

Fossil seeds from the La Cantera Formation, Early Cretaceous, San Luis Province, Argentina

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ABSTRACT. In a study of fossil seeds recovered from the La Cantera Formation, Early Cretaceous, San Luis Basin, we establish a new species, *Carpolithus volantus*, and describe other specimens attributed to *Carpolithus* spp. and *Ephedra canterata*. The botanical affinity of winged seeds assigned to *Carpolithus volantus* is discussed in relation to the fossil flora recovered from this formation. Based on the abundance of Gnetales in the San Luis Basin (pollen grains, reproductive and vegetative structures assigned to *Ephedra*), we propose that *Carpolithus volantus* is affiliated with Gnetales (*Weltwitschia*). We suggest that *Carpolithus* spp. seeds may be angiospermous, because this group, represented by leaves and flowers, dominates the fossil macroflora of the La Cantera Formation. Micro- and macrofloral analyses of the La Cantera Formation and an assessment of available dispersal vectors suggests that wind (anemochory) and water (hydrochory) may have been the most important dispersal strategies for these seeds. The abundance and small size of seeds recovered from the La Cantera Formation, together with their morphological characters, such as the presence of wings in *Carpolithus volantus*, also favour abiotic mechanisms of dispersal such as anemochory or hydrochory.

KEYWORDS: Fossil seeds, *Carpolithus*, La Cantera Formation, Early Cretaceous, Central-western Argentina

INTRODUCTION

Study of reproductive structures is crucial to an understanding of the life cycle of plants; moreover, morphological variations commonly reflect ecological and environmental adaptations (Harper et al., 1970; Haig and Westoby, 1989; Westoby et al., 2002; Tiffney, 2004; Sims, 2012). Seed anatomy contributes to accurate identification of whole-plant taxa (e.g., Vaughan, 1970; Wu et al., 2014; Benedict et al., 2015, 2016; McLoughlin and Pott, 2019), but research on fossil seeds presents many difficulties related to intra- and interspecific variability, as well

as morphologies that might alternatively be related to phylogeny or environmental conditions (Harper et al., 1970; Archangelsky, 2000). The great diversity of seed shape and size is related in part to seed dispersal mechanisms (Eriksson et al., 2000; Moles et al., 2005a,b; Eriksson, 2008; McLoughlin and Pott, 2019), so seeds offer a good starting point for interpreting plant palaeoecology (Tiffney, 1984; McLoughlin and Pott, 2019). The most primitive fossil seeds lack obvious adaptations to specific dispersal vectors (e.g., wind, water, animals) (Moles et al., 2005a), but wind and water probably have been the primary seed dispersal vectors

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since the emergence of terrestrial plants. From the Middle Jurassic to the Early Cretaceous, anemochory was a key strategy for seed dispersal (McLoughlin and Pott, 2019). Numerous fossil fruits and seeds have been described from the Cretaceous, many with excellent anatomical details preserved (Friis et al., 2011). Discussions about their dispersal mechanisms are rare. The most complete Early Cretaceous floras studied, including flowers, fruits, seeds and pollen grains, come from the Potomac Group at the Kenilworth and Puddledock localities, eastern North America (Crane et al., 1993; Pedersen et al., 1994; Friis et al., 2009), the non-marine Wealden Group of southern England (Austen and Batten, 2018), various localities in Portugal (Buarcos, Catefica, Torres Vedras: Lugar d' Almen, Fonte Granda and Almargem formations), and Famalicão (Figueira da Foz Formation) in the Lusitanian Basin (Friis et al., 1999, 2009). Other well-studied floras of this age come from the Jehol Group (Sunjiawan, Fuxin, Jiufotang, Yixian, Zhangjiakou and Tuchengzi formations) in Liaoning Province, China (Chang et al., 2003; Sha, 2007; Wang et al., 2016), and the Koonwarra Fossil Bed (Eumeralla Formation), Australia (Drinnan and Chambers, 1986; McLoughlin and Pott, 2019).

From Argentina there are records of *Carpolithus* in the Piedra Clavada Formation (Early Cretaceous), Quebrada Don Nielsen locality, Santa Cruz Province (Ballent et al., 2011). Seed compressions of angiosperms were described by Frenguelli (1953) from the Mata Amarilla Formation (Late Cretaceous), Santa Cruz Province.

Most Late Cretaceous records in this region come from Patagonia. For example, Gandolfo and Cúneo (2005) described fruit compressions with seeds similar to *Nelumbo* Adans (Nelumbonaceae) from the La Colonia Formation, Chubut Province. From the Neuquén Basin, seeds and angiospermoid reproductive structures from the Portezuelo Formation, Neuquén Group, have been assigned to two species of *Carpolithus* (Passalía et al., 2008).

Seed cuticles provide other evidence of the presence of reproductive structures in the fossil record. Most seed cuticles from the Cretaceous are assigned to the fossil genera *Costatheca* and *Spermatites*, both of uncertain botanical affinity. These “mesofossils”, with dimensions of 0.28–2.50 mm, possibly are related to either angiosperms or gymnosperms, but the chance that some of them are insect eggs cannot be

dismissed (Batten and Zavattieri, 1995, 1996). In Argentina, seed cuticles assigned to *Spermatites* were mentioned from the Plottier Formation (Late Cretaceous) Neuquén Group, (Musacchio and Vallati, 2007), and *Costatheca* was recorded from the Loncoche Formation (Late Cretaceous) at the Calmu-Co section (Papú, 2002), both from southern Mendoza.

The La Cantera Formation (El Gigante Group) has provided one of the most diverse and complete associations of palynomorphs and plant macrofossils from the late Aptian of central western Argentina, including primitive angiosperms (Prámparo, 1990, 1994; Prámparo et al., 2007; Archangelsky et al., 2009; Puebla, 2009, 2010; Puebla et al., 2012, 2017). In addition, reproductive structures including several fossil seeds of different morphological types were identified. Before the present study, these fossil seeds were not described in detail, except for ovulate cones of *E. canterata* published recently by Puebla et al. (2017). Here we provide new photos and descriptions of more specimens of this species. We describe and provide details of the reproductive structures recovered from the La Cantera Formation, San Luis Basin. We discuss their botanical affinities and propose possible forms of dispersal, based on seed morphology. Finally, considering the entire group of plants represented in the fossil record of the basin, we evaluate their possible dispersal strategies and their implications for paleoecological and paleoenvironmental interpretation of mid-latitude Cretaceous floras of central western Argentina, South America.

GEOLOGICAL SETTING

The studied fossils come from the type section of the La Cantera Formation (32°59'25"S, 66°52'48"W) of the El Gigante Group (Flores and Criado Roque, 1972), San Luis Basin, Argentina (Fig. 1). The El Gigante Group consists of six formations: Los Riscos, El Jume, La Cantera, El Toscal, La Cruz and Lagarcito (Flores, 1969; Rivarola and Spalleti, 2006).

The La Cantera Formation is built of laminated greenish grey mudstone, siltstone and claystone, with reddish brown sandstone and grey siltstone interbedded at the top of the succession. It may represent deposition in ephemeral lakes related to a fluvial environment with some periods of a very quiet lacustrine system

allowing the preservation of delicate fossils (Flores and Criado Roque, 1972; Criado Roque et al., 1981; Prámparo, 1989). Recently, Castillo-Eliás et al. (2016) described MISS structures related to a bacterial seal (biofilms), which probably protected the organisms from degradation, making the La Cantera Formation an important source of paleoecological and paleoenvironmental information on a Cretaceous siliciclastic lacustrine system. Prámparo (1999a) interpreted the formation to have been deposited in a shallow freshwater eutrophic environment with some evaporitic episodes, based on the presence of a diverse and abundant phytoplankton (*Scenedesmus*, *Tetrastrum*, *Tetraedron*, *Botryococcus*, *Leiosphaeridia*) (Tab. 1). Aquatic insects, fish, ostracods and spinicaudatans have been recorded in the same sections (Petrulevicius et al., 2010; Arcucci et al., 2015; Giordano, 2017). Based on palynological studies, the La Cantera Formation is late Aptian in age (Prámparo, 1990, 1994, 1999a,b; Prámparo et al., 2007).

