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Diversity of Cretaceous Gymnosperms in the Alchan Depression of Primorye

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Abstract—The diversity of Cretaceous gymnosperms from the Alchan Depression in northwestern Primorye is discussed. The pike of gymnosperm diversity is restricted to the middle of the Late Albian, and a sharp decline took place in the terminal Albian. A new species, *Dictyozamites serafimae* sp. nov., is described.

Key words: gymnosperms, Primorye, diversity, cycadophyte index.

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INTRODUCTION

In northwestern Primorye, plant remains are known from Albian–Cenomanian deposits, mostly in intercourse of the Alchan, Bikin, and Marevka rivers. These deposits are subdivided into Assikaevka Formation, Alchan Formation, and Stolbovskaya Sequence, which are Aptian–lower Middle Albian, upper Middle–Upper Albian, and Cenomanian, respectively (Nevolina, 1990; Volynets, 1997, 2005; Markevich et al., 2000; Amel'chenko et al., 2001; Bugdaeva et al., 2006). Apart from gymnosperms, various polypodipsides and rare lycopodiopsides and equisetopsides are found in the Alchan flora; early angiosperms appear (Bugdaeva et al., 2006). Gymnosperms are the richest and diverse plant taxonomical group. Some members belong to gymnospermous orders which have survived until now; others belong to typically Mesozoic orders such as the Caytoniales, Czekanowskiales, and Bennettitales; Ginkgoales include genera which became extinct in the Cretaceous.

MATERIAL AND METHODS

Plant remains from 75 localities were studied by the author, geologists of Primorye Geological Survey Expedition (PGSE), and paleobotanists Nevolina and Shorokhova (Fig. 1). Collections nos. 1-64 and V-1109 are kept at the IBSS and PGSE, respectively.

The plant remains are mostly represented by leaf imprints, leafy shoots, mineralized trunks, woods, cones, and cone scales. The preservation is satisfactory, but compressions are usually lacking or strongly alternated and do not allow cuticle preparation. Pieces of ore filled with plant debris were bulk-macerated and satisfactory compressions were obtained.

Pieces of ore (up to 50 g) were placed in HF up to total destruction and residue accumulation. The residue was rinsed with water, and cuticles suitable for the further study were treated in Schulze solution after conventional technique. The cuticles were mounted on slides in glycerin jelly. In total, more than 500 pieces of ore were bulk-macerated. The slides were photographed under an Amplival light microscope with an OLYMPUS camera in Jilin University (China). Cuticles of some ginkgoaleans, czekanowskialeans, bennettites, and conifers were studied; the taxonomic composition of gymnosperms was significantly refined.

Cycadophyte index (CI) was calculated by Raunkier formula (Krassilov, 1973):

$$CI = (b_1/a_1 : b/a) \times 100,$$

where a is the total number of genera, b is the total number of cycadophyte genera, and a_1 and b_1 are these parameters for particular stratigraphic units.

DIVERSITY OF GYMNOSPERMS OF THE ALCHAN DEPRESSION AND THEIR ECOLOGY

The region under study is characterized by a mosaic and heterogeneous geological structure (Amel'chenko et al., 2001), that probably stimulated fast diversification of plants. The interaction between abiotic and biotic processes is distinct in the depression under study, since the territory was situated at the boundary between two phytogeographic areas (Siberian-Canadian and European-Sinian areas), that is at the boundary between moderate warm and subtropical climatic

