

# First Miocene megafossil of arrowhead, alismataceous plant *Sagittaria*, from South America

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The first pre-Quaternary representative of Alismataceae from South America is reported based on achenes of *Sagittaria montevidensis* from the Palo Pintado Formation (upper Miocene) in the south of Salta Province, Argentina. Achenes are laterally compressed, have a lateral beak and a single recurved seed inside them. The fruits were found both in the base (10 Ma) and the top of the formation (~5 Ma), suggesting similar environmental conditions during this time period. A cursory review of the Alismataceae family in the fossil record, with a special interest in those South American reports is given. During the Oligocene–Miocene *Sagittaria* may have arrived from tropical Africa to South America and thence to North America.

**Key words:** Alismataceae, *Sagittaria*, achene, aquatic plants, fossil fruits, Neogene, Argentina.

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## Introduction

The monocot family Alismataceae sensu lato (including Limncharitaceae Takhtajan ex Cronquist, 1981) contains about 12 genera and approximately 100 species (Dahlgren 1980; APG III 2009; Chen et al. 2012). The family has a cosmopolitan distribution (Haynes and Holm-Nielsen 1994; Costa and Forni-Martins 2003; Soltis et al. 2005; Lehtonen 2009) and includes aquatic or semi-aquatic herbs with erect or floating leaves (Haynes and Holm-Nielsen 1994). Fossils of this family have been reported from the Lower and Upper Cretaceous and the Paleocene in North America, Europe, Siberia, and Africa (Berry 1925; Brown 1962; Golovneva 1997; Riley and Stockey 2004; Coiffard and Mohr 2018), but researchers disagree about whether all these fossil reports actually represent Alismataceae (Chandler 1963; Haggard and Tiffney 1997; Haynes and Les 2004; Chen et al. 2012).

The alismataceous genus *Sagittaria* has been considered to include up to 139 named species, but only about 20 of

them are currently considered as legitimate (www.tropicos.org; Zepeda and Lot 2005). Species of *Sagittaria*, commonly named arrowheads, are mostly distributed in America, from Canada to Argentina and Chile, although four species are reported in Europe, Asia, and Oceania (Haynes and Holm-Nielsen 1994; Adair et al. 2012). Three species of *Sagittaria* are recorded from Argentina (Rataj 1970, 1972; Matias and Irgang 2006). The fruits of *Sagittaria* consist of aggregates of achenes. These achenes are laterally compressed (flattened) and have different shapes, from sub-circular to lanceolate and oblanceolate. Among the most striking morphological characters, a lateral beak (persistent style) stands out, which has different degrees of development, and a strongly recurved seed. Chen (1989) suggested that *Sagittaria* originated in tropical wetlands and lake areas of Africa, during the Late Cretaceous. Then, it might have dispersed to South America and subsequently to North America (Chen et al. 2012). Data concerning the biogeographic history of Alismataceae family in South America are still scarce.

Recently, Neogene impressions of *Sagittaria* fruits

(described in this paper) were found in the Palo Pintado Formation from northwestern Argentina. This formation has been studied since the 1980-ies and nowadays discoveries still occur. Deposits of the Palo Pintado Formation indicate water bodies of low energy, as a wandering fluvial system that in rainfall periods overflowed from the channel, generating lagoons and swamps during late Miocene to Pliocene (Herbst et al. 1987; Galli et al. 2011).

In order to contribute to the history of the Alismataceae in Argentina and South America, in this paper the following objectives are proposed: (i) to describe the first record of *Sagittaria* from the Palo Pintado Formation; (ii) to perform a review of the Alismataceae in South America; (iii) and associate these data with stratigraphic, sedimentological and paleontological features.

*Institutional abbreviations.*—CTES-PB, Colección Paleontológica de la UNNE Dr. Rafael Herbst, Paleontological Collection of the Universidad Nacional del Nordeste, Corrientes, Argentina.

## Geological setting

The study area is located in the Eastern Cordillera, from 25°30' S to 66°15' W and 25°45' S to 66°00' W, approximately 200 km south of the city of Salta in northwestern Argentina (Fig. 1). Cenozoic sedimentary strata crop out in the Calchaquí Valleys as part of the regional Andean foreland basin that extended into the Eastern Cordillera.

The Payogastilla Group (Díaz and Malizzia 1983) in the Calchaquí Valleys is composed of continental deposits, including in ascending order formations Los Colorados (middle Eocene to Oligocene), Angastaco (middle to upper Miocene), Palo Pintado (upper Miocene) and San Felipe (Pliocene to lower Pleistocene). The Palo Pintado Formation is ~800 m thick and contains a tuff that has been dated at  $10.29 \pm 0.11$  Ma (K/Ar) by Galli et al. (2008). Near the top is another pyroclastic unit that was dated at  $5.27 \pm 0.28$  Ma ( $^{206}\text{Pb}/^{238}\text{U}$ ) by Coutand et al. (2006) and at  $5.98 \pm 0.32$  Ma by Bywater-Reyes et al. (2010). The unit com-

