# SOME LOWER CRETACEOUS CONIFERS OF THE CHEIROLEPIDIACEAE FROM THE U.S.A. AND ENGLAND

*by* JOAN WATSON

ABSTRACT. Five species of Lower Cretaceous conifers assigned to the genera *Pseudofrenelopsis* Nathorst, *Frenelopsis* Schenk, and *Cupressinocladus* Seward of the family Cheirolepidiaceae are redescribed and figured with emended diagnoses. Lectotypes of *P. parceramosa* (Fontaine) comb. nov., *P. varians* (Fontaine) comb. nov., and *F. ramosissima* Fontaine are selected from Fontaine's figured specimens in the collection of the National Museum of Natural History, Smithsonian Institution. A specimen of *F. alata* (K. Feistmantel) from Texas is redescribed and compared with the Czechoslovakian type material and specimens from Portugal. The holotype of *C. valdensis* (Seward) from the English Wealden is rediagnosed and its cuticle figured for the first time. *P. varians* and *F. ramosissima* are unlike any living conifer in having a very slender core of wood separated from a very thick cuticle by a wide, succulent cortex, indicating that these species were probably shrubby plants rather than large forest trees. They may have been quite small, salt-marsh plants.

IN the Lower Cretaceous of Europe, North America, Africa, and Asia there are several conifers distinguished by their smooth, cylindrical stems bearing minute leaves, often at long intervals and having a jointed appearance. Most of these have been placed in the genus *Frenelopsis* Schenk and attributed to the Cupressaceae. The type species of *Frenelopsis* was described by Ettingshausen (1852) as *Thuites hoheneggeri* from the Carpathians. Schenk (1869) also describing material from the Carpathians, which he considered identical to Ettingshausen's, removed it to a new genus, *Frenelopsis*, because he considered it to be closer to the living genus *Frenela* (now *Callitris*) than to *Thuja*. Schenk figured several specimens which almost certainly included more than one species. Unfortunately none of Ettingshausen's or Schenk's specimens can be located. In recent years new Carpathian material has been collected (Reymanówna 1965) which also contains two conifers, one with leaves in alternating whorls of three and one with spirally arranged leaves. This three-leaved species has recently been used as the basis for a rediagnosis of the genus *Frenelopsis* Schenk and the type species *F. hoheneggeri* (Ettingshausen) (Reymanówna and Watson 1976). This new generic diagnosis (slightly emended) is repeated below.

Subsequent to Schenk's work a number of authors used *F. hoheneggeri* for material from many countries and about ten further species of *Frenelopsis* have been erected, though some of these are very unsatisfactory.

Whilst revising the English Wealden flora (Watson 1964) I found shoots of a very similar-looking segmented conifer which, however, differs from *F. hoheneggeri* in bearing leaves one at a node and forming a simple spiral. I tentatively identified this as *F. parceramosa* Fontaine (1889) described from the Potomac Formation of the U.S.A. I have since been able to examine the type material in the Smithsonian Institution and to confirm the identity of the English Wealden specimens. On the basis of the phyllotaxis a new genus, *Manica* (Watson 1974) was erected for species with

[Palaeontology, Vol. 20, Part 4, 1977, pp. 715–749, Pls. 85–97.]

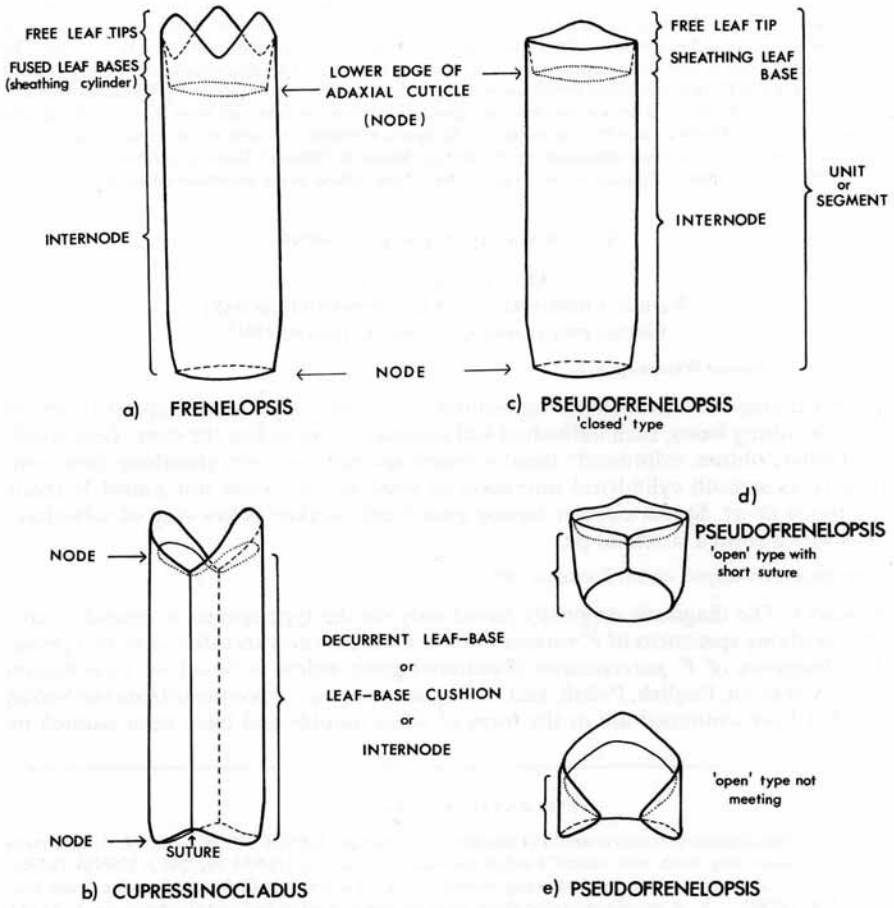
spiral leaf arrangement but otherwise resembling *Frenelopsis*. I have subsequently discovered that Nathorst (1893) erected a genus, *Pseudofrenelopsis*, for shoots of such a species from the Lower Cretaceous of Mexico. Nathorst's type species, *P. felixi* is now known to be identical to material from Glen Rose, Texas described as *F. varians* and *Pagiophyllum dubium* by Fontaine (1893, 1905). This is discussed below in detail but clearly *Pseudofrenelopsis* and *Manica* are synonymous and the diagnosis given for the latter (Watson 1974) will now serve for Nathorst's genus.

Species of *Frenelopsis* and *Pseudofrenelopsis* are sometimes mixed in the same bed and because the leaves are so small may look much alike but are clearly distinguished by their cuticles. An intimate mixture of a *Frenelopsis* species and a *Pseudofrenelopsis* species is present in Lower Cretaceous silicified material from the Sudan (Edwards 1926; Watson in preparation). Reymanówna's Carpathian material is now known to contain *F. hoheneggeri* (Ettingshausen) mixed with *P. parceramosa* (Fontaine) and it is highly probable that Schenk (1869) had the same mixture in his material. When describing *Thuites hoheneggeri* Ettingshausen (1852) also described specimens which he called *Culmites priscus* and regarded as a grass. Schenk (1869) transferred one of these specimens (Ettingshausen 1852, pl. 1, fig. 5) to *F. hoheneggeri*. It consists of two short jointed stems and it may be that *C. priscus* is what is now called *P. parceramosa* (Fontaine) but the figure and description of Ettingshausen do not provide enough information for a clear identification.

Amongst English Wealden material of *P. parceramosa* from the Isle of Wight Dr. K. L. Alvin has found male cones which have yielded *Classopollis* Pflug pollen (to be described elsewhere). *Classopollis* has also been found by Hluštík and Konzalová (1976) in cones attributed to *F. alata* (K. Feistmantel) and by Barnard (1968) and Barnard and Miller (1976) in cones attributed to *Cupressinocladus pseudoexpansum* Barnard and Miller. It therefore seems that these plants hitherto regarded as Cupressaceae should be classified in the family Cheirolepidiaceae. It may be noted here that some authors prefer to use the family name Hirmeriellaceae as the genus *Cheirolepidium* Takhtajan (= *Cheirolepis* Schimper) is no longer in use, being a synonym of *Hirmeriella* Hörhammer.

In describing these jointed cheirolepidiaceous conifers certain difficulties arise in choosing terminology, mainly because the leaf and internode are continuous and the position of the node cannot be seen on the abaxial surface. Text-fig. 1 shows the terminology which is used below for describing the various species of *Frenelopsis*, *Pseudofrenelopsis*, and *Cupressinocladus*. *Cupressinocladus*, which Seward proposed as a form-genus, has whorls of leaves which extend downwards into broad decurrent bases separated by narrow grooves; these are called leaf-base cushions (text-fig. 1*b*). *Frenelopsis* has no such grooves or sutures and consequently no separate basal cushions. The free leaves join laterally to form a cylindrical sheath below which the stem surface is a perfectly smooth cylinder and it seems best to call this internode (text-fig. 1*a*). The node is taken to be the line along which the adaxial cuticle joins the base of the internode above and is more or less transverse. *Pseudofrenelopsis* with its different leaf forms presents further difficulties. Its leaves are one per node and normally have the base of the free part joined into a cylindrical sheath with smooth internode below and a transverse node as in *Frenelopsis* (text-fig. 1*c*; Pl. 85, fig. 4; Pl. 89, fig. 2). In some shoots the leaf is equally broad but does not join into a cylinder

and thus has a suture (Pl. 85, fig. 5; text-fig. 1*d*). Generally in these 'open' leaves the internodes are short and the nodes oblique. In *P. parceramosa* from Portugal Dr. Alvin has seen leaves which are notched in the suture position but are cylindrical below the notch (Alvin 1977). Sometimes the edges of the 'open' type of leaf do not meet (text-figs. 1*e*, 2A) but have a gap filled by the base of the leaf above and in this form it resembles some kinds of *Brachyphyllum*. Clearly in describing these 'open' leaf forms it is convenient to use the terms internode and basal cushion interchangeably.




TEXT-FIG. 1. Diagrammatic representations of disarticulated units of the various genera and the terminology used to describe them in the text.

The purpose of this paper is to redescribe five species from the Lower Cretaceous of the United States and England. They are *P. parceramosa* (Fontaine), *P. varians* (Fontaine), *F. alata* (K. Feistmantel), *F. ramosissima* Fontaine, and *C. valdensis* (Seward).

Fontaine's material was mostly collected last century from several localities in Virginia, Maryland, and Texas. Details of stratigraphic horizons are given with the description of each species. Stratigraphic relations of the Potomac Group localities in Maryland and Virginia are given by Doyle and Hickey (1976).

Most of the American material is housed in the National Museum of Natural History, Smithsonian Institution but one specimen of *F. ramosissima* (bearing a Smithsonian number) is in the Hunterian Museum, Glasgow University. A few of the figured specimens of Fontaine (1889, 1893) and Berry (1911) are missing but most are intact and as Fontaine did not designate holotypes I have selected lectotypes from them. The Glasgow specimen is not recognizable as one of the missing ones. The description of *P. parceramosa* includes figures of English specimens which are in the British Museum (Natural History). Specimen numbers with the prefix USNM are from the Smithsonian Institution, those bearing the letter V. from the British Museum (Natural History), and Pb. the Hunterian Museum, Glasgow. A duplicate set of slides made from American specimens has been deposited in the British Museum (Natural History) (numbers V. 58657–V. 58679) and examples of English *P. parceramosa* have been added to the Smithsonian collection.

## SYSTEMATIC DESCRIPTIONS

### Order CONIFERALES
### Family CHEIROLEPIDIACEAE (HIRMERIELLACEAE)
### Genus PSEUDOFRENELOPSIS Nathorst, 1893

1974 *Manica* Watson, p. 428.

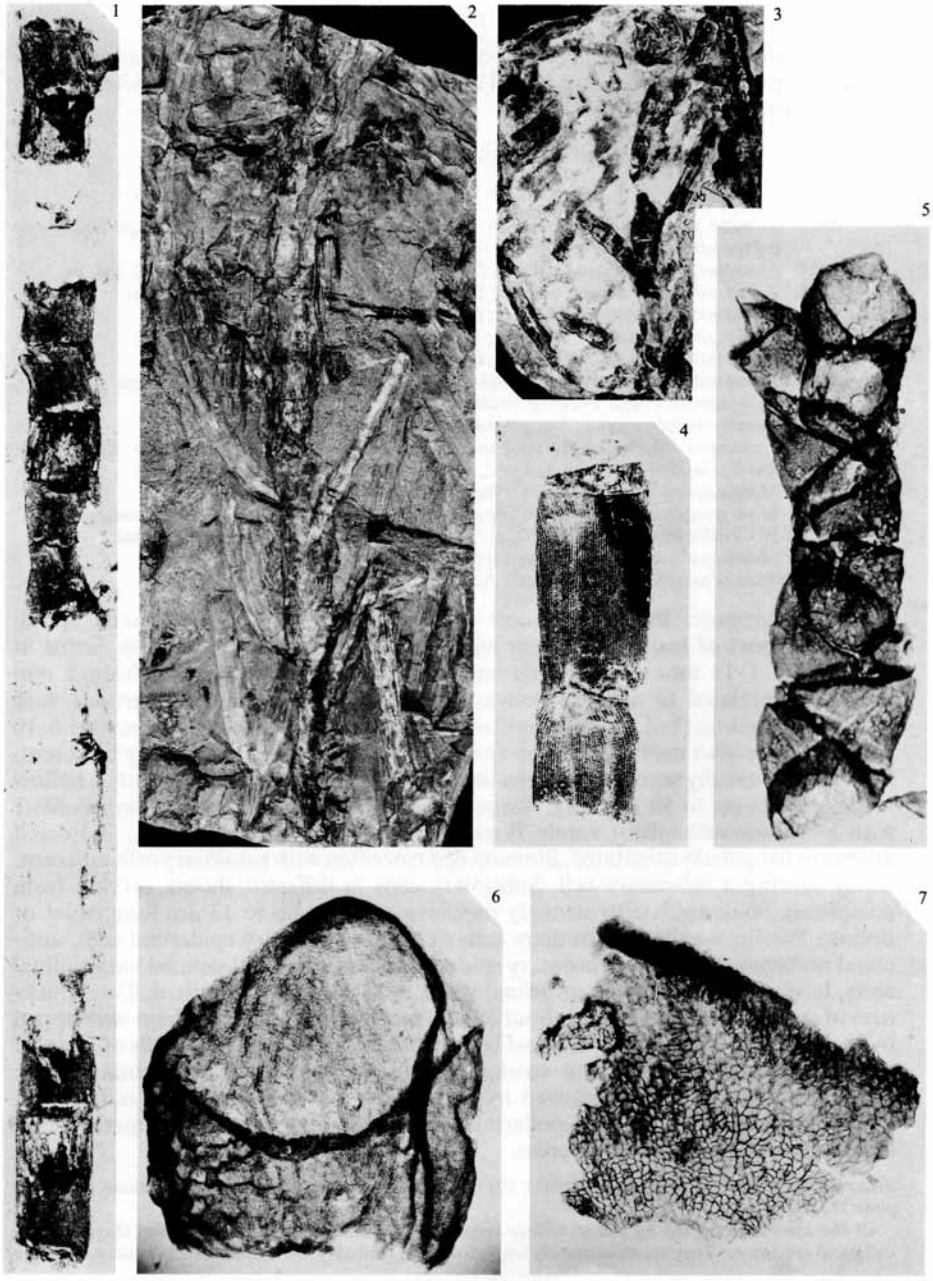
*Emended diagnosis.* Branching, segmented shoots bearing a simple spiral of leaves with sheathing bases, each individual leaf completely encircling the stem. Leaf small, triangular, obtuse, adpressed; usually joined laterally to form sheathing base continuing as smooth cylindrical internode to node below; when not joined laterally internode short. Stoma circular having guard cells sunken below ring of subsidiary cells which form a stomatal pit.

