The Clubmosses in the Carnian Raibl beds

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Strangely in addition to low growing shrubby conifers, characterized by their spinous needles and withered appearance, we encounter in the Upper Triassic (Carnian) Raibl Formation in the Eastern Alps mainly no ferns or horsetails but only lycopods. Especially one *Selaginella* species - *Selaginellites perneri* - is so dominant to cover for hundreds and hundreds of metres the layers. Interesting are their naked and mainly leafless stipes. Fairly common is *Sigillcampeia blaui,* one of the last descendants of the Carboniferous giant Sigillarias. The reasons for the dominance of the lycophyta can be searched probably in a long lasting hypersalinity of the soil, but more in adverse weather conditions, which fulfil all requirements to be classified as immense disaster, the "Raibl-Cataclysm", that prevailed in that time not only in this area, but worldwide.

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A Late Triassic (Carnian) offshore clubmoss landscape of the Lienz Dolomites (Raibl cataclysm)

On the left side grow ***Sigillcampeia blaui,*** a dwarfish descendant of the *Sigillaria*-lycopods, the right side is densely covered by ***Selaginellites perneri.***

It was thought that the giant clubmosses like *Lepidodendron* and *Sigillaria* died out at the end of the Carboniferous-Permian border. But strangely enough we have at the begin of the Triassic with *Pleuromeia* and than in the Alps with *Lycopia dezanchei, Eocyclotes alexawachtleri, Lepacyclotes brandneri* and *Sigillcampeia nana* dwarfish successors of *Lepidodendron* and *Sigillaria.* Especially the representatives of the Sigillarias were present throughout the Triassic with Early-Middle Triassic *Sigillcampeia nana* covering extensive areas in Anisian layers and *Sigillcampeia blaui* reaching from the Middle to the Upper Triassic. They were characterised by their bonsai-like growth, and give a deep insight into the blueprint, growth and fertilisation of this lycopod family. It is also interesting that the cones hold microsporangiate as well macrosporophylls with only one huge sporangia, that in other cases could also be regarded as a seed.

Sigillcampeia blaui WACHTLER 2016

Holotype

SEE 14, **Paratype:** SEE 02 (leaves) (Coll. Wachtler, Dolomythos Museum, Innichen)

Etymology

After their affinities to the lycopod *Sigillaria* and Edith Campei, who found the first specimen. The species-name honours Joachim Blau, Institute for Geo-Sciences, Frankfurt am Main for his researches in the Lienz Dolomites.

Description

Stems: Small heterosporous lycopsid plants, with similar mega- and microsporangiate sporophylls. Stems bulbous, covered with elliptic leaf scars and divided on the apical part into two separated trunks. The apical part of the stems topped on each side with a plume of long, grass-like leaves. Fertile parts on each upper side, revealing two separate tufts of sporophylls. Lower parts covered by leaf cushions in slightly downwards orientated longitudinal rows. Scars smooth and elliptic with one prominent outer rim. Several abscission points situated just over the centre of the leaf scar. Sporophylls cushions sharply delimited at the apex, larger and narrower, undulate. Roots downwards directed.

Leaves: Long, thin, grass-like. From 10 to 20 cm long, 1 to 1.5 cm wide, lanceolote, attached on the whole basal part on the stem. Base slightly concave, crossed vertically entirely from longitudinal veins (about 15 for each centimetre). Apex strongly tapered. Leaves released after maturity and therefore found in high numbers in the layers together with the sporophylls.

Sporophylls: Megasporophylls with megasporangia are situated on the lower part of the fertile cluster, while microsporophylls with microsporangia are present on the upper part. Megasporophylls rounded and smooth, holding only one megaspore. All coated by sterile integuments, only apically opened by a small slit. About 3 cm in size, length and width. Microsporophylls elongated, 5 cm in length, 3 cm wide, filled with microsporangia. Both dropped after maturity.

