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First Finding of Archaeopteridaceae Wood in the Upper Devonian Deposits of the Middle Timan Region

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Abstract—Stem remains of Archaeopteridaceae with a well-preserved anatomical structure were firstly found in the Upper Devonian deposits of the Middle Timan Region. The wood was studied under SEM and REM and was identified as *Callixylon trifilievii* Zalessky. Previous findings of Archaeopteridaceae in the northern part of European Russia and some taxonomic problems of the species were discussed.

Keywords: Late Devonian, Archaeopteridaceae, anatomical structure, cohortoid pitting, and Middle Timan Region.

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INTRODUCTION

Archaeopteridaceae is one of the most mysterious groups of spore plants; it grew circumglobally during the Late Devonian until the Early Carboniferous. Every new finding of these plants extends the suggested territories of the first forest vegetation in the history of the Earth. N.S. Snigirevskaya (1985, 1987, 1995, 2000) investigated the time of the appearance of the first forests and their nature. Her reconstructions became possible because of the discovery by Ch.B. Beck (1960), a well-known American paleobotanist, that Archaeopteridaceae of genus *Callixylon* was a tree. He investigated a large (about 80 cm in length) pyritized stem of *Callixylon zalesskyi* Arnold with a well-preserved anatomical structure from the Frasnian deposits in the state of New York (eastern part of Northern America). Leaves characteristic of *Archaeopteris* cf. *macilenta* Lesquereux were attached to the stem. Hence, he was the first to show an organic connection between *Callixylon* stems and *Archaeopteris* leaves. Somewhat later, Beck (1962) presented a reconstruction of *Archaeopteris* as arborescent plant with a monopodial thick trunk of up to 1 m in diameter at the base and 10 m in height with spiral arrangement of lateral branches.

Archaeopteridaceae combined characters of two different plant divisions: the leaves and reproductive organs were morphologically similar to those of ferns plants, while abundant secondary wood was similar to conifers. The rank of this group of extinct plants is also still a matter of debate: some researchers suggest that they are Archaeopteridales of class Progymnospermopsida (Meyen, 1987), others refer them to an independent division Archaeopteridophyta (Snigirevskaya, 2000); there are those who refer them to division Progymnospermophyta (Taylor et al., 2009).

Archaeopteris Dawson and *Callixylon* Zalessky are the two most thoroughly investigated morphological genera of Archaeopteridaceae. The former is characterized by isolated leaf imprints and related reproductive organs; petrified stems and roots are characteristic of the latter. Although Beck (1960) showed the organic connection between *Archaeopteris* and *Callixylon*, these two morphological genera are still regarded as different morphotaxa, first of all because the relationship of all *Archaeopteris* species to *Callixylon* wood has not been proven and because it was not established that all members of *Archaeopteris* had pseudomonopodial branching of lateral branch systems. Hence, it is possible that not all species of *Archaeopteris* were arborescent plants.

The purpose of our investigation is to thoroughly study the anatomical structure of the new finding of Archaeopteridaceae (genus *Callixylon*) from the Upper Devonian deposits of the Middle Timan Region.

A BRIEF STRATIGRAPHIC DESCRIPTION OF LOCALITY

The studied wood sample came from deposits of the Tsilma and Ust Chirkinsky Formations (which are likely to be nonsegmented), according to the data of I.Kh. Shumilov, who found this sample in the course of field trips in 2007. These formations were distinguished by A.E. Tsaplin in the Middle Timan Region with a stratotype in borehole 333 (Tsilma stone) and were positioned in the uppermost part of the Lower Frasnian Substage by miospore assemblage (*Solution* ..., 1990). The Tsilma Formation was correlated to the lower part of the Timan Horizon, while the Ust Chirkinsky Formation was correlated to its upper part. Attempts to specify the stratigraphic locality of the wood more precisely in the described formations were followed by the conclusion that the wood likely originated from the lower part of the Ust Chirkinsky Formation. This conclusion was based on the unpublished data of A.E. Tsaplin and V.S. Sorokin, who noted the presence of stem and leaf fragments exactly in the lower part of the Ust Chirkinsky Formation. According to their data, the Tsilma Formation and upper part of the Ust Chirkinsky Formation do not contain any plant remains. I.Kh. Shumilov also emphasized cooccurrence of leaf imprints and the wood under study in the Tsilma River bank deposits.