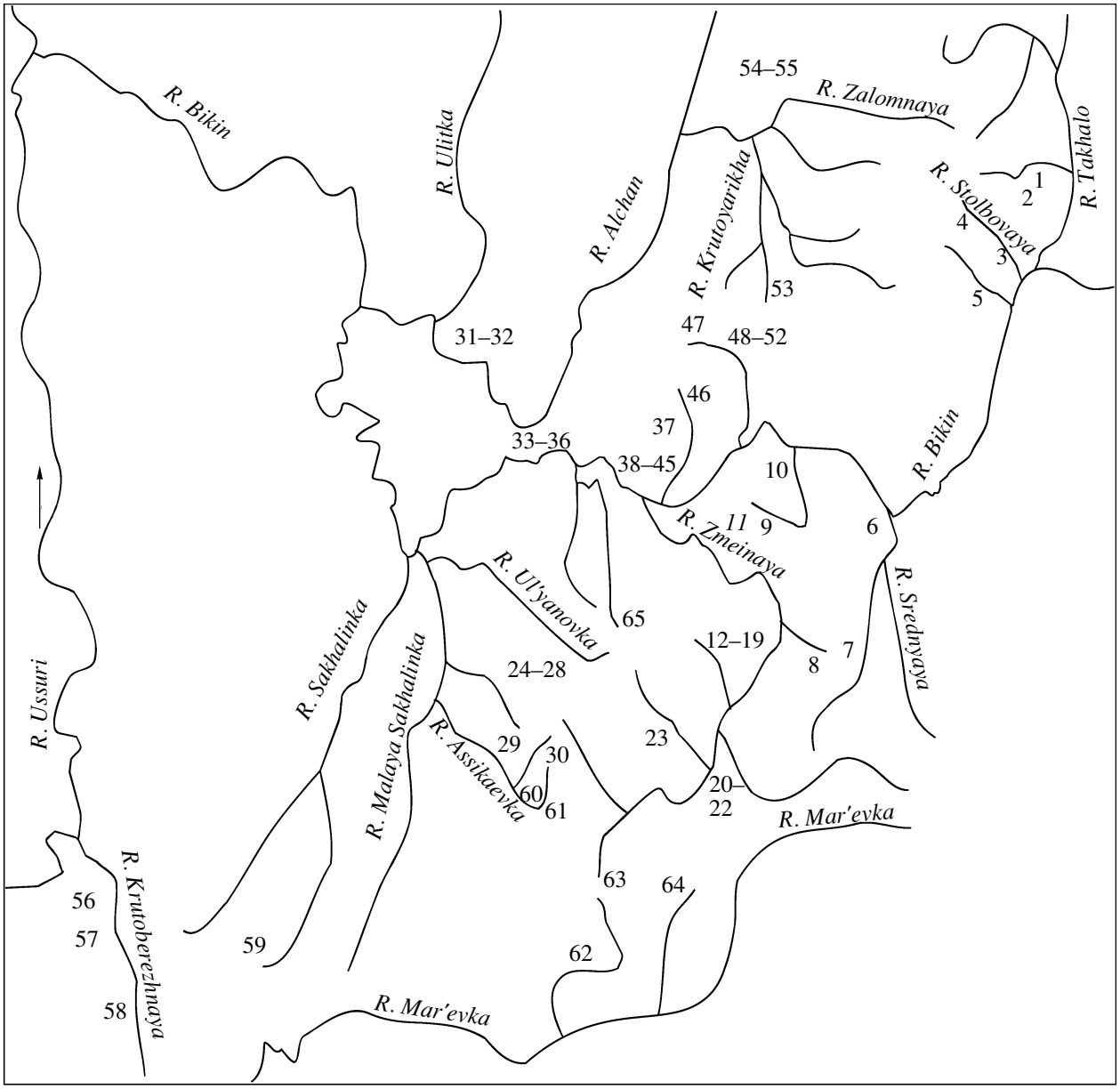


Fig. 1. Albian–Cenomanian localities of gymnosperms in basins of the Ussuri, Bikin, and Marevka rivers of northwestern Primorye. 1:800000, (2) ordinal number of locality.

zones (Vachrameev, 1988; Bugdaeva et al., 2006). Because of the ecotone position of this flora, its taxonomic composition sharply changed as the climate or geology changed. The depression was situated in a volcanic area, and the flora constantly suffered from volcano eruptions, gas pollution, repeated destructions of the substrate, and other events leading to the prevalence of pioneer vegetation (Bugdaeva et al., 2006).

Aptian. Cretaceous sedimentation commenced in the Alchan Depression since the Aptian: deposits of the Lower Assikaevka Subformation were accumulated. They consist of fine and coarse clastic sediments with marine fauna, coaly argillites, and lenses of thin coals with plant remains (Amel'chenko et al., 2001; Volynets, 2005, 2006; Bugdaeva et al., 2006). Plant remains were found in five localities at the left bank of the Bikin River, lower course (Fig. 1, nos. 24–28). Early Assikaevka floral assemblage (FA) was revealed (Volynets, 2005). Gymnosperms are represented by cycadophytes, ginkgoaleans, and conifers (Table 1, Fig. 2). Cycadophytes include members of *Pterophyllum* Brongn. (*P. sutschanense* Pryn., *P. burejensis* Pryn., and *Pterophyllum* sp.) and *Nilssonia* Brongn. (*N. nicanica* Krassil., *N.* ex gr. *brongniartii* (Mant.) Dunk., and *Nilssonia* sp.). Conifers include members of the Podozamitaceae, Pinaceae, and Taxodiaceae. The family Podozamita-

Table 1. Taxonomic composition of Aptian–Cenomanian gymnosperms in the Alchan Depression (relative occurrence of taxon is indicated with an asterisk)

Taxon	Lower Assikaevka Subformation	Upper Assikaevka Subformation	Lower Alchan Subformation	Lower part of the Upper Alchan Subformation	Middle part of the Upper Alchan Subformation	Upper part of the Upper Alchan Subformation	Upper part of the Stolbovaya Sequence
1	2	3	4	5	6	7	8
Caytoniales							
Caytonia orientalis Krassil.				*			
Sagenopteris variabilis (Velen.) Velen.				*	*		
Sagenopteris sp.		*					
Bennettitales							
Anomozamites sp. A					*		
Cycadeoidea bikinensis Krassil.					*		
Cycadeoidea sp. A					*		
Cycadolepis sp.				*			
Dictyozamites serafimae Volynets, sp. nv					*		
Neozamites verchojanensis Vachr.				*			
Nilssoniopteris aff. prynadae Samyl.						*	
Otozamites sp. 1					*	*	
Otozamites sp. 2						*	
Otozamites sp.					*	*	
Pseudocycas sp.					*		
Pterophyllum sutschanense Pryn.	*		*		*		
P. burejense Pryn.	*				*		
Pterophyllum (Tyrmia pterophylloides Pryn.) sp.	*						
Pterophyllum sp.		*			*		
Ptilophyllum sp.		*					
Zamiophyllum ivanovii (Krysht. et Pryn.) Krassil.					*		
Zamiophyllum sp.		*					
Cycadales							
Ctenis sp. 1					*		
Ctenis sp.			*				
Nilssonia densinervis (Font.) Berry			*				
N. ex gr. *orientalis* Heer			*		*		
N. nicanica Pryn.	*		*				
N. canadensis Bell					*		
N. mediana (Leck. ex Bean MS) Fox-Strang.					*		
N. yukonensis Holick					*		
N. ex gr. *brongniartii* (Mant.) Dunk.	*	*	*		*		
Nilssonia sp.	*	*			*		*
Nilssonia sp. 1					*		
Nilssonia sp. 2					*		
Pseudoctenis sp.			*				
Cycadophytes incertae sedis							
Cycadites sp.					*		
Taeniopteris bikinensis Schor.			*		*		
T. cf. *bikinensis* Schor.		*	*				
Taeniopteris sp.				*			

Table. (Contd.)

