

A *FRENELOPSIS* WITH OPPOSITE DECUSSATE LEAVES FROM THE LOWER CRETACEOUS OF PORTUGAL

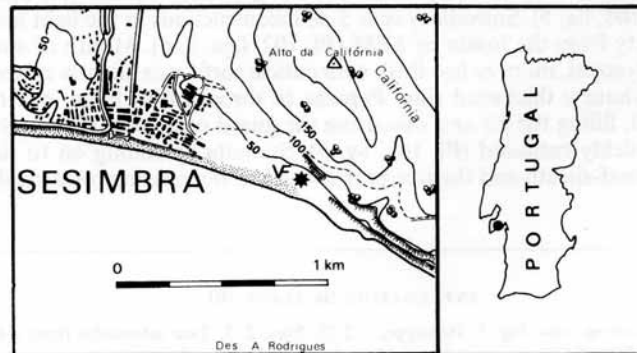
by K. L. ALVIN and J. J. C. PAIS

ABSTRACT. A new species of fossil conifer belonging to the Cheirolepidiaceae (Hirmerellaceae) of Hauterivian or Barremian age is described from Portugal. It differs from other known species of this genus in leaf arrangement and cuticle details. The significance of leaf arrangement in the group is discussed.

FRENELOPSIS Schenk (1869) as amended by Reymanówna and Watson (1976) is distinguished from *Pseudofrenelopsis* Nathorst (1893) (In Felix and Nathorst 1893) [= *Manica* Watson (1974)] by the cyclic as opposed to spiral leaf arrangement. The two genera, both of which are classified in the Cheirolepidiaceae (Hirmerellaceae) on the basis of certain species having been shown to be associated with male cones containing *Classopollis* pollen, have a number of important characters in common. In both, the shoot is strikingly segmented and the leaves are reduced to small teeth, the bases of which typically extend round the stem to form a collar; the internodes are smooth and do not bear decurrent leaf-cushions separated by grooves or 'sutures'. The cuticle and stomatal organization also show a number of important similarities in the two genera (Alvin 1977, Watson 1977).

The new species of *Frenelopsis* we describe here differs from those previously described by having an opposite decussate leaf arrangement.

Material. The plant-bearing bed from which the specimen was collected is believed to be of Hauterivian or Barremian age. It is exposed in the cliff and on the shore just east of Sesimbra (text-fig. 1). Teixeira (1976) has given an account of this deposit



TEXT-FIG. 1. Map showing the position of the fossil plant locality (*).

[Palaeontology, Vol. 21, Part 4, 1978, pp. 873-879, pls. 101-102.]

from which he has described two Bennettitalean leaves, *Pseudocycas tenuisectus* (Saporta) and *Pterophyllum barbaricum* Teixeira. In this paper he briefly referred to the *Frenelopsis* we now describe as well as to the occurrence of fragments of ferns and other conifers in the same bed.

The material consists of a branched twig preserved as a compression in a small block of fine siltstone.

Methods. Cuticle preparations for light microscopy and for scanning electron microscopy were made by the use of the standard maceration and mounting techniques employed previously for similar material (Watson 1977; Alvin, Spicer, and Watson, in press).

SYSTEMATIC DESCRIPTION

Order CONIFERALES

Family CHEIROLEPIDIACEAE (= Hirmerellaceae)

Frenelopsis Schenk emend. Reymanówna and Watson (1976)

Frenelopsis teixeirae sp. nov.

