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Research paper

Heterophylly in *Cordaites*-like foliage from western Gondwana

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ABSTRACT

Cordaitalean plants are an important component of upper Palaeozoic Gondwanan plant fossil assemblages. New fossil axes from western Argentina exhibit the first examples of heterophylly in Gondwanan cordaitaleans. *Cordaites bifolius* sp. nov. was probably a large tree, with its largest branches reaching 17 cm in diameter and leaves reaching at least 55 cm in length. Heterophylly is expressed by the co-attachment of spathulate and needle-like leaves in the twigs. The branches that preserve leaf scars are similar to species of *Cordaicladus*. Associated stout fertile organs are similar to *Cordaitanthus* and bear seeds of *Cordaicarpus*-type.

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1. Introduction

Cordaitales were a very important component of late Palaeozoic floras, but their presence in the Southern Hemisphere remains questionable due to the absence of diagnostic reproductive structures. Records of Gondwanan *Cordaites*-like foliage have been attributed to *Noeggerathiopsis* Feistmantel, *Cordaites* Unger, *Euryphyllum* Feistmantel or *Panthophyllum* Rigby. The oldest records of *Cordaites*-like foliage in Argentina are of late Serpukhovian age (coinciding with the first appearance of monosaccate pollen in the palynofloras) and belong to the *Nothorhacopteris–Botrychiopsis–Ginkgophyllum* (NBG) flora that ranges to the Moscovian (Césari et al., 2011). Cordaitalean leaves also occur in the succeeding "Interval flora" and the Cisuralian *Gangamopteris* flora (Archangelsky and Cúneo, 1984, 1991).

The current investigation is based on specimens from a single locality in the Paganzo Basin of northwestern Argentina. Samples were recovered from outcrops at the Bajo de Véliz site, which is well-known for its rich fossil assemblages that include leaf imprints, insects and palynomorphs; these are referred to the latest Carboniferous or earliest Permian (Pinto and Hünicken, 1980; Hünicken et al., 1981; Gutiérrez and Césari, 2000; Selden et al., 2005).

A robust branch from these deposits resembling the original specimens of *Cordaicladus* described by Grand'Eury (1877) from France bears foliar scars and long leaves. Associated axes have some areas with spathulate leaves and others with needle-like foliage. This represents the first evidence from Gondwana for Trivett's (1992) proposal that Cordaitales expressed heterophylly in heteroblastic series. An associated ovulate structure with densely packed seeds is similar to some fertile structures referred to Euramerican Cordaitales.

2. Geological setting

Specimens studied in this paper were recovered from the Paganzo Basin, a late Palaeozoic continental basin in Argentina (Fig. 1). Sediments accumulated in this western Argentina basin from the Serpukhovian to the Permian (Gulbranson et al., 2010; Césari et al., 2011). The stratigraphic succession is divided into several formations reflecting the alternation of glacial and postglacial deposits, coal-bearing strata and red beds (Limarino et al., 2006). At Bajo de Véliz (32°17′S:65°24′W; San Luis Province), about 25 km west of Santa Rosa city, the Bajo de Véliz Formation is divided into the Cautana, Pallero and Lomas members in ascending stratigraphic order. Since the 19th century (Kurtz, 1895), various authors have documented the palaeontological content of this formation. The diverse plant assemblages are typical of the Argentinian *Gangamopteris* flora, considered to be of early Cisuralian age based on floristic correlations with other units in South America and dating via other fossil groups. Palynological assemblages described by Menéndez (1971) and Gutiérrez and Césari (2000) include about 1% of taeniate pollen represented by *Vittatina* spp., *Protohaploxypinus* spp., *Pakhapites fusus* (Bose and Kar) Menéndez and *Hamiapollenites fusiformis* Marques-Toigo emend. Archangelsky and Gamerro. Palynostratigraphic correlation with units in Brazil and Uruguay supports an earliest Cisuralian age (Césari, 2007; Césari et al., 2011).

The specimens described here occur on bedding planes of thinly bedded, grey argillaceous sandstone. This unit also contains abundant leaves of *Gangamopteris*, *Glossopteris* (Cúneo, 1984), *Velizia*

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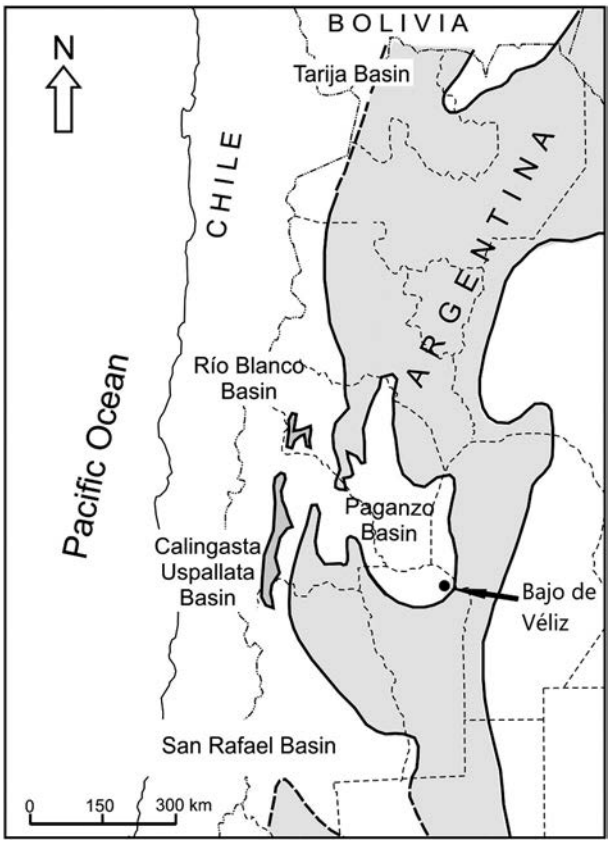

Fig. 1. Map of northwestern Argentina showing the fossil locality. Shaded areas represent highlands.

