



A new angiosperm from the Crato Formation (Araripe Basin, Brazil) and comments on the Early Cretaceous Monocotyledons

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ABSTRACT

The Crato Formation paleoflora is one of the few equatorial floras of the Early Cretaceous. It is diverse, with many angiosperms, especially representatives of the clades magnoliids, monocotyledons and eudicots, which confirms the assumption that angiosperm diversity during the last part of the Early Cretaceous was reasonably high. The morphology of a new fossil monocot is studied and compared to all other Smilacaceae genus, especially in the venation. *Cratosmilax jacksoni* gen. et sp. nov. can be related to the Smilacaceae family, becoming the oldest record of the family so far. *Cratosmilax jacksoni* is a single mesophilic leaf with entire margins, ovate shape, with acute apex and base, four venation orders and main acrodromous veins. It is the first terrestrial monocot described for the Crato Formation, monocots were previously described for the same formation, and are considered aquatics. *Cratosmilax jacksoni* is the first fossil record of Smilacaceae in Brazil, and the oldest record of this family.

Key words: Araripe Basin, *Cratosmilax jacksoni*, Cretaceous, fossil leaf, Gondwana, Monocots.

INTRODUCTION

Leaves are the most visible organs of the plants, composing the majority of the fossil plants records (Wilf 1997, Mohr and Friis 2000, Friis et al. 2011). However, fossil leaves, especially angiosperms, are notoriously difficult to identify and are frequently found isolated as impressions or compressions (Crane et al. 1990, Wilf 2008). Several studies of Cretaceous fossil leaves, including analyses of vein patterns and histology, have brought useful information regarding the

systematic relationships of angiosperms and have contributed significantly to a better understanding of the evolution of early angiosperms (Hickey and Doyle 1977, Upchurch 1984, Upchurch and Dilcher 1990, Friis et al. 2006).

The size, form and venation pattern of fossil leaves are commonly preserved. Additional organic materials, such as cuticular remains, are less frequent and occasionally are also present (Upchurch and Dilcher 1990, Wilf 2008). In the Early Cretaceous, most of these records this record came from three deposits: Potomac Group - United States (Doyle and Hickey 1976, Hickey and Doyle 1977,

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Upchurch 1984), the Crato Formation - Brazil (Mohr and Friis 2000, Mohr and Eklund 2003, Mohr et al. 2006, 2007, Coiffard et al. 2013), and the Yixian Formation - China (Cao et al. 1998, Wu 1999, Leng and Friis 2006). The record of fossil leaves is useful for evolutionary studies, such as floral characteristics (Hickey and Taylor 1991). Several authors used foliar venation for taxonomic purposes and/or species characterization in the description of angiosperms (Melville 1969, Rieger and Fournier 1982, Gerber and Les 1994, Carpenter et al. 2005, Nagalingum 2007).

The Smilacaceae leaves are atypical when compared to the general pattern shown by monocots - leaves with parallel veins - because they exhibit reticulate venation among the acrodromous main veins (Inamdar et al. 1983). Smilacaceae is intimately related to Liliaceae and sometimes included in this family (Barradas and Figueiredo 1974). Most botanists, however, treat Smilacaceae as a distinct family (Hutchinson 1973, Cronquist 1981, Dahlgren et al. 1985, Conran 1989), traditionally containing three genera: *Ripogonum* Forst and Forst, *Heterosmilax* Kunth and *Smilax* L. (Koyama 1960, Hutchinson 1973, Mabberley 1997, Takhtajan 1997, Conran 1998, Cameron and Fu 2000). Recently, only the *Heterosmilax* and *Smilax* have been attributed to Smilacaceae, being the *Ripogonum* genus dismembered and placed in another family, the Ripogonaceae (Conran and Clifford 1985). The Smilacaceae family usually has a climbing habit, petiolate leaves and reticulate venation, with the type genus *Smilax* (Inamdar et al. 1983, Conran 1989) occurring worldwide at tropical and subtropical regions of Africa, Americas, Eurasia and Oceania (Andreata 1980).

This paper describes a new genus and specie of the angiosperms, a monocotyledon from the Crato Formation (Araripe Basin). The paleoflora of the Crato Formation is one of the few equatorial floras from the Early Cretaceous, it is diverse with many angiosperms, especially representatives of the

clades magnoliids, monocotyledons and eudicots (Friis et al. 2011).

GEOLOGICAL SETTING

The Araripe Basin is located in the Northeast region of Brazil, at the central part of the Borborema province (Almeida and Hasui 1984) (Fig. 1). It is an intracratonic basin and the most extensive interior basin of the region (Mabesoone et al. 1994). Because of that, the stratigraphy of the Araripe Basin is very complex and controversial, and it has been through subsequent changes for further detailing (e.g. Beurlen 1962, 1971, Mabesoone and Tinoco 1973, Assine 2007, Brito-Neves 1990, Ponte and Appi 1990, Ponte and Ponte-Filho 1996, Neumann and Cabrera 1999, Viana and Neumann 2002, Valença et al. 2003, Martill 2007a, Kellner et al. 2013). The stratigraphic proposal by Neumann and Cabrera (1999), who carried out a detailed stratigraphic review of the Araripe Basin, raising the Santana Formation to group and Crato, Ipubi and Romualdo members to formations, is used here.

