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Frenelopsis antunesii sp. nov., a new cheirolepidiaceous conifer from the Lower Cretaceous of Figueira da Foz Formation in western Portugal

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Running head: M.M. Mendes and J. Kvaček – *Frenelopsis antunesii* sp. nov. from the Lower Cretaceous of Portugal.

Abstract

Shoots of cheirolepidiaceous conifers assigned to the fossil genus *Frenelopsis* are very common in Portuguese Early Cretaceous mesofossil floras. In this study, a new cheirolepidiaceous conifer *Frenelopsis antunesii* is described from the Lower Cretaceous (upper Aptian –lower Albian) of Figueira da Foz Formation at the Carregueira site, close to the small village of Juncal, in western-central mainland Portugal. The new fossil conifer is described based on morphological characters of vegetative shoots and cuticular features. The new species, *Frenelopsis antunesii*, is characterized by branching segmented shoots with three leaves per node, leaf surfaces distinctly covered by trichomes, leaves with thick cuticles and stomata arranged in short rows. The stomatal apparatus is composed of four or rarely five subsidiary cells. The morphological and anatomical features documented here support the view that *Frenelopsis antunesii* likely grew in a semiarid to arid climate.

***Keywords*:** Fossil plants, Cheirolepidiaceae, *Frenelopsis*, histology, Early Cretaceous, Portugal.

1. Introduction

Members of the extinct conifer family Cheirolepidiaceae are conspicuous and locally dominant elements in Jurassic and Early Cretaceous floras of lower and middle latitudes around the world (Vakhrameev, 1970, 1978; Barnard, 1973). They are represented in the macrofossil record by numerous species based on vegetative shoots, along with associated pollen and seed cones. The Cheirolepidiaceae were initially recognized as a distinct family, based on their distinctive spherical pollen grains with a ring-like germinal groove and striate equatorial band of the *Classopollis* type, notable for its complex ultrastructure (Pettitt and Chaloner, 1964; Barnard, 1968; Vakhrameev, 1970; Alvin et al., 1978; Doludenko, 1978; Pons, 1979; Taylor and Alvin, 1984; Watson, 1988; Zavialova, 2003). In the Northern Hemisphere, the family disappeared at the end of the Cretaceous, but persisted into the Early Paleogene in central Patagonia (Barreda et al., 2012).

The vegetative organs of cheirolepidiaceous conifers are remarkably varied, and include forms that were confused by early authors with Cupressaceae, Araucariaceae and Podocarpaceae. About ten morphogenera include species with characteristic pollen and cones of the family. The genera unequivocally assigned to the family are the Triassic/Jurassic genus *Hirmeriella* Hörhammer and the Cretaceous genera *Frenelopsis* Schenk, *Pseudofrenelopsis* Nathorst, *Tomaxellia* Archangelsky, *Androvettia* Hollick et Jeffrey, *Watsoniocladus* Srinivasan, *Glenrosa* Watson et Fisher and *Otwayia* Pole (Hollick and Jeffrey, 1909; Archangelsky, 1963, 1966, 1968; Watson and Fisher, 1984; Srinivasan, 1992, 1995; Pole, 2000; Kunzmann et al., 2006; Tosolini et al., 2015). In addition, especially in the Jurassic, some species of the morphogenera *Brachyphyllum* Lindley et Hutton, *Pagiophyllum* Heer, and *Geinitzia* Endlicher are also members of the family Cheirolepidiaceae (Barnard, 1968; Vakhrameev, 1970; Watson, 1988; Du et al., 2013).