In the two recent decades, the scientists have actively discussed the age of the Timan Horizon in the context of the lower boundary of the Frasnian Stage in the Timan–Pechora province. The Timan Horizon basement or Upper Timan Subhorizon basement are discussed as variants of this level. The first variant of boundary position was based on the palynological data for the whole Timan–Pechora province (Menner et al., 1989; Larionova et al., 1991). These authors suggested one general palynocomplex, viz., a subzone of abundant *Archaeozonotriletes variabilis*, for the whole Timan Horizon and referred it to the Lower Frasnian Substage. Somewhat later, V.Vl. Menner et al. (2001) indicated one general assemblage of the *Acanthotriletes bucerus* subozone for the Timan and overlying Sargai Horizons, *Archaeozonotriletes variabilis insignis*, but failed to draw the lower boundary of the Frasnian Stage. M.G. Raskatova (2001) studied the palynological assemblages of the Tsilma and Ust Chirkinsky Formations using comprehensive borehole data and referred their deposits to the upper subzone of *Acanthotriletes bucerus*, viz., *Archaeozonotriletes variabilis insignis* of *Contagisporites optivus–Spelaeotriletes krestovnikovii* (OK) zone, but did not show a difference in the composition of miospores in the two mentioned formations. M.G. Raskatova, as well as previous researchers, notes that the Givetian–Frasnian misospore boundary may be drawn in the basement of the *Acanthotriletes bucerus–Archaeozonotriletes variabilis insignis* subzone.

Conodont specialists were among the first to draw the lower boundary of the Frasnian Stage in the Upper Timan Subformation basement corresponding to the Upper Timan Subhorizon and to consider that the boundary of the Frasnian Stage was within the Timan Horizon (Menner et al., 2001; Ovnatanova and Kononova, 2008). O.P. Telnova (2003) described palynological assemblages of the Timan Formation by the 1-Balneological borehole in the South Timan Region and showed differences of the Lower and Upper Timan Subformations in miospores. Significant alterations are characteristic, in her opinion, for the level of the Upper Timan Subformation. This level may be regarded as the Givetian–Frasnian phytostratigraphic boundary and the Timan Horizon may be considered as Upper Givetian (Telnova, 2009). In the palynological spectra of the *Densosporites sorokinii* palynozone, i.e., the uppermost zone of the Timan Horizon, there are significant alterations at the level of higher taxa and the *Densosporites sorokinii* zone may be regarded as a boundary between the Givetian and Frasnian Stages for the entire Timan–Pechora province.

The studied *Callixylon trifilievii* Zalessky wood originates, in our opinion, from the lower part of the Ust Chirkinsky Formation, which corresponds to the Upper Timan Subhorizon. The genus *Callixylon* is widespread in the Upper Devonian deposits of Europe, Asia, America, and Africa. Callixylons have not been found in reliable Givetian deposits yet. This is the reason that deposits that contain *C. trifilievii* are dated to the Late Devonian. In such a way we support the idea that the boundary between the Middle and Upper Devonian Divisions was situated within the Timan Horizon as stated by V.Vl. Menner and O.P. Telnova.

MATERIALS AND METHODS

The studied fossil wood sample was found by I.Kh. Shumilov in Middle Timan (the western part of the Komi Republic) at the left bank of the Tsilma River, which is the left tributary of the Pechora River (Fig. 1). The stratigraphic level of the locality is Upper Devonian, the lower part of the Ust Chirkinsky Formation. The wood sample (Fig. 2a) is pyritized, 24.5 cm in length and 19.5 cm in width, dark gray to black, strongly flattened across its width, and is crushed into fine fragments in some places. Cross, longitudinal, and tangential polished sections were prepared in the grinding workshop of the Faculty of Geology at Moscow State University to study the anatomical structure of the wood (Fig. 2b).

