

# The Aptian–Cenomanian Flora of Primor’e, Part 2: Correlation of Floral Assemblages

E. B. Volynets

Institute of Biology and Soil Science (IBSS), Far East Division, Russian Academy of Sciences, Vladivostok

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**Abstract**—Taxonomic composition of plant fossils from the Aptian–Cenomanian sediments of the Alchan, Razdol’naya, and Partizanskaya depressions of Primor’e is studied in detail. Each of the established floral assemblages characterizes a particular stage of flora stabilization. Correlation of the assemblages is performed. Floral assemblages of the Alchan depression, which occur in association with macrofauna, are suggested to be the standard ones for the southern Far East. New species are described.

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The part one of the work was dedicated to characterization of Aptian–Cenomanian floral assemblages (FAs) from the Alchan, Razdol’naya, and Partizanskaya depressions. In this article, the comparative analysis of assemblages is used to substantiate the suggested correlation chart (the table).

## CONSIDERATION OF RESULTS

In taxonomic composition, the early Assikaevka FA is comparable with the early and late Lipovtsy FAs and with the late Staryi Suchan FA. Taxa in common for the early Lipovtsy and early Assikaevka FAs are *Onychiopsis psilotoides* (St. et W.) Ward, *Coniopteris burejensis* (Zal.) Sew., *Cladophlebis frigida* (Heer) Sew., *Pterophyllum sutschanense* Pryn., *P. burejense* Pryn., *Nilssonina nicanica* Pryn., *N. ex gr. orientalis* Heer., *N. ex gr. brongniartii* (Mant.) Dunk., *Athrotaxites berryi* Bell and *Elatides asiatica* (Yok.) Krassil. Dominants (cycadophytes), subdominants (ferns), and proportions of other plant groups are similar in both assemblages (Figs. 2, 3).<sup>1</sup> An insignificant distinction is as follows: cycadophytes [*Nilssoniopteris rhitidorachis* (Krysht.) Krassil., *Zamiophyllum ivanovii* Krassil., *Cycadites sulcatus* Krysht. et Pryn., *Ctenis yokoyamae* Krysht.] and ferns [*Ruffordia goeppertii* (Dunk.) Sew., *Nathorstia pectinata* (Goepf.) Krassil., *Alsophilites nipponensis* (Oishi) Krassil.] are more diverse in the early Lipovtsy than in the early Assikaevka FA. The latter also contains species in common with the late Lipovtsy FA. These are *Equisetum* cf. *ramosus* Samyl., *Birisia onychioides* (Vassilevsk. et K.-M.) Samyl., *Coniopteris*

*burejensis* (Zal.) Sew., *Cladophlebis frigida* (Heer) Sew., *Pterophyllum sutschanense* Pryn., *P. burejense* Pryn., *Nilssonina ex gr. orientalis* Heer, *N. nicanica* Pryn., *N. ex gr. brongniartii* (Mant.) Dunk., *Elatides asiatica* (Yok.) Krassil., *Athrotaxites berryi* Bell. It should be mentioned also that *Birisia onychioides*, *Pterophyllum burejense*, *Nilssonina nicanica*, and *Athrotaxites berryi* of the early Aptian origin are components of subsequent assemblages, the terminal late Albian ones included. A distinction is that cycadophytes and ferns are dominants and subdominants of the early Assikaevka FA, but in the late Lipovtsy FA these are ferns and cycadophytes respectively, whereas conifers are at the third place in abundance in both FAs (Figs. 2, 3). Besides, a characteristic feature of the early Assikaevka FA is joint occurrence of relict taxa and species of the Aptian origin, while younger advanced species of genera *Arctopteris*, *Osmunda*, *Anemia*, *Taxites* (*Cephalotaxopsis*), and *Sequoia* are more abundant among ferns and conifers of the late Lipovtsy FA. Species in common for the late Staryi Suchan and early Assikaevka assemblages are *Equisetum* cf. *ramosus* Samyl., *Onychiopsis psilotoides* (St. et W.) Ward, *Polypodites verestchaginii* Krassil., *Cladophlebis frigida* (Heer) Sew., *Pterophyllum sutschanense* Pryn., *Nilssonina ex gr. orientalis* Heer, *N. ex gr. brongniartii* (Mant.) Dunk., *Elatides asiatica* (Yok.) Krassil., and *Athrotaxites berryi* Bell. However, dominant plant groups in these two assemblages are different: these are cycadophytes and ferns of the early Assikaevka FA in contrast to ferns and conifers of the late Staryi Suchan FA (Figs. 2, 4). Percentage of “young” evolutionary advanced taxa is insignificant in both assemblages. These are *Anemia dicksoniana* and *Sequoia reichenbachii* in the late Staryi Suchan FA and *Birisia onychioides* in the early Assikaevka FA.

<sup>1</sup> Figures 2, 3, and 4 referred to in this work are published in my earlier work: “The Aptian–Cenomanian Flora of Primor’e, Part 1: Floral Assemblages.”

