Palynological Investigations of Miocene Deposits on the New Siberian Archipelago (U.S.S.R.)[1]

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ABSTRACT. New paleobotanical data (mainly palynological) are reported from Miocene beds of the New Siberian Islands. The palynoflora has a number of distinctive features: the presence of typical hypoarctic forms, the high content taxa representing dark coniferous assemblages and the considerable proportion of small-leaved forms. Floristic comparison with the paleofloras of the Beaufort Formation in arctic Canada allows interpretation of the evolution of the Arctic as a landscape region during Miocene-Pliocene time. This paper is a preliminary analysis of the mechanisms of arctic florogenesis. The model of an "adaptive landscape" is considered in relation to the active eustatic drying of polar shelves.

Key words: palynology, U.S.S.R., New Siberian Islands, Miocene, Arctic, florogenesis

RÉSUMÉ. On rapporte de nouvelles données paléobotaniques (principalement palynologiques) venant de couches datant du miocène situées dans l'archipel de la Nouvelle-Sibérie. La palynoflore possède un nombre de caractéristiques particulières, parmi lesquelles, la présence de formes hypoarctiques typiques, la grande quantité de taxons représentant des assemblages de conifères sombres, ainsi qu'une collection considérable de formes à petites feuilles. Une comparaison floristique avec les paléoflores de la formation de Beaufort dans l'Arctique canadien permet d'interpréter l'évolution de l'Arctique en tant que zone peuplée d'espèces végétales durant le miocène et le pliocène. Cet article est une analyse préliminaire des mécanismes de la genèse de la flore arctique. Le modèle d'un paysage adaptatif est envisagé en rapport avec l'assèchement eustatique actif des plates-formes polaires.

Mots clés: palynologie, U.R.S.S, archipel de la Nouvelle-Sibérie, miocène, Arctique, genèse de la flore

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INTRODUCTION

The late Cenozoic deposits in extreme northeast Asia and in the High Arctic are represented mainly by continental formations, and this considerably hampers correlation both between themselves and with marine deposits of adjacent areas. Because of this, investigations aimed at revealing the common character of paleogeographic environments have become especially urgent. Using paleobotanical data, much of it palynological, it is now possible to reveal phytogeographical components of paleolandscapes and, therefore, to define various landscape zones.

For such investigations, the New Siberian Archipelago is of exceptional importance. The Neogene to Quaternary Nerpichy and Kanarchak beds, which are the northernmost (about 75°N) in the east Asian sector of the Holarctic, are widespread there (Fig. 1). They may be correlated on several grounds (the most important being their phytogeographical position) with the late Cenozoic high-latitude deposits of arctic Canada such as the Beaufort Formation, which occurs from 72° to 80°N. Such correlations and generalizations seem to be the best means for understanding the general themes of florogenesis in the Arctic.

This paper deals primarily with paleobotanical analyses of late Cenozoic deposits situated on the northern coast of Faddeyev Island in the New Siberian Archipelago (Fig. 1). Faddeyev Island carries that name even though, as shown in Figure 1, it is attached by a narrow isthmus to Kotelny Island.

The deposits on Faddeyev Island were first discovered, studied and mapped in the field by Alekseyev, Borovitskaya and Chamov, researchers at the Geological Institute of the U.S.S.R. Academy of Sciences. The Nerpichy Beds were first defined by Trufanov, Belousov and Vakulenko in the course of their work on the New Siberian Islands from 1972 to 1979 (Trufanov *et al.*, 1979).

The area under investigation is part of a post-Early Cretaceous basin including New Siberia, Faddeyev and Bunge Land islands, the eastern part of Kotelny Island and the adjacent water areas (Fig. 1). The western boundary of the basin follows the fault near the Schmidt Ridge, then runs near the eastern coast of Liakhov Island and turns eastward. On the northeast, the boundary of the basin is located along the large fault within the area of weak deformation making up the Bennett massif, e.g., Bennett, Zhokhova and Vil'kitsky islands. The formation of the basin was accompanied by the extrusion of late Mesozoic to Cenozoic acidic rocks.

Palynological study of the Nerpichy Beds was carried out on samples collected near Cape Sango-Balagan and the mouth of the Kanarchak River (Fig. 1). The beds are rather widespread on the New Siberian Islands, outcropping along the northern coast of Faddeyev Island (Cape Nerpichy, the mouth of the Muorastakh River and Cape Sango-Balagan) and New Siberia Island. The same deposits are penetrated by boreholes in the north of Bunge Land and in the Ulkhan-Yuriakh River basin on Faddeyev Island. On Faddeyev Island, Nerpichy Beds unconformably overlie the Eocene Anjouan Suite. At all exposures the top of the Nerpichy sequence has an erosional unconformable contact with overlying deposits of the upper Pliocene to Pleistocene Kanarchak Beds or with middle to upper Quaternary sediments.

The author has analyzed about 40 palynological samples from four localities. Three sequences on Cape Sango-Balagan and at the mouth of the Kanarchak River (Fig. 1) are of Miocene age and one outcrop, also situated at the mouth of the Kanarchak River, is of late Pliocene to Pleistocene age (Trufanov *et al.*, 1979).