MATERIAL AND METHODS

The described specimens were found in finely laminated shales as coalified compressions lacking preserved cuticles. A total of 64 reproductive structures

were studied and compared with published Cretaceous seeds (e.g., Tiffney, 1984; Friis et al., 2014). Modern comparative material was obtained from the collections of Herbario de Plantas Vasculares del Museo de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina (BA).

The fossils were studied using a Leica Mz 125 stereomicroscope and photographed with a Nikon Coolpix 990 digital camera. Some specimens were observed using a LEO 1450VP scanning electron microscope (SEM) of LABMEM (Laboratorio de Microscopía Electrónica y Microanálisis, Universidad Nacional de San Luis). Fossil specimens are housed at Museo Interactivo de Ciencias (MIC) of Universidad Nacional de San Luis (UNSL), San Luis Province, Argentina, under the acronym MIC-P.

COMPOSITION OF THE FOSSIL FLORA

The fossil record of La Cantera comprises impressions and compressions of bryophytes, monilophytes (Equisetidae), gnetophytes (*Ephedra*), angiosperms, and various reproductive structures such as seeds, cones and flowers (Puebla, 2009, 2010; Puebla et al., 2012, 2017) (Tab. 1). The palynoflora was dominated in nearly all the studied assemblages by aquatic forms such as freshwater algae (Prámparo, 1988b, 1990, 1994, 2012). The terrestrial paleoflora was dominated by gymnosperms, with

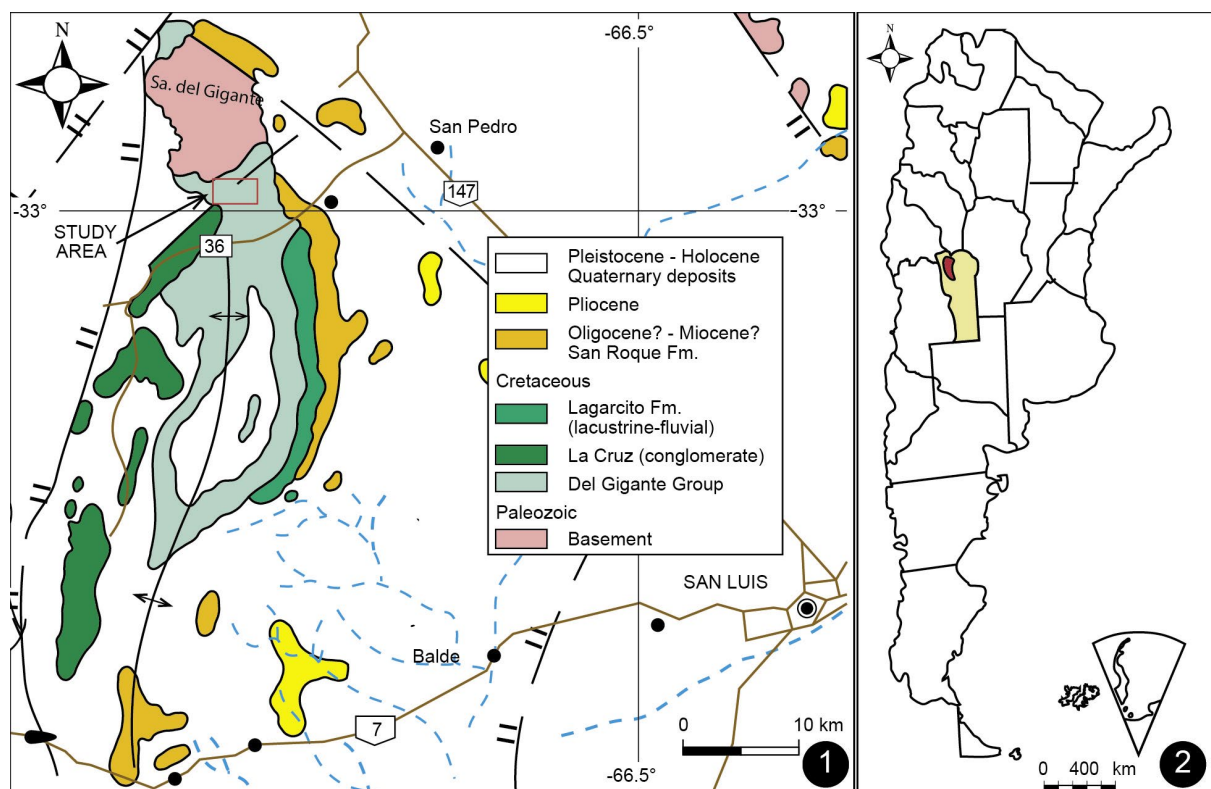


Fig. 1. 1. Geological map showing the La Cantera Formation type locality at Sierra del Gigante (ridge), with exposures of Cretaceous and Cenozoic units in the region (modified from Puebla et al., 2017); 2. Location of San Luis Province, Argentina

Table 1. Micro- and macrofossil record from the La Cantera Formation. In gray are the taxa from the present study (*Carpolithus volutus*, *Carpolithus* spp.)

Macroflora				Microflora			
Taxon	Description	Reference	Algae (Aquatic forms)	Taxon	Description	Reference	
Algae (Aquatic forms)				<i>Crucigeniella?</i> sp.		Prámparo, 1990, 1999a	
				<i>Scenedesmus</i> sp., <i>Tetrastrum</i> cf. <i>multiflorum</i> , <i>Botryococcus</i> sp.	cenobia/colonies	Prámparo, 1990, 1999a	
				<i>Chlorococcaceae</i>		Prámparo, 1999a	
				Algae indet.	spores	Prámparo, 1999a	
Bryophyta	<i>Thalites</i> sp., cf. <i>Hepatites</i> sp.1 and cf. <i>H.</i> sp. 2	Puebla et al., 2012		<i>Cosmapheridium?</i> sp., <i>Leiosphaeridia</i> spp.	hilate spores/cingulate spores	Prámparo, 1990, 1994, 2012	
	<i>Muscites</i> sp.	Puebla et al., 2012		<i>Staplinsporites caminus</i> , <i>Coptospora</i> spp., <i>Zivisporis reticulatus</i> , <i>Tauracosporites segmentatus</i>	zonate spores	Puebla et al., 2012	
				<i>Couperisporites</i> cf. <i>complexus</i> , <i>Triporoletes reticulatus</i> , <i>Foraminisporis asymmetricus</i>	zonate spores	Prámparo, 1990, 1994	
				<i>Aequitriradites</i> cf., <i>A. verrucosus</i>	trilete spores	Prámparo, 1988a, 1989, 1994	
				<i>Leptolepidites macroverrucosus</i> , <i>L. major</i>	trilete spores	Prámparo, 1988a, 1989, 1994	
Monilophyta				<i>Deltoidospora</i> sp., <i>Baculatisporites</i> spp., <i>Osmundacidites</i> spp.	trilete spores	Prámparo, 1988a, 1989, 1994	
				<i>Crybelosporites</i> sp.	trilete spores	Prámparo, 1990	
				<i>Schizaeosporites</i> sp., <i>Cicatricosporites australiensis</i> , <i>Cicatricosporites</i> spp., <i>Appendicisporites macalisteri</i> , <i>A.</i> spp.	monoete/trilete spores	Prámparo, 1989, 1994	
Cupressaceae?	<i>Carpolithus volutus</i>			<i>Podocarpidites</i> spp., <i>Rugubivesiculites</i> spp., <i>Trisaccites microsaccatus</i>	bisaccate/trisaccate pollen grains	Prámparo, 1990, 1994	
				<i>Araucariaceae</i>	hilate pollen grains	Prámparo, 1994	
				<i>Cheirolepidiaceae</i>	rimulate pollen grains	Prámparo, 1990, 1994	
				Coniferales	bisaccate/monosaccate pollen grains	Prámparo, 1990, 1994	
				Gymnospermales	monosulcate pollen grains	Prámparo, 1990, 1994	
				<i>Ginkgoales/Cycadales/Benettitales</i>			
Ephedraceae	<i>Ephedra canterata</i>	Puebla et al., 2017		<i>Ephedripites</i> spp., <i>Steevesipollenites</i> spp., <i>S. pygmaeus</i> , <i>Steevesipollenites</i> sp., <i>Gnetaceapollenites barghoornii</i> , <i>Gnetaceapollenites</i> sp.	plicate pollen grains	Prámparo, 1990, Puebla et al., 2017	
				<i>Retimonocolpites</i> spp., <i>Tucanopolis</i> sp.	pollen grains	Prámparo, 1988a, 1989	
				<i>Stellatopolis barghoornii</i> , <i>Clavatipollenites hughesii</i> , <i>Afropollis</i> aff. <i>jaradinus</i> , <i>A. operculatus</i> , <i>A. zonatus</i> , <i>A.</i> spp., <i>Pennipollis</i> (ex <i>Brenneripollis</i>) <i>peroreticulatus</i> , <i>Asteropollis</i> complex (<i>Stephanocolpites mastandreaei</i> / <i>Huitrinipollenites transitorius</i>)	pollen grains	Prámparo, 1988b, 1989, 1990, 1999a,b, 2012	
				Angiospermales	pollen grains	Prámparo, 1988b, 1989	
				<i>Liliacidites</i> cf. <i>tectatus</i> , <i>Liliacidites</i> spp.	pollen grains	Prámparo, 1988b, 1989	

