



General Palaeontology, Systematics, and Evolution (Palaeobotany)

Leafy branches of *Gangamopteris* from the Gzhelian–Asselian of westernmost Gondwana



Branches feuillues de Gangamopteris du Gzhelian–Assélien à l'Extrême-Ouest du Gondwana

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ABSTRACT

The first reconstructions of glossopterids interpreted this Gondwanan group as arborescent, deciduous plants, with leaves and reproductive structures inserted on short shoots, which were arranged on long branches. The leaves are its most abundant organ in the fossil record, but they are mainly found isolated. The arrangement of the leaves as terminal whorls or tight spirals has been the most accepted phyllotaxis hypothesis. The few examples of leaf impressions preserved in connection with axes correspond mainly to leaves of *Glossopteris* Brongniart, and mostly without clear evidence of the type of insertion. Several specimens of *Gangamopteris* McCoy leaves attached to axes from the Bajo de Véliz Formation (Latest Carboniferous–Earliest Cisuralian) facilitate reconstruction of the foliar arrangement of the genus, to date known mostly from isolated leaves. The available evidence from the new specimens confirms a variation from well-spaced to dense helical insertion of the leaves without forming true whorls, and discards the early notion that they were mainly clustered apically on short shoots in a similar manner to the extant Ginkgoales.

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RÉSUMÉ

Les premières reconstructions de glossoptéridés ont interprété ce groupe de Gondwana comme des plantes à feuilles caduques, arborescentes, avec des feuilles et des structures reproductrices insérées sur de courtes pousses, disposées sur de longues branches. Les feuilles sont son organe le plus abondant dans les archives fossiles, mais elles se trouvent principalement isolées. La disposition des feuilles en tours ou en spirales serrées a été l'hypothèse de phyllotaxie la plus prônée. Les quelques exemples d'empreintes de feuilles conservées en liaison avec des axes correspondent principalement à des feuilles de *Glossopteris* Brongniart et la plupart du temps sans preuve claire du type d'insertion. Plusieurs spécimens de feuilles de *Gangamopteris* McCoy attachés à des axes provenant de la formation Bajo de Véliz (Carbonifère tardif–Cisuralien précoce) facilitent la reconstruction de la disposition foliaire du genre, connue à ce jour principalement à

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partir de feuilles isolées. Les preuves disponibles sur les nouveaux spécimens confirment une variation d'insertion hélicoïdale des feuilles bien espacée à dense sans former de véritables verticilles, et conduisent à abandonner l'idée initiale selon laquelle elles étaient principalement regroupées de manière apicale sur de courtes pousses, de la même manière que les Ginkgoales existantes.

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1. Introduction

The glossopterid leaves are probably the most known and studied Late Paleozoic plant remains from Gondwana (see McLoughlin, 2011; Srivastava and Srivastava, 2016). They are usually preserved detached as impressions, in some cases forming banks of leaves, which have been interpreted as autumnal deposits from deciduous plants (Plumstead, 1958). Evidence of phyllotaxis in glossopterid plants is rare, especially in *Gangamopteris* McCoy, which represents one of the earliest members of the group. New specimens with leaves attached to stems from westernmost Gondwana provide new information about the arrangement of gangamopterid leaves on the branches. The fossils come from the Bajo de Véliz Formation at the Bajo de Véliz locality (Paganzo Basin) in Argentina (Fig. 1), which preserves abundant fossils including plant remains, palynomorphs and insects.

Kurtz (1895) first reported the palaeontological richness of the Bajo de Véliz Formation. The floristic assemblage is referred to the Argentinian *Gangamopteris* flora, considered to be of early Cisuralian age based on correlations with other South American assemblages and dating via other fossil groups (Archangelsky et al., 1987). The formation contains impressions of leaves identified as *Gangamopteris obovata* (Carruthers) White (Archangelsky et al., 1995), *Glossopteris wilsonii* Seward (Cúneo, 1984), *Vélizia inconstans* Césari et Hünicken (Césari and Hünicken, 1992), *Cheirophyllum speculare* Césari et Cúneo (Césari and Cúneo, 1990), *Euryphyllum whittianum* Feistmantel (Leguizamón, 1979) and *Botrychiopsis plantiana* (Carruthers) Archangelsky et Arrondo (Archangelsky and Arrondo, 1971), together with lycopods similar to the northern Chaloneriaceae (Césari et al., 1995), the sphenopsids *Stephanophyllites sanpaulensis* Césari et Hünicken (Césari and Hünicken, 1991), *Tschernovia* Zalesky, *Phyllothea* Brongniart and *Giridia* Pant et al. (Durán et al., 1997), and undescribed coniferophyte leafy twigs. Its age has been debated because fossil plants suggest an Earliest Permian age whereas the insects were considered to be Late Carboniferous in age (Hünicken et al., 1981; Pinto and Hünicken, 1980; Selden et al., 2005).

Palynological associations studied by Menéndez (1971), Gutiérrez and Césari (2000) and Césari and Chiesa (2017) include taeniate pollen (up to 6.5%), such as *Pakhapites fusus* (Bose et Kar) Menéndez, *Hamiapollenites fusiformis* Marques-Toigo emend. Archangelsky et Gamarro, *Protohaploxylinus* spp., *Vittatina* spp. and *Weylandites magmus* (Bose et Kar) Backhouse. Correlation with other palynofloras from Brazil and Uruguay supports a Latest Carboniferous age (Gzhelian) – Earliest Cisuralian age (Césari, 2007; Césari and Chiesa, 2017; Césari et al., 2011).

