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ANA PAULA DE ASSIS OLIVEIRA WESTERKAMP

CRETACEOUS CONIFERS FROM THE ARARIPE BASIN, WITH EMPHASIS ON CONE ANALYSES

FORTALEZA
2018

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Tese apresentada ao Programa de Pós-Graduação em Geologia do Centro de Ciências da Universidade Federal do Ceará, como requisito parcial à obtenção do título de doutor em Geologia. Área de Concentração: Paleontologia e Geologia Histórica

Orientador: Prof. Dr. Roberto Iannuzzi

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To

Dircionita and Christian

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"... nothing in our life makes sense,
if we do not touch the people's hearts."
(Cora Coralina)

"No meio do caminho tinha uma pedra
tinha uma pedra no meio do caminho
tinha uma pedra
no meio do caminho tinha uma pedra.

Nunca me esquecerei desse acontecimento
na vida das minhas retinas tão fadigadas.
Nunca me esquecerei que no meio do caminho
tinha uma pedra
tinha uma pedra no meio do caminho
no meio do caminho tinha uma pedra."

(Carlos Drummond de Andrade)

"Mitten im Weg lag ein Stein
Lag ein Stein mitten im Weg
Lag ein Stein
Mitten im Weg lag ein Stein.

Nie werde ich dieses Ereignis
Im Leben meiner so ermüdeten Netzhaut vergessen.
Nie werde ich vergessen dass mitten im Weg
Lag ein Stein
Lag ein Stein mitten im Weg
Mitten im Weg lag ein Stein."

(German version by Curt Meyer-Clason)

ABSTRACT

Conifers have played a major role in terrestrial ecosystems since the end of the Carboniferous. The arrival of angiosperms in the Aptian (Early Cretaceous) triggered a competition from the Late Cretaceous onwards, finally resulting in an exclusion of conifers from certain regions or habitats. Nowadays, conifers are the most dominant and remarkable gymnosperms in floras throughout the world; they have a high economic and ecological importance. Cones, the conifer reproductive organs, are conspicuous and reflect the adaptive traits developed during the evolutionary process of the group. In the Crato Formation (Santana Group, Araripe Basin) diversity and preservation types of conifer-related fossils were investigated, giving special emphasis on cone structures. Information on whole-plant aspects and pollen records were taken from current literature. Cone data were obtained studying external aspects of the fossils. Vegetative shoot SEM analyses confirmed the presence of charcoal. A total of 140 cone specimens were encountered in the palaeontological collections visited. They were grouped into 26 morphotypes. Conifer macrofossils and palynology prove the occurrence of five conifer families: Araucariaceae, Cheirolepidiaceae, Cupressaceae, Pinaceae, and Podocarpaceae. The number of coalified cones exceeded the sum of all other preservation modes. Iron oxide was second followed by charcoal and impression. All types of preservation were observed in both greyish and yellowish sediments, with higher numbers in the first. Aspects of plant and animal diversity as well as their ecological relationships are presented for the Crato biome. The morphological diversity of the studied cones indicates a richness hitherto unsuspected for conifer species/families in the Araripe Basin. The variety of fossil taxa found in exceptional state of preservation in the Crato Formation reflects the intricate ecological relationships that existed in the Early Cretaceous in northeastern Brazil. .

Keywords: Conifer cones. Cretaceous. Araripe Basin.

RESUMO

As coníferas têm desempenhado um papel importante nos ecossistemas terrestres desde o final do Carbonífero. A chegada das angiospermas no Aptiano (Eocretáceo) desencadeou uma competição do Neocretáceo em diante, resultando na exclusão de coníferas de certas regiões ou habitats. Atualmente, as coníferas são as gimnospermas mais dominantes e notáveis das floras em todo o mundo, com alta importância econômica e ecológica. Seus órgãos reprodutores, os cones, são conspícuos e refletem os traços adaptativos desenvolvidos durante o processo evolutivo do grupo. Foram investigados os tipos de preservação e a diversidade de fósseis de coníferas que ocorrem em calcários laminados da Formação de Crato, com especial ênfase nos cones. Informações sobre macrofósseis e registros polínicos foram retiradas da literatura corrente. Os dados dos cones foram obtidos por observações de aspectos externos dos fósseis. Análises de MEV em fragmentos de um caule confirmaram a presença de charcoal. Um total de 140 espécimes de cones foram encontrados nas coleções paleontológicas visitadas. Eles foram agrupados em 26 morfotipos. Macrofósseis e pólen comprovam a ocorrência de cinco famílias de coníferas: Araucariaceae, Cheirolepidiaceae, Cupressaceae, Pinaceae e Podocarpaceae. O número de cones preservados por coalificação excedeu a soma de todos os outros modos de conservação. Óxido de ferro foi a segunda forma, seguido por charcoal e impressão. Todos os tipos de preservação foram observados em ambos os sedimentos cinza e amarelo, com o predomínio de cones nos acinzentados. Aspectos da variedade vegetal e animal bem como suas relações ecológicas no bioma Crato foram apresentados. A diversidade morfológica dos cones estudados indica uma riqueza até então inesperada de espécies/famílias de coníferas na Bacia do Araripe. A multiplicidade de táxons fósseis encontrados em excepcional estado de conservação na Formação Crato reflete as intrincadas relações ecológicas que existiam no início do Cretáceo no nordeste do Brasil.

Palavras-chave: Cones. Coníferas. Cretáceo. Bacia do Araripe.

ZUSAMMENFASSUNG

Koniferen haben seit dem Ende des Karbons eine bedeutende Rolle in terrestrischen Ökosystemen gepielt. Das Auftauchen der Angiospemen im Apt (Frühe Kreide) hat zu einer Konkurrenzsituation geführt, die schließlich zum Ausschluss der Koniferen aus bestimmten Regionen oder Habitats führte. Heutzutage sind Koniferen die doiminantesten und auffälligsten Gymnospermen weltweit; sie haben eine enorme ökonomische und ökologische Bedeutung. Zapfen, die Fortpflanzungsorgane der Koniferen, sind auffällig und widerspiegeln adaptive Merkmale, die sich während der Evolution der Gruppe entwickelten. In der Crato-Formation (Santana-Gruppe, Araripe-Becken) wurden Diversität und Erhaltungstypen von Koniferen-Fossilien untersucht; Zapfenstrukturen wurden dabei besonders berücksichtigt. Informationen zu Pflanzen und Pollen wurden der aktuellen Literatur entnommen. Zapfendaten wurden durch das Studium der externen Morphologie gewonnnen. REM-Analysen eines vegetativen Sprosses bestätigten das Vorhandensein von Holzkohle. Insgesamt 140 Zapfenfossilien wurden in den besuchten palaeontologischen Sammlungen studiert. Sie wurden in 26 Morphotypen unterschieden. Koniferen-Makrofossilien und -Pollen belegen das Vorhandensein von fünf Familien: Araucariaceae, Cheirolepidiaceae, Cupressaceae, Pinaceae, und Podocarpaceae. Die Anzahl verkohlter Zapfen übertraf die Summe aller anderen Erhaltungsypen. Eisenoxid lag an zweiter Stelle, gefolgt von Holzkohle und Abdrücken. In grauen Sedimenten fanden sich mehr fossile Zapfen als in gelblichen. Aspekte der Pflanzen- und Tiervielfalt im Crato-Biom sowie mögliche ökologische Interaktionen werden vorgestellt. Die morphologische Diversität der untersuchten Zapfen deutet auf einen bisher unvorstellbaren Reichtum an Koniferenarten und -familien im Araripe-Becken hin. Die Vielfalt fossiler Taxa in äußerst gutem Erhaltungszustand in der Crato-Formation spiegelt die komplexen ökologischen Beziehungen wider, die in der Frühen Kreide in Nordost-Brasilien geherrscht haben müssen.

Schlüsselworte: Koniferenzapfen. Kreidezeit. Araripe-Becken.

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1 INTRODUCTION

Conifers are the most dominant and conspicuous gymnosperms in floras throughout the world. Their almost 615 species, 70 genera, and eight families appear in nearly all the major vegetation types, especially in the northern hemisphere where they show thei greatest covering of land. They are present in all climate zones from the Artic and Subantarctic to the Tropics, but absent from the highest altitudes and extreme deserts (FARJON, 2010; FARJON; FILER, 2013).

Conifers have high economic value and many applications. The world trade in coniferous wood represents about 60 % of all wood used for industrial purposes. By far the greatest volume of industrial wood is produced by species from the Family Pinaceae, which occur naturally in the northern hemisphere only, but have been widely planted for this purpose all over the world. Many coniferous species are considered excellent trees for reforestation, and even more are used in horticulture, where several species have yielded valuable cultivars. Additional products include resins and derivatives, such as terpene and essential oils, and even medicinal extracts. Seeds of some species, e.g. *Araucaria angustifolia*, can be tasty and be part of the regional diet. Conifers, thus, display an amazing array of unique potentials (FARJON, 2008; FARJON, 2010).

Conifers also play important ecological roles. Several of the large genera contain species that are highly advanced and adapted to a wide variety of habitats. Many conifers are tolerant of adverse climatic or edaphic conditions unsuitable for other trees. These range from frequent fires in tropical ‘pine savannas’ to extreme climatic conditions at the tree line or beyond in high mountains, from temperate evergreen rain-forests on ocean shores to semi-deserts in the interior of continents. Soils can be sandy, rocky, peaty, dry or wet, and even toxic with heavy metals. This tolerance of such a wide range of climatic and edaphic conditions is unique amongst trees and cannot be achieved by most broad-leaved trees. Natural old growth conifer forests, in with conifers can attain great size and age, are ecosystems sustaining a high level of biodiversity. Many species of plants and animals depend on them. Successional cycles in such forests are long and complex. In other systems, conifers are pioneers capable of establishing a quick forest cover to be replaced later by broad-leaved trees. There are many intermediate forest types between these extremes in which conifers have an important role. Moreover, climate regulation, watershed protection preventing erosion and assuring a steady supply of clean water in streams are other important functions of conifer forests (FARJON, 2008; FARJON; PAGE, 1999).

For these reasons, conifers are very important ecologically and much is still to be learned about them.

Nowadays the diversity of conifers in Brazil is very poor with the record of only nine native species and, except for *Araucaria angustifolia* which is inserted into Araucariaceae, all others belong to the Family Podocarpaceae (FARJON; FILER, 2013). Currently native conifers can be found in all Brazilian regions but in the Northeast Region only in Bahia. This is intriguing because the fossil record of the Araripe Basin shows the abundant occurrence of conifer remains in an area that today corresponds partially to territories of three states, i.e., Pernambuco, Ceará, and Piaui, which do not have any living native species of conifer these days.

Plant fossils from the Araripe Basin are remarkable because of their scientific value, representing the beginning of both the gymnosperm decline and the angiosperm radiation during the Early Cretaceous. And, due to the fascination that the latter plant group exerts on researchers, easily explainable by their dominance in modern vegetation, the study of gymnosperms from Crato has been relegated to the background. Another issue is the degree of preservation of the angiosperm fossils found in this unit. Many of them are preserved more or less entirely, often with roots, stems, leaves, sporangia and flowering structures still connected to each other. The more complete fossils are of immense importance to the paleobotanists once they can reach a more natural classification, key information to fill gaps in the puzzle of the evolution of most of the modern plant groups. The gymnosperms have generally been recorded by means of isolated organs or parts, in particular conifers. Because of all these reasons there is a great lack of knowledge about the conifers of the Crato Formation in the Araripe Basin.

Despite the well-known presence and local abundance of conifer specimens in the Crato Formation layers, there are doubts about identification of various species because their diagnostic differences were not well established. They could simply represent intraspecific and/or ontogenetic variants of few natural species. Moreover, their fertile portions, the cones, are not being studied, thus harming the correct identification of suprageneric taxa (families, etc.), as well as the understanding of the real diversity of the group in the Araripe Basin.

The paleobiogeography of Brazilian northeast is still debatable and the fossils of terrestrial plants could strongly help on determine the correlation between emerged lands during the South Atlantic opening during the Early Cretaceous. On the other hand, plants are sessile organisms so they can accurately reflect the local (habitat) and regional (climate) conditions were they live. The kind of dispersal of conifer seeds, in addition to their presence and diversity, can also collaborate in paleoclimatological interpretation of a region. Thus, an expanded knowledge of this plant group may assist in the reconstruction of terrestrial life in the Araripe region during the Early Cretaceous.

Therefore, the present dissertation is in line to fill part of the gap in the knowledge of the conifers from the Crato Formation flora. For this, besides the analysis of vegetative parts referred to conifers, the study of unpublished specimens corresponding to the fertile portions (cones) was made. It will increase the scope of the results to be obtained in relation to this group, since it is a single relevant collection of conifer fertile portions not yet well analysed.

The aim of this dissertation is to investigate the diversity and the preservation types of conifer-related fossils occurring in the laminated limestones of the Crato Formation from the Santana Group, in the Araripe Basin, with special emphasis on cone structures.

The following questions are proposed:

- what are the preservation types of the conifer remains in the Crato Formation?
- are there morphological characteristics that may reflect the systematic diversity of the conifer remains in the Crato formation?
- is there a spatial distribution of the conifer remains in the Crato Formation?
- which conifer taxa can be tentatively reconstructed as whole plants?

The answers to these questions can contribute to the knowledgement of the role played by conifers in the ancient biomes in which they lived. Thus, this dissertation can contribute to understand neglected adaptation mechanisms of conifers to their specific habitats and climate. It can also help to elucidate the paleobiogeographic context (patterns of distribution *versus* climatic belts, dispersal routes, centers of origin and irradiations, regional endemism, etc.) of this group during the beginning of the break-up of Gondwana.

2 GEOLOGICAL AND PALEONTOLOGICAL BACKGROUND

2.1 Geology of the Araripe Basin

The origin and evolution of the intracratonic basins of Northeast Brazil (fig. 1) were controlled by reactivation of pre-existing tectonic structures in the Precambrian basement during the Jurassic and Cretaceous. This reactivation was closely related to the opening of the South Atlantic Ocean (CARVALHO, 2000). The stability of the Brazilian Platform was broken in the Jurassic. Intense tectonic activity, related to the beginning of the rupturing of the gondwanic crust, resulted in the creation of many small sedimentary basins and led to rapid accumulation of continental sediment (MACHADO JR *et al.*, 1990).

In this context, the Araripe Basin was formed strongly controlled by extensional Early Cretaceous tectonic events related to Occidental Gondwana break-up accompanying the South Atlantic Ocean opening (ARAI *et al.*, 2004; ASSINE, 2007). It is the largest Mesozoic interior sedimentary basin in northeastern Brazil with a surface area of about 12 000 km^2 (fig. 1A). Covering parts of the states Piauí, Ceará and Pernambuco, it is limited by the following geographic coordinates: $38°30' – 40°50'$W and $7°5' – 7°50'$S (ARAI *et al.*, 2004). Showing a complex geological history, it is a basin of polygenetic evolution with stratigraphic framework constituted by megasequences generated in different tectonic regimes (ASSINE, 1992; ASSINE, 2007).

The stratigraphic megasequences have different units that over the years received different denominations (for a historical view, see Assine (1992), Martill (2007c)). Initially proposed by Small (1913), the Santana Formation was subdivided into the members Crato, Ipubi and Romualdo, from base to top, by Beurlen (1971). This denomination was adopted with variations in most of the papers published later (MABESOONE; TINOCO, 1973; PONTE; APPI, 1990; ASSINE, 1990; ASSINE, 1992; MAISEY, 2000; FARA *et al.*, 2005; ARAI, 2006; CASTRO *et al.*, 2006; ASSINE, 2007; MARTILL, 2007c; SCHERER *et al.*, 2015).

In another viewpoint, Neumann (1999) and Neumann e Cabrera (1999) proposed the elevation of the Santana Formation to group in the lithostratigraphic ranking and consequently its members to formations. More recently, Assine *et al.* (2014) and Neumann e Assine (2015) included the Barbalha Formation (ASSINE, 1992) into the Santana Group (ASSINE, 2007) (see table 1).

Stratigraphically, today, the Araripe Basin is constituted by the tectonosedimentary sequences (fig. 2): a) pre-rift, represented by Brejo Santo and Missão Velha formations; b)

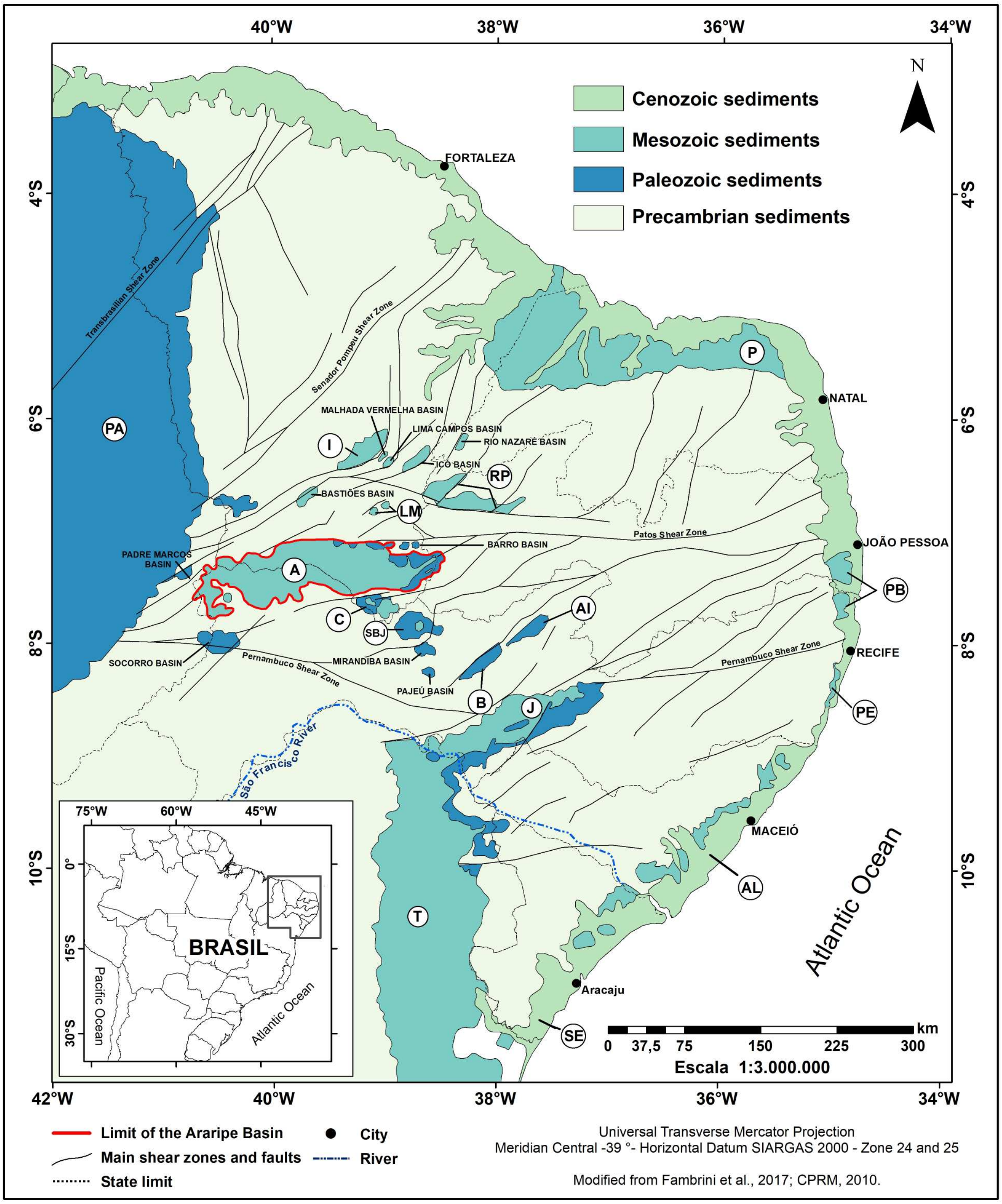


Figure 1 – Phanerozoic intracratonic basins in Northeastern Brazil, showing the Araripe Basin highlighted (rectangle). **A: Araripe**; PA: Parnaíba; I: Iguatu; RP: Rio do Peixe; LM: Lavras da Mangabeira; C: Cedro; SJB: São José do Belmonte; B: Betânia; AI: Afogados da Ingazeira ou Fátima; J: Jatobá; T: Tucano; P: Potiguar; PB: Paraíba; PE: Pernambuco; AL: Alagoas; SE: Sergipe (modified from Fambrini *et al.* (2017), CPRM (2010)).

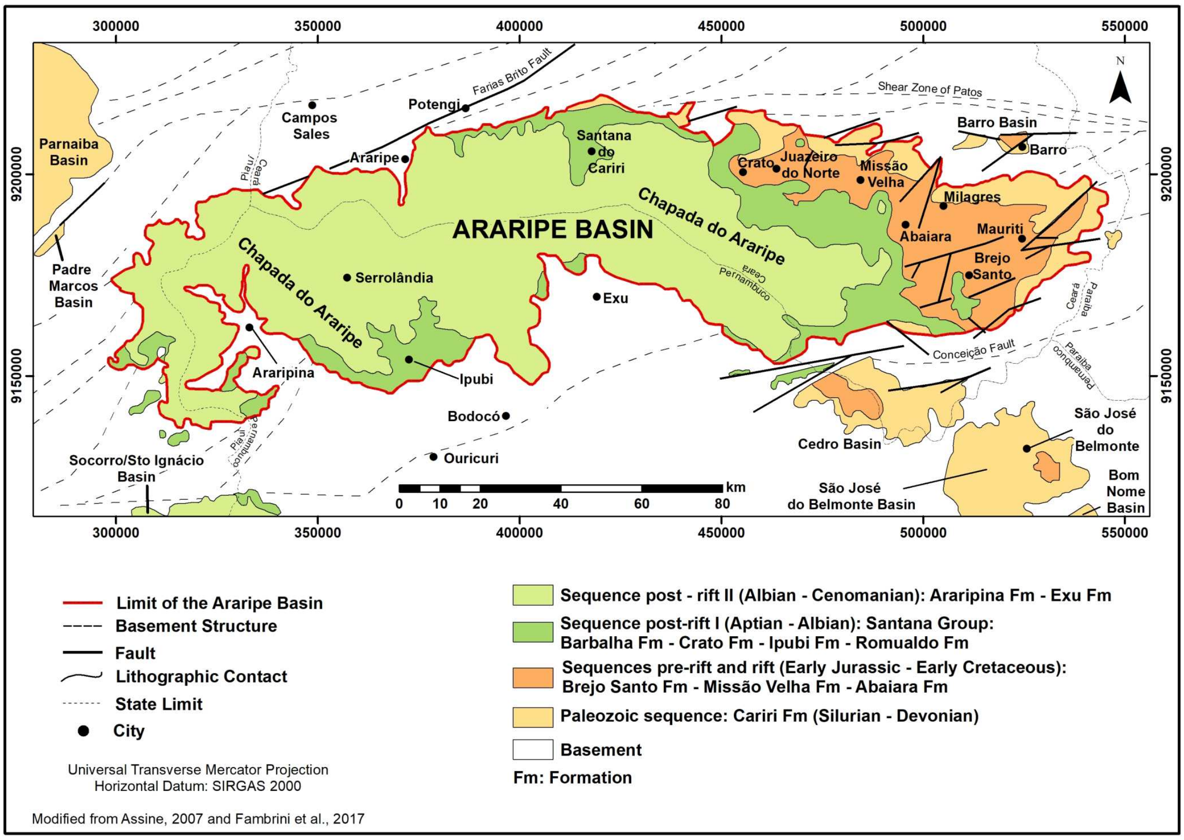


Figure 2 – Simplified geological map of the Araripe Basin (modified from Assine (2007), Fambrini *et al.* (2017)).

rift, composed of Abaiara Formation; c) post-rift I, which includes Barbalha, Crato, Ipubi and Romualdo formations; and d) post-rift II, which includes Araripina and Exu formations (ASSINE *et al.*, 2014; NEUMANN; ASSINE, 2015). These sequences were preceded by a regional Paleozoic sedimentation represented by the Cariri Formation composed of medium and thick sandstones (table 1). Its Ordovician-Devonian continental deposits over the basement occurred under the control of braided fluvial and aeolian depositional systems (ARAI *et al.*, 2004; ASSINE, 2007).

The Thitonian continental deposits of the Brejo Santo and Missão Velha formations (table 1) were the sedimentary response to mechanical subsidence occurred in the interior of northeastern Brazil, induced by the transmission of the strains resulting from rifting processes of Gondwana break up (ASSINE, 1992). The Brejo Santo Formation consists mainly of reddish to greenish argillites probably of continental origin. The Missão Velha Formation is composed of argillites and medium to conglomeratic sandstones with crossbedding, holding petrified gymnosperm trunks attributed to the conifer *Dadoxylon* (ARAI *et al.*, 2004; ASSINE, 2007; FAMBRINI *et al.*, 2017). The Abaiara Formation (table 1) represents the continental deposits that occurred at

Table 1 – Simplified chronostratigraphic column of the Araripe Basin, based on Assine (2007), Assine *et al.* (2014). (* Berriasian - Valanginian - Hauterivian - Barremian)

Geochronology			Lithostratigraphy			Megasequences
Period	Epoch	Stage/Age	Group	Formation	Composition	
Cretaceous	Upper	Cenomanian	Araripe	Exu	sandstones, quartz	Post-Rift II
	Lower	Albian		Araripina	sandstones, siltstones	
		Aptian	Santana	Romualdo	shales, sandstones, limestones	Post-Rift I
				Ipubi	gypsum, anhydrite, shales, carbonates	
				Crato	laminated limestones	
				Barbalha	shales, sandstones	
		BVHB*	Vale do Cariri	Abaiara	shales, siltites, argillites	Rift
Jurassic	Upper	Tithonian		Missão Velha	argillites, sandstones	Pre-Rift
				Brejo Santo	argillites	
Ordovician-Devonian				Cariri	sandstones	Paleozoic

the lowest stage of the Cretaceous (i.e., Berriasian, Valanginian, Hauterivian, and Barremian) formed by shales, siltites and argillites of lacustrine sedimentation (ARAI *et al.*, 2004).

