

Fossil Triassic *Selaginella* species from the Dolomites

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Abstract

Extant Selaginellaceae comprise 700 living species, which 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. 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 by *Selaginellites leonardii* with its heterosporous strobili and *Selaginellites venierii* with characteristic anisophyllous shoots. In the Late Triassic (Carnian) in the same places (Lavanter Alm–Lienz-Dolomites) extensive monocultures of *Selaginellites perneri* n. sp. were found. The plant was characterised by its mimicry leaves and their slender but proportionally elongated sporangiate strobili

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Key words: Fossil lycopods, Alps, *Selaginellites*, Triassic



A Carnian landscape with the lycopod *Selaginellites perneri* covering extended areas

Systematic Paleontology

Division Lycophyta
Order Selaginellales Prantl, 1874
Family Selaginellaceae Willkomm, 1854

Selaginellites ZEILLER, 1906

Taxonomic notes

Renè Zeiller instituted the genus *Selaginellites* in 1906 for fossil heterosporous lycopods resembling recent *Selaginella*.

Selaginellites leonardii WACHTLER ET AL. 2010

Type horizon and age

Dolomites, Early-Middle Triassic, Anisian, Pelson-Illyrian (243 - 241 Mya)

Holotype

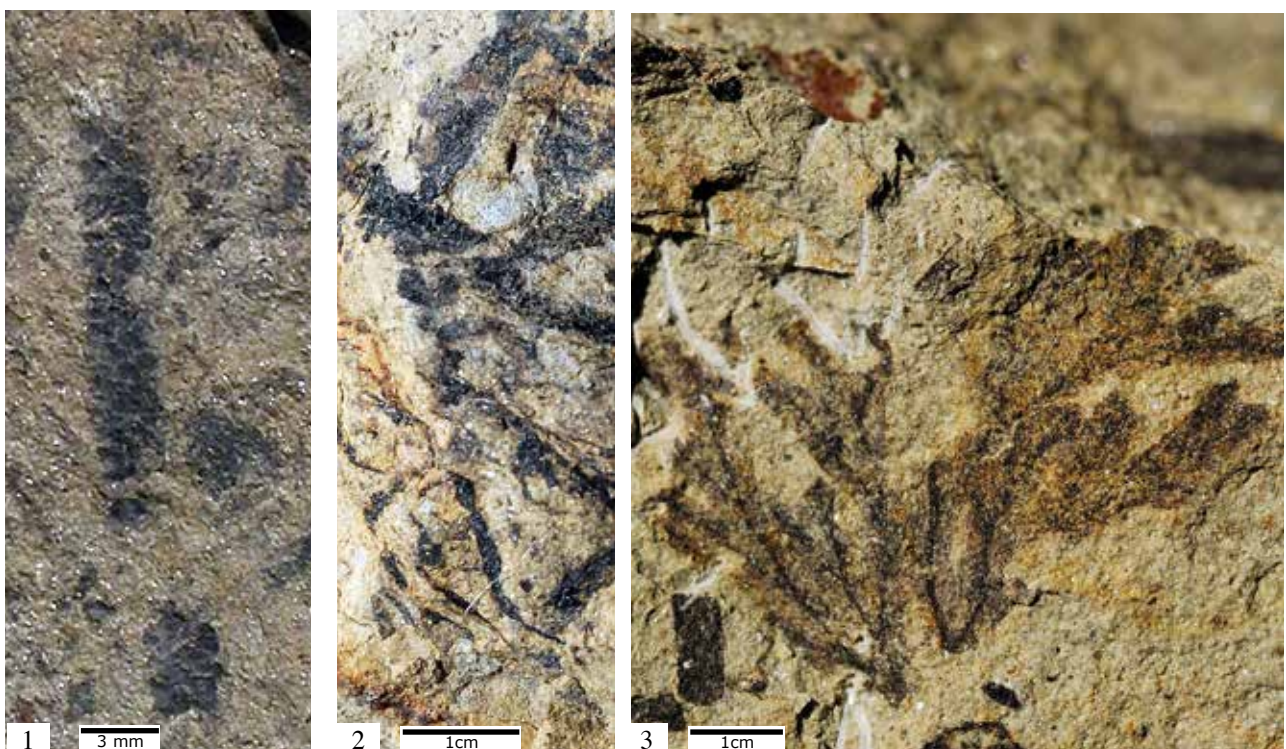
KÜH 1140 (Coll. Wachtler, Natural History Museum Südtirol, Bozen)