The Crato Formation is positioned at the bottom of the Santana Group, it is about 5.500 km² of total area (Viana and Neumann 2002). It consists mainly of micritic laminated gray and cream limestones with halite pseudomorphs (Neumann et al. 2003). The Crato Formation (lacustrine-carbonatic) along with the upper part of the underlying Barbalha Formation (deltaic) constitutes the lacustrine aptian-albian sequence of the post rift phase of the Araripe Basin (Neumann et al. 2002, 2003). The fossiliferous record of this formation is abundant and diverse (Mabesoone and Tinoco 1973). The fossils are found in laminated limestones of lacustrine environment, developed under tropical, arid and semi-arid climatic conditions, with long intervals of dry weather and periodic precipitation (Neumann et al. 2003). The fossil content of Crato Formation includes an immense variety of fauna and flora, which contains plant fragments (Crane and Maisey 1991, Mohr and Friis 2000, Bernardes-de-Oliveira et al. 2003, Lima

et al. 2012), insects (Martins-Neto 2001), ostracods (Berthou et al. 1994), conchostracans (Carvalho and Viana 1993), fishes (e.g. Santos 1947, Castro-Leal and Brito 2004), amphibians (e.g. Kellner and Campos 1986, Baez et al. 2009), pterosaurs (Frey and Martill 1994, Sayão and Kellner 2000, 2006, Frey et al. 2003, Kellner and Campos 2007, Witton 2008, Pinheiro et al. 2011), crocodylomorphs (Salisbury et al. 2003, Figueiredo and Kellner 2009) and feathers (e.g. Sayão et al. 2011). The preservation of fossils is often excellent, conferring to the Crato Formation the status of *Lagerstätte* (Martill and Frey 1998, Kellner and Campos 1999, Sayão and Kellner 2000, Martill 2007a, b), more recently considered as a *Konservat Lagerstätte* (Selden and Nudds 2005).

The specimen MPSC PL 2400 was collected in an outcrop corresponding to the levels of laminated limestone of the Crato Formation, specifically in the quarry "Mina Idemar", city of Nova Olinda, Ceará (24M – 0423025E / UTM 9212692N). The specimen was collected at the C6-level carbonate, according to the proposal of Neumann and Cabrera (1999) (Fig. 1 D). The majority of the species and specimens of fossil plants, described for the Araripe Basin, do not have any stratigraphic and geographic locations. These fossils are often deposited at scattered collections in museums and universities around the world. MPSC PL 2400 is the first fossil plant with precise stratigraphic and geographic location described for the Crato Formation.

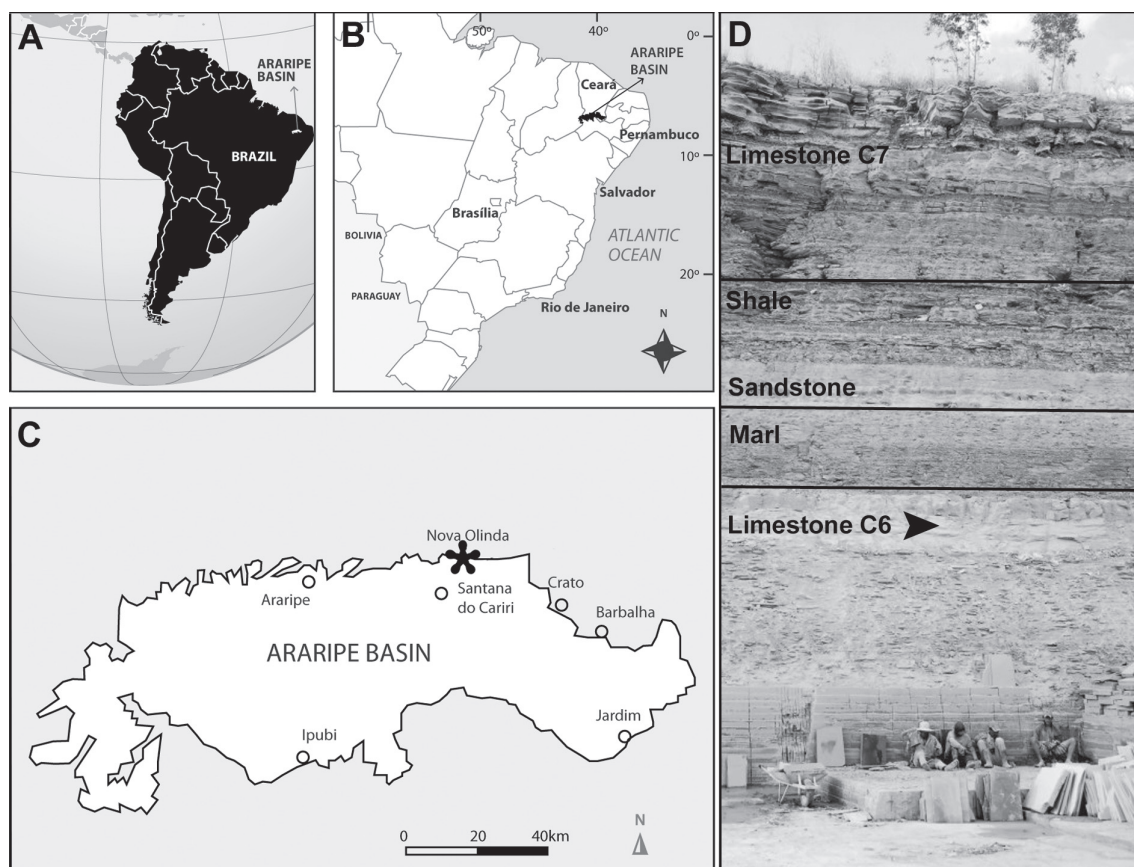


Figure 1 - A. Location of Araripe Basin in South America. B. The Araripe Basin bordering the states of Ceará, Piauí and Pernambuco in northeastern Brazil. C. Outline of the Araripe Plateau, indicating the approximate location of the quarry called "Mina Idemar" in Nova Olinda city, Ceará. D. Crato Formation layering at "Mina Idemar", indicating the laminated limestone C6-level (according to Neumann and Cabrera 1999) where the specimen was collected. Map modified from Sayão et al. 2011.

