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Paleogene Coal-forming Plants of the Zeya–Bureya Basin (Amur River Region)

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Abstract—Coal-forming plants from the Early Paleogene coal mines of the Zeya–Bureya Basin (Amur River Region) were studied. Dispersed cuticles of taxodialeans were obtained from coals for the first time in this region. Since the Danian, taxodialeans became dominant elements in peat-forming environments and provided abundant plant material that transformed into coal.

Key words: Paleogene, Zeya–Bureya Basin, coal-forming plants, taxodialeans.

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INTRODUCTION

Upper Cretaceous and Cenozoic deposits are widespread in the Zeya–Bureya Basin. Our data show that the basin started to fill with sediments in the Santonian. At the base of the stratigraphic sequence, there is the Kundur Formation (Santonian to Campanian), which correlates with the Yongancun and Taipinglinchang formations on the right bank of the Amur River (Markevich et al., 2005b, 2005c). The Tsagayan Formation (Maastrichtian to Danian) conformably overlies the Kundur Formation. On the right bank, the Yuliangzi, Furao, and Wuyun formations occupy the same stratigraphic position as the Tsagayan Formation (*Regional Geology* ..., 1993; *Flora and Dinosaurs* ..., 2001; Akhmetiev et al., 2002; Markevich et al., 2004; Sun et al., 2004; Kezina, 2005a, 2005b).

Long-term studies of the Cretaceous and Early Paleogene palynostratigraphy of the Zeya–Bureya Basin have provided taxonomically rich palynofloras; palynological assemblages of different ages, with characteristic species, have been recognized; wide interregional correlation was performed to date particular strata (Markevich, 1994; *Flora and Dinosaurs* ..., 2001; Markevich et al., 2004, 2005a). The Arkhara–Boguchan, Raichikhinsk, and Wuyun brown coal mines are located in the southeastern part of the Zeya–Bureya Basin (Fig. 1). Our study dated these coals to the Early Paleocene, most likely, Late Danian (Markevich et al., 2004, 2005a; Markevich and Bugdaeva, 2008). At that time, environmental conditions favored the formation of extensive mires. The phytomass became mortmass which in turn was transformed into the brown Amur coals.

MATERIAL AND METHODS

Many elements of the coal-forming plant community can still be identified in the coal. At the time of the mire formation and growth, climatic conditions were such that very little sediment was being transported

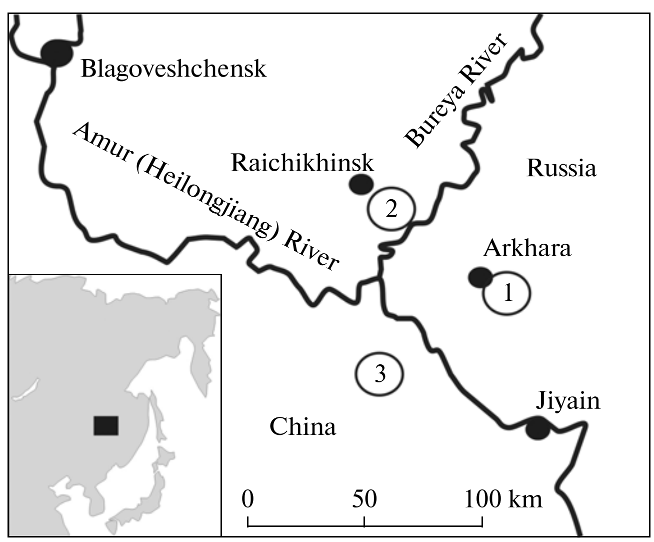


Fig. 1. Distribution of brown coal mines in the southeastern Zeya–Bureya Basin: (*1*) Arkhara–Boguchan; (*2*) "Pioneer" section of Raichikhinsk; and (*3*) Wuyun.

into the basin allowing biogenic sedimentation, with almost complete absence of clastic sediments. Therefore, it is possible to assume that plants that gave rise to the coal deposits were autochthonous and provided the first elements of peat accumulation. Since the clastic deposits represent the material transported from the source area, phytofossil assemblages from the terrigenous deposits between the coal layers are often mixed, consisting of elements from both the slope and lowland communities.

Sections of the Wuyun Coal Mine on the right bank of the Amur River were sampled and described in 2002 and 2008; the Arkhara–Boguchan and Raichikhinsk (section "Pioneer") coal mines, in August 2003. This work was done within the framework of the International Project "Cretaceous Biota and the K–T Boundary of Heilongjiang (Amur) River Area" under direction of Prof. Sun Ge (Jilin University and Shenyang Normal University, Chinese Peoples' Republic).

The following materials were used in this study: Arkhara–Boguchan Coal Mine, 29 samples (collection No. AB1153); Raichikhinsk Coal Mine (section "Pioneer"), 9 samples (collection No. P1107); and Wuyun Coal Mine, 7 samples (collection No. W1076). Dispersed cuticles were separated from coals of the Wuyun mine (Pl. 30). All collections are stored in the Institute of Biology and Soil Science of the Far East Branch of the Russian Academy of Sciences, Vladivostok (IBSS). Samples for the spore–pollen analysis were processed using the standard maceration method proposed by Lüber and Waltz for highly metamorphosed rocks and coals ("Paleopalynology," 1966). To obtain cuticles, the coals were oxidized by concentrated nitric acid, washed with distilled water, then, treated with 10% alkali (KOH) and rinsed.

