New data on *Selaginellites coburgensis* from the Rhaetian of Wüstenwelsberg (Upper Franconia, Germany)

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With 2 figures

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Abstract: A branched shoot with several attached microsporangiate strobili of the Rhaetian (late Triassic) herbaceous lycophyte *Selaginellites coburgensis* is described from Wüstenwelsberg near Coburg, Germany, the locus typicus of the species. The strobili all contain *Uvaesporites*-type microspores, precisely as the single, detached strobilus fragment found in association with one of the original specimens.

Key words: Lycophytes, Selaginellales, Late Triassic, *in situ* microspores

1. Introduction

Several different species in the selaginellalean compression genus *Selaginellites*, as well as dispersed *Uvaesporites*-type spores, have been described from the Triassic of Europe and beyond. However, only few of these taxa are Late Triassic in age, including *Selaginellites hallei* LUNDBLAD 1950 from the Rhaetian of Sweden (LUNDBLAD 1950a, b), *Selaginella anasazia* ASH 1972 from the Norian of the United States (ASH 1972), *Selaginellites yunnanensis* HSÜ 1950 ex LI et al. 1976 from the Upper Triassic/Lower Jurassic of China, and *Selaginellites coburgensis* VAN KONIJNENBURG-VAN CITTERT et al. 2014 from the Rhaetian of Wüstenwelsberg near Coburg (Upper Franconia, Germany). Moreover, reproductive structures (i.e. strobili containing micro- and/or megaspores) have been recorded for only a few taxa; none of these reproductive structures has been found in organic connection to vegetative shoots.

Selaginellites coburgensis as described by VAN KONIJNENBURG-VAN CITTERT et al. (2014) consists of several sterile shoots and a single, fragmentary strobilus with *in situ* microspores from the same stratigraphic horizon. Although sterile and fertile remains were suggested as belonging to the same species, no organic connection or data on epidermal anatomy were available to test this hypothesis. Since the initial description of *Selaginellites coburgensis* a more complete specimen was discovered (in 2014 by G. DÜTSCH) that consists of a twice-branched main axis. Each leafy branch forks several times, and at least in two cases terminal strobili are preserved. This paper describes the new specimen, including in *situ* microspores, which demonstrates that the isolated fragmentary strobilus and the leafy shoots initially assigned as *S. coburgensis* in fact belong to the same taxon. *Selaginellites coburgensis* is significant since it represents a rare element of macropalaeobotanical evidence of the presence of lycophytes in the Rhaetian of Germany. Moreover, *S. coburgensis*

represents the first Triassic *Selaginellites* species for which vegetative shoots and strobili have been documented in organic connection.

2. Material and methods

The new specimen comes from a sandstone quarry near the village of Wüstenwelsberg, approximately 20 km SW of Coburg (Bavaria, Germany; for details, see BONIS et al. 2010 and VAN KONIJNENBURG-VAN CITTERT et al. 2014). The fossiliferous layers are Late Triassic (Rhaetian) in age and are comprised of alternating clay stone and sandstone layers. The fossil comes from the clay layers, one of which (i.e. the so-called 'Hauptton') is up to 10 m thick, belongs to the Contorta beds, and has yielded the majority of the *Selaginellites coburgensis* specimens that formed the basis for the original description.

The specimen is deposited in the collection of G. DÜTSCH (accession number 15Wü14), but will eventually be transferred to the collections of the University of Utrecht, the Netherlands. Fossils were studied with a dissecting microscope and photographed with a Nikon D-700 FX digital camera. Several sporangia were isolated and macerated using Schulze's reagent (30% HNO_3 with $KClO_3$; neutralised in 5% KOH). Microspores were mounted in glycerine jelly, sealed with paraplast, and analysed using normal transmitted light microscopy equipment (Leica). Spores were photographed under an Olympus BX51 transmitted light microscope equipped with an Olympus DP71 digital camera.