Taxon	Lower Assikaevka Subformation	Upper Assikaevka Subformation	Lower Alchan Subformation	lower part of the Upper Alchan Subformation	middle part of the Upper Alchan Subformation	upper part of the Upper Alchan Subformation	upper part of the Stolbovaya Sequence
1	2	3	4	5	6	7	8
Ginkgoales							
Baiera cf. *polymorpha* Samyl.		*					
Ginkgo pluripartita (Schimp.) Heer					*		
G. ex gr. *adiantoides* (Ung.) Heer		*	*		*		*
G. cf. *coreacea* Florin	*						
Ginkgo sp.					*		*
Pseudotorellia aff. *angustifolia* Dolud.						*	
Pseudotorellia sp.						*	
Sphenobaiera cf. uninervis Samyl.						*	
Sphenobaiera sp. 1						*	
Sphenobaiera sp.			*				
Czekanowskiales							
Phoenicopsis ex gr. *angusifolia* Heer				*	*		
Czekanowskia vachrameevii Kiritchk. et Samyl.						*	
C. aff. *ninae* Kiritchk. et Samyl.						*	
C. rigida Heer		*		*	*	*	
Czekanowskia sp.						*	
Coniferales							
Podozamitaceae							
Podozamites ex gr. *lanceolatus* (L. et H.) Schimp.		*	*	*	*		
P. tenuinervis Heer				*	*		
Podozamites sp.	*	*			*		*
Taxa related with the Podocarpaceae							
Nageiopsis ex gr. *heterophylla* Font.			*		*		
Pinaceae							
Pseudolarix (*Pityocladus*) *kolymensis* Samyl.				*			
P. aff. *dorofeevii* Samyl.				*	*		
Pseudolarix sp.			*	*			
Picea sp. 1					*		
Taxa related with the Pinaceae							
Pityocladus pseudolarixoides Samyl.				*			
Pityocladus sp. A				*	*		
Pityophyllum ex gr. *nordenskioldii* Heer		*				*	
Pityophyllum sp.	*	*		*			*
Pityospermum aff. *prynadae* Krassil.				*			
Pityospermum sp.		*					
Pityospermum sp. 1				*			
Pityospermum sp. 2				*			
Pityostrobus piceoides Samyl.					*		
Pityostrobus sp.			*		*		
Pityostrobus sp. A					*		
Pityolepis sp. 1					*		
Pityolepis sp. 2							

Table. (Contd.)

Taxon	Lower Assikaevka Subformation	Upper Assikaevka Subformation	Lower Alchan Subformation	lower part of the Upper Alchan Subformation	middle part of the Upper Alchan Subformation	upper part of the Upper Alchan Subformation	upper part of the Stolbovaya Sequence
1	2	3	4	5	6	7	8
Taxa related with the Taxaceae							
Torreyires cf. *dicksonioides* (Daws.) Bell		*	*				*
Taxites brevifolius (Font.) Samyl.		*			*		
T. acuminatus (Krysht. et Pryn.) Volynets					*		
T. heterophyllus (Holl.) Samyl.							*
Taxites sp. A		*	*				
Taxites sp.							*
Taxodiaceae							
Elatides asiatica (Yok.) Krassil.	*	*	*	*	*	*	
Elatides splendida Bell		*	*	*	*		
Elatides sp. A					*		
Sequoia fastigiata (Sternb.) Heer				*	*		
S. reichenbachii (Gein.) Heer		*	*	*	*		*
S. ex gr. *reichenbachii* (Gein.) Heer					*		
S. ambigua Heer			*		*		
Sequoia sp. 1				*	*	*	
Sequoia sp. 2					*		
Sequoia sp.							*
Sphenolepis ex gr. *sternbergiana* (Dunk.) Schenk		*			*		
Sphenolepis sp.					*		
Athrotaxites berryi Bell	*	*	*		*		
Athrotaxopsis expansa Font. emend. Berry		*	*	*	*	*	
Athrotaxopsis sp.		*					*
Cupressaceae							
Mesocyparis sp.							*
Thuja cretacea (Heer) Newb.							*
Cyparissidium gracile Heer		*			*		
Libocedrus sp.							*
Coniferales incertae sedis							
Brachyphyllum douglassi Bell							*
B. aff. *mamillare* Brongn.					*		
B. ex gr. *obesum* Heer			*	*	*		
Brachyphyllum sp.							*
Elatocladus smittiana (Heer) Sew.							*
Elatocladus sp.		*			*		*
Schizolepis sp. 1		*					
Schizolepis sp. A		*					
Stachyotaxus sp. A					*		
Coniferites sp.		*	*				
Conites sp. 1					*		
Conites sp. 2					*		
Conites sp. A (Metasequoia sp.?)					*		
Conites sp. B					*		
Conites sp.					*		
Pagiophyllum sp.					*		
Gymnosperms incertae sedis							
Desmiophyllum sp.		*	*	*	*	*	

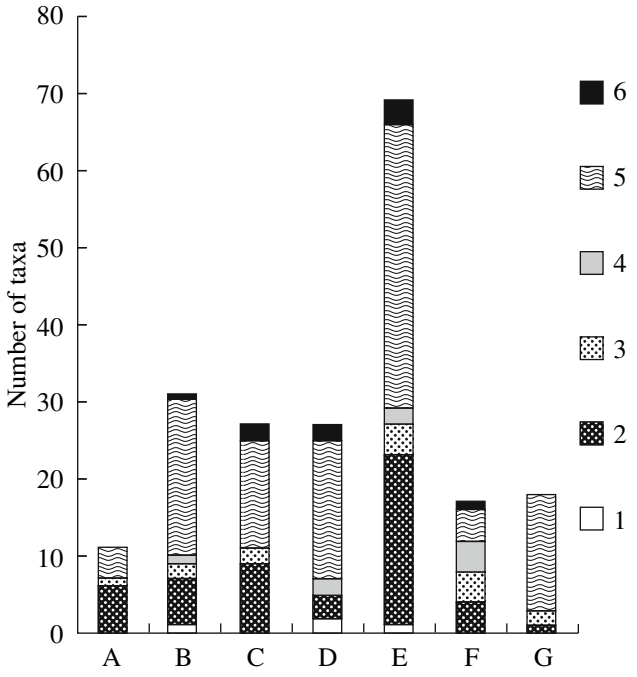


Fig. 2. Ratio between groups of gymnosperms in the Alchan Depression.

(A) Lower Assikaevka Subformation; (B) Upper Assikaevka Subformation; (C) Lower Alchan Subformation; (lD–F) Upper Alchan Subformation: (D) lower portion of section; (E) middle portion of section; (F) upper portion of section; (G) Stolbovaya Sequence, upper portion of section; (1) gymnosperms incertae sedis; (2) conifers; (3) czekanowskiales; (4) ginkgoaleans; (5) cycadophytes; (6) caytonialeans.

ceae is represented by *Podozamites* sp.; and the Pinaceae, by *Pityophyllum* sp. *Athrotaxites berryi* Bell and *Elatides asiatica* (Yok.) Krassil. belong to the Taxodiaceae. *Ginkgo* cf. *coriacea* Florin is the only ginkgoalean member in the flora.

