Dammannia scaratiae nov. gen. n.
A Presumed Early Permian ancestor of the Apiaceae

by Michael Wachtler
P. P. Rainerstrasse 11, 39038 Innichen, Italy; E-mail: michael@wachtler.com

by Thomas Perner
Oregon Institute of Geological Research, 32 SE 139th Ave, Portland, OR 97233-1844

The Early Permian (Kungurian) localities of the Russian Fore-Urals, especially the area around Cherkarda and Matvèevo, are characterised by their richness in broad-leaved plants. In the background, the undergrowth is found covered by low-growing shrubs, creepers and grasses. From one side, they might not have been attractive enough to capture the attention of the fossil-collectors and, therefore, they were overlooked for decades. Fortunately, they can – due to their small size – be recovered in a complete form. A newly discovered plant, *Dammannia scaratiae* nov. gen. n., probably the oldest known representative of the angiosperm family of Apiaceae, will be described. Due to serendipity, it was possible to assemble the complete plant – from the stalk to the leaves to the flowers, fruits and seeds.

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Keywords: Angiosperms, Permian, Angara, Apiaceae

Early Permian landscape from Angaraland with *Dammannia scaratiae,* probably the oldest known representative of the angiosperm family Apiaceae.

Dammannia nov. gen. n. sp. WACHTLER 2020

Etymology

It honours the German researcher Martin Dammann, who found the best specimen

Diagnosis

The plant has an erect stalk and apically forking branchlets with small seeds and the pedicels. The leaves are pinnately dissected or lobed, entire to serrate, with pinnate to palmate venation.

Dammannia scaratiae nov. gen. n. sp. WACHTLER 2020

Type horizon and age

Early Permian, Kungurian, Koshelevka Formation (Irenian substage, uppermost Lower Permian, 275 Mya).

Holotype

CHEK 252 (Dammann Collection, Berlin)

Etymology

It is named after Nika Scarati, who preserved the main slab with caution.

Diagnosis

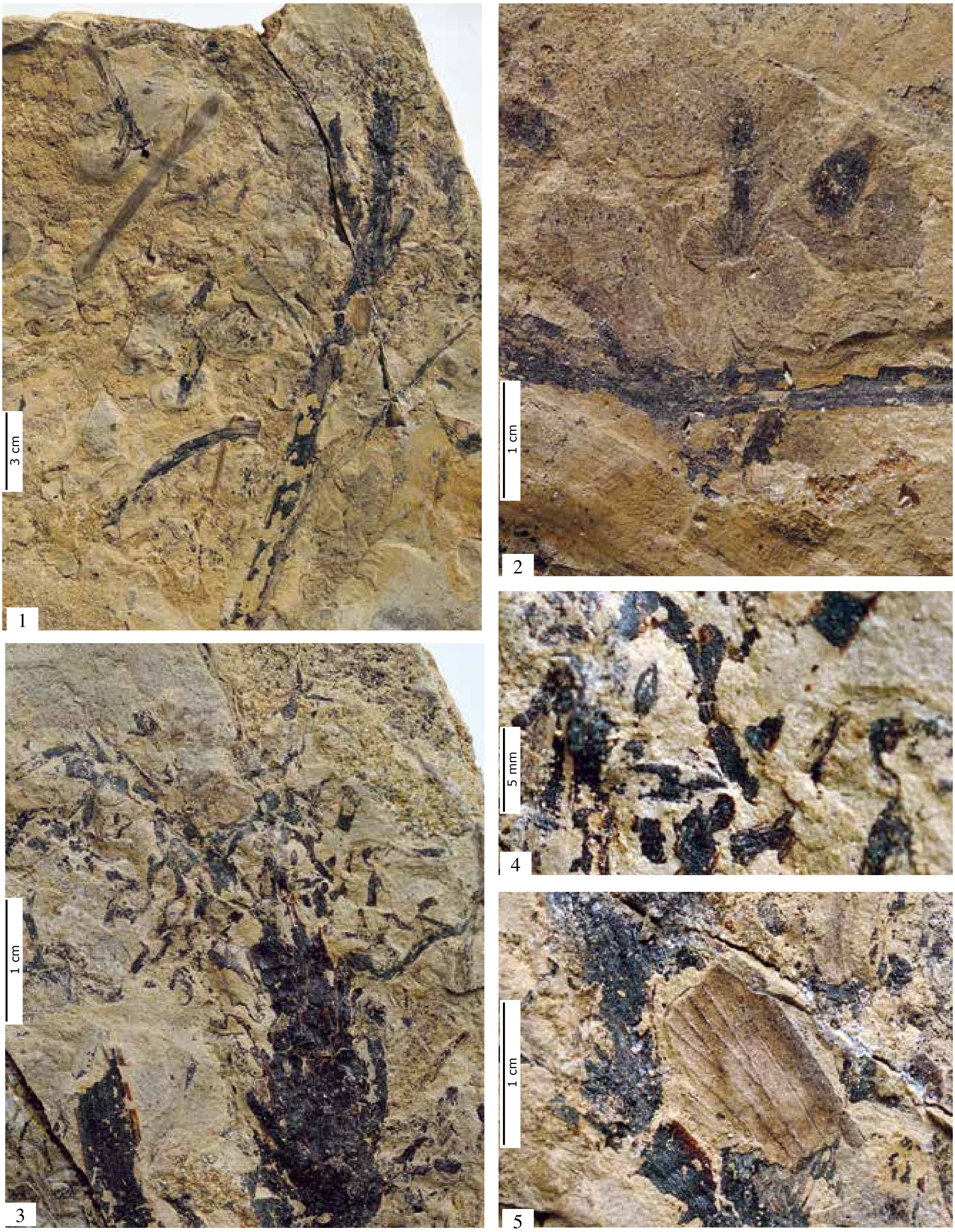
It is a low-growing shrub with palmately compound leaves; the apical part has dividing branchlets and pedicels forming umbels with small elongated seeds.