*Type species. Frenelopsis varians* Fontaine, 1893.

*Remarks.* The diagnosis originally based only ón the type species is emended here after studying specimens of *F. varians* Fontaine which is now transferred to this genus. The diagnosis of *P. parceramosa* (Fontaine) given below is based on information from American, English, Polish, and Portuguese material. Specimens from the Sudan which I have examined are in the form of silica moulds and have been studied by

EXPLANATION OF PLATE 85

Figs. 1–7. *Pseudofrenelopsis parceramosa* (Fontaine). 1, lectotype. USNM 192360, ×2. 2, 3, specimens showing branching, both with 'closed' kind of leaf-base or sheath. 2, USNM 192358, 3, USNM 192362, both ×1. 4, two long internodes showing stomatal rows and very small free leaf on the lower one. USNM 192393, ×3. 5, small macerated shoot showing 'open' kind of leaf and short sutures. V. 51543, ×10. 6, 'closed' leaf with very short internode or basal cushion. V. 51548, ×25. 7, adaxial cuticle with leaf margin at top, line of junction with next highest internode at bottom. V. 51549, ×60.




WATSON, *Pseudofrenelopsis parceramosa*

means of silicone rubber casts (Watson and Alvin 1976). I have not used these for diagnostic purposes as they do not add any information but they seem to be specifically identical.

## *Pseudofrenelopsis parceramosa* (Fontaine) comb. nov.

Plate 85, figs. 1–7; Plate 86, figs. 1–12; Plate 87, figs. 1–10; text-figs. 2, 3

?1852 *Culmites priscus* Ettingshausen, 24, pl. 1, fig. 5 (imperfect figure of what might possibly be a *Pseudofrenelopsis* shoot).
1889 *Frenelopsis parceramosa* Fontaine, 218, pl. 111, figs. 1–5; pl. 112, figs. 1–5; pl. 168, fig. 1.
1905 *Frenelopsis parceramosa* Fontaine; Fontaine in Ward, 544 (name only in lists).
1911 *Frenelopsis parceramosa* Fontaine; Berry, 425, pl. 70, figs. 1–5.
1926 *Frenelopsis parceramosa* Fontaine; Edwards, 97 (mentioned in comparison).
1940 *Frenelopsis parceramosa* Fontaine; Oishi, 390, pl. 40, figs. 1, 5–8.
1946 *Frenelopsis hoheneggeri* (Ettingshausen); Romariz (*pro parte*), 143, pl. 2, figs. 1, 2; pl. 3, fig. 1, *non* pl. 1, figs. 1–3 (= *F. occidentalis*).
1948 *Frenelopsis hoheneggeri* (Ettingshausen); Teixeira, 65, pl. 24, figs. 1–3.
1965 *Frenelopsis hoheneggeri* (Ettingshausen); Reymanówna (*pro parte*), 19, pl. 1, figs. 1, 3, 6; text-fig. 2A, C, E–M, *non* pl. 1, figs. 2, 4–5; text-fig. 2B, D, K (= *F. hoheneggeri*).
1965 *Manica parceramosa* (Fontaine); Reymanówna, 23 (*nomen nudum*).
1974 *Manica parceramosa* (Fontaine) Watson, 428 (generic diagnosis and name change only).
1976 30 CHEIR MaA; Oldham, 462, pl. 72 (code no. used instead of specific name).
1976 *Manica parceramosa* (Fontaine); Reymanówna and Watson, 19.
1977 *Manica parceramosa* (Fontaine); Alvin, 397, pl. 44, figs. 1–8; text-fig. 3.

*Emended diagnosis.* Branched shoots bearing leaves in 2/5 phyllotactic spiral. Triangular part of leaf up to 2 mm high, sheathing base up to 0·8 mm, borne at intervals of 1–11 mm (= internode length); twigs of variable width from 1 mm upwards, unrelated to distance between leaves. Thickly cutinized internode with stomata in well-marked longitudinal rows, uniseriate or imperfectly biseriate; 6–10 rows per mm; rows may continue on to abaxial surface of free leaf or may be absent. Leaf margin usually scarious and microscopically dentate, having unicellular, hollow teeth or hairs up to 80 $\mu$m long. Stomatal apparatus typically 50–80 $\mu$m diameter with 5 or 6 (occasionally 4, rarely 7) more or less equal subsidiary cells; guard-cell apertures irregularly orientated. Stomata of a row often with subsidiary cells adjacent, rarely sharing a subsidiary cell. Subsidiary cells in different shoots varying from completely non-papillate to strongly papillate, papillae up to 13 $\mu$m long, solid or hollow. Perclinal walls of subsidiary cells as thick as ordinary epidermal cells, anticlinal walls much narrower; ordinary epidermal cells forming ill-defined longitudinal rows, having broad, irregular anticlinal walls, 5–15 $\mu$m broad, unpitted. Total thickness of cuticle in mid-internode about 30 $\mu$m, much thinner at base where overlapped by and joined to adaxial cuticle of leaf below. Adaxial cuticle showing cells of variable shape and arrangement, often strongly papillate; few, scattered stomata, often abortive. Well-developed cutinized hypodermis of pitted, thin-walled cells except under stomatal apparatus; hypodermal cells isodiametric under stomatal rows, elongated under non-stomatal areas.

*Material and occurrence.* Lectotype USNM 192360. This specimen was figured by Fontaine (1889) on plate 112, fig. 3.

Of the specimens figured by Fontaine four remain in the Smithsonian Collection and there are two unfigured specimens. They are all extremely fragile and have probably lost numerous leaves since Fontaine

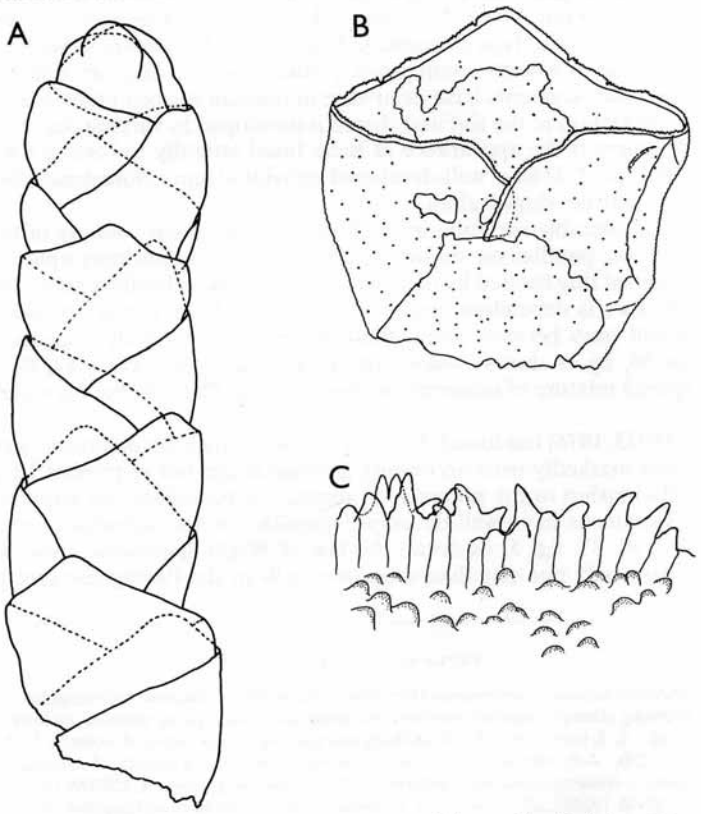
described them. They were all collected from the same locality, Trent's Reach, Virginia which has been dated on the basis of pollen and spore content as Barremian to Aptian (Doyle and Hickey 1976). There is also a very fine specimen (Pl. 85, fig. 4) consisting of two internodes on a piece of borehole core from Louisiana. Information with it suggests that it is the same age as the Glen Rose Formation in Texas which is regarded as late Aptian to earliest Albian (see below under *P. varians*).

The English Wealden specimens are nearly all fragments obtained by bulk maceration of coaly shales from several localities, notably Hastings, Sussex and Hanover Point, Isle of Wight. Oldham (1973, 1976) has found it throughout the Wealden succession (Berriasian to Aptian).

*P. parceramosa* collected by Reymanówna (1965) is from the Grodisht Beds, Przenosza, SE. of Kraków which are Hauterivian–Lower Barremian in age.

The Portuguese material (Alvin 1977) is Aptian–Albian.

The Nubian Sandstone at Jebel Dirra, E. Darfur, Sudan, from which the silicified specimens were collected (Edwards 1926) is of uncertain age (Whiteman 1971, p. 54), but on the evidence of these conifers is presumably Lower Cretaceous.




TEXT-FIG. 2. *Pseudofrenelopsis parceramosa*. A, small shoot with widely 'open' type of leaf, showing phyllotaxis, ×20, V. 51542; B, single 'open' leaf unit showing distribution of stomata, adaxial cuticle has few stomata, ×25, V. 51544; C, scarious leaf margin showing hairs joined laterally, ×300, V. 51545.

*Description.* Despite the abundance of *P. parceramosa* obtained from the English Wealden little is known of the branching of this species. The matrix is extremely friable and though a few small hand specimens have been salvaged most of it was subjected to oxidative bulk maceration yielding only isolated segments (Pl. 85, fig. 6) or short coherent lengths of shoot (Pl. 85, fig. 5). Though few in number the Potomac specimens are much larger and there are two showing branching (Pl. 85, figs. 2, 3) which appears to be alternate in one plane. I could not work out the phyllotaxis from any of the American specimens but using several small English shoots I have satisfied myself that it approximates to 2/5 divergence. The abundant English material has provided all the information about variation in size and leaf form. As would be expected the segments vary greatly in dimensions and doubtless represent large and small stems. The largest I have measured is 11 mm long × 6 mm wide but the proportions vary, e.g. 9 mm long × 3 mm wide; 4 mm long × 4 mm wide; 1·5 mm long × 3·5 mm wide. The 'open' type of segment described earlier occurs in both broad and narrow forms but is always comparatively short. Neither the variable widths nor 'open' and 'closed' segments have been seen in relation to each other *in situ*.

The dentate margin of the leaf and sheath is developed to varying degrees. In some (text-fig. 2c) there is the appearance of hairs fused laterally to form a frill whereas others (Pl. 86, figs. 2, 3) have well-developed individual hairs. Sometimes the scarious margin is scarcely developed at all.

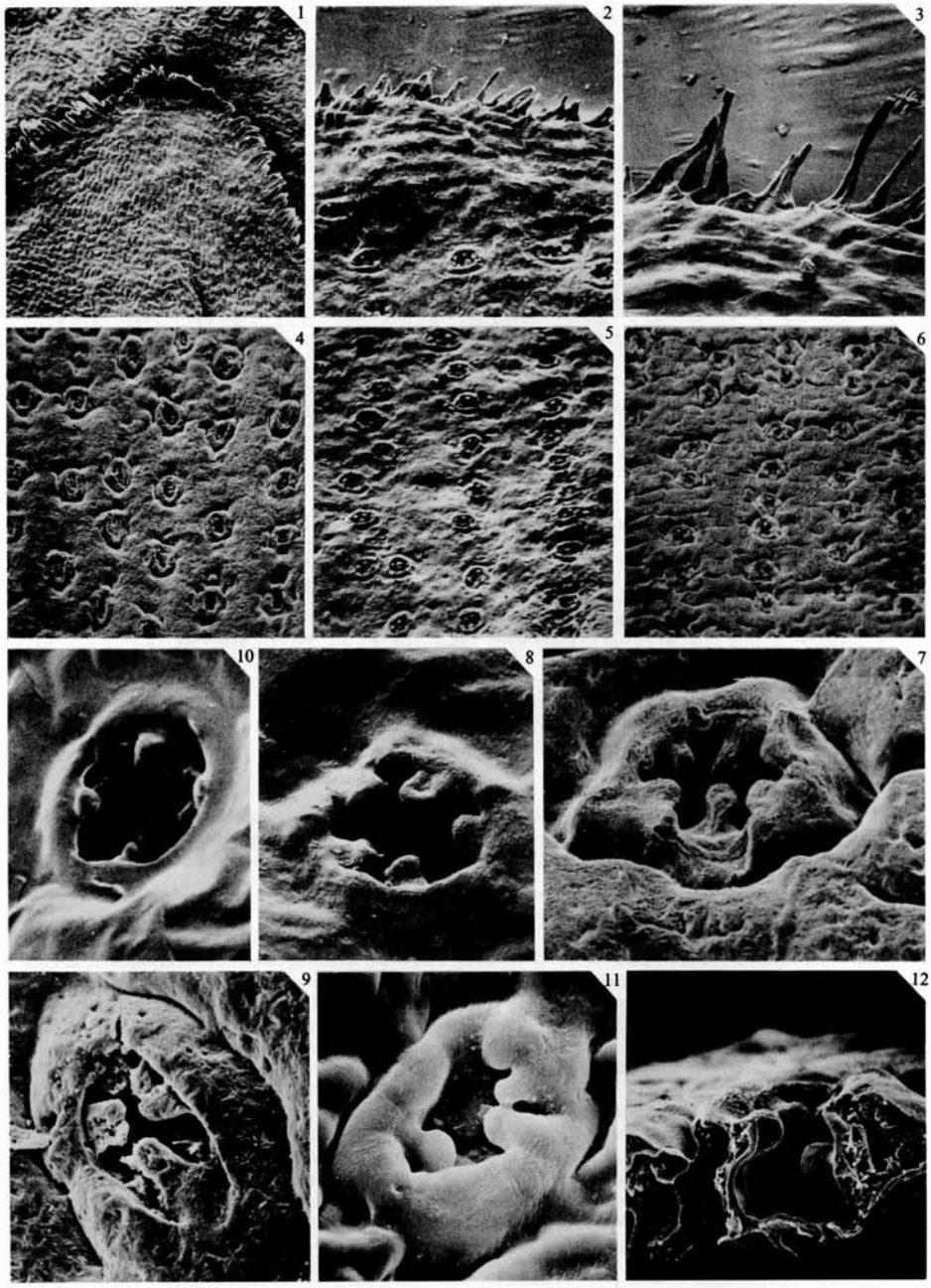
There is considerable variation in the details of the cuticle; mainly in the density of stomatal rows, papillae on subsidiary cells, papillae on ordinary epidermal cells, and the thickened ring formed by the outer surface of the subsidiary cells. The density of stomatal rows is dependent upon the number of biserial rows present and the number of cell rows between them. Plate 86, fig. 6 shows widely spaced uniserial rows; Plate 86, fig. 4 shows closely spaced uniserial rows; Plate 87, fig. 4 shows a closely spaced mixture of uniserial and biserial; and Plate 86, fig. 5 a widely spaced mixture.