## Correlated Aptian–Cenomanian floral assemblages of Primor'ĕ

Stage	Substage	Depression																						
		Alchan				Partizanskaya			Razdol'naya															
		Formation (sequence)	Subformation (member)	Assemblage	Subassemblage	Formation	Assemblage	Subassemblage	Formation	Assemblage														
Cenomanian	upper	Stolbovaya	upper	Stolbovaya			Dadan-shan	Dadan-shan																
	lower		lower				Brovnichi	Brovnichi																
Albian	upper	Alchan	upper	late Alchan	late		Romano-vka	Romano-vka																
							Brovnichi	Brovnichi																
							Kangauz	Kangauz																
							Frentsevo	Frentsevo			late	early	middle	early	late	middle	early	late						
																			Korkino Group (undivided)	Korkino Group (undivided)				
																					early Korkino	early Korkino		
	middle	Alchan	Alchan	lower	early Alchan	early	middle	Frentsevo	Frentsevo	early	late													
												Korkino Group (undivided)	Korkino Group (undivided)											
														late Galenki	late Galenki									
												lower	Assikaevka	Assikaevka	upper	late Assikaevka	early	late	Severnyi Suchan	late Severnyi Suchan	early	late		
																							Korkino Group (undivided)	Korkino Group (undivided)
upper	Assikaevka	Assikaevka	middle	late Assikaevka	early	late	Severnyi Suchan	late Severnyi Suchan	early	late														
											Korkino Group (undivided)												Korkino Group (undivided)	
																								early Galenki
											lower	Assikaevka	Assikaevka	lower	early Alchan	early	middle	Frentsevo	Frentsevo	early	late			
																						Korkino Group (undivided)	Korkino Group (undivided)	
																								late Galenki
Aptian	lower	Assikaevka	lower	early Assikaevka	early	late	Severnyi Suchan	late Severnyi Suchan	early	late														
																						Korkino Group (undivided)	Korkino Group (undivided)	
																								early Lipovtsy
											upper	lower	Assikaevka	upper	late Assikaevka	early	late	Severnyi Suchan	late Severnyi Suchan	early	late			
																						Korkino Group (undivided)	Korkino Group (undivided)	
																								late Lipovtsy
lower	upper	Assikaevka	lower	early Assikaevka	early	late	Severnyi Suchan	late Severnyi Suchan	early	late														
																						Korkino Group (undivided)	Korkino Group (undivided)	
																								late Lipovtsy
											upper	lower	Assikaevka	upper	late Assikaevka	early	late	Severnyi Suchan	late Severnyi Suchan	early	late			
																						Korkino Group (undivided)	Korkino Group (undivided)	
																								late Lipovtsy
lower	upper	Assikaevka	lower	early Assikaevka	early	late	Severnyi Suchan	late Severnyi Suchan	early	late														
																						Korkino Group (undivided)	Korkino Group (undivided)	
																								late Lipovtsy
											upper	lower	Assikaevka	upper	late Assikaevka	early	late	Severnyi Suchan	late Severnyi Suchan	early	late			
																						Korkino Group (undivided)	Korkino Group (undivided)	
																								late Lipovtsy
lower	upper	Assikaevka	lower	early Assikaevka	early	late	Severnyi Suchan	late Severnyi Suchan	early	late														
																						Korkino Group (undivided)	Korkino Group (undivided)	
																								late Lipovtsy
											upper	lower	Assikaevka	upper	late Assikaevka	early	late	Severnyi Suchan	late Severnyi Suchan	early	late			
																						Korkino Group (undivided)	Korkino Group (undivided)	
																								late Lipovtsy

The early subassemblage of the early Assikaevka FA is comparable in taxonomic composition with the early Severnyi Suchan and early Galenki FAs. Species in common for this subassemblage and early Galenki FA are *Onychiopsis psilotoides* (St. et W.) Ward, *Birisia onychioides* (Vassilevsk. et K.-M.) Samyl., *Dicksonia concinna* Heer, *Cladophlebis frigida* (Heer) Sew., *Nilssonsonia* ex gr. *brongniartii* (Mant.) Dunk., and *Elatides asiatica* (Yok.) Krassil. However, the early Galenki FA includes a group of evolutionary advanced species *Birisia onychioides*, *Anemia dicksoniana* (Heer) Krassil., *A. asiatica* Vachr., *Teihardia tenella* (Pryn.) Krassil., *Leptopterophyllum pterophylloides* (Pryn.) Krassil., *Ginkgo pluripartita* (Schimp.) Heer, *Dictyozamites cordatus* (Krysh.) Pryn., *Nilssonsonia densinervis* (Font.) Berry, *Podozamites tenuinervis* Heer, and *Torreyites dicksonioides* (Daws.) Bell. Only two representatives of this group (*Birisia onychioides* and *Torreyites dicksonioides*) are present in the early subassemblage of the early Assikaevka FA, although dominants and subdominants of two floras under comparison are similar. In both, these are ferns (47.1% of the subassemblage under consideration and 30% of the early Galenki FA) and cycadophytes (23.5 and 30% respectively). However, conifers are relatively more abundant in the former (17.6%) than in the latter (13.5%). In addition, the early Galenki FA includes Ginkgoales (10%) and lycophytes (10%), which have not been encountered in the early subassemblage of the early Assikaevka FA (Figs. 2, 3). Species in common for this subassemblage and early Severnyi Suchan FA are *Gleichenites porsildii* Sew., *Onychiopsis psilotoides* (St. et W.) Ward, *Birisia onychioides* (Vassilevsk. et K.-M.) Samyl., *Dicksonia concinna* Heer, *Cladophlebis frigida* (Heer) Sew., *Nilssonsonia* ex gr. *brongniartii* (Mant.) Dunk., *Ginkgo* ex gr. *adiantoides* (Ung.) Heer, *Podozamites* ex gr. *lanceolatus* (L. et H.) Schimp., *Elatides asiatica* (Yok.) Krassil., and *Athrotaxopsis expansa* Font, emend. Berry. Ferns are dominants of both floras containing different subdominants: cycadophytes in the early subassemblage of the early Assikaevka FA and conifers in the early Severnyi Suchan FA (Figs. 2, 4). Characteristic of the latter is also a considerable proportion of evolutionary advanced species representing genera *Osmunda*, *Anemia*, *Birisia* (*B. alata*), *Coniopteris* (*C. asplenoides*), *Nilssonsonia* (*N. canadensis*), and *Taxites*.

The late subassemblage of the late Assikaevka FA is correlative with the middle Galenki and late Severnyi Suchan FAs. Species in common for the subassemblage and middle Galenki FA are *Anemia dicksoniana* (Heer) Krassil., *Ruffordia goeppertii* (Dunk.) Sew., *Adiantopteris yuasensis* (Yabe) Krassil., *Birisia onychioides* (Vassilevsk. et K.-M.) Samyl., *B. alata* (Pryn.) Samyl., *Dicksonia concinna* Heer, *Onychiopsis psilotoides* (St. et W.) Ward, *Arctopteris* cf. *kolymensis* Samyl., *Lobifolia novopokrovskii* (Pryn.) Rasskaz. et E. Lebed., *Cladophlebis frigida* (Heer) Sew., *C. opposita* Pryn., *Nilssonsonia* ex gr. *brongniartii* (Mant.) Dunk., *Podozamites* ex gr. *lanceolatus* (L. et H.) Schimp., *Tax-*