The cuticular membranes were mounted on permanent slides for observation under a light microscope (LM) or were placed on standard stubs, splutter coater with gold and imaged using a scanning electron microscope (SEM). Photographs were produced by L.F. Simanenko, using a Zeiss Axioplan 2 imaging light microscope (FEGI FEB RAS), by N.N. Naryshkina, using a Zeiss EVO-40 scanning electron microscope, and authors, using a Zeiss Axioscop 40 with camera Axiocam HRc light microscope (IBSS FEB RAS).

Arkhara–Boguchan Coal Mine

This mine produces coal from four productive seams (upward in the section): "Nizhnii" (about 2 m thick), "Dvoinoi" (about 8 m), "Promezhutochnyi" (less than 1 m), and "Velikan" (about 10 m). In the section studied, the uppermost coal seam is absent (Fig. 2).

The palynospectrum (sample 01) from a thin (about 25 cm thick) clay bed approximately in the middle of the "Nizhnii" seam is dominated by fern spores, mostly *Cyathidites* Couper and *Laevigatosporites* Ibrahim. Gymnosperm pollen is represented by abundant Pinaceae and Taxodiaceae. Angiosperms are rare, dominated by *Aquilapollenites* Rouse (Fig. 3).

In the palynospectrum from the lower coal seam (samples 02, 03), the number of fern spores and pollen of Taxodiaceae, Cupressaceae, and Taxaceae (TCT) are reduced. The relative abundance of the Pinaceae increases, so that it predominates. Angiosperms are rare, as before; the proportion of plants producing "unica"-type pollen, sharply irreversibly declines. Gymnosperm pollen, mostly TCT and Pinaceae, prevails in the palynospectrum from the clay of the lower plant-bearing bed (samples 04–07, 09–11, 13–15). Spores of *Laevigatosporites* are abundant. The diversity of angiosperms increases with the appearance of *Triatriopollenites* Pflug. Taxonomic diversity of the palynospectrum from a paleosoil (sample 17) is very low. Pollen of the Pinaceae and Taxodiaceae is abundant. Angiosperms are absent.

The proportion of *Laevigatosporites* in the palynospectrum from the lower coal interlayer of the "Dvoinoi" seam (samples 19, 20) sharply increases (57.8%), the proportions of all other main groups decrease. The palynospectrum from the siltstone layer (samples 21, 22) is similar in taxonomic composition to that from the previous layer. *Laevigatosporites* predominates (69%), the proportions of all other plant groups are insignificant.

In sample 25 from the upper coal interlayer of "Dvoinoi" seam, the proportions of the ferns *Cyathidites* and *Laevigatosporites* (18%) and Pinaceae (19%) are almost equal. The proportion of flowering plants, particularly those producing porate pollen, increases to 17%.

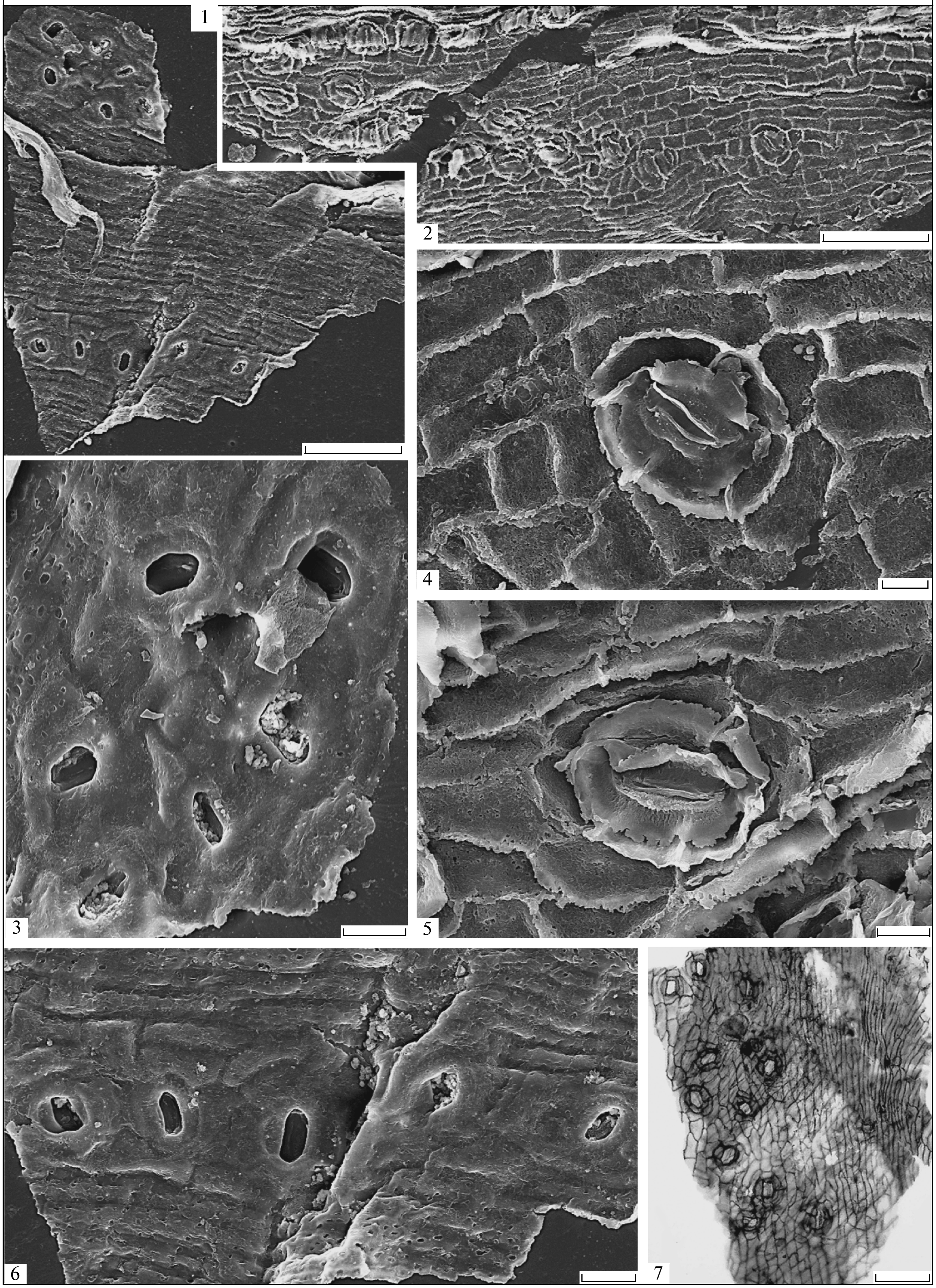
In samples 26–29 from the plant-bearing clay, the proportions of taxodialeans and angiosperms with porate pollen increase considerably (33 and 21%, respectively).