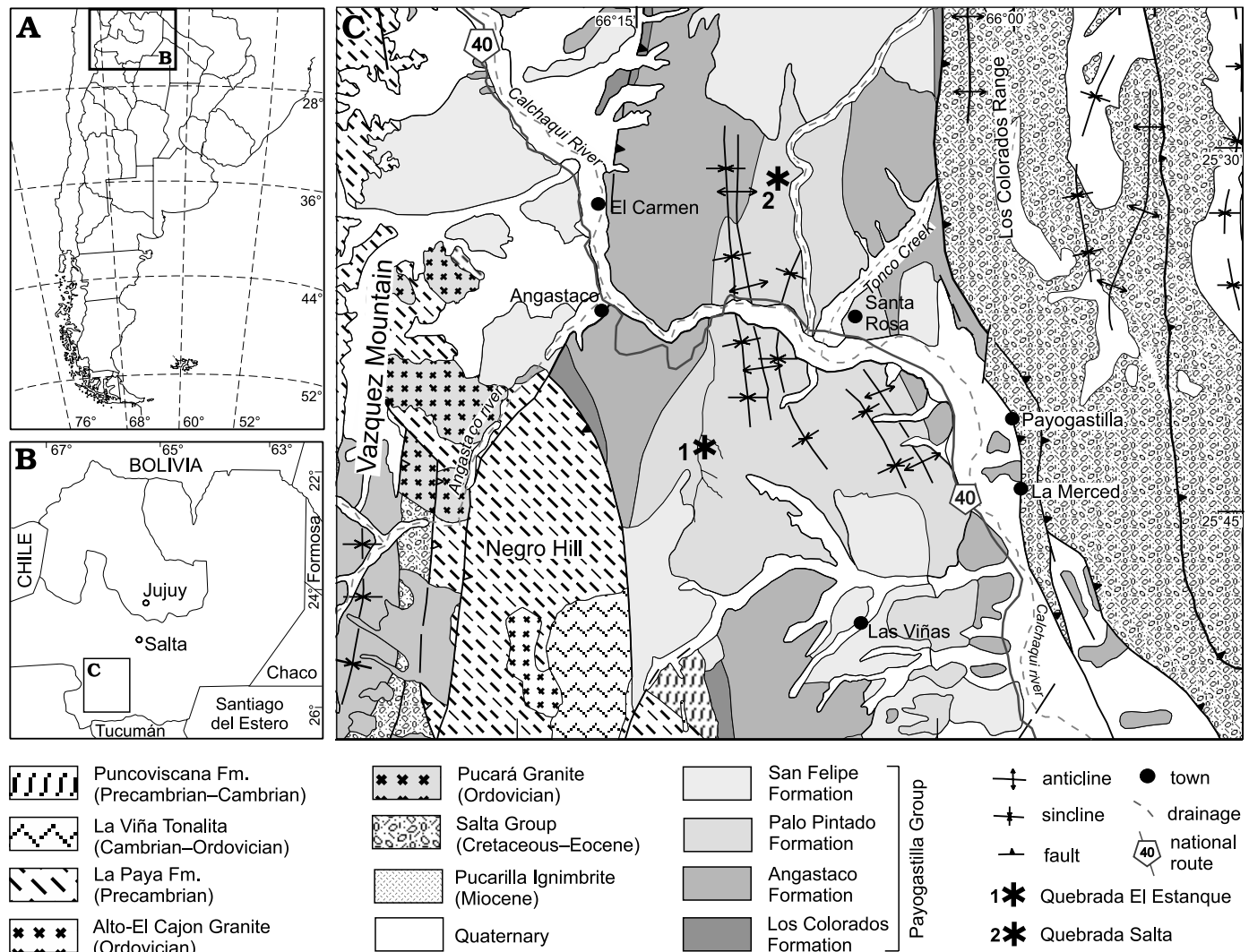


Fig. 1. A, B. Map showing location of the study area within Argentina. C. Geological map with indicated fossil localities of Quebrada El Estanque and Quebrada Salta.

prises thickening and coarsening-upward cycles, including matrix-supported conglomerate, fine to medium sandstone, and fine-grained sublithic sandstone that end in levels of green, brown and gray siltstone. These deposits consist of a transitional style between low- and high-sinuosity rivers that form wandering sand-gravel fluvial systems with small lakes. The geometry and the fluvial architectural characteristics are a direct consequence of allogenic controls, such as tectonic activity, under constant climatic conditions (Galli et al. 2011; Galli and Reynolds 2012). The sedimentological and paleontological evidence indicates that the sediments were deposited while the region was suffering changes regarding the hydric regimen, from a wet phase (late Miocene) to a drier one (Pliocene), due mainly to the formation of an intermountain basin (Angastaco Basin) that was bordered to the west by the Sierra de Quilmes and to the east by the uprising of the Sierras Los Colorados and León Muerto (Starck and Anzótegui 2001; Bywater-Reyes et al. 2010; Rohrmann et al. 2016; Robledo et al. 2020b).

During the late Miocene, the uplift of the basin caused an increase in the sedimentary accommodation/deposition (A/D) rate and was also associated with a change in the petrologic composition of the deposits (Galli et al. 2011, 2017). The resulting orographic barriers produced a warmer and wetter climate (Starck and Anzótegui 2001). The deposits of the San Felipe Formation at the top of the Payogastilla Group are more than 600 m thick in the southeastern Calchaquí Valley and are affected by numerous faults and folds. The transition between the Palo Pintado Formation and the San Felipe Formation is sharp and unconformable; it contains considerable clast-supported conglomerate with overlapping clasts and a lower proportion of sandstone and siltstone, which are interpreted as a gravel-braided fluvial system (Galli and Reynolds 2012). Different analyses of deposits of Palo Pintado Formation, like the presence of clay minerals in the floodplain sub-environment, or the presence of illite, smectite and kaolinite indicate generation by hydrolysis in a temperate-humid climate (Galli et al. 2011); stable isotope data from pedogenic carbonates demonstrated relatively more humid conditions between 10 to 6 Ma (Bywater-Reyes et al. 2010). Paleomagnetism studies in Palo Pintado Formation deposits indicate that at approximately 6.6 Ma there is an increase in the rate of sedimentation of 0.11–0.66 mm/y which is associated with a higher percentage of Salta Group clasts. Paleocurrents from the south to the southeast indicate the tectonic reactivation of the deposition area from the Sierra León Muerto and its continuation to the north as the Sierra Los Colorados (Galli et al. 2014). Isotope analysis of  $\delta Dg$  recorded in volcanic glass reveal that between -6.5 to 5.3 Ma, values from the Angastaco Basin decrease by  $-23 \pm 6\%$  (absolute  $\delta Dg = -95\%$ ), which is interpreted to be the result of surface uplift in this area, with altitude and aridization in a paleoenvironment like the present-day (Pingel et al. 2016).