The Aptian continental deposits of the Barbalha, Crato, and Ipubi formations, and the coastal to marine deposits of the late Aptian to the early Albian Romualdo Formation (fig. 2; table 1) characterize the Santana Group (ASSINE *et al.*, 2014). Chagas *et al.* (2007) recognized two depositional sequences in the Barbalha Formation, distinguished by fining upward arrangement of facies, beginning with fluvial deposits and ending with lacustrine deposits at their tops. In the first cycle, the black bituminous shales of the Batateira Beds are intercalated by limestones with breccia aspect. Thick sandstones and fluvial conglomerates in erosive contact with Batateira Beds represent the beginning of the second sedimentary cycle of the Barbalha Formation. Towards the top, the sandstones become thinner, with intercalations of green-coloured calciferous shales that become dominant at the top of the Barbalha Formation (ASSINE, 2007; CHAGAS *et al.*, 2007).

The Crato Formation (table 1; fig. 13) emerges as discontinuous banks with thickness around 20 metres, interbedded laterally with green shales. It consists predominantly of laminated limestones containing an exceptionally well-preserved and varied fossilized flora and fauna (ASSINE, 2007). The fossil record is abundant and very diverse (MARTILL *et al.*, 2007a), including among others, arachnids, crustaceans, insects, fish, anurans, turtles, crocodiles, lizards, pterosaurs, birds, fungi, gymnosperms and angiosperms (see section 2.3). The Crato Formation is characterized by a rhythmic layering of light and dark laminae (fig. 21) formed via authigenic precipitation of calcite from the upper water column, most probably induced and/or mediated by phytoplankton and picoplankton activities (HEIMHOFER *et al.*, 2010). This unit represents the expansion of the lacustrines systems, indicating low energy conditions in the depositional environment, and common presence of algal filaments (fig. 21) in the carbonates (ASSINE, 1992). The carbonates of the Crato Formation were originated in a lacustrine environment with a dysoxic to anoxic bottom. The lake systems were most likely hydrologically closed, wherein a negative water balance created a hypersaline environment that was hostile to metazoans and favored the development of bacterial mats in shallow water (CATTO *et al.*, 2016). The fossil plant material, the main study objects of this thesis, comes from Crato Formation.

The Ipubi Formation (table 1) has a predominantly evaporitic sedimentation, interbeddeding gypsum, anhydrite, shales and carbonates (ARAI *et al.*, 2004). With maximum thickness of around 30 m, the gypsum layers are lenticular and laterally adjacent to grey-greenish shales, carbonates or even sandstones. The discontinuity of the layers of this member, the existence of intercalation of bituminous shales with fish fragments, carbonized vegetables and non-marine ostracods suggest that there was not a wide marine evaporite basin in the region. The interpretation assumed is that evaporites were originated in coastal environments (supralittoral), susceptible to relative base level variations in arid to semi-arid conditions (ASSINE, 1992; ASSINE, 2007; NASCIMENTO JR *et al.*, 2016).

The Romualdo Formation (table 1) is the top of the Santana Group. It presents pelitic-marl beds, interlayered with bituminous fossiliferous shale, sandstone and limestone banks, especially at the top, where the marine influence was greater (ARAI *et al.*, 2004). The presence of sandstones interstratified with shales characterizes the bottom of the Romualdo Formation. The shales get darker toward the top, where there is 20 metres of rocks rich in organic matter. In these shales, there is an interval of nearly 6 metres thickness where calcareous concretions occur in various shapes and sizes, many of them containing mostly remnants of fishes, other vertebrates and even plants. A few meters above the interval of concretions a coquina layer stands out, which can reach a thickness of one meter, corresponding to the maximum flooding surface in the sequence, according to Assine (2007). The Romualdo Formation comprises a transgressive-regressive cycle characterized by a sea ingression, which has deposited exuberant fossiliferous carbonate concretions and extensive gypsum beds (ASSINE *et al.*, 2014). Recently, data of Custódio *et al.* (2017) support the interpretation that the sea reached the Araripe Basin from the southeast. These authors also suggested that the original size of the epicontinental sea in the interior of north-eastern Brazil was much larger than the present-day area of the Araripe Basin.

The Albian-Cenomanian continental deposits of the Araripina and Exu formations (table 1) comprise the final phase of deposition in Araripe basin. These units have distinct lithological characteristics and are separated by erosional unconformity. The Araripina Formation consists of fine sandstones and clay siltstones of reddish, purplish and yellowish colouration. At the top of the formation, facies suggest meandering fluvial system deposition, characterizing the regressive phase (ARAI *et al.*, 2004). The Exu Formation consists of fluvial quartzose friable and clayish sandstones, that are predominantly reddish and may be whitish in places of intense leaching (ARAI *et al.*, 2004). The presence of alluvial deposits of the Exu Formation, deposited contemporaneously to a global eustatic sea level rising, suggests an epeirogenic uplift early in Albian-Cenomanian times (ASSINE, 1992). The Araripe basin has a polycyclic sedimentary history, like many intracratonic basins (syneclises) and continental margin basins. It differs from these because the conjunction of the eustatic fall, the absence of subsidence and subsequent uplift, which abruptly interrupted sedimentation at the end of Albian-Cenomanian (ARAI *et al.*, 2004).

2.2 The Crato flora – state of the art

Fossil floras are exceptionally well preserved in the Araripe Basin. Dissociated parts as leaves, branches and cones are common in the fossil record, but also whole plants can be found compounding a rich testimony of Cretaceous flora in this region of the globe. A gathering of the main publications about the paleoflora of the Araripe Basin can be found in Bernardes-de-Oliveira *et al.* (2002), Bernardes-de-Oliveira *et al.* (2003), Sucerquia (2006), Fanton *et al.* (2007) and Lima *et al.* (2012). Among the works there are dissertations, theses, publications in congress abstracts, books and scientific journals. In this review, the taxa will be highlighted that were effectively published according to the International Code of Botanical Nomenclature.

Palynological studies of Lima (1979), Lima (1989), Osborn *et al.* (1993), Arai *et al.* (2001), Batten (2007), Heimhofer e Hochuli (2010), Rios-Netto *et al.* (2012) and Portela *et al.* (2014) demonstrate a broad diversity spectrum of spore-bearing and seed plants in the Crato flora. From these studies the presence of algae, pteridophytes, gymnosperms (conifers, cycads and gnetophytes), and angiosperms (monocots and dicots) is obvious. The macrofossils described until now include pteridophytes, gymnosperms and angiosperms. Gymnosperms are dominant, comprising approximately 60 % of the flora remains (MOHR *et al.*, 2007). A summary of macrophyte flora of the Crato Formation is presented below.

2.2.1 Pteridophytes

In terms of lycopsids, the genus *Isoetites* Muenster was first registered in 2000 and 2002 (DILCHER *et al.*, 2000; BERNARDES-DE-OLIVEIRA *et al.*, 2002) and the specimens completely described by Bernardes-de-Oliveira *et al.* in 2003. These authors worked on five specimens bearing short corm stalks with sterile and fertile microphylls. On the other hand, sphenopsids are virtually absent, having been referenced only by Dilcher *et al.* (2000) that reported a short herbaceous specimen of branches with roots and leaves inserted similar to *Schizoneura* Schimper and Mougeot.

Among the pteridophytes, ferns are the most common group assigned in the Crato Formation. Oliveira-Babinski e Lima (1991) reported the filicopsid families Schizaeaceae, Dipteridaceae and Salviniaceae. Bernardes-de-Oliveira *et al.* (1993) registered Schizaeaceae fronds with affinity to the genus *Anemia* Swartz. Later, Bernardes-de-Oliveira *et al.* (2006) identified these fronds as *Ruffordia goepperti* (Dunker) Seward. Recently Mohr *et al.* (2015) described macrofossils of *Ruffordia goeppertii* (Dunker) Seward based on the morphology and in situ spores, taken from organically preserved material. Fanton *et al.* (2007) reported the first record of Caytoniales in the Brazilian Northeast.

2.2.2 Gymnosperms

The gymnosperms macrofossils are apparently represented by only two orders in the Crato Formation, i.e., Coniferales and Gnetales, despite their aforementioned relative abundance within this paleoflora and the presence of pollen grains attributed to cycads.

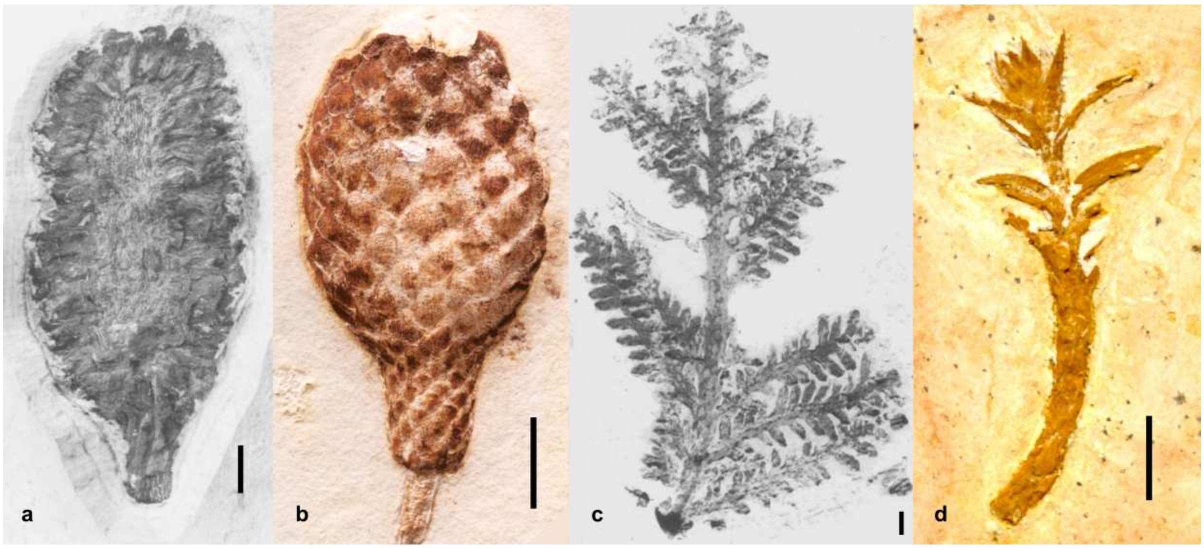


Figure 3 – Coniferales. a) *Araucaria* sp. (KUNZMANN *et al.*, 2004), b) *Araucariostrobus* sp. (KUNZMANN *et al.*, 2004), c) *Brachyphyllum obesum* (KUNZMANN *et al.*, 2004), d) *Tomaxellia biforme* (KUNZMANN *et al.*, 2006). Scale bars: 10 mm.

Coniferales

Araucariaceae and Cheirolepidiaceae are the only two coniferales families found in the Crato flora until now. In Araucariaceae there are isolated leaves, e.g. *Araucaria cartellei* Duarte (CRANE; MAISEY, 1991; BERNARDES-DE-OLIVEIRA *et al.*, 1993; DUARTE, 1993); a cone scale of *Araucarites vulcanoi* Duarte (DUARTE, 1989; DUARTE, 1993); seed cones and isolated cone scales of *Araucaria* Jussieu (fig. 3a) and a juvenile seed cone (fig. 3b) of *Araucariostrobus* Krasser (KUNZMANN *et al.*, 2004). The genus *Brachyphyllum* (Brongniart) Lindley et Hutton, attributed to this family, appears as cone of *B. insigne* Heer (DUARTE, 1993) and leafy branches (fig. 3c) of *B. obesum* Heer (DUARTE, 1985; DUARTE, 1989; DUARTE, 1993; KUNZMANN *et al.*, 2004). Data from Batista *et al.* (2017) support the taxonomic placement of *B. obesum* within Araucariaceae.

Cheirolepidiaceae (fig. 3d, fig. 4a) are represented by leafy branches of *Tomaxellia biforme* Archangelsky (KUNZMANN *et al.*, 2006) and *Frenelopsis* sp. Schenk (KUNZMANN *et al.*, 2006). Sucerquia *et al.* (2015) reviewed *Frenelopsis* sp. (KUNZMANN *et al.*, 2006) and proposed a new species *Pseudofrenelopsis capillata* Sucerquia, Bernardes-de-Oliveira et Mohr. Batista *et al.* (2017) suggested the presence of more than one *Pseudofrenelopsis* species in the Crato Formation.

Coniferales of unknown affinity (fig. 4b-d) have also been reported: *Lindleycladus* sp. Harris (KUNZMANN *et al.*, 2004); *Novaolindia dubia* Kunzmann, Mohr et Bernardes-de-Oliveira

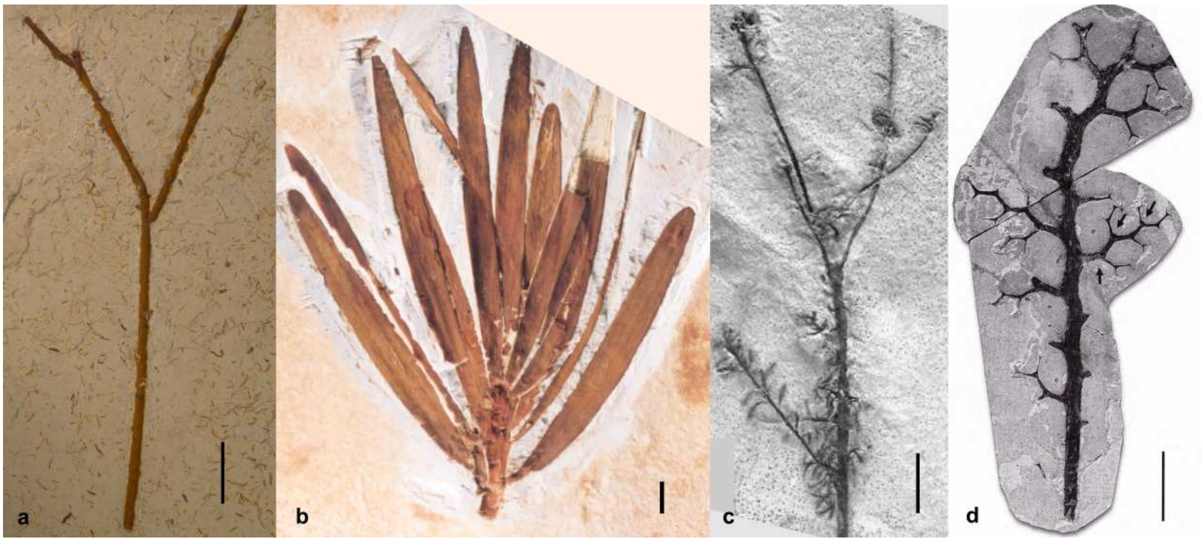


Figure 4 – Coniferales. a) *Frenelopsis* sp. (KUNZMANN *et al.*, 2006), b) *Lindleycladus* sp. (KUNZMANN *et al.*, 2004), c) *Novaolindia dubia* (KUNZMANN *et al.*, 2007), d) *Duartenia araripensis* (MOHR *et al.*, 2012). Scale bars a: 40 mm; b: 10 mm; c: 20 mm; d: 100 mm

(KUNZMANN *et al.*, 2007); *Podozamites* Braun (DUARTE, 1985); *Duartenia araripensis* Mohr, Schultka, Süss et Bernardes-de-Oliveira (MOHR *et al.*, 2012).

Gnetales

Ephedraceae and Welwitschiaceae represent gnetalean plants in the Crato flora. Ephedraceae show leaves and seeds associated to *Ephedra* Linnaeus (BERNARDES-DE-OLIVEIRA *et al.*, 1996; BERNARDES-DE-OLIVEIRA *et al.*, 2000; MOHR; BERNARDES-DE-OLIVEIRA, 2004; FANTON *et al.*, 2006b). Kerkhoff e Dutra (2007) described *Ephedra paleoamericana* Kerkhoff et Dutra, expressed by male reproductive branches. Welwitschiaceae is more diverse and comprehend the cotyledons (fig. 5a) of *Cratonia cotyledon* Rydin, Mohr et Friis (RYDIN *et al.*, 2003), a juvenile branch with cotyledons (fig. 5b) of *Welwitschiella austroamericana* Dilcher, Bernardes-de-Oliveira, Pons et Lott, isolated leaves (fig. 5c) of *Welwitschiophyllum brasiliense* Dilcher, Bernardes-de-Oliveira, Pons et Lott, and axes with pollen cones (fig. 5d) of *Welwitschiostrobus murili* Dilcher, Bernardes-de-Oliveira, Pons et Lott (DILCHER *et al.*, 2005). Löwe *et al.* (2013) described a new gnetalean fossil, *Friedsellowia gracilifolia* Löwe, Mohr, Coiffard et Bernardes-de-Oliveira (fig. 6a), the characters of which point to a close relationship to *Welwitschia* Hook.F.

Other specimens with gnetalean affinity (fig. 6b-d) are *Cearania heterophylla* Kunzmann, Mohr et Bernardes-de-Oliveira (KUNZMANN *et al.*, 2009); *Cariria orbiculiconiformis* Kunzmann, Mohr, Wild et Bernardes-de-Oliveira (KUNZMANN *et al.*, 2011) and *Itajuba yansanae* Ricardi-Branco, Torres, Tavares, Carvalho, Tavares et Campos (RICARDI-BRANCO *et al.*, 2013).

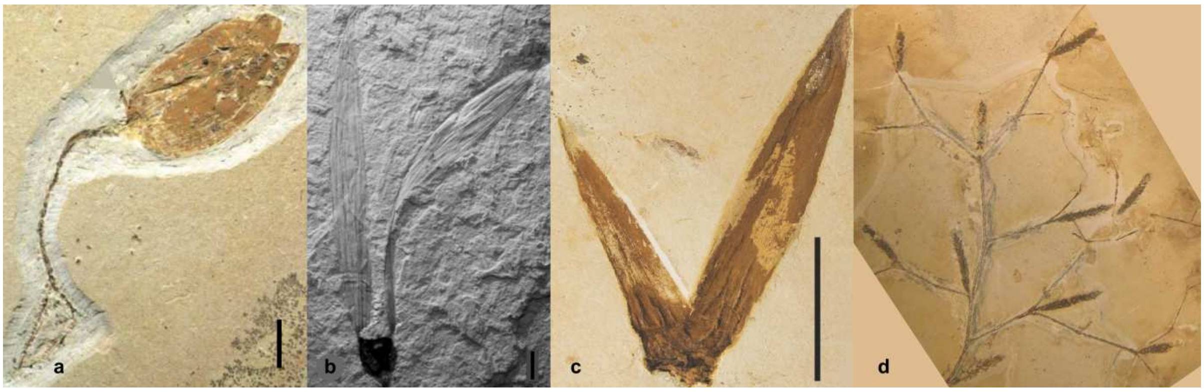


Figure 5 – Welwitschiaceae. a) *Cratonia cotyledon* (RYDIN *et al.*, 2003), b) *Welwitschiella austroamericana* (DILCHER *et al.*, 2005), c) *Welwitschiophyllum brasiliense* (MARTILL *et al.*, 2007a, plate 27d), d) *Welwitschiostrobus murili* (MARTILL *et al.*, 2007a, plate 27e). Scale bars a, b: 10 mm; c: 50mm.

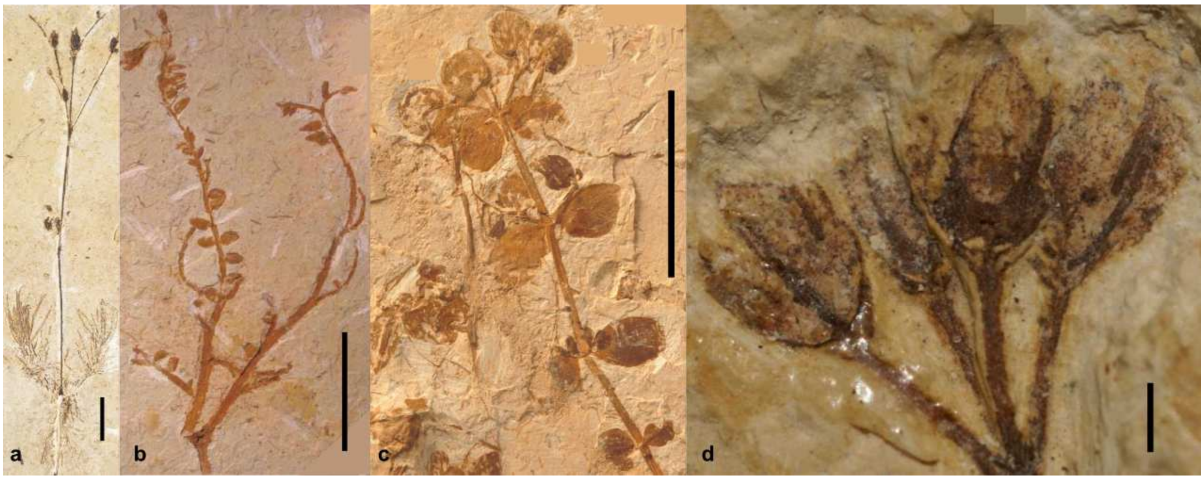


Figure 6 – Gnetales. a) *Friedsellowia gracilifolia* (MARTILL *et al.*, 2007a, plate 28a), b) *Cearania heterophylla* (KUNZMANN *et al.*, 2009), c) *Cariria orbiculiconiformis* (KUNZMANN *et al.*, 2011), d) *Itajuba yansanae* (RICARDI-BRANCO *et al.*, 2013). Scale bars a: 10 mm; b, c: 50 mm; d: 1 mm.

Fanton *et al.* (2006b) proposed a new gnetalean taxon (without naming it) not directly related to the relictual living families or other extinct gnetalean taxa.

2.2.3 Angiosperms

Mohr e Friis (2000) reported the variety of fossil angiosperms in the Crato flora. They mentioned detached leaves, stems with attached leaves and reproductive structures, fruiting structures that occur both isolated and attached to their axes, and complete plants with adhering roots, stems, leaves, and reproductive structures. Three groups of angiosperms are present in the Crato Formation, i.e. basal angiosperms, monocots and dicots.

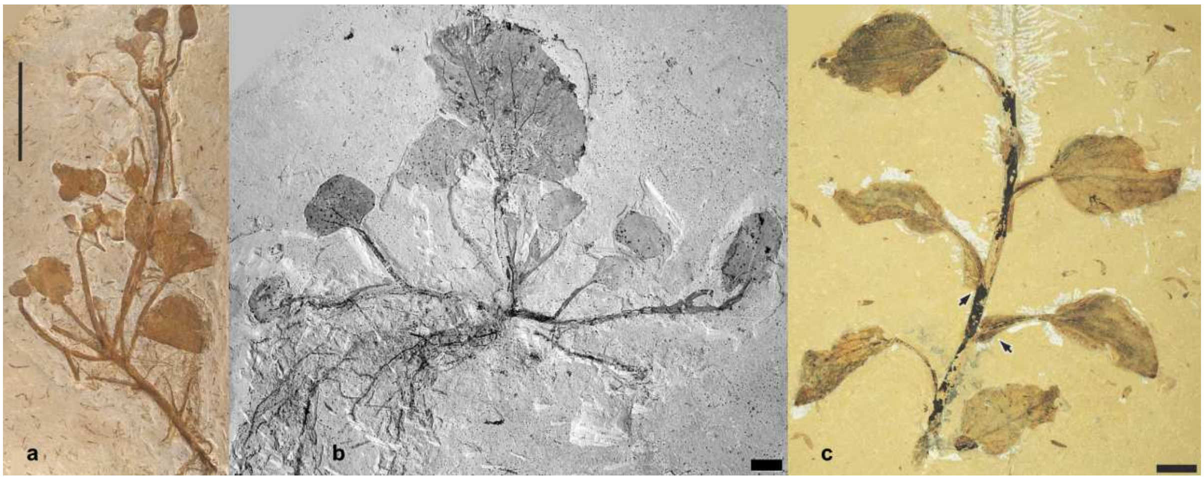


Figure 7 – Basal Angiosperms. a) *Pluricarpellatia peltata* (MARTILL *et al.*, 2007a, Plate 30d), b) *Jaguariba wiersemana* (COIFFARD *et al.*, 2013a), c) *Hexagyne philippiana* (COIFFARD *et al.*, 2014), 2014). Scale bars: 10 mm.

Basal Angiosperms

The basal angiosperms (fig. 7) in the Crato flora are mainly represented by taxons referred to Nymphaeales, e.g., *Pluricarpellatia peltata* Mohr, Bernardes-de-Oliveira et Taylor (MOHR *et al.*, 2008), and *Jaguariba wiersemana* Coiffard, Mohr et Bernardes-de-Oliveira (COIFFARD *et al.*, 2013a), which probably participated in the composition of the aquatic vegetation of the “Crato Lake”. *Hexagyne philippiana* Coiffard, Mohr et Bernardes-de-Oliveira (COIFFARD *et al.*, 2014) is the first macrofossil of a piperalean taxon from the Early Cretaceous (Aptian).

