

Ginkgo from the Lower Jurassic of Middle Europe

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Over the past years, our understanding of the development of the ginkgo tree, despite its small limited geographical area, has expanded. Research has revealed that fully developed ginkgo plants existed from the early Permian period, about 300 million years ago. These ancient plants already exhibited similarities to the modern ginkgos in their berry seeds and pollen organs. However, for many millions of years, they resembled conifers with their needle-like leaves. It was only in the course of the last epochs that the fan-like shape, almost reminiscent of deciduous leaves and similar to the only existing species *Ginkgo biloba*, became apparent. However, throughout the history of research, innumerable names have been assigned to ginkgo ancestors, which today cause more confusion than clarity. Classifications such as *Baiera*, *Sphenobaiera*, *Karkenian*, *Ginkgophyllum* or *Psylmophyllum* are difficult to convey even to those who are interested. This publication deals with the challenges associated with *Baiera*, a ginkgo ancestor first described in 1843 by the German botanist Braun from the German Lower Jurassic, and attempts to identify possible solutions.

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Ginkgos in the Lower Jurassic of southern Germany. On the left is the *Ginkgoites dichotoma* with seed berries and a juvenile pollen cone; on the right, *Ginkgoites hauptmannii* grows with mature male and female fructifications.

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The ancestors of the genus *Ginkgo biloba*, which now comprises a single species, reveal like a mirror image the problems of palaeobotany. This field has made substantial contributions in unravelling the intriguing development of plant life, leading to a niche existence in both scientific and general knowledge. Understanding the evolution of ginkgo trees over the course of 400 million years is akin to solving a puzzle, built on hypotheses and corrections to arrive at reasonably reliable findings.

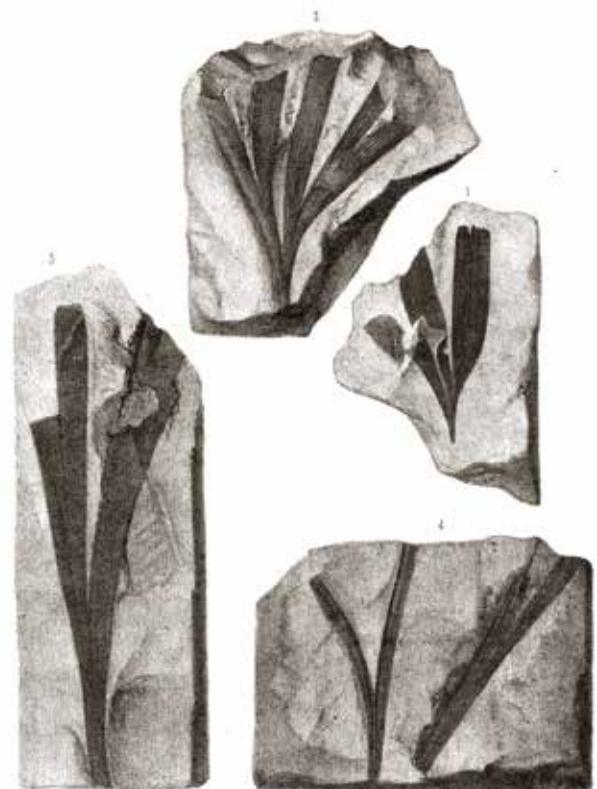
The difficult interpretations of plants present a stark contrast to the animal kingdom, where the reconstruction of the whole organism is easier. The same cannot be said for plants. Each individual part of a plant, from the roots to the leaves, must be carefully put together to form a meaningful whole. Even in the realm of naming, there is a debate regarding whether to prioritise general comprehensibility over strict nomenclature considerations. The exploration of the ginkgo is a prime example of this issue.



From Schenk, 1867, plate 9: The collections described by Braun in Münster (1843) were handed to A. Schenk. He used the name *Jeanpaulia muensteriana* instead of *Baiera dichotoma*.



From Braun in Münster, 1843, Plate XII. First description and illustration of *Baiera dichotoma*.



In addition, Schenk, 1867, figured on plate 5, Fig. 1-4 *Baiera taeniata*.

The natural populations of the ginkgo tree were only discovered around 1730 in southwestern China. Today, it is widely cultivated due to its resistance to environmental influences in temperate zones around the world. The ginkgo avoids excessive cold and heat with low rainfall, so it is believed that it flourished during the Permian and Cretaceous periods, thriving in similar temperatures.

