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Frenelopsis pombetsuensis: a new cheirolepidiaceous conifer from the Lower Cretaceous (Albian) of Hokkaido, Japan

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Abstract. **A new fossil conifer, *Frenelopsis pombetsuensis* sp. nov., is described on the basis of a single specimen obtained from the Lower Cretaceous (Albian) of Hokkaido, Japan. *Frenelopsis pombetsuensis* is similar to *F. choshiensis* from the Lower Cretaceous of Choshi, Kimigahama, in having two leaves at each node. The cuticular feature of *Frenelopsis pombetsuensis* is, however, rather more similar to that of *F. hoheneggeri* from the Lower Cretaceous of Poland than to *F. choshiensis*. The Late Jurassic to Early Cretaceous paleofloras of Japan have been divided into two distinct types: the Ryoseki and Tetori. However, attributions of the Early Cretaceous flora of Hokkaido have not been made because of its hitherto poorly-known fossil record. The genus *Frenelopsis* is one of the most important members of the Ryoseki-type floras and has never been found in the Tetori-type floras. The present fossil is the first record of characteristic taxon of the Ryoseki-type flora from the Lower Cretaceous of Hokkaido.**

Key words: Albian, conifer, *Frenelopsis pombetsuensis*, Hokkaido, Middle Yezo Group, Ryoseki-type floras

Introduction

During Late Jurassic to Early Cretaceous time, two paleofloristic types flourished in Japan and its adjacent areas; the Ryoseki-type and Tetori-type floras (Kimura, 1961, 1975, 1987; Kimura and Ohana, 1992; Ohana and Kimura, 1995). The taxonomic compositions of these two paleofloristic types of floras are quite different. According to Ohana and Kimura (1995), the difference between the two floras is due to climatic factors. Based on the taxonomic compositions of the floras, and the morphological features of fossil plants, they estimate that the Ryoseki-type floras flourished under tropical-subtropical and rather arid climatic conditions, while the Tetori-type floras flourished under warm-temperate and rather humid conditions.

Although a number of fossil plants have been described from the Middle-Upper Yezo Group of Hokkaido (see Nishida, 1991), all of them, except for a single conifer seedling-like structure (Stockey *et al.*, 1990), are dated as Late Cretaceous. Thus, no characteristic plant fossils of the Ryoseki-type or Tetori-type floras have previously been described from Hokkaido.

In the present paper, the author describes a new species of *Frenelopsis* from the Lower Cretaceous (Albian) of Hokkaido. *Frenelopsis* is an extinct conifer genus assigned to the family Cheirolepidiaceae. Frenelopsids, a group consisting of the genus *Frenelopsis* and the closely related genus *Pseudofrenelopsis*, have been used as an indicator of tropical or subtropical and arid climate (Alvin, 1982). In Japan, *Frenelopsis* is one of the characteristic taxa of the Ryoseki-type floras, thought to have flourished under tropical or subtropical and arid or semi-arid conditions (Kimura and Ohana, 1992; Ohana and Kimura, 1995).

Material and Methods

Material.—The compressed conifer shoot was found in the Pombetsu Valley about 60 km northeast of Sapporo City (Figure 1). The specimen was obtained from the mudstone bed of the uppermost strata of the Main part, Middle Yezo Group. Matsumoto (1965) described *Ammonoceratites yezoensis* (Yabe) from the same locality, indicating a middle?- upper Albian age.

Methods.—For the cuticle observation, fossil leaves were treated by Schulze's solution followed by diluted NaOH. Obtained cuticles were mounted in EUKITT for light microscope observation. For SEM observation, cuticles were coated by Pt-Pd with a HITACHI E-1030 ion sputter and photographed by HITACHI S-800.

The specimen is housed in the Mikasa City Museum, Ikushumbets-nishikicho, Mikasa, 068-21 Japan.

