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Paleogene *Salvinia* (Salviniaceae) from Colombia and their paleobiogeographic implications

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A B S T R A C T

Salvinia is a pantropical aquatic fern that has the highest species diversity in tropical America. Its evolutionary history and biogeography is still poorly understood. Contrasting its almost modern pantropical distribution, fossils of *Salvinia* have been found worldwide, including North America, Europe and Asia. Here, we describe fossils of *Salvinia* from four Paleogene localities of Colombia. Based on comparative morphological analyses of sterile organs, we describe two new species: *Salvinia magdalenensis* sp. nov. and *Salvinia bogotensis* sp. nov and assign the fossils from the other two localities to *Salvinia* sp. Available fossil data, together with these new records indicate that *Salvinia* was distributed in tropical latitudes as well as in temperate latitudes of the Northern Hemisphere throughout most of the Cenozoic. Its modern pantropical distribution could be the result of Pleistocene extinction of *Salvinia* in temperate regions due to global cooling climate trend.

1. Introduction

Ferns are distributed worldwide and its highest diversity is found in both wet tropical regions and mountains (Kessler et al., 2014, 2011). Unfortunately, the fern fossil record has not been widely explored in low latitudes (Fig. 1-E, F), therefore many evolutionary and biogeographic questions remain open (Monje-Dussán et al., 2016). Salviniales are heterosporous ferns that include two extant families: Marsileaceae Mirb. and Salviniaceae Martinov (Smith et al., 2006). Salviniaceae are floating aquatic ferns represented today by two genera, *Salvinia* Ség. (~10 species) and *Azolla* Lam (~8 species; The Plant List 2013, accessed 19th July 2016). *Salvinia* has a worldwide distribution, but being mostly in tropical regions of the Americas, Africa, Madagascar, India and Southeast Asia, and subtropical regions in North America, South America, Asia and Europe (Fig. 1-C). Eight of the ten *Salvinia* species are endemic to the Neotropics. There are four species reported in Colombia (*Salvinia auriculata* Aublet, *Salvinia minima* Baker, *Salvinia radula* Baker and *Salvinia sprucei* Kuhn; Bernal et al., 2015).

Salvinia has a unique morphology among ferns, consisting of groups of three leaves, two floating and one submerged (Croxdale, 1981, 1979, 1978). The adaxial sides of the floating leaves are densely covered with trichomes, making the surface extremely water repellent (Barthlott et al., 2009). The submerged leaf is highly dissected and usually petiolate, bears uniseriate, multicellular, apiculate hairs (Schneller, 1990a). This leaf is either sterile or fertile and branches dichotomously into multiple segments. Spore-producing organs borne on fertile submerged leaves, within a branched nonlaminated structure known as sorophore (Nagalingum et al., 2006). In contrast, the morphology of *Azolla* consists of branched rhizomes, simple roots in the ventral side of the axis and small, bilobed, sessile leaves in the dorsal side of the axis (Saunders and Fowler, 1993; Schneller, 1990b). The sorophohore in *Azolla* is borne on the first leaf of a lateral rhizome and it is surrounded by a parenchymatous layer known as the envelope, which is absent in modern *Salvinia* (Nagalingum et al., 2006; Schneller, 1990b). In the fossil record, *Salvinia* and *Azolla* are usually found as impressions of submerged and floating leaves (Collinson, 2001; Shaparenko, 1956). There are few examples of fertile *Salvinia* fossils (Bůžek et al., 1971; Collinson et al., 2001; Collinson, 1991; Weber, 1973), while in *Azolla* fertile whole plants are well known (Collinson, 2001, 1991; Rothwell and Stockey, 1994). Fossil megaspores and microspore massulae from salviniales carry

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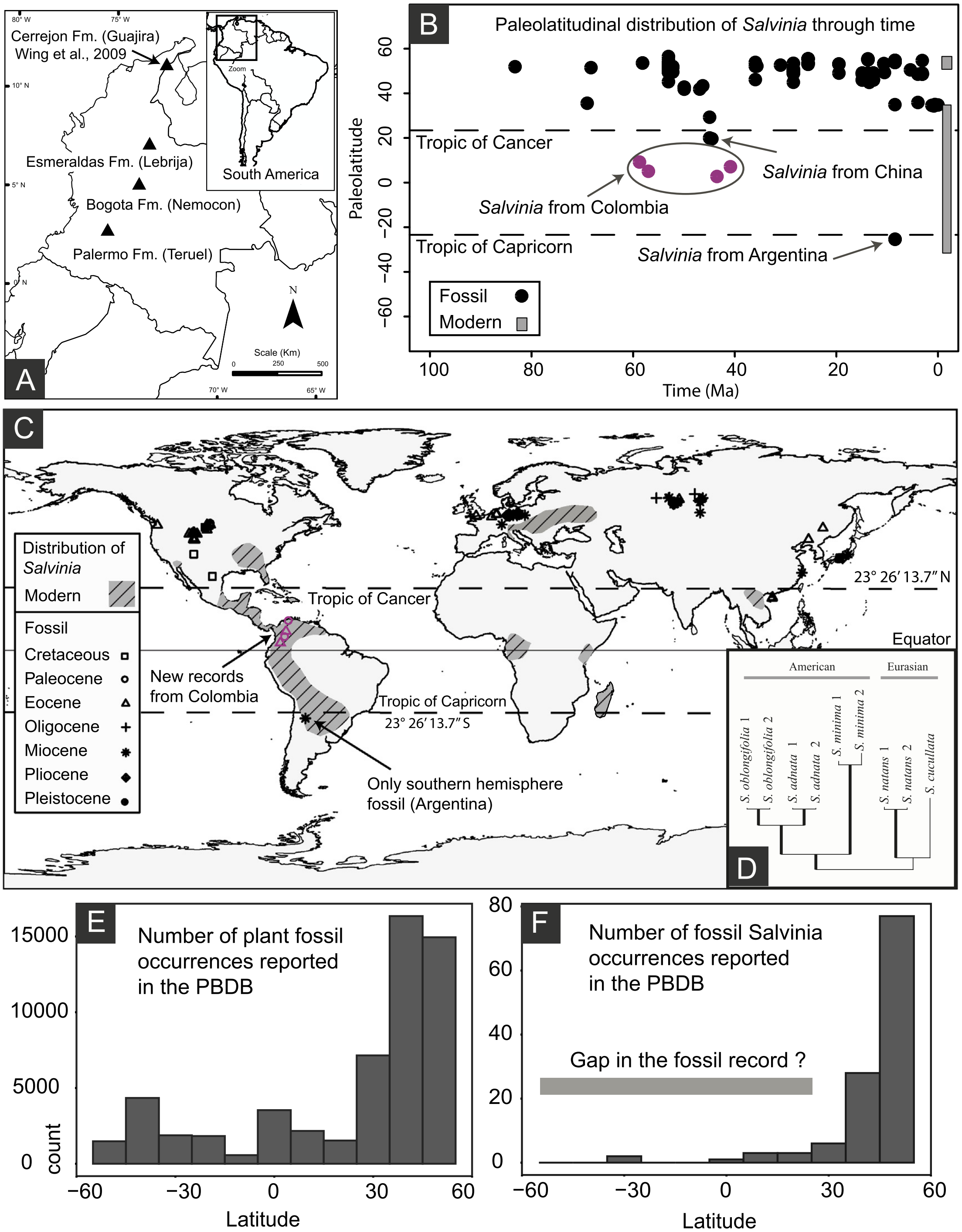


Fig. 1. A - Map of northern Colombia showing the localities with *Salvinia* fossils. B – Paleo-latitude vs. Time graph of *Salvinia*. C - Worldwide fossiliferous localities where *Salvinia* macrofossils have been found. In B and C, purple points indicate new records from Colombia. D - Molecular phylogeny of *Salvinia* from: Nagalingum et al., 2008. E - Frequency histogram of fossil plants occurrences vs. latitude as recorded in the PBDB. F - Frequency histogram of *Salvinia* fossils occurrences vs. latitude as recorded in the PBDB. Data for plots B, C, E and F was downloaded from the PBDB using search terms: Salvinia and plantae.

systematically informative diagnostic characters (see review in Collinson et al., 2013).

The monophyly of *Salvinia* and its phylogenetic relationships within extant ferns is well documented by both morphological and molecular data (Nagalingum et al., 2008; Pryer et al., 1995). The most complete phylogenetic analysis for the genus only included five extant species, and excluded the other five species from South America, Central America Africa and Madagascar (Fig. 1-D, Nagalingum et al., 2008). Two biogeographic clades were proposed: an American clade composed by *Salvinia minima*, *Salvinia molesta* (synonym of *Salvinia adnata* Desv.) and *Salvinia oblongifolia* Martius and a Eurasian clade formed by *Salvinia natans* (L.) All. and *Salvinia cucullata* Roxb.(Nagalingum et al., 2008).

The origin of *Salvinia* and its diversification in tropical regions, where it is most abundant nowadays (Fig. 1), is still poorly understood. Aquatic ferns as Salviniaceae and Marsileaceae appear first in the fossil record in high latitudes of the northern hemisphere during the Cretaceous (Skog, 2001). The earliest known *Salvinia* includes fertile plants with sporocarps, but lacking spores, from Campanian–early Maastrichtian deposits of Mexico (Fig. 1-B: paleolatitude ~35° N; Estrada-Ruiz et al., 2010; Weber, 1973). Cenozoic leaves and spores of *Salvinia* are reported mostly from northern temperate latitudes (Fig. 1B). Records from low latitude floras include leaves from the Paleocene of Colombia (Wing et al., 2009), spore massulae and vegetative remains from the early Paleocene of India (Mahabale, 1950) and leaves and spores (without organic connection) from the Eocene of southern China (Wang et al., 2014).

We describe two new fossil species and four new records of *Salvinia* based on three fossil Paleocene and Eocene localities from Colombia, as well as a previously reported specimen from the Paleocene Cerrejón flora in northern Colombia (Wing et al., 2009). Overall, fossils indicate that *Salvinia* was in the Neotropics at least since the late Paleocene (~60 Ma). We review the fossil record of *Salvinia* in order to understand the modern pantropical distribution and discuss the possible causes that generated its diversity pattern. Furthermore, we discuss the paleogeography of the fossil localities and discuss the geological implications

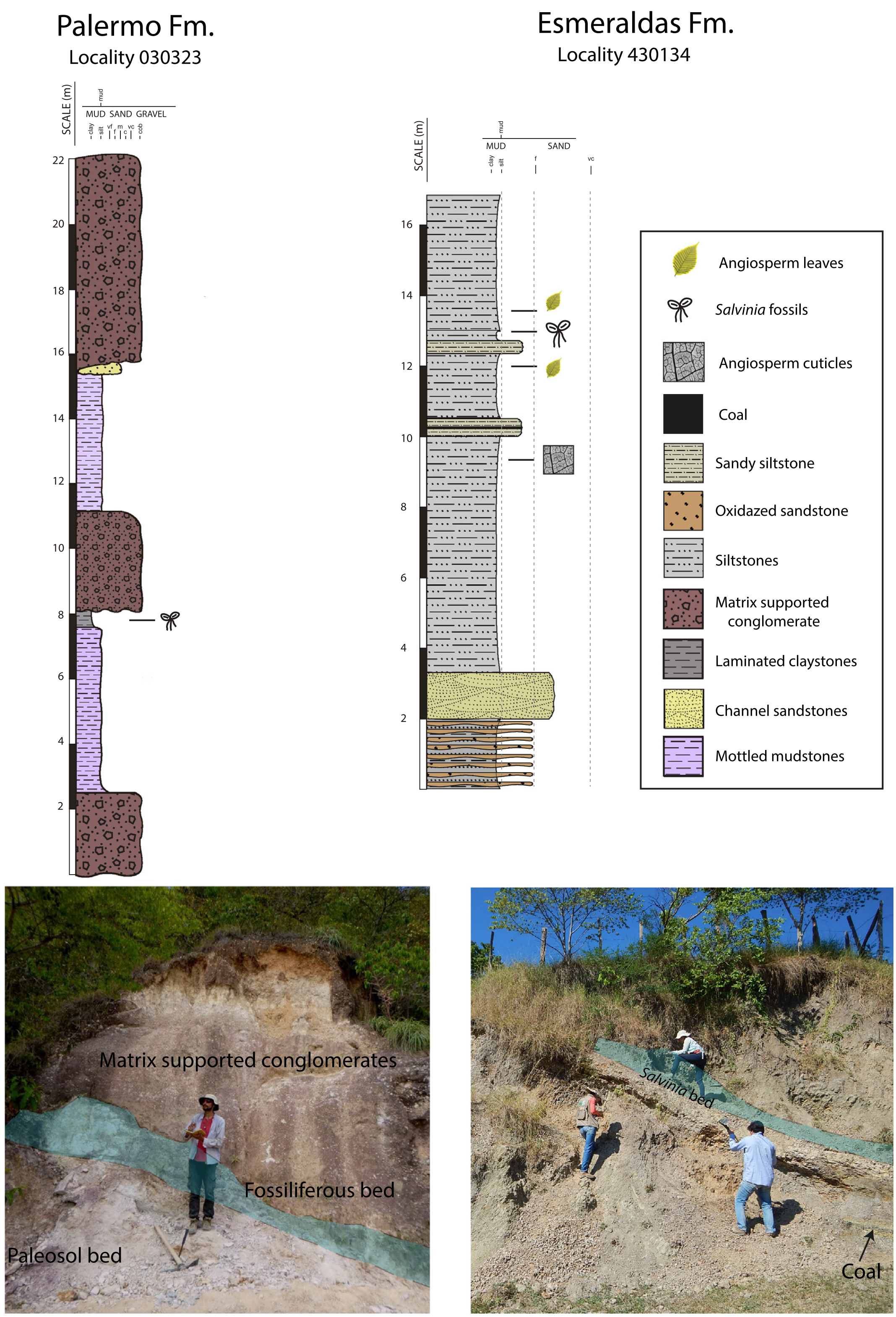


Fig. 2. Stratigraphic columns. A - Palermo Formation. B - Esmeraldas Formation.

of these fossil findings in the Paleogene geology of northern South America.

