The Early Permian (Kungurian) Floras of the Dolomites

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Abstract

While in the Early Permian (Artinskian) of the Dolomites, the flora was still impaired and reduced, probably suffering from the Late Paleozoic Ice Age being effective on the Gondwana-landmass, this changed gradually in the following Early-Middle Permian Kungurian-period. Cycads began to spread, while other gymnosperm families continued to perfect themselves. Strangely we encounter in the Dolomites a "Last of the Mohicans"-taxa in the form of *Wachtleropteris valentinii*, an extremely archaic cycad. Nevertheless, fully evolved cycads like *Taeniopteris nonensis* n. sp. and *Macrotaeniopteris tridentina* nov. comb.—conducting to today's Cycas-line and *Nilssonia perneri,* a progenitor of extant *Zamia*-cycads—were widespread. The Ginkgoales were widely present with *Ginkgoites pohli* nov. comb. They exhibited just all the features of nowadays *Ginkgo biloba*, like leaves coated by a collar and berry-like ovules attached on a stalk. The Pinoidea began to diversify in the five bundled *Férovalentinia cassinisi*, and irregularly from one, two, till three grouped *Férovalentinia angelellii.* Other frequent conifers were the Araucariaceae with *Ortiseia daberi*, the Abietaceae with *Majonica ambrosii* nov. comb. and *Voltzia viallii* nov. com. Poorly represented were the ferns with *Sphenopteris battistii*, additionally some *Peltaspermum*-seed-ferns (*Autunia, Lepidopteris*) or the horsetails with *Neocalamites tregiovensis.*

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Early Permian (Kungurian, about 280 mio years), Tregiovo, Northern Italy

The upper part-sediments of the Tregiovo-Formation were more arid. Two *Pinus* ancestors dominate: Left at the top ***Férovalentinia angelellii,*** with male and female cones, right sprout a branchlet with male and two female cones of the five-needled ***Férovalentinia cassinisi.*** Left below grows the Araucariacea ***Ortiseia daberi*** with male and female cones and some shed one seeded scales. Right below is visible the Abietaceae ***Majonica ambrosii*** with a female cone and some winged seed scales.

The Dolomites can be regarded as an extraordinary window in the history of the Earth and they were therefore included in the list of World Heritage Sites. Beginning from the Early Permian over the whole Triassic, we have an almost uninterrupted succession of sediments that give a deep insight into the evolutionary trends of the fauna and flora. In the plant kingdom, we can experience the evolution of conifers, gingkophyta, cycads, lycopods, ferns and horsetails.
A rich Early Permian (Kungurian) Fossillagerstätte is located in the Val di Non, part of the Autonomous Province Trento in North-Eastern Italy. Between Revò and Laurein, below a large bridge crossing the "Le Fraine" streamlet, crop out variegated layer-pockets that hold not many, but on the whole sufficiently well-preserved plants.

Historical overview

The first geological analysis in the area around the Val di Non was conducted in 1873 by the German geologist **Carl Wilhelm Gümbel** (1823–1898), followed one year later, by **Ferdinand Richthofen** (1833–1905). Afterwards the Austro-Italian naturlalist **Giuseppe Loss** (1831–1880) summarised the informations collected mainly by fellows of the Geological Survey (Geologische Bundesanstalt) of Vienna, comparing them with his own observations about stratigraphically (1877) similar layers in the Dolomites (Wachtler, 2012).
Investigations about the macro-flora began in 1882 by the Czech-Austrian geologist **Michael Vacek** (1848–1925), who correlated the Val di Non sites with well-known German localities. Therefore, he was able to elaborate a distinction between the age-different Lower Permian (Sakmarian-Artinskian) Rotliegend flora with *Walchia piniformis* and *Walchia filiciformis* and the typical Upper Permian (Wuchiapingian) Zechstein plant associations with *Ullmannia frumentaria.* After Vacek (1882 and 1894), in the late twentieth century, several palaeobotanists analysed the plant associations of the Val di Non, especially near the region of Tregiovo (Remy & Remy, 1978; Kozur, 1980; Visscher et al., 2001; Cassinis et al., 2002). In several cases, these investigations led to the assumption that typical Early Permian floras (*Walchia, Lebachia, Autunia conferta*) pertain to the same stratigraphic levels as characteristic plants from the Late Permian (*Ullmannia frumentaria, Ortiseia, Pseudovoltzia liebeana, Taeniopteris eckardtii* or *Peltaspermum martinsii*) (Visscher et al., 2001). Controversies arose therefore, if the Tregiovo Formation was younger and should be placed in the Middle or even the Late Permian period and even specimens were recovered from different geological different sites.
Beginning from 2010, **Michael Wachtler** and the herbalist **Féro Valentini** began their fossil-plant-researches at Tregiovo. Féro Valentini split tons of rocks and slabs and spent many days outdoors in the cold winters with snow and in the heat of summertime in the wilderness of Tregiovo-Le Fraine. "*Only with good statistics we are able to understand an almost 300-million-year-old flora"* was our credo. Our greatest attention was often on ignored plant-parts, such

The Czech-Austrian geologist and paleontologist Michael Vacek (Vaček), was a fellow of the famous researcher Eduard Suess. He elaborated a first geological map of the Val di Non in 1882 and described superficially the first fossil plants from Tregiovo.

as mimicry seeds, scales, and pollen organs. With child-like curiosity, we undertook an intensive examination of every slab. Every day in the field-research, we were able to read better the stone-slabs like a book.

Geology and time-dating

The fossil plant layer bearing horizons of Tregiovo is sandwiched between the older rhyolitic volcanoclastic breccias of the Gries Formation and the pyroclastic flow deposits of the younger Ora Formation. The age of the Tregiovo Basin consisting of lacustrine deposits with alternating marls, limestones and shales was bracketed between radio-isotope ages of the underlying and overlying volcanics with U-Pb-Zircon data respectively related to an age of 276.5 (+-1.2) and 274.1 (+-1.6) Ma., classifying them in the Kungurian (Avanzini et al., 2007; Cassinis & Perotti, 2007; Marocchi et al., 2008; Wachtler, 2015; Wachtler, 2012; Wachtler, 2018).

In the early Permian, developed between the Giudicarie and Foiana faults a small continental basin that was filled by sediments, mostly of volcanic origin from the Athesian Volcanic Complex, one of the largest volcanic spots of that time in Europe (Marchetti et al., 2015). During some inactive periods, some small basins were formed that subsequently were filled with fine sediments and muds. From these events originate the Tregiovo Formation with its 200 m thickness, consisting of many laminated mudstones. They are witnesses of a flat area, periodically or seasonally inundated by floods with phases of dry falling in which mud cracks were formed and animals left their traces. The oxygen-deficient shallow water mixed with anoxic conditions gave origin of some mineralisations, mainly of galena, sphalerite, copper and iron. Digging works in the past were also concentrated on these metals.

Interesting and unusual is the frequency of the so-called Moqui Marbles, sometimes called "Palle del Fèro" (Féro's balls). But whereas the Moqui balls represent iron oxide concretions, the "Palle del Fèro" based on X-Ray diffractometric analysis, are of explicit

The outcrops at Tregiovo–Le Fraine (lower layers).

carbonatic nature, with over 90% calcite created probably by a sulphate reduction in organic C-rich sediments.
Sometimes in the sediments were transported plants. It cannot be established, that some laminas are richer than others, but they occur constantly between all the layers. Unfortunately, the plant material is so compressed and compacted that it impedes cuticular analysis, but the relative abundance of the material allows the development of statistical patterns.

Palaeoecology and Palaeoclimatology

In the Early Permian, Tregiovo was located near or a little South of the Palaeo-equator. In the area, we have to add the last intercontinental habitat because beginning from the Upper Permian the landscape was successively inundated by the Tethys-Sea and this for about more than 200 million years.
Reptile tracks: Rich tetrapod footprints were discovered in the lower part of the Tregiovo Formation. They were dominated by *Dromopus didactylus*. The trackmakers were araeoscelid or bolosaurid reptiles. In minor entity, we encounter the ichnogenera: *Batrachichnus,* basal amphibians or temnospondyls, *Erpetopus,* probably small non-diapsid reptiles and *Hyloidichnus*. The trackmakers were probably captorhinomorphs or derived captorhinids. Sometimes also occur trace fossils of insects (*Helminthoidichnites*) and arachnid tracks like *Octopodichnus* (Gand & Durand, 2006; Marchetti et al., 2015). The reptile footprints, but also the plants attest a not hostile biocoenosis.
An interesting Early Permian flora composition: Superficially can be distinct two plant-assemblage-levels. The lower and slightly older one has a more variegated flora and seems to have had a more wet climate. It holds many different gymnosperm-families and an interesting feature with *Wachtleropteris valentinii*, the most rudimental cycadophyta known (Perner, 2015; Wachtler, 2012). The leaves extended upwards on a stem and branched twice, which is not typical for cycads, and each of the leaves split into two independent branches. The cones, similar to extant *Zamia*-cycads emerge from a modified leave. Nevertheless, we encounter in the same layers fully evolved other cycads like *Taeniopteris nonensis, Macrotaeniopteris tridentina* (*Cycas*-line) and *Nilssonia perneri* (*Zamia*-line). Another important plant from the lower lenses are the *Ginkgoites pohli*, the first unquestionable ginkgophyta. Although equipped with needle-like leaves, it is different from the *Baiera*-tribe. They hold all the features of extant ginkgos: these include a collar-like ring from which the leaves emanate, and one or two ovules/seeds aggregated together. The ovules hang from the end of a distinctive leaf, not a stalk like in modern ginkgo-trees.
The upper sediments of Tregiovo are especially rich in fully evolved Pinoidea-ancestors. *Férovalentinia cassinisi* holds just five needles for each bundle, like todays *Pinus longaeva*, whereas *Férovalentinia angelellii* was equipped with two till three grouped needles. Probably the climate became dryer in the upper and therefore younger lenses, so that the Pinoidea began to dominate the landscape. Otherwise in all sediments we encounter Abietaceae progenitors (*Majonica ambrosii)*, as well as Araucarias (*Ortiseia daberi)* and also Voltziaceae (*Voltzia viallii)* thought *Cryptomeria*-progenitors. Ferns (*Sphenopteris battistii*), seedferns (*Autunia, Lepidopteris)* and horsetails (*Neocalamites tregiovensis*) stand behind the rich gymnosperm-plant assemblage.
Frequent forest fires: The commonness of burned or charcoalified wood indicates that forest fires frequently destroyed the vegetation. They could be caused by activities of the nearby volcanoes or more reasonably a result of thunderbolts (Uhl & Kerp, 2003). Frequent mud-cracks and concretions are indicators of meandering river systems channelling through a climate that was probably also infected by longer periods of drought. But torrential rivers after the monsoons brought enough precipitation from the hinterland to allow the survival of a variegated vegetation. A consistent part of the plants seems to be blown away by wind and storms on the fine sandy areas along the riverbanks where they were buried by the fine-grained sludge.
Springtime assemblage: Because a substantial part of the fertile organs consist of male cones, accompanied by young female fructifications, it can be suggested that short and intensive rainfall periods followed barren periods where most of the lakes and lagoons dried out and conservation was there-

fore no longer possible. Therefore, many plants were deposited in the spring.
The xerophytic character of some plants (*Sphenopteris, Ferovalentinia*) suggests an unusual climate for equatorial regions. The trend beginning in the Early Permian (Artinskian) in the Alps experience its continuation in the Kungurian and ends abruptly in the Late Permian. In all the layers, the winged seed-conifers *Majonica* and *Ortiseia* are present, in minor quantity *Voltzia.* The ginkgos and the cycads appeared in the Kungurian to prosecute with some evolution-trends to the Late Permian.

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Ancient galleries on Tregiovo evidencing mining activities. Galena-silver inclusions near fossilized plants are frequently found.

Certain layers are rich in carbonate nodules of diagenetic origin. They grow due to an alkalinity generated by sulphate reduction in organic C-rich sediments and are rich in calcite and less in fluorite or silica. Their formation process and hardening was just finished with the deposition inside the other fine-grained aerobically digested sludge. Some concretions were carried in the marshes in a semi-hardened condition for a short way and deposited with the plants (*Ortiseia daberi*).

Ferruccio Valentini (Fèro) in 2011 rediscovering the old fossil-site Tregiovo. Above the large bridge begin the upper parts of the Tregiovo-Flora. The sediments are well layered and are especially rich in *Pinus*-ancestor *Férovalentinia.*

Ferruccio Valentini (Fèro) in 2013 working on the lower part of the Tregiovo-Formation. These layers hold apart from other conifers like *Voltzia, Majonica, Ortiseia* also *Wachtleropteris valentinii, Nilssonia perneri, Macrotaeniopteris tridentina* and *Ginkgoites pohli.*

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A bed of conchostracans, small branchiopod crustaceans, probably *Lioestheria*. sp They show a concentric ornamentation.

Arthropod tracks *(Octopodichnus didactylus*)

Tracks of *Dromopus didactylus* often occur. Sometimes they are accompanied by plants. This suggests that the plants were buried near lakes, swamps or marshes.

Charcoalified wood remains from Permian forest fires are common.

Mud cracks of dried-up watering places from Tregiovo

Components of the Tregiovo flora:

Lycophyta
Sigillaria treneri (WACHTLER, 2012, WACHTLER 2021)

Sphenophyta
Neocalamites tregiovensis (WACHTLER, 2012, WACHTLER 2015)

Pteridophyta
Sphenopteris battistii (WACHTLER, 2015)

Pteridospermatophyta
Lepidopteris meyeri (WACHTLER, 2013)
Autunia sp.

Cycadophyta
Wachtleropteris valentinii (WACHTLER, 2012, PERNER, 2013)
Macrotaeniopteris tridentina (WACHTLER, 2012, WACHTLER, 2021)
Taeniopteris nonensis (WACHTLER, 2021)
Nilssonia perneri (WACHTLER, 2012)

Ginkgophyta
Ginkgoites pohli (WACHTLER, 2013, WACHTLER 2021)

Coniferophyta
Ortiseia daberi (WACHTLER, 2012)
Majonica ambrosii (WACHTLER, 2012, (WACHTLER, 2021)
Voltzia viallii (WACHTLER, 2013, (WACHTLER, 2021)
Férovalentinia angelellii (WACHTLER, 2015)
Férovalentinia cassinisi (WACHTLER, 2015)

Lycophyta

When I first described long and fleshly leaves that sometimes are found in the lower layers of Tregiovo, I classified them as conifer with the name *Trentia treneri* (Wachtler, 2012). In this time, I had no knowledge about the rich Early Triassic *Sigillaria*-findings in the Dolomites (*Sigillcampeia*, Wachtler, 2016) with their ovate lanceolate and parallel-veining foliage. More and more I am now convinced that these leaves do not represent a conifer, but a lycopod. Further studies would be able to trace an evolving line from the rich Late Carboniferous *Sigillaria*-deposits in the Carnian mountains till the abundant Triassic *Sigillcampeia*-assemblages in the Dolomites.

Sigillaria treneri nov. comb. (WACHTLER, 2012, WACHTLER 2021)

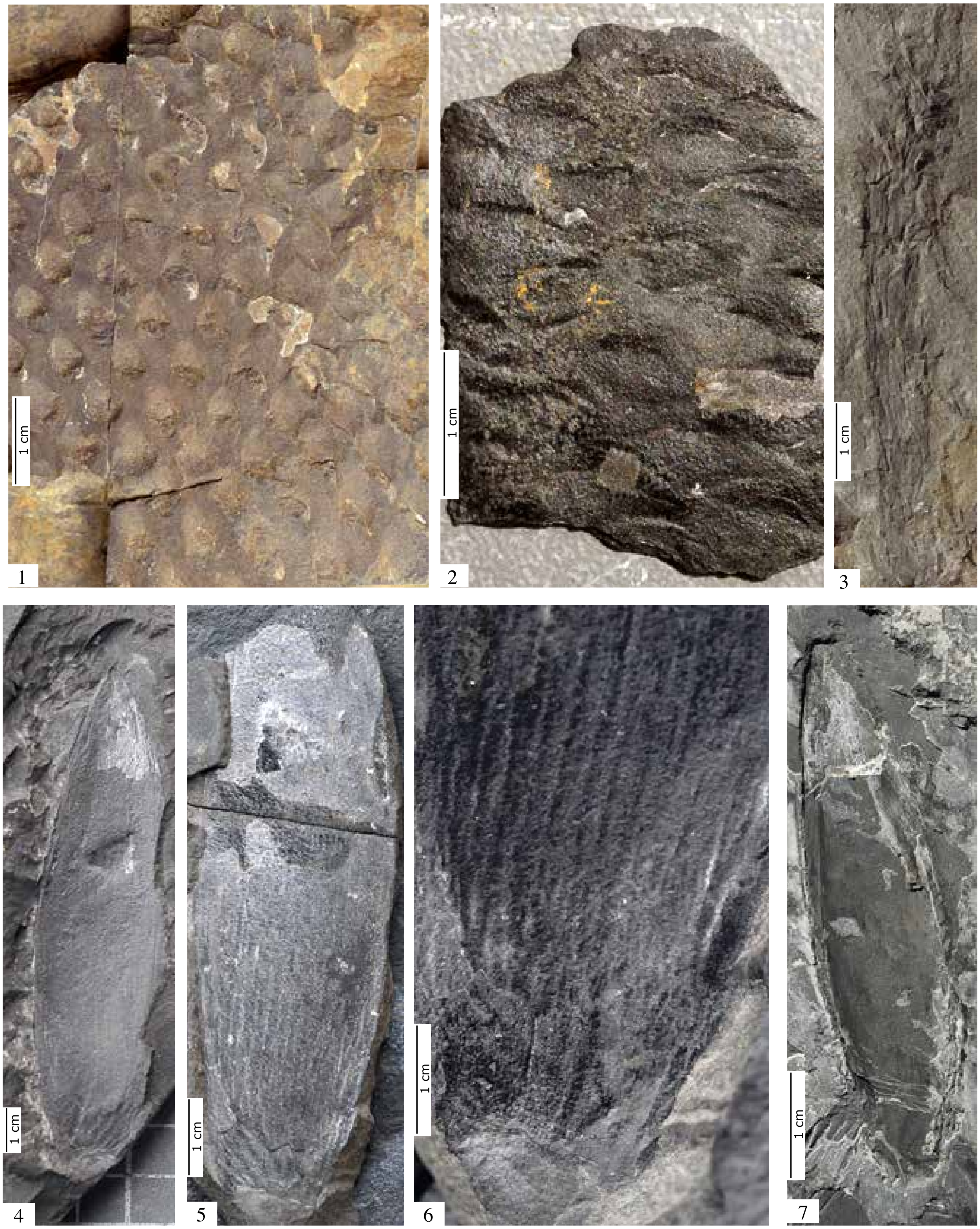
2012 *Trentia treneri,WACHTLER,* pp. 14-17

Etymology
Honouring Giovanni Battista Trener (1877–1954), one of the leading geologists and naturalists of Trentino and first director of the Natural History Museum of Trento. He was also a determined local patriot, fighting with his famous brother-in-law Cesare Battisti in the First World War.

Holotype
TRE 61, **Repository:** Coll. Wachtler, Coll. Valentini; MUSE Trento

Description
Plant: Leaves spirally arranged on stems. They were about 10–12 cm long, from 2 to 3 cm broad and directly attached on the main axis. The abscission point from the branches is large and concave. The leaves are extraordinary fleshy and leathery, with the widest part near or before the middle, tapering gradually to a rounded or bluntly pointed tip. Multiple parallel veins sprout from the base and cross each leaf. (TRE 260, TRE 61 holotype, TRE 55).
Fertile parts: Only in parts known, but TRE 596 has many features of the Sigillariaceae known from the Carnian mountains.

Taxonomic notes
Parallel veined long leaves occurred several times in the fossil record, beginning from the late Carboniferous lycophyta (*Lepidodendron, Sigillaria*) over the enigmatic Cordaites-trees, then in the Triassic they continued with *Sigillcampeia* and *Lycopia* (Wachtler, 2016), or the mysterious conifer *Pelourdea vogesiaca* (Wachtler & Van Konijnenburgh–Van Cittert, 2000. Today inside the gymnosperms we encounter the Kauri trees (*Agathis)*, predominately occurring in the tropical rainforests of the southern hemisphere (Australia, New Zealand) tongue-shaped conifers with veined leaves.
Many of these plants were classified with doubtful arguments, since they were never connected with their fertile organs. The only plants proved beyond doubts are the Triassic lycopods *Sigillcampeia nana* from



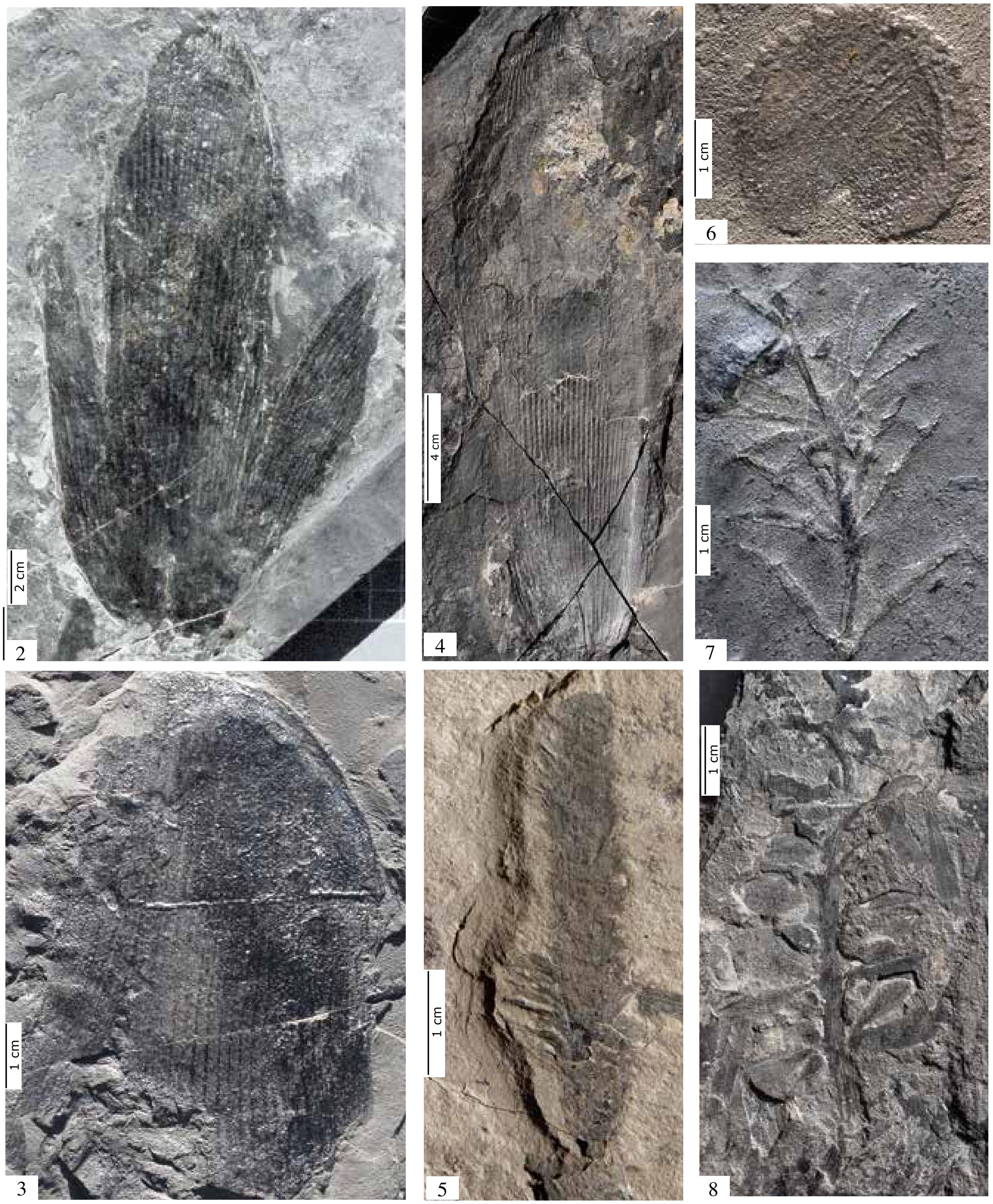
Sigillaria treneri. **Stems and branchlets (Early Permian, Kungurian)**

1. Part of a stem with abscission-points having more *Lepidodendron* character (TRE 510); 2. Apical part of a stem evidencing the abscission points (TRE 260); 3. Suggested fertile part (TRE 596); 4. Isolated leaf (TRE 61B holotype leaf); 5-6. Counterpart evidencing the fine parallel veins. Leaf basis showing the abscise-form from the main stem (holotype, 61A); 7. Isolated fleshy leaf (TRE 55); all Coll. Valentini, Coll. Wachtler; Tregiovo, Le Fraine.

the Anisian, as well as *Sigillcampeia blaui* from the Carnian period recovered as whole plants. Probably the parallel-veined lanceolate leaves of *Pelourdea vogesiaca* classified often as conifer, can be better classified as Sigillcampeiaceae, because typical sporophylls belonging to this lycopod found in the same layers (Wachtler, 2016).
Till now what is not resolved is the problem of the huge Sigillariaceae (also *Sigillaria brardii* from the Early Permian) and the evolving way to the dwarfish *Sigillcampeia* lycopods of the Early Triassic. This is also valid for their different fertile organs that in *Sigillaria treneri* have still a typical character of the *Sigillaria*-lycopods and they do not resemble *Sigillcampeia* macro- and microsporophylls.

Sphenophyta

The first Calamitaceae, a group of horsetails, appeared in the Lower Carboniferous, although they were rare. They spread extensively, especially in the Late Carboniferous splitting in many and sometimes also coeval species like *Calamites multiramis, Calamites equisetiformis*, *Calamites incisum*. Some species in the related genus *Neocalamites* managed to survive into the Late Permian, only to disappear after that from the face of earth. Upper Permian *Neocalamites benckeae* from the Italian Alps can be regarded till now as the last known representatives of the Calamitaceae, because sometimes Triassic species classified (*Neocalamites merianii)* held typical *Equisetites*-like cones and were combined as *Schizoneura merianii* (Wachtler, 2016). Their stems were equipped with characteristic longitudinal ribs and furrow ornament divided by internodal regions. These fossilised pith casts took the name *Calamites.* They are accompanied by the art-form names *Annularia* leaves and *Calamostachys* sporophylls (Wachtler, 2020). The leaves of the Calamitaceae consisted often of verticils surrounding the secondary branchlets like a collar. The strobili hold sporangia encased usually by several sterile bracts. The other group of horsetails the Equisetaceae indeed were characterized by their usually bulbous or elongated reproductive organs segmented in many hexagonal bracts. These peltate shields hold their sporangial sacs hanging down on the underside.



