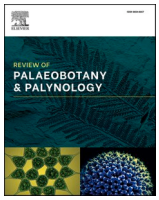
Review of Palaeobotany and Palynology 329 (2024) 105173

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo



Research papers

A new species of *Neocalamites* from the Upper Buntsandstein (Anisian) of Üdingen (Rur Eifel, Germany)

Iris I. Kuipers [a,*], Johanna H.A. van Konijnenburg-van Cittert [b,c], Friederike Wagner-Cremer [a]

[a] Department of Physical Geography, Vening Meinesz Building A, Princetonlaan 8A, 3584 CB Utrecht, the Netherlands
[b] Laboratory of Palaeobotany and Palynology, Vening Meinesz Building A, Princetonlaan 8A, 3584 CB Utrecht, the Netherlands
[c] Naturalis Biodiversity Center, PO Box 9517, 2300 RA Leiden, the Netherlands

ARTICLE INFO

Keywords:
Neocalamites
Anisian
Buntsandstein
Plant fossils

ABSTRACT

Well preserved Early-Middle Triassic plant fossils from Northwest Europe are relatively rare due to the environmental conditions within the Germanic basin during this time period. The only sphenophyte species commonly described in the floras that are found in the area, is *Equisetites mougeotii*. However, only stems without leaf sheaths were ever reported. Here, we describe sphenophyte stems with free standing leaves from the Upper Buntsandstein of Üdingen, Germany, which we attribute to the genus *Neocalamites* based on this characteristic and the difference, mainly in stem size, of the Üdingen material to *E. mougeotii*. Most of the material consists of internodal, infertile stems that are unbranched and vary in width. A few of these stems are three-dimensionally preserved. Due to the difference of the material to the other, rarely present, *Neocalamites* species reported from the Anisian of Western Europe, we propose the plant fossils from Üdingen to be a new species called *Neocalamites vanderburghii* n.sp.

1. Introduction

The North-western European Buntsandstein refers to the characteristic lithostratigraphic unit deposited during the lower to middle Triassic and parallels the Induan to especially Anisian stages. Deposition of the Buntsandstein strata in the Germanic basin occurred under highly continental and arid conditions. The depositional facies has only very limited preservation potential, making fossil floras of this time period extremely rare.

Well known examples of Early-Middle Triassic floras are the Kuhwiesenkopf flora from Italy (Kustatscher et al., 2007), from the margins and the central part of the Germanic basin, the floras from the Vosges (Grès a Voltzia) (e.g., Schimper and Mougeot, 1844; Grauvogel-Stamm, 1978) and the flora from Kommern (Eifel) (Blanckenhorn, 1886), which is the most notable Buntsandsteinflora in Germany. These coeval floras are characterized by the occurrence of the conifers *Voltzia heterophylla* and *Pelourdea vogesiaca* (formerly known as *Yuccites vogesiaca*), the horsetail *Equisetites mougeotii*, the fern *Anomopteris mougeotii*, and the tree fern *Neuropteridium* (Dobruskina, 1994).

The Upper Buntsandsteinflora of Üdingen, located at the northern edge of the Eifel (Germany), has previously been described in a publication by Gothan (1937). The published material includes the horsetails *Equisetites mougeotii* and?*Schizoneura paradoxa*, the conifers *Voltzia heterophylla*, *Albertia latifolia* and *A. elliptica* and the fern *Neuropteridium elegans*. We here present unpublished material from this locality, collected by Dr. J. van der Burgh and identified by J.A. Westerhof (unpublished MSc thesis, 1969). This material mainly consists of conifers, in particular *Voltzia heterophylla*, associated with commonly found *Equisetites mougeotii*. Additional taxa found are *Pelourdea vogesiaca*, *Albertia latifolia, A. elliptica* and *Neuropteridium* sp.. In this study we will focus on the material that had been attributed to *E. mougeotii* but most probably belongs to a different sphenophyte genus.

The horsetail species *Equisetites mougeotii* is historically known from Anisian (Middle Triassic) fossil beds in the Vosges and the Solling Formation in Germany. The leafless, articulated stems were first described by Brongniart (1828, p. 137, pl. XXV figs 4, 5) as *Calamites mougeotii* (also see Schimper and Mougeot, 1844; Blanckenhorn, 1886; Grauvogel-Stamm, 1978). Leaf sheaths of *Equisetites* sp. and *E. mougeotii* have been briefly described and figured by Frentzen (1915) and Grauvogel-Stamm (1978), but in principle leaf sheaths of *Equisetites mougeotii* are very rare.

