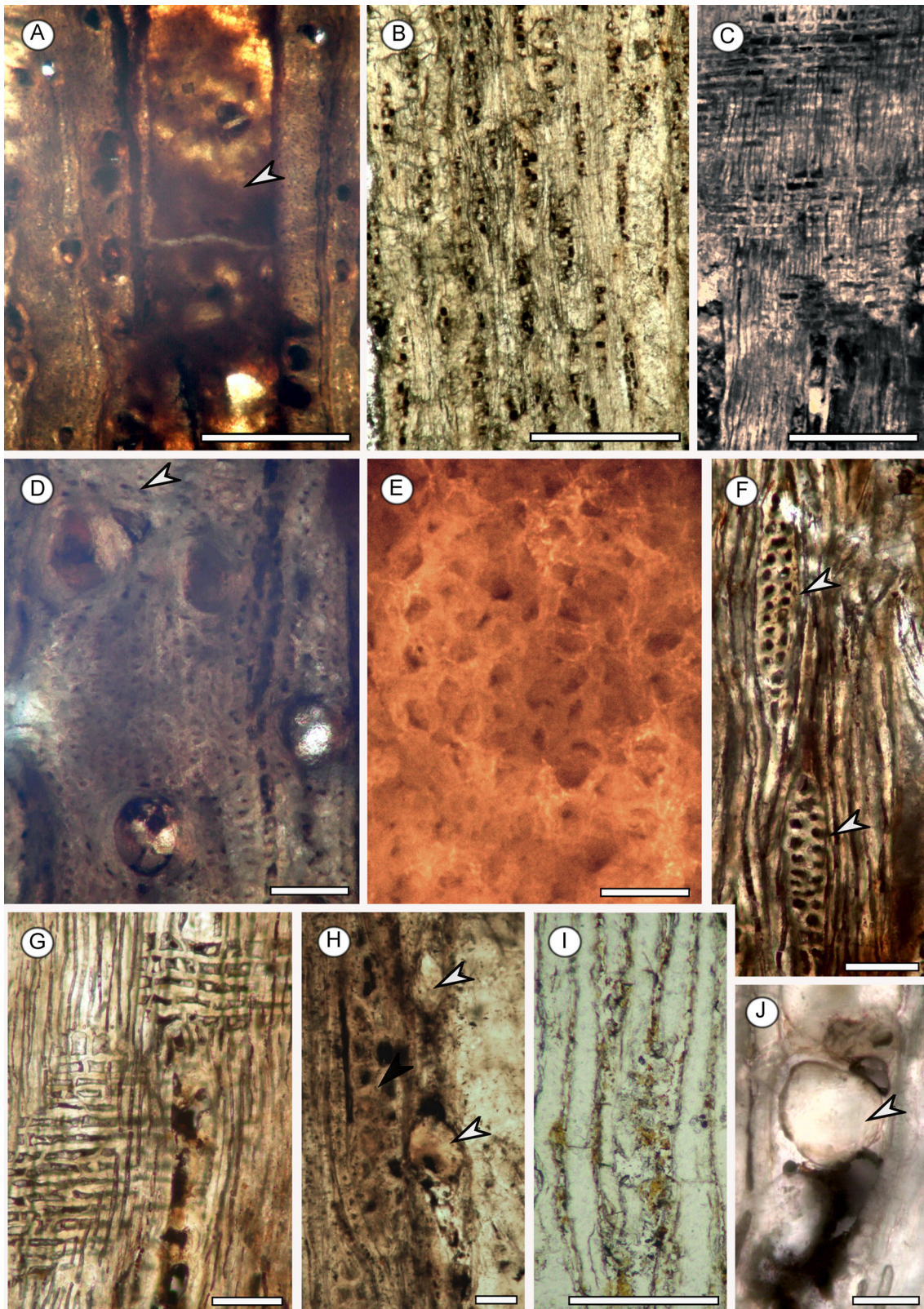
FIGURE 3 *Dolichandra pacei* sp. nov., IANIGLA-PB 313. (A) Transverse section (TS) showing phloem wedges (arrowhead) and xylem with vessels, fibers, and parenchyma. (B) Tangential longitudinal section (TLS) showing a tendency of storied rays. (C) General view of radial longitudinal section (RLS). (D) Detail of the TS showing vessels, fibers, and scanty vasicentric parenchyma (arrowhead). (E) Detail of fibers in TS. (F) Rays (arrowheads) in TLS. (G) Detail of rays in RLS. (H) Perforated ray cells (arrowheads) in TLS. (I) Detail of variant phloem in TLS, sieve tube elements with simple sieve plate. (J) Simple perforated plate (arrowhead). Scale bars: (A, B) = 500 μm, (C) = 300 μm; (D) = 50 μm; (E, H, J) = 30 μm; (F, G, I) = 100 μm
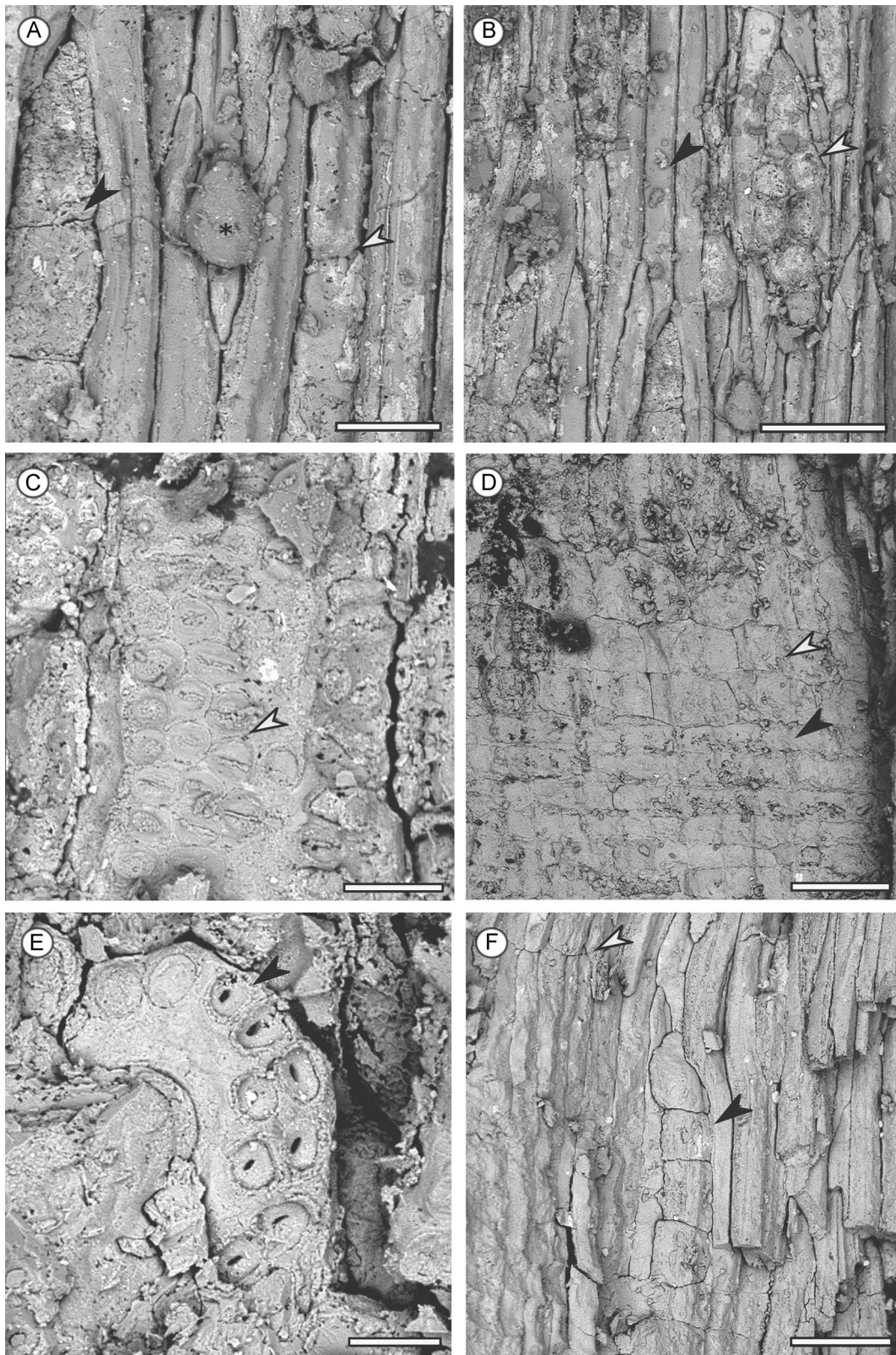
FIGURE 4 *Dolichandra pacei* sp. nov. Scanning electron micrograph (SEM) of the holotype IANIGLA-PB 313. (A) TLS with parenchyma strand (black arrowhead), fiber (white arrowhead), and perforated ray cell (*). (B) Fibers with simple to minutely bordered pits (black arrowhead) and biseriate ray (white arrowhead) in TLS. (C) Intervessel pits alternate and bordered in TLS (arrowhead). (D) Heterocellular ray in RLS (body ray cells procumbent, black arrowhead, with upright or square marginal cells, white arrowhead). (E) Vessel-ray and parenchyma pitting are with distinct borders and similar to intervessel pits in size and shape throughout the ray cell in RLS. (F) TLS with septate parenchyma (black arrowhead) and fiber (white arrowhead). Scale bar: (A) = 20 μm; (B, D, F) = 50 μm; (C, E) = 10 μm