Sigillcampeia blaui. **Microsporophylls**
1. Several microsporophylls on a slab (SEE 02)

***Sigillcampeia blaui*. Lycopod. Reconstructions (Carnian, Late Triassic)**

a. Megasporophyll seen from the upper side (ZOC 08); b. Megasporophyll lateral side evidencing the only megaspore (SEE 14); c. Microsporophyll (SEE 25); d. Leaves with tapered apex and detail of the venation (SEE 02) e. Whole plant; f. Detail of a stem with the abscission points (ZOC 07); All Coll. Wachtler-Dolomythos, Lienz-Dolomites

***Sigillcampeia blaui*. Lycopod. Leaves and Sporophylls (Late Triassic, Carnian)**

1. Megasporophylls and leaves on a slab (SEE 14, holotype); 2. Leaves with tapered apex and basal sporophylls (SEE 02 paratype); 3. Several leaves on a slab (SEE 05); 4-5. Details of different megasporophylls on the same slab (SEE 14); 6. Microsporophyll (SEE 25); 7. Detail of the venation (SEE 02); All Coll. Wachtler-Dolomythos Seekofel, Lienz-Dolomites

***Sigillcampeia blaui.* Lycopod, Stems and Sporophylls (Late Triassic, Carnian)**

1. Megasporophyll and stem (ZOC 07); 2. Detail of the leaf scars with the abscission points (ZOC 07); 3. Stem with leaf scars; 4. Isolated sporophyll (ZOC 08); 5. Plant with attached leaves (ZOC 83) All Coll. Wachtler-Dolomythos Zochenpass, Lienz-Dolomites

Diagnosis, remarks and ecology

Sigillcampeia blaui is more common on the Western part of the Lienz Dolomites beginning from the Seekofel till the Zochenpass. There the characteristic sporophylls, grass-like leaves and the typically divided bulbous trunks can be found in fair amounts. Probably they were well adapted to the flooding areas although always they are accompanied by conifer trees washed in from the mainland. *Selaginellites perneri* in contrast can also build extensive carpets of monocultures (Wachtler, 2016 a, b, c).
Clubmosses with amazing resemblances to the Carboniferous Sigillarias pertain to the most interesting plants in the Triassic. Just in the Earl Middle Triassic (Anisian) we encounter with *Sigillcampeia nana* a first direct ancestor of *Sigillcampeia blaui*. There the leaves were characterized by one strong mid-vein entering the leaf.
Whether *Sigillcampeia* became extinct at the end of the Triassic or if they survived also in the Jurassic is difficult to establish. The only sure observation is that today we do not have any living representative of the Sigillarias - that for so long ruled this planet-, whereas other archaic lycopods, like *Selaginella, Lycopodium* or *Isoetes*, can still be encountered.

Selaginellites perneri
Detail of a plant with strobili (LAV 56), Coll. Wachtler-Dolomythos, Lavanter Alm, Lienz-Dolomites, Carnian)