***Neocalamites tregiovensis*. Stems and branchlets (Early Permian, Kungurian)**

1. Branchlet with leaf-whorls (*Annularia)* (TRE 547); 2. Stem with massive lateral branches. The tangential striae in the lateral whorls are also relatively wide spaced (TRE 299); 3. Apical part of a big stem (24 cm long), (TRE 111, Paratype); 4. Apical part of a stem (TRE 160); 5. Sporophyll (TRE 423); 6. Isolated diaphragms (TRE 115); 7. Part of the secondary whorls and the axis with the leaves (TRE 76, holotype); 8. *Sphenophyllum* sp. These unusual secondary whorls suggest, that in the Tregiovo-Flora different horsetails-species were present (TRE 200); all Coll. Valentini, Coll. Wachtler, Tregiovo)

Neocalamites tregiovensis (WACHTLER, 2012)

2012 *Neocalamites tregiovensis,WACHTLER,* pp. 28-30
2015 *Neocalamites tregiovensis,WACHTLER,* pp. 99-102

Etymology

Named after Tregiovo in the Italian province Trentino.

Holotype

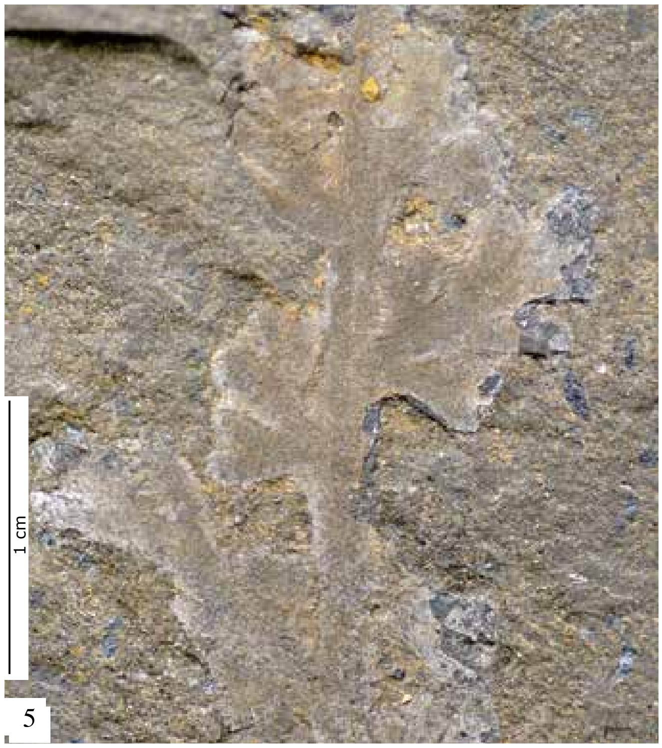
TRE 76, **Paratype** TRE 77 **Repository:** Coll. Wachtler, Coll. Valentini; MUSE Trento

Description

Plant: Sphenophyta with massive stems characterized by broad longitudinal ribs passing without alternation through the nodes. From the main stems diverges consistent upwards growing secondary axis, also with relatively wide spaced striae, holding Annularia whorls with lanceolate leaves.
Fertile parts: Strobili 5–8 cm long, 1 to 1.5 cm wide. A large number of sterile bracts encase the sporangia (TRE 423).

Taxonomic notes

The horsetails were not seldom, but also not very common elements of the flora of Tregiovo. They demonstrate that the climate was wet enough or there were enough rivers or lakes to allow colonisation with Sphenophyta. *Neocalamites tregiovensis* can be regarded as the most characteristic Calamitaceae based on its massive stems and the broad longitudinal ribs with lateral stems diverging from the main axis. It is not to be denied that yet another Calamitaceae existed in the Tregiovo-plant assemblage. Some whorls with fan-shaped rounded whorls had more the character of *Sphenophyllum*-horsetails another group of Sphenophyta belonging to the Calamitaceae. Additionally, isolated diaphragms bear resemblances with the Equisetaceae. But till rounded Equisetites-strobili with its shield-like characteristics were found, species-deductions based only on their stems are difficult. In summary, the importance of these horsetails lies in the contestation of the common belief that the arid Permian age holds a lot of humidity-loving plant representatives. Moist areas or spaces with enough groundwater where their rhizomes reach down to the water-saturated soil were apparently frequent. There, they may have formed extensive monocultures.



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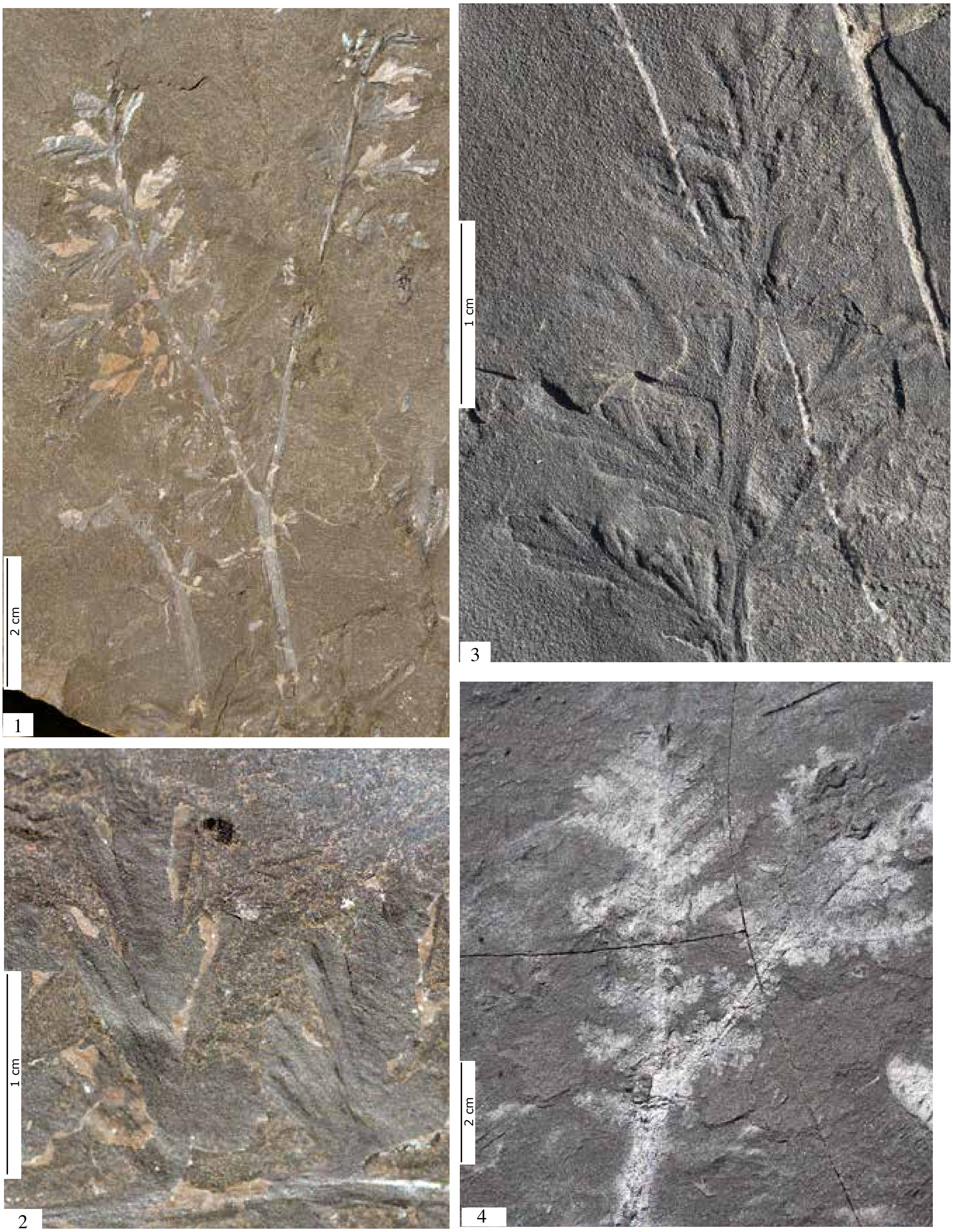


Sphenopteris battistii. Fertile and sterile fronds (Early Permian, Kungurian)

1-2. Part of a frond and detail of the pinnules (TRE 541, designed holotype); 3. Frond (TRE 37B); 4. Sterile frond (TRE 301); 5. Detail of a fertile frond (TRE 448 Paratype); 6. Detail of the sporangia (TRE 201); all Coll. Valentini, Coll. Wachtler; Tregiovo, Le Fraine.

Pteridophyta

The fern *Sphenopteris* was widespread across the Euramerican Early to Late Permian landmass and sometimes it is the only certain fern encountered. Its tripinnate leaflets with a hidden vein-structure were found at many plant fossil sites. Fertile pinnules were skeletonised, with densely arranged sporangia on the lower side of the leaflets. Also in the Southern Alps we have a succession of different species from the Early Permian (Artinskian) Collio Formation with *Sphenopteris suessi* to Tregiovo (Kungurian) *Sphenopteris battistii* or Upper Permian (Lopingian) *Sphenopteris* sp.

Sphenopteris battistii (WACHTLER, 2015)

1999 *Sphenopteris suessi* VISSHER ET. AL. fig. 6,Table 1, *Sphenopteris kukukiana* fig. 12, Table 1

2012 *Sphenopteris dichotoma* WACHTLER, p. 35

2013 *Sphenopteris suessi* WACHTLER p. 127, p 129

2015 *Sphenopteris battistii,WACHTLER,* pp. 62-67

Etymology

Named after the Italian patriot and politician of Austrian citizenship Cesare Battisti (1875–1916), who became a prominent Irrendentist and was sentenced to death.

Holotype

TRE 541, **Paratype** TRE 448, fertile frond
Repository: Coll. Wachtler, Coll. Valentini; Museum of Natural Science, Trento, Dolomythos-Museum, Innichen

Description

Fronds: Low growing fern with tripinnate fronds. Secondary pinnae opposite to alternate, only slightly bifid and incised. Single pinnules are up to 2 cm long and 0.5 cm wide, characteristically segmented into 3 mirror-like leaves concluding with a slightly incised pinnula.

Fertile pinnules: Skeletonised, sporangia densely covering the lower part, mainly encasing the whole leaf. The leaflets are 1 to 2 cm long and 0.5 cm wide.

Taxonomic notes

Sphenopteris ferns in the Kungurian Tregiovo-flora were not very common. Due to the poor preservation recovered there by older researchers, given names like *Sphenopteris dichotoma* (Wachtler, 2012), *Sphenopteris kukukiana* (Visscher et. al., 1999) or *Sphenopteris suessi* (Vissher et. al., 1999; Wachtler, 2013) have to be regarded with caution. They may have been connected with other localities and from different time periods. Several findings from the Tregiovo-Formation have established that the fern *Sphenopteris* is different from the other mostly time differing species. Therefore, it was classified as *Sphenopteris battistii.* Single leaf-pinnulas had a slightly bifid to sometimes dentate form.

From the Upper Permian German Zechstein, several *Sphenopteris*-species have been described (Schweitzer, 1960) (*S. dichotoma, S. geinitzii, S. bipinnata, S. gillitzeri*), often based only on the existence of a single specimen, disregarding the fact that we are dealing with a fern with extremely changeable leaflets (Haubold & Schaumberg, 1985). The only unquestionably Upper Permian fern *Sphenopteris dichotoma*, known mainly from German Zechstein, with some doubtful specimens recovered from the coeval Gröden-Formation from Bletterbach, Recoaro and the Valli del Pasubio, hold, in contrast, smaller leaflets.

In summary, it could be stated that the desiccated looking *Sphenopteris* is not only the most common true fern in the Permian Euramerica. Why the ferns declined so much in the Permian after a peak in the Carboniferous and the sudden rise in the Early Triassic of the Dolomites (Wachtler, 2016) with many genera (*Anomopteris, Ladinopteris, Gordonopteris, Anotopteris, Wachtleria* etc.) is strange, since other water-loving plants like cycads and horsetails were not affected by this decline.

Pteridospermatophyta

The worldwide ranging Peltaspermales, such as *Autunia, Rhachiphyllum, Hurumia, Scytophyllum, Lepidopteris* or *Thinnfeldia*, a group of seed-ferns known for their fronds and leaves, belong to the most suggestive Palaeozoic and Mesozoic flora elements (Perner & Wachtler, 2013), although they seem to be extinct in the Jurassic. Typically for all of these seed-fern tribes are their

***Sphenopteris battistii*. Reconstructions (Early Permian, Kungurian)**

a. Part of a frond (TRE 541), b. Single pinnula, c. Fertile frond (TRE 329), d. Part of a fertile frond, e. Entire plant.

female reproductive organs formed by umbrella-like peltate heads (hence the Latin name *Peltaspermum*). Not totally resolved is the enigma of their pollen organs, because microsporophylls (*Pterosuchus, Antevsia)* are doubtful.

Lepidopteris meyeri (WACHTLER, 2013)

1959 - *Lepidopteris martinsii,* TOWNROW S.345 Text Fig. 1L, 2J, 3G-K, 4A,B 5J, 6D

1990 *Peltaspermum martinsii*, POORT AND KERP, Pl II, III, IV; V.

2012 - *Peltaspermum martinsii* WACHTLER p. 32

2013 - *Lepidopteris meyeri* WACHTLER pp. 120-125

Etymology

Named after German Jürgen Meyer, Zwickau, a profound expert of the Carboniferous-Permian floras.

Holotype

TRE 351, **Repository:** Coll. Wachtler, Coll. Valentini; Museum of Natural Science, Trento, Dolomythos-Museum, Innichen

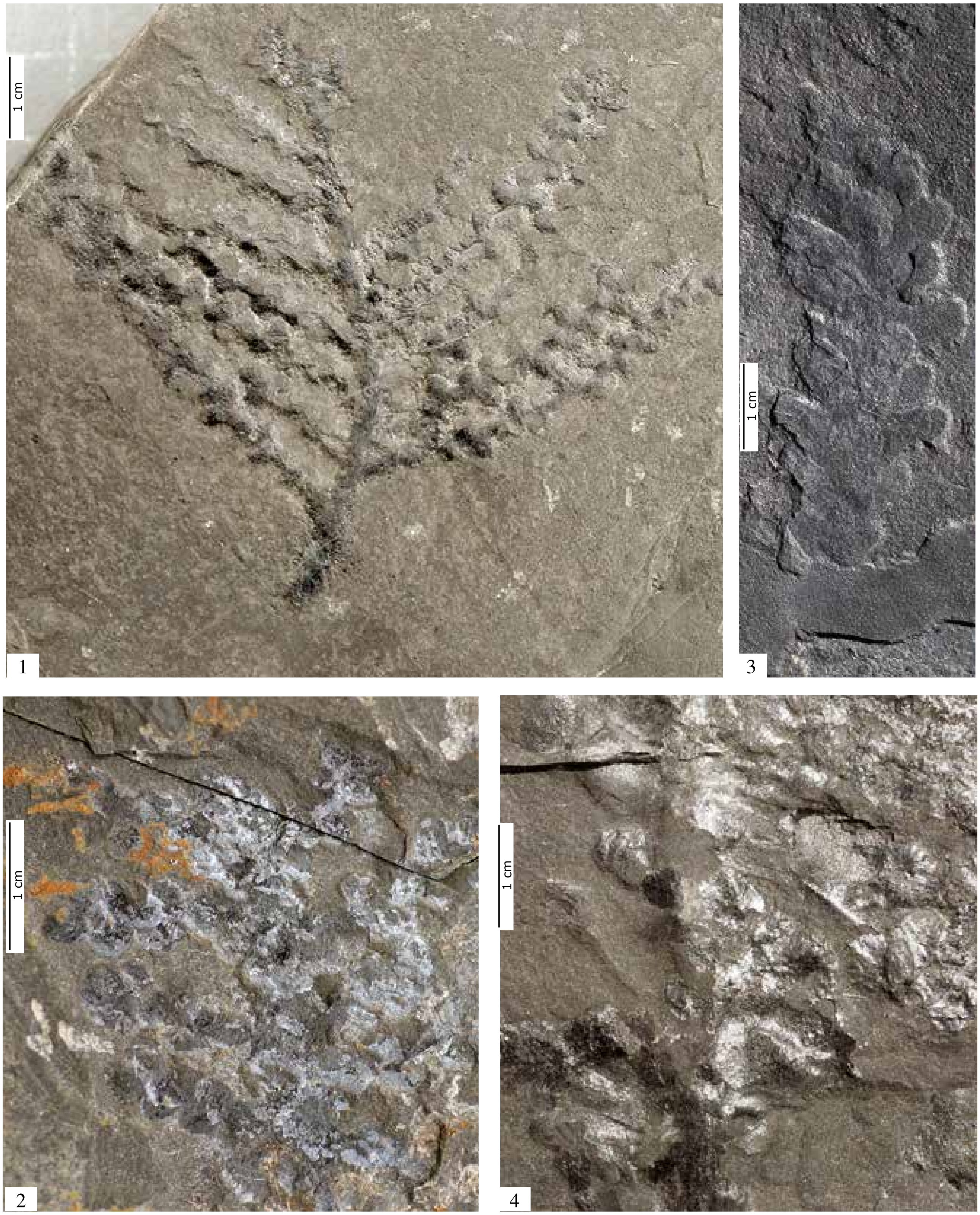
Description

Fronds: Bipinnate fleshy fronds holding minute entire to crenulated small pinnules. The venation is mostly obscured by the thick cuticle, and the mid-vein is relatively weak. The foliage is up to 5 mm long and wide. Sometimes Zwischenfiedern (intercalary pinnulas) cover the axis.

Fertile pinnules: Composed of minute megasporophylls in the form of peltate discs. The ovules are inserted dorsiventrally between from the center starlike outgoing ribs. Megasporophylls papillose, bordered with hairs, global aspect plump. They reach a size from 5 to 8 mm in diameter (TRE 263).

***Lepidopteris meyeri*. Reconstruction (Early Permian, Kungurian)**

a. Frond (TRE 351), b. Pinnula fragment (TRE 71), c. Entire female fructification (TRE 263), d. Megasporophyll front side (TRE 293), e. Megasporophyll back side (TRE 292)



***Lepidopteris meyeri*. Fertile and sterile fronds (Early Permian, Kungurian)**

1. Frond with the minute leathery leaves (TRE 351, designed holotype); 2. Young leaflet (TRE 271); 3. Frond evidencing the "Zwischenfiedern" (Intercalary pinnulas) (TRE 71); 4. Part of frond with several fertile peltate discs (TRE 263); all Coll. Valentini, Coll. Wachtler; Tregiovo, Le Fraine.

Autunia sp.

1893 *Callipteris conferta*, (STERNBERG) BRONGNIART - POTONIÈ 111 Taf. I Fig. 1, 2

1988 *Autunia conferta* (STERNBERG 1826) KERP nov. comb. KERP & HAUBOLD, 143

1988 *Autunia* (al. *Callipteris) conferta* (STERNBERG 1826 KERP nov. comb. KERP, BARTHEL & RÖSSLER 61 pl. 4 fig. 4

2013 *Autunia conferta* WACHTLER, pp. 124-125

Description

Fronds: Bipinnate to tripinnate fronds with alternating to supposite pinnae. Pinnules arising perpendicularly, entirely margined and leathery with a hidden midrib and mainly invisible lateral veins. The midrib extends more than halfway along the pinnula. Apex rounded to slightly tapered.

Ovuliferous organs: They consist of flattened, radially symmetrical umbrella-shaped peltate discs and are subdivided into several (from 8 to 10) segments, dorsiventrally holding the seeds.

Taxonomic notes

The order of Peltaspermales originates mainly on the Permian-Carboniferous boundary (*Autunia dammannii,* Kasimovian-Gzhelian) (Wachtler, 2013). In a relatively short time, they became a widespread group with about 30 genera and 135 species encountered around the world, with Early Permian *Autunia conferta* as one of the most representative plants in the Northern hemisphere. Although their pinnules resemble mostly normal ferns, their attached ovuliferous organs with its peltate shields divided into a fair amount of segments were decisive to classify them as seed-ferns.

The genus *Lepidopteris* was erected in 1869 for ferns with bipinnate or tripinnate fronds, thick pinnules with often-unclear evidenced veins, holding intercalary leaves.

With *Lepidopteris meyeri* and *Autunia* sp., we have to accept that two different *Peltaspermum*-species were present at Tregiovo although both being rare. After this period Autunia-fronds became extinct and only a small-sized, partially skeletal tribe *Lepidopteris (Peltaspermum) martinsii* (Wuchiapingian) survived till the Late Permian, reaching a peltate shield-diameter of only 5–10 mm. After the Early Triassic they increased again in size arriving at 15–25 mm in *Scytophyllum (Peltaspermum bornemannii,* Anisian) (Wachtler, 2011, 2016). Abundant *Lepidopteris (Peltaspermum)* fronds and fragmented fertile peltate shields furnishing cuticle material crop out from the Upper-Permian Gröden-Formation in the Bletterbach-Butterloch and near Recoaro. Entire fronds of *Lepidopteris martinsii* measure in the best cases 18 cm to 30 cm (Poort & Kerp, 1990). Apart from the Alpine flora, *Lepidopteris martinsii* is also well represented in Germany and England, with representatives ranging till China. Some interesting bigger peltate shields, resembling Early Triassic *Scytophyllum*, were found on the Seceda.

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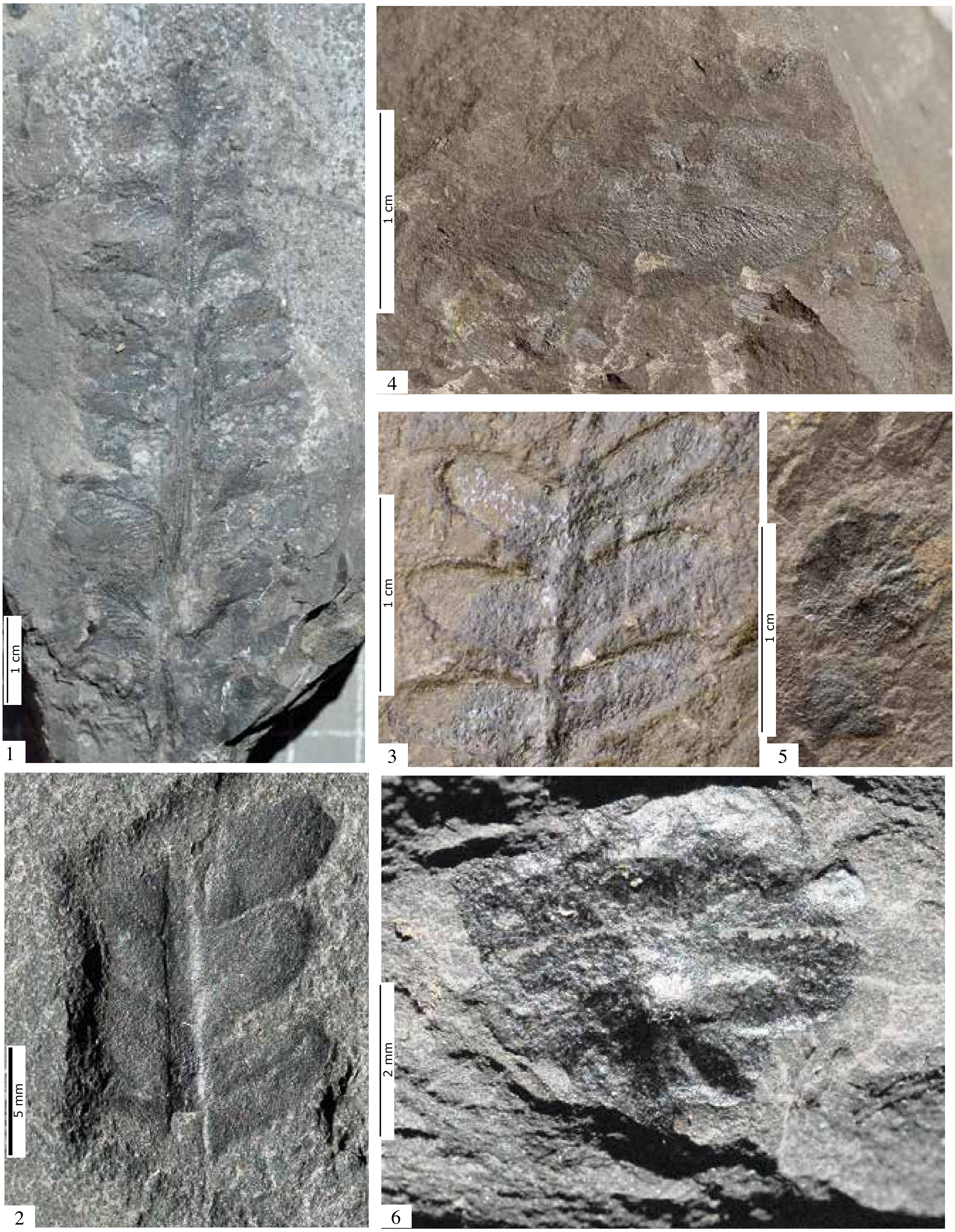


***Autunia sp.* Seed fern (Early Permian, Kungurian)**

1. Frond (TRE 518); 2-3. Small fragments of a pinnules (TRE 308, TRE 403); 4. Detail of a single pinnula (TRE 136); 5-6. *Peltaspermum*-shields thought to belong to *Autunia* (TRE 281, TRE 292); all Coll. Valentini, Coll. Wachtler; Tregiovo, Le Fraine.

Cycadophyta

One of the surprises of the Tregiovo flora is the richness in cycads. With *Macrotaeniopteris tridentina, Taeniopteris nonensis* and *Nilssonia perneri*, which could be defined as true cycad-ancestors due to their bulbous short stems and fertile structures, we encounter with *Wachtleropteris valentinii* an archaic, extremely interesting cycadophyllous plant that can provide information to their earliest genesis.

The cycads still living today consist of 11 genera and 305 species, which make them the second largest group of gymnosperms after the conifers. They spread over the tropics and sub-tropics north and south of the equator, and Central America is considered the region with the greatest diversity of cycads. The palm ferns (another name often used) are generally divided into three large families: the Cycadaceae, the Stangeriaceae, and the Zamiaceae. All cycads exhibit many common features. They all have separate sexes, with male and female fructifications located on separate plants. With the exception of the genus *Cycas,* all species developed similar male and female cones that are easy to differentiate from those of other plants and were located individually or in groups at the tip of the stem between the fronds. For the most part, each sporophyll bore a total of two seeds that are protected by a pair of mirror-symmetrical covers. Only in the genus *Cycas* they hold up to 16 seeds in two rows. The pollen cones of all cycads are relatively uniform with shield-shaped segments that generate the microspores on their underside.

