

WOODY PLANT ASSEMBLAGES AND PALAEOENVIRONMENTS IN THE PLIOCENE OF PAVLOVSKAYA DEPRESSION (SOUTHERN PRIMORY'E)

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Abstract. The additional information on taxonomic diversity of the Russian Far East aboriflora in the Pliocene is given. Representatives of the families Pinaceae, Ulmaceae, Fagaceae, Betulaceae, Salicaceae, Rosaceae, Aceraceae, Araliaceae, Oleaceae and Caprifoliaceae were identified by wood anatomy. Woody plant communities and their environments in the Pliocene of Pavlovskaya Depression (Southern Primory'e) are reconstructed for the first time.

Keywords: Pliocene, Pavlovskaya Depression, Southern Primory'e, Russian Far East, wood anatomy, plant assemblages, palaeoenvironments.

INTRODUCTION

Taphoflora is usually a part of the past plant assemblages since not everything that were buried under sediments could become as fossils. For instance, pollen grains of larches because of a bad ability to fly and easiness to be destroyed occur rather infrequent as fossils in contrast to their resiniferous wood. Coniferous woods are more resistant to destruction than angiospermous ones and usually are more frequent as fossils. Besides, plant remains are often transported before their burial and wood fragments are lesser destroyed during transportation. Thus, plant remains from different sites can be found in the same locality of fossil flora. Wood fragments can be transported by water for a great distance from the place of plant growth to the site of their burial. Despite leaf impressions or palynomorphs are usually more abundant as fossils in contrast to fossil woods, the later can provide sometimes more reliable information about forest dominants and therefore are of some important for a reconstruction of plant assemblages or relief. In the reconstruction of the past plant assemblages the records on various fossil plant remains have to be used in complex.

The information on environments of the related extant species is to be also taken into consideration.

MATERIAL AND METHOD

In the Pliocene of Southern Primory'e (Russian Far East) wood fragments are practically the sole macrofossils, therefore their study is of a great importance for reconstruction of the plant assemblages and interpretation of their environments. However, till now fossil woods from the Pliocene of Primory'e have not been studied.

The abundant wood remains of the Pliocene age were found in Southern Primory'e (Russian Far East) within the Pavlovskaya Depression located in 35 km to the north - east of Ussurisk city (Figure 1).

Fossil woods were collected from the small-pebble conglomerates in the upper part of the Suifunskaya Suite (Plate I, fig. 1) of the Pliocene age (Reshenia IV Mezhdedomstvennogo regional'nogo stratigraficheskogo sovestchania, 1994). However, in the view of Pavlutkin (1998), the Suite is of the Eopleistocene age. This Suite is represented by a series of fluvial sediment rhythms. At the boundaries of the rhythms there are aleurolite lens containing spores and pollen as well as a plant detritus, i.e. remains of needles, fruits and seeds; but leaf impressions are absent.

Wood pieces are abundant, lignitic, light- to dark-brown, range in size, but in mean dimensions are from 6-9 to 23 cm in length and 3-15x5-18 cm in diameter (Plate I, fig. 3). A few logs 40-50 cm in diameter and 3-6 m in length were also found (Plate I, fig. 2). Growth rings are distinct, from 0.2-0.5 to 2-3(4-5) mm (1.5-2 mm on the average) in width and mostly well distinguishable by the unaided eye. Wood fragments, stumps and logs are in horizontal bedding with azimuth of inclination 270° from east to west.

Because wood is characterized by a different anatomical structure in transverse, radial and tangential sections thin transparent slides in these sections have been made of each wood fragment.

The method given in the works by Gammerman et al. (1946) and Nastchokin (1968) has been used for the preparation of slides. In total of more than 4300 thin slides made of 103 wood fragments have been studied in light biological microscope. Fossil woods from the Pliocene of Primory'e have been studied for the first time.

PALAEOBOTANICAL RECORDS

Abies aff. *sachalinensis* Fr. Schmidt, *Pseudotsugoxylon pavlovskiense* Blokh. et Bondar., *Picea* cf. *bicolor* (Maxim.) Mayr, *Piceoxylon pavlovskiense* Blokh. et Bondar., *P. ussuriense* sp. nov., *Larix* aff. *olgensis* A. Henry, *Laricioxylon*

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pavlovskiense Blokh. et Bondar., *L. ussuriensis* sp. nov., *Ulmus* aff. *japonica* (Rehd.) Sarg., *U.* aff. *laciniata* (Trautv.) Mayr, *Quercus pavlovskiense* sp. nov., *Betuloxylon* sp., *Chosenia arbutifolia* (Pall.) A. Skvort., *Padus* aff. *maackii* (Rupr.) Kom., *Malus mandshurica* (Maxim.) Kom., *Cerasus sargentii* (Rehd.) Pojark., *Acer* cf. *tegmentosum* Maxim., *Eleutherococcus* aff. *sessiliflorus* (Rupr. et Maxim.) Seemand, *Fraxinus* sp. and *Sambucus* sp. were identified by wood anatomy. The fossil woods belong to the families Pinaceae, Ulmaceae, Fagaceae, Betulaceae, Salicaceae, Rosaceae, Aceraceae, Araliaceae, Oleaceae and Caprifoliaceae.

