

# Fossil wood *Cedrus penzhinaensis* sp. nov. (Pinaceae) from the Lower Cretaceous of north-western Kamchatka (Russia)

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**ABSTRACT.** A new species, *Cedrus penzhinaensis* sp. nov. is described on the basis of fossil wood anatomy. The wood has been found in Albian or upper Albian (upper Lower Cretaceous) deposits of north-western Kamchatka. This is the first report of fossil wood with *Cedrus* anatomical structure from the Cretaceous of Russian Far East, and is the oldest macrofossil evidence of the genus *Cedrus*. This Cretaceous species differs from the modern species of *Cedrus* as well as from the Palaeogene *C. kamtschatkaensis* by biseriate pits in the tangential walls of tracheids, lower uniseriate rays, and a greater number of epithelial cells lining traumatic horizontal resin canals.

**KEY WORDS:** *Cedrus*, fossil wood, Lower Cretaceous, Kamchatka

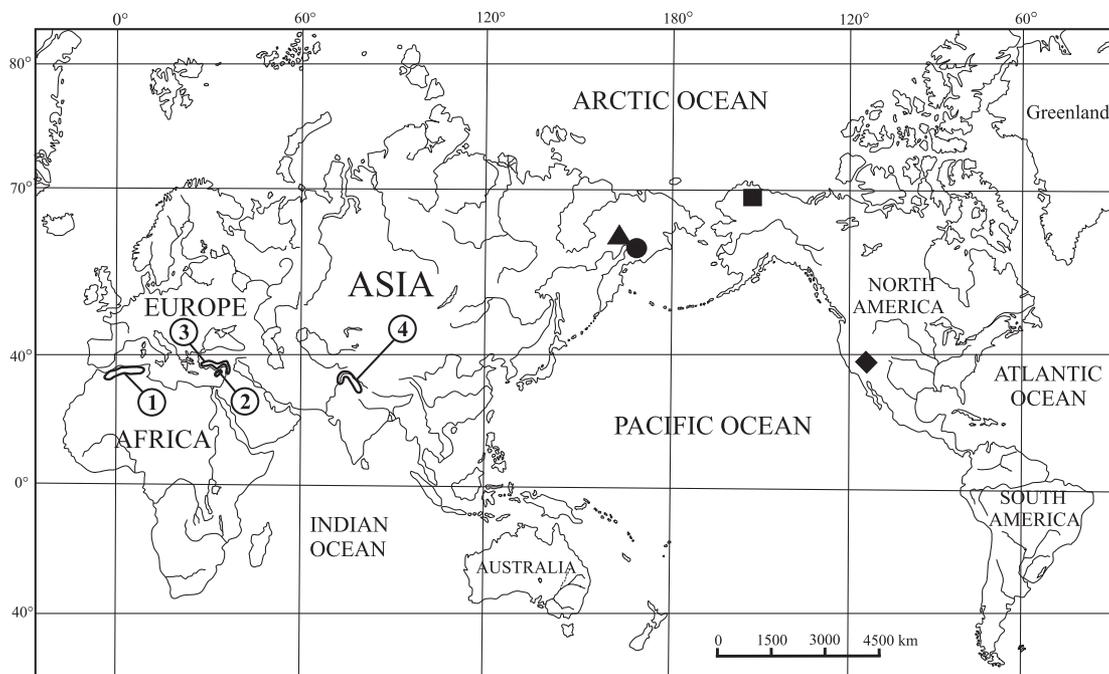
## INTRODUCTION

Fossil woods of the genus *Cedrus* Trew are extremely rare (Fig. 1). Previously, fossil wood remains with anatomical structure of the *Cedrus* had been described from the upper Albian–Cenomanian in the Colville River Basin (northern Alaska, USA) as *Cedrus alaskensis* Arnold (Arnold 1952), from the Palaeocene–Lower Eocene of Chemurnaut Bay (north-western Kamchatka, Russia) as *C. kamtschatkaensis* Blokh. (Blokhina 1998) and from the Miocene of California (USA) as *C. penhallowii* (Jeffrey) Bailey (Barghoorn & Bailey 1938). The latter species was based on well preserved wood, but was established without a complete anatomical description. Generally, *Cedrus* is most frequently represented in the fossil record by pollen grains, with cone scales and seeds much less common. Because the seed cones of *Cedrus* disintegrate when ripe, only unripe cones are preserved intact as fossils making their identification extremely difficult.