For a long time, the doctrine has held that the genus *Cycas* can be considered the most primitive based on the unusual structure of their macrosporophylls, and that all others were derived from it through reduction. Fossil finds, however, indicate that the *Cycas* and *Zamia* groups developed almost simultaneously, ever since the Palaeozoic era.

Cycad-like plants of uncertain classification

The origins and evolution of the cycads have fascinated palaeobotanists for decades. After their first appearance between the Carboniferous and Permian, they became more numerous, remaining nearly unchanged in the development from the Permian to the Triassic. The Tregiovo flora holds some interesting plants that can be inserted into groups of known plants only with difficulty. One of them is represented by *Wachtleropteris valentinii*, probably the most archaic cycad known.

Wachtleropteris valentinii (WACHTLER, 2012 PERNER, 2013)

2012 *Taeniopteris valentinii*, WACHTLER, p. 39- 41
2013 *Wachtleropteris valentinii*, PERNER, p. 139- 144

Etymology

Named after Michael Wachtler who discovered new Permo-Triassic fossil floras in the Alps and described them extensively. The species name is dedicated to the modest forest-man Fèro Valentini from the Val di Non, who worked for many years on the fossil site Tregiovo-Le Fraine and had a passion for the marvels of nature.

Holotype

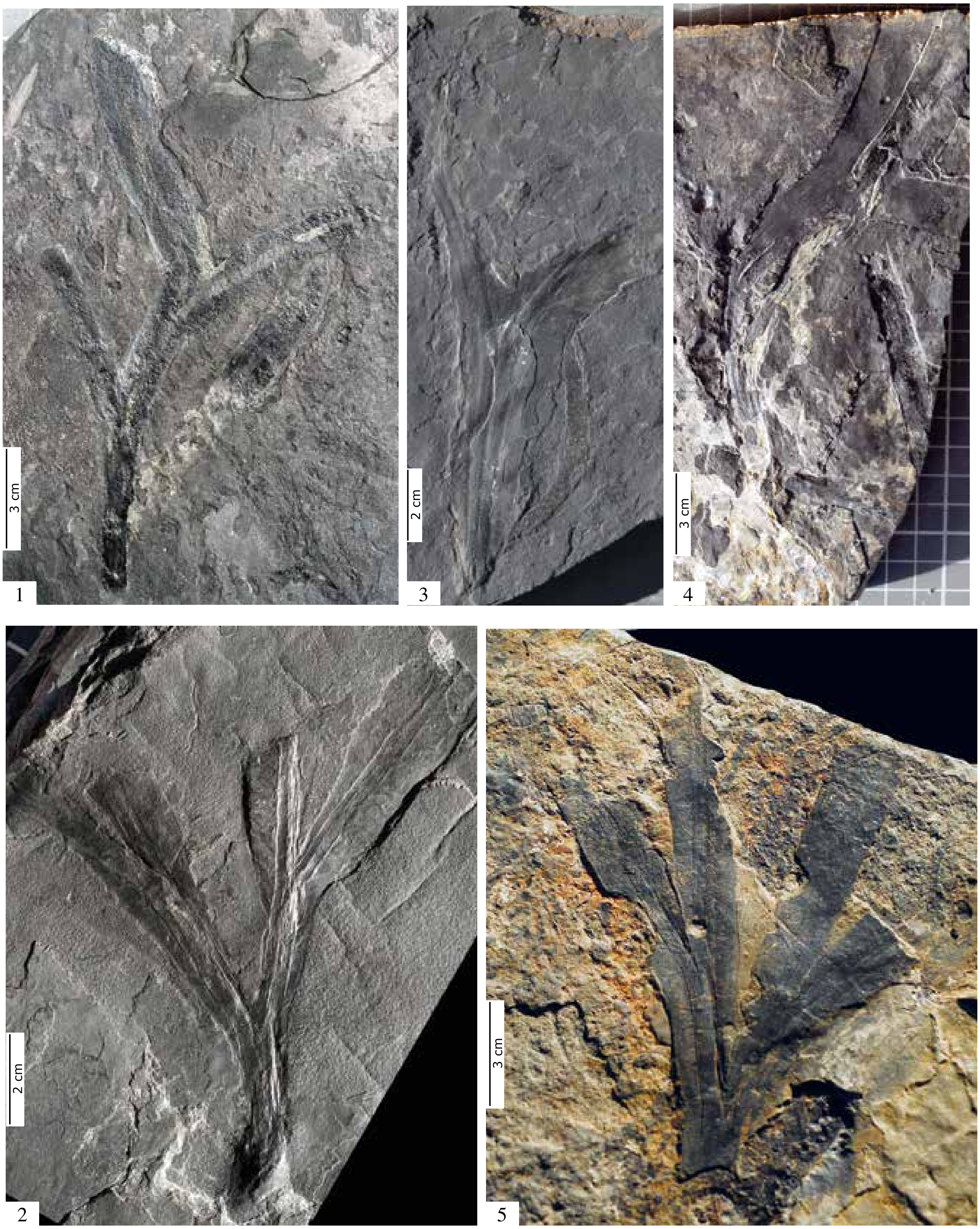
TRE 38, **Paratypes** TREE 39 (Cone), TRE 1 (leaves); **Repository:** Coll. Wachtler, Coll. Valentini; Museum of Natural Science, Trento, Dolomythos-Museum, Innichen

Description

Whole plant: Bushy low-growing plant with several times dichotomously-branched leaflets (TRE 256). The bifurcating leaves end in a rounded apex and generate a consistent central midrib (TRE 01 TRE 38); from which arise, nearly invisible, secondary veins at right angles to it and parallel to each other. Each leaf could reach a length of 10–15 cm and a wide of about 2 cm. Probably the whole plant grew from 30 cm till 50 cm.

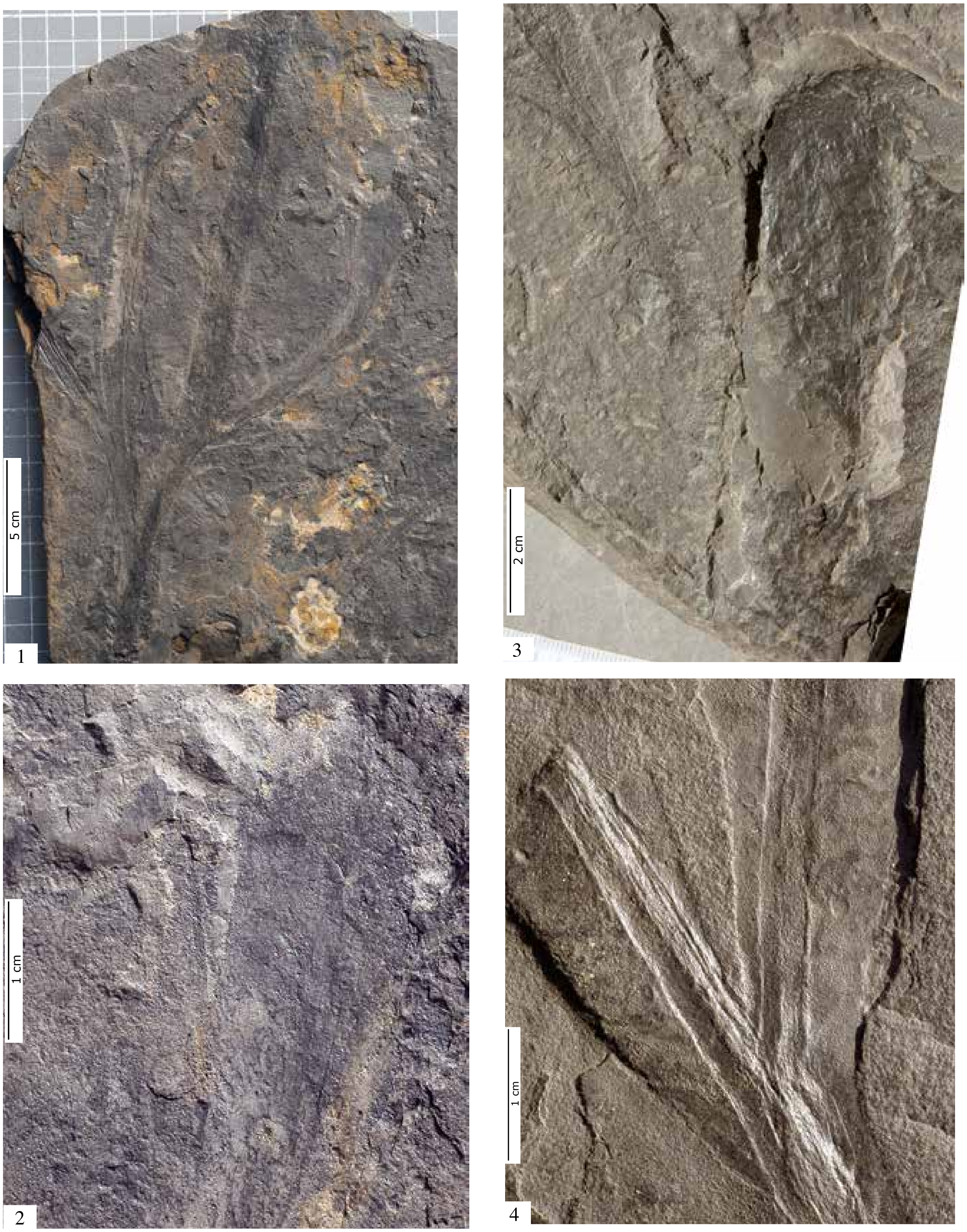
Male organs: Cones from 5 to 8 cm, and 3 cm wide connected with the plant and the foliage by a 1 cm long and 1 cm broad leaf-like petiole. Microsporophylls were spirally arranged on the main axis. The slightly pending sporophylls were 1 cm long, and pointed on the apex with the pollen sacs densely covering the lower surface (TRE 39, TRE 653).

Female organs: Cones from 6 to 10 cm long. Megasporophylls reaching a length of 2.5–3 cm and hanging down. Two seeds are inserted on the lower surface of the leaf-like megasporophyll (TRE 48).



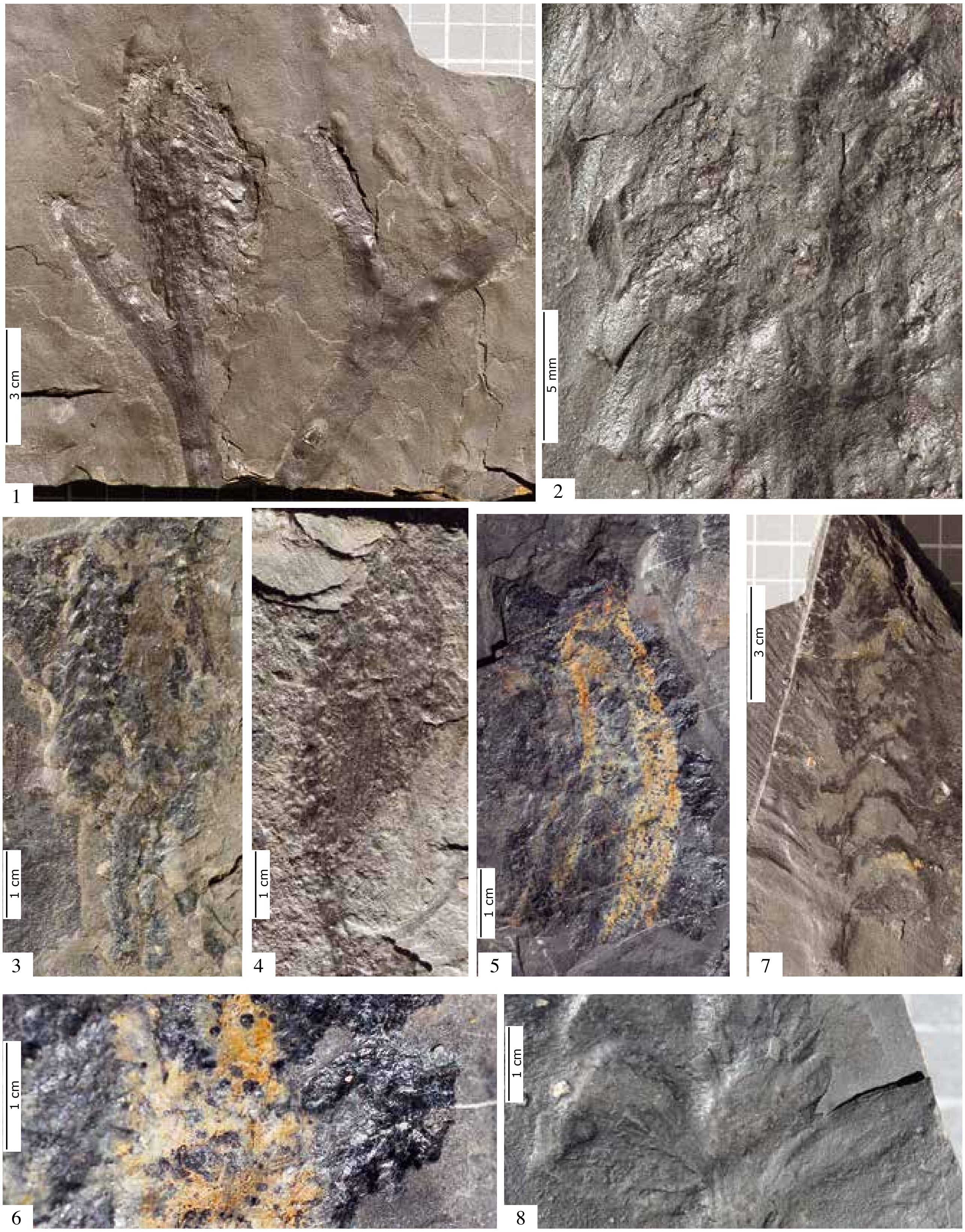
***Wachtleropteris valentinii*. Plant (Early Permian, Kungurian)**

1. Suggested whole plant (TRE 256); 2. Mainly complete plant evidencing the bifurcating foliage (TRE 38, designed holotype); 3. Furcating plant with cone (TRE 65); 4. Several diverging leaves (TRE 90); 5. Plant (TRE 01); All Tregiovo - Le Fraine, all Coll. Valentini, Coll. Wachtler



***Wachtleropteris valentinii*. Plant and cones (Early Permian, Kungurian)**

1-2. Rudimental branching with an juvenile cone (TRE 172); 3. Leaves and attached cone (TRE 653); 4. Part of a plant evidencing the bifurcating foliage (TRE 38, designed holotype); All Tregiovo - Le Fraine, all Coll. Valentini, Coll. Wachtler



Wachtleropteris valentinii. Plant and cones (Early Permian, Kungurian)

1-2. Entire male cone attached on the stem with leaves and detail of the microsporophylls with the pollen on the lower surface (TRE 39, paratype); 3-4. Male cones (TRE 534, TRE 245); 5-6. Male cone and detail of the pollenl (TRE 132); 7-8. Entire female cone and detail of the leaf-like sporophylls with small-sized seeds attached on the lower surface (TRE 48); All Tregiovo - Le Fraine, all Coll. Valentini, Coll. Wachtler

Taxonomic notes

The classification of shrubby *Wachtleropteris valentinii*, reaching a size of probably 50 cm, and relatively often recovered in the lower sediments of Tregiovo is not totally resolved. The leaves extended upwards on a stem and branches twice, which is not typical for cycads, and each of the leaves split into two independent branches. The leaves were tongue-shaped and hold a pronounced midrib. The foliage and the arrangement of the cones on the end of a pinnate leaf identifies them as gymnosperms with affinities to the cycads. In that *Wachtleropteris* forms a bridge from the Devonian until the Permian as the "*last representative of a very old and primitive representative having cycadalean affinities*" (Perner, 2013).

Wachtleropteris valentinii holds some characteristics of the cycads but their expanding bifurcating growth distances it from them. At the same time, due to its ramifying leaves, analogies to some primitive ginkgophyta are evident, but are not sufficient to include them due to their distinguished midrib and the cones in this class, maybe only as a link. Indeed, sometimes when the median rachis is not very well evidenced or obscured in *Wachtleropteris* and the leaves are relatively slender (in most cases they are wide enough to make a sure distinction), it can be confused with *Ginkgoites pohli*. Otherwise, *Gingkoites* is characterised by their circular and often conjoined two seeds/ovules and, when preserved, also a collar on its leaf base.

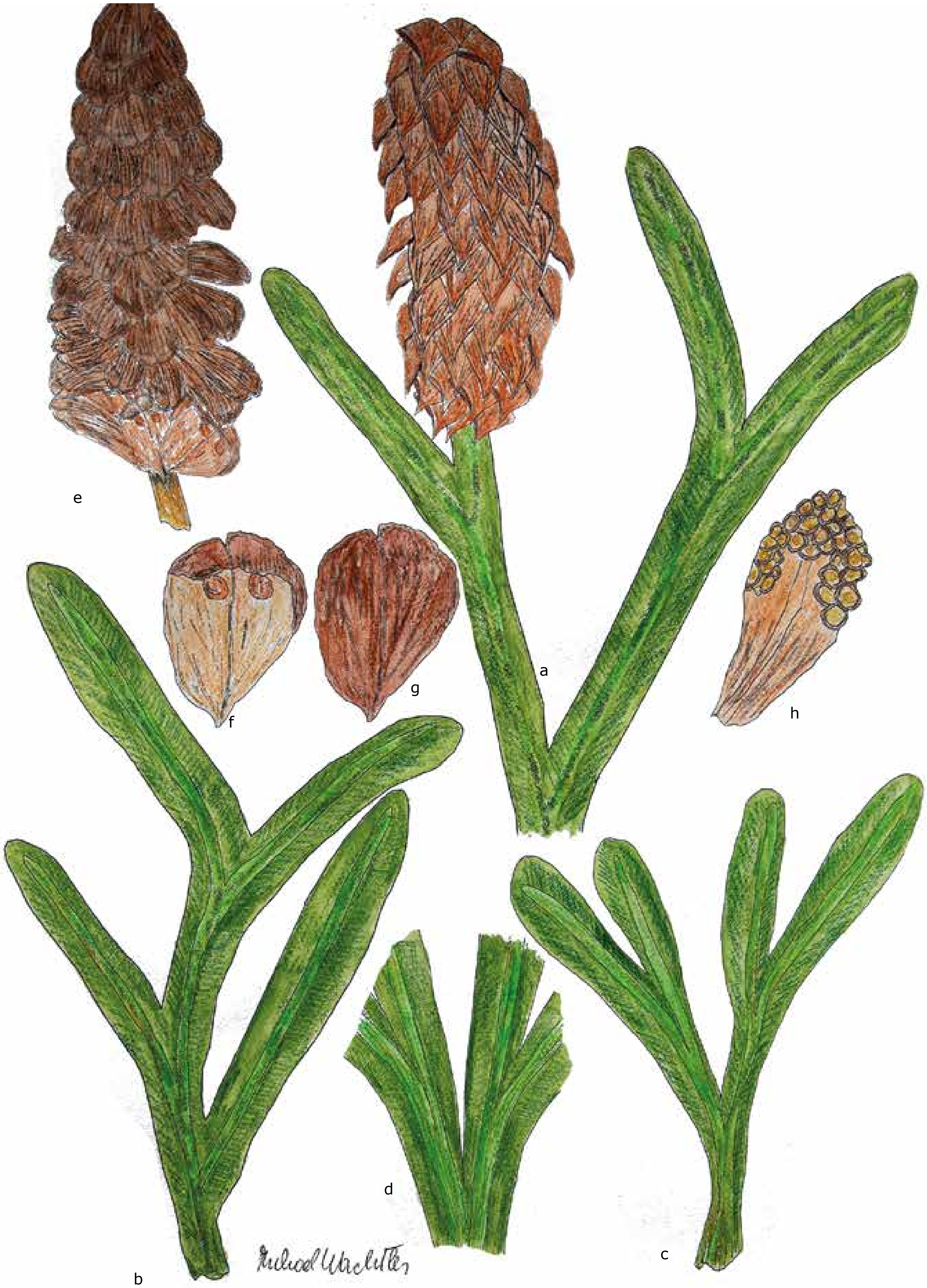
Strangely in the Early Permian Tregiovo-flora, we encounter at the same time other well-formed Cycadophyta, such as *Zamia*-like *Nilssonia perneri* or both *Cycas* resembling *Macrotaeniopteris tridentina* and *Taeniopteris nonensis,* which can be inserted without hesitation in a lineage between Permian and Triassic cycad-ancestors. Male cones of *Wachtleropteris valentinii* hold pending sporophylls. Whereas, the female organs are characterised by their larger, but less numerous sporophylls. Whereas the male and female cones have some analogies with recent fertile organs of the cycads, the arrangement of the leaves on a several times bifurcating stem is unusual and has never been recorded in true cycads. Extant but also fossilised cycads, such as coeval *Nilssonia perneri* are characterised by a bulbous stem, which, in this case, we do not encounter (Wachtler, 2012). *Wachtleropteris valentinii* therefore raises more questions than it resolves. The only way to understand this plant, is to accept the cycadalean affinities, but to agree in the same way that Early Permian Ginkgophyta, especially those from Tregiovo, hold a similar ramifying-concept. In any case, this mysterious plant constitutes one of the most interesting and new flora elements of Permian Tregiovo.

Taeniopteris nonensis n. sp. (WACHTLER 2021)

1978 *Taeniopteris (Lesleya) eckardtii,* Remy & Remy
1999 *Taeniopteris (Lesleya) eckardtii,* Visscher
2012 *Taeniopteris eckardtii,* Wachtler, p. 37

The genus *Taeniopteris* was first described in 1828 by the French palaeobotanist Adolphe Brongniart for tongue-shaped entire-margined cycad-leaves from which densely packed lateral veins extended as far as the end of the blade. He mentioned mostly species from Jurassic–Liassic layers like *Taeniopteris vittata, Taeniopteris latifolia* or *Taeniopteris bertrandi*. In 1839, G.A. Kurtze extended the range with *Taeniopteris eckardtii* up till the Upper Permian German Zechstein, whereas in 1864 August Schenk introduced the species *Taeniopteris angustifolia* for Middle Triassic (Ladinian) foliage thought to be of *Cycas*-like. A plethora of tongue-shaped leaves from the Permian to the Triassic all over the world were then introduced, the main problem being their lack of fertile organs.

In 1864, August Schenk coined the name *Dioonites pennaeformis* for feathered megasporophylls from the German Hauptsandstein (Ladinian) of cycadalean affinities. In the course of time, the view crystallized that the leaf genus *Taeniopteris* and the *Dioonites* megasporophylls can be regarded as belonging to the same plant, although sometimes the confusing name *Dioonitocarpidium* was used. Beginning from the Lower Permian (DiMichele, 2001) till the Triassic similar megasporophylls were found worldwide, all characterised by a sterile apical feather-like frond and a basal blade that holds between 8–30 seeds on each of the two rows. It can be stated that the smaller one belongs to some *Taeniopteris*



***Wachtleropteris valentinii*. Reconstruction (Early Permian, Kungurian)**

a. Plant with rudimental branching and an attached juvenile male cone (TRE 39); b. Part of a plant evidencing the bifurcating foliage (TRE 256). c. Mainly complete plant (TRE 38, holotype); d. Detail of the dividing leaves (TRE 38); e. Female cone (TRE 48); f. Macrosporophyll lower surface with two seeds (TRE 256); g. Upper surface (TRE 256); h. Microsporophyll (TRE 132)

foliage, whereas the bigger and more seeded represent the megasporophylls of *Macrotaeniopteris*.
From the Permian till the Triassic, we encounter also some evolving trends in the Taeniopterides. Whereas the Permian (*Taeniopteris eckardtii,* Wuchiapingian) till the Early-Middle Triassic (*Taeniopteris simplex,* Anisian) hold their sterile leaves/fronds as well the megasporophylls more or less spirally arranged or climbing a central axis, beginning from the Middle Triassic (*Taeniopteris angustifolia)* the leaflets and megasporophylls sprout in one plane from the stem, as we encounter in extant Cycas.

Diagnosis

Leaves are tongue-shaped and parallel-veined with an entire margin ending in a tapered to rounded apex.

Etymology

Named after the Val di Non in the Italian Province Trentino.

Holotype

TRE 598, **Repository:** Coll. Wachtler, Dolomythos-Museum, Innichen

Description

Leaves: Up to 15 cm long and 2–3 cm wide (TRE 228), the tips of the leaflets were pointed (TRE 642) to rounded (TRE 598 holotype). Parallel undivided (only sometimes once divided on the base) veins sprout from the midrib at a slightly offset 90 degree angle, crossing the whole lamina.
Pollen organs (*Androstrobus-type*): Probably bulbous ovoid, composed of spirally arranged microsporophylls on a central axis (TRE 346, TRE 368).
Seed cones (*Dioonites-type*): Till now not recorded with certainty. Probably TRE 70 represents a fertile leaf with the impressions of the seeds on the basal part.

Taxononomic notes

For many decades it was thought that the first cycads originated on the Permian–Triassic boundary. Now it is proven that already in the Early Permian they were fully evolved and, astonishingly, even in the earliest Permian the different extant lines are recognisable. Additionally, similar to the Palaeozoic-Mesozoic genus *Nilssonia*, characterized by its mostly similar male and female cones resembling extant Zamiaceae, we encounter in the Tregiovo-Formation also two distinct Taeniopterides: one with bigger entire fronds, classified as *Macrotaeniopteris tridentina* and the smaller leaved *Taeniopteris nonensis.*
This bisection we can than follow till the Triassic-Jurassic for about 180 million years. Nevertheless there are differences between the Permian-Early Triassic and the following Middle Triassic-Jurassic Taeniopterides. The most obvious difference between today's Cycas-genus and the Taeniopterides were their not segmented fronds. They were for the whole Palaeozoiz-Mesozoic period entire-margined (*Taeniopteris*) or irregularly lacerated due to weather conditions (*Macrotaeniopteris, Bjuvia*).
Interestingly the division of the Taeniopterides into a small-leaved variant (*Taeniopteris*) and one (*Macrotaeniopteris*) with huge leaves (in the Triassic the not segmented fronds could reach also one metre) was operative just from the Early Permian. *Taeniopteris* holds smaller megasporophylls with less seeds (till about 12 for each row), *Macrotaeniopteris* bigger, reaching till 40 ovules for each row. The Taeniopterides were widespread in the Early Permian (T*aeniopteris jejunata, Taeniopteris abnormis* or *Macrotaeniopteris multinervis* in the German Rotliegend (Oberhof-Formation, Sakmarian), and therefore it is assumed that they originated between the Carboniferous-Permian border with roots till the Devonian.

Macrotaeniopteris tridentina nov. comb. (WACHTLER, 2012; WACHTLER, 2021)

2012 *Bjuvia tridentina* WACHTLER, p. 45-46
2013 *Wachtleropteris valentinii*, PERNER, p. 139- 144

Etymology

Named after the Italian province Trentino (Southern Alps), where this Cycadophyta was found for the first time.