Systematic description

Order Coniferales
Family Cheirolepidiaceae Takhtajan, 1963
Genus ***Frenelopsis*** Schenk, 1869

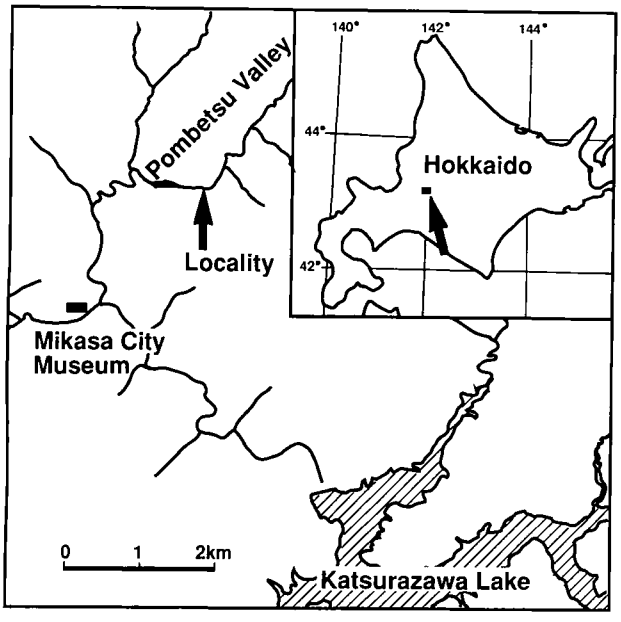

Figure 1. Locality map.

Frenelopsis pombetsuensis sp. nov.

Figures 2A-E, 3A-I

Material.—Holotype, MCM-A573.

Horizon.—Uppermost strata of the main part of Middle Yezo Group (Albian).

Type locality.—Pombetsu Valley, Mikasa City, Hokkaido (Figure 1; roughly 43°16'19"N, 141°59'48"E). The outcrop corresponds to locality no. Ik 2024 of Matsumoto (1965).

Diagnosis.—Internode at least 10 mm long and 1.4 mm wide (Figure 2A). Scale leaves two at each node (Figure 2B). Triangular part of leaf up to 1.5 mm high at a node (Figure 2B). Stomata about the same optical density as rest of cuticle; arranged in longitudinal rows (Figures 2C, D). Subsidiary cells 4-5 in number (Figures 2D; 3C, D).

Internode cuticle about 10 μm in total thickness, with outer periclinal epidermal wall about 3-4 μm thick (Figures 3A, D). Epidermal cells rectangular to polygonal in shape, 30-50 μm in diameter. Outer surface of cuticle smooth, non-papillate (Figure 3E). Hypodermal cells thin-walled, longitudinally arranged, elongate rectangular in shape, 20-40 μm wide (Figure 3I). Stomata arranged in rather irregular longitudinal rows in 100-150 μm interval, each row a single stoma wide; stomata 30-40 per mm^2 in density (Figures 2C, D; 3B, C). Non-stomatal zone 50-100 μm (2-3 cells) wide, consisting of longitudinally arranged epidermal cells. No dorsiventrality observed (Figures 2C, D).

Stomatal complex 65-80 μm in diameter, consisting of a pair of guard cells and 4-5 subsidiary cells (Figures 3C, D). Guard cells sunken about 7 μm below surface; each cell 40-90 μm long and 30-40 μm wide (Figures 3D, G). Mouth of stomatal pit rectangular or polygonal in shape, bounded by a rather thick, lobed canopy (Figures 3E, F); lobes corresponding in number to subsidiary cells. Papillae in throat of pit short and wide; equal in number with that of subsidiary cells (Figures 2E, 3G). Stomatal orientation most frequently transverse (Figure 3H).

Further description.—The branch system of *Frenelopsis pombetsuensis* and the whole length of the internode are uncertain because of fragmental preservation of the fossil.

External and cuticular observations of the specimen clearly indicate the absence of a groove or suture separating the basal cushions, as seen in living cupressaceous species.

The preservation of the cuticle of one side is poor, but is sufficient to observe the number, shape and size of stomata and other epidermal cells.