Fossil woods characterized by anatomical features of the wood of extant *Abies* Mill., *Pseudotsuga* Carr., *Larix olgensis*, *Ulmus* L., *Malus* Mill., *Padus* Mill., *Cerasus* Mill., *Sambucus* L., *Fraxinus* L., *Betula* L., *Eleutherococcus* Maxim., *Chosenia* Nakai., *Acer* L. and *Quercus* L. were found in Russian Far East for the first time.

A new form-genus *Pseudotsugoxylon* Blokh. et Bondar. was proposed for the pinaceous fossil woods characterized by anatomical features of the extant genera *Pseudotsuga* Carr. The Pliocene *Pseudotsugoxylon pavlovskiense* is similar to some extent to the both living North American species *Pseudotsuga menziesii* (Mirb.) Franco and *P. macrocarpa* (Vasey) Mayr (Blokhina & Bondarenko, in press). However, other remains of *Pseudotsuga* (either macrofossils or pollen) were not found in the Pliocene of Russian Far East, including Southern Primory'e. The fact is, *Pseudotsuga* is rather infrequent as fossils, although, the infrequency is, perhaps, simply a result of its difficult identification.

The Pliocene *Eleutherococcus* aff. *sessiliflorus* differs from the extant *E. sessiliflorus* only in the presence of distinct helical thickenings in the walls of some vessels, whereas in the living species helical thickenings are present only in the first growth ring in the vessels located near by the pith.

The fossil *Larix* aff. *olgensis* differs from the extant *L. olgensis* vegetated to date in Primory'e only in the lacking of helical thickenings in the walls of vertical tracheids (Bondarenko & Blokhina, 2003). Although, in the living *L. olgensis* helical thickenings occur only in the juvenile wood (Blokhina & Minkhaidarov, 2000).

Laricioxylon pavlovskiense combines wood anatomical characters of the extant *Larix occidentalis* Nutt., *L. gmelinii* (Rupr.) Rupr. and *L. olgensis* (Blokhina et al., 2003). The fossil *Laricioxylon ussuriensis* is similar by wood anatomy to the extant *Larix leptolepis* (Siebold et Zucc.) Gord. and *L. olgensis* (Bondarenko & Blokhina, 2003). Thus, both the Pliocene *Laricioxylon pavlovskiense* and *L. ussuriensis* show wood anatomical characters of the extant *Larix olgensis*. Thus, one can suppose that in the Pliocene *L. olgensis* vegetated in Primory'e and, perhaps, took place in the hybridization with other

ancient larches. At least, Bobrov (1972, 1978) reports in Primory'e the occurrence of the extant larch hybrids with a participation of *L. olgensis*.

Piceoxylon pavlovskiense is characterized by the presence of wood anatomical features of the extant *Picea koraiensis* Nakai, *P. jezoensis* (Siebold et Zuss.) Carr. and *P. sitchensis* (Bong.) Carr. (Blokhina et al., 2003). A new fossil species *Piceoxylon ussuriense* is similar to some extent to both the living *Picea koraiensis* and *P. likiangensis* (Franch.) Pritz.

Palynomorphs from the aleulite lens are dominated by the moderate broad-leaved species of *Quercus* (58.7%), *Ulmus* (14.4%), *Corylus* L., *Carpinus* L., *Tilia* L. (in total of 11.2%), *Fagus* L. (4.9 %), and *Juglans* L. (0.6%). *Alnus* Mill. (7.6 %), *Betula mandshurica* (Regel) Nakai (4.7 %) and *B. sect. Albae* L. (4 %) are prevalent among the small-leaved angiosperms. Besides, single pollen grains of the exotic for this region *Carya* Nutt., *Pterocarya* Kunth, *Castanea* Mill., *Celtis* L. and *Magnolia* L. are also present. Pinaceae is rather abundant, especially *Picea* A. Dietr. (31 %) and *Pinus* L. (16.6 %), although, *Tsuga* Carr. (1 %) is more rarely. The pollen grains of Cupressaceae-Taxodiaceae (2.2 %) were found (Pavlutkin et al., 1988).