Holotype

TRE 44, **Repository:** Coll. Valentini, MUSE, Trento

Description

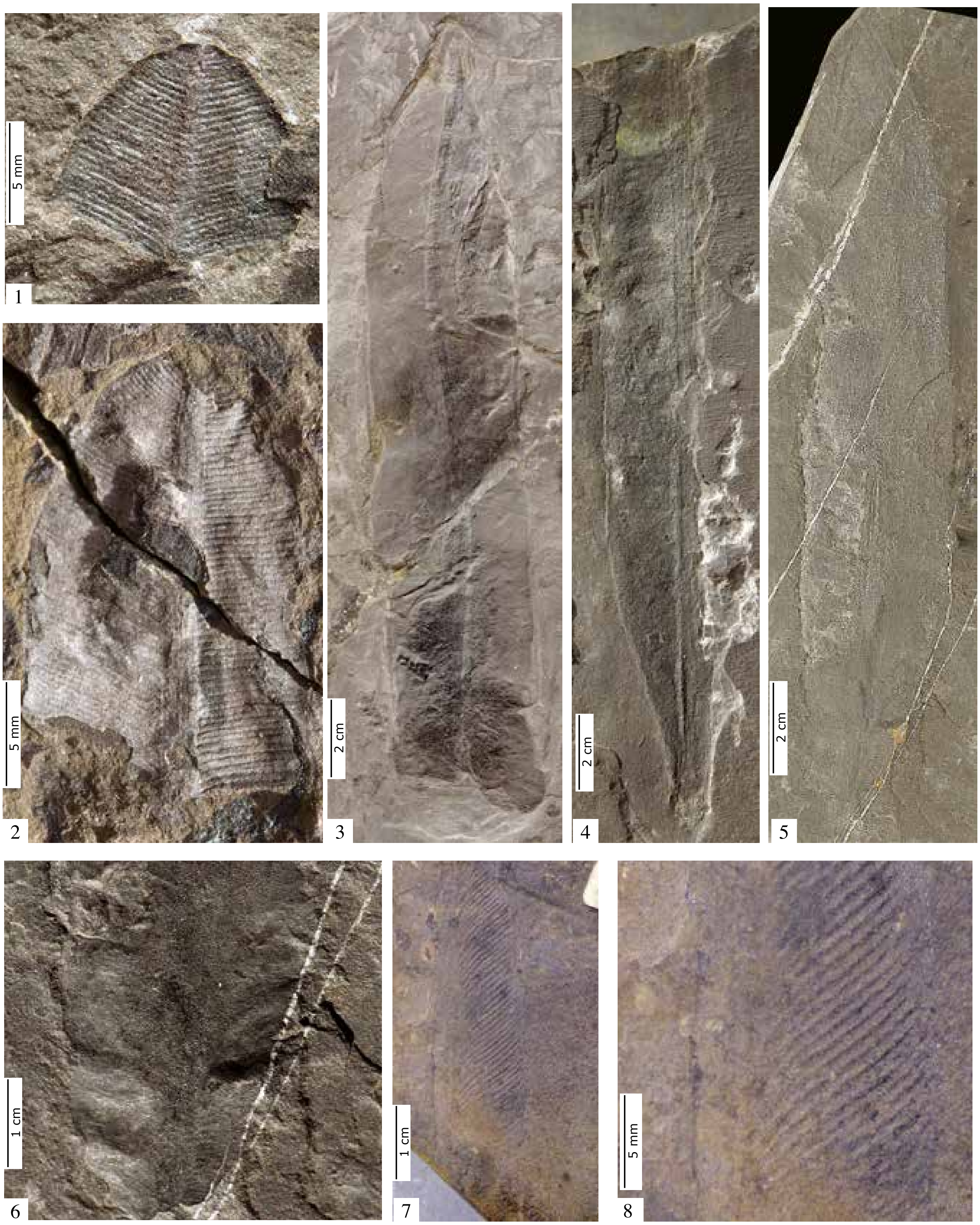
Leaves: Entire marginated foliage that may have been torn several times due to the rig-

Macrotaeniopteris tridentina **and** ***Taeniopteris nonensis*****. Reconstruction (Kungurian)**

a. *Macrotaeniopteris tridentina*, whole plant (TRE 44 holotype), TRE 644, TRE 177); b. Pollen cone, c. Microsporophyll; d. *Taeniopteris nonensis,* whole plant (TRE 598, TRE 642, TRE 228, TRE 508); e. Entire leaf (TRE 228); Apical part of a leaf (TRE 598, holotype)

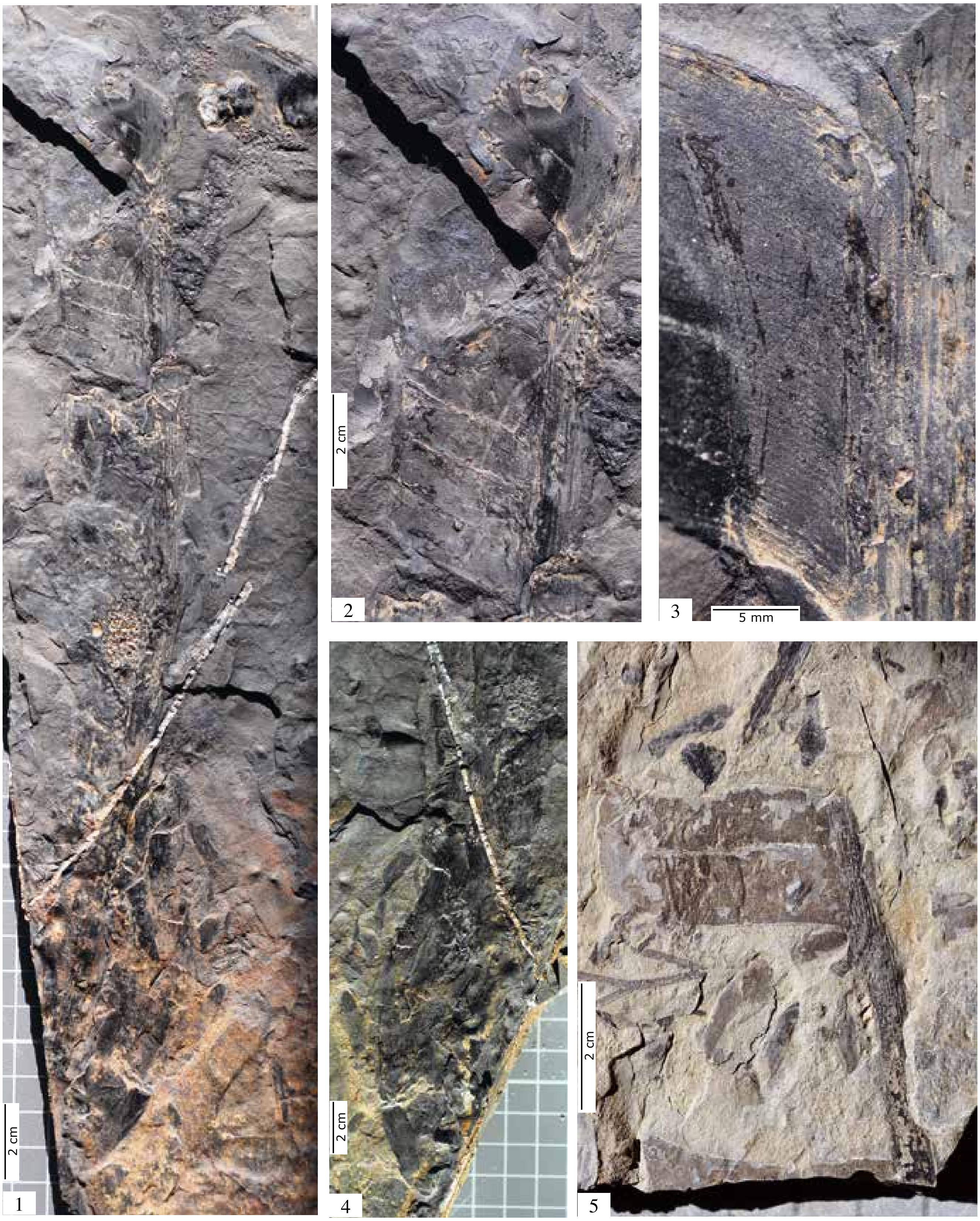
Macrotaeniopteris tridentina nov. comb. (Early Permian, Kungurian)

1. Single apical part of a frond (TRE 44, designed holotype); 2. Entire frond (TRE 644); 3. Lacerated frond (TRE 177); 4. Juvenile frond and detail of the veins (TRE 529); All Tregiovo - Le Fraine, Coll. Valentini, Coll. Wachtler



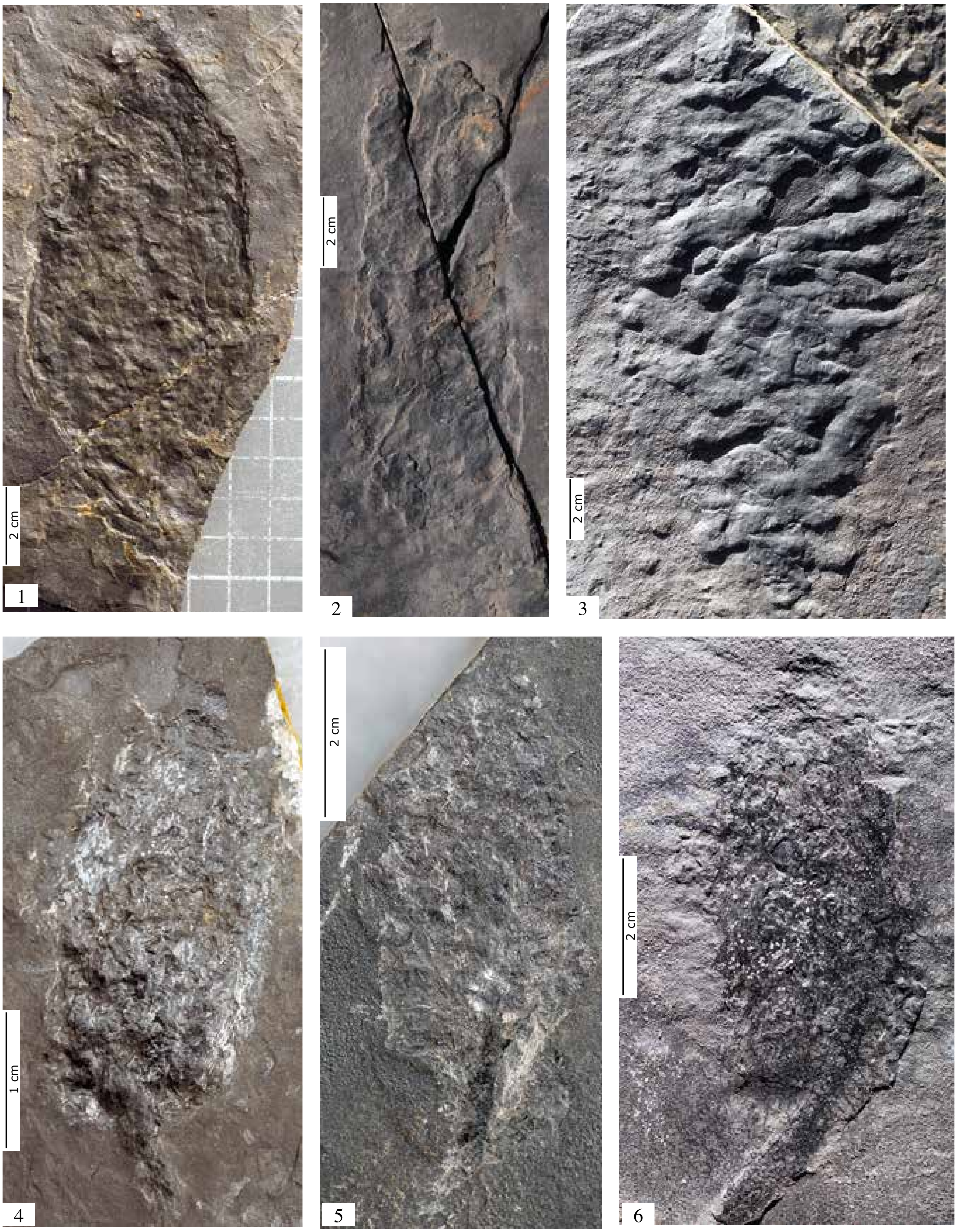
***Taeniopteris nonensis* n. sp. (Early Permian, Kungurian)**

1. Apical part of a leaf (TRE 598 designed holotype); 2. Counterpart of the holotype (TRE 598); 3-4. Single fronds (TRE 642, TRE 228; 5-6. Leaf, basal part probably showing impressions of the seeds (TRE 70); All Tregiovo - Le Fraine, Coll. Valentini, Coll. Wachtler; 7-8. Isolated leaf (Tregiovo, Museo di Scienze Naturali, Brescia)



Nilssonia perneri n. sp. (Early Permian, Kungurian)

1-4. Plant with one entire frond attached on the bulb, and detail showing the veins of a single pinnula (TRE 2, designed holotype). 5. Apical part of a pinnula with a seed on the right upper side (TRE 599); All Tregiovo - Le Fraine, Coll. Wachtler



Undefined cycad cones belonging to *Nilssonia, Macrotaeniopteris* or *Taeniopteris* (Kungurian)

1-6. Various male and female cycad cones with uncertain attribution to one or the other cycad-genus (TRE 175, TRE 557, TRE 47, TRE 346, TRE 368, TRE 224); All Tregiovo - Le Fraine, all Coll. Valentini, Coll. Wachtler;

ours of nature (TRE 44 holotype, TRE 644 (lamina 8 cm long, 5 cm wide, petiole 2 cm long), TRE 177). The leaves are oblong, the apex varies from U-shaped to V-shaped. Unforked secondary veins (or only once divided on the base) arise at right angles from the rachis. The rachis is consistent.

Cones: Male cones of *Thetydostrobus* type. Possible pollen organs can be TRE 175, TRE 47. Due to its poorly conserved character, other information is difficult to establish.

Taxononomic notes

On the basis of deposits of the Rhaetian locality of Bjuv in Sweden, Rudolf Florin established in 1933 the new foliage genus *Bjuvia* for huge cycad leaves, sometimes reaching 1 m and similar to extant banana fronds. All in all, it was not a happy decision. Once because he connected the megasporophylls with the new genus-name *Palaeocycas integer,* also Florin's drawing of *Bjuvia* was fundamentally wrong with its long stem and the superficial arrangement of the sporophylls. In addition, he completely bypassed the earlier literature, not only for the megasporophylls (*Palaeocycas intege*r), since in 1864 August Schenk had introduced the name *Dioonites pennaeformis* for feathered megasporophylls from the German Hauptsandstein (Ladinian).

Somewhat unfortunately also Rühle von Lilienstern (1928) changed the name *Dioonites* to *Dioonitocarpidium (pennaeforme)*, supposing that there was a difference between megasporophylls with and without attached seeds. Moreover, the name *Bjuvia* can only be regarded as synonymous with *Macrotaeniopteris,* a genus name given by the French-German palaeobotanist Wilhelm Philipp Schimper (1808–1880) in 1869 for entire margined huge fronds first accommodated in *Taeniopteris* major from the Jurassic Gristhopre Yorkshire-beds. Although sometimes the validity for the retention of the name *Macrotaeniopteris* was questioned (Van Konijnenburg-van Cittert, 2017), it can be stated that there exist many reasons about the validity of this genus.

Just from the Early Permian the two genera *Taeniopteris* and *Macrotaeniopteris* were already different and easily distinguishable. Huge lacerated fronds in *Macrotaeniopteris*, mostly entire margined small-sized leaves in *Taeniopteris*. This becomes even clearer in the Early-Middle Triassic (Anisian) of the Dolomites with its richness in cycads: the leaves of *Macrotaeniopteris (Bjuvia) olangensis* exceed largely a length of 70 cm with a width of 40 cm. Even greater are the differences in the female organs: big tufts (from 20–30 cm long, 10–15 cm wide) with up to 60 of megasporophylls spirally bearing two rows with up to 20–30 seeds on each characterize *Macrotaeniopteris (Bjuvia).* The featherlike apex was only rudimentary evolved. On the other hand, we have in the Early Triassic with *Taeniopteris simplex* a low-growing shrub, with thin and fragile leaves that reached only a length of 8–15 cm and a width of 1–3 cm. The margin was entire, and only rarely lacerated. The loosely organised sporophylls hold only 6–12 ovules on the lower surface of each row. Their distinguishing feature was a clear evidenced terminal feather-like apex. The same features we encounter in Middle Triassic (Ladinian) *Taeniopteris angustifolia.*

Therefore, it can be clearly stated that they belong to two distinct genera already evident from the Early Permian on and more distinguishable in the Triassic. If they can not be classified as two genera, then the name *Macrotaeniopteris* would have priority in any case about *Bjuvia*. It is obvious that in the Early Permian both—*Taeniopteris* and *Macrotaeniopteris*—had even greater similarities together with their relatively similar and small-sized leaves than in later millions of years. Another question is when or in which part of the world the pinnate leaves became their leaflets geometrically segmented, because all European Taeniopterides from the Permian till the Jurassic evidence only a lacerated blade, but not a frond like today's *Cycas*.

Nilssonia perneri (WACHTLER, 2012)

2012 *Nilssonia perneri,* WACHTLER, p. 130-131

Etymology

Honouring Thomas Perner a German collector and researcher, specialised in fossil cycads.

Holotype TRE 2, Repository: Coll. Wachtler, Coll. Valentini; Museum of Natural Science MUSE, Trento, Dolomythos-Museum, Innichen

***Nilssonia perneri*. Reconstruction (Early Permian, Kungurian)**

a. Whole plant with bulbous stem (TRE 2); b. Single frond; c. Detail of a frond (TRE 515, TRE 599); d. Isolated seed (TRE 599); e. Basal leaf from the stem TRE 2)

Description

Whole plant: Cycadalean-like plant with fine-veined leaves arising at right angles from a broad rachis. They are often and irregularly lacerated, but a tendency to geometrical segmentation is recognisable. Trunk ovoid, formed by elongated leaves, rounded on the apex. Holotype TRE 2 is composed of a single frond, attached on the trunk and constitutes one of the rare cases in which a whole plant could be studied. The entire length of the preserved part of the plant is 36 cm. The bulbous trunk reaches a length of 10 cm by a maximal width of 6 cm. It is covered or consists of densely arranged compact leaves. The foliage of the stem evidences no similarity with the main fronds outgrowing from the upper side of the bulb. The leaves are tightly packed and show neither a central rachis nor veins. They are up to 4 cm long, maximal 0.6 cm wide, and rounded on the apex.

Leaves: The frond is 26 cm long frond arising from the upper side of the trunk. It is irregularly lacerated, although manifesting a disposition to a 1 cm broad segmentation. The consistently main rachis, nerved by several strong and clearly visible mid-veins measures 1 cm. It sometimes holds folded leaves. They are maximal 2.5 wide on each side, delicate and densely arranged. Never forking veins arise in a right angle from the main rachis (TRE 599, TRE 515).

Male cone: (Of *Androstrobus*-type). Various male cycad cones can belong to *Nilssonia perneri*, (TRE 346, TRE 368, TRE 224), but a distinction is difficult, because also *Taeniopteris nonensis* and *Macrotaeniopteris tridentina* generate similar male cones.

Female cone: Probably TRE 175, TRE 557, and TRE 47 represent cones with megasporophylls belonging to *Nilssonia perneri.* They evidence closed macrosporophylls.

Taxonomic notes

With its irregular but still recognisably segmented leaflets, *Nilssonia perneri* from Tregiovo can be considered a potential ancestor of the cycads from the Zamiaceae-line. One specimen from Tregiovo with its attached fronds on the trunk is interesting because for the first time we have unequivocal evidence that a low-growing bulb-like stem is to be found in the first Permian cycads. Moreover, their fertile organs were from the beginning so highly developed that there are minimal difference to the extant one. There are enough parental affinities to regard the Early Permian *Nilssonia perneri* as the precursor of the Upper Permian *Nilssonia brandtii* (Wachtler, 2015) or Middle Triassic *Nilssonia primitiva* (Wachtler, 2015), both from the Dolomites. Also, the male *Androstrobus* and female *Thetydostrobus* cones found in fair amounts in the Permian sediments support this.

Nilssonia perneri cannot be confused with *Macrotaeniopteris tridentina* or *Taeniopteris nonensis* from the same Tregiovo-Formation. The Taeniopterides bear only large, sometimes lacerated foliage, whereas *Nilssonia* clearly holds defined segmented cycad leaflets. Less confounding problems are seen with *Wachtleropteris valentinii*, which is a leaf-forking bushy plant with much smaller leaves. It cannot be disregarded completely that all of these cycadalean plants (*Nilssonia, Macrotaeniopteris, Taeniopteris, Wachtleropteris*) have a Carboniferous common ancestor, although in the Permian they were evolved to completely different lines.

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***Ginkoites pohli*. Reconstruction (Early Permian, Kungurian)**

a. Twig with ovules (TRE 45, TRE 5, TRE 239); b. Leaf (TRE 5); c. Other leaf (TRE 239); d. Seed (TRE 45, TRE 124, TRE 233); e. Inner view of a seed; f. Male cone (TRE 401); g. Single microsporophyll

Ginkgophyta

Today's ginkgo leaves are fan-shaped with veins radiating out into the leaf blade. In the Permian, their leaves were irregularly lobed and needle-like. Especially in the Italian Dolomites the first barely recognizable Ginkgoales with attached seeds and pollen-organs can be studied beginning from the Early Permian (Kungurian) and than their evolution can be followed for many million years till the Late Permian. Early Permian *Ginkgoites pohli* from Tregiovo can be regarded—due to its inchoate and irregular branching system—as the most primitive ginkgo so far recorded. But it has all of the features of real ginkgos: these characteristics include a collar-like ring from which the leaves emanate and two ovules/ seeds aggregated together. The ovules were held by a modified leaf segment and are in that slightly different from those of modern ginkgos that are connected at the end by a distinctive stalk.

Ginkgoites pohli (Wachtler, 2013) comb. nov.

2012 *Sphenobaiera digitata*, WACHTLER, p. 18 - 19
2013 *Baiera pohli* p. 116-119, fig. 1-10

Etymology

Named after the German collector Burkhard Pohl, who helped to develop palaeontology worldwide.

Holotype

TRE 45; **Paratype** TRE 86 Museum of Natural Science MUSE, Trento; **Other:** Repository: Coll. Wachtler, Coll. Valentini; Dolomythos-Museum, Innichen

Description

Leaves: Some are needle-like reaching a considerable length of about 20 cm, by a width of 0.5 cm, and are equipped with basal spur shoots (TRE 86). Other leaves are more small-sized and fork irregularly diverse times (TRE 45, holotype, TRE 5, TRE 544).

Ovules: They are borne in pairs or single at the apex of a modified leaf (TRE 45, TRE 124, TRE 233). The size of the elliptic seeds varies from 0.7 till 1.0 cm in length and about 0.5 cm in width. The stalk/leaf can reach a considerable length of 7 cm (TRE 45, holotype).

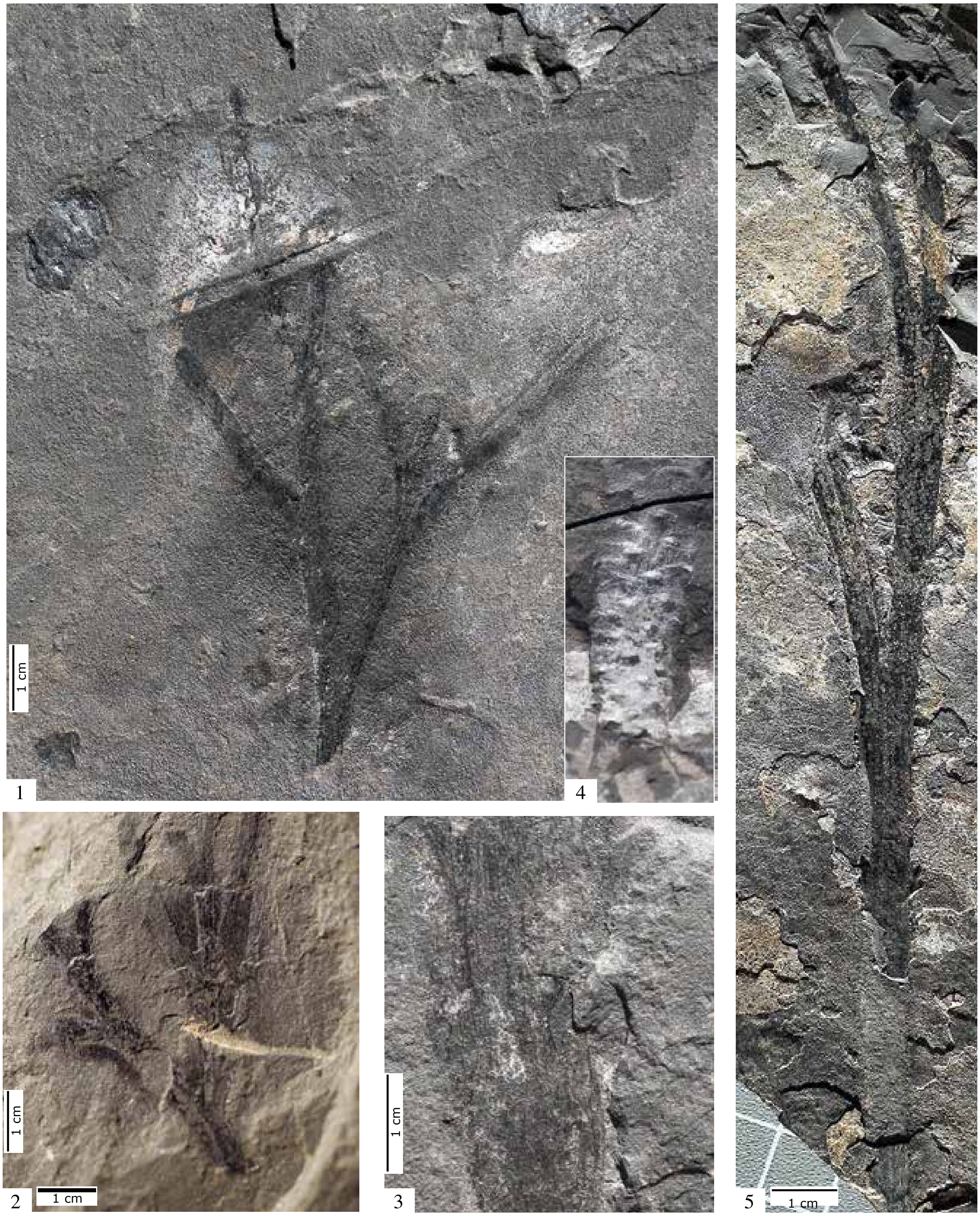
Pollen cone: TRE 401 probably represents a male cone. It consists of a main axis showing divided microsporophylls. From this aspect, it is probably an immature cone.