subordinate angiosperms and free-sporing plants (ferns, bryophytes). The gymnosperms are mainly represented by plicate and rimulate grains. Various species of *Ephedripites*/*Steevesipollenites* of gnetalean affinity frequently co-occur with monosulcate grains of *Cycadopites* and *Monosulcites*. *Classopollis* (Pinopsida: Cheirolepidiaceae) is also abundant in all the sections. Recently, Puebla et al. (2017) described a new fossil species of *Ephedra* (*E. canterata*), based on the presence of ovulate cones associated with vegetative remains and the female reproductive unit (Tab. 1).

SYSTEMATIC PALEONTOLOGY

Wang (2011) proposed conserving the fossil genus *Carpolithus* as an informal category used for fossil fruits and seeds that lack sufficient morphological details to make a more accurate generic assignment. In this work we use *Carpolithus* for relatively simple seeds recovered from

the La Cantera Formation. As in previous studies (Puebla et al., 2017), we follow Yang (2011) and call the reproductive units of ovulate cones “female reproductive units”.

Subdivision GYMNOSPERMAE
Lindley, 1830

Order GNETALES Blume, 1835

Family EPHEDRACEAE Dumort, 1829

Genus *Ephedra* L., 1753

Type species: *Ephedra distachya*
Linnaeus, 1753

Ephedra canterata Puebla et al., 2017

Pl. 1

Materials. (Sixteen specimens) MICP-P797, MIC-P798, MIC-P799, MIC-P801, MIC-P802,

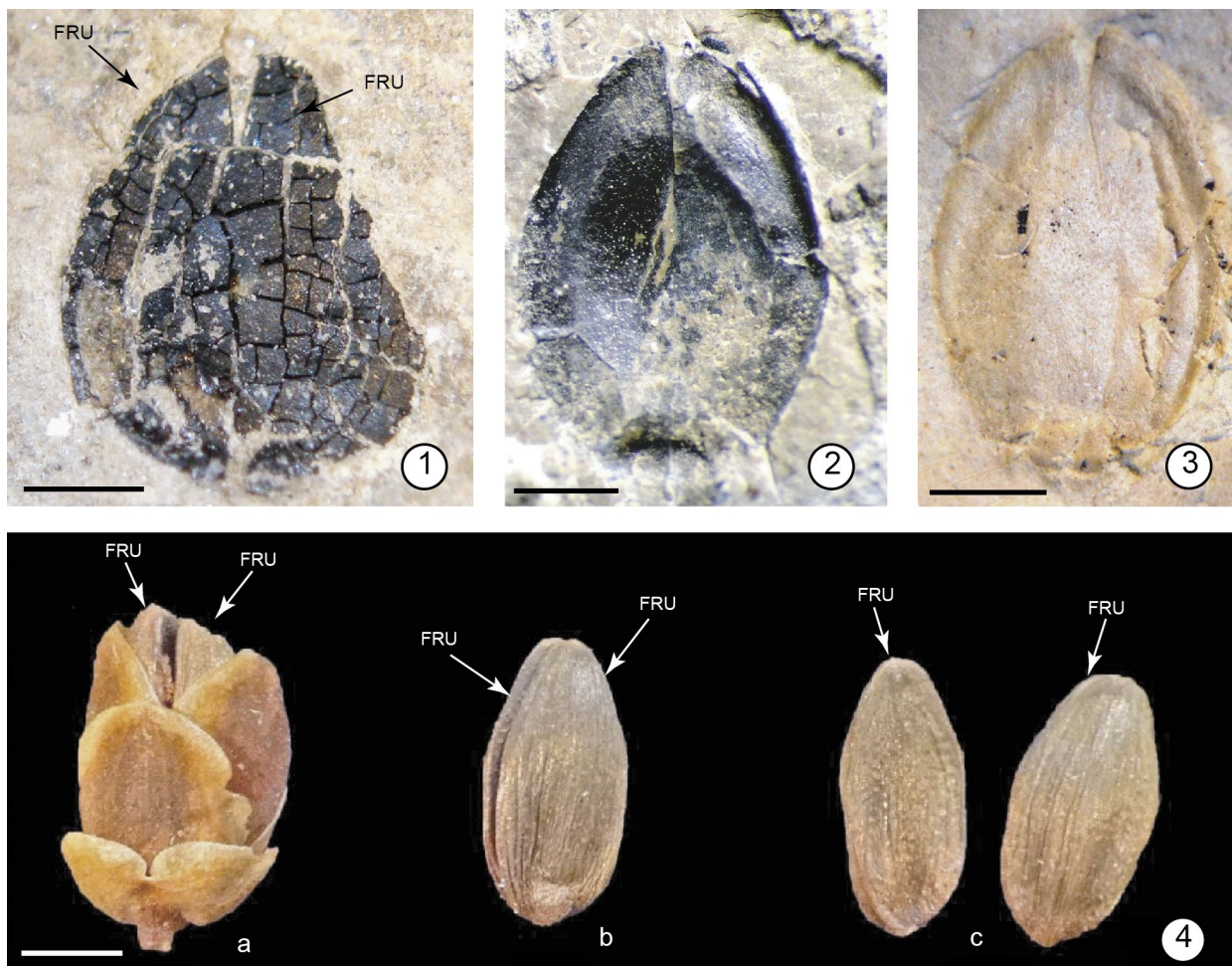


Plate 1. 1–3. Female reproductive units (FRU) of *Ephedra canterata*. 1. Specimen MIC-P684; 2. Specimen MIC-P852; 3. Specimen MIC-P798; 4. *Ephedra chilensis* (extant species), a. ovulate cone with bracts, b. FRU (inside cone), c. FRU isolated. Scale bar = 1 mm (1, 2, 3); 2 mm (4)

MIC–P803, MIC–P804, MIC–P806, MIC–P807, MIC–P811, MIC–P819, MIC–P826, MIC–P830, MIC–P834, MIC–P836, MIC–P852.