Description

Plant: Holotype CHEK 252 is 22 cm long and 24 cm wide and consists of an erect stalk, with a basal width of 1 cm. Leaves are attached to the basal part of the forking secondary branchlets. The apical part of the plant consists of several umbels that hold small seeds.
Foliage: Broad, irregularly lobed and toothed, 3 cm long, 2 cm wide, forming a pinnate or palmate compound of leaflets attached to the common axis (Holotype CHEK 252). The leaves are reticulate with several main veins sprouting from the basal stalk, furcating several times.
Fruits and seeds: Numerous pedicel sprout from the apical parts of the erect stalks. They can be interpreted as main umbels, further divided into several secondary umbelets, which can reach a length of 1 cm. The fruits/seeds are small, sometimes slightly winged and elongated and 1 mm long (CHEK 252). The holotype shows an isolated wing from an insect, probably *Sylvohymen sibiricus*. Other plants (CHEK 143, CHEK 62 and CHEK 327) also evidence secondary umbels with pedicels and some attached, elongated and short-winged seed.

Discussion

Dammannia scaratiae cannot be inserted into one of the known gymnosperm blueprints. As many other (Early Permian) Artinskian-Kungurian plants from the Fore-Urals, it has more similarities with an angiosperm.
Among all the existing families, especially the Apiaceae (Umbelliferae), herbaceous plants appearing usually as creepers or tree-like shrubs have some characteristics with this plant. About 3000 members of this family found all over the world, mainly in the temperate regions and rarely in tropical areas, include some well-known vegetables and herbs, such as the carrots, celery, fennel, coriander and angelica. Some are weeds of hedgerows and woodland (cow parsley and hogweed), and some are grown as ornamental garden plants (*Eryngium, Astrantia* and *Aciphylla*). The Apiaceae are characterised by hollow stems, alternate leaves, often deeply dissected or lobed, entire to serrate, with pinnate to palmate venation. The flowers are small and simple, with five petals aggregated in umbels. The fruits and seeds vary considerably within the group, having small schizocarps connected by an artition, sometimes elongated or spiny seeds. They remain paired until maturity and then fall up apart (Berenbaum, 1990).
A compound leaf with two or more leaflets attached to a common axis can also be seen in *Dammannia scaratiae*, holotype CHEK 252. The apical part of the plant is divided into several branchlets and from each diverge a fair number of small stalks or pedicels forming a compound cluster. The Early Permian localities of the Fore-Urals, especially Chekarda and Matvèevo, are rich in flower-like fossils, multiple-fruit-fructifications, but they are also distinguished from other Euramerican Permian localities



Dammannia scaratiae nov. gen. n. sp. (Kungurian, Early-Middle Permian)

1. Mostly entire plant; 2. Attached leaf; 3. Apical part of the plant evidencing several secondary umbelets with seeds; 4. Detail of the small and elongated seeds; 5. Part of an insect wing (probably *Sylvohymen sibiricus*) All CHEK 252, Chekarda, Kungurian, Coll. Dammann.

Dammannia scaratiae; parts of the plant with seeds (MAT 759, Matvèevo)

Extant *Ferula songorica* belonging to the Apiaceae

due to their richness in insects (Zalesskii, 1939; Martynov, 1940; Naugolnykh, 2014; Zhuzhgova et al., 2015; Wachtler, 2017). Therefore, probably one of the small flowers found there can be considered to be belonging to *Dammannia scaratiae*. In today's Apiaceae, numerous flowers are grouped together in an umbrella-shaped flower head known as a compound umbel.