Monocotyledons

The first monocotyledon referred to the Crato flora was attributed to the genus *Klitzschophyllites* Lejal-Nicol. Later, Mohr *et al.* (2006) made an emended description of *Klitzschophyllites* (fig. 8a), a monocot of uncertain familiar affinity. *Spixiarum kipea* Coiffard, Mohr et Bernardes-de-Oliveira (fig. 8b) is also aquatic and belongs most likely to Araceae (COIFFARD *et al.*, 2013b). The first fossil record of Smilacaceae in Brazil is *Cratosmilax jacksoni* Lima, Saraiva, Silva, Bantim et Sayão (fig. 8c), a plant with terrestrial habits (LIMA *et al.*, 2014).

Dicotyledons

Among dicots, the following magnolialean plants have been assigned (fig. 9a-c): *Araripia florifera* Mohr et Eklund (MOHR; EKLUND, 2003); *Endressinia brasiliana* Mohr et Bernardes-de-Oliveira (MOHR; BERNARDES-DE-OLIVEIRA, 2004) and *Schenkeriphyllum glanduliferum* Mohr, Coiffard et Bernardes-de-Oliveira (MOHR *et al.*, 2013)). *Iara iguassu* Fanton,

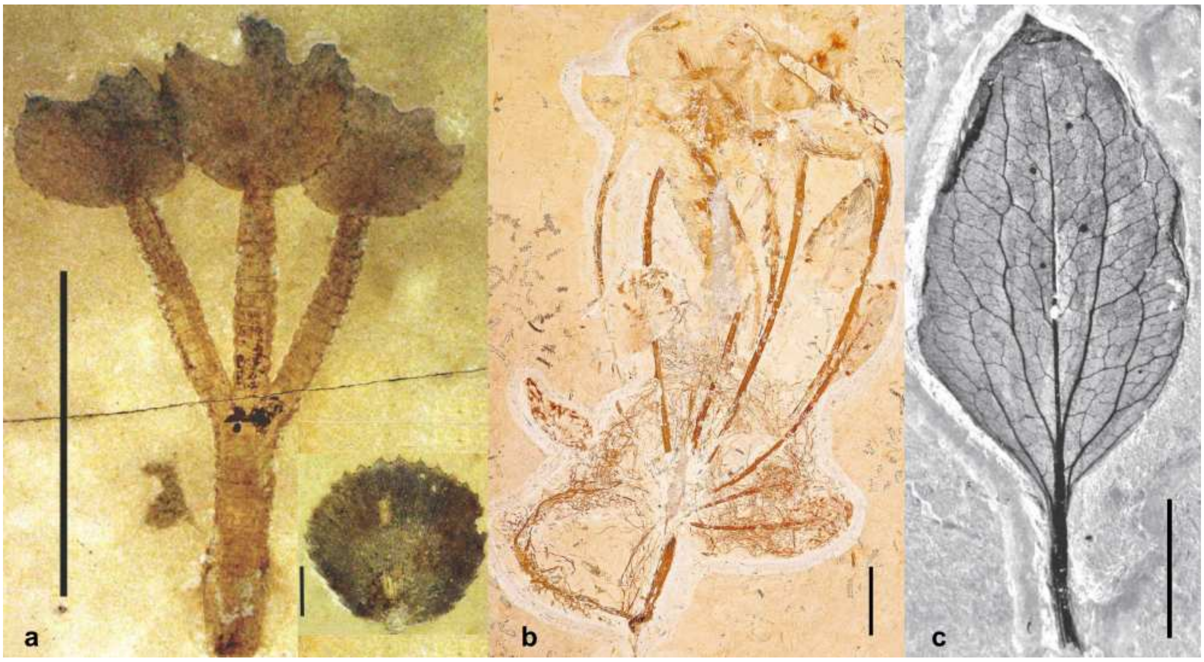


Figure 8 – Monocotyledons. a) *Klitzschophyllites flabellatus* (MARTILL *et al.*, 2007a, Plate 31a/b), b) *Spixiarum kipea* (COIFFARD *et al.*, 2013b), c) *Cratosmilax jacksoni* (LIMA *et al.*, 2014). Scale bars a: 50 mm/10 mm; b: 30 mm; c: 150 mm

Figure 9 – Dicotyledons. a) *Araripia florifera* (MOHR; EKLUND, 2003), b) *Endressinia brasiliana* (MOHR; BERNARDES-DE-OLIVEIRA, 2004), c) *Schenkeriphyllum glanduliferum* (MOHR *et al.*, 2013), d) *Iara iguassu* (FANTON *et al.*, 2006a). Scale bars: 10 mm.

Ricardi-Branco, Dilcher et Bernardes-de-Oliveira (fig. 9d) also is an aquatic flowering plant, probably not related to extant monocots or dicots (FANTON *et al.*, 2006a).

2.2.4 The significance of the Paleoflora

The spectacular flora and fauna fossils preserved in laminated limestones of the Crato Formation earn the Santana Group the status of *Fossil Konservat Lagerstätte* (MARTILL *et al.*, 2007a). The preservation is of more or less entire specimens, often with roots, stems, leaves, sporangia and flowering structures connected to each other; and even the palaeosoils is of immense importance to the palaeobotanists, who often has to deal with dispersed organs, of mostly unknown natural connection (MOHR *et al.*, 2007). The more complete fossils permit a more natural classification, key information to fill gaps in the puzzle of the evolution of a major part of modern plant groups. Beyond their beauty and completeness, plant fossils from the Crato Formation are remarkable because of their scientific value, being on the cusp of the gymnosperm decline and the angiosperm radiation.

Furthermore, the Crato beds were deposited when Gondwana was still reasonably intact; they were located in a sedimentary basin close to the heart of that super-continent, filling a gap that exists in the macrofossil record of plants in the paleotropical belt during the Early Cretaceous. At the same time, both angiosperm diversification and co-evolution with insect pollinators were beginning. These characteristics form a perfect window, allowing the study of plant-pollinator interactions in a Cretaceous Gondwana ecosystem (MARTILL; BECHLY, 2007) beyond the other type of interactions, less symbiotic, such as herbivory and ovoposition, galls and mines (SANTOS FILHO *et al.*, 2017).

The excellent preservation of the palaeoflora of Araripe Basin allows detailed morphological and/or anatomical studies that contribute to the clarification of several aspects on the terrestrial plants as: (i) evolution (DILCHER *et al.*, 2005; KUNZMANN *et al.*, 2011; LIMA *et al.*, 2014; MOHR *et al.*, 2013; RYDIN *et al.*, 2003); (ii) ecology (KUNZMANN *et al.*, 2011; MOHR *et al.*, 2013; SANTOS FILHO *et al.*, 2017); (iii) climatic conditions (DILCHER *et al.*, 2005; KUNZMANN *et al.*, 2004; KUNZMANN *et al.*, 2006; MOHR *et al.*, 2013; RICARDI-BRANCO *et al.*, 2013; SUCERQUIA *et al.*, 2015); (iv) diversity (KUNZMANN *et al.*, 2011; MOHR; EKLUND, 2003; MOHR *et al.*, 2013; RYDIN *et al.*, 2003); (v) morphology (KUNZMANN *et al.*, 2004; MOHR; EKLUND, 2003; COIFFARD *et al.*, 2013a; MOHR *et al.*, 2013; BATISTA *et al.*, 2017); (vi) plant dispersal (DILCHER *et al.*, 2005; COIFFARD *et al.*, 2013b).

2.3 The Crato biome – a brief introduction

By the definition of Odum e Barrett (2005), biome is a large regional or sub-continental system, characterized by a particular type of distinct vegetation that can be differentiated by the predominant plants associated with a certain climate. In this broad spectrum, the flora and fauna of the Crato Formation restricted to the lake and its surroundings is far from being a biome. However, as it represents a clipping, a window, which recorded evidence of various communities that existed associated with Lake Crato, it may represent a model that could be applied to the biome that existed under semi-arid conditions in equatorial Gondwana. It is in this sense that the term biome is used in this section.

2.3.1 Abiotic conditions

Paleoceanographic and paleogeographic changes accompanied the final break-up of Gondwana during the Cretaceous. Flooded continents, large and shallow epicontinental seas, and large marine seaways characterized the paleogeographic situation in these times (SAMES *et al.*, 2016). There was widespread aridity in the equatorial region during the Early Cretaceous (HAY; FLOEGEL, 2012) and the Crato biome was inserted in a hot and arid belt. Recent research about climate indicates a very warm greenhouse in the mid-Cretaceous (Aptian–Turonian/Coniacian) including short-lived hothouse periods (KIDDER; WORSLEY, 2012) with widespread anoxia (HU *et al.*, 2012, Oceanic Anoxic Events 1, 2 and 3) and possible reversals of the thermohaline circulation (KIDDER; WORSLEY, 2012, episodes of Haline Euxinic Acidic Thermal Transgression). Wild fire is another important abiotic factor widespread and frequent in the Cretaceous. Its activity would have affected the health, composition, and structure of the vegetation and, through habitat loss, probably the fauna (BROWN *et al.*, 2012). In addition fire produces charcoal, which can preserve the anatomy of a plant, allowing for taxonomic identification, and permitting an improved understanding of the nature of fire systems in deep time (SCOTT, 2010).

The deposition of laminated limestones of the Crato Formation took place in a lacustrine environment (ASSINE, 2007), under anoxic and, at least during certain episodes, hypersaline bottom water conditions (HEIMHOFER *et al.*, 2010). For Menon (2007), a jigsaw of habitats may have been present around the Crato lagoon during the period in which the limestone sequence was deposited. She considered that as the South Atlantic Ocean opened, the increase in humidity, rainfall and perhaps a change in prevailing wind directions contributed to the heterogeneity of the landscape. The hypothetical paleoflora distribution zones shown in Neumann *et al.* (2003) gives an idea of what the ecosystems around Crato lake would look like. Probably there were: (i) lacustrine zones with changing water level; (ii) periodically flooded lacustrine marginal zones – swamp; (iii) land zones above the lacustrine watertable and (iv) upland zones.

The paleobotanical and paleogeographic data of Neumann *et al.* (2003), suggested that the Crato lacustrine system evolved under a tropical–subtropical, warm paleoclimatic regime, probably characterized by seasonal precipitation and alternating humid–dry cycles. The water column would increase during humid climatic episodes, what could lead to the development of a permanent thermal stratification of water (i.e., thermal meromixis). In periods of water scarcity, the retraction of the lake could generate shallower and more saline water bodies. The renewed input of freshwater during episodes of lacustrine water level rise and spread could result in the development of a strong halocline and cause an ectogenic meromixis. Anoxic conditions prevailing in the hypolimnion is indicated by the occurrence of isorenieratene derivatives in the laminated carbonates of the Crato Formation (HEIMHOFER; MARTILL, 2007). The presence of abundant halite pseudomorphs suggests that hypersaline waters predominated during deposition of the Crato Formation (MARTILL *et al.*, 2007b).

The break of Gondwana and the beginning of the formation of the Atlantic Ocean shaped the Crato biome which probably was the stage of intricate ecological interactions in different ecosystems. The exceptional preservation and variety of fossil taxa found in the Crato Formation provide clues for what could be the ecological relationships existing at that time.

2.3.2 Biotic components

Paleoflora

Regarding the floristic associations, the palynomorph study of Neumann *et al.* (2003) indicates that a typical tropical Early Cretaceous Gondwana flora dominated by Cheirolepidiaceae adapted to arid–semiarid conditions that covered the Crato biome. Ferns (e.g., Schizaeaceae), Gnetales and angiosperms would probably have formed the ground cover of land zones, in proportions changing depending on the level of the lacustrine water-table. Larger conifers would have grown in upland areas while Gnetales would have preferred well-drained soils. Benthic cyanobacterial mats with occasional blooms of *Botryococcus* algae under fresh to brackish water conditions dominated the aquatic communities (NEUMANN *et al.*, 2003).

Nowadays, the fern and lycophyte flora of the semi-arid region in Brazil has a unique identity characterized by an expressive richness of the genus *Anemia* Swartz. Besides that there are high representations of aquatic and heterosporate species, with special survival strategies in some species (e.g., poikilohydric and deciduous seasonal patterns, therophytic life form) and a low representation of epiphytes (XAVIER *et al.*, 2012). *Anemia* Swartz, the closest extant relative of extinct *Ruffordia* Seward found in the Crato Formation, is a common genus of open habitats and well-drained sites, sometimes in savannahs and less often in open or rain forests. In *Ruffordia* Seward, the coriaceous aspect of the frond lamina is consistent, at least in part, with the suggestion of a (seasonally) semi-arid to arid paleoclimate during the time of the deposition of the Crato plattenkalk limestone (MOHR *et al.*, 2015).

Crato conifers exhibit xerophytic characters such as reduced coriaceous leaves, very thick cuticles, deeply sunken stomata, and photosynthetic jointed stems. These morphological and anatomical features support the idea of a warm to hot, temporarily (possibly seasonally) dry climate during the late Early Cretaceous in the paleoequatorial region (KUNZMANN *et al.*, 2004; KUNZMANN *et al.*, 2006; MOHR *et al.*, 2006). Cheirolepidiaceae were ubiquitous in the Araripe Basin because *Classopollis classoides* and disarticulated branchlets were present in both rhythmites and laminated limestones (NEUMANN *et al.*, 2003). The habitat of *Tomaxellia biforme* Archangelsky (fig. 3d) might have been relatively far from the locality of deposition due to its rare occurrence and fragmentary preservation (KUNZMANN *et al.*, 2006). *Pseudofrenelopsis capillata* Sucerquia, Bernardes-de-Oliveira et Mohr was adapted to seasonally dry and/or haline conditions and may have grown in a riparian environment along the borders of a large lake as a minor constituent of the surrounding vegetation (SUCERQUIA *et al.*, 2015). The branches of *Duartenia araripensis* Mohr, Schultka, Süss et Bernardes-de-Oliveira (fig. 4d) arranged in a way that optimizes the presence of small scale leaves and the morphology of the last order branches, that resemble shoot thorns, are features seen today regularly in drought resistant plants. *Duartenia* dense wood with small lumen and thick cell walls could be adaptation to dry conditions or interpreted as compression wood (MOHR *et al.*, 2012).

Extant Gnetales produce pollination drops and are visited and pollinated by insects such as nocturnal moths and dipterans in *Gnetum* L. (KATO *et al.*, 1995), dipterans, hemipterans and hymenopterans in *Welwitschia* Hook.f. (WETSCHNIG; DEPISCH, 1999), and dipterans, lepidopterans and hymenopterans in *Ephedra* L. (BOLINDER *et al.*, 2016). In Gnetales, insect pollination is an ancestral character and an evolutionary shift from insect to wind pollination occurred in *Ephedra* L. prior to diversification of the core clade (BOLINDER *et al.*, 2016). For these reasons, the presence of entomophilous Gnetales in the Crato biome would be expected. Maisey (1990) noted that Gnetales pollen and macrofossils suggested an open, arid environment. The sparse narrow leaves and pronounced primary roots of *Friedsellowia gracilifolia* Löwe, Mohr, Coiffard et Bernardes-de-Oliveira (fig. 6a) are probably adaptations for warm and seasonally dry climate and/or sunny environments close a lake shore, comparable with modern reeds (LÖWE *et al.*, 2013).

Other plants of gnetalean affinities found in the Crato Formation also present adaptive features for seasonally dry climate. *Cearania heterophylla* Kunzmann, Mohr et Bernardes-de-Oliveira (fig. 6b) exhibits heterophylly in different order branches in individual plants. Such uneven growth may have been caused by seasonal or periodical differences in climate (KUNZMANN *et al.*, 2009). *Cariria orbiculiconiformis* Kunzmann, Mohr, Wild et Bernardes-de-Oliveira (fig. 6c) with its herbaceous or small shrubby habit is an r-strategist that may have quickly occupied newly available space in unstable environments (KUNZMANN *et al.*, 2011). *Itajuba yansanae* Ricardi-Branco, Torres, Tavares, Carvalho, Tavares et Campos (fig. 6d) shows ephemeral leaves that may have been a defence of the plant to decrease the evaporative surface, with photosynthesis being the function of new branches. The gross morphology and anatomy suggest that it grew in locations with a definite hydric deficit, at least during some seasons of the year (RICARDI-BRANCO *et al.*, 2013).

Angiosperms constituted a minor element of the vegetation in the Crato biome. They probably occurred scattered among trees of Cheirolepidiaceae and shrubs of pteridospermalean and bennettitalean plants. Various ferns made up most of the vegetation cover. The small leaf size and the predominance of xeromorphic cheirolepidiaceous plants indicate that the Crato angiosperms grew under drier conditions, at least seasonally, probably in a partly open vegetation (MOHR; FRIIS, 2000). *Klitzschophyllites* Lejal-Nicol (fig. 8a) was a xerophyte monocot with reduced leaf surface, relative thickness of the lamina, spines and possibly trichomes. Its habitats were probably seasonally dry areas, perhaps in disturbed environments close to river channels in deltaic to brackish environments (MOHR *et al.*, 2006). The membranaceous to chartaceous leaf texture and the distichous phyllotaxis in *Hexagyne philippiana* Coiffard, Mohr et Bernardes-de-Oliveira (fig. 7c) may indicate an ecology of an understorey plant in a shaded environment (COIFFARD *et al.*, 2014).

Pluricarpellatia peltata Mohr, Bernardes-de-Oliveira et Taylor (fig. 7a), *Jaguariba wiersemana* Coiffard, Mohr et Bernardes-de-Oliveira (fig. 7b), *Spixiarum kipea* Coiffard, Mohr et Bernardes-de-Oliveira (fig. 8b), and *Iara iguassu* Fanton, Ricardi-Branco, Dilcher et Bernardes-de-Oliveira (fig. 9d) were aquatic angiosperms of the Crato lake. *Pluricarpellatia* and *Iara* were hydrophytic while *Spixiarum* probably had a helophytic ecology (COIFFARD *et al.*, 2013b; FANTON *et al.*, 2006a). Possibly, *Jaguariba* was limited to shallow water because the petioles were shorter than those of *Pluricarpellatia* which may have grown in somewhat deeper waters where the plant could reach the surface thanks to its aquatic stems (COIFFARD *et al.*, 2013a).

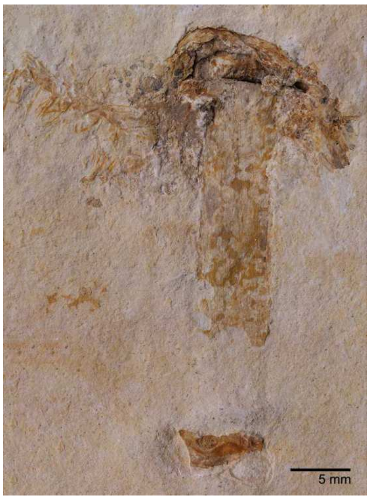


Figure 10 – Crato Formation fungus: *Gondwanagaricites magnificus* (HEADS *et al.*, 2017)

Aquatic macrophytes currently play an important role in structuring communities in aquatic environments. These plants participate in nutrient cycling and provide physical structure by increasing habitat complexity and heterogeneity, consequently affecting various organisms like invertebrates, fishes and waterbirds (THOMAZ; CUNHA, 2010). Probably paleomacrophytes carried out similar ecological activities in the Crato biome. *Endressinia brasiliana* Mohr et Bernardes-de-Oliveira (fig. 9b) and *Schenkeriphyllum glanduliferum* Mohr, Coiffard et Bernardes-de-Oliveira (fig. 9c) are sister taxa that belong to the Magnoliaceae. Both were probably cantharophilous (pollinated by beetles) and would have developed adaptations to dry environments early in history. *Schenkeriphyllum* shares most of the characters with *Endressinia* such as flowers with many parts, including tepals, staminodes and free carpels; organs that have ethereal oil cells; and small to medium-sized, sessil, sheathing coriaceous leaves (MOHR *et al.*, 2013).

Paleofungi

The oldest fossil fungi to date and the first fossil mushroom from Gondwana come from the Crato Formation. Mushrooms are Basidiomycetes of the order Agaricales that produce fleshy, gilled fruiting bodies (called basidiomes, fig. 10) that are rarely fossilized (HEADS *et al.*, 2017). Basidiomycota are decomposers and play an important role in current ecosystems by releasing carbon dioxide into the atmosphere and nitrogenous compounds into the soil (TAYLOR *et al.*, 2009). Besides that, they represent an important food source for fungivorous animals, especially insects. Schmidt *et al.* (2010) found indirect evidence for the presence of fungivorous beetles in the Cretaceous amber forests in France.

Paleofauna

Invertebrates

The Crato biome invertebrate paleofauna is dominated by arthropods, in particular insects, and represents a taphocenosis that may reflect an unusual terrestrial assemblage adapted to riparian settings in an arid or semi-arid hinterland, unique in taxonomic composition and preservation style (MENON; MARTILL, 2007).

The Crato Formation is very important for the centipede record, yielding three of the four known Mesozoic taxa (e.g., fig. 11a). Because of their delicate, unmineralized exoskeletons and their life in litter and soil, they have a very poor fossil record (WILSON, 2001; WILSON, 2003). All are globally distributed, with higher diversity in the tropics (MARTILL, 2007a). Centipedes are top predators in terrestrial detrital food webs. As generalists, they are potentially important in the community composition of the detrital macro- and mesofauna (HICKERSON *et al.*, 2005).

This formation has also the widest range of arachnid groups of the Mesozoic (e.g., fig. 11c). In general, arachnids are predators of other arthropods. As terrestrials, they probably were transported accidentally during floods before fossilization (DUNLOP *et al.*, 2007). Some Crato Dipluridae might have woven funnel-webs to catch jumping prey, such as Orthoptera – abundant in Crato limestone. The suggested paleoenvironment of the Early Cretaceous of north-eastern Brazil is arid or semi-arid, and both, diplurids and their orthopteran prey, are plentiful actually in semi-arid environments (SELDEN *et al.*, 2006).

Scorpions are predators and can feed on anything from annelids to small vertebrates. Rarely, they can be cannibals. Crato scorpions (e.g., fig. 11b) probably ambushed other arthropods, the availability of which could have varied seasonally. Crickets, ground beetles, termites and mayflies, abundant in the formation, could have been among their prey. Centipedes, other scorpions and small vertebrates, all on record, could have been both prey and predator (MENON, 2007).

Registers of mites include feather, leaf-inhabiting and Erythraeoid mites. The latter represent the first unequivocal record of Acari from the Crato biome (e.g., fig. 11l). Erythraeoidea are terrestrial and have a complex life history in which at least one instar is ectoparasitic, either on vertebrates or other arthropods such as Orthoptera and Homoptera that occur quite frequently in this formation (DUNLOP, 2007).

