FOSSIL IMPRINT • vol. 74 • 2018 • no. 3–4 • pp. 317–326
(formerly ACTA MUSEI NATIONALIS PRAGAE, Series B – Historia Naturalis)

NATIONAL MUSEUM

SOME CONIFERS FROM THE EARLY CRETACEOUS (LATE APTIAN – EARLY ALBIAN) OF CATEFICA, LUSITANIAN BASIN, WESTERN PORTUGAL

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Mendes, M. M., Dinis, P., Kvaček, J. (2018): Some conifers from the Early Cretaceous (late Aptian – early Albian) of Catefica, Lusitanian Basin, western Portugal. – Fossil Imprint, 74(3-4): 317–326, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Abstract: Several mesofossil floras discovered in the Early Cretaceous rocks from the Lusitanian Basin of western Portugal comprise numerous well-preserved conifer remains. Here we report the occurrence of four conifer types in the mesofossil flora from the Catefica locality, about 4 km south of Torres Vedras in the Estremadura region on the western Portuguese Basin. The specimens were recovered from rocks belonging to the Almargem Formation, interpreted to be of late Aptian – early Albian age. It includes three Cheirolepidiaceae genera *Frenelopsis* Schenk, *Pseudofrenelopsis* Nath. and *Watsoniocladus* V.Sriniv., and one conifer twig of *Pagiophyllum*-type. These conifers, which co-occurred in the same depositional bed with a well-diversified early angiosperm assemblage including flowers, seeds, fruits and dispersed stamens with pollen in situ, provide new insights into Early Cretaceous palaeoecology.

Key words: conifers, mesofossil floras, Early Cretaceous, Almargem Formation, Catefica, Portugal

Received: October 24, 2018 | Accepted: November 28, 2018 | Issued: December 28, 2018

Introduction

Conifers are the most successful and widespread group of extant gymnosperms (Farjon 2010, Farjon and Filer 2013). They evolved from the late Carboniferous onward and attained their greatest abundance and diversity during the Mesozoic (Hernandez-Castillo et al. 2001, Plotnick et al. 2009). In the Mesozoic, particularly during the Jurassic and Cretaceous, conifers were an important component of plant communities and played an important role in terrestrial ecosystems.

Conifer remains are very common in the mesofossil floras from the Lower Cretaceous strata of the Lusitanian Basin in western Portugal, and these studies have yielded new and important information about plant composition and evolution through the Cretaceous (e.g. Friis et al. 1994, 1999, 2010, Mendes et al. 2011, 2014).

The Catefica locality is a road cut between the villages of Catefica and Mugideira about 4 km SSE of Torres Vedras on the western Portuguese Basin. The mesofossil flora from Catefica was first documented by Friis et al. (1994) from light cross-bedded sands with some darker clay beds rich in plant fragments, and is mostly known for its diversity of angiosperm remains, but also contains an astonishing variety of gymnosperms, mainly conifers (e.g. Friis et al. 1994, 1999, 2009, 2010, 2011, 2013, 2014, 2015a, b, 2018, Mendes et al. 2017).

In this paper we describe the occurrence of four conifer types, which co-occurred with a number of angiosperm mesofossils, forming a unique association in the Catefica flora.

