Swedenborgia nissleri, a characteristic conifer from the Middle Triassic German Hauptsandstein

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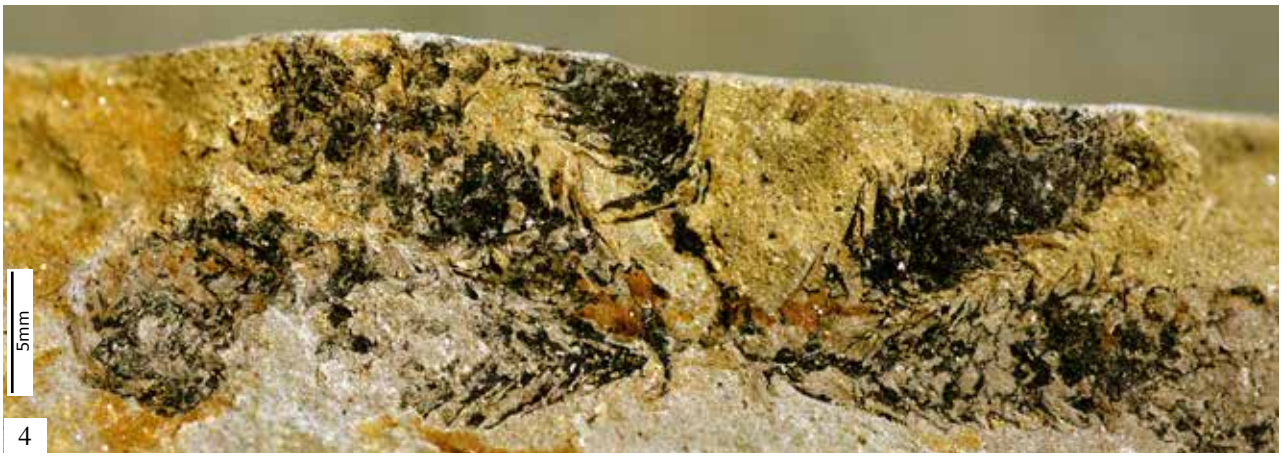
In the German Lower Keuper (Erfurt-Formation, Upper Ladinian, Middle Triassic), specifically owing to their particularly well preserved plant-remains in the well-known locality of Ilsfeld (Baden-Württemberg near Heilbronn), the number of conifer species is small in comparison to the all-dominating horsetail plants and ferns. However, meticulous collection meant that it was still possible to reconstruct the details of a probably bush-like dioecious conifer of the Voltziales order. It is classified as *Swedenborgia nissler*i n. sp. Curiously, there is a large number of large male araucarian *Willsiostrobus silberhorni* n. sp. cones and female *Swedenborgia* seed scales and cones, compared to just a few isolated branch and leaf elements. And if branches are found, then they are characterised by many broken narrow needles.