The deposits which are characterized by the Early Assikaevka FA were formed under shallow-water conditions of a marginal sea and delta front (Konovalov, 1990; Markevich et al., 2000). The plants grew on coastal swampy low-land. Trees and shrubs formed wet coniferous-cycadophyte forests (*Elatides* Heer-*Nilssonia*). Coniferous forests with *Elatides-Athrotaxites* Ung. occupied the majority of deltaic plains in Primorye, Bureya River Basin, and North America (Krassilov, 1967, 1972; Miller and Lapasha, 1984).

CI was calculated in order to obtain a more refined estimation of paleoclimatic changes. Cycadophytes are the most thermophilic group, and the common participation in the vegetation supposedly testifies to climatic optima. The value of CI for the flora of the depression is high and equal to 82.9 (Fig. 3). High values of CI are known for the Aptian of Transbaikalia, Bureya River Basin, and Razdol'nenskaya and Partizanskaya depressions in Primorye; this fact probably indicates that a climatic optimum existed during that time in Eurasia (Krassilov, 1973; Bugdaeva et al., 2006).

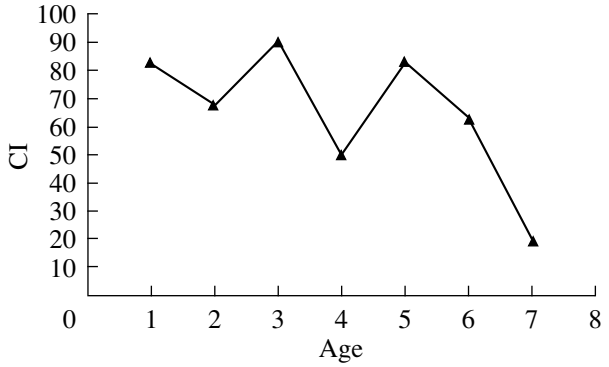


Fig. 3. Variations in cycadophyte index (CI) in the Middle Cretaceous time in the Alchan Depression: (1) Aptian; (2) early Middle Albian; (3) late Middle Albian; (4) early Late Albian; (5) middle Late Albian; (6) terminal Albian; (7) Late Cenomanian; (1–100) CI.

Albian. Deposits of the Middle Assikaevka Subformation were formed in the Early Albian. The territory of the depression was covered with a sea. Submarine volcanic activity took place (Markevich et al., 2000).

Volcanic activity became more active in the first half of the middle Albian. Gradual marine regression took place. Terrigenous deposits of the Upper Assikaevka Subformation were formed; they consist of coarse-grained and fine-grained sediments with admixed volcanic material and lenses of thin coal containing plant remains (Amal'chenko et al., 2001). Plant-bearing layers were found in 13 localities (Fig. 1). Late Assikaevka FA was studied from localities in the lower and middle courses of the Bikin River (Volynets, 2005, 2006; Bugdaeva et al., 2006). Gymnosperms include caytonialeans, cycadophytes, ginkgoaleans, czekanowskialeans, conifers, and genera of uncertain systematic position (Table 1; Fig. 2). Conifers include members of the Podozamitaceae, Pinaceae, Taxodiaceae, Cupressaceae, and Taxaceae, as well as the genera of uncertain systematic position *Elatocladus* Halle, *Schizolepis* Braun, and *Coniferites* Ung. Taxodiaceae are most diverse; *Elatides asiatica* and *Athrotaxites berryi* are common among them. The gymnosperms *Sequoia reichenbachii* (Gein.) Heer, *Elatides splendida* Bell, *Sphenolepis* ex gr. *sternbergiana* (Dunk.) Schenk, and *Athrotaxopsis expansa* Font. emend. Berry first appear. Members of the Taxaceae (*Torreyites* Feistm. and *Taxites* Brongn.) and Cupressaceae (*Cyparissidium* Heer) appear. Cycadophytes *Pterophyllum* (*Pterophyllum* sp.) and *Nilssonia* (*Nilssonia* sp. and *N.* ex gr. *brongniartii*) are still present, and *Zamiophyllum* sp., *Ptilophyllum* sp., and *Taeniopteris* cf. *bikinensis* Schor. appear. Ginkgoaleans include *Ginkgo* ex gr. *adiantoides* (Ung.) Heer and *Baiera* cf. *polymorpha* Samyl. Members of the Caytoniales (*Sagenopteris* sp.) and Czekanowskiales (*Czekanowskia* ex gr. *rigida* Heer) first appear. The taxonomic diversity of gymnosperms enriches at the expense of conifers (20 taxa) and the appearance of

caytonialeans, czekanowskialeans, and some ginkgoaleans.

In that time, the territory of the depression was occupied by a swampy coastal plain, surrounded by a volcanic ridge. The plant communities were more diverse than the Aptian plant communities. In addition to *Podozamites* (Brongn.) Braun and *Elatides, Sequoia* Endlicher and *Athrotaxopsis* Font. become common among conifers. The new genera *Sphenolepis* Nees, *Taxites*, and *Cyparissidium* appear, as well as the orophyte *Torreyites.* Among cycadophytes, *Nilssonia* continues dominating, and the characteristic mangrove element *Ptillophyllum* Morris appears. Krassilov believed (1979) that *Nilssonia-beds*, also named *Nilssonia-marshes*, are mostly restricted to flysch and coal-bearing facies of an overdeltaic plain. Czekanowskialeans first appear, being typical members of Siberian-Canadian phytogeographic area. Bugdaeva (1983) revealed their pioneer role for settling a newly formed land after volcanic eruptions. The depression under study shows a similar situation. After marine regression, plants settle a newly formed land. Because of repeated volcanic eruptions, well-shaped plant communities are destroyed, and r-strategy plants czekanowskialeans and angiosperms (Bugdaeva et al., 2006), as well as the conifers *Athrotaxopsis expansa* and *Sequoia reichenbachii*, start colonizing unpopulated land. Two last species have xeromorphic adaptations helping to survive during long winters with light deficiency. A similar case was described by Herman and Spicer (1999) in phytocenoses of northeastern Russia. The dominance of *Athrotaxopsis expansa* and *Sequoia reichenbachii* in Middle–Late Albian communities of the Alchan Depression is logical. Modern *Sequoia* (*S. sempervirensis* (D. Don) Endl.) is able to produce plentiful young shoots (*Plant* …, 1978). One can suppose that Cretaceous plants had similar characters. The vegetation was repeatedly destroyed in the volcanic area, and these plants could have occupied the newly unpopulated land faster than other plants (Bugdaeva et al., 2006). CI is 67.6 in that time, that is slightly lower than in the Aptian (Fig. 3).