2. Materials and methods

The outcrops of the Bajo de Véliz Formation (32°17'S;65°24'W; San Luis Province) are located 25 km west of Santa Rosa city (Fig. 1). The unit is divided into the Cautana, Pallero and Lomas members in ascending stratigraphic order and the fossil remains are concentrated in the Pallero Member. The studied material includes well-preserved impressions from lacustrine sediments deposited during a postglacial stage (Limarino et al., 2014). The specimens are stored in the collections of the Interactive Science Museum “CONTACTO” (MIC-P) National University of San Luis, National Academy of Sciences in Córdoba (CORD-PB) and the University of Buenos Aires (BAFC-PB). The description of the areolas follows the proposal of Tybusch and Iannuzzi (2008); and the angle of curvature or degree of arching is described following McLoughlin (1994a), considering a midline of the leaf instead of the midrib. This angle was measured in the upper middle part of the leaf. Some selected detached leaves are also described, showing details of venation and size variability.

3. Systematic paleontology

Gangamopteris McCoy, 1875

Type species. *Gangamopteris angustifolia* McCoy, 1875

Gangamopteris obovata (Carruthers) White, 1908

Holotype. *Noeggerathia obovata*, Carruthers, 1869, Plate 4, fig. 1.

General description. Leaves obovate, apex rounded, margin entire, bases arranged in spaced or dense helices on the axes. Veins subparallel at the base, giving rise to arched veins that intersect the margins at acute angles. Degree of arching diminishing towards the apex, varying from ≤ 5 to 18° in the middle part of the lamina. Venation dichotomizing with rare anastomoses and elongate, narrow meshes. Vein concentration is about 13–18 per centimeter in the middle part of the lamina.

3.1. Leaves attached to stems

At least two clusters of leaves, closely attached helically to an axis of 0.9 cm in width (Fig. 2A–D), are preserved on the specimen CORD-PB 3331 (a–b). The leaves are obovate, with rounded apices, attenuate bases, and entire margins. Their sizes range from 5 to 11.3 cm in length and 1.8–3.6 cm in maximum width. Venation is dichotomously branched and anastomosed forming elongate meshes, arising from the base and median line of the leaf; veins are arcuate

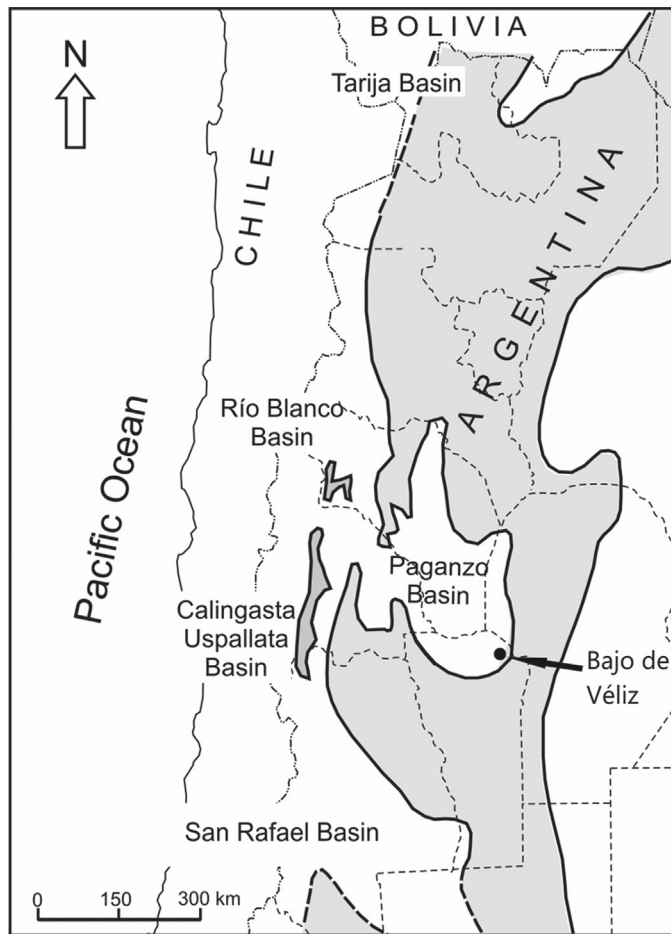


Fig. 1. Map of northwestern Argentina showing the location of the Bajo de Véliz locality.

Fig. 1. Carte du Nord-Ouest de l'Argentine, indiquant l'emplacement de la localité de Bajo de Véliz.

(degree of arching $5\text{--}17^\circ$ in the upper middle part of the leaf), intersecting the margin at acute angles. In the central leaf portion, there are 16 veins per centimeter.

The specimen CORD-PB 2827 (Fig. 3A–B) provides evidence of the helical arrangement of leaves. It represents an axis 14.8 cm long and 0.7 cm wide, which preserves sub-circular or crescent-shaped leaf scars on its leafless lower part. At the top, obovate leaves are arranged in pseudo-whorls. Leaves are up to 5.8 cm long and 2 cm wide, with 17 veins per centimeter in the central leaf portion, which dichotomize and form elongate meshes mainly towards the margins. Meshes are of variable length, with oblique contacts. The venation emerges sub-parallel from the base and curves towards the margin (degree of arching $6\text{--}17^\circ$) intersecting it at acute angles.

Spaced arrangement of leaves is shown in specimen CORD-PB 2932 (Fig. 3C–D), which preserves an axis 9.5 cm long and 0.7 cm wide with helically inserted, alternate, obovate leaves. The more entire leaf is 12 cm long and up to 5.2 cm wide with a narrow base. Veins radiate from the base and are curved towards the margins ($\leq 5\text{--}18^\circ$), which intersect at about 23° . Some dichotomies and anastomoses are observed forming meshes with an oblique contact at

the margins. Vein concentration is 16 veins per cm in the central leaf portion.

A long axis (15.5 cm) of 0.5–0.7 cm in diameter (CORD-PB 2941a–b) preserves some leaves (up to 5 cm long and 1.7 cm wide) with narrow and elongated bases (Fig. 4A, C). The venation, although poorly preserved, emerges sub-parallel from the base and curves at an angle of 15° towards the margins in the medial area of the leaf. Dichotomous veins anastomose and form meshes of small size with oblique contacts, with a density of 16 veins per cm.

