

A. HLUŠTÍK

**FRENELOPSIDACEAE FAM. NOV., A GROUP OF HIGHLY SPECIALIZED
CLASSOPOLLIS-PRODUCING CONIFERS***Frenelopsidaceae* fam. nov. — wysoko wyspecjalizowana grupa szpilkowych
z pyłkiem *Classopollis*

ABSTRACT. On the basis of external morphology, epidermal features, and stratigraphical occurrence *Classopollis*-producing Conifers are re-considered taking their possible diversification into account. An emended diagnosis of *Cheirolepidiaceae* Takht ex Dolud. is presented including *Classopollis* producers of acicular to obtusate foliage of non-segmented axes. The genera *Suturovaginia* Chow et Tsao, *Cupressinocladus* Seward, *Pseudofrenelopsis* Nathorst, *Frenelopsis* Schenk, and *Classostrobus* Alvin, Spicer et Watson are newly suggested as forming an independent extinct family *Frenelopsidaceae* fam. nov. Both the families of *Classopollis*-producing Conifers are substituted under a taxon of superposed level, *Cheirolepidiineae* subord. nov. Principal characteristics of the erected taxa are generally discussed.

INTRODUCTION

The present paper sums up the author's experience in frenelopsid Conifers based on the treatment of Bohemian and Moravian taxa as well as on a valuable international discussion. Results of the research have been incorporated in the postgradual thesis (Hluštík 1981, MS), most of them being dealt with in this paper.

The study is dedicated to graceful memories of both Professor F. Němejc and Professor T. M. Harris, two well experienced students, excellent teachers, and great men. The first led the author through cliffs of *scientiae amabilis*, the latter one let him feel *legem durum* of Mesophytic palaeobotany.

GROUPING OF CONIFEROUS CLASSOPOLLIS PRODUCERS

With respect to the morphology and leaf epidermal structure *Classopollis*-producing Conifers can be characterized as follows:

Cheirolepidiineae subord. nov. (Fig. 1)

Diagnosis. Gymnosperms of coniferous habit producing large, mostly disintegrating female-cones composed of the *Hirmerella*-like scales, ovuliferous scale contained two anatropic ovules; at each scale only one ovule matured. Male-cones composed of a small number of microsporophyll parastichies, microsporangia produced pollen of the *Classopollis*-type. Stomata provided with subsidiary cells in cyclic arrangement, mostly more than four in number (often 5—7), more or less papillate. (Modified after Jung 1968, Reyre 1970, Vakhrameev 1970, Srivastava 1976, Doludenko 1978).

Stratigraphical range. Mesozoic plants, probably becoming extinct during the Upper Cretaceous.

Key to the families and genera:

- A.a. *Classopollis*-producing Conifers with non-segmented axes, leaves free, more or less ascending, stomata on the blade surface only (*Cheirolepidiaceae* Takht. ex Dolud. s. nov.). See B.
- b. *Classopollis*-producing Conifers with more or less distinctive segmentation of axes, leaves adnate, mostly appressed, stomata all over the internode surface (*Frenelopsidaceae* fam. nov.). See C.
- B.a. Phyllotaxy spiral, leaves narrow, more or less acicular, stomata in few bands — „cheirolepidioid forms” (*Cheirolepidium*, *Tomaxellia*, ? *Pagiophyllum* p.p.). See Figs. 1, 2, 3, lineage 1.

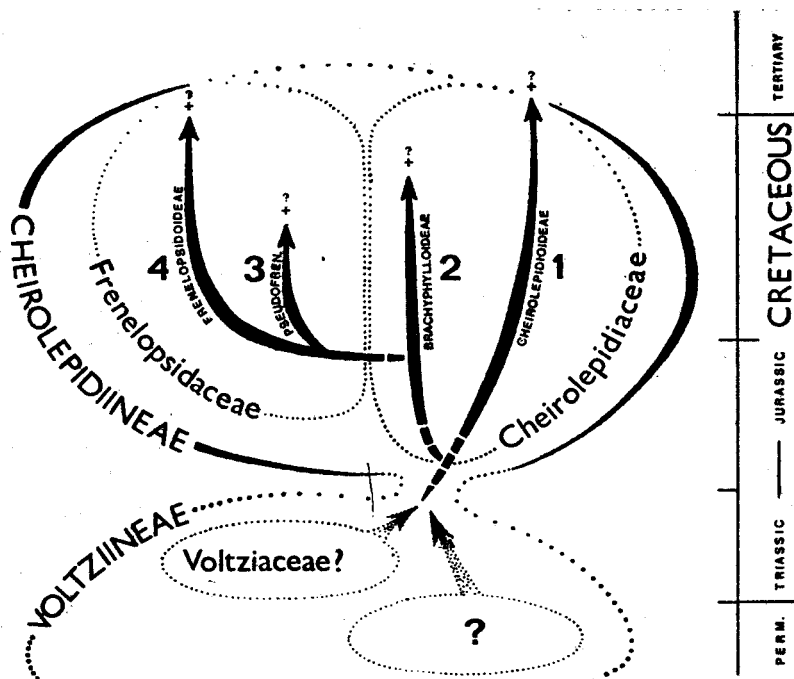


Fig. 1. *Cheirolepidiineae* subord. nov. — the main lineages of phyllotactic morphotypes as suggested here (for explanation see Fig. 2 below). Originally sketched by the author