Comparison and Discussion.—Although the present specimen is frangmental, both external and cuticular features of the specimen correspond well with the diagnosis of *Frenelopsis* Schenk emended by Watson (1988). The opposite arrangement of leaves is similar to that of extant cupressaceous conifers and some cheirolepidiaceous conifer genera such as *Cupressinocladus* Seward. However the present specimen differs from these taxa in the absence of a groove or suture separating the basal cushions.

Among the species of *Frenelopsis* previously described, most have leaves in whorls of three. Only two exceptional species, *Frenelopsis teixeirae* and *F. choshiensis*, have two leaves at each node like the present specimen (Table 1). Of these two species, *Frenelopsis teixeirae*, described by Alvin and Pais (1978) from the Lower Cretaceous of Portugal, differs from the present specimen in its markedly thick cuticle and absence of a lobed ring around the mouth of the stomatal pit. The other species, *Frenelopsis choshiensis*, is described by Kimura *et al.* (1985) from the Lower Cretaceous of Choshi, Japan. *Frenelopsis choshiensis* is clearly distinguished from the present specimen in its large canopy covering the mouth of the stomatal pit, and the presence of a narrow groove surrounding the mouth.

Despite the presence of two leaves at each node, the cuticular features of the present specimen are more similar to *Frenelopsis hoheneggeri* (Ettingshausen) Schenk, having leaves in whorls of three, than to other *Frenelopsis* species with opposite decussate arrangement of leaves (Table 1). *Frenelopsis hoheneggeri* was redescribed in detail by Reymanóna and Watson (1976) based on specimens from the type locality in the Polish Carpathians. The present specimen is distinguished from *Frenelopsis hoheneggeri* only by the number of leaves and cuticle thickness. Despite their different external features, the cuticular features of the present specimen suggest its close relationship with *Frenelopsis hoheneggeri*.

Paleophytogeography.—Since Kimura (1961, 1975) divided the Late Jurassic-Early Cretaceous floras of Japan and its adjacent areas into the Ryoseki-type and Tetori-type floras, his distinction has been extended around Southeast Asia, with some modification (Kimura, 1980, 1987; Kimura and Ohana, 1992; Ohana and Kimura, 1995).

Stopes and Fujii (1910) described some fossil plants from the Upper Yezo Group (Upper Cretaceous) of Hokkaido and, since then, additional specimens have been described from the Upper Cretaceous part of the Yezo Group (see Nishida,