Specimen CORD-PB 3000 (Fig. 4B) resembles those described by Rigby (1967) as *Gangamopteris walkomii* Rigby represented by tufts of leaves of different sizes attached to branches. Small and complete leaves of 3.4–2.9 cm in length and 1.6–1.4 cm in maximum width are preserved. Where complete, they have an obovate shape, entire margins, rounded apices, and elongated, narrow bases. Veins arise subparallel from the base in the central part of the leaf and arch towards the margins (degree of arching $8\text{--}11^\circ$) intersecting them at acute angles. Dichotomous veins are common near the margins but rare near the mid-line of the leaf; anastomoses form longitudinally elongated meshes with oblique type contacts, and some in X-type

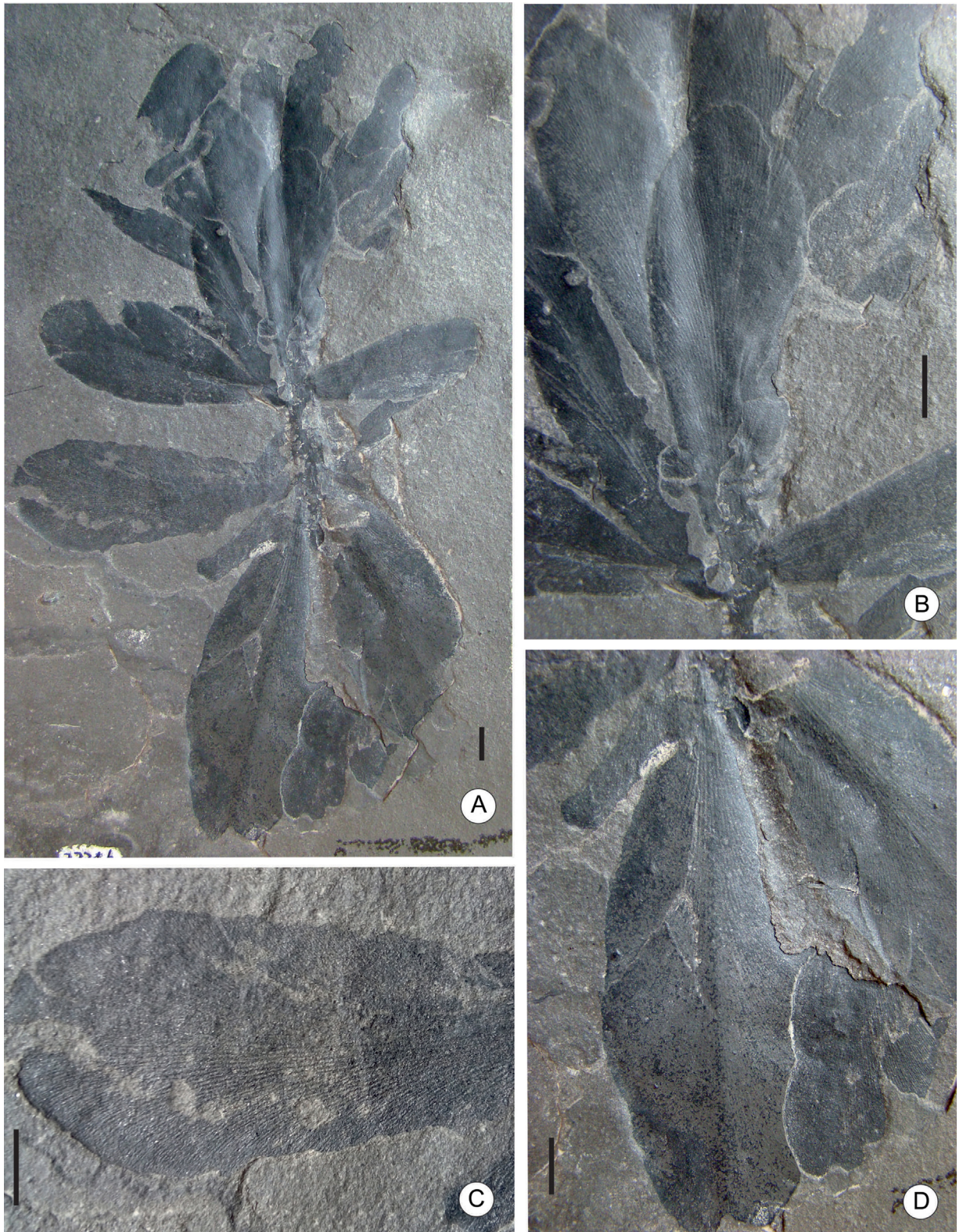


Fig. 2. *Gangamopteris obovata*. CORD-PB 3331. A. General view showing two clusters of leaves attached to the axis. B–D. Detail of the leaves and venation. Scale = 1 cm.

Fig. 2. *Gangamopteris obovata*. CORD-PB 3331. A. Vue générale montrant deux groupes de feuilles attachées à l'axe. B–D. Détail des feuilles et des veines. Échelle = 1 cm.