Apiales are known from the Cretaceous (Maastrichtian), but an exact fossil record of it would be impossible to recreate. Records of all groups existed by the Eocene epoch. Leaf traces or flowers are described from the Eocene-lower Oligocene Florissant flora (Colorado), including fruits (*Paleopanax)* from the Eocene Clarno nut beds of Oregon. *Aralia wellingtoniana* leaves were recovered from the Eocene; other leaves such as *Dendropanax* came from the Eocene of North America (Taylor et al., 2009). Several Araliaceae families date back to the Paleocene (Farabee, 1993), with the oldest pollen record (*Ticolporopollenites armatus*) discovered in France. The Apiaceae has a much more extensive history. Starting with *Hydrocotyle* and *Bupleurum* of the lower Eocene, the fossil record steadily progresses. The genus *Sanicula* has been found in the upper Eocene of England, including pollen deposits in Pliocene localities of Portugal. *Echinophora*, recovered from the upper Eocene, has a characteristic dicolporate and equatorially constricted sculpture. Pliocene *Selinum* was collected from Portugal. Modern plants soon followed similar morphologies (Farabee, 1991). As in other Proto-angiosperms, we still have a gap of many million years between Early Permian and the Cretaceous, with no satisfying fossil record.

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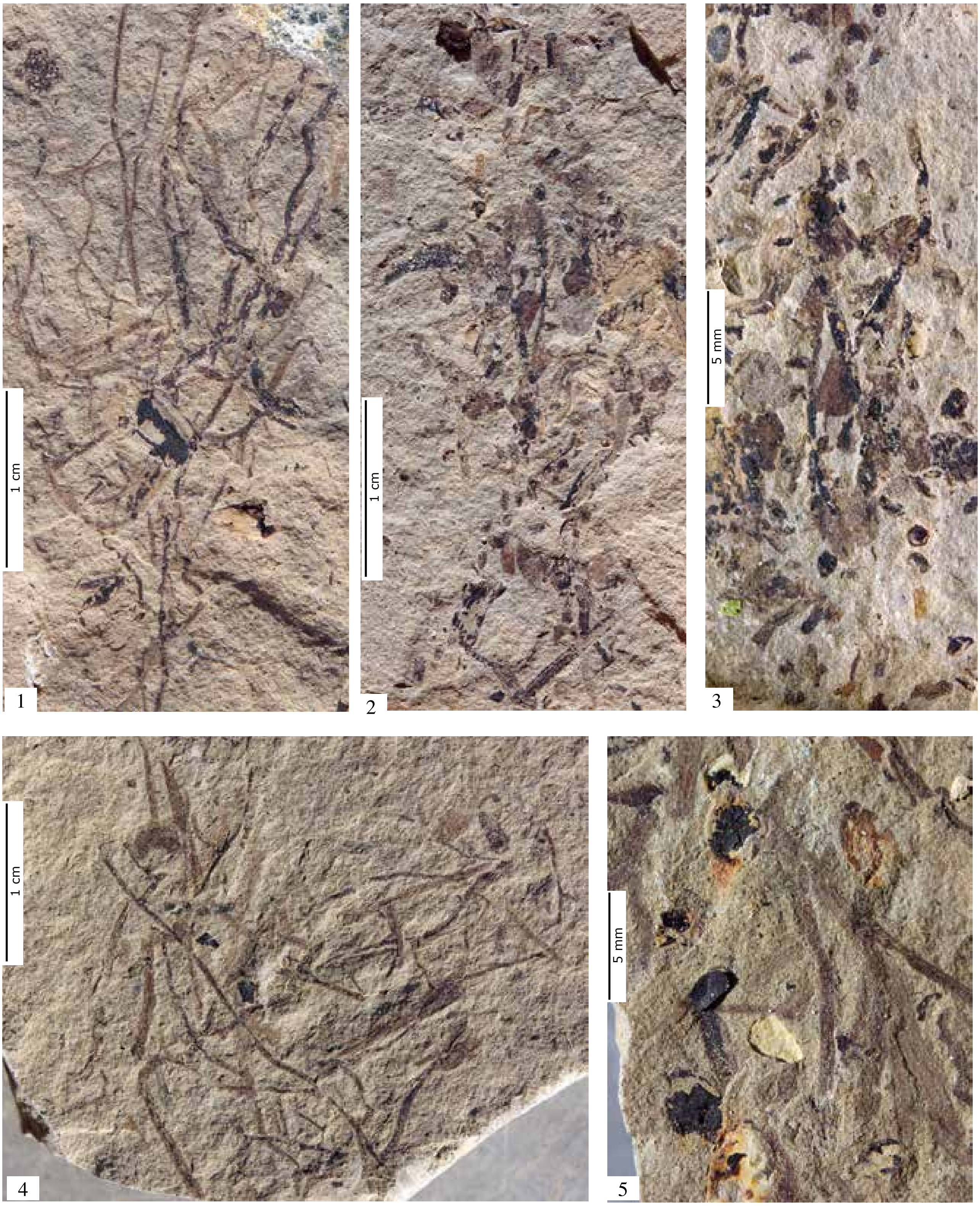
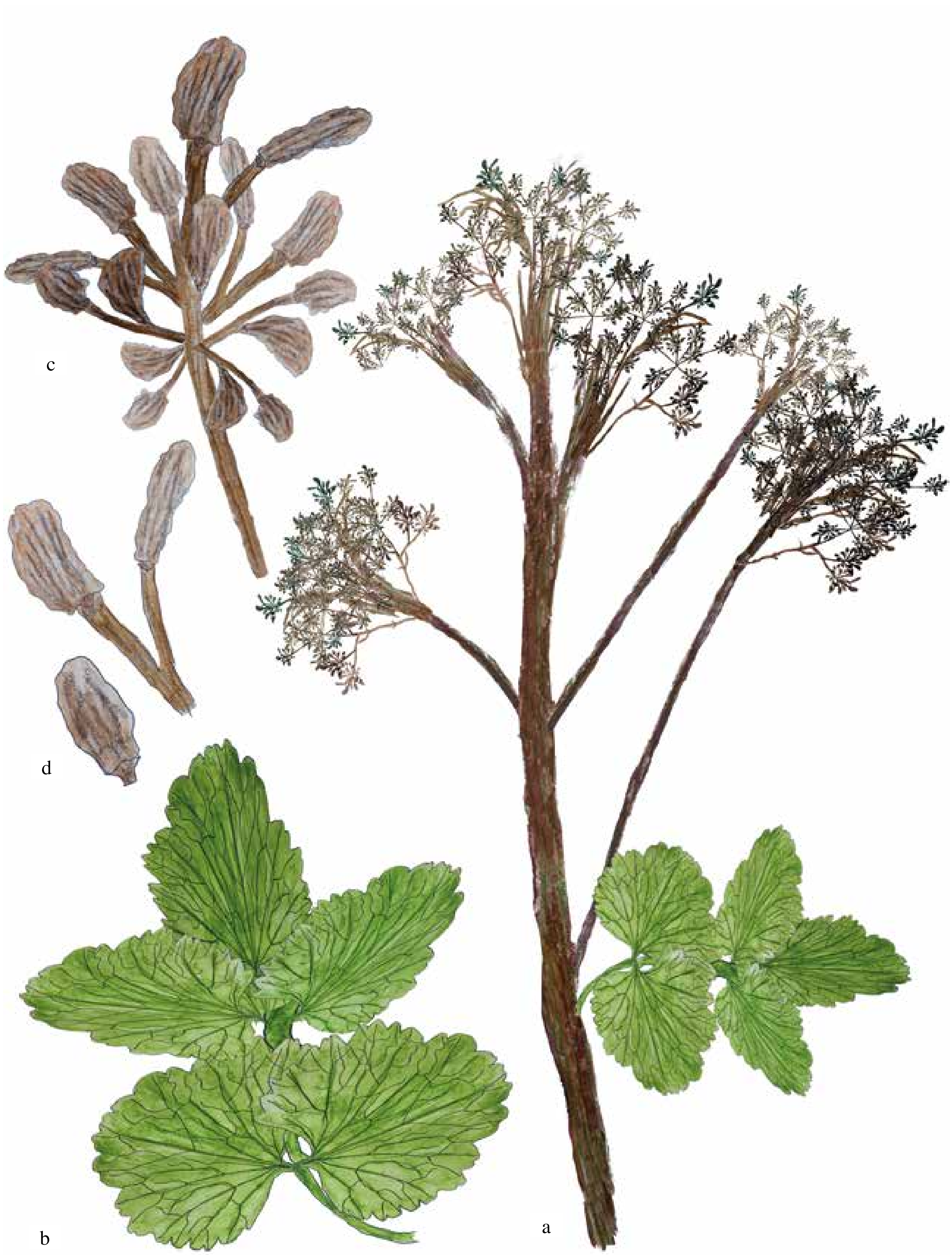


Dammannia scaratiae nov. gen. n. sp. (Kungurian, Early-Middle Permian)

1. Parts of a plant (CHEK 143); 2–3. Parts of the plant with seeds and detail (CHEK 62); 4-5. Apical part with seeds (CHEK 218); All Chekarda, Kungurian, Coll. Wachtler



Dammannia scaratiae **nov. gen. n. sp. (Kungurian, Early-Middle Permian) Reconstructions**

a. Whole plant (CHEK 252 holotype); b. Attached leaf (CHEK 252 holotype); c. Umbel with seeds; d. Single seed All CHEK 252, Chekarda, Kungurian

The Evolution of Magnoliaceae in the Early Permian

by Thomas Perner
Oregon Institute of Geological Research, 32 SE 139th Ave, Portland, OR 97233-1844