Etymology

Remembering Piero Leonardi, a pioneer in the research on the geology of the Dolomites.

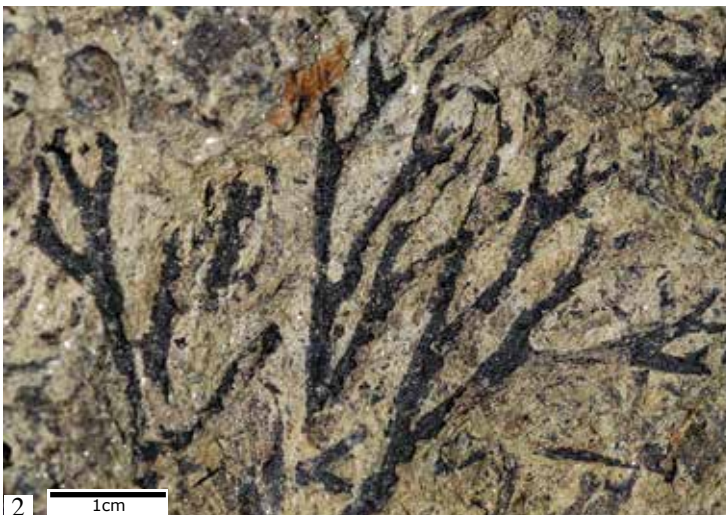
Description

Plant: Stems branch dichotomously and are regularly or irregularly forked or branched. Leaves tightly appressed to ascending on the stems (PIZ 563, 622, 623). Foliage structure linear-lanceolate to slightly falcate at the marginal ranks. Strobili with clusters of overlapping sporophylls are arranged spirally to decussately. Sporophylls ovate, differentiated from vegetative sterile leaves. Heterosporous sporangia in the axils of sporophylls are divided into compact tetrads of trilete microspores, while megaspores are oval to circular with thick spore walls. Stems densely cespitose, ascending, slightly to greatly branched, up to 5 cm high and with dichotomising axes without an apparent decrease in the thickness of lateral branches. Some of the ultimate branchlets are merely short spurs, slightly enlarged at the tip and only a few millimetres in length.



Selaginellites leonardii (Early-Middle Triassic) Plant

1. Heterosporous strobilus (KÜH 1140, holotype); 2. Badly conserved, but attached strobilus (PIZ 622); 8. Shrub with well-preserved juvenile leaves (PIZ 563) All Anisian, Coll. Wachtler)



***Selaginellites leonardii* (Early-Middle Triassic) Plant**

1. Mainly complete branch (PIZ 622); 2. Branches show dichotomous forking (PIZ 623); 3. Axes evidence slightly enlarged short spurs (KÜH 956, paratype); 4. Plant with minute axes (KÜH 1140, holotype); 5. Sterile branchlet (PIZ 165, All Coll. Wachtler, Anisian, Kühwiesenkopf and Piz da Peres)

Leaves: 0.1 to 0.3 cm long and protruding, a little awl-shaped, displaying a subtle needle-like characteristic. Adult branchlets are covered with several rows of minute appressed, narrowly lanceolate and highly overlapping leaves. As a result, they are mostly invisible, suggesting naked shoots.

Strobili: Heterosporous with helically to decussately arranged micro- and macrosporangia, which are aligned in four irregular vertical files (KÜH 1140, PIZ 622). They are about 2 cm long, ovate with a long, acuminate apex and an entire margin and are therefore completely different from the sterile leaves, which are minute and acicular. Strobili, in comparison to the shoots and the dimension of the whole plant, are extraordinarily long (Wachtler et al., 2010).