2. Methods

The fossils described here belong to three fossil floras from Colombia. These include the middle to late Paleocene Nemocon flora (Bogota Formation; 73°50′48.12″W, 5°08′15.00″N; 83 specimens); the late Eocene Topocoro dam flora (Esmeraldas Formation; 7°06′30.24″N, 73°25′45.12″W; 3 specimens); and the late Eocene Teruel Flora (Palermo Formation; 2°44′29.76″N, 75°32′60.0″W; 58 specimens). Additionally, we included a *Salvinia* fossil reported from the middle to late Paleocene Cerrejón Flora (11° 07′40.8″N, 72° 33′18″W; 4 specimens; Wing et al., 2009). We measured a stratigraphic section in both the Teruel Flora (STRI locality 030323) and Topocoro dam Flora (STRI locality 430143; Fig. 2) and present a brief description of the stratigraphy of the Nemocon flora.

2.1. Stratigraphy

Nemocon Flora. It was collected in the middle part of the Bogota Formation. Lithologies include varicolored paleosols intercalated with ribbon-channel sandstones and minor laminated siltstones. *Salvinia* fossils were collected in the laminated silstones. This flora was dated as late Paleocene by correlating the stratigraphic position of this locality with previous biostratigraphic work in the Bogota Formation (zone T-03b-*Foveotricolpites perforatus* Jaramillo et al., 2011).

Topocoro dam Flora. It was collected from the upper part of the Esmeraldas Formation (meter 885 out of 1300 m of the entire formation) and it is dominated by mudstones and siltstones with occasional thin coal beds and fine-grained sandstones. *Salvinia* fossils were collected from gray siltstones (Fig. 2). This flora was dated as late Eocene by correlating the stratigraphic position of our section with the previous biostratigraphic work on the Esmeraldas Formation (Rodríguez-Forero et al., 2012).

Teruel Flora. It was collected from the middle segment of the Palermo Formation, and included thick (up to ~10 m) packages of mud supported conglomerates, interbedded with minor sandstone beds with channel morphologies as well as abundant gray-mottled paleosols (Fig. 2). *Salvinia* fossils were collected from a single layer (~20 cm) of gray laminated mudstone (Fig. 2). This flora was dated as Late Eocene(?) based on the stratigraphic position and a few palynological studies (Beltrán et al., 1968). More studies are required to improve the age of the Palermo Formation.

Cerrejón Flora. *Salvinia* fossils were collected from claystones at the top of the Cerrejón Formation (Locality 0318 from Wing et al., 2009). The stratigraphic section of the Cerrejón Formation includes intercalations of thick packages of sandstones with finely laminated mudstones-claystones and coal beds (Jaramillo et al., 2007). This flora was dated as Late middle to late Paleocene based on the stratigraphic position and previous biostratigraphy of the Cerrejón Formation (Jaramillo et al., 2007).

2.2. Fossil description

All the fossil materials studied are deposited at the paleontological collection of the Mapuka Museum of Universidad del Norte, Barranquilla, Colombia (MUN). Information of samples and localities can be accessed through the Smithsonian Tropical Research Institute (STRI) sample database (http://biogeodb.stri.si.edu/jaramillo2/fossildb/). Each sample has a unique museum ID that starts with MUN and each locality is labeled with a unique ID that starts with STRI. Samples from the Cerrejón Flora are labeled starting with CJ following the original nomenclature (Wing et al., 2009). The material was described based on previous leaf terminology (Collinson et al., 2001; Ellis et al., 2009), and was studied using a Nikon SMZ1500 stereoscope and photographed with a Canon D90s camera with varied low-angle lighting. A scanning electron microscope (JSM-6490LV) was used to reveal venation details. Type specimens were drawn using a camera lucida attached to the stereoscope and digitized with Adobe Illustrator CS5. Measurements were made using ImageJ software (Schneider et al., 2012).

We compared the collected fossils to extant species of *Salvinia* as well as previously described fossil species. Extant species of *Salvinia* were assessed from herbarium collections at the Museo de Historia Natural of the Universidad de los Andes, the L. H. Bailey Hortorium Herbarium, and published descriptions. A morphological character matrix was made to compare collected fossils with available *Salvinia* fossil descriptions (Appendix 2). The characters compared included size and shape of the lamina; venation type; number of secondary veins; shape and size of venation areolas; number of tubercles per areolae; and trichome size and shape. In the submerged leaves, we measured their length, and described their ramification pattern. Characters used to compare the submerged rounded segments were mainly size and the shape of the smaller structures inside them.

We use common terminology to describe fossil *Salvinia* based on comparative tables from previous work (Collinson et al., 2001; Wang et al., 2014). We use the term "rounded structures" to refer to those structures with spherical shape located within the submerged system (Plates II-1, IV). We prefer to use this term and not "floats", "inflated segment" or "floating aids" (Collinson et al., 2001; Collinson, 1991), because these structures seem to have been submerged in their living position, thus we do not find evidence for calling them floating structures (see comments in description of *Salvinia magdalenensis*).

The Paleobiogeography of *Salvinia* was studied using data from the Paleobiology database. We downloaded all occurrences for fossil *Salvinia* as well as the Paleolatitude for each of these fossil localities (Collections fields - Geography fields - Paleolatitude, October 11th, 2017). Furthermore, we explored the scientific literature and add a few additional records for the Paleogene of India (Mahabale, 1950), Eocene of China (Wang et al., 2014), the Miocene of Argentina (Herbst et al., 1987) and Pleistocene of Japan (Nasu and Seto, 1976). Information from each of these occurrences can be consulted in the Appendix 1.

3. Results

3.1. Systematics

Family: Salviniaceae Martinov
Genus: *Salvinia* Séguier
Species: *Salvinia bogotensis* A. Cuervo & N. Pérez, sp. nov.

Plate I. 1–7. Macrofossils of *Salvinia bogotensis* sp. nov.

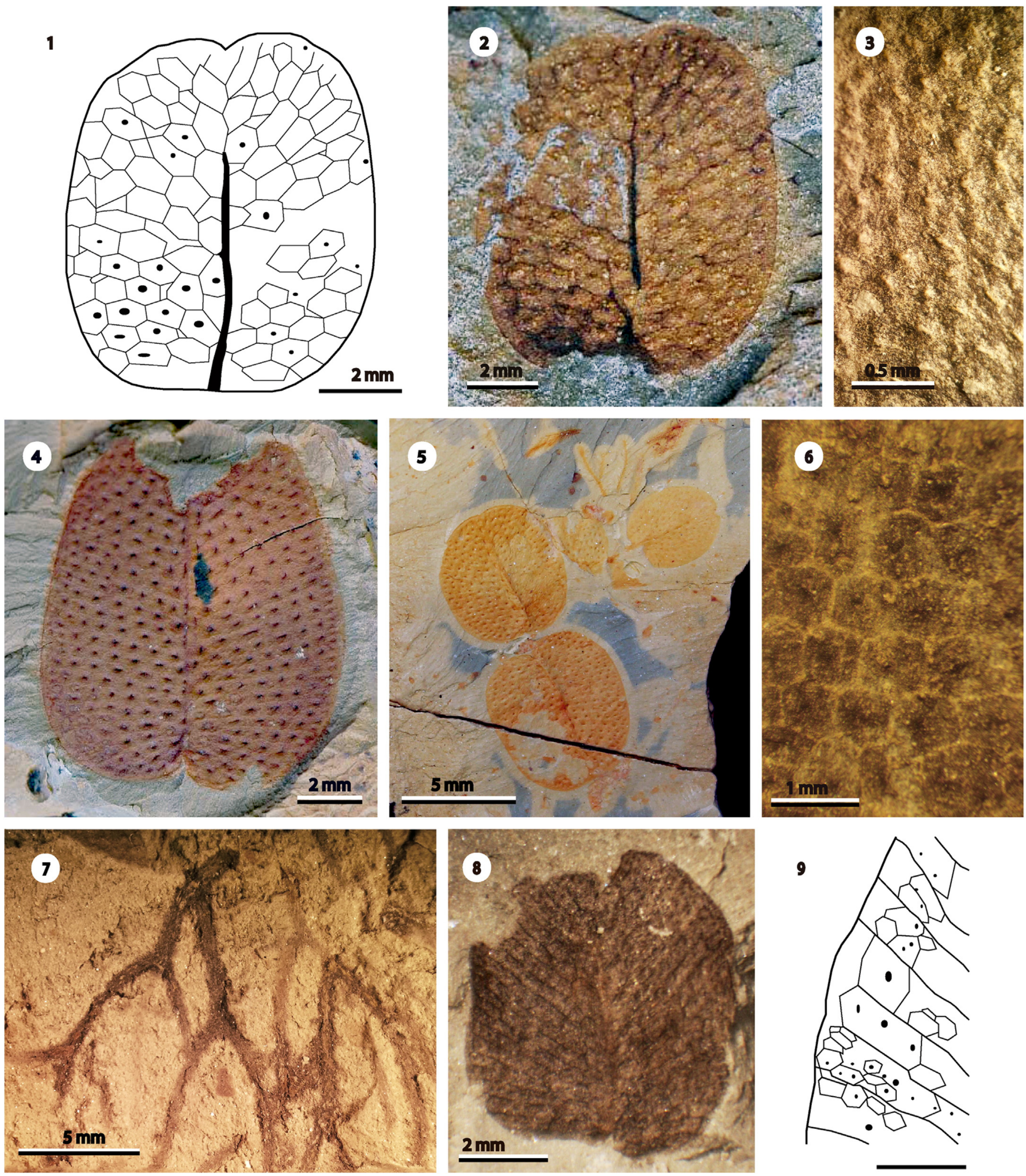
1. Schematic drawing showing the venation patterns of *Salvinia bogotensis*. MUN STRI-12154.
2. Floating leaf with the primary vein and the hexagonal areolas (arrows). MUN STRI-12154.
3. Zoom of a floating leaf showing big tubercles across the lamina. MUN STRI-29896.
4. Floating leaf that exhibits the primary vein and the tubercles in rows parallel to the secondary venation. MUN STRI-12125.
5. Three complete floating leaves with the primary vein and the tubercles. MUN STRI-12121.
6. One big tubercle per hexagonal areola within the floating leaf. MUN STRI-12143.
7. Highly branched submerged organ. MUN STRI-12479.

8–9. Macrofossil of *Salvinia* sp. 1 from the Esmeraldas Fm. MUN STRI-35515.

8. Floating leaf showing primary and secondary veins. MUN STRI-35515.
9. Drawing showing hexagonal areolas with one, two or three tubercles inside. MUN STRI-35515.

Specific Diagnosis:
Floating leaves ovate, elliptical and oblong. Length ranges between 5.3 and 21.2 mm, width ranges between 4 and 15.3 mm. Primary vein thick near base of lamina and thins towards the leaf apex. Areoles hexagonal and rectangular and approximately isodiametric; one tubercle per areole. Submerged leaves with short (one fifth of the total length of the leaf) and strongly branched primary axis.

Holotype hic designatus: MUN-STRI-12125 (Plate III, 4), here designated
Paratypes: MUN STRI-12121 (Plate III, 5), MUN STRI-12125 (Plate III, 4), MUN STRI-12129, MUN STRI-12143 (Plate III, 6), MUN STRI-12154 (Plate III, 1, 2), MUN STRI-12479 (Plate III, 7), MUN STRI-29891, MUN STRI-29896 (Plate III, 3), MUN STRI-29975, MUN STRI-29976, MUN STRI-29982, MUN STRI-29997.