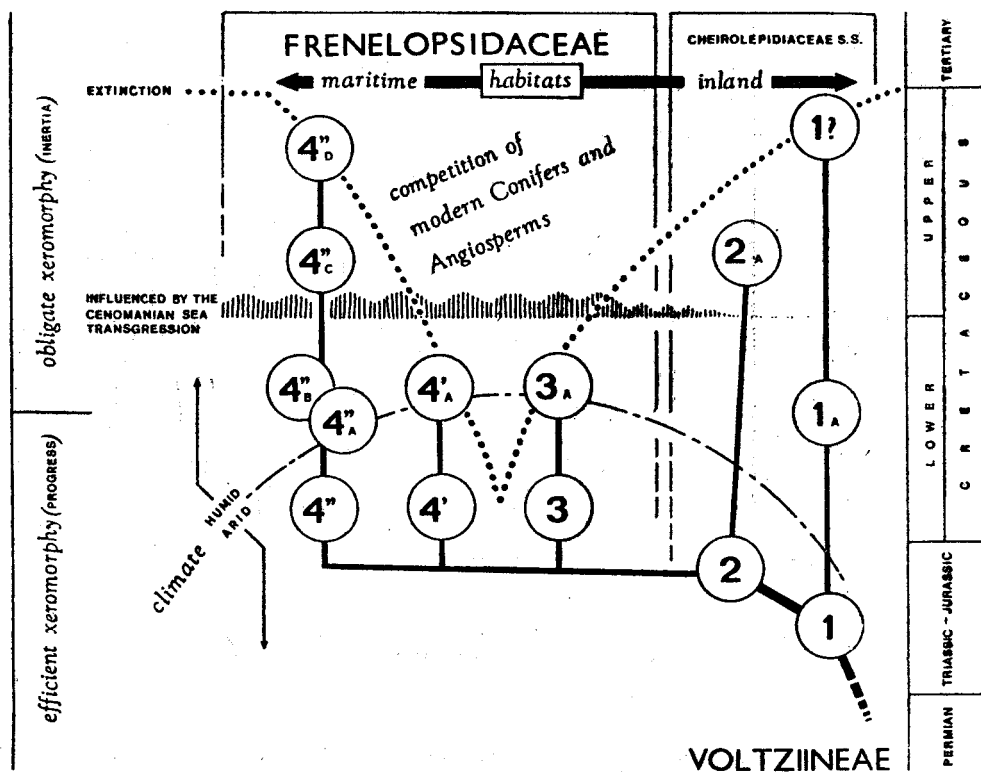


Fig. 2. *Cheirolepidiineae* subord. nov. — principal stages of successive changes of leaf arrangements under possible influences leading to the extinction of *Frenelopsidaceae* fam. nov.: 1 — „cheirolepidioid” lineage (*Cheirolepidium*-stage), 1A — Lower Cretaceous „cheirolepidioid” member (*Tomaxellia*-stage), 1? — hypothetical Upper Cretaceous „cheirolepidioid” member; 2 — „brachyphylloid” lineage (obtusate-leaf-stage), 2A — Upper Cretaceous „brachyphylloid” member (*B. squamosum*-stage, Senonian of Bohemia); 3 — „pseudofrenelopsioid” lineage (*Suturovagina*-stage), 3A — non-sutured „pseudofrenelopsioid” member (*Pseudofrenelopsis*-stage); 4 — „frenelopsioid” lineage, 4' — *Cupressinocladus valdensis*-stage, 4'A — *Frenelopsis teixeirae*-stage, 4'' — ?*Cupressinocladus malaianus*-stage, 4''A — *Frenelopsis ramosissima*-stage, 4''B — *F. hoheneggeri*-stage, 4''C — *F. alata*-stage, 4''D — *F. oligostomata*-stage. Original scheme of the author

- b. Phyllotaxy spiral, leaves broad, mostly obtusate to squamate, stomata in numerous longitudinal rows all over the blade surface — „brachyphylloid forms” (*Brachyphyllum* p.p.). See Figs. 1, 2, lineage 2.
- C.a. Phyllotaxy spiral (Figs. 1—3, lineage 3). See D.
- b. Phyllotaxy decussate or whorled (Figs. 1—3, lineage 4). See E.
- D.a. Leaves more or less encircling the axis, mostly sutured (*Suturovagina*).
 - b. Leaves more or less sheathing, mostly non-sutured (*Pseudofrenelopsis*).
- E.a. Leaves on alternate pairs. See F.
- b. Leaves in alternate whorls. See G.
- F.a. Two opposite leaves at each internode, decussate, sutured (*Cupressinocladus valdensis*-type of foliage).

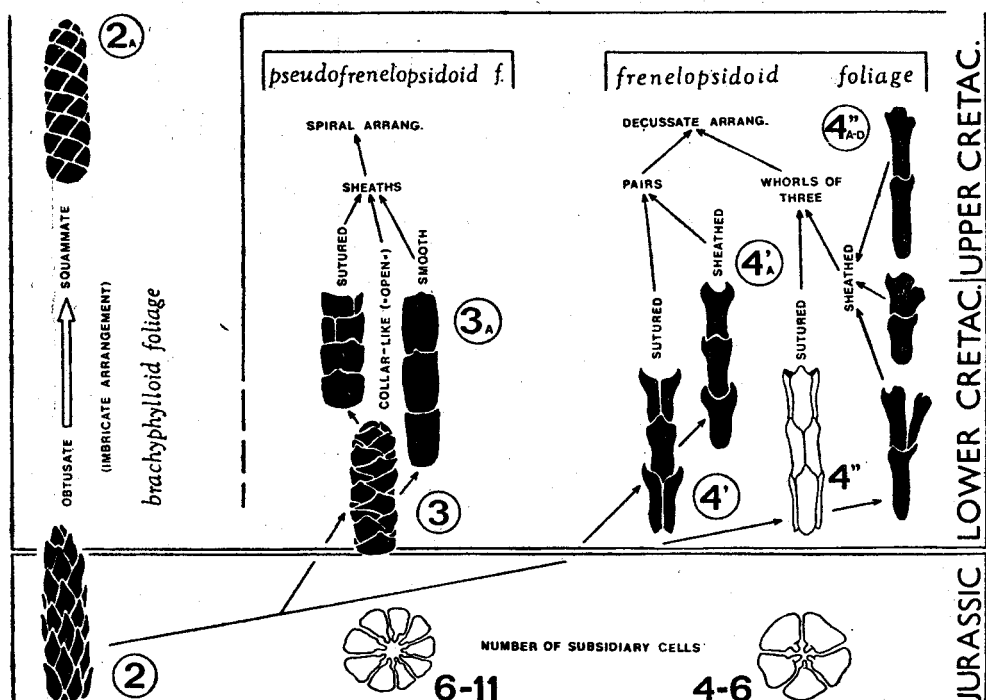


Fig. 3. *Frenelopsidaceae* fam. nov. — detailed explanation of individual phyllotactic morphotypes as probably derived from a hypothetical „brachyphylloid” cheirolepidiinean foliage. Compiled after the authors quoted in the text, for explanation see Fig. 2 here. Original scheme of the author

- b. Two opposite leaves at each internode, decussate, smoothly sheathed (*Frenelopsis teixeirae*-type of foliage).
- G.a. Three leaves at each internode, sutured (*Cupressinocladus malaianus*-type of foliage?).
- b. Three leaves at each internode, smoothly sheathed (*Frenelopsis hoheneggeri*-type of foliage).

(Compiled after Alvin 1977, Alvin & Hlušík 1979, Alvin, Spicer & Watson 1978, Alvin & Pais 1978, Barnard 1968, Barnard & Miller 1976, Doludenko 1978, Doludenko & Reymanówna 1978, Hlušík 1979b, Hlušík & Konzalová 1976a, b, Reymanówna & Watson 1977, Zhou 1983.)

According to the presented key-table four morphological lineages can be pointed out within the proposed *Cheirolepidiineae* subord. nov. The first and, perhaps, the most original one led probably from an unknown praecursor among *Voltziineae* sensu latissimo; it kept a common „coniferous” habit of foliage, e.g. spiral arrangement of mostly aciculate microphylls (here understood as „cheirolepidioid forms”). The second lineage seems to be derived from the previous one as its early Mesozoic adaptation with more fleshy, obtusate to squamate leaves in more or less imbricate arrangement (here related to „brachyphylloid forms”).

This group of cheirolepidiaceous Conifers is preliminary considered as including such types of the *Brachyphyllum*-like plants which yielded *Classopollis* pollen *in situ* only (*B. crucis* Kendall, for example).

The lineages 1, 2 are considered as two morphological phenomena developed parallelly in the family *Cheirolepidiaceae* s. nov. Thus, the family diagnosis is to be followingly modified:

***Cheirolepidiaceae* Takht. ex Dolud. (Doludenko 1978) sensu novo**

Diagnosis emended. *Classopollis*-producing Conifers forming non-segmented axes with free, more or less appressed leaves in spiral arrangement, acicular to squamate in form; male-cones small-sized, probably of the *Masculostrobus*-type. Stomata on the blade surface only.

Typical genus. *Cheirolepidium* Takhtajan, 1963: 249.

Typical species. *Cheirolepidium muensteri* (Schenk) Takhtajan, 1963: 249.

Stratigraphical range. Triassic — Cretaceous.

Remarks. The family substitutes two morphological lineages, probably on the subfamily level. More precise determination of "brachyphylloid" one is now impossible due to rather imperfect knowledge on the pollination in different species of the formal genus *Brachyphyllum* (Srivastava 1976, Hlušík 1978a, b).