Dimensions. Width 1.43–3.70, avg. 2.90 mm; length 2.21–4.75, avg. 3.63 mm.

Description. Two female reproductive units joined by flat ventral face; dorsal face convex (Pl. 1, fig. 4a,b). Split of reproductive units (inside cone) evident only at apex (Pl. 1, figs 1–3, 4a,b). Outer epidermis papillate; among these papillae is a central large rounded protuberance interpreted as a trichome base. Whorls of bracts from ovulate cones not preserved.

Remarks. We include these specimens in *Ephedra canterata* erected by Puebla et al. (2017). The new specimens are consistent with *E. canterata* in size and shape, and they share a papillated outer seed envelope. The original diagnosis includes ovulate cones with fourth whorls of bracts but they are not preserved in the new specimens. The split in the apex probably was due to the arrangement of the ovules in the cone, as occurs in extant species (Pl. 1, figs 1–3, 4a,b).

Isolated Female Reproductive Unit

Pl. 2

Materials. (Fourteen specimens) MIC–P809, MIC–P814, MIC–P827, MIC–P832, MIC–P833, MIC–P838, MIC–P848, MIC–P849, MIC–P850, MIC–P855, MIC–P856, MIC–P858, MIC–P859, MIC–P860.

Dimensions. Width 1–3.42, avg. 2.64 mm; length 2.12–4.92, avg. 3.65 mm.

Description. Seed ovoid-ellipsoid, with acuminate chalaza and rounded apex. These isolated structures are not connected to ovulate cones, and it is not possible to differentiate the three distinctive layers (outer seed envelope, integument and nucellus). Outer epidermis papillated; between the papillae is a large central rounded protuberance, interpreted as a trichome base (Pl. 2, fig. 9).

Remarks. The studied specimens are considered to be isolated seeds because they are not attached to ovulated cones. They have the size, shape and papillae sculpture of the seed envelope, similar to the isolated female reproductive units described by Puebla et al. (2017).

Family Incertae Sedis

Fossil Genus *Carpolithus*
Linnaeus emend. Seward, 1917

Type species: *Carpolithus thalictroides*
Brongniart, 1822

Carpolithus volutus sp. nov.

Pl. 3

Holotype. MIC–P810 (Pl. 3, fig. 4).

Paratype. MIC–P808, MIC–P812, MIC–P813, MIC–P815, MIC–P816, MIC–P817, MIC–P818, MIC–P821, MIC–P822, MIC–P823, MIC–P824, MIC–P825, MIC–P829, MIC–P831, MIC–P844, MIC–P846, MIC–P847 (Pl. 3, figs 1–3, 5–9).

Type locality. Type section of the La Cántera Formation (32°59'25"S, 66°52'48"W), San Luis Province, Argentina.

Derivation nominis. *volutus* (Latin): the specific epithet refers to dispersal strategy by wind.

Diagnosis. Winged and flattened seeds up to 4 mm in width or length, with two symmetric wings flanking a narrow elliptic central seed body.

Dimensions. Width of reproductive structure 1.16–3.96, avg. 2.58 mm, length 1.55–3.61, avg. 2.13 mm; width of seed body 0.42–1.23, avg. 0.75 mm, length 1.24–2.79, avg. 1.92 mm. Width of each wing 0.66–1.70, avg. 1.04 mm, length 0.75–3.61, avg. 1.95 mm (see Fig. 2).

Description. Flattened winged seeds. Central seed body flanked by two membranous wings. Seed body narrow and elliptic, with smooth surface. Acute apex and rounded chalaza. Apex extended into narrow projection probably corresponding to micropylar tube (Pl. 3, figs 4–9). Wings equal in size and shape and wider than body of seed. Some specimens have fine striations at base of wings that extend to more than mid-length. These striations also run along edge of seed body (Pl. 3, figs 1–5). Studied specimens have two wing morphotypes: (a) wings completely surrounding the seed body (Pl. 3, figs 1–3) and (b) wings reaching around half the length of the seed body (Pl. 3, figs 4–9).

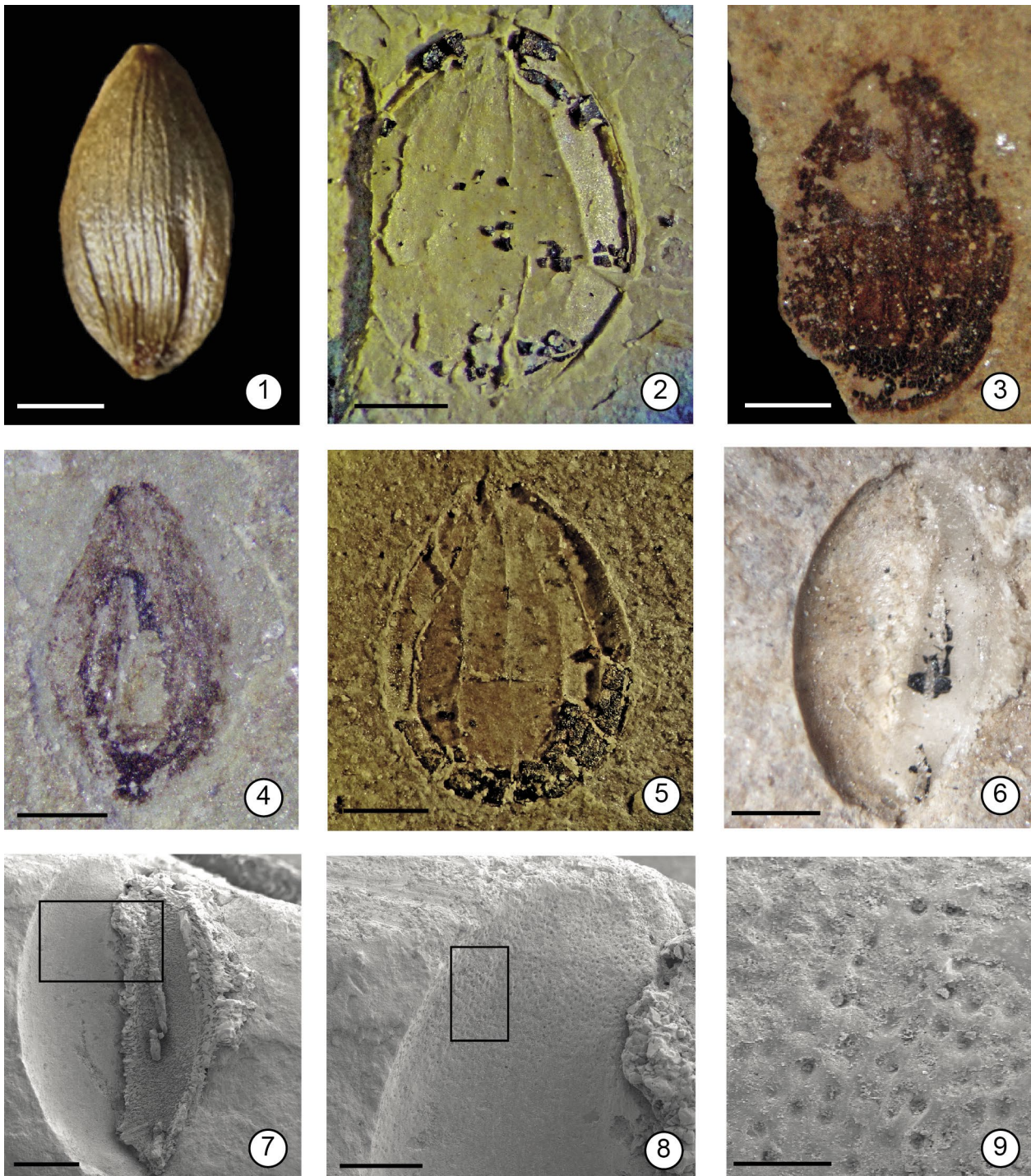


Plate 2. 1. Extant seed of *Ephedra chilensis*. 2–9. FRU isolated from *Ephedra canterata*. 2. Specimen MIC-P856; 3. Specimen MIC-P809; 4. Specimen MIC-P849; 6–9. Specimen MIC-P827; 7–9. SEM images showing impression of outer envelope of seed. Scale bar = 0.5 mm (4); 1 mm (3, 5, 6, 7); 2 mm (1); 200 μ m (8); 100 μ m (9)