This paper deals entirely with the analysis of Miocene deposits; hence only data obtained from the study of the first three sequences are discussed. The data base comes from 25
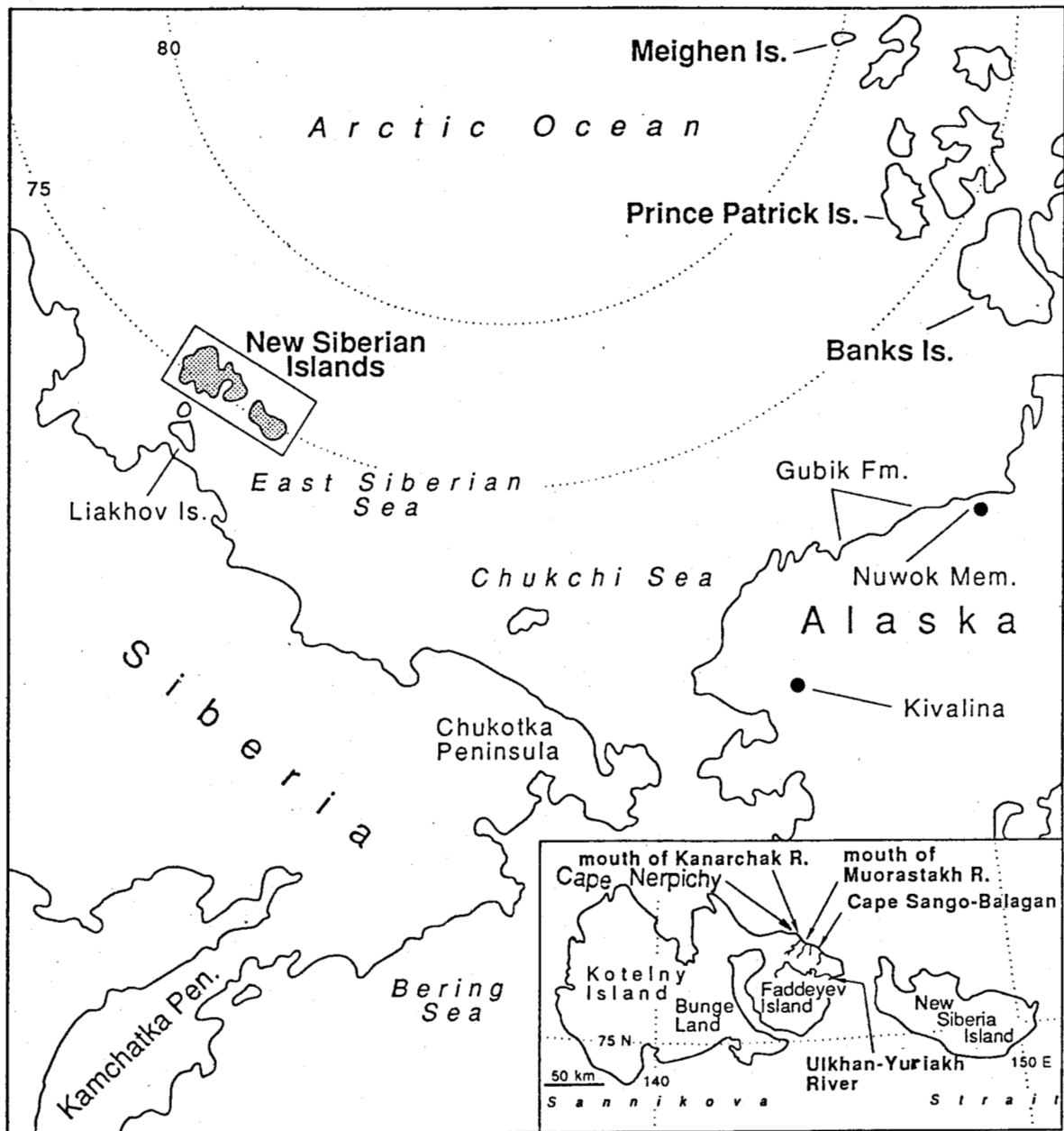
FIG. 1. Approximate distribution of late Cenozoic deposits in the High Arctic and sites on Faddeyev Island.

palynological samples, many of which contained an exceptional abundance of perfectly preserved microfossils (up to 1500 pollen grains counted per sample). In some of them, fewer pollen grains (up to 200 grains counted) were found, although they too were rather well preserved. Some samples contained so few microfossils that they could not be taken into account in the analysis of the palynoflora.

LITHOFACIES ANALYSIS

The deposits of the Nerpichy Beds are lithologically monotonous, being represented mainly by sands of various grain size with pieces of brown coal and coalified wood of autochthonous origin. There are individual units of silt and clay beds as well as small lenses and interbeds of gravel. Grain size decreases and sorting improves from poor to medium to well-sorted from the base of the sequence upward. A rhythmic sort-

ing is seen within many of the units of dipping laminae. The silty and clayey sediments sometimes contain fragments and imprints of thin-valved shells of mollusks. The sands contain mineral segregations of ferruginous carbonate, forming the cement of small dark-brown sheet and cake-like nodules. The sands also contain scattered boulders and pebbles, some of them poorly rounded. Magmatic clasts are more common than those of sedimentary rocks, and most of the former are extrusive rocks (porphyry, felsite).

Palynological samples from the area of Cape Sango-Balagan were collected from alluvial strata with distinctly pronounced channel and floodplain facies (Fig. 2). Characteristic of the channel sand are the dipping, unidirectional, rectilinear and converging beds with rhythmical sorting (Fig. 2, units 3, 5, 6). Weakly pronounced thick, dipping and multidirectional bedding is typical of the sand, with small pebbles at the base of channel alluvium (Fig. 2, unit 2). The floodplain deposits are
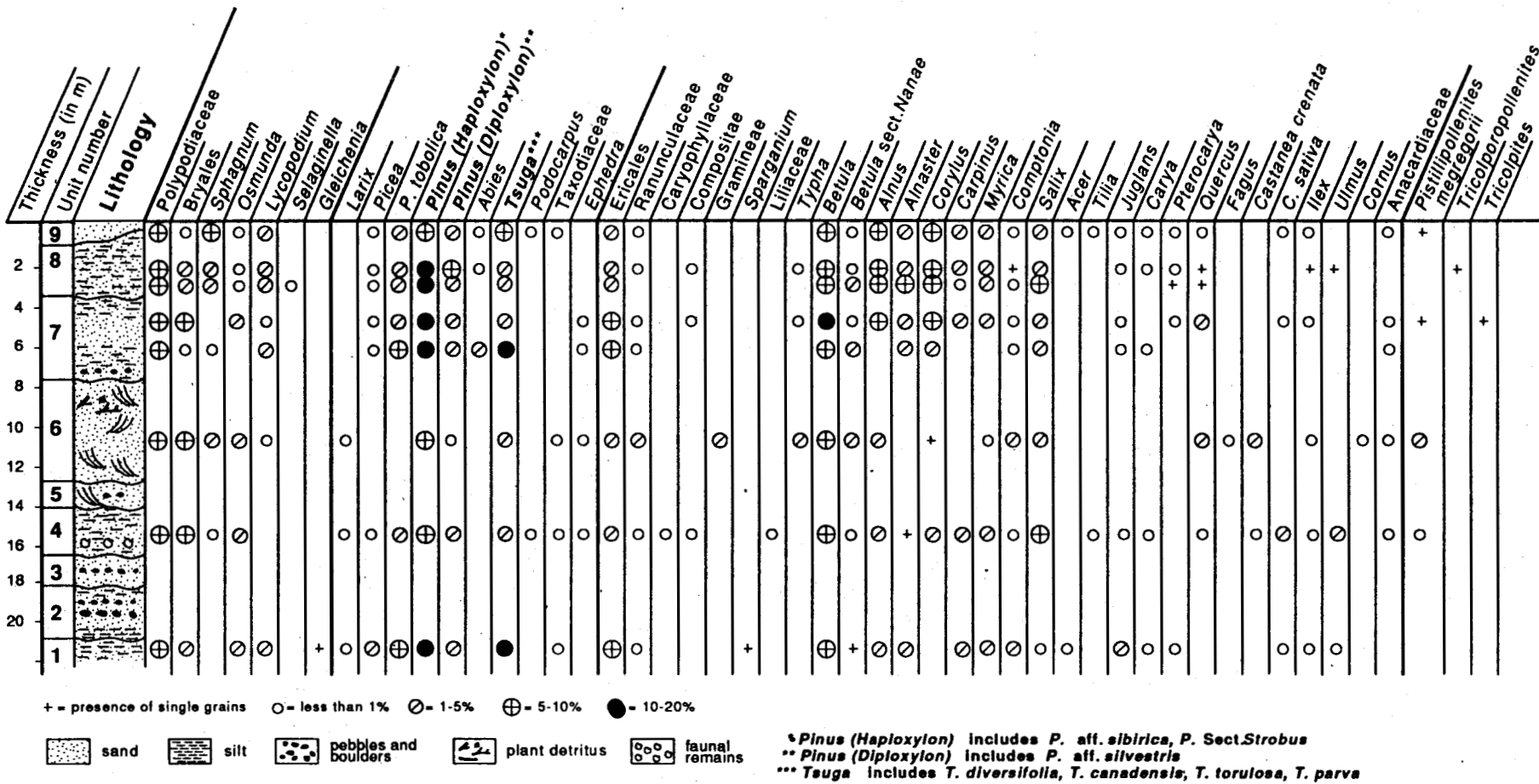
FIG. 2. Pollen flora from the Nerpichy Beds in the Cape Sango-Balagan outcrop.