## PALAEOBOTANICAL RECORDS OF *CEDRUS*

According to Zauer (1954), a maximum development of the genus *Cedrus* took place in the Late Cretaceous with a subsequent decline in the Tertiary. However, Kryshtofovich (cited in Zauer 1954) was of the different opinion suggesting that the earliest macrofossil records of *Cedrus* are not older than the Late Cretaceous, and that the older, even the Early Cretaceous records, are doubtful. Moreover, *Cedrus* is rare in the Late Cretaceous while the records of this genus increase in the Tertiary.

The earliest macrofossil records of *Cedrus* are represented by the fossil woods of *C. penzhinaensis* sp. nov. from the Albian (or upper Albian) of Kamchatka, described in this paper, and *C. alaskensis* described by Arnold (1952) from the Chandler Formation of Alaska dated to the late Albian–Cenomanian (Parrish & Spicer 1988).



**Fig. 1.** Map showing the localities of fossil woods and modern distribution area of the genus *Cedrus* Trew. 1 – *C. atlantica* (Endlicher) G. Manetti ex Carrière, 2 – *C. brevifolia* (Hooker f.) A. Henry, 3 – *C. libani* A. Richard, 4 – *C. deodara* (Roxburgh ex D. Don) G. Don, ▲ – *C. penzhinaensis* sp. nov., ● – *C. kamtschatkaensis* Blokh., ■ – *C. alaskensis* Arnold, ◆ – *C. penhalowii* (Jeffrey) Bailey

The earliest records of *Cedrus* cone scales and seeds come from the early Cenomanian (early Late Cretaceous) of the northern coast of the Okhotsk Sea in north-eastern Russia (Samylina 1988). Seed cones of *C. lopatinii* Heer were described from the Cenomanian of the Chulym-Yenisei interfluvies (Krasnoyarsk Territory, Western Siberia, Russia) by Lebedev (1962) and Golovneva (2004), and from Turonian of the New Siberia Island by Sveshnikova and Budantsev (1969), Filippova and Abramova (1993), and Golovneva (2004). Cone scales of *Cedrus* sp., resembling those of *C. lopatinii*, were described by Filippova and Abramova (1993) from the Cenomanian of the Anadyr River Basin (Chukotka Region, Russia), by Sveshnikova and Budantsev (1969), Filippova and Abramova (1993), and Golovneva (2004) from Turonian of the New Siberia Island, and by Terekhova and Filippova (1983, 1984, cited in Herman 1999) from Coniacian of the Pekul'nei Ridge (North-East of Russia). Probably, *C. lopatinii* was widespread in the Late Cretaceous within the both West and East Siberia. Pollen grains of *Cedrus* have been reported from the coast to the south of Chemurnaut Bay, between the Getkilnin and Rebro Capes (Serova et al. 1989), from the Middle Eocene of Tigil'sky Region, the Mainachsky Section at the boundary of the

Snatol'skaya and Kovachinskaya formations, and from the Upper Eocene of the upper part of the Kovachinskaya Formation (Gladenkov et al. 1991). In north-western Kamchatka, rare pollen grains of *Cedrus* were found in palynological assemblage of the Ilyinskaya and lower Kakertskaya formations (the beginning of the Miocene climatic optimum) along the Kuinivajam river, at the northern coast of Rekinnikskaya inlet (Fradkina 1983).

Summarizing palaeobotanical records, given above, plus our new wood record, we may assume that *Cedrus* was spread in north-western Kamchatka since at least the Albian (late Early Cretaceous) up to the Middle Miocene. Most probably, the earliest appearance of *Cedrus* in north-western Kamchatka was caused by the elevation of the Okhotsk-Chukotka volcanic belt, that created cooler environments on the volcanic plateaus for *Cedrus*, which prefers mountainous habitats.