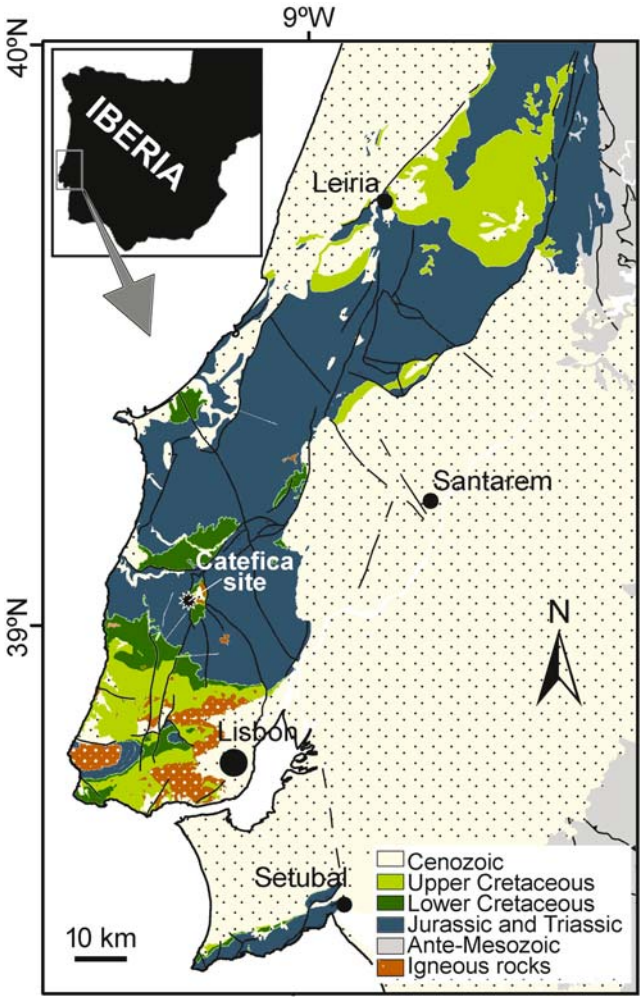
Material and methods

The fossil specimens documented herein were extracted from six rock samples (310, 311, 315, 316, 317 and 318) collected in 2016 by two of us (M. M. Mendes and P. Dinis) from the same plant-bearing horizon in the Catefica exposure (39º 3′ 14.4″ N; 9º 14′ 24.1″ W), in the Estremadura region, Lusitanian Basin, western Portugal (Text-fig. 1). Samples were collected from a dark clay bed belonging to the Almargem Formation and assigned to the "Grés de Torres Vedras" unit (Carta Geológica de Portugal, Folha 30-D

Alenquer; Zbyszewski and Assunção 1965), probably of late Aptian to early Albian in age (Mendes et al. 2017). In the laboratory, the rock samples were disaggregated in water, and washed using a shower through a 125-µm-mesh sieve. The bulk organic matter was cleaned first in 40% hydrofluoric acid (HF), and second in 10% hydrochloric (HCl) acid to remove adhering minerals. They were then thoroughly rinsed in water and dried in air, following standard methods previously described by Friis et al. (1988). Plant fossils were initially investigated under a stereomicroscope. The conifer specimens are both flattened (*Frenelopsis* Schenk and *Pseudofrenelopsis* Nath.) and only slightly compressed and in three-dimensional shape (*Watsoniocladus* V.Sriniv. and *Pagiophyllum*-type conifer).

The specimens selected for more detailed study were mounted on polished aluminium stubs, sputter coated with gold for 60 seconds and examined using a Hitachi Field S-4300 scanning electron microscope (FE-SEM) at 2kV at the Swedish Museum of Natural History, Stockholm.

All photographs were improved for both brightness and contrast, and to remove background irregularities using Adobe Photoshop CS6 software.



Text-fig. 1. Geographical position of the Lusitanian Basin in the western part of the Iberian Peninsula, and detailed map showing the approximate location of the Catefica site where the specimens were collected, indicated by an asterisk.

The fossil specimens are housed in the palaeobotanical collections of the Geological Museum of Lisbon, Portugal (P numbers).

Geological setting

The Catefica outcrop exposure is approximately 4.50 m high, and shows three lithological units (Text-fig. 2):