The distinctive fan-shaped foliage of the ginkgo tree, characterised by fine veins branching out from the leaf blade like a net, sets it apart from a majority of angiosperm leaves. Additionally, it features unique cuffs from leaves of the short shoots emerge, along with one or two seed berries.

Drawing on current knowledge, the following can be summarised: the first precursors of the ginkgo probably developed in the Middle Devonian, 380 million years ago, with leaves like the *Flabellophyllum divisum* from Lindlar having been identified, but the associated ovules remain a mystery (Wachtler,

2023ab). From the Early Permian period, fully developed ginkgos with species-typical single-seeded berries and catkin-like pollen cones existed, especially in the Dolomites with *Ginkgoites pohli*.

One of the most notable differences from the present day lies in the foliage of the ginkgo species. During the Permian period, ginkgo leaves were needle-shaped and irregularly lobed. The ovules arose from a modified leaf and differed slightly from modern ginkgoes, which are connected by a distinct stalk.

A flowering took place in the late Permian period, particularly in the Dolomites, where rich deposits (Montan) containing the long-needed representative *Ginkgoites gasseri* (Wachtler, 2023) were recovered. Alongside the foliage, a variety of seeds and pollen cones were commonly found. However, fan-like leaves (*Ginkgoites munchisonae*) were unveiled in strata of similar age in the Dolomites (Seceda), along with fertile parts (Wachtler, 2021). Another long-needed variant of *Ginkgoites* (*Baiera digitata*) was

From Antevs, 1919 "The Lias-sic Flora from the Hoer-Sandstone": Plate 5. Fig. 18. *Ginkgo geinitzi* Fig. 19. *Baiera muensteriana*; Fig. 20-24. *Baiera taeniata*; Fig. 25. *Baiera longifolia*; Fig. 26. *Baiera angustiloba*; Fig. 27. *Baiera spectabilis*

Many names for similar foliage



From Heer, 1876. Contributions to the fossil flora of Siberia and the Amurland. Plate VII. Ginkgos from different eras. Fig. 1. *Baiera czekanowskiana*; Fig. 2-3. *Baiera longifolia*; Fig. 4 *Ginkgo huttoni*; Fig. 5-6. *Ginkgo schmidtiana*; Fig. 6. *Ginkgo sibirica*; Fig. 7. *Ginkgo lepida*, Fig. 8. *Ginkgo concinna*; Fig. 9 *Ginkgo pusilla*; Fig. 10 *Ginkgo flabellata*.



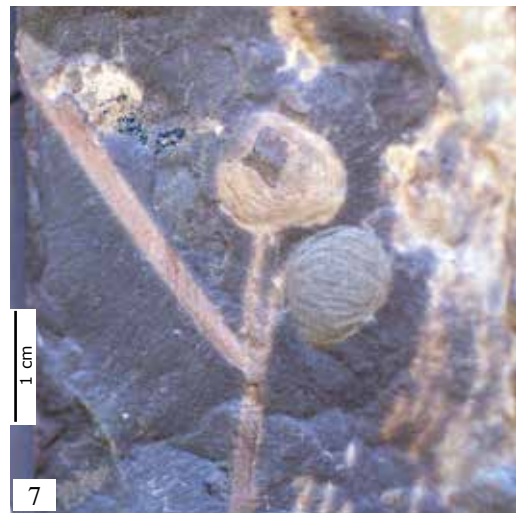
The Ginkgophyte collection of Sepp Hauptmann from the Lower Jurassic of Upper Franconia photographed in his house.



1–2. Branch of a ginkgo tree in the garden of Sepp Hauptmann, as well as a picture of dried leaves and various leaf shapes of the ginkgo in the past; 3–4. Juvenile and overripe pollen cones of *Ginkgo biloba*; 5–6. Mature seeds, as well as dried up seeds on the ground.

discovered in the Zechstein-quarries of Germany. In contrast, the *Psymophyllum* plants found in abundance in the Permian era in the Russian Ural region did not belong to the Ginkgoales family, indicating a different origin. Overall, the Permian and Triassic periods featured larger continental clods with completely autochthonous vegetation, such as the Angara flora of Russia or the Gondwana flora in the southern hemisphere. During the Triassic period, ginkgoes were largely absent from Europe despite the prevalence of fellow plants, such as conifers and cycads. Only after the Raibl catastrophe, towards the late Triassic and early Jurassic, did the ginkgoes appear again almost simultaneously in several distant areas, such as Germany, Sweden, Hungary, eastern Siberia, Kyrgyzstan, and China (Wachtler, 2024). Even during this time, the Permian trend continued, with long-needled variants existing alongside slightly incised fan-like leaves.