#### GEOLOGICAL SETTING

The fossil wood was found on the eastern coast of Penginskaya inlet (north-western Kamchatka peninsula), along the Malayi Unnavajam River (the Talovka River Basin), in the marine terrigenous deposits of the

Kedrovskaya Formation dated to Albian or late Albian (Avdeiko 1968, Paraketsov et al. 1974). This formation is composed of siltstones, with horizons of calcareous concretions (with petrified woods), and interbeds of sandstones and mudstones, with minor amounts of coal, while the base of the formation is formed by gravelstones and conglomerates. According to A.M. Popov (pers. comm.), these deposits contain ammonoids *Neogastropilites* McLearn, *Grantzicerias* Imlay, *Marshallites* Matsumoto, *Anagaudryceras* Shimitzu, the mollusc *Inoceramus* J. Sowerby, and plant remains including petrified woods and solitary leaf imprints of *Nilssonina* (?) Gray type.

## MATERIAL AND METHODS

The fossil wood specimen collected by A.M. Popov is very solid, per-mineralized, dark grey to almost black, 2.7–4.0 × 4.7–7.0 cm in transverse section and 3.8–6.0 cm in length. Growth rings are 0.3–1.5 mm wide and readily distinguishable by the unaided eye. The specimen is a fragment of trunk or large branch.

A conventional petrographic technique was used for preparing thin sections of per mineralized wood (Gammerman et al. 1946). In view of the heterogeneous wood anatomy, necessitated by diverse functions of the tissue, the anatomical sections were made in 3 orientations (transverse, radial and tangential). In total, 7 thin transparent sections (3 transverse, 3 radial and 1 tangential) were studied microscopically and photomicrographs of anatomical structures were taken with "MIKMED" biological light microscopes (LOMO).

The remains of fossil wood are housed in the Institute of Biology and Soil Science, Far Eastern Branch, Russian Academy of Sciences, collection IBSS No. 23/1-6.

## SYSTEMATICS

Genus *Cedrus* Trew, 1757

*Cedrus penzhinaensis* Blokhina  
& M. Afonin **sp. nov.**

Plate 1, figs 1–17

**Holotype.** No. 23/1-6 (Pl. 1, figs 1–17) designated here.

**Repository.** Institute of Biology and Soil Science, Far Eastern Branch, Russian Academy of Sciences, Vladivostok, Russia.

**Type locality.** Malyi Unnavayam River (Talovka River Basin), eastern coast of the

Penzhinskaya inlet, north-western Kamchatka Peninsula.

**Type stratum.** Kedrovskaya Formation, Albian or upper Albian, Lower Cretaceous.

**Etymology.** From Penzhinskaya inlet.

**Diagnosis.** Growth rings distinct. Pits in radial tracheid walls abundant, uni- or biseriate, 16–23(24) µm in diameter, biseriate pits mostly opposite or, occasionally, alternate. Crassulae present between biseriate opposite pits. Torus of pits "fringed". Pits in tangential tracheid walls abundant, uni- or biseriate, 7–8 µm in diameter; biseriate pits more or less opposite or alternate. Axial (wood) parenchyma scanty; transverse walls smooth or with 2–4 small knots, both radial and tangential walls sometimes pitted. Uniseriate rays 1–10(16) cells in height, occasionally with 1–2 rows of biseriate. Ray tracheids smooth-walled, peripheral. Both vertical and horizontal resin canals traumatic. Vertical resin canals surrounded by 6–10 thick-walled epithelial cells, usually destroyed. Horizontal resin canals surrounded by 12–40 thick-walled epithelial cells and, in the same ray, by a different number (from one to three) of ray cell rings. Such resin canals occur in middle part of biseriate, bi-triseriate, triseriate, tri-quadriseiate or quadriseiate rays, with equal (of 1–3 cells) or extremely unequal uniseriate ends: shorter ones consist of 1–3 and longer ones of 4–10 cells. There are 2–4(5) cupressoid or taxodioid pits of 4–6 µm in diameter per cross-field.

**Description.** The growth rings are distinct, 1–3 mm wide. The early/late wood transition is gradual to distinct (Pl. 1, fig. 1). In transverse section, the early wood tracheids are large, thin-walled, with broad lumens, of rounded or rounded-polygonal, sometimes, rounded-rectanguloid in outline, radially elongated. The late wood occupies about 1/4–1/2 (occasionally some more) of the growth ring width. The late wood tracheids are thick-walled, rounded to rounded-rectanguloid, radially flattened, with nearly slit-like lumina at the growth ring boundaries. In radial section, the tracheids ends are rounded, pointed or sock-like.

