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Coniferophytes from the Bajo de Veliz Formation (Gzhelian-Asselian), San Luis Province, Argentina

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ABSTRACT. In this contribution, we analyze the presence of fossil coniferophytes from the Bajo de Veliz Formation (Paganzo Basin) that were initially referred to *Walchia* or *Paranocladus* and have not been described until now. These specimens consist mainly of leafy branches exhibiting foliar heteromorphism characteristic of upper Paleozoic coniferophytes from Gondwana. This group includes *Genoites* sp. with lax arranged ovules on the last order branches, *Krauselcladus* sp. represented by a small vegetative branch with bi- and trifurcated leaves, and *Buriadia* cf. *Buriadia heterophylla* Seward et Sahni emend. Serbet, Escapa, Taylor, Taylor et Cúneo, 2010, showed axes with multifid leaves and ovules on terminal branches. Vegetative fragments with small lanceolate leaves are assigned to *Feruglioclad*us cf. *F. riojanum* Archangelsky et Cúneo, 1987. In addition, an isolated, probably male reproductive structure similar to those known for th latter species was identified. The presence of *Buriadia* is recognized for the first time in the Carboniferous-Permian of Argentina, as well as the identification of vegetative buds or shoots, a previously undocumented characteristic for this Paleozoic coniferophyte from Gondwana.

KEYWORDS: Coniferophyta, Gondwana, Argentina, Carboniferous-Permian, Paganzo Basin

INTRODUCTION

The type of branching, morphological variety of leaves, arrangement, and orientation of the reproductive structure in Paleozoic coniferophytes are of great importance for understanding their evolution in the fossil record (Taylor et al., 2009). Recent advances in knowledge about this extinct group suggest that its diversity during the Carboniferous-Permian of Gondwana maybe even more complex and diverse than previously thought. This variety is evidenced by findings in Argentina (Cúneo, 1985; Archangelsky and Cúneo, 1987; Coturel et al., 2009; César, 2014), India (Singh et al., 2003), Antarctica (Serbet et al., 2010) and Brazil (Fantón et al., 2006; Mune et al., 2016).

A shared characteristic in the Paleozoic coniferophytes of Gondwana is the presence of stems with different orders of irregular branching, bearing simple to heteromorphic leaves, and when preserved, may present lax ovules on terminal branches (Cúneo, 1985; Serbet et al., 2010) or forming compact cones (Archangelsky and Cúneo, 1987).

The latest Carboniferous flora in Argentina is characterized by the *Krauselcladus-Asterotheca* Biozone (formerly known as Interval

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Zone) of Moscovian–Gzhelian age (Carrizo and Azcuy, 2015). The first records of *Krauselcladus argentinus*, *Paranocladus? fallax*, *Paranocladus* sp., and indeterminate conifer-like plants have been reported for central-western Argentina in stratigraphic units of the Río Blanco Basin and Paganzo Basin (e.g. Archangelsky, 1978; Carrizo and Azcuy, 1995, 2015; Coturel et al., 2009).

Two important groups of coniferophytes were described for the lower Permian of Patagonia. Cúneo (1985) described the presence of *Genoites* Feruglio, referred to the Family Buriadiaceae, given the similarity of its lax reproductive structure and morphology of the leaves with *Buriadia* Seward et Sahni. On the other hand, *Feruglíocladus* Archangelsky et Cúneo and *Ugartecladus* Archangelsky et Cúneo were assigned to the Family Feruglíocladaceae by Archangelsky and Cúneo (1987). These taxa are characterized by reproductive structures in the form of compact male and female cones.

In central-western Argentina, fragmentary branches of conifer-like plants were initially described by Kurtz (1895, 1921) from the Bajo de Veliz Formation (Paganzo Basin) and assigned to *Walchia* Sternberg. Later, Florin (1940) reassigned these specimens as *Paranocladus? fallax* Florin. For a long time, *Walchia* was used to describe vegetative stems of primitive Paleozoic conifers without cuticular details and also for reproductive specimens with a single ovule on a dwarf shoot (Clement-Westerhof, 1984; Taylor et al., 2009). The poor preservation of material in the fossil record, lack of anatomical details, and absence of organic connection of the reproductive structures hinder the systematic position of this fossil genus.

New specimens from the Bajo de Veliz Formation including vegetative branches of *Krauselcladus* Yoshida emend. Fanton et al. and *Feruglíocladus* cf. *F. riojanum* Archangelsky et Cúneo are described herein. In addition, fertile specimens of *Genoites* sp., *Buriadia* cf. *Buriadia heterophylla* Seward et Sahni emend. Serbet, Escapa, Taylor, Taylor et Cúneo, 2010, and a reproductive structure were also identified. The new data expand the geographical and stratigraphical distribution of these coniferophytes, and allow comparisons with coeval Gondwanan assemblages from Argentina, Brazil, India and Antarctica.

STRATIGRAPHIC SETTING

The Bajo de Veliz Formation (Flores, 1969) is the more ancient sedimentary deposit in the San Luis province, Argentina (Fig. 1A, B). It has an estimated thickness of 164 m, and comprises the Cautana, Pallero and Lomas members in ascending stratigraphic order (Hünicken and Pensa, 1975). This succession constitutes an excellent example of a fluvial-lacustrine paleosystem (Fernandez et al., 2017) linked to the southeastern extreme of the Paganzo Basin. It yields abundant fossils that indicate a late Carboniferous-early Permian age.

The fossil remains are concentrated in the finely laminated dark mudstones of the Pallero Member and include a rich variety of well-preserved impressions of plants, palynomorphs, arthropods, and traces fossils (Fig. 1C). The macrofloristic material comprises lycopsids, equisetaleans, pteridosperms, coniferophytes, and glossopterids (see references in Césari and Chiesa, 2017). This member is mainly characterized by fine-grained clastic rocks deposited in a lake with variable hydrological conditions, a suitable environment for preserving.

The Bajo de Veliz Formation has been assigned to the early Permian or late Carboniferous according to its paleofloristic or entomofaunal content. The presence of glossopteridales (*Gangamopteris* and *Glossopteris*) allowed this unit to be referred to the early Permian *Gangamopteris* Biozone (Archangelsky et al., 1996). However, according to Hünicken and Pinto (1980), the insects would indicate a late Carboniferous age. Limarino et al. (2014) considered this and coeval successions as characterized by the complete disappearance of striated pavements, diamictites interpreted to be of glacial origin, and the disappearance of other features that indicate glacial climates in Argentina. This paleoflora, as well as the one recovered from the La Colina (=Patquía) Formation (Limarino and Césari, 1984; Césari, 1987), are the best examples in the Paganzo Basin of fossil assemblages characterized by the first occurrence of glossopterids (*Gangamopteris*, *Glossopteris*, and *Eurynphyllum*). According to López-Gamundí et al. (1992) and Gulbranson et al. (2015), during the late Pennsylvanian-Permian, an aridification trend occurred in the region, and the vegetation was confined to scattered wet spots near water bodies where humid conditions prevailed locally, like the assemblages of Bajo de Veliz.