In the field of palaeobotany, a dilemma arises when considering how to classify plants based on their fertile organs. For example, should we categorise plants like the ash maple (*Acer negundo*) and field maple (*Acer campestre*) together, despite their vastly different leaves but similarly paired samaras? Additionally, many pines and araucaria conifers have partially different leaves but similar cones. In this case, all fossil ginkgo precursors would be listed under *Ginkgoites*. Alternatively, should we focus on the deeply worn, almost needle-shaped leaves that have evolved



***Ginkgoites (Baiera) dichotoma*. Leaves and female fructifications**

1-2. Typical foliage (Pechgraben, Urwelt-Museum Upper Franconia, Bayreuth); 3. Long-needle leaves (BT 014957. 00); 4. Leaf (PECH 147, Coll. Wachtler, Dolomythos-Museum); 5-7. Foliage with attached seeds and detail (BT 014956.00) Pechgraben, Urwelt-Museum Oberfranken, Bayreuth

over millions of years as a characteristic, regardless of the fact that all ginkgo ancestors developed seed berries and pollen cones comparable to today's? This raises the question of whether to classify these leaves as *Baiera*.

One or two species of ginkgo can be found in the Lower Jurassic of southern Germany, specifically in the "Locus typicus" – the area where fossil ginkgo research achieved its first milestones. A confirmed species, *Ginkgoites (Baiera) dichotoma*, and potentially another (or even merely a variety), *Ginkgoites (Baiera) hauptmannii*, exhibit slightly different leaf shapes but share the same fertile organs. Before delving into further explanations on this topic, a brief historical description will be provided.

(Ginkgoites) Baiera dichotoma (Braun, 1843)

- 1843 *Baiera taeniata* Braun in Münster, Beitr. VI. p. 21
 1843 *Baiera dichotoma* Braun in Münster, Beitr. VI. p. 21. Tab. 12. Fig. 1-8
 1845 *Jeanpaulia dichotoma*, Unger, p. 112
 1867 *Baiera taeniata*, Schenk pl. V. Fig. 1-4. Pl. VI. Fig. 1-2
 1867 *Jeanpaulia muensteriana* Schenk Pl IX. Fig. 1-13
 1876 *Ginkgo sibirica* Heer, Beiträge zur foss. Flora Sibiriens. Pl. XI, Fig. 1-19
 1876 *Ginkgo lepida* Heer, Beiträge zur foss. Flora Sibiriens. Pl. XII, Fig. 1-10
 1880 *Baiera czekanowskiana* Heer. Beiträge zur foss. Flora Sibiriens. Pl. I. Fig. 12. Pl. II. Fig. 1-3. III Fig. 4-8

Description

Leaves: The leaves of this species feature almost needle-shaped individual leaves that arise at the same level from a petiole about 2 to 3 cm in length, each of which bifurcates once dichotomously. The individual leaves can reach lengths of up to 10 cm and widths of approximately 0.5 cm, which are blunted apically. In the optimal case, these plants form three double-divided leaf bodies.

Female fruitifications: The seeds are slightly oval to rounded, measuring about 1 cm in length and surrounded by a fleshy sarcotesta. They become furrowed in the mature stage, with a woody sclerotesta inside. The seeds are attached to long individual needles that are nearly indistinguishable from the sterile ones.

Ginkgoites (Baiera) hauptmannii (Kirchner & Van Konijnenburg-Van Cittert, 1994) **Wachtler comb. nov. 2024**

1994 *Schmeissneria microstachys* Kirchner & Van Konijnenburg-Van Cittert, Plate I, Fig. 1-2, III, Fig. 1-3, Pl. IV Fig. 1

1994 *Stachyopitys preslii*, Kirchner & Van Konijnenburg-Van Cittert, Pl. IV fig. 1 + 5

1994 *Karkeniania hauptmannii* Kirchner & Van Konijnenburg-Van Cittert, Pl. IV fig. 3,4,6, Pl V, Fig. 1, Pl VI, Fig. 1

Description

Leaves: Each leaf is supported by a short, 1 to 2 cm long petiole, which gives rise to relatively wide individual leaves (up to 1 cm) at the same level. The leaves bifurcate dichotomously at the apex and taper to a pointed end, reaching lengths of up to 10 cm.