Abundance of the Pinaceae (namely, *Picea* and *Larix* Mill.) is characteristic of seed remains. *Salix* L., *Alnus*, *Betula* sect. *Costatae* (Koehne) Rigl., *Padus asiatica* Kom., *P. maackii*, *P. cf. jacutica* Dorof., *Crataegus* L., *Spiraea* L., *Rosa* L., *Aralia* cf. *crassa* Dorof., *Sambucus* were also identified (Pavlutkin et al., 1988; Reshenia IV Mezhdvedomstvennogo regional'nogo stratigraficheskogo sovestchania, 1994).

PLANT ASSEMBLAGES AND PALAEOENVIRONMENTS

In the reconstruction of plant assemblages the records on various fossil plant remains found in the Pliocene of Pavlovskaya Depression have been used in complex. Many of determined fossil species are represented in the modern flora of South Russian Far East or have analogues in the floras of Japan, North-Eastern China, Korea Peninsular or western North America (Table 1, 2). The information on environments of the related extant species was also taken into consideration (Table 3). The information is cited from the works by Ostenfeld & Larsen (1930), Vassiliev (1950), Dylis (1961), Matsenko (1964), Dereviya i kustarniki (1971, 1974), Bobrov (1972, 1978), Gukov (1976), Bukshtynov et al. (1981), Voroshilova & Snezhkova (1984), Klyuikov & Tikhomirov (1987), Nedoluzhko (1987, 1995), Man'ko (1987), Koropachinskiy (1989), Grudzinskaya (1991), Kharkevich (1991) and Yakubov et al. (1996).

Woody plant communities in the Pliocene of Primory'e have been reconstructed for the first time.

In Pavlovskaya Depression the xylotaphocoenosis is presented by a mixing of plant remains from valley and slope habitat conditions. Valley vegetation is characterized by a considerable presence of conifers and elms, while coniferous-hardwood and mixed coniferous forests are characteristic of slope vegetation. Probably, wood remains were transported to the site of their accumulation by water. Perhaps, that was one of the left tributaries of the paleo-Razdol'naya River and has a source somewhere in spurs of the Southern Sikhote-Alin.

On the basis of taxonomical analysis of the fossil plant remains and information on environments of the related extant species the following plant communities have been reconstructed (Figure 2). The bottom-land of valley was covered by willow of *Chosenia arbutifolia* and alder shrubs. The low terrace was overgrown with elm thickets of *Ulmus* aff. *japonica*. In the high terrace they included an admixture of *Padus* aff. *maackii*, *Malus mandshurica*, *Tilia*, *Eleuterococcus* aff. *sessiliflorus*, spruce *Piceoxylon pavlovskiense* as well as larches *Larix* aff. *olgensis*, *Laricioxylon pavlovskiense* and *L. ussuriensis*; *Spiraea* and *Corylus* were present in undergrowth and *Sambucus* - in ravines. Oak forests of *Quercus pavlovskiense* as well as spruce forests may also grow in this terrace, and larch forests occurred there in the lower sites.

Coniferous-hardwood forests of spruce *Piceoxylon pavlovskiense*, larches *Larix* aff. *olgensis*, *Laricioxylon pavlovskiense* and *L. ussuriensis*, *Quercus pavlovskiense*, *Castanea*, *Fagus* and *Carpinus* with an admixture of *Ulmus* aff. *laciniata*, *Padus* aff. *maackii*, *Malus mandshurica*, *Cerasus sargentii*, *Crataegus*, *Corylus*, *Tilia*, *Fraxinus*, birch *Betuloxylon*, *Acer* cf. *tegmentosum* and *Aralia* L. grew in the low belt of hills removed far from the valley. Perhaps, spruce and larch forests also occurred in this belt.

Upslope coniferous forests were presented of spruces *Picea* cf. *bicolor* and *Piceoxylon ussuriense*, larch *Laricioxylon ussuriensis*, *Pinus*, *Abies* aff. *sachalinensis* and *Pseudotsugoxylon pavlovskiense*. Apparently, they grew far from the valley and covered southern spurs of the Sikhote-Alin. Probably, pure spruce and larch forests were also spread there.

As it may testify from the comparative analysis of the Pliocene and modern Primorye flora, during the post Pliocene time *Abies sachalinensis*, *Picea bicolor*, *Pseudotsuga*, *Tsuga*, *Magnolia*, *Celtis*, *Pterocarya*, *Carya*, *Castanea* и *Fagus* have disappeared from this region, and *Larix olgensis* has reduced its area.