The cheirolepidiaceous conifers *Frenelopsis* and *Pseudofrenelopsis*, which are remarkable for the similar appearance of their vegetative shoots, consisting of nodes and internodes, have an extensive fossil record, spanning nearly the entire Cretaceous. *Frenelopsis* and *Pseudofrenelopsis* have been reported and described in detail from several Lower Cretaceous deposits in Asia, Africa, Europe, North America and South America (e.g., Alvin, 1977; Reymanówna and Watson, 1976; Watson, 1977, 1983, 1988; Alvin and Pais, 1978; Doludenko and Reymanówna, 1978; Srinivasan, 1995; Watson and Alvin, 1999; Kvaček, 2000; Gomez et al. 2002; Mendes et al., 2010, 2014; Sucerquia et al., 2015; Barral et al., 2019). In both genera, free parts of leaves in nodes are unusually small relative to the length of the internodes. The phyllotaxis is whorled in *Frenelopsis* (with three leaves per node), and spiral (with one leaf per node) in *Pseudofrenelopsis*.

The vegetative morphology of *Frenelopsis* and *Pseudofrenelospsis* is markedly xeromorphic (highly reduced leaves, thick cuticle, deeply sunken stomata), but the plants appear to have been adapted to a wide range of habitats (Vakhrameev, 1970; Watson, 1977; Alvin, 1982; Francis, 1983, 1984; Archangelsky and Taylor, 1986; Watson, 1988). In the Late Cretaceous, they were particularly frequent in saline environments and brackish coastal marshes (Upchurch and Doyle, 1981; Gomez et al., 2002; Kvaček 2000; Mendes et al., 2010, 2014).

Although much important early work was carried out in the British Wealden and other areas in northern Europe, Early Cretaceous Cheirolepidiaceae are particularly diverse in the Iberian Peninsula (Romariz, 1946; Barale, 1973; Alvin, 1977; Alvin and Pais, 1978; Pons and Broutin, 1978; Álvarez Ramis, 1981; Almendros et al., 1982; Barale et al., 1988; Daviero, 2001; Gomez et al., 2002; Mendes et al., 2010, 2014, 2018; Mendes and Friis, 2018; Barral et al., 2019; Kvaček and Mendes, 2021).

In this article, a new species assigned to *Frenelopsis* is described based on its vegetative shoots and epidermal characters. The new species, *Frenelopsis antunesii* M.M. Mendes et J. Kvaček, is from the Lower Cretaceous of the Figueira da Foz Formation in the Lusitanian Basin, western-central mainland Portugal, and, thus, adds new information to the known diversity and geographic distribution of cheirolepidiaceous conifers in the Northern Hemisphere.

2. Material and methods

The new species described herein is based on shoot fragments extracted from two rock samples (samples Carregueira 348 and Carregueira 353), collected by M.M. Mendes and P.P. Cunha in 2018 from the basal part of Carregueira opencast clay pit complex, close to the small village of Juncal (39º 35' 24.9'' N; 08º 55' 33.1'' W) in the Estremadura region, western-central mainland Portugal (Fig. 1).

The specimens were extracted from a dark-grey, organic rich mudstone layer previously assigned to the "Complexos Gresosos da Nazaré e Cós-Juncal" of Early Cretaceous age (Carta Geológica de Portugal, Folha 26-B Alcobaça; França and Zbyszewski, 1963). This unit is now assigned to the basal part of the Famalicão Member of the Figueira da Foz Formation, just overlying the conglomerates and sandstone of the Calvaria Member (Dinis, 1999, 2001). Sedimentological and lithofacies correlations initially suggested a late Aptian age for the basal part of the Famalicão Member of the Figueira da Foz Formation (Dinis, 2001, Dinis et al., 2002). However, more recent studies suggest a slightly younger age for this unit, probably early Albian (for a more detailed account of the geological context, see Heimhofer et al., 2005 and Mendes et al., 2022).

The Carregueira mesofossil flora includes numerous angiosperm flowers, fruits and seeds, along with abundant fragments of Cheirolepidiaceae and other non-angiospermous seed plants (Mendes, work in progress). Palynological analyses of samples collected from the same stratigraphic level document a palynoflora dominated by various fern spores and conifer pollen. Angiosperm pollen grains have also been recorded, but comprise a minor portion of the palynofloral assemblage (Mendes et al., 2022).