The most part of the investigation is related to the study of wood under SEM and REM. More than 50 small wood fragments from different parts of the stem and branch base were investigated with the help of CAMSCAN SEM in the Borissiak Paleontological Institute of the Russian Academy of Sciences. Some part of wood was studied using GEOL GSM 6480-LV REM in the Laboratory of Local Methods of Substance Studies in the Petrology Department at Moscow State University. As a whole, 15 SEM sessions and 1 REM session were carried out. Study and macrophotography of polished sections were performed at the Paleontology Department of the Faculty of Geology at Moscow State University, and in the Photolaboratory of the Borissiak Paleontological Institute of the Russian Academy of Sciences. Polished sections and test tubes with fine wood fragments that were investigated under SEM and REM are kept in

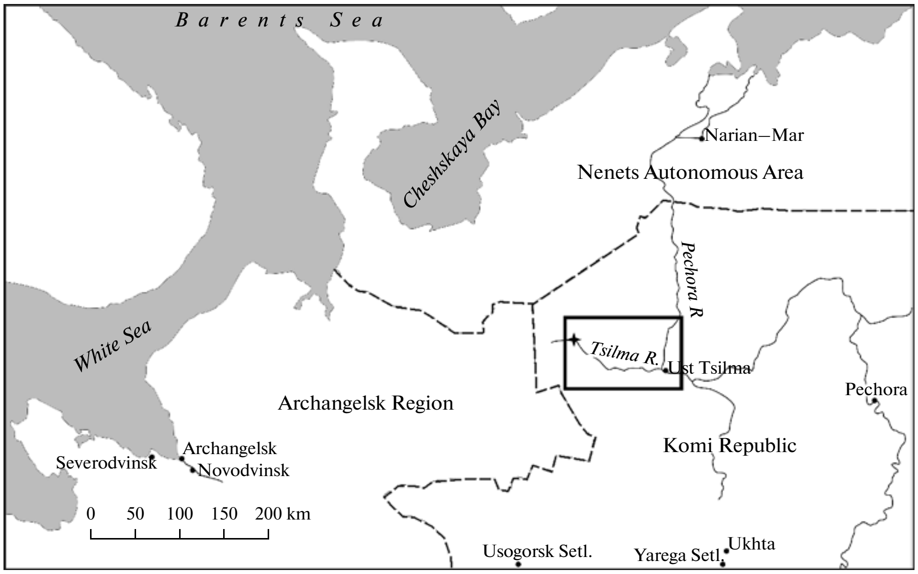


Fig. 1. Geographic locality.

the collection of the Paleontology Department (collection 327).

DESCRIPTION

Division Archaeopteridophyta, Class Archaeopteridopsida, Order Archaeopteridales, Family Archaeopteridaceae, genus *Callixylon* Zalessky, 1911. *Callixylon trifilievii* Zalessky, 1911.

Lectotype: sample 40/1415, isotypes: samples 40a/1415 (cross polished section), 51/1415 (longitudinal polished section), and 48/1415 (tangential polished section); collection is kept at the Chernyshev Central Geological Research Museum (Karpinsky Russian Geological Research Institute, St. Petersburg); collection 1415; the Upper Devonian (Famennian) of Ukraine (Razdolnoe Settlement, Donetsk Region).

Description. ***Morphology.*** The studied sample is a fragment of very flattened vertical stem of 24.5 cm in length and up to 19.5 cm in width. Outer surface is slightly ribbed. Lateral branches are broken closely near basement. In the stem middle part there is a large scar of 75 mm in height and 45 mm in width (Fig. 2a).

Anatomical structure. Primary xylem and pith. The secondary xylem, some elements of primary xylem, and a few pith cells are well-preserved in the studied stem fragments (Fig. 2b). Medullar cells are observed as small clusters containing five to ten irregular rounded cells 80–120 μm in diameter (Fig. 3a). Primary xylem is mesarch in origin due to intrusion of secondary xylem into the zone of primary xylem (Fig. 3b). The metaxylem of secondary branches is observed on wood fragments extracted from the branch basement. It is composed of narrow long tracheids with scalariform bordered pits (Figs. 3b and 3h). Tracheids are characterized by different preservation and are largely observed as inner tracheid and pit moulds. Tracheid outer surface with apertures and borders is occasionally observed. Metaxylem tracheids are polygonal and 12–25 μm in diameter. Pit borders of metxylem tracheids on radial walls are 10–12 μm in width and 3–5 μm in height. Pit apertures of metaxylem tracheids on radial walls are 6–7 μm in width and about 2 μm in height. Most round bordered pits (Fig. 3i) of metaxylem tracheids are found on tangential walls. They are up to 5 μm in width and 4 μm in height, with oval apertures of about 3 μm in width and 2 μm in height. There are scalariform thickenings that are characteristic of Archaeopteridaceae metaxylem tracheids.