In the global context, the ancestor assemblage floras of the current communities already were established and diversifying during the Miocene (Bell et al. 2010). This event

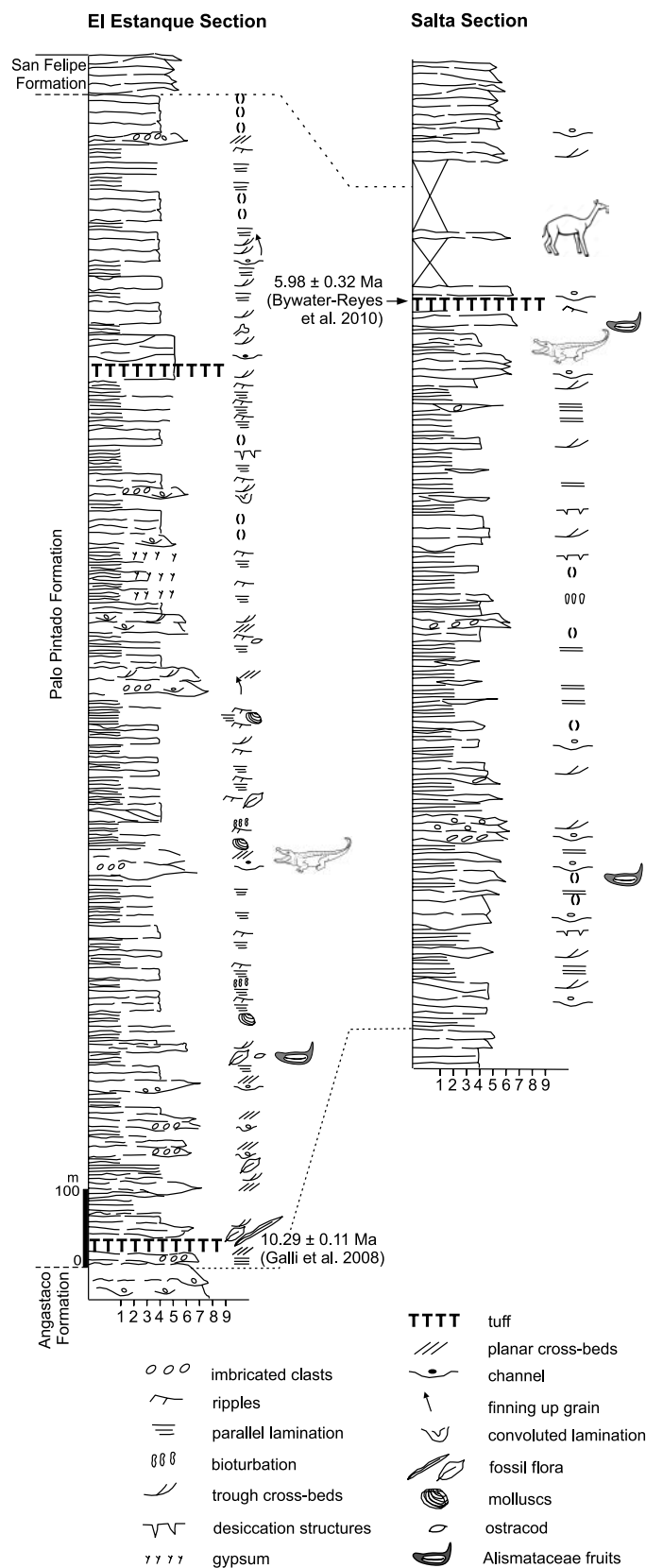


Fig. 2. Stratigraphic correlation of the Quebrada Salta and Quebrada El Estanque localities (Palo Pintado Formation, upper Miocene). 1, clay; 2, limolite; 3, fine sandstone; 4, middle sandstone; 5, coarse sandstone; 6, fine conglomerate; 7, middle conglomerate; 8, coarse conglomerate; 9, ash.

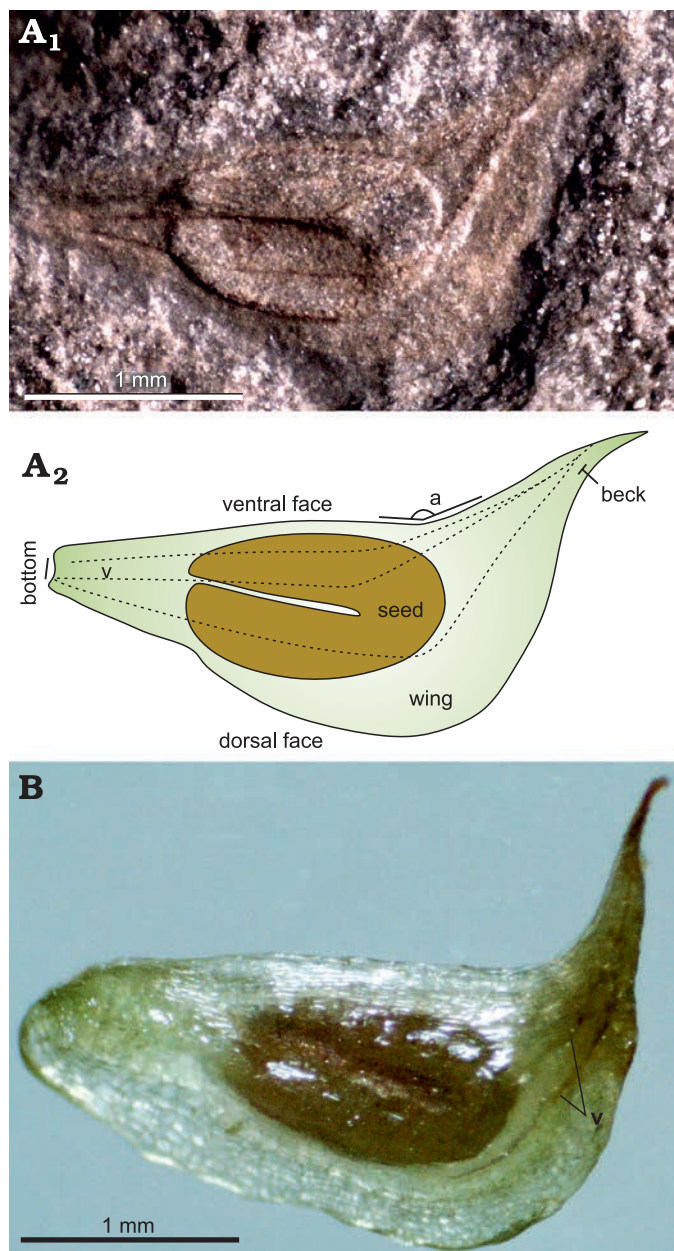


Fig. 3. Fossil and extant fruits of alismataceous plant *Sagittaria montevidensis* Chamisso and Schlectendal, 1827. **A.** CTES-PB 12911, Quebrada El Estanque (Palo Pintado Formation), upper Miocene, fossil fruit (A<sub>1</sub>), explanatory drawing (A<sub>2</sub>), dotted lines (v) represent veins present in the fossil fruit (a, angle formed by the beak and the ventral face); **B.** Recent fruit where the veins (v) are present, but with a slight development. The Recent material is deposited in the CTES herbarium (Corrientes City), as *Sagittaria montevidensis* Chamisso and Schlectendal, 1827 subsp. *montevidensis*.

is also observed in South American paleofloras (Barreda et al. 2007). In turn, the Miocene is a critical moment during which the great spread of the savannas took place (Quade et al. 1989; Cerling et al. 1997; Osborne 2008).