The lineages 3 and 4 seem to be derived from „brachyphylloid” *Cheirolepidiaceae*. Both they are characterized by an extraordinary reduction of the foliage as well as by the segmentation of leafy axes. The lineage 3 is suggested as *Pseudofrenelopsidoideae* subfam. nov., representing *Classopollis* producers with more or less sheathed leaves in spiral arrangement. The lineage 4, that includes Conifers with decussate or whorled leaves, is suggested here as *Frenelopsidoideae* subfam. nov. The two subfamilies are closely related each other.

FRENELOPSID CONIFERS SENSU STRICTISSIMO

The term „frenelopsids” was first used in the connection with certain Cretaceous plants that show such a habit of leafbearing twigs as known in the fossil genus *Frenelopsis* Schenk (Hlušík 1974). Later, the term was rather widened and included the genera *Pseudofrenelopsis* Nathorst, *Suturovagina* Chow et Tsao, and the species *Cupressinocladus valdensis* (Seward) Seward (Hlušík 1979b).

From the point of comparative morphology the fossils resemble living *Callitroideae* most of all. This fact also influenced the authors of initial papers dealing with modern re-investigation of Bohemian species (Hlušík & Konzalová 1976a, b). A rapid progress in studies on „frenelopsids” made us sure of their relations to rather a heterogenous group of *Classopollis*-producing Conifers from the Mesozoic (Watson 1977, Doludenko 1978). Thus, during the last ten years all important characteristics of „frenelopsids” have been obtained. The

present situation allows us to consider them as the best known representatives of *Cheirolepidiineae* subord. nov.

The following data have been compiled from the papers quoted below the key-table (p. 4 here) as well as from studies of Barale (1973a, b), Broutin & Pons (1975), Hlušík (1972, 1978a, b, 1979a, 1981, MS, 1983, MS), Lauverjat & Pons (1978), Li & Zhou (1980), Pons (1979, 1980), Pons & Broutin (1978), Watson (1974), Watson & Alvin (1976), Chow & Tsao (1977), besides modern detailed observations on Bohemian and Moravian material. With help of these information the determination of frenelopsid Conifers s. ss. can be presented as follows:

Frenelopsidaceae fam. nov.

Diagnosis. Woody plants with more or less segmented leafy axes; mature internodes covered by sheathed leaf bases, smooth or sutured; leaves mostly fleshy, appressed, squamiform, tipped, either in spiral arrangement (single leaf at each internode) or in alternate groups (pairs, whorls); epidermis developed all over the surface of each internode and covered by thick cutin membrane; stomata cyclocytic, regularly distributed in more or less dense longitudinal rows on the surface of internodes and leaf tips; stomatal apparatus composed of four to eleven subsidiary cells and two guard cells, sunken; subsidiary cells with distinct anticlinal papillae, stomatal pits craterous, with cutin rims; female-cones of the *Hirmerella*-like type, disintegrating, composed of large scales; ovuliferous scale probably with the only seed matured; male-cones of the *Classostrobus*-like type, producing *Classopollis* pollen; wood structure of shoots similar to that of the *Protopodocarpoxylon*-type; axillary branching developed in both conventional and modified monopodial kinds.

Typical genus. *Frenelopsis* Schenk, 1869 emend. Reymanówna et Watson, 1976:19.

The proposed family includes the following taxa:

Frenelopsidoideae subfam. nov.

Diagnosis. Frenelopsid Conifers with leaves in both alternate pairs or whorls of three, tipped, sutured or smoothly sheathed; axillary branching either conventional one or in its modified form (Alvin & Hlušík 1979).

Typical genus. *Frenelopsis* Schenk emend. Reym. et Watson. Genera et species included:

1. *Frenelopsis* Schenk emend. Reym. et Watson

F. hoheneggeri (Ett.) Schenk emend. Reym. et Watson (generotype, Hauterivian — Albian)

F. alata (K. Feistm.) Knobloch (Cenomanian)

F. choshiensis Kimura, Saiki et Arai (Barremian)

- F. elegans* Chow et Tsao (Aptian — Albian)
F. harrisii Doludenko (Cenomanian)
F. occidentalis Heer (Aptian — Albian)
F. oligostomata Romariz emend. Alvin (Senonian)
F. ramosissima Fontaine (Barremian — Aptian)
F. rubiesensis Barale (? Jurassic — Neocomian)
F. silfloana Watson (Lower Cretaceous)
F. teixeirae Alvin et Pais (Hauterivian — Barremian)
Frenelopsis sp. sensu Watson et Alvin (Cretaceous of Sudan)
 2. *Cupressinocladus* Seward emend. Barnard et Miller
C. valdensis (Seward) Seward emend. Watson (generotype, Wealdenian)
 ?? *C. malaianus* (Kon'no) Barnard et Miller (? Lower Cretaceous)

Pseudofrenelopsidoideae subfam. nov.

Diagnosis. Frenelopsid Conifers with leaves in spiral arrangement, more or less tipped, imperfectly and/or smoothly sheathed, collar-like to cylindrical, one at each internode; axillary branching of a conventional kind; distinct „heterophylly” during a twig development; epidermis heavy cutinized.

Typical genus. *Pseudofrenelopsis* Nathorst, 1893 emend. Watson, 1977: 726—727. Genera et species included:

3. *Pseudofrenelopsis* Nathorst emend. Watson
P. varians (Fontaine) Watson (generotype, Aptian — Albian)
P. dalatzensis Chow et Tsao (Aptian — Albian)
 ? *P. faveolata* Chow et Tsao (Cretaceous of China)
 ? *P. papillosa* Chow et Tsao (Cretaceous of China)
P. parceramosa (Fontaine) Watson (Hauterivian — Albian)
 4. *Suturovagina* Chow et Tsao, 1977 emend. Zhou, 1983
S. intermedia Chow et Tsao emend. Zhou (generotype, ? Lower Cretaceous of China)
 5. *Classostrobus* Alvin, Spicer et Watson, 1978
C. comptonensis Alvin, Spicer et Watson (generotype, Wealdenian)
C. cathayanus Zhou (? Lower Cretaceous of China)

Stratigraphical range of the family: (? Jurassic —) Cretaceous.

Occurrence: marine to brackish deposits of former circumtethyd basins.

Ecology: maritime, seaside and/or riverside biotopes of Cretaceous tropics to sub-tropics, most probably under the influence of arid to semi-arid climatical zone.

DISCUSSION

The presented subdivision of *Classopollis* producers is based on three features: the morphology of twigs, the foliage, and epidermal patterns of leaves. These phenomena have been better known up to now, while information about repro-

ductive organs is very scarce so far. Similarly, we have fragmentary data on morphotypes of the *Classopollis* pollen in the mentioned genera and species.

As to the organization of female-cones, *Cheirolepidiineae* subord. nov. might be generally related to Permo-Triassic types of *Voltziineae* sensu lato. Certain details in the morphology and epidermal structures also indicate that *Classopollis* producers could be compared to *Araucariaceae*, especially, when the development of „embedded” seeds is considered. However, Krassilov (1980) dislikes the idea of the *Hirmerella* seed embedding. He suggests to derive these organs from biovulate pteridospermous cupules. This interpretation seems to be the most stimulative idea taking into consideration possible origins of *Classopollis* producers.

As shown by many authors, *Classopollis* pollen are exceptional not only as to their general morphology and occurrence, but also when possible origin of them as microspores is treated (Médus 1967, Taugourdeau-Lantz 1971, Srivastava 1976, Pons & Broutin 1976, Pons 1979, 1980, Upchurch & Doyle 1981, a.o.). Certain aberrant forms of pollen indicate that *Classopollis* producers might represented separated and old lineage of Conifers, reliable to families *Taxaceae* and *Taxodiaceae*. Thus, the idea of a „cupressaceous” origin of frenalopsids comes into the picture again. The problem is to be solved through a close cooperation between plant morphologists and palynologists, because *Cheirolepidiineae* subord. nov. seem to be excellent objects to study natural connections between macrofossils and pollen favourably preserved.