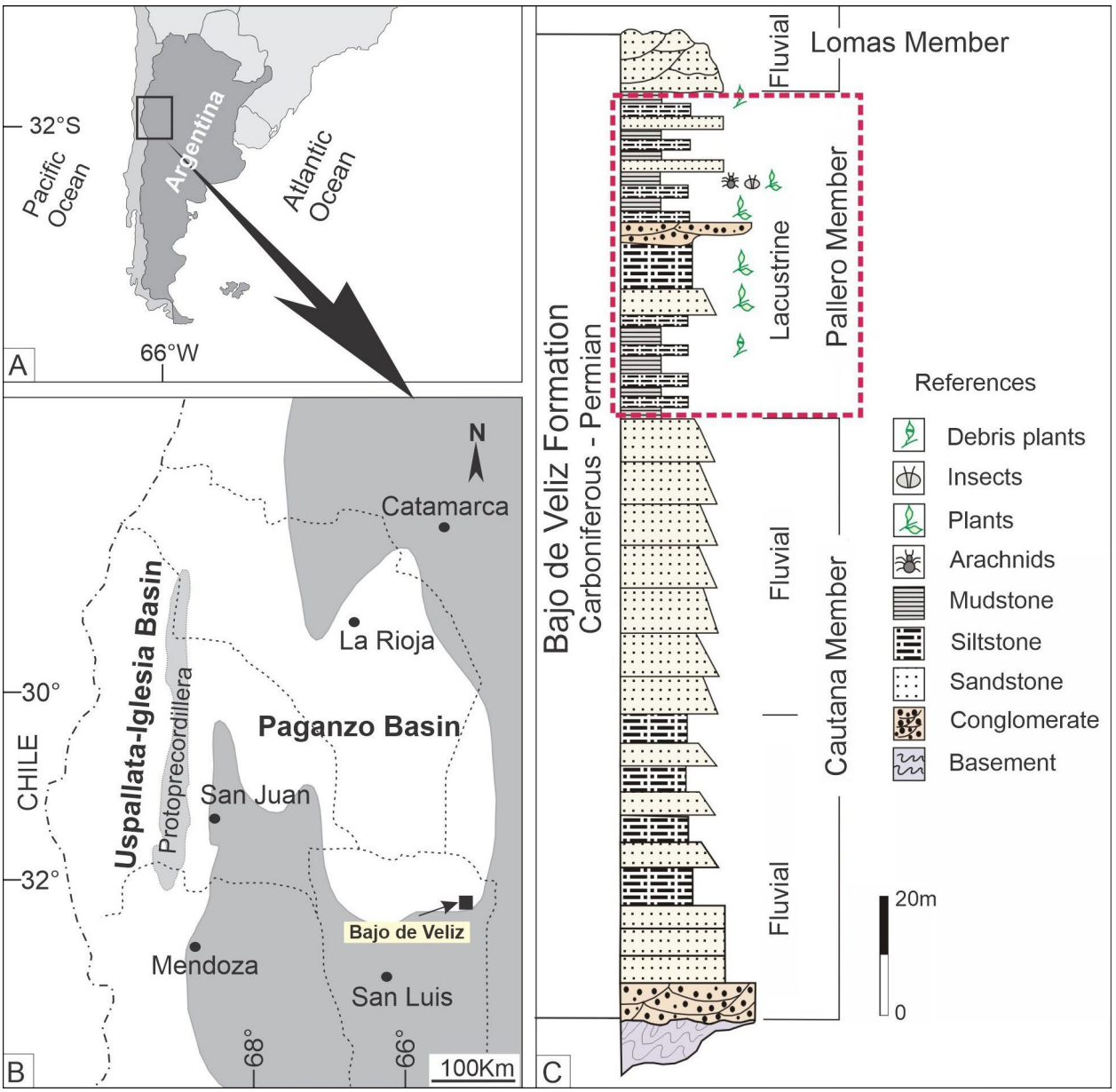

Figure 1. **A**. Map of South America showing the location of the Paganzo Basin; **B**. Palaeogeography of the Paganzo Basin (modified from Limarino et al., 2002), square indicates the locality of Bajo de Veliz in the San Luis province, positive relief is shaded in grey; **C**. Simplified stratigraphic column of the Bajo de Veliz Formation (modified from Hünicken and Pensa, 1975)

Absolute isotopic ages suggest a latest Carboniferous-Permian age for these palaeofloras (César et al., 2011). This age is based on the CA-TIMS U-Pb dating provided by Gulbranson et al. (2010) of 296.09 ± 0.08 Ma obtained from a tuff within eolian deposits overlying the La Torre basalts (dated between 308 ± 6 to 293 ± 6 Ma, see César, 2007) interbedded at the base of the La Colina Formation (Fig. 2), where glossopterids were identified.

Moreover, a review of the palynological content of the Pallero Member allowed César and Chiesa (2017) to refer the palynofloras to the *Pakhapites fusus- Vittatina subsaccata* Biozone (FS), which includes the *Converrucosisporites confluens* Morphon. Their overall composition is similar to that of the palynofloras described for the Carboniferous-Permian boundary stratotype by Dunn (2001) in Kazakhstan and coeval assemblages from Argentina, Brazil, and Namibia (Stephenson, 2009). According to palynological evidence, César and Chiesa (2017) propose an early Gzhelian-Asselian age for the unit, taking into account the radiometric ages obtained in the Ganigobis Shale Member in Namibia of 302 Ma (Gzhelian) where palynofloras contain *C. confluens* spores (Stephenson, 2009). This last species also characterizes palynofloras from Brazil, considered the same age by Souza et al. (2021) based on several radiometric ages.

MATERIALS AND METHODS

The coniferophytes are represented by well-preserved carbonaceous impressions of vegetative and fertile branches recovered from lacustrine facies of the Pallero Member (Fig. 1C). The illustration of the material was made using a Canon optical SONY zoom 4× HD digital camera and a stereomicroscope NIKON SMZ800.

