Sylvocarpus armatus – A Presumed Early Permian ancestor of the Phytolaccaceae

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One of the common flora elements of the Early Permian (Kungurian) Fore-Urals (Russia), especially the localities of Cherkarda and Matvèevo, consist of flowers, inflorescences, racemes, fruits and seeds that can be distinguished in most cases due to some of their characteristic features. They were classified in the past as *Sylvocarpus armatus.* This research examines certain new ideas and concepts and makes the attempt for an evolutionary concept. The fossilised parts of the plant have many similarities with extant Phytolaccaceae, known as pokeweeds, an herbaceous perennial shrub. Probably *Sylvocarpus armatus* can be accepted as their crown ancestor.

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Early Permian landscape with flowers, berries and racemes of *Sylvocarpus armatus*

Left: a complete raceme; **middle and right** are visible isolated berries with the shadows of the seeds inside; **middle**: an insect, *Delopterum rasnitsyni*, searching for food; **right:** the insect, *Agetopanorpa punctata*, can be seen.

Introduction

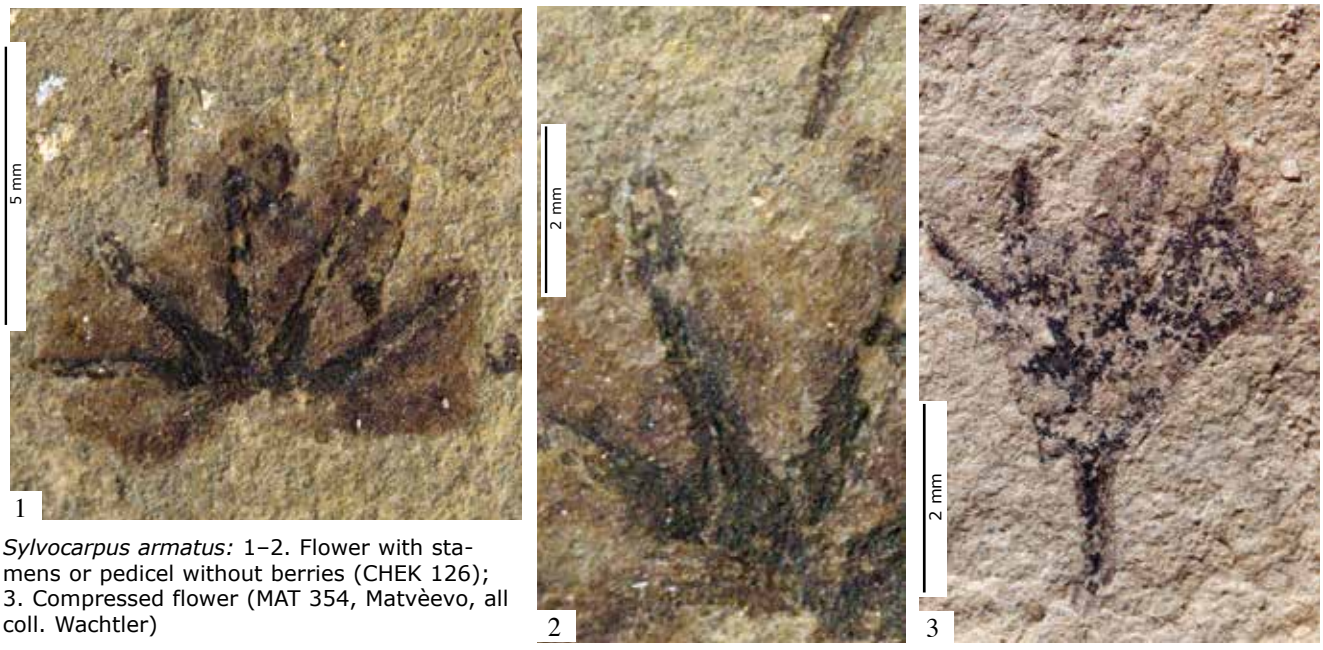
In 2008, the Russian palaeobotanist, Serge V. Naugolnykh, described new "peltate seed-bearing capsules" consisting of umbrella-shaped shields with absent radial ribs on the capsule surface, naming the fruits *Sylvocarpus armatus* and classifying them as Angaropeltidaceae (Doweld, 2001). Effectively these circular flowers/fruits represent a common flora element of the Kungurian sediments from Matvèevo and Chekarda. Due to new specimen, including a completely preserved raceme and many circular seeds and berries, new theories about the importance and further evolution of this interesting plant can be produced.