*ites brevifolius* (Font.) Samyl., *Elatides asiatica* (Yok.) Krassil., *Sequoia reichenbachii* (Gein.) Heer, and *Athrotaxites berryi* Bell. Taxonomic composition of angiosperm genera *Sapindopsis*, *Laurophyllum*, *Dicotylophyllum*, *Nyssidium*, and *Onoana* is also similar. However, ancient Pinaceae (*Pityophyllum* ex gr. *nordenskioldii* Heer), Podocarpaceae, and Podozamitaceae (especially *Podozamites tenuinervis* Heer) are quite abundant in the middle Galenki FA containing a few Taxodiaceae (*Athrotaxites berryi* and *Sequoia reichenbachii*), whereas the last family is well represented in the late subassemblage of the late Assikaevka FA. Besides, Pinaceae and Podozamitaceae are insignificant components of this subassemblage lacking Podocarpaceae. Dominant ferns and subdominant conifers are characteristic of both floras under comparison (Figs. 2, 3). Like the late Severnyi Suchan FA, the subassemblage contains the following species: *Osmunda denticulata* Samyl., *Ruffordia goeppertii* (Dunk.) Sew., *Anemia dicksoniana* (Heer) Krassil., *Gleichenites porsildii* Sew., *Alsophilites nipponensis* (Oishi) Krassil., *Dicksonia concinna* Heer, *Birisia onychioides* (Vassilevsk. et K.-M.) Samyl., *Lobifolia novopokrovskii* (Pryn.) Rasskaz. et E. Lebed., *Cladophlebis frigida* (Heer) Sew., *Nilssonsonia* ex gr. *brongniartii* (Mant.) Dunk., *Ginkgo* ex gr. *adiantoides* (Ung.) Heer, *Podozamites* ex gr. *lanceolatus* (L. et H.) Schimp., *Taxites brevifolius* (Font.) Samyl., *Elatides asiatica* (Yok.) Krassil., *Sequoia reichenbachii* (Gein.) Heer, *Athrotaxites berryi* Bell, and representatives of the genus *Dicotylophyllum*. Ferns and conifers dominant in both floras are associated with cycadophytes and early flowering plants (Figs. 2, 4).

According to taxonomic composition and proportions of main plant groups, the early Alchan FA is similar to the early subassemblage of the Frentsevo FA. Their species in common are *Osmunda denticulata* Samyl., *Ruffordia* ex gr. *goeppertii* (Dunk.) Sew., *Anemia dicksoniana* (Heer) Krassil., *Birisia onychioides* (Vassilevsk. et K.-M.) Samyl., *Onychiopsis psilotoides* (St. et W.) Ward, *Cladophlebis frigida* (Heer) Sew., *Pterophyllum sutschanense* Pryn., *Nilssonsonia densinervis* (Font.) Berry, *N.* ex gr. *orientalis* Heer, *Podozamites* ex gr. *lanceolatus* (L. et H.) Schimp., *Elatides asiatica* (Yok.) Krassil., *Sequoia reichenbachii* (Gein.) Heer, *S. ambigua* Heer, *Athrotaxites berryi* Bell, and *Athrotaxopsis expansa* Font. emend. Berry. Both floras are dominated by ferns (37.5 and 39.1% respectively) and conifers (27.5 and 28.3%), being free of flowering plants (Figs. 2, 4).

The early subassemblage of the late Alchan FA is very close in composition to the early subassemblage of the Frentsevo FA. They both contain fern species *Osmunda denticulata* Samyl., *Birisia onychioides* (Vassilevsk. et K.-M.) Samyl., *Onychiopsis psilotoides* (St. et W.) Ward, *Teihardia tenella* (Pryn.) Krassil.) and conifers *Podozamites tenuinervis* Heer, *Sequoia reichenbachii* (Gein.) Heer, *Elatides asiatica* (Yok.) Krassil., *Athrotaxopsis expansa* Font, emend. Berry,

and *Brachyphyllum* ex gr. *obesum* Heer. Associated angiosperms represent genera *Sapindopsis*, *Araliaephyllum*, *Laurophyllum*, *Sassafras*, and *Dicotylophyllum*. Ferns are dominants, conifers subdominants, and angiosperms subordinate components (Figs. 2, 3). Distinctions are insignificant: the subassemblage of the late Frentsevo FA is lacking Caytoniales, cycadophytes, Czekanowskiales and contains rare Ginkgoales, while the latter are missed from the early subassemblage of the late Alchan FA containing rare cycadophytes.

The late Galenki FA is similar in taxonomic composition to early and middle subassemblages of the late Alchan FA. In this case, species in common are *Osmunda denticulata* Samyl., *Ruffordia* ex gr. *goeppertii* (Dunk.) Sew., *Anemia dicksoniana* (Heer) Krassil., *Gleichenites porsildii* Sew., *Dicksonia concinna* Heer, *Birisia oerstedtii* (Heer) E. Lebed., *Coniopteris asplenoides* Kiritchk., *Onychiopsis psilotoides* (St. et W.) Ward, *Arctopteris kolymensis* Samyl., *Eogymnocarpium* aff. *sinensis* Li et Yeh, *Eogymnocarpium* sp. Ç., *Teihardia tenella* (Pryn.) Krassil., *Cladophlebis frigida* (Heer) Sew., *Caytonia orientalis* Krassil., *Sagenopteris variabilis* (Velen.) Velen., *Neozamites verchojanensis* Vachr., *Pterophyllum sutschanense* Pryn., *P. burejense* Pryn., *Nilssonia* ex gr. *orientalis* Heer, *N. canadensis* Bell, *N. mediana* (Leek ex Bean MS) Fox-Strang., *N.* ex gr. *brongniartii* (Mant.) Dunk., *Ginkgo pluripartita* (Schimp.) Heer, *G.* ex gr. *adiantoides* (Ung.) Heer, *Podozamites* ex gr. *lanceolatus* (L. et H.) Schimp., *P. tenuinervis* Heer, *Pytrolepis* sp. 1, *Taxites brevifolius* (Font.) Samyl., *T. acuminatus* (Krysht. et Pryn.) Volynets, *Elatides asiatica* (Yok.) Krassil., *Sequoia reichenbachii* (Gein.) Heer, *Athrotaxites berryi* Bell, *Athrotaxopsis expansa* Font, emend Berry, and angiosperms of genera *Sapindopsis*, *Araliaephyllum*, and *Laurophyllum*. Dominant plants are ferns. It is necessary to note that specific components encountered in the middle subassemblage of the late Alchan FA are dolioform stems *Cycadeoidea bikinensis* Krassil. and leaves *Zamiophyllum ivanovii* (Krysht. et Pryn.) Krassil., which are missed in the late Galenki FA containing instead leaves *Encephalartopsis vachrameevii* Volynets sp. nov. and “false stems” of fern species *Tempskya* sp. The other distinctions are as follows: angiosperms are subdominants of the subassemblage dominated by ferns and conifers, whereas subdominants of the late Galenki FA are cycadophytes, while flowering plants are of insignificant abundance (3.5%) in this case (Figs. 2, 3).

