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ARTICLE

New plant fossils from the Lower Cretaceous of the Parnaíba Basin, Northeastern Brazil: Southern Laurasia links

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ABSTRACT: *This study reports on the presence of a diverse set of gymnosperm and angiosperm macrofossils from the Codó Formation, Parnaíba Basin, whose assemblage was previously known only by the occurrence of pollen grains, spores, wood fragments, leaves and roots associated with Nympheaceae. In the Brejo municipality, northeastern Maranhão State, marl levels attest a transitional to marginal lacustrine environment, with occasional marine ingressions, demonstrated by the presence of crustaceans, gastropods and fishes. The plant fossils are preserved exclusively by molds and impressions, and its diversity is represented by few specimens, suggesting taphonomic processes of selection and transportation. The taphoflora is composed of Gnetales (?Drewria), conifers (Cupressinocladus and Brachyphyllum), and basal angiosperms (Nympheales, Magnollids, and/or basal Eudicots), which support an upper Aptian – ?Albian age. It displays affinities with both the well-known flora of the Araripe Basin (Santana Formation) as well as those ones identified in deposits from the south of North America (Potomac Group), suggesting that terrestrial links persisted in the equatorial areas of the Pangea at the end of the Early Cretaceous.*

KEYWORDS: *Lower Cretaceous; Macroflora; Parnaíba Basin; Codó Formation.*

INTRODUCTION

In the beginning of the Cretaceous, ferns and gymnosperms dominated the plant communities of a broad equatorial paleofloristic province. At that time, the province included a large part of the modern landmasses of South Hemisphere and southern Laurasia, characterized by assemblages containing elater-bearing pollen grains (Willis & McElwain 2002, Vallati 2013). Tropical, warm, and dry, conditions influenced the climate in this equatorial realm (Vakhrameev 1991).

The Lower Cretaceous floras in Northeastern Brazil (Araripe, Parnaíba, Tucano, Sanfranciscana and Sergipe-Alagoas basins) allow us to infer halophytic forms growing in a xeromorphic vegetation, dominated by conifers and Gnetales, with Bennettitales, Caytoniales, Pteridospermales and early angiosperms as a minor component (Regali *et al.* 1974, Lima 1982, Kunzmann *et al.* 2006, Bernardes-de-Oliveira *et al.* 2007, Mohr *et al.* 2007).

For the Codó Formation, Parnaíba Basin, previous works have only reported the presence of angiosperm wood logs and indeterminate leaves and roots (Moraes Rego 1923, Borges 1937, Duarte 1959), which Duarte and Santos (1993) assigned to a new species, *Nymphaeites choffati* (= *Klitzschophyllites choffati*). The fossil wood log, *Lecythioxylon brasiliense* Milanez, comes from outcropping at the margin of Parnaíba river, in Piauí State, considered correlate with those of the Codó Formation (Milanez 1935).

The palynological assemblage of the Codó Formation, firstly studied by Lima (1982), attests to a flora dominated

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by Gnetales pollen grains (*Equisetosporites*, *Singhia*, *Gnetaceaepollenites* and *Steevesipollenites*), followed in number by conifers (*Classopolis* spp., *Araucariacites* spp. and *Exesipollenites tumulus*), and angiosperms (*Afropollis* (*Reticulatosporites*) *jardinus*). Still little represented (and absent until now in the macroflora), the pteridophytes are diversified, with specimens related to the Cyatheaceae, Dicksoniaceae and Osmundaceae. The presence of *Sergipea* has supported part of the Codó Formation deposits in the Aptian biozone *Sergipea variverrucata* (Pedrão *et al.* 1996, Regali & Santos 1999, Antonioli 2001, Maizatto *et al.* 2011).

In Brejo County, State of Maranhão, focus of this study, the fossil plants occur in limestone beds exposed in open pit mines at two locations: Faveirinha Quarry and Perneta Ranch (Fig. 1), where the occurrence of conifers, Gnetales and angiosperms were preliminarily reported by Lindoso *et al.* (2011, 2013a).

The present study aims to describe these new materials and analyze their relationship with the previously known taxa of other paleo-equatorial basins. Since some of the morphotypes are poorly represented, and others refer to isolate leaves and apical shoots, without associated reproductive structures, its description and illustration try to evaluate their diversity and compare them with other Early Cretaceous floras. With this process, we also intend to make possible inferences based on paleoecology, paleogeology and age.

GEOLOGICAL SETTING

The Parnaíba Basin spreads throughout a wide area in the central portion of northeastern Brazil, including parts of the states of Maranhão, Piauí, Tocantins, Pará, Ceará and Goiás. It has a total area of 600,000 km^2 and its depocenter contains a 500 m thick sedimentary succession of Mesozoic rocks (Campbell 1949, Mesner & Wooldridge 1964a).

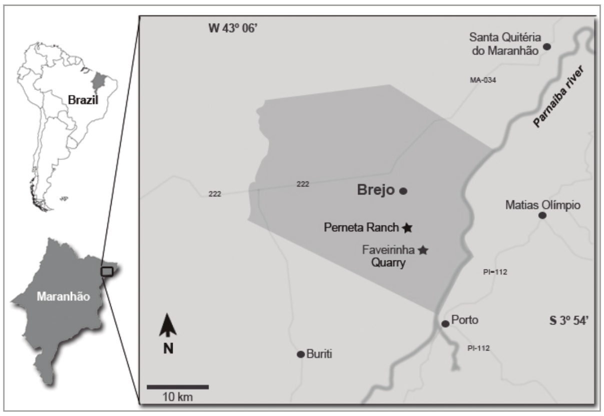

Figure 1. The location is Brejo County, Maranhão State, northeastern Brazil. The black stars indicate the two quarries where the plant fossils were collected.

The Codó Formation is the richest fossiliferous unit in the Parnaíba Basin and is distributed over an area of approximately 170,000 km^2 (Lisboa 1914, Lima 1982). In the last decade, several specimens have been described for this unit, including crustaceans (isopods), mollusks (gastropods and bivalve), fishes, and plants (Lindoso 2016, Lindoso & Carvalho 2012, Lindoso *et al.* 2011, 2013a, 2013b, 2016, Brito *et al.* 2016). Its fossil record in the central-north part of Maranhão State is characterized by a discontinuous occurrence over a wide area, cropping out mainly in the cliffs of the river valleys that drain the central part of the basin (Santos & Carvalho 2009). The fplant fossils herein described come from near the margins of the Parnaiba river, in Brejo County (Fig. 2).

The geology of the Codó Formation was initially reported by Lisboa (1914). Later, Campbell (1949), also classified this unit as bituminous shales associated with limestone and gypsum lenses identified at the Itapecuru river valley, in Codó County. It was then further confirmed by Assine (1992). Additionally, siltstone, sandstone and evaporite levels were also described for the Codó Formation (Vaz *et al.* 2007). Although an Aptian/Albian age was previously suggested for this unit based on palynology (Lima 1982), it was later restricted to the Aptian, based on the lower limit of the overlying unit (Itapecuru Formation), considered upper Aptian in age (Pedrão *et al.* 1996).

The palynological data analyzed by Lima and Leite (1978) indicate marine to brackish lacustrine environments in the Codó Formation. Later, it was confirmed by a facies analysis presented by Rossetti *et al.* (2001). With regard to the inferred lagoon context, three distinct phases were established, evolving in time from central lake to marginal marine environments, influenced by arid to semiarid climate conditions. The marine fossils, recorded at both Parnaíba and São Luís basins, occur in the upper levels of the Codó Formation and they contain fossil plants.

Fish remains (Silva-Santos 1985, Lindoso *et al.* 2016), dinoflagellates (Antonioli 2001), and isopod crustaceans (Lindoso *et al.* 2013b) support the sea-level rise at the end of Aptian (Weissert *et al.* 1998), and in many other coastal basins from Northeast Brazil. According to Arai (2014) and Lindoso *et al.* (2016), the invasion of seawater at that time must have originated from the north and through the Central/Equatorial Atlantic or Eastern Tethys.

The palyno-chronostratigraphic proposal of Antonioli (2001) also divided the Codó Formation into three lithostratigraphic intervals and confirmed that each had the highest influence in open marine conditions along the deposition, with a medium interval characterized by essentially evaporitic deposits. The plant fossils beds are part of the upper interval, which has been interpreted to be an upper shoreface environment, with an interdistributary lagoon/bay, suspension lobes and distributary channels (Paz & Rossetti 2001, Rossetti *et al.* 2001).

