Interesting Paleoangiosperms from the Early Permian Fore-Urals (Russia)

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Some plants from the former Early Permian Angaraland have so many similarities with to-day's angiosperms that it is easy to find connections and solutions to study further evolution of flowering plants. This is valid for *Lyswaia nicolaswachtleri*, a suggested ancestor of the Campanulaceae or *Uraloflos campeiae* nov. gen. n. sp. a low-growing plant with slender leaves and flowers aggregated in umbels. Highly interesting are the fruit capsules resembling extant Leguminosae (Fabaceae) of *Pernerocarpus leguminosa* nov. gen. n. sp. All these plants are characterised by their angiospermy, indicating towards dicotyledons. For future research works, it will be fundamental to find connections between the two mayor flowering plant lineages till the Devonian and look for explanations about the gap in the fossil record till the Cretaceous.

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Two interesting paleoangiosperms from the Permian Fore-Urals: Lyswaia nicolaswachtleri, a suggested ancestor of the Campanulaceae; right: Pernerocarpus leguminosa with fruit pods

In the Early Permian Fore-Urals, herbaceous plants having leaves with a central midrib and fruits capsule containing the seeds were found. Probably campanulate flowers like those of Aspidion decemnervium, first described by M. D. Zalessky in 1937, or Aspidion campanuliformis (Wachtler, 2020) belong to them. The basal leaves are aggregated in tufts. The sympetalous flowers are trumpetshaped to broadly funnelform or nearly bellshaped. Aspidion decemner vium has a flat wheel-shaped corolla and a small tube in the middle; Aspidion campanuliformis is characterised by their tube-shaped corolla forming a cone in the middle. The fruits hang on the corolla and open the capsule to release numerous seeds. The size of the squashed fruit is 20 mm long and about 5 mm wide.

Lyswaia nicolaswachtleri, an ancestor of the Campanulaceae

From all known herbaceous plants of Early Permian Angara, *Lyswaia nicolaswachtleri* (Wachtler, 2017) represents the most interpretable flora element due to some lucky findings. We not only have the campanulalike blossom with its composite flower but also their mature fruit holding dwarfish seeds. Bringing together the complete juvenile plant with a compound of roots and the adult plant, we can establish that the natural size of these angiosperms did not exceed 10 cms. In the Early Permian sediments, herbaceous plants characterised by leaves with a distinctive midrib are encountered in fair numbers.

Searching for a modern representative of *Lyswaia*, we come to the extant Campanulaceae (bellflower family), a cosmopolitan but concentrated in the Northern Hemisphere. The fruits are encapsulated, the flowers are bisexual and bell-shaped, consisting of a narrow, tube-like corolla. The leaves are often characterised by a midrib, such as in *Campanula cespitosa*.

The more difficult questions are why in Early Permian do we have just fully developed Campanulaceae and through which evolutionary way can they be connected with the other herbaceous plants. Although a fusion of several petals into one calyx does not represent a big evolution step, it can be accepted as an obvious way of evolution.

Uraloflos nov. gen. WACHTLER 2020

Etymology

It is from the Ural mountain range and the Latin name for flower.

Diagnosis

It is a low-growing plant with long, slender leaves evidencing a strong midrib; the flowers are aggregated in the umbels.

Uraloflos campeiae nov. gen. n. sp. WACHTLER 2020

Holotype

CHEK 75, Chekarda (Collection Wachtler, Dolomythos, Innichen, Italy

Etymology

It is named after Edith Campei, who preserved and restored many fossils.

Description

Plant: The preserved part of holotype CHEK 75 is about 115 mm long; the leaves reach a length of 40 mm but are only 1–1.5 mm thick. They are slightly curved and have a rounded end. A strong midrib is present in each leaf. The main rachis is on the base, 3 mm thick and smooth. The only preserved inflorescence is 15 mm long and about 20 mm wide and forms an umbel on a short but stout peduncle. It sprouts in middle of the leaves and not terminally. Each single flower/fruit is 5–7 mm long, seems to be composed of five petals and seats on a short pedicel. Other details about the inside of these aggregated flowers are not apparent.

Discussion

Uraloflos campeiae did not form a capitulum, typical of the Asteraceae in the Early Permian layers, such as Naugolnykhia matvéevoi or Asteroforma nicolaswachtleri. The umbel is also different and look like those of Wachtlerosperma stefanperneri. While the leaves in the three genera mentioned did not exist or are only slightly distinctive,



Lyswaia nicolaswachtleri, an ancestor of the Campanulaceae

1–2. Entire plant with detail of a mature and open capsule (MAT 338, Coll. Wachtler); 3. Aspidion decemnervium (MAT 704, Coll. Gerasch, Thomaseum, Langenaltheim); 4. Another campanulate flower, Aspidion campanuliformis (holotype MAT 342, Coll. Wachtler); 5. The flower of Campanula sibirica; 4. Campanula rotundifolia (Bluebell bellflower) capsule containing some seeds, most of them released. It can be compared with MAT 338, which is also an open capsule.