In the early wood, pits in the radial walls of tracheids are abundant, uniseriate (Pl. 1, figs 4–6) or biseriate (Pl. 1, figs 7–9). Uniseriate pits are circular or, rarely, elliptical, horizontally slightly compressed, with an included

aperture (circular or elliptical, respectively). The circular pits are 18–23  $\mu\text{m}$  in diameter and the elliptical pits measure 17–18  $\times$  23–24  $\mu\text{m}$ . The circular apertures are 7.5–10.0  $\mu\text{m}$  in diameter, and elliptical ones 8.0  $\times$  11.5  $\mu\text{m}$ . Pits are scattered, or in more or less close arrangement, occasionally, crowded along of the tracheid length. Biseriate pits are mostly opposite, or occasionally in a mixed arrangement (Pl. 1, fig. 9). In the latter case alternate and opposite pits occur in the same tracheid wall. Pits are circular, 16–23  $\mu\text{m}$  in diameter, with an included circular aperture. Opposite pits are disposed mostly close to the horizontal and vertical contact lines, or in pairs close to the vertical contact. Crassulae are present between biseriate opposite pits (Pl. 1, fig. 7). Both uni- and biseriate pits show a “fringed” torus (Pl. 1, fig. 6), although it was not found sometimes because of rather poor state of preservation of the material. In the late wood, pits in the radial walls of tracheids are uniseriate, scattered or disposed more or less close each to other along of the tracheid length. Pits are circular, 16.5–17.0  $\mu\text{m}$  in diameter. Pits are lacking near the growth ring boundary.

In the tangential walls of tracheids, pits are abundant, uniseriate and biseriate, circular, approximately 7–8  $\mu\text{m}$  in diameter (Pl. 1, fig. 11). Uniseriate pits are scattered, or in more or less close arrangement along of the tracheid length. Biseriate pits are in more or less opposite, or, in alternate arrangement. Axial (wood) parenchyma is scanty and observed in the longitudinal sections (Pl. 1, fig. 10). Transverse walls of parenchyma cells are smooth, or with 2–4 small knots; radial and tangential walls are sometimes pitted.

Rays are numerous, of two types: the linear uniseriate and the spindle-shaped multiseriate with traumatic horizontal resin canals. The uniseriate rays are 1–16 (typically 5–10) cells in height, occasionally with 1–2 layers of biseriate cells (Pl. 1, fig. 13). The horizontal walls of the rays are thickened, and pitted with concavities (Pl. 1, fig. 17); the tangential walls are knotted (Pl. 1, fig. 17). The median ray cells are relatively large, rounded or elliptical and elongated along the ray. The marginal cells are rounded-triangular and approximately of the same size as the median cells. Between ray cells there are rather large intercellular spaces well marked in the tangential section. Ray tracheids are peripheral, i.e. occur along

the ray margins (Pl. 1, fig. 17), the inner walls are smooth. Pits may be observed in the radial wall of ray tracheids.

In the cross-fields, there are 2–4(5) pits (about 4–6  $\mu\text{m}$  in diameter) of a supposed cupressoid or taxodioid type (Pl. 1, figs 5, 12). Pits are arranged in two horizontal rows.

The vertical resin canals are all traumatic, about 56–60  $\mu\text{m}$  in diameter, and surrounded by 6–10 thick-walled, sometimes poorly preserved or destroyed epithelial cells, and parenchyma cells also do not form a continuous lining around a resin canal (Pl. 1, figs 1–3). The vertical resin canals are solitary or, more often, in group of two canals, and there is no ray or layer of tracheids between the canals. Resin canals occur mostly in the late wood, or in the early/late wood transition zone. In one growth ring vertical resin canals disposed in rather long tangential row were observed within the late wood at the growth ring boundary.

The horizontal resin canals are all traumatic and characterized by a fairly well developed and large central canal about 40–110  $\times$  100–500  $\mu\text{m}$  in the mean dimensions (Pl. 1, figs 14–16). The resin canals are surrounded by 12–40 thick-walled epithelial cells and, in the same ray, by a different number (from one to three) of ray cell rings. The resin canals occur in the biseriate, bi-triseriate, triseriate, tri-quadrise-riate or quadrise-riate rays that show equal (of 1–3 cells) or extremely unequal uniseriate ends: the shorter ones consist of 1–3, the longer ones of 4–10 cells. A single ray with 2 traumatic horizontal resin canals was observed (Pl. 1, fig. 15).