In addition to the *Sagittaria* fossils described below, various other vegetal remains were found at the Quebrada Salta and Quebrada El Estanque localities, which developed in an environment with fresh or brackish permanent water. These fossils include algae, ferns, monocots, and dicots (Herbst et al.

1987; Anzótegui and Horn 2011; Horn et al. 2011; Anzótegui et al. 2015). The taxa identified reflect that at least four paleoenvironments have been developed in these localities: aquatic, marsh, riparian and open terrestrial. The fossil fauna recorded here, at the moment corresponds to fragments of a turtle shell, a mandible of *Caiman latirostris* Daudin, 1802 (Bona et al. 2014; Bona and Barrios 2015), a tail tube and osteoderms of two glyptodons, Pampatheriidae osteoderms, fish scales, molluscs (Herbst et al. 2000), and insect wings.

## Material and methods

Two sedimentological profiles from the north and south locations of the Palo Pintado Formation in the study area were analyzed at a scale of 1: 500 (i) Quebrada El Estanque and (ii) Quebrada Salta (Figs. 1, 2), from Salta Province, Argentina. The samples described here were collected from these outcrops of the Palo Pintado Formation. The fossils are deposited at the Colecciones Paleontológicas “Dr. Rafael Herbst”, of the Universidad Nacional del Nordeste, Corrientes Province, Argentina (CTES-PB 12911–12917). The fruits analyzed here are formally considered as achenes, because those are dry fruits with a single seed inside, which does not adhere to the pericarp (Fig. 3). The specimens are well preserved, some samples containing organic remains, although others are incomplete, lacking the bases or the beaks. The fossil fruits were compared with herbarium (CTES-IBONE), field samples, and literature. The fossils were examined with a Nikon binocular stereomicroscope, model SMZ-445, and photographed with a Nikon mounted camera (model 590U). All measurements were digitally performed with the software Micrometrics. Photographs were processed with the software Corel Draw. The systematics in paper are according to APG IV 2016 (Byng et al. 2016).

## Systematic paleobotany

Division: Angiospermae Linnaeus, 1753

Class: Monocotyledoneae De Candolle, 1817

Order Alismatales Brown ex von Berchtold and Presl, 1820

Family Alismataceae Ventenat, 1799

Genus *Sagittaria* Linnaeus, 1753

*Type species:* *Sagittaria sagittifolia* Linnaeus, 1753; Recent, Eurasia.

*Sagittaria montevidensis* Chamisso and Schlectendal, 1827

Fig. 4A–G.

*Material.*—CTES-PB 12911–12917 (Fig. 4A–C, E–G) from Miocene of Quebrada Salta and Quebrada El Estanque outcrops, Palo Pintado Formation, Salta Province, Argentina. All specimens correspond to achenes.