One of the specimens of the sphenophyte material collected in Üdingen features leaves. It shows a narrow stem with a whorl of separate leaves attached to it, a character not found in the genus *Equisetites,* which is characterized by the presence of leaf sheaths. Due to the

* Corresponding authors.
E-mail address: i.i.kuipers@uu.nl (I.I. Kuipers).

https://doi.org/10.1016/j.revpalbo.2024.105173
Received 26 April 2024; Received in revised form 9 August 2024; Accepted 9 August 2024
Available online 10 August 2024

presences of these free leaves, we suggest that the material from Üdingen formerly recorded as *Equisetites mougeotii* should be attributed to the genus *Neocalamites* instead. We propose the species *Neocalamites vanderburghii* for it.

2. Materials and methods

The town of Üdingen is situated in the Rur Eifel. It is intersected by the Düren-Heimbach railway line, which follows the valley of the river Rur. The plant fossils have been collected in a Buntsandstein outcrop that lies next to the railway. A picture of the site can be found in Gothan (1937) and for the locality, see Fig. 1. The lens-shaped Upper Buntsandstein layer is likely of Anisian, early Middle Triassic, age. Gothan (1937) calls the Üdingen flora a "real upper Buntsandstein flora" and likens it to the French floras from the Vosges (Grès-à-Voltzia/Voltziensandstein). However, Grauvogel-Stamm and Kustatscher (2021) call the Üdingen flora stratigraphically and age-wise unclassifiable. They state that the 'Voltziensandstein' was only present on the western edge of the Germanic basin, and in Germany is only found in the Pfalz (Rhineland-Palatinate) and Saarland. This would mean that, according to their categorization, the Üdingen outcrop should belong to the conifer dominated part of the Sollingen Formation, which is of late Olenekian age. Nevertheless, the state border from Üdingen towards the Pfalz state is less than 35 km as the crow flies. Moreover, an important constituent of many floras from the Sollingen Formation is *Pleuromeia*, which is not present in our assemblage. This, together with a lower diversity in conifer species, is the main difference between the Sollingen and Voltziensandstein floras from Germany (Grauvogel-Stamm and Kustatscher, 2021). Lastly, Jux and Pflug (1958) interpreted the description of the lithology of the Üdingen site by Gothan (1937) to be more characteristic of Muschelkalk facies than Buntsandstein. Also given the fact that the plant remains found in the Üdingen area are very similar to the Muschelkalk flora from Blanckenhorn (1886), and the border between the Buntsandstein and Muschelkalk facies lies close to the site, they proposed that the site marks the transition of the Buntsandstein towards the Muschelkalk.

The fossils have been collected between 1966 and 1968 on various excursions led by Dr. J. van der Burgh and originate from two different layers of the same outcrop. The first is a sandstone layer (ca. 200 m NAP) at the top of the outcrop, the second is a yellow clay layer ('Letten') embedded within the sandstone, which was located at the base of the outcrop. The horizontal distance between the two collection sites is around 50 m. The fossils described in the publication by Gothan (1937) did not originate from the sandstone itself but were found in two consecutive layers of green-gray clay, embedded within the sandstone, located in the middle part of the section.

The preservation of the fossils varies, but in general is not excellent. Fossils found in the clay layer are more compressed than those from the sandstone layer). There were cuticle preparations taken from the fossils by using collodium peels, but with limited success, and no slides of *Equisetites mougeotii* were usable.

All fossil material described is stored at the palaeobotanical collection of Utrecht University. The fossils have been photographed with a Nikon D3500/NIKKOR AF-P 18-55 mm 1:3.5–5.6G DSLR camera.

3. Results

A detailed description of the Üdingen material of this taxon is provided; the numbers refer to the registration numbers in the Utrecht University collection.

Class: EQUISETOPSIDA C. Agardh, 1825
Order: EQUISETALES Dumortier, 1829
Family: UNKNOWN[1]
Genus: **Neocalamites** Halle, 1908 emend. Bomfleur et al., 2013
Neocalamites vanderburghii n. sp.

Etymology: vanderburghii after Dr. Johan van der Burgh who curated, documented, studied, and added material to the palaeobotanical collection of Utrecht University for over 50 years. He also collected the material discussed in this study.

Locality: Üdingen, Germany.

Stratigraphic horizon: Upper Buntsandstein.

Age: Anisian.

Holotype: 2075 a + b (part and counterpart), (Plate I, 1,2). Here designated.

Paratypes: 2954 (Plate II, 4, small stem with two attached leaves); 2196j (Plate I, 4, large stem), 2194 (Plate I, fig. 3 showing inner and outer cortex), 2197w (Plate II, 5, showing pith cast with ribs continuing over the node). Here designated.

Diagnosis: straight cylindrical stems, unbranched, divided into three types of varying width; wide ones rare; stems with internodes and sometimes slightly swollen nodes bearing a circle of leaf scars; vascular bundles continuing over the nodes; whorls of straight, free-standing leaves.

