



A new cheirolepidiaceous conifer *Pseudofrenelopsis salesii* sp. nov. from the Early Cretaceous of Brazil (Romualdo Formation, Araripe Basin): Paleocological and taphonomic significance

Maria Edenilce P. Batista ^{a,*}, Lutz Kunzmann ^b, Francisco Irineudo Bezerra ^c, José Artur F.G. de Andrade ^d, Artur A. Sá ^{e,f}, Maria Iracema B. Loiola ^g

^a Programa de Pós-Graduação em Ecologia e Recursos Naturais, Departamento de Biologia, Universidade Federal do Ceará, Av. Mister Hull, CEP 60455-900 Fortaleza, Brazil

^b Senckenberg Natural History Collections, Königsbrücker Landstr. 159, 01109 Dresden, Germany

^c Programa de Pós-Graduação em Geologia, Departamento de Geologia, Universidade Federal do Ceará, Av. Mister Hull, CEP 60455-900 Fortaleza, Brazil

^d Departamento Nacional de Produção Mineral, Praça da Sé, CEP 63100-440 Crato, Brazil

^e Departamento de Geologia, Universidade de Trás-os-Montes e Alto Douro, Quinta de Prados, 5000-801 Vila Real, Portugal

^f Centro de Geociências, Universidade de Coimbra-Polo II, 3030-790 Coimbra, Portugal

^g Departamento de Biologia, Universidade Federal do Ceará, Av. Mister Hull, CEP 60455-900 Fortaleza, Brazil.

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ABSTRACT

Pseudofrenelopsis is a genus of the conifer family Cheirolepidiaceae, whose temporal distribution was restricted to the Early Cretaceous. Its set of features correspond to adaptive responses to rather unstable and stressful environmental conditions, such as aridity and/or groundwater salinity. In this paper, we describe *Pseudofrenelopsis salesii* sp. nov. from the Albian Romualdo Formation of the Araripe Basin, northeastern Brazil, based on anatomical analyses of the stem and leaf epidermis of a new specimen using scanning electron microscopy. The unique combination of features of *P. salesii* sp. nov., such as internodes of uniform sizes, completely sunken stomatal apparatuses, non-papillate subsidiary cells, and multi-layered hypodermis, distinguishes it from the remaining species of the genus, including *Pseudofrenelopsis capillata* from the late Aptian Crato Formation of the same basin. The new fossil species represents both an additional record of Cheirolepidiaceae in the Araripe Basin and the first representative of *Pseudofrenelopsis* formally described from the Romualdo Formation.

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1. Introduction

Pseudofrenelopsis is a genus of the extinct conifer family Cheirolepidiaceae, whose temporal distribution was restricted to the Early Cretaceous (Watson, 1977; Alvin et al., 1981; Alvin, 1982; Upchurch et al., 1994; Axsmith, 2006; Du et al., 2014; Sucerquia et al., 2015). The genus currently encompasses 14 species and its geographical range includes Central Europe, North America, Eastern Asia, Africa and South America (Watson, 1977; Alvin et al., 1981; Zhou, 1995; Srinivasan, 1995; Saiki, 1999; Barale et al., 2002; Haworth et al., 2005; Yang and Deng, 2007; Yang, 2008; Yang et al., 2009; Sun et al., 2011; Kim et al., 2012; Du et al., 2014; Sucerquia et al., 2015; Batista et al., 2017). Morphologically, *Pseudofrenelopsis* is characterized by vegetative shoots subdivided by well-marked nodes and internodes and each node

bearing a single leaf or, rarely, two leaves (Watson, 1977; Srinivasan, 1995; Du et al., 2014). However, the anatomical features of the leaf and stem epidermis vary substantially within the genus and many species can only be set apart from the others based on epidermal-cuticular traits, which are of great taxonomic importance (Sun et al., 2011; Du et al., 2014; Sucerquia et al., 2015). On the other hand, knowledge on internal stem anatomy, in particular on the vascular system of *Pseudofrenelopsis*, is limited and only available for a few taxa. This sort of data were reported from specimens of *Pseudofrenelopsis capillata* and *Pseudofrenelopsis* sp., from the Araripe Basin, northeastern Brazil (Sucerquia et al., 2015; Batista et al., 2017), and *Pseudofrenelopsis parceramosa*, from Arkansas, USA, and Wealden, England (Alvin et al., 1981; Axsmith, 2006).

Pseudofrenelopsis species, as well as others frenelopsid members of Cheirolepidiaceae, are considered as valuable indicators of ancient semiarid and arid climates and/or coastal paleoenvironments under certain influence of brackish water (Upchurch and Doyle, 1981; Alvin, 1982; Du et al., 2014). Many of their features corroborate this inference, such as (i) sunken stomata, generally protected by papillae; (ii) the presence of trichomes; (iii) thick cuticle; (iv) tracheids with thickened

* Corresponding author.

E-mail addresses: edenilcebio@hotmail.com (M.E.P. Batista), Lutz.Kunzmann@senckenberg.de (L. Kunzmann), irineudobezerra@yahoo.com.br (F.I. Bezerra), jartur.andrade@yahoo.com.br (J.A.F.G. de Andrade), asa@utad.pt (A.A. Sá), iloiola@ufc.br (M.I.B. Loiola).

walls; and (v) tracheid pits with thickened tori (Upchurch and Doyle, 1981; Watson, 1988; Hill et al., 2012; Sucerquia et al., 2015; Batista et al., 2017).

In the Araripe Basin, the most significant record of *Pseudofrenelopsis* comes from the late Aptian Crato Formation, especially due to the exceptional preservation of the fossil remains in the lacustrine limestone, including the epidermal cell layer with cuticle and vascular tissues (Sucerquia et al., 2015; Batista et al., 2017). These remains enabled the description of the endemic fossil species *P. capillata*, to date the only formally described *Pseudofrenelopsis* species from that basin (Sucerquia et al., 2015). In contrast to the Crato Formation, the less common specimens of *Pseudofrenelopsis* from the Albian Romualdo Formation are found inside carbonate concretions or as impressions in shales, quite often lacking any anatomical details (Lima et al., 2012; Martill et al., 2012; Lima, 2013).