Fossil plant remains were extracted from rock samples by sieving in water, using a hand-shower through a 125 µm net mesh. The adhering mineral matrix was removed by

treatment with hydrofluoric (40% HF) and hydrochloric (10% HCl) acids, then thoroughly rinsed in water, following standard methods (Friis et al., 1988, 2009).

The fossil specimens were initially investigated using a Nikon SMZ 800 stereomicroscope. Material with preserved morphological details was studied via scanning electron microscopy (SEM). Specimens were mounted on cleaned aluminium stubs using nail polish, coated with gold and examined with a Hitachi S-3700N Environmental Scanning Electron Microscope (SEM) at 2 kV, at the National Museum Prague, Czech Republic.

Selected shoot fragments were used for cuticle analysis. A two-step process was used to remove the opaque coal matter from the target material, and leave clean cuticle for study:

(1) material is macerated with Schulze's reagent (HNO_3 + $KClO_3$) to oxidize the coal matter (for about 30–45 minutes), and subsequently rinsed thoroughly with distilled water, to remove all traces of the acid;

(2) material is treated in a low concentration solution of potassium hydroxide (10% KOH), which dissolves the coal matter oxidized by the Schulze's reagent, then is again thoroughly rinsed with distilled water.

For light microscopy, cuticles were embedded in glycerine and framed with Noyer sealant. Cuticle preparations were examined using an Olympus BX50 light microscope, and photomicrographs were taken with an Olympus DP70 digital camera. Cuticle fragments for scanning electron microscopy were mounted on polished aluminium stubs, coated with gold and examined using a Hitachi S-3700N SEM in the National Museum Prague, Czech Republic.

The SEM-micrographs were enhanced using Adobe Photoshop CS5 software to improve contrast and remove stains from the background.

The fossil specimens and preparations used in this study are all housed in the palaeobotanical collections of the Geological Museum of Lisbon (P numbers).

The specific name of the new fossil is registered in the Plant Fossil Names Registry, hosted and operated by the National Museum, Prague, for the International Organisation of Palaeobotany (IOP).

3. Results

Systematic palaeontology

Order: PINALES Gorozhankin 1904

Family: CHEIROLEPIDIACEAE Turutanova–Ketova 1963

Genus: ***Frenelopsis*** Schenk 1869

Type: Thuites hoheneggeri Ettingshausen 1852, p. 26, pl. 1, figs 6, 7

Remarks on the genus: The genus *Frenelopsis* Schenk was emended by Reymanówna and Watson (1976), and later by Watson (1977). It was established to accommodate vegetative segmented shoots consisting of two or three fused leaves. Basal parts of leaves fused without visible sutures show apically free triangularly shaped tips.

Frenelopsis antunesii M.M.Mendes et J.Kvaček sp. nov. (Plates I-VI)

Holotype: P0861 (Carregueira sample 353; illustrated here in Plates I, II, VI, 1).

Plant Fossil Names Registry Number: PFN002668 (for new species).

Repository: Geological Museum of Lisbon.

Paratypes: P0862 (Carregueira sample 353), P0860 (Carregueira sample 358), P0866, P0867 (both from Carregueira sample 348), P0997 (Carregueira sample 353), P0998, P0999 (both from Carregueira sample 354).

Etymology: In honour of Professor Miguel Telles Antunes for his contributions to palaeontological studies in Portugal.

Type locality: Carregueira opencast clay pit complex, close to the small village of Juncal, Estremadura region, western-central mainland Portugal (39º 35' 24.9'' N; 08º 55' 33.1'' W).

Type unit: Figueira da Foz Formation.

Age: Early Cretaceous (late Aptian–early Albian).

Diagnosis: Segmented axes with leaves arranged in whorls of three. Leaves fused basally without suture, forming nodes. Apical parts of leaves free, triangular. Surfaces of leaves and their margins covered by trichomes and papillae of varying lengths. Stomata in rows surrounded by four and rarely five subsidiary cells. Subsidiary cells bearing two pairs of papillae, one outer pair and one inner pair of papillae within the stomatal pit.