Selaginellites perneri WACHTLER 2016

Holotype

LAV 32 (Coll. Wachtler, Dolomythos Museum, Innichen), **Paratype** LAV 33

Etymology

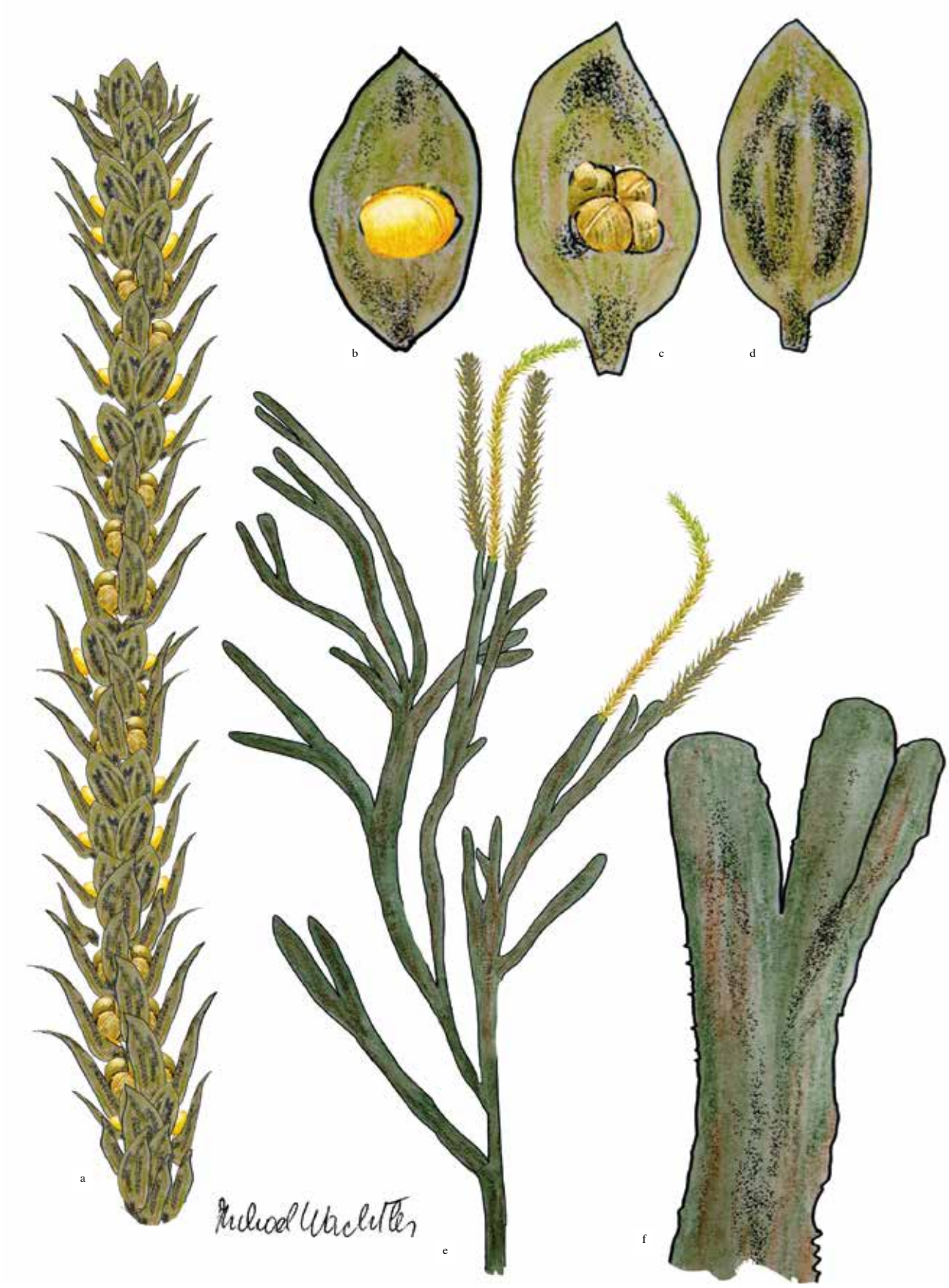
Honouring the researcher and palaeobotanist Thomas Perner, Bad Homburg, Germany. Renè Zeiller instituted the genus Selaginellites in 1906 for fossil heterosporous lycopods resembling recent *Selaginella.*

Taxonomic notes

Extant Selaginellaceae comprise one large genus comprising about 700 living species. They are encountered around the world, with genera adapted to grow in the arctic as frost-tolerant, in deserts as drought-adapted, and in the rainforests as long-lasting humid-resistant. Almost all are characterised by their delicate dichotomously branching stems that develop ranks of minute leaves.