Remarks

Early-Middle Triassic *Selaginellites leonardii* is in fact inconspicuous, but not uncommon,

appearing as understory vegetation between conifers, ferns, cycads and horse-tails, especially in the Prags-Dolomites. The biggest difference to Upper Triassic *Selaginellites perneri* from the nearby Lienz-Dolomites is its size, reaching in best cases only a quarter. This is valid also for the fertile parts (2 cm against 7 cm).

Selaginellites venieri WACHTLER 2011

Type horizon and age

Dolomites, Early-Middle Triassic, Anisian, Pelson-Illyrian (243 - 241 Mya)

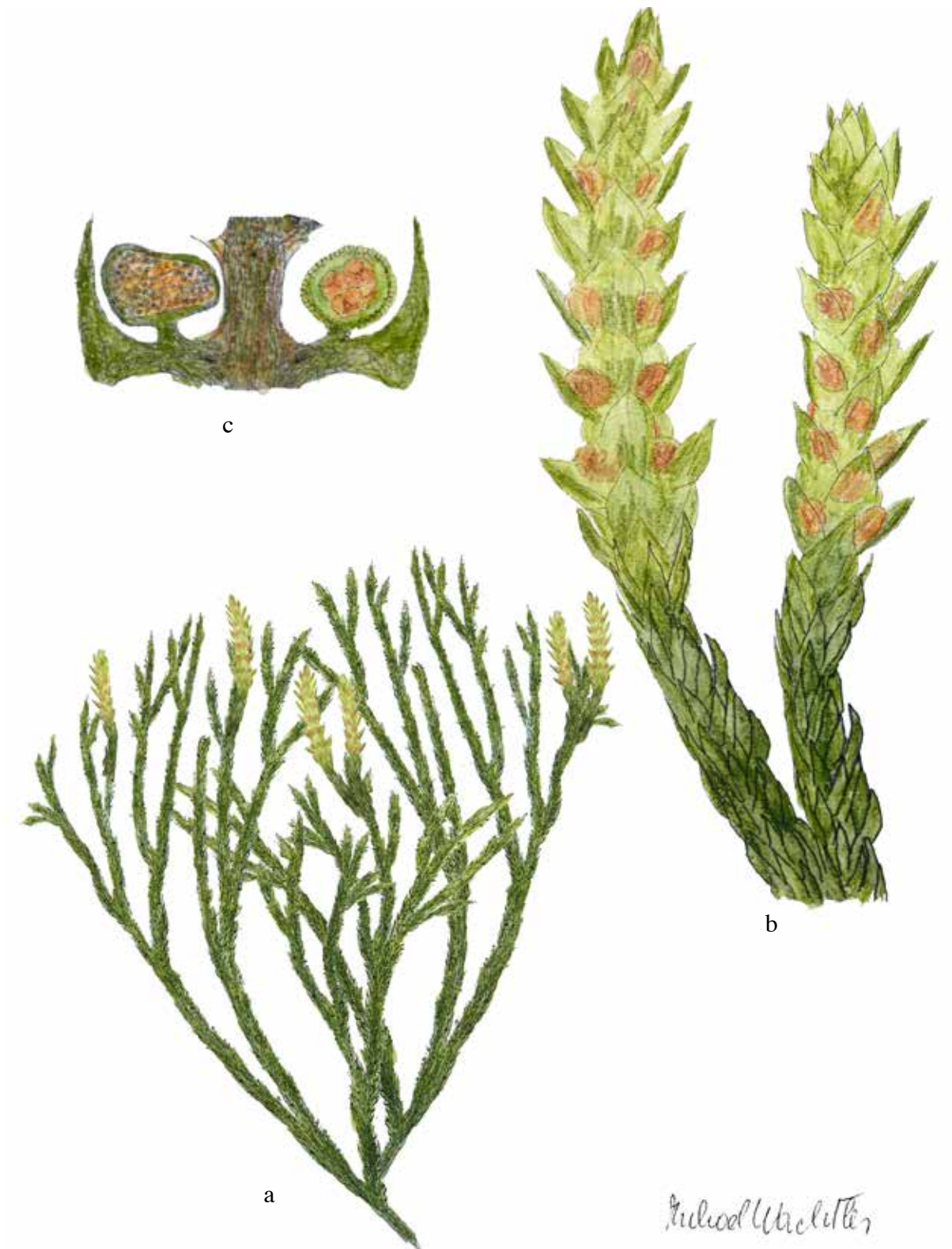
Holotype

PIZ 548 (Coll. Wachtler, Natural History Museum Südtirol, Bozen)



Selaginellites venieri (Early-Middle Triassic) Plant

1-2. Branch with anisophyllous leaves and detail of the leaves (PIZ 548, holotype), Anisian, Piz da Peres, Coll. Wachtler)



***Selaginellites leonardii* (Early-Middle Triassic) Reconstructions**

a. Entire plant with fertile parts (PIZ 622); b. 6. Heterosporous strobili (KÜH 1140, holotype); c. Internal part of a sporophyll displaying macro- and microsporangia

Etymology

For Umberto Venier, who dedicated his life to searching for fossil plants in the Eastern Alps.

Description

Plant: Cespitose low-growing lycopod with a dichotomising axis.

Vegetative branches: Leaves anisophyllous, characterised by their opposite pairs of dorsal and ventral leaves that differ in size and form. The larger leaves are attached laterally and the smaller ones medially on the upper surface. Leaves mostly entire to minutely denticulate. Leaves crowded throughout the stem.