Remarks. *Carpolithus volutus* is the most abundant type of fossil seed recovered from the La Cantera Formation. Unfortunately, all specimens of this species occur isolated, with no organic connection to a reproductive axis.

Botanical affinity and comparisons. Fossil seeds corresponding to *Carpolithus volutus* have morphological characters similar

to gymnosperm seeds of two families: Cupressaceae and Welwitschiaceae. Cupressaceae has an extensive fossil record from the Middle Jurassic (Escapa et al., 2008; Spencer et al., 2015). The Cretaceous was an important time for diversification of this family (Stockey et al., 2005). Extant representatives occur in both hemispheres (Harris, 1979; Rothwell et al., 2011). Seeds from this family are consistent

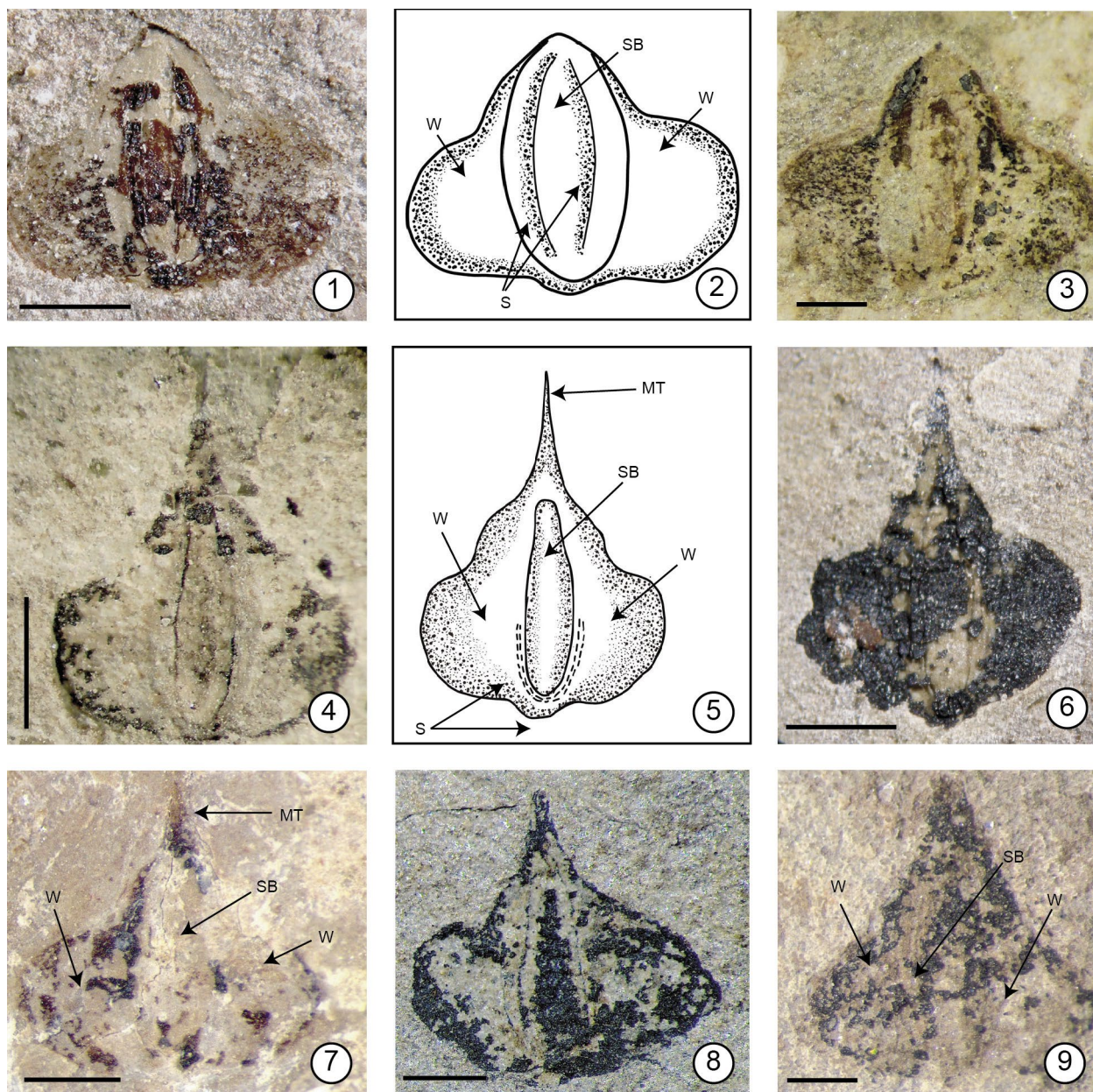


Plate 3. *Carpolithus volutus*; **1.** Specimen MIC–P846; **2.** Line drawing of MIC–P822 showing the striations (S) emerging from base of seed; **3.** MIC–P822 showing wings (W) covering half of seed body; **4–9.** Specimen with wings completely bordering seed body **4.** Specimen MIC–P810 showing narrow projection corresponding to micropylar tube (MT) in apex of seed body (SB); **5.** Line drawing of MIC–P810; **6.** Specimen MIC–P821; **7.** Specimen MIC–P825; **8.** Specimen MIC–P882; **9.** Specimen MIC–P817. Scale bar = 0.5 mm (3, 1); 1 mm (4, 6–9)

within each natural genus and have diagnostic characters for classification in terms of shape and wing arrangement (Kvaček et al., 2000). Moreover, seeds of most Cupressaceae genera have two equal wings (e.g. *Athrotaxis*, *Chamaecyparis*, *Cunninghamia*, *Thuja*, *Sequoiadendron*, *Thujopsis*, *Cupressus*, *Fitzroya*, *Tetraclinis*, *Widdringtonia*, *Neocallitropsis*), like *Carpolithus volutus* (Pl. 3). However, only a few genera (*Athrotaxis*, *Chamaecyparis*, *Thuja*, *Cupressus*, *Fitzroya*) have seeds with dimensions similar to our fossils (< 5 mm). Notably, there are no records of Early Cretaceous

seeds of Cupressaceae similar to those from the La Cantera Formation. Gnetophytes had their peak diversity during the Cretaceous, based on palynological data (Krassilov, 1982; Crane and Upchurch, 1987; Rydin et al., 2003; Dilcher et al., 2005; Taylor et al., 2009). Currently, Gnetales is represented by three monogeneric families: Gnetaceae, Ephedraceae and Welwitschiaceae, which all share reproductive characters (Rydin et al., 2006; Kunzman et al., 2011). *Welwitschia mirabilis*, the single extant species of Welwitschiaceae, is geographically restricted to the arid coastal fringe of Namibia