Key words: Triassic, Keuper, Coniferophyta, Voltziales

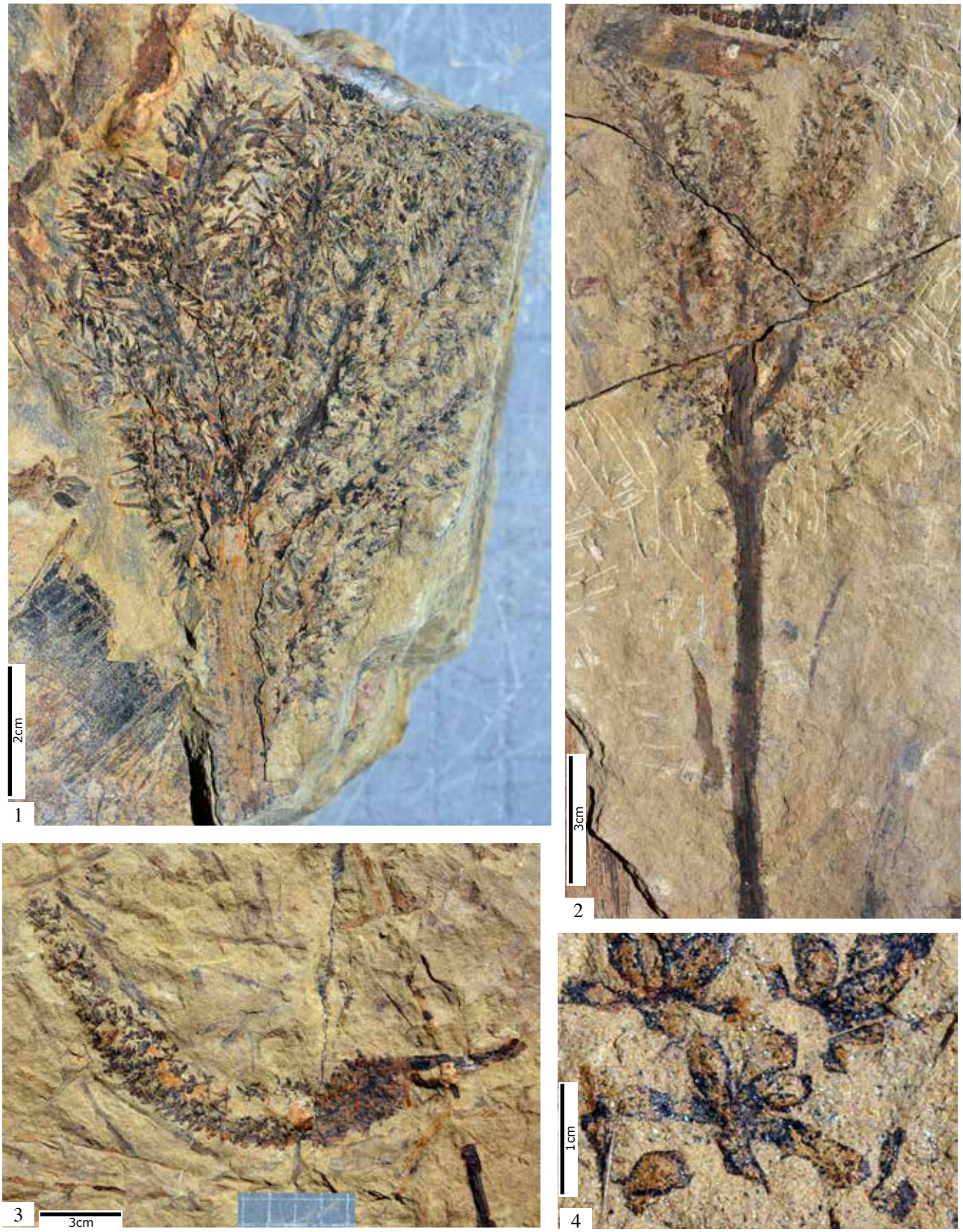
The conifer-genus *Swedenborgia,* mostly associated with its female cones or five-lobed seed scales, stretched from the Middle Triassic to Rhaetian–Liassic and must have died out thereafter. Besides the first described genus *Swedenborgia cryptomerioides* (Nathorst, 1876), from the Liassic of Sweden but spreading as far as Greenland and Asia, other subspecies are known. These subspecies include *Swedenborgia minor* and

Swedenborgia nissleri. 1-2 Different developing stages of female cones (ILS 204, 479); 3. Male cone (ILS 51) All Ilsfeld (Baden-Württemberg, Germany) All Coll. Nißler



***Swedenborgia nissleri n. sp.* (Middle Triassic) Cones twigs and leaves**

1. Holotype (ILS 29) 1. Shoot with ten female cones and one male (Coll. Nißler, Staatliches Museum für Naturkunde (SMNS), Stuttgart); 2-3 Twig and detail of the heterophyllous leaves (ILS 792, Coll. Frieß, ILS 191, Coll. Nißler); 4. Five young female cones connected on the same twig. This compound of several cones was typically for *Swedenborgia* (ILS 544), all Ilsfeld, Ladinian, Longobardian.