ANGIOSPERMS FROM THE CRATO FORMATION

The paleoflora of the Crato Formation comprises representatives of ferns, gymnosperms and angiosperms, with a gymnosperm predominance (Lima 1978, Lima et al. 2012). Palynological and macrofloral data reveal a great variety of ferns and seed plants (Lima 1989, Mohr and Bernardes-de-Oliveira 2004, Batten 2007, Mohr et al. 2007, Heimhofer and Hochuli 2010). It is one of the few floras of North Gondwana which has continuously been studied for many years and thus provides a relatively detailed overview of the composition and diversity of the flora in this paleoequatorial area (Friis et al. 2011). Overall, approximately 35 taxa are recognized, including several gymnosperms and angiosperms (see Lima et al. 2012, for a review). The paleogeographic location is extremely important within the Arid Equatorial Floristic Province (Vakhrameev 1984, Meyen 1987), possibly because it is where the dispersion of the earliest angiosperms occurred (Mohr and Friis 2000, Bernardes-de-Oliveira et al. 2003).

The angiosperms represent the most well-known and best described paleoflora record of the Crato Formation, standing out from the global fossiliferous record due to the preservation of flowering structures connected to vegetative parts (Friis et al. 2011). The angiosperm macrofossils are diverse and preserved as impressions, sometimes with entire plants containing roots, stems, leaves and reproductive structures in organic connection, although generally occurring as isolated leaves (Mohr and Friis 2000, Mohr and Rydin 2002, Mohr and Eklund 2003, Mohr and Bernardes-de-Oliveira 2004, Mohr et al. 2006, 2007). A variety of angiosperm foliar types have already been described, demonstrating moderate paleoequatorial diversity during the Lower Cretaceous (Mohr and Friis 2000). Examples of simple leaf morphotypes were reported for the Crato Formation and include whole leaves, from elliptic to obovate, pinnate and brochidodromous venation (Mohr and Friis 2000,

Mohr and Eklund 2003, Mohr and Bernardes-de-Oliveira 2004, Mohr et al. 2013).

In the Crato Formation many specimens have been previously referenced to the basal angiosperm (magnoliids), representing the majority of the plant record. However, only two taxa have been formally described; the members of the Magnoliales *Endressinia brasiliiana* Mohr and Bernardes-de-Oliveira 2004 and *Schenkeriphyllum glanduliferum* Mohr, Coiffard and Bernardes-de-Oliveira 2013. *E. brasiliiana* is the most ancient fossil described of the flora magnolialeana, which confirms the age of Magnoliales, previously inferred only by dispersed pollen (Mohr and Bernardes-de-Oliveira 2004). *E. brasiliiana* consists of a branching axis with simple ovate leaves closely linked and several small terminal flowers. The *S. glanduliferum* is composed of simple, sessile and branched axes with medium-sized, tightly ovate leaves containing glands and solitary-axillary flowers. Several flowering structures of *S. glanduliferum* are reasonably well preserved in different stages of maturity.

Records of the eudicotyledon are scarce, composed only by *Araripia florifera* Mohr and Eklund 2003. This species is preserved with leaves and flowers connected to a stalk. The combination of characteristics shared with several members of the Laurales, makes *A. florifera* a possible extinct representative of this order (Mohr and Eklund 2003).

Some angiosperms were described as having aquatic habit, commonly occurring in the Crato Formation. *Klitzschophyllites flabellatus* Mohr and Rydin 2002 has affinity to monocots, and the species is known from articulated branches with flabellate leaves, serrated margin, with possibly secreting glands salts. *Pluricarpellatia peltata* Mohr, Bernardes-de-Oliveira and Taylor 2008 is probably related to a basal lineage of Nymphaeales, and consists of plants with flowers with petiolate leaves ovate, peltate and elliptical. *Iara iguassu* Fanton, Ricardi-Branco, Dilcher

and Bernardes-de-Oliveira 2006 supposedly a lineage of aquatic plants with flowers, not related to monocots or existent eudicotyledonous. It has stems with verticils of slender branches and may represent an extinct member. *Jaguariba wiersemaniana* Coiffard, Mohr and Bernardes-de-Oliveira 2013 is a member of Nymphaeaceae and presents a morphology clearly adapted to aquatic environments. The leaves of *J. wiersemaniana* are simple, petiolate, stemming and start directly from a rhizome. *Spixiarum kipea* Coiffard, Mohr and Bernardes-de-Oliveira 2013 belongs to the Araceae, is a monocot with roots highly branched and laterally thin with petiolate leaves.

MATERIALS AND METHODS

The holotype of *Cratosmilax jacksoni* gen. et sp. nov. is deposited in the Museu de Paleontologia of the Universidade Regional do Cariri, located at Santana do Cariri city under the number MPSC PL 2400. The leaves are preserved in abaxial face with the substitution of the organic matter by iron oxide. The specimen was mechanically prepared to show the parts of the fossil that were still covered by the sedimentary matrix (limestone), using the methodology proposed by Fairon-Demaret et al. (1999). Later, a fragment of the leaf surface was submitted to analysis on the Scanning Electron Microscope (SEM), but no microstructure was observed. The preservation of the fossil does not allow any detailed comparison of microstructures with other fossils or any systematic analysis of depth. Linear measurements were made with a digital caliper, and the angular (angle of the base, the apex, the emergence of secondary veins, etc.) with the protractor on implied photos. The surface measurements were calculated according to the formula (length x width x 0.75) suggested by the Manual of Leaf Architecture (Ellis et al. 2009) as a description of leaf architecture and terminology. The work of Conover (1983) was used for comparison and taxonomic identification. The

distribution maps were made based on information from paleobiology database.