The presence of Solifugae (e.g., fig. 11g) supports the general interpretation of an arid environment, typical for the majority of living camel spiders (DUNLOP *et al.*, 2007). As nocturnal

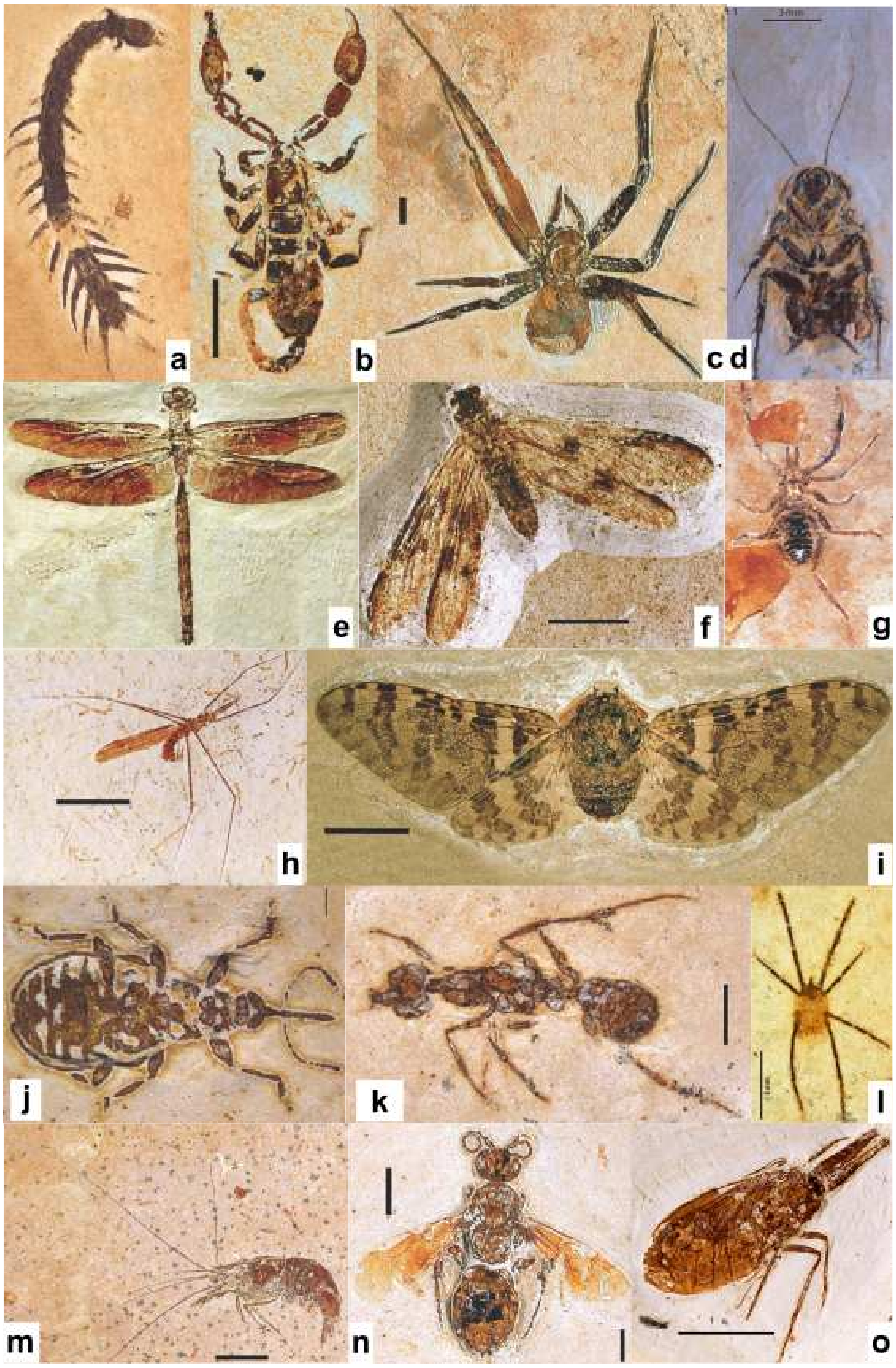


Figure 11 – Crato Formation invertebrates: a) Centipedes: *Cratoraricrus oberlii*; b) Scorpion: *Protoischnurus axelrodorum*. Bar: 10 mm; c) Spider: *Cretaraneus martinsnetoi*. Bar: 1 mm; d) Blattaria: *Perlucipecta santanensis*; e) Odonata: *Araripeliupanshania annesuseae*; f) Ephemeroptera: *Cretereisma antiqua*. Bar: 10 mm; g) Solifugae: *Cratosolpuga wunderlichi*; h) Chresmododea: *Chresmoda* sp. Bar: 20 mm; i) Cicadomorpha: *Baeocossus* cf. *fortunatus*. Bar: 1 mm; j) Coleoptera: Curculionoidea. Bar: 2 mm; k) Formicidae: *Cariridris bipetiolata*. Bar: 2 mm; l) Acari: *Pararainbowia martilli*; m) Crustacea: *Beurlenia araripensis*. Bar: 10 mm; n) Hymenoptera: ?Pompilidae. Bar: 2 mm; o) Hemiptera: *Cratonepa enigmatica*. Bar: 10 mm. (Source: a-c, e, f, h-k, m, n: Martill *et al.* (2007a); d: Lee (2016); g: Dunlop e Martill (2004); l: Dunlop *et al.* (2007); o: Jattiot *et al.* (2012))

(rarely daytime) generalist predators, their prey includes spiders, grasshoppers, termites, other insects, scorpions, mice, lizards, and birds (SELDEN; SHEAR, 1996).

Extant whipscorpions are nocturnal predators, typically inhabiting humid, tropical regions. Some of them have become adapted to arid conditions by obtaining moisture from food and by using their sensitive antenniform legs to detect moist substrates to avoid desiccation. Whipscorpions from the more arid Crato Formation suggest that the behavioural ability of this group had been developed by at least the Lower Cretaceous (DUNLOP, 1998).

The community interactions of whipspiders make them an important component of their ecosystems. The diet of Amblypygids includes diverse arthropods, especially Orthoptera and Blattodea, sphingid and noctuid moths, spiders, scorpions as well as anolis lizards, hummingbirds, and crayfish captured from streams. They fall prey to large lizards, small mammals, lycosid spiders and scorpions. Many amblypygid species prey on animals that are both competitors for prey and potential predators. Whipspiders can be parasitized by mites and chloropid flies. They participate in intraspecific interactions like cannibalism, territoriality, and sociality (CHAPIN; HEBETS, 2016). They are nocturnal and actually occur throughout the tropical and subtropical regions, with some species living in arid environments. Probably some plants in the Crato Formation were local moist settings like an oasis, functioning as a less xeric environment around the original lagoon, hosting part of the arachnid fauna (DUNLOP *et al.*, 2007).

Crato crustaceans (e.g., fig. 11m) appear in few horizons, probably as a consequence of increase in salinity levels and substrate chemistry. Ostracods are more abundant in the geological record, with conchostracans and decapods also present (SCHWEIGERT *et al.*, 2007). The existence of ostracod taxa with different levels of salinity tolerance confirms the hypothesis of lacustrine environments with variations in the salinity level (SOUZA *et al.*, 2017).

The paleoentomofauna is extremely well preserved because of the combination of early diagenetic, microbially induced mineralisation and later in situ weathering (BARLING *et al.*, 2015). The insects with most varied life strategies were found (e.g., aquatic larvae and terrestrial flying and non-flying adults); their taxonomic diversity is high with at least 18 different orders represented and over 350 described species to date (MENON; MARTILL, 2007; BARLING *et al.*, 2015).

Diplura and Zygentoma were present in the Crato biome. Extant japygids (Diplura) are soil-dwelling organisms. They feed on other soil arthropods such as insects, myriapods and mites. Silverfish (Zygentoma), on the other hand, are herbivorous (algae, fungi) (STANICZEK;

BECHLY, 2007). Only one japygoid was described from the locality (see Wilson e Martill (2001)). Sturm (1998) discovered the first two representatives of Zygentoma for the Mesozoic.

Current mayflies (Ephemeroptera) (e.g., fig. 11f) are important elements of the freshwater food chain and the nutrient base for many carnivorous fishes. They are generally halophobics, obligatorily bound to fresh water. The mass occurrence of larvae indicates a presence of streams in the immediate vicinity of the deposit (STANICZEK, 2007). Nymphs of Hexagenitidae (Ephemeroptera) have heads like current Siphlonuridae that are collectors and have debris as preferential diet. They occupy the sand banks at the bottom of lakes or mud, with shallow waters and currents. All their diet elements are documented in the sedimentary record of the Araripe Paleolake; it is consistent to admit that the habitat was the same for Hexagenitidae (MARTINS-NETO, 2006).

The worldwide Odonata are important insect predators. Their larvae live in running and stagnant water (swamps, phytotelmata), a few even in brackish water. The large number of odonate species of the Crato Formation (e.g., fig. 11e) is typical for (sub)tropical habitats with rather diverse aquatic biotopes. The presence of lacustrine biotopes is supported by the occurrence of libelluloid dragonflies and water striders (Hydrometridae) that are usually confined to standing water bodies or at least calmer waters (BECHLY, 2007e).

Earwigs (Dermaptera) live in diverse habitats in most vegetation types. Their diet ranges from strict carnivory over a mixed diet to fungivory and herbivory. The occurrence of only adults in the formation might be a consequence of seasonality (HAAS, 2007).

In Crato, fossil cockroaches (Blattaria) are common and abundant (e.g., fig. 11d), representing about 26 % of all arthropod specimens recovered (LEE, 2016). Their high percentage is typical for a warm climate, that was probably more arid than humid or with strong seasonality. Most Crato cockroach species are characteristic of a shrub vegetation. The cosmopolitan cockroaches are omnivores and live in arid as well as humid environments (BECHLY, 2007a). Vršanský *et al.* (2013) found extinct cockroaches (Blattulidae) in Lebanon amber from the Lower Cretaceous that were feeding on dinosaur faeces.

Termites (Isoptera) are distributed worldwide in all (sub)tropical regions where woody plants are available (BECHLY, 2007c). They indicate a tropical climate and are highly dependent on rainfall in the mating period. Any climatic changes (cold, long periods of drought) interfere with their life cycle. They feed mainly on cellulose but also consume fungi and organic detritus (MARTINS-NETO *et al.*, 2005). The presence of termites in the Crato Formation is indirect evidence for abundant woody plants and trees in the region. Perhaps the abundant gnetaleans have been their source of nutrition (BECHLY, 2007c).

Chresmoids (e.g., fig. 11h) probably represent the only autochthonous aquatic insects in the paleohabitat of the Crato lake (BECHLY, 2007b). Chresmodidae are an extinct family that were presumably carnivorous. Their members possess ultra-articulated tarsi, which may be associated with their capability of skating on the water-surface. Chresmodidae from Araripe probably lived in lacustrine paleoenvironments (NEL *et al.*, 2004).

Most species of the Orthopterida are phytophagous, but there are also predative, fungivorous, and omnivorous species (HEADS; MARTINS-NETO, 2007). Martins-Neto (2006) noted that some morphological characteristics in fossil taxa indicate preferences for five specific niches – from shore habitats to arboreal vegetation. Another phytophagous group, stick insects, were represented by a single species only (HEADS; MARTINS-NETO, 2007).

The Crato homopterans (e.g., fig. 11i) present a great variety of feeding strategies. The radiation of the angiosperms may be related to extinctions amongst phytophagous insect groups (e.g., Paleontinidae: giant cicadas) during the middle part of the Cretaceous (MENON *et al.*, 2005).

Hydrometridae (Heteroptera) are semi-aquatic water striders. They are confined to swampy or slowly moving fresh water environments. Here, they are well adapted to a life on the water surface (GOODWYN, 2002; PÊGAS *et al.*, 2017). Nepid-like bugs are aquatic predators that walk in the mud on the bottom of small ponds and/or hunt among aquatic plants. Near the Crato hypersaline lake were freshwater habitats with aquatic bugs and a diverse aquatic angiosperm vegetation that could have favoured the diversification of Nepidae or nepid-like bugs (e.g., fig. 11o) that were hunting in this newly developed biota (JATTIOT *et al.*, 2012).

The conspicuous size variation of the fossil neuropteran specimens indicates seasonal changes, which also caused seasonal mass mortality. Large-sized neuropterans could represent periods when aridity and high temperatures characterized the climate (MARTINS-NETO; RODRIGUES, 2009). Bechly e Makarkin (2016) pointed out that *Makarkinia* Martins-Neto, 1997 have a long-proboscis that allowed them to feed on plant fluids (secretions and nectar from reproductive organs) like modern butterflies. Nemopteridae might be autochthonous to the boundaries of the Araripe paleolake. They could have occupied the same niche of some kinds of grasshoppers and crickets, with a low vegetation and arid climate, corroborated by an expressive documentation of Elcanidae (Ensifera) (MARTINS-NETO, 2006). Raphidioptera and Megaloptera were probably allochthonous. Extant Raphidioptera are arboreal, found in cold temperate regions, requiring near-freezing temperatures for development and being linked to distinct vegetation, from tundra to more closed mountain forests (JEPSON *et al.*, 2011; MARTINS-NETO; RODRIGUES, 2009). Their abundance and diversity at the beginning of the Cretaceous suggest the presence of vegetated uplands, probably covered by gymnosperms. Megaloptera possess aquatic larvae that link the adults to habitats with sufficient water to support their development. The hypersaline lacustrine environment indicates that megalopterans must have been washed into the lake from the hinterlands because they would not have tolerated such high salinity (JEPSON; HEADS, 2016).

Scarabaeoidea and Curculionoidea (Coleoptera, e.g., fig. 11j) were present in the Crato Formation (WOLF-SCHWENNINGER; SCHAWALLER, 2007). Schigel (2012) indicates that fungivory is common in many Coleoptera families besides sapro- and xylophagy. Chin e Gill (1996) identified a Cretaceous food web with participation of dinosaurs, dung beetles and conifers. They discovered herbivore coprolites with conifer wood and backfilled dung beetle burrows that provide evidence for commensal interactions. Gandolfo *et al.* (2004) suggest that beetle entrapment pollination in water lily (Nymphaeaceae) flowers was present in the earliest part of the Late Cretaceous. The ecological interactions mentioned could also have occurred in the Araripe in the Early Cretaceous since (except for dinosaurs) fungi, beetles, and water lilies were present. Extant Curculionoidea such as Nemonychidae and Belinae are predominantly associated with conifers while Brentidae are almost exclusively associated with angiosperms and Curculionidae feed on virtually all plants (OBERPRIELER *et al.*, 2007). Santos *et al.* (2011) related the Crato Curculioninae to early flowering plants. Gratshev e Zherikhin (2003) predicted the presence of an aquatic gymnosperm plant in the Crato flora because of the type of tarsi similar to those occurring in some living aquatic weevils that they found in a nemonychid genus.

The fossil Hymenoptera assemblage (e.g., fig. 11 k, n) of the Crato Formation suggests a very heterogeneous habitat (OSTEN, 2007), with relatively humid biotopes consist of rather dense vegetation, as well as dry and relatively hot savannah and desert areas with sparse vegetation. The Apoidea abundance suggests a rich flower assemblage as food resource, and also a moderately dry and warm climate. The larval development of the 'Sphecidae' depends on the availability of a large and suitable contingent of insect food. Apidae need a sufficient amount of nectar and pollen available. The Vespoidea representatives indicate a dry, very warm, subtropical climate; they need other insects or spiders for larval development .

Recent scorpionflies (Mecoptera) are carnivorous, phytophagous and saprophytic. They are cosmopolitan, and prefer moist habitats while only a few species are adapted to arid environments. The dry conditions of the Crato habitat probably were unsuitable for Mecoptera. Their extreme rarity can be considered as a further corroboration of arid surroundings of the lake (BECHLY, 2007d). Extinct species of scorpionflies may have established important ecological relationships with early gymnosperms. These taxa had elongate tubular proboscides and fed on gymnosperm pollination drops. They were probably engaged in pollination mutualisms with gymnosperms during the mid-Mesozoic, long before the similar and independent coevolution of nectar-feeding flies, moths, and beetles on angiosperms (REN *et al.*, 2009).

Diptera have a worldwide distribution and can be found in all zoogeographic regions. Species of the Family Asilidae (Asilomorpha) are abundant in the Crato Formation. Extant members of this family prefer arid and semi-arid environments with open vegetation. Stratiomyomorpha presents species with highly specialized proboscides (WILLKOMMEN; GRIMALDI, 2007). Peñalver *et al.* (2015) reported the discovery of long-proboscid flies as pollinators of Cretaceous gymnosperms. As well as in the ecologically analogous scorpionflies (REN *et al.*, 2009), the diversity of proboscis lengths found on flies strongly suggests diverse plant hosts among gymnosperms.

Xavier *et al.* (2014) detected the presence of oviposition possibly carried out by Lepidoptera in a fossil member of Poales. This type of ecological interaction registered in the Crato biome is an example of an intimate relationship between insects and plants that lived and had their evolutionary expansion and adaptive irradiation during the Early Crataceous. In addition to Lepidoptera and Trichoptera (BECHLY, 2007f), the Crato biome has fossils of Mantodea (GRIMALDI, 2007), Fulgoromorpha (SZWEDO, 2007), and Coleorrhyncha (BECHLY; SZWEDO, 2007). The great diversity of insects gives clues about the complexity of the communities that inhabited the region. Recently, Santos Filho *et al.* (2017) reported several evidences of plant-insect interactions in plant remains for Crato Formation increase our knowledge about the the complexe relationships developed in these communities. They record the occurrence of insect galls, leaf margin feeding (herbivory), leaf mines, oviposition of insects and skeletonization. The interactions occurred in a wide range of groups of plants, i.e., ferns, gymnosperms and angiosperms. Herbivore insects that present chewing mouthparts, such as Orthoptera, Lepidoptera, Dermaptera, Isoptera, Coleoptera and Blattodea, probably caused the damages assigned.

Vertebrates

Dastilbe crandalli Jordan, 1910 (fig. 12a) is by far the most abundant fish in the Crato Formation; the mass mortalities recorded in fossils may be due to elevated salinity of the Crato lake (BRITO *et al.*, 1998). The idea that only adults were piscivorous comes from the fact that merely individuals with more than 150 mm length show small fishes in their guts (DAVIS; MARTILL, 1999). *Cladocyclus gardneri* Agassiz, 1841 (fig. 12b) is frequently considered a marine taxon and its tolerance to reduced salinities cannot be ruled out due to its presence in the Crato biome. The presence of marine fish such as *Vinctifer* Jordan, 1919 and *Cladocyclus* suggests at least an intermittent connection of the Crato lake with marine waters, perhaps through a number of restricted channels that prevented wider circulation (BRITO, 2007). Both *Vinctifer* and *Cladocyclus* appear to be surface- or near-surface-living fish. This might suggest that bottom waters were inhospitable.

There are a few articulated anuran remains (e.g., fig. 12c): representatives of the family Leptodactylidae and a possible Pipoidea (BÁEZ *et al.*, 2009). Leite (2013), studying an adult specimen of Leptodactylidae, considered that it most likely lived among small semi-aquatic plants in the marginal areas of a calm and shallow lake. It fed on small insects while serving as diet for small crocodilians. It is important to note that current amphibians do not support water with high salinity, so their presence indicates the occurrence of bodies of exclusively freshwater as part of habitats that composed the Crato biome.

The turtles (e.g., fig. 12g) found are pleurodires. *Araripemys barretoi* Price 1973 may have been a marine form perhaps tolerant of euryhaline conditions. They are rare here, perhaps because the elevated salinity of the Crato lake made it a difficult environment to inhabit (NAISH, 2007).

Lizards are extremely rare in the formation. The described forms are of terrestrial groups, suggesting that the occurrences are largely allochthonous (MARTILL, 2007b). Bonfim-Júnior e Rocha-Barbosa (2006) studied the paleoautecology of *Tijubina pontei* Bonfim-Jr. et Marques, 1997 (fig. 12d). They concluded that *T. pontei* is compatible with an omnivorous terrestrial animal, that could even perform bipedal locomotion. Based on dentition and ecomorphology, its behaviour could be a combination of active and "sit-and-wait" foraging. They also mentioned that *T. pontei* probably lived in a sandy habitat, with vegetation that could bear variations in salinity and high temperatures.

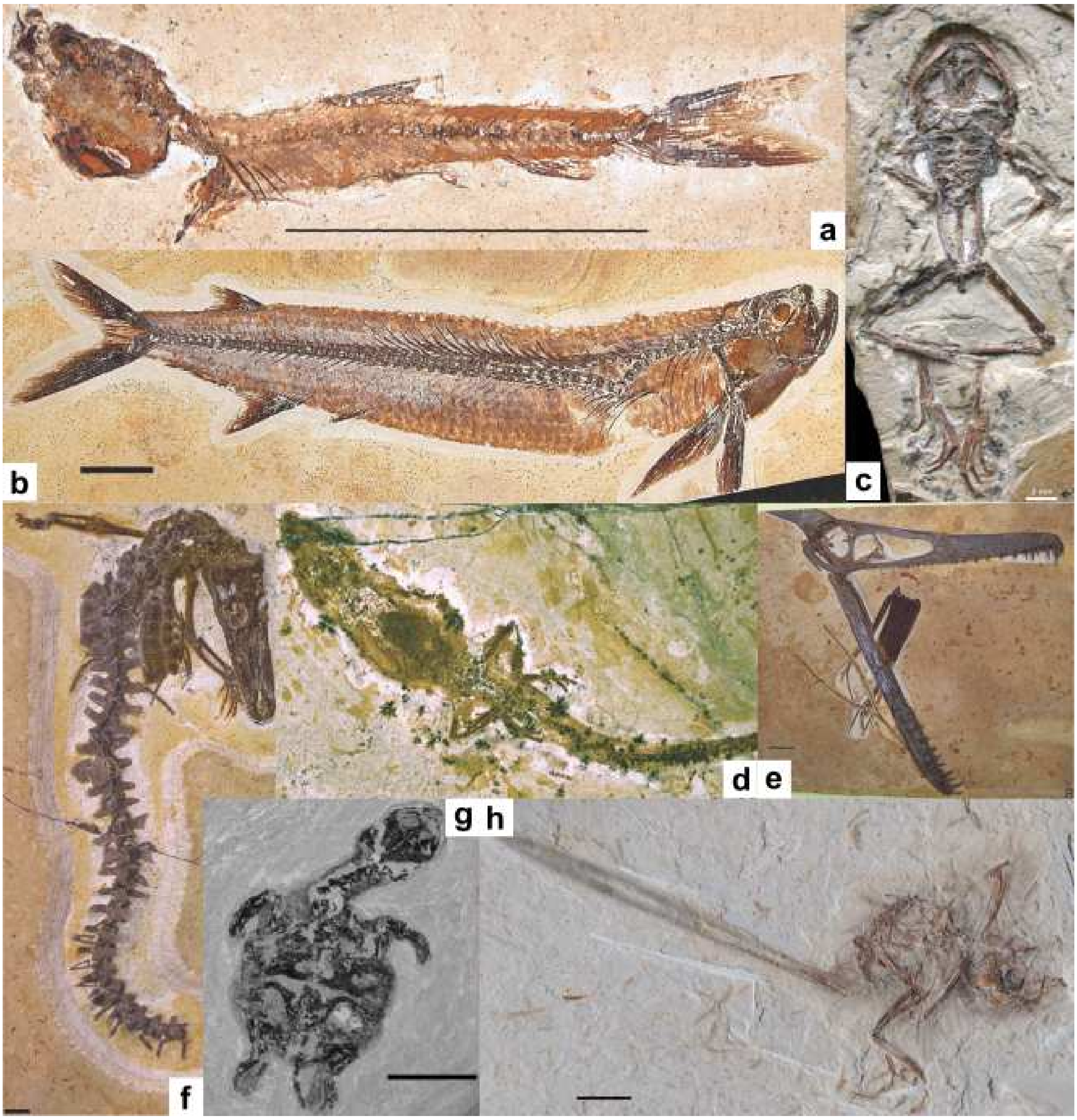


Figure 12 – Crato Formation vertebrates: a) and b) Fish: a) *Dastilbe crandalli*. Bar: 20 mm; b) *Cladocyclus gardneri*; c) Anura: *Arariphrynus placidoi*; d) Lizard: *Tijubina pontei*. Bar: 5 mm; e) Pterosaur: *Ludodactylus sibbicki*. Bar: 50 mm; f) Crocodilian: *Susisuchus anatoceps*. Bar: 10 mm; g) Turtle: Indeterminate juvenile. Bar: 10 mm; h) Bird: *Cratoavis cearensis*. Bar: 10 mm. (Sources: a, b, d-f: Martill *et al.* (2007a); c: Báez *et al.* (2009); g: Fielding *et al.* (2005); h: Carvalho *et al.* (2015))

Crocodilians are extremely rare. They most likely lived in the surrounding hinterland (FREY; SALISBURY, 2007). *Susisuchus* (fig. 12f) most likely lived upstream from the Crato lake in a freshwater river or stream, where it hunted in sheltered shallow waters (FREY; SALISBURY, 2007). The dentition denotes that *Araripesuchus* could be partially herbivorous. A single species found in the Crato biome shows that these terrestrial crocodilians probably avoided the vicinity of the lake, and made their living in the forests of the surrounding uplands (FREY; SALISBURY, 2007).

Pterosaurs (e.g. fig. 12e), intriguing flying reptiles, were present. Ornithocheirids had a well-developed soaring ability, which almost certainly allowed them to reach a large area of food, not necessarily being indigenous in the lake. The tapejarids and 'tupuxuarids' may have been (at least partially) indigenous to the Crato lake area. Their diet is uncertain, with the possibility of having been frugivorous or piscivorous. 'Tupuxuarids' may also have fed upon *Dastilbe*, perhaps by wading in the shallower margins of the lake (UNWIN; MARTILL, 2007).

Several feather types are present in the fossil record (NAISH *et al.*, 2007). They could belong to both, a bird or a non-avian theropod (SAYÃO *et al.*, 2011). Recently, Carvalho *et al.* (2015) documented the first almost complete and articulated skeleton of an Early Cretaceous bird from South America, found in the Crato Formation (fig. 12h). In general, the birds that lived here would have been responsible for predation marks detected on some insects (NAISH *et al.*, 2007).

3 CRETACEOUS CONIFERS

3.1 Systematic overview

The fossil record of woody plants is usually a mosaic of disconnected organs (leaves, stems, pollen, seed cones, pollen cones, seeds, etc.), which makes systematic classification difficult, especially for extinct taxa (FARJON, 2008; KUNZMANN, 2007a). Even for extant species, the systematic positioning is often problematic, despite the modern techniques of genetic and chemical analysis. Among the conifers is no different, there are the classification into eight (FARJON, 2008) and six (ECKENWALDER, 2009; CHRISTENHUSZ *et al.*, 2011) families. Farjon (2008) separates Phyllocladaceae from Podocarpaceae and Cephalotaxaceae from Taxaceae, which does not occur in Eckenwalder (2009) and Christenhusz *et al.* (2011). All the extant conifer families namely Pinaceae, Araucariaceae, Podocarpaceae, Sciadopityaceae, Cupressaceae and Taxaceae appeared in the Mesozoic. In addition to, in the fossil record of the Cretaceous there is the extinct Cheirolepidiaceae that has the last record in the Turonian (FARJON, 2008). The main characteristics and geographical distribution of the current families based on Eckenwalder (2009) and Farjon (2010), besides examples of Cretaceous fossil records are set out below.

Pinaceae Spreng. ex F. Rudolphi

Monoecious evergreen or deciduous, resinous trees or shrubs. Resin canals in wood, barks, leaves and seed cones. Leaves narrow, needlelike, single veined, spirally inserted on long or short shoots, solitary or in tufts. Pollen cones often grouped close together on long shoots, axillary, solitary or clustered from a single bud, catkin-like, deciduous. Microsporophylls numerous, spirally arranged, (sub)peltate, bisaccate or monosaccate or non-saccate pollen. Seed cones compound, small to very large, more or less woody, without any fleshy structures. Bracts free, well developed or rudimentary. Seed scales persistent or deciduous, woody; bearing two inverted seeds with one wing or wingless.