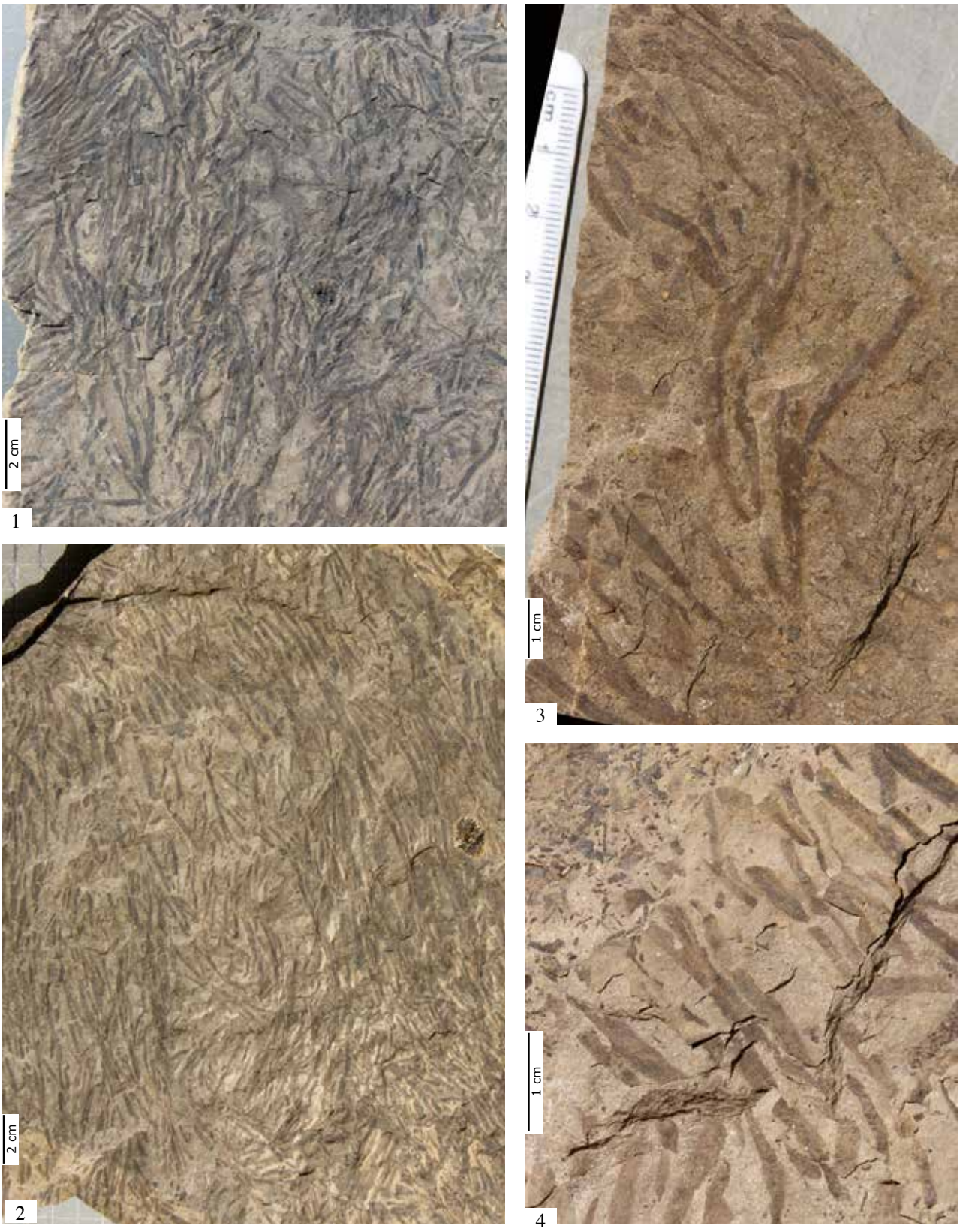
Description

Plant: Stems densely and generously cespitose, reaching up to 30 cm in length and 15 cm in width. Each leafy branch forks dichotomously regularly to irregularly several times. Branches without an apparent decrease in the thickness in direction to the apex (LAV 27).
Leaves: Stems mostly naked, no foliage visible, but only some fine hairy enations.
Fertile parts: Strobili terminal on sterile shoots, elongated, reaching also lengths of 7 cm (LAV 32 holotype), by a width of only 0.2 cm. Heterosporous, mega- and microsporangia, equipped with an elongated pointed apex, occurring in the same strobilus (LAV 33) and therefore easily recognisable from sterile shoots.