3. Systematic palaeobotany

Class Lycopodiopsida

Order Selaginellales PRANTL 1874

Family Selaginellaceae WILLKOMM 1854

Genus *Selaginellites* ZEILLER 1906

Selaginellites coburgensis VAN KONIJNENBURG-VAN CITTERT et al. 2014

Figs. 1 and 2

Description: The specimen comprises a portion of multibranched leafy shoot 55 mm wide and 33 mm long (Fig. 1A). The main axis is dorsiventrally compressed and 2–2.5 mm wide; two lateral branch systems are inserted, both arising at angles of c. 60°. The two lateral branch systems extend from the main axis in opposite direction at a distance of 13 mm. One of the laterals forks dichotomously four times, while the other shows three forkings. Forking usually occurs at angles of 20–60°. The individual axis segments are not narrower distal to dichotomies, precisely as in the original material of *Selaginellites coburgensis*. All axes bear more or less densely spaced leaves (microphylls) arranged in distinct rows. Shoots are anisophyllous, i.e., leaves are arranged into two lateral rows of larger and two median rows of smaller leaves. The leaves have the same dimensions as indicated for the type materials (VAN KONIJNENBURG-VAN CITTERT et al. 2014).

Terminal strobili are attached to at least two (Fig. 1A, B), possibly three or four last order lateral branches. However, two of the imprints are indistinct, and thus render it impossible to determine whether the structures actually represent strobili (Fig. 1A, B). The two unequivocal strobili are 4 and 5 mm long, respectively, and c. 1.5 mm wide. They consist of an axis bearing up to 12 helically arranged, roundish-ovate, entire-margined sporophylls, each of which measures ~1 x 1 mm. Six microsporangia were removed and macerated, and each contained microspores of the *Uvaesporites*-type, precisely as the strobilus that is associated with one of the type specimens (VAN KONIJNENBURG-VAN CITTERT et al. 2014). Most spores occur in tetrads (Fig. 2A, B), but some of the sporangia yielded spores that

apparently were slightly older and occurred more or less separated, although they still cannot be considered fully mature (Fig. 2C-K).

Spores are subcircular and distinctly trilete (Fig. 2D-F), with a mean diameter of 41.0 µm (25 spores measured), extremes 35.2 µm and 45.7 µm; tetrads are 60–71 µm (mean 66 µm) in diameter (Fig. 2A, B). The spores possess a reticulate to verrucate to rugulate ornamentation that is pronounced distally, but weak or absent on the proximal surface (Fig. 2E-H, K). Spores that are more immature sometimes look nearly cavate due to the fact that the exine appears to be subdivided into two distinct layers. In these spores, the thinner exine and the less-developed distal ornamentation form a somewhat cingulate structure that resembles the dispersed spore genus *Densoisporites* (Fig. 2J, K). Occurrence of this feature might be limited to one particular stage of spore development.

4. Discussion

Palynological evidence indicates that representatives from several different lineages of lycophytes occurred in Germany during the Late Triassic and Early Jurassic (the so-called 'Rhaeto-Liassic'; BONIS et al. 2010). However, only two forms, *Selaginellites coburgensis* and *Lepacyclotes kirchneri* BAUER et al. 2014 from the Lower Jurassic of Pechgraben near Bayreuth, have been described to date based on macrofossils. The new specimen of *Selaginellites coburgensis* with attached strobili containing *in situ* microspores is, therefore, important because it links the evidence of the dispersed spore record with the *in situ* spores and – now also unequivocally – with vegetative remains.

4.1 Composition of the strobili

The present-day genus *Selaginella* is heterosporous; mega- and microsporangia usually occur in the same strobilus, but in some species in different strobili (see e.g., VAN KONIJNENBURG -

VAN CITTERT et al. 2014). The strobili of *Selaginellites coburgensis* described in this paper appear to be exclusively microsporangiate. The contents from six microsporophylls from one strobilus were macerated, and all six yielded microspores. The same result was obtained with sporophylls from the detached strobilus described in VAN KONIJNENBURG - VAN CITTERT et al. (2014). As a result, mega- and microsporangia in *S. coburgensis* appear to have been formed in separate strobili, unlike those of, e.g., the Middle Triassic *Selaginellites leonardii* KUSTATSCHER et al. 2010 that developed in micro- and macrosporophylls on the same strobilus.