Description: The majority of the fossils are internodal stem fragments. No fertile material has been found. The stems roughly fit into three different categories: wider stems, medium and very thin stems. There are only a few large stems, which are of similar size. The largest stem (2196j, Plate I, 4) measures 40 mm in width. It has ribs of 2–3 mm wide and oval leaf scars with the former connection to the vascular strand visible as a dot within the scar. The medium sized stems are 10 to 20 mm wide and are commonly better preserved. Most of the material falls into this category. The smallest stems are less than 10 mm wide with the smallest being 3 mm wide. The ribs on the stems are usually spaced less than or around 1 mm apart; however, some of the larger stem fragments have ribs that are 2 mm apart and some of the smaller fragments have relatively wide ribs that are ca. 1 mm apart. The ribs continue over the slightly protruding nodes. The largest fragment is 150 mm long and features one node. Only a few stems, and none of the larger pieces feature multiple nodes. The exact internodal length can thus not be determined but can be said to be relatively large. The internodal length of the smaller side branches varies between 18 and 35 mm, and of the smallest (on a point of growth, no. 2075, Plate I, 1,2) between 2 and 10 mm.

No fossils with leaf sheaths have been recorded from Üdingen. One very small young stem (2954, Plate II, 4) that has almost disarticulated nodes dividing it into six pieces measuring around 2–3 mm each, has 2 attached leaves that measure 12 mm and 13 mm in length. Another narrow stem (2075a, Plate I, 1) is a fragment that is widening upwards (0.4 to 0.9 mm wide) and has a leaf attached, with a leaf scar visible at approximately the same height on the stem. The lowest part of the shoot is coalified and shows several nodes, which are widening rapidly. The upper part is wider, lighter colored and shows the imprints of the vascular bundles. The counterpart of the upper part (2075b, Plate I, 2) is black and has a small, peeling coal layer on the lower end. Another specimen features free standing leaves on a whorl at nodal level (2906a, b, Plate II, 1, 2). There are 7 ribbon-like leaves present; they are max. 28 mm long and less than 1 mm wide. No veins are visible. The stem on which they are attached is ca. 4 mm wide and 7 mm long and has a smooth surface. It is not completely clear whether the leaves are attached or if they are disconnected from the stem.

[1] Family Equisetaceae Micheaux ex De Candolle (1804) is often used to house the genus Neocalamites. Family Neocalamitaceae is also sometimes used, but no author name is known for this family. However, the 2013 emendation by Bomfleur et al. gives an unknown family affiliation, which is what is followed here.