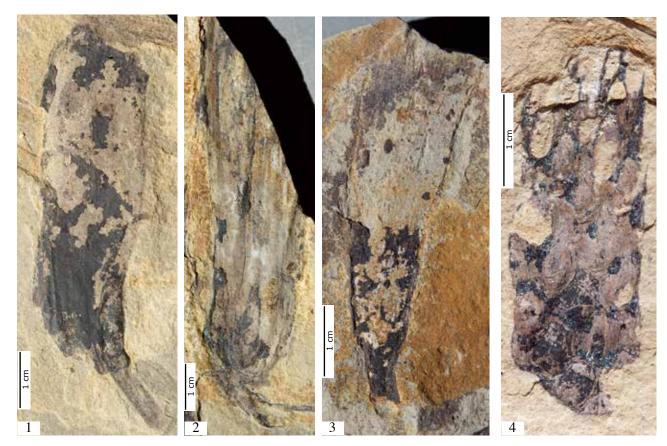


Uraloflos campeiae nov. gen. n. sp.

1. Entire plant with long narrow leaves and aggregated flowers in the upper part (Designed holotype CHEK 75, Chekarda); 2. Detail of the compound corymb from the holotype CHEK 75 (Chekarda, Coll. Wachtler. Dolomythos); 3. Reconstruction of CHEK 75.

in *Uraloflos campeiae*, they are quite pronounced. Therefore, the classification as a new genus is justified and more so when we categorise the different inflorescences. The only one feature that is common among all these herbaceous and low growing plants are their aggregation of many small flowers to form one unit. While gymnosperms never form umbels, it is a common feature in the angiosperms, including the extant ones. It is difficult to establish which plant of today's can be compared with *Uraloflos campeiae*, but many of the monocots or dicots can be worthy of consideration.

It is interesting beyond doubt that aggregated flowers in the form of corymbs, umbels or capitula were frequent in the Early Permian layers of the Fore-Urals, and they debunked the common theory about the relatively late appearance of these kind of flowering plants. Keeping in mind that in former Angaraland, four-petaled flowers like Permotheca colovratica, five-petaled like Claireia pentafolium and Kunguria perneri,



Pernerocarpus leguminosa nov. gen. n. sp. WACHTLER 2020

1. Fruit pod with peduncle (designed holotype MAT 756); 2–3. Other fruit capsules (MAT 758 and MAT 757); 4. Probable inside view of a pod with the seeds (MAT 672), Matvèevo, Coll. Wachtler, Dolomythos Museum.

six-petaled blossoms like Sextupetalum ottiliethomsonae or Sextupetalum smirnovi, multi-petaled flowers like Multifolium petaloides or Nanoflos maueri were found, then the process of evolution to an aggregation of all these flowers is not so far away.

Pernerocarpus nov. gen. WACHTLER 2020

Etymology

It is named after the researcher Thomas Perner, who discovered many plants in the Permian Fore-Urals.

Pernerocarpus leguminosa nov. gen. n. sp. WACHTLER 2020

Holotype

MAT 756 Matvèevo (Collection Wachtler, Dolomythos, Innichen, Italy

Etymology

It is named after their similarity with the Leguminosae, a big group of angiosperms with fruit pods.

Diagnosis

The fruits have the character of pods; these fruit capsules are elongated and robust, with seeds hidden inside. They are connected to the main plant by a peduncle.

Description

Fruit capsules: The smooth pods are 55 mm long (holotype MAT 756) or longer (MAT 758 is probably 100 mm) and 15 mm wide and are held by a robust 10 mm long peduncle. The transition from the stemlet to the fruit capsule is restricted. MAT 672 evidences the inner part of these pods with elongated seeds that are up to 3 mm long and about 1 mm wide. They are inserted in the pod arranged in rows.





Today's Fabacee (Leguminosae)

1. Glycyrrhiza uralensis, also known as Chinese liquorice, is used as a sweetener and in traditional Chinese medicine; an open pod with seeds; 2–3. Halimodendron halodendron, also known as Russian salt tree, belongs to the Fabaceae; an open legume with seeds.

Discussion

Pernerocarpus leguminosa fruit capsules resemble mostly extant Leguminosae (Fabaceae), with over 19,000 species and 730 genera of trees, shrubs and herbs and a worldwide geographical distribution, the third largest family of angiosperms, only surpassed by the Orchidaceae and the Asteraceae. Although the pods of Pernerocarpus were never found in connection with the leaves, some of the many enigmatic fernfronds were never found fertile. Although the first known legumes appeared during the Late Paleocene, about 56 million years ago (Lavin et al., 2005), it can be supposed that just like them, many other paleoangiosperms appeared on the Carboniferous-Permian border of the Fore-Urals, belonging during that time to an isolated continent called Angara. To state the obvious, all properties of Pernerocarpus speak for a classification as the earliest known Leguminosae. However, it is not resolved if they contain the seeds within their pods in one row or like specimen record shows - in two rows.

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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