

Fossil Wood of *Protocedroxylon primoryense* sp. nov. (Coniferales) from the Lower Cretaceous of Southern Primorye (Russian Far East)

M. A. Afonin

Institute of Biology and Soil Science, Far East Branch, Russian Academy of Sciences,
pr. Stoletiya Vladivostoka 159, Vladivostok, 690022 Russia

e-mail: afmaxim@inbox.ru

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Abstract—New species *Protocedroxylon primoryense* (Coniferales) is described from the Lower Cretaceous of southern Primorye based on the fossil wood anatomy. Fossil wood of *Protocedroxylon* was found in the Russian Far East for the first time.

Keywords: wood anatomy, *Protocedroxylon*, Coniferales, Lower Cretaceous, southern Primorye, Russian Far East.

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INTRODUCTION

Protocedroxylon was established in 1910 by W. Gothan on the material from the Upper Jurassic deposits of West Spitsbergen (Norway) and comprises fossil woods of Mesozoic conifers, which combine anatomical features of the woods of Paleozoic conifers and such modern representatives of the family Pinaceae Lindl. as *Abies* Mill., *Tsuga* Carr., *Pseudolarix* Gord., and *Cedrus* Trew. Therefore the fossil wood of *Protocedroxylon* may be considered as a transitional form from ancient (Paleozoic) to modern conifers.

R. Kräusel (1949) united *Protocedroxylon* and *Araucariopitys* Jeffrey; following the priority rules, he considered *Protocedroxylon* as a taxonomical synonym of *Araucariopitys*. However, D. Vogellehner (1967), I.A. Shilkina and R. Khudaiberdyev (1971), M. Philippe and P. Hayes (2010) supposed *Protocedroxylon* and *Araucariopitys* to be independent genera as the wood of their type species differs in the type of pitting of tracheid walls and, especially, cross-fields. Besides, *Araucariopitys* was established on the six-year-old shoot, while *Protocedroxylon* was described by the mature wood of trunk. We also suppose these genera to be independent.

Presently over twenty species of *Protocedroxylon* are known from the Triassic, Jurassic, and Cretaceous of the northern hemisphere.

Before our investigations, in Russia fossil woods of *Protocedroxylon* were described from the islands of Franz Josef Land: *P. dibneri* (Shilk.) Shilk. et Chudajb. from the Upper Triassic deposits of Wiener Neustadt Island, *P. gregussii* (Shilk.) Shilk. et Chudajb. from the Upper Triassic–Lower Cretaceous deposits of the Heiss and Hooker Islands, and *P. poly-*

porosum (Shilk.) Shilk. et Chudajb. from the Lower Cretaceous deposits of the Graham Bell Island (Shilkina, 1967). In addition, the fossil woods of *Protocedroxylon* were found in the Lower Cretaceous deposits of the Kirov Region (*P. kryshstofovichii* Shilk. (Shilkina, 1986) and *P. magnoradiatum* Shilk. (Shilkina, 1989)) and also in the East Siberia: *P. haraulachica* (Shilk.) Vogell. (Shilkina, 1958) from the Lower Jurassic deposits of Kharaula Mountains and from the Upper Jurassic deposits: *P. bojarensis* Shilk. et Blokh. (Blokhina, 1975) from the Boyarka River and *P. ronkinii* Shilk. (Shilkina, 1986) from the Begichev Island.

In the Pacific region the fossil woods of *Protocedroxylon* were described from Japan: *P. mineense* (Ogura) Nishida et Oishi and *P. okafujii* Nishida et Oishi (Nishida and Oishi, 1982) from the Upper Triassic deposits of the Honshu Island, *P. pseudoaraucarioides* Nishida (Nishida, 1973) and *P. japonicum* Nishida (Nishida, 1967) from the Lower Cretaceous deposits of the Honshu Island, and *P. yezoense* M. Nishida et H. Nishida (Nishida and Nishida, 1984) from the Upper Cretaceous deposits of the Honshu Island. The fossil woods of *Protocedroxylon* were also described from China: *P. lingwuense* He et Zhang from the Middle Jurassic deposits of the Henan Province (He and Zhang, 1993) and *P. orientale* He from the Lower Cretaceous deposits of the Inner Mongolia Province (He, 1995). The fossil wood of *P. macgregorii* Medlyn et Tidwell was described from the Upper Jurassic of British Columbia, Canada (Medlyn and Tidwell, 1986).