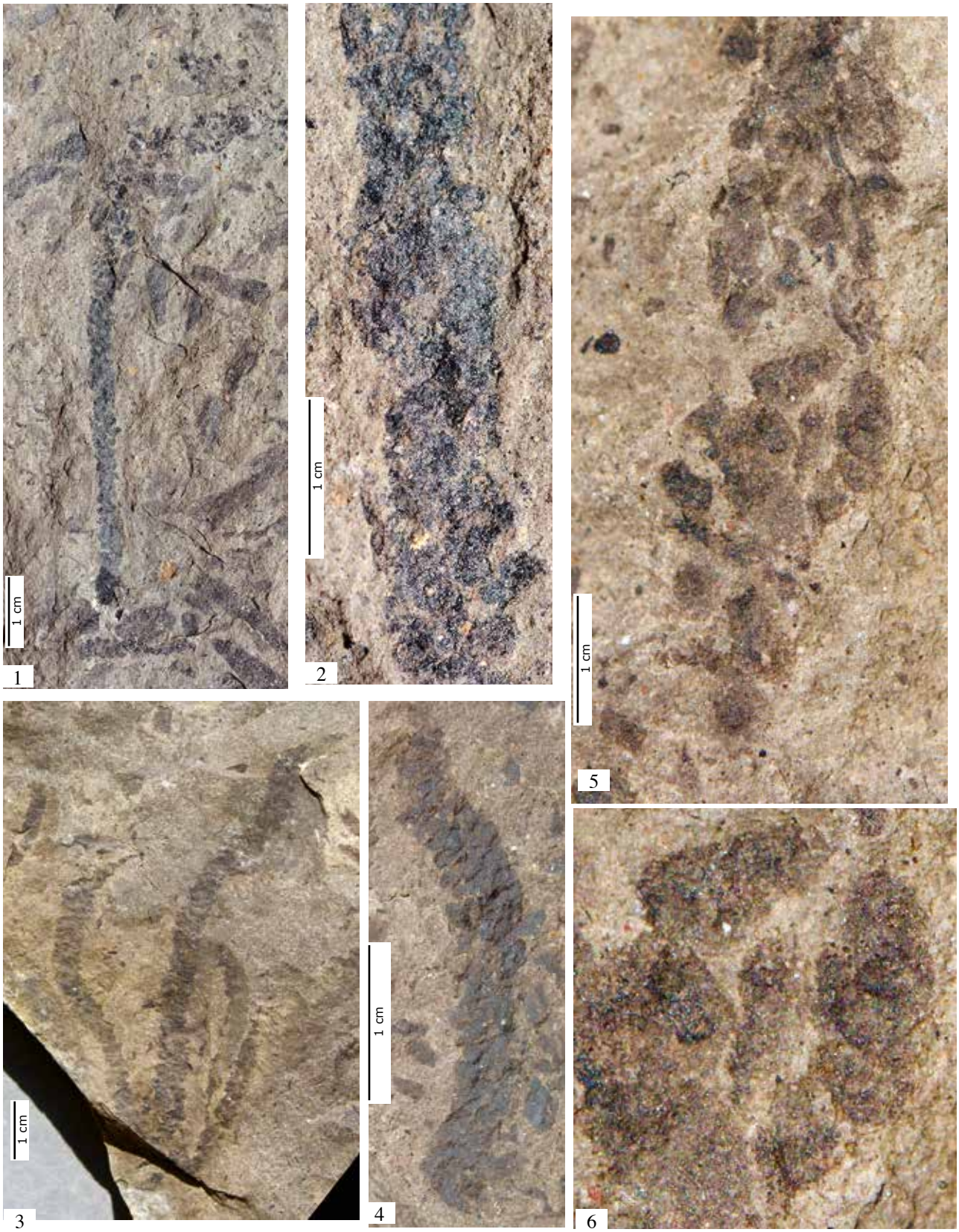
***Selaginellites perneri*. Reconstructions (Late Triassic, Carnian)**

a. Fertile strobilo (LAV 83); b. Microsporangia; c. Macrosporangia; d. Fertile leaf reverse side (LAV 83); e. Apical part of the naked stems (LAV 78); f. Whole plant (LAV 59; LAV 79, LAV 83); Lienz Dolomites



Selaginellites perneri. **Plants (Late Triassic, Carnian)**

1. Big slab with several entire plants (LAV 59); 2. Other big slab with strobili (LAV 60); 3. Detail of a plant LAV 79); 4. Detail of the leafless stipes (LAV 78); All Coll. Wachtler, Lavanter Alm, Lienz-Dolomites, Carnian



***Selaginellites perneri*. Sporophylls (Late Triassic, Carnian)**

1-2. Slab with several sporangiate strobili, one of them measuring 7 x 0.2 cm and detail of the sporangia (LAV 83, designed holotype); 3. Three strobili (LAV 70); 4. Single strobilo (LAV 74); 5-6. Detail of micro and macrosporangia (LAV 83); All Coll. Wachtler-Dolomythos, Lavanter Alm, Lienz-Dolomites, Carnian

Diagnosis, remarks and ecology

In the Triassic of the Dolomites we encounter from the Early till the Late Triassic a continuous presence of fossil *Selaginella* species. They were represented in the Early–Middle Triassic (Anisian) by *Selaginellites leonardii* with its heterosporous strobili and *Selaginellites venierii* with characteristic anisophyllous shoots. In the Late Triassic (Carnian) Dolomites the Selaginellaceae become more dominant to form extensive monocultures with the only one species *Selaginellites perneri.* The plant was characterised by its naked stipes and their slender but proportionally elongated sporangiate strobili.