Female fructifications: The seeds are slightly oval to rounded, reaching about 1 cm in length, surrounded by a fleshy sarcotesta. These are furrowed in the mature stage, with a woody sclerotesta inside. The seeds are located at the top end of the tapered individual needles.

Remarks

In his publication, "*Beiträge zur Urgeschichte der Pflanzen*" (Contributions to the History of Plants), botanist Braun describes two plant species from Strullendorf near Bayreuth under the names *Baiera dichotoma* and *Baiera taeniata*. He mentioned two others, *Baiera huttoni* and *Baiera digitata*, from the Middle Jurassic sites of Gristhorpe Bay (North Yorkshire), as well as *Baiera furcata* from Hayburn Wyke. Braun classified these plants from the Jurassic period under the hydropterids, which are water ferns belonging to the families Salviniales and Marsileales.

However, two years later, in 1845, Austrian palaeobotanist Franz Unger changed the name to *Jeanpaulia dichotoma* without providing further explanations or illustrations. Schenk later adopted this name in 1867 and introduced another species, *Jeanpaulia muensteriana*, while maintain connections to the water ferns.

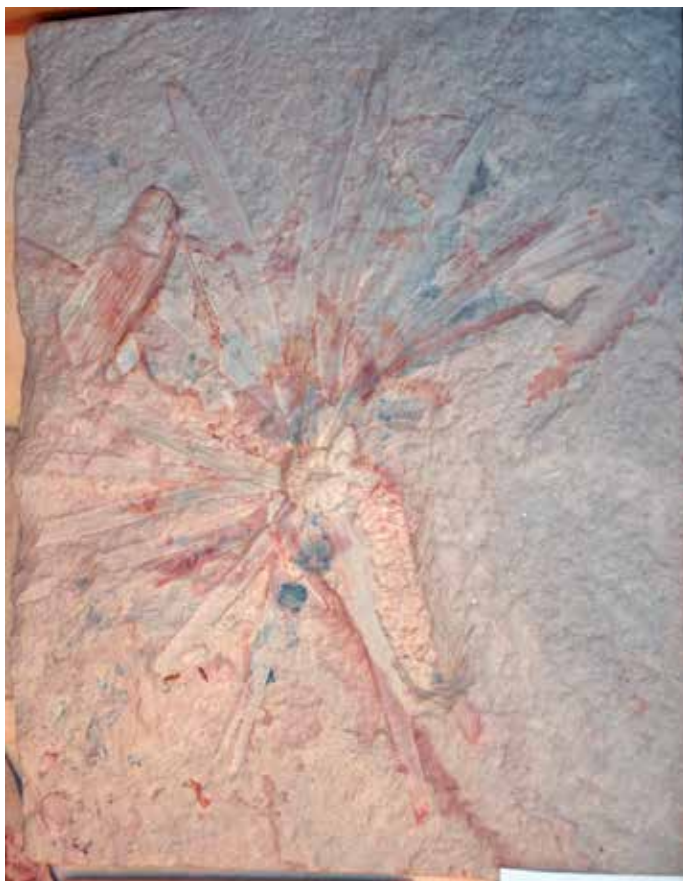
In 1876, Swiss palaeobotanist Heer was the first to notice a connection between these species and the only surviving *Ginkgo*



***Ginkgoites (Baiera) hauptmannii*. Leaves and female fructifications**

1-2. Foliage (BT 014954. 00 Pechgraben, Urvwelt-Museum Oberfranken, Bayreuth); 3. Slightly different foliage (BT 014955.00, Pechgraben, Sandpit Dietz, Urvwelt-Museum Oberfranken, Bayreuth); 4-5. Leaf with seeds (Pechgraben, sandpit Dietz, lent 3, Ex. Coll. Hauptmann, Coll. Tischlinger, Stammham)

biloba. He based his findings on discoveries spanning several eras in Lake Baikal, eastern Siberia, and Pécs in Hungary. In various publications (until 1880), he succeeded in refining these connections by identifying typical ginkgo seed berries and pollen cones. However, he struggled to draw a dividing line between the deeply worn conifer-like Ginkgo precursors and the fan-shaped leaves similar to the modern *Ginkgo biloba*. Consequently, Heer alternated between the names *Baiera* and *Ginkgo* several times, all without presenting clear explanations. In 1919, American palaeobotanist Charles Seward proposed a new interpretation by introducing the name *Ginkgoites* for fossil ginkgo plants. This made perfect sense, as scientists had started to provide such endings for fossil plants. This was already