Taxonomic notes

When I described Early Permian (Kungurian) *Baiera pohli* (Wachtler, 2012, 2013), I had no knowledge about the abundant presence of late Permian (Wuchiapingian) Ginkgoales in the Dolomites (Wachtler, 2021). Only after the recovery of many well-preserved specimen, especially from the Seceda mountain in the Gröden-Valley, I was able to connect better the birth and evolution of the Ginkgoales based on these findings. Therefore, I propose to change the classification to *Ginkoites pohli*, due to the fact that this archaic ginkgo represents probably a direct evolving line to extant ginkgos. Till now *Ginkgoites pohli* was found only in the Kungurian layers of Tregiovo in the Val di Non; in the older Artinskian sediments of the nearby Collio-Formation they are missing, whereas other gymnosperms like Araucaria-ancestor Ortiseia, Abies-progenitor *Majonica* or *Pinus* ancestor *Férovalentinia* are abundant in both localities.

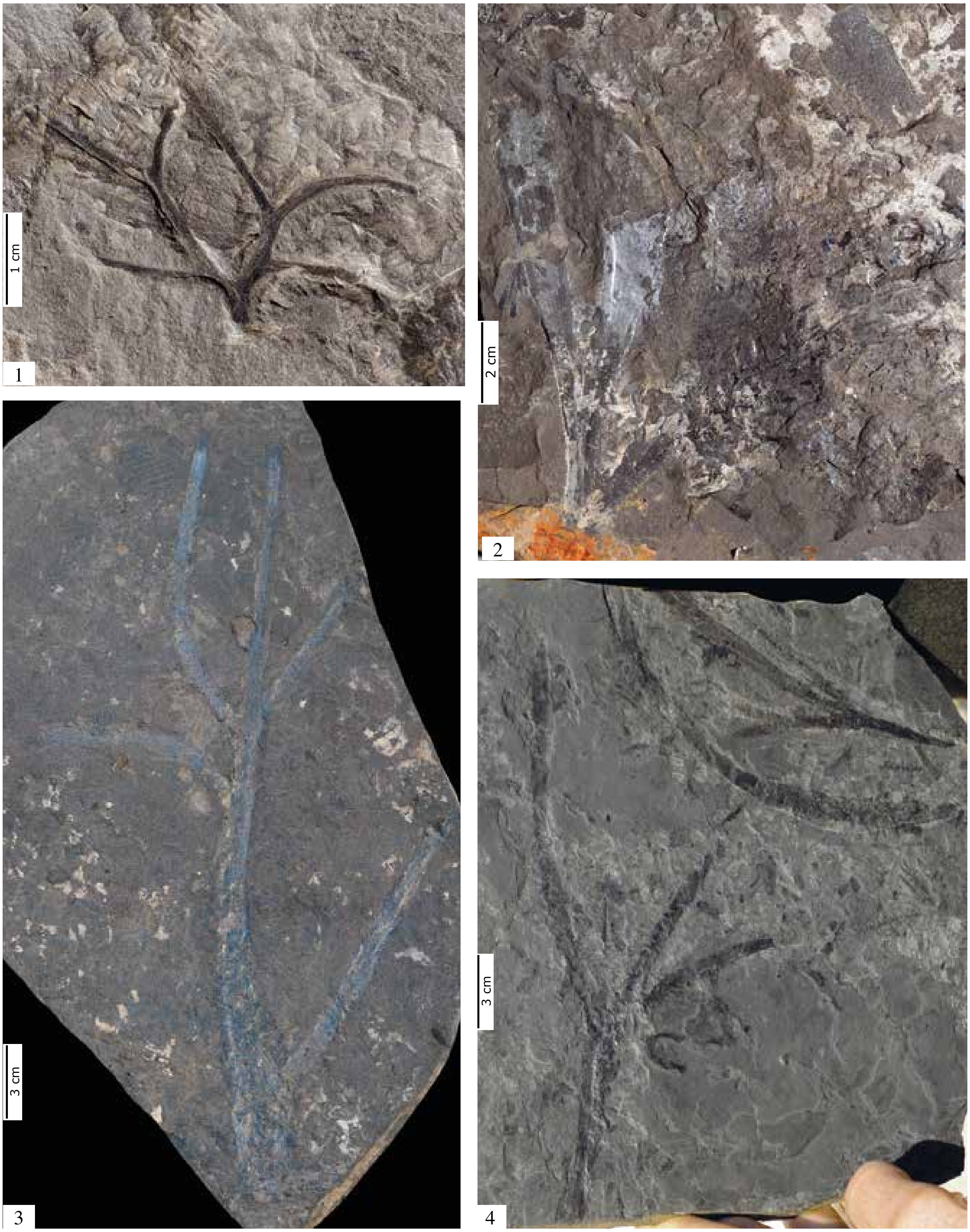
Repeatedly dichotomizing or bilobed leaves based on Rhaetian-Hettangian specimen of Bayreuth were first described as *Baiera dichotoma* (Braun, 1843). Further this genus-name was brought in connection with archaic ginkgos and adopted for various deeply dissected leaves, like late Permian *Baiera digitata* (Heer, 1876). The American researcher Albert Charles Seward introduced than the name *Ginkgoites* (Seward, 1919) for more or less fan-shaped leaves conducting to the only species existing *Ginkgo biloba*. The name *Baiera* remained for an about four-time bilobed leaf-character with a deeper incision in the middle, sometimes enlarged to a fifth or reduced to two or three segments.

Interestingly we encounter beginning from the Carboniferous-Permian just a splitting of two *Ginkgo*-lines. Kasimovian-Gzhelian *Baiera perneri* (Wachtler, 2013, Perner & Wachtler, 2015), as well as Late Permian *Baiera digitata*, both from Middle-European fossil sites were characterized by a short petiole from which sprout in one plane four dichotomously-branched needle-like leaves



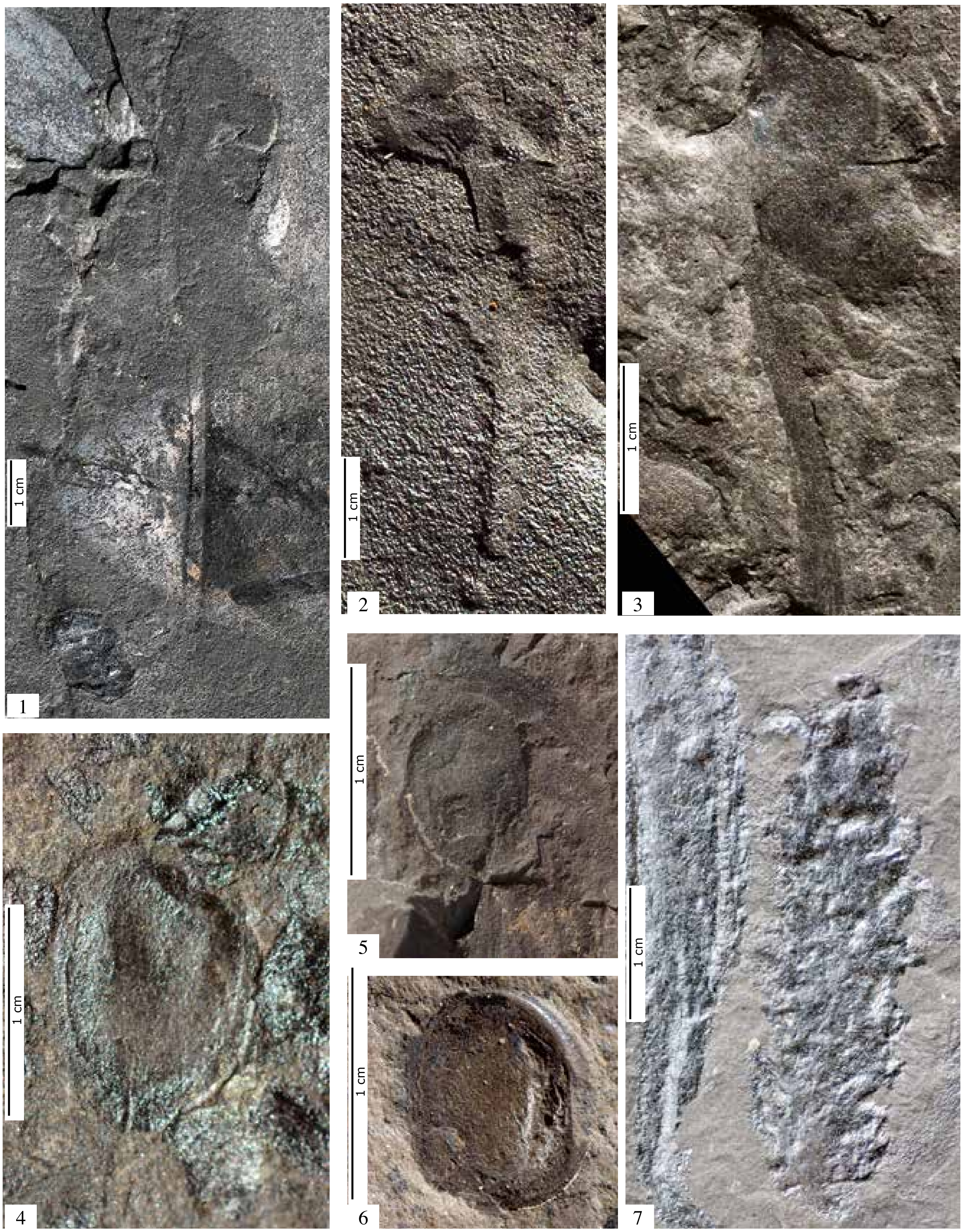
***Ginkgoites pohli.* Leaves. Early Permian (Kungurian)**

1. Leaf with two seeds on the upper right side and one on the left side (TRE 45, designed holotype); 2. Leaf (TRE 5); 3. Detail of a leaf with repeatedly dichotomizing veins (TRE 239); 4. Basal spur shoot with collar (TRE 87); 5. Mature leaf with a basal spur shoot (TRE 86, paratype). All Tregiovo-Trentino; Coll Valentini (MUSE, Trento), Coll. Wachtler (Dolomythos-Museum, Innichen)



***Ginkgoites pohli*. Leaves. Early Permian (Kungurian)**

1-2. Model-like leaf-character (TRE 544, TRE 489); 3. Strangely branching ginkgophyta, characteristic for the Tregiovo-Formation (TRE 242); 4. Several ginkgo-leaves on a slab. In the center two ovules.(TRE 233). All Tregiovo-Trentino; Coll Valentini (MUSE, Trento), Coll. Wachtler (Dolomythos-Museum, Innichen)



***Ginkgoites pohli*. Ovules/Seeds and pollen-organs. Early Permian (Kungurian)**

1-3. Juvenile ovules/seeds attached to their leaves (TRE 45, TRE 124, TRE 233); 4-6. Isolated mature seeds (TRE 589, TRE 220, TRE 590); 7. Suggested pollen cone (TRE 401); All Tregiovo-Trentino; Coll Valentini (MUSE, Trento), Coll. Wachtler (Dolomythos-Museum, Innichen)

with the middle one more segmented. In the other line like Early Permian *Ginkgoites pohli* from the Alps the needle-like leaves originate from a short petiole, but fork irregularly and not on one level, but screwing in the height several times. The leaves of *Ginkgoites pohli* are more rudimental and varies from needle-like resembling some Devonian Progymnosperms with their irregularly furcating leaves till basically fan-shaped, the fructifications, especially their seeds were just fully evolved and gingko-like (Perner & Wachtler, 2015).
In that *Ginkgoites pohli* has also resemblances with the archaic cycadophyta *Wachtleropteris valentinii.* But they are distinct from different ovulate organs, as well as male cones. Isolated *Ginkgoites*-needles from Tregiovo can otherwise be confused with the leaves of the most primitive *Pinus* conifers, *Férovalentinia.* Interestingly, the attached ovules/seeds, as well as the spur shoots are better preserved in the Early Permian Tregiovo-site, as in other Permo-Triassic-Jurassic localities of the world. In a relatively short time Early Permian *Ginkgoites pohli* change till the Late Permian *Ginkgoites murchisonae* to a fan-shaped foliage, a feature which they are perfecting more and more up to today's *Ginkgo biloba.*

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Coniferophyta

The conifers belong to the most frequent flora elements of Tregiovo, but interestingly there are conspicuous differences between the lower and upper layers. Coniferophyta such as the Araucarian-like ***Ortiseia daberi*** (documented by their characteristic one-seeded scales) and Abietoidea-ancestor ***Majonica ambrosii*** (with its winged seed scales) are present everywhere. In addition, in the lower sediments we encounter the more seeded conifer ***Voltzia vialli,*** whereas in the upper part (above the bridge) we have interesting Pinus-ancestors like ***Férovalentinia cassinisi***, characterised by its five-needled bundles or ***Férovalentinia angelellii*** with its irregularly forking groupings of two till three needles.

Araucaria-ancestors

The Araucariaceae evolved from the Artinskian till the Kungurian in the Dolomites considerably and began to dominate the landscape, a development that found its climax in *the late Permian. Especially Ortiseia daberi* can be largely encountered in all layers of the Tregiovo-Formation.

Ortiseia daberi (WACHTLER, 2012)

2012 *Ortiseia leonardii* WACHTLER, p. 12-14
2013 *Ortiseia daberi* WACHTLER, p. 92-95

Holotype

TRE 182, Museum of Natural Science MUSE, Trento; Others: Coll. Wachtler, Coll. Valentini; Dolomythos-Museum, Innichen

Etymology

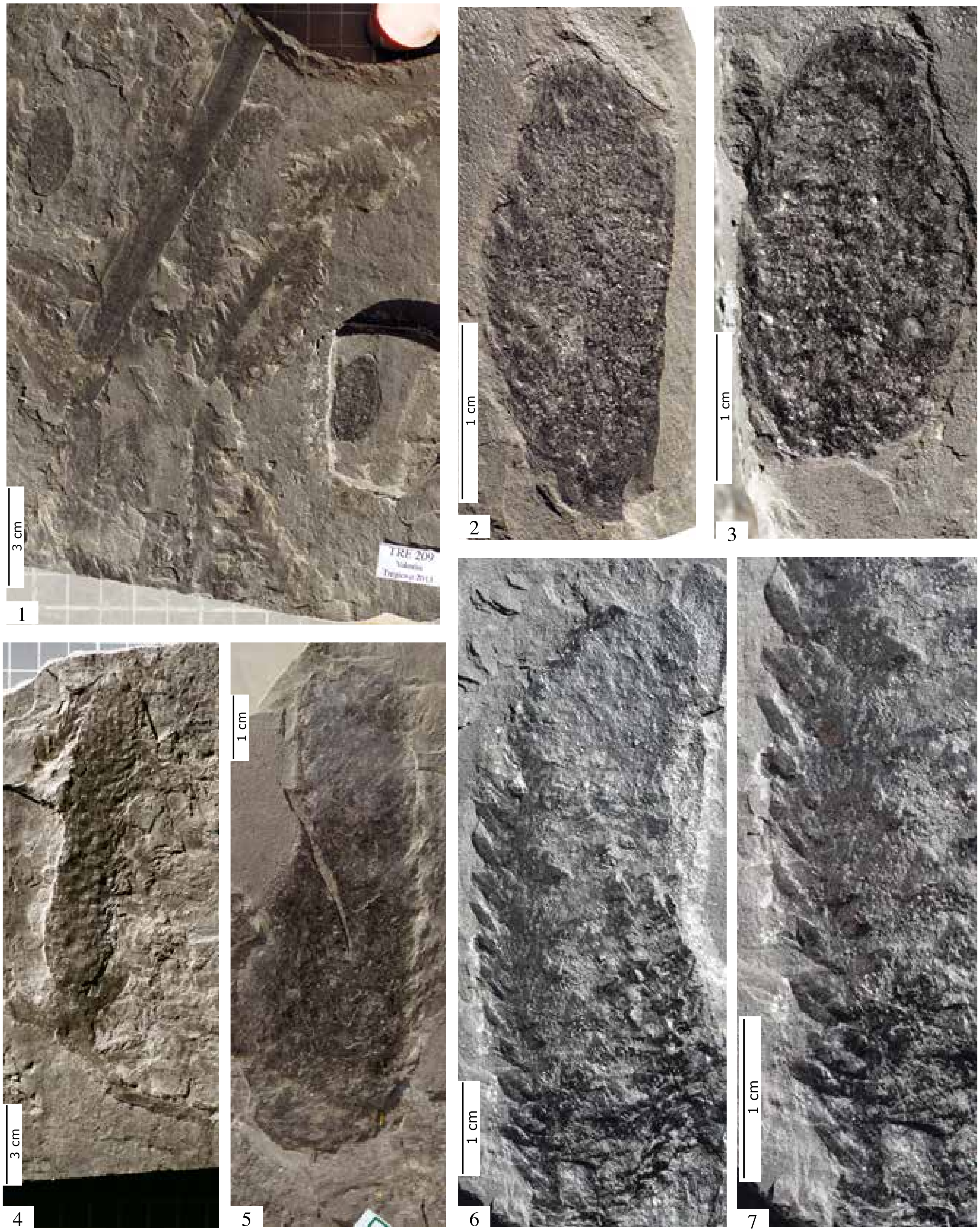
Named after the German palaeobotanist Rudolf Daber, former director of the Museum für Naturkunde Berlin (Natural history Museum, Berlin).

Description

Branchlets and leaves: Shoots pinnately branched, generating hardly overlapping leaves (TRE 500, TRE 182, holotype). Foliage fleshy, with an acute to obtuse apex, leaf base slightly contracted. Nearly invisible grooves crossed the entire foliage whereas in the middle some median emargination

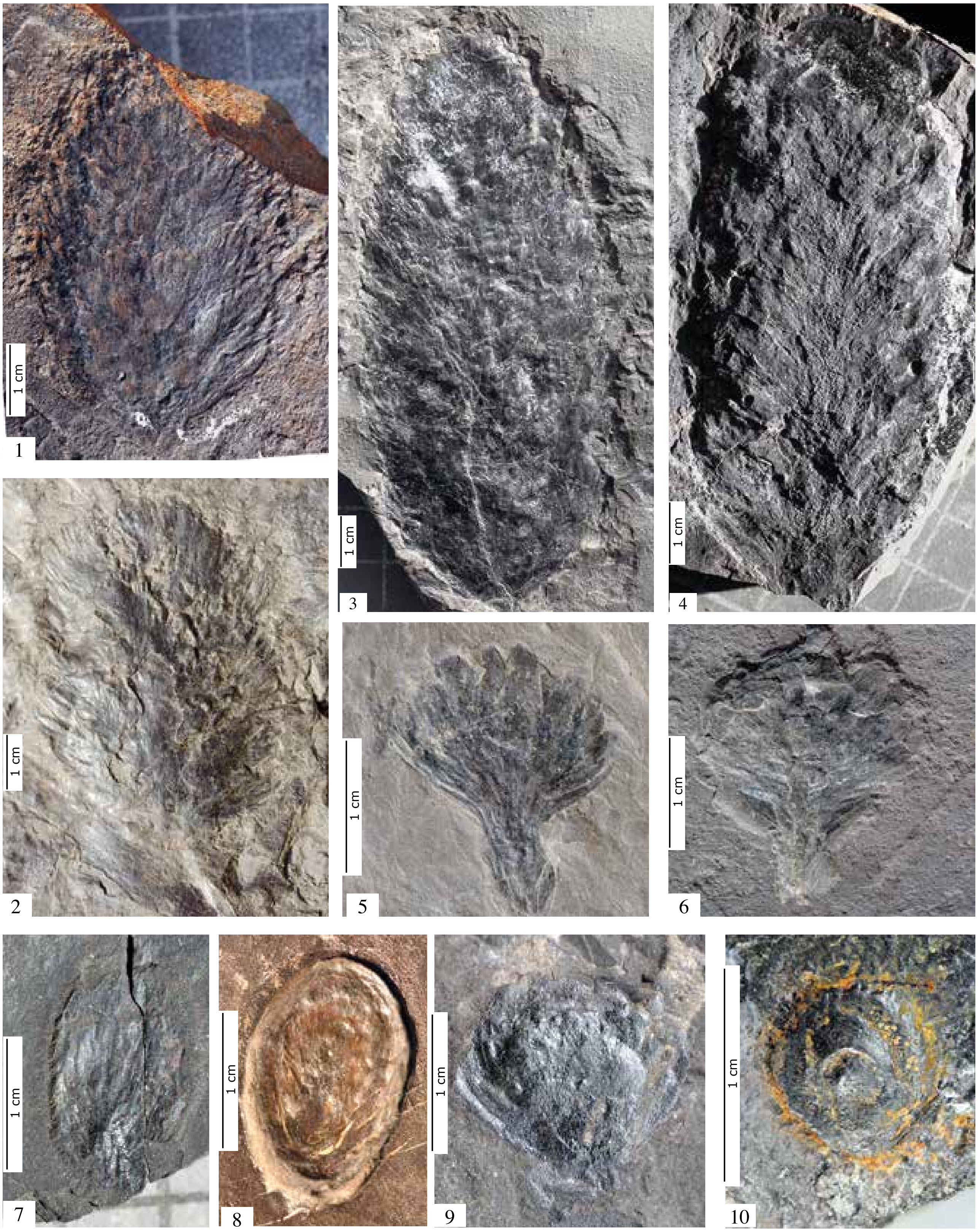
Araucarian-like one seeded *Ortiseia daberi* (Early Permian, Kungurian)

1. Mainly complete branchlet (TRE 500, Coll. Wachtler); 2. Part of a branchlet, (TRE 182, designed holotype, Coll. Valentini); 3. Apical part of a branchlet with juvenile shoot (TRE 564, Coll. Wachtler); 4. Isolated leaves (TRE 573); 5. Leaf evidencing abscission details (TRE 146); 6. Single leave upper side (TRE 270, All Coll. Wachtler); 7. Part of a twig (TRE 116); all Tregiovo Le Fraine, Val di Non.



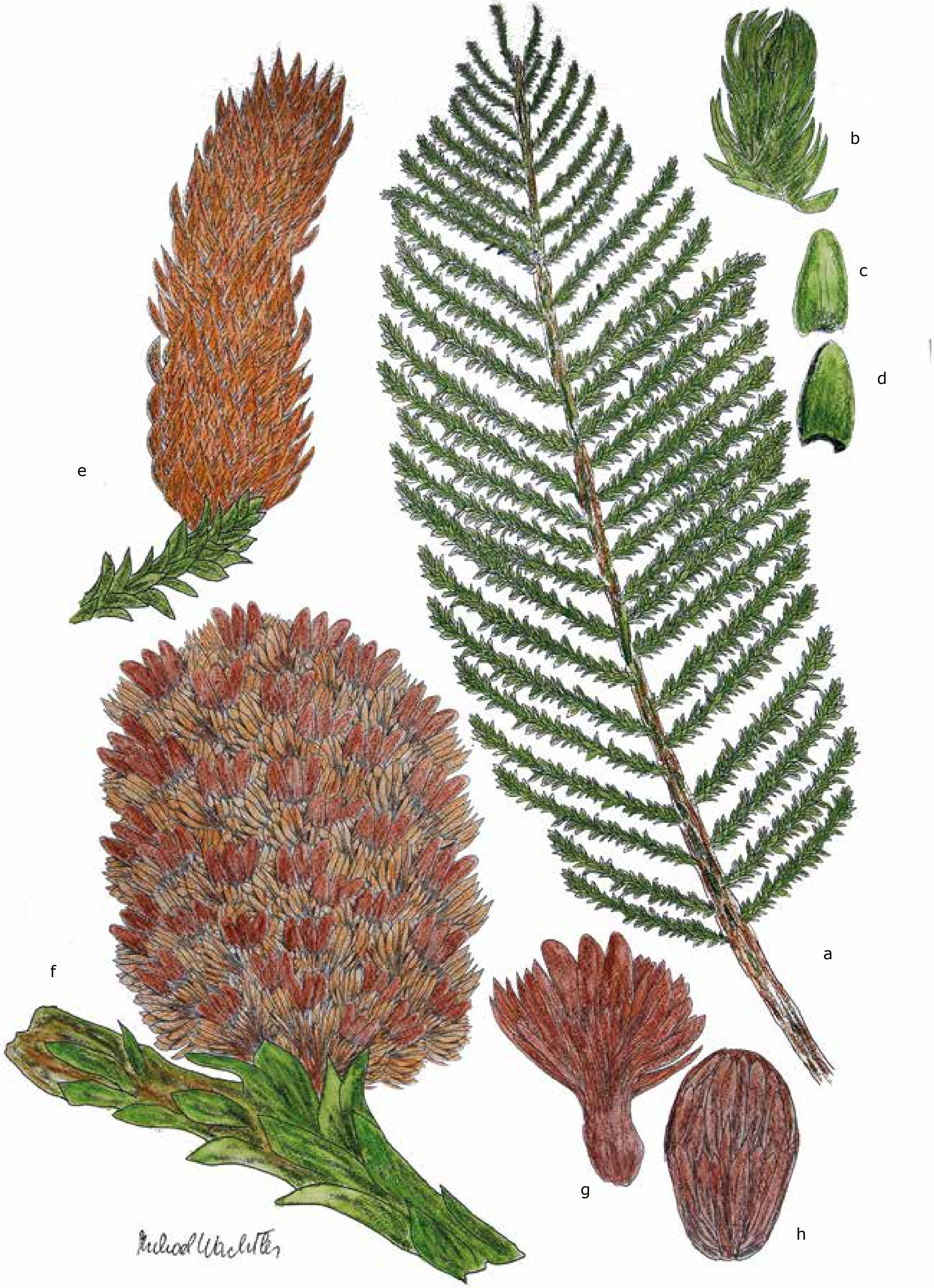
Ortiseia daberi. **Araucaria ancestor. Male cones (Early Permian, Kungurian)**

1-3. Slab with two male cones and *Ortiseia*-twigs (TRE 209); 4. Male cone attached on a branchlet (TRE 49); 5. Male cone (TRE 342); 6-7. Adult male cone, ready to release the pollen and detail of the microsporophylls (TRE 235); all Coll Wachtler, Coll. Valentini, Tregiovo Le Fraine, Val di Non.



***Ortiseia daberi*. Araucaria ancestor. Cones and seed scales (Early Permian, Kungurian)**

1-2. Juvenile female cones, attached on the branchlet (TRE 118 Coll. Wachtler, TRE 585, coll. Valentini); 3-4. Adult female cones (TRE 197, TRE 229, Coll. Wachtler); 5-6. Isolated seed scales with sterile protective leaflets abaxial side (TRE 526, Coll. Valentini, TRE 605, Coll. Wachtler); 7-10. Ovuliferous seed scales (TRE 259, TRE 384, TRE 141, TRE 360, coll. Wachtler); all Tregiovo Le Fraine, Val di Non.