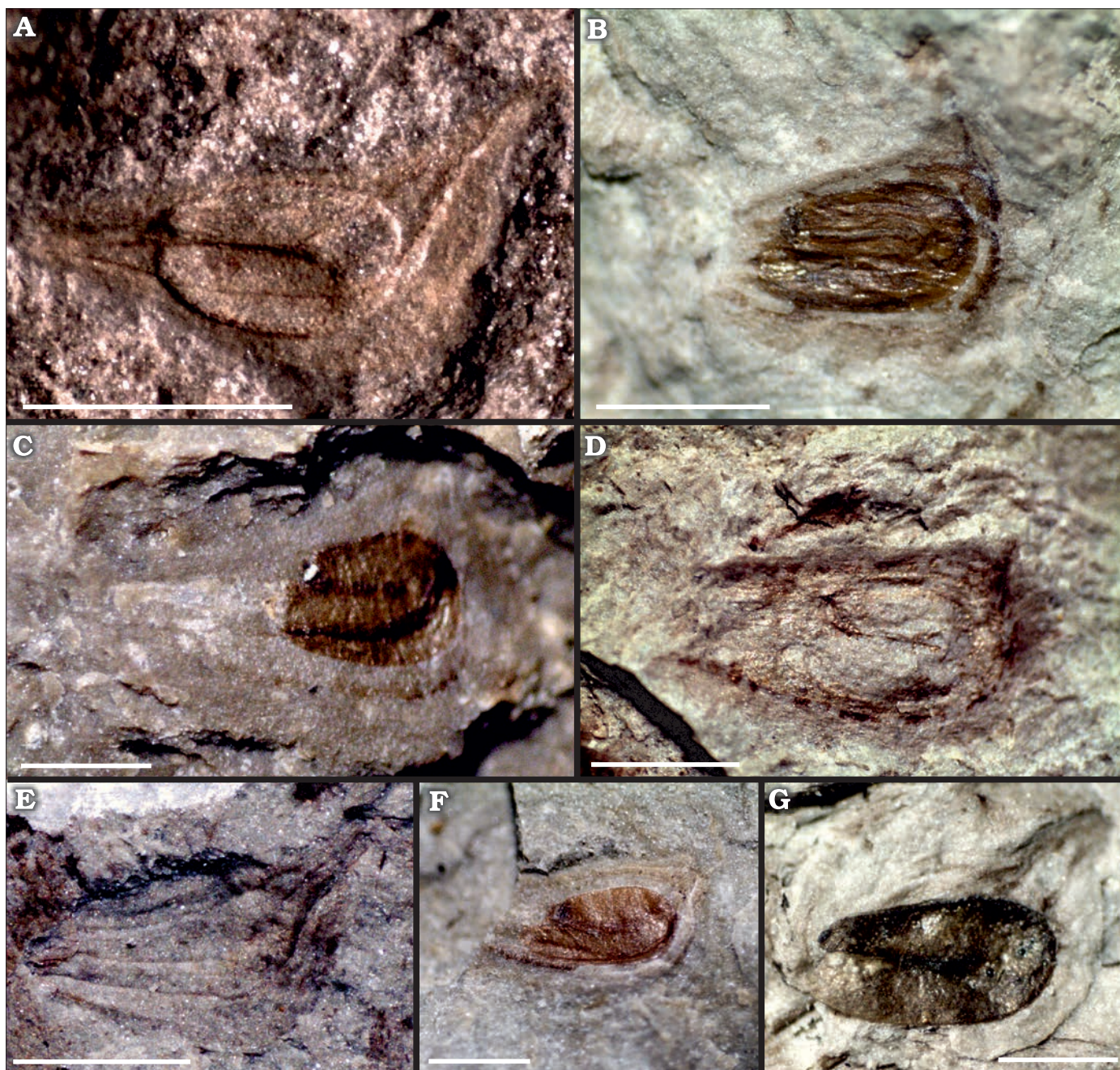


Fig. 4. Achenes of alismataceous plant *Sagittaria montevidensis* Chamisso and Schlectendal, 1827, from the Palo Pintado Formation, Quebrada El Estanque and Quebrada Salta localities, upper Miocene. **A.** Complete achene where the recurved seed and several veins are visible, CTES-PB 12911. **B.** Specimen showing the well-developed beak, almost in straight angle with the ventral face, CTES-PB 12916. **C.** Complete achene with organic remains, CTES-PB 12914. **D.** Fragment of achene where the beak and bottom are lacking, CTES-PB 12917. **E.** Complete fruit showing several veins, CTES-PB 12912. **F.** Incomplete achene where the bottom and beak are lacking, but the seed preserves some organic remains, CTES-PB 12913. **G.** Specimen showing the well-preserved seed inside the achene, CTES-PB 12915. Scale bars 1mm.

*Description.*—The studied material consists solely of fruits preserved as impressions from 1.75 mm (CTES-PB 12915) to 2.58 mm (CTES-PB 12917) in length and 0.75 mm (CTES-PB 12911) to 1.29 mm (CTES-PB 12916) in width. These fossils have a well-developed wing or keel on the dorsal face. All achenes bear an ascending beak ranging from 0.87 mm (CTES-PB 12914) to 1.40 mm (CTES-PB 12913, 12916). The angle formed by the beak and the ventral face ranges be-

tween  $85^{\circ}$  (CTES-PB 12916) and  $153^{\circ}$  (CTES-PB 12911). The curved seeds are preserved inside the achenes in most specimens. These seeds are 0.87 mm (CTES-PB 12914) to 1.40 mm (CTES-PB 12913, 12916) in length and 0.56 mm (CTES-PB 12911) to 0.85 mm (CTES-PB 12917) in width. Several specimens even preserve organic remains from the seeds (CTES-PB 12913–12916). All measurements are listed in Table 1.

Table 1. Characters and measurements (in mm) of all specimens analyzed in this work. “—”, the structure was not observable; (f), the structure was fragmented.

CTES-PB	Length	Width	Angle	Beak	Seed-length	Seed-width
12911	2.12	0.75	152.8°	0.64	0.95	0.56
12912	2.00	1.01	135.8°	0.37	—	—
12913	1.86 (f)	1.07	123.1°	0.48	1.40	0.76
12914	1.84 (f)	0.97	132.5°	0.25 (f)	0.87	0.59
12915	1.75	0.96	140.0°	0.36	1.11	0.57
12916	1.97	1.29	84.8°	0.66	1.40	0.80
12917	2.58	1.20	142.1°	0.21	1.11	0.85

*Remarks.*—According to Keener (2005), the molecular data suggest *Sagittaria montevidensis* is most closely related to *S. intermedia* Micheli, 1881, and *S. calycina* (Engelmann, 1867) Bogin, 1955. Based on morphological similarities, Keener (2005) also suggests *Sagittaria sprucei* Micheli, 1881, as a close species. Fruits of these species are different from those of *S. montevidensis*. *S. calycina* (Fig. 5A) has achenes with broadly developed dorsal wings, the beak turned into a spine and the seed is slightly longer than *S. montevidensis* (Fig. 5N). The achenes in *S. intermedia* (Fig. 5G) have faces tuberculate and the beak is shorter (0.2 mm), while *S. montevidensis* has achenes tuberculate and the beak can reach 1 mm in length. The fruits of *S. sprucei* (Fig. 5U) can be two times longer (6.0 mm) than *S. montevidensis* (3.0 mm), and almost three times wider (4.0 mm in *S. sprucei* and 1.5 mm in *S. montevidensis*). Seeds in *S. sprucei* are slightly smaller (0.9 mm), the beak is two times shorter (0.3–0.5 mm) and the angle formed by the beak and the ventral face is almost horizontal (172°), while the seeds in *S. montevidensis* reach 2 mm, the beak up to 1 mm and the angle is 142°.

Five plesiomorphic species of *Sagittaria* are currently distributed in South America, *S. guayanensis* Kunth, 1816, *S. intermedia*, *S. montevidensis*, *S. planitiana* Agostini, 1970, and *S. rhombifolia* Chamisso, 1835 (Keener 2005; Chen et al. 2012). Three of them are reported from Argentina (*S. guayanensis*, *S. montevidensis*, and *S. rhombifolia*) (Rataj 1970). *S. guayanensis* (Fig. 5F) achenes have similar to those in *S. montevidensis*, but the first presents ribs bearing spiny ridges, both at the dorsal as the ventral faces, while the achenes of *S. montevidensis* have a smooth surface. In turn, *S. rhombifolia* (Fig. 5R) has ovobate achenes without ornaments (smooth surface), but these are from two to four times longer (5–8 mm in length) than achenes of *S. montevidensis*. Other species of *Sagittaria* also have some differences, like an absent or slightly developed beak, as observed in *S. longiloba* Engelmann, 1895 (Fig. 5L) and *S. planitiana* (Fig. 5O). Several species are considerably bigger than *S. montevidensis*, such as *S. lancifolia* Linnaeus, 1758 (Fig. 5I), *S. latifolia* Willdenow, 1805 (Fig. 5J), and *S. trifolia* Linnaeus, 1753 (Fig. 5X). Furthermore, *S. lancifolia* has fruits bearing conspicuous glands. *S. secundifolia* Kral, 1982 (Fig. 5T) presents robust and ornamented ribs. In addition, the beak in this species turned into a spine. More differences regarding measurements, development of beak and ornaments between

*S. montevidensis* and other species of *Sagittaria* are listed in Table 2 and Fig. 5. Wang et al. (2010) reported another three species of *Sagittaria*, these are *S. natans*, *S. pymaea*, and *S. tengtsungensis*. The first is a synonym of *S. subulata* (Haynes and Holm-Nielsen 1994) (Fig. 5V), the remaining two were not illustrated in Fig. 5 because pictures or schemas of these species were not found.