The specimens studied are deposited in the repositories of the Universidad Nacional de San Luis (MIC-P), Academia Nacional de Ciencias-Córdoba (CORD-PB), Museo de La Plata (LPPB) and the Paleobotanical Collection of the Universidad de Buenos Aires (BAFC-PB).

SYSTEMATICS

Division CONIFEROPHYTA

Family BURIADIACEAE sensu Pant 1982

Genus *Genoites* Feruglio emend. Cúneo 1985

Type species *Genoites patagonica* Feruglio 1942

Type locality. Nueva Lubecka, Río Genoa Formation, Chubut, Argentina

***Genoites* sp.**

Fig. 2

Studied material. MIC-P 356-357

Description. Fertile twigs branched up to second order. Incomplete first-order branch, 4.7 cm long and 0.25 cm wide (Fig. 2). Decurrent second-order twigs, arranged radially, irregularly at an angle of 25°–30°, and reaching up to 1.2 cm in length (Fig. 2C). These twigs bear densely helically arranged small, entire and decurrent univeined leaves that do not exceed 0.27 cm in length, with acute apices oriented towards the distal part of the branch (Fig. 2A, B). Lax reproductive structure, with ovules reaching up to 0.17 cm in length, inserted axillary to subaxillary on the second-order axes (Fig. 2A, D–F) by a very short stalk or pedicel. Ovules are subrounded to elliptical and apparently have rounded apices, reaching 1.7 mm in length.

Comparisons. *Genoites* was defined by Feruglio (1942) based on vegetative remains from the Río Genoa Formation (lower Permian, Patagonia). Later, Cúneo (1985) reviewed and studied new material from the same area, expanding the diagnosis and describing fertile specimens of *Genoites patagonica* Feruglio emend. Cúneo. The specimen from the Bajo de Veliz Formation shared with *Genoites* lax reproductive structures located on last orders branches bearing linear simple leaves. However, in *Genoites patagonica* the ovules are larger, reaching 0.4 cm in length (Cúneo, 1985: pl. 2, fig. 2, pl. 3, figs 2–3) and inserted axillary on bifid leaves. Moreover, its needle-shaped leaves are longer (up to 2 cm long and 0.5 cm wide), heteromorphic, varying from entire to slightly or deeply divided, inserted at wide angles and spaced on second-order branches (Cúneo, 1985: pl. 1, fig. 1). The examination of the type material of *Genoites patagonica* (preserved in the Paleobotanical Collection of the Museo Argentino de Ciencias Naturales B. Rivadavia) confirms that the leaves and their phyllotaxis differ from those described here.

Leaves of *Buriadia* identified in the palaeoflora from Bajo de Veliz differ from the specimen described herein in its polymorphic, predominantly dissected laminae with distal margin serrate-incised. Simple leaves in the genus *Buriadia* are lanceolate to ovate-lanceolate in shape. Although, Cúneo (1985) remarked on the generic similarity between *Buriadia* and *Genoites*, Serbet et al. (2010) considered that *Genoites patagonica* differs in its ovules subtended by a bifid leaf (Fig. 3).

It is also distinguished from other Palaeozoic coniferophytes from Argentina, such as *Feruglio*cladus Archangelsky et Cúneo and *Ugarte*cladus Archangelsky et Cúneo because they present reproductive structures of compact and terminal female cones. Their broader, lanceolate leaves closely overlapped on the branches also differ from *Genoites* (Archangelsky and Cúneo, 1987: pl. 1, fig. 1, pl. 3, fig. 1).

Krauselcladus Yoshida, another coniferophyte described for the Carboniferous of Argentina and the Permian of Brazil, differs from the material from Bajo de Veliz by its foliar heteromorphism: linear, straight or falcate and bilobed or multilobed leaves are inserted at wide angle and spaced on the axes (Fanton et al., 2006).