+ = presence of single grains   ○ = less than 1%   ⊘ = 1-5%   ⊕ = 5-10%   ● = 10-20%

sand   silt   pebbles and boulders   plant detritus   faunal remains

* Pinus (Haploxylon) includes P. aff. sibirica, P. Sect.Strobus
** Pinus (Diploxylon) includes P. aff. silvestris
*** Tsuga includes T. diversifolia, T. canadensis, T. torulosa, T. parva

characterized by thin, unidirectionally dipping and converging; thin, dipping striated and rectilinear; or in some places rectilinear, horizontal and horizontally undulating lamination, as well as by gently undulating intercalation of floodplain deposits (Fig. 2, units 7, 8, 9).

In addition to alluvial deposits, the Nerpichy Beds also contain sandy sediments formed by the longshore drift of sediments supplied by rivers to a fluctuating shallow sea. The nearshore marine deposits of this facies are known over a considerable area, from Cape Sango-Balagan to the Kanarchak River basin. Of particular interest is the outcrop near the mouth of the Muorustakh River (Fig. 1), where up to 1 km of dipping, sandy sediments of a delta front are perfectly exposed. These deposits consist of medium-grained sand with thick, inclined, unidirectionally dipping and thinning beds and fine-grained cross-bedded sand. The sorting is intermediate to good and graded inside the inclined laminae. The color is yellow and pale-yellow. Frequently, somewhat charred detritus with vitrinite is present. Rocks of various composition are represented by clasts displaying different degrees of roundness.

That the sedimentation basin was connected with the sea during the Miocene is confirmed by the presence of the imprints of mollusk shells at the base of the section near Cape Sango-Balagan. They occur in weakly bedded (gently undulating) silty sediments alternating with medium-grained sand. Such sediments represent the semi-isolated nearshore zone of a shallow sea (Fig. 2, unit 4).

An abundance of coalified wood, lenses of brown coal and the presence of swamp type vegetation suggest that the strata were deposited in the lower reaches of rivers on or near a delta built into a shallow sea. The delta contained alluvial, lacustrine-paludal and nearshore marine sediments.

THE PALYNOFLORA: STRATIGRAPHIC POSITION AND CHARACTERISTICS

The most reliable palynological results have been obtained by study of the samples collected from the section on Cape Sango-Balagan (Fig. 2). Some of the critical pollen types seen in these samples are shown in Figures 3 and 4. Table 1 is a list of all taxa based on both pollen and macrofossils from the Nerpichy sequence.

The pollen spectra recovered from Cape Sango-Balagan probably represent a single palynoflora. They are characterized by alternate dominance of angiosperm and gymnosperm pollen with less participation of spores. The role of conifers tends to increase gradually up the section at the expense of amentiferous (e.g., catkin-forming) plants, especially the most thermophilic representatives.

Betulaceae pollen dominates the angiosperm component, with *Betula* (≤14%) and *Alnus* (≤9%) predominating and lesser quantities of *Corylus* (4-6%) and *Carpinus* (≤5%). The constant presence of pollen of the shrubs *Betula* sect. *Nanae* and *Alnaster* (in some spectra ≤10%) is notable. Also significant is the presence in all spectra of the pollen grains of *Salix* (4-8%), Ericaceae (≤8%) and Myricaceae (*Myrica* ≤5%, *Comptonia* ≤3%). *Juglans*, *Carya*, *Castanea* and *Quercus* are represented by small quantities of pollen. Single pollen grains of *Tilia*, *Acer*, *Ilex*, *Elaeagnus*, *Cornus* and *Diervilla* are found sporadically. In addition, the spectra contain herb pollen representing the families Ranunculaceae, Caryophyllaceae, Cyperaceae, Rosaceae, Compositae (*Artemisia*) and Gramineae and pollen of aquatic communities such as *Sparganium*, *Potamogeton*, *Typha*, *Nuphar* and *Nymphaea*.
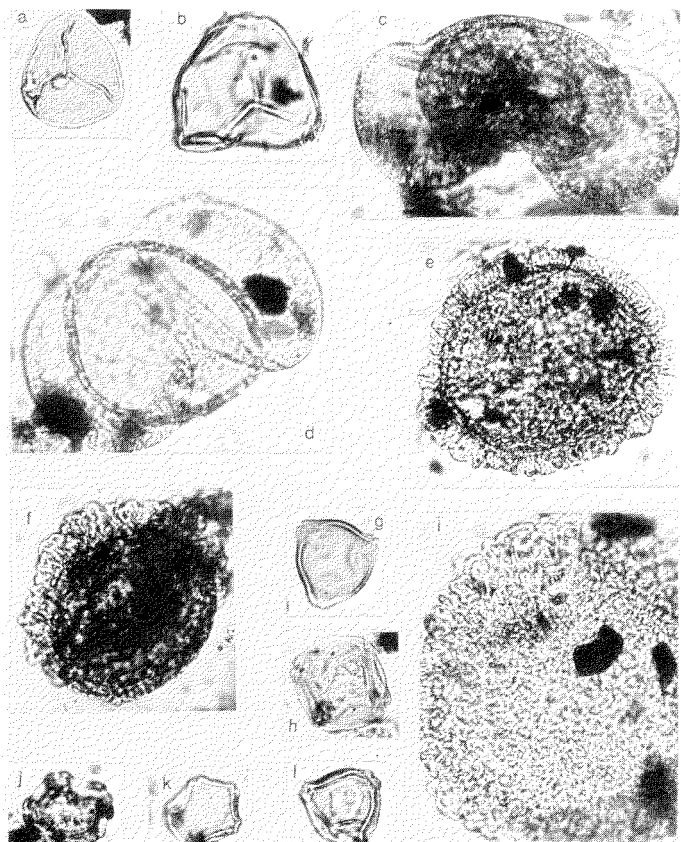