The fossil plants herein described were collected in the Faveirinha (42º44'45.4"W/ 03º49'20.1"S) and Perneta Ranch quarries (42º44'21.1"W/ 03º48'50.0"S), nearly 20 km from Brejo County (Fig. 2). They were collected in massive and fine laminated limestone and interbedded with marls and calcareous concretions, which compose the upper levels of the Codó Formation (Fig. 2A and 2B).

MATERIAL AND METHODS

The plant fossils impressions in the Codó Formation beds, which diversity are represented by few specimens, allows detecting eleven distinct types of branches and leaves linked to gymnosperms and angiosperms. Those related to conifers and Gnetales were compare with others Early Cretaceous previously known morphogenera, and the angiosperm treated by the informal system introduced by Hickey (1973), Hickey and Wolf (1975), and more recently stablished by Ellis et al. (2009). The leaf architecture and venation patterns of the flowering plants were described considering the new taxonomic rules (McNeill et al. 2012) and treated by morphotypes or fossil taxa. Affinities with previously described fossils were proposed, looking for correlations with other preserved assemblages from tropical Cretaceous basins.

Concerning the flowering plants, a code name was used, which follows the procedure applied today in angiosperm fossil materials from levels that precede the Early Miocene (*e.g.*, Pole 1993, Iglesias *et al.* 2007). Here, two initial letters — CF, referring to Codó Formation — and numbers, separate the different morphotypes.

Analyses and illustrations of the fossil material were made using an Olympus SZH Stereomicroscope with a camera lucida. Photographs were taken using a Fujifilm Finepix HS50exr digital camera system. To enhance the contrast and highlight the fine details, a record in low-angle light and

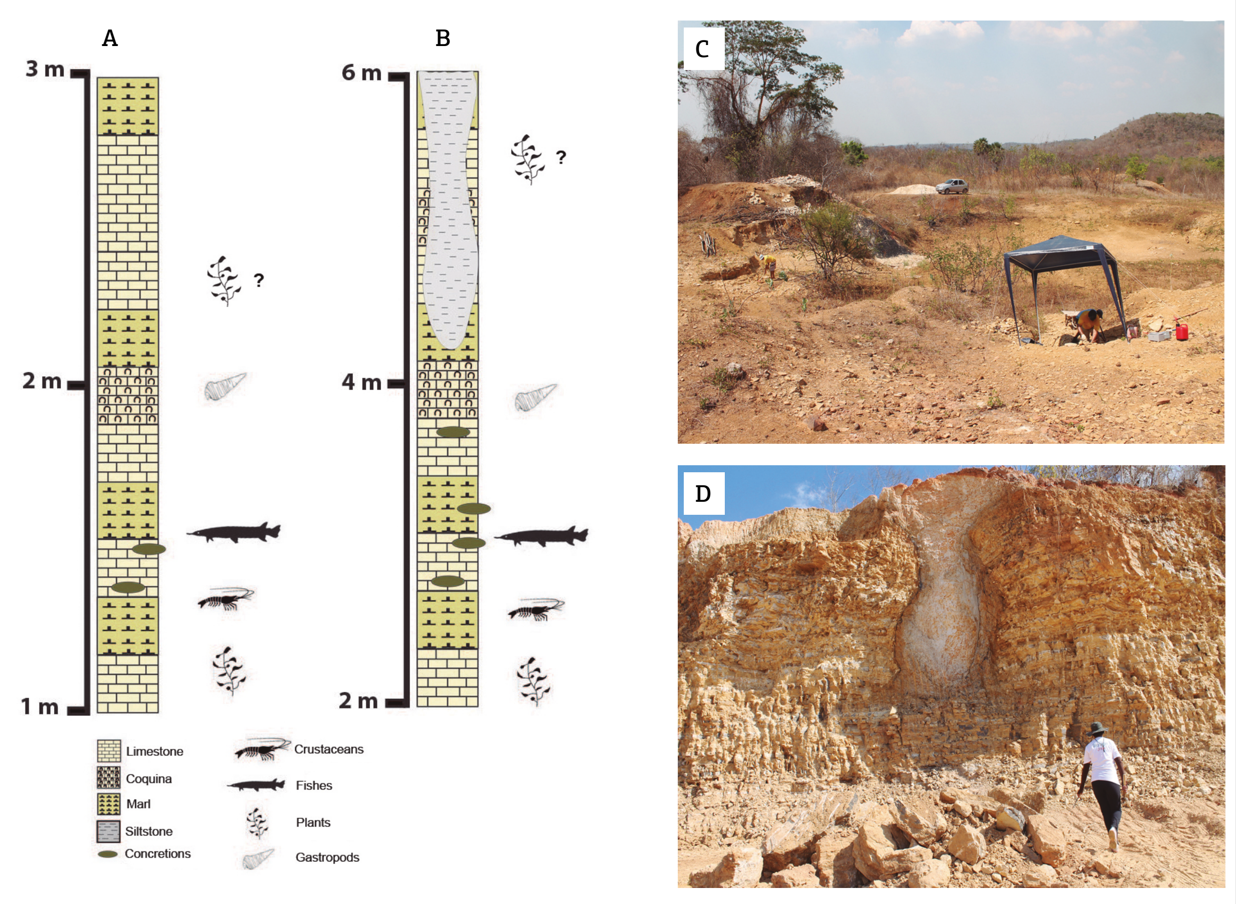

Figure 2. A stratigraphic profile of the Faveirinha Quarry (A) and Perneta Ranch (B), in Brejo City, Maranhão. In (C) and (D) the same outcrops expose the levels of the Codó Formation containing plant fossils.

close-up lens were used. The described samples are housed in the paleontological collection of the Department of Geology at the Universidade Federal do Rio de Janeiro (UFRJ), Brazil, under the following numbers: (UFRJ-DG 1988-Pb, UFRJ-DG 1987-Pb, UFRJ-DG 1944-Pb, UFRJ-DG 1984-Pb, UFRJ-DG 1457-Pb, UFRJ-DG 1986-Pb, UFRJ-DG 1983-Pb, UFRJ-DG 1985-Pb, UFRJ-DG 1800-Pb, UFRJ-DG 1999-Pb, UFRJ-DG 1990-Pb).

DESCRIPTION OF THE FOSSIL PLANTS AND THEIR CORRELATIONS

Gymnosperms

Order GNETALES Luerss 1869

cf. *Drewria potomacensis* Crane et Upchurch Jr., 1987

(Fig. 3A-C)

Material

UFRJ-DG1444-Pb, a cast of a vegetative branch and its associated leaves.

Description

An axillary striate and monopodial vegetative branch with a slender stem (2 mm width) and two lateral branches (1 mm width), one time irregularly forked and planar disposed. Leaves simple, opposite and oblong in form, with entire margins, acute apices, and decurrent bases, diverging from a swollen node. The proximal ones (30 mm long, 4 mm wide on average) have sheathing bases (Fig. 3A-B). The central axis (0.5 mm wide) bear leaves with an apparently highlighted mid vein or vascular bundle, laterally accompanied by parallel veins (Fig. 3C). Weak and rare transverse connections apically oriented (chevrons?) were preserve in a single sector (Fig. 3B).

Remarks

The set of morphological features, as the trifurcate dichotomous branching pattern, striate planar leaf axes, linear elongated sheathing and oblong multi-veined leaves with opposite (decussate?) arrangement, associate to high-order cross veins preserving rare anastomoses in chevrons, approximate this morphotype to those found in previous described gnetophytes (Kunzmann *et al.* 2009, 2011, Seward 2010, Ricardi-Branco *et al.* 2013). Among the known fossils, such morphological features characterize *Drewria potomacensis* Crane (Crane & Upchurch Jr., 1987), described by Doyle and Hickey (1976) to the Zone I Potomac Group. Nevertheless, the Codó branch exhibits some distinct features, like more elongated leaves that are not so clearly decussated in the arrangement, and a slight prominent strand or midrib. Its origin, however, in the branch axis suggests that more than a vein could represent a concentrated bundle of fibers. On the other hand, the convergence of the main veins in the apices of the leaves in the herein described fossil (Fig. 3B) is similar to that mentioned by Crane and Upchurch Jr. (1987) to *Welwitschia* and *Drewria*.