Description: The holotype P0861 represents a fragment of a young, branched axis 4.5 mm long (Plate I, 1–4). Each of the branches is 1 mm thick. The basally and medially fused leaves form an internode. Free triangular leaves are 0.8 mm long and 0.8 mm broad (Plate I, 2). Leaf tip margins are fringed by trichomes similar to those on the epidermal surface. Epidermal cells are quadrangular to polygonal, usually isodiametric, in some cases elongated (20–25 x

20–45 µm); stomata are arranged in short rows, surrounded by typically four and in few cases five subsidiary cells (16–35 x 30–40 µm, Plate VI, 1). Stomata are sunken in deep stomatal chambers; the chamber walls are formed by those subsidiary cells, creating quadrangular or star-shaped openings at the surface. Ordinary cells bear conspicuous trichomes 50–140 µm long (Plate I, 4).

Other studied material of this species consists of branch fragments 5–7 mm long. They are flattened and 1–2 mm broad. Paratype P0997 has apical parts of three leaves, forming an internode in this larger (older) specimen. They are not fused for their entire length, leaving a short unfused gap at the top of the suture (Plate IV, 4). In some specimens (paratype P0862), leaf tip margins are only papillate, rather than hairy. The epidermis of the internode bears fine longitudinal wrinkles (Plate IV, 3). Cuticle of older branches (again P0997) show a rather different pattern, particularly heavier cutinisation, shorter trichomes and circular openings of stomatal pits. All branches have stomata in the internodal area, arranged mostly in rows of varying lengths, but also with sporadic outliers (Plates V, 2, Plate VI, 2); rows mostly perpendicularly and, in some cases obliquely oriented to the twig axis. As in the holotype, each stoma is surrounded predominantly by four or rarely five subsidiary cells (20–35 x 35–60 µm). Subsidiary cells bear papillae pointing into the stomatal chamber, never to the surface. The stomatal chamber is 30–40 µm deep (Plate V, 1, 4). Within the chamber, the papillae are arranged in two oppositely oriented pairs, orientation alternating around the circumference, so that each identically oriented pair each faces each other across the chamber (Plate V, 4). In larger (older) branches, external openings of stomatal pits are circular, rarely star shaped, without papillae or ornamentation, sporadically with a slightly elevated circular rim (Plate III, 4, 5). Ordinary cells are quadrangular to elongate–polygonal, (15–38 x 22–60 µm) in shape. Their anticlinal walls are up to 20 µm high and 2–5 µm thick. The periclinal wall is 15–30 µm thick, including deeply cutinised anticlinal walls; the

thickness of the whole cuticle reaches 35–40 µm. Trichomes on ordinary cells vary in size and distribution within the type material (Plate II, 1). It seems younger branches have longer trichomes, whereas older branches have shorter trichomes. The trichomes are isolated or arranged in groups of two or three. Trichomes or groups of trichomes form longitudinal rows (Plate III, 2, 3¸Plate IV, 3). Other, typically larger (older) studied specimens have short trichomes (Plate V, 1); trichomes are typically 50–80 µm, but can reach 120 µm. In some specimens (paratype P0862), the trichomes are interspaced with papillae (Plate III, 1–5); other specimens completely lack trichomes, having only scattered papillae (Plate IV, 4). Adaxial cuticle from apical parts of leaves is delicate, recording quadrangular elongate ordinary cells 10–30 x 25–45 µm (Plate VI, 4).

4. Discussion

Cheirolepidiaceous conifers related to the fossil genus *Frenelopsis* have an extensive fossil record, spanning nearly the entire Cretaceous. Species with three leaves per whorl have been reported from the Early Cretaceous floras of Africa, Asia, Europe and North America (see Table 1).