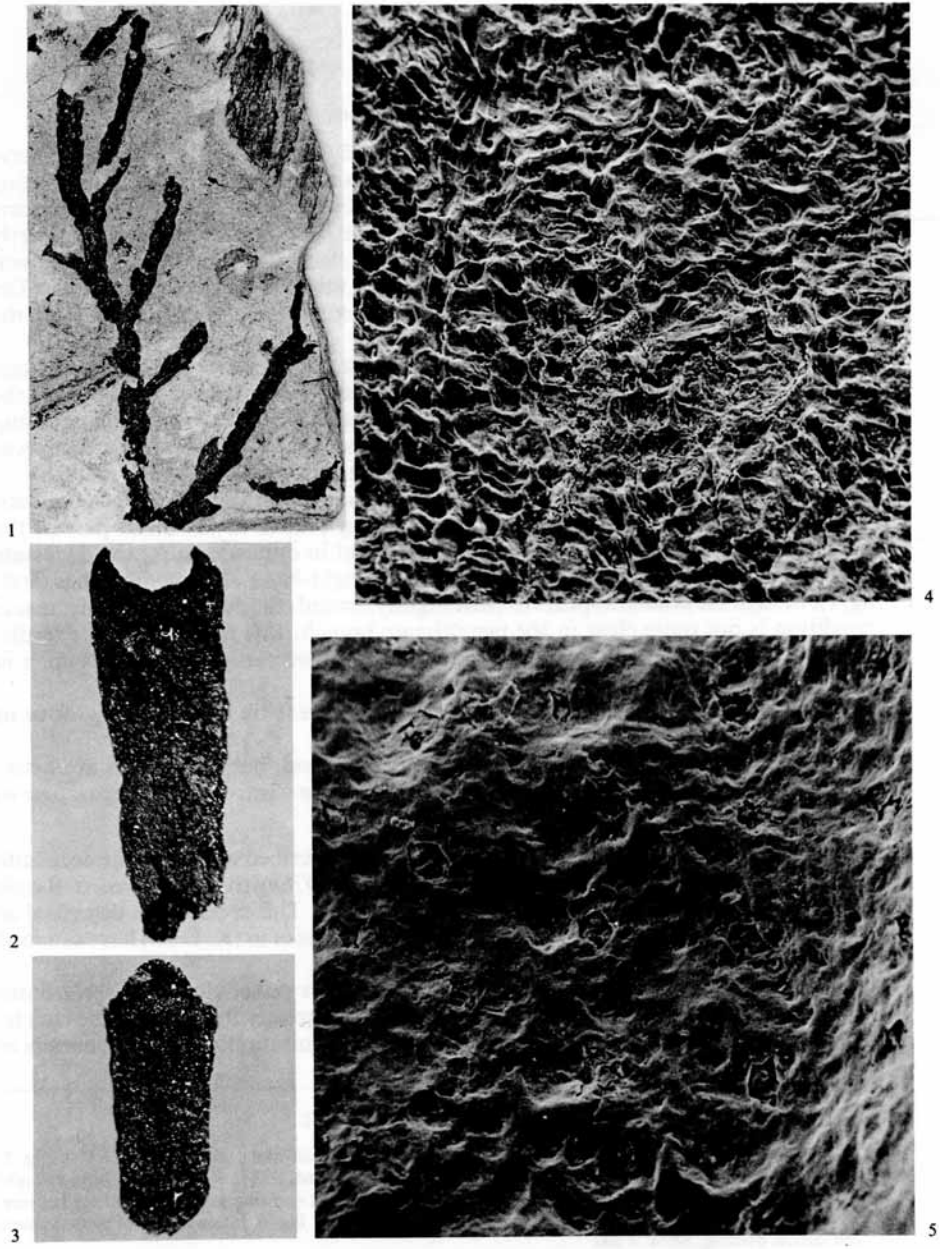
Diagnosis. Branching segmented shoot. Penultimate branch 2.0 mm in diameter, zig-zag; ultimate branchlets arising at about 30°, 1.5 mm in diameter, straight. Segments (internodes) 5.0–6.0 mm long in penultimate branch; 2.5–5.0 mm in ultimate. Leaves in opposite decussate arrangement. Free part of leaf triangular with rounded tip, curving slightly inwards (Pl. 101, figs. 2, 3); tip and edges of leaf very thin, probably scarios, but without discrete hairs; hair-like papillae present on flanks of leaf (Pl. 102, fig. 1).