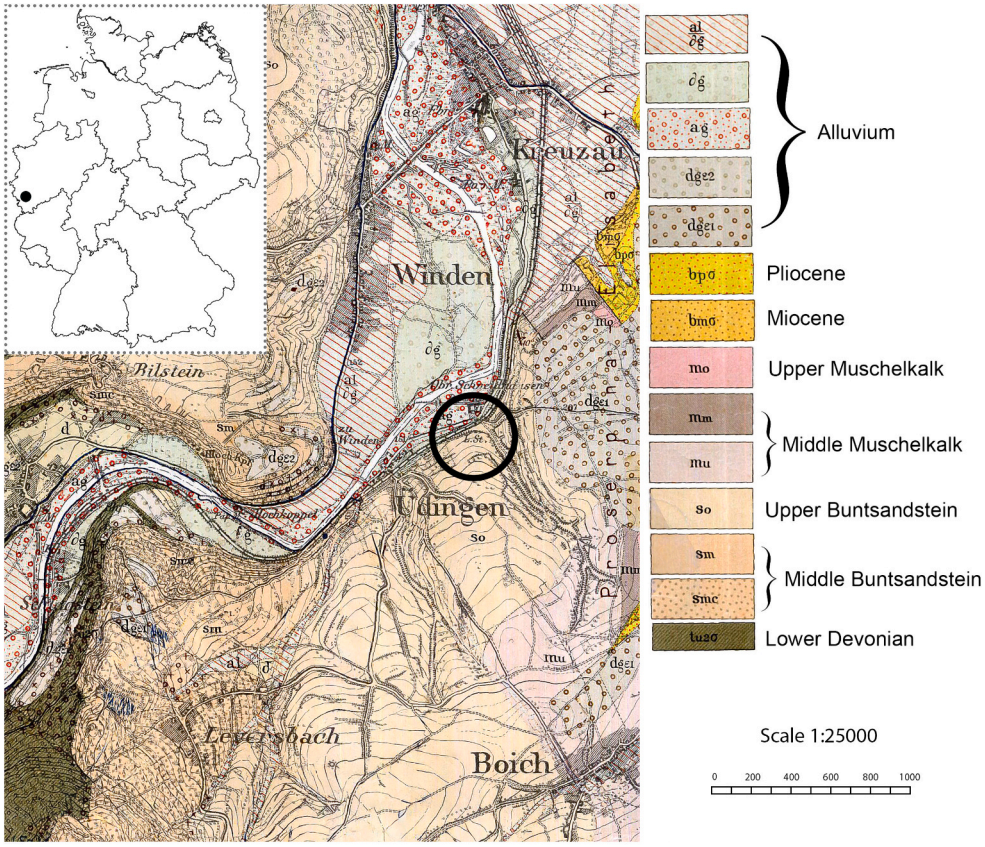


Fig. 1. The location of the Üdingen locality (blue circle). The locality lies in unit **So**, which is Upper Buntsandstein (Anisian) and described as fine grained, clayey sandstones with red layers. Adapted from Holzapfel (1910). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Three stem fragments are more or less three-dimensionally preserved and are in different states of compression. Specimen 2195 measures 57 mm in diameter and is the widest fossil with completely preserved margins but is very compressed. Another three-dimensionally preserved specimen (2194, Plate I, 3), 24 mm wide and 144 mm long, shows a dark, slightly compressed pith cavity. The gray outline that lies on top shows the outer cortical surface of the fossil. There is one node present, which is somewhat protruding and continues from the inner part over to the outer part. The impressions of the vascular bundles on the inner part of the fossil lie very close together, the ridges on the outer part lie further apart. Another almost three-dimensional piece (2197w, Plate II, 5) is a 30 mm long obconical pith cast, which is contorted at its base. It widens quickly towards a node, in which it can been clearly seen that the ribs continue over the nodes. This specimen is most likely a stem rising from the rhizome.

A black, peeling coal layer that reveals the impression of the vascular bundles is present on several specimens. One example is 2899 h (Plate II, 6); this is a narrow, 4 mm wide, 50 mm long piece that has relatively wide ribs (1 mm apart) for its width. Another example can be found on 3183 (Plate II, 3), on which two stems that overlie each other are present. One of them is broken and one still has its entire margins. The first stem is 14 mm wide and has 1 mm wide ribs; the overlying stem has better preservation; it measures 10 mm in width and has relatively wide ribs (1 mm) compared to its width. This last fossil has a black layer of coal with some iron on top, that sometimes peels off to reveal the impression of vascular bundles.

Comparison: For comparison to other contemporary *Neocalamites* spp., see paragraph 4.2 and Table 1.

Remarks: A part of the widest fossil (2196j, Plate I, 4) bears a close resemblance to the stem of *Pelourdea* pictured in Schimper and Mougeot (1844, pl. XXIX, fig. 4). It is 160 mm long and 35 mm wide and bears several sets of rhomboid scars that lie roughly on one line. The distance between these sets is around 20 mm. In some parts, ribbing is visible and the distance between two ribs is max. 3 mm. Instead of *Pelourdea* stems, these two fossils (2196j and the one depicted in Schimper and Mougeot) are most likely horsetail remains: Frentzen (1915) writes in a footnote on page 14 that the fossil depicted in Schimper and Mougeot (1844) might be a deformed inner core of *E. mougeotii*, as he has seen several similar fossils among his material with the ridges having the same scaly appearance.

4. Discussion

4.1. Attribution to Neocalamites

We attribute the here described material to the genus *Neocalamites* because no leaf sheaths are inserted at the nodes, but instead there is at least one whorl of free leaves at a node. Below, we compare the material to other coeval *Neocalamites* species as well as to *Equisetites mougeotti* and *Schizoneura paradoxa*.

4.2. Comparison to other (middle) Triassic Neocalamites species

The oldest fossils of the genus *Neocalamites* are of mid-Permian age (Elgorriaga et al., 2018). In Europe, *Neocalamites mansfeldicus* is for example found in Upper Permian Zechstein deposits in Germany and England (Schweitzer, 1986). However, there are, to our knowledge, no occurrences of *Neocalamites* in the earliest Lower Triassic deposits of Europe. In Anisian floras, occurrences of *Neocalamites* are sparse and determinations are often only made on generic level (e.g., Kustatscher

Plate I. Stems of *Neocalamites vanderburghii* n.sp.. 1, 2) Holotype (part and counterpart), stem with growing points and side stem (2075a,b); 3) Paratype, stem showing inner and outer cortical surface (2194); 4) Paratype, large stem with badly preserved ribbing (2196j). Scale bars: 10 mm.

et al., 2007). However, *Neocalamites merianii* has been recorded from Spain (Borruel-Abadía et al., 2014) and *Neocalamites asperrimus* in Italy and Germany (Labandeira et al., 2016; Kustatscher and Van Konijnenburg-van Cittert, 2008). From the Ladinian onwards, *N. merianii* is the most commonly found species of *Neocalamites* found in European deposits (Dobruskina, 1994) and also in larger quantities (e.g., Kelber, 2015; Kustatscher and Van Konijnenburg-van Cittert, 2008); *Neocalamites schoenleinii* was found by Kelber (2015) but could be a junior synonym of *N. merianii* (Kustatscher and Van Konijnenburg-van Cittert, 2008).