The new species, *Frenelopsis antunesii*, described here, is similar to *F. ugnaensis* Gomez from the upper Barremian of Serranía de Cuenca, Spain (Gomez et al., 2002), in having long trichomes on young shoots. However, *F. antunesii* differs from *F. ugnaensis* in having stomata: (1) arranged predominantly in well-defined rows, (2) lacking external papillae, and (3) positioned in large stomatal chambers.

The new Portuguese species *F. antunesii* is similar to *F. ramosissima* Fontaine, described from the Lower Cretaceous of the Potomac Group of Maryland and Virginia, United States of America (Fontaine, 1889; Watson, 1977; Axsmith and Jacobs, 2005), in having trichomes and papillae. However, *F. antunesii* has stomata arranged predominantly in well-defined rows, whereas *F. ramosissima* has rows arranged more randomly. *Frenelopsis ramosissima* has papillae and short trichomes developed on almost all ordinary cells, which *F. antunesii* does not. Moreover, according to observations by Watson (1977), *F. ramosissima* has younger branches with shorter trichomes and older branches with longer trichomes, which is exactly the opposite of *F. antunesii*.

Frenelopsis antunesii is superficially similar to *F. sifloana* Watson, reported from ~~the~~ Lower Cretaceous strata of Sudan (Watson, 1983). However, ordinary cells of *F. sifloana* bear papillae up to 10 µm long, and stomata are arranged in ill-defined rows, each surrounded by large papillae in the throat of the stomatal pit.

The new species, *F. antunesii*, is also somewhat similar to *F. justae* A. Barral, B. Gomez, V. Daviero-Gomez, C. Lécuyer, M.M. Mendes et T.A.M. Ewin, described from the middle–lower upper Albian Escucha Formation, San Just, Spain, in having of three leaves per whorl and stomatal apparatus arranged in rows. Nevertheless, *F. justae* differs in the absence of trichomes on the internode surface, and in having stomatal apparatus composed of three subsidiary cells (Barral et al., 2019).

Most of the described *Frenelopsis* species have an epidermal surface that is smooth or wrinkled, but never hairy. Those species are *Frenelopsis hoheneggeri* (Ettingsh.) Schenk emend. Reymanówna et Watson from the Hauterivian of the Silesian Carpathians in Poland and Czech Republic (Reymanówna and Watson, 1976), *F. occidentalis* Heer from the Berriasian of Germany (Watson and Alvin, 1999), *F. alata* (K. Feistmantel) Knobloch from the Cenomanian of Central Europe and France (Kvaček, 2000), *F. rubiesensis* Barale from the upper Berriasian to Barremian strata of Spain (Barale, 1973, Gomez et al., 2002), *F. occidentalis* Romariz from the Upper Cretaceous rocks of Portugal and Spain (Alvin, 1977), *F. kaneviensis* Barale et Doludenko from the Albian of Ukraine (Barale and Doludenko (1985), *F. profetiensis* Bartiromo, Barale, Lumaga, Bravi et Barattolo from the middle Aptian of Profeti, Caserta, Italy (Bartiromo et al., 2009) and *F. teixeirae* Alvin et Pais emend. M.M. Mendes, B. Gomez, J. Dinis et J. Pais reported from the Lower Cretaceous of Portugal (Mendes et al., 2010).

Cheirolepidiaceous conifer plants occupied a wide range of environments (Watson, 1977, 1988; Watson and Alvin, 1996, 1999; Barreda et al., 2012; Tosolini et al., 2015). Regarding the present study, rock samples collected from the same stratigraphic level produced a rich and well-preserved palynoflora, dominated by fern spores and gymnosperm pollen. This indicates the presence of wet fluvial environments in the lowlands, and drier but still moderately humid hinterland vegetation, dominated by conifers (Mendes et al., 2022).

Notably, no evidence of marine influence was found. The fragmentary nature of all *F. antunesii* finds to date and the species rarity within the taphocoenosis argues for its allochtonous provenance. It has consistently delicate axes, which are indicative of a small shrub form. The features evident in *F. antunesii* are clearly xeromorphic, not halophytic, evidenced by the ~~total~~ absence of marine phytoplankton in the palynoflora (Mendes et al., 2022), and so are most likely adaptations to a semiarid or arid climate and stressed environmental conditions.