***Ortiseia daberi*. Reconstructions (Early Permian, Kungurian)**

a. Mainly complete branchlet (TRE 500); b. Apical part of a branchlet with juvenile shoot (TRE 564); c. Isolated leaf, abaxial side (TRE 146); d. Single leave adaxial side (TRE 270); e. Male cone (TRE 235); f. Female cone (TRE 585, TRE 197, TRE 229); g. Seed scale, abaxial side (TRE 526, TRE 605) h. Seed (TRE 259, TRE 384) is barely visible. Single *Ortiseia*-leaves are normally 1–2 cm long and at the base up to 1 cm wide (TRE 573, TRE 146, TRE 270).

Male cones: Around a central axis sprout numerous spirally arranged and overlapping microsporophylls. Young cones are characterised by microsporophylls with longer narrowing appendixes. Adult cones, slender at least 10 cm long and 3.5 cm wide (TRE 342, TRE 235) and shortly bracted

Female cones: Cones from round bodied till elongated, at least 10 cm long and 5 cm wide (TRE 118, TRE 585, TRE 197, TRE 229). They are composed of spirally arranged seed scales that generate on their inner side one ovuliferous seed. Minute, elongated, usually pointed to oblate sterile leaves coating densely the outer side of the fruit-blade. Rounded 1 cm big nutlike ovule/seed positioned approximately on the centre of the scale. Scales shed entirely at maturity (TRE 526, TRE 259, TRE 384, TRE 141, TRE 360).

Taxonomic notes

Although Artinskian *Ortiseia dasdanai* and Kungurian *Ortiseia daberi,* both pertaining to the Early Permian geological age, but having a time difference of about 10 million years have a different foliage structure; their fertile parts, especially the ovulate cones are similar. The difference in the leaves can be explained probably by a climate change to more humid and benign weather in the later Early Permian. Effectively we encounter in the Kungurian of the Dolomites for the first time cycads, as well as ginkgoales, although the ferns are missing, with the exception of some rare skeletonized *Sphenopteris*-fern or isolated *Lepidopteris* or *Autunia* seed-ferns. Therefore, the Kungurian flora has more in common with the late Permian, than the Artinskian.

The conifer symbiosis composed of Abietaceae *Majonica, Voltzia,* Araucariaceae *Ortiseia, Pinus*-progenitors *Fèrovalentina* can be followed uninterruptedly over a long time span. The single-seeded *Ortiseia* closes one chapter in the understanding of modern Araucariaceae. The upright standing male and female cones and the arrangement and appearance of the twigs and leaves can be considered typical of all Araucariaceae. The numerous, sterile leaflets that in the Permian densely covered the seeds merged in the following eons and enclosed them densely, as in the Araucaria of today.

Abietoideae-ancestors

When I described in 2012 the conifer *Cassinisia ambrosii* (Wachtler, 2012) I connected it with *Cassinisia orobica* (Kerp et al., 1996) from the nearby Orobian Alps. But just in this publication I stated that "*Due to their poorly preserved fragmented parts and the impossibility of stating if some of the leaf-fragments belong to more conifer species, further analysis or comparisons are necessary*". Now enough material was recovered from Tregiovo to establish that this conifer can better and more logically be placed in the Permian group of Abietaceae-ancestors, the Majonicaceae. Because research has to resolve problems and not to create I propose to change the name for this conifer with once lobed scales bearing two winged seeds in *Majonica ambrosii*.

Majonica ambrosii comb. nov. (WACHTLER, 2012, 2021)

1996 *Cassinisia orobica*, KERP ET.AL. p. 67-68
2012 *Cassinisia ambrosii*, WACHTLER, p. 17-20
2013 *Cassinisia ambrosii*, WACHTLER, p. 96-100

Etymology

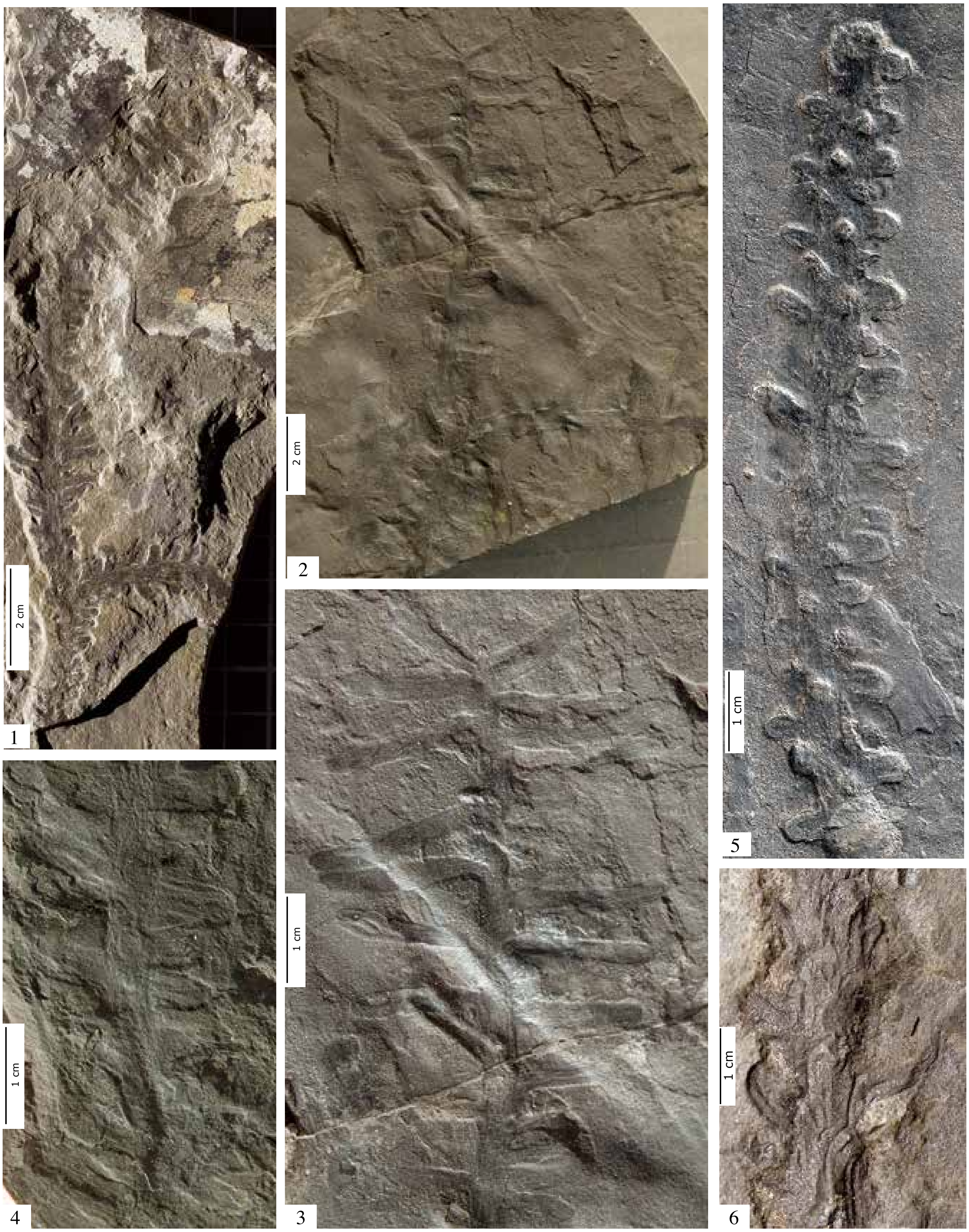
Named after Francesco Ambrosi (Borgo Valsugana, 1821–Trento, 1897), herdsman, autodidact, who increased botanic and palaeontologic knowledge about his territory. Curator of the city museum of Trento, he left an ample naturalistic collection to the Natural History Museum. Additionally, he was a condemned patriot under the Austrian empire.

Holotype

TRE 100; **Paratype** TRE 109; Repository: Museum of Natural Science MUSE, Trento, Other: Coll. Wachtler, Coll. Valentini; Dolomythos-Museum, Innichen

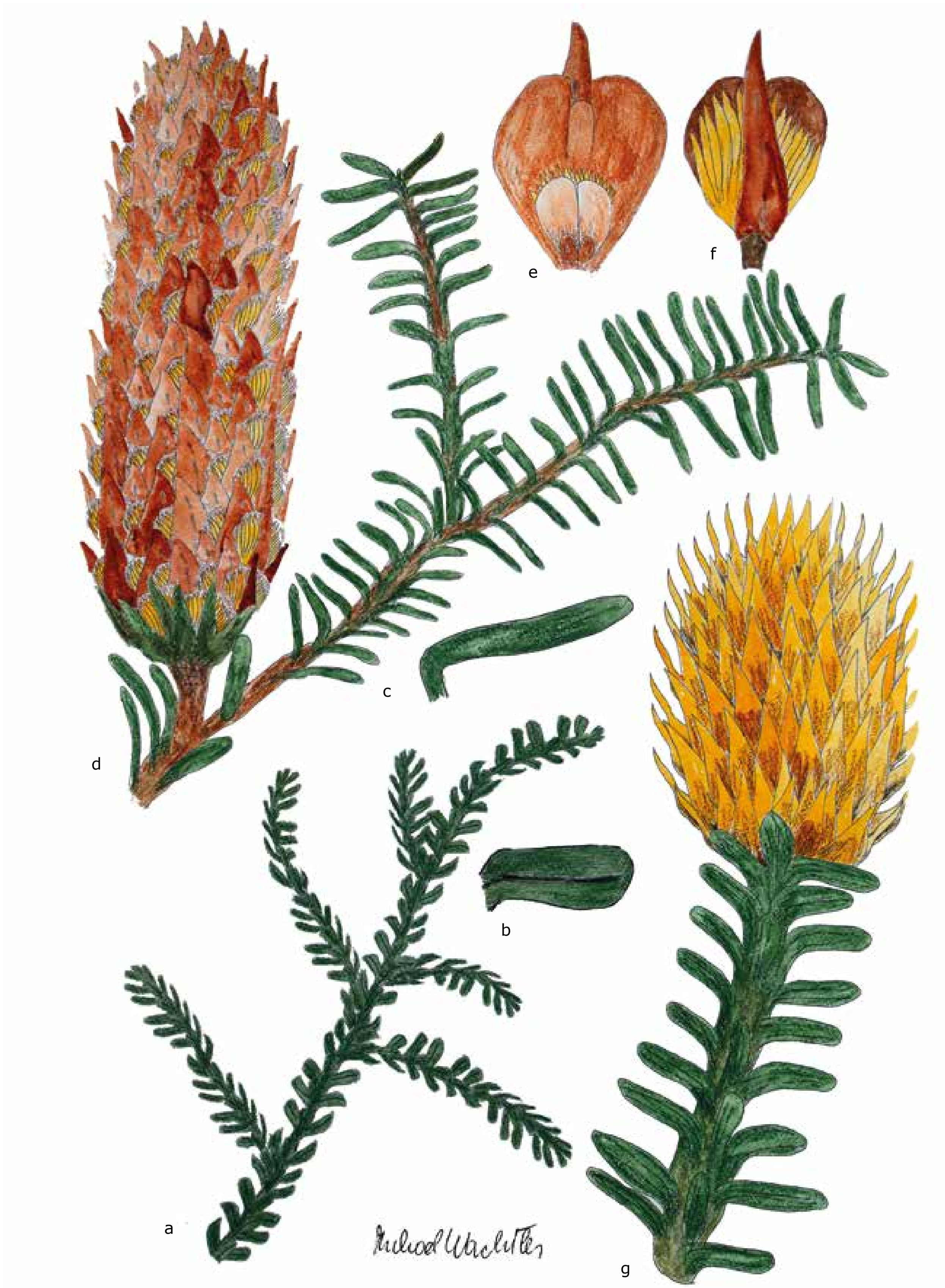
Description

Branchlets and leaves: Twigs pendulous and irregularly diverging in a plagiotropic manner (TRE 190, TRE 100, holotype). The foliage is leathery, sometimes extremely xeromorphic, ending in a square-rounded apex (TRE 660, TRE 171, TRE 105). Usually the leaves are 0.7–1 cm long, and 0.2–0.3 cm wide, but there also exists heterophyllous foliage reaching about 2 cm (TRE 190). The leaves are equally wide for the whole length. One ore two fibrovascular canals expand



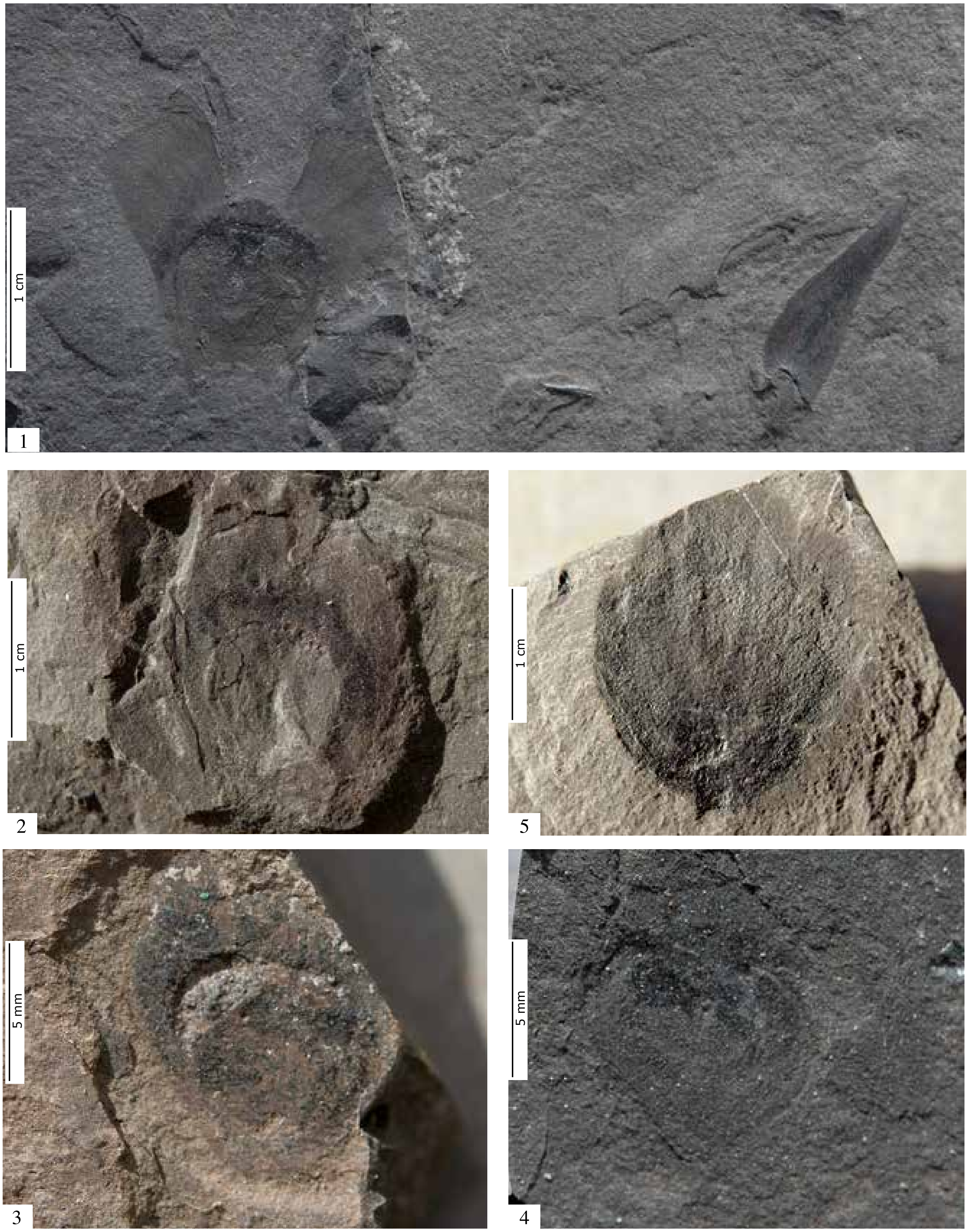
***Majonica ambrosii*. Male and female cones ((Early Permian, Kungurian))**

1. Mostly complete twig (TRE 100 Designed holotype, Coll. Valentini); 2-3. Twig with long needles (TRE 190, Coll. Wachtler-Dolomythos); 4. Shot-fragment with rounded needles (TRE 660, Coll. Wachtler); 5. Leathery branch-fragment (TRE 171); 6. Extremely xerophytic arrangement of leaves (TRE 105); all Tregiovo Le Fraine, Val di Non



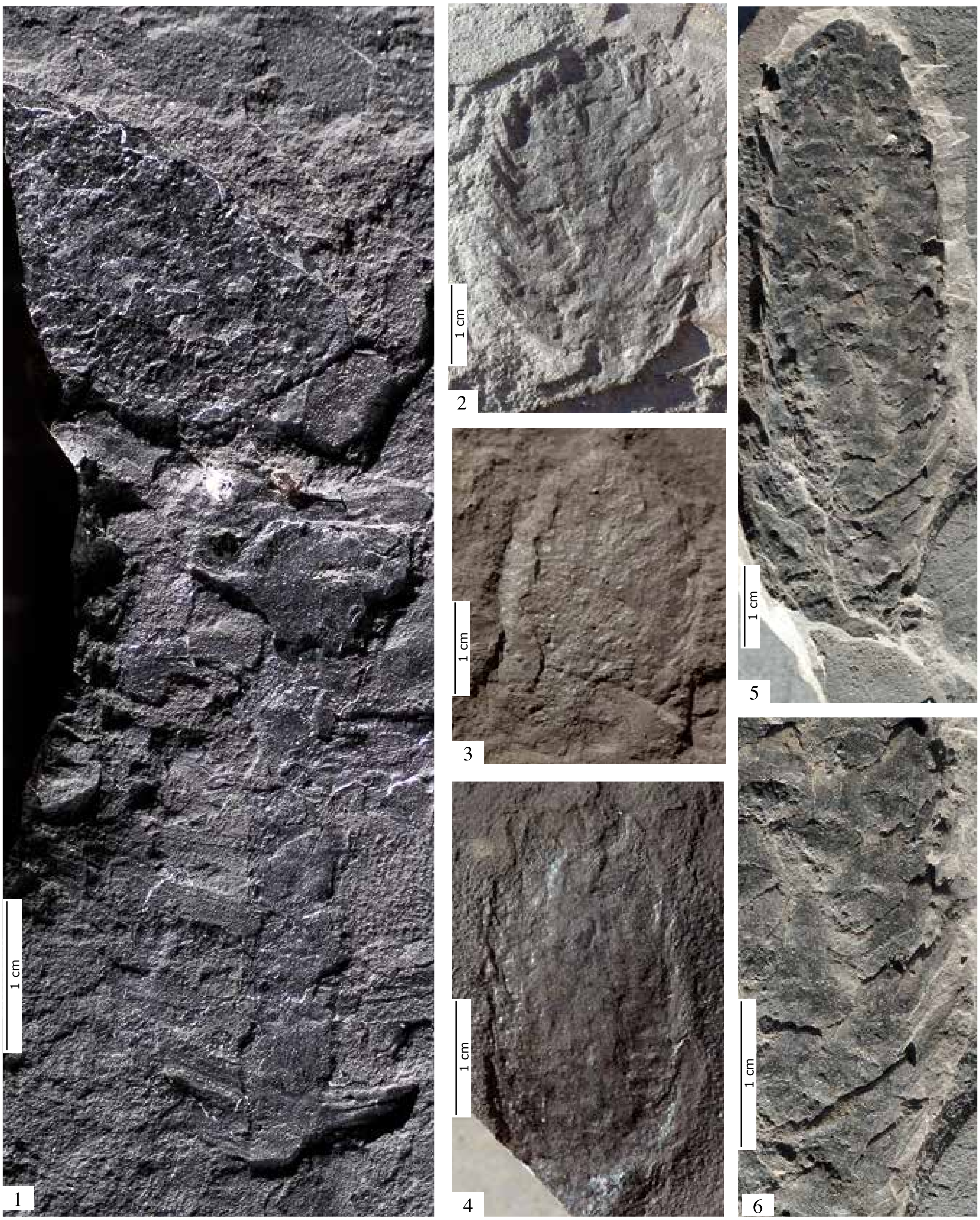
***Majonica ambrosii*. Male and female cones (Early Permian, Kungurian))**

a. Branchlet with xerophytic leaves (TRE 100); b. xerophytic leaf (TRE 171); c. Leaf (TRE 190); d. Female cone (TRE 628); e. Seed scale adaxial side with two winged seeds (TRE 587); f. Seed scale abaxial side (TRE 259); g. Male cone (TRE 158)



Majonica ambrosii. Seed scales (Early Permian, Kungurian)

1. Seed scale an isolated bract (TRE 587); 2-4. Seed scales (seed bearing side) (TRE 594, TRE 414, TRE 575); 5. Seed scale reverse side (TRE 259); all Tregiovo Le Fraine, Val di Non; Coll. Wachtler, Dolomythos-Museum.



Majonica ambrosii. Male and female cones (Early Permian, Kungurian))

1. Male cone connected with a branchlet (TRE 158, Coll. Wachtler - Dolomythos); 2-4. Complete male cones (TRE 629, TRE 140, TRE 276, Coll. Wachtler); 5-6. Juvenile female cone with detail of the elongated protection bracts (TRE 628 Coll. Valentini); all Tregiovo Le Fraine, Val di Non.

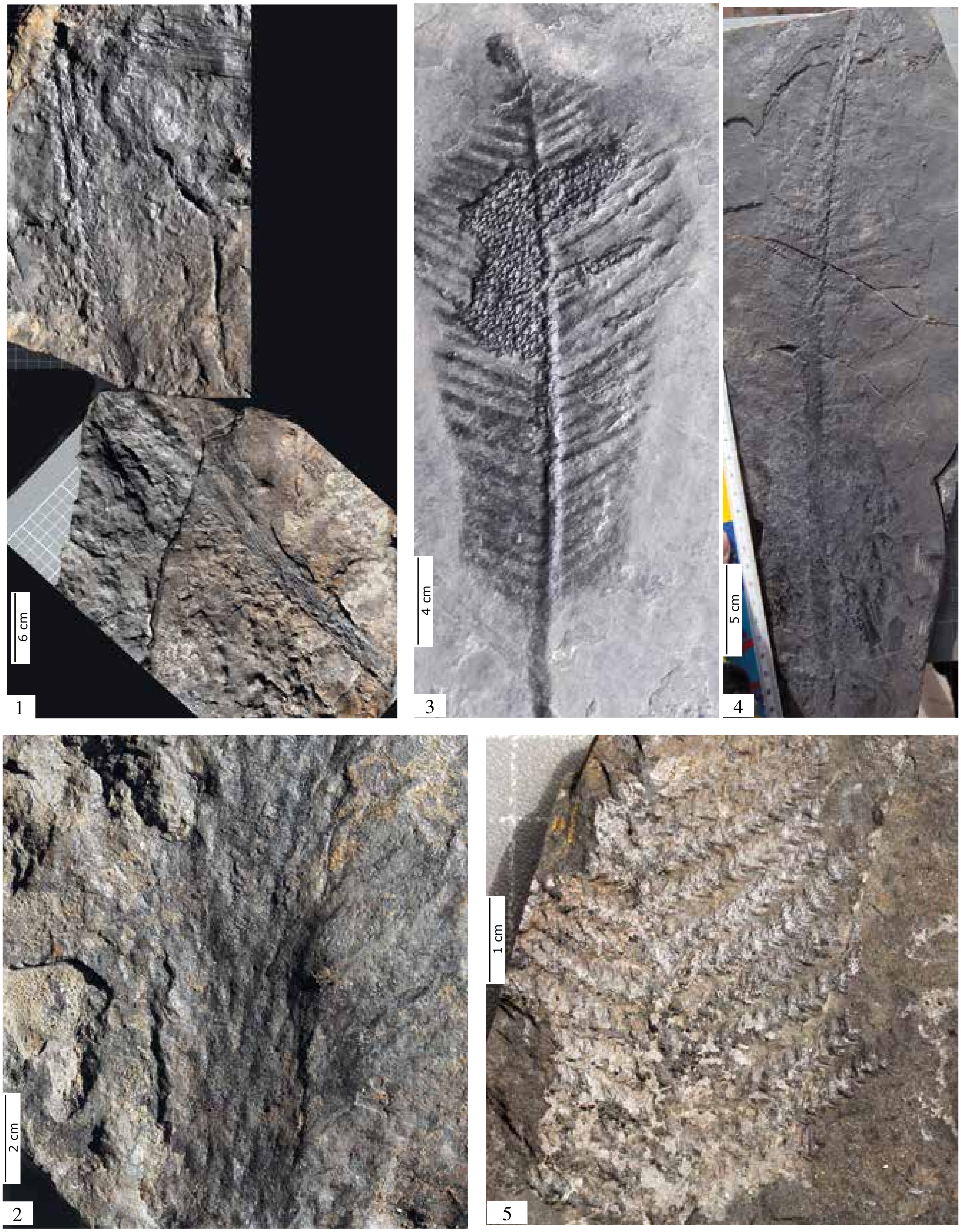
through almost the entire leaf. The needles are slightly decurrent and do not usually overlap each other; they sprout laterally to curve easily upwards, only sometimes they are slightly falcate, from the whole base of the branchlet.
Male cones: They are bulbous till little prolonged, from 2.5–3.5 cm and 1.5–2.0 cm wide (TRE 158, TRE 629, TRE 140, TRE 276). The peltate microsporophylls end in a modestly visible bract.
Female cones: Entire cones are seldom (TRE 628) about 7 cm long and 2 cm wide. They usually decay at maturity. The scale projecting bract is an important distinguishing feature. Two-lobed till completely merged seed scales can be found isolated in the sediments (TRE 587, TRE 594, TRE 414, TRE 575). The outer side of the scales is additionally to the long bract distinct by a fair amount of sterile micro-leaves. The inner seed side holds basally the two alate seeds, covering almost two thirds of the scale.