Here, we analyze the morphology and anatomy of a new specimen of *Pseudofrenelopsis* from the Romualdo Formation (CPCA 3698, Centro de Pesquisas Paleontológicas da Chapada do Araripe/Museu de Paleontologia do Departamento Nacional de Produção Mineral, Crato, Ceará State, Brazil) with its exquisitely preserved epidermal cell structure. Based on this, as well as on the distinct shoot morphology, *Pseudofrenelopsis salesii* sp. nov. is proposed and described. It is the first *Pseudofrenelopsis* species that is formally described from the Romualdo Formation. While doing so, the potential of fossil plants from this stratigraphic unit for paleoecological research, beside the well-known Crato Fossil Lagerstätte and ecosystem, is demonstrated, which promises valuable information on the evolution of paleoequatorial environments and vegetation close to the proto-South Atlantic Ocean.

2. Geological setting

The Araripe Basin is a worldwide known sedimentary deposit, located in the border areas of Ceará, Pernambuco and Piauí states in NE Brazil. It is the most extensive intracratonic basin of that region, covering an area of about 9000 km², and its units were deposited upon the Proterozoic basement known as the Borborema Tectonic Province, as well as Paleozoic series (Fig. 1). Geomorphologically, the basin sediments nowadays form the landscape called Chapada do Araripe, which reaches an altitude of about 900 m above sea level, and, in particular, the sandstones and conglomerates of the Upper Cretaceous Exu Formation represent its cap (Ponte and Appi, 1990; Assine, 1992, 2007; Valença et al., 2003). In the NNE part of the plateau, the Vale do Cariri is an important topographic depression providing an almost complete geological section of the basin including the Romualdo Formation.

The latter lithostratigraphic unit outcrops at the foothills of the Chapada do Araripe high plateau and is mainly characterized by greenish shales and less abundant marls and limestone (Ponte and Appi, 1990; Assine, 1992, 2007; Valença et al., 2003). Within the stratigraphic sequence of the Romualdo Formation, there is a ca. 25 m thick interval which is rich in early diagenetic carbonate concretions. These are often fossiliferous, containing three-dimensionally preserved bioclasts in its core. The fossilization of soft tissues is also proven in some cases, which is why this unit is regarded as a Fossil Lagerstätte. The lithology of the formation and the features of the exquisitely preserved fossils are consistent with the inference of a depositional environment of calm or slack waters and anoxic to sub-anoxic conditions in its bed, which likely delayed the decay and reworking of the deposited organic remains (Martill, 1988; Maisey, 1991; Kellner, 1996; Fara et al., 2005). Regarding salinity, the water body was likely brackish, although fluvial freshwater contributions cannot be ruled out (Assine, 1992, 2007; Valença et al., 2003). On the other hand, true marine conditions are only inferred for specific layers that are rich in fossil gastropods and echinoids (Assine, 1992, 2007; Valença et al., 2003; Sales, 2005; Batista et al., 2015; Prado et al., 2015). In short, paleoenvironmental reconstructions presume a repeated transition between a freshwater lake

and a marginal marine embayment or lagoon, badly or almost not ventilated in its bed. Water depth is currently unknown, as well as the question on distance of the burial place of the fossils to the lake/lagoon shore is unresolved.

The stratigraphic age of the Romualdo Formation is commonly regarded as Albian based on its dinoflagellate cyst and gymnosperm pollen content (Batten, 2007; Heimhofer and Hochuli, 2010), which is 113.0–100.5 Ma according to the most recent chronostratigraphic chart (version 2018/07; Cohen et al., 2013). Higher resolution in the biostratigraphic backbone is still not available.

The paleoflora of the Romualdo Formation is represented to date by angiosperms and gymnosperms, the latter being the most abundant plant megafossils of the assemblage (Duarte, 1985; Lima et al., 2012). Among them, remains of the genera *Brachyphyllum* and *Pseudofrenelopsis* are the most common. However, most specimens of these taxa are found inside concretions and correspond to poorly preserved remains, being often recrystallized (M.E.P.B., personal observation). In fact, recrystallization destroys cell structures, while keeping the general morphology of the remains, thus hampering further anatomical studies which are essential for taxonomic assignments.

3. Material and methods

The precise geographic provenance of the specimen CPCA 3698 is unknown due to its acquisition through seizure by the Departamento Nacional de Produção Mineral (DNPM, Crato, Brazil). However, the matrix enclosing the holotype is quite similar to that of the concretions from the Romualdo Formation, regarding the color and texture, and, as such, the specimen can be considered as coming from that formation.

For observations of epidermal-cuticular features, a small sample was removed from CPCA 3698 and analyzed in a Quanta 400 kV scanning electron microscope (FEI), at the Unidade de Microscopia Eletrônica of the Universidade de Trás-os-Montes e Alto Douro (UTAD), Vila Real, Portugal. On the other hand, in order to analyze the internal structures, another fragment was removed from the same specimen and sputtered with a gold layer of 20 nm. Then, it was observed under a FEI company's Inspect 50 Scanning Electron Microscope, at the Central Analítica of the Universidade Federal do Ceará, Fortaleza, Brazil. This procedure also included an energy dispersive X-rays (EDS) analysis of the inner portion of the stem.

4. Systematic description

Pinidae Cronquist, Takhtajan and Zimmermann, 1966

Cheirolepidiaceae Takhtajan ex Doludenko, 1978

Pseudofrenelopsis Nathorst, 1893 emend. Srinivasan, 1995

Pseudofrenelopsis salesii sp. nov.

Etymology: The specific epithet is named after the paleontologist Dr. Alexandre Sales, who carried out paleontological research in the Araripe Basin, in particular on the Romualdo Formation fossils and passed away in 2016.

Holotype: CPCA 3698 (Fig. 2).

Horizon and locality: Lower Cretaceous (Albian) Romualdo Formation of the Araripe Basin; locality unknown, Ceará State, northeastern Brazil.