Vegetative leaves: Both median and lateral leaves are ranked in two pairs, closely imbricate, narrowly rounded at the tip, strongly oblique to the axis, and ascending at an approximately 45° angle. The lateral side is 1.8 to 2.2 mm long and 0.5 to 0.7 mm wide, while the central part is 0.6 to 0.8 mm long and 0.5 to 0.7 mm wide. The surface area of the external standing leaves is therefore about three times greater than that of the smaller internal leaves (PIZ 548). Anisophylly is typical for many species of extant *Selaginella* species.

Remarks

At least two quite different *Selaginella* species formed part of the Early–Middle Triassic ecosystem in the Dolomites. The isophyllous *Selaginellites leonardii* are characterised by their same-sized leaves, and the anisophyllous *Selaginellites venieri* by their possession of two sets of different foliage on the same rank. Therefore the distinction is not so difficult although *Selaginellites venieri* seems to be much rarer.

Selaginellites perneri sp. nov. WACHTLER 2016

Type horizon and age

Dolomites, Late Triassic, Carnian, (235–228 Mya)

Holotype

LAV 32 (Coll. Wachtler, Dolomythos Museum, Innichen)

Paratype

LAV 33 (Coll. Wachtler, Dolomythos Museum, Innichen)

Etymology

Honouring the researcher and paleobotanist Thomas Perner, Bad Homburg, Germany

Description

Plant: Stems densely and generously cespitose, reaching up to 30 cm in length and 15 cm in width (LAV 33). 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: Foliage minute, densely spaced, tightly appressed to ascending on the stems (LAV 32). As a result, difficult to see, resembling naked stipes.