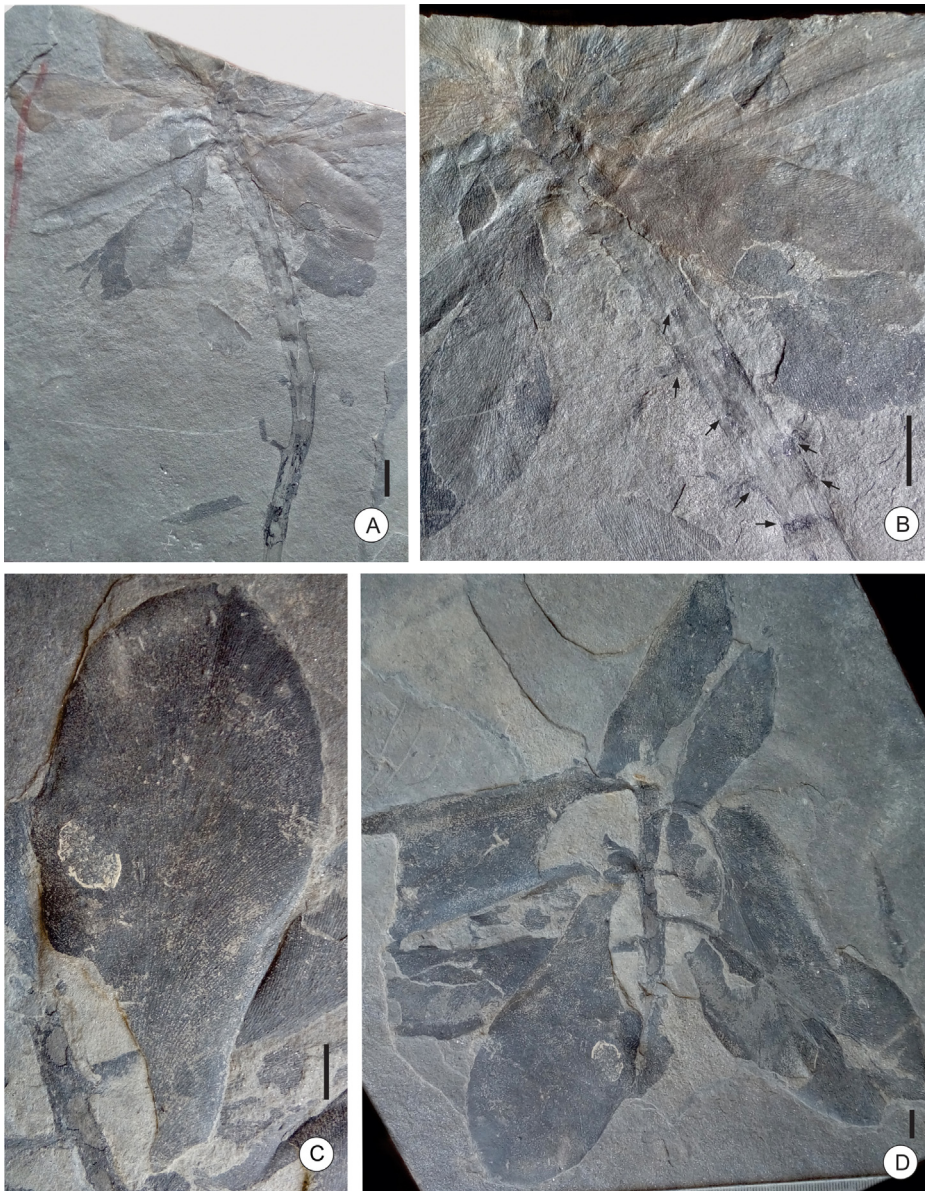


Fig. 3. *Gangamopteris obovata*. A. View of the long axis bearing leaves distally, CORD-PB 2827. B. Detail of leaves and axis illustrated in 1 and leaf scars (arrows). C. Detail of a leaf in specimen CORD-PB 2932. D. Leaves arranged helically on the axis by narrow bases, CORD-PB 2932. Scale = 1 cm.

Fig. 3. *Gangamopteris obovata*. A. Vue du grand axe portant des feuilles en position distale, CORD-PB 2827. B. Détail des feuilles et de l'axe illustrés en 1 et cicatrices des feuilles (flèches). C. Détail de la feuille dans le spécimen CORD-PB 2932. D. Feuilles disposées en hélice sur l'axe par des bases étroites, CORD-PB 2932. Échelle = 1 cm.

arrangement. Vein concentration is up to 9 per 5 mm in the central leaf portion. This specimen, similarly to the Australian representative of *Glossopteris walkomii*, can be interpreted as unexpanded leaves of a new season's flush of leaves (McLoughin, 2011).

An unusual specimen (a possible seedling or young plant?) is a slender and flexuous axis 18 cm long, 0.8 cm wide at the base, and 0.4 cm wide in the distal part (Fig. 4D). At least five attached short leaves are preserved at the distal end of the stem, in a pseudo-whorl arrangement. Leaves are incomplete, 4.8–5.7 cm long and 1.9–3.1 cm wide. They are apparently oval to elliptic, with acute apex probably as a

result of deficient preservation. The venation emerges from the base and curves towards the margins intersecting them at 17° in the middle area. Dichotomies and anastomoses of "oblique" type contact are common in the basal-marginal region of the leaf. Vein concentration is up to 13 per cm in the central leaf portion.

A widely spaced spiral phyllotaxis seems to be represented in specimen BAFC-PB 16735 (Fig. 5B–C). The axis is 26 cm long and 1.5 cm wide and bears well-spaced leaves of variable sizes: the largest is 12.3 cm long and 4.6 cm wide, whereas the smallest is 6.7 cm long and 2.4 cm wide. The leaves are oval-spatulate, with incomplete margins, and