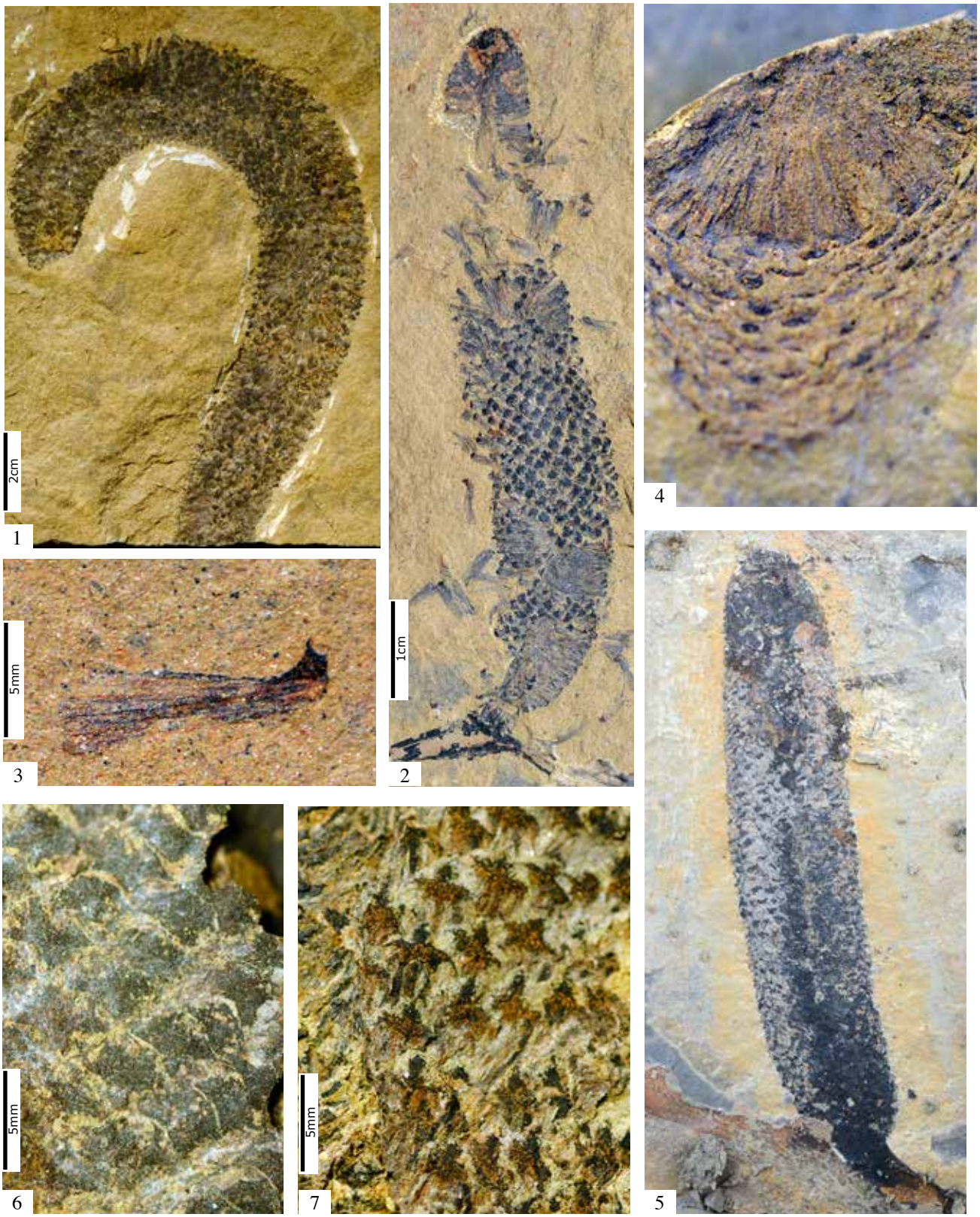


***Swedenborgia nissleri n. sp.* (Middle Triassic) Female cones**

1. Twig with seven female cones (ILS 859); 2. Four female cones. Interesting is the especially long stipe (ILS 858); 3-4. Female cone with a single five-lobed scale and several attached or released seeds (ILS 857) All Ilsfeld, Coll. Pohl.

***Swedenborgia nissleri n. sp.* (Middle Triassic) Female cones**

1. Juvenile cone on a twig (ILS 2); *2*. Mature cone attached on a twig (ILS 144); 3. Adult cone, cross-section (ILS 101); 4. Detail of a long stem on a cone (ILS 742 all Coll. Nißler) 5. Female cone with stipe (ILS 762, Coll. Frieß); 6-7. Accumulation of several five-lobed seed scales (ILS 707, ILS 790 (Coll. Frieß) All Ilsfeld, Ladinian, Longobardian.