Oldham (1973, 1976) has found that the presence of papillae on ordinary epidermal cells increases markedly with decreasing geological age but at present I can see no such age relationship to the presence or absence of subsidiary cell papillae. All the American specimens have well-developed papillae on the subsidiary cells (Pl. 86, figs. 7–9, 11; Pl. 87, fig. 5) as do all the Isle of Wight specimens inspected. Alvin (1977) has seen only non-papillate subsidiary cells in the Portuguese specimens but

---

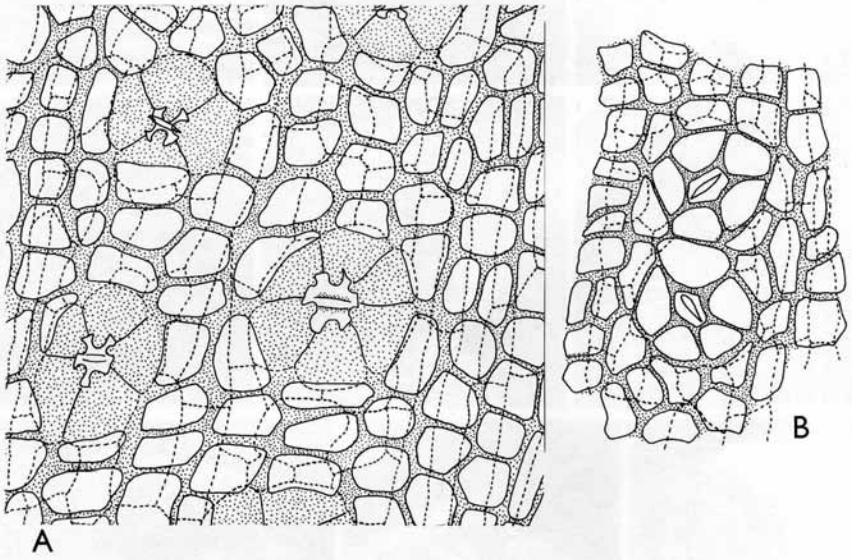
EXPLANATION OF PLATE 86

Figs. 1–12. *Pseudofrenelopsis parceramosa* (Fontaine). All scanning electron micrographs. 1, triangular free leaf showing strongly papillate surface, marginal hairs and sparse stomata in lower part only. V. 58655, × 60. 2, 3, part of leaf sheath showing marginal hairs and extent of stomata. USNM 192358, 2, × 100, 3, × 250. 4–6, internode outer surface showing variation in density of stomatal rows and in form of stoma. 6, showing individual epidermal cells outlined by grooves. 4, USNM 192393, 5, USNM 192358, 6, USNM 192362, all × 100. 7–9, stomata showing subsidiary cell papillae and differences in development of thickened ring and surrounding furrow. 7, USNM 192362, 8, USNM 192358, 9, USNM 192393, all × 1000. 10, silicone rubber cast of stoma from silicified Sudanese material, showing similarity to type of stoma in fig. 8. V. 21708, × 1000. 11, 12, two stomata each with a subsidiary cell papilla inside the stomatal pit. 12, in vertical section. 11, USNM 192363, 12, USNM 192360, both × 1000.




WATSON, *Pseudofrenelopsis parceramosa*

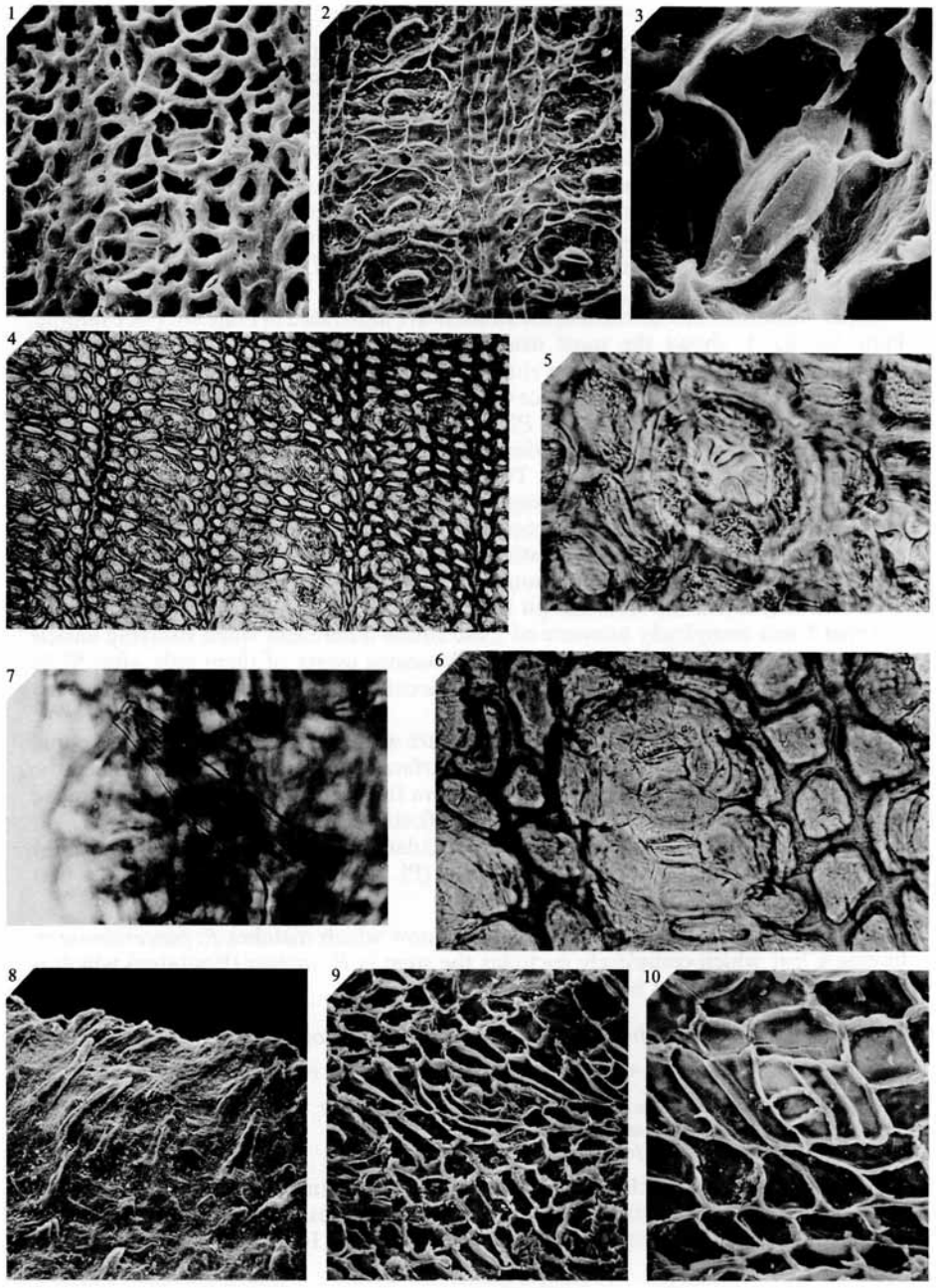
was able to sample only two internodes. In the Hastings material such papillae may be present or absent and I was able to study the variation in numerous isolated segments. There is also variation in the occurrence of papillae on ordinary epidermal cells. I found as a general rule that segments with short internodes (less than 3 mm) have papillate subsidiary cells (text-fig. 3A), whilst those with internodes over 5 mm long have non-papillate subsidiary cells (text-fig. 3B; Pl. 87, fig. 6). Internodes




TEXT-FIG. 3. Cuticle of internode of *Pseudofrenelopsis parceramosa*. A, cuticle of a small unit with papillate subsidiary cells, V. 51546; B, cuticle of a larger unit with non-papillate subsidiary cells, V. 51547. Hypodermal cells shown by dotted lines. Both ×300.

EXPLANATION OF PLATE 87

Figs. 1–10. *Pseudofrenelopsis parceramosa* (Fontaine). 1–3, 8–10, scanning electron micrographs. 1, 2, inner surface of internode cuticle showing stomatal rows. 2, shows a Hastings specimen in which the extensive cutinized hypodermis obscures the ordinary epidermal cells. V. 58654, ×250. 1, a Potomac specimen clearly shows the epidermal cells with only a few pitted hypodermal cells. USNM 192363, ×250. 3, inner surface of a single stoma showing five subsidiary cells, cutinized part of guard cells and stomatal aperture. Subsidiary cell on left shows the entrance of a hollow papilla and the striated ridge which is related to the deep furrow surrounding the stoma on the outer surface. USNM 192363, ×1000. 4, 5, internode cuticle of lectotype showing typical appearance in light microscope. 4, shows both uniseriate and biseriate rows of stomata, ×100. 5, is a single stoma with strongly papillate subsidiary cells, ×500, USNM 192360. 6, internode cuticle of Hastings specimen with non-papillate subsidiary cells, showing two stomata sharing a subsidiary cell. V. 58656, ×400. 7, long, hollow epidermal hair near base of internode of lectotype. USNM 192360, ×500. 8, outer surface of adaxial cuticle with long hairs pointing towards leaf apex. V. 58654, ×250. 9, 10, inner surface of adaxial cuticle. 9, showing stoma on left, ×250. 10, showing an abortive stoma, ×500. V. 58654.




WATSON, *Pseudofrenelopsis parceramosa*

between 3 and 5 mm long may be of one kind or the other or have mixed stomata. On the whole the cell size and, therefore, stomatal diameter, are smaller in non-papillate ones (cf. text-fig. 3A, B). Many of the smallest segments have a solid, central papilla on the surface of the ordinary epidermal cells, occasionally on all cells but more commonly near the base of the leaf cushion only. The longer internodes, particularly those with non-papillate subsidiary cells mostly lack these other papillae too except on the free leaf tip where both abaxial (Pl. 86, fig. 1) and adaxial (Pl. 87, fig. 8) surfaces may have strongly developed papillae or hairs. Only on the lectotype have I found long hairs such as in Plate 87, fig. 7 near the base of the internode (cf. *P. varians* below).

Other variations encountered in the stomata are illustrated in Plate 86. For example, Plate 86, fig. 4, shows the most usual form of stoma with a broad, raised rim surrounding the stomatal pit, the rim in turn surrounded by a deep groove. This groove is related on the inside surface of the cuticle to a raised ridge which frequently has radial striations (Pl. 87, fig. 3). Plate 86, figs. 8 and 10 show stomata where the rim and furrow are much less pronounced. Figure 10 is a silicone rubber cast of the silicified material from the Sudan. This type of stoma is fairly common scattered amongst the usual kind in the Potomac and Sudanese specimens but I have never seen such a stoma in an English specimen. It will also be noted that the subsidiary cell papillae vary in their position in relation to the stomatal pit, either at the top (Pl. 86, fig. 8), slightly below the top and bounded by a groove (Pl. 86, fig. 9), or occasionally even half-way down the stomatal pit (Pl. 86, figs. 11, 12). I think it worth pointing out that I was completely unaware of these subtle differences when studying cuticle preparations with the light microscope and became aware of them only after SEM work. In the light microscope (Pl. 87, fig. 4) the cuticle of *P. parceramosa* is extremely distinctive and, I find, easy to identify.

Plate 86, figs. 6 and 7 show an unusual feature where the outline of each epidermal cell is marked by distinct furrows and the surface is pitted. Dr. Alvin has seen the same feature in a specimen of *Frenelopsis alata* from Portugal (Alvin 1977) and we think it is a preservational feature perhaps reflecting loss of surface wax.

The hypodermis of *P. parceramosa* is particularly well developed and in the SEM often obscures details of the epidermal cells (Pl. 87, fig. 2). Its distribution is best illustrated in text-fig. 3A.

*Comparison.* The only other fossil conifer I know which matches *P. parceramosa* in having a leaf which completely encircles the stem is *P. varians* (Fontaine) which is described and compared below.

### *Pseudofrenelopsis varians* (Fontaine) comb. nov.

Plate 88, figs. 1–9; Plate 89, figs. 1, 2; Plate 90, figs. 1–13; Plate 91, figs. 1–13

1893 *Frenelopsis varians* Fontaine, 273, pl. 40, figs. 1–2; pl. 41, figs. 1–3a.
1893 *Pagiophyllum dubium* Fontaine, 271, pl. 39, figs. 2–11.
1893 *Pseudofrenelopsis felixi* Nathorst, 52, text-figs. 6–8.

*Emended diagnosis.* Branched shoots bearing leaves in simple spiral. Free tip of leaf up to 1·5 mm high, sheathing base up to 0·8 mm; leaves borne at intervals of 1·5–17·0 mm (= internode length); shoots of 3–7 mm wide. Internode cuticle extremely

thick, varying from 50 to 110 $\mu$m in total thickness; outer periclinal wall of subsidiary cell forming almost all this thickness; outer periclinal wall of ordinary cells forming half to three-quarters of total thickness; cuticle much thinner at base of internode where overlapped by leaf below. Stomata scattered in smooth, cylindrical internodes; arranged in uniseriate rows in short internodes where leaf does not join laterally, stomatal rows 8–10 per mm; stomata continuing on to abaxial surface of free leaf but not on to leaf sheath. Leaf margin scarious and microscopically dentate, teeth up to 60 $\mu$m long. Stomatal apparatus varying from 70 to 100 $\mu$m diameter except in extreme basal part of internode where they are much smaller; having 5 to 8 (rarely 4 or 9) subsidiary cells. Guard cells at bottom of deep, parallel-sided stomatal pit formed by extremely thick cuticle of subsidiary cells; aperture randomly orientated. Outer surface of subsidiary cells forming raised rim bounded by deep groove around top of stomatal pit; each cell having hollow papilla overarching pit. Anticlinal walls of subsidiary cells 2–3 $\mu$m broad; those of ordinary epidermal cells 5–6 $\mu$m broad with thickened corners giving rounded lumen; cells haphazard or in short files amongst scattered stomata; in long uninterrupted files between rows of stomata. Each epidermal cell bearing on outer surface a distinct, acutely pointed hair up to at least 80 $\mu$m long. Cutinized hypodermis present (seen only in 'open' leaf-base cushions) except under stomatal apparatus; hypodermal cells square under stomatal rows, elongated between stomatal rows; anticlinal walls 1 $\mu$m broad. Female cones nearly round (largest 18 mm long $\times$ 16 mm wide), surface showing probably 3+5 parastichies of rhomboidal scale ends (no inner parts known); borne on a stalk resembling smaller vegetative stems. Wood forming slender core, less than one-third total width of shoot.

*Material.* Lectotype USNM 192381, figured by Fontaine (1893), plate 41, fig. 3, 3A.