FIG. 3. Examples of the palynoflora of the upper Nerpichy Beds: a) *Sphagnum jakutensis* Rybac.(×1000); b) *Leiotriletes* sp. (×1000); c) *Pinus* aff. *sibirica* Du Tour (×1000); d) *Pinus* sect. *Cembrae* (×1000); e) *Tsuga torulosa* Zakl. (×1000); f) *Tsuga parva* Brutm. (×1000); g) *Myrica* aff. *gale* L. (×1000); h) *Alnus* sp. 1 (×1000); i) *T.* aff. *diversifolia* (Maxim.) Mast. (×1000); j) *Alnus* sp. 1 (×1000); k) *Alnaster* sp. (×1000); l) *Betula* sect. *Nanae* (×1000).
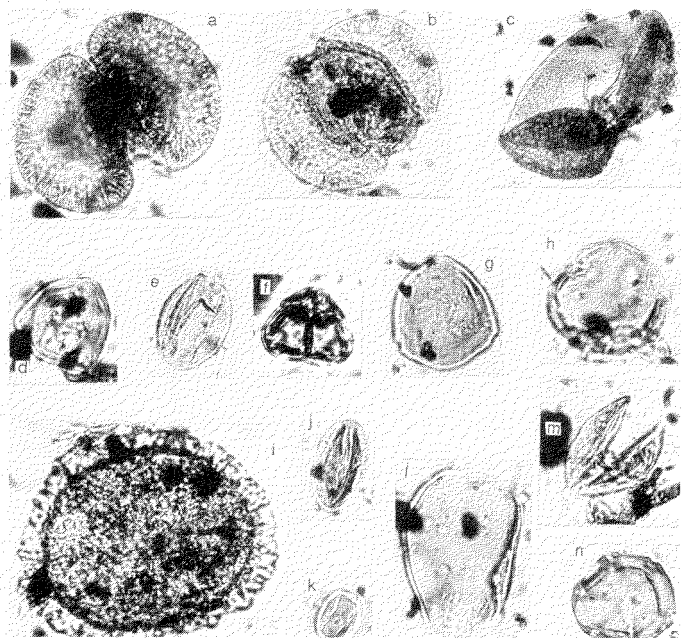

FIG. 4. Examples of the palynoflora of the upper Nerpichy Beds: a) *Podocarpus* sp. (×1000); b) *Pinus* sect. *Strobus* (×1000); c) *Picea tobolica* Pan. (×350); d) *Comptonia* sp. (×1000); e) *Quercus* sp. (×1000); f) Ericales (×1000); g) *Betula* sp. 1 (×1000); h) *Tilia* sp. (×1000); i) *Tsuga torulosa* Zakl. (×1000); j) *Salix* sp. (×1000); k) Rosaceae (×1000); l) Cyperaceae (×1000); m) *Taxodium* sp. (×1000); n) *Alnus* sp. (×1000).

TABLE 1. Fossil flora (pollen and seeds) of the Upper Nerpichy Beds, Faddeyev Island (seed flora determined by Dorofeyev; see Trufanov *et al.*, 1979)

Bryales	++	Gramineae	++
Sphagnum cf. *teres* (Schimp.) Angstr.	++	Cyperaceae	++
Sphagnum	++	*Carex* ex sect. *Vignea*	sd
Lycopodium aff. *alpinum* L.	++	*Carex* sp.	sd
Lycopodium aff. *pungens* La Pyl.	++	Araceae	
Lycopodium aff. *complanatum* L.	++	*Epipremnun crassum* C. et E. Reid	sd
Lycopodium aff. *annotinum* L.	++	Liliaceae	+
Lycopodium sect. *Selago*	+	Salicaceae	
Lycopodium sp.	++	*Salix* spp.	+++
Selaginella aff. *sibirica* (Milde) Hieron	+	*Populus* sp.	+
Selaginella sp.	+	Myricaceae	
Botrychium sp.	++	*Myrica* aff. *gale* L.	++
Adiantum sp.	+	*Myrica* spp.	++
Osmunda sp.	+++	*Comptonia* sp.	+
		Juglandaceae	
Polypodiaceae	+++	*Juglans cinerea* L.	+
Polypodium sp.	+++	*Carya* sp.	+
Gleichenia sp.	+	Betulaceae	
Dryopteris sp.	+	*Betula* sp.	+++
Leiotriletes sp.		*Betula* sp. 1 (large grains with thin exine)	+++
		Betula sect. *Nanae*	++
Gymnosperms		*Alnus* sp.	+++
Podocarpaceae		*Alnus* sp. 1 (large grains with 4 or 5 pores and thin exine)	++
Podocarpus sp.	+	*Alnaster* sp.	++
Pinaceae		*Corylus* sp.	++
Picea sect. *Eupicea*	+++	*Carpinus*	++
Picea tobolica Pan.	+++	Fagaceae	
Picea sect. *Omorica*	+++	*Quercus* sp.	+
Picea sp.	+++	*Fagus* sp.	+
Picea sp. 1 (small grains)	+	*Castanea crenata* Sieb. et Zucc.	+
Abies sp.	+	*Castanea sativa* Mill.	+
Tsuga aff. *diversifolia* (Maxim) Mast.	+++	Ulmaceae	
Tsuga aff. *canadensis* (L.) Carr.	+++	*Ulmus* sp.	++
Tsuga torulosa Zakl.	++	Chenopodiaceae	+
Tsuga parva Brutm.	++	*Corispermum* sp.	sd
Tsuga aff. *sieboldii* Carr. (?)	+	Caryophyllaceae	+
Tsuga sp.	+++	Nymphaeaceae	
Pseudotsuga sp. (?)	+	*Nuphar* sp.	+
Larix sp.	+	*Nymphaea* sp.	+
Pinus subgen. *Haploxylon*	+++	Ranunculaceae	++
Pinus sect. *Cembrae*	++	*Ranunculus* cf. *lingua* L.	sd
Pinus sect. *Strobus*	+	*Ranunculus sceleratus* L.	sd
Pinus subgen. *Diploxylon*	++	*Batrachium* sp.	sd
Pinus aff. *silvestris* L.	+	Aquifoliaceae	
Taxodiaceae		*Ilex* sp.	++
Taxodium sp.	+	Aceraceae	
Cupressaceae		*Acer* sp.	+
Juniperus sp.	+	Tiliaceae	
Ephedraceae		*Tilia* sp.	+
Ephedra sp.	+	Haloragaceae	
		Myriophyllum spicatum L.	sd
Angiosperms		*Menyanthes trifoliata* L.	sd
Typhaceae		Hippuridaceae	
Typha sp.	+	*Hippuris vulgaris* L.	sd
Sparganiaceae		Ericales	+++
Sparganium hyperboreum Laest.	sd	*Arctostaphylos uva-ursi* (L.) Spr.	sd
Sparganium sp.	++	Cornaceae	
Najadaceae		*Cornus* sp.	+
Potamogeton filiformis Pars.		Compositae	+
Potamogeton pectinatus L.	sd	*Artemisia* sp.	+
Potamogeton vaginatus Turcz.	sd		
Potamogeton alpinum Balb.	sd		
Potamogeton natans L.	sd		
Potamogeton praelongus Wulf.	sd		
Potamogeton ex. gr. *maskianus* A. Benn.	sd		
Potamogeton sp.	++		

+ = single grains; ++ = constant presence; +++ = dominant; sd = taxa known from macrofossils only.