Diagnosis: Internodes with uniform size from the base to the top of each branch; one leaf per node completely encircling the stem ('closed' type), consecutive leaves of a branch form a simple helix. Free part of the leaf very small and triangular; adpressed to the stem. Stomatal complex sunken, distributed throughout the whole abaxial leaf surface, and arranged in well-defined longitudinal rows that converge towards the leaf apex; the rows are separated by 2–4 rows of ordinary epidermal cells; within a row, stomata separated by 2–4 ordinary epidermal cells. Stomatal complex cyclocytic; 4–6 non-papillate, ellipsoid subsidiary cells converging towards the central region of each stoma; stomatal pores obliquely oriented; multilayered epidermis; ordinary epidermal

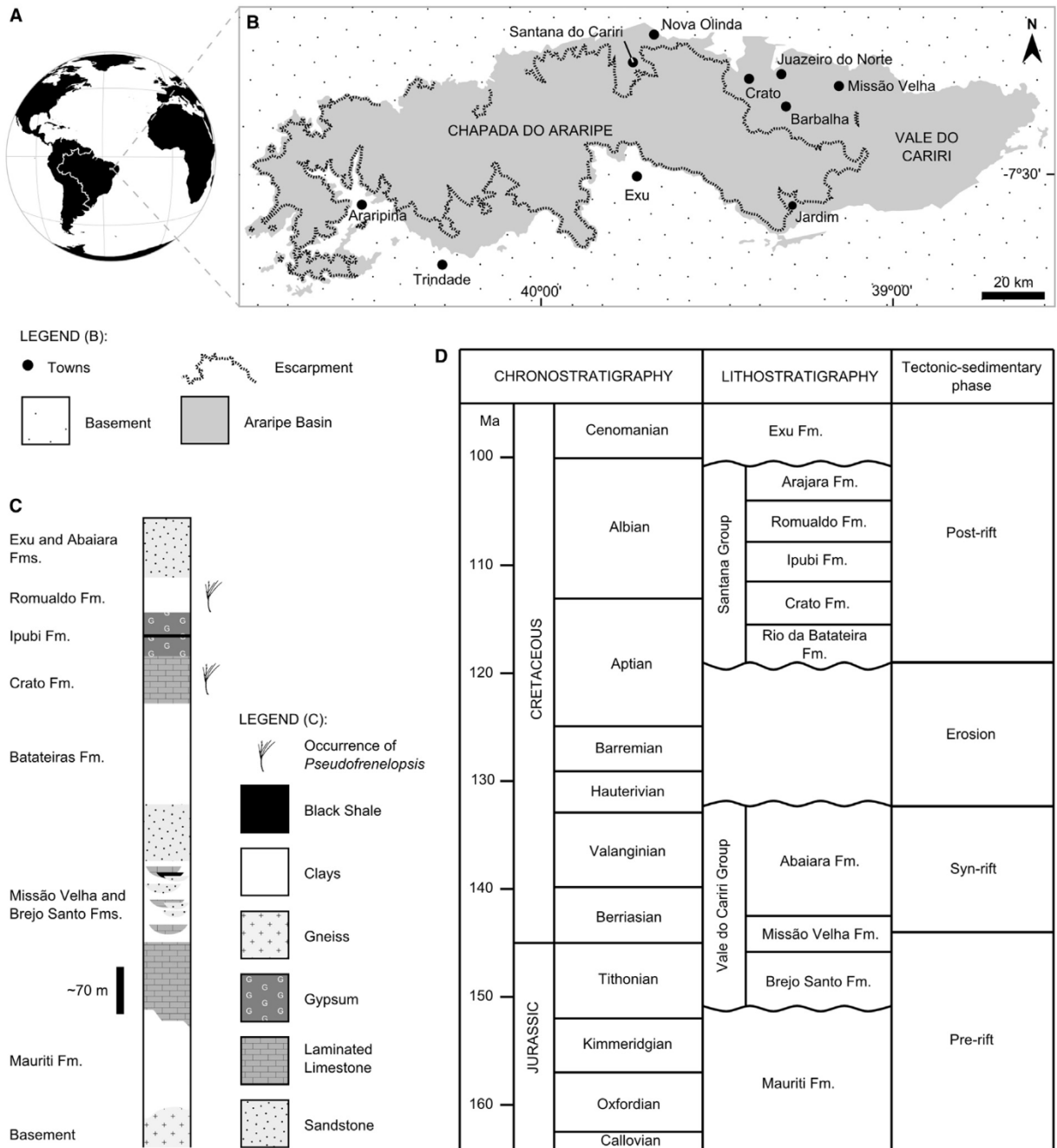


Fig. 1. Location and stratigraphy of the Araripe Basin, northeastern Brazil. A and B, location of the basin and its main geomorphological features. C, generalized stratigraphic log for the north-central part of the basin. D, chronostratigraphic scheme of the basin. Abbreviation: Fm(s), Formation(s). Modified from Martill et al. (2007) and Batista et al. (2017).

cells bearing papillae. Multilayered hypodermis composed of elongated cells; xylem containing tracheids often with areolate pits.

Description: Specimen CPCA 3698 is three-dimensionally preserved. It is 41 cm long and its main branch is 11.92 mm wide, whereas its four secondary branches are 9.5–11.08 mm wide (Fig. 2A). The internodes are short and their sizes are similar from the base to the top of each branch (Fig. 2B). The internodes of the main branch measure between 9.4 and 10.65 mm (average of 9.8 mm) in length and the internodes of the secondary branches are on average 9.36 mm in length. The secondary branches diverge from the main branch in different planes at angles of ca. 29°. Individual branches are built of stem segments, i.e. internodes, which are rugose at their bases and bear a single leaf. The leaf is completely encircling the stem ('closed' type) (Watson, 1977). Positions of free leaf tips of consecutive nodes form a simple helix, i.e. produce a spiral/helical phyllotaxis (Fig. 2B). The free part of the leaf is very

small and triangular (Fig. 2C,D). The free leaf tips are mostly broken-off, but, when present, they slightly overlap the subsequent internode base. Striae in the internodes are visible to the naked eye and correspond to well-defined stomatal rows which run parallel to the long stem axis and cover the whole internode surface converging towards the leaf apex (Fig. 2D).