4.2 Comparisons

Several Triassic and younger Mesozoic *Selaginellites* species from Europe and beyond have been described based on leafy shoots and/or strobili containing microspores are surveyed in VAN KONIJNENBURG - VAN CITTERT et al. 2014. No new relevant literature has been published since. The spores (Fig. 2C-K) macerated from the strobili of *Selaginellites coburgensis* are trilete and characterised by a prominent reticulate to verrucate to rugulate distal ornamentation. These structural features are characteristic of the dispersed spore genus *Uvaesporites,* although in some of the *S. coburgensis* spores the outer ornamentation is less pronounced and more similar to dispersed spores attributed to the genus *Densoisporites* (Fig. 2J, K). The dispersed Triassic spore taxon most closely resembling the *in situ* spores of *S. coburgensis* is *Uvaesporites argenteaeformis* (BOLKHOVITINA 1953) SCHULZ 1967, a typical element of the Triassic–Jurassic of Eurasia. The size range concurs with that of *U. argenteaeformis* (i.e. 40-62 µm), and the distal and equatorial exine of the latter are also covered in a reticulum. In the spores described here, the reticulum is less pronounced as in *U. argenteaeformis*, but we suggest this difference might simply be due to the stage of development of the *S. coburgensis* spores (i.e. not yet mature). *Uvaesporites* has been

reported from numerous localities worldwide and ranges from the Permian to Cretaceous (BALME 1995; MCLOUGHLIN et al. 2014). *Uvaesporites* was probably produced by members of the Selaginellales, based on several *in situ* occurrences, including *Selaginellites hallei* (e.g., LUNDBLAD 1950a, 1950b; BALME 1995) and *S. leonardii* (KUSTATSCHER et al. 2010).

4.3 Palaeoecology

Most specimens of *Selaginellites coburgensis*, including the one described here, are compressions, with the cuticle not preserved or too thin and fragile to be obtained for analysis. As a result, information on the epidermal anatomy that could be used in paleoecological considerations is not available. The overall appearance of the leafy shoots of *S. coburgensis* suggest that this plant was small, delicate, with long prostrate primary axes and dichotomously branching lateral systems, perhaps similar in general appearance to the modern *Selaginella helvetica* (see ZHANG et al. 2013; VAN KONIJNENBURG - VAN CITTERT et al. 2014). Climate conditions during the Rhaetian are reconstructed as hot and arid (PRETO et al. 2010), but more humid conditions may have prevailed locally and for short periods of time, perhaps precisely when and where *S. coburgensis* grew (BONIS et al. 2010). Support for this hypothesis is a spike in horsetail, lycophyte and fern spores, combined with remains of aquatic algae (*Botryococcus* KÜTZING 1849, *Cymatiosphaera* WETZEL 1933 ex DEFLANDRE 1954, *Tasmanites* E. NEWTON 1875) that occurs in the layer from which most *S. coburgensis* fossils come. This spike indicates that bodies of stagnant or slowly running water existed in the Wüstenwelsberg area during the latest Rhaetian (VAN KONIJNENBURG - VAN CITTERT et al. 2014).

5. Conclusions

The new specimen of *Selaginellites coburgensis* substantiates the hypothesis that strobili similar to the detached one described by VAN KONIJNENBURG - VAN CITTERT et al. (2014) were produced on the leafy shoots of this species. The new strobili contain the same *Uvaesporites*-type spores as described previously from the detached specimen, but the microspores of the former are more mature. This supports the idea that most *Uvaesporites* spores in the palynological record of the Triassic were produced by *Selaginellites*-type plants. Moreover, physical connections between strobili, leafy shoots, and *in situ* spores are shown for a Triassic representative of *Selaginellites* for the first time. *Selaginellites coburgensis* from the Rhaetian of Wüstenwelsberg (Upper Franconia, Germany) adds significantly to our understanding of the composition of the understory vegetation, which is typically underrepresented in the fossil record due to the fragility of its components (generally herbaceous, hygrophytic plants with thin and fragile cuticles), of an environment that existed immediately before the end-Triassic mass extinction.

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References

ASH, S.D. (1972): Late Triassic plants from the Chinle Formation in North-Eastern Arizona. – Palaeontology, **15**: 598-618.

BALME, B.E. (1995): Fossil *in situ* spores and pollen grains: An annotated catalogue. – Review of Palaeobotany and Palynology, **87**: 1-323.