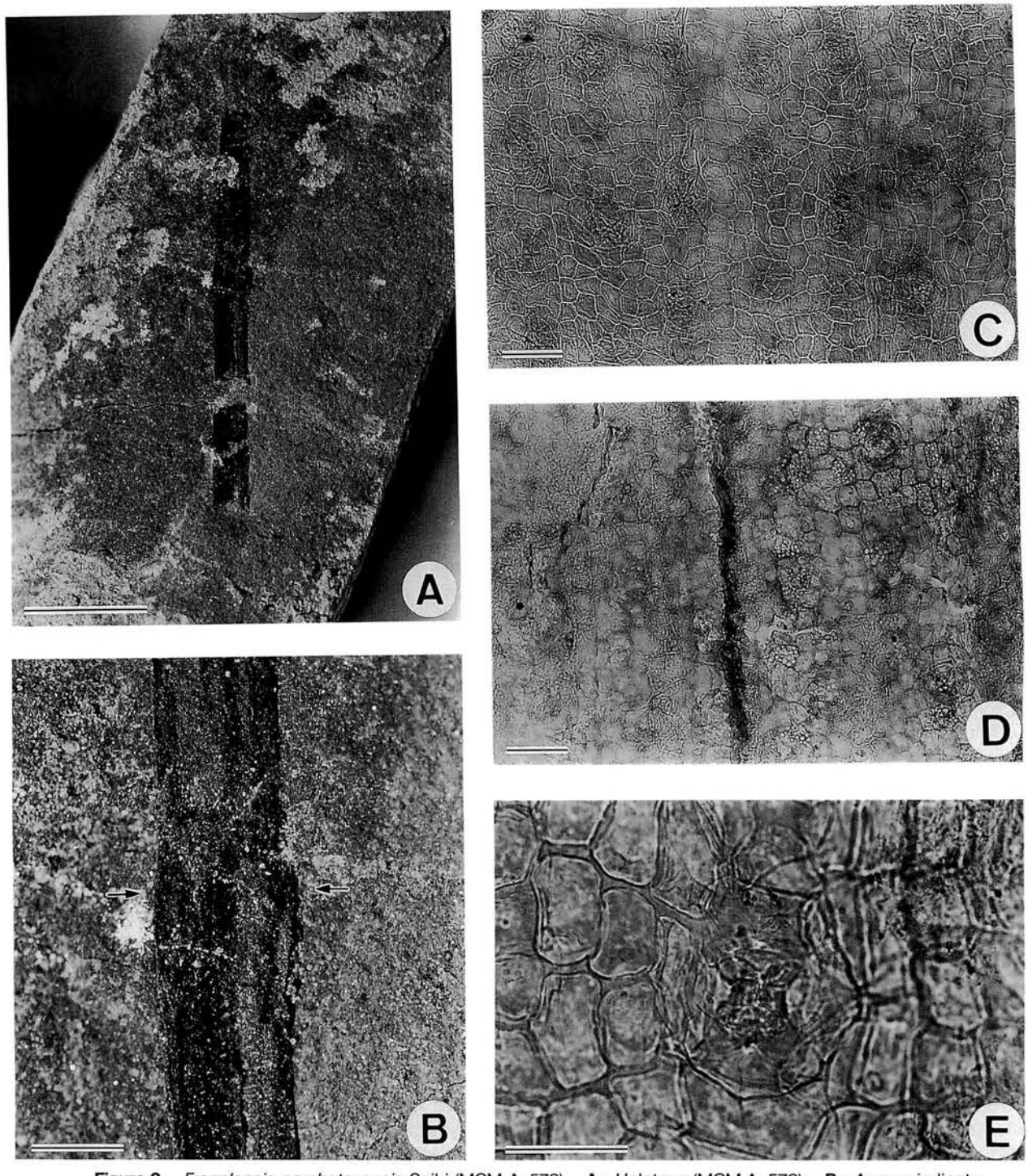

Figure 2. *Frenelopsis pombetsuensis* Saiki (MCM A-573). **A**: Holotype (MCM A-573). **B**: Arrows indicate a pair of leaves. **C**: Cuticle of internode, light microscope. **D**: Cuticle of internode, opposite side of Figure 2C. No dorsiventrality observed. **E**: Stoma, light microscope. Scale bars = 5 mm in A; 1 mm in B; 100 μm in C, D; 50 μm in E.

