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Revision of *Fedekurtzia* (pteridosperm) and allied fronds from the Carboniferous of Gondwana

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ABSTRACT. Carboniferous foliage of *Fedekurtzia argentina* (Kurtz) Archangelsky from Gondwana is systematically described and revised. The frond is reconstructed based on specimens of the late Serpukhovian–Bashkirian *Nothorhacopteris / Botrychiopsis / Ginkgophyllum* flora of western Argentina, especially from the Jejenes, Tupe and Volcán formations. The whole-frond reconstruction emphasizes the variation in pinnule shape throughout the basal, medial and distal sections of the frond. The basalmost rachis possesses cyclopteroid pinnules grading to pinnae with obovate to wedge-shaped pinnules at the medial section of the frond. Distal pinnae are shorter, bearing imbricate and more dissected pinnules. Specimens from the same type locality from which *F. argentina* comes, previously assigned to *Triphyllopteris cuyana* Leguizamón & Vega, are reassigned to *F. argentina*, as well as ovuliferous and microsporangiate structures in organic connection. Two decades ago a revision of the German *Triphyllopteris* genus rejected *T. cuyana* as representative of the taxon, and the Argentinian specimens remained as indeterminate "triphyllopteroid" fronds. The ovulate organ *Polycalyx* Vega & Archangelsky is considered to be in organic connection with vegetative fragments of *F. argentina*, and its cupulate character is discussed. Pollen organs represented by multi-forked axes bearing fusiform sporangia of *Rinconadia* Vega are also in organic attachment and included in the *Fedekurtzia argentina* reconstruction. The pollen or prepollen grains are trilete and with granulate sculpture. The paper presents a comparison with *Botrychiopsis weissiana* Kurtz emend. Archangelsky & Arrondo, which differs in its rounded and entire-margin pinnules. Similar specimens from Australia formerly described as *Rhacopteris*, *Sphenopteridium* and *Archaeopteris* and currently included in *Fedekurtzia intermedia* Rigby share morphological characters with the Argentinian species. A revision of the Australian material is necessary to confirm synonymy. *Fedekurtzia* belongs to the pteridosperms based on the reproductive organs and is here assigned to Austrocalyxaceae. Its reconstruction now constitutes one of the most complete seed-ferns known from the Carboniferous of Gondwana.

KEYWORDS: *Fedekurtzia*, pteridosperms, taxonomy, Carboniferous, Gondwana

INTRODUCTION

The earliest findings of Carboniferous fronds in Gondwana come from its two most distant areas: Australia and Argentina. In Australia, McCoy (1847), Etheridge (1888) and Feistmantel (1878) described the first frond fragments, referring them to different northern genera such as *Rhacopteris*, *Sphenopteridium* and *Archaeopteris*, for which they defined new species. Later, White (1965), Rigby (1969, 1973) and Morris (1975) revised the Australian palaeofloras, proposing new combinations and species. In westernmost Gondwana, Szajnocha (1891) and Kurtz (1894) reported the first records of upper Palaeozoic plants from Argentina. Kurtz (1894) studied a collection made by Brackebusch in San Juan Province and defined a new genus, *Botrychiopsis*, which later was considered a key species of the Pennsylvanian flora of western Argentina (Archangelsky & Azcuy 1985). These first studies

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of Carboniferous floras from Argentina were continued by Frenguelli (1941, 1944, 1946), Archangelsky & Arrondo (1971), Archangelsky (1981, 1983) and Césari (1986), among others. Other typical fronds from Argentina were referred to *Fedekurtzia*, defined by Archangelsky (1981) based on specimens formerly described as *Archaeopteris argentina* by Kurtz (1921). During recent decades, important advances in knowledge of the botanical affinity of some fronds were made by Vega and Archangelsky (2001), who defined the pteridosperm family Austrocalyxaceae. Fronds in organic connection with the fertile organs were referred by these authors to *Triphyllopteris* Schimper or "triphyllopteroid" fronds.

The foliage of these upper Palaeozoic plants shows wide morphological variability, which hinders taxonomic delimitation when small fragments are studied. The aim of this contribution is to present an update of the following taxa described for the Gondwanan Carboniferous flora: *Fedekurtzia* Archangelsky, *Triphyllopteris* Schimper and *Botrychiopsis* Kurtz emend. Archangelsky & Arrondo.

STRATIGRAPHIC SETTING

The Pennsylvanian flora from Argentina is usually assigned to the *Nothorhacopteris argentina–Botrychiopsis weissiana–Ginkgophyllum diazii* (NBG) Biozone.

The NBG Biozone was proposed by Archangelsky and Azcuy (1985); today it displays a widespread distribution in central-western Argentina (Césari et al. 2007). The main components of this flora are lycophytes, cordaitales and pteridosperms. Its age is constrained by several U/Pb datings (Césari et al. 2011) to the late Serpukhovian–Bashkirian. An "Interval" flora was suggested by Archangelsky and Cúneo (1991) to include those latest Carboniferous assemblages where the first occurrences of conifer and fern remains are identified. This flora is now assigned to the *Krauselcladus–Asterotheca* Biozone (Carrizo & Azcuy 2015).

Correlative Pennsylvanian stratigraphic units of central-western Argentina have been given different names in different regions of the country. Among these units is the Tupe Formation, in which many occurrences of the NBG flora have been reported, and which is the namesake of the "Tupense", a regional stage (Archangelsky 1971). However, recent findings extend the stratigraphic range of the NBG flora to the underlying Guandacol Formation. Both units comprise glacial and postglacial deposits which characterize the Lower and Middle Pennsylvanian in westernmost Gondwana (Limarino et al. 2006, 2014). Some coeval stratigraphic units in the Paganzo, Calingasta–Uspallata and San Rafael basins bearing plant remains are the Jejenes, Volcán, Tupe (San Juan Province), El Imperial, Santa Máxima, Tramojo (Mendoza Province) Tupe and Lagares (La Rioja Province) formations. The area between Rinconada and La Carpintería or Retamito (San Juan Province), where the Jejenes Formation crops out, comprises important fossiliferous sites (e.g. Cladera et al. 2000, Vázquez et al. 2016). Type specimens of two key taxa of the NBG flora, *Botrychiopsis* and *Fedekurtzia*, come from these latter localities.

HISTORICAL AND NOMENCLATURAL BACKGROUND

Rigby (1973) described fronds from the Carboniferous of Australia, which he referred to ?*Sphenopteridium intermedium* (Feistmantel) Rigby. This species included Australian specimens originally described by Feistmantel (1878, 1879, 1890) as *Rhacopteris intermedia*, *R. septentrionalis*, *Archaeopteris wilkinsoni* and by Walkom (1934) as ?*Sphenopteridium cuneatum*. Rigby (1973) included also specimens described by Read (1938) as *Rhacopteris* sp. cf. *R. cuneata* from the Peruvian Paracas flora. Later, Rigby (1985) defined *Fedekurtzia intermedia* (Feistmantel) Rigby, combining the specimens described by Feistmantel (1878, 1879) as *Rhacopteris intermedia*, *R. septentrionalis* (figured by Rigby 1973, pl. 3, fig. 10), and *Archaeopteris wilkinsoni* (figured by Rigby 1973, pl. 3, fig. 11a), and selected as lectotype the specimen illustrated by Rigby (1973) in plate 3, figure 12A, from Paterson, New South Wales.

In another contribution to the knowledge of the Australian Carboniferous flora, Morris (1975) considered the variable morphology of pinnae remains found in the same locality (the Paterson area) reviewed by Rigby (1973). She highlighted, for the first time, the presence of a complex of intergrading forms which can be related to several well-defined fossil genera such as *Triphyllopteris* or *Sphenopteridium*.