Eleven genera are distributed almost throughout the northern hemisphere, but also in Central America, Canary Islands, northeastern Africa and Sumatra.

Examples of genera found in the Cretaceous:

Abiocaulis: Belgium (ALVIN, 1960)
Amboystrobus: USA (GANDOLFO *et al.*, 2001)
Cedrus: Russia (BLOKHINA; AFONIN, 2007)
Keteleerioxylon: Russia (BLOKHINA *et al.*, 2006)

Midoriphyllum: Canada (STOCKEY; WIEBE, 2008)

Obirastrobus: Japan (OHSAWA *et al.*, 1992)

Picea: Canada (KLYMIUK; STOCKEY, 2012); Mongolia (HERRERA *et al.*, 2016)

Pinus: Belgium (ALVIN, 1960); USA (MILLER JR; MALINKY, 1986); Japan (STOCKEY; NISHIDA, 1986); UK (RYBERG *et al.*, 2012)

Pityostrobus: France (CREBER, 1960); Canada (STOCKEY, 1981; SMITH; STOCKEY, 2002); California (SMITH; STOCKEY, 2001; SMITH *et al.*, 2016); Russia (FALDERA *et al.*, 1998; RATZEL *et al.*, 2001); Mongolia (HERRERA *et al.*, 2016)

Prepinus: USA (GANDOLFO *et al.*, 2001)

Pseudoaraucaria: England (ALVIN, 1988)

Schizolepidopsis: Mongolia (LESLIE *et al.*, 2013)

Araucariaceae Henkel & W. Hochst.

Dioecious or monoecious evergreen, highly resinous trees. Resin canals in bark, leaves and seed cones. Leaves in helical arrangement or subopposite to opposite; lamina broad and flat or scale-, claw-, or needlelike. Pollen cones catkin-like, axillary to leaves, solitary or in small clusters, sometimes large. Microsporophylls numerous, helically inserted, crowded, with imbricate or tessellate heads, each with 4–20 oblong pollen sacs containing non-saccate pollen. Seed cones large, globose, fairly woody or leathery, mostly disintegrating leaving the tachis on the tree. Seed cone scales predominantly consisting of the bract, but with a fused seed scale bearing a single inverted seed.

Three genera distributed in southern South America and in the western Pacific from Southeast Asia to New Zealand.

Examples of genera found in the Cretaceous:

Agathis: Australia (CANTRILL, 1992)

Agathoxylon: France (PERRICHOT, 2004); Hungary (BARALE *et al.*, 2002)

Alkastrobus: Argentina (DEL FUEYO; ARCHANGELSKY, 2005)

Araucaria: Argentina (CANTRILL; FALCON-LANG, 2001); Australia (CANTRILL, 1992) Brazil (KUNZMANN *et al.*, 2004); Germany (KUNZMANN, 2007b); Mongolia (KRASSILOV, 1982); New Zealand (POLE; PHILIPPE, 2010)

Brachyphyllum: Argentina (ARCHANGELSKY; GAMERRO, 1967, *B. irregulare*); Brazil (KUNZMANN *et al.*, 2004, *B. obesum*)

Dammarites: Spain (BARALE, 1992)

Nothopehuen: Argentina (DEL FUEYO, 1991)
Wairarapaia: New Zealand (CANTRILL; RAINE, 2006)

Cupressaceae Gray (including the former Taxodiaceae)

Aromatic evergreen or deciduous, monoecious or dioecious shrubs or trees, ranging from diminutive prostate shrubs to trees exceeding 100 m. Leaves on (pen)ultimate branchlets linear, claw-, flattened needle- or sacalelike, spirally arranged, ternate or decussate (rarely quadrate) in mature plants. Pollen cones small, terminal, rarely axillary, solitary or sometimes clustered in groups of 2–7. Microsporophylls spirally arranged, ternate or decussate in congruence with leaf phyllotaxis on the cone-bearing shoot, small and thin, (sub)peltate with spherical pollen grains without air bladders. Seed cones terminal, simples or semi compound, globose, ovoid or conical, deciduous or persistent, more or less woody and lacking any fleshy structures. Seed cone scales consisting of transformed bracts, true seed scales absent or sometimes rudimentary. Seeds 1–many axillary to each cone scale, with or without wings.

Thirty genera in both the northern and southern hemispheres, but absent in Africa and South America except for record in central and southern Chile and adjacent Argentina.

Examples of genera found in the Cretaceous:

Athrotaxites: Argentina (CANTRILL; FALCON-LANG, 2001)
Cunninghamites: restricted to the Northern Hemisphere (see a revision in Bosma *et al.* (2012))
Elatides: Belgium (HARRIS, 1953); Mongolia (SHI *et al.*, 2014)
Hubbardiastrobus: Canada (ATKINSON *et al.*, 2014a)
Hughmillerites: Canada (ATKINSON *et al.*, 2014b)
Mikasastrobus: Japan (SAIKI; KIMURA, 1993)
Nephostrobus: EUA (LAPASHA; MILLER JR, 1981)
Oguraxylon: Japan (NISHIDA, 1974)
Rhombostrobus: EUA (LAPASHA; MILLER JR, 1981)
Sphenolepis: Hungary (BARALE *et al.*, 2002)
Taxodium: Canada (AULENBACK; LEPAGE, 1998)
Thuja: Alaska (LEPAGE, 2003)
Widdringtonia: EUA (MCIVER, 2001)

Podocarpaceae Endl.

Dioecious or sometimes monoecious, evergreen, slightly resinous trees or (dwarf) shrubs (one species parasitic on another member of the family). Leaves helically arranged rarely decussate (*Microcachrys*), appressed and imbricate to spreading and remote, shapes highly variable, ranging from small, appressed scale leaves, via thin acicular leaves, to dorsiventrally flattened, linear-lanceolate to broadly lanceolate, large leaves (up to $34 \times 9.5\,\mathrm{cm}^2$). Pollen cones mostly simple, axillary. or terminal, solitary or clustered. Microsporophylls spirally arranged; pollen bi-, tri- or non-saccate. Seed cones axillary or terminal, solitary, mostly much reduced and often swelling to form a succulent receptacle; fertile bracts 1–many. Seed scales single in the axil of a bract, bearing a single initially erect but at pollination more or less inverted ovule. Seeds of most species surrounded by a coriaceous or succulent epimatium; single or sometimes two.

Eighteen genera are distributed throughout the southern hemisphere and north ranging from about 25°N in Mexico and West Indies to about 15°N in East Africa, and 35°N in Japan.

Examples of genera found in the Cretaceous:

Bellingshausium: Argentina (CANTRILL; FALCON-LANG, 2001)
Eromangia: New Zealand (POLE; PHILIPPE, 2010)
Kakahuia: New Zealand (POLE; PHILIPPE, 2010)
Morenostrobus: Argentina (DEL FUEYO *et al.*, 2009)
Podocarpus: Russia (KRASSILOV, 1974)
Podozamites: Australia (CANTRILL, 1991)
Squamastrobus: Argentina (ARCHANGELSKY; DEL FUEYO, 1989)
Trisacocladus: Argentina (GAMERRO, 1965)

Taxaceae Gray

Dioecious or rarely monoecious evergreen shrubs or trees. Slightly resinous with resin in leaves and arils. Leaves helically or decussately inserted, usually pectinately arranged, linear to lanceolate with a single midrib. Pollen cones small, axillary to foliage leaves and solitary or aggregated in umbellate clusters of racemes. Microsporophylls helically decussately arranged; pollen grains spherical, without air bladders. Seed bearing structures consisting of axillary dwarf shoots with decussate scales, with terminal, erect ovules. Seeds usually single, surrounded by a fleshy or succulent aril red, purple, or yellow when ripe.

Currently, six genera spread throughout much of Eurasia and North America and in New Caledonia, with a concentration of genera in eastern Asia.

Examples of genera found in the Cretaceous:

Protocedroxylon: Russia (AFONIN; PHILIPPE, 2014)
Taxaceoxylon: Russia (AFONIN; PHILIPPE, 2014)
Taxus: China (XU *et al.*, 2015)
Vesquia: Belgian (ALVIN, 1960)
Xenoxylon: Russia (AFONIN; PHILIPPE, 2014)

Sciadopityaceae Luerss.

Evergreen, monoecious trees. Foliage consisting of linear cladodes (‘needles’) in pseudo-whorls on shortened terminal sections of long shoots. True leaves much reduced, scale-like. Pollen cones small in terminal or sublateral clusters. Microsporophylls numerous, helically attached in a long, slender stalk; pollen grains spherical, without air bladders. Seed cones terminal or sublateral, ovoid to cylindrical, often exuding resin. Bract-scale complexes helically arranged, consisting of a partly fused bract and exceeding seed scale. Seeds basal to seed scales, inverted with two wings.

One genus, *Sciadopitys*, with a single species occurs in southern Japan today.

Example of genus found in the Cretaceous:

Sciadopityostrobus: Japan (SAIKI, 1992)

Cheirolepidiaceae Takhtajan ex Doludenko, 1978

The extinct conifer Family Cheirolepidiaceae, emerged during the Triassic, formed a significant component in the early Jurassic floras and presented an extraordinary radiation in the Early Cretaceous (AXSMITH; JACOBS, 2005). Cheirolepidiaceous conifers exhibit jointed stems, thick internode cuticles, sheathing leaf bases, and reduced free leaf tips. The possession of the distinctive and unusual pollen grain of the genus *Classopollis* Pflug, 1953 is the single most reliable character on which to base assignment to this family (WATSON, 1988). Some species were trees many meters tall, e.g., *Pseudofrenelopsis parceramosa* (ALVIN, 1983) and *Frenelopsis ramosissima* (AXSMITH; JACOBS, 2005), whereas others have been interpreted as small herbs or shrubs (TAYLOR *et al.*, 2009). The Cheirolepidiaceae has the maximum diversity and abundance during Jurassic and Cretaceous occurring in southern Laurasia and northern Gondwana, occupying a variety of ecological niches (KUNZMANN *et al.*, 2004; AXSMITH; JACOBS, 2005).

Examples of genera found in the Cretaceous:

Androvettia: USA (HUEBER; WATSON, 1988)

Classostrobus: EUA(AXSMITH *et al.*, 2004)

Glenrosa: USA (WATSON; FISHER, 1984)

Pseudofrenelopsis: EUA (AXSMITH *et al.*, 2004); Brazil (SUCERQUIA *et al.*, 2015); Hungary (BARALE *et al.*, 2002); UK (ALVIN *et al.*, 1981)

Otwayia: New Zealand (POLE; PHILIPPE, 2010)

Tomaxellia: Argentina (ARCHANGELSKY; GAMERRO, 1967); Brazil (KUNZMANN *et al.*, 2004)

Watsoniocladus: USA (SRINIVASAN, 1995)

3.2 The South American record

Leslie *et al.* (2012) detected a broad geographic signature imprinted in the evolutionary history of conifers. Their analyses indicate that Northern Hemisphere lineages have a greater proportion of very recent divergence times (i.e., within the past 5 My) and fewer deep divergences than Southern Hemisphere clades. This divergence would be a reflection of complex patterns of migration and range shifts during climatic cycles over the later Neogene in northern clades, leading to elevated rates of speciation and extinction. While in the Southern Hemisphere the scattered persistence of mild, wetter habitats may have favored the survival of older lineages.

Considering extant conifers, South America has a low diversity with only 34 species distributed in nine genera that belong to the three families, i.e., Araucariaceae, Crupessaceae and Podocarpaceae. The Araucariaceae (2 species) and Cupressaceae (3 species) are endemic.

Sucerquia (2006) executed a report of the occurrences of macroflora components described for the Lower Cretaceous of South America, with their respective localities. Their data indicated the presence of conifers in Argentina, Brazil, Chile, Colombia, Ecuador and Peru, representing the families Araucariaceae, Cheirolepidiaceae, Cupressaceae, Podocarpaceae and Pinaceae. Araucariaceae were recorded in the six countries mentioned above, being more abundant in Argentina. The most common genus is *Brachyphyllum* found in all six countries. *B. peruvianum*, however, occurs only in Peru and *B. winklerprinsi* appears only in Colombia. Archangelsky e Del Fueyo (2010) considered *Nothopehuen brevis* and *Alkastrobus peltatus* endemic in the Patagonian Province.

Cheirolepidiaceae were recorded only in Argentina and Brazil. *Tomaxellia* is present in both countries while *Pseudofrenelopsis* occurs only in Brazil and *Tarphyderma* only in

Argentina. Cupressaceae appear in Argentina, Colombia and Peru. The genus *Thuites* was detected in Colombia and Peru while *Athrotaxis* is present only in Argentina. Podocarpaceae was found in Argentina, Brazil, Colombia and Peru. *Podozamites* is the most common genus occurring in Brazil (Romualdo Formation), Colombia and Ecuador. Argentina is the country with the greatest diversity of genera: *Apterocladus*, *Morenostrobus*, *Podocarpus*, *Squamastrobus* and *Trisacocladus*. Pinaceae are restricted to Colombia, with the genera *Pinostrobus* and *Pityostrobus* (SUCERQUIA, 2006).

4 MATERIAL AND METHODS

4.1 Study materials

The studied conifer fossils come from the Crato Formation, in the Santana Group of the Araripe Basin in Northeastern Brazil. This unit overlaps the Barbalha Formation, which is the basis of the Santana Group (table 1) and is composed mainly of yellowish to light greyish brown bedded limestone (Plattenkalk). The outcrops of the Crato Formation can be seen near the municipality of Santana do Cariri, Ceará (fig. 13a). In this region, there are well-known mines for commercial exploration of laminated limestones. The extraction of the rock is made in the form of slabs of limestone for the production of commercial tiles called *Pedra Cariri* (fig. 13b), used for floor and wall coverings, benches, tables and mineral craftworks (SOUSA; VIDAL, 2005). As a result of the action of the workers a great variety of fossil plants and animals arise during the extraction of limestone deposits.

Since the removal of fossils is not scientifically controlled, many sampling and taphonomic data are missing such as, for example, the exact location of where the material was removed, and if occurred and what other fossils occurred at the same level or horizon. Especially in the case of the cones deposited in the scientific collections, the sediment around the fossil was cut, leaving only a small rocky matrix around the fossil, and consequently little taphonomic information available. The conifer remains, as well as the other components of the flora, occur in both the yellow and gray sediments. They are preserved in various ways as light to dark brown coalifications, reddish brown iron oxide compressions, charcoals and impressions, the latter sometimes associated with traces of organic matter coalified. The plant preservation is explained in detail in section 5.2.

Specimens of conifer cones housed in the following scientific paleontological collections were studied: Universidade Federal do Ceará – UFC (acronym LP/UFC CRT); Fundação Paleontológica Phoenix (acronym FPH); Departamento Nacional de Produção Mineral de Crato (acronym DNPM); Universidade de São Paulo – USP (acronym GP3E), and Universidade Federal do Rio de Janeiro – UFRJ (acronym Pb). Their respective collection numbers can be visualized on the plates at the end of this dissertation. In addition, the information about the type of preservation of each cone was placed on the plates where [C] means charcoal, [K] means coalification, [O] means iron oxide, and [I] means impression. The black bar indicates 2 cm.

Figure 13 – Outcrop of the Crato Formation in Santana do Cariri, Ceará. a) Detail of laminated limestones b) Open cast mine for commercial extraction of *Pedra Cariri*.

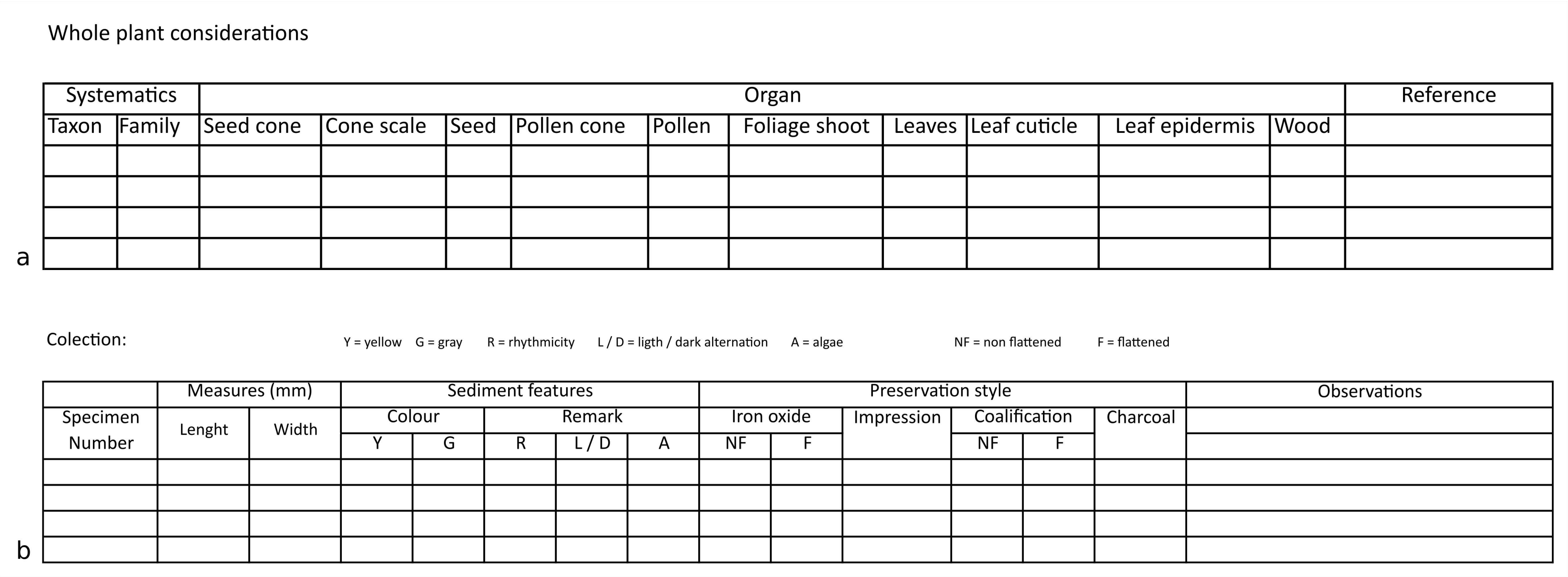
4.2 Methods

The information gathered for whole-plant aspects and pollen records of the conifers was taken from the current literature. For this, a systematic search for scientific texts was carried out during the development of this dissertation, mainly using the Portal de Periódicos CAPES (<www.periodicos.capes.gov.br>). The social network ReserachGate (<www.researchgate.net>) also provided important papers.

Technical visits were made in April 2017 for fossil cone observations in the USP and UFRJ paleontological collections. Regular technical visits to the DNPM-Crato and to UFC were made to study the cones of these collections. Fossils borrowed from the Fundação Paleontológica Phoenix were kept in UFC Paleontology Laboratory. The data on cones were obtained by studying the fossils externally in their respective laboratories.

Information from literature and personal observations was organized in spreadsheets as shown in fig. 14. Cone lengths and maximum cone widths were measured for both seed and pollen cones with a digital caliper. Boxplots were generated using the statistical software R 3.4.4 (<https://www.r-project.org/>) with data from this study and supplementarty material of Leslie (2011a) in <http://rspb.royalsocietypublishing.org/highwire/filestream/45984/field_highwire_adjunct_files/0/rspb20102648supp1.pdf>. Measurements of incomplete transverse sections and fragments were not considered in statistics. When the cones presented more than one type of fossilization, the predominant one was taken into consideration for the calculus based on the tables.

A taxonomic classification being beyond the limits of this dissertation, a documentation of the cone morphological diversity was attempted. To a set of cones or a single cone



Whole plant considerations

Systematics		Organ										Reference
Taxon	Family	Seed cone	Cone scale	Seed	Pollen cone	Pollen	Foliage shoot	Leaves	Leaf cuticle	Leaf epidermis	Wood	

a

Colection:

Y = yellow G = gray R = rhythmicity L / D = ligth / dark alternation A = algae NF = non flattened F = flattened

	Measures (mm)		Sediment features					Preservation style						Observations
Specimen Number	Lenght	Width	Colour		Remark			Iron oxide		Impression	Coalification		Charcoal	
			Y	G	R	L / D	A	NF	F		NF	F		

b

Figure 14 – Observed characteristics for whole-plants (a) and cones (b)

Figure 15 – SEM analyses a) Stubs b) Sputtering c) Quanta FEG 450

with morphological characteristics sufficiently similar but different from the others, the term “morphotype” was applied. They were assorted by the observation of their external morphology. The characteristics of each morphotype are listed in table 3. The definitions proposed by Beentje (2010) helped to characterize the cones.

Cone photos were taken with Nikon Coolpix P510 camera and the plates were composed using the programs IrfanView 4.44, Inkscape 0.92.2 and GIMP 2.8.22.

SEM analyses of vegetative shoots were also made to investigate the presence of charcoal in the Crato Formation. Small fragments of vegetative shoots obtained from specimens of the UFC collection were directly mounted on stubs, sputtered with gold and analyzed in a Quanta FEG 450 Scanning Electron Microscope in the *Central Analítica* da Universidade Federal do Ceará (fig. 15).

5 RESULTS AND DISCUSSION

The conifer macrofossils registered in the Crato Formation are hitherto distributed into two families only, i.e. Araucariaceae and Cheirolepidiaceae. There are, however, also specimens of unknown affinity. On the other hand, the pollen record increases the number of families, adding grains related to Cupressaceae, Pinaceae, and Podocarpaceae (table 2). This distribution goes in favour of the known fossil record of conifers in South America where these five families have also been found (SUCERQUIA, 2006).

In this study, a total of 140 specimens of fossil cones were found in the paleontological collections examined. The cones recovered generally reveal different aspects: lengthwise (whole), lengthwise (cut), transverse, three-dimensional, besides fragments. The specimens fossilized in longitudinal aspect can be seen from inside (fig. 16a) as well as from outside (fig. 16b). The adaxial (visible seeds) and abaxial view of the cone scales can bee seen in the specimens in transversal aspect (fig. 16c, d). The three-dimensional cones are completely detached from the sediment (fig. 16e, f). In addition, diverse fragments of cones were also recorded (fig. 16e, f). The cones were grouped into 26 morphotypes, and their main features are listed in the table 3.

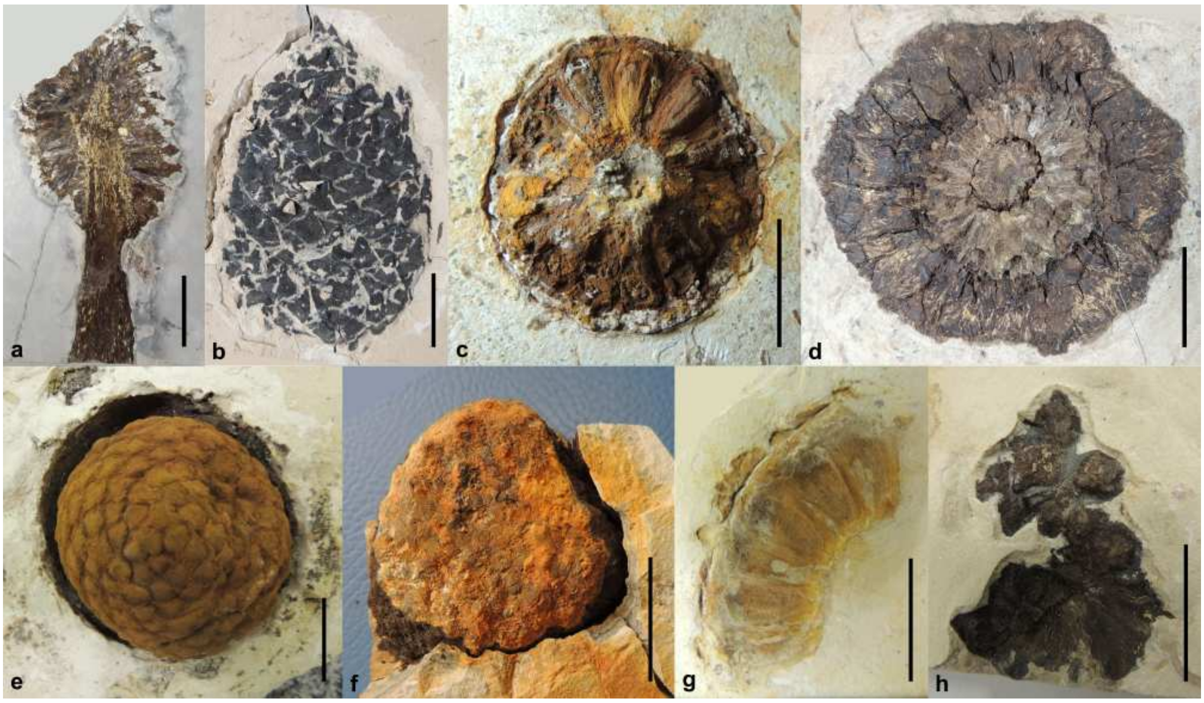


Figure 16 – Conifer cone aspects. Lengthwise: a (LPC/UFC CRT 2315), b (GP3E 9517). Transverse: c (FPH-93-B), d (GP3E 9448). Three-dimensional: e (348 Pb), f (LPC/UFC CRT 2753). Fragments: g (1129 Pb), h (2202 Pb).