marginal cells; fibers septate and non-septate, with simple to minutely bordered pits; axial parenchyma scanty paratracheal, vasicentric, with 3–4 cells per strand; perforated ray cells, presence of cambial variants, and rays and fibers irregularly storied (Carlquist, 1985, 1991; León, 2007, 2009; Angyalossy et al., 2012; Pace and Angyalossy, 2013; Pace et al., 2015).

We also did an InsideWood search using the features tyloses common (56p), axial parenchyma vasicentric (79p), ray width 1 to 3 cells (97p), and other cambial variants present (135p) with 0 allowable mismatches. This search returned *Dolichandra unguis-cati*. Another more specific search 2p 5p 6a 7a 8a 9a 13p 14a 19a 22p 56p 65p 66p 79p 96a 97p 98a 99a 135p with 0 allowable mismatches (see coding of IAWA Committee, 1989) also indicated strong similarities between *Dolichandra unguis-cati* (Inside-Wood, 2004 onward) and the fossil material studied here.

Comparison with fossil taxa

Burnham (2009) established the database Fossil Record of Climbers (FRC) that documents more than 1100 records of climbing plants published in the literature. Fossilized woody stems of angiosperm lianas are known from Cretaceous and Cenozoic deposits (Burnham, 2009; Smith et al., 2013), but no stem had been identified previously as belonging to tribe Bignonieae. Bignonieae fossil included a putative fossil leaf from the Oligocene of Oregon, United States (Chaney and Sanborn, 1933), pollen from the Gatuncillo Formation (Eocene) of Panama, identifying cf. *Fridericia* Mart. and *Tanaecium* Sw. (Graham, 1985), a leaf related to *Fridericia* from the Miocene of Patagonia, Argentina (Berry, 1925), and two leaves from the Miocene of the Loreto, Peru assigned to *Bignonites americana* Berry and *Bignonia neogenia* Berry (Berry, 1922).