Until now only numerous wood remains of conifers *Xenoxylon* Gothan were known from the Lower Cretaceous deposits of the southern Primorye. The fossil wood of *X. latiporosum* (Cramer) Gothan was found in

the upper part of the Lipovtsy Formation (Late Aptian—beginning of Early Albian) on the Muravyov-Amursky Peninsula and in the upper part of the Galenki Formation (middle part of Late Albian) at the western shore of Khanka Lake and on the Muravyov-Amursky Peninsula; fossil wood of *X. hopeiense* Chang was described from the upper part of the Lipovtsy Formation (Late Aptian—beginning of Early Albian) on the Muravyov-Amursky Peninsula (Afonin, 2008, 2010).

The imprints of coniferous shoots, leaves, cones, seed scales, and seeds were also found in the Lower Cretaceous of southern Primorye. Coniferous remains of *Araucariodendron* Krassil., *Elatides* Heer, *Elatocladus* Halle, *Pityostrobus* (Nath.) Dutt, *Podocarpus* l'Héritier, *Podozamites* Schenk, and *Pseudolarix* were described from the Ussuriisk Formation (Barremian) of the Razdol'naya River basin and Muravyov-Amursky Peninsula (Krassilov, 1967); *Araucariodendron*, *Araucarites* Presl, *Athrotaxites* Ung., *Athrotaxopsis* Font., *Brachyphyllum* Brongn., *Cephalotaxopsis* Font., *Cephalotaxus* Sieb. et Zucc., *Elatides*, *Elatocladus*, *Nageiopsis* Font., *Pagiophyllum* Heer, *Parasequoia* Krassil., *Pityolepis* Turut.-Ket., *Pityophyllum* Nath., *Pityostrobus*, *Podocarpus*, *Podozamites*, *Pseudolarix*, *Sciadopityes* Goepf. et Men., *Sequoia* Endl., *Taxites* Brongn., *Tomharrisia* Flor., *Torreya* Arnott, and *Ussuriocladus* Krysht. et Pryn. were found in the Lipovtsy Formation (Aptian—beginning of Early Albian) of the same territory (Krassilov, 1967; Volynets, 2005, 2009). The coniferous remains of *Abietites* Hising., *Athrotaxites*, *Athrotaxopsis*, *Brachyphyllum*, *Elatides*, *Elatocladus*, *Nageiopsis*, *Pagiophyllum*, *Pityolepis*, *Pityophyllum*, *Pityospermum* Nath., *Podocarpus*, *Podozamites*, *Pseudolarix*, *Sequoia*, *Sphenolepis* Schenk, and *Taxites* were described from the Galenki Formation (end of Early—middle part of Late Albian) of the basins of the Amba, Barabashevka, and Razdol'naya rivers, Muravyov-Amursky Peninsula, and western shore of Khanka Lake (Krassilov, 1967; Volynets, 2005, 2009). *Araucariodendron*, *Athrotaxites*, *Athrotaxopsis*, *Elatides*, *Machairostrobus* Pryn. ex Turut.-Ket., *Pityophyllum*, *Podocarpus*, *Podozamites*, and *Sequoia* were described from the Staryi Suchan Formation (Barremian—beginning of Early Albian) and *Araucariodendron*, *Athrotaxites*, *Athrotaxopsis*, *Conites* Sternb., *Elatides*, *Pityocladus* (Nath.) Sew., *Pityophyllum*, *Pityospermum*, *Pityostrobus*, *Podozamites*, *Pseudolarix*, *Sequoia*, *Schizolepis* Braun, and *Taxites* were described from the Severnyi Suchan Formation (Early—beginning of the Middle Albian) (Krassilov, 1967; Volynets, 2005) of the Partizanskaya River basin. Conifers *Athrotaxites*, *Athrotaxopsis*, *Brachyphyllum*, *Elatides*, *Elatocladus*, *Paracmopyle* Krassil., *Pityolepis*, *Pityophyllum*, *Pityospermum*, *Podozamites*, *Sphenolepis*, *Sequoia*, and *Taxites* were described from the Frensevo Formation (end of Middle—beginning of Late Albian) of the Sukhodol and Partizanskaya Rivers basins and eastern shore of the Ussuri Bay (Krassilov,