Secondary xylem of the studied wood is massive, picnoxylic. It is filled by numerous narrow and long tracheids and pith rays (Fig. 3e). Some tracheids are up to 1500 μm in length. Diameter of secondary xylem tracheids varies in radial dimension from 17 to 45 μm, 25–26 μm on average; in tangential dimension from 15 to 41 μm, commonly 25–26 μm. The secondary xylem tracheids are polygonal in shape with cohortoid radial pitting (Fig. 3f). In the studied wood, pits on radial walls of tracheids occur in groups of two–three pit rows (Figs. 3i, 3j), rarely, in one and four pit rows. Distance between the adjacent groups varies from 4 to 44 μm (19–20 μm on average). One group (cohort) commonly contains 5–25 pits, 11–12 pits on average. Pits are rounded hexagonal and are 7–12 μm in diameter (commonly 9.1 μm) with oblique slits crossing in pairs. Average dimensions of pit apertures are 7 × 2 μm. Pits are absent on tracheid tangential walls in secondary xylem. Pith rays are numerous and simple. Height of rays varies from one cell (Fig. 3i) to nine cells (or 23–255 μm). Low rays (three to four cells) are the

(a) (b)

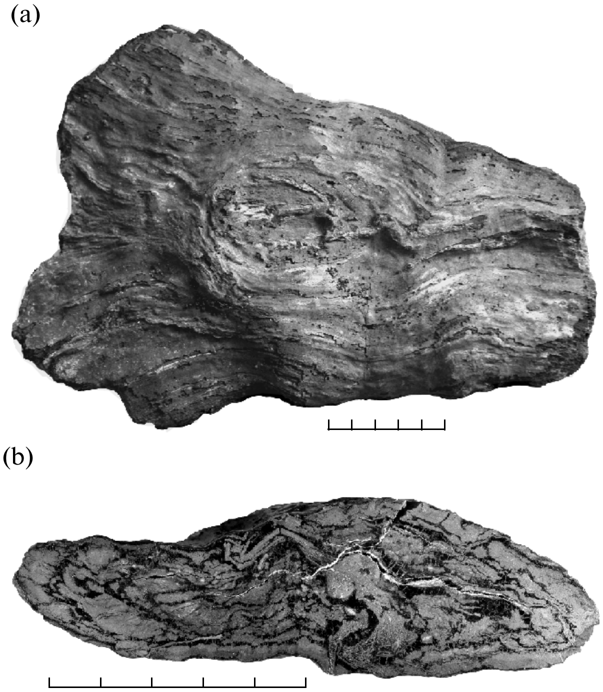


Fig. 2. *Callixylon trifilievii* Zalessky stem fragment from the Upper Devonian deposits of the Middle Timan Region: (a) general view, branch scar is well seen in the central part; (b) polished cross section of the wood.

most common (Figs. 3c, 3i, 3j), while higher rays (up to seven, eight, and nine cells) are sporadic (Fig. 3d). Rays are commonly uniseriate, more rarely, biseriate. They attain 9–39 μm in width. Ray cells are rectangular, of different size, and commonly cover in width 1.5–2 tracheids (Fig. 3e). Ray cells are 9–26 μm in width (15.6 μm on average) and 12–52 μm in height (commonly 25.2 μm on average). Ray pits on radial walls are rare, round, elongate in shape, 8–10 μm in diameter, sometimes free. Ray tracheids are absent. Polyporate–alternate, occasionally, polyporate–opposite pitting of cross-fields is observed (Fig. 3h). In one cross field three to nine (five to six, on average) cupressoid pits with slit-like apertures occur. Cross-field pits are 6–10.2 μm in diameter, commonly 9 μm. Apertures are 7.5 × 2 μm in size on average.

Comparison. The described wood differs in lower and narrower pith rays from *C. newberryi* (Dawson) Elkins et Wieland found in the Upper Devonian deposits of the USA, Germany, Kazakhstan, and Russia.