(César and Hünicken, 1992), *Cheirophyllum* (César and Cúneo, 1990), *Euryphyllum* (Leguizamón, 1979) and *Botrychiopsis* (Kurtz, 1895), together with lycopods similar to the northern Chaloneriaceae (César et al., 1995), the sphenopsids *Stephanophyllites* (César and Hünicken, 1991), *Tschernovia*, *Phyllotheca* and *Giridia* (Durán et al., 1997), and undescribed coniferophyte leafy twigs. As these fossils lack cuticle it has been impossible to determine if the *Cordaites*-like leaves belong to *Cordaites sensu stricto* or to *Noeggerathiopsis*, a typical Gondwanan leaf form for which anatomical and cuticular characters are known.

3. Systematics

Genus *CORDAITES* Unger, 1850
Type species: *Cordaites borassifolius* (Sternberg) Unger, 1850.
Cordaites bifolius sp. nov. (Plates I–III, Fig. 2)
Holotype: Specimen CORD-PB 3324.
Paratypes: Specimens CORD-PB 3028 (Plate II) and CORD-PB 2659 (Plate II) represent small branches with zones of spathulate leaves alternating along the branch with zones of needle-like leaves.
Repository: Paleobotanical Collection of Córdoba University (CORD-PB).
Type locality: Bajo de Véliz, San Luis Province, Argentina.
Stratigraphic horizon: Bajo de Véliz Formation.
Age: early Cisuralian.
Derivation of name: from the Latin *bi* (two) and *folium* (leaf).
Diagnosis: Cordaitalean plants with leaves helically arranged; leaves of two types: needle-like and spathulate. Small branches bear zones of needle-like leaves alternating with zones of spathulate leaves with apex obtuse to broadly rounded. Leaves variable in size, the largest being unique to larger branches. Leaf veins straight, parallel to margins and to each other, with sparse dichotomies and usually with interveinal linear features. Surface of large branches with downward-curved to subrhomboidal scars, usually with small distinctive vascular scars aligned horizontally.

3.1. Description of the holotype

Specimen CORD-PB 3324 (Plate I, 4) represents a leafy twig with alternate zones of spathulate and needle-like leaves arranged helically. The apical zone, 9.5 cm long and 4.5 cm wide, bears small closely spaced needle-like leaves adpressed to the axis forming a covered bud. Larger, spathulate leaves (up to 9.5 cm long and 1.5 cm wide) with a rounded apex are borne at the base of the apical zone forming a pseudowhorl. These leaves have parallel venation, with several dichotomies and approximately 16 veins per centimetre near the apex. Fine, interstitial linear features are evident between the veins. Proximal to these leaves, another segment of the axis (7.5 cm long and 4 cm wide) is fully covered by spirally arranged small needle-like leaves and this zone is delimited at its base by another pseudowhorl of larger spathulate leaves. The proximal part of the axis represents a third zone covered by scale leaves with a basal pseudowhorl of spathulate leaves.

3.2. Description of the paratypes

Specimen CORD-PB 2659 (Plate II, 3) is a leafy twig with an apical bud of closely adpressed small needle-like leaves, 2.5 cm long (Plate II, 1). Larger, spathulate leaves are borne at the base of the bud forming a pseudowhorl. These leaves are 6 cm long and 1.2 cm wide with 16 veins per centimetre at the rounded apex. Proximally, the axis bears 5-cm-long needle-like leaves that are better preserved along the stem's lateral margins (Plate II, 2). This zone is delimited proximally by spathulate leaves.

Specimen CORD-PB 3028 is an axis fragment 21 cm long and approximately 1 cm wide with two short segments (each 7 cm long), fully covered by needle-like leaves, separated by a longer part (9 cm long) bearing spathulate leaves (Plate II, 7). Helically inserted, adpressed, acicular leaves reach 30 mm long and 4 mm wide, each with a rounded base (Plate II, 5). Spathulate leaves are 11 cm long and 1.5 cm in maximum width, with four veins at the base and 15 veins per centimetre at the apex, which seems to have a crenate margin (Plate I, 3). Venation is parallel, with several dichotomies (Plate II, 4) and one or two interstitial fine features (Plate III, 6).

3.3. Description of additional specimens

Specimen CORD-PB 2722 (Fig. 2) is a laterally compressed large branch bearing incomplete leaves at the apex. The branch fragment is 9 cm wide and 19 cm long and its surface bears indistinct downward-curved leaf scars. Leaves attached at the apex of the branch are large, entire and thick, with parallel margins, linear to spathulate, up to 7 cm wide and at least 55 cm long. No leaf tips have been preserved. The vein density varies from 5 to 15 per centimetre along the leaf.

An isolated incomplete leaf (specimen CORD-PB 3025, Plate I, 2), 7.5 cm wide and 21 cm long, has parallel margins and a widened and thickened base. The appearance of the base with numerous small wrinkled grooves seems to correspond to the presence of hypodermal sclerenchyma fibres in the epidermis, similar to the leaf bases of extant *Araucaria araucana* or palms.

Specimen BAPb16 (Plate I, 1) represents a pseudowhorl with 17 incomplete leaves arranged radially around a central axis, probably of a distal branch or twig. These spathulate leaves have obtuse to rounded apices and reach 10 cm long and 1.3 cm wide.

3.4. Comparisons

This new cordaitalean is characterized by a wide variation in the size of the leaves, with small needle-like and spathulate leaves occurring on