In the Cenozoic, numerous species of climbers were present, and phylogenetic diversity is restricted to ferns and angiosperms (Burnham, 2009). In Argentina, only two species of vines or lianas have been previously identified from fossil stems: *Lardizabaloxylon lardizabaloides* Schönfeld, 1954 (Lardizabalaceae) from Patagonia, and *Ranunculodendron anzoteguiae* Lutz and Martínez, 2007 (Ranunculales, family incertae sedis) from the Palo Pintado Formation (Upper Miocene), Salta. Also, two twigs from the Mariño Formation were found and described (Franco et al., 2015). These materials were retained under open nomenclature and have features akin to dicotyledonous lianas or vine-like or small shrub species (Franco et al., 2015). *Dolichandra pacei* sp. nov. differs from these fossil woods in having cambial variants, in the diameter of the vessel lumina, and in the absence of tylosis and helical thickenings in vessels.

Bignoniaceae non-lianescent woods were found from the lower Cenozoic to the Pleistocene in Asia, Africa, and South America (see Table 1). The only Bignoniaceae fossil wood previously recorded in America is *Bignonioxylon americanum* Moya and Brea from the Late Pleistocene Arroyo Feliciano Formation, Entre Ríos Province, Argentina (Moya and Brea, 2018). This specimen exhibits anatomical features similar to the *Tabebuia* alliance and *Tecoma* and differs from *Dolichandra pacei* sp. nov. in the absence of cambial variants, the presence of aliform and confluent parenchyma, and the presence of rays composed exclusively of procumbent cells; mainly uniseriate, among others (Moya and Brea, 2018).

Wood anatomy evolution, paleoecology, and paleobiogeography

Evolution

Pace and Angyalossy (2013) proposed that two main aspects played a critical role in the evolution of wood anatomy in Bignoniaceae: ecophysiological factors and the lianoid habit. Habitat and habit transitions strongly influenced the patterns of the evolution of wood in the family. The evolutionary response of wood to selective pressures also enabled the occupation of new habitats, habits, and niches by the family (Pace and Angyalossy, 2013).

Bignoniaceae and Verbenaceae are two clades nested well within the Lamiales (Olmstead, 2013). These clades have a South American ancestral area, then diversified throughout the continent, and established toeholds on other continents too (Olmstead et al., 2009; Marx et al., 2010). Both families were found in the Mariño Formation, and with Solanaceae, represent a lineage with a probable Gondwana origin. Its diversification coincided with the geological and climatological changes that South America experienced since its isolation from the other continents (Olmstead, 2013). The plant fossil evidence from Mariño Formation, with the record of Bignoniaceae and Verbenaceae, suggests that these families could have diversified in the Andean region, probably related to dry or seasonally dry habitats. These records, with phylogenetic and biogeographical studies, are important for understanding plant diversification in South America.

The tribe Bignonieae is exclusively American, and most of its species are tropical, with the center of diversity in Brazil (Gentry, 1980; Lohmann and Taylor, 2014). Also, a South American origin was inferred for this tribe (Olmstead, 2013; Lohmann et al., 2013). Lohmann et al. (2013) suggested that the crown group of the Bignonieae probably originated in the South American rainforest in the early Eocene.

Dolichandra reunites four genera previously treated as separate: *Dolichandra*, *Macfadyena* A.D.C., *Melloa* Bureau, and *Parabignonia* Bureau ex K. Schum. (Fischer et al., 2004; Pace et. al., 2015; Fonseca et al., 2017); it presently includes nine recognized species: *D. cynanchoides*, *D. dentata*, *D. uncata*, *D. hispida*, *D. unguis-cati*, *D. chodatii*, *D. stermarkii*, *D. unguiculata*, and *D. quadrivalvis* (Lohmann and Taylor, 2014; Fonseca et al., 2017). Members of this genus share a unique type of cambial