If we compare the *Neocalamites* species from Üdingen to these other early/middle Triassic species, we recognize distinct differences. Probably the most morphologically different species is *N. asperrimus* with its characteristic superficial undulations. It could be that these are due to taphonomic processes (Kelber, 2015); no signs of superficial ornamentations are present on the specimens from Üdingen, and we can, therefore, discount this species. *Neocalamites merianii* has much broader ribbing on the outer cortex compared to its fine ribbing when the outer

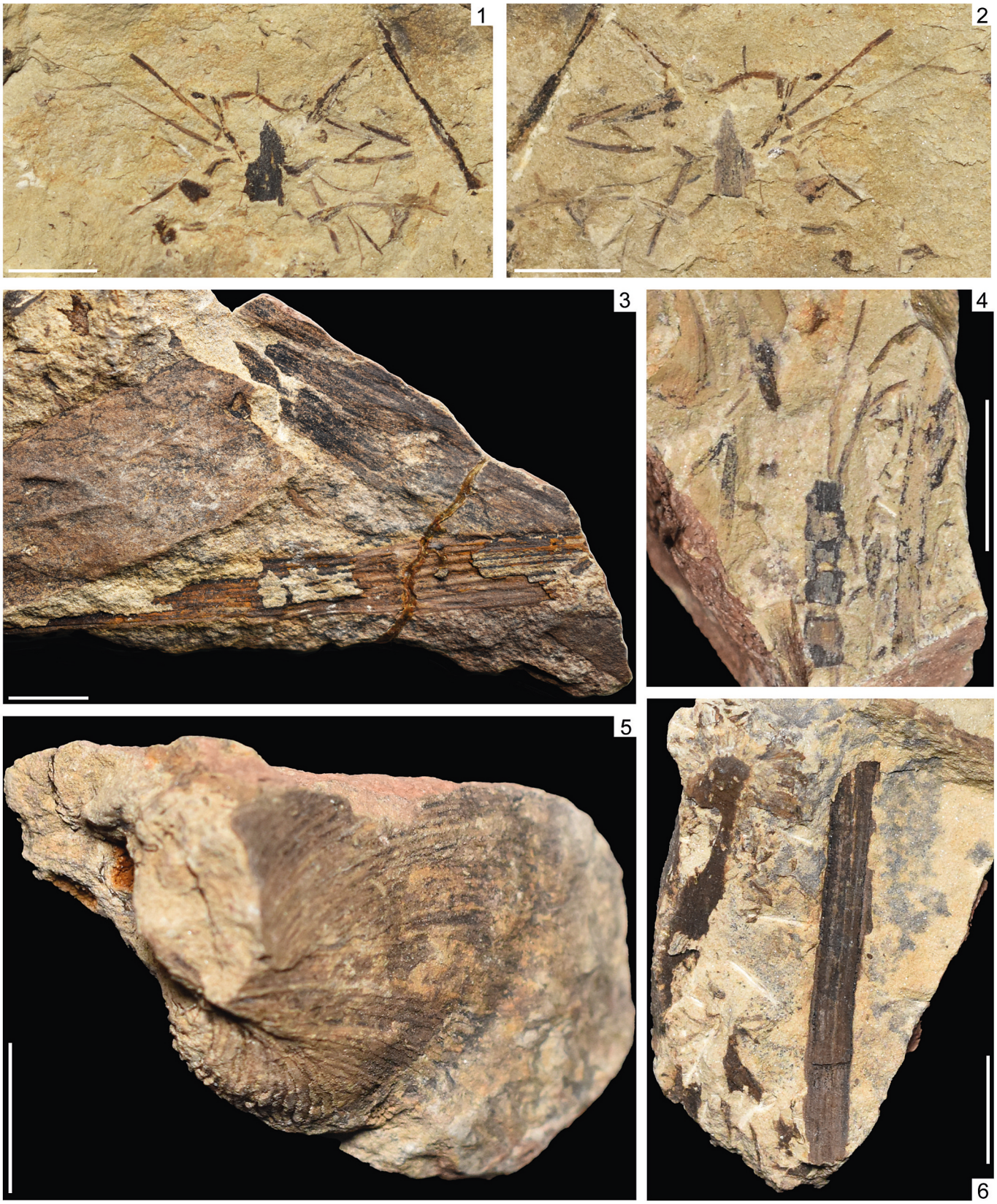


Plate II. *Neocalamites vanderburghii* n.sp., various parts of the stem and leaves. 1,2) stem fragment with a number of leaves (2906a,b); 3) stem fragment with peeling coalified outer cortical surface (3183); 4) Paratype, narrow stem fragment showing multiple nodes and 2 attached leaves (2954); 5) Paratype, three-dimensionally preserved stem fragment showing rhizome attachment (2197w); 6) stem fragment showing impression of the vascular bundles (2899 h). Scale bars: 10 mm.