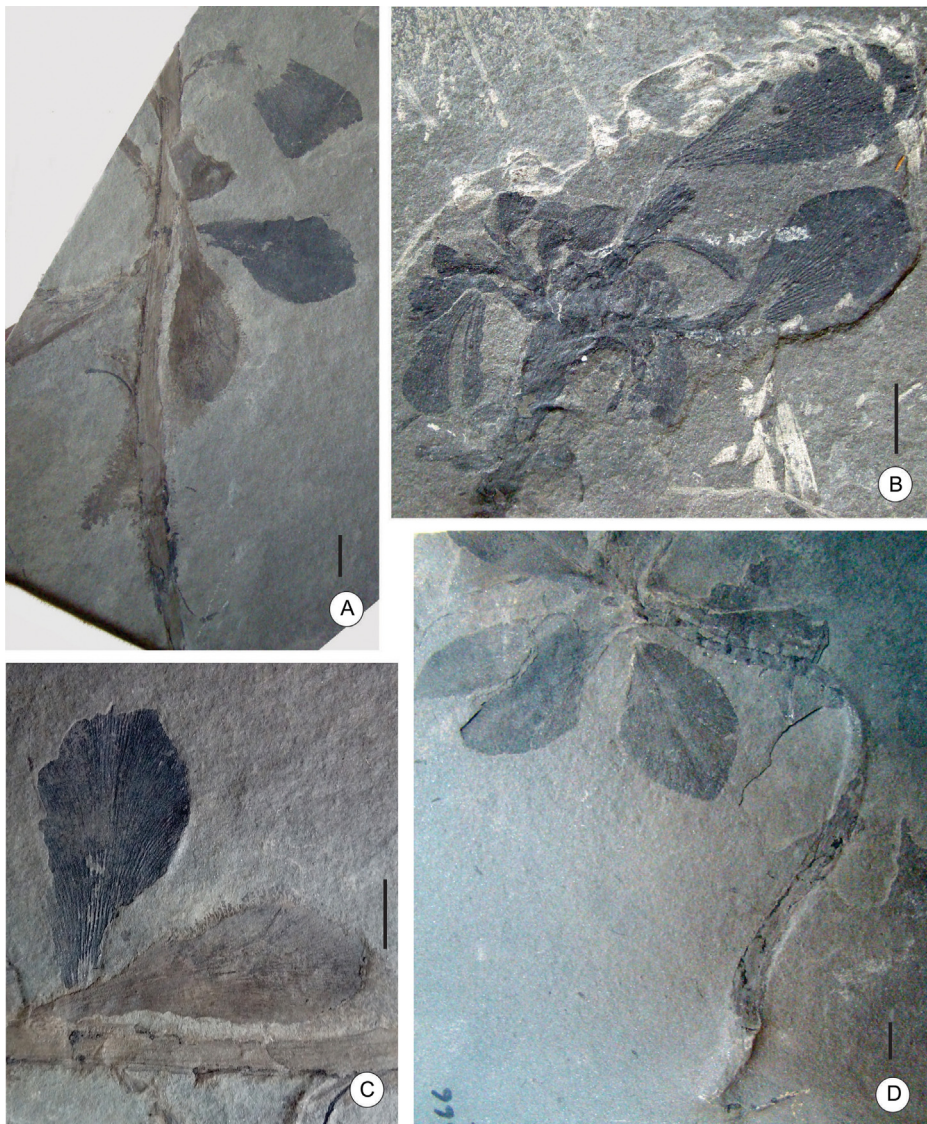


Fig. 4. *Gangamopteris obovata*. A. Axis associated and in connection with leaves partially incomplete, CORD-PB 2941. B. Small, probably unexpanded leaves attached to the axis, CORD-PB 3000. C. Detail of leaves in A. D. Long and narrow axis bearing distally a pseudo-whorl of incomplete leaves and leaf scars (arrows) CORD-PB 2666. Scale = 1 cm.

Fig. 4. *Gangamopteris obovata*. A. Axe associé et en relation avec des feuilles partiellement incomplètes, CORD-PB 2941. B. Petites feuilles, probablement non développées, attachées à l'axe, CORD-PB 3000. C. Détail des feuilles en A. D. Axes longs et étroits portant distalement une pseudo-spirale de feuilles incomplètes et de cicatrices de feuilles (flèches) CORD-PB 2666. Échelle = 1 cm.

apparently obtuse apex, and are inserted widely spaced by a broad base. The venation arises from the base and curves ($\leq 5\text{--}15^\circ$) towards the margins, intersecting them at acute angles in the central leaf portion. The vein concentration is 16 per cm in the central leaf portion.

3.2. Isolated leaves

Some dispersed leaves collected from the Bajo de Véliz Formation share the characteristics of the more complete specimens described above. In particular, the specimen CORD-PB 2931a-b (Fig. 5A–B) represents a bunch of overlapped leaves probably attached to the same axis, which

is not exposed on the surface. Leaves are up to 14.2 cm long and 4.5 cm wide, with narrow bases. Veins are approximately parallel at the base and then curve (degree of arching $8\text{--}11^\circ$) intersecting the margins at acute angles in the middle-upper portion of the leaf. Dichotomies and anastomoses form oblique meshes, and the vein concentration is about 13 per cm in the middle portion of the leaf.

Specimen CORD-PB 2990a-b (Fig. 6A) is a typical obovate leaf 9.6 cm long and 3.5 cm wide at the middle-upper section. Veins dichotomies occur mainly in the margins and basal-middle part of the leaf. Anastomoses form rhombic areolas with “oblique” and some “X” contacts.



Fig. 5. *Gangamopteris obovata*. A and B. Tuft of leaves, CORD-PB 2931b. B. Detail of venation, CORD-PB 2931b. Scale = 1 cm.
Fig. 5. *Gangamopteris obovata*. A et B. Touffe de feuilles, CORD-PB 2931b. B. Détail de la veine, CORD-PB 2931b. Échelle = 1 cm.

Incomplete basal fragments of leaves preserve a distinct venation pattern, such as specimen MIC-P 48 (Fig. 6D), with veins subparallel in the middle part and curved towards the margins (degree of arching 15–20°). The veins dichotomize and anastomose, forming areolas of variable size. In the middle part of the leaf, the areolas are long, whereas towards the margins they are shorter and rhombic. The three types of “oblique”, “transverse” and “X” contacts are evident. However, oblique contacts are the most common.

A large incomplete specimen has a narrow base (Fig. 6E). This fragment is 10 cm long and 8.5 cm wide with entire margins and a narrow base. Veins dichotomize and anastomose, to form meshes of variable size and rhombic morphology; the usual contact is “oblique”. Another large leaf at least 10 cm wide, probably representative *G. obovata*, is represented by an incomplete, distal fragment (Fig. 6F). It possesses the characteristic venation without a midrib, and a vein concentration of approximately 16 per cm, arising from the base and arching at 10° to the margins.