According to Gandolfo *et al.* (2000), the presence of a midvein in some elongated leaves is not a definitive criterion to discard the Gnetales from possible affinities, since modern *Gnetum* have a well-developed main vein. Moreover, similar morphologies to that of *Drewria*, including “chevrons”, characterize *Welwitschia* and the even now dubious Early Cretaceous monocot *Acaceaephyllum* Fontaine. However, the latter, like *Gnetum*, has a pinnate venation (Sender *et al.* 2012).

With other gnetalean from Lower Cretaceous of Brazil, the Codó branch only shares the longitudinally striated axes, here without visible nodes. The preserved specimens, *Itajuba yansanae*, *Cearania heterophylla*, and *Cariria orbiculiconiformis*, differ in sympodial axes and have round and short leaves, or are represented by reproductive structures and woods (Kunzmann *et al.* 2009, 2011, Ricardi-Branco *et al.* 2013). As such, it is impossible to compare them with the vegetative branch herein described.

As previously observed, the Gnetales are an important component in the palynological assemblage of the Codó Formation, the Santana Formation (Portela *et al.* 2014) and the basal Potomac Group (Doyle & Hickey 1976). For Crane and Upchurch Jr. (1987), the absence of extensive secondary tissues in the Gnetales and in *Drewria*, indicates that it is an herbaceous plant.

Recently, Yang *et al.* (2015) proposed that the decussate phyllotaxy in the reproductive shoots of *D. potomacencis*, and its leaf morphology, similar to that of *Ephedra multinervis* from China, guarantees that *Drewria* and other Gnetales are in an intermediate phylogenetic position, between Ephedrales and Welwitschiales.

Order CONIFERALES *sensu* Farjon, 2010

?Family Cheirolepidiaceae Tahktajan, 1963

Cupressinocladus Seward, 1919

(Fig. 3D)

Material

UFRJ-DG1987-Pb, part of an ultimate shoot.

Description

Erect and short, one-branched, leafy stem (c. 30 mm long, 6–7 mm wide). Leaves bifacially disposed, cushion-like and keeled (5–3 mm long, 3–2 mm wide), rhomboidal in transverse section, with fleshy to leathery texture apparently opposite to sub-opposite (helically?) arranged. The broad basal part of the leaves is sessile attached to the axis and the middle and distal ones are free. Apex varies between acute-obtuse to slightly falcate. Venation indistinct and margins apparently irregular.

Remarks

Leafy branches with decussate to slightly helically arranged leaves, longer than wide, with a broad basal cushion and free apices, characterize the extant Cupressaceae. In the fossil record, they are generally related to the morph

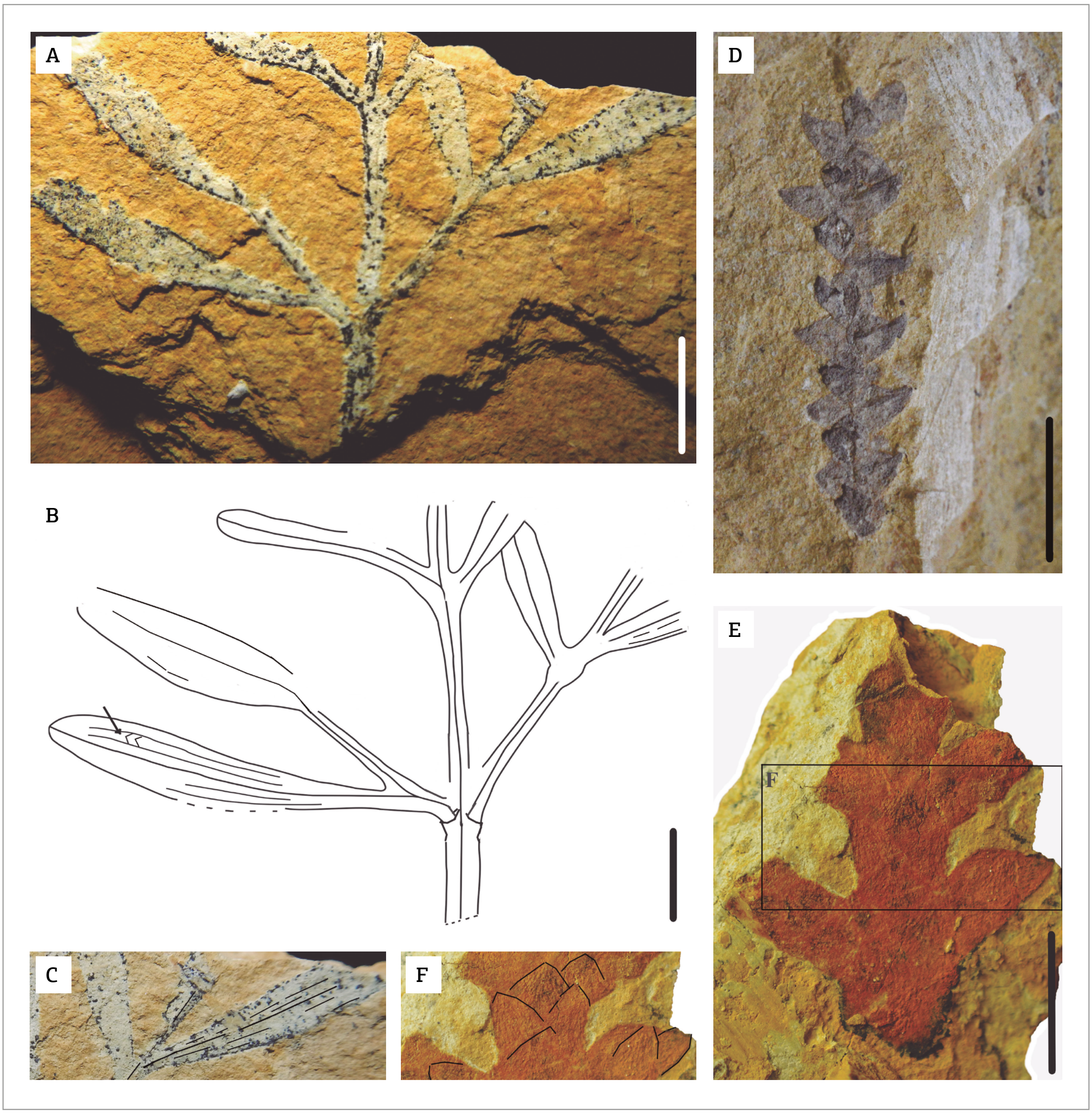

Figure 3. Gnetales (A,B,C) and conifer-related forms (D,E,F) in the Codó Formation flora. (A) Monopodial and trifurcate dichotomous branch, one time irregularly forked, carrying opposite, oblong leaves, comparable to those associate of the reproductive structure of *Drewria potomacencis* Crane and Upchurch (UFRJ-DG1444-Pb); (B) outline of the shoot in A, showing the fine details of venation with probable apically orientated chevrons (arrow); (C) detail of the axillary branch venation; (D) *Cupressinocladus* sp. (UFRJ-DG1987-Pb), branch impression with sub-opposite spreading bifacial, cushion-like and keeled leaves; (E) cf. *Brachyphyllum* sp. (UFRJ-DG1988-Pb), impression of an apical branch and of the sub-alternate to opposite second order branches; (F) detail of E, highlighting the apical contours of the spirally disposed leaves and their radial striations. Figures 3C and 3F are detailed reproductions of the figures 3A and 3E, respectively. Scale bars: 1 cm.

genera *Cupressinocladus* Seward (link to the Cupressaceae by Seward 1919) or to *Pagiophyllum* Heer (*sensu* Stewart & Rothwell 1993, fig. 29.7B). Among them, the homogeneous round to rhomboidal leaves of *Cupressinocladus*, flattened and oppositely disposed along the shoot, are closer to the morphotype herein described. In general, when including in the Cheirolepidiaceae, some researchers prefer to maintain its affinities unresolved (Pons 1988, Pole 2000, Van Waveren *et al.* 2002, Gee 2010).

Related shoot morphologies is until now rare in the Cretaceous assemblages of northeastern Brazil, the only exception being an isolated shoot that is still undescribed from the Riachuelo Formation (Aptian-Albian), Sergipe-Alagoas basin (Dutra *et al.* 2002), and in some decurrent leaves of the heterophilic shoots of *Tomaxelia* Archangelsky, identified in Santana Formation, Araripe Basin by Kunzmann *et al.* (2006), and included in the Cheirolepidiaceae. However, *Tomaxelia* has helically arranged leaves, a distinct phyllotaxy to that of the branch herein preserved.