1967; Volynets, 2005). *Athrotaxites*, *Elatides*, *Elatocladus*, *Pagiophyllum*, *Pityophyllum*, *Pityospermum*, *Pityostrobus*, *Podozamites*, *Sphenolepis*, and *Sequoia* were mentioned from the Kangauz Formation (middle part of Late Albian) and *Coniferites* Ung., *Elatocladus*, and *Pityophyllum* were mentioned from the Romanovka Formation (end of Late Albian) of the Partizanskaya River (Volynets, 2005).

MATERIAL AND METHODS

The described in the present paper wood of the new fossil species of *Protocedroxylon* was found in 2008 by the author and E.B. Volynets on the Firsov Cape (Muravyov-Amursky Peninsula, southern Primorye).

The fossil wood (specimen no. 32A/2) was found in the upper part of the Lipovtsy Formation, which on the Firsov Cape consists of middle- and fine-grained sandstones and siltstones with five interbeds of coaly rocks and coals. These deposits also contained fossil woods of *Xenoxylon latiporosum* (Afonin, 2008, 2010), remains of mosses (*Thallites* Walt.), clubmosses (*Lycopodites* Lindl. et Hutt.), horsetails (*Equisetum* L.), ferns (*Adiantopteris* Vassilevsk., *Arctopteris* Samyl., *Birisia* Samyl., *Eogonocormus* Deng, *Cladophlebis* Brongn., *Coniopteris* Brongn., *Lobifolia* Rasskaz. et E. Lebed., *Osmunda* L., *Ruffordia* Sew., *Teilhardia* Sew.), Caytoniales (*Sagenopteris* Presl), Cycadales (*Cycadites* Sternb., *Nilssonia* Brongn., *Pseudoctenis* Sew., *Pterophyllum* Brongn., *Williamsonia* Carruth.), Ginkgoales (*Ginkgo* L.), Czekanowskiales (*Czekanowskia* Heer), and conifers (*Araucariodendron*, *Athrotaxites*, *Athrotaxopsis*, *Elatides*, *Pityophyllum*, *Podozamites*, *Pseudolarix*, *Sequoia*, *Taxites*) (Krassilov, 1967; Volynets, 2009). The upper part of the Lipovtsy Formation is dated by the Late Aptian—beginning of the Early Albian (Bugdaeva et al., 2006; Volynets, 2006).

The fossil wood studied is very dense, mineralized, dark gray, almost black, with annual rings well visible to the naked eye. The collection studied is stored at the Institute of Biology and Soil Science, Far East Branch of the Russian Academy of Sciences (IBSS), coll. no. 32A.

The transparent thin sections of dense mineralized wood have been prepared by the standard petrographic method (Gammerman et al., 1946). Since the wood performs various functions, it has heterogeneous structure; therefore the preparations for its anatomical study have been made in three perpendicular planes: transverse, radial, and tangential. Sixteen thin sections have been made and studied. The thin sections have been studied microscopically with optical biological microscopes Micmed (LOMO); photomicrographs of the anatomical structures have been made with a microscope AxioScop-40, camera AxioCamHR, and modular system AxioVision 3.0 (Carl Zeiss). The wood anatomy was described using the terms proposed by A.A. Yatsenko-Khmelevskii (1954) and "IAWA List

of Microscopic Features for Softwood Identification” (Baas et al., 2004).