5. Conclusions

A new species, *Frenelopsis antunesii*, was described based on distinctive shoot characters and cuticle morphology. Thick cuticle, sunken stomata protected by papillae and long trichomes are probably adaptations to extreme environmental conditions (especially water stress) for *F. antunesii*. Moreover, the marginal hairs might have served to capture moisture condensation during the night in semiarid to arid palaeoenvironments. Interestingly, the epidermis of *F. antunesii* has the longest hairs among *Frenelopsis* species. The new cheirolepidiaceous conifer probably grew far from rivers. Furthermore, within the taphocoenosis, its allochthonous provenance is strongly suggested by the relatively rare occurrence and fragmentary nature of the fossil twigs. It has relatively delicate axes, which imply that it was a small shrub.

Frenelopsis is highly characteristic for the Cretaceous Tethys realm, and this new species adds to the diversity of an already species–rich genus.

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Figure captions

Figure 1. (A) Geographical position of Lusitanian Basin in western part of Iberian Peninsula. **(B)** Detailed map showing approximate location of fossil site where specimens were collected indicated by asterisk.

Plate I. SEM images of *Frenelopsis antunesii* sp. nov. from Lower Cretaceous of Carregueira, Juncal, central-western Portugal. **1.** Fragmented twig showing typical ultimate branchlet (Holotype, P0861, sample Carregueira 353). **2, 3.** Detail of holotype showing tips of leaves fringed by trichomes (Holotype, P0861, sample Carregueira 353). **4.** Specimen showing detail of trichomes (Holotype, P0861, sample Carregueira 353). **Scale bars:** 1 mm (1, 2, 3), 200 µm (4).

Plate II. SEM images of *Frenelopsis antunesii* sp. nov. from Lower Cretaceous of Carregueira, Juncal, central-western Portugal. **1.** Internode surface covered by trichomes interspaced with papillae (Holotype, P0861, sample Carregueira 353). **2.** Epidermal surface of internodal area, showing trichomes and stomatal pits with star-shaped openings (Holotype, P0861, sample Carregueira 353). **Scale bars:** 200 µm (1), 100 µm (2).

Plate III. SEM images of *Frenelopsis antunesii* sp. nov. from Lower Cretaceous of Carregueira, Juncal, central-western Portugal. **1.** Fragmented twig showing sparse branching and different internode lengths (Paratype, P0862, sample Carregueira 353). **2, 3.** Internodes with long hairs and three free leaves (Paratype, P0862, sample Carregueira 353). **4, 5.** Detail of internode showing shorter trichomes and circular openings of stomatal pits. **Scale bars:** 1 mm (1, 2, 3), 200 µm (4), 100 µm (5).

Plate IV. SEM images of *Frenelopsis antunesii* sp. nov. from Lower Cretaceous of Carregueira, Juncal, central-western Portugal. **1, 2.** Internodes of different lengths and leaf apices showing hairs at apical edge (Paratypes, P0866 and P0867, both from sample Carregueira 348). **3.** Detail of internode with groups of hairs arranged in two or three per group (Paratype, P0867, sample Carregueira 348). **4.** Detail of hairs at apical part of leaf (Paratype, P0997, sample Carregueira 353). **Scale bars:** 1 mm (1, 2), 500 µm (3, 4).