"Cupressoid" foliages are, however, common in other Equatorial areas of South America (Zijlstra & Kvaček, 2010), especially in the levels of the Paja Formation, in Colombia, where seven distinct species assigned to *Cupressinocladus* were recorded (Pons 1988, Van Waveren *et al.* 2002, Plate 4, Fig. 1; Sucerquia 2013), and included in the Cheirolepidiceae (Meyen 1987, Taylor *et al.* 2009). First detected in Gondwana assemblages, their older lineages (Berriasian-Barremian) came from southern Eurasia (Kimura *et al.* 1992, Coiffard *et al.* 2007), where *Cupressinocladus* is commonly registered with *Brachyphyllum* and *Frenelopsis/Pseudofrenelopsis*.

Younger similar planar shoots and cushion-like leaves were found in other putative Cheirolepidiaceae of North America (Glen Rose Formation, Texas), like *Glenrosa* (Watson & Fisher 1984 emend. Srinivasan 1992), which is characterized by keeled leaves with free acute-obtuse apices and fringed margins (*e.g.*, *G. falcata* Gomez, Gomez *et al.* 2012). It has a broad temporal (Barremian to Cenomanian) and paleogeographic distribution in tropical areas and has been found to be associated to hypersaline lagoons and bay deposits (Srinivasan 1995, Zhou *et al.* 2000, Gomez *et al.* 2012, Moreau *et al.* 2015). In the coastal marine environments of the Potomac beds, it occurs along with other xerophytic Cheirolepidiceae (Watson & Fischer 1984, Srinivasan 1995, Zhou *et al.* 2000, Tanrikulu *et al.* 2015), in paleoenvironmental conditions similar to those of the from Santana and Codó Formations deposits (Antonioli 2001).

Also, *Sedites* Geinitz, from the German Cretaceous (upper Turonian "Plänerkalk" horizon of Geinitz 1842), shares the spread disposed leaves in apparent four rows of opposite decussate pairs (Kunzmann 2010). In *S. rabenhorstii* Geinitz, opposite pairs of leaves with decurrent bases (35 mm long) are arranged along an unbranched terminal shoot and are represented by scarce materials. Kunzmann (2010) associated it with a dubious Cheirolepidiaceae.

The apical shoot herein associated to *Cupressinocladus* differs, however, from two other Cretaceous conifers of low latitudes, carrying decussate disposed leaves, *Geinitzia* and *Frenelopsis*. *Geinitzia* Endl. has bilateral and more elongated leaves which are helically disposed (Stewart & Rothwell 1993). *Frenelopsis* Schenk emend. Watson, has slender spreading leaves that are disposed in whorls (Barale & Ouaja 2002, Gomez *et al.* 2002, Kunzmann *et al.* 2006, Burger & Ward 2016).

In a more recent study, Arens and Allens (2014) confirm the difficulty in discriminating a preferable family to *Cupressinocladus*, considering their convergent characteristics shared with more than one conifer family. In extant conifers, besides the Cupressaceae, short and acute leaves that are oppositely arranged can also be found in the heterophilic shoots of Podocarpaceae (Page 1999, Seward 2010, Fontes & Dutra 2010, Mao *et al.* 2012, Du *et al.* 2013). In the absence of reproductive structures or preserved cuticles, we follow here the recommendation of Schweitzer (1974) that proposes to include "cupressoid" foliages in *Cupressinocladus* genus and, for the herein commented reasons, with an uncertain familiar relation with the Cheirolepidiaceae.

?Araucariaceae/Cheirolepidiaceae

cf. *Brachyphyllum* Lindley and Hutton emend. Harris 1979
(Figs. 3E and 3F)

Material

UFRJ-DG1988-Pb, impression of a single, ultimate branch.

Description

Fragment of a planar branch, with short and broad (5 mm large) ramifications that are opposite to sub alternate, and disposed in 45° angles. The scale leaves show triangular contours and poorly visible radiated striae diverging from the leaf apex.

Remarks

The leaf shoot impression, with uniformly wide branches of opposite to subalternate arrangement, bearing weakly preserved leaves of obtuse apex appressed to the stem, and covered by longitudinal and radial divergent striations (Fig. 3E), indicates a resemblance with forms comprised in the *Brachyphyllum* morphogenus. In the genus, by the stout branch, approximates from the species B. *obesum* Heer (Yabe & Kubota 2004, Du et al. 2013).

B. obesum is an important component of the paleotropical floras, including those from Northeastern Brazil, where is registered in all known lower Cretaceous deposits This is the case of the sedimentary successions from Japoatã and Riachuelo formations, in Sergipe-Alagoas Basin, Marizal Formation in the Tucano Basin, and Romualdo, Missao Velha, and Santana formations, from Araripe Basin (Teixeira 1948, Duarte 1985, Dutra *et al.* 2002, Kunzmann *et al.* 2004, Sucerquia 2006, 2013, Lima *et al.* 2012, Batista *et al.* 2017).

In South America, diversified species of *Brachyphyllum* were also register to the rain shadow areas of the western Andean basins, Chile to Venezuela (Berry 1922, Archangelsky 1963, Baldoni 1979, Romero *et al.* 1995, Van Waveren *et al.* 2002, Monje-Dussán *et al.* 2016).

Still the familiar placement of the genus remains dubious, it has been normally included in the *Cheirolepidiaceae*, due to its morphological resemblance with the non-frenelopsid members of this family and the common presence of *Classopollis*-type pollen in the assemblages (Kerp 1990). However, *B. obesum* from the Santana Formation was assigned to the Araucariaceae based on its cuticle micromorphology and wood features (Kunzmann *et al.* 2004, Sucerquia 2013, Batista *et al.* 2017). The absence of those anatomical features in the preserved form of the Codó Formation, and the associated occurrence of both *Classopollis* and *Araucariacites* pollen grains in the Codó Formation (Lima 1982), make difficult to confirm its insertion into the Cheirolepidiaceae.

Spermatophyta incertae sedis

CF1 morphotype
(Figs. 4A-4F)

Material

UFRJ-DG 1457a-Pb, 1457b-Pb (holomorphotype *sensu* Ellis *et al.* 2009), referring to the part and counterpart (cast) of an isolated three lobed leaf; UFRJ 1983-Pb, 1994-Pb, partial impression of the leaf base, and UFRJ-DG 1986 Pb, has a preserved, folded leaf branch.

Description

Palmate dissected leaf (7 cm long and 5 cm wide), apparently coriaceous in texture, with three planarly disposed symmetrical lobes of linear-oblong outline and without basal constriction or a distinct petiole. The cuneate base is a continuum of the broad axis (0.6 cm wide, 2.5 cm long in the preserved portion) and does not have a visible sheath. The prominent central lobe (4.5 cm long, 1 cm wide) is separated from the lateral ones (diverging in angles of 35-40º) by deep sinusoidal incisions. Lobes with basal entire margins and irregular (serrate?) ones near apices. The ramified main vein (1 mm wide) splits when entering the lobes and ends at their apices without other visible ramifications. The very fine secondary veins (or striae) diverge at straight angles from the main veins, and do not reach the leaf margin. They probably end (they are not visible) in the weak marginal venation that merges at the apex. The black dots of iron oxi-hydroxides, organized in parallel rows over the blades, may represent aligned stomatal complexes (Fig. 4B).

Remarks

CF1 is the most abundant morphotype in the Codó Formation flora, despite the partial preservation of the additional related materials. It shows a characteristic leaf type, of difficult affinity and comparison with the previously described fossils from Brazil, and even in its insertion in the high clades.

The close relative in morphological appeals are *found in* the shoots carrying decussate leaves with three symmetrical lobes (similar to a "birdfoot") assigned to *Novaolindia dubia* identified in the Santana Formation beds (Kunzmann *et al.* 2007, Plate I.7 and II 1–3). However, N. *dubia*, has simple and lobate leaves in the same axis, a feature that is impossible to be detected in the unique lamina herein preserved. Despite this limitation, a single basal leaf, visible in the folded leafy shoot related to CF1 (Fig. 4F), could correspond to those found in N. *dubia*. However, Kunzmann *et al.* (2007) had no mention about the presence of veins or surface irregularities over the leaf blade of N. *dubia*. Based in the anatomical features (longitudinally aligned anomocytic to probably cyclocytic stomata) and the presence of capsule-like fertile organs, the authors propose a preferable relation of N. *dubia* with the gymnosperms. In the absence of organic materials preserved in CF1, and of venation features in N. *dubia*, more specific comparisons are difficult. Additionally, the CF1 leaves are nearly four times larger and broader lobes of nearly entire margins, distinct characters when compared with N. *dubia*.