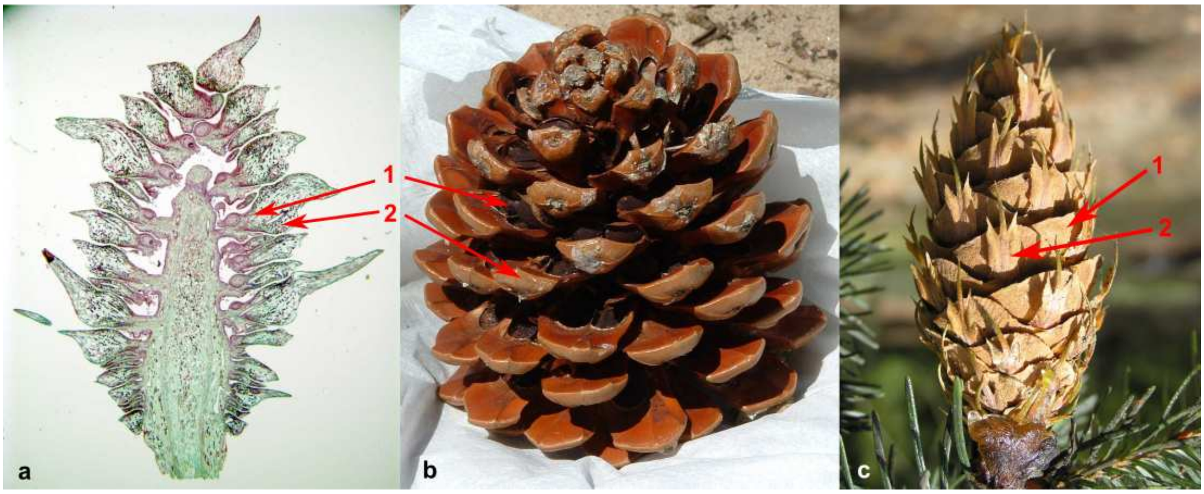


Figure 17 – Seed cones. a) *Pinus* sp. light micrograph of a longitudinal section (Photo: Curtis Clark, from Wikimedia Commons), b) *Pinus pinea* (Photo: Nuno Tavares, from Wikimedia Commons), c) *Pseudotsuga menziesii* (Photo: Beentree, from Wikimedia Commons). Legend: 1 = ovuliferous scale, 2 = pherophyll.

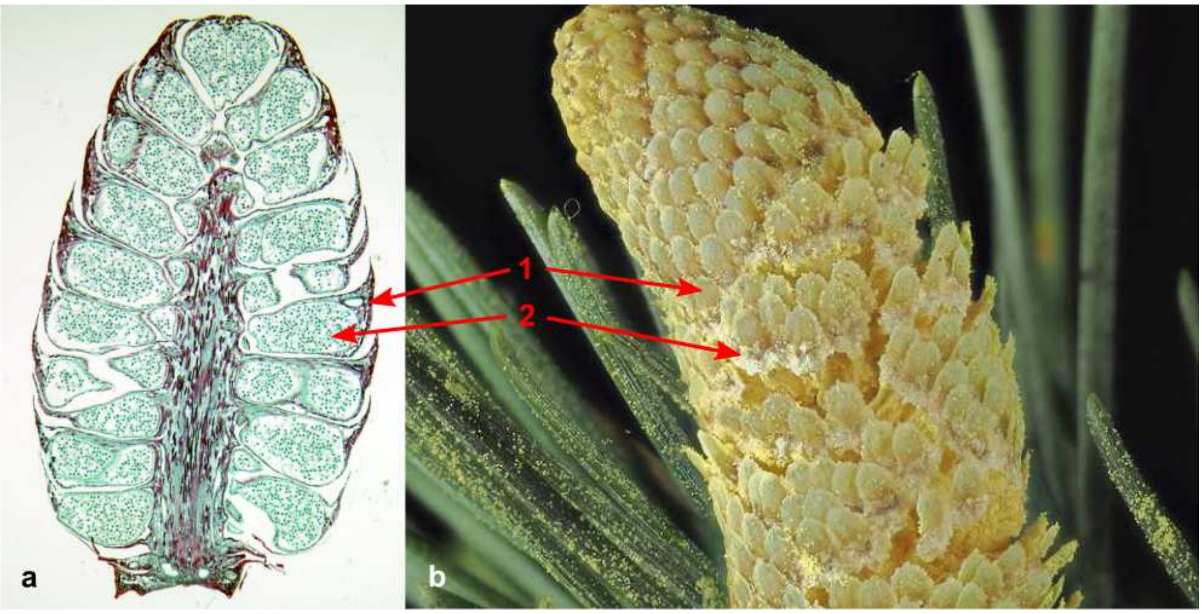


Figure 18 – Pollen cones. a) *Pinus* sp. light micrograph of a longitudinal section (Photo: Curtis Clark, from Wikimedia Commons), b) *Cedrus atlantica* (Photo: John Rusk, from Flickr). Legend: 1 = microsporophylls with microsporangia 2 = pollen grains.

The simple occurrence of a good diversity of cone morphotypes seems to indicate the presence of a greater number of conifer species and/or families in the Araripe Basin.

5.1 Conifer morphotypes

The word conifer means cone-bearer; this character named the group. Cones are reproductive organs were seeds and pollen grains are produced. Seed cones are reproductive

Table 2 – Coniferales of the Crato Formation [*] (∗ M: macrofossil , P: pollen)

Family	∗	Taxon	References
Araucariaceae	M	*Araucaria* sp.	Kunzmann *et al.* (2004)
	M	*Araucariacites* sp.	Batten (2007); Heimhofer e Hochuli (2010)
	P	*Araucariacites australis*	Lima (1979); Arai *et al.* (2001); Coimbra *et al.* (2002); Neumann *et al.* (2003); Portela *et al.* (2014)
	P	*Araucariacites guianensis*	Lima (1979)
	P	*Araucariacites limbatus*	Lima (1979)
	M	*Araucariostrobus* sp.	Kunzmann *et al.* (2004)
	M	*Brachyphyllum obesum*	Kunzmann *et al.* (2004); Batista *et al.* (2017)
	P	*Callialasporites* sp.	Batten (2007)
	P	*Callialasporites dampieri*	Lima (1979); Arai *et al.* (2001); Coimbra *et al.* (2002); Neumann *et al.* (2003); Portela *et al.* (2014)
	P	*Callialasporites lucidus*	Lima (1979); Portela *et al.* (2014)
	P	*Callialasporites segmentatus*	Lima (1979); Portela *et al.* (2014)
	P	*Callialasporites trilobatus*	Lima (1979); Arai *et al.* (2001); Coimbra *et al.* (2002); Neumann *et al.* (2003)
Cheirolepidaceae	P	*Circulina meyeliana*	Lima (1979); Portela *et al.* (2014)
	P	*Circulina minima*	Lima (1979)
	P	*Circulina parva*	Lima (1979)
	P	*Classopollis* sp.	Batten (2007); Heimhofer e Hochuli (2010)
	P	*Classopollis* sp. (cf. *C. intrareticulatus*)	Lima (1979)
	P	*Classopollis alexi*	Lima (1979)
	P	*Classopollis brasiliensis*	Lima (1979)
	P	*Classopollis classoides*	Arai *et al.* (2001); Coimbra *et al.* (2002), Neumann *et al.* (2003); Portela *et al.* (2014)
	P	*Classopollis torosus*	Lima (1979)
	P	*Cycadopites* sp.4 Antonioli, 1998	Portela *et al.* (2014)
	P	*Dicheiropollis* sp.A	Arai *et al.* (2001)
	P	*Dicheiropollis etruscus*	Arai *et al.* (2001)
	M	*Pseudofrenelopsis* sp.	Batista *et al.* (2017)
	M	*Pseudofrenelopsis capillata*	Sucerquia *et al.* (2015)
	M	*Tomaxellia biforme*	Kunzmann *et al.* (2006); Mohr *et al.* (2012)
Cupressaceae	P	*Exesipollenites tumulus*	Lima (1979); Coimbra *et al.* (2002)
	P	*Exesipollenites scabratus*	Lima (1979)
	P	*Inaperturopollenites simples*	Portela *et al.* (2014)
	P	*Inaperturopollenites turbatus*	Portela *et al.* (2014)
	P	*Properinopollenites* sp.	Lima (1979)
	P	*Spheripollenites scabratus*	Neumann *et al.* (2003)
Pinaceae	P	*Alisporites* sp.	Lima (1979)
	P	*Cerebropollenites carlylensis*	Lima (1979)
	P	*Laricoidites magnus*	Lima (1979)
	P	*Protopinus* sp.	Lima (1979)
Podocarpaceae	P	*Podocarpidites* sp.	Arai *et al.* (2001)
	P	*Podocarpites* sp. (cf. *P. epistratus*)	Lima (1979)
Unknown affinity	M	*Duartenia araripensis*	Mohr *et al.* (2012)
	M	*Lindleycladus* sp.	Kunzmann *et al.* (2004)
	P	*Protoconiferus* sp.	Lima (1979)
	P	*Uesuguipollenites callosus*	Portela *et al.* (2014)

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[*] The species of the genus *Zonalapollenites* (*Z. dampieri, Z. lucidus, Z. segmentatus*, and *Z. trilobatus*) reported by Lima (1979) are treated as synonyms of *Callialasporites* according to Raine *et al.* (2011) and therefore do not appear with their original name in the table

shoots consisting of a central axis clothed with infertile scales (pherophylls), compactly arranged spirally, each bearing ovuliferous scales in their axils (fig. 17). In some species the pherophyll can be morphologically very distinct from the ovuliferous scale (e.g., *Pseudotsuga menziesii* (Mirb.) Franco; fig. 17c). The actual seed cones are frequently woody (Pinaceae, Araucariaceae, Sciadopityaceae and most Cupressaceae) but can also be fleshy (Podocarpaceae, Taxaceae and *Juniperus*, a Cupressaceae genus) (ECKENWALDER, 2009). Conifer seed cones perform a variety of functional roles as summarized by Leslie (2011b): (i) they serve as sites for pollen capture and their morphology often facilitates the movement of pollen grains towards ovules; (ii) they enclose and protect developing seeds from predators; (iii) their morphology must in some way facilitate the dispersal of mature seeds, through either abiotic processes or biotic agents. Similar functions can be also attributed to the seed cones that existed in the Crato biome.

The conifers are mostly anemophilic (wind pollinated), with many species producing pollination drops as, e.g., *Pinus mugo* Turra. Pollination in *P. mugo* occurs when the wind-blown saccate pollen arrives at the cone; on ovuliferous scales, it slides towards the central axis and glues to the extended arms of the micropyle immediately above (fig. 19a); later, the ovule secretes a pollination drop that dissolves the sticky mass. The liberated grain then swims upward, thanks to the gas-filled balloons and thus may arrive at the micropyle s.str. (STÜTZEL; RÖWEKAMP, 1999). However, pollination drops are also exploited as a source of insect nutrition. These drops together with the morphology of the ovuliferous scales might in some cases indicate the occurrence of entomophily (insect-mediated pollination). This insect-plant interaction may have existed in Cheirolepidiaceae in the Cretaceous. An example might be *Alvinia bohemica* Kvaček, a seed cone related to *Frenelopsis alata* (K. Feistmantel) E. Knobloch (LABANDEIRA, 2010; LABANDEIRA *et al.*, 2007). This seed cone exhibits distinctive and unique specializations of the ovuliferous scales (for details see Kvaček (2000)) that strongly suggest insect pollination. Labandeira *et al.* (2007) proposed that long-proboscid mecopteroids and dipterans may have acted as pollinators of *A. bohemica*. Similar insect-plant interactions may have occurred in the Crato biome since Cheirolepidiaceae, mecopteroids (fig. 19b) and dipterans (fig. 19c) were also recorded in this formation.

Pollen cones have a central axis with several microsporophylls (fig. 18), each with one or multiple microsporangia where pollen is housed before release (FARJON, 2010). Schulz *et al.* (2014) studied the variability in current pollen cone properties and observed that: (i) their diversity ranges from simple to compound cones; (ii) their spatial distribution on the tree is

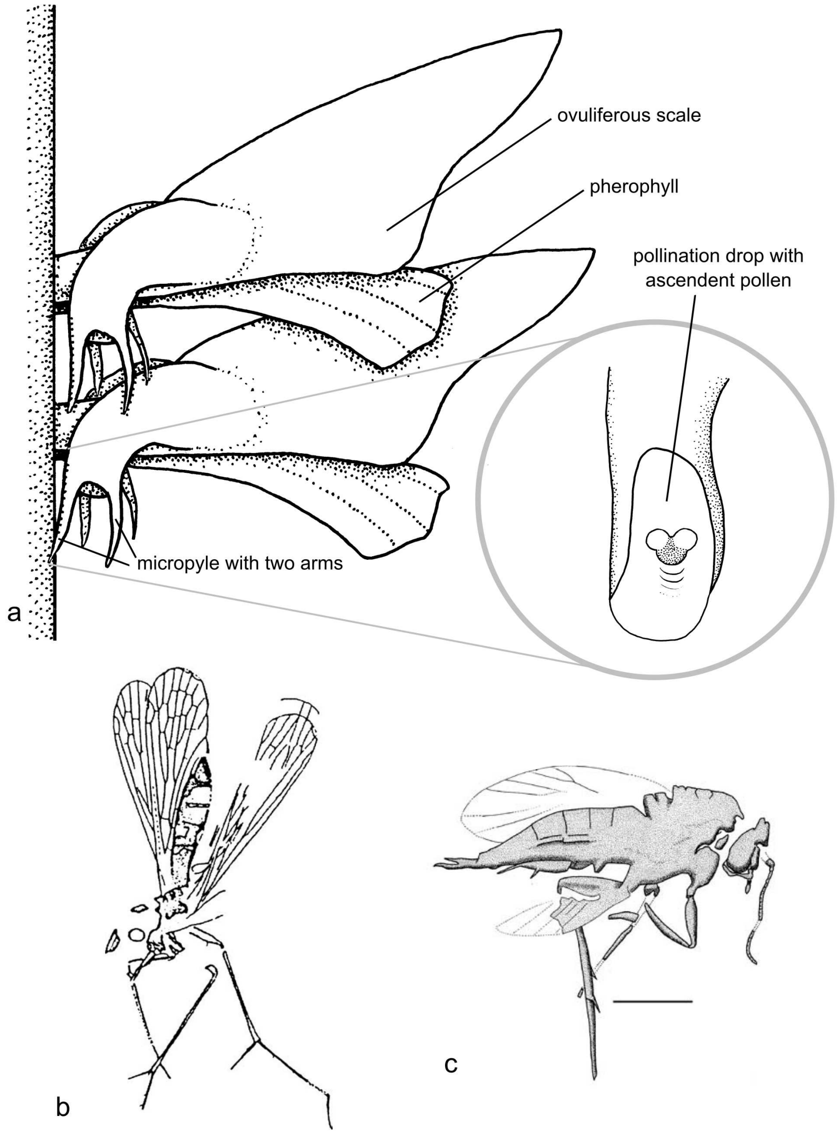

Figure 19 – Pollination participants. a) Schematic *Pinus mugo* scales; in detail: pollination drop with saccate pollen in ascendent movement; b) Crato Formation Mecoptera. Scale unknown. c) Crato Formation Diptera. Bar: 1mm. (Source: a: Christian Westerkamp, modified from Stützel e Röwekamp (1999); b: Bechly (2007d); c: Willkommen e Grimaldi (2007).

related to the type of cones, i.e., simple cones are solitary or in aggregations (fasciculate or clustered) while compound cones only appear in aggregations (fasciculate or clustered); (iii) their different spatial distribution patterns are correlated with distinct leaf types and variable branching frequencies; (iv) the number of sporangia per sporangiophore and the number of sporangiophores per cone are important and fast-evolving characters. Among the 140 cone specimens studied herein, only four are possibly pollen cones (Morphotypes 24, 25 and 26; Plate X). Their scarcity in the fossil record may be related to a difficulty in fossilization since pollen cones show a very short time of duration, a limited growth, and never get woody (FARJON, 2010).

Size differences between seed and pollen cones are obvious throughout the geological history of conifers. On average, seed cones are larger both in the fossil record and in recent species (LESLIE, 2011a; LESLIE, 2011b). Averages of the analyzed cones can be seen in fig. 20 and confirm this pattern. Interestingly, the Crato cone data show that both seed and pollen cones are larger (fig. 20) as compared to other Early Cretaceous specimens and to living material (data from Leslie (2011a)). This author believes that the relative amount of tissue invested in pollen cones has remained constant through time, while seed cones show a sharp increase in proportional tissue investment in the Jurassic that has continued to intensify to the present day. The study of these changes over the time has helped in the understanding of shifting functional roles in the evolutionary history of conifer cones.

5.2 Taphonomy of Conifer remains

The study of the transition (in all their details) of animal remains from the biosphere into the lithosphere was denominated taphonomy by Efremov (1940). This initial concept has undergone alterations over the years and became much wider and currently embraces the study of the processes of preservation and how they affect information in the fossil record (BEHRENSMEYER; KIDWELL, 1985; BEHRENSMEYER *et al.*, 2000). Gastaldo (1988) already emphasized the importance of understanding the processes of fossilization through necrology, biostratinomy and diagenesis for the phytotaphonomy. This more integrated view of the fossil with its environment is important for understanding the functioning of paleobiomes.

Most of the conifer vegetative structures registered in the literature from the Crato Formation are preserved as iron oxide fossils (KUNZMANN *et al.*, 2004; KUNZMANN *et al.*, 2006; MOHR *et al.*, 2012; SUCERQUIA *et al.*, 2015). There are also impressions (KUNZMANN *et al.*, 2006; SUCERQUIA *et al.*, 2015) and compressions (SUCERQUIA *et al.*, 2015). The amount of cones in

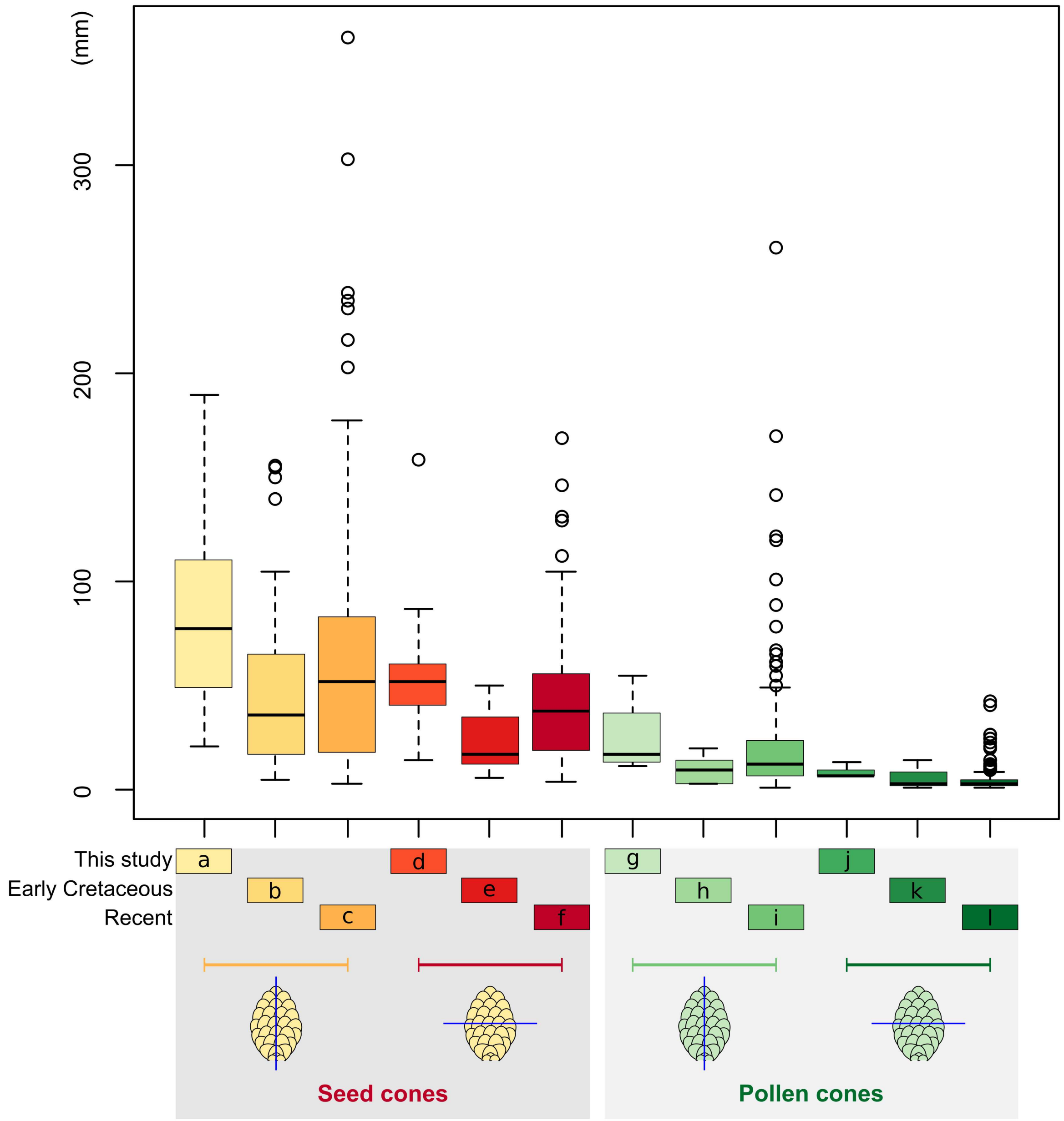

Figure 20 – Boxplot of seed and pollen cone average sizes. Length (mm): a (n = 99), b (n = 38), c (n = 209), g (n = 4), h (n = 10), i (n = 292). Width (mm): d (n = 127), e (n = 38), f (n = 209), j (n = 4), k (n = 10), l (n = 292). Early Cretaceous and recent data (supplementary material of Leslie (2011a)).

Table 3 – Cone morphotypes (Mt) as proposed herein for the Crato Formation

Mt	Characteristics	Plate
1	Seed cones with scales inserted on a well-defined narrow cylindrical central axis; presence of a single seed per scale; specimens with elongated ellipsoid aspect when preserved lengthwise	I, II
2	Elongated ellipsoid seed cones; scales densely amassed; stunted peduncle much wider as compared to Morphotype 1	III, IV
3	Seed cones broadly ovoid; scales very pronouncedly acuminate	V
4	Presence of obvious resin channels in the central axis; in some specimens the resin channels extend towards the scales	VI, VII
5	Cylindrical seed cones with a central axis slightly curved next to peduncle	VIII
6	Cylindrical seed cones; two-seeded scales; quasi impression only	VIII
7	Ovoid seed cones; small scales of oval shape	VIII
8	Globose seed cones with scales nearly circular	VIII
9	Globose seed cones; densely distributed scales much wider than long, with a shortly pointed apex	IX
10	Globose to ovoid seed cones; scales wider than long with a rounded apical margin	IX
11	Ellipsoid seed cones; scales with irregular apical margins that give them a worn aspect	IX
12	Ovoid seed cones with few large scales	IX
13	Ovoid seed cone; loose pherophylls (Deckschuppe) protruding prominently from the cone; narrow peduncle densely covered by pointed leaves	IX
14	Oblate seed cone, with the free end of the peduncle somewhat retracted to within the cone, giving its base a cordate shape in longisection	IX
15	Seed cone with a thick round central axis; apically rounded seed scales inserted radially, each one with two seeds (with apical wings?) and diverse resin channels; at least one structure protruding from the cone: pherophyll?	IX
16	Cylindrical seed cone, incomplete: final part broken off; small number of 2-seeded (?) scales with acuminate apex; central axis slightly curved next to peduncle	X
17	Blunt broadly ovoid seed cone; two-seeded (?) scales in the axil of irregularly-shaped shortly-pointed membraneous pherophylls	X
18	Base of a broken (?) or globose seed cone with some thick distally rounded scales and a narrow peduncle covered with appressed pointed minuscule leaves	X
19	Seed cone fragment wit no visible axis; scales with hexagonal (sometimes pentagonal) circumference and an umbonate centre	X
20	Poorly preserved ovoid (?) cone with protruding pherophylls (?); tangential longitudinal section with no trace of an axis	X
21	Transverse view of a cone; numerous pherophylls (?) surrounding a thick central axis; maybe base of a cone with end of peduncle with lots of minuscule appressed leaves	X
22	Undefined fragment with several scales (of at least two different types) arranged around a central axis, the peduncle of which broke off	X
23	Base of a non-coniferous cone	X
24	Probably male cones; elliptic shape, surrounded by an involucre at the base; thick peduncle	X
25	Possibly male cone; narrowly ovoid with tapering apex; slender peduncle	X
26	Possibly male cone; long cylindrical form; combined central axis and peduncle curved next to their contact, numerous stout scales with rhomboid circumference	X

Table 4 – Cones from the Crato Formation distributed by their preservation style and sediment features (n: total of specimens; R: rhythmicity; L/D: light/-dark alternation; A: algae).