The Magnoliaceae played an important role in the evolution of angiosperms, with a documented macrofossil record going back till the Early Cretaceous. New recoveries from the Russian Fore-Urals in the Early Permian (Kungurian) forming an isolated continent called Angara evidence that we have to search the origin of the Magnolias and other tribes of angiosperms on the Carboniferous-Permian border. *Geraschia wachtleri* nov. gen. n. sp. is described as a flowering plant that evidences mostly all the features of today's Magnolias. Also, supposed flower buds and multiple fruits were recovered in association. The fact that they were found together with a plethora of insect families emphasizes a symbiosis between animals and plants, regarded commonly as prerequisite for the evolution of flowering plants. Along with *Geraschia*, we find not only the ancestors of samara-, acorn- and drupe-bearing plants but also presumed members of the Rosaceae and the Asteraceae family. In that, these early Magnoliaceae cannot be regarded as more primitive than other angiosperms, but it can be established that almost all of today's plant tribes had their evolution stage just between Devonian and Early Permian.

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Keywords: Angiosperms, Magnolias, Permian, Angara

Genus *Geraschia* nov. gen. PERNER 2020

Etymology

It honours the German researcher Thomas Gerasch, who found and preserved the first specimen.

Diagnosis

The flower consists of distinct whorls of fruit-leaves and surrounds an inner part of reproductive organs that can be interpreted as stamens and carpels.

Geraschia wachtleri nov. gen. n. sp. PERNER 2020

Type horizon and age

Early Permian, Kungurian, Koshelevka Formation (Irenian substage, uppermost Lower Permian, 275 Mya).

Holotype

CHEK 05 (Museum Thomaseum, Gerasch Collection, Langenaltheim), counterplate (Dolomythos-Museum, Innichen, Italy)

Etymology

It honours Michael Wachtler for his lifelong research work and publications in palaeobotany.

Diagnosis

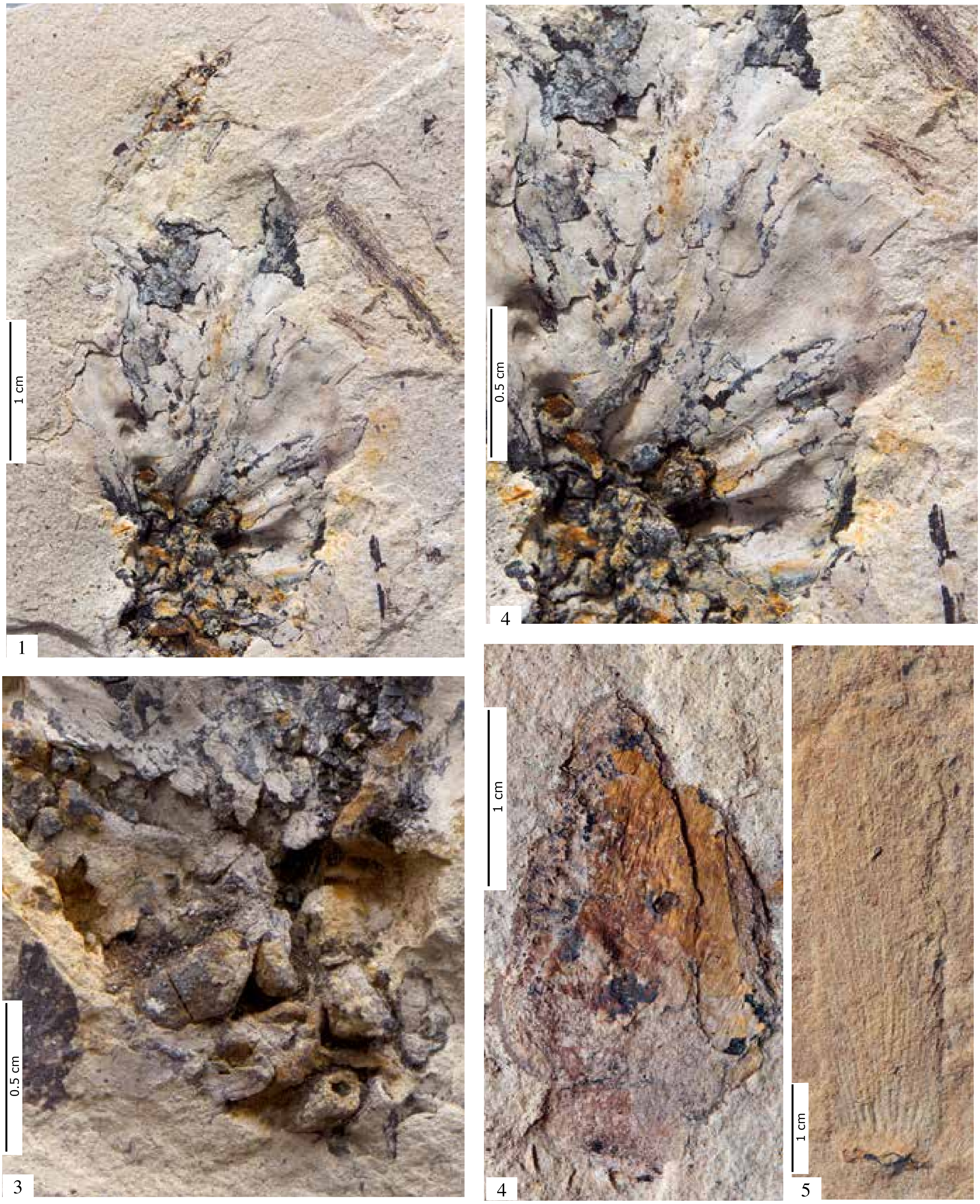
The whorls of leaves seen grouped spirally around an axis that protect the inner reproductive organs; cone-like fruits originate from a short stem and contain multiple seeds.