RESULTS

SYSTEMATIC PALEONTOLOGY

Division **Magnoliophyta** Cronquist 1981

Class **Monocotyledoneae** Cronquist 1981

Order **Liliales** Perleb 1826

Family **Smilacaceae** Ventenat 1799

Cratosmilax gen. et

TYPE SPECIES

Cratosmilax jacksoni sp. nov.

ETYMOLOGY

Generic name "*Cratosmilax*" (= smilax of the Crato Formation) = Crato derives from Crato Formation, geological formation of the Araripe Basin where important species of angiosperms were found, and smilax = due to its similarity with the genus *Smilax*, a Smilacaceae up to now known only from the Holocene.

DIAGNOSIS

Same as type species

Cratosmilax jacksoni sp. nov. (Fig. 2)

TYPE SPECIMEN

Holotype MPSC PL 2400 deposited at the Museu de Paleontologia of the Universidade Regional do Cariri, Santana do Cariri - Ceará.

TYPE LOCALITY

Quarry "Mina Idemar", Nova Olinda city, Ceará. Stratigraphic unit: Crato Formation, Santana Group, Araripe Basin. Age: Lower Cretaceous (Aptian-Albian).

ETYMOLOGY

The specific epithet "*jacksoni*" is named after the geologist Francisco Jackson Antero de Sousa, professor and environmentalist. Defensor of the Araripe Basin natural patrimony.

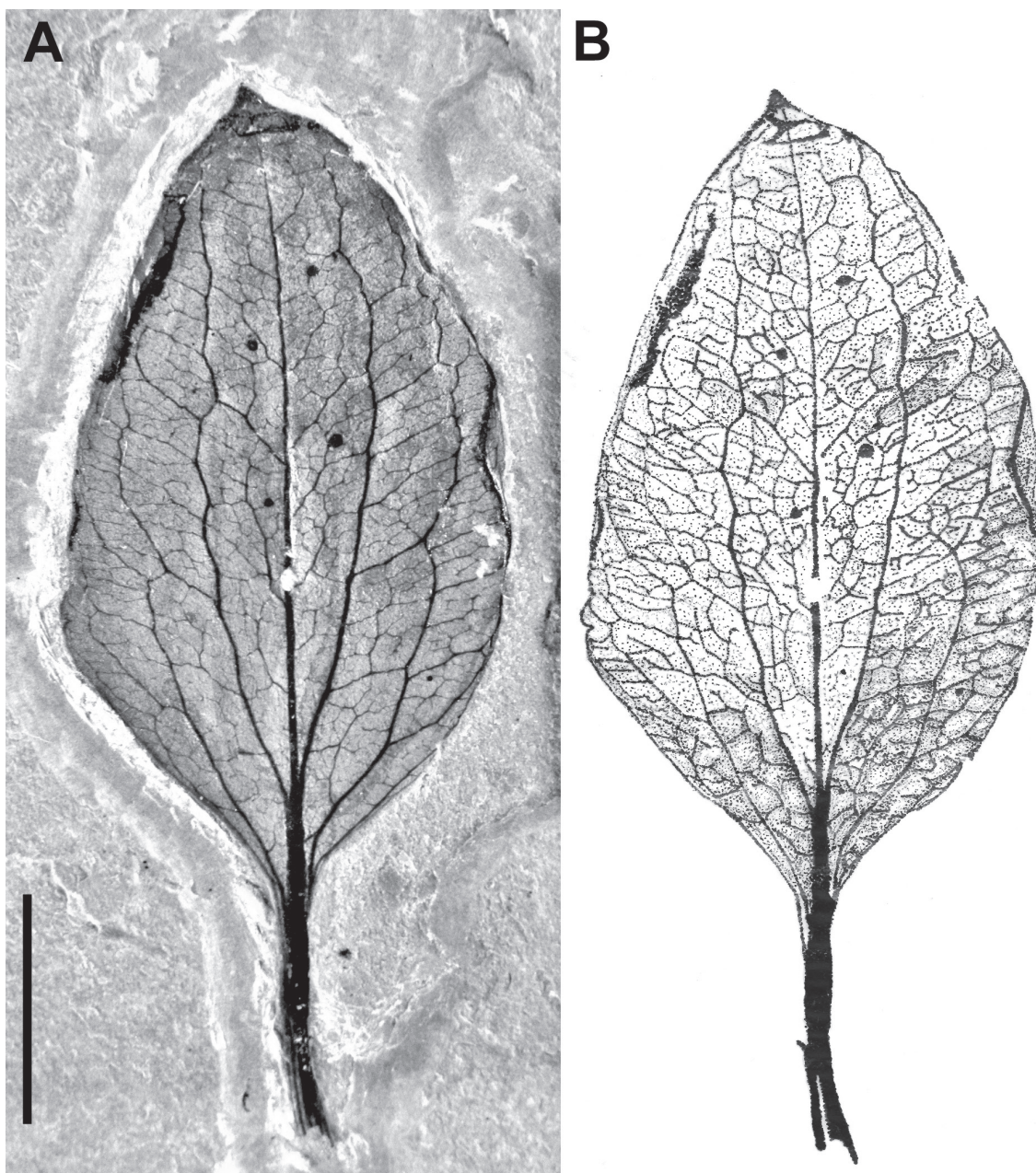


Figure 2 - *Cratosmilax jacksoni* gen. et sp. nov. **A.** Holotype, specimen MPSC PL 2400. **B.** Drawing of the Holotype emphasizing the venation pattern. Scale bar = 150 mm.