Type locality: Cogua locality, Cundinamarca, Bogota Formation. STRI locality: FH0903: 5°04′36.1″N, 73°57′18.9″W
Paratype localities: Cogua locality, Cundinamarca, Bogota Formation. STRI locality: FH0801: 73°50′48.12″W, 5°08′15.00″N.
Age: late Paleocene (60–58 Ma, Jaramillo et al., 2011)
Repository: Mapuka Museum of Universidad del Norte, Barranquilla, Colombia (MUN).
Etymology: The specific epithet refers to the name of the geological Formation and the capital city of Colombia where the fossils were found.
Detailed description:
These fossils comprise whole plants and detached floating leaf compressions. Floating leaves have shapes that vary between ovate, elliptical and oblong; leaf length ranges from 5.3 mm to 21.2 mm (measured at the longest point; SD = 3.71, n = 39) and width ranges from 4 mm to 15.3 mm (measured at the widest point; SD = 2.48, n = 39); base of lamina is generally cordate (Plate I, 4) but can be rounded (Plate I, 1, 5); apex shape is rounded (Plate I, 5) or emarginated (Plate I, 1, 2). Primary vein is conspicuous near base of the leaf, its thickness decreases towards apex where it disappears (Plate I, 1, 2). Secondary veins are alternate and there are from 22 to 46 per leaf. Angle between primary and secondary veins increases towards base of lamina, being 90° to 82° at the base; ~78° to 65° at the middle of the leaf and 64° to 50° towards apex (Plate I, 4). Areoles have hexagonal and rectangular shape. Areole length ranges between 0.3 mm and 1 mm and width ranges between 0.5 mm and 1 mm. Each areole has conspicuous one tubercle (Plate I, 1, 2, 6). Tubercles are arranged in rows that are parallel to secondary veins (Plate I, 3, 4).
Submerged leaves are covered with abundant simple trichomes. Size of submerged leaf segments varies from 3.7 mm to 21.5 mm in length. Primary axis is short (one fifth of the total length of the leaf) and strongly branched (Plate I, 7).
Morphological comparison of *Salvinia bogotensis* sp. nov. with extant taxa:

Salvinia bogotensis has hexagonal or quadrangular areoles, like those seen in some living species such as *Salvinia auriculata*, *Salvinia sprucei* and *Salvinia biloba*. However, areoles of *S. biloba* have a length:width ratio of 1:3 (Forno, 1983) and size of areoles of *S. sprucei* is highly variable across the lamina, contrasting with a nearly isodiametric areole shape seen in leaves of *S. auriculata* (Forno, 1983) and *S. bogotensis*. *S. auriculata* differs from *S. bogotensis* in having a submerged organ with a long primary axis (Forno, 1983; Lichtenstein, 1939). Furthermore, *S. bogotensis* has one tubercle per areole, whereas *Salvinia oblongifolia* has four trichomes per areole and *Salvinia natans* has 4 to 8 (Shaparenko, 1956).

Morphological comparison of *Salvinia bogotensis* sp. nov. with fossil taxa:

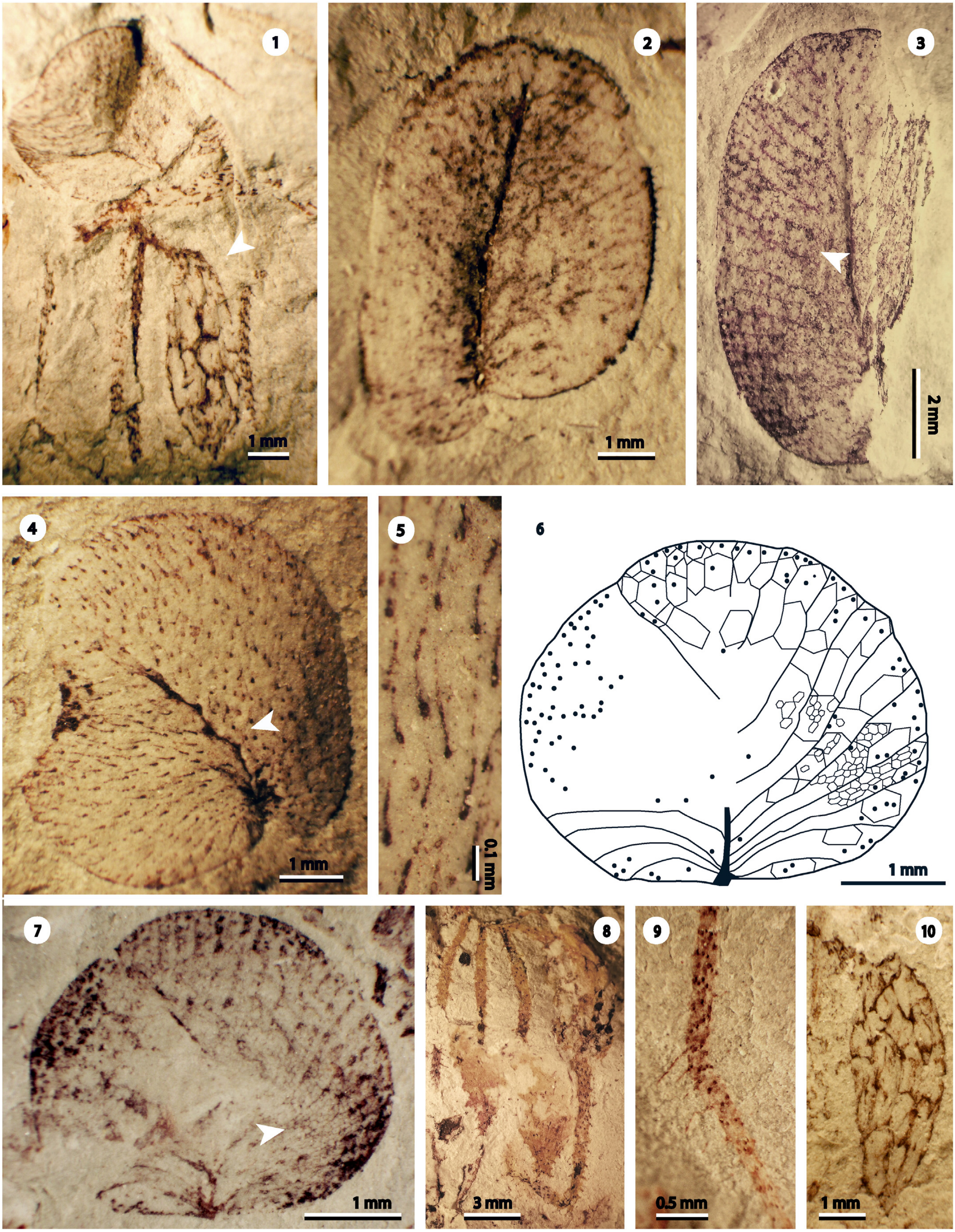
Salvinia bogotensis sp. nov. differs from all other previously described fossil species of *Salvinia*. Most distinctive characters of *S. bogotensis* are its conspicuous tubercles (one per areole), isodiametric areoles and its lack of a keel. *Salvinia magdalenensis* sp. nov. differs from *S. bogotensis* because it has 1–2 tubercles per areole and hexagonal areolas; *Salvinia hainanensis* has a distinct keel and areoles that decrease in size towards margin (Wang et al., 2014); *Salvinia xiananshanensis* Li has pentangular to polygonal areoles with 2 to 4 tubercles in each one (Sun et al., 2010); and *Salvinia mildeana* has mostly quadrangular areoles with 4 tubercles (Collinson et al., 2001). *Salvinia pseudoforma* also has one tubercle per hexagonal to quadrangular areole (Ôishi and Huzioka, 1943), however, it is different from *S. bogotensis* because its tubercles are not conspicuous. Areoles of *Salvinia coahuilensis* are hexagonal but length:width ratio is 2:1 (Weber, 1973) instead of 1:1 as in *S. bogotensis*. *Salvinia reussii* has 4 tubercles per areole (quadratic in shape) and much larger submerged leaves than *S. bogotensis* (up to 100 mm; Bůžek et al., 1971).

Species: *Salvinia* sp. 1
Specimens examined: MUN STRI-35660, MUN STRI-35515 (Plate III, 8, 9) and MUN STRI-36164.
Locality: Topocoro dam, Santander, Colombia. Esmeraldas Formation. STRI locality 430143: 7° 06′30.24″N, 73° 25′45.12″W.
Age: late Eocene for the upper segment of the Esmeraldas Formation (Rodríguez-Forero et al., 2012).
Repository: Mapuka Museum of Universidad del Norte, Barranquilla, Colombia (MUN).
Detailed description:
These fossils consist on detached floating leaf compressions. Shape of floating leaves varies between oblong and ovate; width is 6.2 mm (n = 1, only one specimen was found complete), and length is 7 mm (n = 1); base of lamina is cordate and apex is rounded (Plate I, 8). Primary vein narrows distally. Floating leaves have 28 secondary veins, which are alternate, have straight courses, and remain parallel to each other from base to apex (Plate I, 8). Angle between primary and secondary veins increases towards base of lamina; proximal secondary veins have an angle between 110° and 80°; middle secondary veins have an angle between 60° to 50° and distal secondary veins between 50° to 38° (Plate III, 8). Areoles have hexagonal shape in outline; its width ranges from 0.4 mm to 0.7 mm, and its length ~ 0.2 mm to 0.4 mm. Usually, there is 1 tubercle per areole is 1, but sometimes there are 2 (Plate III, 8, 9). Tubercles are arranged in parallel rows that follow orientation of secondary veins.
Comparison:
Salvinia sp. 1 has 1 or 2 tubercles per areole as seen in *Salvinia magdalenensis* and different from other fossil species as *Salvinia xiananshanensis* Li which has areoles with 2 to 4 tubercles in each one (Sun et al., 2010) or *Salvinia mildeana* that has areoles with 4 tubercles. Floating are larger than those of *S. magdalenensis* but smaller than *Salvinia bogotensis*. Shape of the floating leaves is variable as seen in many fossil and living taxa. The primary vein of *Salvinia* sp. 1 narrows toward the apex, similarly to *Salvinia reussii*, *Salvinia coahuilensis* and *S. bogotensis*.
Comments:
The measurements included in the description were based uniquely on one specimen of a floating leaf in which venation and shape characters were well preserved.

Species: *Salvinia magdalenensis* A. Cuervo & N. Pérez, sp. nov.
Specific diagnosis:
Floating leaves oblong, elliptical, to ovate. Leaf length ranges between 4.5 and 10 mm and width ranges between 3 and 7 mm. Primary vein distinct, decreasing in gauge distally, sometimes exhibiting a zigzag pattern towards the distal half of the leaf blade. Primary areoles hexagonal, usually broader than longer, having one or two tubercles per areole. Secondary areoles hexagonal and smaller than primary areoles. Submerged leaves length ranges between 5 and 17 mm with a short, strongly branched primary axis bearing submerged rounded segments.
Holotype hic designatus: MUN STRI-36738 (Plate II, 1)

Plate II. Macrofossils of *Salvinia magdalenensis* sp. nov.

1. Floating leaf attached to submerged leaves bearing a submerged rounded structure (arrow). MUN STRI-36738.
2. Floating leaf showing some tubercles, first and second order venation. MUN STRI-36736.
3. Impression of a floating leaf with primary and secondary veins, hexagonal areola (arrow) and tubercles. MUN STRI-36705.
4. Floating leaf showing the distribution of the trichomes, the primary vein and its zigzag pattern (arrow). MUN STRI-36716.
5. Close up view of the trichomes of the floating leaf. MUN STRI-36716.
6. Schematic drawing showing the venation pattern of *Salvinia magdalenensis*. MUN STRI-36708.
7. Floating leaf with second order venation and secondary hexagonal areolas (arrow). MUN STRI-36708.
8. Submerged leaves bearing rounded structures and showing its ramification pattern. MUN STRI-36749.
9. Zoom of one submerged segment showing some simple trichomes and tubercles. MUN STRI-36721.
10. Submerged rounded segment with the internal structures. MUN STRI-36731.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2 mm
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5
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6
1 mm
7
1 mm
8
3 mm
9
0.5 mm
10
1 mm

Paratypes: MUN STRI-36716 (Plate II, 4), MUN STRI-38288, MUN-STRI-36705 (Plate II, 3), MUN STRI-36708 (Plate II, 6, 7).
Type locality: Teruel, Huila. Palermo Formation. STRI locality 030323: 2°44′29.76″N, 75°32′60.0″W. Palermo Formation.
Age: Late Eocene(?). The Palermo Formation has not been well dated. It has been considered as Eocene based on stratigraphic position and a few palynological studies (Beltrán et al., 1968).
Repository: Mapuka Museum of Universidad del Norte, Barranquilla, Colombia (MUN).
Etymology: The specific epithet refers to the Magdalena River.
Detailed description:
These fossils comprise whole plants and detached floating leaf compressions. Floating leaves have shapes that vary between oblong, elliptical and ovate; leaf length ranges from 4.5 to 10 mm (measured at the longest point; n = 46; SD = 1.39), and width ranges from 3 to 7 mm (measured at the widest point; n = 46; SD = 0.98); base of lamina is generally cordate (Plate II, 2, 4) but in some cases rounded (Plate II, 1, 7); apex shape is rounded (Plate II, 2) or emarginated (Plate II, 3,7). Primary vein is markedly thickened to the base of the leaf, and tapers towards its apex (Plate II, 2–4); at the most distal end of the leaf the primary vein is absent (Plate II, 2, 3). Secondary veins are alternate, nearly parallel (Plate II, 2, 3) and occasionally curving apically at leaf margin (Plate II, 6, 7); there are from 16 to 38 secondary veins per leaf. Angle between primary and secondary veins increases towards base of lamina (Plate II, 2, 3); proximal secondary veins diverge at 110° to 55°, whereas most distal secondaries diverge at 30–50°. Tertiary veins form a hexagonal areole pattern between secondaries. Areoles are broader than longer and measure ~0.2–1 mm in width and ~0.07–0.5 mm in length. Number of tubercles in each areola varies from 1 to 2 (Plate II, 3, 6). In a few specimens, there are multiple hexagonal secondary areolas, smaller than primary ones (Plate II, 6, 7). Trichomes are arranged in parallel rows that follow the orientation of secondary veins (Plate II, 4), are straight, thicker at base and thinning upwards, and are approximately 0.1 mm to 0.4 mm long (Plate II, 4, 5).