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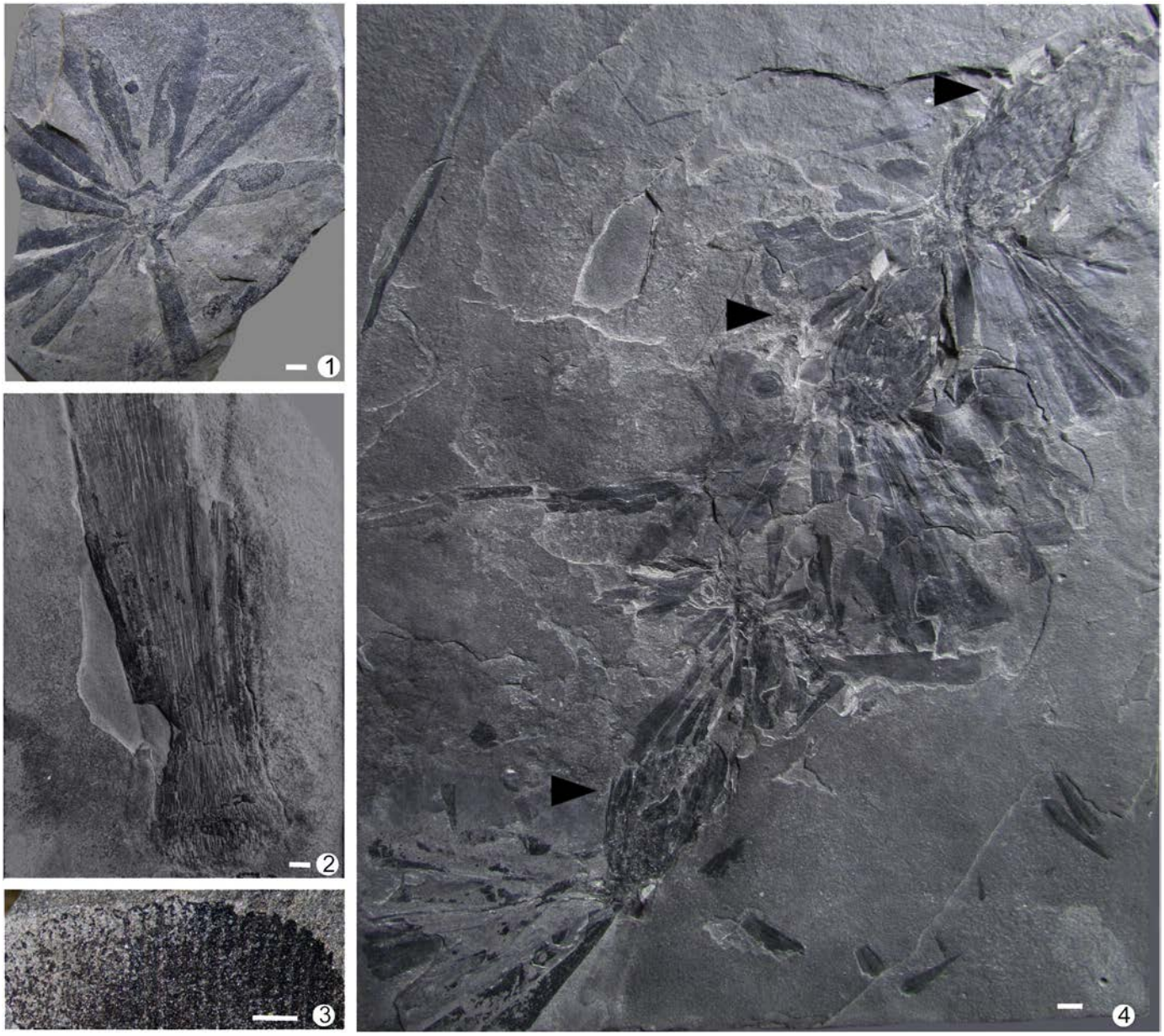

Plate I. *Cordaites bifolius* sp. nov.

1. Pseudowhorl of spathulate leaves, BAPb16. Scale bar = 1 cm.
2. Large leaf with thickened and widened base, CORD-PB 3025. Scale bar = 1 cm.
3. Detail of the leaf apex, CORD-PB 3028. Scale bar = 1 mm.
4. The holotype. Leafy twig with alternate segments of spathulate and needle-like leaves, CORD-PB 3324. Scale bar = 1 cm.

the twigs or small branches, whereas large branches have only long spathulate leaves. Our specimens allow comparisons based on three main features of the leaves: shape, venation and the expression of heterophylly. As all examples lack cuticle and anatomical details it is impossible to determine whether the spathulate leaves conform precisely to Euramerican *Cordaites* or *Noeggerathiopsis sensu* Pant and Verma (1964) or McLoughlin and Drinnan (1996). Because the type specimens of both genera lack preserved cuticle, several authors (e.g. Seward and Sahni, 1920; Walton, 1929; Archangelsky and Leguizamón, 1980) have preferred the use of *Cordaites*, which has nomenclatural priority, for leaf impressions. Where cuticles have been recovered from similar-shaped Gondwanan leaves, they have been found to differ from Euramerican *Cordaites*. This led Rigby (1984) to establish *Pantophyllum* for "*Noeggerathiopsis*-type" leaves with cuticles. McLoughlin and Drinnan (1996) considered the erection of different genera an unnecessary nomenclatural duplication. However, Maheshwari and Singh (1999) favoured the use of *Pantophyllum* for leaves with cuticular characters and discussed the validity of *Noeggerathiopsis* Feistmantel. One of the most important features used to differentiate *Cordaites* leaves from *Noeggerathiopsis* is the presence of prominent sclerenchyma bundles and columns within the mesophyll in the Euramerican genus. Many Gondwanan forms apparently lack these fibre bundles but, at least in Antarctic specimens, bear stomatiferous abaxial grooves between the veins (McLoughlin and Drinnan, 1996). Interstitial linear features are evident between the veins of the new specimens, in *Cordaites riojanus* Archangelsky and Leguizamón and other Carboniferous cordaitalean leaves described from Argentinian assemblages (Archangelsky and Leguizamón, 1980; García, 1990; Coturel et al., 2009) and also elsewhere in Permian of Gondwana (e.g. *Noeggerathiopsis hislopi* in