SYSTEMATIC PALEOBOTANY

Order Coniferales

Genus *Protocedroxylon* Gothan, 1910

Protocedroxylon primoryense M. Afonin, sp. nov.

Plate 15, figs. 1–22

E t y m o l o g y. From Primorye.

H o l o t y p e. Institute of Biology and Soil Science (IBSS), Far East Branch, Russian Academy of Sciences, coll. no. 32A, specimen no. 32A/2, fossil wood; southern Primorye, Muravyov-Amursky Peninsula, Firsov Cape; upper part of the Lipovtsy Formation, Upper Aptian–lowermost Lower Albian; Pl. 15, figs. 1–22.

D i a g n o s i s. Growth rings distinct. Pitting in the radial walls of tracheids uniseriate, biseriate, occasionally triseriate; sometimes in stellate pit clusters (3–4(6) pits). Uniseriate pits in a close arrangement or scattered along the tracheid length, biseriate pits in alternate or occasionally mixed arrangement, triseriate pits in alternate arrangement. Circular, penta- and hexagonal pits 14–19 μm and elliptic pits 14–16 \times 15–18 μm in diameter. Pits in tangential walls of tracheids and crassulae absent. Axial parenchyma scanty, diffuse; transverse walls smooth. Rays 1–22(35) cells high, uniseriate, occasionally with 1–5 layers of biseriate cells. Rays with marginal cells resembling ray tracheids. Cupressoid and taxodioid pits 1–4 per cross-field, 4–6 μm in diameter. Traumatic vertical resin canals present.

D e s c r i p t i o n. The wood consists of tracheids, ray and axial parenchyma, and epithelial cells of resin canals.

The growth rings are distinct, 2–6 mm wide, but strongly contorted; the transition from early to late wood is gradual; the late wood occupies from one-fifth to one-third of the growth ring width. In cross-section the tracheids of early wood are relatively large, thin-walled, with large lumina, rounded square, rounded rectangular, or rounded polygonal, and radially elongated. The tracheids of late wood are thick-walled, rounded rectangular, strongly radially flattened, with nearly slit lumina near the growth ring boundary. In

radial section the ends of tracheids are pointed and rounded.

The pits in radial tracheid walls of early wood are abundant and uniseriate (Pl. 15, figs. 4, 6, 7), biseriate (Pl. 15, figs. 5–10), rarely triseriate (Pl. 15, figs. 10, 11). Sometimes radial tracheid walls bear stellate pit clusters consisting of 3–4, sometimes 6 pits in each cluster (Pl. 15, figs. 6, 8). The uniseriate pits are elliptic, horizontally elongated, sometimes circular, with elliptic or circular apertures, respectively, usually closely and adjacently arranged along the tracheid length, sometime scattered; the circular pits are 14–19 μm and elliptic pits are 14–16 \times 15–18 μm in diameter. The biseriate pits are circular, elliptic, penta- and hexagonal, with rounded and oval apertures, 15–18 μm in diameter; pits are in alternate or occasionally mixed arrangement. The triseriate pits are circular, penta- and hexagonal, 14–18 μm in diameter, with rounded and oval apertures; pits are in alternate arrangement. The crassulae are absent. The pits in radial tracheid walls of late wood are uniseriate, circular, and scattered along the tracheid length. The pits in tangential tracheid walls are absent; possibly they did not preserve.

The axial parenchyma is scanty and diffuse; its transverse cell walls are smooth (Pl. 15, figs. 16, 17); sometimes traumatic axial parenchyma with notched transverse and pitted tangential walls occurs.

The rays are numerous, uniseriate, 1–22 (35) cells in height, sometimes with 1–5 layers of biseriate cells (Pl. 15, figs. 18, 19). The horizontal and tangential walls of ray cells are pitted (Pl. 15, figs. 12–15). The median ray cells are elliptic, rounded rectangular, and elongated along the ray; the marginal ray cells are rounded triangular. The pitting of ray cells (Pl. 15, fig. 20) and the intercellular spaces between the ray cells (Pl. 15, figs. 18–20) are well seen in tangential section. True ray tracheids are absent, but occasionally occur marginal cells with circular, 4–5 μm in diameter, and scattered in radial walls pits; the ray cells sometimes form relatively elongated rows along the rays margins, which are very similar to the ray tracheids (Pl. 15, figs. 14, 15).