TABLE 1 Summary of Bignoniaceae fossil woods

Identification	Geological age	Geographic source	Reference
Bignonioxylon americanum Moya and Brea	Late Pleistocene	Temperate South America (Northeast Argentina)	Moya and Brea, 2018
Catalpa wuhanensis Yang	upper Cenozoic	Temperate Asia (Hubei, China)	Yang et al., 1993
Catophractes sp. aff. *C. alexandri* D.Don	Pliocene	Tropical Africa	Dechamps, 1983
			Dechamps and Maes, 1985
Dolichandrone wuhanensis Yang in Qi, Yang and Xu	upper Cenozoic	Temperate Asia (Wuhan, China)	Qi et al., 1997
Heterophragmoxylon indicum Shete and Kulkarni	lower Cenozoic (Maharashtra, India)	Central South Asia	Shete and Kulkarni, 1982
Kigelia africana (Lam.) Benth	Pliocene	Tropical Africa	Dechamps, 1976
Kigelia fo africana Gros (1990) (unpub. thesis; invalid name)	Pliocene/Pleistocene	Tropical Africa	Gros, 1990
Markhamia preobtusifolia Bande, Dechamps, Lakhanpal and Prakash	Miocene?	Tropical Africa	Bande et al., 1987
Stereospermoxylon eoacuminatissimum Prakash, Awasthi and Lemoigne	Miocene-Pliocene	Tropical Africa (Canon in Blue Nile Valley)	Prakash et al., 1982
cf. *Stereospermoxylon eoacuminatissimum* Prakash, Awasthi and Lemoigne	Miocene	Tropical Africa (Ethiopia)	Wheeler et al., 2007
Stereospermoxylon grambasti Prakash, Awasthi and Lemoigne	Miocene-Pliocene	Tropical Africa (Canon in Blue Nile Valley)	Prakash et al., 1982
Stereospermum sp. cf. *S. kunthianum* Cham.	Pliocene	Tropical Africa	Dechamps, 1983
			Dechamps and Maes, 1985

variant (Lohmann, 2006; Pace et al., 2009, 2015), known as "multiple-dissected" phloem wedges, supporting the circumscription of these genera proposed by Lohmann and Taylor (2014). All these species share four main synapomorphies: (1) stems with multiple-dissected phloem wedges in cross section, (2) trifid and uncate tendrils, (3) psilate and 3-colpate pollen, and (4) capsules with four lines of dehiscence (Fonseca et al., 2017). The genus is monophyletic and originated in the Eocene or Oligocene (36.43–26.23 Myr ago), probably in eastern South America, and diversified during the Oligocene and Miocene, with a great geographical movement after the speciation (Fonseca and Lohmann, 2015). The finding of these new fossil stems would indicate that *Dolichandra pacei* sp. nov., a representative of the genus *Dolichandra*, was present at least since the Miocene of the Southern Andean region.

Paleoecology

The presence of cambial variants is more common in lianas than in any other life form (Pace et al., 2011). These soft tissues that intermingle with stiff secondary xylem increase the flexibility of the stem for climbing (Rowe et al., 2004; Pace et al., 2011; Pace and Angyalossy, 2013) and are an essential mechanical and hydraulic feature in the success of

lianas (Rowe et al., 2004). The feature of multiple-dissected phloem wedges, present in *Dolichandra pacei* sp. nov., could have been important in providing more flexibility to the stem because the more phloem wedges it has, the more flexible it will be (Pace and Angyalossy, 2013). Furthermore, the presence of cambial variants is also important in injury repair, water storage, xylem development, and better conduction of photosynthates (Dobbins and Fisher, 1986; Carlquist, 2001; Pace et al., 2011; Angyalossy et al., 2012).

Based on two fossil stems, we calculate a maximum diameter of 48 mm and a minimum diameter of 35 mm for *Dolichandra pacei* sp. nov. According to the literature, *Dolichandra unguis-cati* stems commonly measure up to 60 mm (Gentry, 1973). The calculated stem diameter is reduced in comparison to the diameter of a tree trunk and can be thought of as a mechanical adaptation to the climbing habit, allowing reduced allocation to structural support and an increase in stem flexibility too (Angyalossy et al., 2012).