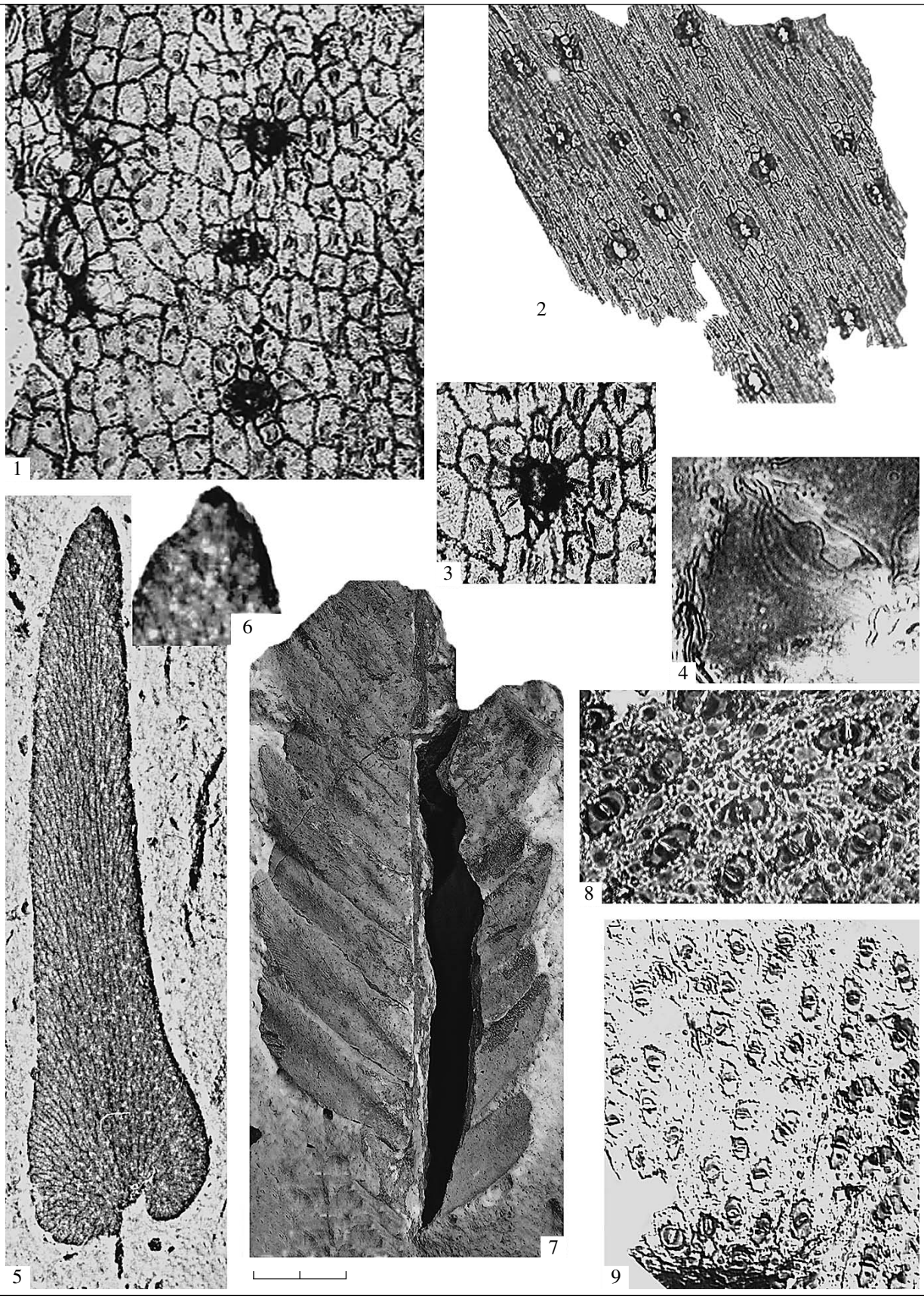
During the second half of the Middle Albian, the highest pike of terrestrial volcanic activity took place, and marine conditions only existed in the extreme north of the depression (Markevich et al., 2000). Terrigenous volcanogenic deposits of the Lower Alchan Subformation were accumulated. Sublayers of coaly argillites and coals were observed among the deposits of this subformation. Plant remains from 11 localities were studied (Fig. 1). Early Alchan FA was revealed in the lower and middle course of the Bikin River (Volynets, 2005, 2006; Bugdaeva et al., 2006). Gymnosperms of this assemblage are represented by cycadophytes, ginkgoaleans, conifers, and *Desmiophyllum* sp., a conifer taxon of uncertain position (Table 1; Fig. 2). Among conifers, members of the Podozamitaceae, Pinaceae, Taxodiaceae, Taxaceae, and genera of uncertain position *Brachyphyllum* Brongn. and *Coniferites* are present, and podocarp *Nageiopsis* ex gr. *heterophylla* Font. appears. Members of the Taxodiaceae are still diverse and include *Elatides asiatica, E. splendida, Sequoia reichenbachii, Athrotaxitas berryi, Athrotaxopsis expansa*, and newly appearing *Sequoia ambigua* Heer. The cycadophytes *Pterophyllum, Pseudoctenis* Sew., *Taeniopteris* Brongn., *Nilssonia*, and *Ctenis* Lindl. et Hutton are present. *Ctenis* sp. and *Pseudoctenis* sp. appear for the first time. The genus *Nilssonia* is most diverse and includes four species (Table 1). The ginkgoaleans *Ginkgo* ex gr. *adiantoides* and *Sphenobaiera* sp. are present. In total, the gymnosperm diversity slightly decreases.