Taxonomic notes

Conifers with cones that were characterised by two-winged seeds are recorded from the Carboniferous–Permian border on (*Wachtlerina bracteata*) (Perner & Wachtler, 2013). They split relatively fast in two distinct lines: the Middle-European—distinguished till the Early Permian by symmetrically arranged combs—and the "Alpine" line with their pendulous plagiotropic branchlets like today's Abietaceae (*Majonica suessi* (Artinskian), *Majonica ambrosii* (Kungurian), *Majonica clementwesterhofae* and *Majonica alpina* (Wuchiapingian). Moreover, their pollen cones diminished in size from the early Permian on, but remain considerably larger than today's.
Nevertheless, it is possible to draw parallels with the modern fir trees (Abies), conifers that dominate many landscapes of the Northern hemisphere today. Their woody and slender seed cones are composed of numerous, spirally arranged ovuliferous scales that bear two winged seeds on their upper surface that are only attached at the base. Certain living species such as the bristlecone fir (*Abies bracteata*) are characterised by sterile cover bracts that extend far beyond the ovuliferous scales being in that identical with *Majonica ambrosii.* Only the bilobed scale merged from the Permian till the present, that today the dichotomy of the seed scales is hardly recognizable any more. It is certain that winged seeds had formed by the beginning of the evolution of conifers, and that the ability to spread seeds carried by the wind over long distances became a model for success. This direction line was no less advanced than the nuts offered by other conifers to animals as food. We can only speculate, but a series of distinct characteristics indicate that on the Carboniferous–Permian border Araucariaceae and Abietoidaceae were still so closely related as to give some difficulties in telling them apart.

More seeded Early Permian conifer-scales

Due to the scarce material, it took decades to recognize the real structure of the Voltziaceae, being so frequent between the Permian and the Triassic on the Euramerican landmass. The most important feature was not the considerably varying foliage-type, but their female cones and especially their fertile scales. The Voltziaceae hold in comparison with other conifers normally three till five (or more) elliptic ovules/seeds on each scale distributed on each distinct fertile lobe. Accompanying sterile protective leaves especially on the outer side were normal. The hanging ovules were usually small-sized (only in *Pseudovoltzia* (Brandt, 1997) they were bigger) and evidence a clawing micropyle on the hanging basal side. They were connected on the apical side by an abscission point, that can often be detected on the upper side of the scale-lobes.
There were also found in the Permian, as well as in the Triassic scales with more than three seeds. In the Middle Triassic *Swedenborgia*, as well as *Aethophyllum* hold five seeds (Wachtler, 2016). In the Early Permian *Thuringiostrobus meyenii* was characterized by six or more seeds. Additionally, from the former Angara-continent (today's Ural region/Russia) also interesting multi-seeded and small-sized cones were recovered *(Taxodiella bardaeana*).
The Voltziaceae and their multi-lobed scales can be seen in a direct evolution-line beginning on the Carboniferous-Permian border with *Voltzia niederhauseni* (Perner & Wachtler, 2015), prosecuted by the Alpine tribes Artinskian *Voltzia triumpilina*, Kungurian *Voltzia viallii* till Late Permian *Voltzia sjerpii* (Clement-Westerhof, 1987) or *Pseudovoltzia liebeana* from the German Zech-



***Voltzia viallii*. Twigs (Early Permian, Kungurian)**

1-2. Entire adult twig and detail of the central axis (TRE 50, designed holotype, Coll. Wachtler, MUSE Trento); 3. Juvenile twig (TRE 53, Paratype, Coll. Valentini, MUSE, Trento); 4. Branchlet (TRE 273, Coll. Wachtler); 5. Banchlet with detail of the needles (TRE 266, Coll. Wachtler); all Tregiovo-Le Fraine, Val di Non.

stein. They overpass the Permo-Triassic crisis without mayor changes and were present in Europe with many sub-species just in the Anisian like *Voltzia rietscheli* or *Voltzia agordica* arriving till the Late Triassic (Carnian) with *Voltzia carinthica* (Wachtler 2016).

***Voltzia viallii* nov. comb. (WACHTLER, 2012, WACHTLER 2021)**

2012 *Alpia viallii, WACHTLER,* p. 23
2013 Walchia vialli, WACHTLER, p. 103-105
2013 *Dolomitia nonensis,* p. 100-102

Etymology

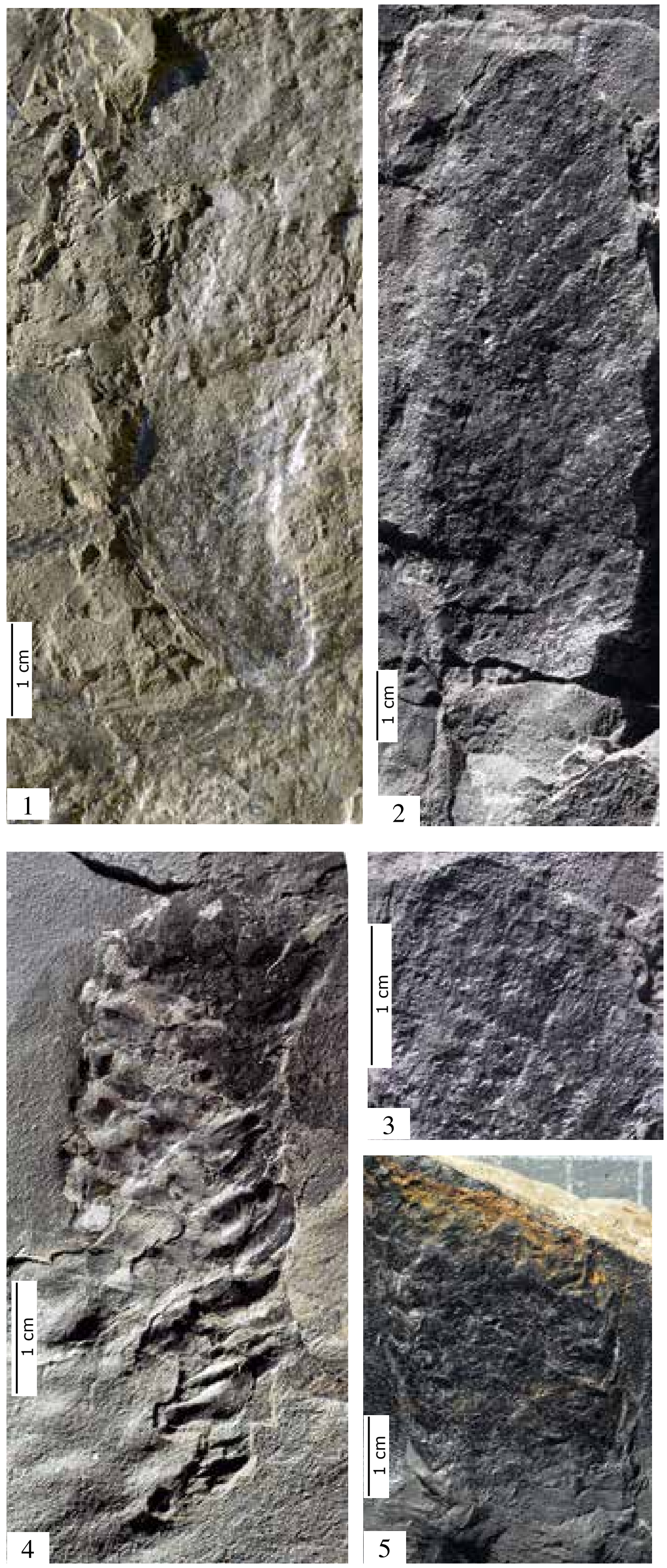
Named in honour of Vittorio Vialli (Cles 1914–Bologna 1983), an Italian geologist and palaeontologist, who was deported under the Nazi regime to a concentration camp. There, he took innumerable pictures undercover, which appeared in a famous book (*"Ho scelto la prigionia"—I chose the prison)* following the war.

Holotype

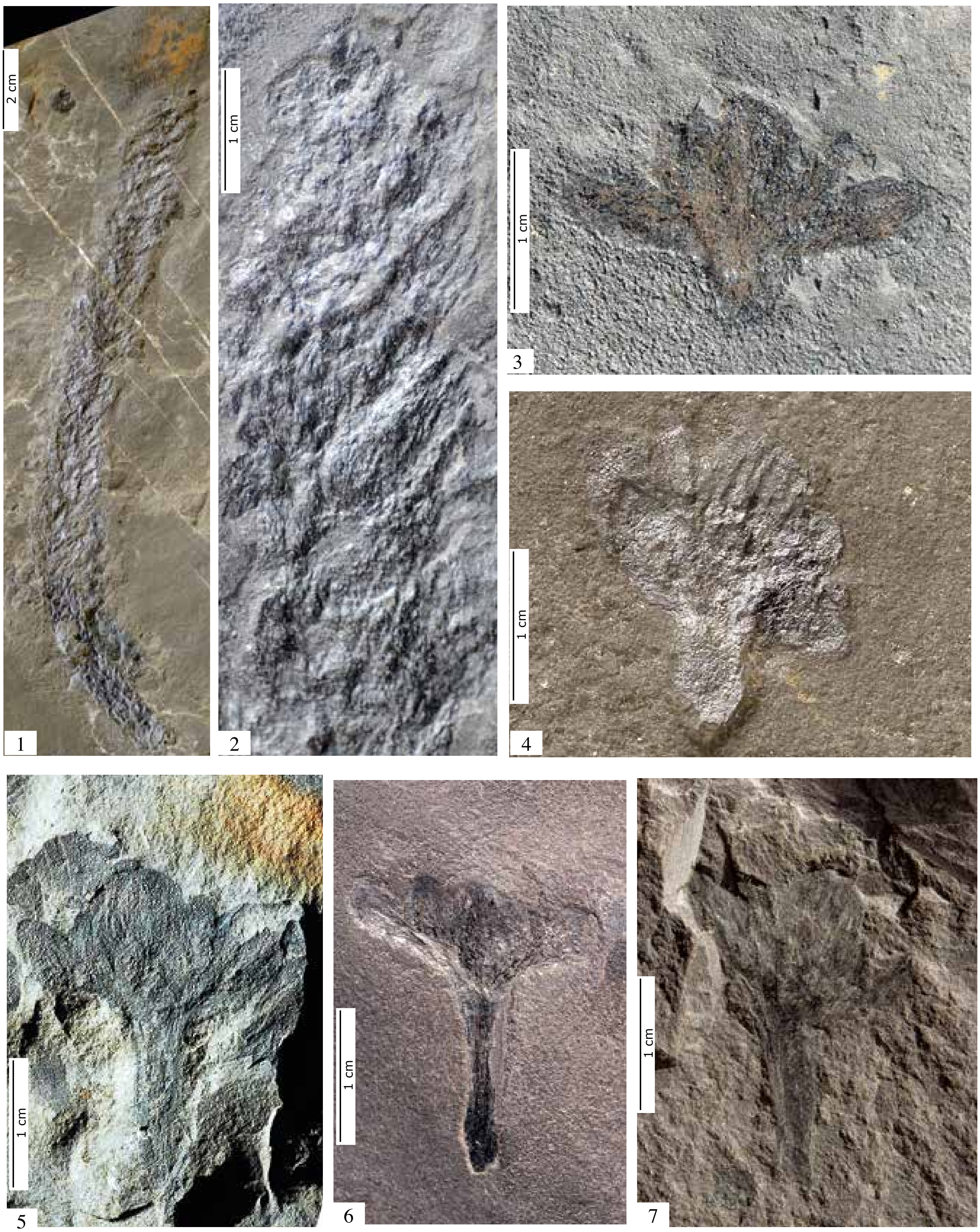
TRE 50; **Paratype** TRE 53; TRE 335 (Scale) Repository: Museum of Natural Science MUSE, Trento, Other: Coll. Wachtler, Coll. Valentini; Dolomythos-Museum, Innichen

Description

Branchlets and leaves: Protruding, slender bipinnate twigs, densely covered with small-sized, falcate only sometimes overlapping needles. Foliage maximal 1 cm long, sharply pointed at the apex. Leaves on the main trunk till 5 cm long and lanceolate (TRE 50, TRE 53, TRE 273, TRE 266).
Male cones: Usually 5–7 cm long, 1.5–2 cm wide, ovoid to elongated. Microsporophylls with short bracts (TRE 411, TRE 226).
Female cones: Slender, almost 15 cm long (TRE 408), 2–3 cm wide. Ovuliferous seed-scales provided with a fair amount of protection leaves and one flat three-lobed apically rounded fertile scale. The scales reached a length from up to 1.5 to 2.0 cm and a width from 1.4 to 1.8 cm and are bilaterally symmetrical with a slightly bigger middle lobe. The axis is sometimes very long in proportion to the rest of the scale. The accompanying sterile leaves are minute, with a pointed apex (TRE 176, TRE 335, TRE 88, TRE 83, TRE 387, TRE 611).



***Voltzia viallii*. Male cones (Permian, Kungurian)**
1. Male cone in connection with branchlet (TRE 411, Coll. Valentini); 2-3. Male cone and detail of the short bracted microsporophylls (TRE 226, Coll. Wachtler); 4-5 Male cones (TRE 148, TRE 121, Coll. Wachtler); all Tregiovo-Le Fraine, Val di Non.



***Voltzia viallii*. Cones and seed scales (Early Permian, Kungurian)**

1-2. Female cone and detail of the seed scales (TRE 408); 3-4. Seed-scales adaxial view with the place of the ovule attachment. 15 mm x 10 mm (TRE 335, TRE 88); 5-7. Seed scales abaxial view evidencing well the sterile microleaves (TRE 83, TRE 387, TRE 611); Coll. Wachtler, Coll. Valentini; all Tregiovo Le Fraine, Val di Non.

Taxonomic notes

When I described this conifer in 2012, based on branchlet with incurved subtle needles, connecting seed scales were missing. When the first flat three-fingered apically rounded seed scales were recovered—based on Clement-Westerhof's (1987) term for Voltzia seed scales, I introduced the new species-name *Dolomitia nonensis* (Wachtler, 2012). But due to the fact that they can well be connected with *Voltzia viallii* branchlets and male cones, this name proved to be superfluous. The foliage-type of the Voltziaceae varied considerably over the Permo-Triassic. In the Early Permian, as well as in Artinskian *Voltzia triumpilina*, and also Kungurian *Voltzia viallii* the branchlets were symmetrical pinnate and spread almost horizontally or slightly oblique whereas the needles were usually small-sized and dwarfish. Beginning from the Late Permian, especially with *Pseudovoltzia liebeana* the leaves and twigs changed to an irregular habitus, which can seen over the whole Triassic (*Voltzia rietscheli, Voltzia agordica, Voltzia dolomitica, Voltzia carinthica*) (Wachtler, 2016). The female cones were in the Early Permian huge but slender reaching 10–15 cm or more. From the Late Permian on they diminished considerably. A feature were their shed seed scales after maturity, so that sometimes whole scale lawns can be found in the sediments. The pollen cones were medium-sized, usually equipped with a short bract and resembled in their apically and dorsiventrally hanging pollen sacs the Araucariaceae.

Early Permian (Kungurian) Pinoidea ancestors

In 2015, I described a new genus of Permian conifers from the Kungurian locality Tregiovo that most resembled today's Pinoideae, thus naming them *Valentinia*, I honoured Féro Valentini, who discovered the fossilised plants at the Kungurian site Tregiovo in the Val di Non (Dolomites, Northern Italy) and decided after retirement to dedicate his further life to science.

Soon afterwards it was recognized that this name was treated as a taxonomic synonym of a Liliaceae, although being not more in use because replaced by the genus *Maianthemum* (Fabricius, 1763, Heister, 1730), but being still valid. Therefore, I proposed to change the illegitimate fossil conifer name *Valentinia* to *Férovalentinia* (Wachtler, 2018). It honours in the same way Féro Valentini. Included are the species: *Férovalentinia angelellii* distinguished by its shorter irregularly forking needles grouped in bundles of one, two or three and *Férovalentinia cassinisi* holding five long needles per bundle both described by Michael Wachtler, 2015. Of course also the genus name *Férovalentinia wachtleri* from the Early Permian (Artinskian) Collio-Formation in the Italian Alps, described by Thomas Perner (2015) has to be changed. Till now *Férovalentinia wachtleri* represents the oldest known ancestor of the Pinoidea, based less to its female and male cones, that are similar to the Kungurian species, but due to its archaic needles, that do not form geometrically definable bundles.

Férovalentinia angelellii (WACHTLER, 2015

2015 *Valentinia angelellii,* WACHTLER, pp. 89-90

Etymology

Named after Francesco Angelelli, scientific curator of the Palaeontological collections of ISPRA (Institute for Environmental Protection and Research), Rome, who sustained the researches at Tregiovo.

Holotype

TRE 480; **Paratype** TRE 548 (female cone); TRE 488 (Male cone), Repository: Museum of Natural Science MUSE, Trento, Other: Coll. Wachtler, Coll. Valentini; Dolomythos-Museum, Innichen

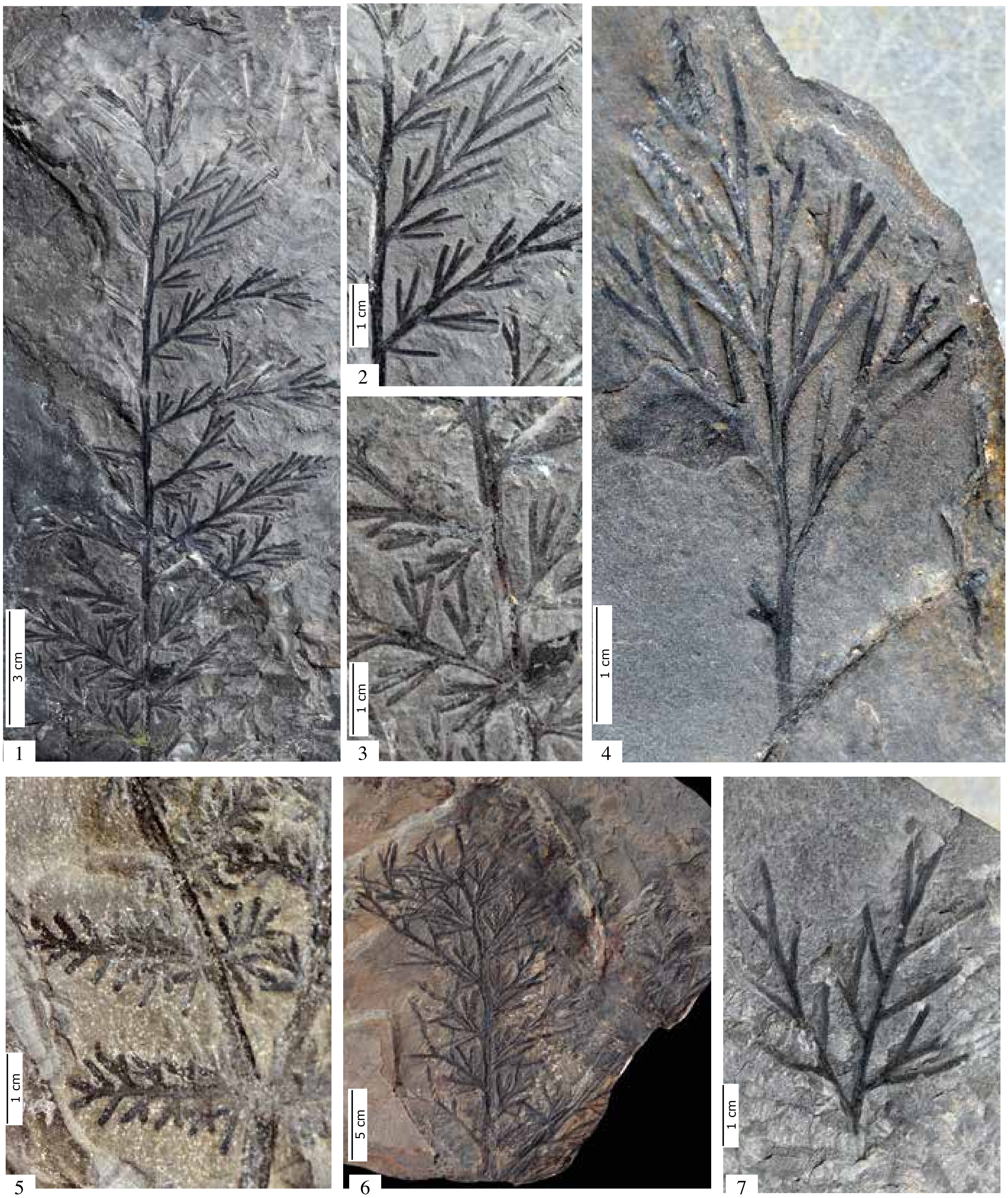
Description

Branchlets and leaves: From a main axis, sometimes equipped with deep longitudinal ribs fork irregularly lateral branches (TRE 565), TRE 649, TRE 788). Stiff and short needles spread grouped in one, two, till three bundles on protruding to ascending secondary branches. Single needles are 1–2 cm long, but only 0.1 cm wide and end pointed to slightly curved.

Male cones: Sprouting single on a needle/leaf. They are small-sized rounded till ellipsoid, only 1 cm long and 0.5–0.8 cm wide, forming catkin-like structures. The micro-

Voltzia viallii. Reconstruction (Early Permian, Kungurian))

a. Part of a branchlet (TRE 5, TRE 53); b. Arrangement of the needles (TRE 266); c. Male cone (TRE 411, TRE 226); d. Female cone (TRE 408); e. Seed scale with shed seeds (TRE 335, TRE 88); f. Seed scale with attached seeds; g. Isolated seed; h. Seed scale reverse side (TRE 83, TRE 387, TRE 611)

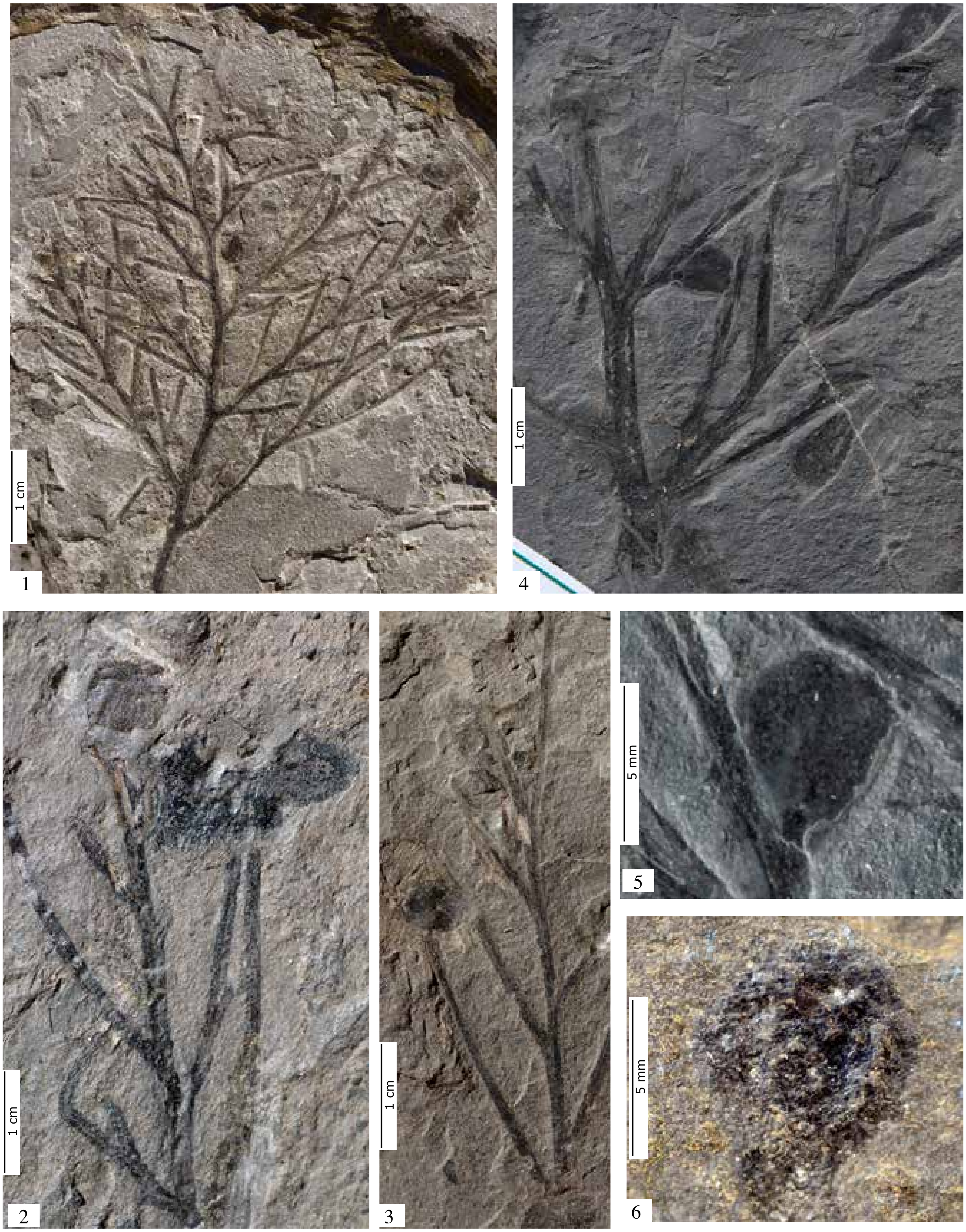


***Férovalentinia angelellii*. Twigs and needles (Early Permian, Kungurian)**

1-3. Superb preserved branchlet (15 cm long) bundled sometimes in two needles (especially on the upper part) or three needles (mainly on the lower part), (TRE 565); 4. Part of a branchlet (6 cm long) (TRE 516); 5. Juvenile branchlet (TRE 649); 6. Huge branchlet (TRE 788); 7. Arrangement of the needles (TRE 525); Coll. Valentini, Coll. Wachtler, all Tregiovo Le Fraine, Val di Non.

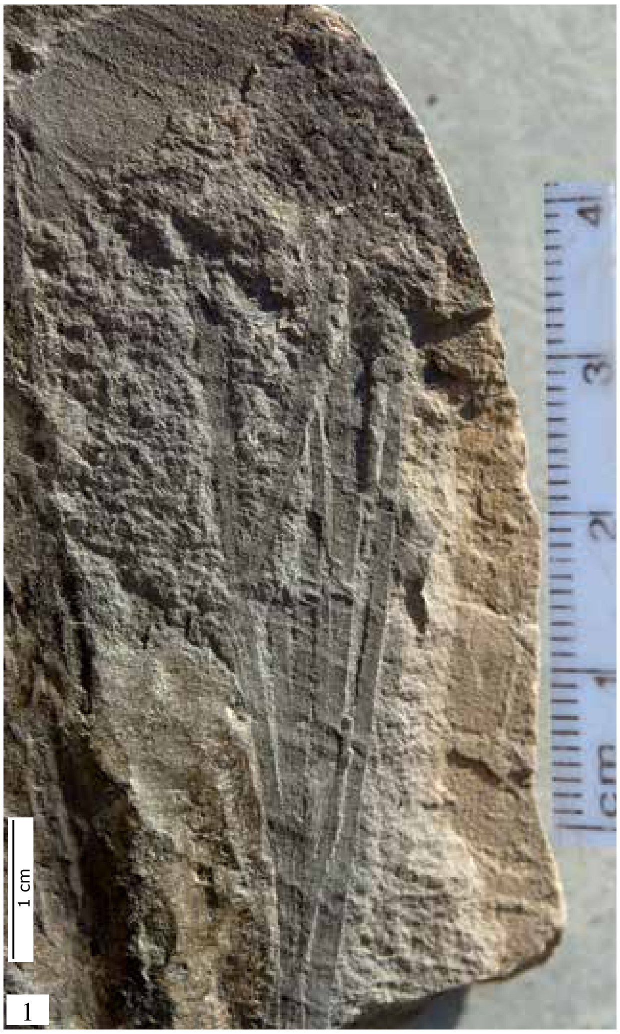
***Férovalentinia angelellii*. Twigs and needles (Early Permian, Kungurian)**

1. Branchlet (TRE 480, holotype); 2. Branchlet (TRE 486); 3-4. Twig and detail with the concept of the needles (TRE 542); 5. Branchlet (TRE 627); Coll. Valentini, Coll. Wachtler, all Tregiovo Le Fraine, Val di Non.