The middle subassemblage of the late Alchan FA is most similar in composition to the Kangauz FA. They both contain *Onychiopsis psilotoides* (St. et W.) Ward, *Anemia dicksoniana* (Heer) Krassil., *Birisia alata* (Pryn.) Samyl., *B. onychioides* (Vassilevsk. et K.-M.) Samyl., *Gleichenites porsildii* Sew., *Onychiopsis psilotoides* (St. et W.) Ward, *Teihardia tenella* (Pryn.) Krassil., *Podozamites tenuinervis* Heer, *P.* ex gr. *lanceolatus* (L. et H.) Schimp., *Elatides asiatica* (Yok.) Krassil.,

*Sequoia reichenbachii* (Gein.) Heer, *S. ambigua* Heer, *Athrotaxites berryi* Bell, *Sapindopsis variabilis* (Font.) Berry, *S. brevifolia* Font., *Sassafras* aff. *ussuriensis* Krassil., and representatives of genera *Marchantites*, *Isoetites*, *Lycopodites*, *Equisetum*, *Osmunda*, *Anemia*, *Coniopteris*, *Sagenopteris*, *Dictyozamites*, *Pagiophyllum*, *Pityostrobus*, *Sequoia*, *Sphenolepis*, *Vitiphyllum*, *Celastrorhynchium*, and *Kenella*. Dominant in the Kangauz FA are ferns and conifers constantly occurring in association with flowering plants. However, this assemblage is four times less diverse than the subassemblage under comparison, because it is lacking Ginkgoales and Czekanowskiales, and its cycadophytes are represented by the genus *Dictyozamites* only (Figs. 2, 4).

The late subassemblage of the late Alchan FA is correlative with the early Korkino, Romanovka, and Brovnichi FAs. Species in common with the early Korkino FA are *Anemia dicksoniana* (Heer) Krassil., *Coniopteris* ex gr. *arctica* (Pryn.) Samyl., *Onychiopsis psilotoides* (St. et W.) Ward., *Pityophyllum* ex gr. *nordenskioldii* Heer., *Elatides asiatica* (Yok.) Krassil., and *Dicotylophyllum* forms representing flowering plants. Distinctions: xerophytes of the genus *Otozamites*, which are rather abundant in the subassemblage, have not been encountered in the early Korkino FA that is also lacking Sphenobaieraceae, Czekanowskiales, and Pseudotorelliaceae. Besides, typical of the late subassemblage of the late Alchan FA are dominant angiosperms, subdominant conifers, and quite abundant cycadophytes and Czekanowskiales, whereas dominant ferns and subdominant conifers of the early Korkino FA coexist with rare specimens of flowering plants (Figs. 2, 3). The subassemblage contains species *Onychiopsis psilotoides* (St. et W.) Ward that is also characteristic of the Romanovka FA showing in distinction a considerable proportion of xerophytes from the genus *Otozamites* and lacking Sphenobaieraceae, Czekanowskiales, and Pseudotorelliaceae. Percentages of principal plant groups are also different: ferns, cycadophytes, and conifers are equally abundant in the Romanovka FA (23.1% per each group) containing 15.3% of angiosperms, whereas the late subassemblage of the late Alchan FA is dominated by angiosperms occurring in association with subdominant conifers and subordinate cycadophytes and Czekanowskiales (Figs. 2, 4).

Xerophytes of the genus *Otozamites*, ferns *Anemia dicksoniana* (Heer) Krassil., conifers representing genera *Athrotaxopsis*, *Elatocladus*, *Taxites*, *Pityophyllum*, and flowering *Araliaephyllum* forms are taxa in common for the Brovnichi FA and late subassemblage of the late Alchan FA. The Brovnichi FA lacking Sphenobaieraceae, Czekanowskiales, and Pseudotorelliaceae (Figs. 2, 4) contains however the more diverse flowering plants, species *Araliaephyllum obtusilobum* Font. and *Cercidiphyllum* aff. *sachalinensis* Krysht. included.

The Stolbovaya and Dadanshan FAs comparable in taxonomic composition are dominated by angiosperms, especially by broad-leaved Platanaceae. Their taxa in common are *Anemia dicksoniana* (Heer) Krassil., *Toreyites* cf. *dicksonioides* (Daws.) Bell, *Sequoia reichenbachii* (Gein.) Heer, and species of genera *Gleichenites*, *Cladophlebis*, *Ginkgo*, *Podozamites*, *Taxites*, *Brachyphyllum*, *Elatocladus*, *Magnolia*, *Cissites*, *Araliaephyllum*, and *Menispermites*. Proportions of main plant groups (dominant angiosperms, subdominant conifers, associated ferns) are also similar. A distinctive feature is absence of cycadophytes in the Dadanshan FA (Figs. 2, 4).

### CONCLUSIONS

(1) Taxonomic composition of plant remains from Aptian–Cenomanian deposits is studied in detail. In the Alchan depression, they are divided into five floral assemblages. These are the early and late Assikaevka assemblages, the latter consisting of two subassemblages, the early and late Alchan assemblages each consisting of three subassemblages, and Stolbovaya assemblage. The early and late Lipovtsy, early, middle and late Galenki, and early Korkino assemblages characterize fossil plants of the Razdol'naya depression. Eight assemblages of the Partizanskaya depression correspond to the late Saryi Suchan, early and late Severnyi Suchan, Frentsevo (two subassemblages), Kangauz, Romanovka, Brovnichi, and Dadanshan floras (the table).

(2) The distinguished floral assemblages (FAs) are correlated, and their ages are established more precisely. The FAs of the Alchan depression, which occur in association with fossil fauna, are regarded as reference standards. As is established, the assemblages correspond in age to the following chronostratigraphic intervals: the early Assikaevka and early Lipovtsy FAs to the early Aptian; the late Lipovtsy and late Saryi Suchan FAs to the late Aptian–initial early Albian; the early subassemblage of the late Assikaevka FA, early Galenki and early Severnyi Suchan FAs to the terminal early Albian; the late subassemblage of the late Assikaevka FA, middle Galenki and late Severnyi Suchan FAs to the initial middle Albian; the early Alchan FA and early subassemblage of the Frentsevo FA to the terminal middle Albian; the early subassemblage of the late Alchan FA and late subassemblage of the Frentsevo FA to the initial late Albian; the middle subassemblage

of the late Alchan FA, late Galenki and Kangauz FAs to the middle late Albian; the late subassemblage of the late Alchan FA, early Korkino and Romanovka FAs to the terminal late Albian; the Brovnichi FA to the terminal late Albian–early Cenomanian; the Stolbovaya and Dadanshan FAs to the late Cenomanian.