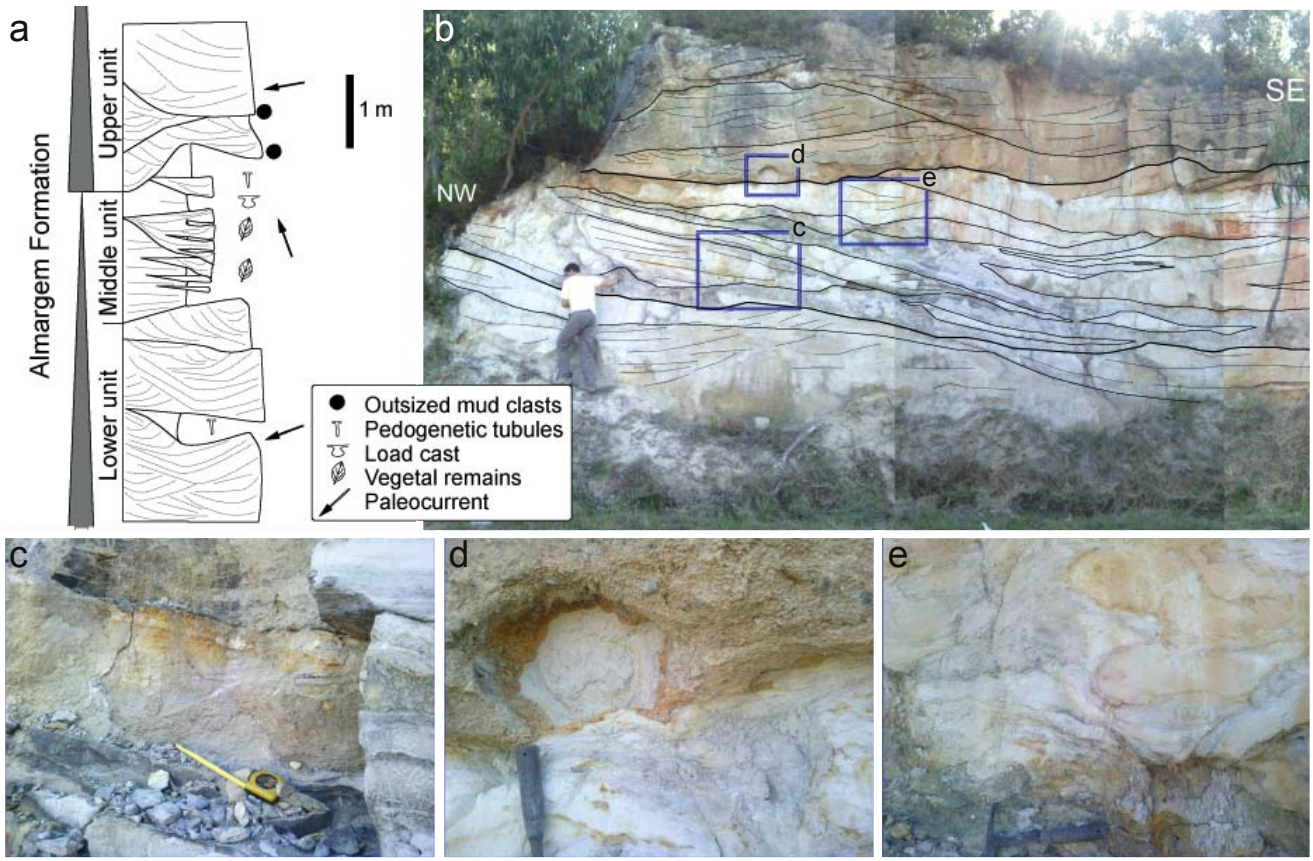
(a) The lower unit mainly consists of white to light grey trough cross-bedded pebbly sandstones. Decimetre-thick mudstone lenses are occasionally interbedded. The contact with the middle unit is occasionally highlighted by a cm-thick iron crust.

(b) The middle unit consists of structureless or cross-bedded, fine to medium-grained sandstones interbedded with organic-rich horizontal laminated, silt-dominated mudstones and very fine-grained sandstones. These beds are lens-shaped, decimetre- to metre-thick, and can be traced laterally for several metres, being organised in an inclined heterolithic depositional unit. The fine to medium-grained sandstones are usually white or light grey, and show a concave lower surface and plane upper surface, although a plane lower surface and convex upper surface also occur. This unit also shows load casts in its lower portion and pedogenetic tubular mottles near the top. The rock samples containing the conifer fossils studied herein were collected from the organic-rich fine-grained beds.

(c) The upper unit consists of yellowish-brown or grey trough cross-bedded pebbly sandstones, and is characterised by amalgamated metre-thick concave-up beds. Its lower boundary is a sharp erosive surface that can be associated with over-sized mudclasts, up to 10–20 cm in diameter.

Rey (1993) interpreted this succession as related to a system of relatively large braided rivers. The lithology and geometry of the middle unit suggest that it is probably related to a lateral accretion architectural element generated by sinuous channels within this river system. Similar environments were described elsewhere (e.g. Makaske and Nap 1995, Miall 1996). The fine-grained beds containing the plant mesofossils were probably deposited during periods of low discharge into the site. The presence of load casts indicates that renewed discharge responsible for sand deposition occurred when the fine-grained beds were still wet. High sedimentation rates account for the low oxidation and bioturbation, which are common only near the top of this middle unit. The amalgamated coarse-grained beds of the upper unit are attributed to a higher energy episode. Steeper relief and the presence of highly mobile channels explain the absence of fine-grained beds within this upper unit.

On the basis of the sharp unconformities and lithological contrast, the three units may correspond to distinct stratigraphic intervals. The lower unit was probably deposited during a sea level highstand that Rey (1993, 2006) considered as belonging to the lower member of the Almargem Formation, which is early Aptian in age (for a more detailed account of the geology see Mendes et al. 2017). The rock samples containing the studied conifer mesofossils were collected from a dark clay bed of the middle unit, probably belonging to the base of the upper member of the Almargem Formation, which is likely of late Aptian to early Albian age (Mendes et al. 2017).