Neighboring stomatal rows are separated by 2–4 rows of ordinary epidermal cells, but in most cases they are separated by three rows (Fig. 3A,B). Within each stomatal row, neighboring stomata are separated by 2–4 or, rarely, by a single ordinary epidermal cell, and they never share subsidiary cells (Fig. 3B). In general, there are 9–10 stomatal rows/mm and ca. 60 stomata/mm².

Stomata are sunken and stomatal complexes are cyclocytic, ranging in diameter from 50 to 75 μm, although the diameter of most of them is 56–68 μm. Each stomatal complex has 4–6, mostly five subsidiary cells

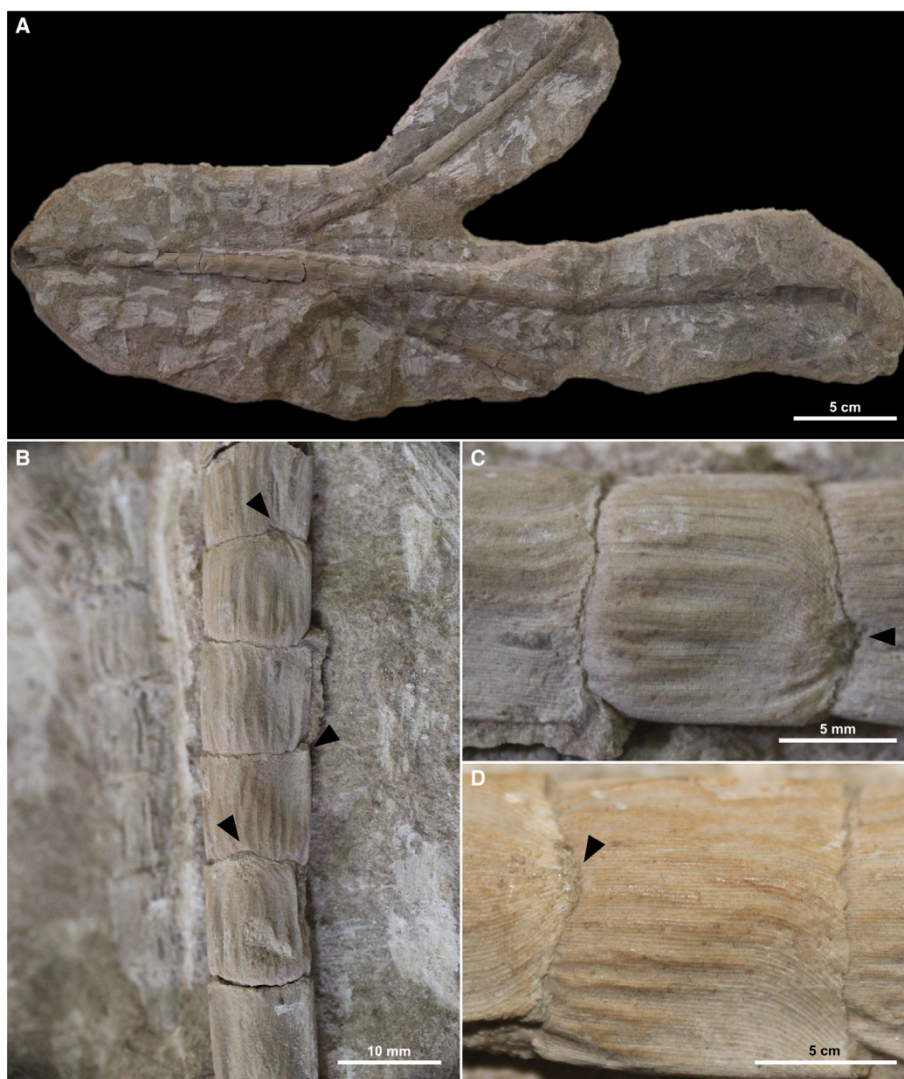


Fig. 2. *Pseudofrenelopsis salesii* sp. nov. (A) specimen CPCA 3698 (holotype). (B) Detail of a branch showing triangular leaves with spiral phylotaxis (arrowhead). (C) Detail of a leaf with its apex deteriorated (arrowhead). (D) Leaf with well-marked longitudinal rows converging to the apex (arrowhead).

(Fig. 3C). These cells are ellipsoid and non-papillate but project towards the central region of each stoma, giving a stellate aspect to the stoma complex, especially when it is covered by solids (Fig. 3D). Subsidiary cell are 15–33 μm wide. The guard cells are more sunken than the subsidiary cells. They are kidney-shaped and are 20–30 μm long and 4.5 μm wide (Fig. 4A). All observed stomatal pores are obliquely oriented (Fig. 4C) and some of them, at the base of the internodes, are open (Fig. 4B).

The epidermal surface has ordinary cells that can be squared, rectangular, rounded or even irregular in shape, and most of them bear a single papilla (Fig. 4A,D,E). The papillae are rounded and their diameter is ca. 10 μm (Fig. 4B). The base of the leaf is visible (Fig. 5A,B). In cross-section, the epidermis is multilayered, with two or three cell layers (Fig. 5C). Ordinary epidermal cells are 13–28 μm wide and 11–36 μm long, depending on their shape. Cells of the lower layers are irregular in shape.

Below the epidermal cells, the multilayered hypodermis contains elongated cells, interrupted in the stomatal region (Fig. 5C,E). Below the hypodermis, the mesophyll is composed of tightly packed elongated cells of the palisade parenchyma and oval-shaped cells from the spongy parenchyma (Fig. 5D,E).

In the cortical region, there are juxtaposed cells, most of which display on their surface bump-like projections of unknown origin (Fig. 5F). Regarding the poorly preserved vascular system, it is composed of tracheids with areolate pits (Fig. 5G).