DIAGNOSIS

Simple leaf, ovate, with acute apex, attenuate base and entire margin, petiolated with channeled petiole finishing in a sheath. The main vein is prominent and straight. Two pairs of secondary veins run from the base of the lamina and end up on the upper portion being lost before reaching

the apex, the secondary veins do not converge at the apex. The secondary veins are acrodromous and transverse veins are irregular. Thin quaternary veins, reticulate and orthogonal subparallel are present among the tertiaries forming an asymmetrical reticulate transversely disposed to the primary and secondary veins.

DESCRIPTION

Cratosmilax jacksoni is composed of a single leaf with an entire margin (430 mm long by 240 mm wide) corresponding to a mesophyll leaf. The leaf is ovate, with the base (210 mm) wider than the apex (15 mm) and the center is 210 mm wide. The apex is acute in an angle of 70° and the base is acute in an angle of 80° . The leaf has a long, channeled, striated petiole preserved with 150 mm long by 2 mm wide, ending in a sheath. The specimen shows four orders of venation, with suprabasal acrodromous secondary veins (Fig. 3). The primary vein is straight with 430 mm in length and is more prominent in the proximal portion of the limbo and thinner in the distal portion. There are two pairs of secondary veins in an opposite distichous way from the base of the lamina. Secondary veins emerge at a decurrent angle ranging from 5° to 10° , parallel courses that do not converge at the apex, disappearing even before reaching the edge of the leaf. Left secondary veins converge at the apex with the main vein. Probably the secondary right vein would have reached the apex too, but the preservation of the specimen did not allow this observation to be made.

The secondary veins are the acrodromous, forming an angle of 10° at the base of the main vein. The first pair of secondary veins are 330-350 mm long and the second pair of secondary veins are 330-340 mm long. The angle between the main vein and the first pair of secondary veins is approximately 10° and with the second pair is approximately 30° . Tertiary veins are quite evident and form an asymmetric transversal reticulate compared to primary and secondary veins ranging from 20 mm to 50 mm. It shows quaternary fine veins, orthogonal subparallel reticulate between the tertiary, forming an asymmetrical reticulate transversely disposed to the primary and secondary veins. The angle between the main vein at the margin of the lamina is approximately 40° .

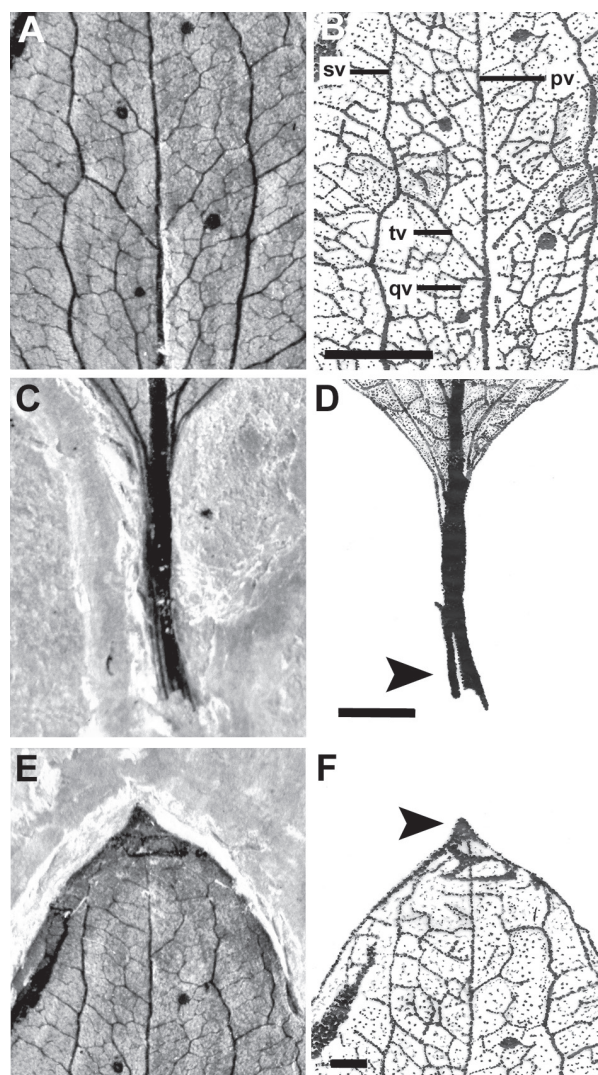


Figure 3 - A. Detail of venation of *Cratosmilax jacksoni* gen. et sp. nov. B. Drawing showing the presence four orders of venation: pv - primary vein; sv - secondary vein; tv - tertiary vein; qv - quaternary vein. C. The long petiole terminates in a sheath. D. Drawing showing details of the petiole. E. Acute foliar apex. F. Details of the acute apex forming an angle of 70° in the drawing. Scale bars = 10mm in A-B; 5mm in C-D; 2mm in E-F.

The leaf margin is folding in both midline and apex areas. This feature is observed in leaves that are in the process of resecting (Mader 1995). Probably the resecting occurred before the fossilization of *Cratosmilax* holotype. In taphonomic ways, the preservation of the whole leaf with delicate and acute apex indicates none or little transportation

(Mohr et al. 2006). The iron oxide in the fossil, usually found in Crato Formation, can sometimes make them brittle and fragile.

DISCUSSION

The monocots have a long record in the fossil history, which began in the Early Cretaceous (Daghlian 1981, Herendeen and Crane 1995, Gandolfo et al. 2000, Bremer 2000). In the Upper Cretaceous it was expected that the monocots were both widespread and diverse (Herendeen and Crane 1995), however the fossil record has shown this group with mostly Laurasian distribution with the exception of a record in Brazil. Many orders of monocots are not fully represented during the Upper Cretaceous or consist only of scattered

records (Friis et al. 2004). Nevertheless, the records of Cretaceous monocots are not common, when compared to the large amount of data on eudicotyledons of the same age (Doyle 1973, Daghlian 1981, Hotton et al. 1994, Herendeen and Crane 1995, Cox et al. 1995) (Fig. 4). The monocots usually occur more in the fossil palynoflora than in the macrofossil record (Hotton et al. 1994, Cox et al. 1995). *Cratosmilax jacksoni* reinforces the presence of monocots in the Early Cretaceous, as proposed before by the occurrence of *Klitzschophyllites flabellatus* and *Spixiarum kipea* (Doyle 1973, Walker and Walker 1984), not in accordance with Gandolfo et al. (2000), who stated that the first fossils of monocotyledons were securely identified for the Turonian.