According to Morris (1975), the most common species was named *Rhacopteris digitata* by Etheridge (1888) together with variable aphlebia of *Rhacophyllum diversiforme* Etheridge. She also proposed an intergradation between fronds of *Aneimites austrina* Etheridge and *Dactylophyllum digitatum* (Etheridge) Morris.

When Archangelsky (1981) combined the species *Archaeopteris argentina*, formerly described by Kurtz (1921), as the new genus *Fedekurtzia*, he included in the diagnosis specimens originally referred to *Sphenopteris*, *Eremopteris*, *Archaeopteris*, *Rhacopteris*, *Sphenopteridium*, *Adiantites*, or *Triphyllopteris* from Argentina, Peru, and Australia. According to the original illustrations (Fig. 1), Kurtz (1921) observed variation in the morphology of the pinnules and pinnae throughout the frond. This heteromorphism was corroborated by Césari (1986), adding more complete specimens from the Tupe Formation in La Rioja Province, showing significant variation in the morphology of the pinnae and pinnules of this species. Archangelsky (1981) regarded the specimens illustrated by Morris (1975) under the name *Triphyllopteris austrina* as possibly conspecific with *Fedekurtzia argentina*, but later Archangelsky (1983) proposed that they represent a *Botrychiopsis* frond, as suggested by Retallack (1980); its incomplete preservation hampered close comparison with any species. After that, Rigby (1985) considered that *Aneimites austrina* Etheridge and *Triphyllopteris austrina* (Etheridge) Morris should be included together with *Otopteris ovata* M'Coy in *Botrychiopsis ovata* (M'Coy) Rigby.

Archangelsky (1981) also described the presence of spike-like male fructifications, which were interpreted to be in organic connection to a specimen of *Fedekurtzia argentina* collected by Frenguelli in Mendoza Province.

Leguizamón and Vega (1991) reported, for the first time, the presence of *Triphyllopteris* Schimper in Argentina and described a new species, *T. cuyana*, which was considered to be different from *Fedekurtzia*; this distinction is relevant because the specimens were found in the same stratigraphic unit and fossiliferous area (Cladera et al. 2000) from which comes the lectotype of *Fedekurtzia argentina* Archangelsky. Later, Vega and Archangelsky (1997) described fertile structures in organic connection with these fronds.

Gutiérrez (1994) also described fertile structures associated with fragments of pinnae referred to *Fedkurtzia argentina*. One of them comes from the same stratigraphic levels where Césari (1986) illustrated nearly complete fragments of fronds of that species for the first time. The ovuliferous organ is very similar

Fig. 1. **A** – Reproduction of figs. 2, 3 (plate XXIX) from Kurtz (1921), originally assigned to *Archaeopteris argentina*. **B** – Reproduction of fig. 9 (plate XVIII) from Kurtz (1921) originally assigned to *A. argentina*. Scale bar: 1 cm

to those described as *Polycalyx* by Vega and Archangelsky (2001), associated with triphyllopteroid foliage. The latter authors did not compare these specimens.

Vega (1995a) defined the microsporangiate species *Rinconadia archangelsky* based on fertile frond specimens bearing lobed pinnules and pinnae identical with *Triphyllopteris cuyana* Leguizamón & Vega. However, Vega (1995a) remarked upon the uncertain generic assignment of the Argentinian species, following Knaus's (1994) revision of the northern representatives of this genus. The same criterion was followed by Vega and Archangelsky (2001) when they referred to those fronds as "triphyllopteroid" type without precise generic endorsement.

When Knaus (1994) assigned a neotype for *Triphyllopteris collombiana* Schimper (type species of the genus), she rejected the species *T. cuyana* Leguizamón & Vega and *T. peruviana* Jongmans from the genus. Moreover, she noted the need for revision of the original Feistmantel specimens described by Etheridge (1894) and Morris (1975) as *T. austrina* and moved to *Botrychiopsis* by Retallack (1980) or *Fedekurtzia argentina* by Archangelsky (1981). Knaus (1994) constrained the distribution of *Triphyllopteris* to the European region, and the similar genus *Genselia* to North America.

Knaus's reconstruction of the *Triphyllopteris* frond defines a rhombic bipinnate frond with the longer pinnae at the base, which bear 3- or 5-lobed pinnules. The distance between pinnae decreases toward the apex and the pinna arrangement is subopposite. The basal pinnules are rhombic and usually trilobed, the distal pinnules are entire or in some cases slightly lobed, and the apical pinnules are unlobed and ovate to lanceolate.

MATERIAL AND METHODS

This revision is based on specimens collected in the Jejenes and Volcán formations (San Juan Province) and Tupe Formation (La Rioja Province); we also compared additional material from coeval units. These well-preserved imprints of foliage allowed reconstruction of the frond architecture and a comparison with isolated or incomplete specimens described under different species from other stratigraphic units.

The holotype of *Fedekurtzia argentina* deposited in the Palaeontological Collection of Córdoba University (CORD PB) was re-examined, as well as many specimens from the Palaeobotanical Collection of La Plata Museum (LPPB), the Palaeobotanical Collection of the Museum of Natural Sciences of San Juan (PBSJ), the Palaeobotanical Collection of the Museo Argentino de Ciencias Naturales (BA Pb) and the Palaeontological Collection of Buenos Aires University (BAFC PB).

Descriptions follow the terms used to describe multipinnate frond architecture in upper Palaeozoic seed ferns (e.g., rachis, pinna, pinnule). The reconstruction of the frond follows the criteria used by Knaus (1994, 1995) with similar Carboniferous material. The specimens were selected mainly if at least two pinnae as well as their most apical pinnulae were attached to a rachis.

To represent the available evidence, linear tracings over photographs were made and then placed in the reconstruction according to the measured parameters.

SYSTEMATICS

Family Austrocalyxaceae
Vega & Archangelsky 2001

Fossil genus ***Fedekurtzia***
(Archangelsky) emend.

Original diagnosis. Frond with a main axis bearing pinnate segments, helicoidally inserted and bilaterally disposed at acute angles. Mature pinnae oval elongate, close to superposed, with pinnules of two types: a) separated at the base, entire, subcircular to oval or wedge-shaped and b) distal or apical, confluent, decurrent, wedge-shaped, narrow, having 2 or 3, rarely more lobes. Venation uniform, dichotomous and fan-shaped. Spike-like fructifications disposed on the same rachides with pinnae, consisting of an axis with compactly arranged free oval to fusiform bodies (sporangia?), distally rounded and perpendicularly placed on the axis; no visible dehiscence markings.

Emended diagnosis. Frond heteromorphic, bipinnate, elliptic in outline and slightly asymmetrical; longest pinnae occurring in middle section. Pinna arrangement subopposite to alternate, and angles of attachment becoming progressively more acute apically. Basalmost rachis with cyclopteroid pinnules and heteromorphic pinnules in pinnae of medial section of frond; distal pinnae reduced in length, with densely spaced pinnules. Pinnules of medial and distal portions of frond obovate to wedge-shaped, decurrent, and having deep or incipient lobation. Venation uniform, dichotomous and fan-shaped. Apical microsporangiate organ consisting of multiforked axis with free sporangia arranged at tips. Ovuliferous organs apically attached to a pinnate rachis, comprising leaf-like receptacles with ovules inserted on one side.