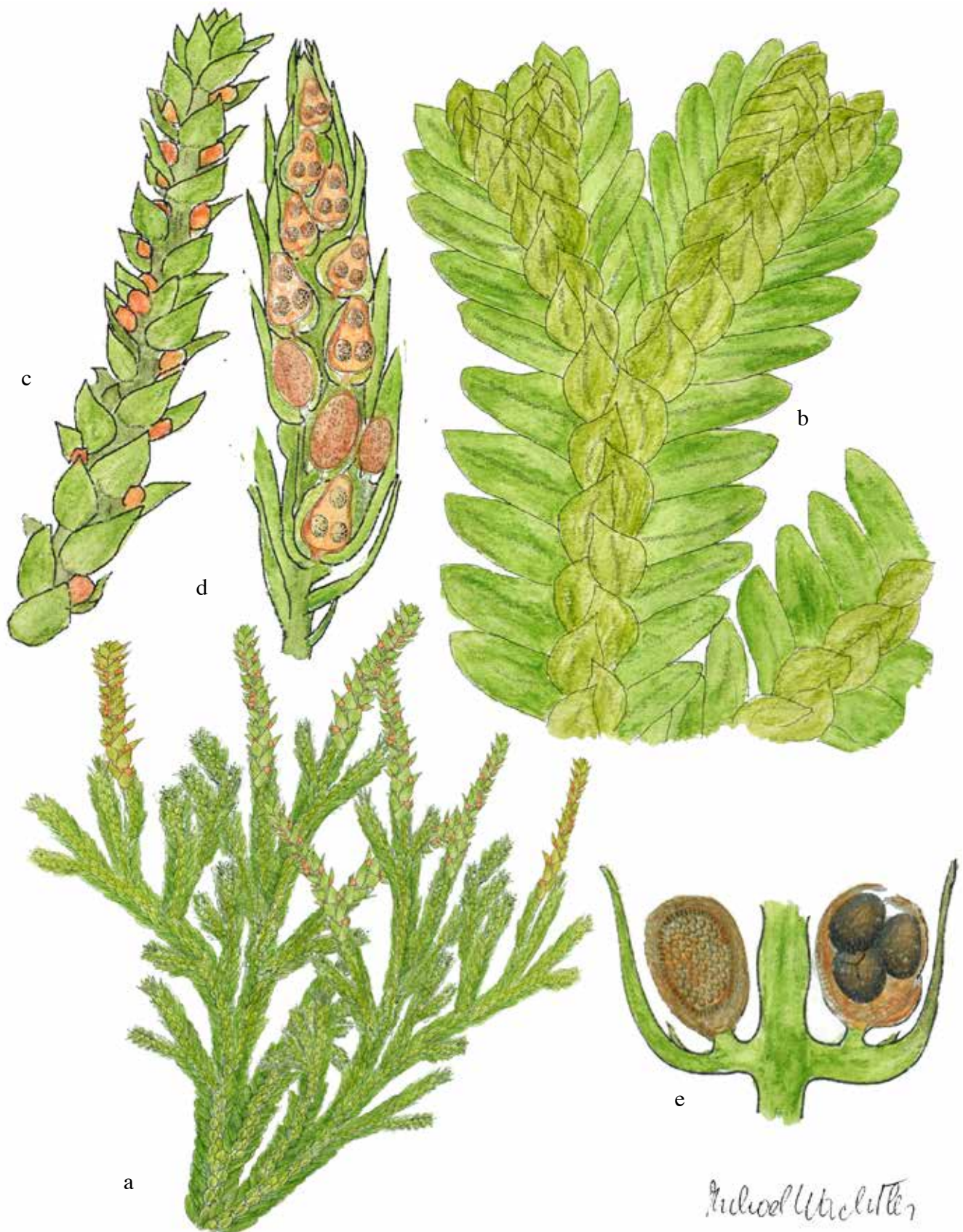
Fertile parts: Strobili terminal on sterile shoots, elongated, reaching a length of 7 cm (LAV 32 holotype), by a width of only 0.2 cm. Heterosporous, mega- and microsporangia, equipped with an elongated pointed apex, occurring in the same strobilus (LAV 33) and therefore easily recognisable from sterile shoots.

Remarks

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 Lavanter Alm. Probably due to their plainness but also the area's remoteness (a long walking-distance of about three hours) till now they had never attracted attention. Interestingly they occur in abundance with one 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 rough and stormy.