Description

Flower: The complete flower of the holotype CHEK 05 is 37 mm long and 30 mm wide, with a fair amount of tepals in whorls that are spirally attached to the main base; single obovate tepals, 15–20 mm long and

Tillyardembia antennaeplana **(G. Zalessky, 1938)**

Counterplate with the well-preserved insect, *Tillyardembia antennaeplana*, a plecoptera (stonefly), Dolomythos-specimen; (CHEK 05, Chekarda, Detail of the holoytype, Coll. Gerasch, Dolomythos-Museum)

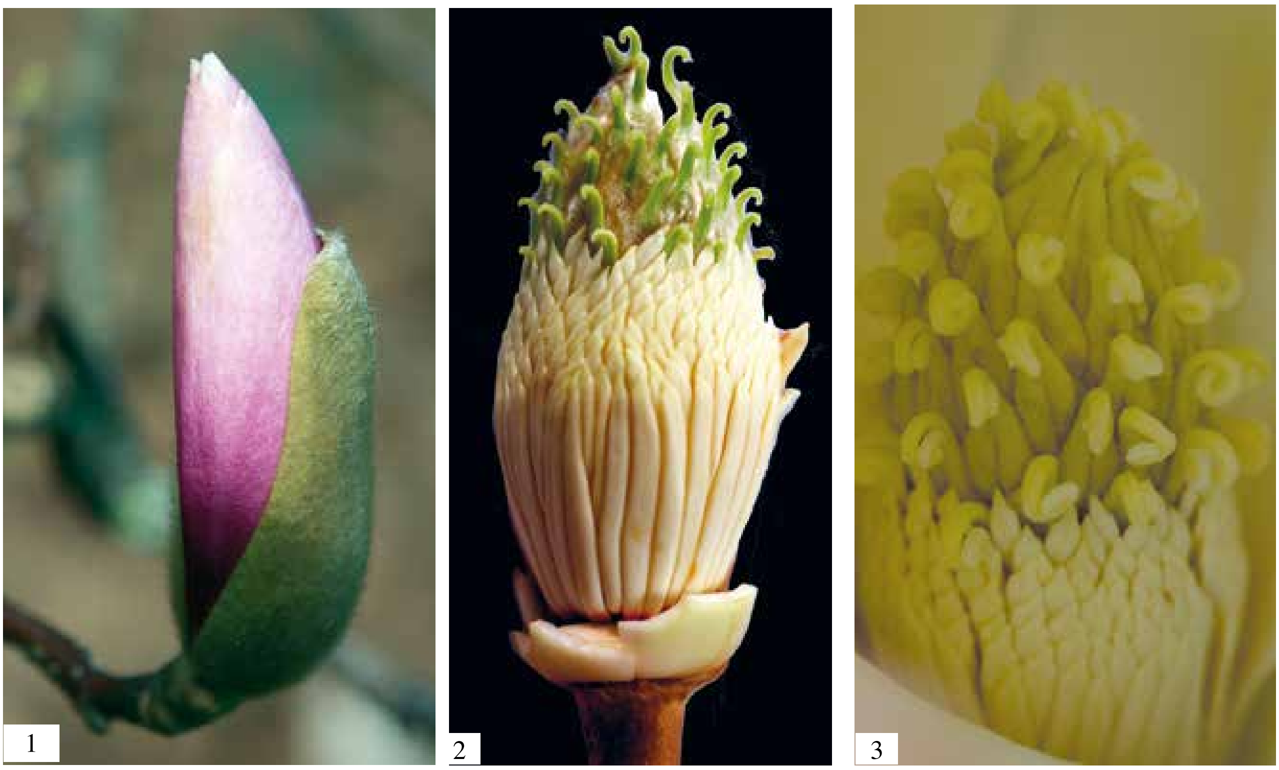


Geraschia wachtleri nov. gen. n. sp. (Kungurian, Early-Middle Permian)

1–2. Flower with the broken basal part evidencing the interior blueprint of the plant and detail of the various tepals (CHEK 05, holotype, Thomaseum-specimen); 3. Detail of the exposed numerous adnate carpels on the basal part (CHEK 05, Coll. Gerasch, Dolomythos-Museum); 4. More evolved flower bud (MAT 406); 5. Suggested flower leaf (CHEK 129, 5 cm); MAT = Matvèevo, CHEK = Chekarda; Kungurian.