Some species of *Echinodorus* (Alismataceae) have similar achenes to those in *Sagittaria*, but their fruits are mainly terete (cylindrical), rather than flat. The achenes of *Echinodorus berteroi* (Spreng, 1825) Fassett, 1955 and *E. paniculatus* Micheli, 1881, are similar in shape (Lehtonen 2009), although these are almost straight from the base to the beak, whereas in *Sagittaria montevidensis*, the beak and the ventral face form an angle that can even reach 90°. Moreover, the achenes of *E. berteroi* and *E. paniculatus* are proportionally bigger than the achenes of *Sagittaria montevidensis*, also they present well-developed ribs that in some cases are dichotomized (*E. paniculatus*), while *S. montevidensis* is not ribbed.

*Stratigraphic and geographic range.*—Miocene of Argentina and Recent from North and South America.

## Discussion

**The fossil record of Alismataceae.**—The fossil fruits of *Sagittaria montevidensis* are the first Neogene report of Alismataceae from South America. In one previous work, pollen grains corresponding with Alismataceae were reported from Paso Otero locality (late Pleistocene–Holocene), in the Pampean region of Argentina (Gutiérrez et al. 2011). The specimens were dated between 9900–7700 BP, although the authors only mentioned the finding of Alismataceae pollen and do not provide descriptions or illustrations permitting the comparison with other palynological records.

After an analysis of the current distribution of its Recent species Chen (1989) suggested Late Cretaceous age for the origin of *Sagittaria*. Later Chen et al. (2012) interpreted late Eocene and the Miocene time of origination from DNA analysis. This suggestion is consistent with the oldest records of *Sagittaria* accepted by Haggard and Tiffney (1997) who rejected the age proposed by Chen (1989). Furthermore, Chen et al. (2012) suggested an African origin of *Sagittaria*