***Swedenborgia nissleri n. sp.* (Middle Triassic) Male and female cones**

1. Mature 20 cm long cone (ILS 45, Coll. Nißler); 2-3. Male cone and isolated microsporophyll (ILS 860, 4. Naturally broken pollen cone (*Willsiostrobus silberhorni* holotype) with nice detail of the pollen tubes (ILS 833, Coll. Silberhorn) 5. Cone on a naked twig (ILS 572); Coll. Pohl); 6. Closed microsporophylls (ILS 412); 7. Open microsporophylls with free hanging araucaroid pollen-tubes (ILS 454, all Coll. Nißler); All Ilsfeld, Ladinian, Longobardian.

S. major from the Liassic, S. benkerti from Bayreuth, *S. megasperma, tyttosperma, S. longiloba* from the Russian Donezbecken (Stanislavsky, 1971), and *Swedenborgia lata, rigida, coreanica, onoyamai, attenuata* (Kon'no, 1944) from the Liassic of Japan, China and Korea. Owing to the finding of an exceptionally rich Upper Ladinian (Langobardian) flora in the German Ilsfeld (Baden-Württemberg), the blueprint of an enigmatic conifer, *Swedenborgia nissleri,* could be reconstructed now in all detail.

Division CONIFEROPHYTA
Order Voltziales
Family Aethophyllaceae (Grauvogel-Stamm, 1978)
Genus *Swedenborgia*, Nathorst, 1876

Swedenborgia nissleri n. sp. WACHTLER 2016

Diagnosis

Conifers with female cones consisting of five-lobed seed scales, each containing five seeds hanging upside-down from the top edge. Pollen cones large, araucarian-like with pollen tubes hanging from the tip. Branches with slightly crooked and narrow pointed needles.

Stratigraphic horizon

Erfurt Formation (Lower-Keuper), Upper Ladinian, Longobardian.

Etymology

In honour of Christoph Nißler from Echterdingen, who collected systematically in Ilsfeld and uncovered many valuable missing links.

Holotype

ILS 29, Coll. Nißler, Stuttgart Museum of Natural History (D)

Description

Plant: Probably shrub-like low-growing conifer with male and female cones on the same tree.
Leaves: Irregular branching with sometimes crooked pointed needles of 1 cm in length (Holotype ILS 29, 252), but also showing heterophyllous foliage with narrow needles up to 3 cm long (ILS 315, 191, 226). Easily decomposing branches and needles.
Pollen organs (*Willsiostrobus silberhorni* type): Narrow elongated cones up to 25 cm long with several from the lower hanging pollen sacs.
Seed organs: 10–15 cm long, 3 cm wide cones, attached to the branches with narrow stems of up to 5 cm length. Seed scales with five lobes, tapering to a point and without bracts. On each of the five lobes an elliptical elongated seed, approximately 0.5 cm long hanging dorsiventrally at the top end.

Willsiostrobus silberhorni n. sp. WACHTLER 2016

Diagnosis

Pollen cones, large, araucarian character. Microsporophylls with short pointed to lightly rounded bract attachments. Pollen tubes hanging down dorsiventrally from the upper section towards cone shaft.

Etymology

In honour of Peter Silberhorn from Langenbrettach, for his contribution to the palaeobotanic research of the Lower Keuper.