PALAEOCLIMATE RECONSTRUCTION BASED ON

WOOD ANATOMY

Some wood anatomical attributes are correlated with habitat conditions. The presence of distinct growth rings in the fossil woods studied is the evidence that trees vegetated under condition of well-pronounced seasonality. The widest growth rings were found in *Larix* aff. *olgensis* (4 mm) and *Ulmus* (5 mm), while the narrowest rings (0.2 mm) occur in *Piceoxylon pavlovskiense* and *P. ussuriense*.

Late wood occupies not more than 1/2 of the growth ring width (1/5-1/4 on the average). The narrowest zone of late wood was found in *Piceoxylon ussuriense* (1/7 of the ring width) as well as in *Abies* aff. *sachalinensis* and *Laricioxylon pavlovskiense* (1/6 of the ring width). The widest zone of late wood was found sometimes in *Piceoxylon pavlovskiense*, *P. ussuriense* and *Pseudotsugoxylon* (up to 1/2 of the ring width).

Transition from early to late wood is rather abrupt or well pronounced in *Pseudotsugoxylon*, *Larix-Laricioxylon* and *Ulmus*; although, more or less gradual transition can be observed in the widest growth rings of *Larix*- and *Pseudotsuga*-wood. On the other hand, transition from early to late wood in *Cerasus*, *Eleutherococcus*, *Abies* and *Picea-Piceoxylon* is gradual; although, rather marked transition can be observed in narrow rings of the *Picea*-wood. Apparently, trees vegetated under relatively mild warm temperate climate throughout the year with considerable humidity during autumn-winter season.

False rings occur in *Piceoxylon pavlovskiense* and *Larix* aff. *olgensis*. Abundant traumatic vertical resin canals or cysts were found in *Abies* aff. *sachalinensis*, *Piceoxylon pavlovskiense* and *P. ussuriense*. Disturbance of tracheid growth ("twisted tracheids") occurs in *P. pavlovskiense*. Most likely, all these anatomical structure features are the reaction of cambium activity in response to damages on account of insects, animals, winds, frosts, etc.

Thus, on the basis of fossil woods anatomy, it may be supposed that climate was, probably, well pronounced seasonal, relatively warm temperate throughout the year and with rather snowy and mild winter. Although, there were, perhaps, years with more severe weather conditions.

CONCLUSIONS

Fossil woods from the Pliocene of both Primorye and Russian Far East as a whole have been studied for the first time. As a result of this study the additional information on taxonomic diversity of the Russian Far East arboriflora in the Pliocene has been obtained. Representatives of the families Pinaceae, Ulmaceae, Fagaceae, Betulaceae, Salicaceae, Rosaceae, Aceraceae, Araliaceae, Oleaceae and Caprifoliaceae were identified by

wood anatomy.

In Pavlovskaya Depression (Southern Primory'e) the xylophocoenosis is presented by a mixing of plant remains from valley and slope habitat conditions. Valley vegetation is characterized by a considerable presence of conifers and elms, while coniferous-hardwood and mixed coniferous forests are characteristic of slope vegetation. Probably, wood remains were transported to the site of their accumulation by water that was, perhaps, one of the left tributaries of the paleo-Razdol'naya River and has a source somewhere in spurs of the Southern Sikhote-Alin.

On the basis of taxonomical analysis of the fossil plant remains and information on environments of the related extant species the following plant communities have been reconstructed. The bottom-land of valley was covered by willow and alder shrubs. The low terrace was overgrown with elm thickets. In the high terrace they included an admixture of *Padus*, *Malus*, *Tilia*, *Eleuterococcus*, spruce and larches; *Spiraea* and *Corylus* were present in undergrowth and *Sambucus* - in ravines. Oak forests as well as spruce forests may also grow in this terrace, and larch forests occurred there in the lower sites.

Coniferous-hardwood forests of spruce, larches, *Quercus*, *Castanea*, *Fagus* and *Carpinus* with an admixture of *Ulmus*, *Padus*, *Malus*, *Cerasus*, *Crataegus*, *Corylus*, *Tilia*, *Fraxinus*, birch, *Acer* and *Aralia* grew in the low belt of hills removed far from

the valley. Perhaps, spruce and larch forests also occurred in this belt.

Upslope coniferous forests were presented of spruces, larch, *Pinus*, *Abies* and *Pseudotsugoxylon*. Apparently, they grew far from the valley and covered southern spurs of the Sikhote-Alin. Probably, pure spruce and larch forests were also spread there.

Woody plant communities and their environments in the Pliocene of Pavlovskaya Depression like of Primory'e as a whole were reconstructed for the first time. During the post Pliocene time *Abies sachalinensis*, *Picea bicolor*, *Pseudotsuga*, *Tsuga*, *Magnolia*, *Celtis*, *Pterocarya*, *Carya*, *Castanea* и *Fagus* have disappeared from Primory'e and *Larix olgensis* has reduced its area.