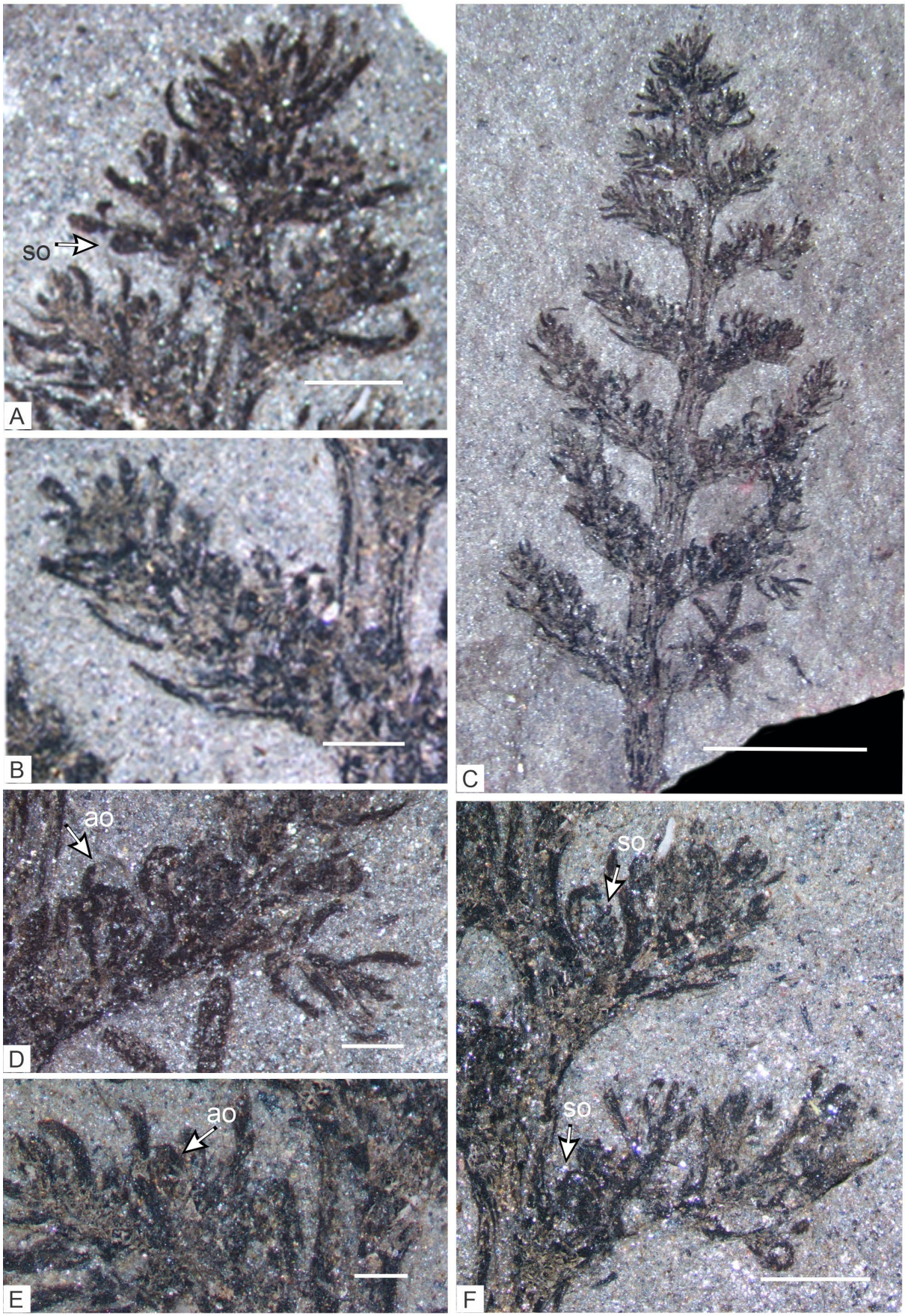

Figure 2. *Genoites* sp. MIC-P 356-357. **A**. Apical portion of a shoot, small, linear, curved upward; **B**. Secondary axis covered by linear leaves inserted in thigh spiral; **C**. Low magnification image of the specimen showing the leafy secondary axes; **D–F**. Details of subaxillary (so) and axillary (ao) ovules inserted between the leaves by a short pedicel. Scale bars = 1 cm in C; 1 mm in A, B, D, E, F

Genus *Krauselcladus*
Yoshida emend. Fanton, Ricardi-Branco, Torres-de-Ricardi et Rohn, 2006

Type species *Krauselcladus canoinhensis*
Yoshida emend. Fanton, Ricardi-Branco, Torres-de-Ricardi et Rohn, 2006

Type locality. Canoinhas, Santa Catarina, Brazil

***Krauselcladus* sp.**

Fig. 4

Studied material. BAFC-PB 187

Description. Fragment of vegetative shoot with two branching orders. The first order branch is 4 cm long and 0.1 cm wide (Fig. 4). Second order branches arise decurrently at approximately 30°–35°, bearing helically spaced heteromorphic leaves which are closer distally (Fig. 4C). Leaves diverge from the stem at wide angles, are 0.3–0.5 cm long and 0.1 cm wide, and range from simple and linear to bifurcated and trifurcated in the same branch (Fig. 4A, B). In some leaves the bifurcation can reach 2/3 of the lamina, with lobes of entire margins and subrounded to acute apices. Indistinguishable venation.

Comparisons. *Krauselcladus* Yoshida is a coniferophyte defined for the early Guadalupian of the Paraná Basin (Brazil) based on compressions of vegetative branches several times branched orders. Yoshida (1970) defined two species, *K. canoinhensis* and *K. catatinensis*. Subsequently, based on new anatomically preserved material, Fanton et al. (2006) emended the diagnosis of the genus and proposed the synonymy of these species, being *K. canoinhensis* valid by priority.

The specimen studied herein is comparable to *Krauselcladus* from Brazil by the heteromorphism of the leaves arranged on the last branching orders (Fanton et al., 2006: pl. 3, fig. 1, pl. 4, figs 1, 2). In the Argentinean material, simple and linear leaves are also observed on the same branch, bifurcated and trifurcated, with subrounded to acute apices, spaced on the second-order axes (Fig. 3). Although it resembles *Genoites patagonica* by the relatively long and spaced leaves, usually inserted at 60°–70°, it differs by its deeply bifurcated and trifurcated leaves. Moreover, the presence of ovules in *Genoites* distinguishes it from the Brazilian taxon (Cúneo, 1985).

In Argentina, *Krauselcladus* is already represented by the species *Krauselcladus argentinus* Archangelsky from the Carboniferous Trampeadero Formation (Paganzo Basin). That species differs from the one described here by its homomorphic leaves arranged densely or loosely along the branch (Archangelsky, 1978).

Buriadia Seward et Sahni emend. Serbet, Escapa, Taylor, Taylor et Cúneo, 2010, is distinguished from the Argentinian material by its irregular branching and the heteromorphy of the multifid lanceolate leaves, forming an incised distal margin.

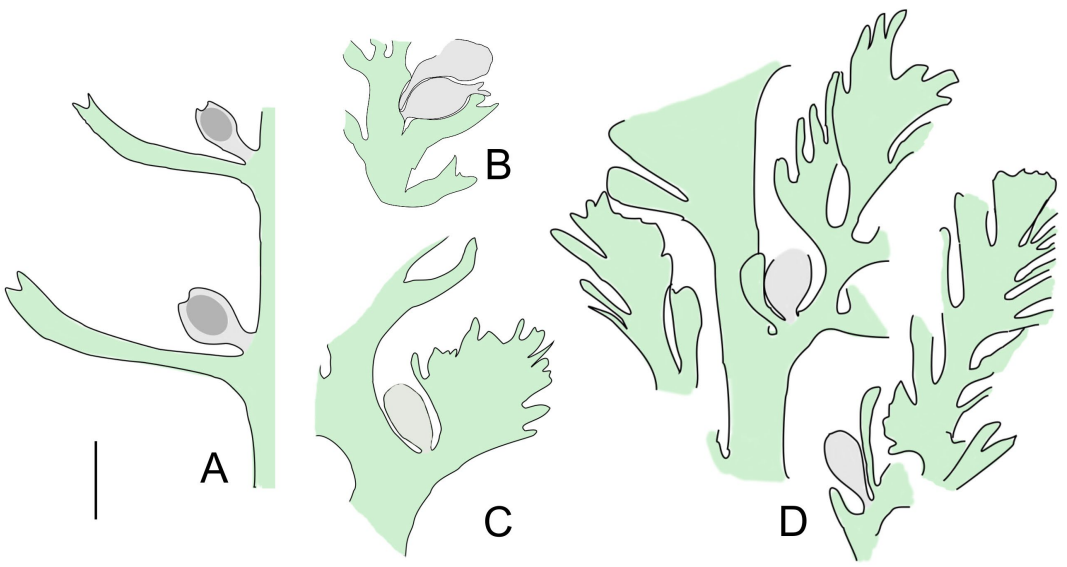

Figure 3. Line drawings of fertile leafy branches. **A**. *Genoites patagonica* (modified from Cúneo, 1985); **B**. *Buriadia heterophylla* (modified from Serbet et al., 2010); **C**, **D**. Specimens of *Buriadia* cf. *B. heterophylla* described here. Ovules in grey