The gymnosperm pollen is represented almost entirely by the Pinaceae, including ≤28% *Pinus* (e.g., *Pinus* sect. *Cembrae*, *P*. aff. *silvestris*, *P*. sect. *Strobus*), ≤16% of the group including *Tsuga* sp., *T. torulosa*, *T. parva*, *T*. aff. *diversifolia*, *T*. aff. *canadensis*, *T*. aff. *sieboldii* (?), "*Pseudotsuga* type" and ≤35% of the group containing *Picea* sp., *Picea* sect. *Omorica*, *P*. sect. *Eupicea* and *P. tobolica*. There are small quantities of *Larix*, *Abies* and *Cedrus* pollen. Cupressaceae is represented by single pollen grains of *Juniperus*. *Ephedra* and *Podocarpus* were seen in some samples.

Among the sporophytes, ferns dominate: Polypodiaceae (≤12%), *Dryopteris* (≤2%), *Adiantum* (≤1%), *Osmunda* (≤5%) and *Botrychium* (≤1%). Mosses (*Sphagnum* and *Bryales*) are considerably less abundant. Various lycopods are also represented by a small quantity of spores (≤5% in total). *Lycopodium annotinum* and *L. complanatum* are represented by percentages of ≤3% and 1% respectively. *Lycopodium pungens*, *L*. sect. *Selago*, *L. alpinum* and *Selaginella sibirica* are less frequent.

The main problem in the consideration of any palynoflora is to define the relationship between the vegetation composition and the types of pollen spectra — i.e., to define the most important regularities influencing the formation of the latter. There exists an enormous literature on various aspects of the formation of palynocoenoses, such as the estimation of the distance of pollen transportation, composition of spectra as a function of sediment type, pollen redeposition, etc. (e.g., Volkova, 1977; Krassilov, 1972; Permiakov, 1971). Various authors have come to different conclusions concerning these problems and this fact alone illustrates the difficulty of making objective conclusions. Some recent studies have shown that quantitative analyses of palynological data can be used to identify the dominant plant genera in palynocoenoses (Krassilov, 1972). However the author believes that the sharp differences in productivity, transportation potential and resistance to degradation of pollen grains preclude the use of such quantitative criteria for determining the relationship of vegetation to pollen. The most that can be said about the palynoflora discussed here is that: 1) the spectra are not dominated by any one type, which is evidently related to the types of enclosing deposits; and 2) the vegetation of the area where the deposits accumulated was in the boreal zone *senso lato*. However, these conclusions are supplemented by the floral composition of the assemblages — that is, by their taxonomic diversity and content of pollen representing forest-forming taxa.

Before interpretation of the pollen spectra, it is necessary to identify redeposited palynomorphs. Redeposited grains were noted, and following an artificial classification the author identified these mainly as *Tricolporopollenites*. However, the Nerpichy sequence is complex and its total age range is not yet known precisely. Thus it would be logical for one to conclude that the single representatives of Eocene vegetation within "boreal" Miocene assemblages are redeposited.

Nevertheless, judging from Figure 2 and the list in Table 1, as well as by the present-day structure of dark coniferous communities, one might also postulate the existence of both pure tracts of *Tsuga* and mixed forests containing species of *Pseudotsuga*, spruce, fir and lesser numbers of pine and small-leaved amentiferous plants. The actual composition of such communities at any one time would depend on the local successional stage. In a more general phytocoenological context and in an attempt to explain the evolution of the plant cover, it is possible to invoke the concept of segregation. Segregated

associations arise in two ways: 1) by survival of certain taxa to become members of an undifferentiated complex when other components disappear, and 2) by some of the taxa occupying new areas. Sochava (1946), taking the Manchurian mixed forest as an example, regarded the segregation process as the transformation of weakly differentiated warm-temperate Tertiary formations under the influence of exogenic factors into the present-day types of predominantly homogeneous forest. It has been emphasized repeatedly that segregation is not a universal phenomenon in the evolution of a plant cover. However, for nemoral types of vegetation, segregation seems to have played a considerable role in the formation of many present-day associations (Sochava, 1946; Grossgeym, 1948).

PLANT MACROFOSSILS FROM THE NERPICHY BEDS

The lithological and palynological characteristics of the deposits suggest that they most likely represent the upper part of the Nerpichy Beds. It is the author's opinion that these deposits are late middle Miocene in age and they are floristically correlative with the Miocene Beaufort Formation of arctic Canada. Sediments of the Beaufort Formation have yielded a combination of paleobotanical information (microfossils, mosses and leaf and seed floras) as well as fossil insects. According to the latest data (Matthews and Ovenden, 1990; Fyles *et al.*, 1991), marine beds of the Beaufort Formation from Meighen Island are late Pliocene in age. Matthews and Ovenden (1990) believe that the Beaufort Formation from Prince Patrick and Banks islands may be the same age or slightly older. It seems highly unlikely, in view of such data, that tundra would have already existed on the Chukchi Peninsula and Bering land bridge in late Miocene time (Matthews and Ovenden, 1990; Zyryanov *et al.*, in press). Floras of the Beaufort Formation indicate that forests existed in arctic regions during the Pliocene. It is highly unlikely that the paleovegetation trend could represent only the last warm interval of the Pliocene, now dated at approximately 3.1 Ma (Fyles *et al.*, 1991).

Because the plant macrofossils from the Beaufort Formation are mostly seeds and fruits, comparisons with the Nerpichy Beds need to be based on fossil seeds and fruits. Most of the Nerpichy macrofossils come from the middle and upper parts (north coast of Faddeyev Island, Cape Nerpichy) of the sequence. They were studied and identified by Dorofeyev (Trufanov *et al.*, 1979).

The taxa represented by macro-fossils may be grouped according to their autecology (Table 2). *Potamogeton* is one of the common fossils in Paleogene and Neogene deposits of West and East Siberia; less frequently it is found in the Soviet northeast. It is known in Miocene deposits of arctic Canada (Matthews and Ovenden, 1990). *Sparganium* is a dominant form in the Neogene of eastern Europe and west Siberia. It is frequently found in Miocene deposits of central Yakutia (Mamontova Gora) but is a rare form in the Soviet northeast. In the Nerpichy Beds (Faddeyev Island) and the Beaufort Formation (Banks and Meighen islands) it is represented by a single species.

Menyanthes is at present a monotypic genus represented by a single species *M. trifoliata* L. The present-day distribution area of this species is extremely extensive, embracing all the extra-tropical regions of the Northern Hemisphere, i.e., the Holarctic. Two fossil species of *Menyanthes* are known: the Oligocene to early Miocene west Siberian *M. parvula* Nikit.