5. Comparisons and discussion

Specimen CPCA 3698 can be unambiguously attributed to the genus *Pseudofrenelopsis*, because it has only one ‘closed-type’ leaf per node, helically arranged, which are diagnostic features of the genus (Watson, 1977). It cannot be attributed to the genus *Frenelopsis*, because the latter has consistently three leaves per node (the whorled arrangement; Watson, 1977, Sucerquia et al., 2015). The fossil is characterized by a unique combination of morphological and anatomical characters which is why *P. salesii* sp. nov. is proposed.

Although *P. salesii* is clearly distinct, it shares a number of features with other congeneric species (see Tables S1 and S2). Among the latter, *P. capillata* from the Crato Formation is the most similar one. However, some features of the Romualdo Formation species, such as internodes of uniform sizes, non-papillate subsidiary cells, stomata spread along the whole leaf, and the presence of a hypodermis (Tables S1 and S2), differ from those of *P. capillata* (Sucerquia et al., 2015). Nevertheless, considering diagnostic characters of frenelopsid species in general these points are proper features for the definition of a new species.

Pseudofrenelopsis salesii also partially resembles the specimen from the Crato Formation considered as *Pseudofrenelopsis* sp. by Batista et al. (2017), especially regarding the shape of the stomatal complexes. However, *P. salesii* has papillae on ordinary epidermal cells in proximity to stomatal complexes and the stomata are distributed along the entire

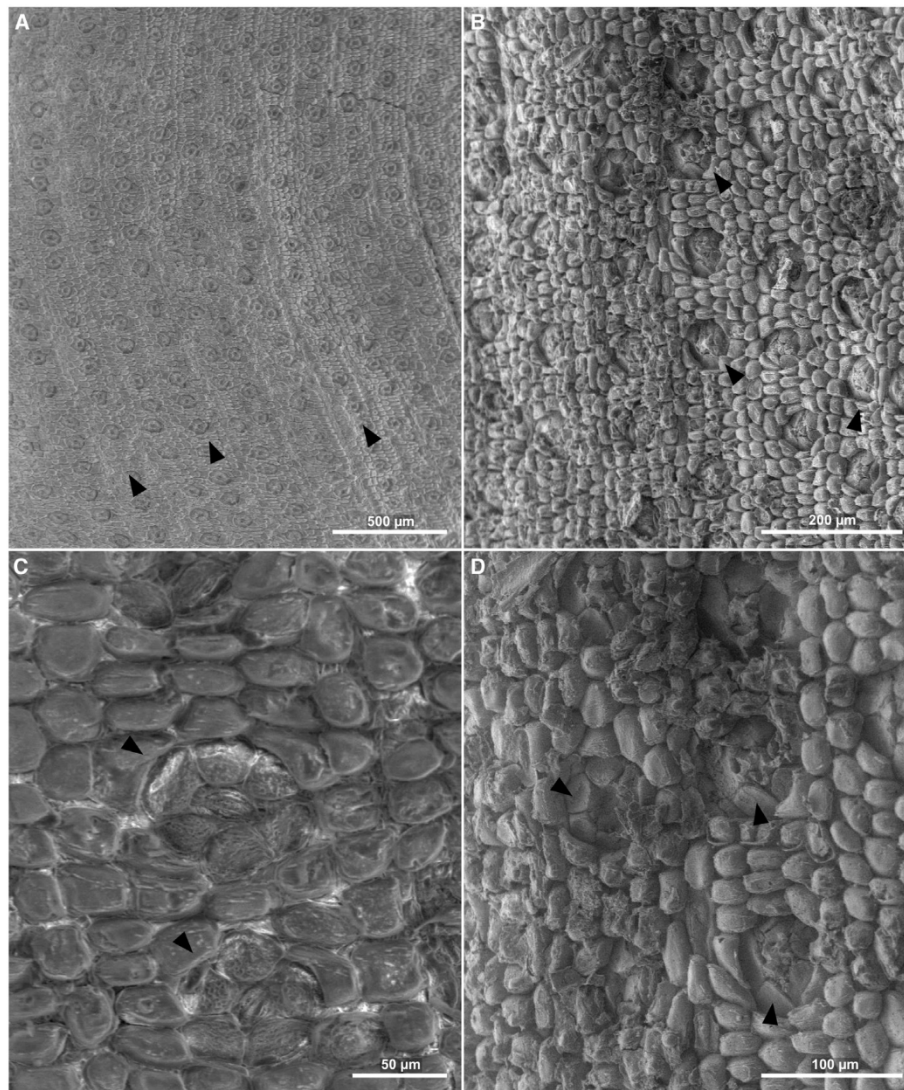


Fig. 3. Epidermal features of *Pseudofrenelopsis salesii* sp. nov. (A) Well-defined stomatal rows (arrowheads). (B) Stomatal complex completely sunken (arrowheads) and separated by ordinary epidermal cells. (C) Cyclocytic stomata with six and five subsidiary cells (arrowheads). (D) Stomatal complex with ellipsoid subsidiary cells (arrowheads) projecting towards the central portion of each stomatal aperture.

leaf surface, whereas the specimen of *Pseudofrenelopsis* sp. has non-papillate ordinary epidermal cells close to the stomata and the distribution of stomata differs between different sections of the leaf surface, with the basal region of leaves presenting less stomata than the other sections (Batista et al., 2017).

Among the features most commonly shared by *Pseudofrenelopsis* species are the papillate ordinary epidermal cells. These structures were already observed in *P. varians*, *P. dalatzensis*, *P. papillosa*, *P. narthorstiana*, *P. liupanshanensis*, and *P. capillata* (Table S2; Watson, 1977; Zhou, 1995; Srinivasan, 1995; Yang et al., 2009; Sun et al., 2011; Du et al., 2014; Sucerquia et al., 2015). However, these species have some features that are not observed in *P. salesii*. For example, *P. varians* has papillate subsidiary cells and irregularly oriented stomatal pores and only its guard cells are sunken (Table S2; Watson, 1977). *Pseudofrenelopsis dalatzensis*, *P. papillosa*, *P. liupanshanensis*, *P. glabra*, *P. guixiensis*, *P. heishanensis*, and *P. parceramosa* have subsidiary cells with their papillae projecting towards the stomatal opening (Watson, 1977; Alvin et al., 1981; Zhou, 1995; Saiki, 1999; Yang et al., 2009; Sun et al., 2011; Du et al., 2014). *Pseudofrenelopsis narthorstiana* has papillate ordinary cells and their stomatal pores are irregularly oriented (Srinivasan, 1995), whereas *P. gansuensis* and *P. intermedia* do not

have trichomes, hairs or papillae on their ordinary epidermal cells (Yang and Deng, 2007; Du et al., 2014), thus differing from *P. salesii* too.