4. Comparisons

Pant (1982) included the leaf genera *Glossopteris* Brongniart ex Brongniart, *Gangamopteris* McCoy, *Palaeovittaria* Feistmantel, *Rubidgea* Tate, *Euryphyllum* Feistmantel, *Rhadotaenia* Pant, *Belemnopteris* Feistmantel emend. Pant et Choudhury and *Pteronilssonina* Pant et Mehra in *Glossopteridales* based on their similarities in form, the general pattern of venation and cuticular structure. Srivastava (1991) recognized two groups of *Glossopterid* leaves based on the absence (*Euryphyllum*, *Palaeovittaria*, *Rhadotaenia*, and *Rubidgea*) or presence (*Belemnopteris*, *Gangamopteris*, and *Glossopteris*) of anastomoses (meshes) in the venation. Later, additional leaf genera have been erected and related to *Glossopteridales*, such as *Gondwanophyllites*

Srivastava, *Laceyphyllum* Chauhan, *Maheshwariphyllum* Srivastava, and *Surangephyllum* Chandra et Singh (Srivastava and Srivastava, 2016).

The specimens from Bajo de Véliz are included in *Gangamopteris* based on the absence of midrib or a cluster of distinctive central parallel veins and the presence of anastomoses. The assignment to *G. obovata* (Carruthers) White, is based on the venation radiating from the base and reaching the margins at acute angles, the overall size (3.4–14 cm in length and 1.4–5.5 cm in width), and the shape of the leaves. The type specimen of *G. obovata* (Fig. 7A) is a long and narrow leaf (17 × 4 cm), its L/W ratio is 4.25, whereas the studied specimens usually have ratios ranging from about 2 to 3. However, leaves usually assigned to *G. obovata* in Brazilian studies (Adami-Rodrigues et al., 2004) are similar in size and L/W relation to those analyzed herein; and the Argentinian specimen CORD-PB 2991 (Fig. 7D) possesses a L/W ratio (17.5 cm in length and 3.6 cm in width) identical to the type specimen of *G. obovata* illustrated by Carruthers (1869).

4.1. Two controversial species: *G. obovata* and *G. cyclopteroides*

Kurtz (1895) was the first to mention the presence of *Gangamopteris* in the Bajo de Véliz Formation, mentioning the presence of *G. cyclopteroides* Feistmantel. Later, Kurtz (1921) described two varieties, *G. cyclopteroides* forma *typica* Feistmantel and *G. cyclopteroides* forma *attenuata* Feistmantel. Archangelsky et al. (1995) reassigned those specimens to *G. obovata* (Carruthers) White, species that they considered synonymous and to have priority over *cyclopteroides*.

Gangamopteris cyclopteroides was defined by Feistmantel (1876) from the Talchir Group (Lower



Fig. 6. *Gangamopteris obovata*. A. Detached leaf, CORD-PB 2990. B. Detail of the leaf figured in C. C. Axis bearing spaced and incomplete leaves, BAFC-PB 16735. D. Basal fragment of the leaf; the arrows indicate connections between veins, MIC-P 908. E. Basal fragment of the leaf with narrowed base, CORD-PB 2924; F. Apical fragment of a large leaf, CORD-PB 2994. Scale = 1 cm.

Fig. 6. *Gangamopteris obovata*. A. Feuille détachée, CORD-PB 2990. B. Détail de la feuille représentée en C. C. Axe à feuilles espacées et incomplètes, BAFC-PB 16735. D. Fragment basal de la feuille ; les flèches indiquent les connexions entre les veines, MIC-P 908. E. Fragment basal de la feuille à base rétrécie, CORD-PB 2924. F. Fragment apical d'une grande feuille, CORD-PB 2994. Échelle = 1 cm.

Permian) of India, with a short diagnosis and without illustration. Later (Feistmantel, 1879) enlarged the diagnosis as: "Leaves oblong-oval, symmetrical or oblique, entire; without midrib, its place is only indicated by some thicker veins, especially in the base; veins radiate from the base with anastomosis forming meshes long to somewhat broad in the middle part of the leaf, but narrow towards the margin. Base attenuated, amplexicaule." Feistmantel (1879) recognized three varieties of the species: *G. cyclopteroides* var. *subauriculata*, *G. cyclopteroides* var. *areolata* and *G. cyclopteroides* var. *attenuata*, based on differences in size and shape of the base. Arber (1905) considered the three

varieties as intraspecific variations of the same species, *G. cyclopteroides*. The specimens illustrated by Feistmantel (1879) in his plate VII, figs. 1 and 2, which were described as the original specimens of the "Cyclopteris-like" leaf from the Talchir shales, may be considered characteristic of the species. Enlarged portions of one of the Feistmantel's leaves, were figured by Feistmantel in plate VIII and IX, fig. 1, showing the presence of central parallel veins (Fig. 7C). According to Pant and Singh (1968) those specimens are untraceable because are not recorded in the Type Register of the Geological Survey of Indian Museum. Pant and Singh (1968) selected as lectotype the specimen G.S.I.