**Comparison.** The combination of such characteristics of wood anatomy as the presence of distinct growth rings with distinct transition from early to late wood, large thin-walled early wood tracheids of rectangular outline and radially elongated (in transverse section), abietoid pitting in the walls of tracheids and ray cells, scanty axial parenchyma, heterogeneous rays (i.e. with ray tracheids), small bordered pits several in number per cross-field, and alongside with the both vertical and horizontal resin canals of traumatic origin, allow to attribute the described fossil wood to the family Pinaceae Lindley.

The fossil wood under study is characterized by the combination of typical anatomical features of the genus *Cedrus* such as the

absence of any normal resin canals and the presence of traumatic canals both vertical and horizontal ones (the latter with excessively developed central canals), as well as the presence of smooth ray tracheids, mixed pitting in radial walls of early wood tracheids (araucarioid pitting occasionally occurs alongside with abietoid pitting), a "fringed" torus with uneven marginal indentations, and scanty axial parenchyma.

The fossil specimen studied differs from the fossil wood of *Cedrus alaskensis* (Arnold 1952), firstly by ray tracheids (they are absent in *C. alaskensis*) and by equal development of both uni- and biseriate pits in the radial walls of tracheids. In the *C. alaskensis* biseriate pits are prevalent, and pits are smaller than in the described *C. penzhnaensis* from Kamchatka. In addition, in the fossil wood studied, triseriate pits are lacking, and biseriate pits occur also in the tangential walls of tracheids. The other difference from *C. alaskensis* are lower uniseriate rays and a greater number of pits per cross-field. More detailed comparison is not possible because the Arnold's description (Arnold 1952) does not provide information about such characters as diameter of pits in the tangential walls of tracheids, type of cross-field pits, structure of horizontal resin canals, and number of epithelial cells in both vertical and horizontal traumatic resin canals (Tab. 1).

There are also several distinctions between the wood of the new described species and the *Cedrus kamtschatkaensis* (Blokchina 1998). The studied wood differs by the presence of biseriate pits in the tangential walls of tracheids, whereas in the Palaeogene wood of *C. kamtschatkaensis* biseriate pits are absent. It differs also by lower uniseriate rays and shorter biseriate regions in those rays, and a greater number of epithelial cells lining traumatic horizontal resin canals. In addition, in the fossil wood studied, piceoid pits were not found in the cross-fields (Tab. 1).

The description of *Cedrus penhallowii* from the Miocene of California (USA) given by Barghoorn and Bailey (1938) does not provide information about important characters such as cross-field pitting, pitting of tangential walls of tracheids, diameter of pits in radial walls of tracheids, structure and height of rays, structure of horizontal resin canals, and number of epithelial cells in both vertical and horizontal traumatic resin canals. Unfortunately, the

species *C. penhallowii* was established without a complete anatomical description. Therefore, it was not possible to accomplish a more detailed comparison. However, the studied fossil wood differs from *C. penhallowii* by the presence of ray tracheids (Tab. 1).

The described species is anatomically slightly different from all extant *Cedrus* species by equal development of both uni- and biseriate pits in the radial walls of tracheids. In living species the uniseriate pits are prevalent, and pits are smaller. In addition, in the fossil wood studied, biseriate pits occur also in the tangential walls of tracheids, and those pits are smaller than that of the wood of living *Cedrus*. The fossil specimen is also characterized by lower uniseriate rays, the presence of a different number of ray cell rings surrounding traumatic horizontal resin canals within the same ray, and a little greater number of epithelial cells in horizontal canals (Tab. 1).

#### SYSTEMATICAL REMARKS AND CONCLUSIONS

The formal genus *Cedroxylon* for the fossil pinaceous wood without normal resin canals has been erected by G. Kraus in 1872 (Kraus in Schimper 1872). According to Kräusel (1949), the earliest findings of *Cedroxylon* Kraus are known from the Lower Cretaceous. However, the diagnosis given by Kraus allowed to include in this form-genus not only the Pinaceae, but also conifers from other families. Later Gothan (1905) revised the original diagnosis of *Cedroxylon* Kraus and included it in the unambiguous pinaceous wood remains only (Yatsenko-Khmelevsky 1954). At the same time, the emended genus as defined by Gothan (1905) comprised several natural genera of Pinaceae without normal resin canals and ray tracheids or with the latter but poorly developed, as in *Abies* Mill., *Tsuga* Carr., *Pseudolarix* Gord., and *Cedrus*. Thus, Yatsenko-Khmelevsky (1954) recommended that the name *Cedroxylon* should be applied to poorly preserved fossil wood remains alone, and only the better preserved material should be assigned to one of the above listed extant genera. Moreover, the generic name *Cedroxylon* was differently interpreted and applied by subsequent authors. It seems to be useful only in the case when the