Text-fig. 2. The Catefica locality. (a) Stratigraphic log. (b) General view of the Catefica outcrop. (c) Detail of the fine-grained organic rich fossil beds between sandstones. (d) Out-sized mud clasts at the base of the upper unit. (e) Load casts in the middle unit.

Systematic palaeobotany

Order Coniferales
Family Cheirolepidiaceae Takht., 1963

Genus *Frenelopsis* Schenk, 1869

Type. *Frenelopsis hoheneggeri* (Ettingsh.) Schenk, 1869, p. 13, pl. 4, figs 5–7, pl. 5, figs 1–2, pl. 6, figs 1–6, pl. 7, fig. 1.

***Frenelopsis* cf. *turolenis* B.Gomez in Gomez et al., 2002**
Text-fig. 3a–c

Description. Shoot fragments from bulk macerated material consist of one or two internodes – whorls of three fused leaves each. Whorls alternate at 60º. Leaves are fused along almost their entire lengths, forming an internode (sheath) with no suture in between. The internodes show terminally short triangular free tips with scarious margins (Text-fig. 3a) being up to 13 mm long, and 4 mm wide (the latter corresponding to half a perimeter). The three leaf tips are usually less than 0.5 mm, but they are 2.1 mm in one specimen (Text-fig. 3a). Cuticle surface is papillate to generally smooth. Stomata are arranged in parallel but rather ill-defined longitudinal rows running along to the internode axis. They have typically 4, but sometimes 5 subsidiary cells, each bearing outer papillae (Text-fig. 3c, arrowed). The compound structure of the stomatal chamber shows inner and outer papillae (Text-fig. 3c, arrowed).

Discussion. Through the present, based on the study of their cuticles, up to 20 species of *Frenelopsis* have been described from the Valanginian – Maastrichtian of Belgium, China, the Czech Republic, France, Germany, Goban Spur, Greenland, Italy, Japan, Poland, Portugal, Spain, Sudan, Tajikistan, Ukraine and USA (e.g. Watson 1988, Kvaček 2000, Gomez et al. 2002, 2008, Mendes et al. 2010, Bartiromo et al. 2012, Batten et al. 2014, Barral et al. 2016).

The studied material most closely matches *Frenelopsis turolenis* from the Albian of Spain, but has some characters in common with *F. ugnaensis* B.Gomez from the Barremian of Spain (Gomez et al. 2002). Our material shares the characters of a small inner papillae and a cuticle that is rather papillate, but not hairy, with *F. ugnaensis*. Therefore, we leave it for further study to determine whether the material definitively belongs to *F. turolensis*. Both species show cuticles with stomata arranged in rows. Their stomata are surrounded by typically four subsidiary cells. Typical number of subsidiary cells is a character in which our material differs from other three-leaved *Frenelopsis* species with approximately smooth cuticle: *F. rubiescensis* Barale from the Berriasian – Barremian of Spain (Gomez et al. 2002), *F. occidentalis* Heer from the Early Cretaceous of Portugal and Germany (Alvin 1977), *F. oligostomata* Romariz from the Late Cretaceous of Portugal and Spain, *F. kanevensis* Barale et Doludenko from the Albian of Ukraine (Barale and Doludenko 1985). *F. ramosissima* Fontaine from Barremian – Albian of the USA (Berry 1910, Watson 1977) differs from our material in having stomata surrounded typically by five subsidiary cells and round rim of stomatal pit.

Genus *Pseudofrenelopsis* Nath., 1893

Type. *Pseudofrenelopsis felixii* Nath. in Felix and Nathorst 1893, p. 52, text-figs 6–9.

Note. The genus was emended by Watson (1977) and we accept this emendation here.