In conclusion, because of the unique combination of features, i.e. uniformly sized internodes of the same branch, stomata in longitudinal rows that are equally distributed on the whole internode surface, stomata sunken, non-papillate and cyclocytic, and ordinary epidermal cells of internodes bearing papillae, *P. salesii* represents a hitherto unknown species, being in particular distinct from the older *P. capillata* of the Crato Formation of the same basin, and beyond from any other *Pseudofrenelopsis* species.

5.1. Paleocological significance

Pseudofrenelopsis is commonly considered as a xerophytic group of plants, able to occupy a wide range of ecological niches (Axsmith, 2006; Du et al., 2014; Sucerquia et al. 2015). Its morphology and anatomy support such an inference, as many species have features that are regarded as responses to water stress, i.e. discontinuous water availability, such as reduced leaves, sunken stomata protected by papillae, and thick cuticles (Lewis, 1972; Bernardes-de-Oliveira et al., 2014; Du et al., 2014). Some authors also regard this genus as halophytic plants

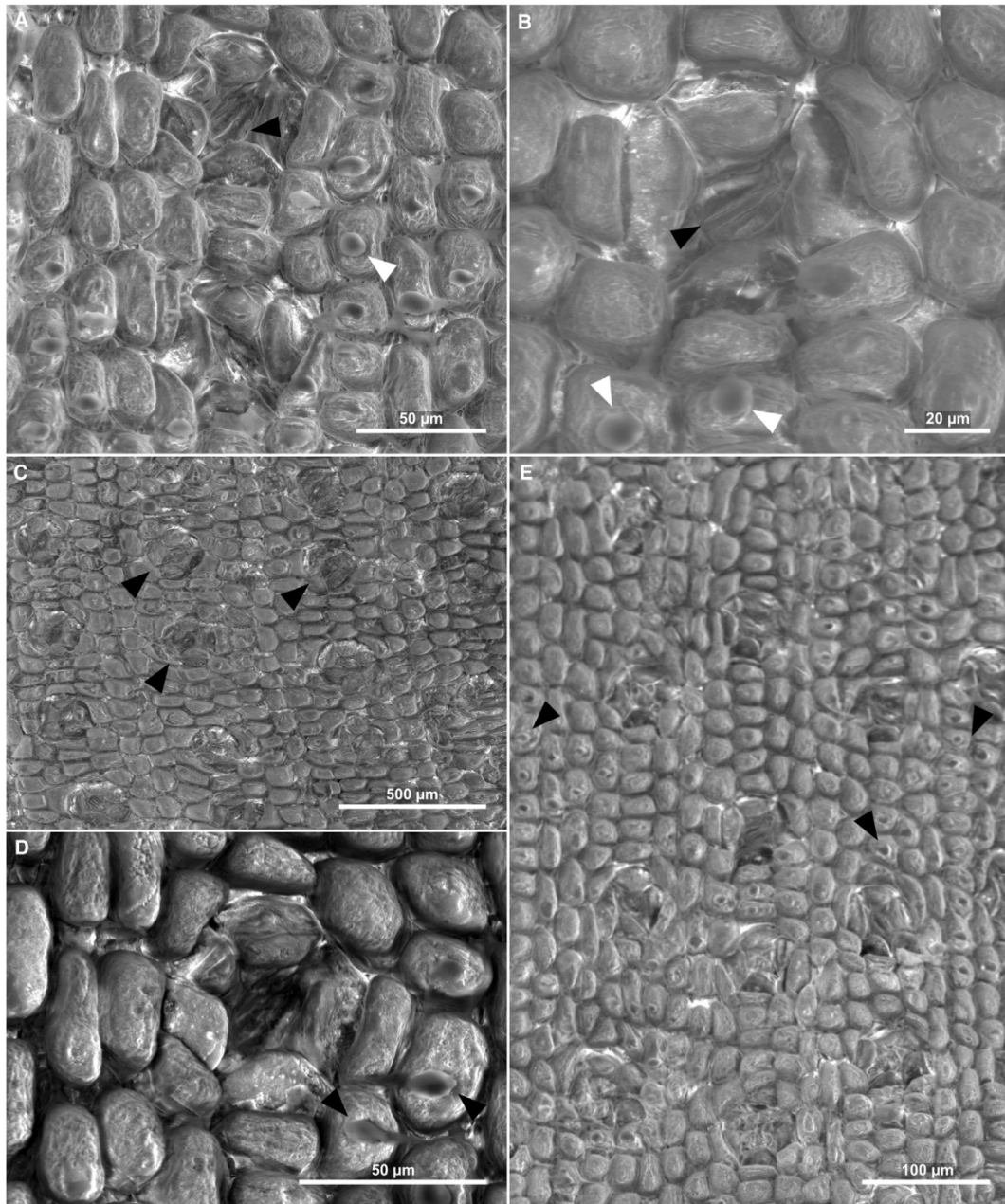


Fig. 4. Epidermal features of *Pseudofrenelopsis salesii* sp. nov. (A) Stomatal complex with kidney-shaped subsidiary cells with oblique stomatal opening (black arrowhead) and papillate epidermal cells (white arrowhead). (B) Detail of the base of an internode showing a stomatal opening (black arrowhead) and epidermal cells with rounded papillae (white arrowheads). (C) Stomata with oblique openings (arrowheads). (D) Detail of a stomatum and epidermal cells with papillae (arrowheads). (E) Detail of an internode showing various stomata and papillate ordinary epidermal cells (arrowheads).