The Smithsonian Collection contains all Fontaine's figured specimens of *P. varians* together with a number previously unfigured. They were all collected from the Trinity Group of the Lower Cretaceous at Glen Rose, Texas where they occur in the Glen Rose Limestone together with an abundant marine fauna. The Glen Rose Formation is considered to be late Aptian to earliest Albian (Stephenson *et al.* 1942).

*Description.* The specimens now described as *P. varians* (Fontaine) were separated by Fontaine into two distinct species, *F. varians* and *Pagiophyllum dubium*. He attributed all the female cones to *P. dubium*. In his account Fontaine (1893, p. 274), describing the leaves of one specimen of *F. varians*, points out how they '. . . strikingly resemble the leaves at the summit of the cone-bearing twigs of *Pagiophyllum dubium*'. On examination of the cuticles it is immediately obvious that they are different leaf forms of a single species.

At the same time as Fontaine was describing this material from Texas, Nathorst (1893) was unknowingly describing the same plant from Mexico under another name. Nathorst compared his specimens to *F. parceramosa* Fontaine, suspecting that they were the same species and at the same time mildly criticizing Fontaine for describing the *F. parceramosa* specimens as articulated. Not wishing to use the genus *Frenelopsis* for shoots other than those with leaves in whorls of three or four Nathorst erected a new genus, *Pseudofrenelopsis*, with the Mexican specimens as a new species, *P. felixi*. Fontaine (1905) in correcting the criticism about the jointed nature of *F. parceramosa* pointed out that Nathorst's *P. felixi* was identical to his own

*Pagiophyllum dubium* from Texas, i.e. what is now the 'open' leaf form of *Pseudofrenelopsis varians*. I think Fontaine was correct, notwithstanding the absence of the Mexican specimens and details of their cuticle. In joining these species I have chosen to retain the specific epithet *varians* because shoots given that name by Fontaine more clearly typify the species and include the lectotype.

There are only two branching specimens in the collection (Pl. 88, fig. 1; Pl. 89, fig. 1), both are strikingly jointed with a stiff, sparsely branched appearance. All the other specimens are lengths of shoot of up to a dozen segments (Pl. 88, figs. 2–6) or short lengths of shoot bearing a cone (Pl. 88, figs. 7–9). As with *P. parceramosa* there is no specimen which shows the 'closed' and 'open' leaf forms together on the same shoot. However, both long and short segments are present in specimen USNM 192378 (Pl. 89, fig. 1) on the lowest right-hand branch which has segments of variable length in the lowest part, long segments in the middle with an abrupt change to short, narrow segments in the distal region. As noted by Fontaine, the shoots in their smallest form are very like those of *P. parceramosa*. The small leaves below the cones are of either the 'closed' or 'open' variety but not mixed as far as I can tell. The cuticle of these small leaves (Pl. 90, fig. 11) easily identifies the cones as belonging to *P. varians*.

Variation in details of the cuticle is chiefly associated with differences in the epidermal hairs. The long cylindrical internodes have, in the main, short sharply pointed hairs (Pl. 90, figs. 2, 5) or the eroded remains of such hairs (Pl. 90, fig. 6). In the basal region of some internodes patches of considerably longer hairs occur (Pl. 91, figs. 11, 12). The epidermal hairs of the 'open' leaf type are often densely packed (Pl. 91, fig. 10) particularly on the free part of the leaf (Pl. 90, figs. 8, 9) where they tend to join laterally and point towards the apex.

There is little variation in the external appearance of the stoma which is usually as seen in Plate 90, fig. 7 but occasionally the thickened rim has the form of a low cone as seen in Plate 90, fig. 5.

The long, wide internodes consistently contain a very narrow cylinder of wood (Pl. 89, fig. 2) separated from the cuticle by a wide gap where all the tissue has vanished, I imagine because it was parenchyma. Several of the internodes have numerous small holes puncturing the cuticle (Pl. 91, fig. 13) which were clearly made when the plant was living because they have a callus around them. It seems to me quite likely that they were made by the proboscis or ovipositor of an insect, either to suck at the juicy tissue below or to lay eggs in it.

---

EXPLANATION OF PLATE 88

Figs. 1–9. *Pseudofrenelopsis varians* (Fontaine). 1, lectotype showing jointed, sparsely branched appearance, with long cylindrical internodes. USNM 192381, ×1. 2–4, short lengths of shoot with the 'open' type of leaf. 3, cone probably not attached. 2, USNM 192364, ×1, 3, USNM 192371A, ×1, 4, USNM 192365, ×2. 5, 6, shoots with 'closed' type of leaf but much shorter internodes than lectotype. 5, shows very small free leaves in 5th and 6th segments from bottom, USNM 192380, ×2. 6, is a shoot apex and shows a free leaf on the 3rd segment up, USNM 192379, ×3. 7–9, female cones attached to short lengths of shoot which have been identified by their cuticle. 7, USNM 192368, 8, USNM 192367, 9, USNM 192376, all ×1.

*Comparison*. There is a strong superficial resemblance between some shoots of *P. varians* and *P. parceramosa* (cf. Pl. 85, fig. 1 and Pl. 88, fig. 5) but they are easily separable on cuticle differences which are summarized in Table 1. The fragmentary shoots of *P. parceramosa* which abound at Hanover Point, Isle of Wight are intimately associated with considerable amounts of fossil wood and the cliff section is only a matter of metres away from the famous 'pine-raft' on the foreshore. Any relationship between wood and leafy shoots has yet to be established but clearly there are indications that *P. parceramosa* may have been a sizeable tree. On the other hand, the very small size of the stele in *P. varians*, about one-quarter of the total diameter of the shoot, leads me to suppose that it was not a tree at all but a small shrub. This is further discussed below in comparison with *F. ramosissima*.

## Genus FRENELOPSIS Schenk 1869

1976 *Frenelopsis* Schenk; Reymanówna and Watson, 19.

*Diagnosis* (slightly emended after Reymanówna and Watson). Branching, articulated shoots consisting of cylindrical internodes each extending at the upper margin into a whorl of equal, scale-like, adpressed, triangular leaves (usually three, sometimes two); successive whorls alternating; internode surface smooth, showing no grooves or sutures. Stomatal apparatus circular, monocyclic, or incompletely amphicyclic, having guard cells sunken below a ring of subsidiary cells which form a stomatal pit.

*Type species. Thuites hoheneggeri* Ettingshausen 1852, 26.

*Remarks*. The diagnosis above is slightly emended because shoots with two leaves per node have recently been found. These are at present being studied (Pais, Alvin pers. comm.) and do not match any known species, but they lack the sutures of *Cupressinocladus* so will be included in *Frenelopsis*. So far there is no evidence of both two-leaf and three-leaf whorls in one species, contrary to expectation.

### *Frenelopsis alata* (K. Feistmantel) Knobloch

Plate 89, figs. 3, 4; Plate 92, figs. 1–9

Selected synonomy:

1881 *Sclerophyllum alatum* K. Feistmantel, 96, pl. 7, fig. 1*a–k*.
1888 *Frenelopsis bohemica* Velenovský, 590, pl. 1, figs. 1, 2, 10.
1893 *Frenelopsis hoheneggeri* (Ettingshausen); Fontaine, 275, pl. 42, fig. 4, 4*a*.
1926 *Frenelopsis bohemica* Velenovský; Němejc, 133, pl. 1, figs. 1–3; pl. 2, figs. 1–5; pl. 3, figs. 1–4.
1946 *Frenelopsis lusitanica* Romariz, 144, pl. 3, figs. 2, 3; pl. 4, figs. 1, 2.

---

EXPLANATION OF PLATE 89

Figs. 1, 2. *Pseudofrenelopsis varians* (Fontaine). 1, branched specimen showing variable internode length, particularly on lowest, right-hand branch. USNM 192378, ×1. 2, portion of long cylindrical internode showing free leaf (slightly eroded) at back left, and the slender core of wood. USNM 192371A, ×8.

Figs. 3, 4. *Frenelopsis alata* (K. Feistmantel). Branched specimen with only one intact whorl of leaves which is shown in fig. 4. The position of this whorl is indicated by the arrow on fig. 3, and a dotted line in fig. 4. USNM 3750, 3, ×1, 4, ×6.


WATSON, *Pseudofrenelopsis*, *Frenelopsis*

1971 *Frenelopsis alata* (K. Feistmantel) Knobloch, 44 (name change only).
1972 *Frenelopsis alata* (K. Feistmantel); Hluštík, 210.
1974 *Frenelopsis alata* (K. Feistmantel); Hluštík, 265, pl. 1, figs. 3, 4; pl. 3, figs. 1, 2.
1976 *Frenelopsis alata* (K. Feistmantel); Hluštík and Konzalová, 38, pls. 1–6 (description of male cone).
1977 *Frenelopsis alata* (K. Feistmantel); Alvin, 388, pl. 41, figs. 1–5; pl. 42, figs. 1–6; text-fig. 1A.

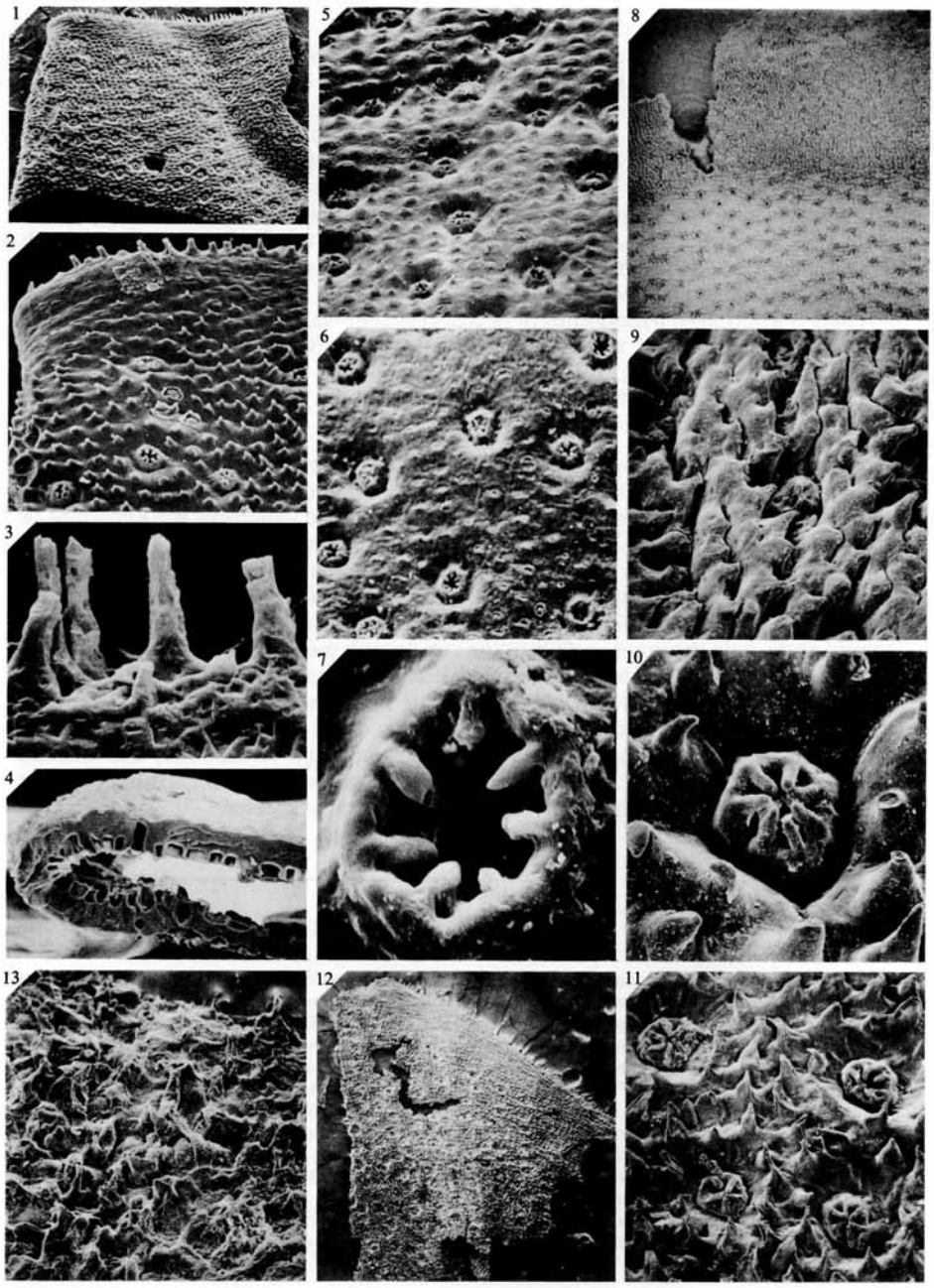
*Material.* USNM 3750. The lectotype is in the National Museum, Prague, Czechoslovakia.

*Description.* Only one specimen of this species (Pl. 89, figs. 3, 4) is present in the Smithsonian Collection. It is from Glen Rose, Texas and was found amongst specimens of *P. varians* (Fontaine). Only one node shows well-preserved leaf arrangement (Pl. 89, fig. 4; Fontaine 1893, pl. 42, fig. 4*a*) and this is clearly a whorl of three. Fontaine states that the leaves in successive whorls alternate but I certainly could not verify this on examining the specimen. However, this feature has been clearly established in European specimens. The free leaf was not sampled and the description below is based on only two slide preparations and one SEM preparation from the internode. Also I was unable to ascertain whether the leaf is bordered by a fringe of hairs as are all the other species of *Frenelopsis* and *Pseudofrenelopsis* I have examined. The specimen is branched but the details are not clear. As far as I can tell the segments are 1·5–2·0 cm long and 3·5–5·0 mm wide. The free leaf tip is about 1·0 or 1·2 mm high but I do not know the extent of the leaf sheath. The leaves show a distinct series of ridges and furrows radiating from the apex (Pl. 89, fig. 4), a feature commonly seen in specimens of *Frenelopsis*. The epidermis of the internode has stomata in fairly ill-defined uniseriate rows with 10 or 12 rows per mm and with 1–4 rows of ordinary epidermal cells between the stomatal rows. Within a row the individual stomata are irregularly spaced.