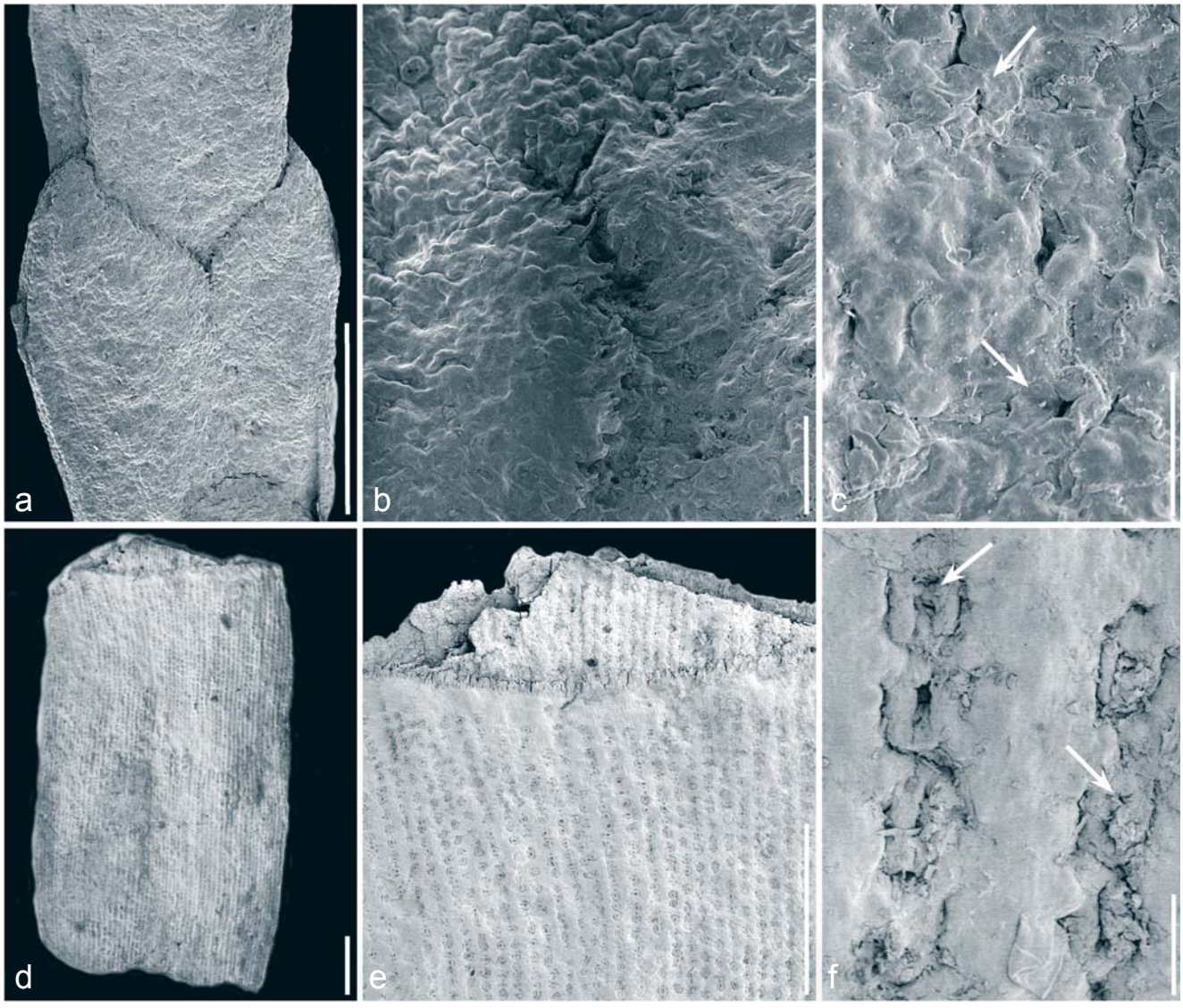
Pseudofrenelopsis cf. *parceramosa* (Fontaine) J.Watson, 1977

Text-fig. 3d–f

Description. The studied mesofossils represent fragments of axes and single stocky leaves. The axes consist of nodes and internodes. Each leaf shows one short free tip (Text-fig. 3d). The flat internodes are up to 6.9 mm long and 3.6 mm wide (the latter corresponding to half a perimeter). The distal margins of leaves bear dense, long, hairy papillae. The leaf tips are up to 0.7 mm long. Stomata are arranged in well-defined parallel longitudinal rows running parallel to the internode axis (Text-fig. 3e). Stomata are circular to elliptical in outline and show a raised elliptical rim (Text-fig. 3f, arrowed). They are surrounded by about 5 papillae set on periclinal walls of the same number of subsidiary cells (Text-fig. 3f, arrowed).

Discussion. *Pseudofrenelopsis* includes 12 species that have been reported from the Berriasian – Albian in Brazil, the Czech Republic, China, Columbia, England, Mexico, Korea, Poland, Portugal, Spain, Sudan and USA (e.g. Nathorst 1893, Reymanówna and Watson 1976, Watson and Alvin 1976, Alvin 1977, Watson 1977, 1983, 1988, Alvin et al. 1981, Zhou 1983, Hluštík 1988, Srinivasan 1995, Saiki 1999, Deng et al. 2005, Axsmith 2006, Moreno Sánchez et al. 2007, Yang and Deng 2007, Mendes et al. 2010, Sun et al. 2011, Kim et al. 2012, Hill et al. 2012, Villanueva-Amadoz et al. 2014, Sucerquia et al. 2015, Peixoto Batista et al. 2017).