Sample 30 collected from sandstone is similar in the proportions of taxodialeans and angiosperms with porate pollen (27%) to the sample just below it from clay. The two groups are dominants in the palynospectrum from sandstone.

Explanation of Plate 30

Figs. 1–8. Dispersed cuticle of *Taxodium* sp., sample no. WII-146,2, coals of the Wuyun Coal Mine in the Zeya–Bureya Basin, Amur River Region, Wuyun Formation: (1) stomatal band, internal view; (2) two stomatal and nonstomatal bands, external view; (3) distribution of stomata in the band, internal view; (4) concentric arrangement of the stomata around cutinized cell, external view; (5, 6) stoma, internal view; (7) stomatal band, with stomata oriented transversely relative to veins, external view; (8) stomatal and nonstomatal bands. Scale bar in (1, 4, 7) 20 μm, (2, 3, 8) 100 μm, (5, 6) 10 μm. (1–7) SEM, (8) LM.

Plate 30



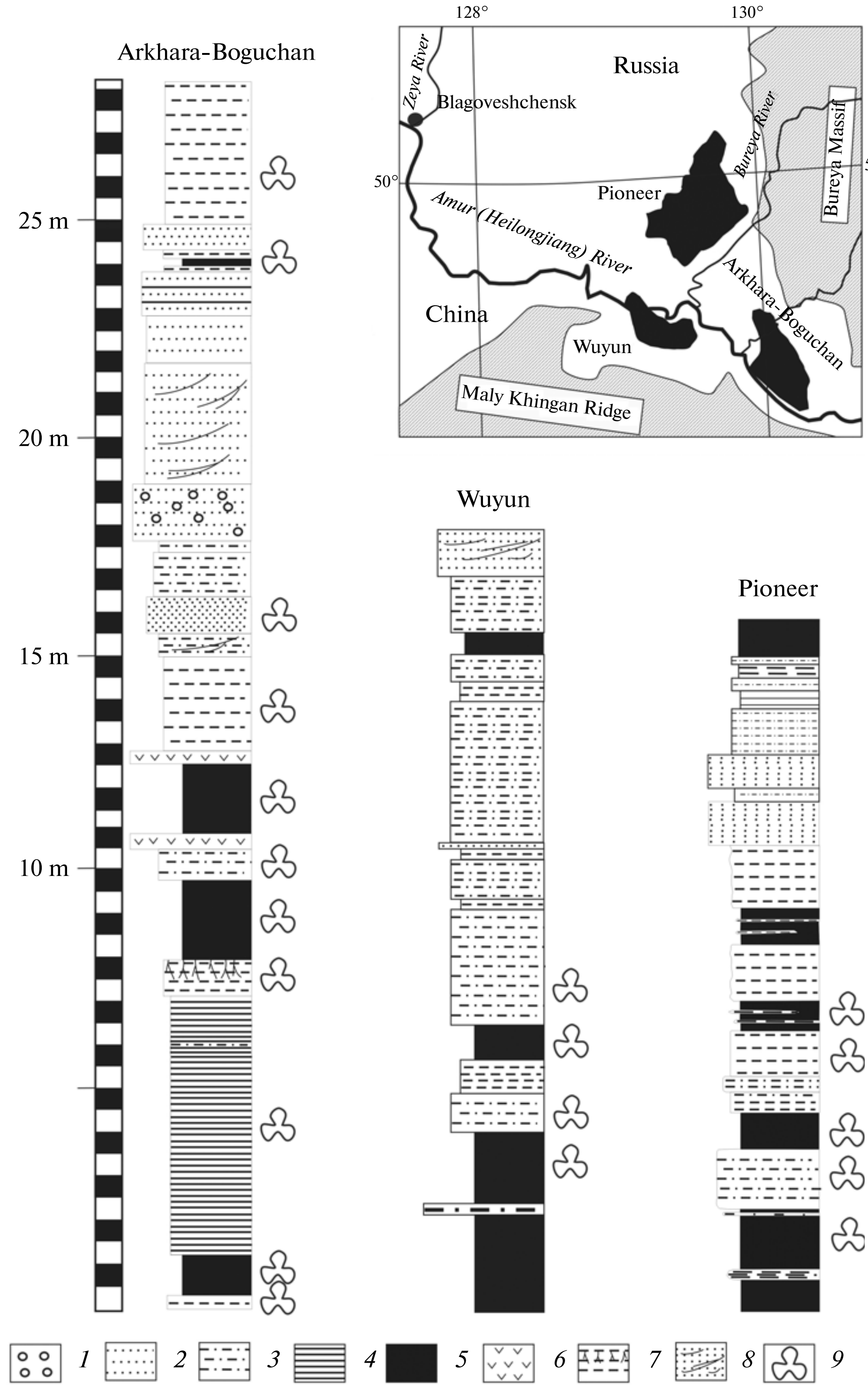


Fig. 2. Geological sections of the Arkhara–Boguchan, Wuyun, and "Pioneer" brown coal mines. Inset is a schematic paleogeographic map of the time of coal formation in the Zeya–Bureya Basin, where white color shows the valley, gray is mountainsides framing the valleys, black is swamp lowlands; designations: (*1*) conglomerate, (*2*) sandstone, (*3*) siltstone; (*4*) clay, (*5*) coal, (*6*) rhyolite tuff; (*7*) paleosoil; (*8*) cross-bedding structures; (*9*) points of sampling.

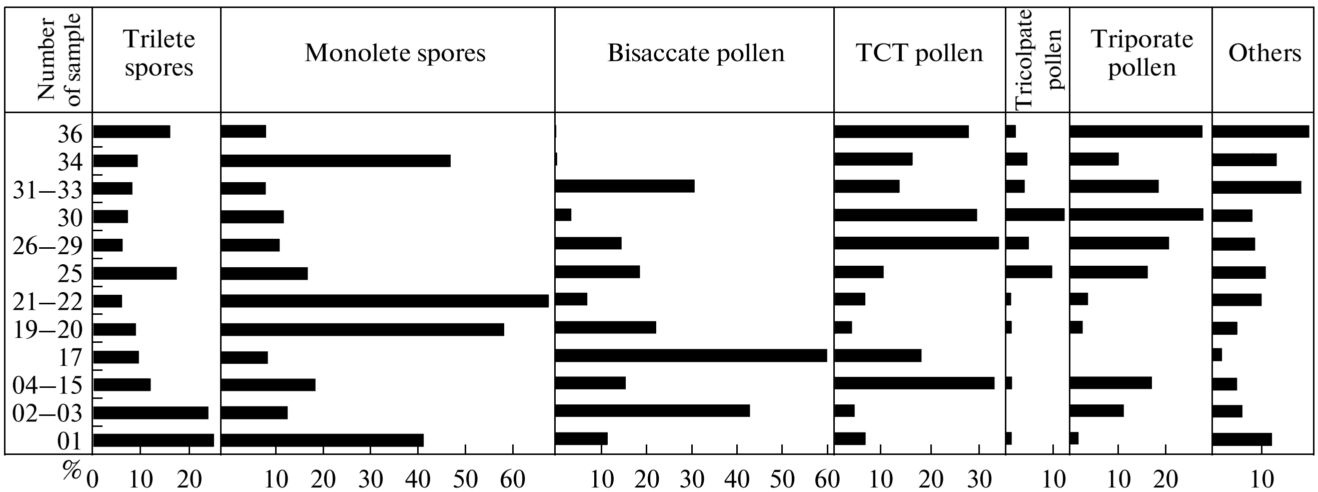


Fig. 3. Relative abundance of the major groups of spores and pollen in the palynospectra from the Arkhara–Boguchan Coal Mine.

The palynospectra of siltstone samples 31–33 are dominated by Pinaceae, the proportions of ferns and taxodialeans are reduced, and the proportion of angiospermous pollen remains the same.

In a thin coal seam (sample 34), the proportion of *Laevigatosporites* sharply increases to 47%, at that of angiosperms decreases to 14%. Conifers are rare, with the taxodialeans at 16%, Pinaceae are almost absent.