**Table 1.** Comparative anatomy of the fossil wood *Cedrus penzhinaensis* Blokhina & M. Afonin sp. nov. and the wood of extinct and extant species of *Cedrus* Trew. Legend: (+) – presence, (–) – absence, (+ +) – prevail, (+ –) – rare, (?) – no data

Species Anatomical characters	Extinct species				Extant species			
	<i>Cedrus penzhinaensis</i> Blokh. & M. Afonin sp. nov.	<i>Cedrus alaskensis</i> Arnold (Arnold 1952)	<i>Cedrus kamchatkaensis</i> Blokh. (Blokhina 1998)	<i>Cedrus penhalowii</i> (Jeffrey) Bailey & Bailey 1938)	<i>Cedrus atlantica</i> Manetti (Yatsenko-Khmelevsky 1954, Budkevich 1961, Greguss 1955, 1963, Alexeeva 1964, Chavchavadze 1979)	<i>Cedrus brevifolia</i> Henry (Greguss 1955, 1963, Budkevich 1961, Chavchavadze 1979)	<i>Cedrus libani</i> A. Rich (Budkevich 1961, Greguss 1955, 1963, Alexeeva 1964, Chavchavadze 1979)	<i>Cedrus deodara</i> (D. Don) G. Don (Yatsenko-Khmelevsky 1954, Budkevich 1961, Greguss 1955, 1963, Alexeeva 1964, Chavchavadze 1979)
Pits in radial walls of tracheids:								
uniseriate	+	+	+	+	+	+	+	+
biseriate	+	++	+	+	+	–	+	+
triseriate	–	+	–	–	–	–	–	–
diameter of pits (µm)	16–23(24)	21.5	15–24	?	13–19	13–21	9–17	10–20
Pits in tangential walls of tracheids:								
uniseriate	+	+	+	?	+	+	+	+
biseriate	+	–	–	?	–	–	–	–
diameter of pits (µm)	7–8	?	9–15	?	7–13	10–16	7–10	7–13
Uniseriate rays:								
height (in cells)	1–10(16)	2–30	1–40	?	1–45(70)	1–32	1–35	1–32(60)
number of biseriate layers	1–2	–	1–4(6)	?	1–8	1–4	+	+
Traumatic vertical resin canals:								
number of epithelial cells	6–10	?	(4)7–12	?	4–10	?	5–12(13)	4–10
Traumatic horizontal resin canals:								
number of epithelial cells	12–40	?	6–18(30)	?	?	?	6–12(17)	6–12(17)
diameter of resin canal in tangential section (µm) -								
long	100–500	?	90–420	?	?	?	up to 450	100–200
short	40–110	?	30–180	?	?	?	up to 140	15–100
Cross-field pitting:								
number of pit per cross-field	1–4(5)	2–4	1–4(5)	?	1–4(5)	1–4(5)	1–3(5)	1–3(4)
diameter of pits (µm)	4–6	6	5–7	?	5–6	4–8	4–6	5–6
Type of pits:								
cupressoid	+	?	+	?	–	+	–	+
taxodioid	+	?	+	?	–	+	+	+
piceoid	–	?	+	?	+	–	–	+

assignment of a fossil wood to an extant genus is rather doubtful.

A "fringed" torus with uneven marginal indentations is one of diagnostic characters of the genus *Cedrus*. In conifers the "fringed" torus is a rare feature. It is variably expressed in some tracheids and in certain wood specimens alone being relatively constant in *Cedrus* and *Tsuga*. However, in the latter genus the torus is typically smooth, whereas a dentate torus occurs in occasional pits only. In addition, the toral dents in *Tsuga* wood are smaller than in *Cedrus* (Chavchavadze 1979). In practice, however, this feature is difficult to apply to fossil conifers, in which border pits are often filled with various substances, whereas the pit membranes are partly or completely destroyed.