During that time, a volcanic area with less diverse phytocenoses existed in the territory of the Alchan Depression. Anthracophilic plants, such as *Podozamites, Pterophyllum, Nilssonia*, and others, become rare; the orophytes *Torreyites, Pseudolarix* Gordon, and *Sequoia* occur more often (Table 1). Swampy valleys with *Elatides-Podozamites-Ctenis-Nilssonia* and ferns and horsetails are formed in pauses between volcanic events, that is confirmed by the occurrence of thin coal sublayers in sections (Amel'chenko et al., 2001). *Pseudolarix* and *Nageiopsis* Font. appear in conifer forests. CI reaches the highest value (90.2), testifying to the climatic optimum for the area. The Early Cretaceous cycadophytes *Nilssonia, Taeniopteris*, and *Ctenis* form large aggregations near coal beds (Krassilov and Shorokhova, 1989). Slightly increased diversity of cycadophytes at the generic level and decreased diversity of gymnosperms and other plants resulted in a higher value of CI (Fig. 3).

In the Late Albian, the region included several mountain ranges and river valleys with disjointed volcanic structures; coastal marine environments only remained in the extreme north of the depression. Terrigenous volcanogenic deposits of the Upper Alchan Subformation continue accumulating. The subformation is predominantly formed by small lenses of coaly argillites, tuff-sandstones and tuff-siltstones beds with fossil plants and mollusks (Amel'chenko et al., 2001).

Deposits of the lower part of the Upper Alchan Subformation were accumulated at the beginning of the Late Albian (Volynets, 2006). Plant-bearing beds were found in six localities at the right and left banks of the Bikin River, in its middle course, in the basins of the Vasil'evka and Zmeinaya rivers and Alenkin Creek (Fig. 1). Early subassemblage of the Late Alchan FA was revealed (Volynets, 2005; Bugdaeva et al., 2006). Among gymnosperms, caytonialeans, cycadophytes, czekanowskialeans, conifers, and gymnosperms of uncertain systematic position are present (Table 1; Fig. 2). Caytonialeans include *Caytonia orientalis* Krassil. and *Sagenopteris variabilis* (Velen.) Velen., and czekanowskialeans include *Czekanowskia* ex gr. *rigida* and *Phoenicopsis* ex gr. *angustifolia* Heer. Cycadophytes are represented by *Neozamites verchojanensis* Vachr., *Cycadolepis* sp., and *Taeniopteris* sp. Members of the Podozamitaceae, Taxodiaceae, and Pinaceae are

Plate 32



Explanation of Plate 32

Figs. 1–3. *Czekanowskia vachrameevii* Kiritchkova et Samylina, middle course of the Bikin River, upper course of the Stolbovaya River, Lower Cretaceous, Albian: (1) IBSS, no. 4, T.2517/12, epidermis of the lateral surface of a leaf, ×160; (2) IBSS, no. 4, T.2517/10, epidermis of the lower surface of a leaf, ×160; (3) IBSS, no. 4, T.2517/12, stoma, epidermis of the lateral surface of a leaf, ×320.

Fig. 4, 8, 9. *Nilssoniopteris* aff. *prynadae* Samylina, middle course of the Bikin River, upper course of the Stolbovaya River, Lower Cretaceous, Albian: (4) IBSS, no. 4, T.2517/10-1, stoma, epidermis of the lower surface of a leaf, ×480; (8) IBSS, no. 4, T.2517/10-2, epidermis of the lower surface of a leaf with finely undulated cellular walls, ×150; (9) IBSS, no. 4, T.2517/10-2, epidermis of the lower surface of a leaf, stomata, ×60.

Figs. 5–7. *Dictyozamites serafimae* sp. nov.: (5) IBSS, no. 53, T.4561/10, isolated segment, middle course of the Alchan River, left bank, lower course of the Krutoyarikha River, Lower Cretaceous, Albian, ×3.2; (6) IBSS, no. 53, Alchan, left bank, upper course of the Krutoyarikha River, Lower Cretaceous, Albian, ×12.8; (7) holotype, IBSS, no. 9, T.5599/6, leaf imprint, middle course of the Bikin River, Zabytyi Creek, Lower Cretaceous, Albian, ×1.6.

known among conifers, as well as the species of uncertain systematic position *Brachyphyllum* ex gr. *obesum* Heer. Two former families do not change significantly their taxonomic composition. For the first time, the taxonomic diversity increases in the Pinaceae, at the expense of *Pityocladus* (Nath.) Sew., *Pityospermum* Nath., and *Pseudolarix.* During this interval, the taxonomic diversity of gymnosperms increases at the expense of conifers and several new species of other groups.

The divided relief of the depression that was formed to that time predetermined the diversity of plant communities. Arborescent slope vegetation mostly consists of members of the Pinaceae with participation of the Taxodiaceae. Underbrush of wet sites included caytonialeans (*Caytonia* Thom. and *Sagenopteris* Presl). Czekanowskialeans (*Czekanowskia* Heer and *Phoenicopsis* Heer) grew in lower areas of river valleys, near swamps. Angiosperms again appear. Siberian bennettite *Neozamites* Vachr. appears in some plant communities. CI decreases up to 49.6 (Fig. 3), that apparently testifies to climatic cooling and southern shift of the moderate zone.