In the palynospectra from plant-bearing clay (sample 36), the proportions of ferns, taxodialeans, and angiosperms with porate pollen are almost equal, 22, 28, and 28%, respectively.

Detailed paleobotanical studies of this locality were carried out by M.A. Akhmetiev, T.M. Kodrul, S. Manchester, M.G. Moiseeva, and V.A. Krassilov. The most abundant floristic assemblage comes from the clay member between the layers "Nizhnii" and "Dvoinoi" (Akhmetiev et al., 2002; Kodrul et al., 2006). In the basal part of plant-bearing clays, the taphocenoses are dominated by *Taxodium* (L.) Richard, *Sequoia* (D. Don) Endl., *Mesocyparis rosanovii* Kodrul, Tekleva et Krassilov, and *Nyssa* L. In other layer, *Dyrana flexuosa* (Newb.) Golovn. dominates. Upward in the section, leaves of *Taxodium* are common, *Onoclea* L. and *Averrhoites* Hickey are locally abundant. *Mesocyparis rosanovii* and members of the Platanaceae are rare. In the burial from the upper part of clays, *Taxodium* becomes subordinate, as the monocots are dominant here. *Trochodendroides* Berry, *Zizyphoides* Newberry, *Beringiaphyllum* Manchester, Crane et Golovneva, and Platanaceae become dominants. The Platanaceae are represented by leaves and reproductive organs (Maslova and Kodrul, 2003; Maslova et al., 2007; Kodrul and Maslova, 2007). These plants apparently grew close to the place of burial and have not undergone long transportation. The megafloral assemblage from the clay roof of "Dvoinoi" seam includes taxodialeans, *Trochodendroides*, *Zizyphoides*, and members of the Platanaceae (Akhmetiev et al., 2002).

Raichikhinsk Coal Mine, Section Pioneer

The section studied is situated in the southeastern part of the Rajchikhinsk Brown Coal Mine (Figs. 1, 2). It is represented by alternating siltstones, sandstones, and five coal seams, the thickness of which varies from 0.5 m to 2.5 m.