Considering the presence of fine secondary veins, transversally disposed in relation to the primary veins, and of a continuous marginal vein (Fig. 4B), the Codó leaf seems to be more probably link to a dubious angiosperm. Among them, the North Hemisphere forms assigned to *Araliaephyllum* Fontaine (which is considered a Magnoliopsida) share features in common, like the trilobate palmate leaves with lanceolate lobes, and acute or rounded apices. For other side, the leaves in this Cretaceous morphogenus have distinct actinodromous venation and dentate margins in the middle-upper part of the blade (Greguš & Kvaček 2015, Plates 14.3 and 15.4-6).

Another trilobed leaf from the Crato Member, *Araripea florifera* Mohr and Eklund (Mohr & Eklund 2003), was also considered to be in the angiosperms by the actinodromous

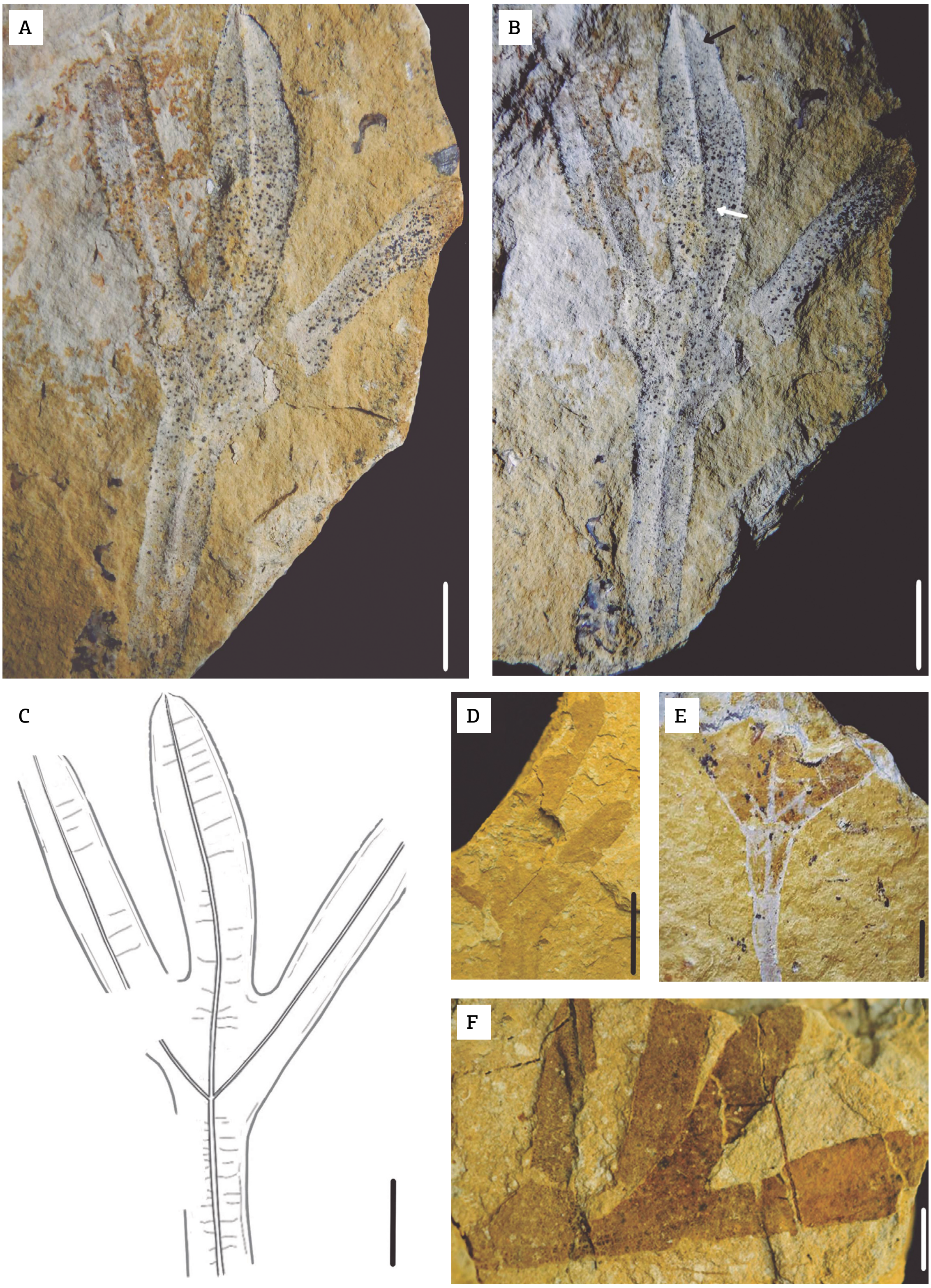

Figure 4. CF1 holomorphotype (UFRJ-DG 1457a-1457b Pb). (A, B) Mold and cast (mineralized) of a trilobed "birdfoot"-like leaf. The white arrow in B points to probable aligned stomata or glands over the central lobe. The black one indicates the fine marginal vein; (C) drawing of B, highlighting the weak visible secondary and marginal veins; (D, E) additional related leaf fragments, with partial axes and basal leaf impressions (UFRJ-DG 1983, 1994 Pb); (F) A folded leafy shoot showing an apparent additional unilobed leaf (UFRJ-DG 1986 Pb). Scale bars = 1 cm, except in figure F = 0.5 cm.

venation. However, it has leaves with a strong decurrent base which is closer to the following CF3 morphotype herein described.

ANGIOSPERMS

? Nympheales

CF2 morphotype
cf. *Pluricapellatia peltata* B. Mohr, Bernardes-de-Oliveira & David W. Taylor 2008
(Fig. 5A-B)

Material

A broad leaf impression associated with, but not connected to a bifurcate axis (UFRJ-DG1984-Pb), and an isolated ramified leaf branch (UFRJ-DG 1985-Pb).

Description

Impression (replica) of an eccentrically reniform-wide peltate leaf (3 cm long, 3.8 cm wide) diverging from a weakly jointed petiolate axis (Fig. 5A, white arrows) of 1.7 cm long and 0.2–0.3 mm wide, with an apparently very reduced sheath. The leaf base is truncated. The margins serrate to doubly serrate with short triangular and irregular teeth visible in a few sectors (Fig. 5A, black arrows). There is no evidence of organic connections between the superimposed leaf axis and the associated branch.

Remarks

The morphological features of the CF2 leaf, with its apparently broad reniform blade and long axis, that seems connected to a cut in the base of the leaf, make this leaf morphotype similar to other eccentric peltate ones found in Lower Cretaceous beds, like, for example, *Proteaephyllum reniforme* Fontaine (Aptian) and *Nelumbites* Berry (Albian) of the Potomac Group (Doyle & Hickey 1976, Doyle & Upchurch Jr. 2014). They are distributed along the tropical areas of southern Laurasia and northern Gondwana (Mohr & Rydin 2002, Mohr *et al*. 2006, 2008, Doyle 2015).

With regard to the previously described specimens of Brazilian deposits (Araripe and Areado basins), they can partly be compared to *Nymphaeites choffati* Saporta, firstly described in Portugal (*N. chofatii* Teixeira, 1948), and latter in the Santana Formation (Duarte 1985). To the Codó Formation it was until now the only macrofossil described, and considered relate with the Nymphaeaceae and the genus Nymphaeites Sternberg. emend. Heer by Duarte and Santos (1993).

The distinctive characters between CF2 and the holotype of N. *choffati*, are the more fan-shaped leaf (2.5-4.5 cm in length and 2.5-3.0 cm wide) and the well preserved reticulate venation in the Santana Formation leaves. However, it can result of the distinct preservation modes and make difficult a more detailed comparison. The CF2 impression seems to represent a dorsoventrally deformed leaf or where the upper part of the margin was folded. No venation feature was preserved, probably because of its more coriaceous texture, which is highlighted by the cracked iron oxide-hydroxide deposits on top of the impression. They both share the same general leaf size and axis, dentate margins (but with broader teeth and glands in *N. choffati*) and a long petiolate axis with transversal lines (arrows in Fig. 5A). Duarte and Santos (1993) have suggested that N. *choffati* had an aquatic habitat and link it to the Nympheales by the presence of root aggregates, with well-developed calyptras, and by the jointed petiolar axis, which have been interpreted as aerenchymatous tissues by the authors.