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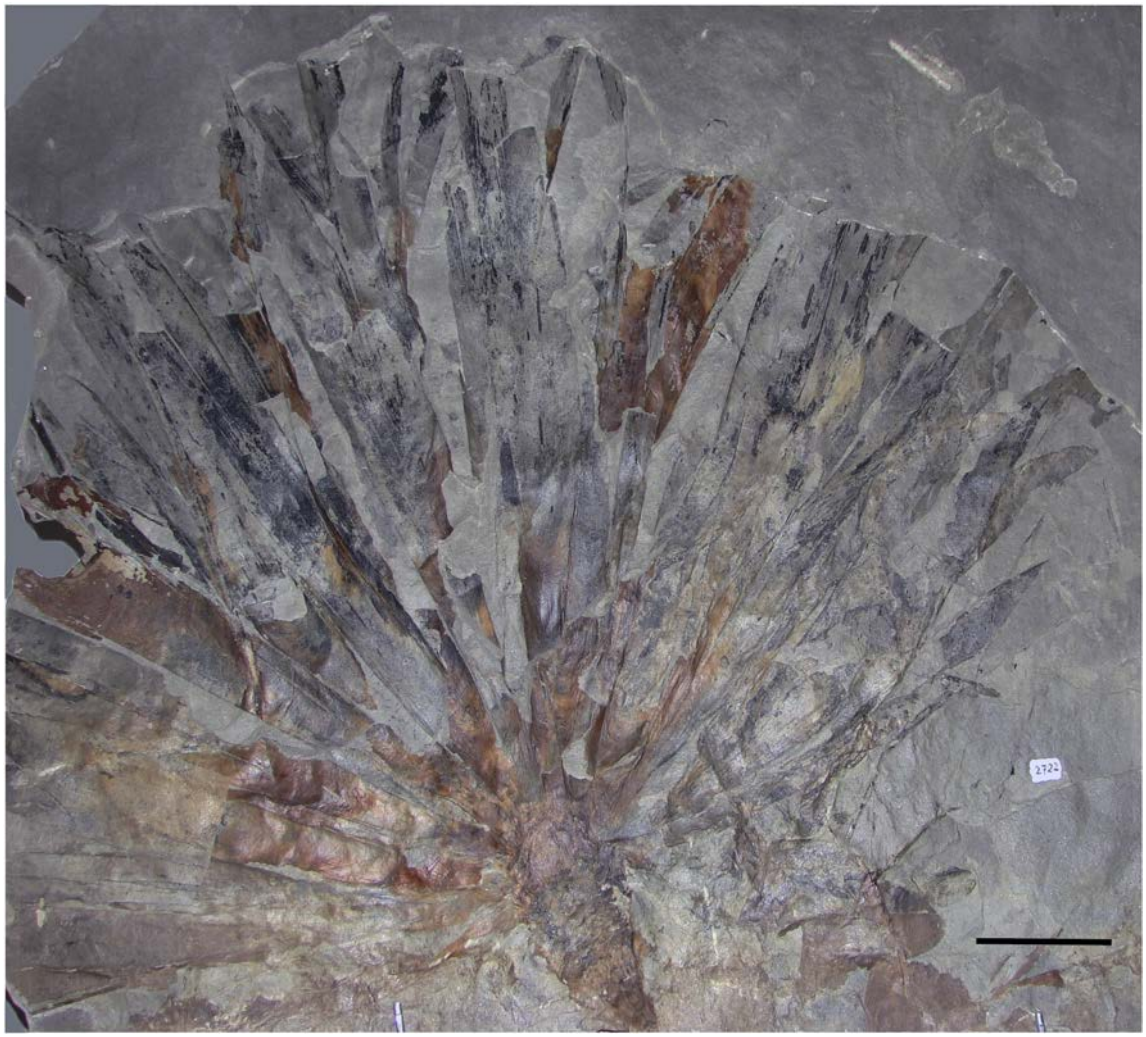

Fig. 2. *Cordaites bifolius* sp. nov., fragment of branch bearing large, incomplete leaves at the apex, CORD-PB 2722. Scale bar = 10 cm.

Walkom, 1922; *Cordaites dumanii* Chandra and Srivastava, 1991). The absence of preserved cuticle makes it impossible to confirm whether these thickenings correspond to fibres or alternatively are the remnants of stomatiferous grooves.

Šimůnek et al. (2009) interpreted the type species *Cordaites borassifolius* to represent a large tree bearing large, entire, thick, ovate-lanceolate leaves with bluntly pointed or, in some cases, deeply lacerated apices, and medium to dense veins. They described the

Plate II. *Cordaites bifolius* sp. nov.

1. Detail of apical bud of fig. 2, CORD-PB 2659. Scale bar = 1 cm.
2. Detail of axis of fig. 2, showing departure of needle-like leaves. Scale bar = 1 cm.
3. A paratype. Leafy twig with apical bud and alternate spathulate and needle-like leaves, CORD-PB 2659. Scale bar = 1 cm.
4. Detail of venation of leaf from fig. 7. Scale bar = 1 mm.
5. Acicular leaf from fig. 7. Scale bar = 1 cm.
6. Seed associated with specimen in fig. 7, short black arrow. Scale bar = 1 mm.
7. Twig with spathulate and acicular adpressed leaves. CORD-PB 3028.
8. Detail of acicular leaves (long black arrow in 7) and leaf scars (white arrow in 7).

Scale bar = 1 cm.

Plate III. 1, 3, 6. *Cordaites bifolius* sp. nov. (see on page 6)

1. Large stem with helically arranged subrhombic leaf scars, CORD-PB 2670. Scale bar = 10 cm.
3. Detail of leaf scars of fig. 1, CORD-PB 2670. Scale bar = 10 cm.
6. Detail of venation showing interstitial bands of organic matter (arrowed), CORD-PB 3028. Scale bar = 1 mm.

2, 4, 7. *Cordaitanthus* sp. 1, CORD-PB 2858. Scale bar = 1 cm.

2. Detail of ovules of fig. 4. Scale bar = 1 cm.
4. Fragment of axis showing the basal part with rounded downward-facing scars and the upper section covered by ovules. Rounded scars (short white arrows) correspond to the incomplete bracts (black arrows), CORD-PB 2858. Scale bar = 1 cm.
7. Detail of a downward-facing scar, CORD-PB 2858. Scale bar = 1 cm.
5. *Cordaitanthus*? sp. 2, bud covered by adpressed bract scales (white arrow), note supposed fertile scales curved upwards at the lateral margins (black arrow), CORD-PB 2839. Scale bar = 1 cm.