A total of five layers were sampled. The palynospectrum from the lower coal seam (sample IV) is dominated by gymnosperms, with abundant bisaccate pollen of Pinaceae (34%). Pollen of the families Taxodiaceae, Cupressaceae, and Taxaceae amounts 15.2%. The contribution of spore plants is substantial (24%). The role of angiosperms is insignificant; they are represented mostly by porate pollen of plants close to Juglandaceae (Fig. 4).

In the palynospectrum from siltstone (sample VIII), which overlies the lower coal seam, bisaccate pollen predominates (46%). TCT pollen accompanies it (26%). The proportions of spore plants (11%) and angiosperms (less than 10%) decrease sharply.

In the palynospectrum from the second coal seam (samples IX–XII) bisaccate pollen still predominates (40.2%). The significance of TCT pollen (38%) increases. The proportions of both spore plants and angiosperms slightly decrease, 11 and 8.7%, respectively. It should be noted that the diversity of spores, despite a decrease in their number, increases due to the appearance of spores of Gleicheniaceae, Osmundaceae, and Schizaeaceae as well as lycopods and bryophytes, such as liverworts.

In the palynospectrum from the overlying siltstone layer (samples XIV, XV), both pollen Pinaceae (27%) and Taxodiaceae (28%) almost equally predominate. The proportions of spore plants and angiosperms

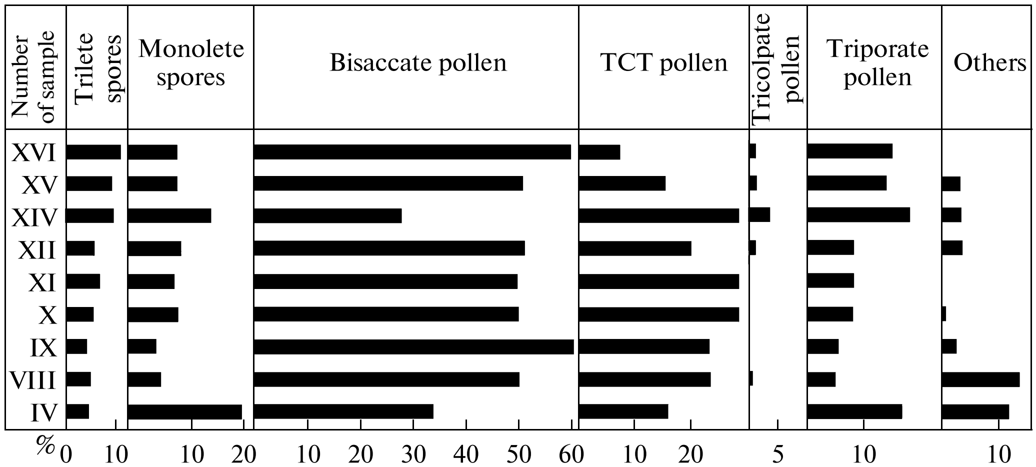


Fig. 4. Relative abundance of the major groups of spores and pollen in the palynospectra from the "Pioneer" section of Raichikhinsk Coal Mine.

increase (14 and 16%, respectively). Bryophytes almost disappear (0.3%).

In the palynospectrum from the third coal seam (sample XVI), Pinaceae becomes absolute dominant (60%). Taxodialeans lose their dominant role (7.5%). The relative abundance of spore plants and angiosperms remain constant.

Plant megafossils were collected in the coal bottom and roof layers (the main part of the collection) of the section (Akhmetiev et al., 2002; *The 2nd International Symposium ...,* 2003). A large number of remains of conifers, primarily Taxodiaceae (*Metasequoia disticha* (Heer) Miki, *Taxodium dubium* (Sternb.) Heer, *Glyptostrobus europaeus* (Brongn.) Heer), as well as Cupressaceae and Pinaceae were found. Impressions of Platanaceae, *"Acer" arcticum* Heer and *Trochodendroides arctica* (Heer) Berry, are common. The male inflorescences, presumably belonging to plants with leaves *Trochodendroides* have been found (Golovneva, 2006; Krassilov and Kodrul, 2008).

Note that opinions differ as to the composition of the genus *Trochodendroides.* For example, Kryshtofovich and Baikovskaya (1966) recognized the following leaf forms: (1) *Trochodendroides arctica* (Heer) Berry, (2) *T.* cf. *genetrix* (Newb.) Brown, (3) *T. richardsonii* (Heer) Krysht., (4) *T. smilacifolia* (Newb.) Krysht., (5) *T. speciosa* (Ward) Berry, (6) *T. elliptica* (Newb.) Krysht., (7) *Cercidiphyllum crenatum* (Ung.) Brown, (8) *Tetracentron amurensis* Krysht., (9) *Zyzyphus fibrillosa* Lesq., (10) *Z. hyperborea* Heer, (11) *Z. phosphoria* Krysht., (12) *Paliurus* cf. *colombii* Heer, and (13) *Ficus praetrinervis* Knowlt.