Type species: ***Fedekurtzia argentina*** (Kurtz) Archangelsky 1981

Fedekurtzia argentina (Kurtz) Archangelsky emend.

Pl. 1–3

1991 *Triphyllopteris cuyana* Leguizamón & Vega: 306, pl. 1, figs 1 and 2.

1995b *Triphyllopteris cuyana* Leguizamón & Vega; Vega, pl. I, fig. 2, pl. II, fig. 6.

Additional synonymy in Archangelsky 1981: 1133.

Lectotype. Specimen CORD Pb 402 (Pl. 2, fig. 3) and counterpart CORD Pb 400 (designed by Archangelsky 1981).

Emended diagnosis. Rachis straight at base, somewhat flexuous at middle part of frond, tapering apically. Attachment of pinnae to rachis at 75° to 40° in middle to distal sections of frond; pinnae arrangement subopposite to alternate, with spacing regular in basal and mid-sections and overlapping of pinnules on apical sector. Basalmost rachis with broad, cyclopteroid, rounded, decurrent pinnules passing upward to pinnules with undulate margins and narrower bases, followed by trilobed pinnules. Number of pinnules and degree of segmentation per pinna increasing distally along frond. Venation uniform, dichotomous and fan-shaped. First pinnae of mid-section five-lobed, lobes decurrent, obovate to wedge- shaped; distal lobe elongate, slightly bilobed. Longest pinnae bearing alternate to subopposite pinnules attached by a narrow base and slightly bi- or trilobed; basal anadromous pinnules obovate, larger than the catadromic. Pinnules wedge-shaped towards apex of pinna, and apical pinnule unequally emarginate. In distal section of frond pinnae are shorter, bearing imbricate pinnules, with basal pinnules three to four-lobed and apical elongate pinnules, bilobed at apex.

Ovulate structures borne apically on pinnate fronds of diverse grades of development. Main rachis forking twice, each branch supporting a relatively large receptacle consisting of two orbicular laminae with distal margin laciniate into narrow and acute lobes. Oval, elongate ovules, with terminal long and narrow lobes, inserted on adaxial and proximal surface of each lamina. Sporangial masses emerge from terminal multi-forked apex of pinnate rachis. Fusiform sporangia with finely and helically striated surface, containing trilete spores.

Remarks. The original diagnosis of the species was emended and expanded; the first was presented by Césari (1986), mentioning the wide variation in the morphology of the pinnules along the frond. Gutiérrez (1994) added the character of the venation in the basal part of the frond and the association with multiovulate cupules. The present emended diagnosis is based on revision of the holotypes of *Fedekurtzia argentina* and *Triphyllopteris cuyana*, an analysis of many specimens, which allowed reconstruction of the frond (taking into account the available evidence on complete and incomplete fragments), and revision of the fertile material.

It should be noted that the almost complete specimen illustrated by Leguizamón and Vega (1991, pl. 1) probably represents an early ontogenetic stage in which the morphology of the pinnules changes rapidly from one sector of the fragment to another, but replicating the leaf forms described below for each section of an adult frond. According to the scale in plate 1 of Leguizamón and Vega (1991), the specimen is ca 300 mm in length, not 520 mm as was mentioned in the text, and thus there is no basis to support the suggestion that the fragment is a third-order pinna in a very large frond.

Description. The measurements of the main specimens analysed are detailed in Table 1 and 2. They represent fragments of different plants and probably of different sizes.

Basal section of frond. This section includes the most basal simple pinnules identified, attached to the main rachis up to the first pinna with two pairs of pinnules (arrow in Pl. 1, fig. 3). The basal fragments of the fronds bear opposite to subopposite, rounded to obcordate and lobed pinnules, with venation dichotomous and fan-shaped (Pl. 1, figs 7, 8). The bases of the lowermost pinnules are decurrent, forming a narrow wing along the rachis. Upwards in the frond the incipiently lobed pinnules pass to

Table 1. Measurements of the basal section in the main specimens analysed

Basal section	Rachis	Pinnule		
Specimen	Width (mm)	Distance (mm)	Length (mm)	Width (mm)
PBSJ 1021	4	15	13	14
PBSJ 1015	2.5	9–12	16–17	14
BAFCPB 12858	6	22.5	19–32	24–25
BAPB 5330	6	20	31	22.5
BAFCPB 12838	5	20	20–25	22.5–25
BAPB 12232	4	18	23	16