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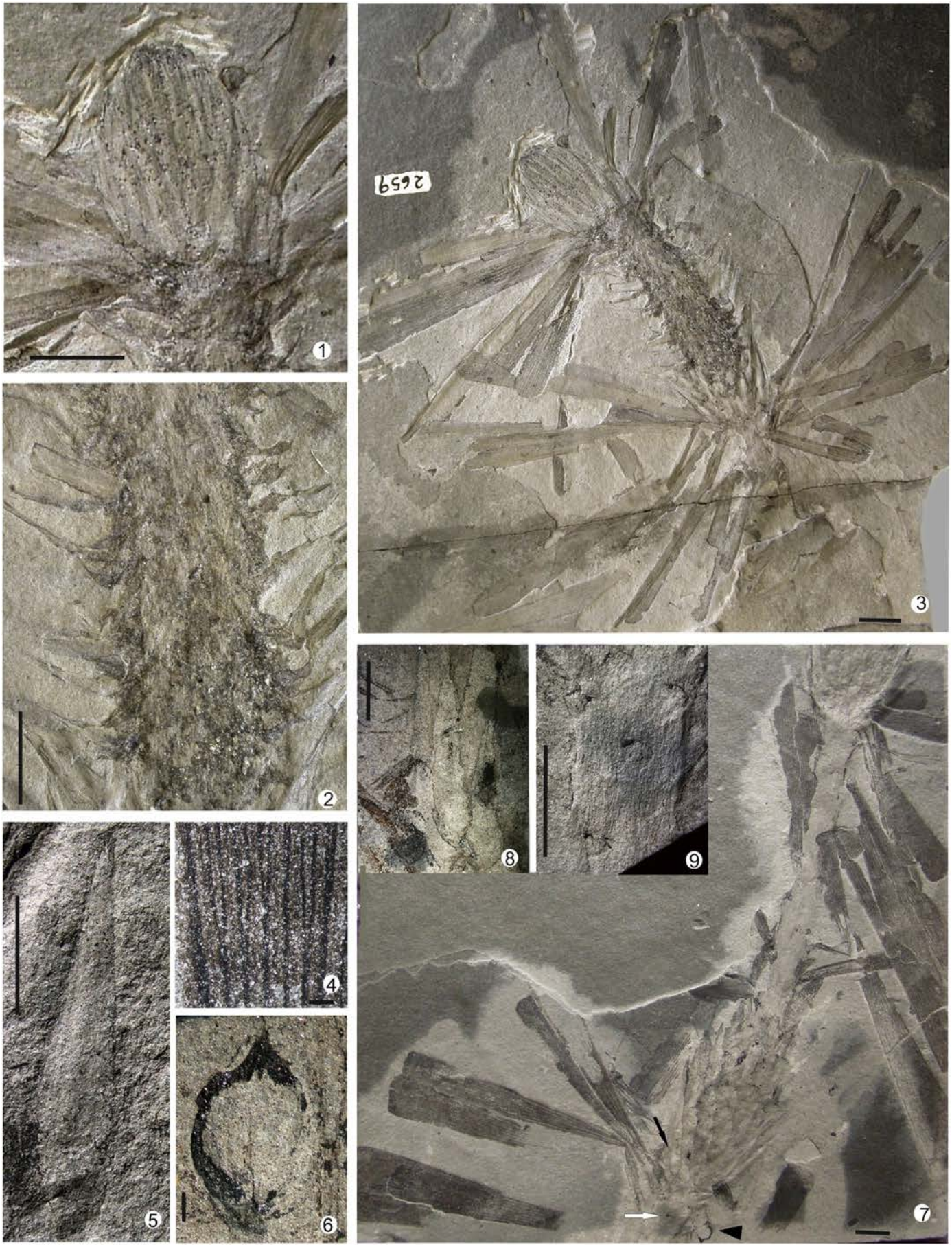

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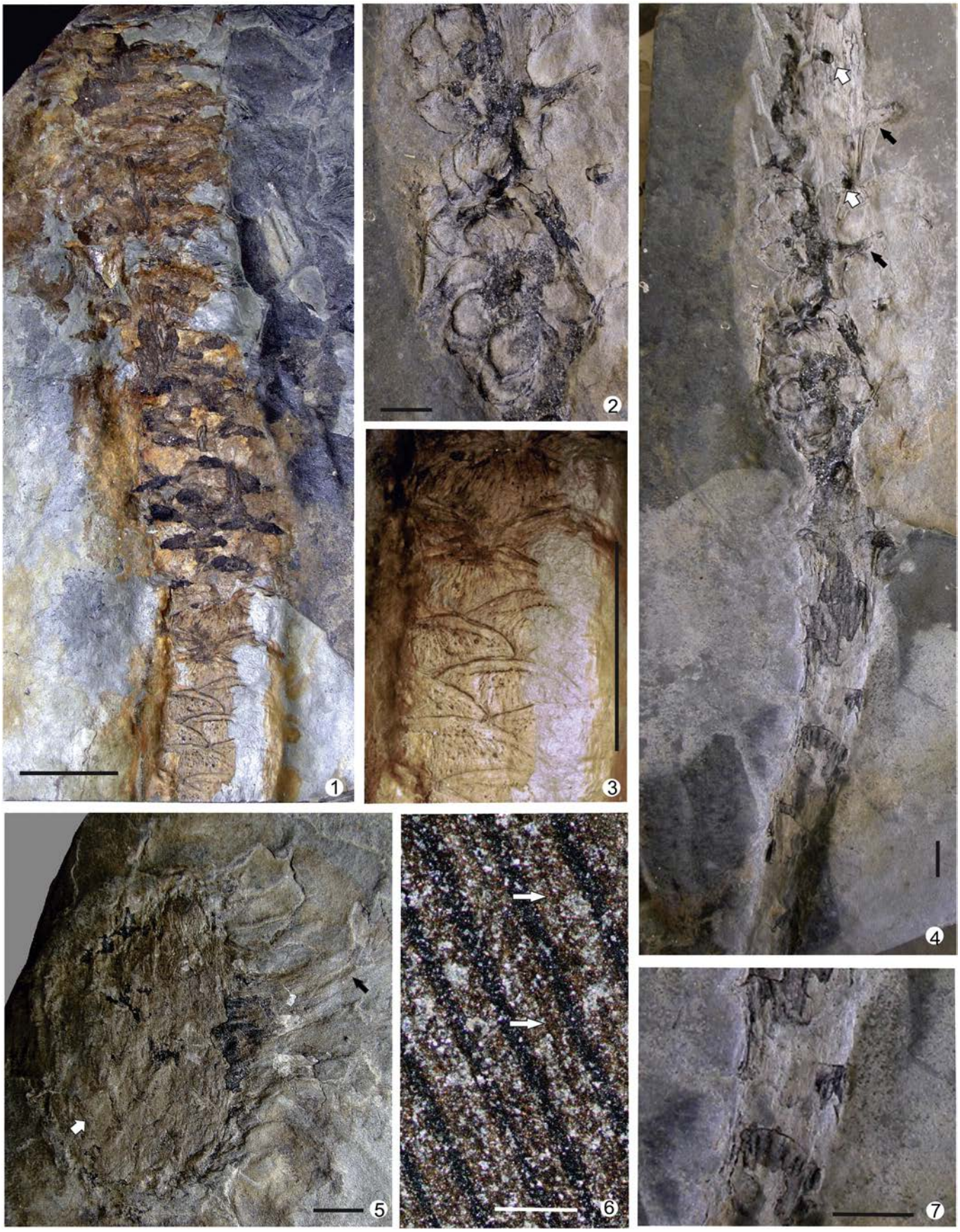