Krassilov (1976) believed that the genus *Trochodendroides* is polymorphic and all the above forms are variations of one species, *T. arctica* (Krassilov,. According to Akhmetiev et al. (2002), the genus *Trochodendroides* comprises leaves with palmate venation and evenly spaced shallow crenate teeth with apical glandules, while leaves similar to *Trochodendroides* in morphology, with entire margin or with margin having rare, irregularly arranged, rounded teeth with an apical glandule or without it, belong to the genus *Zizyphoides.*

The study of male inflorescences, tentatively assigned to plants with leaves *Trochodendroides*, allowed for the first time to obtain data on their pollen grains (Krassilov and Kodrul, 2008). Pollen grains are relatively small, tricolpate, with long furrows and sculpture ranging from fine reticulate to verrucous–scabrous. These authors proposed that *Trochodendroides* which produced similar pollen grains, is related to Hamamelidaceae (Krassilov and Kodrul, 2008). However, the palynospectra from Paleocene sediments of the region display a small proportion of hamamelidaceous pollen, although *Trochodendroides* is a dominant of this flora. Apparently, these plants were transported by water flows during floods rather than grew in lowlands. Note that the genus *Trochodendroides* is marked as the fourth most important coal-forming plant after the Taxodiaceae, Cupressaceae, and Araucariaceae (Kezina, 2005a), whereas our data show that, in the palynospectra from the coal deposits studied, pollen of Hamamelidaceae is almost absent (less than 1%).

It is believed that, during the Kivda Time, the flora changed significantly (Akhmetiev et al., 2002). Although taxodialeans and *Trochodendroides* still dominate plant communities, Betulaceae, Myricaceae, Juglandaceae, and Ulmaceae begin to play an important role; in particular, *Ulmus furcinervis* (Bors.) Ablaev, which is typical for Early Paleogene floras of the Far East, appears; it is described from the Bogopol'e and Takhobe formations of eastern Sikhote-Alin and the Wuyun Formation of northeastern China (Ablaev, 1974; Feng et al., 2003). In the spore–pollen spectra, these changes are manifested in

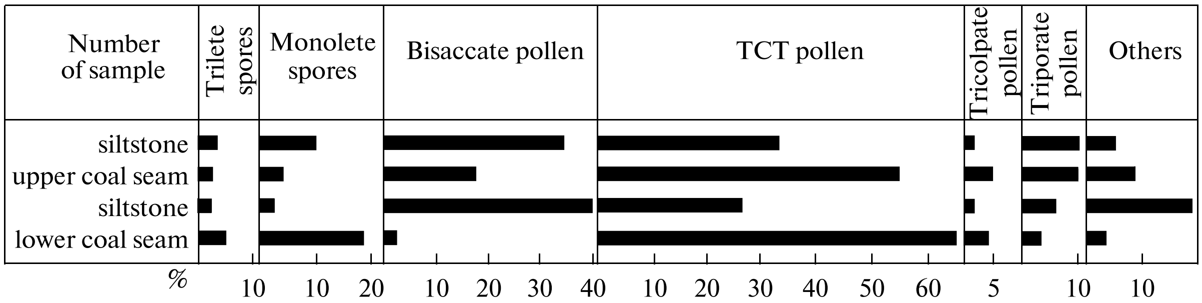


Fig. 5. Relative abundance of the major groups of spores and pollen in the palynospectra from the Wuyun Coal Mine.

an increase in the proportion of porate pollen of Betulaceae, Myricaceae, Juglandaceae, and Ulmaceae combined with the maintenance of dominant positions of Taxodiaceae and Pinaceae.

Wuyun Coal Mine

The Wuyun Coal Mine is located on the right bank of the Amur River (Figs. 1, 2). The section starts with a thick coal seam (palynological samples were taken in its upper part) overlain by 1.5-m-thick aleuropelites. Upward in the section, there is another coal seam (about 0.5 m thick). The sequence is finalized by interbedding sandy and clayey deposits.

The palynospectrum from the lower coal seam is dominated by members of the families Taxodiaceae, Cupressaceae, and Taxaceae (65%). Monolete spores of *Laevigatosporites* follow TCT pollen in abundance. The proportion of palynomorphs of all other plant groups is insignificant (Fig. 5). During coal maceration, abundant xylem elements of taxodiaceous wood and dispersed cuticle of leaves, mostly representatives of the Taxodiaceae, were obtained (Pl. 30).

In the palynospectrum from mudstone overlying the lower coal seam, the proportion of TCT pollen decreases (28%) and the content of bisaccate pollen of Pinaceae increases to 39%. Pollen of *Ginkgocycadophytus* Samoilovich, Ericaceae, *Schizoporites parvus* Cook. et Dettm., and pteridophyte spores of *Osmundacidites wellmanii* Coup., *Concavissimisporites asper* Pock., lycopods *Retitriletes subrotundus* (K.-M.) Sem. occur in a small number.

In the palynospectrum from the upper coal seam, TCT pollen dominates again (55%), while bisaccate pollen decreases to 17%. Throughout the sequence, the proportion of triporate pollen gradual increases; in this seam, it is 10%. Megafossils in residue of this coal are represented by dispersed cuticle and, to a lesser extent, taxodiaceous wood.

In the palynospectrum from mudstone overlying the second coal seam pollen of Pinaceae (35%) and TCT (35%) predominate. Monolete spores and triporate pollen are less frequent (10%). The number of other palynomorphs is insignificant, about 10%. Plant megafossils are abundant. The Wuyun Coal Mine has yielded ferns, ginkgoaleans, Taxodiaceae (*Metasequoia disticha* (Heer) Miki, *Sequoia chinensis* Endo emend. Wang et Li, *Glyptostrobus* sp., *Taxodium* sp.), Cupressaceae (*Thuja cretacea* (Heer) Newb.), and many angiosperms (Tao and Xiong, 1986; *Fossil Floras …,* 1995; Manchester et al., 1999; Feng et al., 2003; Wang et al., 2006; Herman et al., 2009).