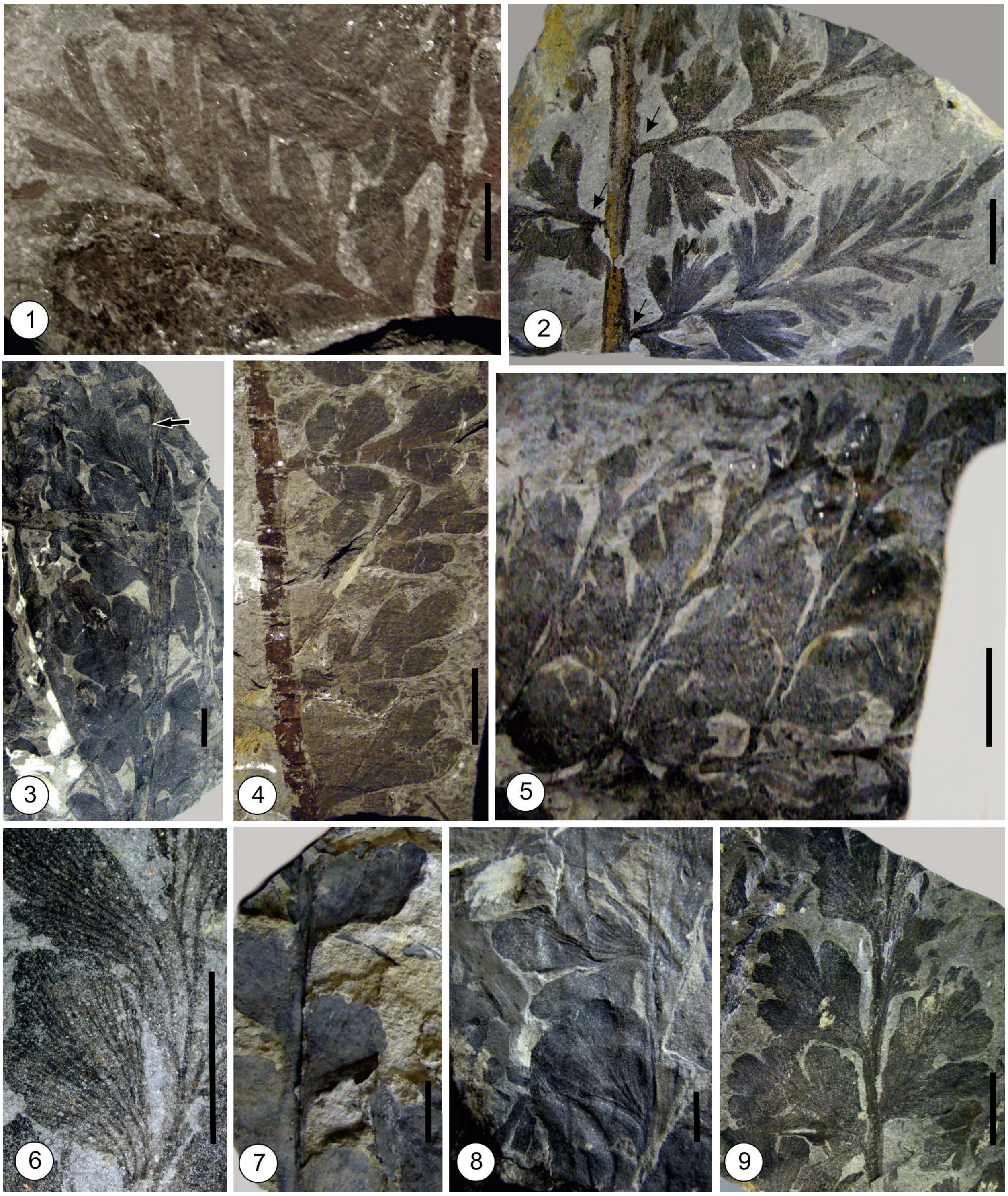

Plate 1. *Fedekurtzia argentina*. **1**. Detail of distal pinnae in specimen illustrated in Plate 2, fig. 5. Scale bar: 1 cm; **2**. Distal pinnae with apparent torsion in their insertion (arrows), bearing incised pinnules with their apices artificially truncated by preservational factors, Volcán Formation, PBSJ 1018. Scale bar: 1 cm; **3**. Trilobed basal pinnules grading to pinna with two pairs of lateral pinnules (arrow), Tupe Formation, BAFCPb 12858. Scale bar: 1 cm; **4**. Detail of basal pinnules of the specimen figured in Plate 2, fig. 2. Scale bar: 1 cm; **5**. Medial pinnae, Volcán Formation, PBSJ 1013. Scale bar: 1 cm; **6**. Detail of venation, Volcán Formation, PBSJ 1016. Scale bar: 1 cm; **7**. Basalmost pinnules, Volcán Formation, BAPb 12232. Scale bar: 1 cm; **8**. Basal pinnules, Tupe Formation, BAFCPb 12838. Scale bar: 1 cm; **9**. Trilobed basal pinnules, Volcán Formation, PBSJ 1015. Scale bar: 1 cm

distinctly lobed pinnules of a narrow base (Pl. 1, fig. 9). Trilobed basal pinnules are also identified in the specimen described by Vega (1995b) as *Triphyllopteris cuyana* (arrow in Pl. 1, fig. 4).

The first foliar laminae can be compared with heteromorphic basal elements of fern-like fronds from the Carboniferous of Europe. Cyclopteroid leaves have rounded laminae

Table 2. Measurements of the medial and distal sections in the main specimens analysed

Middle section	Main Rachis	Pinna				Basal pinnule		Apical pinnule	
Specimen	Width (mm)	Distance (mm)	Length (mm)	Width (mm)	Rachis (mm)	Length (mm)	Width (mm)	Length (mm)	Width (mm)
PBSJ 1013	1.4	17.1	48–54	26	0.85	14–17	10	13	7–10
PBSJ 1017	4.1	26	59.5	24	1	14	13	17	7–10
PBSJ 1014	2.5	16	44	15	2	10	9	10	5
BAFCPB 12821	5	25	45–90	3–3.4	1.5–2	25	13	25	5
CORD-PB 402	3	30	70	30	1.5	22	15	15	7
LP Pb 10543	2	10	28	14	1.5	11	0.75	11	6

Distal section	Main rachis	Pinna				Basal pinnule		Apical pinnule	
Specimen	Width (mm)	Distance (mm)	Length (mm)	Width (mm)	Rachis (mm)	Length (mm)	Width (mm)	Length (mm)	Width (mm)
PBSJ 1018	4	24	62	26	2	15	14	14	4–5
PBSJ 1019	2	10	40–20	7–13	1	12	7	13	4–2
BAFCPB 12837	3	22	40	20	1.2	20	8	17	2.5–3
BAPB 5331	1–2	14–20	87	25–30	1.5–2	17.5	10	13	2.5

with entire margins or dissected to irregularly lobed leaflets. Bomfleur et al. (2012) mentioned the possibility that the basal outgrowths in the Triassic fronds of *Dicroidium* are an atavistic expression of the ancestral pinnules of late Paleozoic seed-fern taxa such as *Nothorhacopteris* and *Botrychiopsis*. According to Bomfleur et al. (2012), aphlebia and/or cyclopteroid pinnules in the basal part of a *Dicroidium* frond are early leaf-ontogenetic architectural units, which are ephemeral and may be shed during ensuing leaf maturation. However, isolated aphlebia-like pinnules are rare in the assemblages from the Argentinian NBG flora.

Middle section of frond. The holotype of *Fedekurtzia argentina* (Pl. 2, fig. 3), the specimen illustrated in Plate 2, fig. 1, and the fragment of a frond formerly described as *Triphyllopteris cuyana* (Pl. 2, fig. 2) represent middle sections of fronds. Both specimens possess slight asymmetry due to the development of shorter pinnae on one side of the axis, although the three shorter pinnae on the left side of the specimen in Plate 2, fig. 2, could be attached to an axis not visible underlying the one bearing long pinnae. The holotype of *T. cuyana* (Leguizamón & Vega 1991, pl. I) and the specimen figured in Plate 2, figs 1, 2, are the larger specimens collected, reaching up to 30 cm in length.

The longest pinnae have at least five pinnules to each side of the secondary rachis. Basal anadromous pinnules may be shallowly lobed and slightly larger than the equivalent catadromous ones. The pinnules range from rounded, with margin slightly bi- or trilobed at the base of the pinna, to distally narrow, wedge-shaped, slightly bilobed pinnules. The apical pinnule is long and sub-bilobed, with the catadromous lobe smaller. The venation is dichotomous and fan-shaped (Pl. 1, fig. 6).

The holotype of *F. argentina* is a fragment of a frond not very well preserved, with the pinnules superimposed and their apical margins incomplete (Pl. 2, fig. 3), so Kurtz's illustration of the proximal pinnules is not accurate (Fig. 1).

It must be noted that the differences between *F. argentina* and *Triphyllopteris cuyana* suggested by Vega (1995b) consist in the helical insertion of the pinnae and the shape of the proximal pinnules in the first species. However, the helical insertion of the pinnae was only illustrated by Archangelsky (1981, figs 3, 4) in one small specimen. Slight torsion of the pinnae can be observed in both species as shown in Plate 1, fig. 2 and Plate 2, fig. 5, even though preservation can mask that true phyllotaxis. The proximal pinnules of the mid-section of the frond are similar in both forms; the similarity can be obscured by the insertion and preservation, which can produce superposition and damage of their apices.

Distal section of frond. The specimens illustrated in Plate 1 (figs 1, 2) and Plate 2 (figs 4, 5) represent the distal section of the frond, where the pinnae decrease in length and their pinnules increase their dissection, looking like a very packed zone with superposition of pinnules. The angle of insertion of the pinnae is more acute in this section than in the mid-section. The proximal pinnules