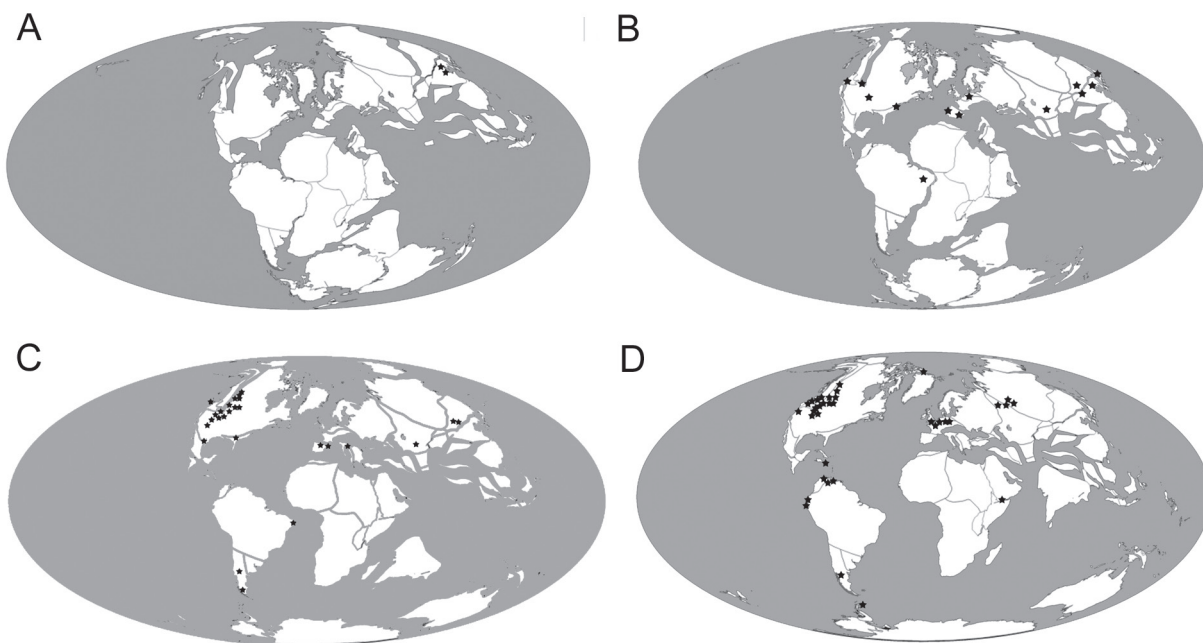


Figure 4 - Distribution map of angiosperms during Mesozoic and Cenozoic: **A.** First records at the Upper Jurassic. **B.** Early Cretaceous. **C.** Upper Cretaceous. **D.** Paleogene.

Previous works proposed parallel venation of the leaves as an apomorphy of the monocots (Doyle and Hickey 1976, Dahlgren et al. 1985, Borsch et al. 2003, Conran et al. 2009). However, this characteristic is absent in some Araceae, Dioscoreaceae, Smilacaceae and other members

of this group (Dahlgren et al. 1985, Stevenson et al. 2000). Since some evidences support the idea that reticulate venation evolved secondarily in these taxa, parallel veins should be considered as plesiomorphic (Doyle and Endress 2000, Wilson and Morrison 2000).

Most angiosperm synapomorphies are related to the reproductive system, but the vegetative parts, such as the leaves of most angiosperms, also possess a suite of features that are not seen in other plant groups (Friis et al. 2006). The main characteristics that differ angiosperms leaves from other groups is the presence of a hierarchical system of successive finer veins, veins with free termination and anastomosed between two or more orders, forming a reticulate venation pattern (Doyle 1973, Hickey and Wolfe 1975). Stipules are also considered typical of angiosperms, although not common among monocots (Friis et al. 2005). Similar to what occurs to pollen grains, the systematic determination of fossil leaves at lower levels is often complicated due to broad patterns of convergent evolution (Friis et al. 2005). In the past, many works had solely used leaves in their systematic determinations (Hickey and Doyle 1977, Upchurch 1984). With the discovering of new and more complete fossils, this kind of analysis became untrustworthy. The only way to assert the taxonomic status of a leaf is by using the venation pattern (Hickey and Wolfe 1975) and the cuticular structures (Dilcher 1974). This has significantly improved the possibilities for useful comparative studies (e.g. Upchurch and Dilcher 1990). *C. jacksoni* is a narrow monocot leaf with several orders of venation after the primary and although it could exhibit stipule this has not been preserved. The ovate form, margin entire, veins acrodromous with reticulate venation of *C. jacksoni* are common architectural features in some recent monocot leaves, especially Liliales (Cronquist 1981, Dahlgren et al. 1985). Inside this order *C. jacksoni* shares reticulate venation with Dioscoreaceae (especially *Dioscorea* L.). However, the main leaf venation of *Dioscorea* is percurrent opposite alternate, where the tertiary veins cross the secondary adjacent, forming parallel paths with no branch (Conover 1991, Ding and Gilbert 2000, Raz 2002). This venation is different in *C. jacksoni*, which presents the tertiary

veins crossing the secondary in a disorganized and opposite way, but forming a branch-shaped network. While there are similarities between *C. jacksoni* and *Ripogonum* (Ripogonaceae), the latter differs by having a blade leaf with a second pair of suprabasal lateral veins, acute to acuminate apex, without stipules. Furthermore, in many cases there is a well-developed drip tip (Conran and Clifford 1985, Conran 1989, 1998, Conran et al. 2009). *C. jacksoni* has no pairs of suprabasal lateral veins, and the drip tip is considerably shorter, these features, however, are not sufficient to include it in Ripogonaceae family.