On the basis of fossil woods anatomy, it may be supposed that climate was, probably, well pronounced seasonal, relatively warm temperate throughout the year and with rather snowy and mild winter. Although, there were, perhaps, years with more severe weather conditions.

Acknowledgments

The authors are grateful to the Russian Foundation for Basic Research (grant No 01-04-48095) and Presidium of the Far Eastern Branch of the Russian Academy of Sciences (grant No 03-1-0-06-002) for supporting of this work.

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PLATES, TABLES AND FIGURES EXPLANATIONS

FIGURE 1.

Map of Russian Far East showing location of the studied area

FIGURE 2.

Scheme of the possible high altitude zonation of the Pliocene woody assemblages within Pavlovskaya Depression

TABLE 1

Fossil woods of the Pinaceae from the Pavlovskaya Depression and their related extant analogues

TABLE 2

Fossil woods of Dicotyledones from the Pavlovskaya Depression and their related extant analogues

TABLE 3

Environments of the related extant species

PLATE I.

Figures 1-3. Collecting site of the Pliocene fossil woods (Pavlovskaya Depression, Southern Primory'e).

Fig. 1. Section of the Suifunskaya Suite. An arrow indicates the upper part of the Suite containing fossil wood remains.

Fig. 2. Palaeobotanist O.V. Bondarenko. Fossil wood log in horizontal bedding.

Fig. 3. Piece of the lignitic fossil wood approximately 75 cm in length and 12x30 cm in diameter.

WOODY PLANT ASSEMBLAGES AND PALAEOENVIRONMENTS IN THE PLIOCENE OF PAVLOVSKAYA DEPRESSION (SOUTHERN PRIMORYE)