The diameter of the stomatal apparatus varies from 52 to 77 $\mu$m and most have 5 subsidiary cells though sometimes 4 or 6. The form of the stomatal pit is highly distinctive (Pl. 92) having a stellate opening (up to 20 $\mu$m across) which is formed by a lobed canopy arching over the pit. The number of lobes appears to equal the number of subsidiary cells. Half-way down inside the pit is a ring of large, hollow papillae again equal in number to the subsidiary cells. On the outer surface the canopy is surrounded by a deep furrow (Pl. 92, figs. 3, 9). The guard cells are very thinly cutinized

EXPLANATION OF PLATE 90

Figs. 1–13. *Pseudofrenelopsis varians* (Fontaine). All scanning electron micrographs. 1, part of long internode showing scattered stomata. USNM 192383, ×25. 2, part of same showing epidermal papillae, marginal hairs, and absence of stomata from leaf sheath, ×100. 3, long hairs of leaf sheath margin. USNM 192383, ×500. 4, transverse section of internode showing extreme thickness of cuticle. USNM 192383, ×100. 5, surface of internode with short epidermal papillae and cone-shaped rim of stomatal pit. USNM 192380, ×100. 6, 7, surface of internode with severely eroded papillae and ring of thickening around stomatal pit. USNM 192378, 6, ×100, 7, ×1000. 8, 'open' type of leaf with stomata in rows, showing difference in papillosity between internode (lower half) and free leaf. USNM 192371A, ×25. 9, 'open' leaf with papillae joined in rows and pointing towards apex, stomata somewhat stunted. USNM 192364, ×250. 10, stoma from mid-internode of a specimen with strongly developed pointed papillae and hairs. The base of this specimen is seen in Plate 91, figs. 11, 12. USNM 192378, ×500. 11, 12, 'open' scale-leaf from below female cone. The cuticle is very similar to that in fig. 10. USNM 192372, 11, ×250, 12, ×25. 13, outer surface of adaxial cuticle. USNM 192378, ×250.




WATSON, *Pseudofrenelopsis varians*

and did not survive maceration but Dr. Alvin has seen some in Portuguese specimens and thinks they are randomly orientated. Plate 92, figs. 4 and 5 show the absence of guard cells so that the papillae inside the stomatal pit are clearly seen. Plate 92, fig. 5 shows that these papillae are hollow. The cells immediately surrounding the subsidiary cells tend to form a definite ring and occasionally a stoma has a cell which appears to be a genuine encircling cell. The other ordinary epidermal cells are arranged in irregular longitudinal files and may be rounded, squarish, or slightly elongated; they are 25–50 $\mu$m long and 20 $\mu$m wide with anticlinal walls 3–6 $\mu$m broad. The inner surface of the periclinal walls is often finely sculptured (Pl. 92, figs. 6, 7) but the outer surface (Pl. 92, fig. 1) is quite smooth with no hint of papillae.

There is a cutinized hypodermis of pitted, very thin-walled cells, elongated between stomatal rows, squarish within the stomatal rows, often slightly overlapping the subsidiary cells (Pl. 92, fig. 5).

The total thickness of the internode cuticle is about 40 $\mu$m (measured on SEM photographs).

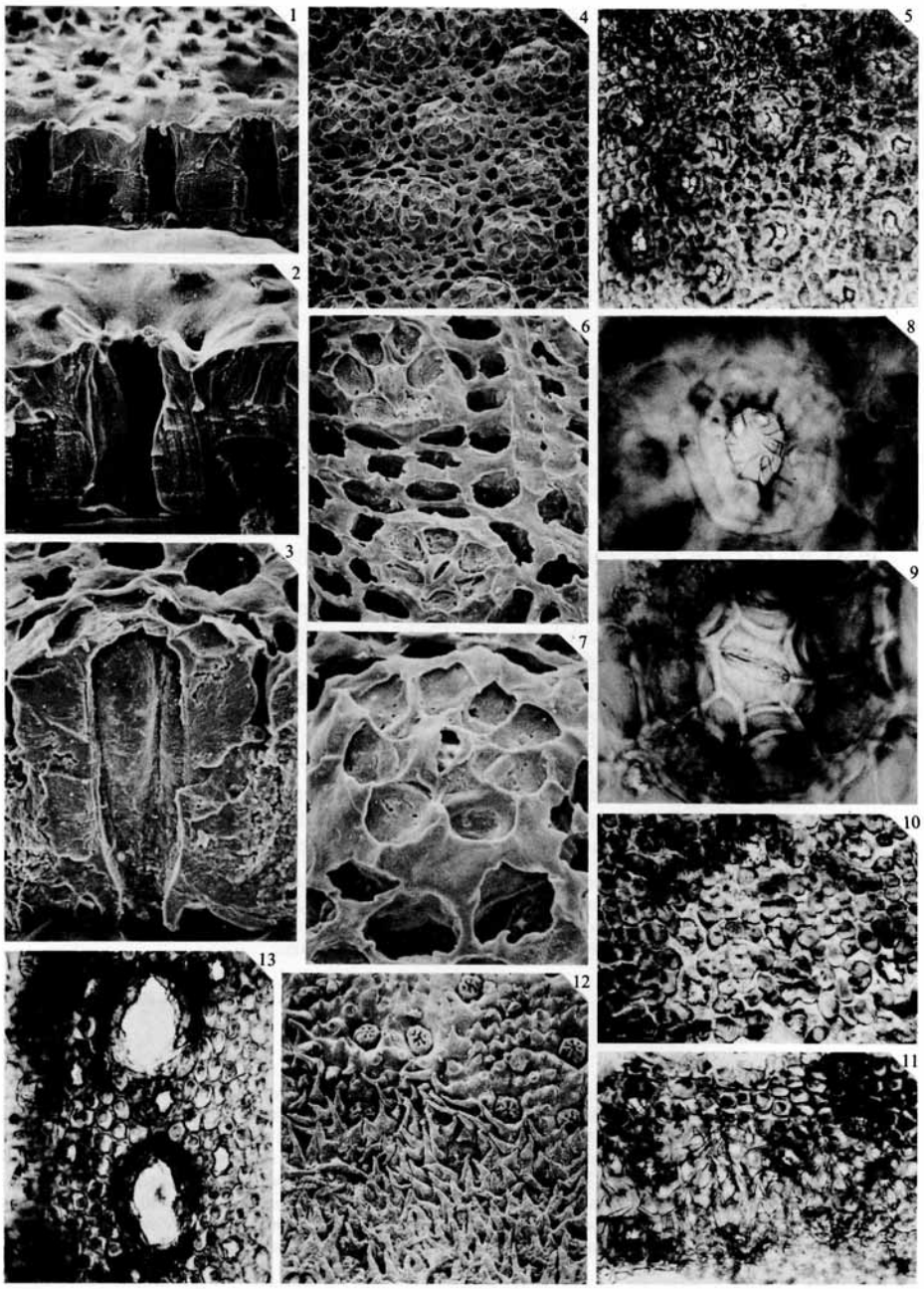
*Discussion and comparison.* I have examined the cuticle of the Portuguese material assigned to *F. alata* by Alvin (1977) and compared it with USNM 3750 and it seems to me that they are specifically identical. The Portuguese specimens are known to be Cenomanian whereas the Texas specimen can only be early Albian at the youngest. Hluštík (1974) has figured the cuticle of Czechoslovakian *F. alata* and comparing his light micrograph (pl. 1, fig. 3) to the cuticle of USNM 3750 I can see only minor differences such as slightly shorter epidermal cells. His scanning electron micrographs show only the inner surface of the cuticle with guard cells intact so that I cannot tell if the stoma has the same distinctive structure as described above. However, Hluštík has examined Alvin's photographs of Portuguese *F. alata* and is satisfied that the determination is correct.

The silicified *Frenelopsis* from the Sudan (Watson and Alvin 1976) has stomata closely similar to those of *F. alata* but studying them only as silicone rubber casts it is difficult to be certain whether or not they are the same species.

---

EXPLANATION OF PLATE 91

Figs. 1–13. *Pseudofrenelopsis varians* (Fontaine). 1–4, 6, 7, 12, are scanning electron micrographs. 1, 2, cuticle in section showing tubular stomatal pits with papillae at top and cutinized guard cells at bottom. 2, shows that the cuticle of the subsidiary cell is twice as thick as that of the adjacent epidermal cell. USNM 192378, 1, ×250, 2, ×500. 3, vertical section of thickest cuticle sampled (over 100 $\mu$m), inside uppermost. USNM 192380, ×400. 4, inner surface of internode cuticle with scattered stomata. USNM 192380, ×100. 5, light micrograph of internode cuticle, outside uppermost. USNM 192378, ×100. 6, inside of cuticle showing guard cells and hypodermal cells, USNM 192380, ×250. 7, stoma with eight subsidiary cells showing small lumen compared to other epidermal cells. USNM 192380, ×400. 8, stoma outside uppermost showing subsidiary cell papillae. USNM 192378, ×500. 9, stoma inside uppermost showing aperture and that stomatal pit is fluted in section. USNM 192378, ×500. 10, cuticle of 'open' leaf-cushion with papillae more prominent than stomata. USNM 192371A, ×100. 11, 12, light and scanning micrographs of the same internode with very long epidermal hairs at base. USNM 192378, both ×100. 13, possible insect bites in cuticle. USNM 192378, ×100.




WATSON, *Pseudofrenelopsis varians*

The same basic type of stoma with papillae inside the pit occurs in several other species of *Frenelopsis* and also in *Cupressinocladus valdensis* but they all have differences in external details of the pit opening. *F. oligostomata* Romariz from Portugal (Alvin 1977) has a thick ring around the pit entrance and rather short papillae inside. *F. hoheneggeri* (Ettingshausen) from Poland (Reymanówna and Watson 1976) has a stellate pit opening surrounded by large pouch-like papillae; the papillae inside the pit are large and obscure the guard cells. *F. occidentalis* Heer from Portugal (Alvin 1977) also has very large papillae in the pit but the pit opening is flush with the smooth outer surface. This is very similar to the stoma of *C. valdensis* (Seward) described below. *F. ramosissima* Fontaine is the only species of *Frenelopsis* I have seen without this kind of stoma.

## *Frenelopsis ramosissima* Fontaine

Plate 93; Plate 94, figs. 1–5; Plate 95, figs. 1–4; Plate 96, figs. 1–10; Plate 97, figs. 1–5

1889 *Frenelopsis ramosissima* Fontaine, 215, pls. 95–99; pl. 100, figs. 1–3; pl. 101, fig. 1.
1910 *Frenelopsis ramosissima* Fontaine; Berry, 305, text-figs. 1, 2.
1911 *Frenelopsis ramosissima* Fontaine; Berry, 422, pls. 71, 72.

*Emended diagnosis.* Lateral branches profusely branched in one plane, bearing leaves in whorls of three. Triangular part of leaf up to 2·0 mm high, sheathing base up to 0·5 mm; leaf margin dentate, teeth up to 100 μm long. Thickly cutinized internodes with stomata occurring roughly in longitudinal rows, irregularly spaced within rows; rows close together in ultimate branches (10–12 per mm), widely spaced (one per mm) and less well defined in older orders of branching; few stomata present on free leaf. Stomata with 4–6 (usually 5) subsidiary cells; diameter of stomatal apparatus 50–75 μm; guard cells at bottom of shallow pit, apertures tending to be horizontally orientated. Outer surface of subsidiary cells forming thickened rim around stomatal pit, lobed or with papillae (one per subsidiary cell) overhanging pit, rim bounded by distinct groove. Outer surface of each ordinary epidermal cell bearing a papilla or hair, up to 120 μm long; ordinary epidermal cells with thin periclinal walls, arranged roughly in files, often wider than long in older branching orders.

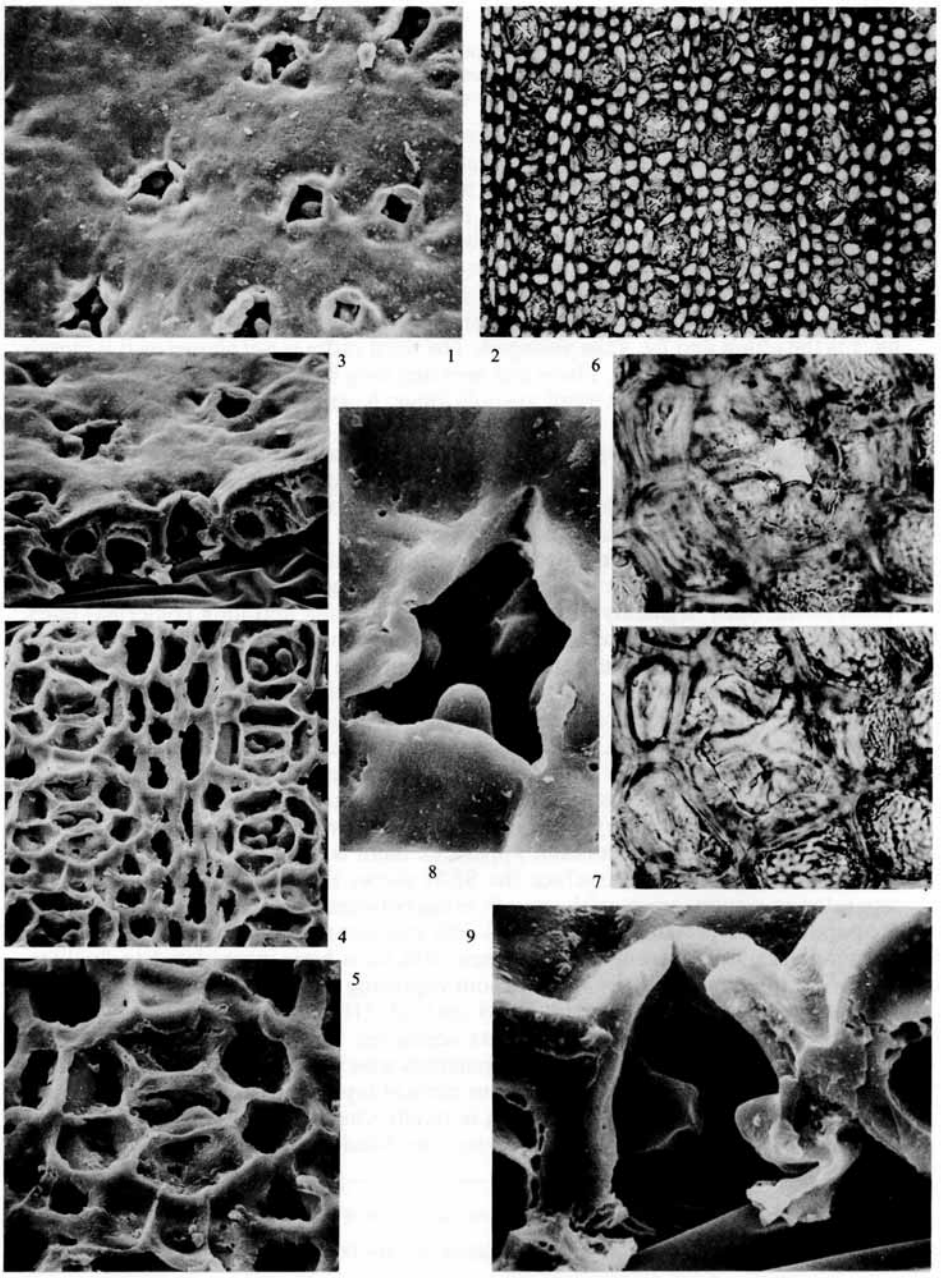
*Material and occurrence.* Lectotype USNM 192385, figured by Fontaine (1889), plate 96, fig. 2.

There are about twelve specimens remaining in the Smithsonian Collection, all from Fredericksburg, Virginia though Fontaine and Berry listed other localities. It seems probable that at least some of the missing specimens were exchanged with other museums many years ago.