Cuticle of internode about 50 μm in total thickness (measured in folds under light microscope) with the outer periclinal wall of the epidermis about 15 μm . Epidermal cells mostly isodiametric, not in well defined longitudinal rows; anticlinal walls 5–10 μm thick. Hypodermal cells not clearly marked except sometimes between stomatal rows (Pl. 101, fig. 4).

Stomata about the same optical density as the rest of the cuticle (Pl. 102, fig. 4); arranged in rather irregular longitudinal rows, generally 75–125 μm apart within the rows (Pl. 101, fig. 5). Subsidiary cells 5–6, inconspicuous in the light microscope, but seen clearly from the inside by SEM (Pl. 102, figs. 3, 6). Mouth of stomatal pit stellate or polygonal, more or less flush with cuticle surface or slightly raised (Pl. 102, fig. 2) but without a thickened ring. Papillae in throat of pit large, one from each subsidiary cell, filling the pit and obscuring the guard cells from above. Guard cells moderately thickly cutinised (Pl. 102, fig. 5). Stomata extending on to the abaxial cuticle of the leaf-sheath and the free part of the leaf but ceasing towards the tip and margins.

EXPLANATION OF PLATE 101

Frenelopsis teixeirae sp. nov. Fig. 1. Holotype, $\times 1.75$. Figs. 2, 3. Two internodes from a branchlet of ultimate order with the leaves in, and at right angles to, the plane of compression respectively. Fig. 4. Inside view of internode cuticle, SEM $\times 200$. Fig. 5. Outside view of internode cuticle, SEM $\times 200$.



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Locality. Sesimbra, Estremadura, Portugal.

Horizon. ?Hauterivian or Barremian.

Depository of Holotype. Serviços Geológicos de Portugal, Lisbon.

Further description. The single specimen (Pl. 101, fig. 1; text-fig. 1) apparently represents three orders of branches: we interpret the axis labelled 1 in text-fig. 1 as being the main axis on which the penultimate branch (2) is borne as a lateral. Axis 1 appears thicker and woodier than the other portions of the specimen and has become partly decorticated; only two internodes are reasonably clear. Possibly there is a fragment of a second penultimate branch (2?) represented at the bottom of the specimen. The penultimate axis bears possibly alternately arranged ultimate branchlets, though the ones given off to the left are poorly represented.

A branch apparently arises at nearly every node on the penultimate axis, though branches may cease in the distal part. No node bears more than one branch and the insertion of a branch is associated with a slight displacement of the succeeding segment of the axis producing a somewhat zig-zag shape. The branch system was probably not planate; it does not all lie in one flat bedding plane of the matrix.

The opposite decussate leaf arrangement is best seen in the ultimate branchlets. The segments (Pl. 101, figs. 2, 3) removed from a branch in the distal part of the specimen demonstrate clearly the leaf arrangement in opposite pairs; the decussate alternation is clear in the middle one of the three right-hand ultimate branches (text-fig. 1), though the branch appears to twist slightly towards the distal end. The decussate condition is not quite clear in the penultimate branch; this is probably due to distortion associated with branching and perhaps to compression of the specimen in fossilisation.

Internodes such as that in Pl. 101, fig. 2, make it clear that there is no groove or 'suture' extending down from between the two leaves.