Geraschia wachtleri nov. gen. n. sp. (Kungurian, Early-Middle Permian) - Juvenile cones

1. Multiple fruits in an early stage of growth, resembling juvenile Magnoliaceae, although it also has some features of the lycophyta (CHEK 311, Coll. Perner); 2. Flower bud (CHEK 205); 3. Twig (CHEK 105, Chekarda); 4. Leaves (MAT 648, Matvèevo); Kungurian, Coll. Wachtler, Dolomythos-Museum, Italy



1 2 3

Magnolias today

1. Flower bud of *Magnolia liliiflora*; 2–3. *Magnolia grandiflora,* cone with the tepals detached and detail of the stamens (below) and the carpels (upper part)

5–10 mm wide, with complete and unlobed margins; venation not visible; apices of the tepals acute, straight and basally concave; numerous tubiform spirally arranged stamens at the base of a cone-like structure are visible due to a broken opening by the fossilisation; tubes of about 2 mm diameter visible.

Fruits: Suggested reproductive organs are cone-like, sitting on a stout peduncle. They consist of densely settled multiple fruits and are elongated or ovoid (CHEK 311 is 85 mm long and 35 mm wide). Some cones (CHEK 205 is 50 mm long and 35 mm wide; MAT 406 is 19 mm long and 12 mm wide) can also be a result of aborted floral shoots released into the soil after or during the blooming period. Other multiple fruit cones were described as *Uralofructa magnoliformae* (MAT 355, MAT 364, MAT 376, MAT 679 and CHEK 214) representing multiple partially-decomposed fruits. On some bracts, rounded or elongated seeds of about 5 mm diameter are found attached.

Foliage: Suggested leaves are shortly petiolate, broadly ovate; margins are unlobed or slightly lobed and apices are acute or rounded; primary venation is pinnate, secondary venation is irregularly spaced and tertiary veins are irregular reticulate; the length varies from 40–60 mm (CHEK 105, MAT 648 and MAT 514) and width from 10–15 mm.

Discussion

The Artinskian-Kungurian localities from the Fore-Urals are rich in flower-like fossils and multiple-fruit-fructifications, and they are additionally distinguished from other Euramerican Permian localities by their richness in insects. Apart from a few horsetails, ferns, lycopods and conifers, the others do not correspond with gymnosperm families like ginkgos, cycads or conifers, commonly known and widespread in Euramerican sediments during this period.

The reason behind this abundance of Proto-Angiosperms are not entirely resolved yet, but it can be attributed to the simple fact that we cannot accept millions of years' gap between the Early Permian and the presumed origin of the angiosperms in the Cretaceous.

The discovery of Early Permian *Geraschia wachtleri*, a flower with an accompanying insect on the same slab, from Chekarda by

***Geraschia wachtleri* - branchlet**

Entire twig, probably belonging to this plant; leaves of this type are fairly common in the sediments (MAT 514, Matvèevo; Kungurian, Coll. Wachtler, Dolomythos-Museum, Italy).

Thomas Gerasch can be regarded as the "century's finding". Connected fossil plant-insect interactions are rare; beautiful preservations are even more so. So, if fortunate fossilisation conditions allow a broken part of the flower to provide an insight into the blueprint of the carpels and stamens, then this can be regarded as a "lucky punch". The flower CHEK 05 is interesting not only because of the enveloping tepals but also for the basal opening or damage by sedimentation when some of the fertile inner parts were exposed. The tubiform channels have resemblances with the stamens, sprouting from the lower part of today's Magnolias.

Although mutual plant-insect sedimentation can mean all or nothing, it is nevertheless a valuable source of a symbiosis, as it happens today in many angiosperm families (Wachtler, 2017). So why was it different nearly 300 million years ago?

One of the most complex problems in palaeobotany is a fait accompli that the various parts of a plant can only seldom be found in direct connection, such as leaves with the fruits or cones, or even flowers with their fruits. Therefore, it is important to accurately search through stratigraphically coherent lenses or layers till enough material for fairly reliable statistics is gained. In this case, we tried to combine all the parts of the thought Early Permian Magnoliaceae *Geraschia wachtleri*, with the risk of possible misinterpretation. Science must find solutions and not create confusion!