Preservation style		Sediment features							
		Yellow				Grey			
		n	R	L/D	A	n	R	L/D	A
Coalification (83)	non-flattened (49)	11	11	4	11	38	38	38	34
	flattened (34)	8	6	7	7	26	25	26	19
Iron oxide (37)	non-flattened (23)	21	3	3	21	2	2	1	2
	flattened (14)	14	9	9	14	0	0	0	0
Charcoal (12)		3	2	2	2	9	8	8	8
Impression (8)		7	6	6	6	1	1	1	1

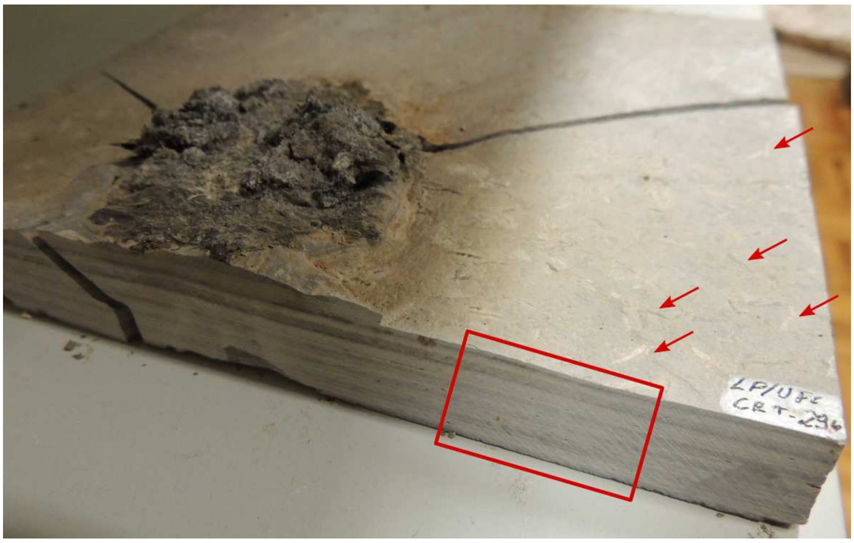

Figure 21 – Sediment features. LP/UFC CRT 296 specimen preserved in greyish sediment with presence of algae (arrows). The rectangle highlights the lateral layers with rhythmicity (approximately the same thickness) and the alternation between light and dark in coloration.

the coalification type (59.3 %) exceed the sum of the other preservation modes (table 4). The second most common type was iron oxide (26.4 %) followed by charcoal (8.6 %) and impression (5.7 % (table 4). Sucerquia (2013), analysing conifer leafy branches and cones, emphasized the iron oxide mode of preservation as the most common, although she also recorded the occurrence of coalification and impression in the fossils from the Crato Formation. It seems that the preservation of the fossils in the Crato Formation is partly linked to the rocky nature of the outcrop and partly to the original specimen morphology (MENON; MARTILL, 2007).

Coalification is an increase in the carbon percentage of plant remains by hydrogen and oxygen being driven off as consequence of increasing temperature and pressure. The plant tissues are transformed into peat and then into soft brown coal by both aerobic and anaerobic biochemical processes, and then with further increase in the coalification rank to hard coal and finally graphite (SPICER, 1991). It was possible to recognize 83 cones preserved by coalification herein (e.g., fig. 22a). They have a black colouration ranging from softer tones to strong ones (e.g., LP/UFC CRT 1963, FPH-95-B, Plate II; GP3E 9517, Plate V). Most of them are not flattened; they are predominantly found in the greyish carbonatic sediments (table 4). Consequently, coalification was the dominant preservation mode for the cones studied, differently of Sucerquia (2013) that considered the coalified plant remains of the Crato Formation scarce. She also believed that they could be generated in more anoxic phases at the bottom waters of the lake when the organic material would not be decomposed, but distilled during the diagenetic processes.

Preservation by iron oxide occurs through precipitation of authigenic minerals in sediment pore space around the organic fragment. It usually involves very early cementation in soft sediment that preserve surface configurations of organic parts. External or internal molds may result from authigenic preservation and some traces of very delicate form can be conserved (SCHOPF, 1975). There were 37 cones preserved by iron oxide (e.g., fig. 22b; table 4). They are characterized by an orange-brown colouration (e.g., LP/UFC CRT 2479, GP3E 9514, Plate I; GP3E 9511, FPH-93-B, Plate II). Most of them are not flattened and they rarely appear in the greyish sediment (e.g., GP3E 9533, Plate III; 1484-Pb, Plate X). Sucerquia (2013) considered the molds in iron oxide as a frequent type of preservation among the macrophytofossils of the Crato Formation. This type of preservation is also common in insects of the Crato unit (BARLING *et al.*, 2015; OSÉS *et al.*, 2016). Barling *et al.* (2015) and Menon e Martill (2007) suggested that microbial induction should have occurred during fossilization. Osés *et al.* (2016) considered that biofilms of sulphate reducing bacteria (SRB) had a central role in insect decay and mineralisation. They proposed that during early diagenesis, SRB acted in the formation of pyrite by reducing sulphate (SO_4^{2-}) to hydrogen sulphide (H_2S) and, possibly, ferric iron (Fe^{3+}) to ferrous iron (Fe^{2+}) dissolved in pore water solutions. Their analyses have also shown that the supergene oxidation and/or hydration of pyrite resulted in the formation of iron oxides/hydroxides. Sucerquia (2013) found structures similar to bacteria and fungus hyphae that could evidence the action of microorganisms in the formation of phytofossils of the Crato Formation.

Osés *et al.* (2017) proposed that bacterial respiration processes are involved both in pyritization and kerogenization in the Crato Formation. Recent studies have contributed to

Figure 22 – Cone preservation modes in the Crato Formation. a) Coalification: GP3E 9449; b) Iron oxide: GP3E 9461; c) Charcoal: LP/UFC CRT 2755; d) Impression: FPH-82-B. Scale bar = 2 cm

the understanding of the microbial influence on the formation of laminated limestones of the Crato unit. Catto *et al.* (2016) detected the presence of calcified coccoid, filamentous bacteria, calcified biofilms and extracellular polymeric substances in the laminated limestones. Warren *et al.* (2017) record stromatolite microbialites originated by the action of microbial mats present in the ancient Araripe lacustrine system. These discoveries confirm the existence of metabolic activity of microorganisms and the biologically induced mineralization in the Crato limestone morphogenesis.

Conifer stem fragments analysed herein by scanning electron microscopy (SEM) confirmed the existence of charcoal in the Crato Formation. Bordered pits typical of conifers can be seen in fig. 23a. The thick cell walls common in charcoalified plants are visible in fig. 23b. In this case the plant had not yet been fully charred because the middle lamella is still present (fig. 23b). According to Scott (2010), in temperatures of about 500 °C the carbonization stage is complete and the cell walls become homogenized. Brown *et al.* (2012) considered the Cretaceous a "high-fire" world because the widely distribution of charcoalified plant mesofossils throughout this period. Twelve cones were found with charcoal preservation mode (e.g., fig. 22c), nine of which are preserved in the grey sediment (table 4). They have a characteristic dark colouration (e.g., GP3E 9527, LP/UFC CRT 1055, Plate II; GP3E 9508, GP3E 9532, Plate VII) and leave black traces on the fingers when touched.

Impression fossils form when the organ decayes, leaving a void in the sediment (LOCATELLI, 2014). Eight cones were found as impressions (e.g., fig. 22d). Most of them are found in the yellowish carbonatic sediments, with only one (713 Pb; Plate III) in the greyish sediment (table 4). Generally they present some parts of specimens coalified (e.g., LP/UFC RT 2034; DNPM 3695, Plate VIII), but most of the material of the fossils has been weathered leaving only impressions in the surrounding matrix.

After burial, plant matter inevitably undergoes some degree of compaction or flattening as additional sediment is deposited above it. The only exception to this is when mineralization occurs almost immediately and before significant sediment loading has taken place (SPICER, 1991). Despite of this, the study cones preserved by coalification and iron oxide were classified as flattened and non flattened with the predominance of the latter in both cases (table 4). This result may be due to the way the cone appears and is collected in the sediment. Often only a half of the cones are visible because they are separated in the part and counterpart at the time of gathering of the outcrop, leaving only one of them, the most prominent, in the collections.

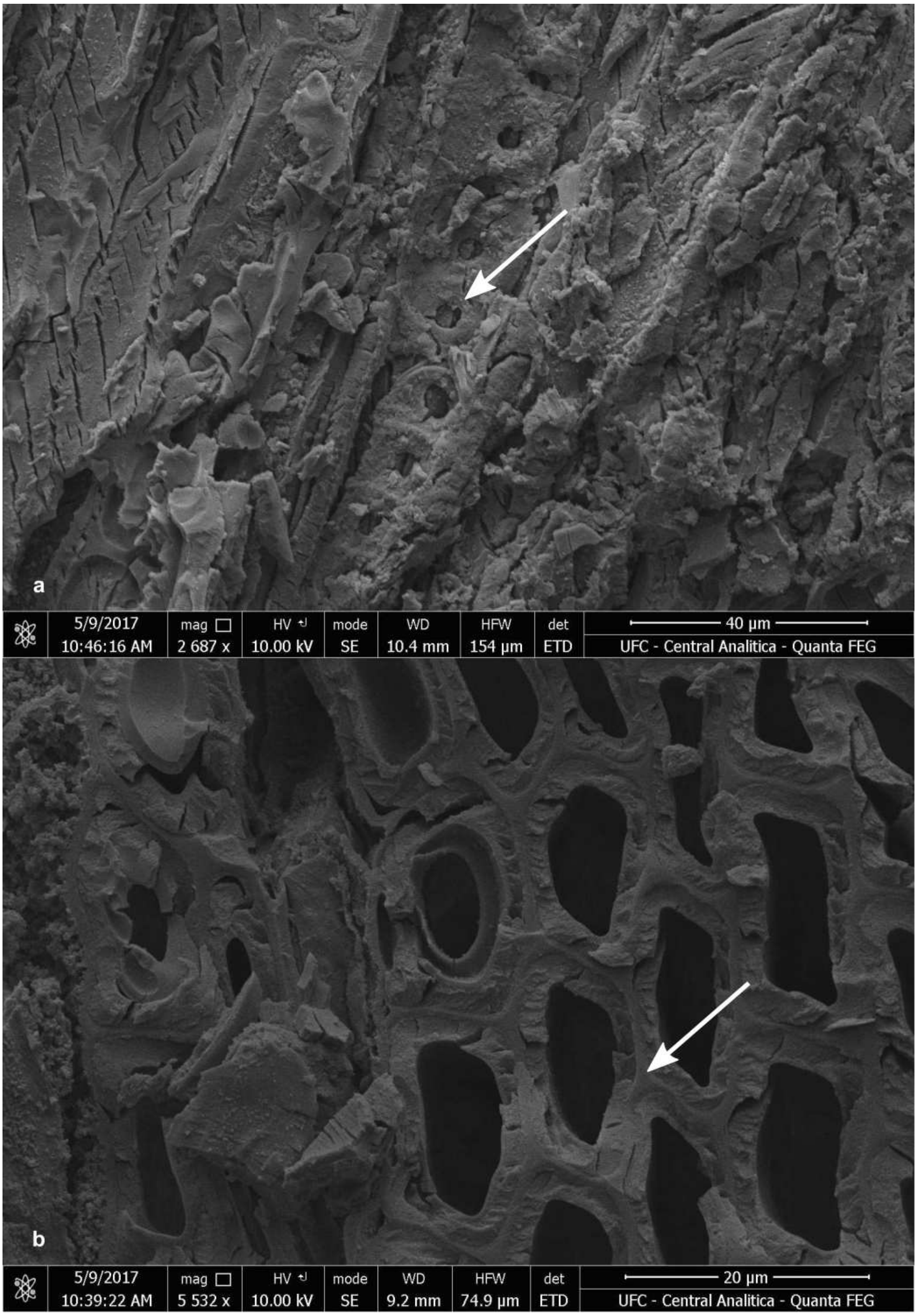

Figure 23 – Charcoal wood of the Crato Formation. Scanning electron micrographs of the conifer stem LP/UFC CRT 2759 specimen. a) Radial longitudinal section showing tracheids with bordered pits (arrow). b) Transverse section showing tracheids with thick wall and middle lamella (arrow). Photos: Central Analítica – UFC.

Considering the sediment colour, the cones were fossilized in both greyish (54.3 %) and yellowish (45.7 %) sediments (table 4). Osés *et al.* (2017) related taphonomic modes of fossil fish soft-tissue preservation to different microfacies. Their study revealed that the orange iron oxyhydroxide fossils were pyritized in beige limestone microfacies and the black carbonaceous compression fossils were kerogenized in greyish limestone microfacies. They proposed that the different taphonomic pathways were controlled by distinct sedimentation rates in two different microfacies. For the cones of this work this is not the rule since both coalification and iron oxide preservation styles were found in both yellowish and greyish sediments. However, most cones with preservation of coalification type are found in the greyish (77 %) sediment and those with iron oxide mode of fossilization are in the yellowish (94.6 %) sediment (table 4).

By observing the layers of laminated limestone on the sides of the sediment where the cones were fossilized, it was possible to record the rhythmicity and alternation between light and dark. The presence of regularity at the thickness of the layers of laminated limestone was considered as rhythmicity. When there was a difference in the colour of the sediment between one layer and another of laminated limestone, it was considered a light/dark alternation. The presence of algae in the upper and/or lower parts of the fossil was also recorded (fig. 21). From the total of 140 cones, 133 were preserved in rhythmic sediments, 105 in limestone showing light/dark alternation and 126 in association with algae (table 4). Catto *et al.* (2016) characterized the rhythmic microfacies as interbedded submillimetric to millimetric lenses of micritic calcite, organic matter and clay. They also found that these lenses form pairs of light and dark micritic lenses with restricted concentrations of organic matter and clay.

Concerning the spatial distribution of cones in the Crato Formation, almost no information was obtained. Only the cones deposited in the collection of UFRJ (62 specimens; 44.3 % of the total) presented the register of geographical coordinates from where they were found. For these cones, the latitude varied between 7°5′40″ S and 7°12′12.1″ S and the longitude varied between 39°41′90″ W and 39°44′11.8″ W, indicating that they were found close to each other. Therefore there is the possibility of a distinct cone bed, which can only be confirmed with more data acquired in the future. Lima Felix (2017) conducted an ethno-stratigraphic research with workers of the quarries of Nova Olinda, Ceará. She correlated fossils and their stratigraphic positions in the layers of the Nova Olinda Member of the Crato Formation, using the vernacular names applied by the miners. The registered layers, from the base to the top, were: ‘Sete Cortes’, ‘Matracão’, ‘Lajão Branco’, ‘Pão de Milho’, ‘Veio da Piaba’, ‘Lajão Doidão’, ‘Lajão Amarelo’, and ‘Lajão dos Besouros’. Plant fossils, i.e., *Ruffordia*, *Welwitschiophyllum*, *Brachyphyllum*, incarbonized woods, and cones occur in all layers, except for ‘Matracão’. The ‘Veio da Piaba’ layer was the one with the largest amount of *Brachyphyllum* remains recovered while the highest concentration of cones and incarbonized woods was found in the most basal ‘Sete Cortes’ layer. These two layers have in common the presence of vertebrates, such as fishes (e.g., *Dastilbe* and *Cladocyclus*), and tetrapodes (e.g., Order Anura, turtle *Araripemys*, crocodilians), and invertebrate remais, such as the insects of the Blattaria and Odonata orders, and arachnids. Pterosaurs of the Family Tapejaridae also only appear in the ‘Sete Cortes’ layer while insects of the Family Gryllidae and Order Homoptera only occur higher in the section, in the ‘Veio da Piaba’ layer.

Regardless of the preservation modes and sediment characteristics, the conifer fossils of the Crato Formation are relatively resistant, nonetheless, particle detachment may occur upon touching. The fact that the conifers found so far in the Crato unit have been terrestrial indicates that the species were transported into the depositional setting, i.e., they are allochthonous. The transport to the Crato lake may have occurred by the initial action of rain and wind, releasing parts of the plant that were later carried by the stream of water bodies that drained into the lake. It is natural for plants to lose aerial organs from time to time, but the large amount of loose leaves, pieces of branches and isolated cones recovered in the Crato Formation may be a consequence of the transport that the individuals suffered until deposition in the lake. Cones can float and thus could be transported for longer distances along the lake surface like other plant litter. With little currents, induced by wind, they could have floated to distinct places of the lake and built mass accumulations in certain areas. Then they sank to the bottom of the lake and settled horizontally. This resulted in the fossils in longitudinal aspect (fig. 16 a, b). Pieces of broken cones (with diameter much larger than axis) turned over as they reached the bottom of the lake, just as a thrown coin always falls onto its face; they originated the fossils in transversal aspect (fig. 16 c, d). The fact that the analyzed cones are closed can be explained by the hygrophilic mechanism of cone opening and closing. In the presence of moisture pine cones close in a passive movement. It is the response of the scales to changing relative environmental humidity (fig. 24 a, b). Each scale has a bilayer composed of sclerenchyma fibres in the inner surface and sclerids in the outer surface. When exposed to humidity, the outer layer cells respond by expanding longitudinally (fig. 24 c); they shrink when drying (fig. 24 d), while the inner layer does not respond as strongly (DAWSON *et al.*, 1997; SONG *et al.*, 2015) . This hygroscopic response triggers a global movement

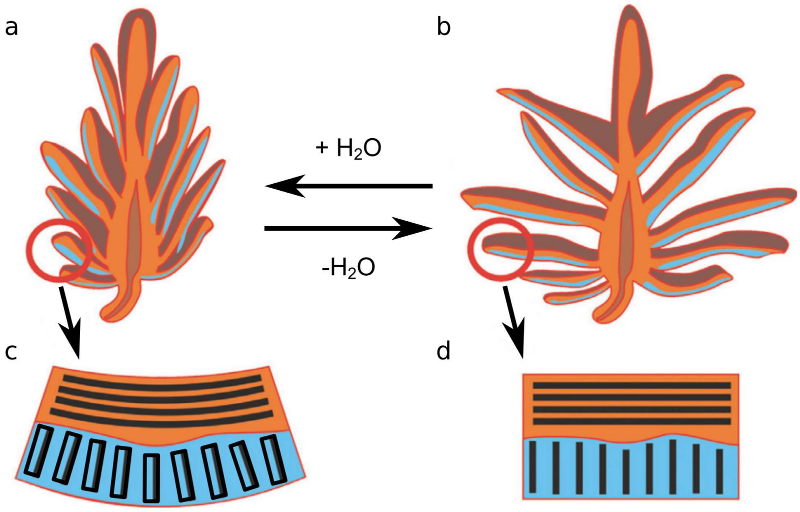

Figure 24 – Pine cone response to humidity. a) closed cone in wet conditions; b) open cone in dry conditions. c) and d) bilayer composed by sclerenchyma fibres in the inner (orange) surface and sclerids in the outer (blue) surface (modified from: Dunlop *et al.* (2011))

of cone opening or closing. This phenomenon is observed even in fossil cones (POPPINGA *et al.*, 2017).

Probably the natural habitat of conifers was not distant because, although isolated, the organs are mostly complete, with no signs of breakage or other damages. Kunzmann *et al.* (2004) considered that larger, almost completely preserved shoots of *Brachyphyllum obesum* and well preserved shoots that bear more than a dozen completely preserved leaves of *Lindleycladus* probably did not come very far away from the place where the remains were embedded in the sediment. The habitat of *Duartenia araripensis*, however, may have been relatively far from the Crato lake because the specimens known are fragmentary, represented mostly by defoliated branches and/or small fragments of twigs (MOHR *et al.*, 2012).

5.3 Whole-plant reconstructions

Whole plants are rarely found in the fossil record and reconstructing ancient plant forms is often a laborious process requiring great skill and long time. In practice very few whole plants are (e.g., Alvin (1983)), or can ever be, reconstructed (SPICER, 1991). The occurrence of dissociated vegetative and reproductive structures is common among conifer fossils of the Crato Formation. Vegetative shoots, leafs, branches, cones, scales and pollen grains are found isolated compounding a complex puzzle of difficult solution. Until now, there is no record of a specimen containing the cones attached to branches, for instance. The maximum that occurs are

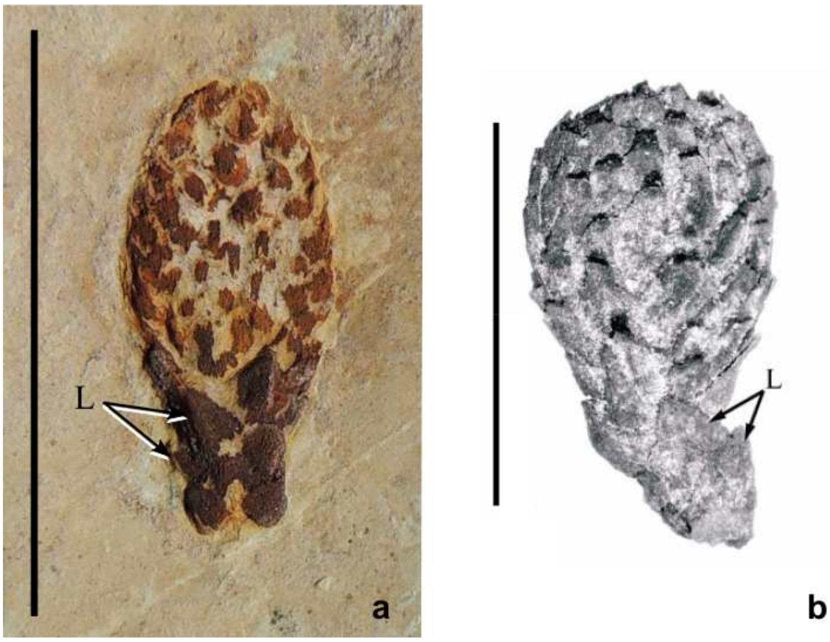

Figure 25 – Morphological aspects of pollen cones. a) Specimen FPH-92-B. Scale bar = 2 cm (Photo: AP Westerkamp). b) *Classostrobus arkansensis*. Scale bar = 1 cm (AXSMITH *et al.*, 2004, figure 2.4). L = leaves.

cones with a portion of their peduncle still preserved (e.g., FPH-88-Ba, Plate II). Under these conditions, what can be done by comparison with the existing literature are assumptions.

Axsmith *et al.* (2004) described the Cheirolepidiaceous conifer pollen cones *Classostrobus arkansensis*. It was still attached to *Pseudofrenelopsis parceramosa* Fontaine in the Holly Creek Formation of the Lower Cretaceous (Aptian/Albian) from Arkansas, USA. The base of the cone (fig. 25b) is covered by an involucre of small leaves with acute apex that also cover the small section of the stem. The same situation can be observed in our specimen FPH-92-B (fig. 25a). As there is the presence of at least one species of *Pseudofrenelopsis* registered in the Crato Formation, i.e. *Pseudofrenelopsis capillata*, it is suggested that FPH-92-B were related to this genus.

5.4 Paleoecology of conifer remains

It seems that the gymnosperms dominated the vegetation of the Crato biome and that the conifers constituted a relatively large part of the flora (MOHR *et al.*, 2007; KUNZMANN *et al.*, 2004). They shared the environment with pteridophytes, gnetales and angiosperms. Morphological characters of leaves and epidermal features show that the conifers were adapted to a possibly seasonally dry climate. The xerophytic characters present in the other plant groups also suggest a warm and dry paleoenvironment. However, it should be noted that there was enough water availability in this ecosystem over time capable of sustaining the presence of large trees, as suggested by the existing remains of Cheirolepidiaceae. Whether from the perennial lake Crato, or from the rainwater discharges, the water was sufficient for the growth of individuals of arboreal habit around that lake. It is worth mentioning that the vegetation should be adapted to the natural occurrence of fire, indicated by the presence of charcoal in the Crato Formation.

The diversity of cones morphotypes could mean a greater number of species of conifers that were responsible for much of the terrestrial primary productivity of the Crato biome, since they appear as the only group of plants that possibly produced arboreal individuals, constituting perhaps the canopies in side lake forest formations. If this is true, conifers promoted the development of a richer and more complex ecosystem around the Crato lake, housing several other species of plants and animals under their canopies and increasing the amount of biomass available. In this way, conifers could establish important ecological relationships with the rich and diverse fauna recorded in the Crato Formation. For example, their trunk bark could be a shelter for insects, their ovule cones could nourish visitors (and thus be pollinated), their seeds could feed frugivorous animals, and their leaves could be consumed by herbivores, among many other possible interactions.

6 CONCLUSIONS

The diversity of cone morphotypes suggests a greater number of conifer species and/or families in the Araripe Basin, as already suggested by the palynological record. In the future, a taxonomic classification of these distinct morphotypes can extend the record of conifer types in Western Gondwana, helping to understand dispersal and irradiation of conifer families during the Early Cretaceous.

Future paleometrical (non destructive) analyses as, e.g., scanning electron microscopy (SEM), energy dispersive X-ray fluorescence (EDXRF), particle induced X-ray emission (PIXE), and Raman spectroscopy, should be carried out to confirm the cone fossilization types of the Crato Formation.

More detailed studies on the relationships between plant fossil preservation modes and local sediment types are necessary and will improve the knowledge on the fossilization process in the Araripe Basin.

Cones are also key components for identifying pollination and dispersal syndromes as well as other ecological interactions like predation that drove conifer evolution through time.

Natural fires present in the Crato Formation may have contributed to natural selection of the conifer vegetation.

The variety of fossil taxa found in exceptional state of preservation in the Crato Formation reflects the intricate ecological relationships that existed in the Early Cretaceous in northeastern Brazil.