BAUER, K., KUSTATSCHER, E., DÜTSCH, G., SCHMEISSNER, S., KRINGS, M. & VAN KONIJNENBURG-VAN CITTERT, J.H.A. (2015): *Lepacyclotes kirchneri* n. sp. (Isoetales, Isoetaceae) aus dem unteren Jura von Oberfranken, Deutschland. – Berichte der Naturwissenschaftlichen Gesellschaft Bayreuth 2015, **27**: 429-443.

BONIS, N.R., KÜRSCHNER, W.M. & VAN KONIJNENBURG-VAN CITTERT, J.H.A. (2010): Changing CO_2 conditions during the end-Triassic inferred from stomatal frequency analysis on *Lepidopteris ottonis* (Goeppert) Schimper and *Ginkgoites taeniatus* (Braun) Harris. – Palaeogeography, Palaeoclimatalogy, Palaeoecology, **295**: 146-161.

KUSTATSCHER, E., WACHTLER, M. & VAN KONIJNENBURG-VAN CITTERT, J.H.A. (2010): Lycophytes from the Middle Triassic (Anisian) locality Kühwiesenkopf (Monte prà della Vacca) in the Dolomites (Northern Italy). – Palaeontology, **53**: 595-626.

LI, P.J., CAO, Z.Y. & WU, S.Q. (1976): Mesozoic plants from Yunnan. – In: Nanjing Institute of Geology and Palaeontology, Academia Sinica (Ed.): Mesozoic fossils from Yunnan, 1: 87-150; Beijing (Science Press).

LUNDBLAD, A.B. (1950a): Studies in the Rhaeto–Liassic floras of Sweden. I. – Kungliga Svenska Vetenskapsakademiens Handlingar, **1** (8): 1-82.

LUNDBLAD, A.B. (1950b): On a fossil *Selaginella* from the Rhaetic of Hyllinge, Scania. – Svensk Botanisk Tidskrift, **44**: 477-487.

MCLOUGHLIN, S., JANSSON, I.-M. & VAJDA, V. (2014): Megaspore and microfossil assemblages reveal diverse herbaceous lycophytes in the Australian Early Jurassic flora. – Grana **53**; http://dx.doi.org/10.1080/00173134.2013.848234

POTT, C., SCHMEIßNER, S., DÜTSCH, G. & VAN KONIJNENBURG-VAN CITTERT, J.H.A. (submitted): Bennettitales in the Rhaetian flora of Wüstenwelsberg, Bavaria, Germany. – Review of Palaeobotany and Palynology

PRETO, N., KUSTATSCHER, E. & WIGNALL, P.B. (2010): Triassic climates – state of the art and perspectives. – Palaeogeography, Palaeoclimatology, Palaeoecology, **291**: 1-10.

VAN KONIJNENBURG-VAN CITTERT, J.H.A., KUSTATSCHER, E., BAUER, K., POTT, C., SCHMEISSNER, S., DÜTSCH, G. & KRINGS, M. (2014): A *Selaginellites* from the Rhaetian of Wüstenwelsberg (Upper Franconia, Germany). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **272** (2): 115-127.

ZEILLER, R. (1906): Bassin houiller et Permien de Blanzy et du Creusot. II. Flore fossile. Études Gîtes Minéraux de la France. – 265 pp.; Paris (Ministère des Travaux Publics).

ZHANG, X.C., NOOTEBOOM H.P. & KATO, M. (2013): Selaginellaceae. – In: WU, Z.Y., RAVEN P.H. & HONG, D. Y. (Eds.): Flora of China, Vol. 2-3 (Pteridophytes), 37-66 ; Beijing (Science Press).

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Figure Captions:

Fig. 1. *Selaginellites coburgensis* VAN KONIJNENBURG - VAN CITTERT et al. 2014 from the Rhaetian (uppermost Triassic) of Wüstenwelsberg, Upper Franconia: Branched leafy shoot with attached strobili. **A** –15Wü14, shoot system with at least two attached strobili (white arrows) and several indistinct imprints of putative strobili (black arrow).
B – 15Wü14, detail of A, indicating the attached strobili.
Scale bars = 1 cm.

Fig. 2. *Selaginellites coburgensis* VAN KONIJNENBURG - VAN CITTERT et al. 2014 from the Rhaetian (uppermost Triassic) of Wüstenwelsberg, Upper Franconia: *In situ* spores from 15Wü14. **A**, **B** – Spore tetrads. **C**-**K** – Single spores. Scale bars = 50 µm.