At present we have the *Classopollis* pollination in frenalopsid Conifers for granted. It was ascertained in *Pseudofrenelopsis*, *Suturovagina*, and *Frenelopsis*. Basing on palynological assemblages, ecological conditions of certain frenalopsids were reconstructed (Upchurch & Doyle, l.c.). In pseudofrenelopsidoid forms male-cones are known under generic name *Classostrobus*, where the attachment of microsporophylls is supposed as a spiral one, most probably derived from the shoot phyllotaxy. Similar situation is now known in *Frenelopsis alata* from Bohemian Cenomanian, too (Hlušík 1983, MS). Microsporophylls of the species were organized in alternate whorls of three, identical to the triads of leaf tips at leafy shoot internodes.

The morphology of frenalopsid female-cones is known rather less satisfactorily. Pons & Broutin (1978) described a *Hirmerella*-like ovuliferous scale related with the species *Frenelopsis oligostomata*. In the Peruc Member Flora similar scales were described by Velenovský (1889) as „*Araucaria*” *bohémica*. The latest studies on these rare fossils indicate that this Cenomanian „species” might also be connected with *Frenelopsis alata* (Hlušík 1983, MS).

Unfortunately, up to now we have no indubitable evidence of similar large female-cones in *Pseudofrenelopsidoideae* subfam. nov. On the other hand, the fact of disintegrating female-cones in *Frenelopsidaceae* fam. nov. well corresponds to the scarcity of their appearance in sediments: individual scales were mostly detached from original cone axes.

In the majority of *Frenelopsidaceae* fam. nov. a common, ordinary type of

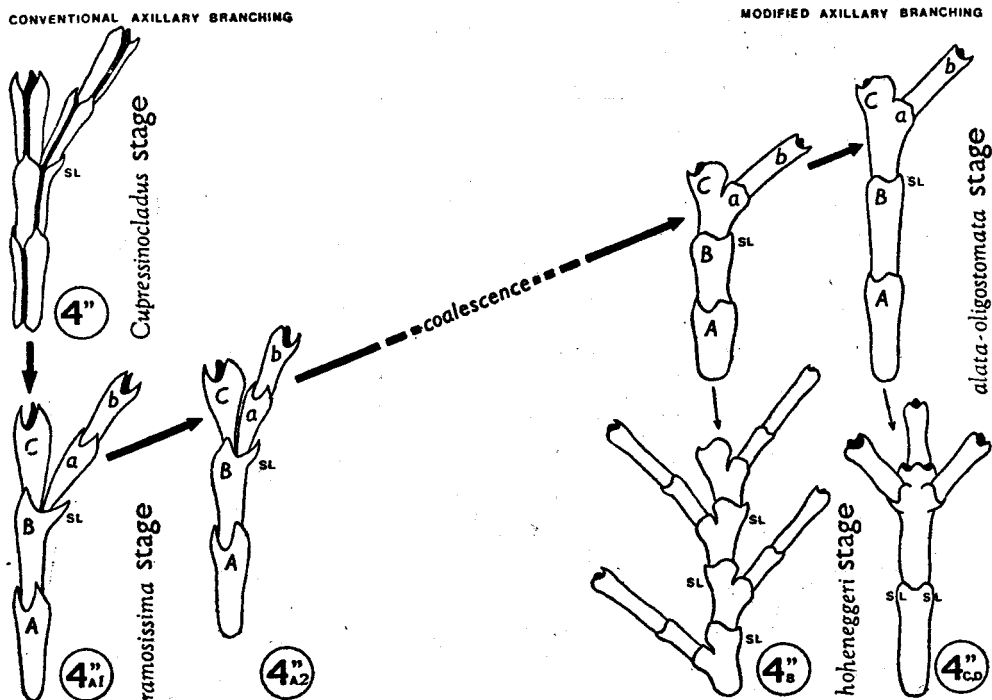


Fig. 4. *Frenelopsidaceae* fam. nov. — individual stages of the modified axillary branching development in species of the genus *Frenelopsis* Schenk (alternate triads of leaves): 4'' — ? *Cupressinocladus malaianus*-stage (sutured leaves), 4'' A₁ — *Frenelopsis ramosissima*-stage (birch-like habit?), 4'' A₂ — *Frenelopsis* sp. (Watson and Alvin 1976, Sudan), 4'' B — *F. hoheneggeri*-stage (complanate branching), 4'' C, D — *F. alata-oligostomata*-stage (birch-like to pendulate forms). Explanation of characters: A, B, C — internodes of parent axis, a, b, c — internodes of lateral axis, SL — position of subtending leaf. After the data of authors quoted in the text. Original sketch of the author

monopodial branching can be observed. Lateral branchlets developed in axillary position above a subtending leaf on parent axis (here named as *conventional axillary branching*). In pseudofrenelopsidoid genera it well fits spiral arrangement of leaves (Watson 1977, Zhou 1983). In frenelopsidoid genera important differences can be seen when individual species are studied.

As shown in Fig. 4, in *Frenelopsis* an artificial lineage of subsequent stages can be arranged to explain a probable development of the *modified axillary branching* sensu Alvin & Hluštík (1979). This phenomenon has been unknown in both fossil and living Conifers up to now. Moreover, in late Cretaceous species *F. alata* and *F. oligostomata* certain „regression” to original (*conventional*) axillary branching occurred: the lateral branchlets' insertions are secondarily moved upright, e.g. in nearly axillary position. It was probably caused by a rapid elongation of basal segment of the branchlet-bearing parent internode. In this way, the process led to the origin of a „pseudoparent” internode, when lateral bran-