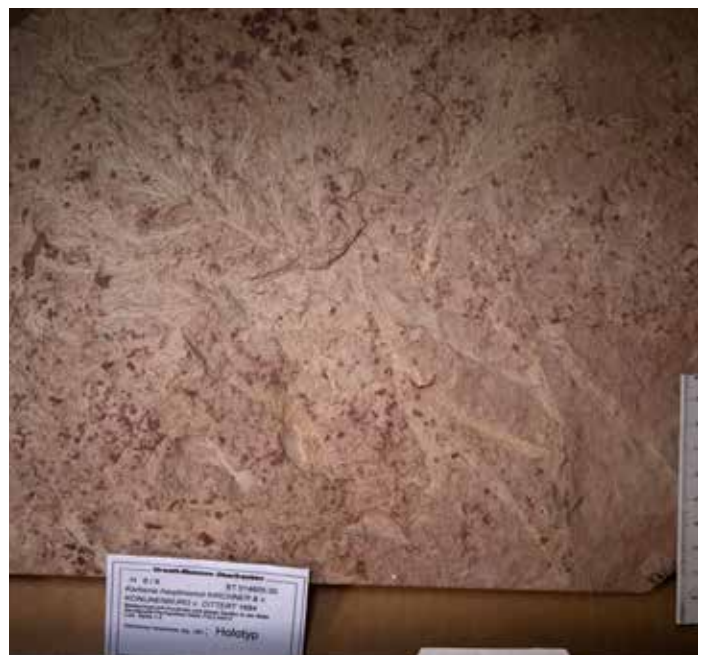


The holotype of the supposed ginkgophyte *Karkeniania hauptmannii* figured in the publication Kirchner and Cittert (1994). However, it is a short shoot of the conifer *Podozamites distans*, with the laterally embedded sheath cuff in the upper part being turned from above. Moreover, the leaves are not dichotomously divided in a ginkgo-specific manner (Pechgraben, Coll. Hauptmann, Urweltmuseum Oberfranken, Bayreuth).

the case for *Equisetites* (Sternberg, 1833), resembling today's *Equisetum* horsetails, *Todites*, *Danaeites* and *Cyatheites* for fossil ferns. However, the Swedish palaeobotanist Rudolf Florin (1936) further complicated the classifications of ginkgophytes by introducing the genus name *Sphenobaiera* for leaves lacking a petiole. However, he failed to answer whether these leaves were naturally broken off or if they had varying lengths of petioles, as is typical for ginkgos.

***Karkeniania hauptmannii*, a Frankenstein Monster?**

A special case is presented by *Karkeniania hauptmannii* from the Lower Jurassic of Upper Bavaria. In 1994, Kirchner and Cittert published a paper that attracted considerable attention, prompting some to question if this newly combined plant could even be considered "A missing link to angiosperms?" (Wang et al., 2007). An analysis of the publications and original illustrations revealed that the desire to find a connection led to the amalgamation of various plant parts from at least four different families.



The second holotype declared in the Urweltmuseum Oberfranken, Bayreuth as *Karkeniania hauptmannii*. The appendages declared as cones represent sterile needle sheaths and probably belong to *Swedenborgia liasokeuperianus* (Pechgraben, sandpit Dietz, Lent 3, Coll. Hauptmann).



Above: A drawer with the questionable *Karkenia hauptmannii* from the Sepp and Traute Hauptmann collection. On the right is a watercolour illustration by Sepp Hauptmann ("Rich finds enabled a complete reconstruction of the flowering branch."). The illustration should be correct, including the male pollen organs *Stachyopitys preslii*. However, they belong to the conifer *Podozamites distans*.

Middle: The supposed pollen organ *Stachyopitys preslii* forms an immature sporophyll of the fern *Thinnfeldia rhomboidales*, which is widespread in the Lower Jurassic of Franconia. The apically dichotomously divided leaves belong to the ginkgo ancestor *Ginkgoites dichotoma* and are well documented alongside seed berries (Pechgraben, sandpits Dietz and Küfner).

Below: The "cones" declared as female ovules with the name *Schmeissneria microstachys* represent needle sheaths of the conifer *Podozamites distans* (Pechgraben, sandpit Dietz, Coll. Hauptmann, Urweltmuseum Oberfranken, Bayreuth).