---

EXPLANATION OF PLATE 92

Figs. 1–9. *Frenelopsis alata* (K. Feistmantel). 1, 3–5, 8, 9, scanning electron micrographs. All USNM 3750. 1, outer surface of internode cuticle. ×250. 2, light micrograph of internode cuticle showing stomatal arrangement. ×100. 3, cuticle tilted at 60° to show stoma in vertical section. ×250. 4, inner surface of internode cuticle. Note that guard cells are not preserved. ×250. 5, single stoma showing openings to hollow papillae in stomatal pit. The papillae can be clearly seen here because the guard cells are absent. ×500. 6, stoma in high plane of focus to show stellate opening to stomatal pit. ×500. 7, same stoma in low plane of focus showing large papillae inside stomatal pit. ×500. 8, outer view of single stoma showing pit papillae below the lobed canopy. ×1000. 9, vertical section of a stoma. ×1000.




WATSON, *Frenelopsis alata*

*Localities*. Fredericksburg, Virginia and Federal Hill (Baltimore), Maryland which are both lower Albian (Doyle and Hickey 1976); Chinkapin Hollow, Virginia is probably Doyle and Hickey Zone I (Barremian–lower Albian) but has not yielded pollen for dating (Hickey pers. comm.).

*Description*. The Fredericksburg locality produced a profusion of handsome specimens and though many are missing the larger ones remain (Pl. 93 and Pl. 94, fig. 2) together with some lengths of wide stem (Pl. 94, fig. 1). Thus it has been possible to sample the cuticle more extensively than in any of the other species.

The cuticle of *F. ramosissima* is immediately distinguishable from other species by its epidermal papillae and hairs which may be extremely long; Plate 96, fig. 10 shows them at their smallest and Plate 97, fig. 2 at their longest. Plate 97, figs. 1–4 show the cuticle of four of the five orders of branching of the Glasgow specimen (Pl. 95, fig. 1); fig. 1 is the oldest and fig. 4 the youngest. The third order is not shown as it is closely similar to the second (fig. 2). I have not seen any long hairs in the youngest segments and clearly there is a distinct trend towards longer hairs in the older orders with some mixing of different lengths.

The rim around the stomatal pit is somewhat variable. The subsidiary cells may each have a well-developed papilla overhanging the stomatal pit (Pl. 96, fig. 5 and Pl. 97, fig. 4). Usually I found these in the youngest segments with dense stomatal rows and small epidermal cell papillae. Plate 97, fig. 2 shows stomata where the subsidiary cell papillae are less strongly developed and do not overhang the pit, and Plate 96, fig. 4 shows the rim as a gently undulating ring. This type of stoma is usually found in the older segments with widely spaced stomata and long epidermal hairs. However, these combinations of characters are not consistent: Plate 96, fig. 10 shows a young segment with scarcely any epidermal papillae and a lobed stomatal rim.

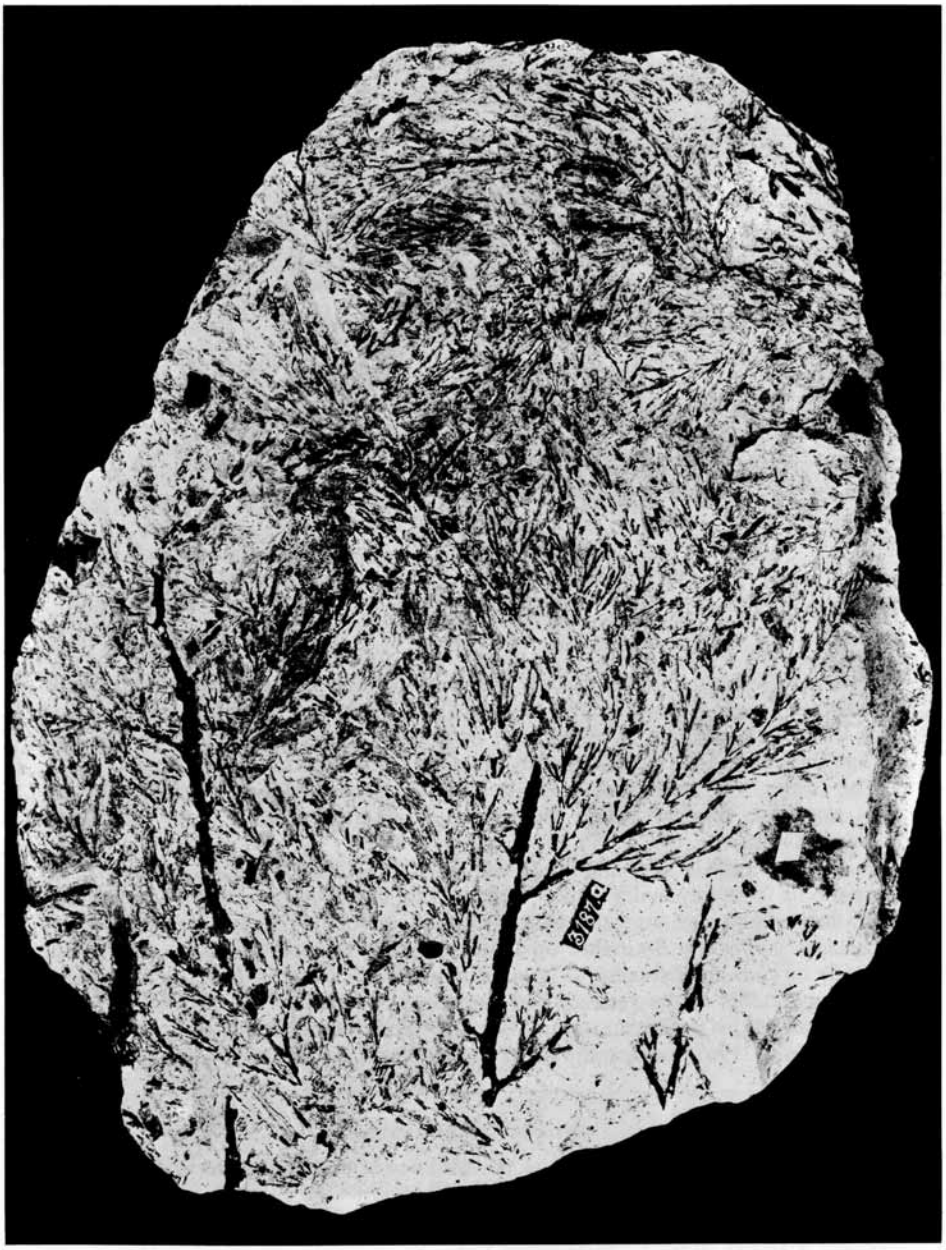
The specimen in Plate 94, fig. 1 is of especial interest because this is a stem 2 cm in diameter with persistent cuticle and there are similar specimens with persistent leaves (Fontaine 1889, pl. 96, fig. 3). The epidermal cells of this specimen are considerably elongated horizontally with a somewhat stretched appearance, but in places there is clear evidence of continuing cell division, mostly in a vertical plane (text-fig. 4). The stomata are very widely spaced (one row per mm) but are in no way distorted and around the stomatal apparatus there is both vertical and horizontal cell division. On the outer surface the SEM shows the epidermal papillae widely separated in sinuous tracts with smooth areas between (Pl. 97, fig. 5). I assume that the papillae were present on the original cells and that the smooth areas, which show stretch-marks, are where most of the new cells have been intercalated to facilitate expansion in diameter of the stem without rupturing the epidermis.

Fontaine's account of this plant (1889, pp. 215–218) indicates that *F. ramosissima* had very little woody tissue. He reports seeing the woody axis in the form of jet 'always much smaller than the tube of epidermis which incloses it'. He suggested that the stem originally had a 'thick succulent cortical layer' and quite commonly found 'the shrunken remains of the twigs lying in molds which are now considerably larger than themselves, and which they evidently once filled'.

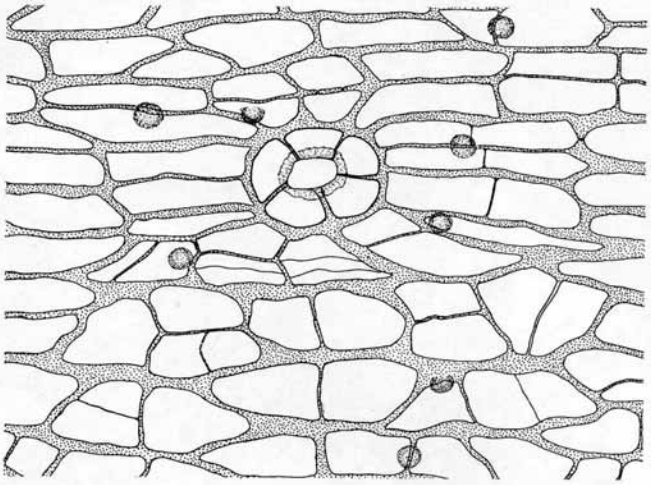
---

EXPLANATION OF PLATE 93

Fig. 1. *Frenelopsis ramosissima* Fontaine. The lectotype. USNM 192385. ×$\frac{2}{3}$.



WATSON, *Frenelopsis ramosissima*



TEXT-FIG. 4. Cuticle of the wide stem of *Frenelopsis ramosissima* in Plate 94, fig. 1 showing horizontally elongated cells with continuing cell divisions in horizontal and vertical planes; stomata now widely isolated from one another but undistorted; a few epidermal papillae can be seen.

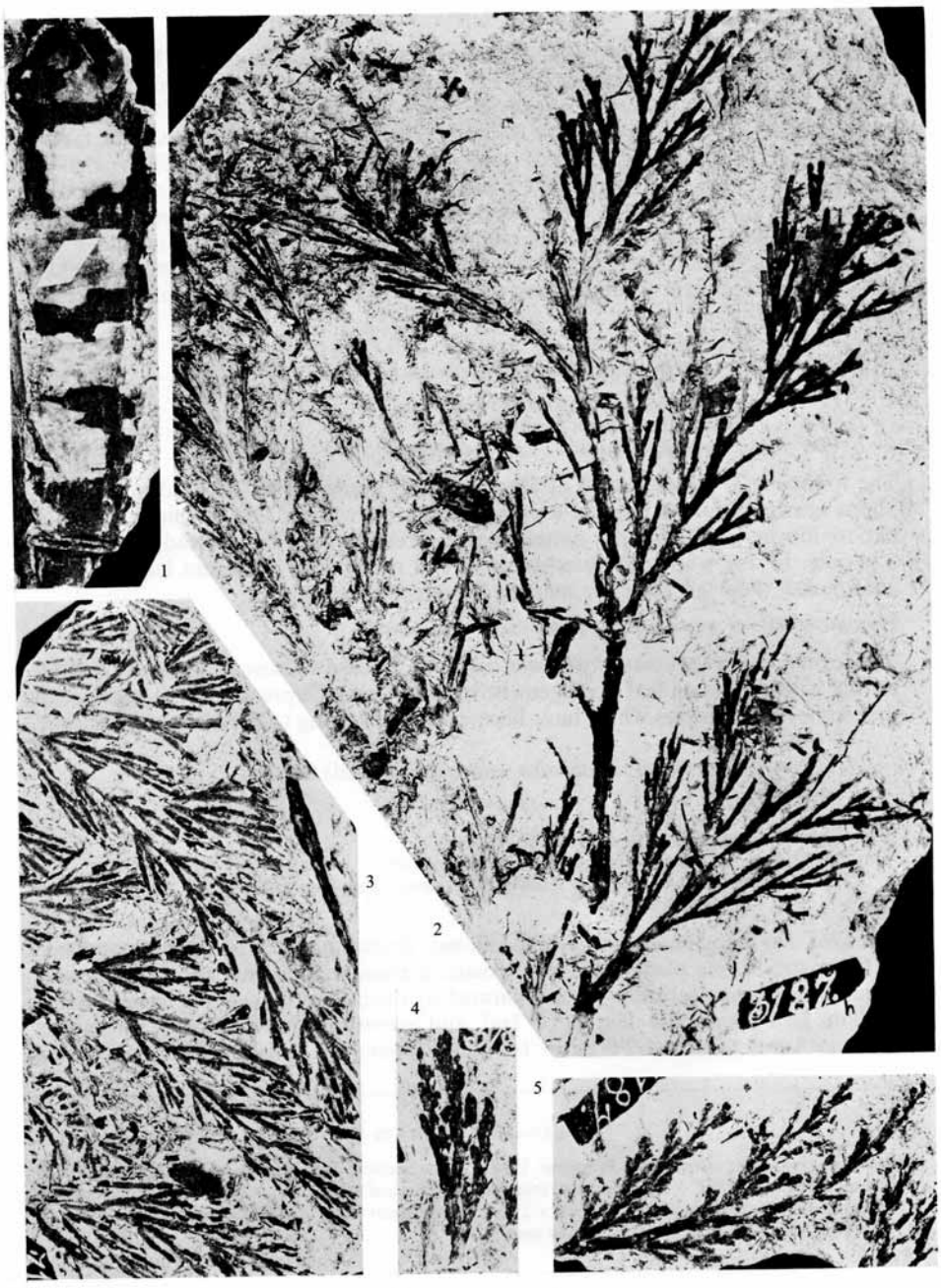
*Comparison.* Clearly *F. ramosissima* was rather similar in morphology and habit to *Pseudofrenelopsis varians*, as well as in surface features of the epidermis. However, they differ considerably (see Table 1) in their branching, leaf number per node, cuticle thickness, and, of course, they have not been found in association.

The stoma of *F. ramosissima*, unlike all other species of *Frenelopsis* I have seen, does not have papillae inside the stomatal pit and is much more like that of *P. parceramosa.*

*Frenelopsis* and the very similar *Pseudofrenelopsis* differ strikingly in the aspect of their shoots from any living conifer. Particularly *F. ramosissima* and *P. varians* seem much more like some stem succulent dicotyledon, such as *Salicornia* of the Chenopodiaceae. *Salicornia* flourishes on marshes where the soil is loaded with sodium chloride or sodium carbonate. The predominance of *Classopollis* pollen in coastal, marine sediments of the Jurassic and Cretaceous has led to the suggestion that the plants bearing this pollen may have been stilt-rooted mangrove species (Hughes and Moody-Stuart 1967) or dominant on the seaward margin of lowland forests (see

EXPLANATION OF PLATE 94

Figs. 1–5. *Frenelopsis ramosissima* Fontaine. 1, the widest stem in the collection. This specimen has cuticle which shows the continuing cell division of the epidermis, seen in text-fig. 4. USNM 192387, ×1. 2, 3, profusely branched specimens with fairly long internodes, photographed dry. 2, USNM 192388, ×1, 3, USNM 192390, ×1. 4, 5, unexpanded shoots with short internodes, crowded branching, and bud-like tips. 4, USNM 192386, 5, USNM 192391, both ×1.