Plate III (*caption on page 4*).

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holotype as an apex of a twig bearing leaves up to 425 mm long and 58 mm wide in their middle part with 50 veins per centimetre.

Cordaitalean leaf morphotaxa are very similar in shape and some closely match *Cordaites bifolius* sp. nov., but none has been described as imprints of foliage attached to stems that also bear needle-like leaves. Some northern species such as *Cordaites aequalis* Göppert depicted by Zalessky (1912, Plate I, fig. 31) have crenate leaf apices, like the Argentinian specimens but this feature is not usually preserved as was noted by Zalessky (1912).

Gondwanan cordaitalean leaves preserved as imprints are usually referred to *Noeggerathiopsis hislopi* (Bunbury) Feistmantel, a Permian species from India lacking interstitial veins or fibres (Singh et al., 2007). A pseudowhorl of incomplete leaves 17 cm long assigned to *N. hislopi* from Australia (Walkom, 1921) is comparable to the specimen BAPb16 described here. The presence of interstitial features between veins was not mentioned by Rigby et al. (1980) in the similar Australian species *Cordaites spatulata*; however McLoughlin and Drinnan (1996) noted that the type specimen shows linear features that can be interpreted as abaxial grooves. Although these Permian species are similar to the small spathulate leaves described here, considering the presence of heterophylly a diagnostic character, they are retained as different species.

The Pennsylvanian cordaitalean small leaves from Argentina known as *Cordaites riojanus* Archangelsky and Leguizamón are characterized by two or three interstitial linear features between veins. Cordaitalean Permian leaves from northwestern Argentina and Brazil were assigned to *Cordaites* (*Noeggerathiopsis*) *hislopi*, *Noeggerathiopsis hislopi* or *Cordaites* sp. (Leguizamón, 1972; Millan and Dolianiti, 1981; Guerra-Sommer and Cazzulo-Klepzig, 2000). *Cordaites casildensis* Archangelsky et al. (1981) from the Permian of Patagonia is clearly different to the leaves from Bajo de Véliz.

Large *Cordaites* leaves have also been reported in Euramerica (e.g. Falcon-Lang and Bashforth, 2004, 2005; Šimůnek et al., 2009; Taylor et al., 2009) reaching 100 cm in length. Our specimen CORD-PB 2722 seems to be the largest reported from western Gondwana, where incomplete leaves up to 20 cm long have been described by previous authors (Archangelsky and Leguizamón, 1980; Millan and Dolianiti, 1981), although Anderson and Anderson (1985) described *Noeggerathiopsis elongata* from southern Africa reaching 60 cm in length and 5 cm in width. This latter species differs from the one described here in shape and lower density of veins.

The presence of heterophylly in *Cordaites* was first cited by Rothwell and Warner (1984). They described *Cordaixylon dumusum* with needle-like leaves at the base of branches and spathulate leaves up to ca. 3 cm wide distally on some branches and needle-like leaves only on others. This heterophylly was only identified in anatomically preserved branch fragments, but not seen in impressions or compressions of foliage. Trivett (1992) also described the intergradation of strap-shaped and needle-like leaves on the same branch of permineralized specimens of *Cordaixylon iowensis* (Wilson and Johnston) Trivett. Additionally, needle-like leaves also characterized the Cathaysian *Cordaites sinensis* Bateman and Wang (Wang et al., 2003; Hilton et al., 2009).

3.5. Leafless stems

3.5.1. Description

Branch up to 17 cm wide and 72 cm long, parallel-sided and showing no conspicuous tapering, with helically arranged subrhomboidal leaf scars (Plate III, 1). There are 9–11 scars per gyre in a low spiral (45–55°). Leaf scars are subrhomboidal, 75–94 mm wide and 44–30 mm high, acute at lateral ends with the apex rounded and the base acute (Plate III, 3). The distal margin shows a narrow rim, below which are many (more than ten) small aligned vascular scars. The rest of the scar surface bears radial striations.

Specimen studied: CORD-PB 2670.

3.5.2. Comparisons

Although no leaves were found attached to this large trunk fragment, its surface clearly resembles the characteristics of the robust branch and twigs bearing cordaitalean leaves from the same locality, allowing to include them in a single species.

Grand'Eury (1877) pointed out that *Cordaicladus* is easily recognized by its downward curved and decurrent leaf scars, with raised edges as in monocotyledons. When vascular scars are distinctive, they are small and horizontally aligned. Grand'Eury (1877) described *Cordaicladus subschnorrianus* as constituting branches up to 10 cm wide with scars, some of them rounded, with or without underlying smaller scars, the surface being marked by irregular striae, more or less interrupted by transverse irregular wrinkles. *Cordaicladus selenoides*, *C. idoneus* and *C. ellipticus* differ in the outline of their scars and arrangement of the striae.