Also, the immature (CHEK 311), as well as the mature cones (MAT 406 and MAT 679) have many resemblances with today's Magnolias. Today the family of the Magnoliaceae includes about 210 species divided between the genera, *Magnolia* and *Yuvalia*. They have a classic disjunct distribution with the centre in east and southeast Asia and a secondary agglomeration in Eastern North America, Central America, the West Indies and some species in South America. Although having a global distribution extending into the temperate zones of both hemispheres, most of their diversity flourishes in tropic to subtropic areas (Zagórska-Marek, 2011).

Magnolia flowers do not have true petals and sepals but are composed of petal-like tepals. The flowers grow at the end of the tree's branches. They are composed of numerous spirally arranged stamens at the base of a cone-like receptacle where they do not pro-

Today Magnoliaceae - Foliage and flowers

1–2. Single leaf and wilted flowers of *Magnolia grandiflora*; 3. Leaves of *Magnolia virginiana*

duce true nectar, rather a large quantity of pollen grains. On the upper part, they give rise to a fair amount of spirally arranged carpels. At maturity, the carpels develop into a woody, cone-like aggregate containing the seeds. The fruit flesh then splits open, exposing the individual seeds covered by a fleshy aril.
Another resembling plant family is *Liriodendron.* The flower is similar, the fruit is also cone-like, but it produces winged samaras.
As known till date, the Magnoliaceae appear in the macrofossil record about 100 million years ago. Often, therefore, they are regarded as the most primitive angiosperms that give valuable indications regarding the origin and evolution of flowering plants (Romanov & Dilcher, 2013). The Magnoliaceae are known from the Early Cretaceous Aptian-Albian Crato Formation in Brazil, representing one of the few known equatorial paleofloras holding various angiosperm fossils. Two of them, *Endressinia brasiliana* (Mohr & Bernardes-de-Oliveira, 2004) and *Schenkeriphyllum glanduliferum* (Mohr et. Al., 2014), were linked with the Magnoliaceae because of the sheathing leaf base and dry fruit wall. That they belong to the Early Cretaceous angiosperms can be accepted, but the difference in the blueprint of today's genus Magnolia is obvious.
Another multifollicular angiosperm fruit from the Middle Cretaceous (Albian-Cenomanian) of Kansas is represented by *Archaeanthus* (Dilcher & Crane, 1984). Clusters of samaras (other interpretation) follicles (Romanov & Dilcher, 2013) were borne terminally at the apex of a stout branch. *Archaeanthus linnenbergeri* was connected with *Liriophyllum kansense* leaves (Dilcher & Crane, 1984). Hence, it can be stated that Middle Cretaceous *Archaeanthus*-samaras and *Liriophyllum*-leaves have striking resemblances with today's *Liriodendron tulipifera*, and a gap of about 100 million years in the fossil record of angiosperms can be filled. One unresolved question is how closely are samara-bearing *Liliodendron* and follicle-holding *Magnolia* parented?
From the Cretaceous till the Permian, we have effectively filled a gap in the angiospermian and magnolian fossil record of about 160 million years. However, interestingly, we have strange breaks in the gymnosperms: from the first Early Permian Abies ancestors (*Majonica*) till Eocene firs (Wachtler, 2015) like *Abies milleri* or Early Permian Pinus ancestors (*Férovalentinia wachtleri, Férovalentinia angelellii, Férovalentinia cassinisi*) (Wachtler, 2013) till Eocene *Pinus macrophylla* or *Pinus lataensis,* we have even longer interruptions. Causes for the above can be the Permo-Triassic crisis, a continental drift causing a change from temperate forests to a tropical vegetation or even difficulty for plants to migrate over long distances due to huge moun-

***Geraschia wachtleri* Early-Middle Permian Magnolia**

Left: a juvenile flower bud ((MAT 406); middle: a whole flower with open stamens (CHEK 05); **right:** two cones (MAT 355 and CHEK 214); some Tillyardembia antennaeplana insects are seen flying above the flowers.

tain ranges or uniform climates over long periods. Among all the proposed ancestors, *Geraschia wachtleri* matches the concept of a real Magnolia from the flower till the floral buds or cone-like aggregates more than the others. Some of the Early Permian Vojnovskyales from the Fore-Urals (Neuburg, 1965; Naugolnykh, 2001) can also be inserted in these schemata.
The "invention" of the flower with pistil and stamen surrounded by protecting leaves in the form of tepals, petals or sepals was just finished in the Early Permian, as well as the characteristic features of samaras, acorns, pappus and drupes in the Early Permian Angaraland. During the same time, on the Euroamerican landmass, we experience a coeval perfection of winged seeds like *Majonica* or coating of the seeds with fleshly arils from ginkgo ancestors like *Baiera.* All these steps in evolution were milestones in the development of the singular plant families, and no one could be regarded as more difficult in the evolution process than the other.

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Early Permian Flowering Plants

Edited by
Michael Wachtler and Thomas Perner

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