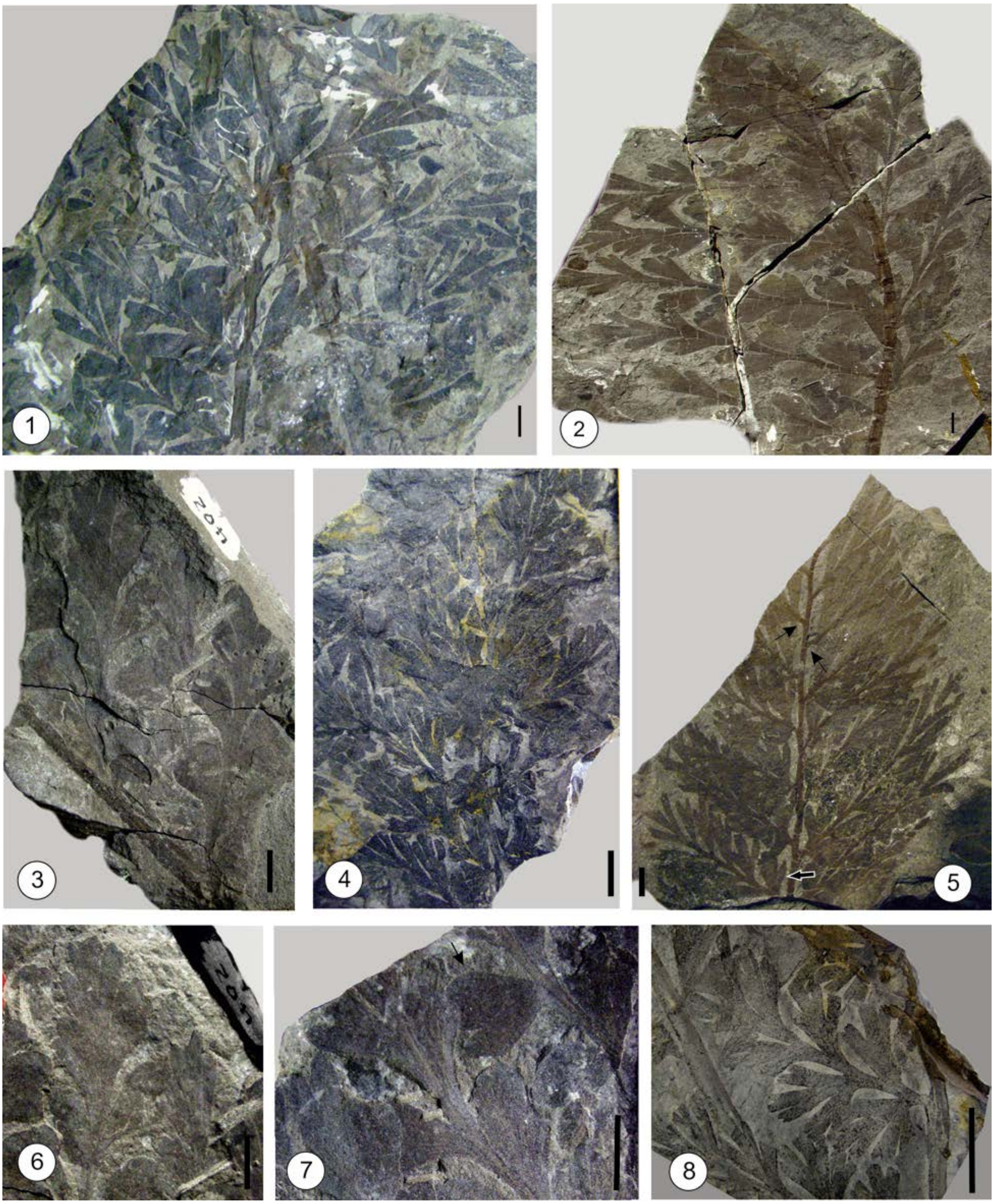

Plate 2. *Fedekurtzia argentina*. **1**. Specimen representing medial sector of frond, Tupe Formation, BAFCPb 12821. Scale bar: 1 cm; **2**. Medial frond fragment, originally described as *Triphyllopteris cuyana* by Vega (1995b), Jejenes Formation, BAPb 5330b. Scale bar: 1 cm; **3**. Lectotype, Jejenes Formation, CORD Pb 402. Scale bar: 1 cm; **4**. Distal portion of frond, Volcán Formation, PBSJ 1019. Scale bar: 1 cm; **5**. Distal sector of frond, described as *Triphyllopteris cuyana* by Vega (1995b), Jejenes Formation, BAPb 5331, white arrow indicates proximal pinnule; black arrows indicate small torsion in insertion of pinnae. Scale bar: 1 cm; **6**. Lectotype. Detail of distal pinnules, Jejenes Formation, CORD Pb 402. Scale bar: 1 cm; **7**. Lectotype. Detail of slightly bilobed pinnule, Jejenes Formation, CORD Pb 402. Scale bar: 1 cm; **8**. Incised pinnules, Volcán Formation, PBSJ 1017. Scale bar: 1 cm

are trilobed, with the central lobe commonly slightly dissected and the lateral lobes sometimes also slightly dissected. The distal pinnules are sub-bilobed and resolve at the apex with a long, wedge-shaped apical pinnule of the bilobed margin. These examples are similar to the specimen illustrated by Césari (1986, pl. 2, fig. 3) from the Tupe Formation.

The specimens illustrated in Plate 1 (figs 1, 2, 5) show how differences in preservation change the shape of the pinnules: although the outline of the pinnules is rounded in Plate 1, fig. 1, the pinnule margin is slightly covered or broken, making it appear to be straight and rough-looking in Plate 1, fig. 2. The fragment originally identified by Kurtz (1921) as *Sphenopteris fonsecae* Kurtz looks similar to pinnules of *Fedekurtzia argentina* when poorly preserved.

Microsporangiate specimens. A revision of specimen LPPB 10519 (Pl. 3, fig. 5), from Mendoza Province described by Archangelsky (1981) as a fertile fragment of a frond allowed us to make a new interpretation of these plant remains. There are three incomplete pinnae aligned so that they seem to emerge from a rachis (Pl. 3, fig. 5), which is not preserved and should be located to the bottom of the figure. The fusiform sporangia are preserved close to a robust rachis (arrow in Pl. 3, fig. 8) disconnected from the pinnae; they are closely grouped and aligned at the apex of a short bifurcate axis, numbering at least fifteen. Other masses of sporangia appear isolated on the matrix; the sporangia are fusiform, 3.2–2 mm long and 0.6–0.8 mm wide, and finely striated helically (Pl. 3, fig. 10). This new analysis of the specimen questions the suggestion that the fertile structures arise laterally from the same main rachis bearing pinnae, as has been proposed (Archangelsky 1981, Carrizo & Archangelsky 2013). However, the sporangia and arrangement are similar to those described by Vega (1995a) and Vega & Archangelsky (2001) as *Rinconadia archangelskyi* in association with *Triphyllopteris* fronds.

We consider the specimens of *Rinconadia archangelskyi* illustrated by Vega (1995a) and Vega and Archangelsky (2001) to be fertile specimens of *Fedekurtzia argentina*, owing to the similarity of the foliar region and the frequent occurrence of such fertile structures associated with frond fragments (Césari et al. 2001, Coturel & Gutiérrez 2005). The vegetative part of the holotype of *Rinconadia archangelskyi* (Pl. 3, fig. 1) is bipinnate, with two subopposite basal pinnae or pinnules. One of them preserves two anadromic pinnules and a narrow apical pinnule with the apex slightly bilobed. On the other side of the rachis is a rounded pinnule slightly lobed into at least four lobes. The upper pair of pinnae bears three

Fig. 2. Reconstruction of *Fedekurtzia argentina* (Kurtz) Archangelsky emend. Scale bar: 1 cm. Sporangia out of scale

pinnules on each side of the secondary rachis, and an elongate apical pinnule. The pinnules are wedge-shaped and the first basal catadromic pinnule is apically bilobed. Apically, the main axis bifurcates twice, bearing at the apex sporangial masses with fusiform sporangia 1–1.7 mm long and 0.3–0.8 mm wide. The vegetative sector of the holotype conforms to the reconstruction proposed here for *F. argentina*.