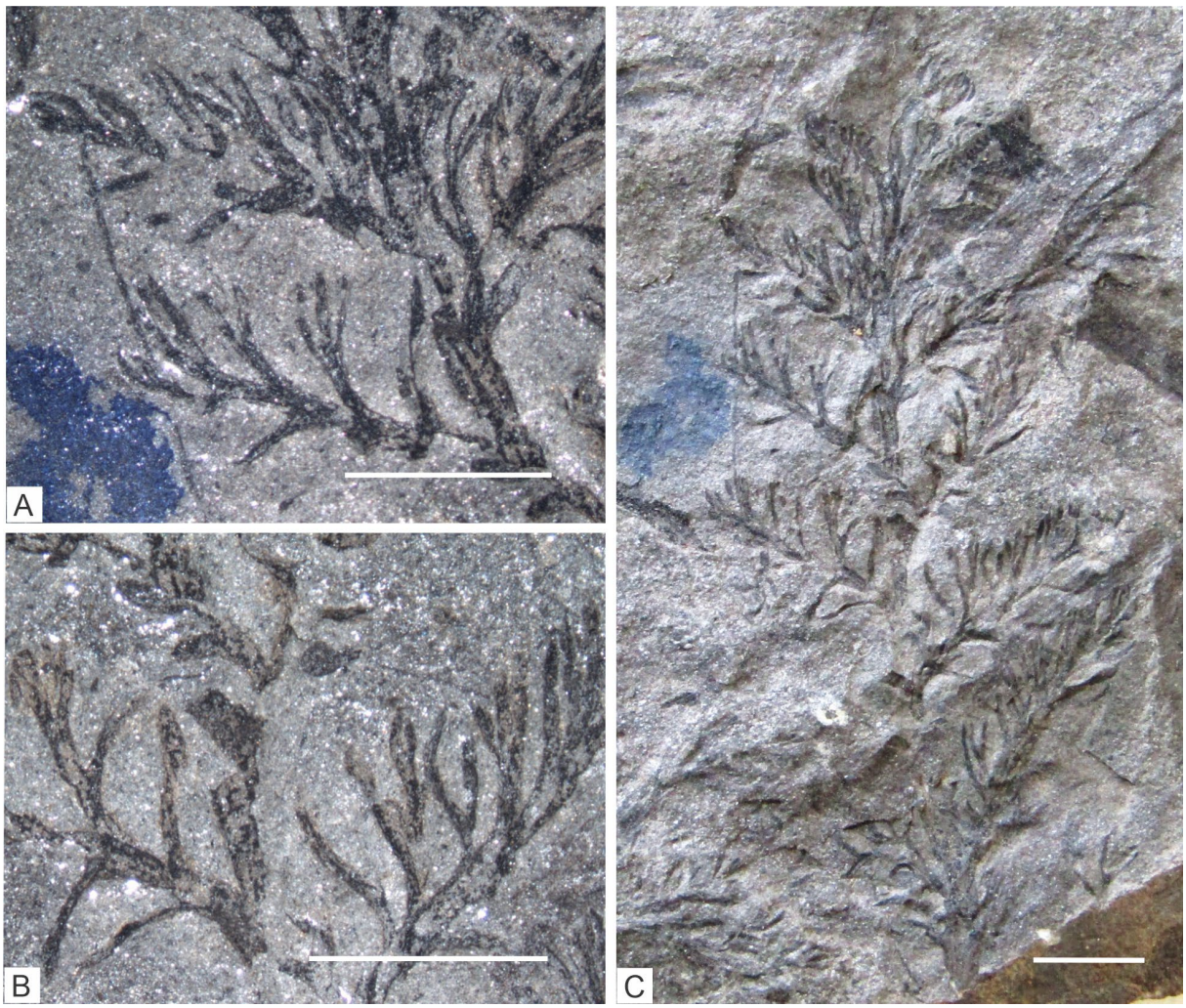

Figure 4. *Krauselcladus* sp. BAFC-PB 187. **A**, **B**. Detail of the second order branches, showing spaced to closer arranged heteromorphic leaves: entire linear, bifurcate and trifurcate; **C**. General view of the specimen with two branching orders. Scale bars = 5 mm

Genus *Buriadia*
Seward et Sahni emend. Serbet, Escapa, Taylor, Taylor et Cúneo, 2010

Type species *Buriadia heterophylla*
Seward et Sahni, 1920

Type locality. Mount Gran, Victoria Land, Antarctica.

Buriadia* cf. *Buriadia heterophylla
Seward et Sahni emend. Serbet, Escapa, Taylor, Taylor et Cúneo, 2010

Fig. 5

Studied material. CORD-PB 2816, CORD-PB 3310 (A-B), CORD-PB 3323, MIC-P 914.

Description. Vegetative shoots with irregular branching. The most complete specimens (MIC-P 914 and CORD-PB 3323) have incomplete main branches 7.2–10 cm long and 0.5 cm wide (Fig. 5A, D). Young shoots or buds (axillary?) up to 7.5 cm long, covered by overlapping leaves, arise from the main axis. Second order branches 3.5–9.5 cm long and 0.2 cm wide, bear axes with heteromorphic leaves closely arranged. Leaves are polymorphic, predominantly multifid with distal margin serrate-incised forming deeply dissected laminae with multiple simple apices (0.5 cm long), with apex acute 0.4 cm long and 0.1 cm wide (Fig. 5C, E, I). Indistinguishable venation. The specimen MIC-P 914 bear ovules 0.3–0.4 cm long and 0.1 cm wide, subrounded to elliptic, inserted to a lateral branch by a narrow base or very short petiole or peduncle, and associated with multifid leaves forming lax structures (Fig. 5F, G, H). Smaller specimens correspond to distal branches (CORD-PB 2816 and CORD-PB 3310) (Fig. 5B). These first-order axes do not exceed 5 cm in length and 0.2 cm in width, and second-order branches up to 1.6 cm long.