The other diagnostic character of the genus *Cedrus* is a capacity of forming both vertical and horizontal traumatic resin canals in the absence of normal resin canals. This feature is shared with two other pinaceous genera, namely, *Abies* and *Tsuga*, however, they develop vertical traumatic resin canals alone. Despite the fact that vertical traumatic resin canals are relatively common in *Cedrus*, they do not constitute a constant feature, being present in some specimens and annual rings, while lacking in others (Yatsenko-Khmelevsky 1954). In *Cedrus* horizontal traumatic resin canals have excessively developed central canals surrounded by 2 or 5 rings of ray cells. Horizontal traumatic resin canals occur in bi-, tri- and quadriseriate rays. As a rule, the horizontal resin canals differ from the vertical ones, their canal diameters decrease with the distance from the latter.

The presence of smooth, mostly peripheral ray tracheids constitute an additional distinctive character of the genus *Cedrus*. This character is shared with other pinaceous genus *Tsuga*. However, in *Tsuga*, ray tracheids occur along ray margins alone, while in *Cedrus* they are also present at places in the middle part of the ray. In *Abies* ray tracheids are typically lacking in normal wood, occurring, according to Chrysler (1915), in traumatic wood alone. Although, in the opinion of Budkevich (1961) and Chavchavadze (1979), in *Abies* as well as in *Pseudolarix* real ray tracheids are absent, and so-called ray tracheids are actually short cells of different shapes containing crystals of calcium oxalate. Such cells occur in the periph-

eral ray tiers. However, in *Cedrus* ray cells containing crystals of calcium oxalate occur sometimes together with real ray tracheids along ray margins.

The presence of scanty axial parenchyma with smooth or knotted transverse walls of parenchyma cells is also characteristic of the genus *Cedrus*. According to Chavchavadze (1979), in *Cedrus* the radial and tangential walls of parenchyma cells are pitted. There are 5–10 cupressoid or piceoid pits per parenchyma cell. Pits occur in diffuse or alternate arrangement. In the genus *Cedrus* there are cupressoid, taxodioid and piceoid pits in cross-fields, although, taxodioid and piceoid pits are prevalent (Budkevich 1961, Greguss 1963, Chavchavadze 1979). However, *C. atlantica* is characterized by the presence of piceoid pits only, and *C. libani* by the presence of taxodioid pits, whereas, the presence of both cupressoid and taxodioid pits are characteristic of *C. brevifolia*, and three types of pits (cupressoid, taxodioid and piceoid) are typical of *C. deodara* (Chavchavadze 1979).

One more characteristic feature of the wood of *Cedrus* is araucarioid pitting that occasionally occurs in radial walls of early wood tracheids alongside with abietoid pitting. Such mixed pitting is rather common in the wood remains of Mesozoic conifers, being sometimes characteristic of higher taxa, notably the archaic pinaceans of the so-called Protopinaceae group. Shilkina and Yatsenko-Khmelevsky (1980) suggested that the mixed type represents a certain stage of structural evolution of the Pinidae in general. Latter this type was replaced by abietoid pitting that, since the Jurassic period, has appeared in all conifer groups, except the araucarians. Among the modern Pinaceae, the tendency to araucarioid pitting occurs also in the wood of *Keteleeria davidiana* (Bertrand) Beissner (Bailey 1933, Budkevich 1961).

Thus, the fossil species *Cedrus penzhinaensis* sp. nov. is characterized by all the above diagnostic wood anatomical features of the genus *Cedrus*. Therefore, following the recommendation of Yatsenko-Khmelevsky (1954), we have assigned the species to this genus. Nevertheless, its anatomical characteristics do not fully coincide with any published fossil species and any extant ones of the genus *Cedrus*.