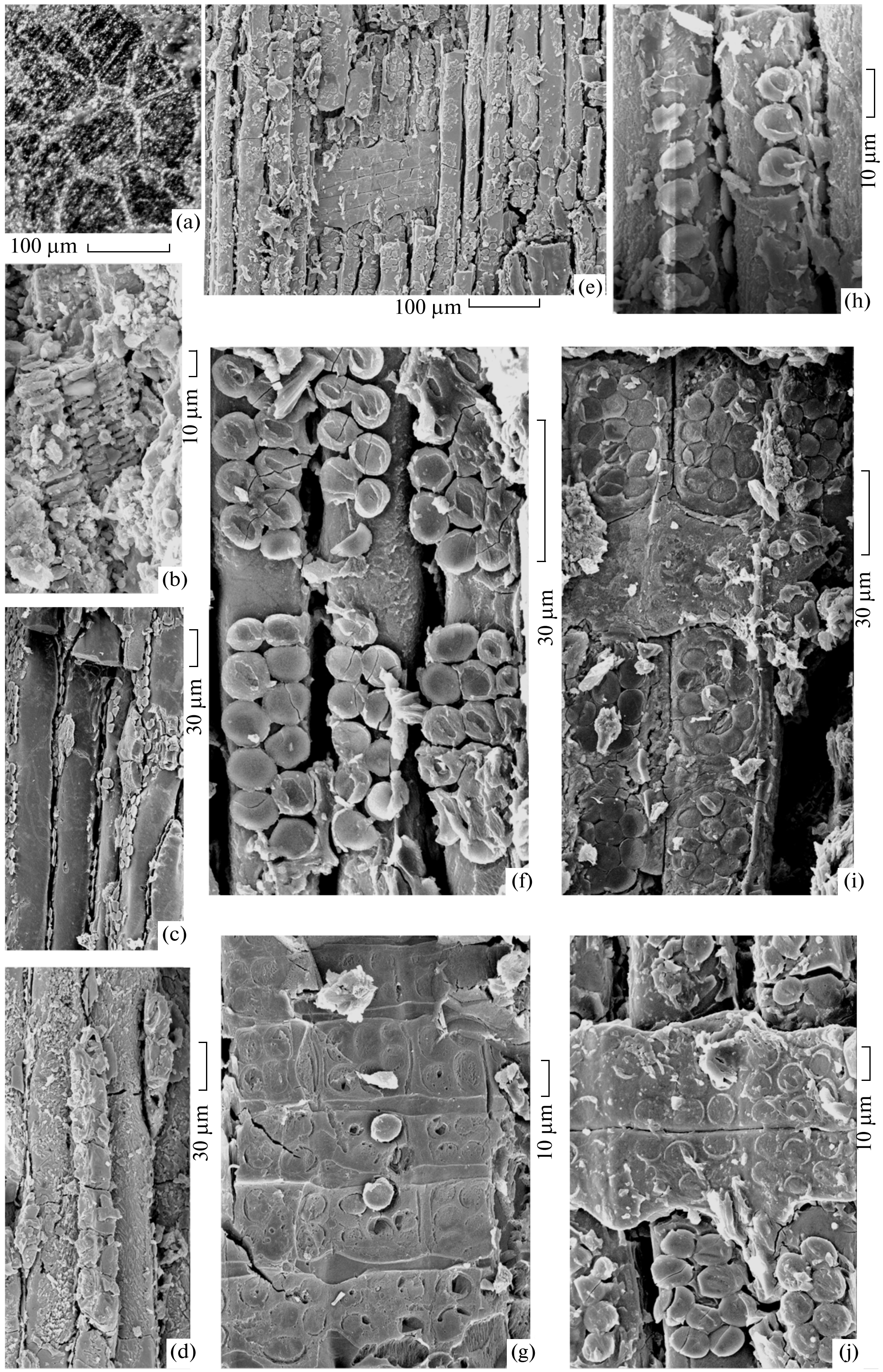
Remarks. In the course of preliminary brief description of the wood (Orlova et al., 2009), we noted the presence of ray tracheids. However, in the course of further more detailed and thorough investigation of the sample, we established that the dimensions of the ray cells varied significantly in tangential cross section; for a certain type of preservation they were very similar to ray tracheids, which nevertheless were not observed in longitudinal sections and thus were absent in the studied wood fragment.