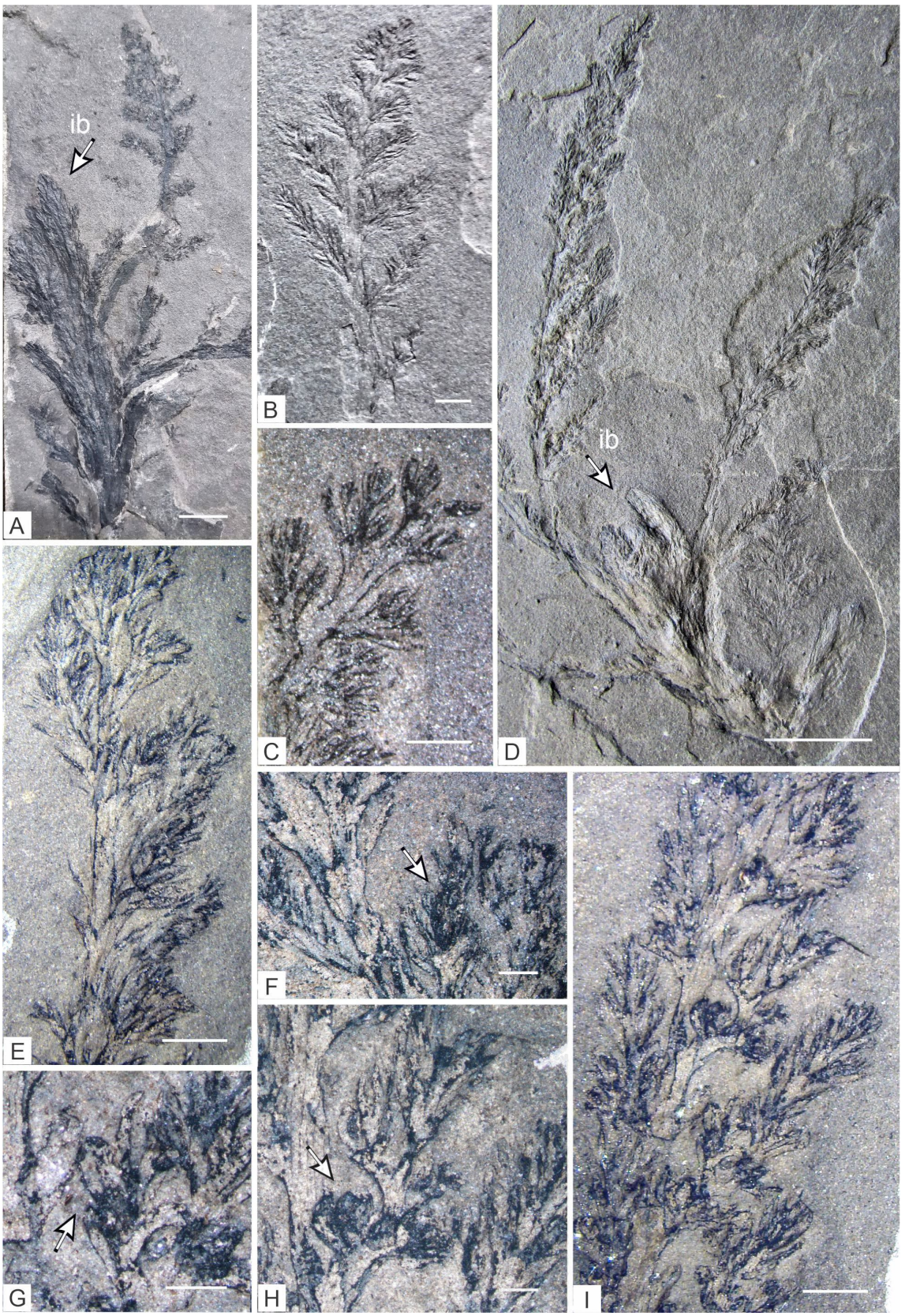

Figure 5. *Buriadia* cf. *Buriadia heterophylla*. **A**. CORD-PB 3323, low magnification image of the specimen showing buds or immature buds (ib) arising from the main axis; **B**. CORD-PB 2816, distal portion of a leafy branch with two orders of ramification; **C**. MIC-P 914, distal portion of a secondary axis bearing decurrent leaves repeatedly divided; **D**. MIC-P 914, specimen with leafy branches bearing ovules and buds or immature buds (axillary?) (ib) on the main axis; **E**. MIC-P 914, detail of secondary axis bearing leafy branches; **F**. MIC-P 914, detail of oval ovule (arrow) inserted to a lateral branch; **G**. MIC-P 914, ovule (arrow) inserted by a very short peduncle and associated to divided leaves; **H**. MIC-P 914, ovule (arrow) apically incomplete, inserted to the axis, axillary to a simple? leaf; **I**. MIC-P 914, general view of the leafy axes bearing the ovules illustrated in G and H. Scale bars = 1 cm in A, B; 2 cm in D; 2 mm in F, G, H; 5 mm in E, I

Comparisons. *Buriadia heterophylla* Seward et Sahni was initially reported from the late Paleozoic of India, and it was the subject of several controversial interpretations. Singh et al. (2003) reviewed the holotype, paratypes and lectotypes described by Feistmantel (1879, 1881) and Pant and Nautiyal (1967). They studied new specimens from the Permian of India and emended the species, discarding an organic connection with reproductive structures. Later, Serbet et al. (2010) described and illustrated *B. heterophylla* conifer-like branches from Antarctica. These specimens bear heteromorphic leaves arranged helically and orthotropic ovules of bifid apex attached to last-order branches by a short peduncle (Fig. 3). This organic connection was observed in at least two ovules. Although the material analyzed by Serbet et al. (2010) comes from another region, they proposed a new emendation of the Indian genus. Ricardi-Branco et al. (2015) and Mune et al. (2016) also reported the presence of *B. heterophylla* in Permian strata of Brazil.

The specimens studied from the Bajo de Veliz locality can be compared with *B. heterophylla* from India and Antarctica because of their similar vegetative and reproductive parts. The second-order branches bear two types of leaves: simple and with multiple bifurcations that form a complex lamina. The Argentinean leaves are multifid with distal margin incised into multiple simple apices of apex acute, whereas, in the Antarctic specimens the apices are mainly bifurcate (Serbet et al., 2010: pl. 1, figs 1–6, pl. 2, fig. 4).

The reproductive structures composed of lax ovules are also comparable to those described for *B. heterophylla* in terms of size and their insertion on the axes of ultimate branches (Serbet et al., 2010: pl. 3, fig. 2), but differ by lacking a bifid apex (Fig. 5G, H). The ovules in the Argentinian specimen are similar to those illustrated from India.