(3) Ages of local stratigraphic units are tuned to new phytostratigraphic data. The Assikaevka Formation is of the Aptian–initial middle Albian age, the Alchan Formation of the terminal middle–late Albian age, and the Stolbovaya Formation of the Cenomanian age. The Lipovtsy Formation is correlated with the Aptian–lowermost Albian, the Galenki Formation with the uppermost lower and mid-upper Albian, while the undivided Korkino Group is attributed to the uppermost Albian–Cenomanian. An upper part of the Saryi Suchan Formation is dated back to the Aptian–earliest Albian, the Severnyi Suchan Formation to the early–initial middle Albian, and the Frentsevo Formation to the terminal middle–initial late Albian. The Kangauz and Romanovka formations span intervals of the middle and terminal upper Albian respectively. The Brovnichi Formation is of the terminal late Albian–early Cenomanian age, and the Dadanshan Formation corresponds in age to the late Cenomanian.

(4) Fossil plants from undivided deposits of the Korkino Group, the Razdol'naya depression, are studied for the first time. As is established in the Tret'ya Kamenka River basin, flora containing *Aralia lucifera* (Krishtofovich, 1929; Krassilov, 1967) is from the Kangauz Formation.

Description of two new species is presented below along with emended characterization of one taxon.

### FAMILY PTERIDACEAE

#### Genus *Adiantopteris* Vassilevskaja, 1963

*Adiantopteris grandis* Vachrameev emend. Volynets, emend. nov.

Plate I, figs. 1–4, 6

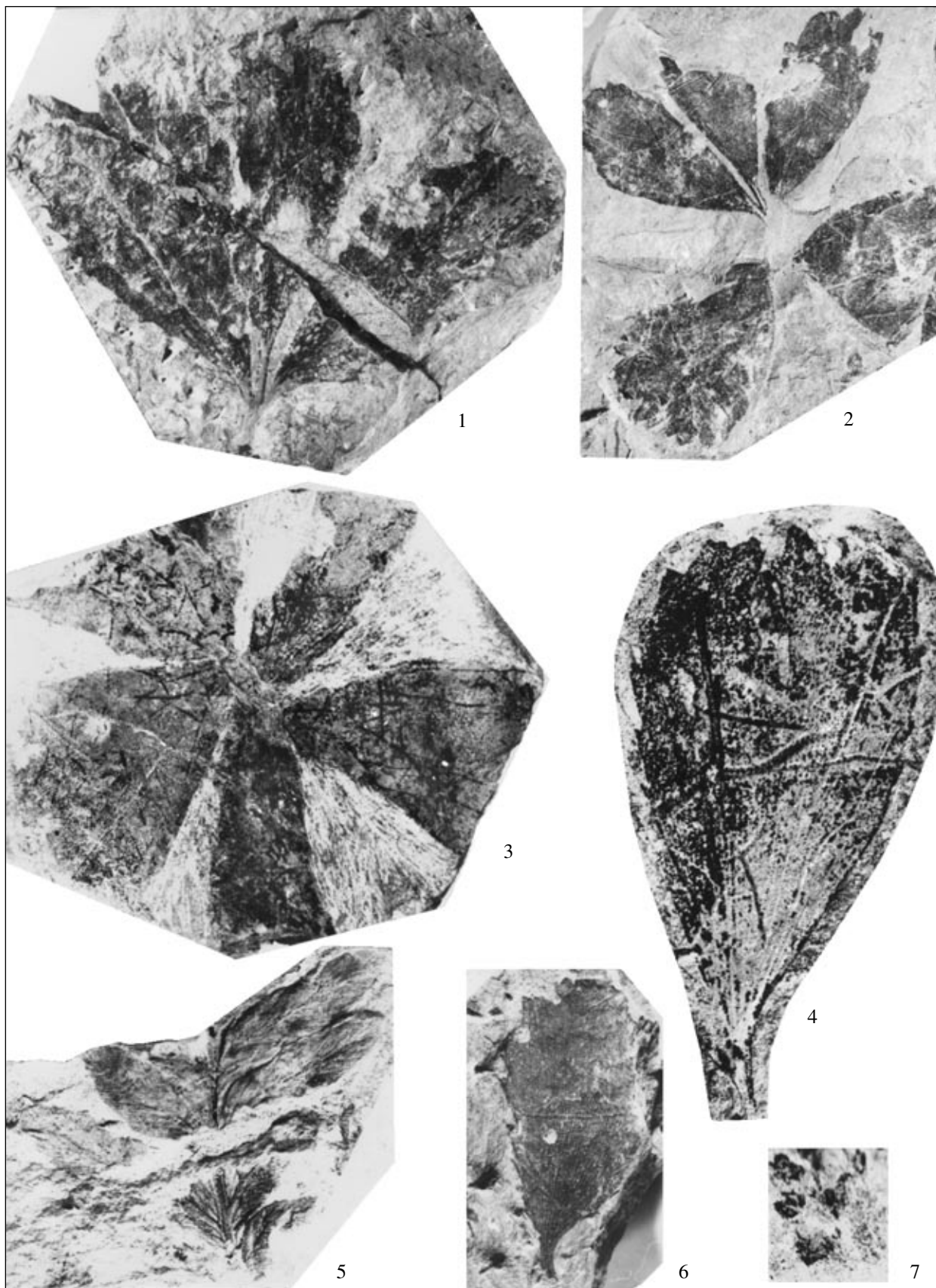
*Adiantopteris grandis*: Vachrameev, 1968, Plate IV, figs. 2–4

**Holotype:** collection GIN RAS, no. 417-2.

**Topotype:** IBSS FED RAS, no. 41/1 (Plate 1, fig. 1), southwestern Primor'e, Bolotnyi Creek, Barabashevka River basin; Lower Cretaceous, Galenki Formation.