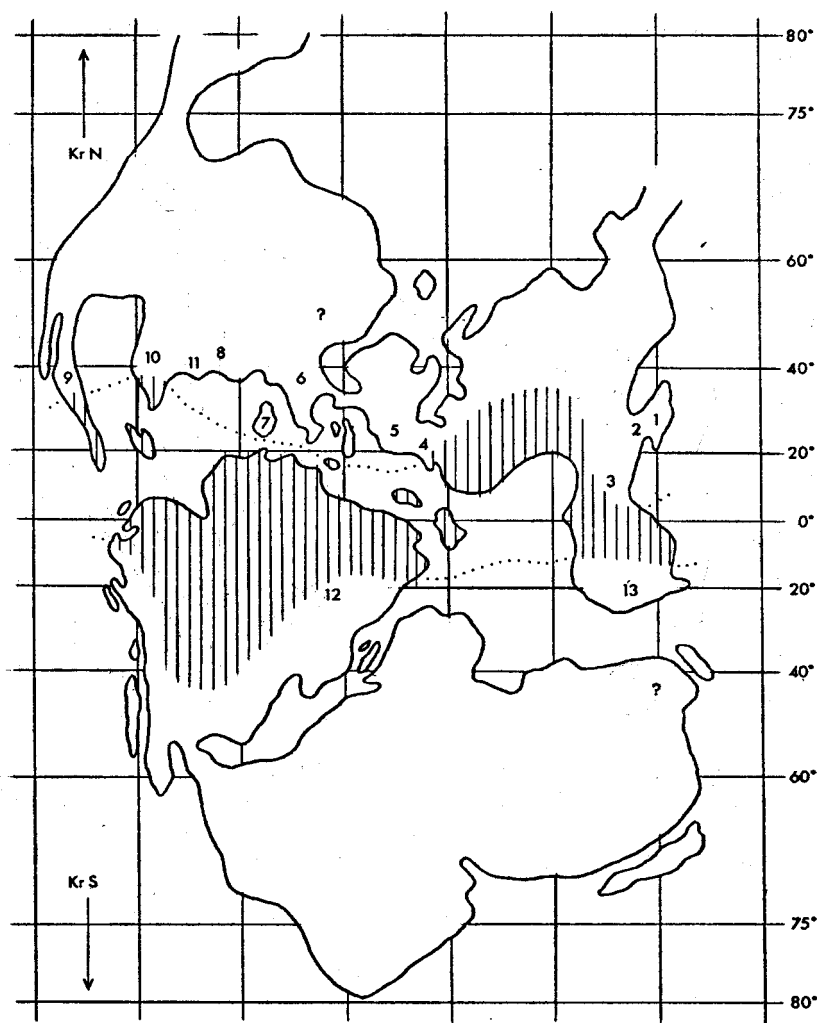


Fig. 5. Palaeogeographical situation of Neocomian continents. Figures indicate approximate location of different species of *Frenelopsidaceae* fam. nov. as recently known from sedimentary formations all over the world: 1 — Japan, 2 — Korea, 3 — China, 4 — Tajikistan, 5 — Ukraine, 6 — Czechoslovakia, Poland, NW Germany, France, England, 7 — Spain, Portugal, 8 — Maryland (USA), 9 — Mexico, 10 — Texas (USA), 11 — Virginia (USA), 12 — Sudan, 13 — Malaya, ? — uncertain and/or possible appearance of frenelopsidacean fossils (non-revised data); possible extension of arid/semi-arid areas during the Cretaceous is marked by vertical and dotted lines. Modified after Kremp 1978, Vakhrameev 1984, and authors quoted in the text. Sketched by the author

chlet insertion was moved up on the distance of nearly one-internode-length. The author believes that this phenomenon was in accordance to ecological condition oscillations which Cretaceous frenelopsidoid Conifers had to live under.

The arrangement of leaves serves as one of taxonomical arguments for the

presented subdivision of new family. In Fig. 3 a comparative survey of individual kinds of phyllotaxy is given. In the author's opinion, the foliage in genera *Suturovagina* and *Cupressinocladus* represents an intermediate stage leading from „brachyphylloid” types to pseudofrenelopsidoid and frenelopsidoid ones.

The reduction of „brachyphylloid” foliage is well visible especially in the species *Suturovagina intermedia*, where transitions from „open” to „closed” sheathing of collar-like leaves are supposed also by Zhou (1983). Similar kind of „heterophylly” observed Watson (1977) in the genus *Pseudofrenelopsis*, too. It probably reflects some morphological, ecologically conditioned differentiation within *Cheirolepidiineae* subord. nov. during early Mesozoic (? the uppermost Jurassic). In *Pseudofrenelopsis* barrel-like internodes are more frequent in fossil record. Collar-like leaves, perhaps, developed at very young twigs. In any case, in the genus some remains of suturae are still visible at barrel-like sheathing leaves (Hlušík 1978a, 1979a).

In the subfamily *Frenelopsidoideae* subfam. nov. similar trend of sheathing can be supposed. The transitional stage was probably coded in cupressinocladous Conifers, either they bore two or three leaves at each internode. Cupressinocladous types might also develop from a brachyphylloid form with less closed spiral arrangement of leaves. Namely, frenelopsidoid twigs show an evident ability to elongate their internodes. This ability might be of a very old date, and could be understood as a start-point not only for the development of rapidly elongated, decurrent leaf bases (*Cupressinocladus*), but also for the origin of the mentioned modified axillary branching of smoothly sheathed segmented axes of *Frenelopsis*.

One of the most surprising features is to be seen in the degree of epidermal cutinization in *Frenelopsidaceae* fam. nov. The formation of cutin layers reached enormous dimensions in representatives of both subfamilies (Fig. 6a—j).

Pseudofrenelopsidoid types produced cuticular membranes up to 200 μm thick, while frenelopsidoid twigs were covered by the cuticle 35 to 50 μm thick. This extreme epidermal cutinization of leaves and internodes had to be evidently accompanied by changes in stomatal function. Subsidiary cells with elongated anticlinals partially covered sunken guard cells as well as enclosed deep stomatal pit. The rim of craterous pit was formed by a ring-like cutin elevation, and anticlinals of subsidiary elements were papillously thickened. Sometimes, the papillae were of such dimensions that nearly filled the pit: in light microscope it appears as a „star-like” or „rosette-like” stomatal aperture (see Zeiller 1882, Thompson 1912, Bayer 1921, Němejc 1926, etc.); it led to a curious idea of a large number of guard cells acting simultaneously at the bottom of stomatal pit (Bayer, l. c., for example). In certain species also large hairy emergences as well as papillous thickenings have been observed at periclinals of epidermal cells (Watson 1977, Doludenko 1978, Zhou 1983, etc.). In all types of frenelopsidaceous Conifers more or less distinctive hypodermal cutinization took a part as well.

As a total, these all phenomena indicate a tendency of frenelopsidaceous

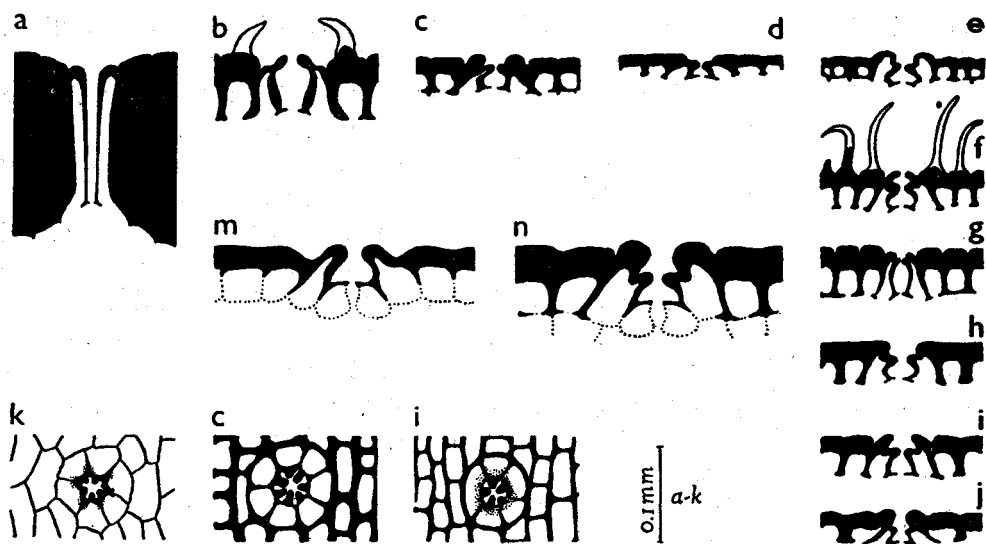


Fig. 6. *Frenelopsidaceae* fam. nov. — comparative survey of the cutinization in different species (cross-sections of stomata): a — *Suturovagina intermedia*, b — *Pseudofrenelopsis varians*, c — *P. parceramosa*, d — *Cupressinocladus valdensis* (an approximative restoration!), e — *Frenelopsis hoheneggeri*, f — *F. ramosissima*, g — *F. harrisii*, h — *F. teixeirae*, i — *F. alata*, j — *F. oligostomata*; left below schematized surface views of cuticles are given as follows: k — *Conifere Typ 5* after Barthel (1964), Upper Permian of Germany, c — *Pseudofrenelopsis parceramosa*, Lower Cretaceous of Europe, i — *Frenelopsis alata*, Upper Cretaceous of Europe; in the centre a comparison between *Agathis* sp. (m) and *Frenelopsis* sp. (n) stomatal apparatus is expressed (rather more enlarged). After different authors, quoted in the text, modified the author

plants to protect their physiological regime against dessication as much as possible (Fig. 6b, f).