The studied material shows important diagnostic characters of *P. parceramosa* – smooth cuticle with stomata



Text-fig. 3. SEM micrographs of two types of conifers from the Early Cretaceous mesofossil flora of Catefica, Portugal. (a) Shoot fragment of *Frenelopsis turolensis* with terminally short triangular free tips (P0357, sample Catefica 310). (b) Outer surface with papillae and stomata arranged in longitudinal rows (P0357, sample Catefica 310). (c) Stomatal chamber with outer and inner papillae (arrows) (P0357, sample Catefica 310). (d) Flat internode of *Pseudofrenelopsis* cf. *parceramosa* (P0132, sample Catefica 315). (e) Outer view of the abaxial surface showing stomatal rows (P0132, sample Catefica 315). (f) Detail of stomatal rows showing massive rings around the stomatal pits (arrows) (P0132, sample Catefica 315). Scale bars = 1 mm (a, d, e); 100 µm (b); 50 µm (f); 5 µm (c).

arranged in well-defined rows (Alvin 1977, Watson 1977). The aperture of the stomatal pit is rounded, formed by a well-developed rim (Florin ring). However, its papillae on subsidiary cells sunken in stomatal pits are not always visible. In this preliminary study we assign it to the species *P. parceramosa*, which was described by Alvin (1977) from the Early Cretaceous of Portugal. This species was reported from the Late Cretaceous of USA (Fontaine 1889, Watson 1977), Portugal (Alvin 1977), Great Britain (Watson and Alvin 1976, Alvin et al. 1981, Watson 1977, 1983, 1988), Poland (Reymanówna and Watson 1976) and is generally one of the best known frenelopsids (Watson 1988).

Genus *Watsoniocladus* V.Sriniv., 1995

Type. *Watsoniocladus valdensis* (Seward) V.Sriniv., 1995, p. 267 ≡ *Thuites valdensis* Seward, 1895, p. 209, pl. 20, fig. 6.

***Watsoniocladus* cf. *virginiensis* V.Sriniv., 1995**
Text-fig. 4a–g

Description. These conifer twigs consist of unbranched stems bearing decussately or semi-decussately arranged leaves of *Brachyphyllum*-type. They are usually borne so tightly together along the stems that the latter are not visible (Text-fig. 4a, e). The apices are usually pointed and falcate in outline, but some specimens show the most distal leaves being rounded (Text-fig. 4e, f). The leaves are up to 2.5 mm long and 1.2 mm wide. The abaxial surfaces are convex and keeled, whilst the adaxial surfaces are concave and unkeeled. The leaves are amphistomatic. Ordinary cells of abaxial cuticle bear papillae, particularly in their terminal parts. The stomata are surrounded by a raised rim with finger-like outer papillae. The papillae form star-shaped stomatal apertures (Text-fig. 4d, arrowed). The stomata are arranged in ill-defined rows (Text-fig. 4c).

Discussion. Based on the opposite decussate leaf arrangement and cuticle characters, the present fossil material is ascribed to the genus *Watsoniocladus*. *Watsoniocladus* consists of at least 6 species collected from the Early Jurassic – Albian of England, France, Germany, Israel, Iran, Japan, Spain and USA (e.g. Watson and Alvin 1999, Srinivasan 1995, Néraudeau et al. 2012, Buscalioni et al. 2018). Due to presence of elongate leaves and papillae borne rather outside then inside the stomatal pits, we compare the studied material with *W. virginensis* V. Sriniv. and *W. florinii* V.Sriniv. described from the Early Cretaceous (early to middle Albian) flora of the Potomac Group in eastern North America (Srinivasan 1995). Both species have papillae and trichomes on their outer abaxial surfaces, papillate stomatal rims and stomata arranged in ill-defined stomatal rows. The present material shows separate leaves, and is therefore assigned to *W. virginiensis* rather than to *W. florinii*, in which adjacent leaves are fused (Srinivasan 1995).

Family indet.

Fossil-Genus *Pagiophyllum* Heer, 1881

Type. *Pagiophyllum crinicum* (Saporta) Heer, 1881, p. 11, pl. 10, fig. 6 ≡ *Pachyphyllum crinicum* Saporta, 1873, p. 37.

Note. The material described here is preliminarily assigned to the genus *Pagiophyllum*. It shows that genus's principal diagnostic characters: helically arranged leaves in which length exceeds their width (Harris 1969). It differs from *Geinitzia* Endl. and *Elatides* Halle in lacking any reproductive structure. From *Cunninghamites* C.Presl it differs in having leaves triangular in cross-section, usually falcate and lacking the conspicuous leaf base cushion and corresponding scar (Kvaček 1999, Bosma et al. 2012).