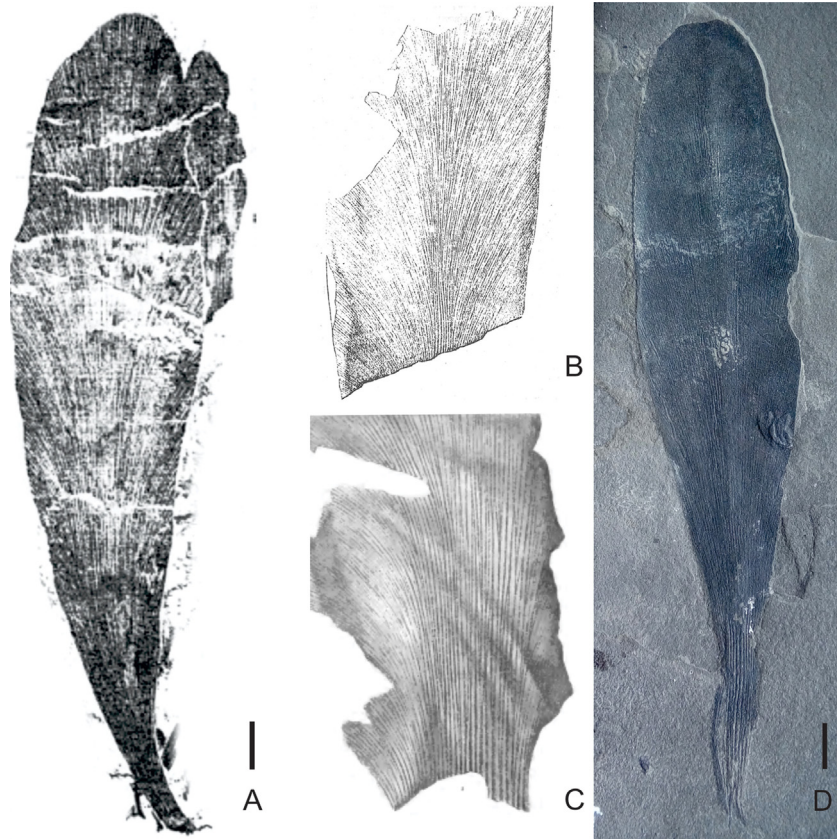


Fig. 7. A. Type specimen of *G. obovata* (Carruthers) White, taken from Carruthers (1869). B. Lectotype of *G. cyclopteroides*, taken from Feistmantel (1879, plate XIII, fig. 5). C. *G. cyclopteroides*, taken from Feistmantel (1879, plate IX, fig. 1). D. Specimen from the Bajo de Véliz Formation CORD-PB 2991. Scale = 1 cm.
Fig. 7. A. Spécimen type de *G. obovata* (Carruthers) White, extrait de Carruthers (1869). B. Lectotype de *G. cyclopteroides*, tiré de Feistmantel (1879, planche XIII, fig. 5). C. *G. cyclopteroides*, extrait de Feistmantel (1879, planche IX, fig. 1). D. Spécimen de la formation Bajo de Véliz CORD-PB 2991. Échelle = 1 cm.

5013 figured by Feistmantel (1879) in his plate XIII, fig. 5, which preserves the cuticle, but the leaf is unfortunately incomplete at the apex and base (Fig. 7B). Srivastava et al. (2012) described *G. cyclopteroides* with 4–6 parallel distinctive veins in the central region of the leaf.

Previously, Carruthers (1869) had defined *Noeggerathia obovata* from the Candiota coals (Brazil), with a brief description: “Fronde sessile flat, entire, elongate-obovate, attenuated towards the base; nerves dividing dichotomously, parallel”. Owing to the apparent absence of anastomoses, Zeiller (1895) assigned the specimen to *Euryphyllum wittianum*, but Arber (1905) and Seward (1908) considered it to be identical with *Gangamopteris cyclopteroides* Feistmantel. Arber (1905) described the *N. obovata* specimen illustrated by Carruthers (1869) as an almost complete leaf, oval-spatulate, lacking a midrib but having veins emerging from the base, with dichotomies and anastomoses in the distal part of the lamina (Fig. 7A).

White (1908) transferred Carruthers’ species to *Gangamopteris* and noted that *G. obovata* had priority over *G. cyclopteroides* defined by Feistmantel (1876) from India and included the varieties *attenuata* and *major* in the former species. The variety *subauriculata* was provisionally distinguished from *G. obovata*. White (1908) redescribed the Brazilian species as: “Leaves elongated obovate-spatulate,

or oval-spatulate to obovate-lingulate, contracted, usually, with concave lower borders, in a narrow, sometimes very narrowly cuneate, often rather slender base, the apex of the leaf being rounded or ovate-round, lamina thick, often convex ventrally between the nerves; venation rather coarse, from many close parallel and vertical dichotomous and rarely anastomosing primary veins in the basal portion, the outer veins arching very gently to the border in the lower part of the leaf, and more strongly in the higher portions, while forking and anastomosing more frequently especially near the border, where the nervilles are very close, with a much shorter mesh; curvature of the lateral nervation varying greatly in the lower part of the leaf in accordance with the width of the base of the leaf, the nervilles arching more strongly in the broader leaf forms; scale fronds cuneately obovate, narrow, and somewhat concavo-convex.”

Later, Kovács-Endrödy (1979) proposed *Gangamopteris* as a junior synonym of *Glossopteris* and emended again the diagnosis of *G. obovata* based on the holotype, which was illustrated. The new diagnosis emphasized characters that separate it from *G. cyclopteroides*, such as the rounded apex of the oblanceolate leaves with a narrow base, venation radiating from the basal portion of the lamina, with long and narrow meshes that are difficult to distinguish.

Maithy (1965) distinguished Indian *G. cyclopteroides* as leaves with the maximum width at the mid-length of the lamina, similar to the interpretation by Kovács-Endrödy (1979), who described the species as having elliptical leaves. Some specimens described here possess similar type of leaves (Fig. 2) but maintain a L/W ratio not higher than three. Tybusch et al. (2016) and Tybusch and Iannuzzi (2008) evidenced once more the difficulty in differentiating the two species, due to their wide range of intraspecific variability. However, Tybusch et al. (2016) proposed to distinguish *G. cyclopteroides* from *G. obovata* “by the absence (in the Brazilian species) or presence (in the Indian species) of straight sharp subparallel veins in the middle region of the lamina from the base to the apical region of the leaf, just below the apex”. We consider that the presence, or not, of a cluster of central veins along the lamina, the shape of the leaves and the proportion of meshes may be useful characters to distinguish these similar species.