The rest of the specimens from Bajo de Veliz (CORD-PB 2816, CORD-PB 3310, CORD-PB 3323) correspond to sterile branches, where the decurrent second-order branches of variable size bear small heteromorphic leaves helically arranged. These characteristics are shared with *B. heterohylla*.

The presence of non-apical vegetative buds or young shoots arranged on the main axis and between secondary branches in specimens from the Bajo de Veliz Formation is a character not previously described for these Paleozoic conifers.

Although *Genoites patagonica* (Cúneo, 1985), an allied genus of *Buriadia* (Cúneo, 1985), shares the arrangement and type of lax ovule without bifid apex, but differs by its entire or apically bifurcate linear leaves (Cúneo, 1985: see fig. 3), while the specimens here described have multifid leaves (Figs 3, 5F, G, H).

The vegetative branches of *Krauselcladus* present two morphological types of leaves: simple (linear, straight or falcate) and lobed leaves (bilobed or trilobed) arranged spaced and densely on the axes, which differ from the multifid leaves with incised distal margin of the specimens here described.

Family FERUGLIOCLADACEAE Archangelsky et Cúneo, 1987

Genus *Feruglіocladus* (Feruglio) Archangelsky et Cúneo, 1987

Type species *Feruglіocladus riojanum* Archangelsky et Cúneo, 1987

Type locality. Anzulón, Arroyo Totoral Formation, La Rioja Province, Argentina

Feruglіocladus* cf. *F. riojanum Archangelsky et Cúneo, 1987

Fig. 6

Studied material. BAFC-PB 184, MIC-P 913

Description. Vegetative leafy axes up to second order of branching. First order axes reach a length of 2.8 cm to 3.5 cm and a width of 0.6 cm to 0.8 cm (including leaves) (BAFC-PB 184 and MIC-P 913). In their distal portion, these present two ramifications that reach 2.5 cm to 4.1 cm in length and 0.4 cm in width (Fig. 6A, C). All branches are covered by small, lanceolate leaves, appressed at the base and slightly overlapping, with parallel margins and acute and straight apices, slightly curved towards the apex of the branch, arranged in spiral phyllotaxis on very thin central axes (Fig. 6B, D, E). These leaves reach a length of 0.3 cm to 0.4 cm and a width of 0.1 cm. Indistinguishable venation.

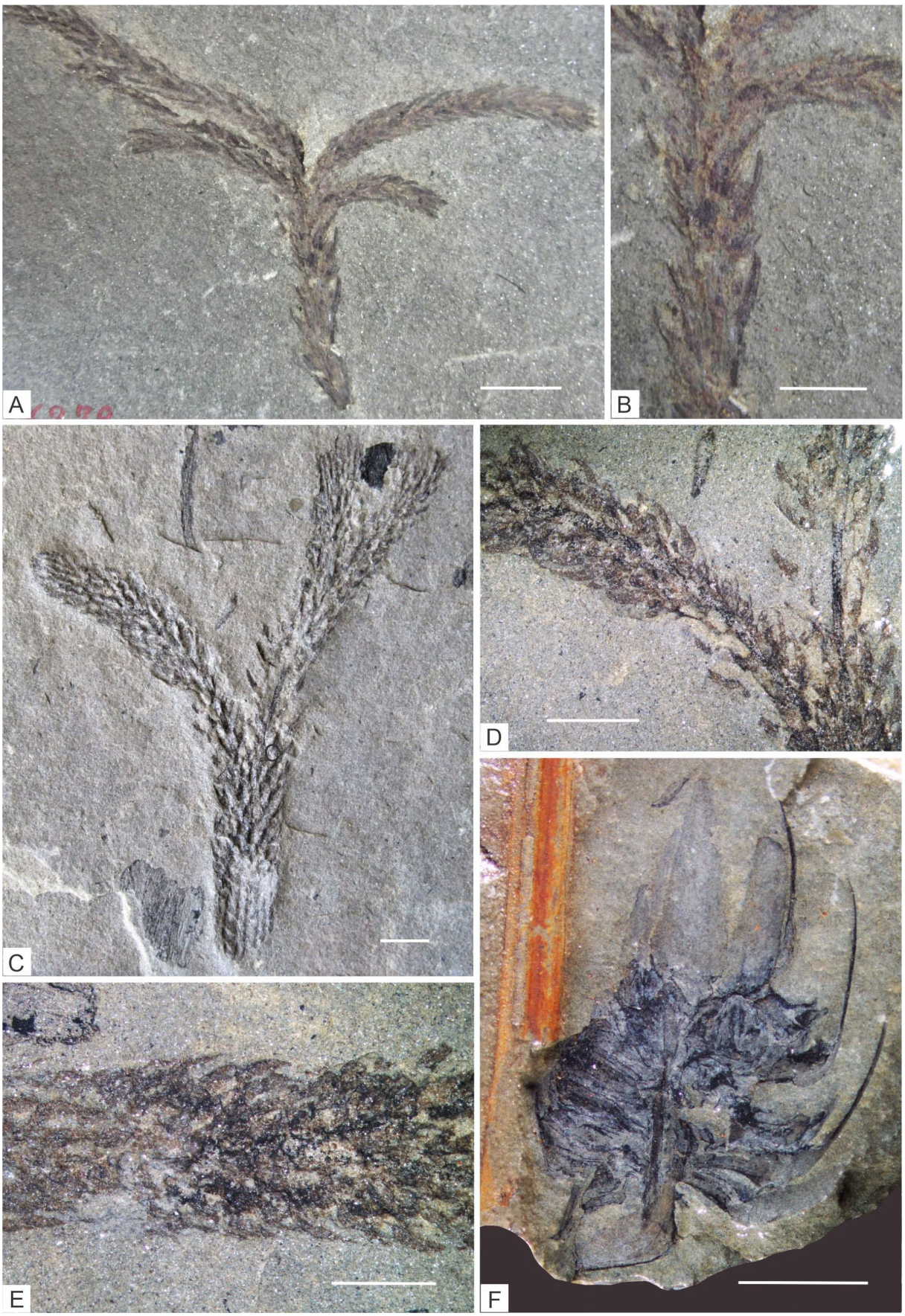

Figure 6. *Feruglioclados riojanum*. **A**, **B**. BAFC-PB 184, **A**. Vegetative axis with second order branching covered by small overlapped leaves, **B**. Detail of axis bearing densely arranged leaves; **C–E**. MIC-P 913, ramified specimen showing small leaves, **D**, **E**. Details of the leaves and the central narrow axis; **F**. LPPB 1452, incomplete male? cone showing a central axis bearing microsporophylls strongly curved upwards. Scale bars = 1 cm in A, 5 mm in B, C, D, E, F

Associated reproductive structure

Fig. 6F

Studied material. LPPB 1452

Description. The specimen LPPB1452 corresponds to an incomplete male cone. The structure is 1.6 cm long and 1.3 cm wide (Fig. 6F). Central axis 0.8 cm long and 0.2 cm wide. Microsporophylls are 1 cm long and 0.2 cm wide, lanceolate, inserted perpendicular to the axis and strongly curved towards the apex of the structure, overlapping each other. Given the fragmentary nature and preservation it is not possible to observe anatomical details.