Submerged leaves have 3 to 6 segments covered with abundant simple trichomes (Plate II, 9). Some of these segments bear rounded structures (Plate II, 8, 10; Plate III, 2–6) 2.5–7.5 mm long and 1–3.5 mm wide. These rounded structures bear several (n = 15–30) distinct, elliptical to spherical segments (Plate II, 1, 10; Plate III, 5, 6). Submerged leaf segments range 5–17 mm in length, while segments that bear rounded

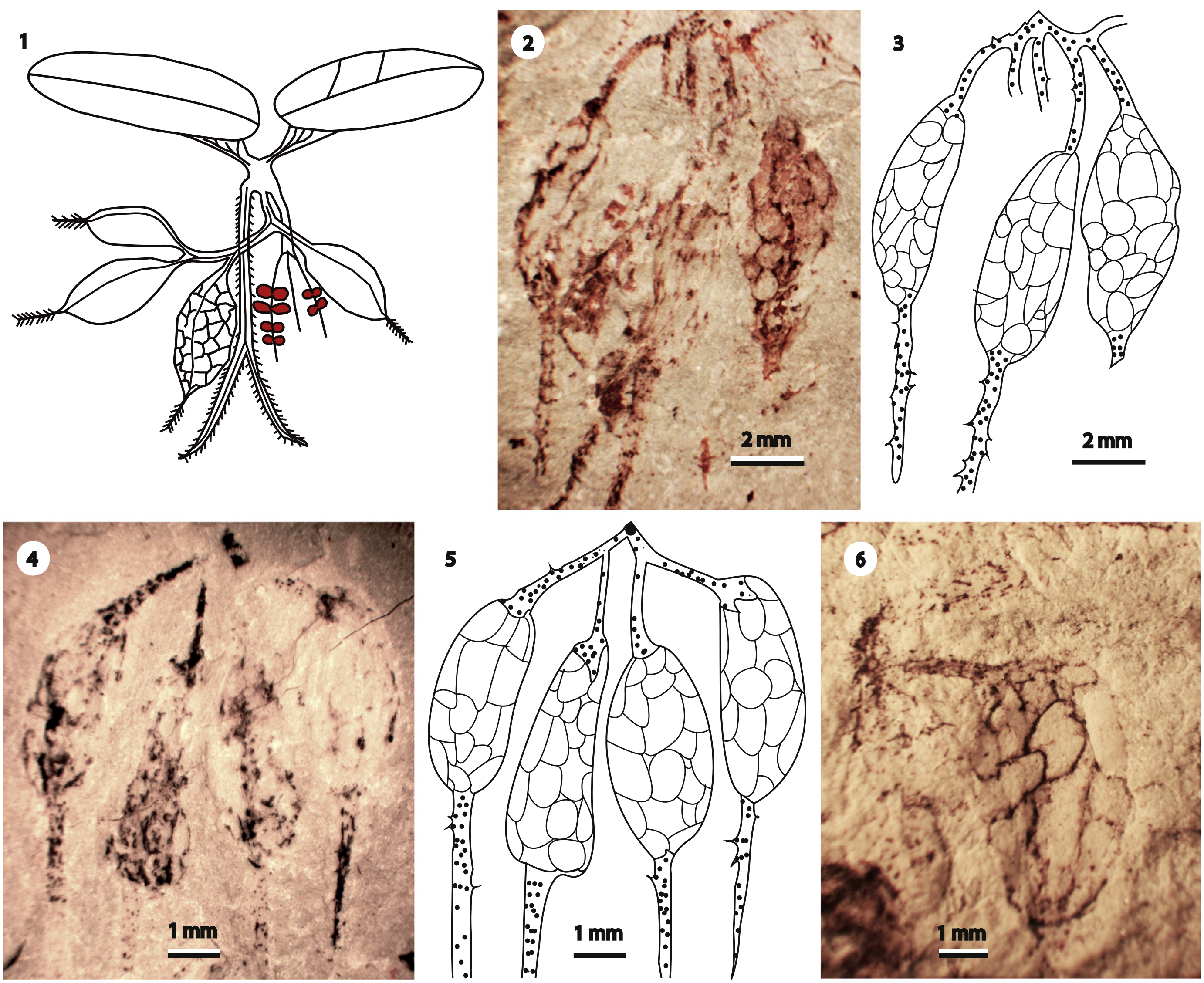

Plate III. Submerged rounded structures of *Salvinia reussii* and *Salvinia magdalenensis* sp. nov.

1. Schematic reconstruction of *Salvinia reussii*, Miocene, Bohemia (Bůžek et al., 1971) bearing submerged rounded structures. Modified from Collinson, 1991.
2–5. Submerged rounded structures attached to node of the submerged leafs, and their respective schematic diagrams. MUN STRI-36782 and MUN STRI-32288.
6. Isolated submerged rounded structure and associated submerged leaf. MUN STRI-36731.

structures range between 1.5–3.4 mm in length. Primary axis of leaves is short (one fifth of the total length of the leaf) and lateral segments are generally highly ramified (Plate III, 3, 5), although sometimes they appear without ramifications.

Morphological comparison of *Salvinia magdalenensis* sp. nov. with extant taxa:

Salvinia magdalenensis has a smaller size range than any other extant or fossil species (3–7 mm × 4.5–10 mm; Appendix 2) and has rounded structures which all extant species lack. Among the vegetative characters of *S. magdalenensis* that differ from those of extant species are areole shape (hexagonal) and size. *S. magdalenensis* resembles *Salvinia sprucei* because it also has a zigzag pattern in the primary vein but can be distinguished from *S. sprucei* because latter has areolas with quadrangular to hexagonal shape and their width varies, increasing towards the primary vein. *Salvinia oblongifolia*, *Salvinia nymphellula* Desvaux and *S. natans* have rectangular areoles (Shaparenko, 1956), and *Salvinia herzogii* de la Sota has elongated areoles (Forno, 1983). *Salvinia auriculata* and *Salvinia biloba* Raddi have quadrangular to hexagonal areoles larger than those of *S. magdalenensis* (Forno, 1983; Lichtenstein, 1939). *S. magdalenensis* has 1–2 trichomes per areole, while *Salvinia natans* has 4 to 8 trichomes per areole and *S. oblongifolia* has 4 trichomes per areole (Shaparenko, 1956). The submerged leaves of *S. auriculata*, *S. herzogii* and *S. biloba* have a long, stalk-like main axis which is short in *S. magdalenensis* (Forno, 1983).

Morphological comparison of *Salvinia magdalenensis* sp. nov. with fossil taxa:

The primary vein of *Salvinia magdalenensis* does a zigzag in the middle, not previously described for other *Salvinia* fossil (Plate II, 4). Areoles of *S. magdalenensis* and *Salvinia coahuilensis* Weber have hexagonal shape (Weber, 1973), however, the size of the areoles in *S. magdalenensis* (l = 0.2, w = 0.5) is much smaller than those of *S. coahuilensis* (l = 2, w = 0.8), and the length-width proportions are different. *Salvinia hainanensis* Wang and *Salvinia pseudoforma* Heer have one tubercle per quadrangular or hexagonal areole, in *S. magdalenensis* there are 1–2 tubercles per areole (Wang et al., 2014). Submerged rounded segments have also been described for *Salvinia mildeana* Goeppert from upper Miocene of Sosnica, Poland (Collinson et al., 2001) and *Salvinia reussii* Ettingsh (Plate III, 1) from upper Oligocene of Germany and lower Miocene of Bilina, Czech Republic (Bůžek et al., 1971). However, these species consistently differ from *S. magdalenensis* in characters of floating leaves such as shape of areoles and number of tubercles per areole.

Submerged rounded structures are absent in extant species of *Salvinia*. These rounded structures have been interpreted as floats to aid buoyancy (Bůžek et al., 1971; Collinson et al., 2001). Rothwell and Stockey, 1994 suggested that these rounded segments could be the wall or envelope of large multisoral sporocarps. In terms of the new terminology (Nagalingum et al., 2006), these structures could represent sorophore envelopes surrounding the sorophore structures. This interpretation has implications in the evolution of the heterosporous ferns Salviniaceae and Marsileaceae, given that the extant species of *Azolla* and all of the species from Marsilaceae possess soropohore envelope, but it is absent in modern *Salvinia*. Nevertheless, no spores have been found within any rounded structures (Collinson et al., 2001), therefore, there is no strong support for them to be sorophores. Spore remains were not observed in the samples of *Salvinia magdalenensis* when scanned under SEM, yet, it is possible that spores do not preserve well.

Species: *Salvinia* sp. 2
Age: middle to late Paleocene (Jaramillo et al., 2007).
Specimens examined: CJ42-1, CJ42-2, CJ42-3 and CJ42-4 (Plate IV)
Locality: Cerrejón coal mine, Guajira, Colombia. Cerrejón Formation. STRI locality 0318: 11° 07′40.8″N, 72° 33′18″W.
Repository: Mapuka Museum of Universidad del Norte, Barranquilla, Colombia (MUN).
Description:
These fossils comprise detached floating leaf compressions. Floating leaves have elliptic (Plate IV, 1–3) to oblong (Plate IV, 4) shape in outline; width is 9.6–9.7 mm (n = 2) and length is 9.1–12.5 mm (n = 2); base of lamina is rounded (Plate IV, 3) and apex is rounded (Plate IV, 3) or emarginated (Plate IV, 2). Primary vein absent at the apex. Secondary veins are alternate and sometimes curving apically at leaf margin. Angle between primary and secondary veins increases towards base of lamina (Plate IV, 1, 4). Areoles have quadrangular shape decreasing in size at leaf margin (Plate IV, 4).
Comparison:
Salvinia sp. 2 has quadrangular areolae as seen in *Salvinia pseudoforma*, *Salvinia mildeana* and the extant species *Salvinia auriculata* and *Salvinia biloba*. Floating are larger than those of *Salvinia magdalenensis*, *Salvinia bogotensis* and *Salvinia* sp. 1. The primary vein of *Salvinia* sp. 2 also narrows toward the apex, similarly to *Salvinia reussii*, *Salvinia coahuilensis*, *Salvinia* sp. 1 and *S. bogotensis*.

Comments:
Specimens are not assigned to a specific species due to the poor preservation of the fossil, which does not allow us to provide a complete description.

4. Discussion

The current understanding of the phylogenetic relationships based on molecular data among species of *Salvinia* supports the presence of two major clades, Eurasian and American (Fig. 1-D; Nagalingum et al., 2008). However, only five species were used in this analysis (Eurasian clade: *Salvinia cucullata* (unaccepted) and *Salvinia natans* and American clade: *Salvinia minima*, *Salvinia molesta* (currently *Salvinia adnata*) and *Salvinia oblongifolia*). The scarce Cretaceous fossil record of *Salvinia*, mostly reported from high latitude regions of North America, and the small amount of paleobotanical collections in tropical regions might be obscuring our understanding of the origin and diversification of this group. The four records of *Salvinia* for the Paleogene of Tropical South America described here, indicate that *Salvinia* was present in tropical latitudes at least since the middle Paleocene (~58 Ma). Here we discuss the fossil record of *Salvinia* and its modern distribution and paleobiogeography in light of the new fossil findings. Furthermore, we discuss the geological and paleogeographical implications of the localities where *Salvinia* fossils were found.

Of the ten accepted species of *Salvinia* (http://www.theplantlist.org/; accessed 10th October), six are restricted to South-Central America (*Salvinia adnata*, *Salvinia auriculata*, *Salvinia Biloba*, *Salvinia oblongifolia*, *Salvinia radula and Salvinia sprucei*), One species is shared between North America and South-Central America (*Salvinia minima*), two species are restricted to Africa (*Salvinia hastata* Desv. and *Salvinia nymphellula*) and one species is restricted to Europe and South East Asia (*Salvinia natans;* European Red List, IUCN 2011). One further species, *Salvinia cucullata*, has not been taxonomically resolved but is known from south east Asia (Nagalingum et al., 2008) and *Salvinia adnata* (synonym *Salvinia molesta*) seems to have been introduced in Australia (McCarthy and Orchard, 1998; Nagalingum et al., 2008). The phylogenetic relationships of the African species are unknown, although they are expected to form a clade with the American species if they share a Gondwanan origin.