In the cross-fields, there are 1–4 cupressoid and taxodioid pits, 4–6 μm in diameter; 2–3 pits are arranged in a single horizontal row and 2–4 pits are

Explanation of Plate 15

Figs. 1–22. *Protocedroxylon primoryense* sp. nov., specimen no. 32A/2: (1) cross-section, chain of traumatic vertical resin canals; (2) and (3) cross-section, traumatic vertical resin canal; (4) radial section, uniseriate pitting in tracheid walls; (5) radial section, biseriate pitting in tracheid wall; (6) radial section, uniseriate pitting and pits in tracheid wall arranged in stellate cluster; (7) radial section, uniseriate and biseriate pitting in tracheid walls; (8) radial section, biseriate pitting and pits in tracheid wall arranged in stellate cluster; (9) radial section, biseriate pitting in tracheid walls; (10) radial section, bi- and triseriate pitting in tracheid wall; (11) radial section, triseriate pitting in tracheid wall; (12) and (13) radial section, ray cell walls; (14) and (15) radial section, ray cell walls, marginal ray cells resembling ray tracheids; (16) radial section, axial parenchyma; (17) radial section, biseriate pitting in tracheid wall, axial parenchyma; (18) and (19) tangential section, uniseriate rays, uniseriate ray with biseriate region and intercellular spaces; (20) tangential section, pitting of ray cells, intercellular spaces; (21) and (22) radial section, cross-field pitting; southern Primorye, Muravyov-Amursky Peninsula, Firsov Cape; Upper Aptian–lowermost Lower Albian, upper part of the Lipovtsy Formation.