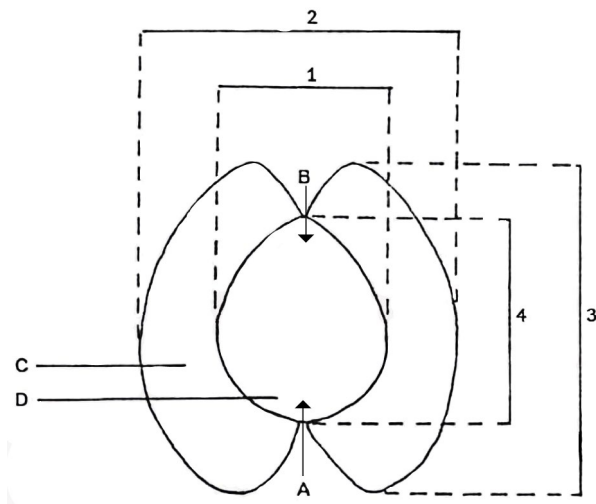


Fig. 2. Line drawing (modified of Lele, 1969) showing the main dimensions considered in descriptions of seed morphology: 1. Width of seed body; 2. Total width of seed; 3. Length of wings; 4. Length of seed body. A. Chalaza; B. Apex; C. Wing; D. Seed body

and Angola (Bornman et al., 1972). This species produces enclosed seeds in a membranous winged perianth and generally measures more than 2 cm long (Hooker, 1863; Kubitzki, 1990). *Carpolithus volutus* shares some morphological characters with *Welwitschia*, such as membranous wings with a smooth surface that surround the seed body.

The best-studied fossil records of *Welwitschia*-like seeds correspond to *Bicatia* from the Early Cretaceous of Portugal and North America (Friis et al., 2014). This fossil taxon has been assigned to *Welwitschia*-like plants, based on the combination of the external morphology of their seeds and *in situ* pollen (Friis et al., 2014). *Bicatia* shares with *Carpolithus volutus* the flattened winged seed, but it does not exceed 1 mm width and 1.3 mm length; *Carpolithus volutus* is more than 1 mm wide and 1.5 mm long (Pl. 3). Additionally, *Bicatia* has a rough surface that differs from the smooth surface of *Carpolithus volutus*.

Krassilov and Schrank (2011) described *Qataniaria* with a probable affinity to Gnetales from the upper Albian of the Hatira Formation, Makhtesh Qatar, northern Negev, Israel. The associated fruiting bodies are enclosed in cataphylls similar to the foliage. The structures are also considered gnetophytic, with lobed wings that probably correspond to persistent bracteoles as in *Welwitschia*. *Qataniaria* shares with *Carpolithus volutus* the presence of wings and similar measurements. However, the fossils from Israel lack a detailed description for further comparisons.

Subdivision ?ANGIOSPERMAE
Lindley, 1830

Family Incertae Sedis

Carpolithus spp.

Pl. 4

Referred materials. (sixteen specimens) MIC-P800, MIC-P820, MIC-P835, MIC-P837, MIC-P839, MIC-840, MIC-P842, MIC-P851, MIC-P853, MIC-P864.

Dimensions. Width 0.68–2, avg. 0.99 mm, length 0.68–2, avg. 1.29 mm.

Description. Isolated seeds small (<2 mm), rounded or narrow and elliptic. Rounded apex and chalaza. Some specimens have smooth surface (Pl. 4, figs 1–6) and others have keel-like structure (Pl. 4, fig.7). Some have micropyle-like structure at apex (Pl. 4, figs 1–3, 7–8).

Remarks. The specimens included in *Carpolithus* spp. are less than 2 mm in size; they are smaller than the other fossil seeds described from the La Cantera Formation. Although some differences between the specimens included in *Carpolithus* spp. can be observed, they do not preserve many anatomical characters to assign them a definite botanical affinity.

Botanical affinity and comparisons. The diminutive seeds included in *Carpolithus* spp. lack any obvious architectural modifications for dispersal (Pl. 4). Angiosperms dominate the macroflora of the La Cantera Formation and are represented by a record including leaves and reproductive structures (Archanglesky et al., 2009; Puebla, 2009, 2010; Tab. 1). These early fossil flowers are very small and presumably produced tiny seeds. Based on their abundance and small size, *Carpolithus* spp. could be related to angiosperms.

DISCUSSION

THE EVOLUTION OF SEED SIZE

Seed size is critical to many aspects of plant ecology and evolution (Harper et al., 1970; Westoby et al., 1996; Leishman et al.; 2000; Moles et al.; 2005a,b; Eriksson, 2008). Several authors have shown a correlation between

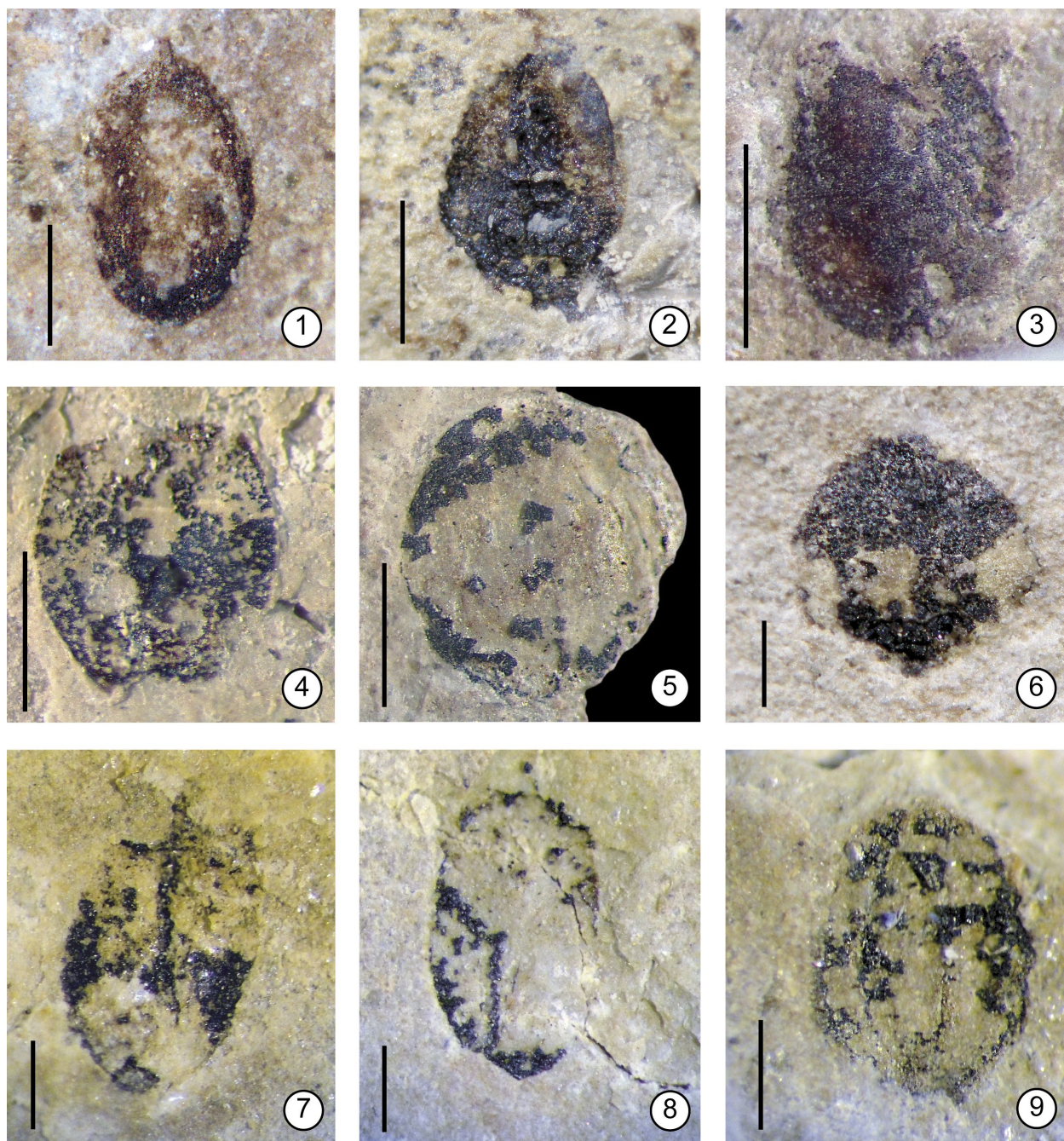


Plate 4. *Carpolithus* spp. 1. Specimen MIC-P800; 2. Specimen MIC-P820; 3. Specimen MIC-P880; 4. Specimen MIC-P853; 5. Specimen MIC-P881; 6. Specimen MIC-P671; 7. Specimen MIC-P839; 8. Specimen MIC-P835; 9. Specimen MIC-P851. Scale bar = 0.5 mm