(Upchurch and Doyle, 1981; Sucerquia et al., 2015). For instance, *P. varians* from Texas, USA, might have been indeed a halophyte, inhabiting swampy coastal areas (Upchurch and Doyle, 1981). Actually, water stress can be due to various factors, such as lasting droughts, high salinity in ground water and/or soil, volcanism, or two or more factors simultaneously (Rotondi et al., 2003; Bernardes-De Oliveira et al., 2014; Grigore et al., 2014).

Regarding the Araripe Basin species, *Pseudofrenelopsis* sp. and *P. capillata* from the Crato Formation have, in general, similar features to those observed in *P. salesii* (Sucerquia et al., 2015; Batista et al., 2017). Sucerquia et al. (2015) suggested that the xeromorphism of *P. capillata* might have been an adaptation mainly to the hypersaline and/or arid conditions of its habitat in the Crato Formation. However, the precise habitat conditions are a matter of debate as the fossil remains are embedded in lacustrine limestones and the particular

growing place conditions such as soil characteristics and potential influence of brackish groundwater are still unknown.

In the case of *P. salesii*, reduced leaves, the succulent aspect of the stem, sunken stomata and multilayered hypodermis are the clearest xeromorphic adaptations of this species. Moreover, specimen CPCA 3698 is well-preserved and shows almost no evidence of abrasion. Its branching and relatively large size are rarely seen in other *Pseudofrenelopsis* specimens, as they are usually broken at the nodes (Yang and Deng, 2007) producing shorter sections of axes. This suggests that the Romualdo Formation specimen might not have undergone relatively long-distance transport from its growing site to its burial place (Scheihing and Pfefferkorn, 1984; Ferguson, 1985; Gastaldo et al., 1996) which was a lake and/or lagoon. Thus, the adaptations for water stress of *P. salesii* may have been also due to the assumed saline condition of the lagoonal lakeshore during the deposition of the Romualdo

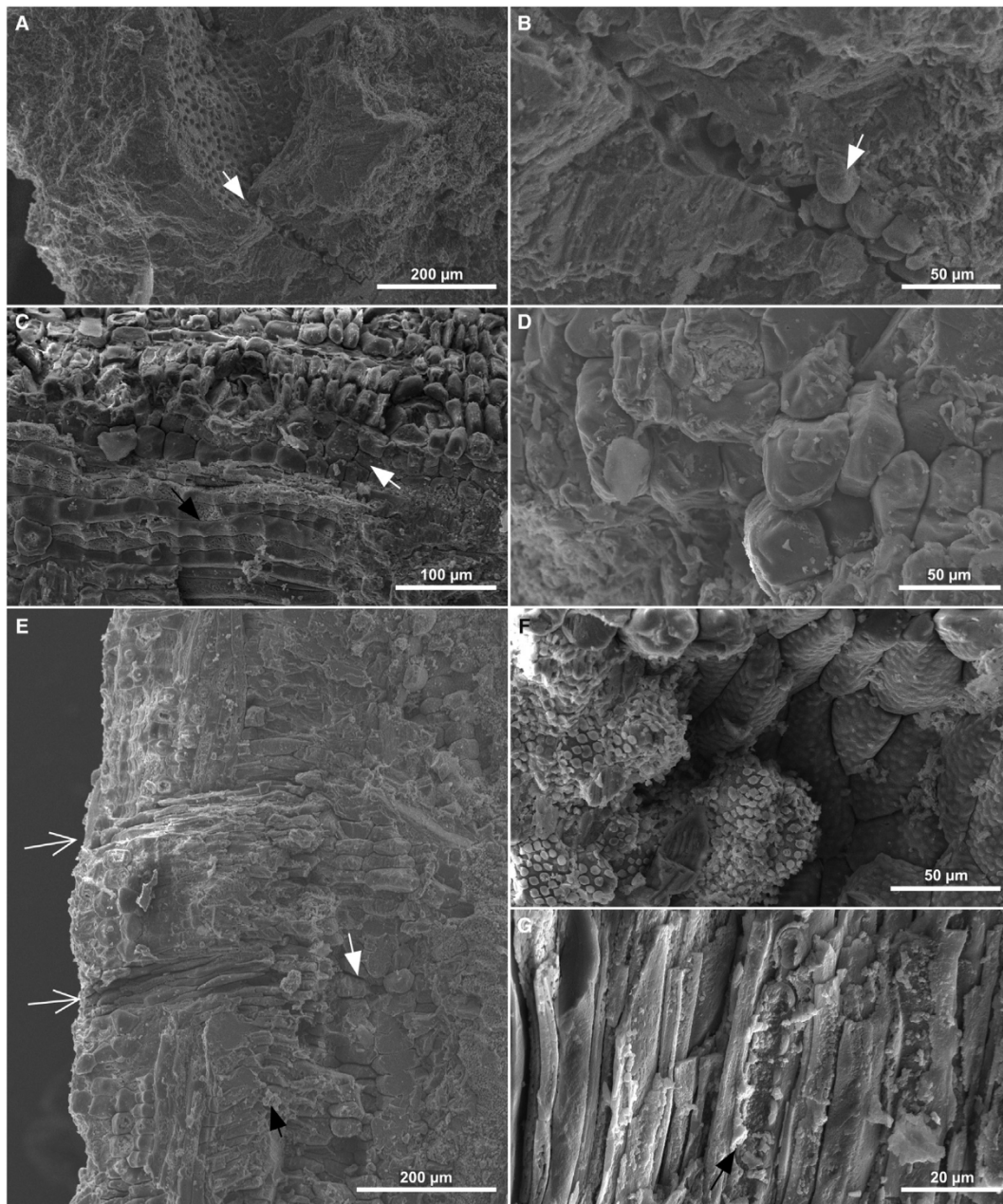


Fig. 5. Anatomical features of *Pseudofrenelopsis salesii* sp. nov. (A) Base of the node displaying epidermal cells (white arrow). (B) Detail of the area shown in (A). (C) Multilayered epidermis (white arrow) and hipodermis (black arrow). (D) Detail of the cells of the spongy parenchyma. (E) General view of the multilayered epidermis and hipodermis, palisade (black arrow) and spongy (white arrow) parenchyma, and stomatal chambers (white open-headed arrows). (F) Cells of the cortical region displaying bump-like projections on their surface. (G) Xylem composed of tracheids and areolate pits (arrow).