Plate 15

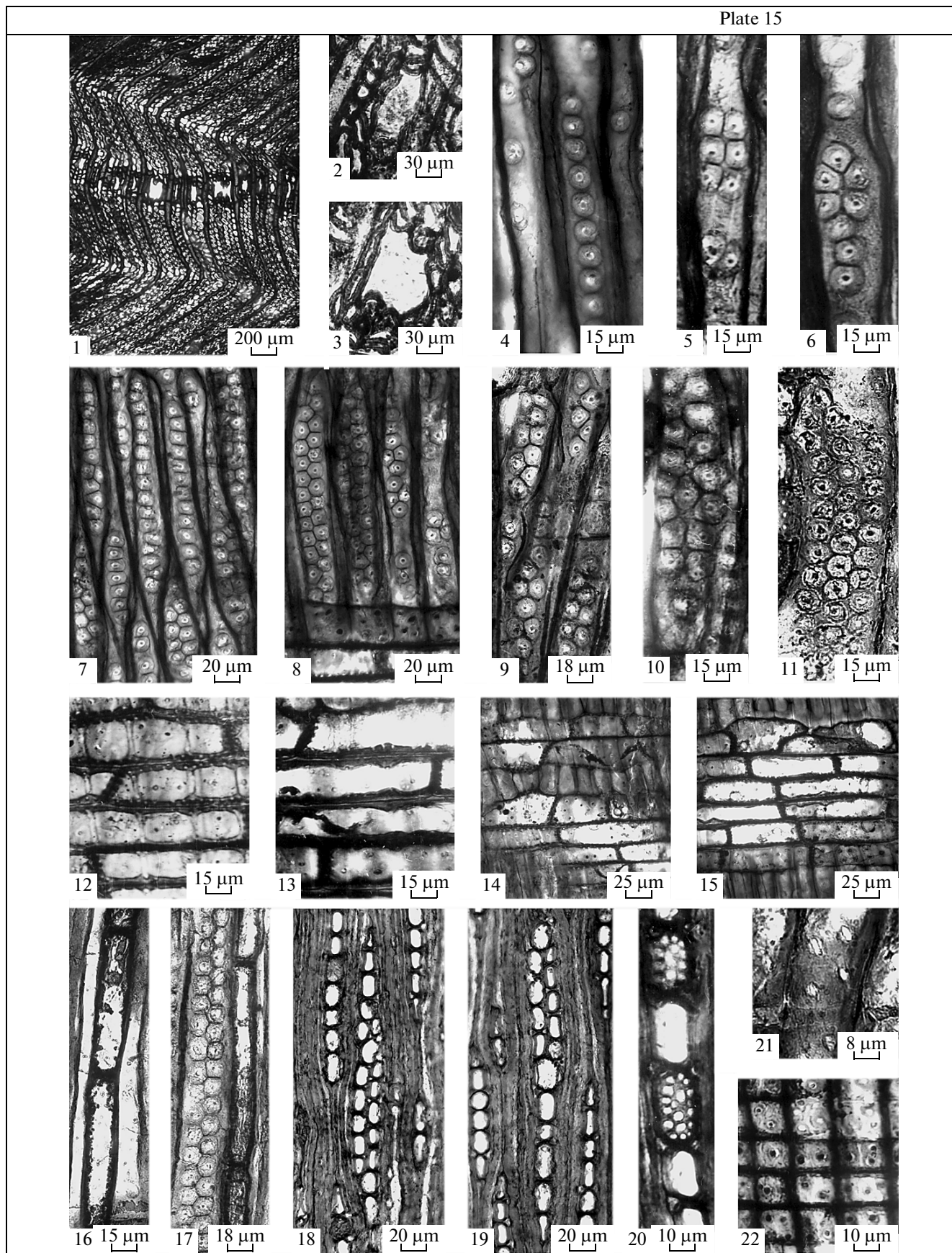


Table 1. Comparative characterization of the fossil wood anatomy of *Protocedroxylon primoryense* M. Afonin, sp. nov. and wood of related species of *Protocedroxylon* Gothan.

Anatomical characters	<i>Protocedroxylon primoryense</i> sp. nov.	<i>Protocedroxylon dibneri</i> (Shilkina) Shilkina et Chudajberdyev (Shilkina, 1967)	<i>Protocedroxylon ronkinii</i> Shilkina (Shilkina, 1986)	<i>Protocedroxylon kryshstofovichii</i> Shilkina (Shilkina, 1986)
Pitting in radial tracheid walls:				
uniseriate	+	+	+	+
biseriate	+	++	+	++
triseriate	+–	+	+	+
Pitting in tangential tracheid walls	–	+	+	+
Axial parenchyma	+	+	+	+
Uniseriate rays:				
height (in cells)	1–22(35)	1–11(19)	1–20(30)	1–10
biseriate regions (length in cells)	1–5	+	1–2	+–
Marginal ray cells resembling ray tracheids	+	–	–	–
Traumatic vertical resin canals	+	–	–	+
Number of pits in cross-fields	1–4	2–3(4)	2–4	?

Note: (+) Character present, (++) prevail, (–) absent, (+–) rare, (?) no data.

arranged in two horizontal rows per cross-field (Pl. 15, figs. 21, 22).

The normal resin canals are absent, but some growth rings have traumatic vertical resin canals (Pl. 15, figs. 1–3). The canals are circular or elliptic, 30–120 µm in diameter, with 4–10 thick-walled epithelial cells, which sometimes do not form continuous layer; the traumatic vertical resin canals are arranged in long chains in the early wood (Pl. 15, fig. 1).

Comparison. Among known fossil woods of *Protocedroxylon*, the fossil wood of the new species is most similar to the wood remains of *P. dibneri* (Shilkina, 1967) from the Upper Triassic of Franz Josef Land, *P. ronkinii* (Shilkina, 1986) from the Upper Jurassic of East Siberia, and *P. kryshstofovichii* (Shilkina, 1986) from the Lower Cretaceous of Kirov Region.