Karkenia hauptmannii was found to be composed of the fertile juvenile organ of a *Thinnfeldia* fern (*Stachyopitys preslii*), the stubby spur shoots (*Schmeissneria microstachys*), pollen organ, and leaves of the conifer *Podozamites distans*, the leaves of the Ginkgophyte *Baiera*, and the branches and pollen cones of the conifer *Swedenborgia liaso-keuperianus*.

The name *Karkenia hauptmannii* was chosen for the new combination of all these plant parts, after a genus described by the South American palaeobotanist Sergio Archangelsky in 1965, which is suspected of having a connection to ginkgoes from the Late Cretaceous period from Patagonia, Argentina.

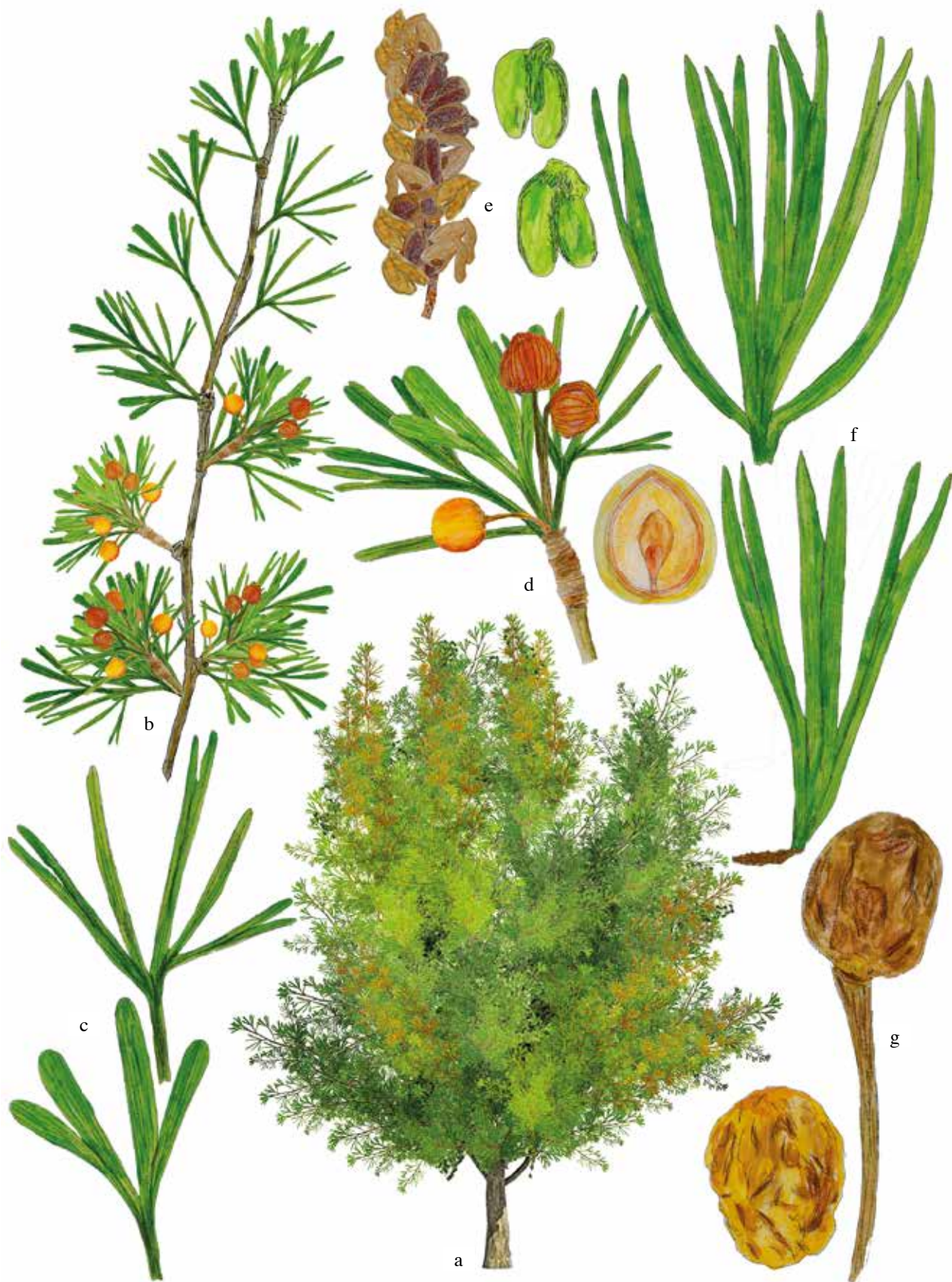
Despite the challenges in linking the *Glossopteris* flora, which develops independently in the southern hemisphere, with Euro-American plants of the northern hemisphere, *Karkenia hauptmannii* served as an example of the creation of a "mon-