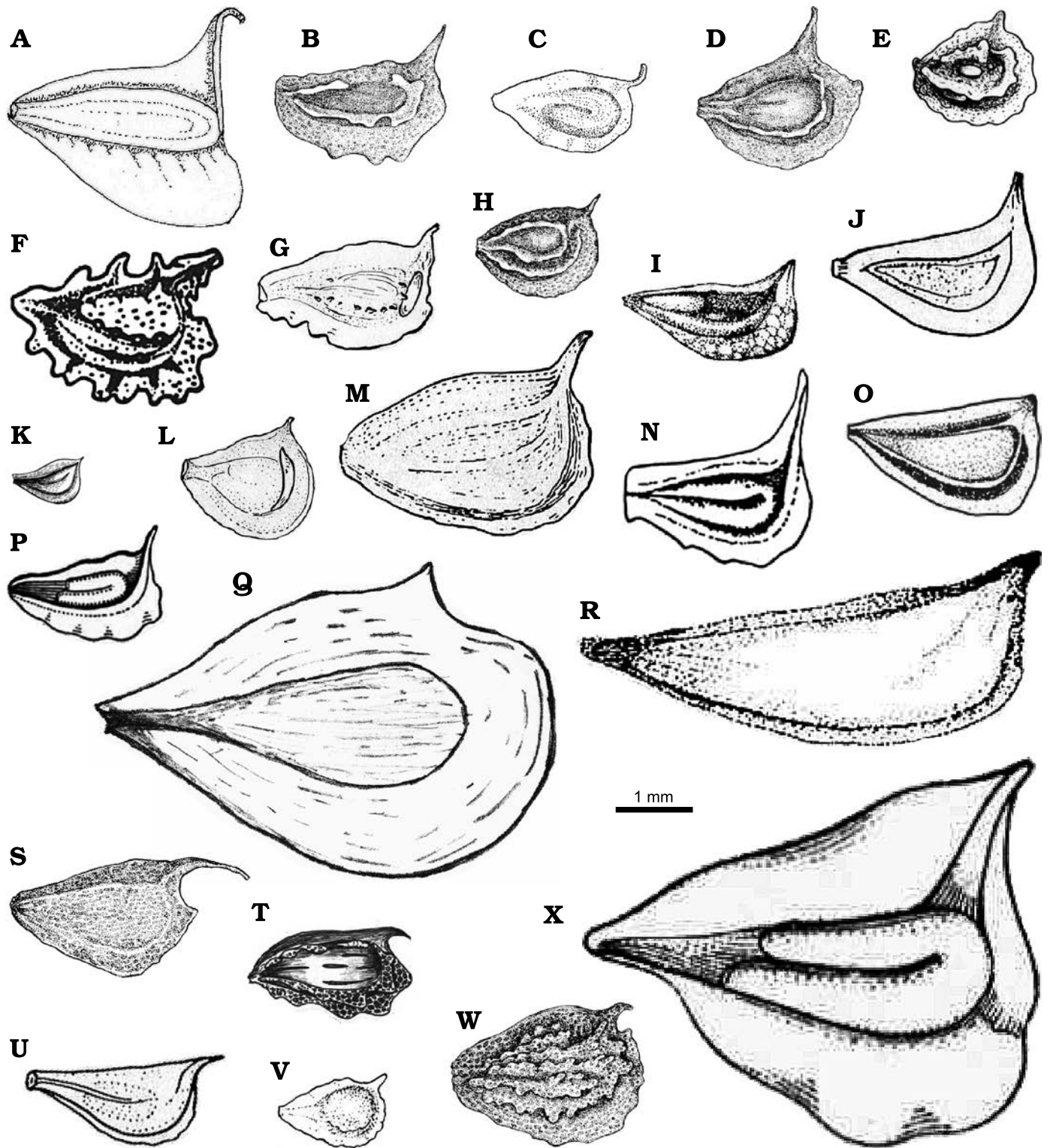


Fig. 5. Illustrations of species detailed in Table 2. A. *Sagittaria montevidensis* ssp. *calycina* (Ricketson 2018) (*S. calycina* following Keener 2005). B. *Sagittaria cristata* (Wooten 1973). C. *Sagittaria demersa* (Smith 1895). D. *Sagittaria fasciculata* (Wooten 1973). E. *Sagittaria graminea* ssp. *graminea* (Haynes and Holm-Nielsen 1994). F. *Sagittaria guayanensis* (Rataj 1970). G. *Sagittaria intermedia* (Haynes and Holm-Nielsen 1994). H. *Sagittaria isoetiformis* (Wooten 1973). I. *Sagittaria lancifolia* (Matias and Irgang 2006). J. *Sagittaria latifolia* (Haynes and Holm-Nielsen 1994). K. *Sagittaria lichuanensis* (Wang et al. 2010). L. *Sagittaria longiloba* (Haynes and Holm-Nielsen 1994). M. *Sagittaria macrophylla* (Haynes and Holm-Nielsen 1994). N. *Sagittaria montevidensis* ssp. *montevidensis* (Rataj 1978). O. *Sagittaria planitiana* (Matias and Irgang 2006). P. *Sagittaria platyphylla* (Den Hartog 1957). Q. *Sagittaria potamogetonifolia* (Wang et al. 2010). R. *Sagittaria rhombifolia* (Matias and Irgang 2006). S. *Sagittaria rigida* (Wooten 1973). T. *Sagittaria secundifolia* (Kral 1982). U. *Sagittaria sprucei* (Haynes and Holm-Nielsen 1994). V. *Sagittaria subulate* (Haynes and Holm-Nielsen 1994). W. *Sagittaria teres* (Wooten 1973). X. *Sagittaria sagittifolia* ssp. *S. leucopetala* (Den Hartog 1957) (*S. trifolia* following Lim 2015).

Table 2. Comparative chart (measurements in mm) of current *Sagittaria* fruits. Data obtained from: Smith (1895); Den Hartog (1957); Godfrey and Adams (1964); Rataj (1970, 1978); Wooten (1973); Kral (1982); Haynes and Holm-Nielsen (1994); Zepeda and Lot (1999); Matias and Ir-gang (2006); Moreira and Bove (2010); Wang et al. (2010); Matias and Sousa (2011); Lim (2015); Hall and Gil (2016); Canalli and Bove (2017); Ricketson (2018). \*, authors differ in this character; –, the dimension could not to be established.

Species	Length	Width	Angle (in °)	Seed length	Seed width	Beak	Presence/development of keels and/or ornaments	Illustration on Fig. 5
<i>S. calycina</i>	2.6	1.9	118	2.4	0.7	0.9	dorsal wing broadly developed	A
<i>S. cristata</i>	2.1	1.2	120	1.4	0.5	0.6	crenate wings	B
<i>S. demersa</i>	1.5–2.0	1.0	135–178	1.0	0.6	1.1	without keel	C
<i>S. fasciculata</i>	2.1	1.3	116	1.0	0.6	0.6	dorsal wing broadly developed	D
<i>S. graminea</i> ssp. <i>graminea</i>	1.5–2.8	1.1–1.5	115	1.1	0.5	0.2	without keel; 1–2 conspicuous glands	E
<i>S. guayanensis</i>	1.5–2.7	1.2–2.0	155	1.7	1.0	0.2–0.5	keeled; margins echinate	F
<i>S. intermedia</i>	1.5–2.2	1.0–1.4	111	1.1	0.6	0.2	without keel, face tuberculate	G
<i>S. isoetiformis</i>	1.5	1.1	120	0.9	0.5	0.3	keeled; horizontal beak	H
<i>S. lancifolia</i>	1.2–2.5	0.7–1.1	139–145	0.6–1.6	0.1–0.5	0.3–0.7	keeled	I
<i>S. latifolia</i>	2.5–3.5	1.9–2.0	108–131	2.0	0.9	1.0–2.0	without keel	J
<i>S. lichuanensis</i>	0.8–1.0	0.4–0.6	130	0.6	0.3	0.1	narrowly winged	K
<i>S. longiloba</i>	1.2–2.5	0.8–1.6	148	1.0	0.7	0.1–0.6	keeled	L
<i>S. macrophylla</i>	3.1–3.5	1.8–2.4	122–132	1.8–1.9	0.9	0.6–1.2	without keel	M
<i>S. montevidensis</i>	2.0–3.0	1.0–1.5	142	1.1–2.0	0.69	0.3–1.0	without keel; smooth surface	N
<i>S. planitiana</i>	1.5–2.4	1.0–1.44	142–144	1.5	0.6	0.1–0.3	keeled*	O
<i>S. platyphylla</i>	1.2–2.2	0.8–1.3	118–158	0.8–1.4	0.4–0.7	0.3–0.6	without keel; 2-ribbed	P
<i>S. potamogetonifolia</i>	5.0–7.0	4.5–6.0	105	3.0	1.5	0.5	dorsal wing undulated	Q
<i>S. rhombifolia</i>	4.0–7.0	2.0–3.0	130–135	4.9	1.5	0.7–1.2	keeled	R
<i>S. rigida</i>	2.4	1.5	165	1.6	0.7	1.0	horizontal beak	S
<i>S. secundifolia</i>	2.1	1.1	172	1.5	0.6	0.3	beak turned in a spur; margins crested	T
<i>S. sprucei</i>	2.1–6.0	0.9–4.0	172	0.9	0.4	0.3–0.5	without keel	U
<i>S. subulata</i>	1.4–2.0	0.9–1.5	143	0.8	0.6	0.2–0.4	keeled, crenate wings	V
<i>S. teres</i>	2.4	1.7	173	–	–	0.4	keeled; horizontal beak; irregularly crenate dorsal wing	W
<i>S. trifolia</i>	3.0–5.0	1.5–3.0	150	1.5	0.6	0.5	dorsal wing broadly developed	X

and four potential dispersion routes during the Oligocene–Miocene: (i) the first route suggests that *Sagittaria* has migrated from tropical Africa to South America and later to North America; (ii) the second one proposes an initial dispersal to Europe, followed by dispersal to North America, and then to South America. The remaining routes hypothesize the arrival in (iii) Madagascar and (iv) Asia. Considering the great dispersal capacity of *Sagittaria*, including possible large distances by water in streams and rivers, both by asexual (tubers) as sexual reproduction (achenes) (Gordon 1996; Zhang et al. 2010), and since in the late Oligocene–late Miocene range, about 20 million years have elapsed, we consider that both routes (i) and (ii) would explain the presence of *Sagittaria montevidensis* in South America during the late Miocene. The first route seems more plausible, because besides of *Sagittaria montevidensis*, other four plesiomorphic species have a current South American distribution (*S. guayanensis*, *S. intermedia*, *S. planitiana*, and *S. rhombifolia*) (Keener 2005; Chen et al. 2012).