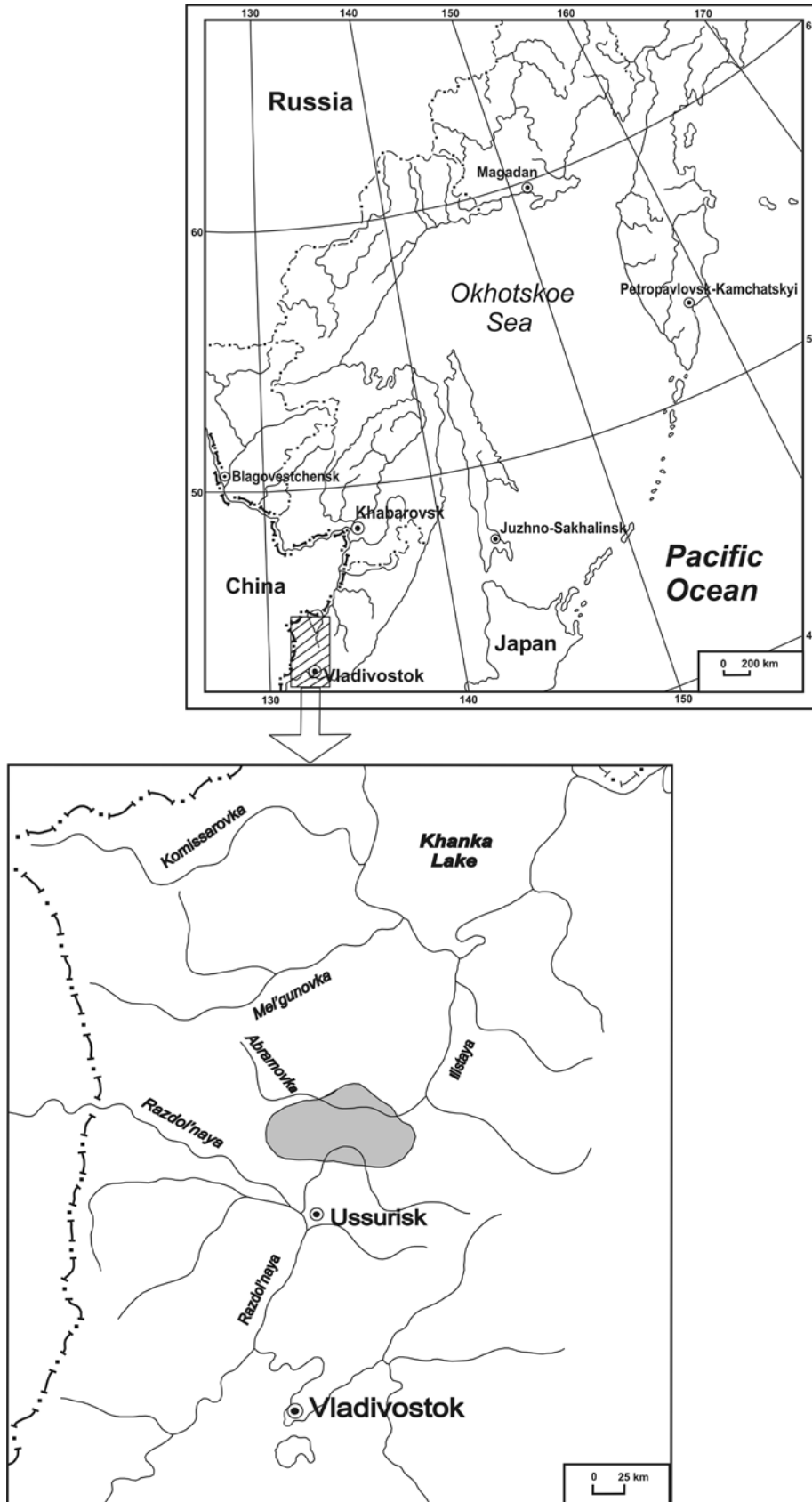


Figure 1. Map of Russian Far East showing location of the studied area.