The feature of diffuse-porous wood, present in the fossil stem, is an ancestral state for the family Bignoniaceae (Pace and Angyalossy, 2013). Moreover, the presence of diffuse-porous wood is common in tropical genera, while temperate-zone genera have ring-porous wood (Fischer et al., 2004). The scanty axial parenchyma is also a common feature present in lianas and can be correlated with the presence of septate fibers, which occur in only a few non-lianescent

Bignoniaceae (Metcalfe and Chalk, 1950; Carlquist, 1985; Pace and Angyalossy, 2013). It has been hypothesized that septate fibers, which store starch, could assume the role of the parenchyma axial in those woods (Pace and Angyalossy, 2013). Both features are preserved in the fossil stem studied here. Another feature strongly correlated with the lianoid habit in Bignoniaceae and found in *Dolichandra pacei* sp. nov. is the presence of perforated ray cells. This feature is likely another source of hydraulic conduction safety and efficiency (Pace and Angyalossy, 2013).

The vulnerability (*V*) index predicts which species can live in dry environments (Carlquist, 2001). Xylem hydraulic efficiency depends on the diameter and frequency of vessels per unit in cross-sectional area (Giménez et al., 2014). Hydraulic conductivity in lianas is more efficient than trees or shrubs because they have developed a greater number of vessels, of all sizes, per unit transection that offer less resistance to the water movement from roots to leaves (Rosell and Olson, 2014), but dysfunctions in the xylem such as embolisms and cavitation from water stress can impede the efficiency of water transport (Grossiord et al., 2020). Xylem embolism resistance is one of the most important traits determining plant drought resistance (Chen et al.). Lianas and trees tend to have the same relationship of hydraulic safety versus efficiency, but lianas show a tendency for greater maximum stem-specific conductivity and less-resistant xylem (De Guzman et al., 2017). The *V* index in the fossil stems has a value of 1.71, which is relatively low value and, with TIA, indicates some features that could contribute to hydraulic safety: small, numerous and short vessels, simple perforation plates, and small intervessel pits (Carlquist, 1977, 1984; Lindorf, 1994; Baas and Wheeler, 2011; Martínez-Cabrera et al., 2014). Thus, *Dolichandra pacei* sp. nov. probably grew in a dry or seasonally dry forest. The climate interpretation based on anatomical features of the fossil plant is consistent with the reconstruction of the paleoenvironments by sedimentological data, which suggests that the Mariño Formation was deposited under arid or semi-arid conditions (Yrigoyen, 1993; Irigoyen, 2000, 2002; Cerdeño et al., 2006, 2018; and references therein). Evidence for these climatic conditions includes the occurrence of oxidized floodplain deposits, incipient calcrete bands, and fluvial sandstone lithofacies that suggest deposition under ephemeral flow regimes, and a thick succession of eolian deposits (Franco et al., 2015; Cerdeño et al., 2018).

Paleobiogeography

Lianas are among the most important components of tropical forests (Gentry, 1991; Angyalossy et al., 2012; Malizia et al., 2015). They are more diverse and abundant in tropical than temperate forests. Many tropical lianas grow in wetlands (e.g., along riverbanks) and do not need safety mechanisms because they are not exposed to water stress and frost. Other lianas can grow in areas where drought or frost are moderate, but not in extreme drought or cold (Gentry, 1973; Carlquist, 1985).

Bignoniaceae and Leguminosae are nearly always the dominant liana families in neotropical lowland forests (Gentry, 1991; Angyalossy et al., 2012). Bignoniaceae, the most speciose liana family in the dry forest (Gentry, 1991), is distributed in warm tropical regions, with perhaps no more than seven or eight species (ca. 1% of New World diversity) occurring further than ca. 35° north or south of the equator (Olmstead, 2013). The tribe Bignonieae is mainly neotropical with decreasing diversity toward Central America and North America (Gentry, 1991, 1992). Bignonieae form part of the liana floras in the wet tropical forest, including Amazonian and Atlantic coastal forests, and probably originated in those ecosystems, but successfully colonized dry, fire-prone cerrado Brazil, most probably one but perhaps multiple times (Lohmann et al., 2013; Olmstead, 2013).