Holotype

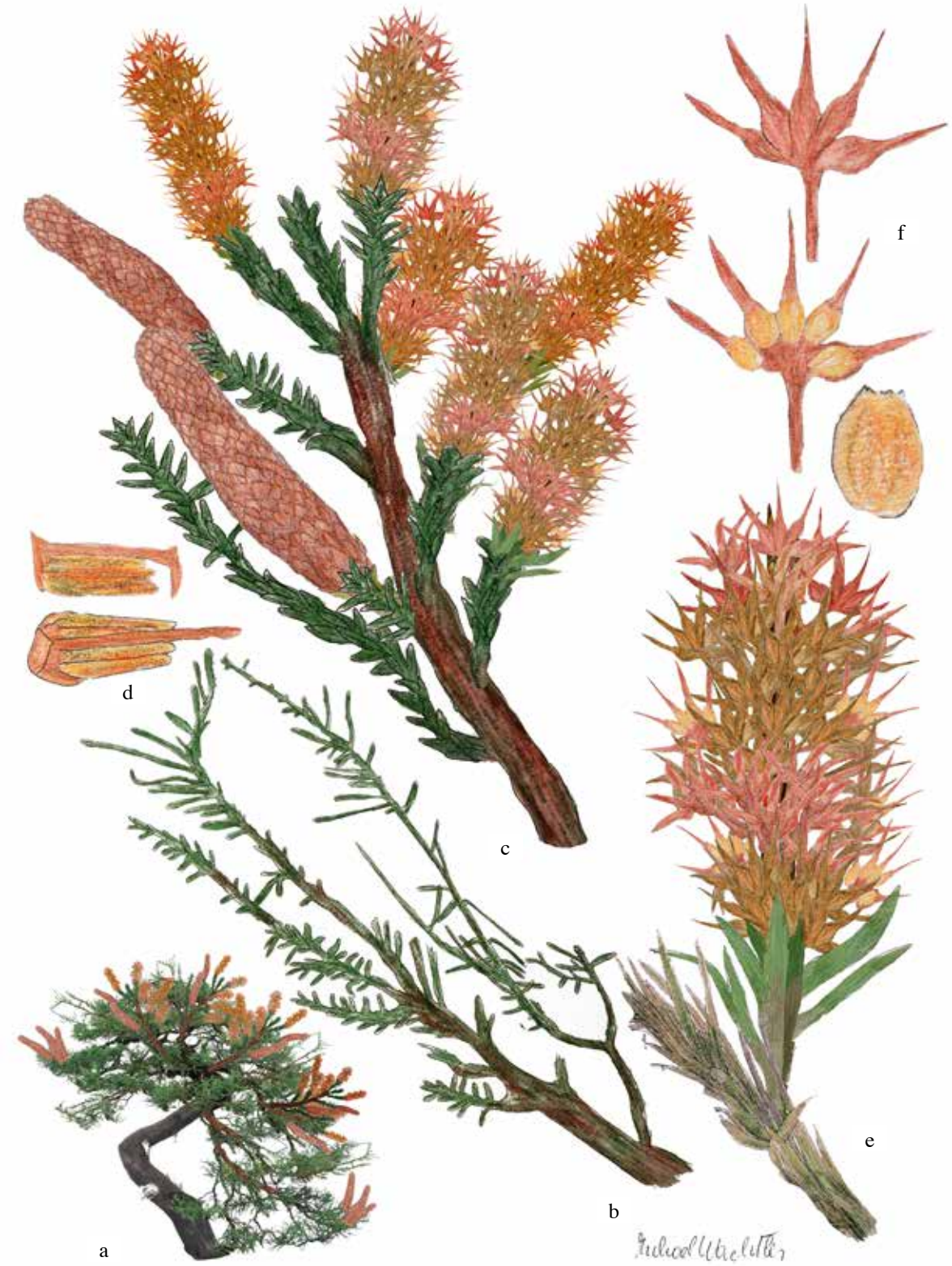
ILS 833, Coll. Silberhorn, Stuttgart Museum of Natural History (D)

Description

Weighty pollen cones up to 20–25 cm long and 3 cm thick. Situated on the ends of the branches attached by a solid 2 cm long and 0.5 cm thick stalk (ILS 572, 208, 51). Microsporophylls araucarian with slightly pointed to rounded tips. On the apical undersides, pollen tubes hanging down towards the cone shaft.

Remarks

Although conifers—particularly those of the Voltziaceae family—characterised many Triassic landscapes, in the Lower Keuper of Ilsfeld, they play a subordinate role; indeed, it seems they did not exist at all in the form of trees. In the midst of the



The conifer *Swedenborgia nissleri*. Middle Triassic. Reconstructions

a. Whole plant; b. Sterile twig ILS 315; ILS 191); c. Branchlet with six female and two male (*Willsiostrobus silberhorni)* cones (ILS 29); d. Microsporophylls from the male cone (ILS 454, 45); e. Female cone (ILS 2, 204) f. Seed scale from the outside and the inner side with five seeds (ILS 10), isolated seed (ILS 479)

horsetail swamps, the only common conifer, *Swedenborgia,* with its large female and especially male cones—otherwise apparently low growing—was probably the only type that survived to become widely established in the hinterland areas, such that the branches dried out and were destroyed during the sedimentation journey, whilst the more robust cones suffered less.