DISCUSSION

Coal-forming plants from different strata of the Arkhara–Boguchan Coal Mine are largely similar in composition: they are represented by ferns and Pinaceae. However, the palynospectrum from the upper coal interlayer of the seam "Dvoinoi" (sample 25) differs from that of two underlying coal beds (samples 02, 03 and 19, 20) in the greater proportion (over 30%) of angiosperms (Figs. 2, 3). A thin layer of rhyolite tuff overlays this coal interlayer. It is assumed that the swamp, where plants subsequently forming the coal grew, were buried by volcanic ash. These disturbed habitats are favorable for angiosperms because of their explerent nature. Apparently, flowering plants penetrated into plant communities of swampy lowland and occupied stable positions, which are reflected in the composition of the palynospectrum from the upper coal interlayer.

Based on seimentological features, two environments are recognized for the time of the coal formation; at the beginning, there were mires and marshes, which were subsequently reduced. Suzuki et al. (2004) reconstruct environments of a marshy lake surrounded by forest or valley with braided streams and shallow interchannels overgrown with trees. Paleosoils indicate surface conditions. Subsequently, environments changed. Fine-grained cross-bedded sandstone suggests the formation of deposits in fluvial conditions (Suzuki et al., 2004).

Changes in the composition of vegetation is closely linked with paleoenvironmental changes; judging from palynological data, wet valley coniferous forests with the fern understory were replaced by broad-leaved forests with Taxodiaceae and Cupressaceae. Based on the composition of plant remains, it is possible to reconstruct coniferous–broad-leaved forests with the Taxodiaceae, Cupressaceae, Platanaceae, and Cornaceae, which were replaced by coniferous–broad-leaved forests dominated by Taxodiaceae, *Trochodendroides*, Platanaceae, and Betulaceae (Akhmetiev et al.; 2002; Maslova and Kodrul, 2003; Kodrul, 2004; Kodrul et al., 2006; Maslova et al., 2007; Kodrul and Maslova, 2007; Herman et al., 2009; etc.).

The coal-forming plants of the Raichikhinsk Coal Mine (section "Pioneer") are dominated mostly by plants producing bisaccate pollen (Fig. 4). In the lower coal seam, pteridophyte spores play an important role; however, in the overlying coal layers, they decrease in proportion. Taxodiaceae pollen is the second most abundant. Mire vegetation was composed of conifers (Pinaceae, Taxodiaceae, and Cupressaceae) and ferns, with an admixture of angiosperms.

It should be noted that the proportion of pollen of Taxodiaceae increases in clastic beds between coal seams and decreases in coals. In all likelihood, the territory of the recent coal mine was occupied by a flowing marsh, which was flooded from time to time. In addition, sedimentological data suggest the presence of a depression with a subdued relief, the paleocurrents in which flowed from the east–northeast. Inverted grading reflects the formation of fluvial deposits under flooding conditions (Suzuki et al., 2004).

The Taxodiaceae played the major role in the composition of coal-forming plants from the Wuyun Coal Mine (Fig. 5). Note that the proofs were obtained from pollen, leaf remains, and fossil wood. Pollen can be transported from all area of the drainage basin and buried in the lowlands, while leaves and wood in the coals are evidence of short transportation distances.

In clastic sediments between coal seams of the Wuyun Coal Mine, the role of TCT pollen decreases and the role of bisaccate pollen increases. In the Wuyun Coal Mine, conglomerates have not been recorded. Cross-bedded sandstones and clays occur between coal seams. The cross-bedded sands terminate this sequence (Okada, 2004).

The question arises why in the coeval Arkhara–Boguchan and Pioneer coal mines the main coal-forming plants are Pinaceae and ferns, and in the Wuyun Coal Mine, Taxodiaceae. For coals of the Paleocene Fort Union Formation in North America almost the same situation was revealed, the palynospectra from thick coal seams are dominated by TCT pollen (up to 75%), whereas in the palynospectra from thin seams this proportion drops sharply to 6–8% (Nichols, 1995). Nichols attributed this difference to different sedimentation environments.

In the coal mines investigated on the left bank of the Amur River, coal seams are relatively thin and, in the Wuyun Mine, the lower coal seam is more than 5 m thick (Fig. 2). Thick coal seams indicate the formation in environment of a forested swamp, modern analogues of which can be found in swampy forests with *Taxodium* and *Nyssa* in the southeastern United States. In the palynospectra from clastic beds of the Wuyun Mine, the proportion of bisaccate pollen sharply increases (Fig. 5), which strongly suggests that it was transported from the slopes. This is confirmed by facies features: sandstone undoubtedly accumulated in the river environments (Okada, 2004).

Relatively thin coal seams of Arkhara–Boguchan and section Pioneer undoubtedly formed under different conditions. These were probably nonforested mires; the banks of streams and rivers flowing into them were occupied by taxodialeans. Apparently, bisaccate pollen of Pinaceae, which occupied the surrounding slopes, was easily transported and buried in the lowlands, where peat accumulated. Note that the relative abundance of pollen of arboreal plants in the palynospectra from the coals is low (Figs. 3–5). It increases in clastic beds between coals. These beds also contain remains of leaves, shoots, and reproductive organs of plants, which were brought from their habitats.

Misunderstanding of these taphonomic features leads to erroneous conclusions about the composition of ancient mire communities (Kezina, 2005a, 2005b). In particular, Kezina believes that one of the main coal-forming plants of the Arkhara–Boguchan and Raichikhinsk coal mines were Platanaceae. It is known that Platanaceae are representatives of riparian rather than mire plant communities. Recent plane trees inhabit riparian levees and crevasses (*Life of Plants*, 1980). Add that, in coals of the above-mentioned mines, the proportion of tricolpate pollen, which may have been produced by the Platanaceae, ranges from 0 to 4%.