Table 1
Comparison between *Neocalamites vanderburghii* and the most common Triassic *Neocalamites* species from Europe. [1](Brongniart) Halle, 1908, [2](Franke) Shen, 1990, [3]Schenk in Schönlein, 1865, [4](Schimper) Harris, 1961.

	Neocalamites vanderburghii	*Neocalamites merianii*[1]	*Neocalamites asperrimus*[2]	*Neocalamites schoenleinii*[3]	*Neocalamites hoerensis*[4]
Geographic and stratigraphic range	Germany; Anisian	Germany, Switzerland, Austria, Svalbard; Ladinian to Carnian	Germany; Carnian	southern Germany; Ladinian	Greenland, Sweden, Germany; Rhaetian to Hettangian
Stems	Straight, cylindrical, unbranched, 40 to <10 mm wide.	Bush-like growth, clear difference between primary and secondary shoots. 40–60 mm wide	Superficial undulations, narrow stems.	See *N. merianii*	Up to 50 mm wide; clear ridges, ca. three times no. of leaf scars. Main stem large, branches rare.
Nodes/ internodes	Slightly swollen nodes bearing a circle of leaf scars; vascular bundles continuing over the nodes.	Swollen nodes	See. *N. merianii*	See *N. merianii*	Internodes typically 120 × 40 mm. Nodes without diaphragm, very slightly protruding. Outer surface of internode nearly smooth in smaller stems but showing ridges due to vascular strands in large stems.
Ribbing	Usually spaced less than or around 1 mm apart.	Much broader ribbing (ca. 7–17 mm) on the outer cortex compared to inside. Vascular bundles 6-10x no. of outer cortex ridges.	See *N. merianii*	See *N. merianii*	Longitudinal ridges on main stems 10–15 per cm. In main stem, ridges about 3-4x no. of leaves, in smaller stems ca. 2x, in smallest stems equal.
Leaves	Ribbon-like; free standing at base; max. 28 mm long, <1 mm wide.	Free at the base; slender and linear; 10–24 leaves per whorl; only present on the lateral shoots; small midrib present.	See *N. merianii*	Broader leaves than *N. merianii.*	Main stems leafless, medium and small stems usually with leaves. Leaves per whorl equal, ca. 120 mm long, 2 mm wide in the middle and basal thirds, tapering in the upper third. Midrib broad, ill-defined, not keeled; margins entire, flat; lamina showing rather large transfusion cells.

cortex is absent, and impressions of the vascular bundles are shown. In those specimens from Üdingen in which both the outer cortex is preserved and the impressions of the vascular bundles are visible, no such size difference in ribbing is visible. Wider ribbing is visible in some specimens; however, this is not nearly as wide as can be seen in *N. merianii* (e.g., Kustatscher and Van Konijnenburg-van Cittert, 2008). Another European middle Triassic *Neocalamites* species is *N. schoenleinii*. Both Schenk (in Schönlein, 1865) and Kelber (2015) argue that *N. schoenleinii* is a separate species based on the broadness of its leaves. Schenk, unlike a.o. Kustatscher and van Konijnenburg-van Cittert (2008), first regarded the material belonging to this species not as a junior synonym of *N. merianii* but as older branches of *N. merianii,* however, he changed his view after seeing wider leaves on apical parts of branches. Wide leaves on smaller stems are also present on the material from Üdingen. However, the similarity between the stems of *N. merianii* and *N. schoenleinii* in regard to the wide ribbing, on top of the lack of consensus over the validity of *N. schoenleinii* as a separate species, makes it unwise to assign the present material to this species.

None of the characteristics of previously described species from the Early/Middle Triassic exactly fits the material from Üdingen. Therefore, we propose to make this a new species of *Neocalamites,* i.e., *Neocalamites vanderburghii*.

4.3. Comparison to Equisetites mougeotii and Schizoneura paradoxa

Equisetites mougeotii is the most common constituent of the fossil assemblage from Üdingen as described by Gothan (1937). Horsetail stems are the second most common fossil found in our material after *Voltzia heterophylla*. *Equisetites mougeotii* has been reported from a large number of Lower Triassic deposits, making it a characteristic species of this interval (Alvarez-Ramis, 1982). It has been consistently found in France, Germany, Italy and Spain (e.g., Frentzen, 1915; Alvarez-Ramis, 1982; Kustatscher et al., 2007). It is, therefore, of interest to determine whether (part of) the horsetail stems from Üdingen belong to *Equisetites mougeotii.*