Comparisons. Specimens BAFC-PB 184 and MIC-P 913 from Bajo de Veliz are alike to *Feruglíocladus riojanum* Archangelsky et Cúneo (1987: pl. 2, figs 1–2). This species was defined from the Arroyo Totoral Formation (Paganzo Basin) by Archangelsky and Cúneo (1987). The leaves are similar in arrangement and morphology, although they are smaller (up to 0.4 cm) whereas in *F. riojanum* they can reach 1 cm in length.

The specimen LPPB-1452 is an isolated structure comparable to the compact male cones of *F. riojanum* by the size of the sporophylls (up to 1 cm long) inserted perpendicularly to a central axis, strongly curved towards the apex of the cone. *F. patagonicus* from Río Genoa Formation (Tepuel-Genoa Basin) differs by its leaves markedly lanceolate, straight, with acute apex and wide base, and are up to 1.8 cm long.

Feruglíocladus riojanum, illustrated and described by Césari et al. (2014: pl. 2, figs 2–7) from the Ansilta Formation (Calingasta-Uspallata Basin), only differs from the material studied herein by having slightly larger leaves (up to 0.6 cm long) with leathery or woody appearance.

This fossil genus and *Ugartecladus* were included in the family Feruglíocladaceae by Archangelsky and Cúneo (1987) for the early Permian of Gondwana from vegetative branches and reproductive organs in organic connection. Both genera share similar vegetative branches and female cones but differ because in *Feruglíocladus* the ovules and seeds are larger, have a bifurcated apex, and more developed wings. It should be noted that in the palaeofloristic record of the Bajo de Veliz locality those typical seeds or ovules with forked apex have not yet been identified. Although these vegetative axes could be referred to the genus *Paranocladus*, it is preferred to assign them to *Feruglíocladus* due to the finding of associated cones that characterize the latter genus of known distribution in Argentina.

DISCUSSION AND CONCLUSIONS

During the latest Carboniferous-earliest Permian, significant floristic changes occur in the vegetation of westernmost Gondwana, with the appearance of glossopteridales characterizing the *Gangamopteris* Biozone (Archangelsky et al., 1996; Césari et al., 2007). This biozone, typified by the abundance of *Gangamopteris* over *Glossopteris*, includes the palaeoflora from Bajo de Veliz. Coniferophytes are already recorded in the late Pennsylvanian *Krauselcladus-Asterotheca* Biozone, although they are rare components in the floras of central-western Argentina.

Kurtz (1895, 1921: pl. 13, figs 134–137) referred and illustrated for the first time leafy branches as *Walchia* from the Bajo de Veliz Formation which were reassigned by Florin (1940) to *Paranocladus? fallax* Florin, a taxon whose specimens lack preservation of cuticular-anatomical features. This type of coniferous vegetative branches was also described by Coturel et al. (2009) from the Solca Formation (Paganzo Basin) and by Césari (2014) in the Cisuralian Tasa Cuna Formation.

Fertile coniferophytes were initially described in the Paganzo Basin (Arroyo Totoral Formation) by Archangelsky and Cúneo (1987) and referred to *F. riojanum*. The genera *Feruglíocladus* and *Ugartecladus* characterize the Family Feruglíocladaceae, and given their extensive areal distribution, they are included in the *Feruglíocladus* Biozone of Patagonia (Archangelsky and Cúneo, 1985). In Patagonia, *Feruglíocladus patagonicus*, *Ugartecladus genoensis* and *Genoites patagonica*, are the most important coniferous species from the lower Permian of the Río Genoa Formation (Cúneo, 1985; Archangelsky and Cúneo, 1987), of which the genus *Genoites* is apparently more primitive (Cúneo et al., 2022).

Correa et al. (2012) reassigned to *Feruglíocladus patagonicus* specimens formerly described as *Krauselcladus argentinus* from the Andapaico Formation, proposing its

younger age (lower Permian) and the presence of the *Feruglíocladus* Biozone in this unit of the southern Paganzo Basin. Additionally, Césari et al. (2014) reported the presence of *Feruglíocladus riojanum* in the lower Permian Ansilta Formation (San Juan province).

Genoites is another fertile taxon recognized in the Bajo de Veliz Formation; this genus, formerly constrained to the Permian of Patagonia, now has an expanded distribution to central-western Argentina.

Complete specimens from Bajo de Veliz allow the identification of *Buriadia*, a distinctive coniferophyte with simple and deeply incised leaves supporting randomly interspersed ovules. Their probable belonging to *B. heterohylla*, which had so far been reported from lower Permian strata of India (Singh et al., 2003), Antarctica (Serbet et al., 2010) and recently for Brazil (Ricardi-Branco et al., 2015; Mune et al., 2016), is a novel finding for Argentina.

In summary, the coniferophytes of the Bajo de Veliz Formation represent the two main upper Paleozoic groups of Argentina. Those that form lax reproductive structures like those of the Buriadiaceae Family from the lower Permian of Patagonia (Cúneo, 1985), and those that form compact male and female cones with associated seeds of the Feruglíocladaceae Family (Archangelsky and Cúneo, 1987) also from the lower Permian of Patagonia and Paganzo Basin.

The specimens studied consist of vegetative branch impressions with different branching orders and, in some cases, bearing fertile organs. *Feruglíocladus* cf. *F. riojanum* is represented so far only by vegetative axes with simple linear leaves and detached male reproductive structure, similar to those known for this species. Another vegetative branch, but showing heteromorphic leaves (simple, bifurcate to trifurcate), is assigned to *Krauselcladus* sp., a fossil genus with previous records in the late Pennsylvanian of the Paganzo Basin. Two allied genera are represented by fertile specimens of *Genoites* sp., initially described from Permian assemblages of Patagonia and the first record of *Buriadia*, a coniferophyte previously known from other Gondwanan areas.

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ADDITIONAL INFORMATION

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