■ - Pavlovskaya Depression

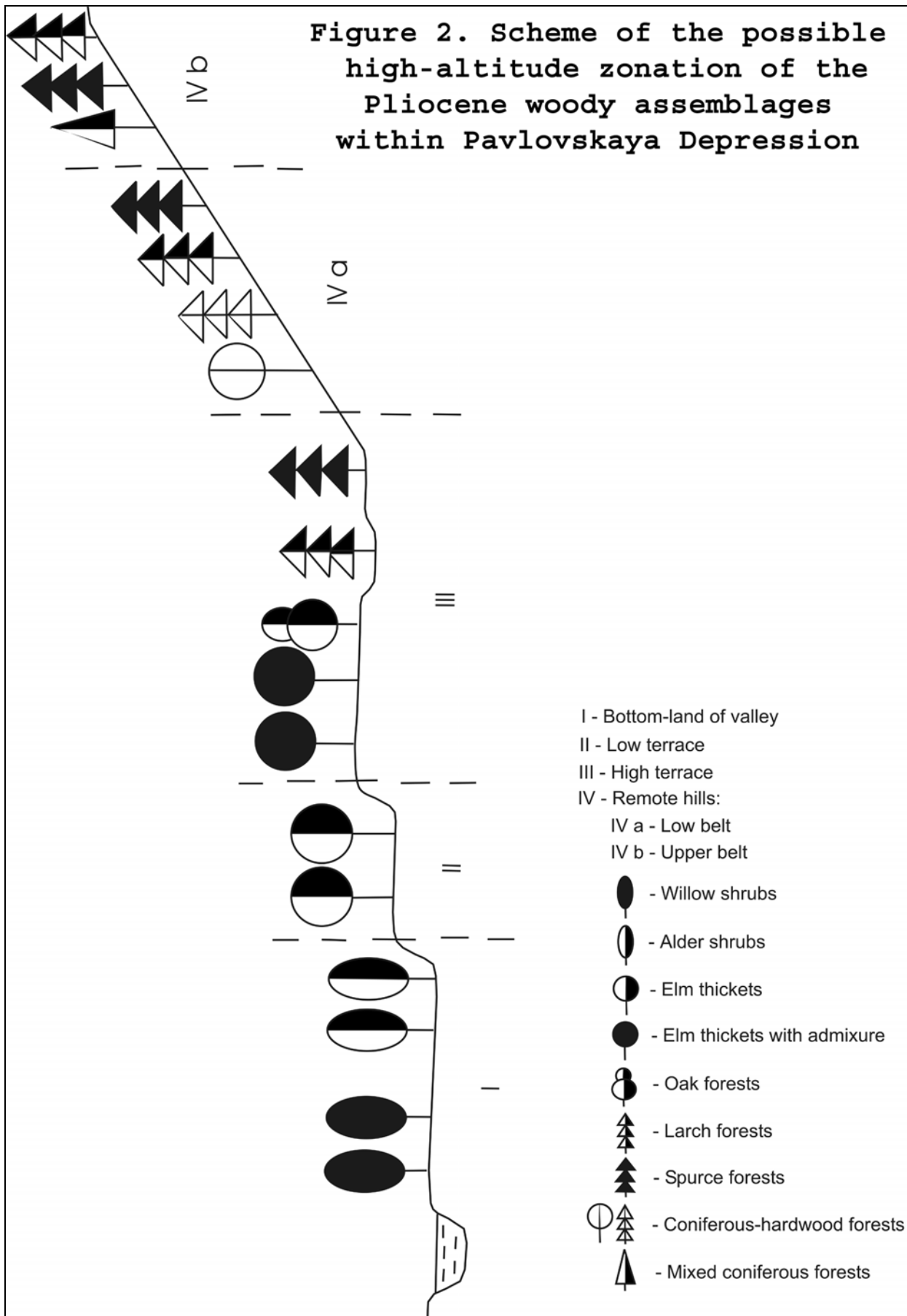


Table 1

**Fossil woods of the Pinaceae from the Pavlovskaya Depression and
their related extant analogues**

No	Fossil species	Related extant species	
		species	areal
1.	<i>Abies</i> aff. <i>sachalinensis</i> Fr. Schmidt	<i>Abies sachalinensis</i> Fr. Schmidt	Sakhalin, the southern Kuril Islands, northern Hokkaido
2.	<i>Pseudotsugoxylon</i> <i>pavlovskiense</i> Blokh. et Bondar.	<i>Pseudotsuga menziesii</i> (Mirb.) Franco <i>Pseudotsuga macrocarpa</i> (Vasey) Mayr	the pacific coast of Canada and the USA northern California Peninsula (Mexico), southern the state California (USA)
3.	<i>Picea</i> cf. <i>bicolor</i> (Maxim.) Mayr	<i>Picea bicolor</i> (Maxim.) Mayr	central Japan
4.	<i>Piceoxylon</i> <i>pavlovskiense</i> Blokh. et Bondar.	<i>Picea koraiensis</i> Nakai <i>Picea jezoensis</i> (Siebold et Zucc.) Carr. <i>Picea sitchensis</i> (Bong.) Carr.	Southern Primory'e, Korea Peninsula central Kamchatka, the Okhotskoe Sea coast, the Middle Amurian Basin, Primory'e, Sakhalin, the southern Kuril Islands, north- eastern China, Korea Peninsula, Japan the states: western British Columbia (Canada); southern Alaska, Oregon, north- western California (USA)
5.	<i>Piceoxylon</i> <i>ussuriense</i> sp. nov.	<i>Picea koraiensis</i> <i>Picea likiangensis</i> (Franch.) Pritz.	(see no. 4) China
6.	<i>Larix</i> aff. <i>olgensis</i> A. Henry	<i>Larix olgensis</i> A. Henry	Primory'e (the coast from Valentine to Vladimir Bays)
7.	<i>Laricioxylon</i> <i>pavlovskiense</i> Blokh. et Bondar.	<i>Larix occidentalis</i> Nutt. <i>Larix gmelinii</i> (Rupr.) Rupr. <i>Larix olgensis</i>	the states: British Columbia (Canada); Washington, Montana, Idaho (USA) Middle and Eastern Siberia, northern Inner Mongolia, north-eastern China (see no. 6)
8.	<i>Laricioxylon</i> <i>ussuriensis</i> sp. nov.	<i>Larix olgensis</i> <i>Larix leptolepis</i> (Siebold et Zucc.) Gord.	(see no. 6) central Honshu

Table 2

Fossil woods of Dicotyledones from the Pavlovskaya Depression and their related extant analogues

N o	Fossil species	Related extant species	
		species	Areal
1.	<i>Ulmus</i> aff. <i>japonica</i> (Rehd.) Sarg.	<i>Ulmus japonica</i> (Rehd.) Sarg.	Eastern Siberia, Russian Far East, Mongolia, China, Japan
2.	<i>Ulmus</i> aff. <i>laciniata</i> (Trautv.) Mayr	<i>Ulmus laciniata</i> (Trautv.) Mayr	Khabarovskiy Territory, Primory'e, Sakhalin, the Kuril Islands
3.	<i>Quercus pavlovskiense</i> sp. nov.	<i>Quercus crispula</i> Blume.	Sakhalin, the Kuril Islands, Korea Peninsula, Japan
4.	<i>Chosenia arbutifolia</i> (Pall.) A. Skvort.,	<i>Chosenia arbutifolia</i> (Pall.) A. Skvort.	Russian Far East
5.	<i>Padus</i> aff. <i>maackii</i> (Rupr.) Kom.	<i>Padus maackii</i> (Rupr.) Kom.	Amurian Region, Khabarovskiy Territory, Primory'e
6.	<i>Cerasus sargentii</i> (Rehd.) Pojark.	<i>Cerasus sargentii</i> (Rehd.) Pojark.	Southern Primory'e, Sakhalin, Kunashir, north-eastern China, Korea Peninsula, Japan
7.	<i>Malus manshurica</i> (Maxim.) Kom.	<i>Malus manshurica</i> (Maxim.) Kom.	Southern Primory'e
8.	<i>Eleutherococcus</i> aff. <i>sessiliflorus</i> (Rupr. et Maxim.) Seem.	<i>Eleutherococcus sessiliflorus</i> (Rupr. et Maxim.) Seem.	southern Khabarovskiy Territory, Priamury'e, Primory'e, northern China, northern Korea Peninsula
9.	<i>Acer</i> cf. <i>tegmentosum</i> Maxim.	<i>Acer tegmentosum</i> Maxim.	Priamury'e, Khabarovskiy Territory, Primory'e