In the middle of the Late Albian, deposits of the middle part of the Upper Alchan Subformation were accumulated (Amel'chenko et al., 2001). I studied plant remains from 47 localities, situated in the interfluve of the Bikin and Marevka rivers and basins of the Dostupnaya, Petlyanka, Zmeinaya, Assikaevka, Izmailikha, Sakhalinka, Krutoberezhnaya, Medovaya, Vasil'evka, and Krutoyarikha rivers (Fig. 1). The middle subassemblage of the Late Alchan FA was revealed (Volynets, 2005, 2006; Bugdaeva et al., 2006). Gymnosperms of the subassemblage include conifers, cycadophytes, ginkgoales, czekanowskialeans, and one species of caytonialeans; gymnosperms of unclear systematic position are represented by *Desmiophyllum* Lesq. (Table 1; Fig. 2). Members of the Taxodiaceae are most taxonomically diverse among conifers: *Elatides, Sequoia*, and *Athrotaxopsis* still occur, and *Sphenolepis* and *Athrotaxites* reappear. The Pinaceae includes *Pityophyllum* Nath., *Pseudolarix, Pityocladus, Pityostrobus piceoides* Samyl., *Pityolepis* sp. 1, and *Picea* sp. 1, *Podozamites* ex gr. *lanceolatus* (L. et H.) Schimp., *P. tenuinervis*, Heer and *Podozamites* sp. are still present among members of the Podozamitaceae. The family Taxaceae includes *Taxites brevifolius* (Font.) Samyl. and *T. acuminatus* (Krysht. et Pryn.) Volynets; the Cupressaceae, *Cyparissidium gracile* Heer, and the Podocarpaceae, *Nageiopsis* ex gr. *heterophylla* Font. Conifers of unclear systematic position are *Brachyphyllum, Pagiophyllum* Heer, *Stachyotaxus* Nath., *Elatocladus* Halle, and *Conites* Sternb. The diversity of cycadophytes is increased at the expense of *Anomozamites* Schimp., *Dictyozamites* (Oldh.) Medl. et Blanf., *Otozamites* Braun, *Cycadeoidea* Buckl., *Cycadites* Sternb., *Pseudocycas* Nath., *Zamiophyllum* Nath., and *Ctenis*; *Pterophyllum, Nilssonia*, and *Taeniopteris* constantly occur. No changes were detected in the composition of ginkgoaleans (*Ginkgo pluripartita* (Schimp.) Heer, *G.* ex gr. *adiantoides,* and *Ginkgo* sp.), czekanowskialeans (*Czekanowskia* and *Phoenicopsis*), and caytonialeans (*Sagenopteris*).

Volcanic activity became slightly weaker during that time, the depression became more strongly divided, river valleys and small lakes became more numerous, and the diversity of plant communities increased. Cycadophytes became more prominent, inhabiting both wet and dry sites: *Nilssonia, Taeniopteris*, and *Ctenis* and *Cycadeoidea, Zamiophyllum,* and *Otozamites*, respectively. CI is high (82.9), testifying to the existence of a climatic optimum (Fig. 3). Various conifers with scaly shoots participated in the plant communities: *Athrotaxopsis, Cyparissidium, Brachyphyllum*, and *Pagiophyllum*. Many cenoses existed with *Sequoia, Elatides, Sphenolepis*, and *Taxites* as forest-forming elements. These genera are characteristic members of moist conifer forests of subtropical or moderate climate with a small difference between winter and summer temperatures (Krassilov, 1967, 1971). In addition to *Cycadeoidea, Zamiophyllum*, and some other typically subtropical elements, the phytocenoses are actively participated by moderate plants, such as czekanowskialeans, that testifies to the existence of favorable conditions for both moderate and subtropical plants.

In the terminal Albian, deposits of the upper part of the Upper Alchan Subformation were accumulated; they are tuffites, tuff sandstones, and siltstones. Plant bearing beds were found in two localities: in the middle

course of the Bikin River (basin of the Stolbovaya and Zmeinaya rivers) and the Storozhevoi Creek (Fig. 1). Here, a late subassemblage of the Late Alchan FA was found (Volynets, 2005, 2006; Bugdaeva et al., 2006). The subassemblage includes cycadophytes, ginkgoaleans, czekanowskialeans, conifers, and gymnosperms of unclear systematic position (Table 1; Fig. 2). Among cycadophytes, members of *Otozamites* and *Nilssoniopteris* Nath. (*N.* aff. *prynadae* Samyl.) are present (Pl. 32, figs. 4, 8, 9). Ginkgoaleans include *Sphenobaiera* Florin and *Pseudotorellia* Florin; and czekanowskialeans, *Czekanowskia vachrameevii* Kiritchk. et Samyl. (Pl. 32, figs. 1–3), *C.* aff. *ninae* Kiritchk. et Samyl., *C.* ex gr. *rigida,* and *Czekanowskia* sp. Conifers are represented by members of the Taxodiaceae (*Elatides asiatica, Sequoia* sp. 1, and *Athrotaxopsis expansa*) and Pinaceae (*Pityophyllum* ex gr. *nordenskioldii* Heer). Gymnosperms of unclear systematic position are represented by *Desmiophyllum.* In total, gymnosperms become less diverse.

A pause happened in the volcanic activity during this period. Mountainous ridges and river valleys were main components of the relief of the territory; plains most probably prevailed over mountains. The vegetation composition became much poorer due to the disappearance of many cycadophytes and conifers. Plant communities with *Otozamites* and *Desmiophyllum* dominated. Although the diversity of phytocenoses decreases, new genera of cycadophytes (*Nilssoniopteris*) and ginkgoaleans (*Sphenobaiera*) appear. Czekanowskialeans and conifers (*Elatides* and *Sequoia*) still participate in the plant communities. Coalified compressions of leaves of *Sphenobaiera, Pseudotorellia, Czekanowskia*, and *Nilssoniopteris* occur among remains of *Otozamites* sp. in siltstones of the upper part of the subformation (localities 4 and 8). Remains of *Otozamites* sp. are morphologically close to *Otozamites lacustris* Krassil. from lacustrine deposits of Mongolia (Krassilov, 1982) and *Otozamites* sp. from Dalazi Formation (*Fossil* …, 1995). It is supposed that a lake existed in the middle course of the Bikin River, in the upper course of the Stolbovaya River, to the north of the Storozhevoi Creek. The lithological composition shows that neither dolomites nor shales were accumulated in the lake (Amel'chenko et al., 2001). Apart from *Otozamites* and *Desmiophyllum*, the coastal vegetation was participated by *Czekanowskia* and *Nilssoniopteris*; more elevated sites were inhabited by *Pseudotorellia* and *Athrotaxopsis.* The vegetation of the terminal Albian was a sort of cycadophyte chaparral with rare conifers, ginkgoaleans, and angiosperms (Bugdaeva et al., 2006). The sharply reduced diversity, decreased value of CI (Fig. 3), disappearance of ferns, many cycadophytes, and conifers from the coastal vegetation, and increased contribution of *Otozamites* probably testify to the existence of unfavorable climatic conditions.