Description of *Sylvocarpus armatus*

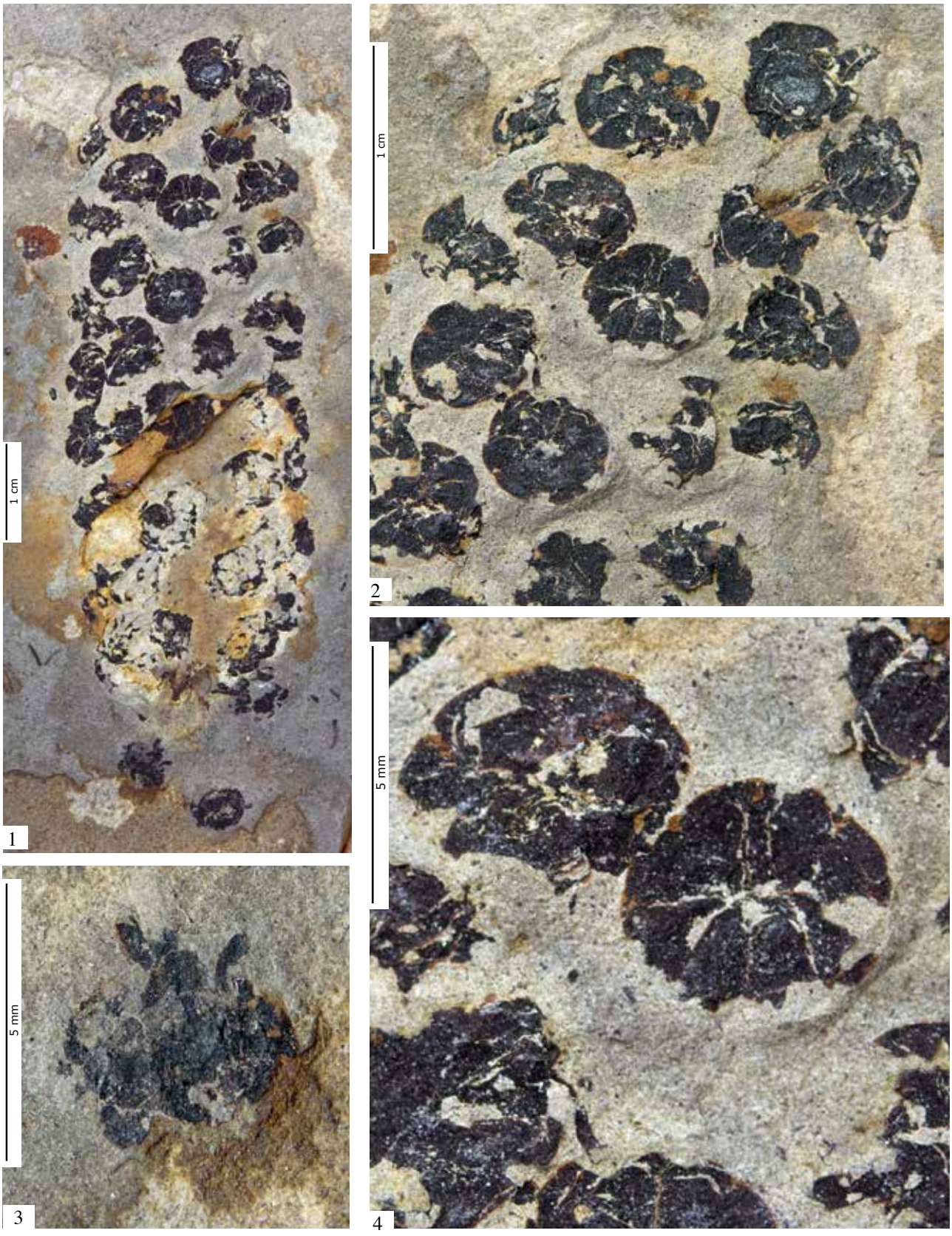
A short diagnosis can state that *Sylvocarpus armatus* represents an agglomeration of individual circular flowers/fruits to form an inflorescence which changes to a raceme after maturation. The developing berries covered by a fleshy aril hold a fair amount of small elongated seeds inside.
The completely preserved raceme (MAT 252) is 70 mm long and 35 mm wide and consists of an aggregation of about 70–100 individual flowers/fruits. Each one is circular and slightly segmented and has a diameter of about 5 mm. Stamen and pistil are preserved on some flowers on the lower part of MAT 252. A flower with ovary and stamens also represents MAT 354. By looking at CHEK 126, one cannot decide if it can be regarded as a flower with stamen and carpels or it represents a pedicel with the berry dropped off. MAT 719 evidence a part of a fully grown inflorescence/raceme, with the flowers/fruits attached on a short stalk.
The seeds or berries – usually 7–8 in number – are circular and have a diameter between 6 mm (MAT 635) and 8 mm (CHEK 334). A smooth berry peel coats the inner fleshy pulp, and the elliptic to elongated seeds of about 1 mm diameter are inserted on the outer margin. MAT 635 shows a fruit covered with a protective skin; in CHEK 334, altogether seven seeds can be counted that lay exposed.
The foliage definitely remains unknown till date, but probably short petiolate leaves like those of CHEK 81, CHEK 101 or leaf CHEK 121 can belong to *Sylvocarpus armatus*. They are oblong, entire on the margin, tapering slightly apically and have a reticulate venation, typically for the Early-Permian locations of the Fore-Urals.