habit, habitat, size and seed number. For example, ephemeral plants of open or unstable habitats generally produce many small seeds that can be widely dispersed, often by abiotic mechanisms (Salisbury, 1942; Harper et al., 1970; Silvertown, 1981; Tiffney, 1984; Shipley and Dion, 1992; Eriksson, 2008). Openness of vegetation explains why seeds remained small during the Cretaceous and biotic dispersal was not promoted (Eriksson et al., 2000). A comparative study of angiosperm seed size from the Early Cretaceous to the Neogene

suggests that small seeds prevailed until the Late Cretaceous, and seed dispersal was mostly abiotic (Eriksson et al., 2000; Moles et al., 2005b). From the Late Cretaceous to the Paleogene there was a marked increase in the average size of seeds, equivalent to about 2–3 orders of magnitude (Eriksson, 2008). Therefore it is probable that the earliest angiosperms were herbaceous plants (Doyle, 1996; Eriksson, 2008). The angiosperm fossil leaves recovered from the La Cantera are small (0.1–2.7 cm long, 0.1–1 cm wide), so it is inferred

that they were probably herbaceous (Puebla, 2009, 2010), and some of the specimens studied here (*Carpolithus* spp.) could belong to this group (Pl. 4).

The difference in seed mass between gymnosperms and angiosperms is evident both in the fossil record and in the extant species. In the Cretaceous, the smallest gymnosperm seeds are about two orders of magnitude larger than the smallest angiosperm seeds (Moles et al., 2005b). Small Cretaceous seeds probably belonged to angiosperms that were shrubs, small trees or even herbs (Wing and Tiffney, 1987; Wing and Boucher, 1998; Eriksson, 2008). The European and North American fossil angiosperms from Cretaceous strata all have small reproductive organs, with the dimensions of seeds, fruits and flowers varying between 0.5 and 3 mm (Frumin and Friis, 1999; Rydin et al., 2006).

ANALYSIS OF DISPERSAL STRATEGIES IN SPORES, POLLEN GRAINS AND SEEDS

We analyzed the dispersal strategies of plants from the La Cantera Formation, based on micro- and macrofossils (Tab. 1).

Bryophyta

The bryophytes *sensu lato* were important components of early terrestrial floras (Bateman et al., 1998; Renzaglia et al., 2007), with a wide range of habitats (Mishler, 2001). The Cretaceous saw an evolutionary radiation and dispersion of bryophytes. Fossil remains found from this period are easily assigned to extant genera because their morphology is conservative (Frahm, 1994; Taylor et al., 2009). In the La Cantera Formation, spores together with diverse macrofossils belonging to Bryophyta were recovered from the same fossiliferous strata. Puebla et al. (2012) found predominance of spores and thalli with hepatic affinities within the assemblage. The record of trilete spores of Bryophytes is sparse, represented by the hilates such as *Couperisporites* sp. cf. *C. complexus*, *Aequitridites* sp. cf. *A. verrucosus*, *Foraminisporis symetricus*, *Zlivisporis reticulatus* and *Coptospora* spp. (Puebla et al., 2012) (Tab. 1).

Bryophytes are ecologically sensitive, small (a few millimeters to decimeters), niche-specific, and intolerant to seawater. Generally they need a humid environment for their

development (Bates et al., 2009). The La Cantera Formation represents ephemeral lake deposits of a fluvial floodplain setting (Flores and Criado Roque, 1972), which allowed preservation of delicate structures such as bryophyte thalli.

Sexual reproduction of these plants is strongly related to the availability of water because male gametes move only short distances (Longton and Schuster, 1983; Hedderston and Longton, 1995; Bell and Hemsley, 2000; During, 2007; Frahm, 2007; Vanderpoorten and Goffinet, 2009; Devos et al., 2011). In asexual reproduction, spores disperse mainly by wind (anemochory) (Zander, 1979).

Monilophyta

During the Early Cretaceous, ferns grew and accumulated under warm conditions in moist environments including wetlands, mires, riverbanks and the understory of forests (Collinson, 2002; Van Konijnenburg-van Cittert, 2002). Two families were particularly important during the Early Cretaceous: Osmundaceae and Schizaeaceae. Modern Schizaeaceae are distributed in warm and humid environments (Skog, 2001). Their spores are dispersed mainly by wind and water (Traverse, 1988). Most ferns are homosporous. These ferns have free-living bisexual gametophytes, so they can establish new populations in distant places by scattering individual spores. For these reasons, ferns can respond more readily to environmental changes than flowering plants can (Kato, 1993). Monilophyta are represented in the La Cantera paleoflora by diverse but not abundant spores (Prámparo, 1989). Spores belonging to the homosporic ferns Lycopodiaceae, Cyatheaceae, Dicksoniaceae and Schizaeaceae, and the heterosporous ferns Marsileaceae and Selaginellaceae, occur in the palynoflora (Prámparo, 1989, 1990, 1994) (Tab. 1). So far, ferns have not been recorded in the macroflora.

Gymnospermae

During the Mesozoic, gymnosperms including cycads, conifers and ginkgos reached their peak in species richness and ecological importance (Harris, 1979; Thomas and Spicer, 1986; Henry, 2005). The Mesozoic is considered the golden age of conifers, given their expansive

radiation and floristic dominance (Harper et al., 1970).

Gnetales are a group of interest to botanists because their relationships with other seed plants are still unknown (Crane et al., 2004; Ickert-Bond and Renner, 2016). Recently the new species *Ephedra canterata* was described from the La Cantera Formation, based on vegetative and reproductive remains (Puebla et al., 2017). Plicate pollen grains are also very abundant and diverse in the palynoflora (Tab. 1). The *Ephedripites* complex (= pollen grains of gnetalean affinity) includes *Ephedripites* spp., *Gnetaceapollenites* spp., *Steevesipollenites* spp. and *Jugella* spp. (Prámparo, 1990; Prámparo et al., 2018; Puebla et al., 2017). The abundant plicate pollen grains associated with the macrofossils confirm the strong representation of this group in the basin (Puebla et al., 2017).

The modern representatives of *Ephedra* grow in dry environments; their abundance during the Cretaceous could be related to the warmer and drier environments that developed in tropical and subtropical regions during this period (Scotese et al., 1999; Wang and Zheng, 2010). The cones of *Ephedra canterata* have dry membranous bracts and small seeds, so anemochory is inferred as the mechanism of dispersal of these seeds (Puebla et al., 2017). This morphology is evident in seeds of some extant species of *Ephedra* (Section *Alatae*), which are wind-dispersed (Hollander and Wall, 2009; Hollander et al., 2010). The abundant record of *Ephedra* in the La Cantera Formation (indicative of dry, even arid conditions) suggests a marked arid season in the basin during the late Aptian (Puebla et al., 2017; Prámparo et al., 2018).