#### Plate I. Leaf impressions of Albian ferns from Primor'e:

(1–4, 6) *Adiantopteris grandis* Vachrameev emend. Volynets, emend. nov. (Barabashevka River basin, Bolotnyi Creek): (1) topotype, flabellate pinna, specimen IBSS no. 41/1; (2, 3) umbellate (?) shape of leaves, specimen IBSS nos. 41/2 (2), specimen IBSS no. 41/3; (4, 6) individual pinnules with details of venation and crenate margins, (4) specimen IBSS no. 41/4 (×1.5), (6) specimen IBSS no. 41/5. (5, 7) *Anemia sutschanica* Volynets sp. nov. (Partizanskaya River basin, Olenii–Ostrosopkovyi interfluvium): (5) a fragment of the leaf lower part with details of venation, specimen IBSS no. 60/10 (×1.5); (7) a fragment of sporiferous, specimen IBSS no. 60/11 (×10).



**Emended diagnosis.** Leaves of umbellate form (?) and radial attachment. Pinnules are flabellate, 35–70 mm long and 25–50 mm wide. Pinnules have aculeate-dentate lateral margins and composite-dentate upper margin. Acropetal venation is of flabellate-dichotomous type: initial vein taking origin at petiole base branches into three veins, two marginal and one intermediate.

**Description.** The collection includes one impression of bipinnate umbellate (?) leaf (Plate I, figs. 2, 3). Two flabellate pinnae of the leaf consist in turn of three ovate or obovate pinnules. The main rachis of pinna is of unknown thickness. In pinnules, rachis is straight and broad (up to 2 mm), having median sulcus. Rachis of lateral pinnules is 5 to 10 mm long. In each group of three pinnules, the lateral ones are oriented under angle of 40–50° relative to the rachis and the median pinnules under angle 90°. Lateral margins of pinnules are aculeate-dentate in basal part, acutidentate in the middle, and composite-dentate in the upper one. First denticles with one vein entering them appear 5 mm above the pinnule base (Plate I, figs. 4, 6). Aculeate denticles are visible not everywhere, because lateral margins of pinnules are plunged into the rock or overlapped by adjoining pinnules. Near the upper margin, one vein enters each denticle and two or three veins approach saddle in between, whereas saddles near the pinnule base are lacking veins. The pinnules base is laticuneate. Petioles are 5 to 15 mm long and up to 2 mm thick. Initial vein taking origin at the petiole base divides into three veins. Multiply dichotomizing, two lateral veins create main venation patterns in pinnules, while the medial one tends upward dichotomizing rarely near the upper margin (Plate I, fig. 4). Venation is of flabellate type with 10 veins per 5 mm of the pinnules width in the lower part and 14–15 veins in the upper one. Sporulation is unknown.

**Comparison.** In distinction from close *Adiantopteris sewardii* (Yabe) Vassilevskaja, the described species has larger umbellate leaves with pinnules of the other laticuneate shape, which have dentate lateral margins and more complicated venation.

**Distribution:** Lower Cretaceous (Albian, Galenki Formation), the Razdol'naya depression.

**Material:** 32 samples, no. 41 (specimens 41/1–41/32), upper reaches of the Bolotnyi Creek, left bank, Barabashevka River basin, southwestern Primor'e.

## FAMILY SCHIZAEACEAE

### Genus *Anemia* Swartz, 1806

*Anemia sutschanica* Volynets, sp. nov.

Plate I, figs. 5, 7; Plate II, figs. 1–8, Plate III, fig. 2

**Holotype:** IBSS FED RAS, nos. 60/1, 60/2 (Plate II, fig. 1; Plate III, fig. 2); Olenii Creek in middle courses of the Partizanskaya River, southeastern Primor'e; Lower Cretaceous, Severnyi Suchan Formation.

**Diagnosis.** Bipinnate leaves have winged rachis rounded, straight, about 3 mm thick, with a long furrow in the middle. Intermediate triangular pinnules are attached to the pinna rachis. Alternate linear-lanceolate pinnae narrowing gradually toward the apex are attached to the rachis under angle of 45°. Pinnules are predominantly opposite or intimate-opposite, asymmetrical, with *Eboracia*-type venation and occasional anastomosis near the rachis and midrib. The midrib in pinnules is normal. The fertile pinnae are strongly reduced. Sources are confined to apical veins of pinnules.