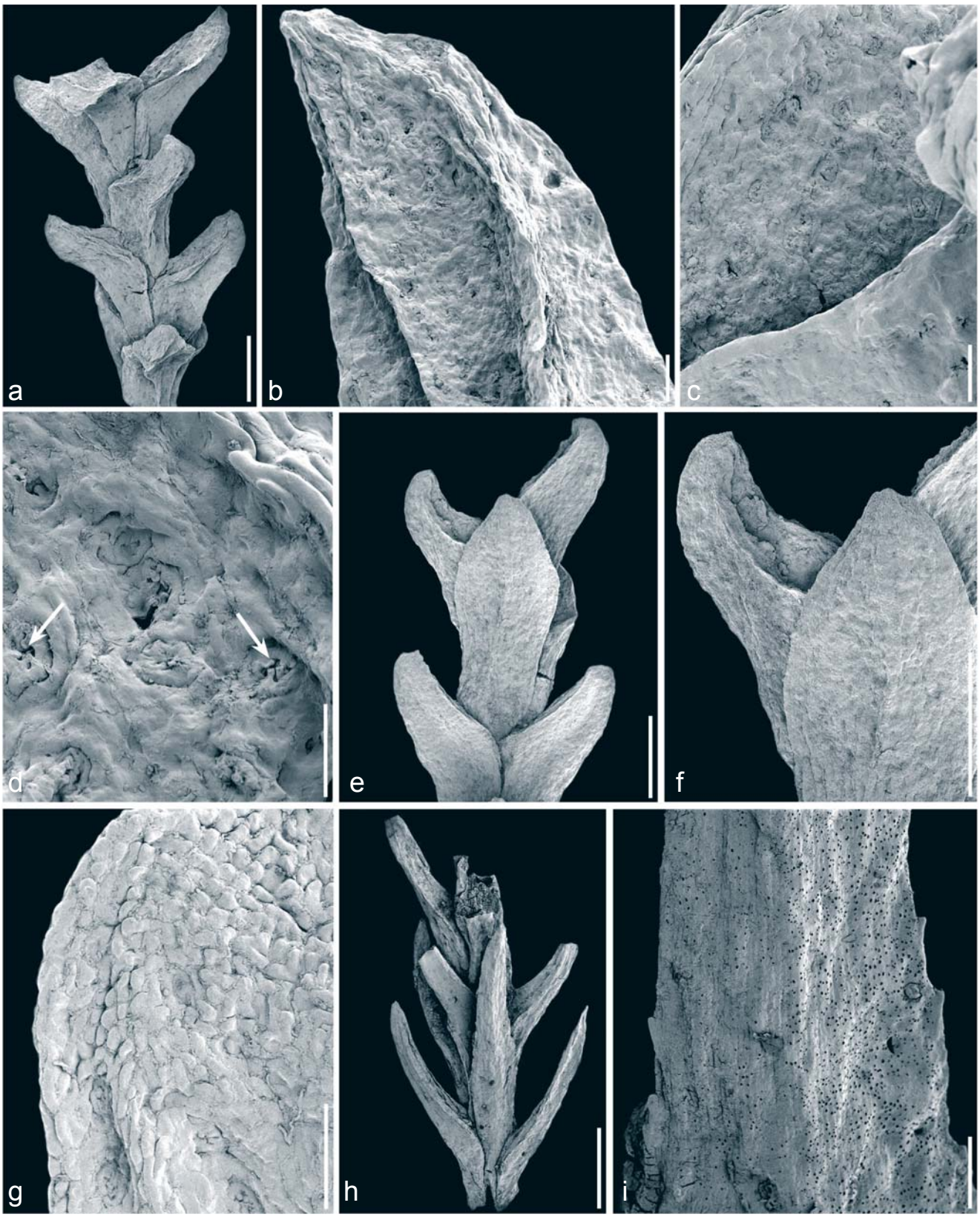
***Pagiophyllum* sp.**
Text-fig. 4h, i

Description. The fragmentary shoot specimens consist of long, slender leaves arranged helically along unbranched axes (Text-fig. 4h). The leaves are up to 3 mm long and 0.6 mm wide. Their leaf cushion is narrowly elongate. They represent a continuation of a basal part of the leaf, without any particular broadened part (Text-fig. 4h). The abaxial surfaces are convex and keeled, whilst the adaxial surfaces are concave. Leaf margins show tiny, regular teeth (Text-fig. 4i). Leaves hypostomatic, stomata lack papillae.