TABLE 2. Groups of plants according to autecology

Herbaceous aquatic plants
  Potamogetonaceae
    Potamogeton filiformis Pers., *P. pectinatus* L., *P. vaginatus* Turcz., *P. alpinum* Balb., *P. natans* L., *P. praelongus* Wulf., *P.* ex gr. *maskianus* A. Benn.
  Sparganiaceae
    Sparganium hyperboreum Laest.
  Haloragaceae
    Myriophyllum spicatum L.
  Menyanthaceae
    Menyanthes trifoliata L.
  Ranunculaceae
    Ranunculus cf. *lingua* L., *R. sceleratus* L., *Batrachium* sp.
  Hippuridaceae
    Hippuris vulgaris L.

Mesic herbaceous plants
  Araceae
    Epipremnum crassum C. et E. Reid
  Cyperaceae
    Carex sp., *C.* sect. *Vignea*

Forest and low-schrub taxa
  Ericaceae
    Arctostaphylos uva-ursi (L.) Spr.

River-floodplain plants
  Chenopodiaceae
    Corispermum sp.

and Miocene *M. orientalis* Nikit. from the Okhotsk region. In the Miocene of the High Arctic *Menyanthes* is represented by a single species *M. trifoliata* L. *Hippuris* is represented in the U.S.S.R. by *H. vulgaris* L., which is found everywhere from tundra to the Far East and Central Asia. The species was recorded in the deposits of the Nerpichy Beds and Beaufort Formation. Of all the flowering plants in the Hypoarctic flora, *Carex* is the genus with the greatest number of bog species.

Epipremnum is represented at present by herbaceous, frequently climbing (lianas) plants. Fourteen species of *Epipremnum* are distributed in the tropics and subtropics of East Asia and Australia. In the Tertiary the genus is represented by more than ten described species and was widespread throughout Eurasia from the Eocene (and possibly from the Paleocene) to the Pliocene (Nikitin, 1979). In Nikitin's opinion (1979), *E. crassum* C. et E. Reid is a typical Miocene to Pliocene Euro-Siberian species.

The first thing to note when examining this seed assemblage is its exceptional intrazonality. Virtually all the fossils, except some single forms, represent the biota inhabiting oxbow lakes. *Sparganium, Potamogeton, Myriophyllum, Hippuris* and *Menyanthes* occur more or less in the water, while *Carex, Ranunculus, Batrachium,* etc., grow on moist shorelines. Baranova *et al.* (1976) showed that similar plant communities were characteristic of the environments of the extensive Miocene boreal forests at Mamontova Gora on the Aldan River.

DISCUSSION

Phytogeography

Because of the rather rich specific diversity and good preservation of the Nerpichy fossil flora, it is possible to speculate at somewhat greater length on the characteristic paleogeographic features of the New Siberian Archipelago region.

The palynoflora (excluding redeposited microfossils) has a number of interesting features: 1) the presence of typical Hypoarctic forms, such as shrub forms of birch and alder, willow and their various morphotypes (perhaps species); 2) the presence of the pollen of forbs and low shrubs; 3) the high-content of taxa representing dark coniferous (*Tsuga, Picea, Abies*) and, to a lesser extent, light coniferous taiga (*Pinus, Larix*); and 4) the considerable proportion of small-leaved forms.

Using the data presented here and the latest information on the Miocene Beaufort Formation (Matthews and Ovenden, 1990; Fyles *et al.*, 1991), whose leaf and seed flora also reflect the various analogs of present-day Hypoarctic landscapes, it is possible to attempt to explain this somewhat strange thanatocoenosis. According to the pollen analyses, the palynoflora from Faddeyev Island appears to represent a combination of at least two landscape zones. The outer zone was probably situated on the coast of the arctic basin, at first only as a narrow strip. The proximity of a rather cold ocean would have increased the severity of climate in this zone, lowering the summer temperatures. Because the ocean froze in the winter, the winter temperatures would not have been any warmer (Tolmachov, 1986). It was in this environment that the primary Hypoarctic landscapes formed.

In appearance these early Hypoarctic landscapes probably resembled plant formations such as the present sparse birch stands of the Kuril-Kamchatka type, with large-shrub alder stands and small-tree and shrub willow stands (Tolmachov, 1986). The inner zone was evidently situated at a considerable distance from the coast and was dominated by dark coniferous taiga assemblages (boreal dark coniferous plant formation). The available palynological data suggest that in middle Miocene (the period of the longest eustatic regression of the polar shelf) the present-day New Siberian Archipelago was within this zone. It is logical to suppose that an ecotone existed between the outer and inner zone and formed a proto-forest-tundra landscape. The open spaces there, as in the outer zone, would have been occupied by proto-Hypoarctic communities. Forest strips would have consisted of the representatives of dark coniferous taiga assemblages and small-leaved amentiferous plants.

Within the Asian sector of the Holarctic there is no hard evidence for the location of the northern boundary of closed forests during the late Cenozoic. However, within the North American sector, Meighen Island, the northernmost position of the Beaufort Formation (about 80°N) has yielded fossil tree trunks of a small size. This may indicate a dwarfed forest similar to that existing at present near the tree line. However, it is essential to note that the taxonomic composition of fossil assemblages from Meighen Island is more diverse than that of a present-day boreal forest (Matthews, 1987). Thus, the proposed paleogeographic model provides the basis for a new phytogeographic interpretation: the synchronous existence of the various types of zonal vegetation in the High Arctic during the second half of the Miocene-Pliocene.

It is necessary to discuss some important concepts of this newly proposed phytogeographic model. The most essential one is the botanical basis for interpreting the taxonomic composition of palynospectra in the Nerpichy sequence. At present, the study of the qualitative composition of recent pollen spectra has shown that the best pollen representation of regional vegetation and flora occurs in the spectra from the sediments of large lakes. Such sediments are represented in

the Nerpichy sequence. Freshwater sediments in the Nerpichy sequence are also indicated by the presence of certain water plants that are normally restricted to fluvial-lacustrine biotopes (see Tables 1 and 2).

Having stated the taphonomic principles that are the basis of interpreting the qualitative composition of the palynospectra, it is now necessary to consider the possibility of the existence of other paleogeographic environments. The most popular scheme, which has become conventional in the analysis of palynofloras, is to suppose the existence of vertical differentiation of plant communities, i.e., altitudinal effects. Such a concept is quite valid in the case of paleolandscapes with dissected topography. However, it is the author's opinion that the phyto-indicators discussed here provide no objective criteria for postulating differences in vertical and lateral plant zonality. The most reliable information on paleo-altitudes comes from the character of the sedimentary strata. It is manifested, first of all, by a shift in sediment type across a basin, which may indicate change in the elevation and dissection of source lands. Thus, the existence of rather elevated source lands results in thick accumulations of coarse clastic deposits (Khomutova, 1987). The presence of known high elevation source lands, such as the Verkhoyansk Mountains and Aldan massif for the Miocene deposits of the Lower Aldan basin (Baranova et al., 1976), also indicates a potential for fossil plant assemblages to reflect altitudinal differences. When these various indicators are evaluated for the Nerpichy Beds, it becomes clear that they represent low-relief topography. Furthermore, it is difficult to conceive that elevated areas that might have produced floristic differences could have existed on arctic shelf regions in the late Miocene.