The ginkgo over the course of 300 million years

1. The oldest confirmed ginkgoes come from the Lower Permian (*Ginkgoites pohlii* with seed berries, Kungurian, 275 million years, Tregiovo, Coll. Valentini, MUSE, Trento); 2. The leaf needles resembled conifers (MON 350); 3. Fossil pollen cones (MON 253) show that from the beginning they had characteristics of those of today (*Ginkgoites gasseri*, Upper Permian, 260 million years, Montan, Dolomites, Coll. Wachtler, Dolomythos Museum). 4. At that time there were already fan-shaped leaves (*Ginkgoites munchisonae*, Wuchiapingian, 255 million years, Seceda, Dolomiten, Coll. Wachtler, Dolomythos). 5. While ginkgos were largely absent in the Triassic, they experienced a new bloom in the Jurassic. Needle-shaped variants alternated with fan-shaped ones (*Ginkgoites marginatus* with seeds, Lower Jurassic, 200 million years, Hettangian, Gromadzice, Zagaje Formation, Poland; 6. *Ginkgoites huttonii*, 166 million years Battonian, Middle Jurassic, Scalby Ness, Yorkshire, England); 7-8. Prosecuting the sites already known to Oswald Heer on Lake Baikal (7-8. *Ginkgoites sibirica*, Tshyta Area, Aptian, 110 million years, Middle Cretaceous), to the Paleocene (9-10. *Ginkgo cranei*, male cone and seed, North Dakota, 60 million years), the Eocene (11. *Ginkgo gardneri*, Middle Eocene, 45 million years, Stonerose Fossil Center, Republic, Washington, USA) and the Miocene (12. *Ginkgoites adiantoides*, 15 million, Lavanttal Carinthia, and the present, there were hardly any major developments especially regarding their fertile organs (All except 11, Coll. Wachtler, Dolomythos Museum)



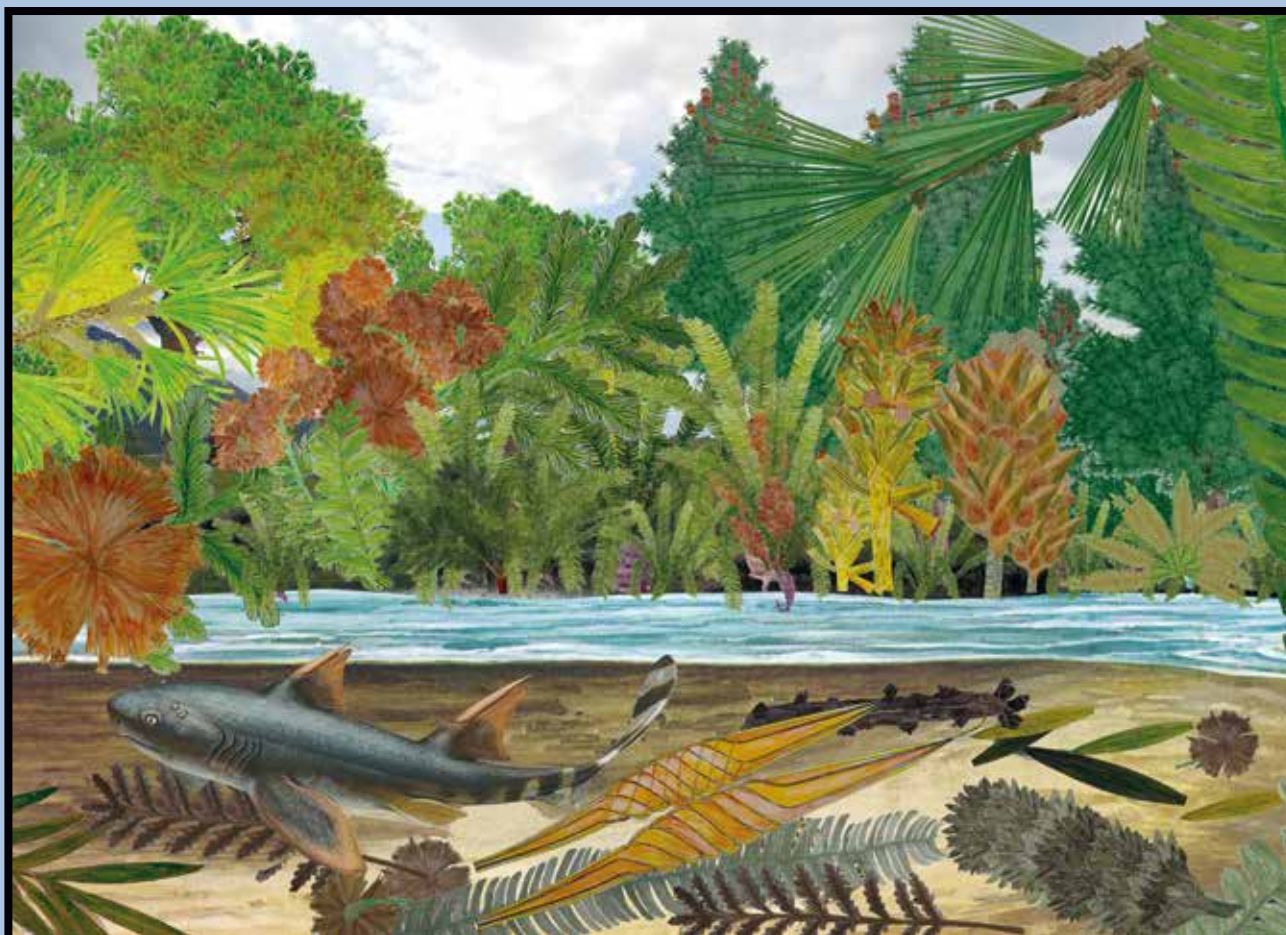
***Ginkgoites (Baiera) dichotoma* and *Ginkgoites (Baiera) hauptmannii*. Reconstructions**