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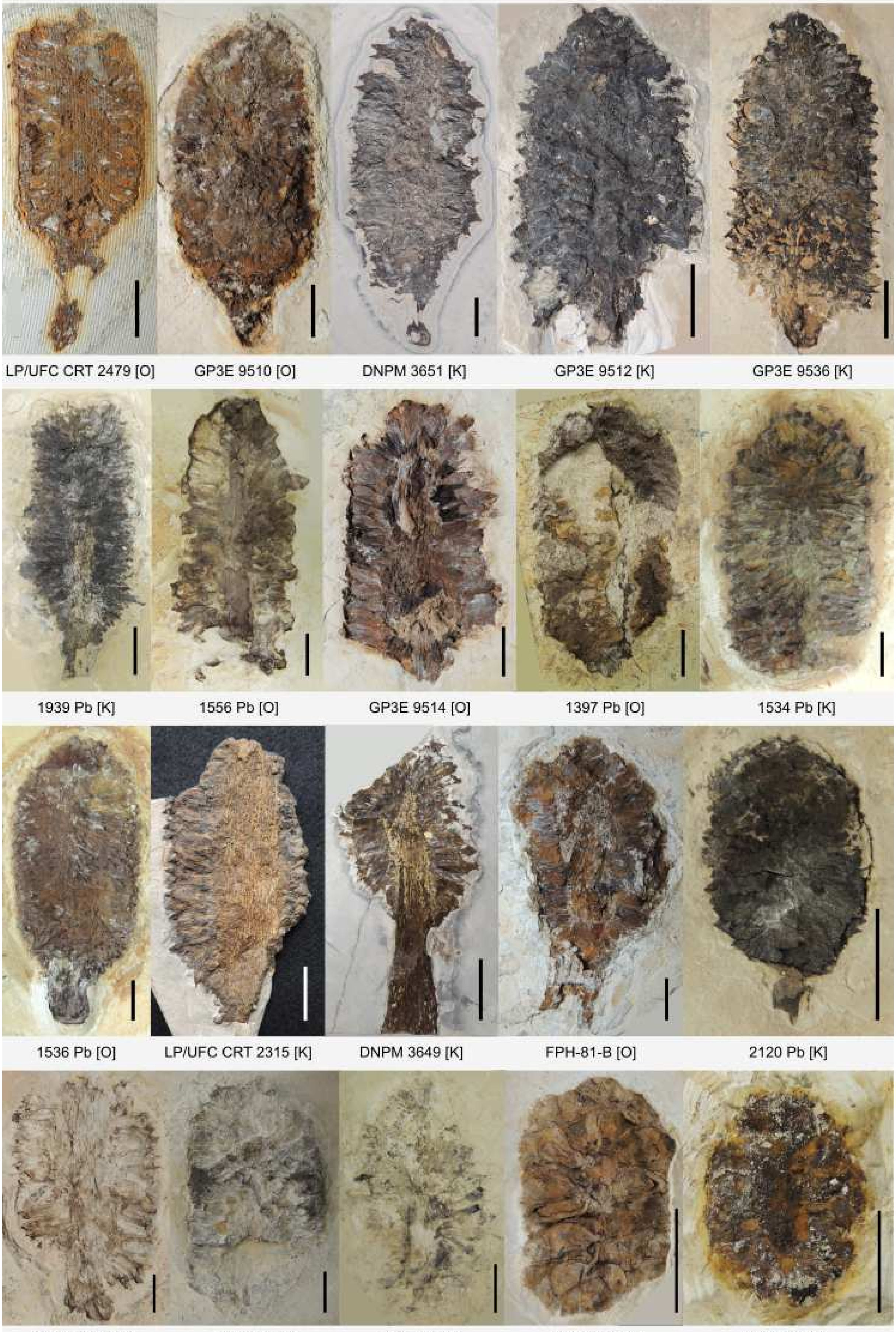
APPENDIX A – PLATE I



Morphotype 1

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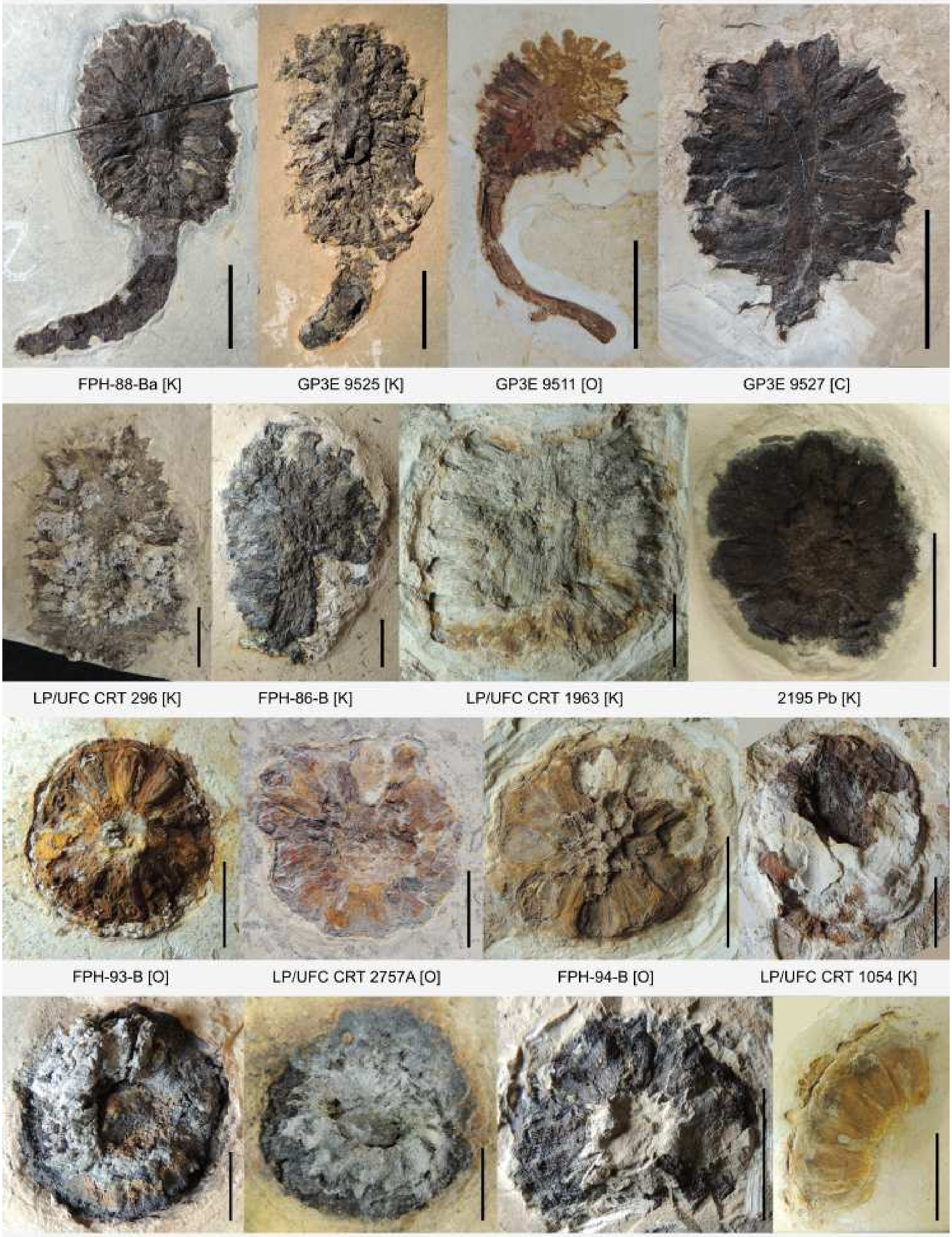
1939 Pb [K] 1556 Pb [O] GP3E 9514 [O] 1397 Pb [O] 1534 Pb [K]

1536 Pb [O] LP/UFC CRT 2315 [K] DNPM 3649 [K] FPH-81-B [O] 2120 Pb [K]

GP3E 9513 [K] 2081 Pb [K] 1547 Pb [O] FPH-91-B [O] 2360 Pb [O]

APPENDIX B – PLATE II

Morphotype 1



FPH-88-Ba [K]
GP3E 9525 [K]
GP3E 9511 [O]
GP3E 9527 [C]
LP/UFC CRT 296 [K]
FPH-86-B [K]
LP/UFC CRT 1963 [K]
2195 Pb [K]
FPH-93-B [O]
LP/UFC CRT 2757A [O]
FPH-94-B [O]
LP/UFC CRT 1054 [K]
LP/UFC CRT 1055 [C]
1962 Pb [O]
FPH-95-B [K]
1129 Pb [O]

APPENDIX C – PLATE III

Morphotype 2

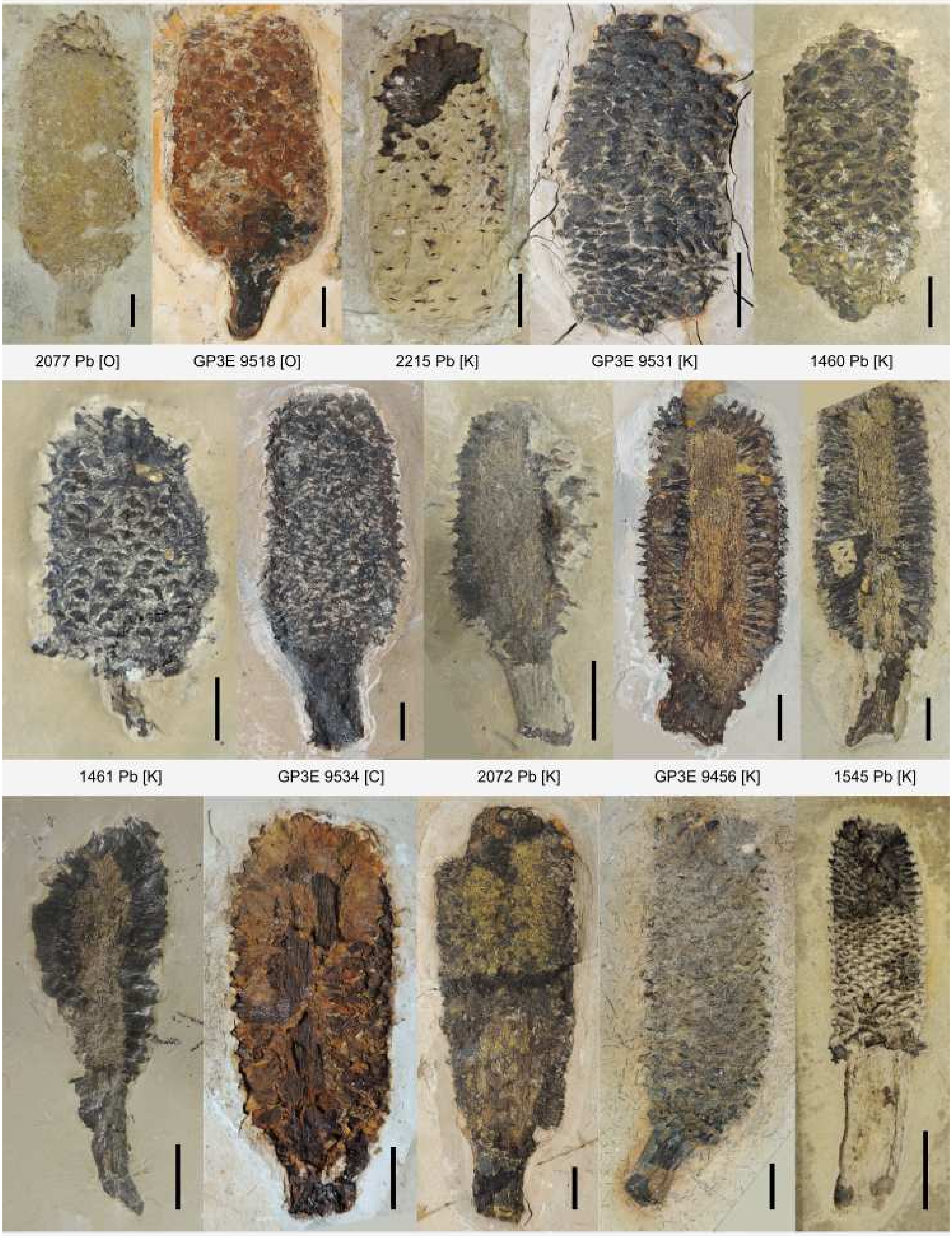
DNPM 3650 [I]
2332 Pb [O]
DNPM 3648 [O]
GP3E 9528 [O]
GP3E 9519 [O]

GP3E 9533 [O]
GP3E 9537 [O]
713 Pb [I]
2053 Pb [I]
GP3E 9454 [K]

1971 Pb [K]
2208 Pb [K]
LP/UFC CRT 943 [K]
DNPM 3652 [C]
2141 Pb [K]

APPENDIX D – PLATE IV

Morphotype 2

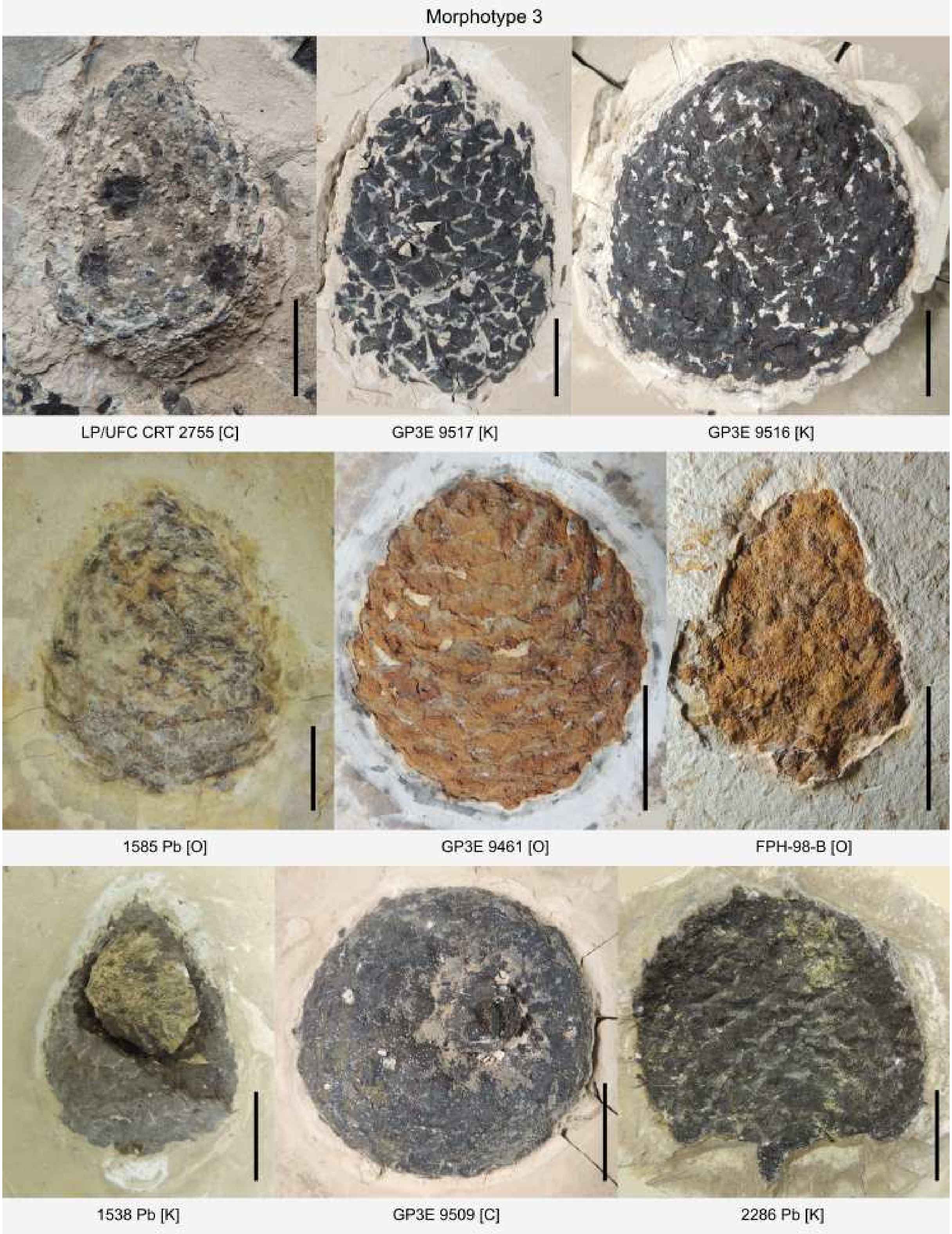


2077 Pb [O] GP3E 9518 [O] 2215 Pb [K] GP3E 9531 [K] 1460 Pb [K]

1461 Pb [K] GP3E 9534 [C] 2072 Pb [K] GP3E 9456 [K] 1545 Pb [K]

2119 Pb [K] GP3E 9520 [O] GP3E 9535 [C] 2216 Pb [K] 2127 Pb [K]

APPENDIX E – PLATE V



Morphotype 3

LP/UFC CRT 2755 [C]

GP3E 9517 [K]

GP3E 9516 [K]

1585 Pb [O]

GP3E 9461 [O]

FPH-98-B [O]

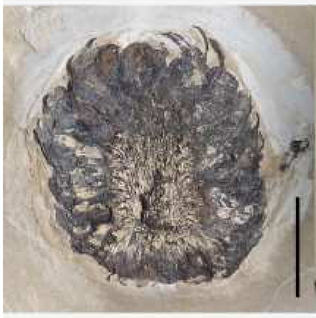
1538 Pb [K]

GP3E 9509 [C]

2286 Pb [K]

APPENDIX F – PLATE VI

Morphotype 4


GP3E 9506 [K]


2263 Pb [K]


DNPM 3694 [K]


GP3E 9526 [C]


1577 Pb [K]


1976 Pb [K]


2134 Pb [K]


2325 Pb [K]


FPH-96-B [K]


1959 Pb [K]


2082 Pb [K]


1391 Pb [K]


GP3E 9507 [K]

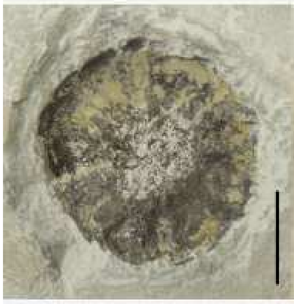

FPH-89-B [K]

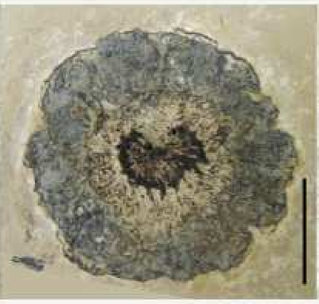

2249 Pb [K]


2337 Pb [K]

APPENDIX G – PLATE VII

Morphotype 4


2017 Pb [K]


1543 Pb [K]

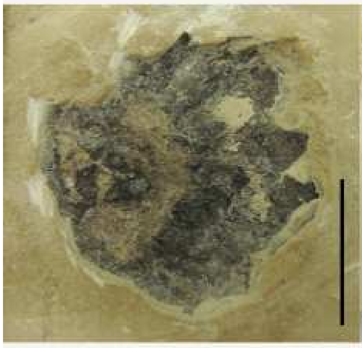

GP3E 9448 [K]


GP3E 9508 [C]


2079 Pb [K]


LP/UFC CRT 779A [K]


1493 Pb [K]


1829 Pb [K]


2202 Pb [K]


1539 Pb [C]


LP/UFC CRT 2492 [K]


GP3E 9532 [C]


2126 Pb [K]


GP3E 9521 [K]


GP3E 9529 [K]

APPENDIX H – PLATE VIII

Morphotype 5


GP3E 9453 [K]


2316 Pb [K]


FPH-99-B [K]


2234 Pb [K]

Morphotype 6


DNPM 3647 [I]


LP/UFC CRT 2034 [I]


FPH-82-B [I]

Morphotype 7


348 Pb [O]

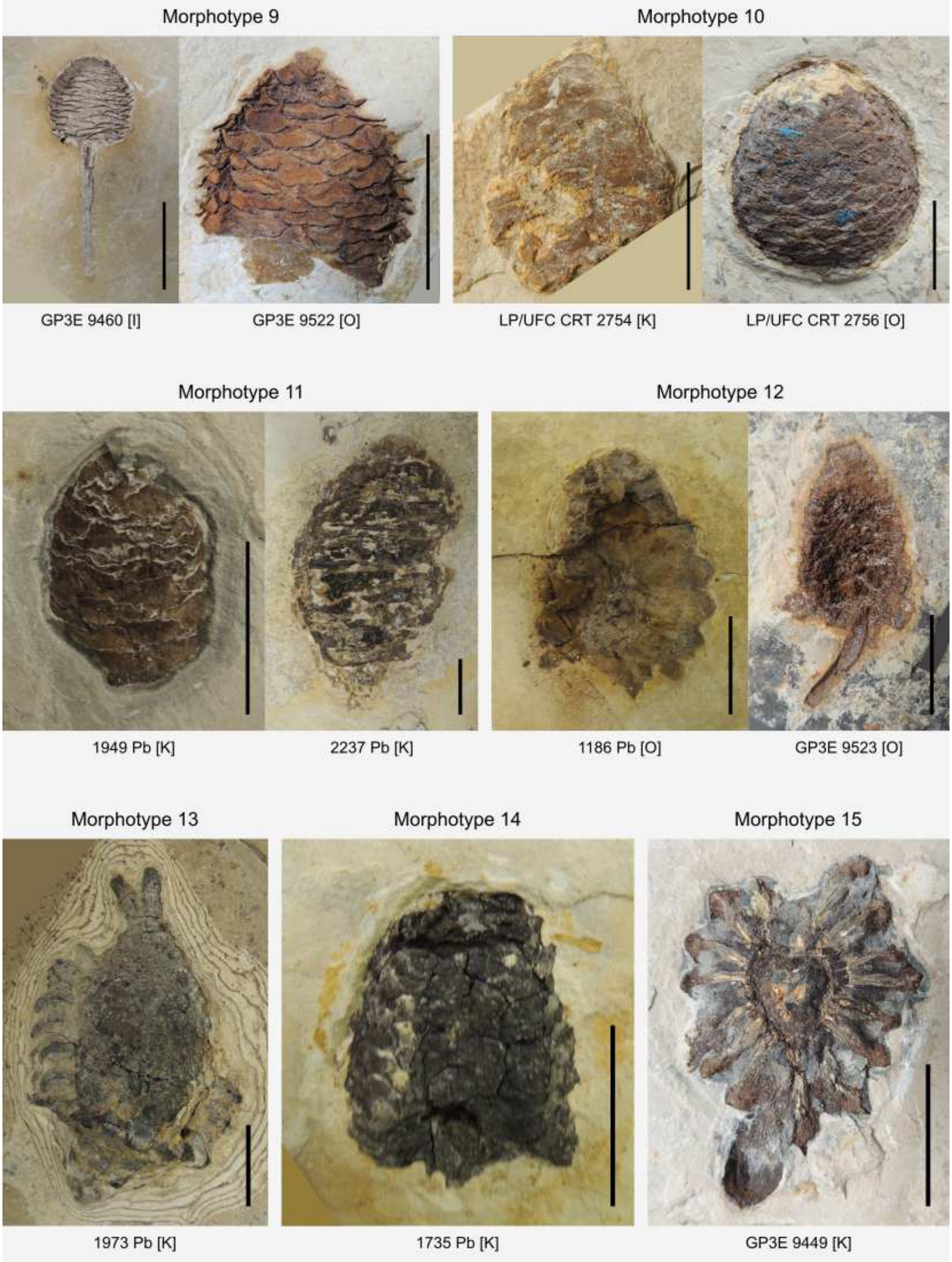

LP/UFC CRT 2753 [C]

Morphotype 8


FPH-87-B [K]


DNPM 3695 [I]

APPENDIX I – PLATE IX



APPENDIX J – PLATE X

Morphotype 16

2133 Pb [K]

Morphotype 17

FPH-90-B [K]

Morphotype 18

1484 Pb [O]

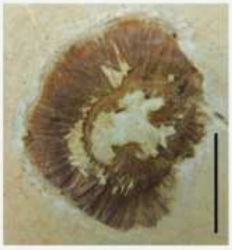
Morphotype 19

FPH-84-B [K]

Morphotype 20

1754 Pb [K]

Morphotype 21



867 Pb [O]

Morphotype 22

1554 Pb [K]

Morphotype 23

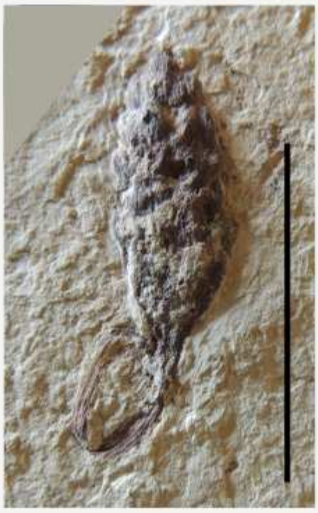
FPH-83-B [K]

Morphotype 24

1182 Pb [O]

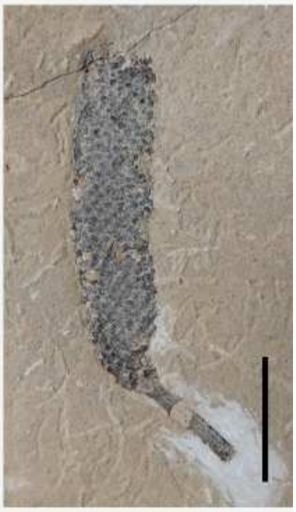
FPH-92-B [O]

Morphotype 25



FPH-97-B [K]

Morphotype 26



FPH-85-B [K]