Plant Communities during the Initial Stage of Arctic Florogenesis

The lithofacies analysis of the Nerpichy Beds provides information on a complex assemblage of deposits representing a more or less gradual transition from alluvial and deltaic terrestrial facies to nearshore marine sediments. The rhythmic structure of sequences can be explained by the repeated migrations of both limnic and paralic morphological elements. Following the concept of catena or changeable-dominant complexes (Krassilov, 1972; Meyen, 1987), the author has attempted to reproduce the dynamics of vegetation evolution in the environment of a maritime fluvial-deltaic plain. The task is complicated in this particular case because in addition to vegetation change as a function of geomorphic level (Fig. 5), there exists the problem of the vegetation of an "adaptive zone" formed from areas emerging as a result of the eustatic drying of polar shelves. By the beginning of the most intense drying of shelves in the second half of the Miocene the vertical zonality and physiognomic structure of dark coniferous vegetation, which at that time represented the widespread and probably circumpolar dark coniferous boreal plant formation, apparently had formed. The florogenesis of this formation was to some extent demonstrated by Yurtsev (1972). It was related, first of all, to the fall of temperature noted for the latest Miocene throughout the Northern Hemisphere (Biske, 1975). Such climatic changes resulted in a down-slope shift of vegetation zones onto constructional low plains (Meyen, 1987). In the course of arctic florogenesis, the dark coniferous complex occupied maritime lowlands, having descended from elevated areas, where it had existed in Tertiary arctic forests as an inde-

pendent belt above the deciduous broad-leaved and thermophilic coniferous associations. Once dark coniferous forests had occupied the plains, the dominants probably formed the following vertical series: 1) maritime lowlands and slopes of river terraces with fairly moist air and 2) areas with well-moistened (possibly even relatively salinized) soils and frequent bogs. These sites were occupied by various species of Tsuga with an admixture of spruce, while spruce stands with some firs grew on the more elevated areas.

After the start of the emergence of the shelf, a growing unvegetated "adaptive zone" appeared. It would have been first occupied by communities of pioneer plant species. Within the present boreal taiga zone such sites are occupied by communities made up mostly of deciduous trees, with species of birch, aspen, poplar, willow and alder constituting the initial (pioneer) forest-forming plants. Studies on the settling regularities of present-day seed plants (e.g., Udra, 1988) demonstrate that common characteristics of the above-mentioned pioneer taxa are their wide ecological amplitude and their hardiness in the face of extreme ecological conditions, such as poor or immature soils, areas of exposed underlying rock or areas of drought and/or excess moisture. Most are also adapted for long-distance transport (e.g., abundant light seeds with various devices such as hairs, alar projections, etc.), and this contributes to their ability to quickly invade new areas. These properties allow the pioneeer deciduous taxa mentioned above to be the first to occupy areas free of forest vegetation.

In addition to the above-mentioned taxa, light coniferous trees such as pines of the Diploxylon subgenus and larches are also pioneer plants. However, despite the fact that they can occupy areas for a much longer time than the deciduous pioneer species, their migration abilities are considerably lower. These species, apparently, represent the second stage of the expansion. For example, at present in southeastern Alaska, where the main (climax) type of forest is represented by Tsuga heterophylla, with Picea sitchensis in a subordinate role, vegetation-free areas such as moraines are occupied by such pioneer species as Salix barclayi, S. sitchensis, S. alaxensis, Alnus crispa subsp. sinuata and Populus trichocarpa, which are later replaced by spruce (Heusser, 1969).

The above is the probable sequence for explaining the colonization of the spaces that became free during the regression of the Arctic Ocean. Allogenic changes usually characterize succession in dark coniferous forests. In other words, the pioneer species fill the treeless spaces, paving the way for the more competitive species of the next stage. However, in Miocene time in the High Arctic regions this next successional stage probably failed to occur, possibly having been precluded by the cooling temperature trend of the time. Ecological niches, therefore, remained "vacant" (Krassilov, 1986). No plants, other than the pioneers themselves, could fill them, and the pioneers had to change their vital strategy for that. The paleobotanical materials demonstrate that the pioneer communities made up of deciduous tree taxa, lacking competition on the one hand and allogenic changes on the other, increased their taxonomic complexity as a means of surviving new conditions. This is indicated in the pollen spectra by the appearance of several different pollen morphotypes of birch, alder and willow. At present there are no data to show the exact sequence of changes during the Miocene, but it probably started with communities with high-trunk forms, then through a number of derivatives to shrub and low-shrub forms, which evidently resulted in a proto-Hypoarctic vegetation.
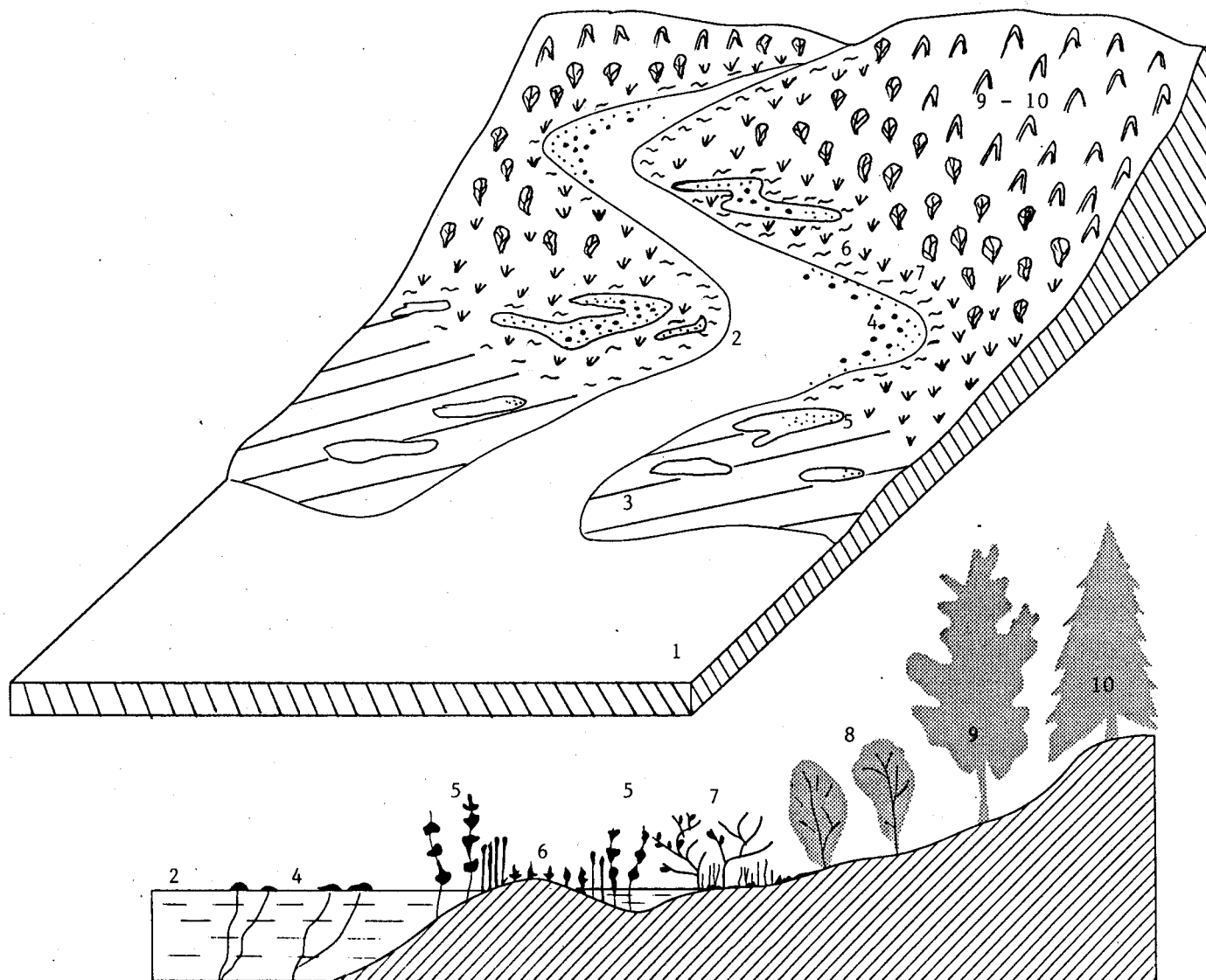
FIG. 5. Distribution of plant communities in the coastal delta plain environments. 1) sea level; 2) freshwater-body level; 3) dried areas where pioneer groups develop; 4, 5) aqueous vegetation — 4: relatively deep-water forms (*Myriophyllum, Potamogeton natans*), 5: nearshore shallow-water forms (*Typha, Sparganium, Hippuris vulgaris*); 6) dwellers of moist flooded bank areas (*Ranunculus, Batrachium*); 7) vegetation of floodplain bogs (*Myrica, Carex*); 8) riparian stands (*Alnus, Salix, Ulmus*); 9, 10) dark coniferous forest — 9: association represented by *Tsuga* with the admixture of spruce, 10: spruce stands with some firs.