A Proposal to Insert *Sylvocarpus armatus* in the crown-group of the Phytolaccaceae

Sylvocarpus armatus can be regarded as one of the most interesting plants of the Early Permian Fore-Urals. It can be commonly found and therefore, flowers, racemes and berry fruits through different growing stages

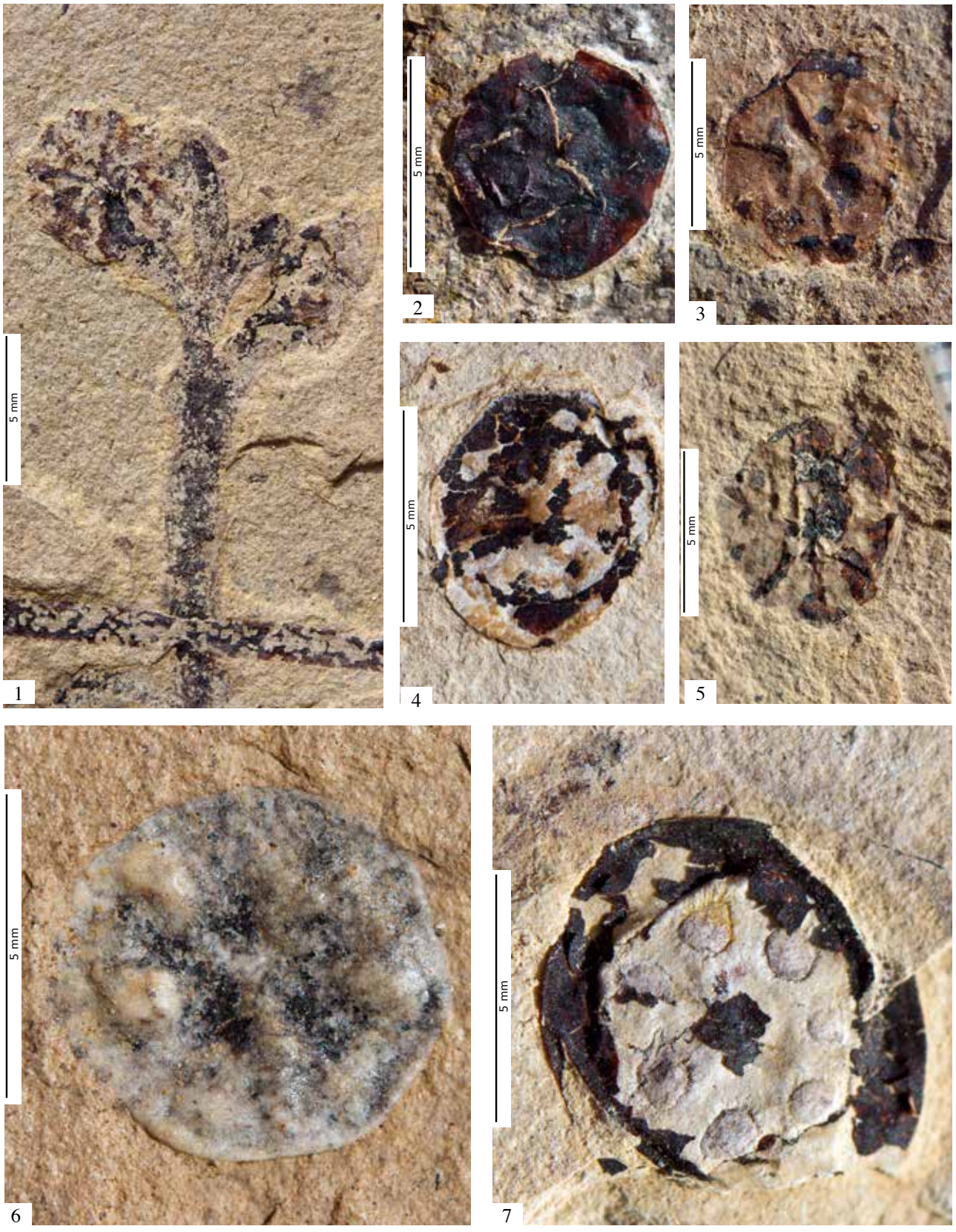


Sylvocarpus armatus: 1–2. Flower with stamens or pedicel without berries (CHEK 126); 3. Compressed flower (MAT 354, Matvèevo, all coll. Wachtler)



***Sylvocarpus armatus*, (Kungurian, Early-Middle Permian)**

1. Complete raceme; 2. Upper part of the inflorescence; 3. Isolated flower from the basal part with pollen anthers and supposed stigma; 4. Detail of closed berries; MAT 104 (Matvèevo, Lyswa, Coll. Gerasch, Thomaseum, Langenaltheim)



***Sylvocarpus armatus*, (Kungurian, Early-Middle Permian)**

1. Part of a raceme/inflorescence (MAT 719, Coll. Gerasch); 2. Isolated berry (MAT 590); 3–5. Developing fruits (MAT 663, MAT 670 and MAT 532); 6. Fruit berry coating some seeds (MAT 635); All Matvèevo, Lyswa, 7. Fruit berry with seven exposed seeds; CHEK 334, (Chekarda; All Coll. Wachtler, Museum Dolomythos, Innichen, Italy)

***Sylvocarpus armatus* nov. gen. n. sp. Suggested leaves**

1. Twig (CHEK 81); 2. Single leaf (CHEK 121); (Chekarda; All Coll. Wachtler, Museum Dolomythos, Innichen, Italy)

have been recorded, although sometimes it is not easy to recognise berries, especially isolated ones. In Matvèevo especially, springtime inflorescences predominate racemes and flowers of *Sylvocarpus armatus*; in Chekarda, more mature berries, fruits or seeds can be found. Although the leaves are not known with certainty, and therefore, the appearance of the whole plant is speculative, just their fertile parts can be regarded as sensational for its different growing stages. Also, sometimes the recovered stamina and ovaries give valuable clues about the flora evolution in the Early Permian (Wachtler, 2017).