5. Discussion

Reconstructions of the glossopterids have been mainly based on disarticulated organs (e.g., Gould and Delevoryas, 1977; Pant, 1977; Plumstead, 1958; Retallack and Dilcher, 1988). Etheridge (1895) presented the first reconstruction of *Glossopteris* as a small woody plant, and Plumstead (1958) developed one of the first attempts to reconstruct the habit of glossopterids as deciduous, woody plants, with an arborescent habit, and with leaves and reproductive structures borne on short shoots, a few of which developed into long shoots to form branches. She noted great size diversity amongst the glossopterid leaves, which occur tightly packed, without signs of withering before burial and rarely bent or folded, in the same bed, and postulated that: “The more probable explanation is, therefore that, the banks of leaves represent normal autumnal deposits from deciduous plants, dropped into still water, for they show no fraying attributable to transportation”.

The assumption that glossopterid leaves were borne in whorls or tight helices apically on short shoots was initially the most accepted phyllotaxy (Table 1 in Pigg and Taylor, 1993), but anatomical studies by Pigg and Taylor (1993) demonstrated that leaves on small twigs (about 1 cm in diameter) of *Glossopteris schopfii* Pigg and *G. skaarensis* Pigg were arranged helically in a two-fifths phyllotaxy, with long and short internodes. Other records of leaves associated with reproductive structures attached to anatomically preserved stems (Nishida et al., 2014, 2018) also favor a spiral phyllotaxy.

The first report of leaves attached to stems was presented by Dana (1849) who illustrated a clump of *Glossopteris browniana* Brongniart ex Brongniart attached to a stem, and Etheridge (1895) described *Glossopteris* as “a clump of leaves at the end of a caudex bearing leaf scars”. Bunbury (1861) described and figured a small specimen referred tentatively to *Glossopteris*, which preserves four leaves attached to a stem. Oldham (1897) illustrated a cluster of eleven leaves of *Glossopteris communis* Feistmantel and Seward (1910) figured a group of *Glossopteris browniana* leaves at the end of a stem.

Plumstead (1958) described some specimens of glossopterid leaf clusters from Wankie, southern Rhodesia. Some of them preserve groups of leaves of *Gangamopteris indica* Srivastava and *Gangamopteris obovata* var. *attenuata* White, although the connection with the axes is unclear. She interpreted the clusters to have been shed as a whole, leaving probably a single large oval, or pear-shaped scar and that in many cases the leaves remained together until they were buried.

Rigby (1967) described *Gangamopteris walkomii* Rigby as a plant having leaves arranged into tightly adpressed spirals on long and short shoots. Some of the specimens described by Rigby (1967) were also illustrated by White (1990, figs. 119 and 131) and McLoughlin (2011). Rigby (1969, fig. 1) reconstructed the *Glossopteris/Gangamopteris* plant as a tall tree with small whorled leaves growing in terminal tufts, and also as a small unbranched tree with a crown of large leaves at the top, similar to some modern cycads.

Pant and Singh (1974) described two small leaves attached to an axis that they referred to *G. cyclopteroides* Feistmantel. These authors also illustrated, as *G. cf. cyclopteroides* var. *cordifolia* Feistmantel, four leaves connected to an axis. In both specimens, the precise phyllotaxis is difficult to discern.

Numerous other authors have reported the occurrence of glossopterid leaves attached to stems with longitudinal striations, wrinkles or leaf scars (Anderson and Anderson, 1985; Bunbury, 1861; Feistmantel, 1881; McLoughlin, 1994b; Pant, 1967; Pant and Singh, 1974; Rigby, 1967). Pigg and Taylor (1993) reported that specimens with lenticular or rhombic scars, like the axis described by Etheridge (1895), show short internodes, whereas in other specimens (e.g., Dolianiti, 1954) the individual leaves are more widely spaced. This variation in internodal length could reflect different stem types (long and short shoots) as suggested by Plumstead (1958) and Pant and Singh (1974), or the position on the plant or along a branch.

The new specimens presented here support, in part, recent proposals (McLoughlin, 2011) suggesting that glossopterid leaves were attached either widely spaced or densely packed. However, clear evidence of long and short shoots is not available in the studied material. Axes of similar lengths and diameters may bear either widely spaced or tightly packed leaves. These differences in internodal length could reflect variations along a branch in a tree with proleptic branching (Pigg and Taylor, 1993). Although a great diversity is inferred to have existed within the large group of glossopterid plants, it is possible to consider this helical phyllotaxis for *Gangamopteris obovata* specimens of west-central Argentina to be a consistent feature of the earliest glossopterid representatives.

These results, together with previous examples of glossopterid leaves attached to axes, prove that these plants had a distinctly different phyllotaxy from leaves with superficially similar morphology from the Mesozoic. For example, *Contriglossa* from the South African Triassic Molteno Formation flora (Anderson and Anderson, 1989, 2003) has leaves that are of very similar shape and venation patterns to glossopterids, but their whorled insertion

provides good evidence that they belong to a plant group unrelated to glossopterids (probably Gnetales).

6. Conclusions

Since glossopterid leaves are rarely preserved in organic connection to subtending branches, specimens from the Gzhelian–Earliest Permian Bajo de Véliz Formation, contribute to resolving the phyllotaxis of gangamopterid plants. Leaf attachments in the new material vary from widely to tightly spaced helical patterns and provide an advance in our understanding of the variability in foliar arrangements in this group. The presence of long and short internodes in the earliest representatives of glossopterids confirm the proposal of Pigg and Taylor (1993) for more advanced (Late Permian) glossopterids. The impressions of branches of similar length and diameter bearing variable-sized leaves of *G. obovata* confirm that minor variations in morphology can be attributed to ontogeny or position on the plant. True leaf whorls are not recognized in the Argentinian specimens, and the available evidence suggests the absence of apical clusters of leaves on short shoots like in the extant Ginkgoales.

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