4.1. Paleobiogeography

The Cretaceous record of *Salvinia* is restricted to temperate regions of northern hemisphere (n = 4), and therefore, it has been proposed that the group originated there (Hall, 1974; Skog, 2001; Fig. 1-B).

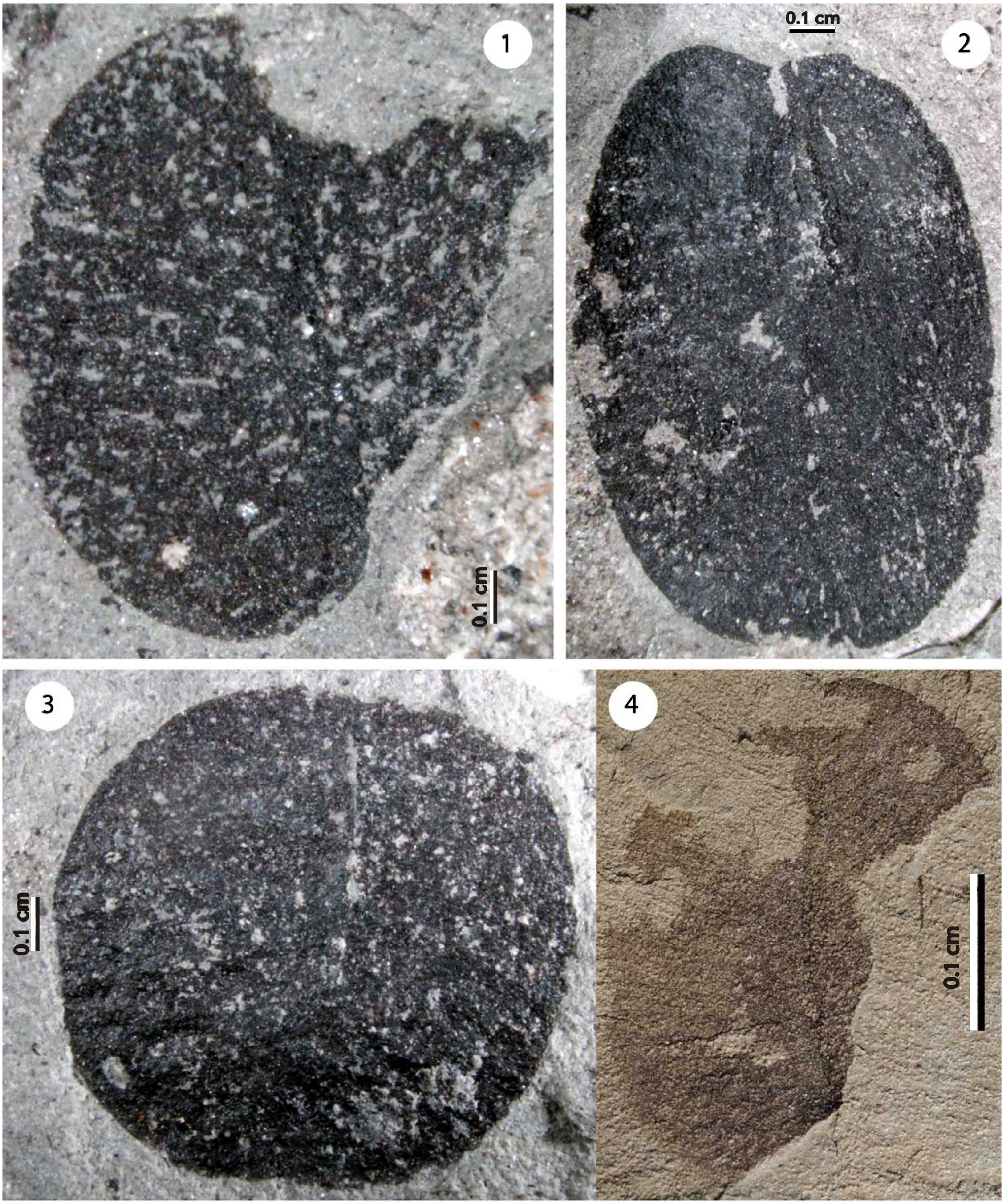

Plate IV. Macrofossils of *Salvinia* sp. 2 from the Cerrejon Fm. Pictures obtained from the supplementary material of Wing et al., 2009.

However, the number of well-studied Cretaceous floras from tropical latitudes is very scarce (Fig. 1-E, F), and thus further exploration of tropical Cretaceous sites is necessary to confirm this hypothesis.

The Cenozoic record of *Salvinia* has a worldwide and wide latitudinal distribution (Fig. 1-B, C), although high latitude localities in the northern hemisphere are strongly dominant. Cenozoic floras outside the northern temperate regions are scarce and include the early Paleocene of India (Mahabale, 1950), Colombia (reported by Wing et al., 2009 and described here), Eocene of southern China (Wang et al., 2014) and Miocene from Argentina (Herbst et al., 1987; Fig. 1-B).

A Laurasian origin of *Salvinia* has been previously proposed (Skog, 2001). Assuming the origin of *Salvinia* in high latitudinal regions of North America during the Cretaceous (Skog, 2001), would imply either an dispersal in the mid Cretaceous to Gondwana to explain its distribution across South America, Africa and Madagascar, or a Paleocene dispersal to South America, and from there a subsequent dispersal to Africa/Madagascar at some point during the Cenozoic, as the Gondwanan form a distinct clade (Fig. 1).

The Cenozoic latitudinal distribution of *Salvinia* is different from its modern distribution. *Salvinia* was common in high latitude northern regions (North America, Europe and Asia) during most of the Cenozoic, and today it is still present in high latitudes but restricted to small fragments, while it is mostly distributed along tropical regions (Fig. 1-B, C). The absence of *Salvinia* in the fossil record of tropical latitudes could be related to the lack of studies of megafloras in the region. The restriction in the longitudinal distribution of *Salvinia* across high latitudes probably occurred during the Pleistocene (Fig. 1-B). This change in distribution could be related to the reduction of global temperature and the increase in latitudinal temperature gradients (Savin, 1977). Experiments on modern *Salvinia adnata* show that it does not survive on temperatures below 5° or above 43 °C after a few hours (Whiteman and Room, 1991), thus northern hemisphere glaciations could have affected the modern distribution of the genus.

4.2. Paleoenvironments and paleogeography

The northern Andes are divided in the Western, Central and Eastern cordilleras, separated by the intermountain basins of the Cauca and Magdalena rivers (Fig. 3). Paleogene paleogeography of the fossil *Salvinia* localities was quite different from today (Fig. 3). The northern Andes could be broadly classified as a syn- to post-collisional margin (Cardona et al., 2014; Weber et al., 2010), where an intraoceanic arc diachronously swept along from south to north causing deformation along the western margin of the Central cordillera of Colombia, and the Santa Marta massif. These mountains formed at the time of the collision, while there were only discontinuous hills in the Eastern cordillera (Bayona et al., 2011, 2013; Lamus et al., 2013; Mora et al., 2010). All occurrences of *Salvinia* here reported would have then been located in lowlands, probably along a piedmont or foreland basin that would have been facing directly to the Amazon or Maracaibo basins to the east (Fig. 3).

To the north, Paleocene strata of the Cerrejón Formation contains the record of very high temperatures (Head et al., 2009) and precipitations (Wing et al., 2009) in an oscillating paralic swampy environment very favorable to coal accumulation (Jaramillo et al., 2007). Provenance analyses (Bayona et al., 2007) and growth strata (Montes et al., 2010) indicate that the mountains that today block direct communication with neighboring Maracaibo basin were not present at that time. The Paleocene Bogota Formation and the Eocene Esmeraldas Formation would have been located in a paleogeographic situation far removed from the piedmont of the Central cordillera, in lowlands connected to the Amazon basin (Fig. 3). Strata of the Esmeraldas Formation contains

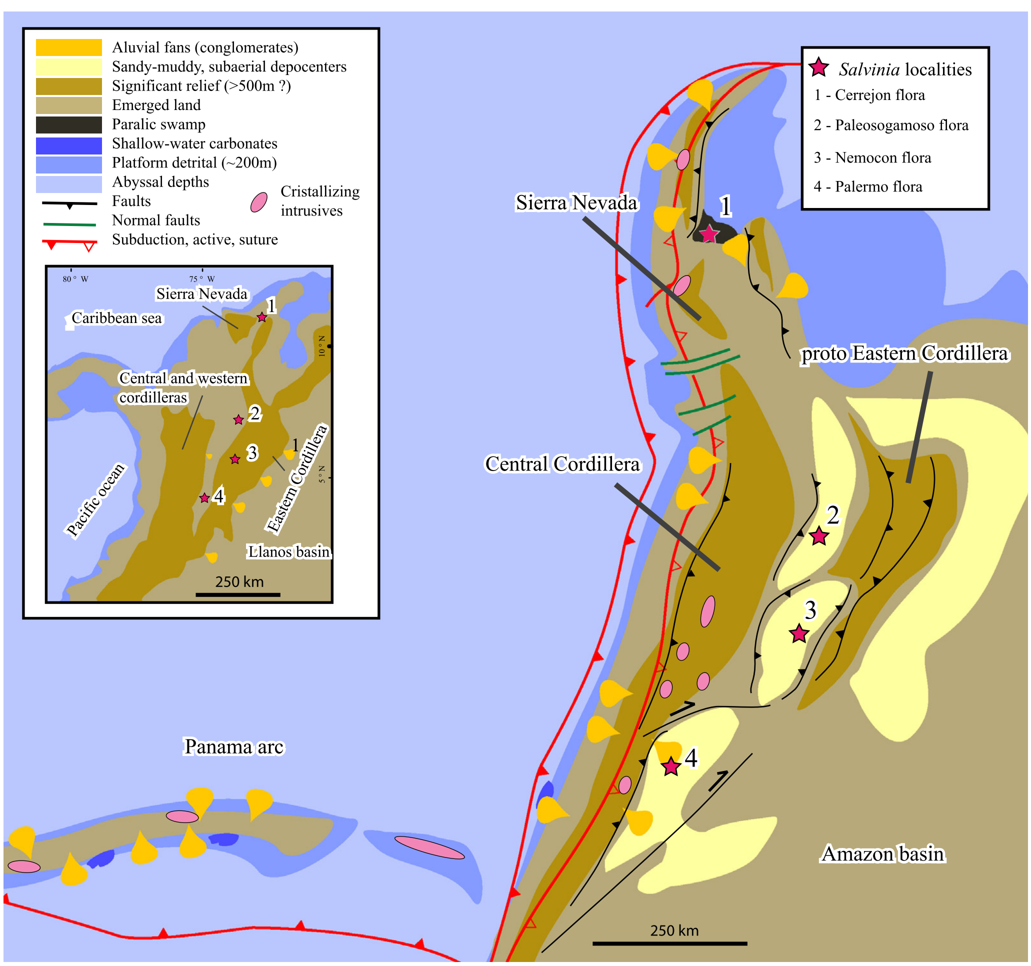

Fig. 3. Paleogene paleogeographic reconstruction of northern South America. Modified from: Cardona et al., 2014.

the record of initial Eastern cordillera rise (Nie et al., 2010), so at least hills with perhaps complex drainage patterns could have been present at that time. The Palermo Formation in contrast, would have been located in a steep piedmont where very coarse-grained, high energy fluvial fans drained the highlands of the Central cordillera (Anderson, 1972; Caicedo and Roncancio, 1994). These fans could have hosted fine-grained, low-energy and short-lived ponds where *Salvinia* could flourish. Current estimates suggest that even by Oligocene times the Eastern cordillera would not have been an effective barrier (Anderson et al., 2016), and today's Magdalena valley was open to the Amazon basin. Syn-tectonic deposits of the Eastern cordillera, however, were already developing (Bayona et al., 2013; Lamus et al., 2013), and suggest that this mountainous barrier may have been present, perhaps discontinuously, at that time (Fig. 3).