Férovalentinia angelellii. male cones (Early Permian, Kungurian)

1. Twig with several male cones (TRE 576); 2-3. Male cones sprouting from needles/twigs (TRE 488, Paratype, TRE 576); 4-5. Twig with several male organs and detail of a single cone (TRE 602, Coll. Wachtler); 6. Mature pollen cone (TRE 491); Coll. Valentini, all Tregiovo Le Fraine, Val di Non.



***Férovalentinia cassinisi*. Male cones**

1-2. Twig with a male cone and detail of the microsporophylls (TRE 421); Coll. Wachtler); Tregiovo Le Fraine, Val di Non.

sporophylls are densely arranged on a small central axis (TRE 576, TRE 488 Paratype, TRE 576, TRE 602).

Female cones: Female cones symmetrical rounded, sessile on the final part of a minute needle. Scales swollen, ending apically slightly incised in the middle. Each reaches a diameter size of 1–2 cm. Only a few (3-4) scale-rows form a cone. The branchlet facing side is deeply crenate, the upper side of the megasporophyll flat and glossy, holding two seeds. The ovules/seeds are nut-like till shortly winged. A distinction between those of *Férovalentinia cassinisi* cones is till now not possible.

Taxonomic notes

Most of the *Férovalentinia* specimen at Tregiovo are found in layers on the upper side of the road from Revò to Laurein in the vicinity of the bridge. There they constitute the most common plant-genus, whereas in the slightly older layers of the lower Tregiovo-Formation they are rare or not present. Interestingly they can be clearly divided into two subspecies: *Férovalentinia angelellii* is distinguished by its shorter irregularly forking needles grouped in bundles of one, two or three. An evolution in the direction to extant diploxyl pines is suggested.

Férovalentinia cassinisi generate bundles of five long needles, a feature that is valid also today in many Pines like *Pinus longaeva* or *Pinus cembra*. In that we encounter an interesting evolution between the several million years older, Artinskian *Férovalentinia wachtleri,* which does not yet allow the division into different subspecies and the two encountered in the Kungurian.

Férovalentinia cassinisi (WACHTLER, 2015)

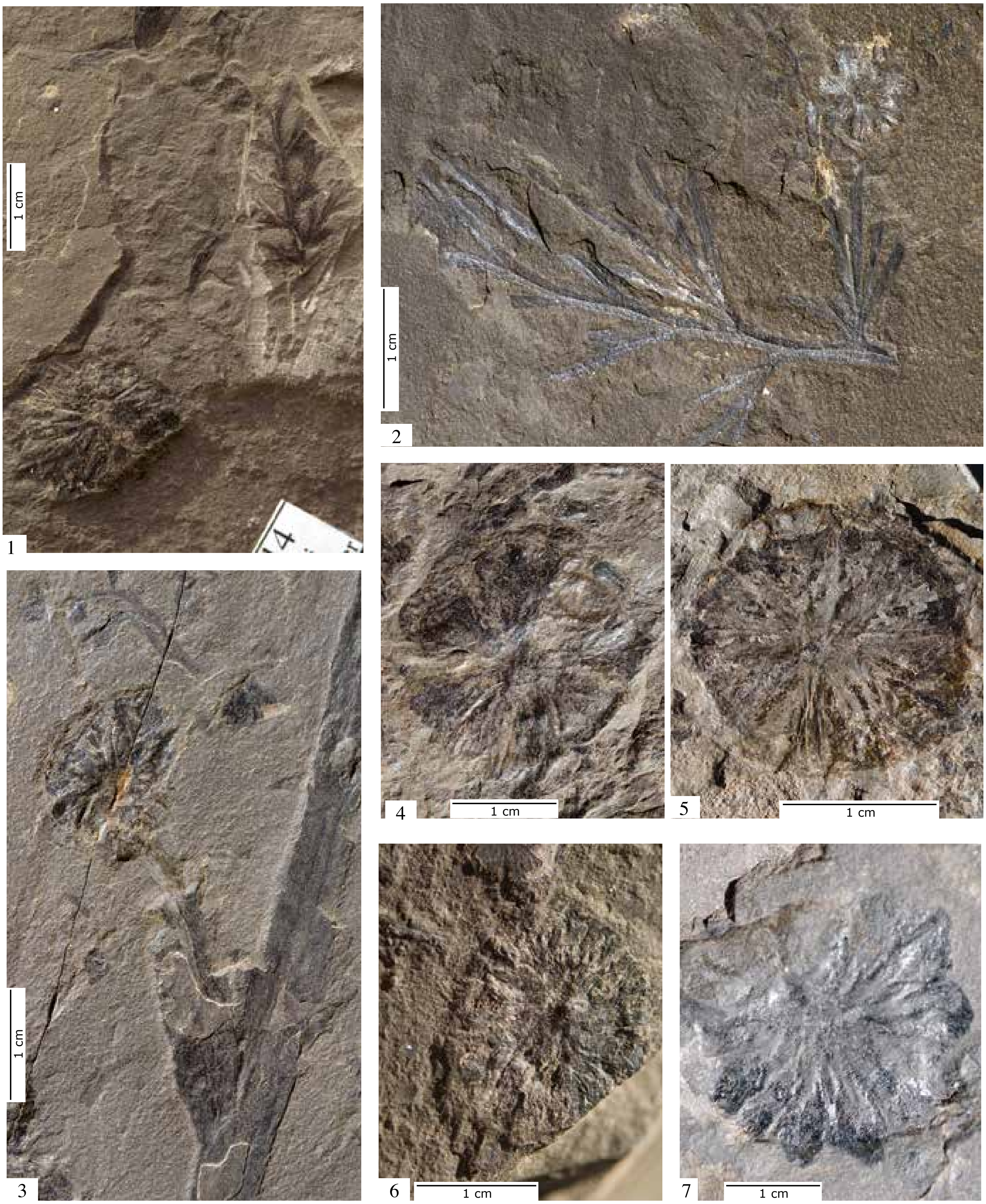
2015 *Valentinia cassinisi,* WACHTLER, pp. 91-98

Etymology

Honouring Giuseppe Cassinis, professor emeritus of the University of Pavia, who organised many researches at Tregiovo.

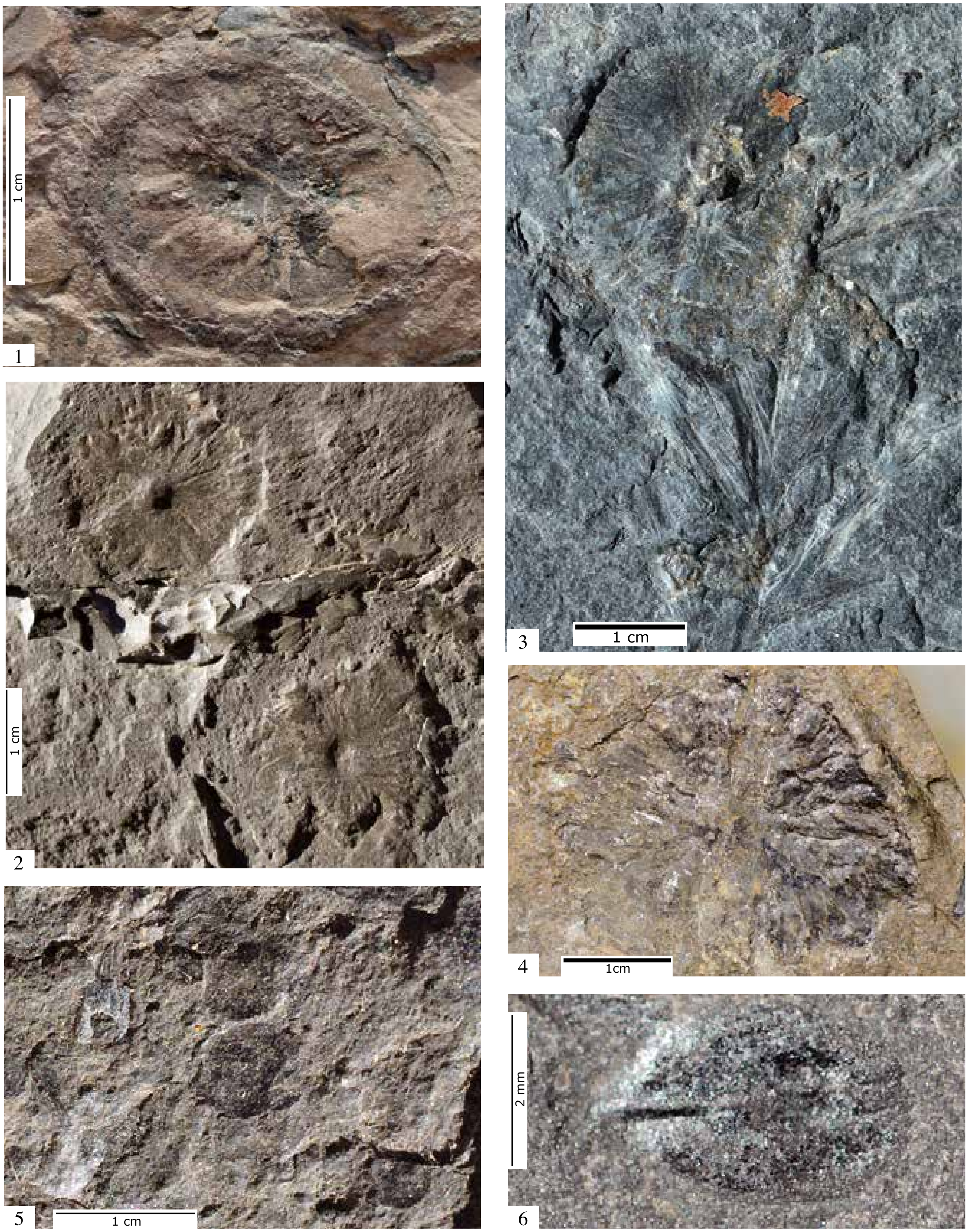
Holotype

TRE 490; **Paratype** TRE 421 (male cone); Repository: Museum of Natural Science MUSE, Trento. Other: Coll. Wachtler, Coll. Valentini; Dolomythos-Museum, Innichen



***Férovalentinia angelellii* or *Férovalentinia cassinisi*. Female cones (Early Permian, Kungurian)**

1. Branchlet and a female cone (TRE 614); 2-3. Female cones sprouting from *Férovalentinia angelellii*-twigs (TRE 505, TRE 425); 4-5. Cones upper seed side (TRE 548, TRE 610); 6-7. Female cones, lower side (TRE 453, TRE 456); Coll. Valentini, Coll. Wachtler, all Tregiovo Le Fraine, Val di Non.



***Férovalentinia angelellii* or *Férovalentinia cassinisi*. Female cones and seeds (Kungurian)**

1. Female cone, upper seed-side (TRE 520; 2. Two female cones (TRE 631); 3. Female cone (probably belonging to *Férovalentinia cassinisi (*TRE 652); 4. Female cone basal side (TRE 453); 5. Colluvium of seeds (TRE 548, Paratype); 6. Single seed (seed size 0.4 x 0.2 cm, TRE 570); Coll. Wachtler, all Tregiovo Le Fraine, Val di Non.

Description

Branchlets and leaves: Slender branchlets with relatively long and minute needles. Shoots rough with small cataphylls. Needle-tufts sometimes extremely agglomerated together. Needles from 5–8 cm long but only 0.1 cm wide, grouped in bundles of five (TRE 483, holotype). Sometimes they are attached on the stem with long and persisting fascicle sheaths (TRE 490, TRE 601, TRE 455, TRE 490).

Male cones: Collocated on the end of a minute needle/shoot, relatively small, not exceeding 1 cm or a width of 0.5 cm. Microscopic microsporophylls arranged in clusters and grouped together on a small axis (TRE 421).

Female cones: Ovuliferous strobili growing at the end of an elongated needle. They are compact and ovoid till rounded. Few macrosporophylls growing spirally around an axis, on each scale two ovules lying on the base. Umbo flimsy incised on the upper side, thickened on the end. Lower part of the macrosporophylls furrowed.

Taxonomic notes

If in *Férovalentinia angelellii* the exact geometry of their needles was not fully completed and it is more difficult to find direct extant descendants (because it can be regarded as a potpourri of many possible pine-species), *Férovalentinia cassinisi* could easily be transplanted into a contemporary landscape without attracting a particular attention. It holds just five long needles per bundle, being in that a potential ancestor of today's haploxyl pines.

The biggest challenges arise therefore shortly after the sudden onset of the pine-progenitors in the Early Permian. Strangely just in the Late Permian of the Alps—where we have a large presence of Araucariaceae-, Abietaceae-, Ginkgo-, or Cycadaceae-ancestors, the Pinoideae vanished abruptly. We do not encounter them in the German basin, being located around the 20th parallel to the north, nor in the Alps, lying in that time near the equator. And we have not or only extremely doubtful evidence in the following 150 till 200 million years. The same occurred with the Abietaceae and also the extremely diversified proto-angiosperms from the Permian Ural-region (Wachtler, 2020).

But it did not happen with the cycads, providing a comprehensive documentation from the Early Permian till today, or the ginkgos, ferns, or horsetails. The Mesozoic entered in geological history as age of the cycads, and they were widely present in the Alps, before being occupied by the pine-trees.

Maybe the very cold adapted Pines found in the hostile climate influenced in Early Permian by the Gondwana Ice-age an ideal habitat and vanished beginning from the Late Permian when the weather conditions became more humid and especially in the Triassic changed to tropical that for the pines was to inadequate, otherwise with the present state of knowledge we are faced with an insoluble task. The ovoid to ellipsoid woody female cones of all the Early Permian *Férovalentinia* species were similar. They hold only a few rows (maximum four) of megasporophylls around an axis, but they can just be identified as typically Pinus-like.

A number of Pinyon-pines, like *Pinus edulis, Pinus monophylla, Pinus remota* or *Pinus quadrifolia* with its few scales for each cone, are a good example of the blueprint of all Early Permian *Férovalentinia*-species (Wachtler, 2015). The lower parts of the scales with their rugged and wrinkled surfaces are also identifiable as Pinus, as well as the two seeds for each megasporophyll. It seems that they were nut-like or maximally shortly winged. *Férovalentinia angelellii* can be defined as more primitive, having closer affinities with *Férovalentinia wachtleri* from the older (Sakmarian-Artinskian) Collio Formation (Perner, 2015).

Male cones were dwarfish rounded, composed of many densely aggregate small-sized microsporophylls. Both, male and female, sit on the apical part of a modified needle. Interestingly the splitting from the other conifers, such as *Ortiseia, Voltzia* or *Majonica* must have occurred just many million years earlier. Too great are the differences in the cones, but also the needles. As distant related could only be taken in consideration Late Carboniferous P*erneria thomsonii.*

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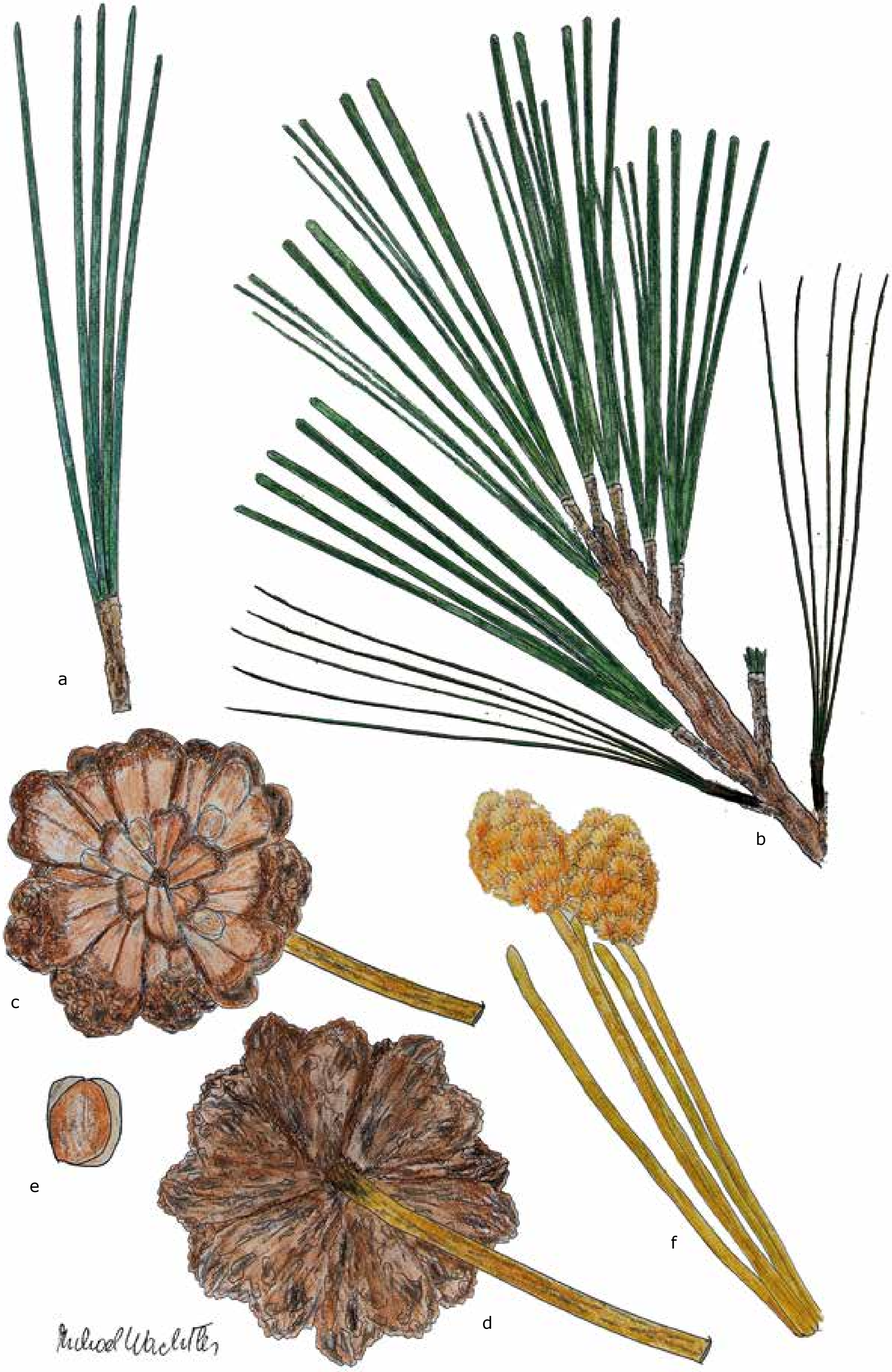
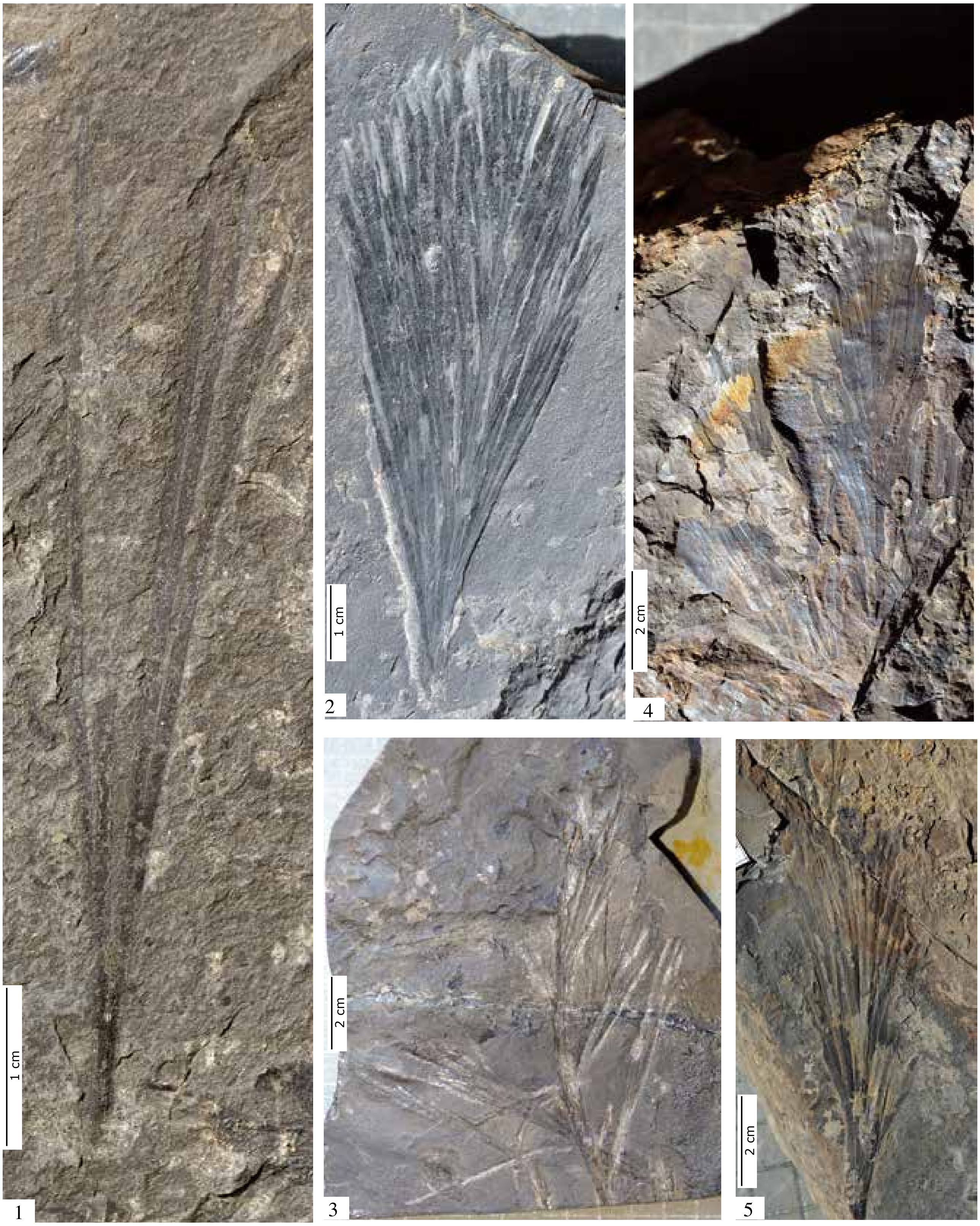
***Férovalentinia angelellii*. Reconstruction (Early Permian, Kungurian)**

a. Branchlet (TRE 565); b. Detail of a twig (TRE 516); c. Adult female cone upper side (TRE 548, TRE 610) d. Twig with several male cones (TRE 576); e. Juvenile male cone (TRE 505); f. Mature pollen cone (TRE 491); g. Detail of a microsporophyll outside; h. Microsporophyll with two pollen sacs.



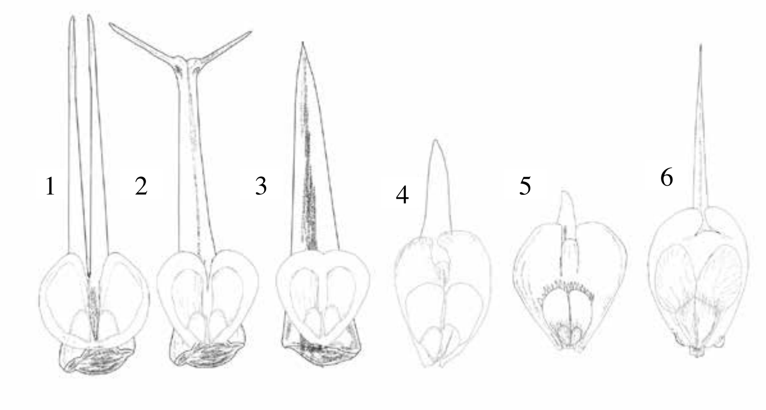
***Férovalentinia cassinisi*. Reconstruction (Early Permian, Kungurian)**

a. Fascicle with five attached needles encased by a sheath (TRE 483, holotype); b. Branchlet (TRE 601); c. Adult female cone upper side (TRE 520, TRE 621); d. Female cone basal side (TRE 453); e. Single seed (TRE 570); f. Mature pollen cones (TRE 421) on a fertile shoot



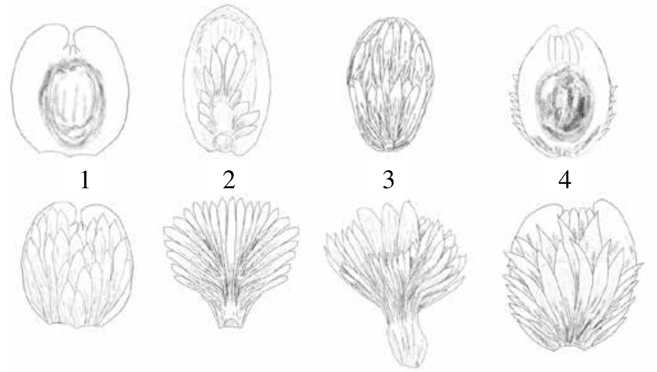
***Férovalentinia cassinisi*. Twigs and needles (Early Permian, Kungurian)**

1. Exemplary fossilized fascicle (7 cm long) with five attached needles encased by a sheath (TRE 483, holotype); 2. Branchlet (10 cm long) with large branching shoots (TRE 490); 3. Branchlet (TRE 601); 4. Several needle-tufts aggregated on a twig (TRE 455); 5. Tuft of leaves (TRE 490); Coll. Valentini, Coll. Wachtler, all Tregiovo Le Fraine, Val di Non.



Permian Majonica-Abies-evolution

1. Abies ancestor (Moscovian); *2. Gomphostrobus bifidus* 3. *Wachtlerina bracteata* (Kasimovian); 4.*Majonicas suessi* (Artinskian); 5 *Majonica ambrosii* (Kungurian); 6. *Majonica alpina* (Wuchiapingian)



Permian Ortiseia-Araucaria-evolution

1. *Ortiseia uhli* (Kasimovian); 2. *Ortiseia dasdanai* (Artinskian); 3. *Ortiseia daberi* (Kungurian); 4. *Ortiseia leonardii* (Wuchiapingian)

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