Discussion and ecology

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



***Selaginellites venieri* (Early-Middle Triassic) Reconstructions**

a. Whole plant; b. Detail, evidencing the arrangement of the anisophyllous leaves; c. Fertile strobilo; d. Inside view of a fertile strobilo; e. Detail of the micro- and macrosporangia

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 and are included in one large genus of about 700 species. 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 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 lanceolate 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 Rhaetian *Selaginellites coburgensis* is now relatively well documented. It holds a multibranched leafy shoot (5.5 cm wide 3.3 cm long, the main axis 0.2–0.25 cm wide). All axes bear more or less densely spaced leaves arranged in distinct rows. The leaves are arranged into two lateral rows of larger and two median rows of smaller leaves also anisophyllous, and therefore it cannot be regarded as closely related with *Selaginellites perneri*. Also the mega- and microsporangia appear to grow on separate strobili (Van Konijnenburg-Van Cittert et al., 2014, 2016). *Selaginellites perneri* seems therefore to be closely related to Early–Middle Triassic *Selaginellites leonardii* that manifest micro- and macrosporophylls on the same strobilus.

From the extant Sellaginellaceae the well-known *Selaginella lepidophylla* has some similarities with *Selaginellites venieri*, being also anisophyllous.

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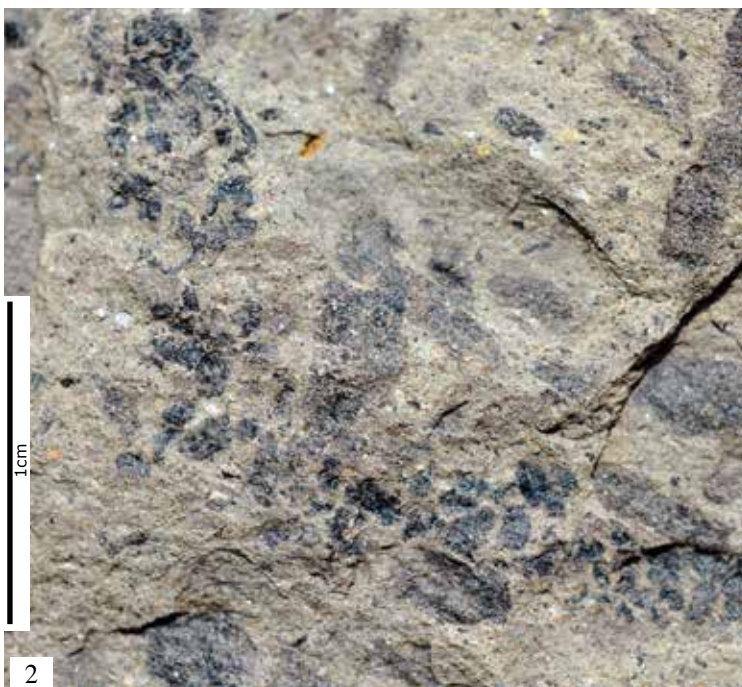
***Selaginellites perneri* (Late Triassic) Reconstructions**

a. Whole plant (LAV 33); b. Apical part of a sterile branchlet (LAV 27); c. Sporangiate strobilo (LAV 32); d. Apical part of the fertile strobilo; e. Macrosporangia and f. microsporangia; g. Inside view of a cone. Lienz Dolomites



***Selaginellites perneri* n. sp. (Late Triassic) sporophylls**

1. Two mainly entire plants, the left having a length of about 30 cm (LAV 33 designed paratype). 2-3. Specimen evidencing the size of the single leaves (0.3 cm) (LAV 26); 4. Isolated part of a branchlet (LAV 27); All Coll. Wachtler, Lavanter Alm, Lienz-Dolomites, Tyrolean part, Carnian)



***Selaginellites perneri* n. sp. (Late Triassic) sporophylls**

1. Slab with several sporangiate strobili, one of them measuring 7 x 0.2 cm; 2. Detail of the apical semi-destroyed microsporangia; 3. Detail of the lower macrosporangia (All LAV 32, designed holotype) All Coll. Wachtler, Lavanter Alm, Lienz-Dolomites, Tyrolean part, Carnian)