Remarks, discussion and ecology

Of all *Selaginellites* species in the Triassic Dolomites *Selaginellites perneri* is by far the most widespread covering extensive areas in the Carnian sediments of the Lienz Dolomites. Probably due to their plainness but also the area's remoteness from any passable roads, till now they had never attracted the attention of the researchers. Most places can only be reached by a long walking-distance of about three hours, starting from the Dolomitenhütte, till climbing first the Laserz-Törl than descending for about 400 elevation gain and after that torture climbing again the 400 m attitude till reaching the Schwärza Törl. And all these going back with a heavy rucksack filled with huge lycopod stone-slabs.

Interestingly they occur in abundance with one shrubby Cupressaceae conifer *Pusteria maribelae,* characterised by small-sized cones and stunted branchlets and long-tapered needles. It can therefore be suggested that in the Upper Triassic the climate in this part of the world near the Tethys ocean was extremely rough and stormy.

Extant Selaginellaceae belong to a widely distributed family of herbaceous lycopods, well adapted to various climate conditions and soil types. Some species can resist extreme weather, such as those prevalent in alpine or arctic circles. They can also colonise barren and dry deserts. One of the most well known, *Selaginella lepidophylla,* is called the resurrection plant because it can survive years without rainfall. They reach their highest diversity in tropical areas under the forest canopy, protected from direct sunshine, or around riverbanks, marshes or waterfalls. The presence or absence of leaves of two distinct sizes has been used as a criterion for subdividing extant Sellaginellaceae.

Anisophylly, or two ranks of different sized needles, is characteristic for the subgenera *Heterostachys* and *Stachygynandrum,* whereas *Tetragonostachys, Selaginella* and *Ericetorum* are isophyllous, or equipped with identical foliage. Selaginellaceae are delimited from herbaceous Lycopodiaceae by their heterosporous fructifications in contrast to the isosporous lycopods.

The earliest fossil evidence of Selaginellaceae comes from the Carboniferous (Visean 345.3 to 328.3 million years ago) and from the Late Carboniferous with *Selaginellites*

Detail of *Selaginellites perneri* with its creeping appearance (LAV 59); Coll. Wachtler-Dolomythos, Lavanter Alm, Lienz-Dolomites, Carnian

1

2

3

4

5

Selaginella species today

1 *Selaginella sanguinolenta* (Altai, foto courtesy by Sergej Smirnov); 2-5. *Selaginella tamariscina; 4.* Cusp of fertile sporophylls; 5. Detail of a sporophyll with micro- and macrosporangia

gutbieri, when branching stems that bore minute leaves were widespread in Coal Measure floras. *Selaginellites gutbieri,* recorded in extraordinary complete and spectacular specimens from Westphalian D of Germany, had a well-developed planar branching. The arrangement of the leaves is anisophyllous, with two ranks of larger lateral leaves, ovate to lanceolote with acute apices, and two ranks of smaller median leaves. Surprisingly, at that time, isophyllous and anisophyllous species just coexisted.

A delimitation to other Lycopodaceae is that *Selaginellites* is restricted to heterosporous species, whereas *Lycopodites* includes isosporous taxa and other species that are not known to be heterosporous (Zeiller, 1906). Although fossil Selaginellas are known from such a long time ago, their remains are very rare, because of their inconspicuousness and fragility.

Only a few, sometimes poorly preserved, Triassic *Selaginellites* species are currently known, most of them found in Upper Triassic rocks. These include Norian *Selaginella anasazia* in Arizona (Ash, 1972), Greenland (Selaginellites polaris), Rhaetian *Selaginellites hallei* and *Lycopodites scanicus* from Sweden (Lundblad, 1950), *Selaginellites yunnanensis* from China (Li et al., 1976), and also in Germany (*Selaginellites coburgensis*), found in connection with fertile parts (Van Konijnenburg-Van Cittert et al., 2016). From all of them Upper Triassic (Rhaetian) *Selaginellites coburgensis* can give an interesting inside of a slow recovering of the Selaginellaceae. Whereas the stipes of Carnian *Selaginellites perneri* are naked the descendants *Selaginellites coburgensis* are just equipped with shoots with densely spaced leaves.

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