WATSON, *Frenelopsis ramosissima*

Hughes 1976, p. 37). Vachrameev (1970) favours an upland habitat and Batten (1974) has reconstructed several alternatives including those above. Current work continues to link more plants with *Classopollis* (Archangelsky 1968; Lorch 1968; Hluštík and Konzalová 1976; Barnard and Miller 1976) and it is now clear that the family Cheirolepidiaceae includes a wide variety of shoot types. It may well be that its members also exhibited a much wider range of habitat than has hitherto been supposed and some of them, such as *P. varians* and *F. ramosissima*, may have been low, coastal succulents and even salt-marsh inhabitants (Jung 1974). Dr. S. Baksi and Professor P. Allen (pers. comm.) have found, *in situ*, a small *Frenelopsis*-like plant in brackish clays at the top of the Indian Gondwanas where a Wealden facies has now been recognized.

### Form-genus *Cupressinocladus* Seward 1919: 307

1960 *Cupressinocladus* Seward; Chaloner and Lorch, 237.
1969 *Cupressinocladus* Seward; Harris, 250.
1976 *Cupressinocladus* Seward; Barnard and Miller, 43.

The following is the diagnosis of Harris slightly emended by Barnard and Miller. Shoot bearing leaves in decussate pairs or alternate whorls. Leaves small and scale-like or longer, dorsiventrally flattened and spreading, not constricted basally into a petiole. In any whorl where adjacent lateral margins of decurrent leaf bases are contiguous, their junctions are marked by conspicuous sutures.

*Type species. Thuites salicornoides* Unger (selected by Andrews 1955).

The form-genus *Cupressinocladus* was made by Seward to accommodate vegetative shoots with decussate leaf arrangement like the living Cupressaceae. It now seems that some of the species which have been described belong to the Cheirolepidiaceae.

### *Cupressinocladus valdensis* (Seward) Seward

Plate 97, figs. 6–11

1895 *Thuites valdensis* Seward, 209, pl. 20, fig. 6.
1919 *Cupressinocladus valdensis* (Seward) Seward, 309.
1960 *Cupressinocladus valdensis* (Seward); Chaloner and Lorch, 236 (brief comparison with *C. ramonensis*).

*Emended diagnosis* (based on holotype alone). Branching of lateral shoots opposite or alternate, in one plane. Leaves opposite, decussate; free part short, adpressed, surmounting long decurrent bases separated by distinct sutures. Some leaves having median keel along the length of leaf and decurrent base; largest internodes 10 mm × 4 mm; smallest 2·0 mm × 1·5 mm. Stomata on abaxial surface (including

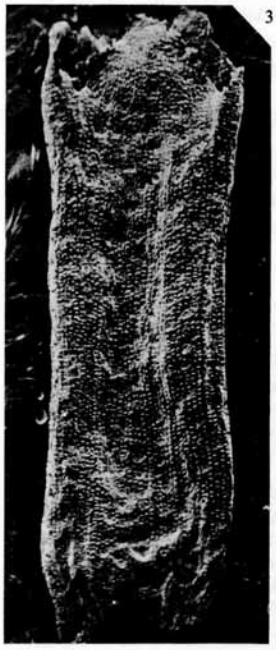
---

EXPLANATION OF PLATE 95

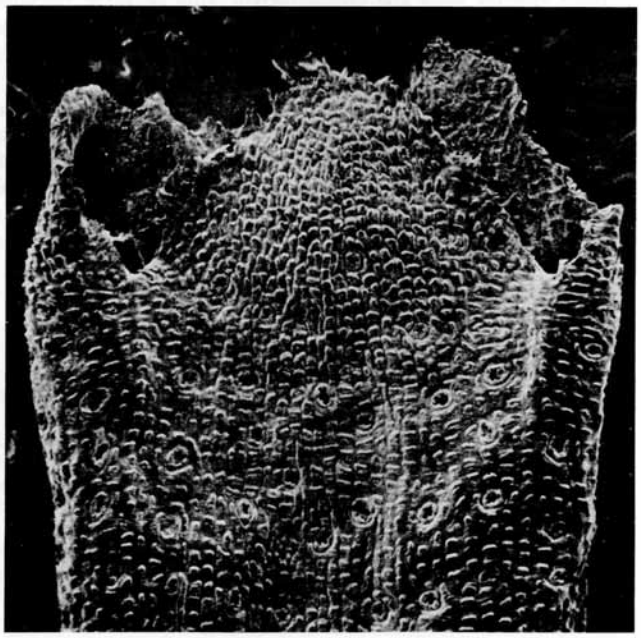
Figs. 1–4. *Frenelopsis ramosissima* Fontaine. 1, part of the specimen in Glasgow Museum photographed under paraffin. Pb 2207, × 2. 2, the same magnified to show leaf whorls. × 5. 3, SEM of a single segment from an ultimate branch. USNM 192385, × 25. 4, SEM of a leaf whorl of the same segment. The marginal hairs are mostly missing but a few can be seen. × 75.

1

2



3



4

WATSON, *Frenelopsis ramosissima*

whole leaf-base cushion) occurring in longitudinal rows, uniseriate or imperfectly biseriate, 9–11 rows per mm. Stoma monocyclic having guard cells sunken below ring of 4–6 subsidiary cells which form a stomatal pit; opening of stomatal pit level with epidermal surface. Over-all diameter of stomatal apparatus 65–85 $\mu$m; each subsidiary cell having a large papilla inside the stomatal pit obscuring guard cells. Guard cells randomly orientated. Epidermal cells non-papillate, thick walled, squarish or rectangular tending to be in longitudinal rows; stomatal rows separated by up to four rows of such cells. Hypodermis of thin-walled rectangular cells under non-stomatal regions, square cells under stomatal regions but absent under stomatal apparatus.

*Material.* Holotype and only known specimen B.M. (N.H.) V. 2138.

The locality in the English Wealden is given as Ecclesbourne, Hastings though the exact horizon is not known but it must be Berriasian in age (Hughes 1975).

This specimen was originally well preserved but was cellulose varnished in 1940 which damaged the cuticle. However, I was able to get satisfactory preparations from the surfaces facing the rock and from side branches previously unexposed. Even so the preservation is poor by comparison to the other material described in this paper.

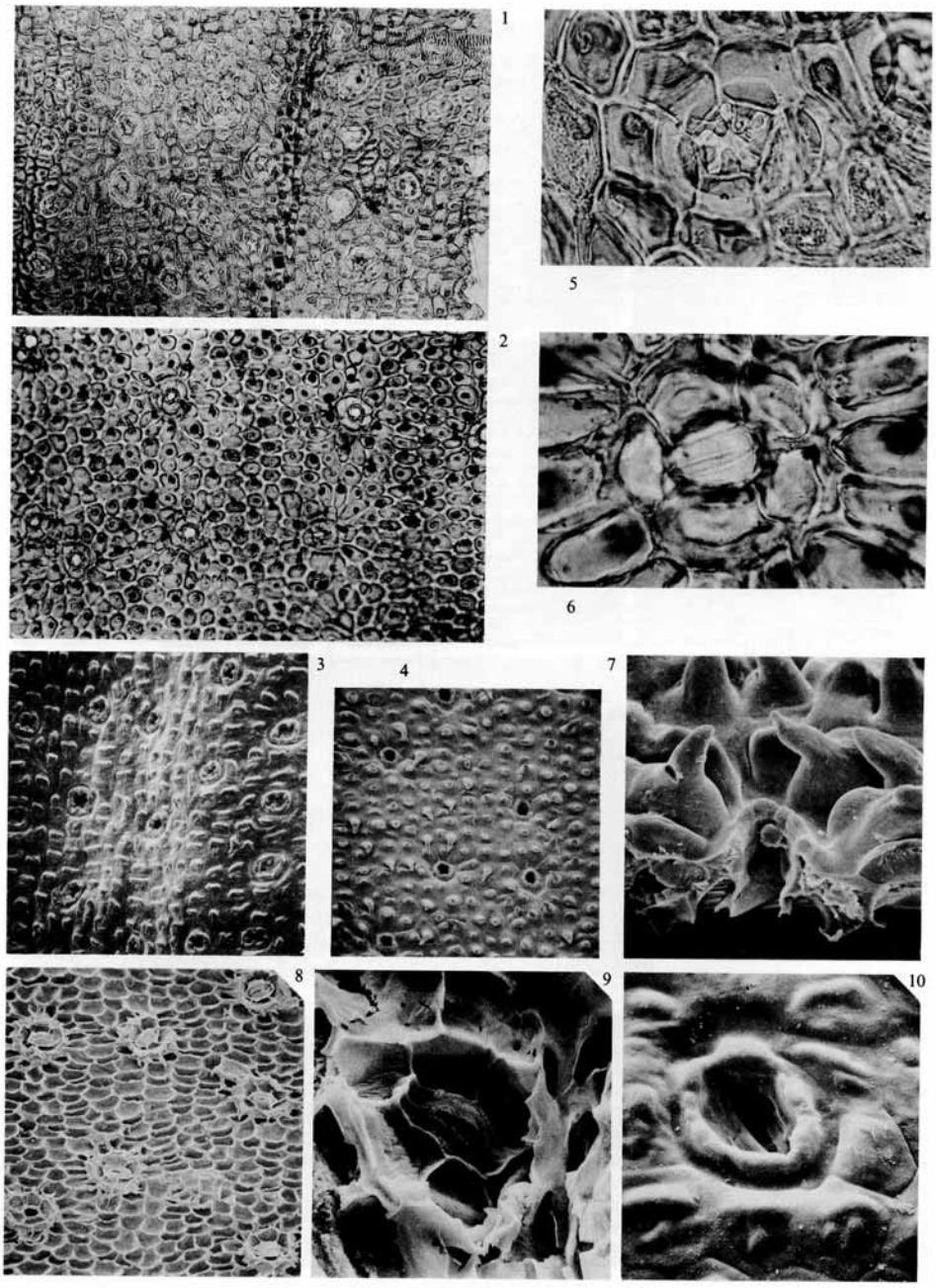
*Description and comparison.* The cuticle of *C. valdensis* is now known to have the same distinctive type of stoma as various species of *Frenelopsis*. *F. occidentalis* Heer from the Lower Cretaceous of Portugal has a closely similar stoma in that the opening of the stomatal pit has no thickening around it and is flush with the general cuticle surface which is totally featureless (Pl. 97, fig. 8) except for these simple pit openings. Both species have the characteristic ring of large papillae inside the stomatal pit, entirely filling it and obscuring the guard cells from above. The leaf number of *F. occidentalis* has not been determined (Alvin 1977) but it is clear that there are no sutures.

Two species with leaf arrangement and sutures like *C. valdensis* are *C. acuminifolia* Kon'no and *F. malaiana* Kon'no from the Cretaceous of Malaya (Kon'no 1967, 1968). The latter species which clearly has sutures should not be included in *Frenelopsis* and has recently been transferred to *Cupressinocladus* by Barnard and Miller (1976) who think it may have its leaves in whorls of three. Unfortunately there are no cuticle details of either species. *C. ramonensis* Chaloner and Lorch (1960) from the Lower

---

EXPLANATION OF PLATE 96

Figs. 1–10. *Frenelopsis ramosissima* Fontaine. 1, internode cuticle of a young branching order showing closely arranged papillate stomata. USNM 192390, ×100. 2, internode cuticle of an older branching order showing widely spaced stomata. USNM 192385, ×100. 3, SEM of cuticle similar to that in fig. 1. USNM 192385, ×100. 4, SEM of cuticle similar to that in fig. 2. USNM 192385, ×100. 5, single stoma from specimen in fig. 1 showing strongly papillate subsidiary cells. ×500. 6, single stoma from specimen in fig. 2 showing subsidiary cells without papillae. In this stoma the subsidiary cells form a fluted ring as in figs. 4, 10. ×500. 7, cuticle tilted at 60° in SEM to show vertical section of stoma. USNM 192385, ×500. 8, inner surface of cuticle of older branching order, from same piece as fig. 4. USNM 192385, ×100. 9, inside view of stoma (young branching order) showing guard cells and some cutinized, pitted hydrodermal cells. USNM 192385, ×500. 10, stoma on young branch, scarcely papillate and without subsidiary cell papillae, showing guard cells at bottom of shallow stomatal pit. USNM 192385, ×500.




WATSON, *Frenelopsis ramosissima*

TABLE 1. Comparison of the species in this paper together with *Frenelopsis hoheneggeri* (from details given by Reymanówna and Watson 1976).

| SPECIES / KNOWN DETAILS | *Pseudofrenelopsis parceramosa* | *Pseudofrenelopsis varians* | *Frenelopsis ramosissima* | *Frenelopsis alata* | *Frenelopsis hoheneggeri* | *Cupressinocladus valdensis* |
|---|---|---|---|---|---|---|
| BRANCHING | sparse | sparse | profuse | moderate | moderate | moderate |
| INTERNODE LENGTH | 1 - 11mm | 1.5 - 17mm | up to 2cm | up to 1.5cm | typically 8mm | up to 1cm |
| INTERNODE WIDTH | 1mm upwards | 3 - 7mm | up to 2cm | up to 5mm | typically 3mm | up to 2mm |
| PRESENCE OF SUTURE | in some 'open' forms | no | no | no | no | yes |
| LEAF NUMBER PER NODE | 1 (2/5 phyllotaxis) | 1 | alternating whorls of 3 | alternating whorls of 3 | alternating whorls of 3 | 2 -opposite & decussate |
| MAXIMUM LENGTH OF FREE LEAF | 2mm | 1.5mm | 2mm | about 1mm | 1.5mm | 2mm |
| DEPTH OF SHEATHING BASE | 0.8mm | 0.8mm | 0.5mm | up to 1mm | 1mm | – |
| LEAF MARGIN | hairs up to 80µm | hairs up to 60µm | hairs up to 100µm | fringe of hairs | scarious | not known |
| INTERNODE CUTICLE THICKNESS | 30µm | 50 - 110µm | 38µm | 30 - 40µm | 40µm | about 20µm |
| STOMATAL ARRANGEMENT | well defined rows | scattered in 'closed' forms rows in 'open' forms | ill defined rows | ill defined rows | well defined rows | well defined rows |
| DENSITY OF STOMATAL ROWS | 6 - 10 per mm | 8 - 10 per mm | 10-12 per mm less with age | 10 - 12 per mm | 10 - 12 per mm | 9 - 10 per mm |
| DIAMETER OF STOMATAL APPARATUS | 50 - 80µm | 70 - 100µm | 50 - 75µm | 52 - 77µm | 60 - 70µm | 65 - 85µm |
| NUMBER OF SUBSIDIARY CELLS | usually 5 or 6 rarely 4 or 7 | usually 5 - 8 rarely 4 or 9 | 4 - 6 usually 5 | usually 5 occas. 4 or 6 | 4 - 6 usually 4 | 4 - 6 |
| ORIENTATION OF STOMATAL APERTURE | random | random | horizontal | ?random | horizontal | random |
| PAPILLAE INSIDE STOMATAL PIT ? | no | no | no | yes | yes | yes |
| TRICHOMES ON EPIDERMAL CELLS | none to very long hairs | up to 80µm | up to 120µm | none | none | none |
| RIM OF STOMATAL PIT | round:- with or without papillae | round:- with papillae | round:- lobed or papillate | stellate | stellate | stellate |
| STRATIGRAPHIC RANGE | Berriasian-Albian | Aptian-Albian | Barremian - Albian | Aptian - Cenomanian | Hauterivian | Berriasian |