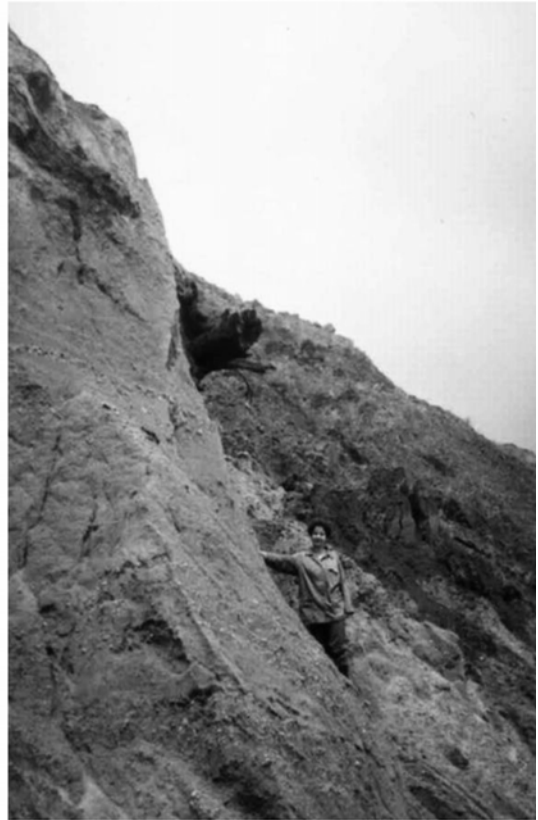
Table 3

Environments of the related extant species

Extant species	Environments
<i>Abies sachalinensis</i>	Mountain mixed dark-coniferous forests together with <i>Picea jezoensis</i> and <i>Larix gmelinii</i> , sometimes pure <i>Abies</i> -forests; (400) 800-1100 m above sea level.
<i>Pseudotsuga menziesii</i>	Coniferous and coniferous-hardwood forests; up to 1800 m above sea level.
<i>P. macrocarpa</i>	Mixed coniferous forests.
<i>Picea bicolor</i>	Mountain forests.
<i>P. koraiensis</i>	Marshy valley forests together with <i>Abies nephrolepis</i> and <i>Picea jezoensis</i> .
<i>P. jezoensis</i>	Dominant in dark-coniferous forests; mountain dark-coniferous forests, an admixture in low terrace forests.
<i>P. sitchensis</i>	Mixed or pure <i>Picea</i> -forests along on the flooded river; mountain forests up to 900-1000 m above sea level.
<i>P. likiangensis</i>	Mountain forests; 2500-4000 m above sea level.
<i>Larix olgensis</i>	Coniferous-hardwood forests; up to 100-500 m above sea level.
<i>L. occidentalis</i>	Mixed coniferous forests or sometimes pure <i>Larix</i> -forests; 600-1200 m above sea level.
<i>L. gmelinii</i>	Pure <i>Larix</i> -forests or with an admixture of hardwoods.
<i>L. leptolepis</i>	Mountain forests, 500-2300 m above sea level.
<i>Ulmus japonica</i>	Coniferous-hardwood forests together with <i>Pinus koraiensis</i> , <i>Picea</i> , <i>Larix</i> ; hardwood forests; rarely - valley forests together with <i>Populus</i> and <i>Salix</i> .
<i>U. laciniata</i>	Coniferous-hardwood forests; up to 600-700 m above sea level.
<i>Quercus crispula</i>	An admixture in hardwood and coniferous-hardwood forests, sometimes pure Oak-forests; up to 220-400 m above sea level.
<i>Chosenia arbutifolia</i>	Pure or mixed willow on the bottom-lands of mountain rivers; up to 700-800 m above sea level.
<i>Padus maackii</i>	Coniferous-hardwood or rarely hardwood forests; usually on slopes in the low belt of hills.
<i>Cerasus sargentii</i>	Mixed coniferous-hardwood forests; in the low belt of hills.
<i>Malus mandshurica</i>	Hardwood and coniferous-hardwood forests, in the low belt of hills.
<i>Eleutherococcus sessiliflorus</i>	Mixed coniferous-hardwood forests.
<i>Acer tegmentosum</i>	Mixed coniferous-hardwood forests.



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