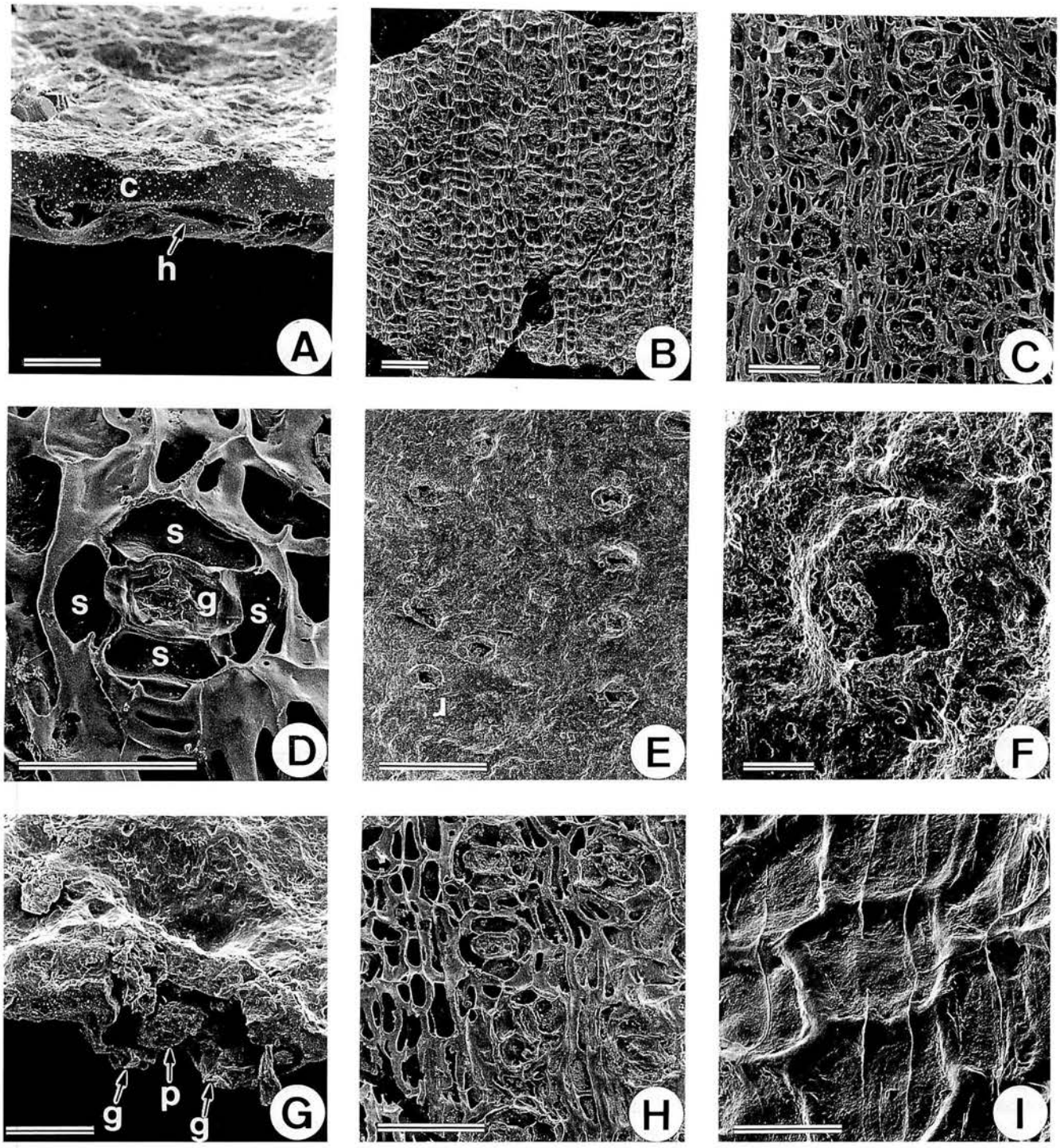

Figure 3. SEM micrographs of cuticle of *Frenelopsis pombetsuensis* Saiki (MCM A-573). **A**: Section of cuticle showing cutinized epidermis (c) and hypodermis (h). **B**: Cuticle of internode, showing longitudinally arranged rows of stomata. **C**: Internode cuticle seen from inside showing transversely oriented stomatal pit. **D**: Stomatal complex showing a pair of guard cells(g) and four subsidiary cells(s). **E**: Internode cuticle from outside showing mouth of stomatal pit. Surface of cuticle smooth, without any papillae or trichome. **F**: Single stoma from outside showing rectangular mouth of the stomatal pit and papillae in throat. **G**: Section of stoma showing guard cells(g), and papillae in throat of stoma (p). **H**: Internode cuticle. Epidermal layer covered by hypodermal layer in lower right of this photograph. **I**: Polygonal epidermal cells covered by longitudinally elongated hypodermal cells. Scale bars=10 μm in A, F, G; 100 μm in B, C, E, H; 50 μm in D, I.