However, the fossil wood of the new species differs from the wood of *P. dibneri* in the absence of pits in tangential tracheid walls, slightly higher rays, and presence of traumatic vertical resin canals and marginal cells resembling ray tracheids (Table 1).

It differs from the wood of *P. ronkinii* in the gradual transition from early to late wood, absence of pits in tangential tracheid walls, and presence of traumatic vertical resin canals and marginal cells resembling ray tracheids (Table 1).

The new species differs from the wood of *P. kryshstofovichii* in the gradual transition from early to late wood, absence of pits in tangential tracheid walls, higher rays, and presence of marginal cells resembling ray tracheids (Table 1).

In addition, the descriptions of the anatomy of *P. dibneri*, *P. ronkinii*, and *P. kryshstofovichii* lack data on the dimensions of pits in radial and tangential tracheid walls and in cross-fields; thus preventing a more detailed comparison.

Remarks. The mixed type of pitting of radial tracheid walls, pitted walls of ray cells, and absence of normal resin canals (occasional presence of traumatic canals) are evidence that the wood belongs to *Protocedroxylon*.

In the course of evolution many conifers changed the typical araucarioid pitting, which was mainly characteristic of the wood of ancient (Paleozoic) conifers,

to the abietoid pitting of modern type. The mixed pitting combines araucarioid and abietoid pitting in the wall of one tracheid and is supposed to be the transitional stage between araucarioid and abietoid pitting (Yatsenko-Khmelevskii, 1954; Chavchavadze, 1979; Shilkina and Yatsenko-Khmelevskii, 1980). The mixed type of pitting is the specific feature of wood of many Mesozoic conifers. The Mesozoic, which includes the Cretaceous period, is the transitional stage in the development of pitting in radial tracheid walls, when the type of pitting changed almost in all structural types of wood (Chavchavadze, 1979; Shilkina and Yatsenko-Khmelevskii, 1980).

The radial tracheid walls of the fossil wood of *P. primoryense* sp. nov. have both the mixed type of pitting and typical araucarioid pitting, which in *P. primoryense* sp. nov. consists of biseriate and triseriate penta- and hexagonal pits alternating along the tracheid length.

The ray tracheids developed in Mesozoic in conifers and provided radial flow of water solutions (Shilkina and Yatsenko-Khmelevskii, 1980). The marginal ray cells resembling ray tracheids are considered as transitional form to the true ray tracheids (Greguss, 1955).

The fossil wood of *P. primoryense* sp. nov. has marginal cells resembling ray tracheids and differs in this feature from all earlier described fossil woods of *Protocedroxylon*, which lack both true ray tracheids and marginal cells resembling ray tracheids. In this feature *P. primoryense* sp. nov. is possibly most evolutionary advanced of all other known representatives of *Protocedroxylon*. According to E.V. Budkevich (1961), the wood of modern Pinaceae *Abies*, *Pseudolarix*, and *Keteleeria* Carr. sometimes contains similar marginal ray cells.

The origin of resin canals is associated with the development of axial parenchyma and is one of its evolutionary stages. Vertical traumatic structures (schizogenous intercellular spaces and resin cysts) were the most ancient and primitive structures and possibly gave rise to traumatic resin canals. Later normal vertical and horizontal resin canals arose in the wood of conifers together with traumatic resin vesicles (Chavchavadze, 1979).

The fossil wood of *P. primoryense* sp. nov. lacks normal resin canals; however, traumatic vertical resin canals sometimes occur. Among modern members of the Pinaceae, *Abies*, *Tsuga*, *Pseudolarix*, and *Cedrus* lack normal resin canals. Traumatic vertical resin canals may occur in *Abies*, *Tsuga*, and *Cedrus*, but *Cedrus* sometimes also has horizontal traumatic resin canals (Budkevich, 1961; Chavchavadze, 1979).

As the type of the fossil wood studied does not completely coincide with the wood of any known representatives of *Protocedroxylon*, it should be described as a wood of a new species, *P. primoryense* sp. nov.

M a t e r i a l. Holotype.

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