After Mohr and Rydin (2002) include N. *chofatti* in the synonym of *Trifurcatia flabellata*, preserved by reddish brown impressions in the Crato Member of the Santana Formation. They were based on their common leaves with serrate margins and conspicuous nodes and internodes in the axes. The authors pointed to their similar sizes, amplexicaule leaf blades, and the number of marginal triangular teeth they have (14–28 in *N. chofatii* and 20–25 in *T. flabellata*). However, in the diagnosis of *T. flabellate*, there was no mention or comparison made with *N. choffati*. Because of its major acrodromous/parallelodromous venation, its irregularly zigzagging secondary and transversal tertiaries, and because of the presence of gland like structures, *T. flabellata* is related to an ancient monocot that probably grows in a seasonally dry context.

In a revision of the early monocots distributed in the Cretaceous deposits of tropical areas, Mohr *et al.* (2006) included *T. flabellata* (and thus *N. choffati* from Portugal, Brazil and Northern Africa) in the diversity of *Klitzschophyllites* Lejal-Nicol (Lejal-Nicol 1987). A genus emendation was proposed in addition to its relationship with a putative monocot that adapted to drought and/or haline environments. For Mohr *et al.* (2006), the inclusion of *N. choffati* in the new genus was based on what previously Mohr and Rydin (2002) had been considering as an erroneous association of the Codó species with the Nymphaeaceae. The Brazilian specimens of *T. flabellata* from the Codó and Santana formations were associated with the *K. flabellatus* species, and were compared with the other two confirmed species, *K. aegyptiacum* Lejal-Nicol from Egypt (Barale & Ouaja 2002) and *K. choffatii*, from Portugal and Tunisia. They were associated together due of their similar dentate

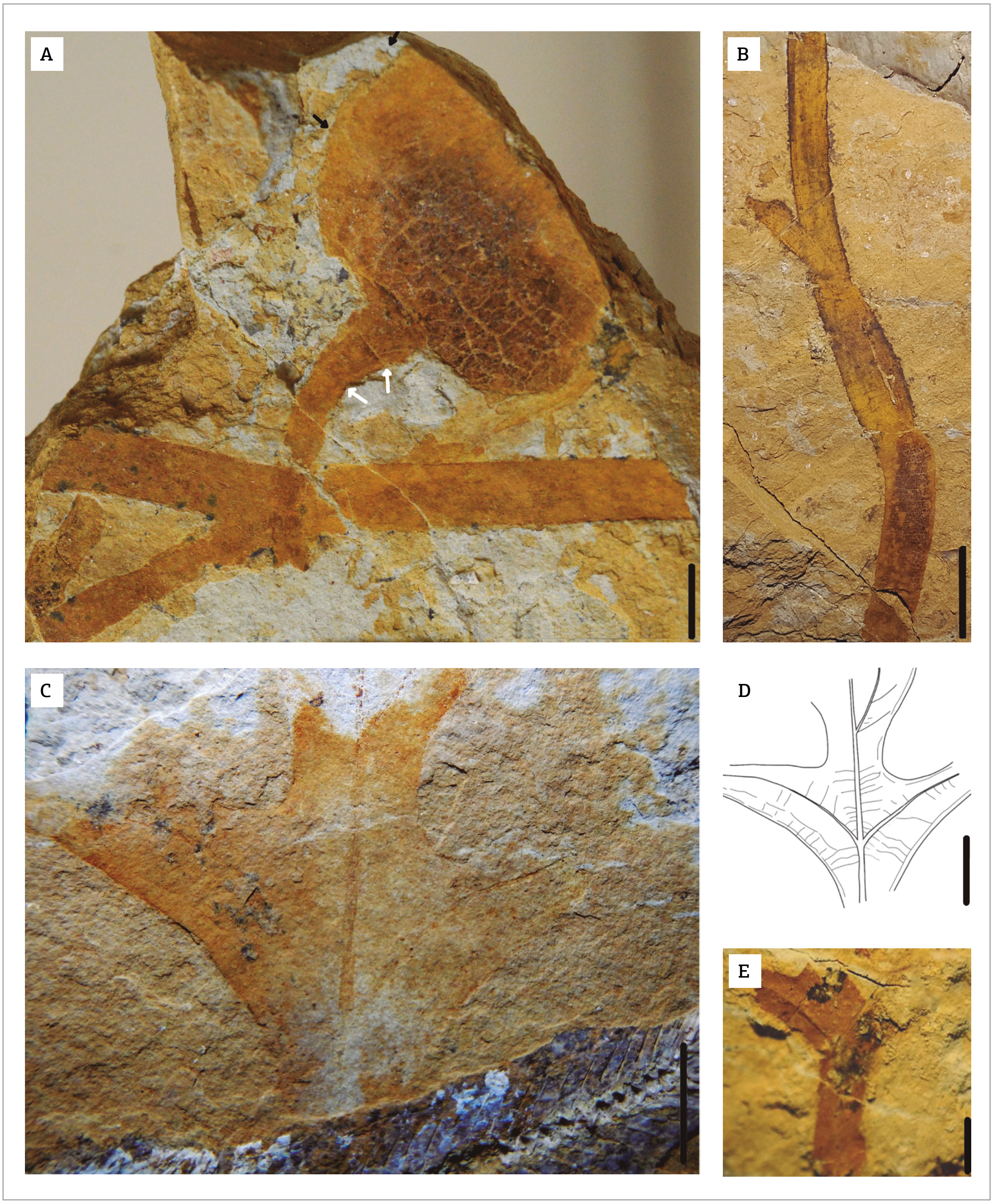

Figure 5. (A, B) CF2 morphotype. A. reniform leaf (UFRJ-DG 1985-Pb) eccentrically inserted in a slender petiole and covered by dehydrated coats of iron minerals. Black arrows point to the weakly preserved triangular teeth more visible in the middle part of the margin. White arrows indicate the poorly developed (or preserved) nodes or grooves along the axes; (B) part of an associated axis with a short-ramified shoot (UFRJDG1984-Pb). Delicate striations over it could indicate a nodular character or the presence of aerenchymatous tissues; (C-E) CF3 morphotype (UFRJ-DG 1800-Pb), showing partially preserved pinnatilobed leaf, with decurrent lateral lobes of entire margins; (D) outline of C, highlighting the pinnate main vein and the irregular pattern of the secondary veins (semicraspedodromous?); (E) an additional cast of an incomplete fragment, showing the long and well-preserved swollen petiolate base (UFRJ-DG 1990-Pb). Scale bar = 1 cm.

margin and sizes (2–3 cm wide on average), except for the little Egypt form, which was slightly distinct in its leaf outline (Mohr *et al.* 2006, Fig. 2B and 2C). However, regarding the CF2 Codó morphotype herein described, and taking into account the eccentrically position of the reniform leaf in the axis the more probable and next affinity of CF2 is with the *Klitzschophyllites choffatii specimens* from Portugal (Mohr *et al.* 2006, Fig. 2B).

Gomez *et al.* (2009), which later described specimens from northeast Spain, also consider that the Codó leaf must be related to this species. They also propose an emended diagnosis of *K. choffatii* (Saporta) and associate it with an aquatic basal Eudicot. Additionally, with regard to the Crato Member specimens, Gomez *et al.* (2009) proposed to maintain its validity within the species *Trifurcatia flabellata*, because of its trifurcate axis and its relation with the monocts.

If the reniform character of CF2 leaf is confirmed by additional new materials it would also be comparable to the large eccentrically peltate leaves with crenulated margins that characterizes *Pluricarpellatia peltata* Mohr, Bernardes de Oliveira and Taylor, and the "Nymphaeales Taxon A" of Mohr *et al.* (2008), from the Crato Member, Araripe Basin. *P. peltata* is represented by a complete plant with aquatic shoots and flowers and in the variable leaf forms illustrated by Mohr *et al.* (2008). With them, CF2 shares the size and irregular margins containing small teeth and differs only by the more slender and longitudinal striated petiole of *P. peltata*. Additionally, some specimens of *P. peltata* (Mohr *et al.* 2008, Fig. 3) exhibit bifurcated branches that resemble the isolated axis here preserved (Fig. 5B). Due to its carpel morphology and simple petiolate and peltate leaves of laminar placentation *P. peltata* was assigned to a Cabombaceae of herbaceous habit (Mohr *et al.* 2008).