The cyclocytic composition of stomata in the described plants is due to a higher number of radially orientated subsidiary cells. In pseudofrenelopsidoid types it reaches up to eleven cells, in frenelopsidoid ones the number varies about four to six. In this connection it is interesting to compare the described stomata to those of the *Conifere Typ 5* from the Upper Permian of Germany (Barthel 1964, here also Fig. 6k, c, i, below). The above mentioned anticlinal papillae in stomatal pits closely resemble similar forms in many lebachiacean and voltziacean plants, as figured by Barthel (l.c.). The average number of subsidiary cells tends to be a non-even one, mostly five. Their radial orientation probably corresponds to the distribution all over abaxial surface of leaves, too. The secondary thickening of twigs and shoots with collar-like and/or sheathed leaves caused lateral tractions within epidermal and hypodermal tissues. It had to lead to the development of more convenient form of stomata — cyclic to transversely ellipsoidal, with stomatal apertures obliquely directed.

PHYSIOLOGICAL AND ECOLOGICAL CONSIDERATIONS

Upchurch & Doyle (1981) brought an idea of different ecology of both frenelopsidoid and pseudofrenelopsidoid plants. Detailed studies on the material all over the world seem to support their model in general.

While external habit of pseudofrenelopsidoid Conifers is well comparable to that of many living obligate halophytes, the morphology of frenelopsidoid types still more recalls a coniferous one, comparable, as mentioned above, to the living *Callitroideae* most of all. Like other Conifers, frenelopsidaceous plants had their phylogenetical handicap in the wood structure, e. g. in tracheids. They could be called „physiologically predetermined xerophytes”. This predisposition is of a very old date, having originated in the time of late Palaeozoic continental environments. Although, at present times Conifers participate in the vegetation of different bioms, they evidently have preferred mesic habitats. Only several taxa are to be assigned to xerophytes in conventional sense, e.g. mostly *Cupressaceae* as such. According to their morphology, frenelopsidaceous plants could be considered approximatively as their ecological, especially edaphic analogies.

The xeromorphy of cupressaceous forms have seemed to represent a maximal degree of xeromorphic adaptation, possible in Conifers up to now. The habit, the foliage reduction as well as epidermal organization and cutinization of frenelopsidaceous fossils are in an evident contradiction to this assumption.

In no living coniferous taxa can we see such a smoothly sheathed foliage, sharply developed internodes, large papillae overhanging stomatal pits, and last but not least, such a production of protective cutin layers upon the surface of epidermis. All these features indicate that *Frenelopsidaceae* fam. nov. underwent substantial adaptations, starting probably with the latest Jurassic. The process could be simply called as a „xeromorphization of xeromorphy”.

The handicap in the vascularization was substituted by a formation of succulent-like penultimate/ultimate twigs, maximal limitation of free leaf laminae (in many frenelopsidaceous species they persisted as omittuous tips!), dispersion of the leaf innervation, and, perhaps also by a reduction of the life form of plant as a total (low tree, shrubs?). In this respect our fossils resemble some modern angiosperms of arid and/or semi-arid zones first of all.

Physiological problems were probably solved also by stomatal organization. As shown in Fig. 7a—c, the degree of cutinization and composition of stomata are clearly comparable to those of recent succulents and halophytes (see also Watson 1977, Zhou 1983, a.o.). In frenelopsidaceous plants stomatal pits are very similar to those of mangrove plants, halophytes, and certain succulents coming from desert inlands (Walter 1964). These Conifers might inhabit similar biotopes, now occupied by more progressive and plastic angiospermous vegetation under conditions of salty soils, higher insolation, dry climate, tidal oscillations, rocky substrates, etc.

The function of stomata in frenelopsidaceous species is to be treated in detail here. They represent the most tangible indicators of physiological events within

the plants. Under such a layer of cutin much more delicate stomatal cells had to be limited in their action. The cutin membrane sheltered inner tissues not only from an excessive transpiration but also from a short-waved radiation. The radiation is an important component of the insolation in maritime as well as dry-climate regions. Moreover, solar radiation enormously warmed up the plant surface in such areas.

On the other hand, the light is necessary to the photosynthetic activity, e.g. papillous thickenings over periclinals of epidermal cells might serve as concentrating lenses.

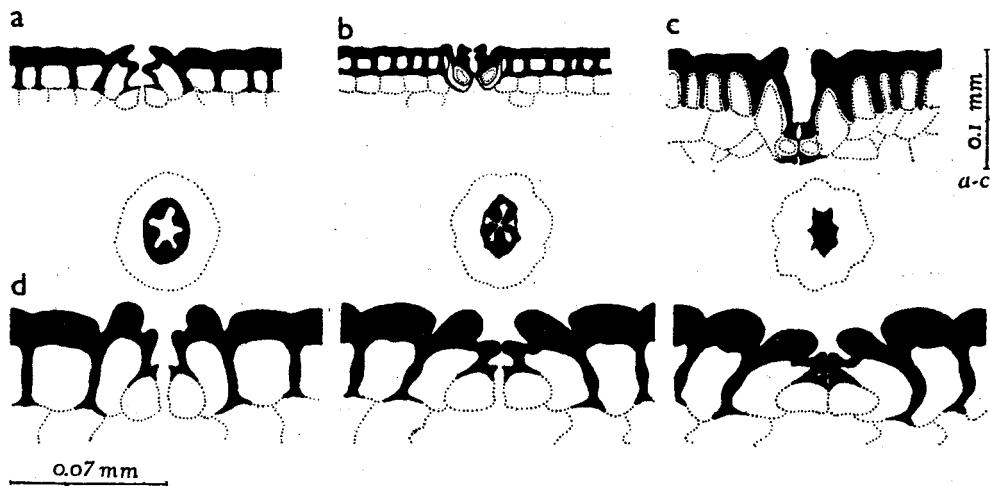


Fig. 7. A comparative survey of the cutinization in *Frenelopsis* sp. (a), *Rhizophora mucronata* (b), and *Sansevieria cylindrica* (c) showing that living halophytes and succulents form similar adaptations of stomatal apparatus as seen in different species of *Frenelopsidaceae* fam. nov.: see, for example, the organization and cutinization of *Sansevieria* compared to *Suturovagana* (Fig. 6 here); after Walter (1964). Hypothetical phases of possible function of a stoma in *Frenelopsis* sp. (d), where subsidiary cells might act as additional elements. Originally sketched by the author

The existence of deeply sunken stomata is a very normal phenomenon in Conifers. But, tongue to finger-shaped papillae upon the pit anticlinals of subsidiary cells are to be explained as a certain re-duplication of guard cells, so far unknown in living Conifers (Fig. 7d). The papillae were probably hollow, corresponding evidently with elevations of anticlinal cell walls. Under the turgor pressure had to be kept stiff, sticking out over the pit crater. After a moderate decreasing of the tension, papillae might slightly subside: although they partially closed the pit above guard cells, numerous microscopic perforations still remained. Thus, the mentioned „star-like” guard cells of certain previous authors (Zeiller 1882, Němejč 1926, a.o.) were in action. These perforations, limited by margins of overhanging papillae, allowed to perform the exchange of gases. If the turgor had decreased dangerously, the subsidiary cells pressed papillae into the pit: the stoma was safely closed by both ordinary guard cells and anticlinal papillae.