Archangelsky and Archangelsky (1987) also illustrated groups of sporangia associated with specimens of *Fedekurtzia argentina* from the Tramojo Formation (Mendoza Province). Césari et al. (2001) described a specimen of *Rinconadia* in close association with *F. argentina* from the Trapiche Formation, which has excellent preservation allowing recognition of four successive dichotomies in each lateral branch, and recovery of spores from the sporangia (Pl. 3, fig. 2). The trilete spores sculptured by small grana (Pl. 3, fig. 9) are similar to those obtained from many lyginopterid seed ferns (see Orlova et al. 2009, Serbet et al. 2016) and considered to be prepollen by Stewart and Rothwell (1983). These spores, when dispersed, have been assigned to *Cyclogranisporites rinconadensis* Césari & Limarino,

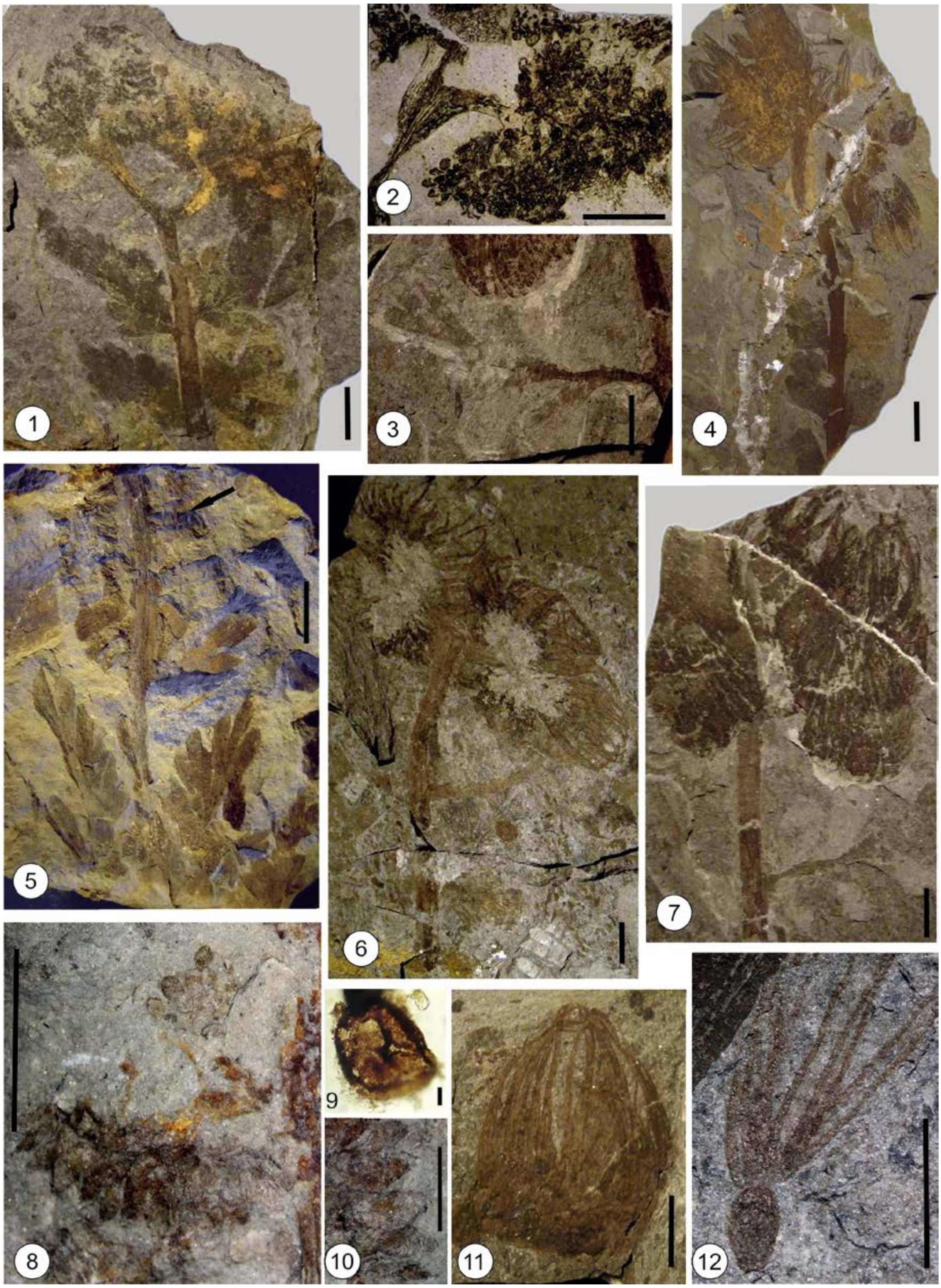

Plate 3. **1**. Holotype of *Rinconadia archangelskyi* Vega, Jejenes Formation, BAPb 5348. Scale bar: 1 cm; **2**. Detail of *Rinconadia archangelskyi* Vega, showing group of sporangia, Volcán Formation, BAPb 12235. Scale bar: 5 mm; **3**. Detail of fig. 3, showing pinna with elongate pinnules. Scale bar: 1 cm; **4**. Specimen described by Vega & Archangelsky (2001) as *Poycalyx laterale*, with trilobed basal pinnules and distal ovulate organs, Jejenes Formation, BAPb 5363. Scale bar: 1 cm; **5**. Specimen preserving groups of sporangia (arrow) described by Archangelsky (1981), Santa Máxima Formation, LP Pb 10519. Scale bar: 1 cm; **6**. Holotype of *Polycalyx laterale*, Jejenes Formation, BAPb 5364. Scale bar: 1 cm; **7**. Specimen described by Vega & Archangelsky (2001) as *Polycalyx tetramera*, Jejenes Formation, BAPb 5362. Scale bar: 1 cm; **8**. Detail of 5, showing a short forked axis bearing fusiform sporangia. Scale bar: 1 cm; **9**. Trilete spore recovered from the sporangia illustrated in Fig. 2. Scale bar: 10 µm; **10**. Detail of sporangia in Fig. 8. Scale bar: 3 mm; **11**. Small ovuliferous organ with distal long and narrow lobes, Jejenes Formation. BAPb 5366. Scale bar: 1 cm; **12**. Small ovule with long distal Jejenes Formation, described by Vega (1995b), BAPb 5346. Scale bar: 1 cm

a component of palynofloras from central-western Argentina (Césari & Limarino 2002).

The sporangiate organ of *Genselia uberis* (Skog & Gensel) Knaus is similar to *Rinconadia* in its apical position and attachment to bifurcated axes. As in *Rinconadia* specimens, the fertile branch has immature or characteristic pinnules of basal fronds with few lobes per pinna.

Diplopteridium teilianum Walton, a member of the Lyginopteridaceae, bears sporangia at the apex of dichotomously branched axes, resembling the structure of *Rinconadia*, but the architecture of the bifurcate frond is different (see Walton 1940). The *Rinconadia* pollen organs are also similar to some species of *Pteruchus* Thomas, the most common reproductive structure of Triassic Corystospermales, which have alternately arranged microsporophylls attached to an axis and bearing elongate pollen sacs with bisaccate pollen grains. Although *Rinconadia* lacks a distinctive narrow microsporophyll lamina, the pattern of organization is comparable. Moreover, similarities are recognized with the peltasperm organ *Antevsia* Harris, which includes branched axes that bear groups of elongate pollen sacs at their distal tips. These pollen organs contain monosulcate grains.