Discussion. This taxon shows helically arranged leaves with stomata lacking papillae. It provides completely different characteristics than the first described group of conifers belonging to the Cheirolepidiaceae. Its stomata do not show any papillae. This type of foliage with falcate, helically arranged leaves may indicate Cupressaceae s.l., but its stomata are not arranged in bands. Due to its fragmentary preservation, the material is left in open nomenclature and its systematic affinity remains questionable. Additional studies should provide more details to its more precise identification.

Discussion and conclusions

Co-occurrences of *Frenelopsis* plus *Pseudofrenelopsis* (e.g. Watson 1977, 1983, Hluštík 1988, Mendes et al. 2010, Moreno Sánchez et al. 2007), *Pseudofrenelopsis* and *Watsoniocladus* (e.g. Watson and Alvin 1996)) and *Frenelopsis* and *Watsoniocladus* (e.g. Watson and Alvin 1999, Buscalioni et al. 2018) in the same plant assemblage have been reported several times. However, all three, *Frenelopsis*, *Pseudofrenelopsis* and *Watsoniocladus* were previously only collected together once, from the Puddledock locality (Potomac Group, Early Cretaceous) in eastern North America (Srinivasan 1995). Remarkably, the Puddledock mesofossil flora is highly diverse, including bryophytes, lycopods, ferns, conifers, and angiosperm flowers and fruits (Friis et al. 2009 and references therein). The Catefica mesofossil flora is similar to the latter, comprising well-preserved angiosperm flowers, fruits and seed as well as dispersed stamens with pollen in situ, conifers, numerous fragments of ferns and thalloid liverworts, several selaginellaceous shoots and megaspores. *Classopollis* pollen grains are very abundant in the Catefica palynoflora (Mendes et al. 2017), as well as in the Potomac Group (Tanrikulu et al. 2018), suggesting a dominance of cheirolepidiaceous conifers in the warm temperate and subtropical Early Cretaceous



Text-fig. 4. SEM micrographs of two types of conifers from the Early Cretaceous mesofossil flora of Catefica, Portugal. (a) Leafy twig of *Watsoniocladus* cf. *virginiensis* with opposite-decussate leaves showing convex, keeled, abaxial surface and concave, unkeeled, adaxial surface (P0127, sample Catefica 316). (b), (c) Details of the leaf apex showing amphistomatic abaxial and adaxial surfaces (P0127, sample Catefica 316). (d) Detail of stomata surrounded by a raised rim with finger-like outer papillae showing star-shaped stomatal apertures (arrows) (P0127, sample Catefica 316). (e), (f) Leafy twig of *Watsoniocladus* cf. *virginiensis* showing hook-shaped leaves in outline (P0129, sample Catefica 317). (g) Detail of the abaxial surface showing stomata arranged in ill-defined rows (P0129, sample Catefica 317). (h) Leafy twig of *Pagiophyllum* sp. showing convex, keeled, abaxial surface and concave, unkeeled, adaxial surface (P0126, sample Catefica 318). (i) Detail of the abaxial leaf surface showing serrate margin and scattered stomata (P0126, sample Catefica 318). Scale bars = 1 mm (a, e, f, h); 100 µm (b, c, g, i); 50 µm (d).

palaeoenvironments. *Frenelopsis* and *Pseudofrenelopsis* are usually reconstructed as shrubs and trees (Alvin 1983, Watson 1988, Axsmith 2006, Barral et al. 2016). Such a long-lived conifer tree forest was certainly a diversified plant ecosystem. We can speculate that early angiosperms could occur in its understory. Some palaeoclimate data has indicated a global warming and increased precipitation during the late Aptian – early Albian in the Lusitanian Basin (e.g. Heimhofer et al. 2012, Bonin et al. 2016). This climate change could be one of the reasons for increased angiosperm abundance, and their eventual dominance (Coiffard et al. 2012).

Acknowledgement

This research was supported by grants from the Amadeu Dias Foundation, the Portuguese Science Foundation (FCT) grant UID/MAR/00350/2013 to CIMA of the University of Algarve. JK was financially supported by the Ministry of Culture of the Czech Republic (DKRVO 2018/05, National Museum, 00023272). We are also grateful for their comments to Johanna H. A. van Konijnenburg-van Cittert (Naturalis, Biodiversity Center, Leiden) and Alexei Herman (Geological Institute, Russian Academy of Sciences, Moscow), who reviewed the manuscript.

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