Among the existing angiosperms, the family of *Phytolacca*, also known as pokeweed – herbaceous perennial and robust, non-woody shrubs – have major similarities with Early Permian *Sylvocarpus armatus*. Pokeweeds are native to Eastern North America, the Midwest and the Gulf Coast, but they are also naturalised in parts of Europe and Asia, comprising about 65 species in 18 genera. The entire leaves alternate on the stem and are elongated. The flowers

develop in racemose clusters. Each blossom is radially symmetric, equipped with usually five sepals and no petals. The number of stamens fluctuate between five and 30 and are inserted in one or several whorls. Also, the number of carpels vary from five to 16. They are united on the base (or free) and inserted in a ring. Each encloses a single anatropous ovule. The flowers are self-fertile (Ronse De Craene et al., 1997).
In autumn, the racemes hang from the plant showing soft berries that are round and equipped with a flat indented top and bottom. Pedicels with the berries released have a distinctive and rounded five-part calyx.
Pokeweeds reproduce only by their glossy and lens-shaped seeds, contained in a fleshy, celled berry. A plant can, in that way, produce 1,500 to 7,000 seeds annually. The seeds have an extraordinary long viability and can remain fertile in the soil for up to 50 years. After the germination follows a rapid growth.
That *Sylvocarpus armatus* forms a raceme, meaning an unbranched inflorescence holding pedicellate flowers and does not correspond to a spike bearing sessile flowers or a

***Sylvocarpus armatus,* (Kungurian, Early-Middle Permian) reconstructions**

a. Part of a raceme/inflorescence (MAT 104, holotype); b. Flower with anthers (MAT 104); c. Single anther; d. Maturing berry (MAT 719); e. Raceme with berry partially lost (CHEK 126); f. Fruit berry with seven exposed seeds (CHEK 334) g. Single leaf; h. Twig (CHEK 81)

Phytolacca recent

1. *Phytolacca acinosa*, (Indian Poke) flowers; 2. Raceme and fruits; 3. Mature flower with fused carpels and wilted anthers; 4. Detailed view of a mature berry.

5. Pedicels without berries have a distinctive and rounded five-part calyx; 6. Squeezed berry; 7. Dried berry showing 7–8 seeds; 8. Leaf

panicle with its multi-branched inflorescences can be seen well on holotype MAT 104.
Due to fortunate circumstances, racemes were found (MAT 104), as well as CHEK 334). From the outer appearance, racemes of *Sylvocarpus armatus* have many similarities with extant *Phytolacca*.
The fact that *Sylvocarpus armatus* is different from the *Peltaspermum* discs from Euramerican floras was just noted (Naugolnykh, 2008) due to the absence of radial sectors on the shield surface. The Permo-Triassic Peltaspermales were widespread, especially in the Mesozoic in Europe, and were regarded as pteridosperms, meaning seed bearing ferns. But the classification as *Angaropeltum* was not satisfied because it leaves parental affinities further vacant, especially when it is regarded as a gymnosperm.
Phytolacca-like fossil has been described from the Upper Cretaceous Cerro del Pueblo Formation, Coahuila, Mexico as *Coahuilacarpon phytolaccoides.* Multiple infructescences composed of berries with six locules, each containing a single seed, were recorded. The embryo developed in a curved ovule with pendulous placentation, a berry anatomy that is similar to that of the genus *Phytolacca* (Cevallos-Ferriz et al., 2008). Other Phytolaccaceae are also known from the Pleistocene (Chen, 2011).
Though plants with multiple-flowers and fruits forming racemes are common in the extant flora kingdom, such as the *Sorbus* (rowan berry), *Hippocastanus* (chestnut), also the Piperales, among all of them, the Phytolaccaceae are most similar to *Sylvocarpus armatus.* These also due the fact that similar berries are mostly known from the Phytolaccaceae.
Interesting but unresolved is the question whether other plants from Early Permian are parented with *Sylvocarpus armatus*, although certainly not samara evolving plants and not those forming parachutes either. Also, the development of the stone fruits must have occurred in another way. As of now, it can be stated that in the Early Permian Russia/Siberia, racemes with multiple flowers had fully evolved, and these concern not only *Sylvocarpus armatus* but also other Protoangiospermous plants. They were hermaphroditic and developed berries containing multiple seeds. Therefore, *Sylvocarpus armatus* has its origin just between the Devonian till the Carboniferous, as many other plants in the former Angaraland.

Contributions

Thomas Gerasch, Martin Dammann, Thomas Perner, Nicolas Wachtler and Michael Wachtler made fossil specimens available. Michael Wachtler analysed the data, made the drawings, photos and wrote the paper. Thomas Perner supported the work financially.

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