According to the Angiosperm Phylogeny Group II system (APG II 2003), the Smilacaceae already contains *Smilax* and *Heterosmilax* (Ding et al. 2011). Usually the leaves of *Heterosmilax* blades have a broad form (large blade and petiole) ovate or lanceolate oblong, based cordate and entire or slightly lobed margin (Chen et al. 2000). *C. jacksoni* cannot be associated with *Heterosmilax*, since the basis, the number of major veins and the way the veins converge in the apex are distinct.

Cratosmilax shares some features with *Smilax*, especially regarding the venation which is typically reticulate acrodromous venation. Besides this characteristic, several species of the genus *Smilax* present an acute ovate blade to linear-lanceolate (Caponetti and Quimby 1956, Andreatta and Pereira 1990, Andreatta 1997, 2000, Guaglianone and Hurrell 2009). The *Smilax* species are variable in habit, leaf form, number of main veins, etc (Fig. 5). Some species show absolutely diagnostic features, but most are differentiated by a set of unremarkable details, closely relatable, not always easy to interpret (Andreatta 2000, Guaglianone and Gatusso 2006). The number of major veins (3-5-7) can be a useful characteristic in separating or grouping of species of *Smilax* (Barradas and Figueiredo 1974, Martins 2009), but the remarkable difference between *Smilax* and the *Cratosmilax* is that main veins do not converge completely at the apex.

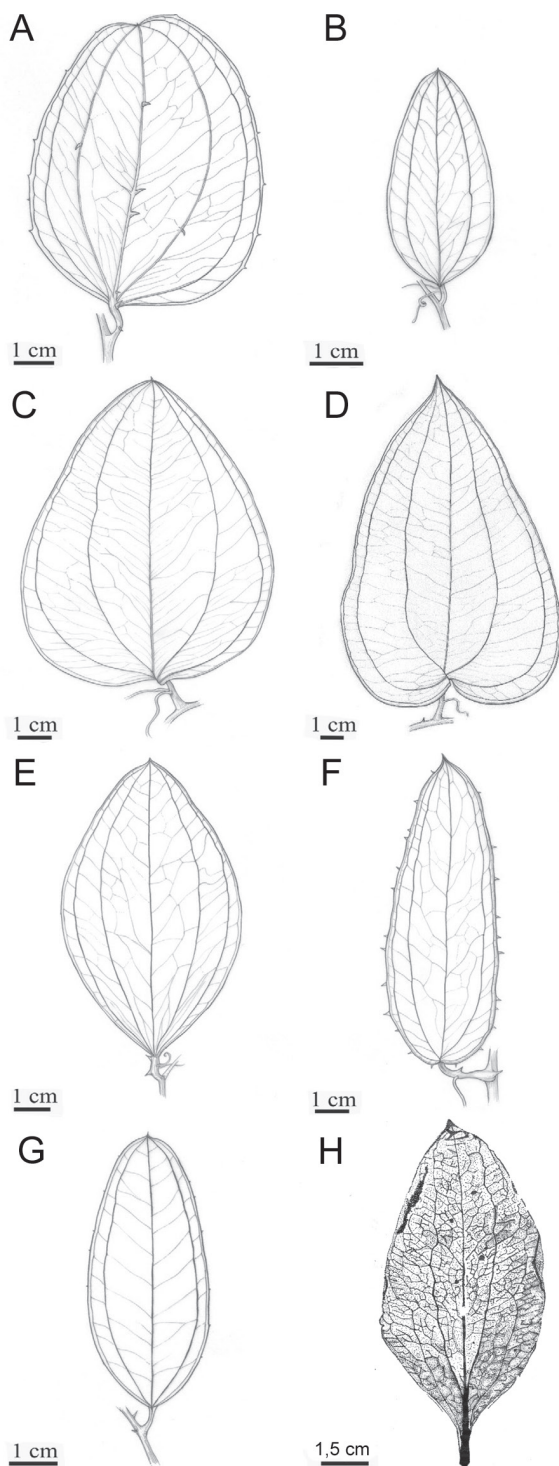


Figure 5 - Comparison among the external leaf morphologies of *Cratosmilax jacksoni* gen. et sp. nov. and seven species of *Smilax*. **A.** *Smilax brasiliensis*. **B.** *Smilax campestris*. **C.** *Smilax cissoids*. **D.** *Smilax fluminensis*. **E.** *Smilax goyazana*. **F.** *Smilax oblongifolia*. **G.** *Smilax rufescens*. **H.** *Cratosmilax jacksoni*. From A to G after Martins et al. 2013

Several fossil species of *Smilax* were reported for different locations in the Upper Cretaceous, Eocene and Miocene (e.g. Berry 1929, Morita 1931, MacGinitie 1953, Sun and Dilcher 1988, Dilcher and Lott 2005, Macovei and Givulescu 2006, Erdei and Rákosi 2009) (Fig. 6). Reliable fossil records of *Smilax* occurred frequently throughout the Cenozoic northern hemisphere (Conran et al. 2009). Generally, fossil plants are identified based on the macrostructures of leaves, but some species with similar forms, as some Cenozoic angiosperms, are generally classified by their epidermal characteristics (Bainian et al. 2004). Up to now there is no record of Smilacaceae even in the Crato palynoflora, as well as in other deposits of Early Cretaceous age. The early record of pollen of such plants comes from the Upper Cretaceous of Antarctic Peninsula (Dutra 2004) and the Pachaco Formation in Argentina (Prámparo et al. 1996).