In addition to the South American occurrences reported herein, a large number of fossil records of Alismataceae from the Cretaceous and Cenozoic times have been re-

ported in the Northern Hemisphere (Berry 1925; Teixeira 1948; Brown 1962; Doyle 1973; Muller 1981; Cevallos-Ferriz and Ramírez 1998; Retallack 2004). Before the year 2000, most of the authors agreed that the oldest remains of Alismataceae were the genera *Alisma* and *Caldesia*, from the Oligocene of Europe and early Miocene of the United States respectively (Daghlian 1981; Friis 1985; Haggard and Tiffney 1997). Recently, other authors proposed again that the Alismataceae have originated at the end of Mesozoic, most likely around the mid-Cretaceous (Chen et al. 2012; Smith 2013; Coiffard and Mohr 2018). Among the reports that undoubtedly correspond to Alismataceae, Riley and Stockey (2004) described the species *Cardstonia tolmanii* Riley and Stockey, 2004, from St. Mary River Formation (Campanian–Maastrichtian of Canada). Originally the species was included in Limnocharitaceae, but this family was later included into Alismataceae (APG III 2009; Chen et al. 2012). Furthermore, Smith (2013) suggested that *Haemantophyllum* Budantsev, 1983, a genus from Cretaceous of Russia (Golovneva 1997), correspond to the Alismataceae family. More recently, Coiffard and Mohr (2018) described an Alismataceae (*Alismataceae* gen. et sp. indet.), which



corresponds to an almost complete leaf from the Upper Cretaceous of Egypt and firstly assigned to *Echinodorus cf. cordifolius* by Kahlert et al. (2009).

**The fossil record of *Sagittaria* in the late Miocene context.**—The *Sagittaria* fossils studied here were recovered from late Miocene units ranging from approximately 10–5 Ma. According to Herbert et al. (2016) between 7–5.4 Ma, both hemispheres were affected by a drought, an increase in seasonality, and a restructuring of terrestrial plant and animal communities. These events were especially observed in the subtropical areas, but they were typically attributed to regional tectonic forces (Herbert et al. 2016). During the Neogene, the uplift of the Andes Mountains occurred in discrete periods, progressing from south to north and from west to east (Amarilla et al. 2015). The region experienced a deformation and compartmentalization of the basin, which extended during the Pliocene. These processes modified the environment, from a humid foreland to an elevated and hydrologically restricted semi-arid intermontane basins (Pingel et al. 2016). The Andes Mountains became the sole barrier to atmospheric circulation in the Southern Hemisphere (Amarilla et al. 2015). However, the fossil assemblages and the sedimentological evidence from the Palo Pintado Formation are not consistent with dry environments. During the deposition of this formation, a warm climate with seasonal rainfall is observed without significant climatic changes. Bywater-Reyes et al. (2010) suggested relatively more humid conditions between 10 to 6 Ma, although with seasonal conditions (Galli et al. 2011; Anzótegui et al. 2019). Changes to more arid environments started about 5 Ma until reaching the current conditions to 1 Ma ago (Pingel et al. 2016). Other Neogene locations close to the studied sites, such as the Quebrada del Toro locality (Miocene–Pliocene; Salta Province), also reflect similar conditions, with the presence of plant remains associated with marshy environments (Robledo et al. 2020a). This evidence suggests that the changes to a drier environment in the Palo Pintado Formation would have been gradual.

The achenes of *Sagittaria montevidensis* were found in different sections of two outcrops of the Palo Pintado Formation (see Fig. 2). The Quebrada El Estanque locality yielded a smaller number of *Sagittaria* fruits but they were the most complete fossils. In turn, the Quebrada Salta locality yielded a greater number of *Sagittaria montevidensis* impressions, including both complete and incomplete fruits. In both localities, these fossils are related to the marsh and lacustrine environments and they would have developed under a warm and humid climate with dry seasonality suggested for the Palo Pintado Formation (Galli et al. 2011). These conditions are some of the characteristic environments where *Sagittaria* currently develops. The arrowheads like *Sagittaria montevidensis* are rooted aquatic plants that grow in freshwater and slow current wetlands (i.e., swamps and marshes), wet or flooded soils, alongside

streams or in drainage channels (Costa and Forni-Martins 2003; Haynes and Les 2004; Lehtonen 2009, 2018). Their presence in the outcrops studied would suggest these types of environments during the Neogene in the study area. Additionally, Demetrio et al. (2014) suggested that this species could morphologically modify its corm as an adaptive response to environmental stress, as flood periods or dry seasons, both events proposed for Palo Pintado Formation. *Sagittaria montevidensis* coexisted with other aquatic or marsh plants (for example, *Cabomba*, *Salvinia*, *Azolla*, *Mayaca*, and *Equisetum*), previously recorded from sediments of the Palo Pintado Fm., attesting to the great diversity of aquatic plants preserved in these wetland deposits (Anzótegui et al. 2017, 2019).

## Conclusions

The Miocene Alismataceae record introduced here is the first Neogene fossil belonging to this family in South America and the most well substantiated fossil record of *Sagittaria* found of the continent.

The finding of *Sagittaria* in these Neogene sediments supports the possibility of a migratory route from Africa to South America and thence to North America.

This record constitutes another evidence that the environment during the deposition of the Palo Pintado Formation was warm and humid, in the interval of 10–5 Ma. During the late Miocene these *Sagittaria* would have inhabited a fluvial paleoenvironment in a warm climate with seasonal rainfall and without significant climatic changes, very different from the current dry conditions of the place, where it is now part of the South American Arid Diagonal.

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