Stomatal transpiration, the gas exchange and evaporation were cut off, and cuticular transpiration was limited at minimal level. The plant resisted a dry period under the shelter of heavy cuticle. The hairy cover and periclinal papillae (sometimes also enormous!) might serve as diffusors of the light, as a protection from salt microcrystals, and, perhaps, also as condensators of steams.

The presented mechanism of stomatal activity probably varied in different taxa of *Frenelopsidaceae* fam. nov. In *Suturovagina*, for example, tubular subsidiary cells most probably operated as such, e.g. during the oscillations of the turgor tension. They were able to control the narrow, cylindrical pit throughout its profile as a whole.

Cheirolepidiinean Conifers as a total might be predisposed for extreme living conditions by other features, too. The plants produced a specialized type of pollen (*Classopollis* s.l.) and formed disintegrating female cones. Just the disintegrability of the cones had to serve to better germination of matured seeds. Similarly, the morphology of *Classopollis* pollen can be a reflection of some specific conditions: the germination of the microspores might be limited by a very short period, similarly to many living desert ephemerids.

At the begining of Cretaceous period we can also suppose a rapid radiation of Angiosperms. These plants were probably able to occupy the majority of late Mesozoic biotopes. While more „mesophyllous” *Cheirolepidiaceae* s. nov. stepped back into the inland localities (similarly to the living *Cupressaceae*!) and participated in a mixed vegetation, *Frenelopsidaceae* fam. nov. were squeezed in less favourable biotopes bordering both arid and oceanic zones.

This presumption seems to be evaluated by the appearance of frenelopsidaceous fossils when set in palaeogeographical configuration of Cretaceous continents (Fig. 5). The situation clearly evokes an idea of „frenelopsid” adaptation of certain *Cheirolepidiineae* subord. nov. on very special conditions along former oceanic shore as well as proposed zone of arid climate (see also Hlušík 1978a, b). The adaptations might vary depending upon topographic and hypsometric circumstances.

Concluding considerations on frenelopsidaceous adaptations the author believes that the habit of these plants reflects their original biotopes as well. A much more halophytic habit of *Pseudofrenelopsidoideae* subfam. nov. indicates that they participated in the vegetation inert to a higher and/or oscillating salinity of soils (coastal marshes, inland salinas, playas, sabkhas, etc.). *Frenelopsidoideae* subfam. nov. probably occupied more variable habitats, on the contrary.

Early Cretaceous forms, *Frenelopsis ramosissima* and *F. hoheneggeri*, resemble true xerophytes. In fossil state they are known as distinctively wood and fragments of shoots. They might be analogous to the recent *Callitroideae* first of all (durillignose forests, scrubs, chaparrals, macchias, highland vegetation, etc.).

The Upper Cretaceous types seem to be rather regreding to the mesophylly. After the data obtained from the Peruc Member (Cenomanian of Bohemian Massif), the species *Frenelopsis alata* inhabited coastal areas of the archipelago.

Due to the existence of flat seashores, some analogy to the recent gallery forests and mangroves cannot be excluded *a priori*. The same role probably played *F. oligostomata* from the Senonian. The above described modification of axillary branching seems to support not only the rule of the evolution irreversibility, but also an unique return to the pre-hoheneggeri pattern of branching.

The cuticles of *F. alata* and *F. oligostomata* are also more delicate than those of Lower Cretaceous species. The number of subsidiary cells varies about four to five, and papillae at the subsidiary cell anticlinals are much less distinctively developed. These phenomena should be explained as re-adaptation on less dry conditions. The tidal regime of tropical or sub-tropical seashores with lagoons, deltas, estuaries, brakish swamps and relatively higher aerial humidity might be just the correct environment for the mentioned Upper Cretaceous species.

Although fossil mangrove-like bioms have not been indubitably proved up to now, the described adaptation was able to include them in the maritime areas of the Bohemian Massif. As shown by Hlušík & Konzalová (1976a, b), *F. alata* produced pollen *Classopollis* cf. *classoides* (Pflug, 1953) Pocock et Jansonius, 1961. Svobodová (1984, MS) newly recorded that this type of classopollid pollen was dominating in brakish to marine facies of the Peruc Member (Lower to Middle Cenomanian). In fluvial to lacustrine sediments of the same member the pollen appear quite scarcely. The data were obtained from cores drilled in the area of Slaný (Central Bohemia, N of Prague) where the lectotype and syntypes of *F. alata* come from (Hlušík 1972). In the light of these facts a presence of *F. alata* in the vegetation of brakish environment seems to be more than probable. Although they are not elements of a mangrove flora, *Taxodium* and *Chamaecyparis thyoides* seem to be the nearest living analoga for Upper Cretaceous swampy Conifers of *Frenelopsidaceae* fam. nov.

CONCLUSIONS

Frenelopsidaceae fam. nov. represents a group of highly xeromorphous Conifers producing *Classopollis* pollen. They underwent their own differentiation during the Cretaceous. Lower Cretaceous *Pseudofrenelopsidoideae* subfam. nov. represented most probably woody halophytes. Within the subfamily *Frenelopsidoideae* subfam. nov. (Lower to Upper Cretaceous) there are included successive forms of Conifers developing from xerophytes up to re-adapted mesophytes. As a total, *Frenelopsidaceae* fam. nov. resemble the living *Callitroideae* most of all, although, they belonged to an extinct group of *Classopollis*-producing Conifers, here erected as *Cheirolepidiineae* subord. nov.

ACKNOWLEDGEMENTS

The author is much obliged to all colleagues from Argentina, England, France, China, Spain, and U.S.S.R. for their valuable discussion and comparative materials. Special thanks are due to Dr. habil. Maria Reymanówna, Dr. Joan Watson, and Dr. Kenneth L. Alvin

for their personal discussion as well as friendly help. The author also expresses his cordial thanks to all Czech colleagues for their criticism and technical help.