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Appendix 1. List of all the fossils of *Salvinia* and *Azolla* considered in the latitudinal analysis. Downloaded and modified from the Paleobiology Data Base

Data Provider	The Paleobiology Database
Data Source	The Paleobiology Database
Data License	Creative Commons CC-BY
License URL	http://creativecommons.org/licenses/by/4.0/
Documentation URL	http://paleobiodb.org/data1.1/occs/list_doc.html
Data URL	http://paleobiodb.org/data1.1/occs/list.csv?limit=all&base_id=56125&show=coords,attr,loc,prot,time,strat,stratext,lith,lithext,geo,rem,ent,entname,crmod,paleoloc&showsource

Species name	Reference	Age	Longitude	Latitude	Country	State	Formation	Paleolongitude	Paleolatitude
Salvinia magdalenensis	This article	Eocene	−75.55	2.7416	CO	Huila	Palermo	_	_
Salvinia sp.	This article	Eocene	−73.4292	7.1084	CO	Santander	Esmeralda	_	_
Salvinia bogotensis	This article	Paleocene	−73.9553	5.0767	CO	Cundinamarca	Bogota	_	_
Salvinia preauriculata	Hickey, L. J. (1977). Stratigraphy and paleobotany of the Golden Valley Formation (early Tertiary) of western North Dakota. Geological Society of America Memoirs, 150, 1–296.	Eocene	−103.25	45.5	US	North Dakota	Golden Valley	−74.14	52.13
Salvinia preauriculata	Hickey, L. J. (1977). Stratigraphy and paleobotany of the Golden Valley Formation (early Tertiary) of western North Dakota. Geological Society of America Memoirs, 150, 1–296.	Paleocene	−102	46.983334	US	North Dakota	Golden Valley	−67.96	53.86
Salvinia preauriculata	Hickey, L. J. (1977). Stratigraphy and paleobotany of the Golden Valley Formation (early Tertiary) of western North Dakota. Geological Society of America Memoirs, 150, 1–296.	Paleocene	−102.050003	47.983334	US	North Dakota	Golden Valley	−67.36	54.8
Salvinia preauriculata	Hickey, L. J. (1977). Stratigraphy and paleobotany of the Golden Valley Formation (early Tertiary) of western North Dakota. Geological Society of America Memoirs, 150, 1–296.	Eocene	−102.833336	47.166668	US	North Dakota	Golden Valley	−72.81	53.61
Salvinia preauriculata	Hickey, L. J. (1977). Stratigraphy and paleobotany of the Golden Valley Formation (early Tertiary) of western North Dakota. Geological Society of America Memoirs, 150, 1–296.	Eocene	−102.833336	47.083332	US	North Dakota	Golden Valley	−72.86	53.54
Salvinia preauriculata	Hickey, L. J. (1977). Stratigraphy and paleobotany of the Golden Valley Formation (early Tertiary) of western North Dakota. Geological Society of America Memoirs, 150, 1–296.	Eocene	−101.949997	47.383331	US	North Dakota	Golden Valley	−71.74	53.62
Salvinia preauriculata	Hickey, L. J. (1977). Stratigraphy and paleobotany of the Golden Valley Formation (early Tertiary) of western North Dakota. Geological Society of America Memoirs, 150, 1–296.	Eocene	−102.816666	47	US	North Dakota	Golden Valley	−72.89	53.45
Salvinia preauriculata	Wing, S. L., Alroy, J., & Hickey, L. J. (1995). Plant and mammal diversity in the Paleocene to early Eocene of the	Eocene	−108.051331	44.292519	US	Wyoming	Willwood	−80.01	52

Appendix 1 (*continued*)

Species name	Reference	Age	Longitude	Latitude	Country	State	Formation	Paleolongitude	Paleolatitude
Salvinia preauriculata	Bighorn Basin. Palaeogeography, Palaeoclimatology, Palaeoecology, 115(1), 117–155.								
Salvinia peauriculata	Wing, S. L., Alroy, J., & Hickey, L. J. (1995). Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin. Palaeogeography, Palaeoclimatology, Palaeoecology, 115(1), 117–155.	Eocene	−108	44	US	Wyoming	Willwood	−80.09	51.71
Salvinia preauriculata	Wing, S. L., Alroy, J., & Hickey, L. J. (1995). Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin. Palaeogeography, Palaeoclimatology, Palaeoecology, 115(1), 117–155.	Eocene	−108.052132	44.298218	US	Wyoming	Willwood	−80.01	52.01
Salvinia preauriculata	Wing, S. L., Alroy, J., & Hickey, L. J. (1995). Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin. Palaeogeography, Palaeoclimatology, Palaeoecology, 115(1), 117–155.	Eocene	−107	44	US	Wyoming	Willwood	−78.98	51.5
Salvinia preauriculata	Wing, S. L., Alroy, J., & Hickey, L. J. (1995). Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin. Palaeogeography, Palaeoclimatology, Palaeoecology, 115(1), 117–155.	Eocene	−107	44	US	Wyoming	Willwood	−78.98	51.5
Salvinia preauriculata	Wing, S. L., Alroy, J., & Hickey, L. J. (1995). Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin. Palaeogeography, Palaeoclimatology, Palaeoecology, 115(1), 117–155.	Eocene	−109	44	US	Wyoming	Willwood	−81.21	51.92
Salvinia preauriculata	Wing, S. L., Alroy, J., & Hickey, L. J. (1995). Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin. Palaeogeography, Palaeoclimatology, Palaeoecology, 115(1), 117–155.	Eocene	−109	44	US	Wyoming	Willwood	−81.95	51.73
Salvinia preauriculata	Wing, S. L., Alroy, J., & Hickey, L. J. (1995). Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin. Palaeogeography, Palaeoclimatology, Palaeoecology, 115(1), 117–155.	Eocene	−108.220711	44.446411	US	Wyoming	Willwood	−80.13	52.19
Salvinia preauriculata	Wing, S. L., Alroy, J., & Hickey, L. J. (1995). Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin. Palaeogeography, Palaeoclimatology, Palaeoecology, 115(1), 117–155.	Eocene	−108.071724	44.354496	US	Wyoming	Willwood Formatin	−80.01	52.07
Salvinia preauriculata	Wing, S. L., Alroy, J., & Hickey, L. J. (1995). Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin. Palaeogeography, Palaeoclimatology, Palaeoecology, 115(1), 117–155.	Eocene	−108.333336	44.5	US	Wyoming	Willwood	−80.23	52.26
Salvinia preauriculata	Wing, S. L., Alroy, J., & Hickey, L. J. (1995). Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin. Palaeogeography, Palaeoclimatology, Palaeoecology, 115(1), 117–155.	Eocene	−109	44	US	Wyoming	Willwood	−81.21	51.92
Salvinia preauriculata	Wing, S. L., Alroy, J., & Hickey, L. J. (1995). Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin. Palaeogeography, Palaeoclimatology, Palaeoecology, 115(1), 117–155.	Eocene	−109	44	US	Wyoming	Willwood	−81.21	51.92
Salvinia preauriculata	Wing, S. L., Alroy, J., & Hickey, L. J. (1995). Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin. Palaeogeography, Palaeoclimatology, Palaeoecology, 115(1), 117–155.	Eocene	−109	44	US	Wyoming	Willwood	−81.21	51.92

(*continued on next page*)

Appendix 1 (*continued*)

Species name	Reference	Age	Longitude	Latitude	Country	State	Formation	Paleolongitude	Paleolatitude
Salvinia preauriculata	Wing, S. L., Alroy, J., & Hickey, L. J. (1995). Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin. Palaeogeography, Palaeoclimatology, Palaeoecology, 115(1), 117–155.	Eocene	−108.550079	44.156311	US	Wyoming	Tatman	−80.63	51.98
Salvinia preauriculata	Wing, S. L., Alroy, J., & Hickey, L. J. (1995). Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin. Palaeogeography, Palaeoclimatology, Palaeoecology, 115(1), 117–155.	Eocene	−110	44	US	Wyoming	Willwood	−82.33	52.13
Salvinia preauriculata	Wing, S. L., Alroy, J., & Hickey, L. J. (1995). Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin. Palaeogeography, Palaeoclimatology, Palaeoecology, 115(1), 117–155.	Eocene	−109	44	US	Wyoming	Willwood	−81.21	51.92
Salvinia natans cf.	Ozaki, K. (1991). Late Miocene and Pliocene floras in central Honshu, Japan. Bull. Kanagawa Pref. Mus., Nat. Sci., special issue, 244.	Miocene	139	36.25	JP	Gunma	Itahana	137.39	35.9
Salvinia miocenica	Mai, D. H., & Walther, H. (1988). Die pliozänen Floren von Thüringen, Deutsche Demokratische Republik. Quartärpaläontologie, 7(55), 297.	Pliocene	10.066667	50.966667	DE	Thuringia		10.63	50.25
Salvinia rhenana	Mai, D. H., & Walther, H. (1988). Die pliozänen Floren von Thüringen, Deutsche Demokratische Republik. Quartärpaläontologie, 7(55), 297.	Pliocene	11.2	50.849998	DE	Thuringia		11.63	50.3
Salvinia cerebrata	Mai, D. H., & Walther, H. (1988). Die pliozänen Floren von Thüringen, Deutsche Demokratische Republik. Quartärpaläontologie, 7(55), 297.	Pliocene	10.8	51.516666	DE	Thuringia		11.24	50.97
Salvinia miocenica	Mai, D. H., & Walther, H. (1988). Die pliozänen Floren von Thüringen, Deutsche Demokratische Republik. Quartärpaläontologie, 7(55), 297.	Pliocene	10.033333	50.849998	DE	Thuringia		10.47	50.31
Salvinia rhenana	Mai, D. H., & Walther, H. (1988). Die pliozänen Floren von Thüringen, Deutsche Demokratische Republik. Quartärpaläontologie, 7(55), 297.	Pliocene	10.866667	50.766666	DE	Thuringen		11.3	50.22
Salvinia tuberulata	Mai, D. H., & Walther, H. (1988). Die pliozänen Floren von Thüringen, Deutsche Demokratische Republik. Quartärpaläontologie, 7(55), 297.	Pliocene	10.866667	50.766666	DE	Thuringen		11.3	50.22
Salvinia sp.	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Oligocene	66.5	57.5	RU	Tiumensky		63.74	52.63
Salvinia preauriculata cf.	Burnham, R. J. (1994). Paleoecological and floristic heterogeneity in the plant-fossil record-an analysis based on the Eocene of Washington. Bulletin/US. Geological survey.	Eocene	−121.966667	47.25	US	Washington		−102.14	52.81
Salvinia cerebrata	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Oligocene	83	57	RU	Tomsk		78.93	53.54
Salvinia cerebrata	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Oligocene	83	57	RU	Tomsk		78.93	53.54
Salvinia sp.	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Oligocene	83	57	RU	Tomsk		78.93	53.54
Salvinia preauriculata cf.	Burnham, R. J. (1994). Paleoecological and floristic heterogeneity in the plant-fossil record-an analysis based on the Eocene of Washington. Bulletin/US. Geological survey.	Eocene	−121.966667	47.25	US	Washington		−102.14	52.81
Salvinia cerebrata	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	14.183333	51.433334	DE	Saxen		15.86	48.93
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	14.183333	51.433334	DE	Saxen		15.86	48.93

Appendix 1 (*continued*)

Species name	Reference	Age	Longitude	Latitude	Country	State	Formation	Paleolongitude	Paleolatitude
Salvinia cerebrata	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.766667	51.733334	DE	Brandenburg		15.47	49.24
Salvinia mildeana	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	14.25	51.549999	DE	Brandenburg		16.05	48.84
Salvinia cerebrata	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.533333	51.450001	DE	Brandenburg		15.49	48.56
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.533333	51.450001	DE	Brandenburg		15.49	48.56
Salvinia cerebrata	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.75	51.549999	DE	Brandenburg		15.7	48.65
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.75	51.549999	DE	Brandenburg		15.7	48.65
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.75	51.549999	DE	Brandenburg		15.45	49.05
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.75	51.549999	DE	Brandenburg		15.7	48.65
Salvinia cerebrata	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.75	51.549999	DE	Brandenburg		15.7	48.65
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.75	51.549999	DE	Brandenburg		15.45	49.05
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.9	51.549999	DE	Brandenburg		15.59	49.05
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.9	51.549999	DE	Brandenburg		15.59	49.05
Salvinia cerebrata	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.9	51.549999	DE	Brandenburg		15.59	49.05

(continued on next page)

Appendix 1 (*continued*)

Species name	Reference	Age	Longitude	Latitude	Country	State	Formation	Paleolongitude	Paleolatitude
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.9	51.549999	DE	Brandenburg		15.59	49.05
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.9	51.549999	DE	Brandenburg		15.59	49.05
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.9	51.549999	DE	Brandenburg		15.84	48.65
Salvinia cerebrata	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.9	51.549999	DE	Brandenburg		15.59	49.05
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.9	51.549999	DE	Brandenburg		15.59	49.05
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.9	51.549999	DE	Brandenburg		15.59	49.05
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.9	51.549999	DE	Brandenburg		15.59	49.05
Salvinia aspera	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Oligocene	81	59.049999	RU	Tomsk		76.72	55.46
Salvinia cerebrata	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Oligocene	81	59.049999	RU	Tomsk		76.72	55.46
Salvinia aspera	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Oligocene	81	59.049999	RU	Tomsk		76.72	55.46
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.833333	51	DE	Brandenburg		15.5	48.5
Salvinia cerebrata	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	14.7	51.516666	DE	Brandenburg		16.35	49
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.933333	51.549999	DE	Brandenburg		15.87	48.65
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.933333	51.549999	DE	Brandenburg		15.87	48.65
Salvinia cerebrata	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.933333	51.549999	DE	Brandenburg		15.87	48.65