Two monocots have been recorded in the Crato Formation paleoflora: *Klitzschophyllites flabellatus* and *Spixiarum kipea*. The plant of aquatic habits *K. flabellatus*, has orbicular leaves attached to stems trifurcated with the main veins and venation flabellate longitudinally and transversely thinner between the large veins forming an array (Mohr and Rydin 2002, Doyle et al. 2008). In *K. flabellatus* the fine venation is typical of monocots, but the main venation, is ending in spines at the leaf margin (Mohr and Rydin 2002). Based on leaf characteristics of *K. flabellatus* it is noticeable that it differs completely from *C. jacksoni*. The second record of the Crato Formation monocot is *S. kipea*, a herbaceous plant with petiolate leaves, characterized by several orders of parallel acrodromous veins converging apically and finer transverse veins, the leaves are ovate with acute base (Coiffard et al. 2013). Although it has similarities with *C. jacksoni* the leaf architecture size, form and disposal of the veins are different. *K. flabellatus* and *S. kipea* are aquatic plants or adapted to live in water (Mohr and Rydin 2002, Coiffard et al. 2013), therefore, *Cratosmilax*

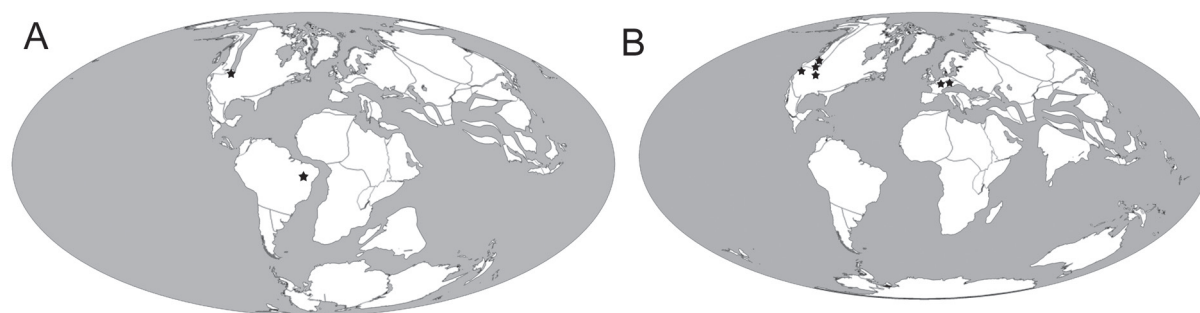


Figure 6 - First distribution patterns of Smilacaceae during Mesozoic and Cenozoic. **A.** In the Cretaceous, limited to Brazil and USA. **B.** In the Paleogene the records are limited, up to now to the Northern Hemisphere (USA and Europe).

jacksoni is the first monocot plant described with terrestrial habit for the Crato Formation.

Although dispersed fossil leaf no clear evidence about the systematic relationships of plants, they supply information on the level of complexity in leaf architecture. It may also, to some extent, be used to infer the paleoecology of the study area, height and habits of angiosperms, complexity and density of venation, which are key features in the leaf function (Boyce et al. 2009, Feild et al. 2011, Sack et al. 2012). The veins are considered one of the most visible traces of the leaves, which provide support, water distribution, carbohydrates exportation and are crucial for maintaining adequate amounts of water and amount and photosynthetic capacity (Sack and Holbrook 2006).

CONCLUSION

The unique architectural characteristics of the leaf presented by *Cratosmilax jacksoni* supports that this fossil corresponds to a new genus and species of Smilacaceae. Based on the leaf structure (presence of sheath) and venation pattern (reticulated acrodromous), *Cratosmilax jacksoni* is placed as monocot angiosperms. This taxon would be the first monocot plant with terrestrial habits described so far to the Crato Formation, only known before for aquatic plants *Klitzschophyllites flabellatus* and *Spixiarum kipea*. The description of this taxon brings new information to the Crato paleoflora,

one of the few localities in the paleoequatorial region and, therefore, of great interest for climate reconstructions of the Early Cretaceous. *Cratosmilax jacksoni* represents the first fossil of Smilacaceae family in Brazil, composing the oldest record of this family of angiosperms so far.

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RESUMO

A paleoflora da Formação Crato é uma das poucas floras equatoriais do Cretáceo Inferior. É diversificada, com

muitas angiospermas, especialmente representantes dos clados magnoliids, monocotiledôneas e eudicotiledôneas, confirmando a hipótese de que a diversidade das angiospermas durante a última parte do Cretáceo Inferior era relativamente alta. A morfologia de uma nova monocotiledônea fóssil é estudada e comparada com outros gêneros de Smilacaceae, especialmente a venação. *Cratosmilax jacksoni* n. gen. n. sp. pode ser relacionada com a família Smilacaceae, tornando-se o registro mais antigo da família, até então. *Cratosmilax jacksoni* consiste de uma única folha mesófila com margem inteira, ovada, com ápice e base agudos, quatro ordens de venação e veias principais acródomas. É a primeira monocotiledônea terrestre descrita para a Formação Crato, monocotiledôneas foram anteriormente descritas para a mesma formação, e são consideradas aquáticas. *Cratosmilax jacksoni* é o primeiro registro fóssil da família Smilacaceae no Brasil, e o registro mais antigo desta família.

Palavras-chave: Bacia do Araripe, *Cratosmilax jacksoni*, Cretáceo, folha fóssil, Gondwana, Monocotiledôneas.

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