Ovulate specimens. The first female fertile organs associated with *Fedekurtzia* were described by Gutiérrez (1994) from the Agua Colorada and Tupe formations in the Paganzo Basin. One specimen from the same locality (La Cortadera creek) where Césari (1986) recovered the complete fronds of *F. argentina* (Pl. 2, figs 1, 4) preserves an orbicular laminar structure with a narrow base and the apex divided into narrow and long lobes. Scars of possible attachment of oval ovules are aligned over the lower part of the lamina. The finding of ovules attached to this type of structure by Vega and Archangelsky (1997) validated the interpretation given by Gutiérrez (1994) as female reproductive organs.

Vega and Archangelsky (1997) reported the finding of compound cupulate receptacles in organic connection with a rachis bearing pinnae with wedge-shaped to obovate pinnules. The rachis forks apically, bearing bivalve cupules (Pl. 3, figs. 4, 6, 7) encircling oblong ovules with long and narrow distal integumentary lobes. These authors described the vegetative frond as "triphyllopteroid", and it is worth noting that the sample comes from the type locality of *Fedekurtzia argentina*. Later, Vega and Archangelsky (2001) established the genus *Polycalyx* to encompass these female structures. Revision of the vegetative pinnae associated with *Polycalyx*, according to the reconstruction presented here, allows us to assign them to *Fedekurtzia argentina*. The vegetative parts of *Polycalyx* show lobate pinnules similar to those of *F. argentina* fronds (Pl. 3, figs 3, 4).

However, two species of *Polycalyx* were distinguished by Vega and Archangelsky (2001): *P. laterale* and *P. tetramera*, according to the presence of two or four apical multiovulate organs. In our analysis of fertile specimens we identified four laminar structures with a rounded base and deeply laciniate in their distal part. The specimen illustrated as *P. laterale* in Vega and Archangelsky (2001, pl. 1, fig. 1) has a main rachis which divides at a wide angle into two short axes bearing rounded, deeply laciniate, laminar receptacles. The right secondary axis (Pl. 3, fig. 6) seems to divide once more, and each division bears a laminar structure according to the orientation of the long lobes. On the counterpart of this specimen can be seen the ovules and their points of insertion arranged in the same concentric pattern observed by Gutiérrez (1994) in specimens from the Tupe Formation. Vega and Archangelsky (2001, pl. 2, fig. 3) illustrated another specimen showing only two ovulate structures but the other two may be buried in the matrix.

The platyspermic ovules described by Vega and Archangelsky (2001) in the ovulate structure have long apical lobes as well as dispersed ovules associated (Pl. 3, fig. 12) that resemble *Jejenia alata* Vega and Archangelsky, which preserves some internal structural information (Vega & Archangelsky 2000).

Vega and Archangelsky (2001) interpreted the drooping multiovulate organs as rigid and globose cupules, but these leaf-like reproductive receptacles are usually preserved split into flat valves (Pl. 3, fig. 11). We find it difficult to suppose that the small pinnae would support large, heavy, fleshy structures. Moreover, the flattened and leaf-like features of *Polycalyx*, its unusually large size and the ovules embedded on one side (apparently the adaxial surface) suggest that it should be interpreted as a megasporophyll rather than a cupule, which implies a set of structures surrounding one or more ovules or seeds (Taylor et al. 2009).

As well as in *Rinconadia*, the pinnules attached to the main axis of *Polycalyx* represent the basal to mid-sections of *Fedekurtzia*'s frond, suggesting that reproductive structures could be developed on young plants. The specimens illustrated in Plate 3 resemble the architecture of the extant fern *Botrychium boreale* Milde, which was also compared by Kurtz (1894) with *Botrychiopsis*, a closely related Gondwanan frond.

Associated stems. Anatomically preserved stems have been described from the same deposits from which the holotype of *Fedekurtzia argentina* and fertile specimens were recovered. Césari et al. (2005) described *Amosioxylon australis*, a single stem 6 cm in diameter with several vascular segments surrounded by secondary xylem. The primary xylem is two- or three-ribbed and the rays are heterocellular, with tracheids having reticulate or spiral thickenings. The tissue between the vascular strands shows reticulate thickenings. The pycnoxylic wood is characterized by triseriate-bordered pitting of the tracheids in the tangential and radial walls; the cross-fields show 5–10 simple circular pits. The presence of transverse tracheids was also recognized in *Callixylon* by Beck (1970), and suggests shared characters with the progymnosperms. However, the presence of more than one vascular strand, which is considered a primitive character, also promotes comparisons with early pteridosperms.

Associated palynological assemblages. Gutiérrez and Césari (1987) reported a poorly preserved palynological assemblage from the same levels of the Jejenes Formation bearing original specimens of *Fedekurtzia argentina* in the San Juan Province. Monosaccate pollen predominates, represented by *Plicatipollenites malabarensis* (Potonié & Sah) Foster, *Potonieisporites novicus* Bharadwaj, *Caheniasaccites* sp. and *Crucisaccites* sp., together with subordinate spores which include *Lundbladispora braziliensis* (Pant & Srivastava) Marques-Toigo & Pons. The presence of pollen grains supported the inferred Bashkirian-Moscovian age of the unit. Nearby fossiliferous outcrops of the Jejenes Formation provided palynofloras studied by González Amicón (1973), Gutiérrez and Césari (1987) and Césari and Bercowski (1997), characterized also by abundant pollen and more diverse spores. All these palynofloras have been included in the *Raistrickia densa*/*Convolutispora muriornata* Biozone (DM) defined by Césari and Gutiérrez (2000).

Similarly, specimens of *Fedekurtzia argentina* from the Tupe Formation are associated with palynological assemblages studied by Césari (1985), which characterize Subzone B of the *Raistrickia densa*/*Convolutispora muriornata* (DM) Biozone.

COMPARISONS

Coeval Pennsylvanian floras from Australia are characterized by the so-called enriched *Nothorhacopteris* flora or *Sphenopteridium* flora by Morris (1985) or *Nothorhacopteris argentinica*/*Fedekurtzia* floras by Rigby (1985). These are characterized by *N. argentinica*, *Fryopsis frondosa* (=*Cyclopteris* sp. *sensu* Rigby), *Botrychiopsis ovata*, *Dactylophyllum digitatum* (=*Fedekurtzia intermedia sensu* Rigby) and *Sphenopteridium* sp. The last three species are bipinnate fronds with a leafy footstalk, and occur associated with fertile organs described as *Dictyothalamus* by Morris (1985). Unlike the palaeoenvironmental conditions in Argentina, this Australian flora underlies glacial deposits.

Among those species, *Fedekurtzia intermedia* (Feistmantel) Rigby is most comparable to *F. argentina*. The original specimen figured by Feistmantel (1878, pl. 2, fig. 2; 1890, pl. IV, fig. 3), although lost, is similar to the basal section of *F. argentina*. The neotype selected by Rigby (1973) resembles distal pinnae of *F. argentina*, even though the pinnules would be slightly buried in the sediment. Rigby (1973) remarked that pinnules are better preserved in the specimen illustrated in his plate 3, figure 11b. Other specimens synonymized with *F. intermedia*, such as *Rhacopteris septentrionalis* Feistmantel and *Archaeopteris wilkinsoni* Feistmantel, are also closely comparable to mid- and distal sections of *F. argentina* according to the reconstruction presented here (Fig. 2). New specimens from the Australian flora need to be analysed in order to confirm the relationship between *F. intermedia* and *F. argentina* fronds.