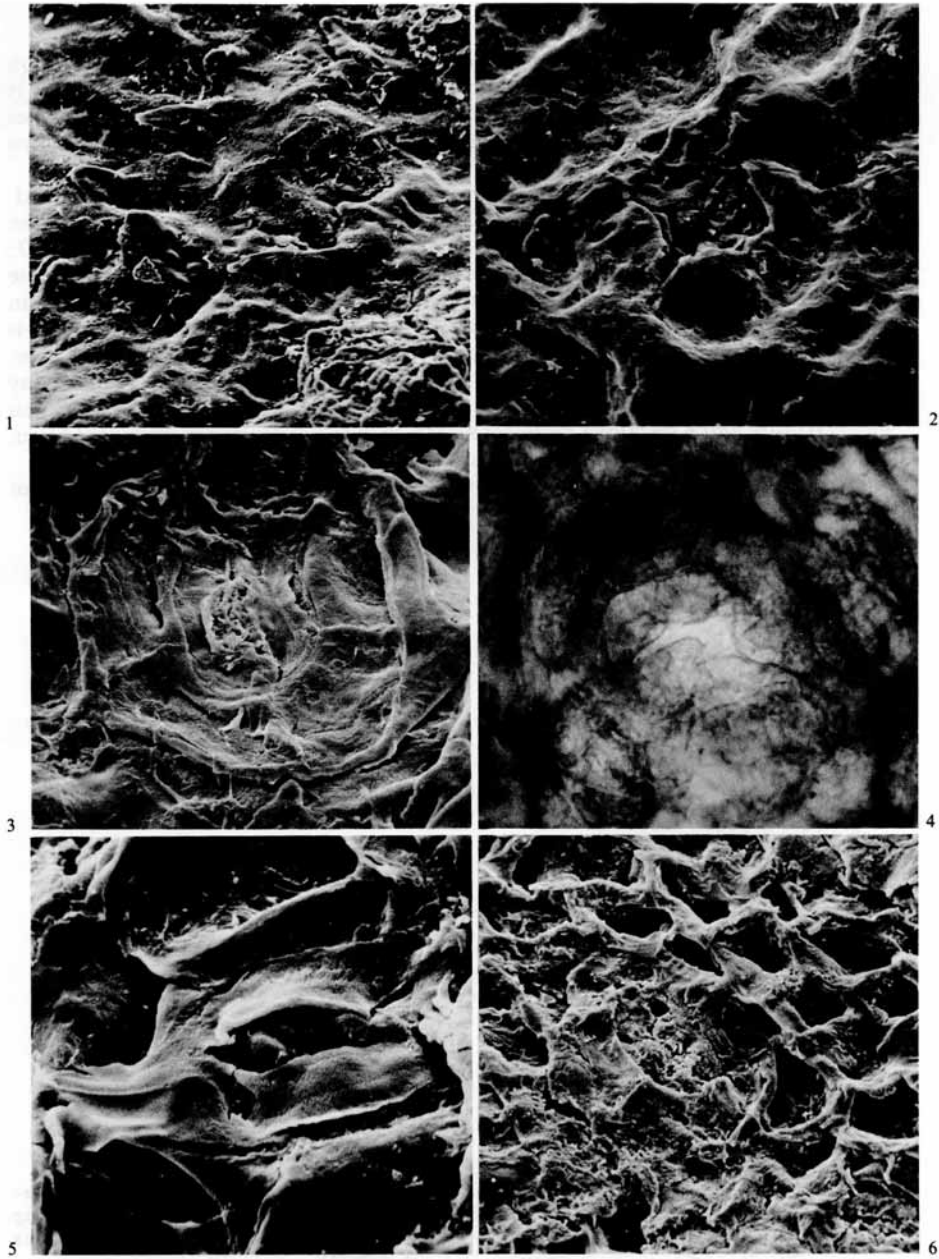
The preservation of the cuticles is generally not good, but some areas are better preserved than others. It has not been possible to make a satisfactory preparation of the adaxial leaf cuticle.

Discussion. No other species of *Frenelopsis* has been described with opposite decussate leaves. The reference by Hlušík and Konzalová (1976b) to *F. rubiesensis* Barale (1973) as having leaves in pairs seems to be a mistake. This species was described as having leaves in whorls of three and specimens which one of us (K. L. A.) has examined in the British Museum (Natural History) confirm this.