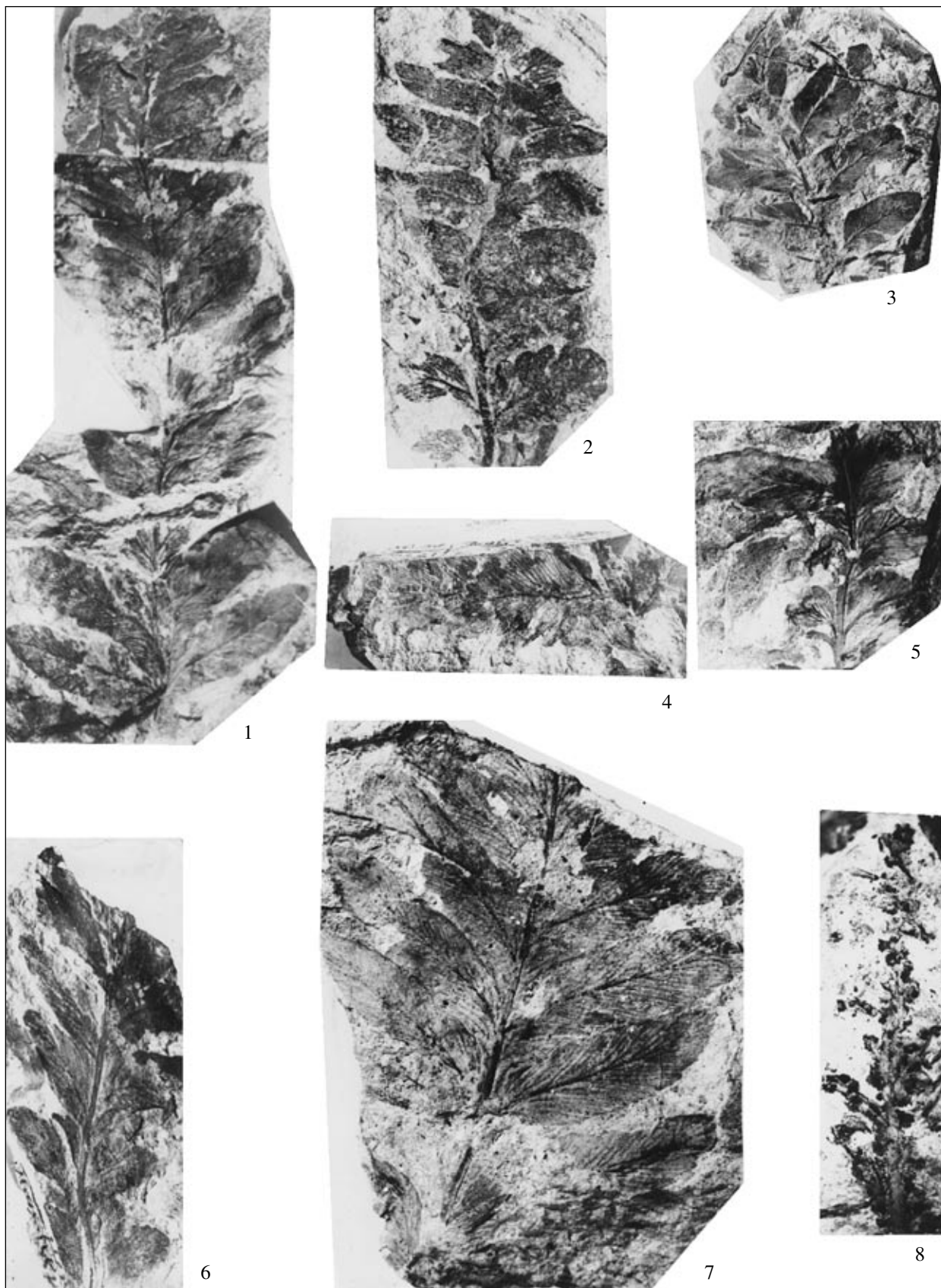
**Description.** The collection studied includes more than 50 leaf specimens. Leaves are large, bipinnate (?). They have thick (3 mm) winged round and straight rachis with axial furrow. Intermediate triangular pinnules are attached to the pinna rachis (Plate II, fig. 5). Alternate or intimate-alternate linear-lanceolate pinnae are oriented relative to the rachis under angle of 45°. Pinnae are 8–19 cm long and 2–12 cm wide. Their size is depending on position at the rachis: they are longer and wider in the lower part of leaves than in the middle and near the top. Pinnules are linear, broad-lanceolate to triangular, attached to the rachis in the opposite (Plate II, figs. 2, 5, 7) or intimate-opposite manner (Plate II, figs. 1, 3, 6; Plate III, fig. 2) under angles of 35 to 40°. In the upper part of pinna, pinnules are attached to the rachis with their entire base and have broad rounded apices (Plate II, figs. 3, 6). Pinnule margins are denticulate (serrate). Denticles 1 mm long and 2 mm wide have straight lateral sides and acute apices. They are divided by acute-angled saddles. In many impressions, pinnule margins are invisible being concealed in the rock, folded inside or overlapped by neighboring pinnules.

The imperfect venation resembles that of *Eboracia* leaves. The midrib straight or slightly sinuous enters pinnules under acute angle close to basisopic margin and, bending to the median position, dichotomizes 3 to 7 times near the tip (Plate I, fig. 5; Plate II, figs. 4, 7).

#### Plate II. Leaf impressions of Albian ferns from Primor'e:

(1–8) *Anemia sutschanica* Volynets sp. nov. (Partizanskaya River basin, Olenii–Ostrosopkovyi interfluvium): (1) holotype, specimen IBSS no. 60/1; (2) a middle part of pinna illustrating shape of pinnules, their attachment mode, and details of venation, specimen IBSS no. 60/2 (×1,5); (3) an upper part of pinna with visible venation patterns, specimen IBSS no. 60/3; (4) an isolated pinnule in the leaf middle part illustrating dichotomizing veinlets and their anastomosis near the midrib, specimen IBSS no. 60/4 (×1,5); (5) a lower fragment of pinna, specimen IBSS no. 60/5; (6) an upper fragment of pinna, specimen IBSS no. 60/6 (×2); (7) a middle part of pinna with crenate margins and venation in pinnules with anastomosis near the midrib, specimen IBSS no. 60/7 (×2); (8) a fragment of sporiferous pinna, specimen IBSS no. 60/8 (2).

Plate II





Basal lateral veinlets (1 to 5) of catadromous row deviate under acute angle directly from the pinna rachis, dichotomize 1–3 times, and bend downward to the pinnules margin (Plate II, figs. 1, 7). Near the midrib of some pinnules, there is visible anastomosis (Plate I, fig. 5; Plate II, figs. 1, 3, 4, 6). In the well-developed pinnules, individualized basal veins are close in rank to the midrib, and their bifurcating veinlets form a network in the winged rachis and basal areas of pinnules (Plate I, fig. 5, Plate II, fig. 1). The basal vein of anadromous row takes origin at the pinnule rachis and dichotomizes 2 to 6 times. Some lateral veins situated near the rachis are interconnected due to anastomosis. Anastomosing veins form quadrilateral cells of irregular shape and size (Plate II, figs. 4, 7).

Sporiferous pinnae are strongly reduced (Plate II, fig. 8; Plate III, fig. 2). The leaf axis straight and firm bears the alternate or approximate-alternate pinnae deviating under angles 40 to 45°. Linear-lanceolate pinnae 60 × 20 mm in size are gradually narrowing toward the tip. Their firm rachises bear 14 to 16 pairs of pinnules oriented under angle of 40°. Numerous sporangia are glabrate, situated on both sides of terminal veins (Plate I, fig. 7). Structures of soruses and some sporangia are poorly preserved. Colorless trilete spores extracted from sporangia by chemical treatment underwent a quick decay. In opinion of V.S. Markevich, the extracted spores belong to the genus *Anemia*, family Schizaeaceae.

**Comparison.** The described species is similar to *A. asiatica* Vachr. (Vakhameev, 1959) in the attachment mode of middle and terminal pinnae. Characteristic of both species are also the common type of venation inside pinnules and presence of intermediate pinnules attached to the leaf rachis. However, pinnules of the new species are shorter (up to 50 mm) and broader near the tip, and besides it has fertile pinnae.

The species under consideration is also close to *A. dicksoniana* (Heer) Krassil. (Krassilov, 1979) in the shape of sporiferous leaves, which have similar disposition and structure of soruses and sporangia. In addition, sterile leaves of both species are tri- or bipinnate, have winged rachis, and show catadromous arrangement of asymmetric pinnae with *Eboracia*-type venation. They differ from each other in leaf dimensions, amount of pinnules attached to the rachis, and in venation patterns within basicopic part.