Plate V. SEM images of *Frenelopsis antunesii* sp. nov. from Lower Cretaceous of Carregueira, Juncal, central-western Portugal. **1.** External view of internodal cuticle showing trichomes, and detail of stomata with inner and outer papillae (Paratype, P0997, sample Carregueira 353). **2.** Internal view of internodal cuticle showing stomata in rows (Paratype, P0997, sample Carregueira 353). **3.** Detail of previous specimen showing perpendicularly and obliquely oriented stomata surrounded by four or five subsidiary cells (Paratype, P0997, sample Carregueira 353). **4.** Perpendicular cut view of cuticle showing stomatal chamber with three papillae (of presumably four) indicated by arrows, with alternating heights (Paratype, P0997, sample Carregueira 353). **5.** Detail of stoma, inner part of internodal cuticle (Paratype P0997, sample Carregueira 353). **6.** Perpendicular cut view of cuticle showing anticlinal and periclinal walls of ordinary cells (Paratype, P0997, sample Carregueira 353). **Scale bars:** 100 µm (1, 3), 200 µm (2), 20 µm (4), 50 µm (5), 20 µm (6).

Plate VI. Transmitted light photomicrographs of *Frenelopsis antunesii* sp. nov. from Lower Cretaceous of Carregueira, Juncal, central-western Portugal. **1.** Internodal cuticle showing stomata surrounded by four or five subsidiary cells (Holotype, P0861, sample Carregueira 353). **2.** Overview of cuticle showing stomata arranged in short rows (Paratype, P0997, sample Carregueira 353). 3. Detail of previous specimen showing stomata surrounded by four

subsidiary cells (Paratype, P0997, sample Carregueira 353). **4.** Adaxial cuticle detail showing ordinary cells. **Scale bars:** 50 µm (1, 3), 100 µm (2), 50 µm (4).

Table 1. Morphological features in some described species assigned to the *Frenelopsis* genus.

Species	Leaves per node	Trichomes or hairs on the internode surface	Stomatal arrangement	Number of subsidiary cells	Papillae in throat of stomatal pit	Stratigraphy	Occurrence	Selected references
F. alata	3	Absent	Ill-defined rows	4-5, occasionally 6	Present	Albian-Cenomanian	Czech Republic, France, Portugal, USA	Kvaček (2000)
F. antunesii	3	Present	Well-defined rows	4-5, usually 4	Present	Upper Aptian-Lower Albian	Portugal	Herein
F. hoheneggeri	3	Absent	Well-defined rows	4-6, usually 4	Present	Hauterivian	Czech Republic, Poland	Watson (1988)
F. justae	3	Absent	Bifurcate rows	3-6	Present	Middle-Upper Albian	Spain	Barral et al. (2019)
F. kaneviensis	3	Absent	Ill-defined rows	4-6	Present	Upper Albian	Ukraine	Barale and Doludenko (1985)
F. occidentalis	3	Absent	Well-defined rows	5-6	Massive papillae	Aptian-Albian	Portugal, Germany	Alvin (1977)
F. profetiensis	3	Absent	Well-defined rows	4, rarely 5	No	Middle Aptian	Italy	Bartiromo et al. (2009)
F. ramosissima	3	Present	Ill-defined rows	4-6, usually 5	No	Barremian-Albian	USA	Axsmith and Jacobs (2005)
F. rubiesensis	3	Absent	Well-defined rows	4-6, usually 4	Large rounded	Upper Berriasian-Barremian	Spain	Barale (1973)
F. siflorana	3	Absent	Ill-defined rows	4-5	Present	Lower Cretaceous	Sudan	Watson (1988)
F. teixeirae	2	Absent	Ill-defined rows	5-6	Large	Hauterivian-Barremian	Portugal	Alvin and Pais (1978)
F. ugnaensis	3	Present	Ill-defined rows	usually 4	Present	Upper Barremian	Spain	Gomez et al. (2002)