Living taxodialeans are remnants of the formerly widespread family. At present, they occur within isolated ranges in North America and eastern Asia, while, in the Paleogene and Neogene, these plants were important components of forests widespread throughout the Northern Hemisphere.

In the Santonian of the Zeya–Bureya Basin, taxodialeans were constituents of plant communities, but these plants were less abundant (Fig. 6). As L.B. Golovneva established, the Santonian flora of this region includes the *Sequoia* sp. and *Metasequoia* sp. (Markevich et al., 2005b, 2005c). During the Campanian Age, the diversity of this group increased due to the appearance of *Glyptostrobus* sp. and *"Taxodium"* sp., although palynological data suggest that the proportion of taxodialean pollen decreased. In the Early and Middle Maastrichtian palynospectra, the proportion of Taxodiaceae pollen increased; in the Late Maastrichtian flora, taxodialeans prevailed, as follows from both palynological and paleobotanical data. We found *Taxodium* sp. in the beds of this age.

The Tsagayan Flora of the Danian Age includes *Taxodium olrikii* (Heer) Brown, *Metasequoia disticha*, and *Sequoia reichenbachii* (Geinitz) Heer (Krassilov, 1976), remains of which are abundant in burials. In the younger Kivda Flora, taxodialeans retain their positions

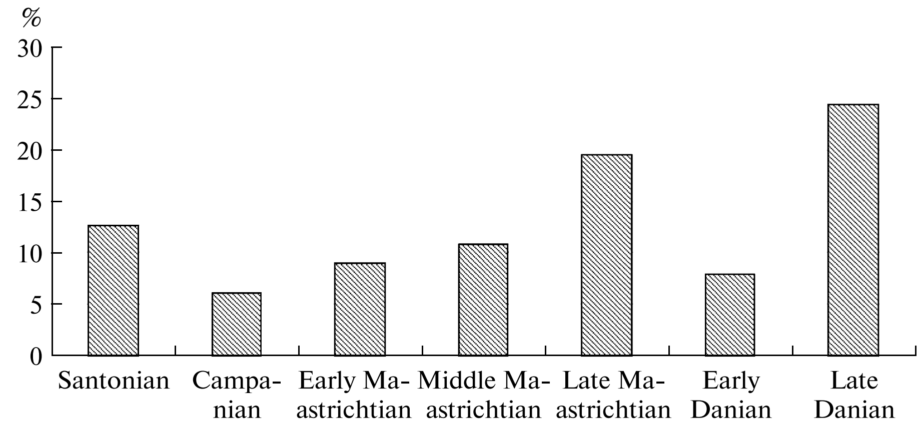


Fig. 6. Changes in the proportion Taxodiaceae in Santonian to Paleocene palynofloras of the Zeya–Bureya Basin (based on palynological data).

as one of the main components (Akhmetiev et al., 2002). In the Eocene, the flora changed abruptly. It was dominated by angiosperms, with a significant proportion of thermophilic forms (Bratceva, 1969; Akhmetiev, 1973; Kamaeva, 1990). The contribution of Taxodiaceae to the flora decreases considerably.

CONCLUSIONS

Coal-forming plants of the Arkhara–Boguchan Coal Mine are ferns and Pinaceae. However, the palynospectrum from the upper coal seam overlying a thin layer of rhyolite tuff, differs from that of two underlying coal layers in the greater proportion of angiosperms (over 30%). The influx of volcanic ash is recorded in this sequence. Perhaps, the mire was covered with ash fall. Angiosperms colonized this volcanic desert. Apparently, flowering plants penetrated into plant communities of swampy lowlands, where they acquired stable positions.

At the time of the formation of these coal-bearing deposits, two environments are recognized; initially, there were mires and swampy lowlands which were replaced by river valleys. Changes in vegetation composition were closely linked with paleoenvironment changes: the wet valley coniferous forests with fern understory were replaced by broad-leaved forests with a significant admixture of Taxodiaceae.

Coal-forming plants of the Raichikhinsk mine were dominated by plants producing bisaccate pollen. Taxodiaceous pollen was second most abundant. Conifers and ferns with some participation of angiosperms were the main contributors of mire vegetation. The area of this coal mine was occupied by a flowing marsh, which was flooded from time to time.

In the composition of coal-forming plants of the Wuyun Coal Mine, the Taxodiaceae play the main role, as is evident from pollen, leaf remains, and fossil wood. Thick coal seams of this mine formed in environment of forested swamps, similar to the modern swamp forests with *Taxodium* and *Nyssa* of the Atlantic coast of the United States. Relatively thin coal layers of the Arkhara–Boguchan Mine and Pioneer section undoubtedly formed under different conditions. Perhaps, these were mostly nonforested swamps at the confluence of streams and rivers, which were overgrown with Taxodiaceae. Apparently, bisaccate pollen of Pinaceae, which inhabited surrounding slopes, was transported and buried in the lowlands, where peat accumulated.

In the Santonian of the Zeya–Bureya Basin, the Taxodiaceae (*Sequoia* sp. and *Metasequoia* sp.) were included in plant communities, although they were less abundant. During the Campanian Age, the diversity of this group increased due to the appearance of *Glyptostrobus* sp. and *"Taxodium"* sp.; however, palynological data suggest that it decreased in abundance. In the Maastrichtian palynospectra, relative abundance of taxodiaceous pollen increased; in the Late Maastrichtian flora, taxodialeans prevailed, judging from both palynological and paleobotanical data. The peak of this plant group occurred at the beginning of the Cenozoic, when they began to play an edificator role. In the Eocene and later on, the role of Taxodiaceae decreased sharply.

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