Equisetites (Calamites) mougeotii was first described by Brongniart (1828) from a locality in the Vosges. Brongniart defined *Calamites mougeotii* as having "nodes smaller than the diameter of the stem; a side branch is sometimes inserted at a node; ribs on the stem are parallel, regular, broad, flat". Schimper and Mougeot (1844) also described *E. mougeotii* from the Vosges: *"Articulations ('nodes') rather spaced and a little swollen; ribs far apart, more or less protruding; scars of the branches arranged in whorls all around the articulations (nodes); thick woody cylinder, surrounding a medullary body with narrow and very numerous ribs."*. The relatively large internodal length, finer ribbing of the internal casts and the swelling around the nodes corresponds to our material, but the broad ribbing does not. pl. XXIX, fig. 1 in Schimper and Mougeot (1844) shows an internal cast that is very smooth with the ribs 10 mm apart. This is unlike any of the specimens from Üdingen.

Equisetites mougeotii is also the most commonly found fossil in the flora from Kommern (Eifel), which Blanckenhorn published in 1886. Larger stems are rare in this assemblage and most fossils have fine ribs that lie close together and nodes that lie far apart. These remains are from the upper parts of the plant. This description matches our material very well. The main difference is that the ribs alternate over the nodes, but that is not visible in any of his illustrations. In none of these publications attached leaves were described.

Frentzen (1915) gave a very detailed anatomical description of *E. mougeotii* from different Buntsandstein localities in Baden, Germany. The diameter of the largest specimen exceeds the Üdingen records, likely due to the large amount of material available in this study. Frentzen described the outside of the shaft as widely striped with flat ribs and sides that barely protrude. Some shafts that are 20–30 mm in diameter have 2 ribs per centimeter, which is much less than we observe on similar sized fossils. But he also noted that the width of the ribbing varied with the growth stage of the stems, and that the ribs were often difficult to discern.

Finally, Grauvogel-Stamm (1978) described an abundance of *Equisetites* material from the Vosges. However, a number of them have attached leaf sheaths and are, therefore, not attributed to *E. mougeotii*, but to *Equisetites* sp. (Grauvogel-Stamm and Kustatscher (2021; pl. 4. fig. 1.)) have later figured one of those stem fragments, but now identified as *E. mougeotii*.

Wills (1910) proposed that the internal casts of the leafless stems from the Vosges that were previously assigned to *E. mougeotii* might be internal casts of larger stems of *Schizoneura paradoxa* as they are virtually indistinguishable. Gothan (1937) found leaf fragments and one larger stem in Üdingen that he assigned to *S. paradoxa* (his pl. 31, fig. 3), although only provisionally as the node from which the leaves originate is not clearly visible. *Schizoneura paradoxa* was first described by Schimper and Mougeot (1844) and is typified by leaves that arise from the nodes in two bundles. Although some similarities between their pl.

XXVI, fig. 1 and specimen 2906 (pl. II, 1, 2) from Üdingen could be observed since the pictured leaves are rather slender, the specimens shown on the other plates are rather dissimilar. Wills (1910) described *S. paradoxa* in Keuper outcrops located in Worcestershire, England. The different specimens of *S. paradoxa* that feature leaves provided in Wills (1910) (pl. XV, fig. 1; pl. XVI, fig. 2; pl. XVII, fig. 7) nicely show the characteristic leaves of *Schizoneura*, which are strap-shaped bundles of leaves that come out of a leaf sheath that is usually split into two halves in mature material (Bomfleur et al., 2013). The pictures in Gothan (1937) and Frentzen (1915) on the other hand are less clear. Both authors describe *S. paradoxa* as very rare in their assemblages; but Frentzen (1915) figured and drew *S. paradoxa* in his pl. XII figs. 6 and 7, where the arising leaves are not clearly arranged into two bundles. We have not found any distinct *Schizoneura* with 2 bundles of leaves at the nodes, in the Üdingen assemblage. Yet, it is not impossible that some of our leafless stem fragments might belong to *S. paradoxa*. But, given the characteristics of the leaves and their arrangement, it is most likely that most of the material belongs to the genus *Neocalamites*: the leaves of *Neocalamites* are long, linear and narrow, free standing, and appear in whorls at the nodes, whereas the leaves of *Schizoneura* are fused at the base to form 2 bundles of leaf-sheath segments (Bomfleur et al., 2013). Moreover, the emended diagnosis of *Schizoneura* by Bomfleur et al. (2013) states that the leaves of immature whorls are entirely fused laterally. Given the size of our specimen, it could be an immature branch, making it even less likely to belong to *Schizoneura.* Finally, it is also possible that the few *S. paradoxa* specimens described by Frentzen (1915) and Gothan (1937) are, in fact, *Neocalamites*.