Five-lobed seed scales are commonly found in Europe from the beginning of the Triassic. In general, they were classified as *Aethophyllum* and supported by fossil results classed as low-growing bushy conifers with a dioecious character. That is, having pollen and seed cones on the same plant, a characteristic to be found in extant Araucaria like Australian *Wollemia,* which was not discovered until the 20th century. *Aethophyllum* conifers are also characterised by their narrow elongated leaves, which can reach lengths of 5 to 30 cm (Grauvogel-Stamm, 1978). Particularly, *Aethophyllum stipulare* from the Buntsandstein (Olenekian-Anisian) is deemed one of the characteristic conifers of Central Europe and is spread across a wide area as far as Spain (Juàrez & Wachtler, 2015). However, it is rare or entirely absent in the southern Alpine areas near Tethys (Wachtler, 2011).

For statistical reasons Lea Grauvogel-Stamm created the genus *Willsiostrobus* for Triassic Voltziales pollen cones (Grauvogel-Stamm, 1978). In this concept, the male cone *Willsiostrobus rhomboidalis* (Grauvogel-Stamm & Schaarschmidt, 1978), thought to belong to *Pelourdea* (ex *Yuccites) vogesiaca,* and *Willsiostrobus acuminatus* (Grauvogel-Stamm & Grauvogel, Grauvogel-Stamm & Schaarschmidt 1978), can be correlated with bushy *Aethophyllum stipulare* or *Willsiostrobus silberhorni (*Wachtler, 2016) pertaining to *Swedenborgia nissleri.* Furthermore, *Willsiostrobus willsii* (Townrow, Grauvogel-Stamm & Schaarschmidt 1978) is suggested as being the pollen cone of *Voltzia heterophylla*. In contrast, there are many pending doubts about *Willsiostrobus cordiformis, W. denticulatus* and *W. ligulatus W. cordiformis,* and *W. bromsgrovensis* (Grauvogel-Stamm & Schmidt, 1978).

There are also major differences in the male cones, which in the case of *Aethophyllum stipulare* (described as *Willsiostrobus acuminatus*) were much smaller and narrower and characterised by 1–2 cm long bracteal appendages. These, on the other hand, are completely absent in *Swedenborgia nissleri (Willsiostrobus silberhorni*).

In contrast to the tree-like *Voltzia* widespread in the Early Triassic epoch and still in the Middle Upper Triassic, where no clusters of female cones were found, for both *Aethophyllum* and *Swedenborgia*, there are numerous apically clustered female cones. Isolated *Swedenborgia* seed scales are found only rarely, whereas with *Voltzia,* this is the norm and only occasionally are juvenile female cones found complete, torn off by storms. It can therefore be assumed that the female cones of *Swedenborgia* generally decayed on the ground, if at all, only after maturity, whereas *Voltzia* cones decomposed on the tree, similar to many extant Araucaria.

References

Grauvogel-Stamm, L., (1978). La flore du Grès à Voltzia (Buntsandstein supérieur) des Vosges du Nord (France). Morphologie, anatomie, interprétations phylogénique et paléogéographique. Sciences Géologiques, Mémoire 50, 1–225.

Juárez , J., Wachtler M. (2015): Early-Middle Triassic (Anisian) Fossil Floras from Majorca (Spain), Dolomythos, Innichen, p. 1- 40.

Kon'no, E. (1944): Contribution to our knowledge of *Swedenborgia*. Japan. J. Geolog. Geogr., 19, p. 27 - 66, 14 fig. 5 pl. Tokyo.

Stanislavsky, F. A., (1971): Flore fossile et stratigraphie des d´depots du Trias superérieur du Bassin du Donetz (en russe) Acad. Sci. Kiev, 140 p., 36 pl.

Wachtler, M., (06/2011): Evolutionary lines of conifers from the Early-Middle Triassic (Anisian) Piz da Peres (Dolomites - Northern Italy), Dolomythos, Innichen. p. 95 - 164

Swedenborgia nissleri: Many young female cones connected on the same twig and detail (ILS 714), Ilsfeld, Ladinian, Coll. Perner