Rigby (1969) described a specimen from New South Wales (Australia) that he referred to *Cordaicladus adamsii* (Feistmantel) Rigby, a species that had earlier been assigned to *Caulopteris* by Feistmantel (1878, 1890). The Australian leaf scars are very similar in shape to the specimen described here.

3.6. Associated fertile organs

Cordaitanthus sp. 1
Plate III, 2, 4 and 7
Specimen studied: CORD-PB 2858.
Description. Fragment of axis up to 190 mm long and 20 mm wide (Plate III, 4). The basal part preserves rounded downward scars that probably correspond to leaf bases. The upper section is covered by ovate ovules ca. 12 mm long and 85 mm wide. The ovules are orthotropous surrounded by a narrow rim (sarcotesta) that forms a short micropyle at the distal end and the surface of the sclerotesta is smooth (Plate III, 2). The presence of bracts is inferred by incomplete remains on the lateral margin and subcircular scars on the axis (Plate III, 4). Bracts arise at ca. 45° and are 4.25 mm wide in lateral view.
Comparisons. The ovules attached to the axis have the same morphology as the seed associated with CORD-PB 3028 (Plate II, 6, 7). All the ovules are positioned tightly on the axis and the method of attachment is not clearly determined. The lack of evidence regarding a stalk or pedicel attaching the ovules to the axis supports the interpretation of bracts subtending the ovules. We consider that this specimen could be the ovuliferous organ of *Cordaites bifolius* sp. nov., although evidence of a physical connection is missing. Although incomplete, the fertile structure resembles specimens assigned to *Cordaitanthus* Feistmantel from Laurasia. However, this Gondwanan organ shows only individual axillary bracts subtending ovules on a long shoot rather than fertile (bract- and ovule-bearing) short shoots attached to the main axis. The ovules are also very similar to *Cardiocarpus annularis* (Sternberg) Lesquereux, a species found in association with *Cordaites borassifolius* (Šimůnek et al., 2009).

Fructifications with sessile ovules that are solitary or subtended by sterile bracts have been described by Grand'Eury (1877) and Lesquereux (1880a,b). Ignatiev and Meyen (1989) proposed *Grandeuryconus* to encompass this type of fertile organ where the bract-axillary complex organization is very simple. *Krylovia* Chachlov, a fertile structure associated with *Rufloria* leaves from the Angara flora, differs from the Argentinian specimen in having elongated pedicels with terminal ovules. A closed allied Gondwanan genus is *Arberia* White, a branching structure with branches terminating in uniovulate cupules whose affinity is controversial between Cordaitales and glossopterids (Millan, 1967; Meyen, 1987). The fertile organ of *Velizia inconstans* Césari and Hünicken, also from the Bajo de Véliz Formation, differs in being an ovate and shorter structure where the morphology of the ovules is not clearly discernible.

Since the pioneer works of Grand'Eury (1877) it was inferred cordaitalean affinities for *Cordaicarpus*-like seeds. Many Gondwanan

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species referred to this genus share a similar morphology and usually show an intergradation, generally without taxonomic significance. Dispersal ovules or seeds are common in plant fossil assemblages of western Argentina. *Cordaicarpus famatinensis* Gutiérrez et al. (1992) seeds are similar to those described here but this species has an older stratigraphic range. However, similar Cisuralian seeds from Brazil were described as *C.* cf. *famatinensis* (Marques de Souza and Iannuzzi, 2009).

Cordaitanthus? sp. 2
Plate III, 5
Specimen studied: CORD-PB 2839.

The bud is 6.5 cm long and 4.3 cm wide (Plate III, 5). It is fully covered by adpressed bract scales (1.2 cm long and 5 mm wide) with acute apices. The surface of the bracts is marked by longitudinal furrows. Distally arched and tapered scales up to 45 mm long with a wide base occur at the lateral margins of the cone.
Comparisons. The scales are wider than the vegetative needle-like leaves of *Cordaites bifolius* sp. nov., and are associated with apparently interspersed long and distally narrow lamina, interpreted as putative fertile scales that can be seen on the laterals. This presumed fertile bud resembles the male fructifications of *Cordaitanthus* and other gymnosperms based on the presence of compact, spirally arranged scales.

Cladostrobus Zalessky described by Maheshwari and Meyen (1975) is similar in its external morphology with the specimen described here. Both organs have spirally arranged rhomboid scales bearing longitudinal, irregular wrinkles. However, the microsporophylls in *Cladostrobus* consist of long stalks with a distal lamina.

4. Discussion

Euramerican Cordaitales have eustelic stems bearing helically arranged strap-shaped leaves. The reproductive organs are compound, monosporangiate strobili up to about 25 cm long, in which either platyspermic ovules or saccate pollen is produced. Cones occur either as axillary branches or as branches with no definite relationship to the leaves. *Cordaites* leaves are roughly spathulate, entire, up to 1 m long, with veins that dichotomize infrequently and appear to be parallel. The surface of most large cordaitalean leaves is characterized by longitudinal ridges that correspond to the positions of veins and interspersed sclerenchyma bundles, and furrows that lie embedded within the normal mesophyll tissue. According to Rothwell (1988), cones have a flattened primary axis from which bracts arise on opposite sides, and when compressed are easily recognized because none of the appendages overlies the primary axis, instead appearing to be borne in a decussate arrangement. The permineralized cordaitean ovules have a cordate base and pointed apex when flattened. The best known northern cordaitaleans include *Cordaixylon dumusum*, *C. iowensis*, *Mesoxylon priapi* and *M. birame*. These taxa refer to whole plant associations based on anatomical, morphological and reproductive information.