Cenomanian. Terrestrial variegated deposits of the Stolbovaya Sequence were accumulated during the Cenomanian. The deposits are coarse- and fine-grained clastic rocks. Plant remains come from the upper part of the Stolbovaya Sequence (Late Cenomanian), in the basin of the Zalomnaya River (Fig. 1); Stolbovaya FA was revealed (Volynets, 2005, 2006; Bugdaeva et al., 2006). Gymnosperms include cycadophytes, ginkgoaleans, and conifers (Table 1; Fig. 2). *Nilssonia* sp. is the only cycadophyte of the assemblage. Ginkgoaleans are represented by *Ginkgo* ex gr. *adiantoides* and *Ginkgo* sp. Among conifers, a considerable diversity was recorded in the families Taxodiaceae (*Sequoia reichenbachii, Sequoia* sp., and *Athrotaxopsis* sp.), Taxaceae (*Torreyires* cf. *dicksonioides* (Daws.) Bell, *Taxites heterophyllus* (Holl.) Samyl., and *Taxites* sp.), and Cupressaceae (*Mesocyparis* sp., *Thuja cretacea* (Heer) Newb., and *Libocedrus* sp.). The role of the Podozamitaceae (*Podozamites* sp.) and Pinaceae (*Pityophyllum* sp.) decreased. Conifers of unclear systematic position are represented by *Brachyphyllum* and *Elatocladus.* Angiosperms became dominants of the FA, mostly represented by the Platanaceae; aquatic plants appeared (Volynets, 2005).

During the Late Cenomanian, the territory was occupied by an alluvial plain, surrounded by low mountainous ridges. The plant communities were dominated by angiosperms, mostly by the Platanaceae. Remains of the aquatic angiosperms *Quereuxia* Krysht. and *Potamogeton* L. and floating fern *Salvinia* Micheli were found (Volynets, 2005). The new genera *Thuja* L. and *Mesocyparis* McLver et Basinger. appeared among conifers. The fact that the dominants of the plant communities changed points out that a crucial turn-over took place. The prevalence of riparian platanaceous forests and common settlement of aquatic sites testify to the existence of a humid climate.

The increased floristic diversity in the middle Late Albian apparently testifies to the most favorable conditions and is probably explained by the existence of a climatic optimum. Contrariwise, the sharply decreased diversity in the terminal Albian is an index of unfavorable conditions. Dominants of phytocenoses changed in the Late Cenomanian, and a new plant formation appeared: platanaceous forests.

A new species is described below.

SYSTEMATIC PALEOBOTANY

Gymnospermae

Order Bennettitales (Cycadeoideales)

Genus *Dictyozamites* (Oldham) Medlicott et Blanford, 1879

***Dictyozamites serafimae* Volynets, sp. nov.**

Plate 32, figs. 5–7

Dictyozamites sp. A: Bugdaeva et al., 2006, pl. XIV, figs. 4, 5.

Otozamites sp. 1: Bugdaeva et al., 2006, pl. XIV, fig. 10.

E t y m o l o g y. In honor to the paleobotanist S.I. Nevolina.

H o l o t y p e. IBSS, no. 9, T.5599/6; leaf; Primorye, middle course of the Bikin River, left bank, water

divide of the Bikin and Zmeinaya rivers; Lower Cretaceous, Albian (Pl. 32, fig. 7).

Diagnosis. Leaves pinnate, 90 × 50 mm. Segments attached to rachis at angle of 40°, asymmetric, oblong-lanceolate, with strongly expanded basis, developed auriculars, and convex-concave margin. Segment apices acuminate, with thickened gland. Venation reticulate.

Description. The collection contains five imprints of segments and one fragmentary leaf. The leaf is pinnate, regularly segmented, 90 mm long, and up to 50 mm wide in the middle and lower parts. The rounded rachis is 3 mm thick. The segments are situated oppositely, attached with the middle part of their base at an angle of 40°. The base is cordate, with distinct auricles. The length of the segments is 30–40 mm, and the width is 6–10 mm, with the maximum at the lower part. The segment margins are convex-concave, the apex is narrowing and acuminate, with a thickened gland on the tip (Pl. 32, fig. 6). The venation is reticulate. The veins are fan-shaped. They dichotomize forming elongated meshes 0.5–0.6 mm wide, which are situated in parallel to the margin and reach 3–6 mm long and become shorter up to 1–2 mm in the lower and marginal areas of the segments. Twenty-six to twenty eight veins occur per 1 cm of the leaf margin; eighteen, in the middle part; and twenty-three, in the upper part.

Comparison. The new species differs from numerous previously published species of *Dictyozamites* by distinctly asymmetrical segments and a narrowing apex. It differs from *D. falcatus* (Morris) Medl. et Blanf. from the Early Cretaceous of Primorye (Krassilov, 1967) by larger segments, convex-concave margins of the segments, a pointed apex, and denser venation. The new species differs from *D. obliquus* Samyl., described by Samylina (1964) from the Early Cretaceous of the Sikhote Alin Range (upper course of the Bikin River) by smaller segments, convex-concave margins, a pointed apex, and widened bases of the segments, and looser venation in the segments.

D. auriculatus Kimura et Sekido (Kimura and Sekido, 1976) from the Early Cretaceous of Japan (Oguchi Formation) resembles the new species by the mode of segment attachment to the rachis, but differs by more distinctly asymmetrical bases of segments, having an upper auricle that is much better developed than the lower auricle, and looser venation in the segments (Kimura and Sekido, 1976).

Occurrence. Primorye, Bikin River Basin, Zabytyi Creek; Alchan River Basin, Krutoyarikha River; Lower Cretaceous, Alchan Formation, Upper Subformation.

Material. One fragmentary leaf and five isolated segments, specimen nos. 9 T.5599/6-9 and 53 T.4561/26-27.

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