Finally, some common features also exist between CF2 and *Jaguariba wiersemana* (Coiffard, Mohr and Bernardes-de-Oliveira) and other Nympheales from the Santana Formation (Coiffard *et al.* 2013), including the long petiole, which is eccentrically attached to a nano-to notophyllous elliptic-ovate lamina. They differ because the CF2 leaf is bigger and has irregular margins.

Magnollids

CF3 morphotype

cf. *Araripia florifera* Mohr and Eklund 2003
(Figs. 5C-E)

Material

Basal-middle portion of a pinnate tri-lobed leaf (UFRJ-DG 1800-Pb); dispersed fragments from the basal part of the leaves (UFRJ-DG 1990-Pb; UFRJ-DG 1999-Pb).

Description

Pinnate tri-lobed notophyll leaf (6 cm wide, partly preserved), with symmetrical lobes separated by open and rounded sinus that have entire margins. The broad base forms a continuum with the also wide petiole (1 cm wide, 3 cm long) of the swollen base (Fig. 5E). The primary vein highlighted (10–5 mm wide) has two suprabasal and opposite inserted secondaries (5 mm large) that supply the lateral lobes and diverge from the primary vein in broad angles (60º), following a sharp convex course. An additional upper pair of secondaries is visible and diverges from the primary vein in a more acute angle (25º). Afterward, it curves upward in a semicraspedodromous pattern (Fig. 5D). The percurrent opposite tertiary veins have a sinuous course and cross the high order veins, which seem to end in the fine intramarginal vein.

Remarks

Pinnately lobed leaves (three or five lobes) that are similar to those of the CF3 morphotype have been reported in distinct Early Cretaceous deposits of Laurasia and Gondwana (Krassilov 1977, Thomas & Spicer 1986, Romero & Archangelsky 1986, Crabtree 1987, Sun & Dilcher 2002, Puebla 2009). For Doyle (2015), in the Potomac Group, this kind of leaf architecture only appears in the basal middle Albian (Subzone IA), as part of the "platanoid" (Doyle & Hickey 1976, Doyle & Upchurch Jr. 2014) or platanophyllic (Crabtree 1987) morphological complex, and coincides with the first appearance of the reticulate tricolpate pollen grains.

In Brazilian basins, such pinnate trilobed leaves are rare, but because of their suprabasal decurrent secondaries, they are comparable to some reproductive branches of *Araripia florifera* Mohr and Eklund, of the Crato flora (Mohr & Eklund 2003, Pls. 1 and 3.1), included in the Magnollid. However, *A. florifera* leaves might have an irregular number of lobes and craspedrodomous secondary veins. These features, unfortunately, are impossible to detect in this partially preserved margin of CF3. However, the upward curved upper pair of secondaries may suggest a semicraspedodromous venation. The main distinct characteristics between CF3 and *A. florifera* are the size of the lower leaves and their more irregular lobes (2–3 cm wide). However, these features usually vary in lobate leaves and can be controlled by environmental adaptations as well as ontogenetically. Mohr and Eklund (2003) compared *A. florifera* with *Sassafras* (Laurales) and with the leaf of *Sassafras officinalis* Nees Rugel.

The "leaf type 5" from Mohr and Friis (2000, Fig. 2G), another pinnately lobed leaf of the Santana Formation, shares some morphological features with CF3, like the full margins and the semicraspedodromous venation with the exmedial inflexion of the proximal pair of secondaries. However, it is different (or not preserved in CF3) in the high number of lobes (at least 7) of irregular size in the Crato Member leaves. Like in this case, this morphotype is represented by only one sample and has distinct types of round to ovate leaves, which are linked to the Nympheales, some of which are included later in the same species herein discussed with regard to the CF2 morphotype.

Additionally, it is important to call attention to the ternately platanoid lobed leaves initially mentioned, and its similarity to those present in *Vitiphyllum. Vitiphyllum* generally represents a basal eudicots (Doyle & Upchurch Jr. 2014) which also share features with CF3. However, they normally characterize younger Albian levels of the mid-latitude Eastern Laurasia assemblages that have the first tricolpate pollen grains (Mohr & Eklund 2003, Doyle & Upchurch Jr. 2014). This makes its presence in the Brazilian Equatorial basins less probable.

Concerning pinnate venation, suprabasal secondary and marginal veins, the CF3 leaf supports an affinity with the Magnollids, which was also proposed by Mohr and Eklund (2003) in relation to *Araripea florifera*. CF3 shows also a probable affinity with the Laurales and with "Sassafras" leaf type, considering the broad petiole and the inflexion in the basal secondaries (Little 1980). Those morphological appeals, the swollen basal petiole and the membranaceous texture, seem to suggest a deciduous plant or a plant with a vine habit (Naidu 2012, Pole 2015).

DISCUSSION

The tectonic and depositional context of the north Brazilian basins in the beginning of Cretaceous confirmed that they are part of a rift system derived from the breakup between South America and Africa. (Françolin & Szatmar 1987, Chang *et al.* 1992, Varejão *et al.* 2016). This conditioning led to a sedimentary deposition that was controlled by the presence of marginal areas, and, during the upper Aptian, by seawater ingressions, probably through a still incipient Equatorial Atlantic gateway (Milani & Thomaz-Filho 2000, Rossetti *et al.* 2001, Mizusaki *et al.* 2002, Castro 2011).

The Early Cretaceous carbonate beds (*e.g.*, the Marizal and Santana formations, respectively from the Recôncavo and Araripe basins, and the Codó Formation in the Parnaíba Basin), preserve fish related materials, gastropods and crustaceans, which are associated with plant fossils that can confirm the oceanic influence over and between the main lacustrine successions that conditioned the deposition (Mesner & Wooldrige 1964b, Darros de Matos 2000; Rossetti *et al.* 2001, Amaral & Brito 2012, Lindoso & Carvalho 2012, Lindoso *et al.* 2016). More recently, the beds also give support to a Tethyan influence across the northern Brazilian areas (Arai 2014). In the terrestrial and marginal areas, the palynological assemblages join pollen grains and spores that have a cosmopolitan distribution in South Laurasia, like *Classopollis* and *Exesipollenites*, associate to *Sergipea* and *Tucanopolis*, which are until now exclusive from the Gondwana (Tanrikulu *et al.* 2015).

The Codó Formation macroflora herein described, and its associated microflora (Lima 1982, 1989, Pedrao *et al.* 1996) confirm those data, despite their more limited preservation when compared with the well-preserved and known flora of the Santana Formation. Although its taxonomic placement was normally restricted to high rank clades, it had a vegetation sample that is not far from that which characterizes other Lower Cretaceous deposits, including Gnetales (cf. *Drewria*) and putative Cheirolepidiaceae/Araucariaceae?, which are associated with morphotypes that can attest to the conjunct occurrence of Nymphaeales, Magnoliids and other, still uncertain, early flowering plants.

Due to its general morphological features CF1 morphotype could be associated with both an angiosperms and a gymnosperms. The peltate round to ovate leaves of CF2 can be found in the Nympheaceae, in Monocots and in basal aquatic Eudicots. The morphotype "Spermatophyta *incertae sedis*", for other side, have no comparison in the known fossil record and could represent a putative angiosperm. This information reinforces a previous unsuspected initial diversity of the lower Cretaceous angiosperms, and also its fast adaptation in the expanding lacustrine contexts and sunny open areas (in general with a dry climate), of the interior areas of tropical Pangea (Wing & Boucher 1998, Gandolfo et al. 2000, Martin-Closas *et al.* 2006, Coiffard *et al.* 2007, Gee 2010, Wang *et al.* 2016).

In the Codó Formation assemblage, palmate lobed leaves represent two (CF1 and CF3) of the three morphotypes that are probably related to the angiosperms and were also a common component of the Early Cretaceous assemblages. This has been known since the pioneering work of Berry (1919) and recognized by its role in age inferences (Doyle & Hickey 1976) with regard to the phylogeny of the first angiosperms (Doyle & Endress 2010, Doyle 2015). As observed by Crane and Upchurch Jr. (1987), from work within levels of the Potomac Group Zone I of Virginia, conifers and angiosperms are still rare in Aptian assemblages and, as shown herein, are represented by a few fragmentary and incomplete samples. Many associated ferns suggest that some moister climates characterize the Southern United States at this moment.