Table 1. Comparative morphometrics of *Frenelopsis pombetsuensis* sp. nov. and related species. 1 : Kimura *et al.* (1985), 2 : Alvin and Pais (1975), 3 : Reymanówna and Watson (1976).

Characters\Species	*F. pombetsuensis*	*F. choshiensis*[1]	*F. teixeirae*[2]	*F. heheneggeri*[3]
Internode length	at least 10 mm	4-4.5 mm	2.5-5 mm	8 mm
Internode width	1.4 mm	1.5-2 mm	1.5 mm	3 mm
Leaf number per node	2	2	2	3
Maximum length of free leaf	up to 1.5 mm	0.5 mm	—	1.5 mm
Leaf margin	—	hairs up to 4 μm	scarious	scarious
Total thickness of cuticle	10 μm	50 μm	50 μm	40 μm
Stomatal arrangement	ill defined rows	ill defined rows	ill defined rows	well defined rows
Density of stomatal row	7-9 per mm	—	—	10-12 per mm
Density of stomata	30-40 per mm^2	200 per mm^2	—	—
Diameter of stomatal complex	65-80 μm	45-75 μm	—	60-70 μm
Number of subsidiary cells	4-5	4-6, usually 4	5-6	4-6, usually 4
Orientation of stomatal aperture	horizontal	horizontal	—	horizontal
Surface around stomatal pit	thickened ring	grooved	slightly raised	thickened ring
Papillae in throat of stomatal pit	present	present	present	present
Trichomes on epidermal cells	none	none	—	none
Stratigraphic range	Albian	Barremian	Hauterivian-Barremian	Hauterivian

1991). All of these specimens have been obtained from Upper Cretaceous sediments. This marked absence of fossil plants from the Lower Cretaceous of Hokkaido, has prevented a comparison of the Early Cretaceous flora of Hokkaido with the Ryoseki- and Tetori-type floras. *Frenelopsis pombetsuensis* is therefore important because it is the first report of a characteristic taxon of the Ryoseki-type flora from the Lower Cretaceous (Middle Yezo Group) of Hokkaido.

Based on their distribution in the fossil record, frenelopsids are interpreted as thermophilous plants. Alvin (1982) plotted the Berriasian-Cenomanian distributions of frenelopsids on the paleogeographical maps. They seem to lie essentially at the edge of the tropical or subtropical and arid belt of low paleolatitudes. *Classopollis*, the pollen produced by cheirolepidiaceous conifers, also supports the thermophilous nature of frenelopsids. The occurrence of *Classopollis* corresponds well with estimated tropical or subtropical and arid paleoclimates (Vakhrameev 1970, 1980, 1981, 1991).

Although the thermophylly of the frenelopsids is not in dispute, their xerophytic or halophytic nature is certainly controversial (Alvin, 1982 ; Watson, 1988). Halophytic and xerophytic plants have evolved similar features to prevent excessive water loss due to high salinity. Frenelopsids have a distinctly succulent appearance which is sometimes compared with modern halophytic angiosperm plants such as *Salicornia* L. (Zeiller, 1882 ; Reymanóna and Watson, 1976). A relatively thick cuticle and a deeply sunken stoma surrounded by papillae are the characteristic features not only of xerophytes but also of halophytes. Moreover, sedimentological evidence clearly indicates a coastal habitat of some frenelopsids, such as *Frenelopsis harissii* Doludenko and Reymanóna and *Pseudofrenelopsis varians* (Fontaine) Watson (Alvin, 1982). Thus, it is inappropriate to use frenelopsids as an indicator of arid climates without any additional supporting evidence.

The Ryoseki-type flora is thought to have flourished under tropical-subtropical climatic conditions with a fairly long-term arid season in each year (Ohana and Kimura 1995). The occurrence of frenelopsids supports the presence of tropical-subtropical climate in Hokkaido area. However, the remarkably thinner cuticle of *Frenelopsis pombetsuensis* in relation to other frenelopsids, and the non-papillate surface of its cuticle, may also indicate rather humid conditions.

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