As to the both fossil woods *C. alaskensis* (Arnold 1952) and *C. penhallowii* (Barghoorn

& Bailey 1938), they are characterized by the absence of ray tracheids, although, the presence of ray tracheids is one of the important diagnostic features of the genus *Cedrus*. Furthermore, in *C. alaskensis*, biseriate pits are abundant and prevalent, and triseriate pits frequently occur in radial walls of tracheids; these features are not typical of *Cedrus*. Besides, in the pictures presented by Arnold (1952, pl. 1 fig. 3, and pl. 4, fig. 1) horizontal and tangential walls of ray cells are entirely smooth, and, in cross-field 4 pits are disposed in one horizontal row that is characteristic of the Taxodiaceae wood. Therefore the identification of specimen from the Cretaceous of Alaska as a wood of the *Cedrus* (Arnold 1952) is rather doubtful. The same one can say about the fossil wood *C. penhallowii* from the Miocene of USA (Barghoorn & Bailey 1938), which was correctly described earlier by Jeffrey (1904) as *Sequoia penhallowii* Jeffrey.

In terms of wood anatomy, the individual extant species of *Cedrus* are characterized by rather uniform structure (Tab. 1) and are difficult to differentiate. However, their wood anatomy has not been adequately studied, and the published descriptions are incomplete. Besides, wood anatomy of the living species is very similar to that of the published fossil species of *Cedrus*. Thus, it may be assumed from the comparative analysis, that xylem evolution in the genus was, probably, relatively conservative, and wood anatomy of *Cedrus* has undergone, perhaps, relatively small specialization since the Cretaceous. However, the available fossil records, are insufficient yet for indubitable conclusions.

However, we may suppose that in the course of evolution, the number of pit rows in tracheid walls decreased from the equally common uni- and biseriate pits in the both radial and tangential walls to predominantly uniseriate ones in radial walls and only uniseriate – in tangential walls. In the case of tangential pitting, simultaneously with the decrease of pit rows, the pit diameters increased from 7–8  $\mu\text{m}$  (in the Cretaceous *C. penzhinaensis* sp. nov.) to 9–15  $\mu\text{m}$  (in the Palaeogene *C. kamtschatkaensis*), and 10–16  $\mu\text{m}$  in the living species. The maximum number of epithelial cells in the traumatic horizontal resin canals decreased from 40 (in the Cretaceous) to 30 (in the Palaeogene) and 17 in the extant species. The height of uniseriate rays and

the length of biseriate regions in the rays have increased, most likely, since the early Palaeogene (Tab. 1). Cross-field pits in the living *Cedrus* are represented by three types: cupressoid, taxodioid and piceoid (Budkevich 1961, Greguss 1963, Chavchavadze 1979). Such pitting was observed also in the early Palaeogene *C. kamtschatkaensis*, whereas in the Cretaceous *C. penzhinaensis* sp. nov., cupressoid and taxodioid pits occurred in cross-fields. Thus, piceoid pits have appeared in *Cedrus*, perhaps, in the early Palaeogene. However, the number of pits per cross-field and the diameters of such pits, as well as the number of epithelial cells in the traumatic vertical resin canals, were probably constant during the evolution of this genus.

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## PLATE

### Plate 1

*Cedrus penzhinaensis* sp. nov., holotype IBSS, No. 23/1-6, Lower Cretaceous, north-western Kamchatka (Russia)

#### 1–3. Transverse section

1. Growth rings, early/late wood transition, traumatic vertical resin canal in late wood
2. Tangential row of traumatic vertical resin canals
3. Traumatic vertical resin canal shown in the fig. 1

#### 4–9, 17. Radial section

4. Uniseriate pits on tracheid walls
5. Uniseriate pits on tracheid walls, and cross-field pitting
6. “Fringed” torus
7. Crassulae between biseriate opposite pits
8. Radial section: biseriate opposite pits on tracheid walls
9. Mixed type of tracheid walls pitting

#### 17. Marginal ray tracheid

#### 10–16. Tangential section

10. Axial parenchyma
11. Uniseriate ray and pits on tracheid walls
12. Cross-field pitting
13. Biseriate region in uniseriate ray
14. Traumatic horizontal resin canal
15. Ray containing two traumatic horizontal resin canals
16. Traumatic horizontal resin canal

Scale bars: 1 – 120  $\mu\text{m}$ ; 2 – 116  $\mu\text{m}$ ; 3 – 17  $\mu\text{m}$ ; 4, 5, 7–9 – 40  $\mu\text{m}$ ; 6 – 14  $\mu\text{m}$ ; 10, 11, 17 – 35  $\mu\text{m}$ ; 12 – 16  $\mu\text{m}$ ; 14 – 44  $\mu\text{m}$ ; 15 – 73  $\mu\text{m}$ ; 16 – 65  $\mu\text{m}$ .