***Ginkgoites dichotoma*:** a. Tree with fruits; b. Fertile branch with short and long shoots; c. Foliage variation; d. Fertile short shoot with cut seed; e. Male cone and immature microsporophyll; ***Ginkgoites hauptmannii*:** f. Different leaves; g. Mature seeds

ster plant" that bridges the evolutionary gap between ferns, conifers, and ginkgoes. However, it is only now possible to draw new conclusions and build on the findings of previous generations with advancements in large-scale prospection techniques. The initial situation was made more difficult by the presence of three gymnosperms (*Podzamites*, *Swedenborgia*, *Ginkgoites*) with spur shoots in the Lower Jurassic of Upper Franconia. The subtle difference in leaf sheaths between these genera, as well as the need for intensive study of hundreds of specimens to classify pollen organs accurately, complicated the situation further. In summary, the plant *Karkeniania hauptmannii* never existed and was only a human construct.

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The Fossil Flora of Early Jurassic

A catastrophic decline in vegetation during the Upper Triassic period was followed by a remarkable resurgence of flora in the Lower Jurassic era. However, the family of flowering plants, which is prevalent today, was clearly absent during this time. Even potential ancestors of these plants remain unidentified. During the Lower Jurassic period, conifers such as *Podozamites*, *Swedenborgia*, and *Hirmeriella* dominated, although they are now only found in limited areas in East Asia, represented by species like the golden larch (*Pseudolarix*), umbrella fir (*Sciadopitys*), *Taiwania*, and precursors of ginkgo (*Ginkgoites*). Cycads, including the two-seeded *Nilssonina* and *Ctenis*, as well as the multi-seeded *Macrotaeniopteris*, were also quite common. Interestingly, ferns that are now rare, such as *Matonia* (*Phlebopteris*, *Laccopteris*) and ancestors of *Dipteris* (*Thaumatopteris*, *Chlathropteris*, *Dicytophyllum*, *Sagenopteris*, *Otozamites*), played an important role during this period. Another notable fern, *Thinnfeldia*, which can be classified within the large *Schizaeales* group due to its distinct trophophyll and sporophyll fronds, was abundant. Precursors of *Marattiales* (*Marattiopsis*) were numerous. Horsetails were represented by *Equisetites* and *Schizoneura*, while strange clubmosses such as *Bernettia*, *Bavaroostrobus* and *Lepacyclotes* also had a notable presence, with no clear descendants identified.

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