In general cuticle features this new species resembles rather closely *F. occidentalis* Heer emend. Alvin (1977). Indeed the differences (the greater thickness of the cuticle, the smoother outer surface, the more continuous cutinisation of the hypodermis in

EXPLANATION OF PLATE 102

Frenelopsis teixeirae sp. nov. Fig. 1. Part of flank of leaf showing hair-like papillae, SEM, $\times 600$. Fig. 2. External view of stoma, SEM, $\times 800$. Fig. 3. Internal view of stoma, SEM, $\times 800$. Fig. 4. Stoma. Light microscope, $\times 800$. Fig. 5. Internal view of well preserved stoma showing guard-cell cuticles between which can be seen some papillae of the stomatal pit, SEM, $\times 1600$. Fig. 6. Internal view of stoma; guard cell cuticle missing, SEM $\times 500$.

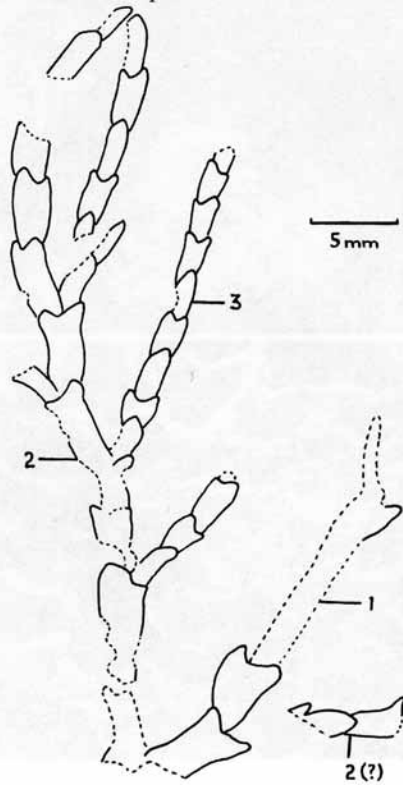


ALVIN and PAIS, *Frenelopsis*

F. occidentalis) could be explained simply in terms of a greater extent of cutinisation and therefore of no very great taxonomic significance. However, *F. occidentalis* is probably younger (Aptian-Albian) and the only known specimen unfortunately does not permit the leaf arrangement to be determined unequivocally. We regard the two species as being distinct.

The two genera *Frenelopsis* and *Pseudofrenelopsis* are probably closely related. Indeed it is doubtful if there are any clearly distinguishing characters other than the different leaf arrangement. On the basis of detailed recent observations (Alvin 1977; Watson 1977) it would appear that the stoma in *Frenelopsis* typically has papillae extending from the sides of the pit, as in the new species described here, whereas in *Pseudofrenelopsis* the papillae, if present, are at the mouth of the pit, though it remains to be shown whether this difference is consistent throughout; in any case, it would seem a small difference. Little is yet known of the reproductive organs of any species, though the microsporophyll and pollen of male cones attributed to *Frenelopsis alata* (Hlušík and Konzalová 1976a, b) and to *Pseudofrenelopsis parceramosa* (Alvin, Spicer, and Watson 1978) present remarkable similarities.

Our new species with two leaves at the node might at first seem to provide an



TEXT-FIG. 2. *Frenelopsis teixeirae* sp. nov. Drawing of the holotype to illustrate the branching and leaf arrangement. Numbers represent orders of branches.

intermediate between the one-leaf condition of *Pseudofrenelopsis* and the three-leaved condition of other species of *Frenelopsis*, but on the basis of the taxonomy of Recent conifers, the important distinction is between the spiral and the cyclic arrangement, and in this *F. teixeirae* falls clearly into *Frenelopsis*. Until more is known of the reproductive and other character of these extinct conifers, it will be convenient to regard the two genera as distinct.

It is possible that leaf arrangement in *Frenelopsis* trees varied from one shoot to another. Although such variation is rare among Recent conifers, it is noteworthy that in *Cupressinocladus pseudoexpansum* Barnard and Miller (1976), another member of the Cheirolepidiaceae, the leaves were in whorls of three on penultimate branches, but opposite decussate on the ultimate. As far as we can tell from our one specimen, the leaf arrangement was the same on three orders of branches.

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