Dolichandra is a genus of neotropical lianas within tribe Bignonieae and comprises nine species. It is centered in Paraguay, southern Brazil, and northeastern Argentina, where six species occur and three are endemic. The species of *Dolichandra* are generally climbers in dry and wet lowland forests, also growing in swamps and gallery forests (Fonseca et al., 2017). *Dolichandra unguis-cati* is a species widely distributed in tropical America, from Baja California in Mexico to Argentina, including the Caribbean Islands (Figure 5). This species is common in dry forests and becomes progressively less common in premontane moist forests and rare in premontane wet forests and tropical wet forests (Gentry, 1973; Fonseca et al., 2017). The present distribution of *Dolichandra unguis-cati* does not reach the region of Precordillera in Mendoza Province, where the fossil stems were found, indicating that the neotropical flora was more widespread in the past (Figure 5).

Lohmann et al. (2013) investigated the biogeographical history of Bignonieae and proposed that ancestral area of the tribe is in the rainforest in eastern South America. For the crown node of the core Bignonieae, in which *Dolichandra* is included, they proposed a widespread ancestral distribution, including eastern South America and lowland Amazonia. Their analysis also suggested that the diversification occurred during the time that the neotropical climate dried and the Andes uplifted. Sixteen possible ancestral states were estimated for *Dolichandra*, but the most likely ancestral area in the analysis was eastern South America, except for two nodes with the South American dry areas. This number of possible ancestral areas suggests that the biogeographical signal could have been lost due to the changes in species distributions (Fonseca and Lohmann, 2015). Also, these authors indicated that the ancestral area reconstruction in *Dolichandra* has high levels of uncertainty. Therefore, *Dolichandra pacei* sp. nov. has great importance for future time-calibrated phylogenetic and biogeographic studies of the tribe Bignonieae and the genus *Dolichandra*. Their evolution was probably influenced by the Andean uplift and a dry Neotropical climate during the Miocene.

The presence of *Dolichandra pacei* sp. nov. in the Miocene of the south-southwestern Andean Precordillera in Mendoza

FIGURE 5 Map showing the distribution *Dolichandra unguis-cati* (o) and the Potrerillos fossiliferous locality (★) where the fossil materials described here were collected

Province, central-west Argentina, does not refute the hypotheses proposed by Lohmann et al. (2013) and Fonseca and Lohmann (2015) about the biogeographic history of the tribe and the genus. The fossil stem represents a derived lineage and the tribe diversified during the Eocene.

CONCLUSIONS

The stems from the Mariño Formation represent a new taxon of Bignonieae, *Dolichandra pacei* sp. nov., which adds to the previous paleobotanical records from this formation, increasing the number of known families. *Dolichandra pacei* sp. nov. confirms the presence of Bignonieae lianas in the neotropics by the early Miocene and provides the first and oldest evidence of the climbing habit in this family.

Paleobotanical records from the Miocene of Patagonia and central-western Argentina are still very scarce. Therefore, further paleobotanical studies in the Mariño Formation could be essential to understand the biogeographic history of the families Bignoniaceae and Verbenaceae and the evolution of South American floras. Anatomical features indicate that *Dolichandra pacei* sp. nov. probably grew in a dry or seasonally dry forest, agreeing with the reconstruction of the paleoenvironments by sedimentological data. The discovery of this fossil stem in the Miocene of the south-southwestern Andean Precordillera (Argentina) could be proof that the diversification of *Dolichandra* was related to a dry neotropical climate and the Andes uplift. The present study provides new evidence about the importance of the Miocene for plant diversification in the neotropics.

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DATA AVAILABILITY STATEMENT

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