Material. One sample of well-preserved pyritized wood from the left bank of the Tsilma River (the left tributary of the Pechora River), the Middle Timan Region (western part of the Komi Republic); the Upper Devonian, (?) lower part of the Ust Chirkinsky Formation.

DISCUSSION

By the major structural features of its primary and secondary xylem, the studied stem fragment may be referred to *Callixylon trifilievii* found for the first time in the Upper Devonian deposits of the Middle Timan Region. Five Late Devonian localities (Leningrad,

Fig. 3. Main anatomical features of *Callixylon trifilievii* Zalessky wood from the Upper Devonian deposits of the Middle Timan Region: (a) group of irregular rounded cells of pith in cross section; (b) scalariform thickening of primary xylem tracheids in oblique-radial section; (c) low uniseriate pith rays of secondary xylem in oblique-tangential section; (d) medium-high pith ray of secondary xylem in tangential section; (e) pith ray and numerous narrow tracheids of secondary xylem in longitudinal section; (f) cohortoid pitting of secondary xylem tracheids in longitudinal section; (g) cross-field pitting of secondary xylem in longitudinal section; (h) narrow tracheids of primary xylem with uniseriate pitting on radial and tangential walls; (i) multiseriate pitting of secondary xylem tracheids in longitudinal section; (j) secondary xylem tracheids and pith ray in longitudinal section, oblique slit-like apertures are seen in the lower part of the figure.


(a)
100 μm
(b)
10 μm
(c)
30 μm
(d)
30 μm
(e)
100 μm
(f)
30 μm
(g)
10 μm
(h)
10 μm
(i)
30 μm
(j)
10 μm

Murmansk, Vologda, Archangelsk Regions, and Northern Timan Region) of Archaeopteridaceae petrified stems of *Callixylon* and leaves of genus *Archaeopteris* were previously known in the northern part of European Russia (Snigirevskaya and Snigirevsky, 2001). *Callixylon trifilievii* wood, which comes from the Frasnian deposits of the Gnevashevo Formation, is described only in one locality, Andoma Mount (Vologda Region). The investigated *C. trifilievii* found in the Middle Timan Region extends the range of *Callixylon* occurrence to the east of the northern part of European Russia and adds the species description.

In conclusion, the species diversity of genus *Callixylon* is discussed. The only revision of the genus was carried out more than 25 years ago by French (Lemoigne et al., 1983) and Russian paleobotanists. However, new data on the mentioned genus accumulated over the last two decades was sufficient for a new revision. Which features of genus *Callixylon* are generic and which are specific? That question was raised when we investigated the new finding of *Callixylon* from the Upper Devonian deposits of the Middle Timan Region. We failed to answer that question, because most findings of *Callixylon* stems were fragmentary. Moreover, only massive secondary xylem is commonly preserved in fossil state. When M.D. Zalessky (1911) erected the new genus *Callixylon*, he noted unusual pitting on the radial walls of secondary xylem tracheids among other numerous features. In the following investigations, for historical reasons, that very cohortoid pitting (Snigirevskaya, 2000) became a major feature that was used to include the petrified samples in the genus *Callixylon*, in spite of the fact that Zalessky (1911) noted that the mesarch origin of xylem was the most important feature in the identification of the genus. Nevertheless, mesarch xylem may be observed only if elements of primary xylem are preserved completely or at least partially, while the cohortoid pitting of secondary xylem tracheids is observed at any preservation degree of petrified stems. So, what features should be used to define certain species of genus *Callixylon*? We studied typical collections of polished sections of most *Callixylon* species to trace the specific features of this genus.

It was established that the width of the secondary xylem ray is the most important feature in species diagnosis. Other important features are average height of pith rays, presence/absence of ray tracheids in secondary xylem, character and number of pits in the cross field, presence of pits on tangential walls of tracheids. The following category of features includes so-called "individual" features, for example, the vertical or horizontal position of the aperture. As for features of primary xylem in the case of its preservation, they include wide or narrow pith relative to the entire diameter of the stem, the number of mesarch bundles (if the diameter is preserved), as well as some specific features. Hence, according to the new revision of the genus *Callixylon*, the features of the secondary xylem play the most important role in the identification of genera and species of Archaeopteridaceae petrified samples.

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