Based on this succession, which extends from the Aptian to the Cenomanian, Doyle (2015, Fig. 1) recently showed that palmate and trilobed morphotypes, will have been irradiated in the Albian and dispersed worldwide until the Cenomanian.

Trilobate leaves have occured since the archetypic aquatic plant *Archaefructus* from the Aptian of China (Sun *et al.* 2002) and led Doyle and Upchurch Jr. (2014) to suggest that they predate (with exception of *Vitiphyllum*) the consistent presence of the tricolpate pollen of the Eudicots in the upper Aptian deposits of northern Gondwana, as well as in those from the Aptian-Albian boundary of Laurasia. Such a proposal is coherent with the likelihood-based analysis of Geeta *et al.* (2012), which confirms that the lobate character evolved early on in the leaves of the Eudicot stem lineage.

The peltate leaf with palinactinodromous venation of the CF3 morphotype (Fig. 5C-E), for example, differs from other related known fossils being analyzed. On the other hand, it shows ancestral features (like low-order veins, which are less organized or asymmetrically distributed along the leaf) that are also found worldwide. They were distributed in the Early Cretaceous Magnollids and in the first Eudicots (Feild *et al.* 2011, Sack & Scoffoni 2013, Zhang *et al.* 2015). Other components of Codó and Potomac floras also exhibit low vein densities with values in the same range as in distinct non-angiosperm clades, supporting the idea that this were probably an ancestral feature of angiosperms, like proposed by Feild *et al.* (2011).

An analysis of the previous record shows that many lobate leaf designs were experienced by the flowering plants (Dutra & Batten 2000, Pole 2015), and so difficulting its taxonomic insertion, especially when dealing with isolated leaves like here. Additionally, leaves can vary from entire to multiple lobate in the same branch or tree (Nicotra et al. 2011). This well-known leaf plasticity is today better understood. Considering the traditional forms for which they were conceived and the textures that were influenced by their habits and adaptations (or as a defence against herbivores), the important role of KNOX genes is now well recognized about its influence in this process (Royer *et al.* 2010, Nicotra *et al.* 2011, Dkhar & Pareek 2014, Ferris *et al.* 2015).

On the other hand, the palmate-lobed leaves, which are common in extant herbs, vines and trees, grow today mostly along tropical and subtropical belts (Takayama *et al.* 2006, Cheek 2007, Maes *et al.* 2009), and could be a good proxy in detecting zones of the past that were submitted to this condition, in addition to the environmental adaptive processes in the fossil record. Regardless of its taxonomic classification, the small lobate leaves herein described suggest opportunistic deciduous, herbaceous or creeping habits, which colonize freshly disturbed substrates and have a climatic context subject to seasonal dry periods (Taylor & Hickey 1992, Royer *et al.* 2010, Nicotra *et al.* 2011, Jud 2015).

Halamski (2013), working with Cretaceous fossil plants, proposed that communities composed of palmate and lobed leaves (like *Debeya*), and those that are accompanied by the conifer *Geinitzia reichenbachii* (which shares some common characteristics with *Cupressinocladus*), support the idea of a xeromorphic flora that grows in disturbed environments along river systems. For Arens and Allen (2014), *Cupressinocladus* is a genus characteristic of more drained areas around rivers or deltas, and Alvin (1983) considers that the Cheirolepidiaceae is an indicator of seasonally arid conditions.

Thus, as expressed by the types discussed in this study, and from other ones present in the Early Cretaceous floras of Brazil (Duarte & Santos 1993, Ferreira *et al.* 2008, Portela *et al.* 2014), the temporary resistant condition of the vegetation to drought and to hypersaline environments, proposed by Mohr *et al.* (2006), seems to be confirmed and coincides with the evaporitic depositional context of the Codó Formation.

In addition to the discussion regarding the plausibility of the first angiosperms having arrived in the tropical or in the high latitude areas, another impressive debate regards their initial adaptation to the environment. The herbaceous to shrubby habit here proposed in reference to CF1 and CF3, or/and an aquatic adaptation (in CF2), is suggested nowadays by many authors when dealing with the early angiosperms (based on the associated roots), and there has been a long-time debate about its adaptive evolution. An herbaceous to shrubby habit was inferred in relation to *Drewria* by Crane and Uchurch Jr. (1987), in relation to *Archaefructus* by Sun *et al.* (2002), and in relation to the early Eudicots by Jud (2015). As previously showed, the Aptian Codó flora shows its arrival from the near, wet coastal areas. It was submitted to a tropical and seasonally dry climate in a community composed mainly by Gnetales and conifers, as demonstrated in the macro and microflora, with the unique distinction of having ferns spores in the latter.

The contribution of Codó flora to age and correlations

Except by the lack of pteridophytes remains in the macroflora (despite present in the microflora, which also includes the upper Aptian *Sergipea variverrucata* of Regali & Santos, 1999), an older age is supported to

Codó Formation when compared with that of Santana Formation (Coimbra *et al.* 2002; Heimhofer *et al.* 2008), like was propose by Lima (1982). This age inference shows to have a cosmopolitan character confirmed by the occurrence of similar assemblages, containing lobate leaves (3 to 5 lobes) with "bird-foot" design, in the basal Aptian Potomac floras. In Southernmost South America, palmate lobed leaves of putative angiosperms are also record (Archangelsky *et al.* 2009) and at Albian arrive at the southern tip of Patagonia and northern Antarctic Peninsula (Rees & Smellie 1989, Cantrill & Nichols 1996, Dutra & Batten 2000, Cantrill 2001).

The presence of the described macroflora in the Codó beds expands the knowledge about Early Cretaceous plant fossils in low-latitudes, which were well-known in Brazil only to the Araripe Basin. Also attest a critical moment of plant evolution (the evolutionary turnover from gymnosperm-to angiosperm-dominated ecosystems) and of profound paleogeographic changes. The breakup of the continuous landmasses, after this time interval, would have a direct influence on the vegetation taking into account their dependence of terrestrial areas for its dispersion.

CONCLUSION

The allochthonous-parautochthonous assemblage from the youngest levels of the Codó Formation, with forms related to the Gnetales, conifers and to those representing the stem group of angiosperms (Nympheales and Magnollids), give also support to the Aptian-Albian age proposed to its succession. Some other similar plants in the fossil record indicate a vegetation composed of aquatic and herbaceous/shrubby habits, growing in fluvial/deltaic, lacustrine, and coastal open areas, which were probably fed by river systems whose banks sheltered and allowed for the growing of conifers. Cyclical invasions of marine waters and climate variations between arid and wet conditions were inferred from palynomorphs and characterize the same upper levels that contain the macroflora. As noticed herein, analogous fossil assemblages characterize the paleotropical areas of Southern Laurasia and northern Gondwana at the same time interval.

The macro and microfloristic assemblage from the Codó Formation stands out partly from that of Araripe Basin, because of the initial presence of many pteridophytes (proven only in the microflora) and the almost complete lack of established Eudicots, which could have resulted from their slight age differences, or from their near coastal location, which was probably more influenced by oceanic humidity. The Early Cretaceous plant fossils of the Codó Formation, together with other Brazilian basins precede the first efforts of the break-up between North and South America, and Africa, and the arrival of the north Atlantic Ocean waters to Tethyan areas, ending with the terrestrial links between those lands. Therefore, with other floras of the Equatorial belt, they are aligned with the latter floras that show a cosmopolitan vegetation inherited of the Pangea times.

Although representing only a partial portrait of the original vegetation that grew in what today corresponds to the northeastern coast of Maranhão State, the herein discussed plant fossils and their associated facies, seem to support one of the numerous strategies suggested with regard to the first appearance of flowering plants and their subsequent diversification. Initially proposed by Doyle in 1969, they conceived of the emergence and initial radiation of angiosperms on disturbed, aquatic or dry areas, near the coastal plains. By a fortunate coincidence, the studied fossiliferous area of Maranhão State is today a good analogous to the paleoecological context that conditioned the grown of its plant fossils. Nowadays locates in a similar latitude to that occupied at the beginning of the Cretaceous, and still submitted to arid to semiarid conditions, their ephemeral floods and coastal lagoons, with scarce vegetation, are a good portrait of ancient times here aborded.

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