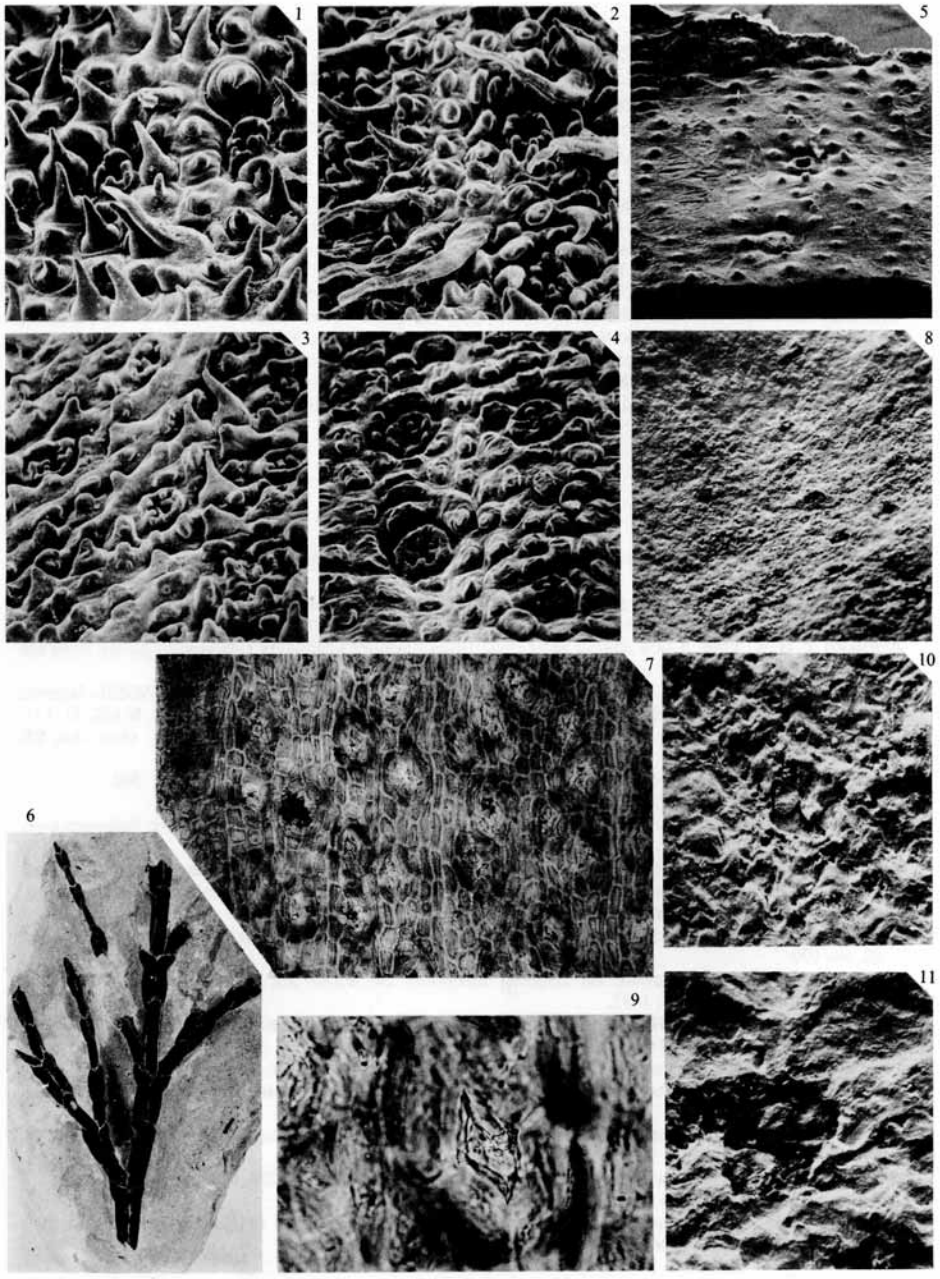
Jurassic of Israel which is very similar in appearance to *C. valdensis* is thought to have borne a *Masculostrobus* cone with *Classopollis* pollen (Lorch 1968). From the middle Jurassic of Iran Barnard and Miller (1976) have recently described *C. pseudoexpansum* which has leaves in whorls of three. It is profusely branched with short leaf-base

EXPLANATION OF PLATE 97

Figs. 1–5. *Frenelopsis ramosissima* Fontaine. 1–4, four of the five successive branching orders of the Glasgow specimen. 1, is the oldest; 5, is the youngest; 2, the second order is closely similar to the third order which is omitted. Pb 2207, all ×250. 5, cuticle from the wide stem in Plate 94, fig. 1 showing widely spaced sinuous rows of papillae on original cells separated by smooth areas showing stretch-marks where new cells have been intercalated. USNM 192387, ×100.

Figs. 6–11. *Cupressinocladus valdensis* (Seward), B.M. (N.H.) V. 2138. 6, holotype and only known specimen. ×1. 7, cuticle of leaf-base cushion. ×100. 8, outer surface of leaf-base cushion showing stomatal pits flush with surface. ×100. 9, single stoma showing stomatal pit opening. ×500. 10, 11, stomata showing large papillae inside stomatal pit. 10, ×500, 11, ×1000.

Figs. 1–5, 8, 10, 11, scanning electron micrographs.




WATSON, *Frenelopsis*, *Cupressinocladus*

cushions and a completely different appearance to *C. valdensis*, nor does it have a similar stoma. However, it is known to bear a male cone containing *Classopollis* pollen and is therefore clearly cheirolepidiaceous.

At the moment there is no evidence for any species having both two- and three-leaf whorls nor can I say if any of them are succulent like *P. varians* and *F. ramosissima*.

*Acknowledgements.* I am most grateful for the opportunity to study the collection in the National Museum of Natural History, Smithsonian Institution and especially thank Dr. Leo Hickey for his continuing help. My visit to Washington D.C. was partly financed by the Royal Society and the University of Manchester.

I also thank the following who have been enormously helpful: Dr. K. L. Alvin for use of his unpublished manuscript, help with SEM work, and endless discussion; Professor T. M. Harris, F.R.S., for invaluable help with the manuscript; Dr. Alan Charlton for his patient discussion of the various botanical problems posed by these plants; Mr. James P. Ferrigno of the Smithsonian Institution for all the photography of hand-specimens; Mr. Brian Atherton of Manchester University for all the printing of the micrographs; Department of Textile Technology, U.M.I.S.T. for use of the SEM. A donation from the W. H. Lang Fund, Manchester University has helped towards the cost of the plates in this paper and is gratefully acknowledged.

## REFERENCES

ALVIN, K. L. 1977. The conifers *Frenelopsis* and *Manica* in the Cretaceous of Portugal. *Palaeontology* **20,** 387–404.

ANDREWS, H. N., Jun. 1955. Index of generic names of fossil plants, 1820–1950. *U.S. Geol. Surv. Bull.* **1013,** 262 pp.

ARCHANGELSKY, S. 1968. On the genus *Tomaxellia* (Coniferae) from the Lower Cretaceous of Patagonia (Argentina) and its male and female cones. *J. Linn. Soc.* (*Bot.*), **61,** 153–165.

BARNARD, P. D. W. 1968. A new species of *Masculostrobus* Seward producing *Classopollis* pollen from the Jurassic of Iran. Ibid. 167–176.

—— and MILLER, J. C. 1976. Flora of the Shemshak Formation (Elburz, Iran), Part 3: Middle Jurassic (Dogger) plants from Katumbargah, Vasek Gah and Imam Manak. *Palaeontographica*, **B 155,** 31–117.

BATTEN, D. J. 1974. Wealden Palaeoecology from the distribution of Plant Fossils. *Proc. Geol. Ass.* **85,** 433–458.

BERRY, E. W. 1910. The epidermal characters of *Frenelopsis ramosissima*. *Bot. Gaz.* **50,** 305–309.

—— 1911. *In* Lower Cretaceous. *Maryland Geological Survey*, 622 pp.

CHALONER, W. G. and LORCH, J. 1960. An opposite-leaved Conifer from the Jurassic of Israel. *Palaeontology*, **2,** 236–242.

DOYLE, J. and HICKEY, L. J. 1976. Pollen and leaves from the Mid-Cretaceous Potomac Group and their bearing on Early Angiosperm Evolution. *In* BECK, C. B. (ed.). *Origin and Early Evolution of Angiosperms.* Columbia University Press, New York. Pp. 139–206.

EDWARDS, W. N. 1926. Fossil plants from the Nubian Sandstone of Eastern Darfur. *Q. Jl geol. Soc. Lond.* **82,** 94–100.

ETTINGSHAUSEN, C. 1852. Beitrag zur näheren Kenntniss der Flora der Wealdenperiode. *Abh. geol. Bundesanst., Wien*, **1** (3/2), 1–32.

FEISTMANTEL, K. 1881. Der Hangendflötzung im Schlan—Rakonitzer Steinkohlenbecken. *Arch. naturw. LandDurchforsch. Böhm.* **4** (6), 96–98.

FONTAINE, W. M. 1889. The Potomac or younger Mesozoic Flora. *Mon. U.S. Geol. Surv.* **15,** 1–377.

—— 1893. Notes on some fossil plants from the Trinity Division of the Comanche Series of Texas. *Proc. Nat. Mus.* **16,** 261–282.

—— 1905. *In* WARD, L. F. Status of the mesozoic floras of the United States. *Mon. U.S. Geol. Surv.* **48,** 616 pp.

HARRIS, T. M. 1969. Naming a fossil conifer. *J. Sen Memorial Volume*, 243–252. Calcutta.

HLUŠTÍK, A. 1972. *Frenelopsis alata* (Cupress. fossil). *Taxon*, **21,** 210.

—— 1974. New finds of *Frenelopsis* (Cupressaceae) from the Cretaceous of Czechoslovakia and their problems. *Čas. Miner. geol.* **19,** 263–268. [In Czech, English summary.]

HLUŠTÍK, A. and KONZALOVÁ, M. 1976. Polliniferous cones of *Frenelopsis alata* (K. Feistm.) Knobloch from the Cenomanian of Czechoslovakia. *Vest. ústřed. Úst. geol.* **51,** 37–45.

HUGHES, N. F. 1975. Plant succession in the English Wealden strata. *Proc. Geol. Ass.* **86,** 439–455.

—— 1976. *Palaeobiology of Angiosperm Origins.* Cambridge University Press, 242 pp.

—— and MOODY-STUART, J. C. 1967. Palynological facies and correlation in the English Wealden. *Rev. Palaeobotan. Palynol.* **1,** 259–268.

JUNG, W. 1974. Die Konifere *Brachyphyllum nepos* Saporta aus den Solnhofener Plattenkalk (unteres untertithon), ein Halophyt. *Mitt. bayer. Staatsamml. Palaont. hist. Geol.* **14,** 49–58.

KNOBLOCH, E. 1971. Neue Pflanzenfunde aus dem böhmischen und mährischen Cenoman. *N. Jb. Geol. Paläont. Abh.* **139,** 43–56.

KON'NO, E. 1967. Some younger Mesozoic plants from Malaya. Contributions to the Geology and Palaeontology of Southeast Asia, 38. *Geol. palaeont. S.E. Asia,* **3,** 135–164, Tokyo.

—— 1968. Additions to some younger Mesozoic plants from Malaya. Contributions to the Geology and Palaeontology of Southeast Asia, 48. Ibid. **4,** 139–155. Tokyo.

LORCH, J. 1968. Some Jurassic conifers from Israel. *J. Linn. Soc.* (*Bot.*), **61,** 177–188.

NATHORST, A. G. 1893. *In* FELIX, J. and LENK, H. *Beiträge zur Geologie und Paläontologie der Republik Mexico,* **2,** 51–54. Leipzig.

NĚMEJC, F. 1926. On the identity of *Sclerophyllum alatum* Feistm. and *Frenelopsis bohemica* Vel. *Sb. st. geol. Úst. čsl. Repub.* **6,** 133–142. [In Czech, English Summary.]

OISHI, S. 1940. The Mesozoic floras of Japan. *J. Fac. Sci. Hokkaido Univ.* **5,** 123–480.

OLDHAM, T. C. B. 1973. The Plant debris beds of the English Wealden. Unpublished Ph.D. Thesis, University of Cambridge, No. 8681.

—— 1976. Flora of the Wealden Plant-debris beds of England. *Palaeontology,* **19,** 437–502.

REYMANÓWNA, M. 1965. On *Weichselia reticulata* and *Frenelopsis hoheneggeri* from the Western Carpathians. *Acta palaeobot., Cracov,* **6,** 15–26.

—— and WATSON, J. 1976. The genus *Frenelopsis* Schenk and the type species *Frenelopsis hoheneggeri* (Ettingshausen) Schenk. *Acta palaeobot., Cracov,* **17,** 17–26.

ROMARIZ, C. 1946. Estudo e revisão das formas portuguesas de *Frenelopsis. Bolm. Mus. Lab. miner. geol. Univ. Lis.* (4) **14,** 135–150.

SCHENK, A. 1869. Beiträge zur Flora der Vorwelt. III. Die fossilen Pflanzen der Wernsdorfer Schichten in den Nordkarpathen. *Palaeontographica,* **19,** 1–34.

SEWARD, A. C. 1895. The Wealden Flora, Part II. Gymnospermae. Catalogue of Mesozoic Plants in the Department of Geology, British Museum (Natural History), xii+259 pp.

—— 1919. *Fossil Plants.* A Textbook for Students of Botany and Geology, 4. Cambridge University Press, 543 pp.

STEPHENSON, L. W. *et al.* 1942. Correlation of the outcropping Cretaceous Formations of the Atlantic and Gulf Coastal Plain and Trans-Pecos Texas. *Bull. geol. Soc. Am.* **53,** 435–448.

TEIXEIRA, C. 1948. Flora Mesozoica Portuguesa. I Parte. Servicos Geologicos, Lisboa, 118 pp.

VACHRAMEEV, V. A. 1970. Range and palaeoecology of Mesozoic conifers, the Cheirolepidiaceae. *Paleont. Jour.* **1,** 12–25.

VELENOVSKY, J. 1888. Ueber einige neue Pflanzenformen der böhmischen Keideformation. *Sber. K. böhm. Ges. Wiss.* **29,** 590–598.

WATSON, J. 1964. Revision of the English Wealden Fossil Flora. Unpublished Ph.D. Thesis, University of Reading, R. 1146.

—— 1974. *Manica*: A new fossil conifer genus. *Taxon,* **23,** 428.

—— and ALVIN, K. L. 1976. Silicone rubber casts of silicified plants from the Cretaceous of Sudan, *Palaeontology,* **19,** 641–650.

WHITEMAN, A. J. 1971. *The Geology of the Sudan Republic.* Clarendon Press, Oxford. 290 pp.

JOAN WATSON
Departments of Botany and Geology
The University
Manchester M13 9PL

Typescript received 3 June 1976
Revised typescript received 20 November 1976