Geoindustria, n. p. Praha, U průhonu 32, Praha 7 — Holešovice, ČSSR

REFERENCES

- Alvin K. L. 1977. The conifers *Frenelopsis* and *Manica* in the Cretaceous of Portugal. *Palaeontology*, 20: 387—404.
- , Fraser C. J. & Spicer R. A. 1981. Anatomy and palaeoecology of *Pseudofrenelopsis* and associated conifers in the English Wealden. *Ibid.*, 24: 759—778.
- & Hlušík A. 1979. Modified axillary branching in species of the genus *Frenelopsis*: a new phenomenon among conifers. *Bot. J. Linn. Soc.*, 79: 231—241.
- & Pais J. J. C. 1978. A *Frenelopsis* with opposite decussate leaves from the Lower Cretaceous of Portugal. *Palaeontology*, 21: 873—879.
- , Spicer R. A. & Watson J. 1978. A *Classopollis*-containing male cone associated with *Pseudofrenelopsis*. *Ibid.*, 21: 847—856.
- Barnard P. D. W. 1968. A new species of *Masculostrobus* Seward producing *Classopollis* pollen from the Jurassic of Iran. *Bot. J. Linn. Soc.*, 61: 167—176.
- & 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—177.
- Barthel M. 1964. Coniferen- und Cordaiten-Reste aus dem Rotliegenden des Döhlener Beckens. *Geologie*, 13: 60—89.
- Bayer E. 1921. Zbarvené mikroskopické praeparaty fosilní kutikuly některých rostlin křídových z českých vrstev peruckých. *Čas. Mus. Král. Čes.*, 95: 41—54 (in Czech, French summary).
- Broutin J. & Pons D. 1975. Nouvelles précisions sur la morphologie et la phytodermologie de quelques rameaux du genre *Frenelopsis* Schenk. C. r. 100^e Congr. Nat. Sav. Sci. (Paris 1975), 2: 29—46.
- Chow T. & Tsao Ch. 1977. On eight new species of conifers from the Cretaceous of East China with references to their taxonomic position and phylogenetic relationship. *Acta Palaeont. Sin.*, 16 (2): 165—181.
- Doludenko M. P. 1978. Rod *Frenelopsis* (Coniferales) i ego nachodki v melu SSSR. *Palaeont. Zh.*, 4 (1978): 107—121 (in Russian).
- & Reymanówna M. 1978. *Frenelopsis harrisii* sp. nov. from the Cretaceous of Tajikistan, USSR. *Acta Palaeobot.*, 19 (1): 3—12.
- Hlušík A. 1972. *Frenelopsis alata* (Cupress. fossil). *Taxon*, 21 (1): 210.
- 1974. Nálezy *Frenelopsis* (Cupressaceae) v křídě Československa a jejich problematika. *Čas. Miner. Geol.*, 19 (3): 263—268 (in Czech, English summary).
- 1978a. Frenelopsids and their position within Mesozoic vegetation. C. r. 1^{re} Tab. Ronde sur les Écosyst. contin. Mésoz. Paris.
- 1978b. Frenelopsid plants (*Pinopsida*) from the Cretaceous of Czechoslovakia. *Univerzita Karlova (Proceed. Palaeontol. Conf. Prague 1977)*: 129—141.
- 1979a. Fossil gymnosperms from the Pláňava Formation (Hauterivian), Štramberk (Moravia). *Čas. Mor. Mus.*, 64: 25—36.
- 1979b. Frenelopsidy — málo známé fosilní jehličnany. *Živa*, 27: 16—17.
- 1981. Čeled *Frenelopsidaceae* fam. nov. (*Pinopsida*) a její zástupci v křídě Československa. Postgradual thesis (MS), ÚGG ČSAV Prague (Library), 131 pp. (in Czech).
- & Konzalová M. 1976a. Polliniferous cones of *Frenelopsis alata* (K. Feistm.) Knobloch from the Cenomanian of Czechoslovakia. *Věst. Ústř. Úst. Geol.*, 51: 37—45.
- & Konzalová M. 1976b. *Frenelopsis alata* (K. Feistm.) Knobloch, a new plant producing *Classopollis* pollen. *Proceed. Conf. Evolut. Biology (Prague 1976)*: 125—131.

- Jung W. 1968. *Hirmeriella münsteri* (Schenk) Jung comb. nov., eine bedeutsame Konifere des Mesozoikums. *Palaeontographica*, B, 122: 59—93.
- Krassilov V. 1980. Notes on *Hirmeriella*. IOP Newsletter, 13: 5.
- Kremp G. O. W. 1978. The earliest appearance worldwide of tricolpate pollen and origin of Angiosperms. 11th Ann. Meet. Amer. Assoc. Stratigr. Palynol. (Phoenix), Abstracts: 23.
- Lauverjat J. & Pons D. 1978. Le gisement Sénomien d'Esgueira (Portugal): Stratigraphie et flore fossile. C. r. 103^e Cong. Nat. Sav. Sci. (Nancy 1978), 2: 119—137.
- Li X. & Zhou T. 1980. Palaeofloristic provinces in the Cretaceous of South Eastern China. Inter. Palaeobot. Conf. (Reading 1980), Abstracts: 40.
- Médus J. 1967. Contribution au problème de l'affinité botanique du genre de forme *Classopollis*. Ann. Fac. Sci. Marseille, 39: 143—147.
- Němejc F. 1926. O totožnosti Feistmantelovy specie *Sclerophyllum alatum* a *Frenelopsis bohémica* Vel. Sbor. Stát. Geol. Úst. ČSR, 6: 133—142 (in Czech, English summary).
- Pons D. 1979. Les organes reproducteurs de *Frenelopsis alata* (K. Feistm.) Knobloch, *Cheirolepidiaceae* du Cénomaniien de l'Anjou, France. C. r. 104^e Cong. Nat. Soc. Sav. Sci. (Bordeaux 1979), 1: 209—231.
- 1980. Comparison between the male reproductive organs (cones and pollen „in situ”) of *Frenelopsis alata* (K. Feistm.) Knobloch and *F. oligostomata* (Romariz) Alvin (*Cheirolepidiaceae*). Inter. Palaeobot. Conf. (Reading 1980), Abstracts: 35.
- & Broutin J. 1978. Les organes reproducteurs de *Frenelopsis oligostomata* (Crétacé, Portugal). C. r. 103^e Cong. Nat. Soc. Sav. Sci. (Nancy 1978), 2: 139—159.
- Reymanówna M. & Watson J. 1976. The genus *Frenelopsis* Schenk and the type species *Frenelopsis hoheneggeri* (Ettingshausen) Schenk. Acta Palaeobot., 17: 17—26.
- Reyre Y. 1970. Stereoscan observation on the genus *Classopollis* Pflug 1953. *Palaeontology*, 13: 302—322.
- Srivastava S. K. 1976. The fossil genus *Classopollis*. *Lethaia*, 9: 437—457.
- Svobodová M. 1984. Palaeofloristic assemblages, palynology, palaeofacies and palaeogeography of Cenomanian deposits near Hamr na Jezeře. Postgradual thesis (MS), ÚGG ČSAV Prague (Library), 136 pp. (in Czech).
- Taugourdeau-Lantz J. 1971. Á propos du genre *Classopollis* (Pflug) Pocock et Jansonius, un phénomène nouveau. *Rev. Micropaléont.*, 14 (1): 50—54.
- Thompson W. P. 1912. The structure of the stomata of certain Cretaceous conifers. *Bot. Gaz.*, 54: 63—67.
- Upchurch G. R. jr. & Doyle J. A. 1981. Palaeoecology of the conifers *Frenelopsis* and *Pseudofrenelopsis* (*Cheirolepidiaceae*) from the Cretaceous Potomac Group of Maryland and Virginia. *Geobotany*, 2: 167—202.
- Vakhrameev V. A. 1970. Zakonomernosti rasprostraneniya i paleoekologia mezozojskich chvojnykh *Cheirolepidiaceae*. *Paleont. Zh.*, 1 (1970): 19—34 (in Russian).
- 1984. Floras and climates of the Lower Cretaceous. *Soviet. Geologia*, 1 (1984): 41—49 (in Russian).
- Velenovský J. 1889. Květena českého cenomanu. *Rozpr. Král. čes. spol. nauk*, 7 (3): 1—75 (in Czech).
- Walter H. 1973. Die Vegetation der Erde in öko-physiologischer Betrachtung. I. Die tropischen und subtropischen Zonen. G. Fischer Verlag VEB, Jena.
- Watson J. 1974. *Manica*: a new fossil conifer genus. *Taxon*, 23: 428.
- 1977. Some Lower Cretaceous conifers of the *Cheirolepidiaceae* from USA and England. *Palaeontology*, 20: 714—749.
- & Alvin K. L. 1976. Silicone rubber casts of silicified plants from the Cretaceous of Sudan. *Ibid.*, 19: 641—650.
- Zeiller R. 1882. Observations sur quelques cuticules fossiles. *Ann. Sci. Nat., Bot.*, 6 (13): 217—238.
- Zhou Z. 1983. A heterophyllous cheirolepidiaceous conifer from the Cretaceous of East China. *Palaeontology*, 26: 789—811.