**Distribution:** Primor'e, Lower Cretaceous, Severnyi Suchan and Frentsevo formations of the Partizanskaya basin and eastern coast of the Ussuriiskii Bay.

**Material:** specimens 60/1–60/62 from a bedrock outcrop in the Olenii–Ostrosopkovskii interfluve, middle courses of the Partizanskaya River, Severnyi Suchan Formation.

## CYCADOPHYTES OF THE ORDER CYCADALES

### Genus *Encephalartopsis* Fontaine, 1899

*Encephalartopsis vachrameevii* Volynets, sp. nov.

Plate III, figs. 1, 3, 4

*Sphenozamites* sp.: Krassilov, 1967, p. 152, Plate XLIII, figs. 4, 5.

The species is named in honor of paleobotanist V.A. Vakhrameev.

**Holotype:** IBSS FED RAS, no. T.B. 18/1 (Plate III, fig. 1); Primorskii krai, Lake Khanka; Lower Cretaceous, Albian, Galenki Formation.

**Diagnosis.** Pinnate leaves with oblong oblanceolate leaflets having horny cuneate base are attached to the apical surface of the rounded axis with linear midrib. The leaflet margins are composite-dentate. Marginal denticles are widely spaced, acuminate or attenuate, and aculeate at the tip. The dichotomous venation includes single areas of anastomosis. Veins are distinct, ending mostly in denticles and dens. The epidermis structure is unknown.

**Description.** In the studied collection, there are 10 leaf impressions and over 20 leaflet impressions. Holotype corresponds to a distal part of leaf 100 mm long and up to 100 mm wide. Round rachis is straight, 1.5 to 2.5 mm thick, having distinct axial furrow. Lateral leaflets are oblong, oblanceolate-taeniate, with a narrow sphenoid base grading into callus. They are attached to the upper part of rachis. Phylotaxis is pairwise-intimate in lower and middle parts of the leaf and opposite in the distal one. The leaflet–rachis angles range from 90° in the lower part to 50° in the distal one. Leaflets 50 to 60 mm long are getting wider at the levels 1/5–1/6–1/10 from the base. They are from 4 to 12 mm wide depending on their position at the rachis. Narrowed tips of leaflets have four closely spaced and elongated denticles (Plate II, fig. 3). Leaflet margins are crenulate to crenate. Basicopic leaflet margins are crenate, complicated by subulate denticles in the lower part of leaf and acroscopic ones are crenulate. In the distal part of leaf, both margins are crenulate. Deflected denticles jut out for 2–4 mm above the leaflet margin. They are acuminate awl-like, irregularly spaced for 5–10 mm from each other, and not always visible, when leaflet margins are folded or concealed in the rock.

### Plate III. Leaf impressions of Albian ferns and cycadophytes from Primor'e:

(1, 3, 4) cycadophyte *Encephalartopsis vachrameevii* Volynets sp. nov. (outcrops at the southwestern coast of the Lake Khanka): (1) holotype, pinnate leaf, specimen IBSS no. T.B. 18/1; (3) a middle fragment of pinnate leaf (see holotype) illustrating the attachment mode of leaflets, their dentate tips, and details of venation, specimen IBSS no. T.B. 18/1 (×2); (4) a middle part of pinnate leaf, specimen IBSS no. T.B. 18/2; (2) *Anemia sutschanica* Volynets sp. nov. (Partizanskaya River basin, Olenii–Ostrosopkovyi interfluve), sporiferous leaf, specimen IBSS no. 60/9.

Plate III



Venation is dichotomizing, rarely anastomosing near basiscopic margins of leaflets. Veins are thick and distinct. Three veins taking origin at the basiscopic margin of leaflets form fascicles at the acroscopic, middle, and basiscopic margins of leaflets. By frequently dichotomizing venation in basiscopic area, individual veinlets enter each of the marginal denticles, being interconnected sometimes due to anastomosis. In the middle part of leaflets, where dichotomy is less frequent, venation consists of straight parallel veins. In the acroscopic margin, initial veins dichotomize first after 3 mm of its length and then after 5 mm and longer segments. All the veins have their ends in dens and denticles. From 8 to 12 veinlets have been counted per 6-mm-wide segment of a leaflet.

One more specimen (Plate III, fig. 4) characterizes a middle part of leaf, where basiscopic margins of all leaflets are crenate, and leaflets showing alternate attachment to the rachis have wider tips. Remains of cuticle have not been discovered.

**Comparison.** As compared to *Encephalartopsis nervosa* Font. (Fontaine, 1899, p. 174) from the Lower Cretaceous of North America, the described species has lesser leaflets of another shape, a lower amount of veins counted across leaflets, and anastomosing venation near the basiscopic leaflet margins only.

In distinction from *Encephalartopsis vassilevskajae* Krassil, Golov. et Nessov (Krassilov et al., 1990, p. 213), leaflets of the described species are of the other shape and size, being spaced wider at the rachis, and have lesser amount of veins taking origin at the leaflet base. Phytoleims are absent.

In comparison with *Encephalartites leihzigii* Vachr. (Vakhrameev, 1962), leaflets of the species are attached to the rachis in different way. Being of the other shape and size, they are narrower at the base, where the venation pattern is different.

**Remarks.** In the leaf morphology, the described species is close to present-day cycads of genera *Encephalartos*, *Zamia*, *Dioon*, and *Bowenia* (*The Life of Plants*, 1978, V. 4, p. 273, fig. 164). For instance, leaves of *Encephalartos*, *Dioon*, and *Bowenia* have spiniform marginal denticles. In the attachment mode of leaflets, the species is identical to *Encephalartos*, *Zamia*, and *Bowenia*, whereas leaves of *Dioon* are attached to grooves at the upper surface of rachis.

Krassilov (1967) described *Sphenozamites* sp. from the lower Cretaceous of Primor'e (Galenki Formation, Konstantinovka site), which has no principal distinctions from *Encephalartopsis vakhrameevii*. In the studied collection, there are identical or very close impressions from the Konstantinovka site, which belong most likely to the species described above.

**Distribution:** Primor'e, Lower Cretaceous, Galenki Formation.

**Material:** southern coast of the Lake Khanka, west suburb of settlement Kamen Rybolovov, Galenki For-

mation (specimens T.B.-18/1-45); Konstantinovka site, Galenki Formation (specimens T.B.-560/1-4).

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