REFERENCES

BARANOVA, YU.P., ILYINSKAYA, I.A., NIKITIN, V.P., PNEVA, G.P., FRADKINA, A.F., and SHVAREVA, N.YA. 1976. The Miocene of Mamontova Gora flora. Moscow: Nauka. 283 p. (In Russian.)

BISKE, S.F. 1975. The Paleogene and Neogene of the extreme northeast of the U.S.S.R. Novosibirsk: Nauka. 264 p. (In Russian.)

FYLES, J.G., MARINCOVICH, L., Jr., MATTHEWS, J.V., Jr., and BAREN-DREGT, R. 1991. Unique mollusc find in the Beaufort Formation (Pliocene) on Meighen Island, Arctic Canada. In: Current Research, Part B, Geological Survey of Canada, Paper 91-1B:105-112.

GROSSGEYM, A.A. 1948. Plant cover of the Caucasus. Moscow: Izdatelstvo Moskovskogo Obshchestva Ispytatelei Prirody. 265 p. (In Russian.)

HEUSSER, C.J. 1969. A Pleistocene phytogeographical sketch of the Pacific northwest and Alaska. In: Wright, H.E., Jr., and Frey, D.G., eds. The Quaternary of the United States. Moscow: Mir. p. 111-132. (In Russian.)

KHOMUTOVA, V.I. 1987. Pollen complexes. In: Martinson, G.G., and Neustroeva, I.U., eds. History of lakes in the late Paleozoic and Mesozoic. Leningrad: Nauka. p. 69-72. (In Russian.)

KRASSILOV, V.A. 1972. Paleoecology of terrestrial plants. Vladivostok: Dalnevostochniy Nauchiy Tsentr. 208 p. (In Russian.)

———. 1986. Unsolved problems of the evolution theory. Vladivostok: Dalnevostochniy Nauchiy Tsentr. 165 p. (In Russian.)

MATTHEWS, J.V., Jr. 1987. Plant macrofossils from the Neogene Beaufort Formation on Banks and Meighen islands, District of Franklin. Geological Survey of Canada Paper 87-1A:73-87.

MATTHEWS, J.V., Jr., and OVENDEN, L.E. 1990. Late Tertiary plant macrofossils from localities in arctic/subarctic North America: A review of the data. Arctic 43(4):364-392.

MEYEN, S.V. 1987. General paleobotany. Supplement to: Principles of paleobotany. Moscow: Nedra. 201 p. (In Russian.)

NIKITIN, V.P. 1979. Neogene floras of the U.S.S.R. Northeast. In: Shilo, N.A., and Baranova, J.A., eds. Continental Tertiary deposits of northeast Asia. Novosibirsk: Nauka. p. 130-149. (In Russian.)

PERMIAKOV, A.I. 1971. On the dependence of pollen spectra on the origin of enclosing deposits. In: Neishtadt, M.I., ed. Methodological problems of palynology. Novosibirsk: Nauka. p. 46-54. (In Russian.)

SOCHAVA, V.B. 1946. Problems of the florogenesis and phylocaeno-genesis of the Manchurian mixed forest. In: Materials on the history of the U.S.S.R. flora and vegetation. Leningrad: Izdatelstvo Academii Nauk U.S.S.R. p. 283-315. (In Russian.)

TOLMACHOV, A.I. 1986. Problems of the genesis of arctic floras. In: Malyshev, L.I., and Krasnoborodov, I.M., eds. Methods of comparative floristics and florogenesis problems. Novosibirsk: Nauka. p. 91-131. (In Russian.)

TRUFANOV, G.V., BELOUSOV, K.N., and VAKULENKO, A.S. 1979. Materials on the stratigraphy of the Cenozoic deposits in the New Siberian Archipelago. In: Shilo, N.A., and Baranova, J.A., eds. Continental Tertiary sequences of the Asian Northeast. Novosibirsk: Nauka. p. 22-30. (In Russian.)

UDRA, I.F. 1988. Settling of plants and problems of paleogeography and bio-geography. Kiev: Naukova dumka. 197 p. (In Russian.)

VOLKOVA, V.S. 1977. Stratigraphy and the history of vegetation evolution of West Siberia in the late Cenozoic. Moscow: Nauka. 235 p. (In Russian.)

YURTSEV, B.A. 1972. Problems of the origin of dark coniferous taiga in the light of the recent paleobotanical investigations. Botanecheskii Zhurnal 57:1-11. (In Russian.)

ZYRYANOV, E.V., POLYAKQVA, E.I., and LAUKHIN, S.A. In press. Pollen and diatoms of the Neogene Northeast Chukotka. Moscow: Doklady Academii Nauk U.S.S.R.