Cheirolepidiaceae is an extinct conifer group dating to the Late Triassic (Axsmith and Jacobs, 2005); it disappeared around the Cretaceous/Paleogene boundary in most areas, except in southern Argentina, where it has also been recorded from the Early Paleogene (Barreda et al., 2012). This family was a characteristic and abundant element of low-latitude Cretaceous floras, mainly represented by *Classopollis* pollen (Alvin, 1982). It is also a frequent and abundant component of Early Cretaceous palynofloras of Argentina (Quattrocchio et al., 2011; Villar de Seoane and Archangelsky, 2014; Prámparo et al., 2018) and other high-latitude parts of Gondwana (Tosolini et al., 2015). *Classopollis*, together

with pollen grains of Gnetales (mainly those with *Ephedra* and *Welwitschia* affinity), have been used as indicators of aridity in paleoclimatic reconstructions, mainly in low to middle latitudes (Herngreen, 1996; Mejia-Velasquez et al., 2012; Prámparo et al., 2018).

The La Cantera Formation yielded abundant pollen grains of *Classopollis* at some levels (Prámparo, 1989, 1990, 1994). The abundance of these pollen grains, together with Gnetalean pollen, both inferred to be drought-resistant, indicate an expanding hot arid climate during the Aptian–Albian in the middle and low latitudes of Argentina (Prámparo et al., 2018). However, there are no records of conifer macrofossils in the basin. The La Cantera Formation palynoflora contains monosulcate grains of the fossil genera *Cycadopites* and *Monosulcites* (Prámparo, 1989, 2012) (Tab. 1). Most of the *Cycadopites*/*Monosulcites* pollen grains from the Late Jurassic to Early Cretaceous originated from Ginkgoales, Cycadales and Bennettitales that grew in lowland vegetation (Vakhrameev, 1991; Abbink et al., 2004). In addition, pollen grains related to Podocarpaceae (*Podosporites* sp. 1, *Rugubivesiculites* spp. 1–2 and *Trisaccites microsaccatus*), Araucariaceae (*Balmeiopsis limbatus*) and other Coniferales (*Alisporites similis*, *Calliasporites australiensis*) have been found in La Cantera (Prámparo, 1990, 1994) (Tab. 1). However, there are no records of these taxonomic groups in the macroflora so far.

Most gymnosperms are wind-pollinated, but beyond this, two main dispersal syndromes are known for the group. One of the dispersal syndromes consists of woody or coriaceous cones that generally contain winged seeds that are dispersed by wind (anemochory) or by gravity (barochory). The other consists of fleshy “fruits”/arils that surround wingless seeds that are dispersed by animals (zoochory) (Giddy, 1974; Givnish, 1980; McLoughlin and Pott, 2019).

The seeds included in *Carpolithus volantus* of the La Cantera Formation are double-winged (Pl. 3). The presence of such appendages indicates that anemochory was an important dispersal strategy (McLoughlin and Pott, 2019). Seed wings, especially double wings, provide improved aerodynamic properties, reducing the rates of descent and optimizing seed dispersal (Souza and Iannuzzi, 2012; Stevenson et al., 2015). The presence of this

morphological feature in *Carpolithus volutus* emphasizes anemochory as the main dispersal strategy for these seeds.

Angiospermae

The Cretaceous is crucial for understanding the evolution and radiation of angiosperms, one of the most important events in the history of the Earth's biota (Taylor and Hickey, 1990; Sun and Dilcher, 2002; Friis et al., 2006). The oldest unequivocal angiosperm remains come from Cretaceous strata and are represented by remains of leaves (Hickey and Doyle, 1977), flowers and floral organs (Friis et al. 2011).

Mesofossil assemblages from Cretaceous (Barremian–Aptian) strata contain an enormous diversity of isolated fruits and seeds (Friis et al., 1999, 2009, 2011). The study of these fossils has great potential for elucidating early angiosperm evolution (Friis et al., 2011). During most of the Cretaceous, angiosperm seeds were small and unspecialized (Tiffney, 1984; Friis and Crepet, 1987; Friis et al., 1995, 1997; Erikson et al., 2000), so their dispersal was probably abiotic (hydrochory or anemochory) (Tiffney, 1984; Eriksson et al., 2000; Eriksson and Kainulainen, 2011; McLoughlin and Pott, 2019). In the La Cantera Formation palynoflora, angiosperms are represented by *Afropollis* (*A. operculatus*, *A. zonatus*, *A. aff. jadinus*), *Retimonocolpites* sp., *Stellatopollis* sp., *Clavatipollenites* sp., *Tucanopollis*, *Penipollis* (ex *Brenneripollis*) *reticulatus* and the *Asteropollis* complex (*Stephanocolpites mastandrei*/*Huitrinipollenites transitorius* (Prámparo, 1999b; Prámparo et al., 2007). In addition, early angiosperm remains have been found as leaves, some of which are assigned to the eudicots (*LC-Microphyll trifoliolate*) (Archangelsky et al., 2009; Puebla, 2009), and small flowers (Puebla, 2010) (Tab. 1). These remains are all small (0.1–2.7 cm; Puebla, 2009, 2010).

The seeds included in *Carpolithus* spp. from the La Cantera Formation are very small (<2 mm) and unspecialized morphologically (Pl. 4). Seeds of *Archaeofructus liaoningensis* Sun et al. 1998 and *Sinocarpus decussatus* Leng et Friis 2003 also have no distinctive characters and are generally smooth, ellipsoidal and 1–2 mm long (McLoughlin and Pott, 2019). Therefore, based on the characters of *Carpolithus* spp., it is inferred that this type of seed could have been produced by small angiosperms and may be related to the small fossil

flowers recovered from the basin. Owing to its proximity to a lacustrine environment, *Carpolithus* spp. (<2 mm) could have been dispersed by wind or water.

CONCLUSIONS

Fossil seeds from the late Aptian of the La Cantera Formation, San Luis Basin, central western Argentina, are described and illustrated here for the first time. We described a new species of *Carpolithus*, plus additional specimens attributed to *Carpolithus* and *E. canterata*. These new fossils expand the floristic diversity of the San Luis Basin during the Early Cretaceous.

We discussed the botanical affinity of winged seeds assigned to *Carpolithus volutus* in the context of the entire plant association recovered from the formation. Thus, two alternative affinities are possible for the winged seed types: Cupressaceae or Welwitschiaceae. Their preservation as impressions or thin compressions precludes a detailed anatomical comparison (Pl. 3). Nevertheless, it is noteworthy that there is currently no evidence (within the macro- or microflora) of the presence of Cupressaceae in the La Cantera Formation. On the other hand, the discovery of *E. canterata* and abundant and diverse polylicate pollen grains confirms the strong representation of Gnetales in the San Luis Basin (Tab. 1). Furthermore, among polylicate grains, those that have a longitudinal aperture and probable affinity to *Welwitschia* were recognized in the microflora (Puebla et al., 2017). Thus, we deduced a more probable relationship of *Carpolithus volutus* to Gnetales.

Angiosperms are the dominant group in the macroflora of the La Cantera Formation (Puebla, 2010), being represented by small leaves (0.1–2.7 cm long, 0.1–1 cm wide) and flowers (<6 mm) (Puebla, 2009, 2010), so it is inferred that they were herbaceous plants. We suggest that some of the seeds studied here (*Carpolithus* spp.) could belong to this group.

Our analysis of the total floristic association (micro- and macroflora) of the La Cantera Formation and their morphological adaptations indicates that their dispersal strategy was mainly anemochory. However, we cannot exclude hydrochory as a dispersal strategy for small seeds.

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