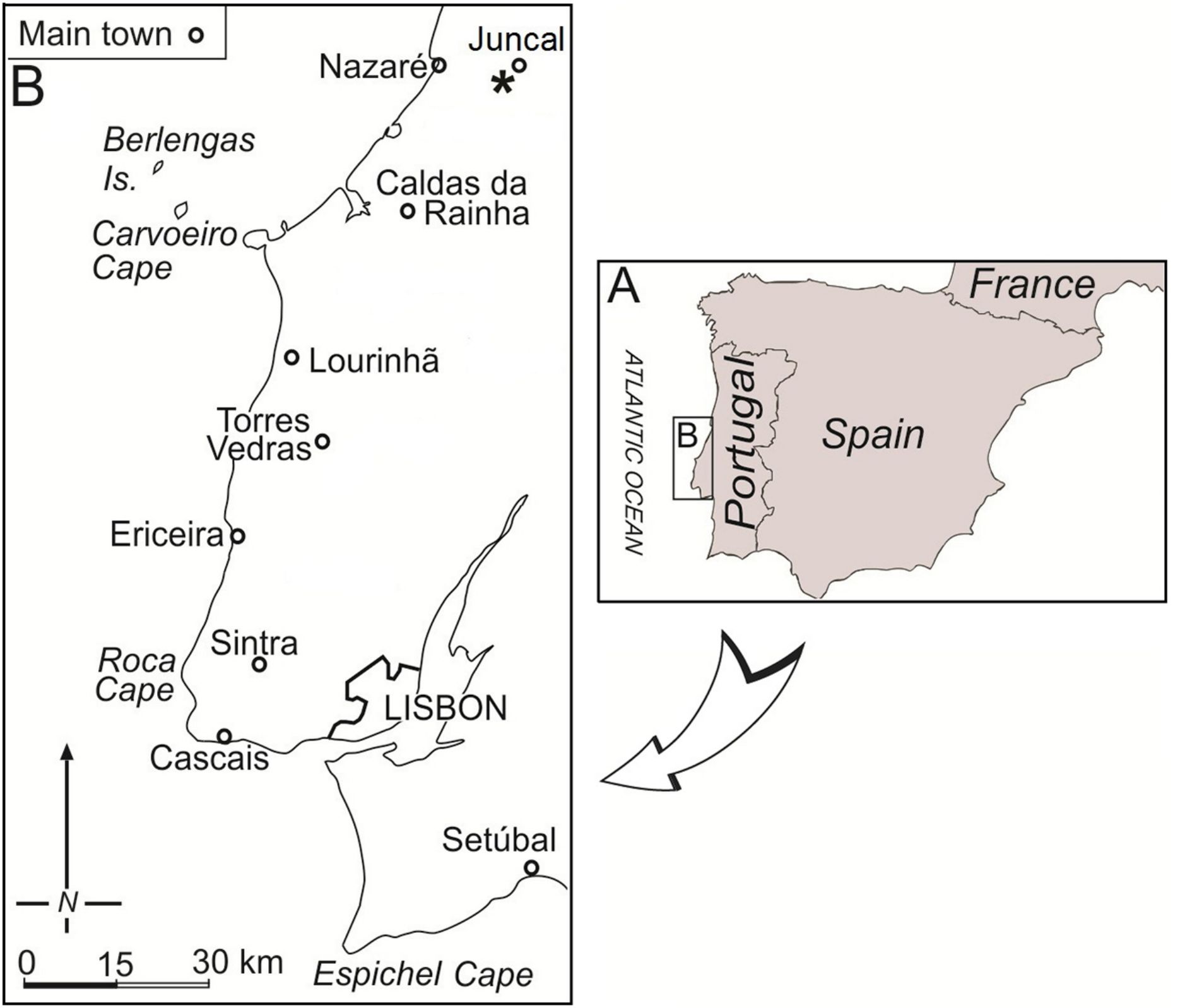
Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Highlights

- A new cheirolepidiaceous conifer is described from the Lower Cretaceous of Portugal.
- *Frenelopsis antunesii* sp. nov. shows segmented shoots with three leaves per node.
- The new species adds new information on the morphological variation in frenelopsids.
- Supports the importance of the cheirolepidiaceous conifers in the Cretaceous floras.


Main town
B
Juncal
Nazaré
Berlengas
Is.
Caldas da
Rainha
Carvoeiro
Cape
Lourinhã
Torres
Vedras
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Roca
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France
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Spain
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Figure 1