Appendix 1 (*continued*)

Species name	Reference	Age	Longitude	Latitude	Country	State	Formation	Paleolongitude	Paleolatitude
Salvinia aspera	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Oligocene	81	59.049999	RU	Tomsk		76.72	55.46
Salvinia aspera	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Oligocene	81	59.049999	RU	Tomsk		76.72	55.46
Salvinia sibirica	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Oligocene	82.5	56.5	RU	Tomsk		78.57	53.01
Salvinia sp.	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Oligocene	82.5	56.5	RU	Tomsk		78.57	53.01
Salvinia cerebrata	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	74.5	56.5	RU	Omsk		71.67	53.15
Salvinia sp.	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	74.5	56.5	RU	Omsk		71.67	53.15
Salvinia cerebrata	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Oligocene	83.5	57	RU	Tomsk		79.23	53.42
Salvinia cerebrata	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Oligocene	83.5	57	RU	Tomsk		79.23	53.42
Salvinia intermedia	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	83	52	RU	Tomsk		80.12	49.05
Salvinia intermedia	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	83	56	RU	Tomsk		79.57	53.04
Salvinia cerebrata	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	71.099998	57.483334	RU	Omsk		69.19	55
Salvinia intermedia	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	71.099998	57.483334	RU	Omsk		69.19	55
Salvinia cerebrata	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	71.366669	57.700001	RU	Omsk		69.42	55.22
Salvinia sp.	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	71.366669	57.700001	RU	Omsk		69.42	55.22
Salvinia cerebrata	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	84	57.5	RU	Tomsk		81.32	55.42
Salvinia intermedia	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	84	57.5	RU	Tomsk		81.32	55.42
Salvinia nikitinii	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	73.01667	55.216667	RU	Omsk		71.54	53.28
Salvinia cerebratella	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	73.01667	55.216667	RU	Omsk		71.54	53.28
Salvinia intermedia	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	73.01667	55.216667	RU	Omsk		71.54	53.28
Salvinia intermedia	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	73.01667	55.216667	RU	Omsk		71.91	53.81
Salvinia cerebratella	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	73.01667	55.216667	RU	Omsk		71.91	53.81
Salvinia natans	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Pliocene	73.01667	55.216667	RU	Omsk		72.6	54.69
Salvinia nikitinii	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	73.449997	55.466667	RU	Omsk		72.31	54.07
Salvinia cerebratella	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	73.449997	55.466667	RU	Omsk		72.31	54.07
Salvinia intermedia	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	73.449997	55.466667	RU	Omsk		72.31	54.07
Salvinia sp.	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	73.449997	55.466667	RU	Omsk		72.31	54.07
Salvinia nikitinii	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	73.449997	55.466667	RU	Omsk		72.31	54.07
Salvinia cerebratella	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	73.449997	55.466667	RU	Omsk		72.31	54.07
Salvinia intermedia	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	73.449997	55.466667	RU	Omsk		72.31	54.07
Salvinia intermedia	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	74.400002	55.75	RU	Omsk		73.22	54.37
Salvinia cerebratella	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	74.400002	55.75	RU	Omsk		73.22	54.37
Salvinia intermedia	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	74.73333	56.116669	RU	Omsk		73.52	54.74
Salvinia cerebratella	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	74.73333	56.116669	RU	Omsk		73.52	54.74
Salvinia intermedia	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	74.73333	56.116669	RU	Omsk		73.52	54.74
Salvinia cerebratella	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	74.73333	56.116669	RU	Omsk		73.52	54.74
Salvinia intermedia	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	74.73333	56.116669	RU	Omsk		73.52	54.74
Salvinia cerebratella	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Miocene	74.73333	56.116669	RU	Omsk		73.52	54.74
Salvinia cerebratella	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Eocene	75.116669	57.016666	RU	Omsk		70.81	52.2

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Appendix 1 (*continued*)

Species name	Reference	Age	Longitude	Latitude	Country	State	Formation	Paleolongitude	Paleolatitude
Salvinia intermedia	Dorofeev, P. I. (1963). Tretichnye flory zapadnoi Sibiri.	Eocene	75.116669	57.016666	RU	Omsk		70.81	52.2
Salvinia turgaica	Mai, D. H., & Walther, H. (1978). Floren der Haselbacher Serie im Weisselster-Becken (Bezirk Leipzig, DDR).	Oligocene	12.433333	51.066666	DE	Saxony		15.9	45.99
Salvinia reussii cf.	Mai, D. H., & Walther, H. (1978). Floren der Haselbacher Serie im Weisselster-Becken (Bezirk Leipzig, DDR).	Oligocene	12.433333	51.066666	DE	Saxony		15.9	45.99
Salvinia turgaica	Mai, D. H., & Walther, H. (1978). Floren der Haselbacher Serie im Weisselster-Becken (Bezirk Leipzig, DDR).	Oligocene	12.433333	51.066666	DE	Saxony		15.9	45.99
Salvinia reussii cf.	Mai, D. H., & Walther, H. (1978). Floren der Haselbacher Serie im Weisselster-Becken (Bezirk Leipzig, DDR).	Oligocene	12.433333	51.066666	DE	Saxony		15.9	45.99
Salvinia sp.	Mai, D. H., & Walther, H. (1978). Floren der Haselbacher Serie im Weisselster-Becken (Bezirk Leipzig, DDR).	Oligocene	12.45	51.066666	DE	Saxony		15.92	45.99
Salvinia sp.	Mai, D. H., & Walther, H. (1978). Floren der Haselbacher Serie im Weisselster-Becken (Bezirk Leipzig, DDR).	Oligocene	12.433333	51.150002	DE	Saxony		15.91	46.07
Salvinia reussii cf.	Mai, D. H., & Walther, H. (1978). Floren der Haselbacher Serie im Weisselster-Becken (Bezirk Leipzig, DDR).	Oligocene	12.383333	51.049999	DE	Saxony		15.86	45.98
Salvinia turgaica	Mai, D. H., & Walther, H. (1978). Floren der Haselbacher Serie im Weisselster-Becken (Bezirk Leipzig, DDR).	Oligocene	12.383333	51.049999	DE	Saxony		15.86	45.98
Salvinia sp.	Mai, D. H., & Walther, H. (1978). Floren der Haselbacher Serie im Weisselster-Becken (Bezirk Leipzig, DDR).	Oligocene	12.35	51	DE	Saxony		15.82	45.93
Salvinia sp.	Mai, D. H., & Walther, H. (1978). Floren der Haselbacher Serie im Weisselster-Becken (Bezirk Leipzig, DDR).	Oligocene	12.366667	51.116669	DE	Saxony		15.85	46.04
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.933333	51.549999	DE	Brandenburg		15.62	49.05
Salvinia cerebrata	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	14.6	51.333332	DE	Brandenburg		16.25	48.82
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	14.6	51.433334	DE	Brandenburg		16.01	49.32
Salvinia miocenica	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	14.6	51.433334	DE	Sachsen		15.21	50.5
Salvinia cerebrata	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	14.6	51.433334	DE	Sachsen		16.37	48.72
Salvinia crassiuscula	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und	Miocene	14.6	51.433334	DE	Sachsen		16.37	48.72

Appendix 1 (*continued*)

Species name	Reference	Age	Longitude	Latitude	Country	State	Formation	Paleolongitude	Paleolatitude
Salvinia crassiuscula	Paläobiologie. Palaeontographica Abteilung B, 1–85.								
Salvinia cerebrata	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.616667	51.466667	DE	Brandenburg		15.57	48.57
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	14.783333	51.400002	DE	Sachsen		16.42	48.88
Salvinia cerebrata	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	14.183333	51.566666	DE	Brandenburg		15.86	49.06
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.8	51.533333	DE	Brandenburg		15.62	48.84
Salvinia intermedia	Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. Palaeontographica Abteilung B, 1–85.	Miocene	13.75	51.533333	DE	Brandenburg		15.57	48.84
Salvinia mildeana	Chandler, M. E. J. (1961). Flora of the Lower Headon beds of Hampshire and the Isle of Wight. British Museum (Natural History).	Eocene	−1.6	50.75	UK		Headon Beds	3.96	44.94
Salvinia boveyana	Chandler, M. E. J. (1957). The Oligocene flora of the Bovey Tracey lake basin, Devonshire. British Museum (Natural History) Geology.	Oligocene	−3.683333	50.583332	UK		Bovey Tracey Lignite	1.22	46.15
Salvinia preauriculata	Wilf, P. (2000). Late Paleocene–early Eocene climate changes in southwestern Wyoming: Paleobotanical analysis. Geological Society of America Bulletin,112(2), 292–307.	Eocene	−107.802902	41.71579	US	Wyoming	Wasatch	−80.9	49.48
Salvinia preauriculata	Wilf, P. (2000). Late Paleocene–early Eocene climate changes in southwestern Wyoming: Paleobotanical analysis. Geological Society of America Bulletin,112(2), 292–307.	Eocene	−107.881241	41.686062	US	Wyoming	Wasatch	−80.99	49.47
Salvinia preauriculata	Wilf, P. (2000). Late Paleocene–early Eocene climate changes in southwestern Wyoming: Paleobotanical analysis. Geological Society of America Bulletin,112(2), 292–307.	Eocene	−108.200691	41.68745	US	Wyoming	Wasatch	−81.35	49.54
Salvinia preauriculata	Wilf, P. (2000). Late Paleocene–early Eocene climate changes in southwestern Wyoming: Paleobotanical analysis. Geological Society of America Bulletin,112(2), 292–307.	Eocene	−108.384697	41.826618	US	Wyoming	Wasatch	−81.49	49.71
Salvinia preauriculata	Wilf, P. (2000). Late Paleocene–early Eocene climate changes in southwestern Wyoming: Paleobotanical analysis. Geological Society of America Bulletin,112(2), 292–307.	Eocene	−108.027077	41.815781	US	Wyoming	Wasatch	−81.1	49.62
Salvinia preauriculata	Wilf, P. (2000). Late Paleocene–early Eocene climate changes in southwestern Wyoming: Paleobotanical analysis. Geological Society of America Bulletin,112(2), 292–307.	Eocene	−108.17292	41.916618	US	Wyoming	Wasatch	−81.22	49.75

(*continued on next page*)

Appendix 1 (*continued*)

Species name	Reference	Age	Longitude	Latitude	Country	State	Formation	Paleolongitude	Paleolatitude
Salvinia preauriculata	Wilf, P. (2000). Late Paleocene–early Eocene climate changes in southwestern Wyoming: Paleobotanical analysis. Geological Society of America Bulletin,112(2), 292–307.	Eocene	−108.217079	42.330002	US	Wyoming	Wasatch	−81.09	50.16
Salvinia preauriculata	Wilf, P. (2000). Late Paleocene–early Eocene climate changes in southwestern Wyoming: Paleobotanical analysis. Geological Society of America Bulletin,112(2), 292–307.	Eocene	−108.160698	42.335098	US	Wyoming	Wasatch	−81.02	50.15
Salvinia mildeana	Collinson, M., Kvacek, Z., & Zastawniak, E. (2001). The aquatic plants Salvinia (Salviniales) and Limnobiophyllum (Arales) from the late Miocene flora of Sosnica (Poland). Acta Palaeobotanica, 41(2). ISO 690	Miocene	16.783056	51.033054	PL		Poznan	18.42	48.28
Salvinia intermedia complex informal	Collinson, M., Kvacek, Z., & Zastawniak, E. (2001). The aquatic plants Salvinia (Salviniales) and Limnobiophyllum (Arales) from the late Miocene flora of Sosnica (Poland). Acta Palaeobotanica, 41(2). ISO 690	Miocene	16.783056	51.033054	PL		Poznan	18.42	48.28
Salvinia aureovallis n. sp.	Jain, R. K., & Hall, J. W. (1969). A contribution to the early Tertiary fossil record of the Salviniaceae. American Journal of Botany, 527–539.	Eocene	−103.248055	47.393055	US	North Dakota	Golden Valley	−73.94	53.77
Salvinia aureovallis n. sp.	Jain, R. K., & Hall, J. W. (1969). A contribution to the early Tertiary fossil record of the Salviniaceae. American Journal of Botany, 527–539.	Eocene	−102.991112	46.865002	US	North Dakota	Golden Valley	−73.94	53.22
Salvinia sp.	Jain, R. K., & Hall, J. W. (1969). A contribution to the early Tertiary fossil record of the Salviniaceae. American Journal of Botany, 527–539.	Eocene	6	51.316666	NL	Limburg	Tienen	12.05	43.37
Salvinia sp.	Jain, R. K., & Hall, J. W. (1969). A contribution to the early Tertiary fossil record of the Salviniaceae. American Journal of Botany, 527–539.	Eocene	4.216667	50.416668	NL	Leval-Trahegnies	Tienen	10.81	41.84
Salvinia sp.	Jain, R. K., & Hall, J. W. (1969). A contribution to the early Tertiary fossil record of the Salviniaceae. American Journal of Botany, 527–539.	Eocene	6.216667	51.416668	BE	Leval-Trahegnies	Tienen	12.6	42.76
Salvinia sp.	Jain, R. K., & Hall, J. W. (1969). A contribution to the early Tertiary fossil record of the Salviniaceae. American Journal of Botany, 527–539.	Eocene	6.216667	51.416668	BE	Leval-Trahegnies	Tienen	12.6	42.76
Salvinia sp.	Robison, C. R., Hunt, A., & Woldberg, D. L. (1982). New Late Cretaceous leaf locality from lower Kirtland Shale member, Bisti area, San Juan Basin, New Mexico. New Mexico Geology, 4, 42–45.	Cretaceous	−108.24472	36.271111	US	New Mexico	Kirtland	−69.72	45.21
Salvinia sp.	Bolliger, T. (1992). Kleinsäugerstratigraphie in der lithologischen Abfolge der miozänen Hörnlischüttung (Ostschweiz) von MN3 bis MN7. Eclogae Geologicae Helvetiae, 85(3), 961–993.	Miocene	8.083611	47.475834	CH	Aargau		9.99	44.9
Salvinia HC312 informal	Johnson, K. R. (2002). Megaflora of the Hell Creek and lower Fort Union Formations in the western Dakotas: Vegetational response to climate change, the Cretaceous-Tertiary boundary event, and rapid marine transgression.Geological Society of America Special Paper, 361, 329–391.	Cretaceous	−104.00528	46.459442	US	North Dakota	Hell Creek	−62.79	56.5
Salvinia CJ42 informal	Wing, S. L., Herrera, F., Jaramillo, C. A., Gómez-Navarro, C., Wilf, P., & Labandeira, C. C. (2009). Late Paleocene fossils from the Cerrejón Formation, Colombia, are the earliest record of Neotropical rainforest. Proceedings of the National Academy of Sciences, 106(44), 18,627–18,632.	Paleocene	−72.555	11.128	CO		CerrejÃ³n	−52.13	9.21
Salvinia minima cf.	Herbst, R., Anzótegui, L. M., & Jalfin, G. (1987). Estratigrafía, paleoambiente y	Miocene	−66.08667	−25.678333	AR	Provincia de Salta		−64.15	−25.35