Formation. Saline or brackish conditions are also evidenced by the presence of dinoflagellates (Arai, 2009). However, the paleoenvironment of the Romualdo Formation was characterized by both lagoonal and arid settings and it is thus not distinguishable if the xeromorphic character is more an adaptation to the regional climate, or the expression of a salt-tolerant autecology. Actually, as proposed for the Crato Formation species too, it is likely that the xeromorphic characters of *P. salesii* are adapted to both salinity of ground water or soil and (semi-)aridity.

5.2. Taphonomy

The Romualdo Formation is well-known for the exceptional preservation of its fossils mostly enclosed in carbonate concretions. Previous studies on fossils from Romualdo Formation reported delicate morphological and anatomical features and taphonomic aspects, such as

uncrushed preservation and complete skeletal remains (Martill, 1988; Hirayama, 1998; Kellner and Campos, 2002; Freire et al., 2014; Oliveira et al., 2015). On the other hand, plant remains fossilized inside concretions are less common in Romualdo Formation and this is the first time that a well-preserved plant megafossil from this unit is described in detail.

Under normal conditions, a *Pseudofrenelopsis* leafy shoot exposed for a few days under hot (semi-)arid climate would easily dry out, shrink and start decaying. However, CPCA 3698 epidermal cell structure is very well-preserved (Figs. 3 and 4), along with the very delicate parenchyma cells and the residual vascular tissues in the inner portion of the stem (Fig. 5G and Fig. S1A). Possibly, this specimen was directly broken from the mother plant and quickly carried to the depositional environment without any dwelling time as air-exposed plant litter on a forest floor. The anoxic to subanoxic conditions of the lake or lagoon floor of

the Romualdo Formation strongly favored its good preservation, reducing the decomposition by microorganisms (Heimhofer et al., 2008).

On the other hand, the formation of the concretion was especially important for the preservation of the delicate structures of CPCA 3698, as its early diagenesis prevented the crushing of the specimen, keeping its three-dimensionality. In general, the origin of fossiliferous carbonate concretions is associated with local pH changes due to the anaerobic decomposition of the organic matter by sulphate-reducing bacteria (Mortimer et al. 1997; Zatoń and Marynowski, 2004; Heimhofer et al., 2008). When the pH reaches 7–8, calcite may precipitate (Pettijohn, 1975). In this case, the initial anaerobic decomposition of the plant remains was likely responsible for local pH fluctuations. This, in turn, enabled a nucleation site creating a favorable microenvironment for the precipitation of calcium carbonate around the plant remains. This is generally known as autigenic preservation (Schopf, 1975).

Another peculiar feature of CPCA 3698 is that recrystallization, common in concretion fossils from the Romualdo Formation, did not destroy the anatomical structures; the opposite is usually the case for most plant remains from this unit, especially *Brachyphyllum* specimens (M.E.P.B., personal observations).

In relation to the chemical composition, the EDS analyses showed that CPCA 3698 is dominated by calcium, reflecting the abundance of calcite, which constitutes most of the fossil (Figs. S1B and S2). There are also great concentrations of carbon, especially in the inner region of the stem, where the residual vascular tissue is present, indicating this tissue itself as the biogenic source (Figs. S1B and S2). As the precipitation of calcium carbonate took place adjacent to the specimen, the innermost region of the stem was likely less altered by fossil diagenetic processes, partly keeping its original organic constitution. The magnesium content is low for the first carbonates formed in organic-rich sediments (Figs. S1E and S2; Hendry, 1993).

In short, all the processes highlighted above likely contributed to preserve the delicate anatomical features of the specimen CPCA 3698, which enables us to describe, for the first time, the anatomy of a fossil plant from the Romualdo Formation. This is an example of an exceptional preservation, probably, due to two factors: (1) the rapid burial in an anoxic environment, preventing plant tissue degradation by oxidation and microbiological decay; and (2) the early formation of the concretion after the burial of CPCA 3698, which prevented the crushing of its fragile structures and, hence, preserved the anatomical traits important for establishing the taxonomic affinity of this specimen.

6. Conclusion

For the first time, an anatomically preserved plant fossil is described from the Albian Romualdo Formation of the Araripe Basin in NE Brazil. Based on the unique combination of features of the studied fossil specimen, *Pseudofrenelopsis salesii* sp. nov. is proposed. This discovery is meaningful, because it is the first *Pseudofrenelopsis* species formally described from the Romualdo Formation and the second from the late Early Cretaceous Araripe Basin formations. In addition, based on its autecological features, this discovery contributes to the characterization of the paleoenvironment of the Romualdo Formation landscape.

The stratigraphic positioning and xeromorphic characteristics support the hypothesis that the new species was well adapted to hot and (semi-)arid climate, or was even halophytic. This is in accordance both with geological evidence from the Romualdo Formation and with autecological characters of most of the *Pseudofrenelopsis* species. However, based on CPCA 3698 specimen alone, it is not possible yet to determine if the xeromorphism of *P. salesii* was mainly the expression of a single cause, in particular regional climate or halophytic autecology, or if it comprised adaptive responses to both factors. More specimens collected with rigorous lithostratigraphic control, embedded in a depositional model for the Romualdo Formation, might shed new light on this issue. The exceptional preservation of *P. salesii* indicates short-term subaerial exposure and minimal reworking, if at all. Hence, we

suggest that the conifer grew relatively close to the lake shore. It remains an open question if the new taxon was a tree or a shrub.

The leafy shoot of the *P. salesii* is enclosed in a carbonate concretion. This sedimentological structure is built around organic remains during an early phase of cementation and associated calcite nucleation. Indeed, this process avoided the crushing of the fossil plant remains as well as allowing for the preservation of many delicate cell structures of various plant tissues. Our study has demonstrated great potential of the fossil content of this stratigraphic unit, due to the unique three-dimensional preservation process of cell tissues, for paleobotanical and paleoecological studies on a macro- and microscopic scale.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.revpalbo.2018.08.002>.

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