Specimens illustrated by Morris (1975, 1980) as *Triphyllopteris austrina* have been reassigned to *Botrychiopsis* by Rigby (1985), Archangelsky (1983) and Iannuzzi and Pfefferkorn (2002), or with doubts to *Fedekurtzia* by Archangelsky (1981). Archangelsky (1981) was the first to consider that the original specimen of *Aneimites austrina* Etheridge (1888) figured by Rigby (1973, pl. 1, fig. 2) corresponds to *Botrychiopsis plantiana* (Carruthers) Archangelsky & Arrondo. Iannuzzi and Labandeira (2008) illustrated frond fragments that conform in part to *Triphyllopteris austrina*, from the same locality where Morris (1975, 1980) reported the species, and concluded that they and the holotype of *Aneimites austrina* Etheridge should be excluded from *B. plantiana* and *F. argentina*. Specimens illustrated by Iannuzzi and Labandeira (2008) as *T. austrina* "minor form" are similar to medial pinnae of *F. argentina* but the pinnules differ in their entire apical margins apparently being diminutively crenulate.

Similar foliage from the Peruvian Paracas flora (late Visean to early Serpukhovian in age) was described by Iannuzzi and Pfefferkorn (2002). In that flora, *Sphenopteridium* sp. is represented by a bipinnate fragment with a robust axis bearing pinnules irregularly and deeply subdivided into wedge-shaped segments. Although fragmentary, the pinnules resemble distal sections of *F. argentina*. These authors also described the presence of *Triphyllopteris boliviana* with small pinnules with many lobes, which are different even from the more laciniate pinnules of the Argentinian species.

Botrychiopsis weissiana is another Argentinian taxon applied to identify comparable Pennsylvanian fronds, related to cold palaeoenvironmental conditions (Jasper et al. 2003). Unfortunately, the holotype from the Retamito locality (Jejenes Formation) is a bipinnate fragment with the pinnules partially buried in the sediment, obscuring their complete outline (Archangelsky & Arrondo 1971, pl. 2, fig. 4). This specimen coincides in its dimensions and morphology with a more complete sample from the Tupe Formation at the Mina La Negra locality (Archangelsky & Arrondo 1971, pl. 4), which allows a more precise characterization of the genus. According to Archangelsky (1981), *Fedekurtzia* differs from *Botrychiopsis* because "*Botrychiopsis* never have truly bipinnate fronds (at most they are imperfectly bipinnate); pinnules have fused bases, entire margins, and are more rounded."

Despite the abundance of *Botrychiopsis weissiana* specimens in the Carboniferous of Argentina, the structure of its frond was not reconstructed up to now. Two sectors can be differentiated in *Botrychiopsis* fronds: the basal, with rounded and entire pinnules fused with the main rachis through a narrow wing; and the mid- and upper sections, with regular, 5-pinnule rounded symmetrical pinnae. There is no development of a distinctive pinnae rachis along the frond and each pinnule is rounded and broadly inserted, and even though the pinnules tend to be subtriangular they are attached broadly. The apical pinnule is larger, spathulate, and with an entire margin (Fig. 3).

The most conspicuous character to differentiate *Botrychiopsis weissiana* from *Fedekurtzia* pinnae is that the first genus shows a broad basal insertion of the pinnae and pinnules, which are rounded with an entire and regular margin, whereas even the most rounded pinnules from *Fedekurtzia* have at least an incision and/or irregular apical margin. A close relationship between *Botrychiopsis* and *Fedekurtzia* is suggested by the degree and types of shape differences between these two foliage genera, variation that is comparable to that seen among some species of the extant fern genus *Botrychium* (e.g. *Botrychium boreale* Milde, *Botrychium pinnatum* St. John). Moreover, fragments of *Rinconadia* have been described in close association with *B. weissiana* pinnae (Artabe et al. 1987, Césari & Limarino 1988).

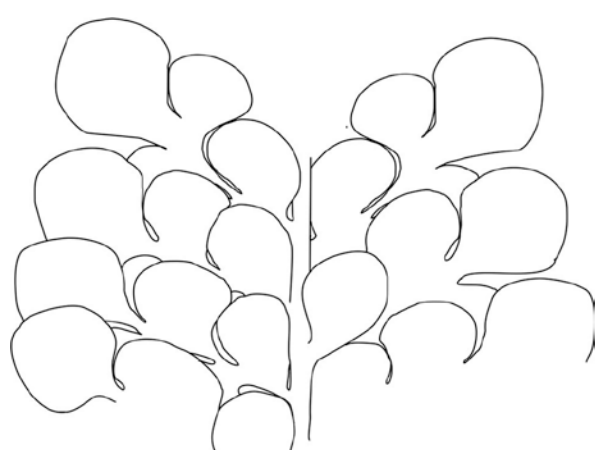

Fig. 3. Reconstruction of medial pinnae of *Botrychiopsis weissiana* Kurtz emend. Archangelsky & Arrondo. Scale: 1 cm

Fedekurtzia argentina differs from the North American tryphyllopteroid *Genselia* Knaus in the presence of cyclopteroid basal elements, the regular spacing between pinnae along the rachis, the intra-pinna heteromorphy, the continuous presence of rough or incised pinnules, and the absence of a distinctive rachis in the pinnae of the basal and medial sections of the frond. The overall tendencies of pinnule incision and the diminishing heteromorphy along the frond are considered enough to maintain the separation between these genera.

Thus, the Austrocalyxaceae are now interpreted as pteridosperms, which include monopinnate and heteromorphic bipinnate fronds (*Nothorhacopteris*, *Fedekurtzia* and, probably, *Botrychiopsis*). The fertile fronds have the main rachis, unforked or distally forked, bearing apical reproductive structures. Megasporangiate fronds bear cupule-like laminar structures with a rounded base and distally laciniated (*Polycalyx*, *Austrocalyx*), with ovules inserted on the adaxial and proximal surface of each lamina. The dispersed ovules have elongate apical integumentary lobes. Microsporangiate fronds are composed of multiply dichotomized axes forming clouds of fusiform sporangia (*Rinconadia*); the recovered prepollen is trilete with small grana (*Cyclogranisporites*-type).

CONCLUSIONS

Our revision of some Argentinian Carboniferous fronds and the associated reproductive organs confirms the absence of the genus *Tryphyllopteris* in southern Gondwana. The palaeogeographic distribution of this type of foliage is represented by *Tryphyllopteris* in Europe, *Genselia* in North America, and *Fedekurtzia* on the western and eastern margins of Gondwana. Despite their foliar similitude, their relationship and botanical affinities should be corroborated with the findings and a comparison of their reproductive structures.

Although the fronds of *Botrychiopsis* are certainly different from those of *Fedekurtzia*, some dispersed pinnae of both genera can be erroneously referred to any one of the genera. We conclude in this study that the most conspicuous characters to differentiate these pinnae are both the nature of the margin and the shape of the pinnule, being entire and rounded in *Botrychiopsis*, whereas a notched margin having at least one incision is seen in the wedge-shaped pinnules of *Fedekurtzia*. It is likely that *Botrychiopsis* belongs to Austrocalyxaceae, in view of its association with *Rinconadia* remains and the foliage variation within *Fedekurtzia*'s fronds.

Two taxa, *Polycalyx* and *Rinconadia*, are interpreted as fertile organs of *Fedekurtzia* according to the foliage in organic connection. In the revision of the ovulate organs we addressed the nature of the leaf-like structure containing the ovules, which was originally interpreted as a large and globose, fleshy, cupulate organ, but it is proposed here that the structure could be described as a flattened megasporophyll-like receptacle.

The architecture of the different fossil genera (*Nothorhacopteris*, *Fedekurtzia*, *Botrychiopsis*) associated with the Austrocalyxaceae suggests that they were small bushes with reproductive structures growing in different ontogenetic plant stages.

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