Noeggerathiopsis Feistmantel is a Gondwanan morphogenus that includes Carboniferous and Permian linear to spathulate leaves with parallel venation. Pant and Verma (1964) pointed out the resemblances between the form and venation of *Cordaites* and *Noeggerathiopsis*; however they proposed retaining both genera owing to the imperfect knowledge of the internal anatomy of *Noeggerathiopsis* and its stems at that time, and the absence of any indubitable fructification of *Cordaianthus* type in Gondwana. Those authors suggested that "both genera may represent leaves of closely related plants because their form, venation and cuticular structure are not only similar among themselves but quite distinct from those of other gymnosperms". Leaves from the Angaran floras originally referred to *Noeggerathiopsis* have been transferred to *Rufloria* or *Cordaites* depending on the presence or absence of interveinal furrows (Meyen, 1963). Singh et al. (2007) distinguished *Noeggerathiopsis* and *Cordaites* on external morphological criteria. According to those authors, *Noeggerathiopsis* leaves have simple veins of uniform thickness throughout the lamina, whereas *Cordaites* possesses comparatively thick veins separated by thin parallel interveinal fibres.

McLoughlin and Drinnan (1996) also described *Noeggerathiopsis* as an exclusive Gondwanan genus of uncertain botanical affinities owing to the absence of associated fertile organs. The more complete anatomy of *Noeggerathiopsis* reported from Antarctic permineralized specimens is characterized by prominent abaxial stomatiferous furrows protected by dense epidermal hairs and lacking fibre bundles (McLoughlin and Drinnan, 1996). The Antarctic leaves do not possess mesophyll sclerenchyma, a distinctive feature of Euramerican *Cordaites* leaf anatomy. The exclusive presence of prominent abaxial stomatiferous furrows and hirsute lower epidermis in the Antarctic specimens was extrapolated to all Gondwanan cordaitalean leaves and considered a differential character. Cuticular characters usually have taxonomic and phylogenetic value but, as with any other feature, the capacity of such characters to provide useful information varies greatly from taxon to taxon (Stace, 1966). Foliar anatomy was considered useful for distinguishing species of some fossil pteridosperms (Cleal and Shute, 2012) and *Cordaites* (Šimůnek, 2007), but the anatomical evidence in Gondwana cordaitaleans still seems insufficient for its clear differentiation from the Euramerican leaves. This group of plants inhabited diverse environments during approximately 80 Myr, therefore much detailed information is required to distinguish characters reflecting environmental adaptations, ontogenetic stages or position on the plant from those that reflect inherited (phylogenetically significant) stages.

Cordaites bifolius sp. nov. shares the presence of heterophylly with some northern Cordaitales. This character is considered the most significant in establishing the affinities of the species. Rothwell and Warner (1984) described small and large leaves in *Cordaixylon dumusum* and proposed that they represent a heteroblastic series. Trivett (1992) enlarged the diagnosis of *Cordaixylon* including the presence of needle-like to spathulate leaves usually arising in a heteroblastic series. According to Trivett (1992), some branches of *Cordaixylon iowensis* are characterized by an intergradation from the narrow leaves to the more spathulate ones distally. Analogies with rhythmic growth of modern plants corresponding to Rauh's model were suggested for *C. iowensis* by Trivett (1992). Rhythmic extension of leafy axes is a common growth pattern in modern plants, and is expressed by alternating periods of dormancy and active shoot extension via meristem activity (prolepsis). A growth unit (the portion that develops during a continuous period of extension) is generally identified because it is limited by a zone of short internodes and/or cataphylls (i.e. scale leaves) corresponding to the protective organs of the bud (Barthélémy and Caraglio, 2007). The specimens described here displaying these features allow us to propose a rhythmic growth in at least some Gondwanan cordaitalean plants. It is probable that the extremely scarce record of branches with attached leaves has generally prevented the recognition of heterophylly elsewhere.

Shanxioxylon, a cordaitalean whole plant exhibiting needle-like leaves (Wang et al., 2003) from Cathaysia was considered by Hilton and Bateman (2006) and Taylor et al. (2009) to be important in understanding conifer and cordaite phylogeny. Similarly, the species *Cordaites bifolius* sp. nov. from Gondwana, exhibiting heterophylly with needle-like leaves, should also be taken into consideration.

The recent discovery of permineralized trunks in the Late Carboniferous–Cisuralian San Ignacio Formation (Césari et al., 2011) reinforces the presence of Cordaitales in the westernmost Gondwanan floras. The permineralized specimens represent trees up to 28 m tall with anatomical characters very similar to the northern cordaitean stems.

5. Conclusions

Cordaites bifolius sp. nov. has both needle-like and spathulate leaves that distinguish it and some other cordaitalean species from the classical

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reconstructions with only strap-like leaves. As in conifers, the needle-like leaves are imbricate and adpressed to the axis suggesting a close relationship to this group. This type of foliage was observed exclusively in twigs where zones bear needle-like leaves alternating with zones of spathulate leaves.

This first report of heterophylly in Gondwanan cordaitalean foliage reveals no intergradation between the needle-like and spathulate leaves, as was proposed for anatomically preserved Euramerican *Cordaites*. Specimens from Argentina suggest that the acicular leaves are not young or immature leaves but likely represent heterophylly produced by prolepsis. Associated large branches bear leaf scars similar to *Cordaicladus*, a genus also affiliated with Cordaitales.

The presence of linear interveinal thickenings in the leaves may be related to mesophyll sclerenchyma or stomatiferous furrows, characters proposed to differentiate Euramerican and Gondwanan cordaitaleans. Both presumed fertile organs associated with the foliage have similarities to cordaitalean fructifications of the Northern Hemisphere and represent the first indication of reproductive structures in Gondwana associated with *Cordaites*-like leaves.

Advances in knowledge of the Cordaitales have shown that this was a very diverse group, evolving for approximately 80 Myr in various habitats. Traditionally, isolated leaves have been referred to different genera according to their geographical origin and cuticular characters. McLoughlin and Drinnan (1996) suggested that the similarities between the northern *Cordaites* and *Rufloria* and the southern *Noeggerathiopsis* and *Euryphyllum* represent the retention of plesiomorphic characters and interchange between the floras. Future studies should determine whether or not the presence of heterophylly in some Euramerican and Gondwanan cordaitaleans must be considered a plesiomorphic feature.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.revpalbo.2013.04.001. These data include Google map of the most important areas described in this article.

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