Appendix 1 (*continued*)

Species name	Reference	Age	Longitude	Latitude	Country	State	Formation	Paleolongitude	Paleolatitude
Salvinia minima cf.	dos especies de Salvinia Adanson (Filicopsida), del Mioceno superior de Salta, Argentina. Facena, 7, 15–42.								
Salvinia graui	Herbst, R., Anzótegui, L. M., & Jalfin, G. (1987). Estratigrafía, paleoambiente y dos especies de Salvinia Adanson (Filicopsida), del Mioceno superior de Salta, Argentina. Facena, 7, 15–42.	Miocene	−66.099998	−25.733334	AR	Provincia de Salta		−64.16	−25.41
Salvinia coahuilensis	Weber, R. (1973). Salvinia coahuilensis nov. sp. del Cretácico Superior de México. Ameghiniana, 10(2), 173–190.	Cretaceous	−101.216667	27.933332	MX	Coahuila		−65.22	35.56
Salvinia natans	Nasu, T., & SETO, K. (1976). Fossil macrospores and massulae of Salvinia natans from the Pliocene and the Quaternary sediments in the Kinki and Tokai districts, Japan. Bulletin of the Osaka Museum of Natural History, 30, 37–48.	Pliocene	136.850006	34.783333	JP	Aichi Prefecture		136.05	34.59
Salvinia natans	Nasu, T., & SETO, K. (1976). Fossil macrospores and massulae of Salvinia natans from the Pliocene and the Quaternary sediments in the Kinki and Tokai districts, Japan. Bulletin of the Osaka Museum of Natural History, 30, 37–48.	Pleistocene	135.350006	34.450001	JP	Kishiwada city		134.97	34.35
Salvinia natans	Nasu, T., & SETO, K. (1976). Fossil macrospores and massulae of Salvinia natans from the Pliocene and the Quaternary sediments in the Kinki and Tokai districts, Japan. Bulletin of the Osaka Museum of Natural History, 30, 37–48.	Pleistocene	135.766663	35.083332	JP	Kyoto City		135.38	34.98
Salvinia natans	Nasu, T., & SETO, K. (1976). Fossil macrospores and massulae of Salvinia natans from the Pliocene and the Quaternary sediments in the Kinki and Tokai districts, Japan. Bulletin of the Osaka Museum of Natural History, 30, 37–48.	Pleistocene	135.766663	34.883331	JP	Kyoto City		135.38	34.78
Salvinia natans	Nasu, T., & SETO, K. (1976). Fossil macrospores and massulae of Salvinia natans from the Pliocene and the Quaternary sediments in the Kinki and Tokai districts, Japan. Bulletin of the Osaka Museum of Natural History, 30, 37–48.	Holocene	135.733337	34.916668	JP	Kyoto city		135.73	34.92
Salvinia hainanensis	Wang, L., Xu, Q. Q., & Jin, J. H. (2014). A reconstruction of the Fossil Salvinia from the Eocene of Hainan Island, South China. Review of Palaeobotany and Palynology, 203, 12–21.	Eocene	110.11778	19.634167	CH	Hainan Island	Changchang Formation	_	_
Salvinia hainanensis	Guo, S.X., 1979. Late Cretaceous and Early Tertiary floras from the Southern Guangdong and Guangxi with their stratigraphic significance. In: Institute of Vertebrate Paleontology and Paleoanthropology and Nanjing Institute of Geology and Palaeontology, Academia Sinica (Eds.), Mesozoic and Cenozoic Red Beds of South China. Science Press, Beijing, pp. 223–231 (in Chinese).	Eocene	110.354578	20.003902	CH	Hainan Island	Changchang Formation	_	_
Salvinia sp.	He, C.X., Tao, J.R., 1997. A study on the Eocene flora in Yilan County, Heilongjiang. Acta Phytotaxon. Sin. 35, 249–256 (in Chinese with English abstract).	Eocene	129.390562	46.171801	CH	Yilan Coal Mine	Dalianhe Formation	_	_
Salvinia sp.	Writing Group of Cenozoic Plants of China (WGCPC), 1978. Cenozoic Plants from China. Fossil Plants of China, vol. 3. Science Press, Beijing, pp. 5–6 (in Chinese).	Eocene	123.95722	41.88088	CH	Fushun	Guchengzi Formation	_	_
Salvinia sp.	Sun, K.Q., Cui, J.Z., Wang, S.J., 2010. Fossil Flora of China. Fossil Pteridophytes in China, vol. 2. Higher Education Press, Bejing, pp. 295–296 (in Chinese).	Miocene	121.428509	29.287163	CH	Ninghai	Xiananshan Formation	_	_

Appendix 2. Comparison table of *Salvinia* from this study and other fossil records. Modified from Wang et al., 2014

Taxon	Reference	Age	Floating leaves size (mm)	Shape of leaves	Primary venation	Shape of venation areolas	Areolas size (mm)	Trichomes/ tubercles per areola	Submerged leaves	Inflated segments
S. magdalenensis sp. nov.	This article	Eocene	3–7 × 4.5–10	Obovate - oblong - elliptical - ovate	Thick in the base - zigzag in the middle	Hexagonal	0.2–1 × 0.07–0.5. The wide being two times the length (2:1)	1&2	4–6 segments, 5–17 mm long	2.5–7.5 mm long and 1–3.5 mm wide
S. bogotensis sp. nov.	This article	Paleocene	4–15.5 × 5.5–21.5	Ovate - elliptical - oblong	Thick in the base	Hexagonal or rectangular	0.5–1 × 0.3–1. The wide is usually the same as the length (1:1)	1	Highly dissected. Segments 4–21.5 mm long	–
Salvinia sp.	This article	Eocene	6.2 × 7	Oblong to ovate	Thick in the base	Hexagonal	0.4–0.7 × 0.2–0.4	1&2	?	–
S. hainanensis Wang	Wang et al. (2014)	Eocene	6–14 × 11–21	Rounded to ovate to elongate	Thick in the base	Quadrangular or hexangular	?	1	Strongly branched, at least 25 mm long	–
S. fushunensis Li	WGCPC (1978)	Eocene	7.5–11 × 12–16.5	Oval	?	?	?	?	?	–
S. xiananshanensis Li	Sun et al. (2010)	Miocene	8.5 × 10.5	Oval	?	Pentangular to polygonal	?	2 to 4	?	–
S. pseudoforma Heer	Ôishi and Huzioka (1943)	Miocene	5–12 × 8–13	Rounded - ovate	?	Regular hexangular, quadrangular or polygonal		1		–
S. reussii Ettingsh	Bůžek et al. (1971), Collinson et al. (2001)	Miocene	8–30 × 10–45	Ovate oval to elongate oval	Tappers towards the apex	Mostly quadratic, sometimes hexagonal	?	4	Strongly branched, up to 100 mm long	Regularly developed, one segment bearing 2 to several floats, typically 5–15 mm long and 2–5 mm wide.
S. mildeana Goeppert	Wang et al. (2014), Collinson (2001)	Miocene	5–16 × 8–16	Elliptical - elongate	?	Mostly quadrangular		4	10 mm long with segments bearing root-like or inflated segments	One segment bearing 2–3 floats typically 8 mm long and 2 mm wide
S. coahuilensis Weber	Weber (1973)	Maastrichtian	11 × 7.5	Elliptical to ovate	Barely seen in the apex. Dicotomic venation	Hexagonal	2 × 0.8, the wide is half the length (1:2).	?	<20 mm long	–
S. preauriculata Berry	Berry (1925)	Eocene	Less than 10 × 16	Elliptical	Well defined	?	?	?	25 mm long	–
S. auriculata Aublet	Forno (1983), Lichtenstein (1939)	Extant	20–30 × 15–20	?	Reticulate	Hexagonal to quadrangular	Similar in length	?	Usually, the main axis is short and divides into 2 or 3 slightly recurved branches at the end. The main axis of the submerged organ is long and stalk-like and may reach up to 100 mm before dividing.	–
S. bilova Raddi	Forno (1983)	Extant	?	?	Reticulate	Quadrangular to hexagonal	The longest side being three times the length of the shortest (1:3)	?	Mostly, the main axis is stalked without recurved branches. At the end distal to the rhizome it divides into 2 or 3 slightly recurved branches.	-
S. herzogii de la Sota	Forno (1983)	Extant	?	?	?	Elongate	The longest side being six times the length of the shortest (1:6)	?	The main axis varies in length from 2 to 14 mm.	–
S. oblongifolia Martius	Shaparenko (1956)	Extant	12–15 × 35–45	Oval	?	Mostly rectangular		4	?	–
S. nymphellula Desveaux	Shaparenko (1956)	Extant	4–8 × 6–13	Rounded - ovate	?	Mostly rectangular		?	?	–
S. natans Allioni	Shaparenko (1956)	Extant	7–9 × 12–14	Rounded - ovate	?	Long rectangular		4 to 8	?	–

Appendix 3. List of all the fossils collected and studied, with reference to the locality

Locality	Locality coordinates	MUN-STRI-ID	MUN-STRI-ID	MUN-STRI-ID	MUN-STRI-ID
Bogotá Formation	5.0767 N; 73.9553 W	12112	12157	12679	12154
		12115	12158	12690	12125
		12116	12159	12698	
		12117	12160	29890	
		12118	12161	29891	
		12119	12162	29892	
		12120	12163	29893	
		12121	12164	29894	
		12123	12165	29895	
		12124	12166	29896	
		12126	12167	29973	
		12127	12479	29974	
		12128	12529	29975	
		12129	12591	29976	
		12130	12599	29978	
		12132	12614	29979	
		12133	12144	29980	
		12134	12145	29981	
		12135	12146	29982	
		12136	12149	29996	
		12137	12150	29997	
		12138	12151	29998	
		12139	12152	30008	
		12140	12153	30011	
		12141	12154	30013	
		12142	12155	30166	
		12143	12156	36706	
Palermo Formation	2.7416 N; 75.55 W	36783	38291	36719	
		36784	36717	36711	
		36785	36705	38293	
		36748	36703	36782	
		36699	36736	32288	
		36749	36737	36731	
		36787	36517		
		36745	38291		
		36743	38288		
		36729	36731		
		36750	36738		
		36704	36730		
		36742	36713		
		36747	38289		
		36707	38290		
		36726	38311		
		36752	36740		
		36741	36716		
		36708	36715		
		36702	36739		
		36725	36723		
		36751	36722		
		36748	36724		
		36728	36721		
		36786	36709		
		36700	36718		
		36701	36720		
Esmeralda Formation	7.1084 N; 73.4292 W	35660			
		35515			
		36164			

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