4.4. Ecology

During the time of deposition of the Upper Buntsandstein layers in the Eifel, the fluvial environment that was present in the Germanic basin changed into a deltaic or tidal environment when the sea that deposited the overlying Muschelkalk prograded westwards (Mader, 1983; Gall and Grauvogel-Stamm, 1999). The carbonate containing sandstones of the Upper Buntsandstein were deposited by river channels and are interlaced with the fine clay layers ('Letten'), which were deposited in a brackish environment (Jux and Pflug, 1958; Gall and Grauvogel-Stamm, 1999), evidence that points to marine influences in these mainly terrestrial deposits.

As mentioned before, Jux and Pflug (1958) proposed that the Üdingen site marks the transition between Buntsandstein and Muschelkalk strata. This boundary is characterized by shifts between terrestrial and marine environments. Van Konijnenburg-Van Cittert et al. (2021) suggest possible environmental differences in habitat between *Neocalamites* and *Equisetites,* where *Neocalamites* may grow in moving water and *Equisetites* only grows in standing water. This is supported by the fact that some of the sphenophyte fossils from Üdingen were found in a sandstone layer rather than clay, which is indicative of a higher energy environment. The presence of *Neocalamites* in Üdingen, rather than the *Equisetites* species commonly found in coeval floras such as in the Vosges, might thus reflect a divergent local environment at this site.

Specifically looking at the fossils of *Neocalamites,* we propose that *Neocalamites* could indicate a higher energy environment. Lastly, the flora of Üdingen is species-poor in terms of macrofossils. This could be due to the clonal growing habitat of sphenophytes, which might result in large areas dominated by only one species (Pott et al., 2008). However, pollen analysis shows that most contemporary floras are more species rich than the macrofossil assemblages indicate (Gall and Grauvogel-Stamm, 1999).

5. Conclusions

The specimens formerly identified as *Equisetites mougeotii* from Üdingen resemble the discussed material of *E. mougeotii* from the Vosges (Brongniart, 1828; Schimper and Mougeot, 1844; Grauvogel-Stamm, 1978) and Germany (Blanckenhorn, 1886; Frentzen, 1915) in the appearance of the internal casts, the nodes and the continuation of the vascular bundles over the nodes. However, the width between the vascular bundles varies greatly, which might just be an indicator of the growth stage and thickness of the plant remains. The most important difference between the specimens of *E. mougeotii* from the Vosges and other areas in Germany and the material from Üdingen that was previously assigned to the species, is the presence of free-standing leaves that are attached to the nodes rather than leaf sheaths. Thus, the material bears more similarities to the genus *Neocalamites.* Compared to other species within that genus, our material features finer ribbing, especially on the outer surface. It is also slightly older than the most common middle Triassic species, *Neocalamites merianii*. Therefore, we propose that the formerly identified '*Equisetites mougeotii*' from Üdingen in fact belongs to the genus *Neocalamites* and is a new species of *Neocalamites,* viz. *N. vanderburghii*.

This proposition could indicate that *Neocalamites* might be not only present in the flora from Üdingen, but also in some of the known fossil floras from the Anisian which, in turn, has possible implications in terms of the interpretation of the paleoenvironment.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We are grateful to the editor-in-chief Dr. Carrion and two anonymous reviewers for their constructive comments that improved the paper considerably. We also like to thank Onno Tijsma for his support in the paleobotanical collection.

References

Alvarez-Ramis, C., 1982. Presencia de *Equisetites* en el Buntsandstein de la Cordillera Ibérica. COL-PA 37, 33–36.
Blanckenhorn, M., 1886. Die fossile Flora des Buntsandsteins und des Muschelkalks der Umgegend von Commern. Palaeontographica 32, 117–154.
Bomfleur, B., Escapa, I.H., Serbet, R., Taylor, E.L., Taylor, T.N., 2013. A reappraisal of *Neocalamites* and *Schizoneura* (fossil Equisetales) based on material from the Triassic of East Antarctica. Alcheringa 37 (3), 349–365.
Borruel-Abadía, V., Galán-Abellán, A.B., Kustatscher, E., Diéguez, C., López-Gómez, J., De la Horra, R., Barrenechea, J.F., Arche, A., 2014. Palaeoenvironmental reconstruction of the early Anisian from sedimentology and plant remains in the SE Iberian Range (E Spain). Palaeogeogr. Palaeoclimatol. Palaeoecol. 414, 352–369.
Brongniart, A., 1828. Histoire des végétaux fossiles, ou Recherches botaniques et géologiques sur les Végétaux renfermes dans les divers couches du globe. I. Paris 1–488.
Dobruskina, I.A., 1994. Triassic Floras of Eurasia, 10. Springer-Verlag, New York, pp. 1–422.
Elgorriaga, A., Escapa, I.H., Rothwell, G.W., Tomescu, A.M., Cúneo, R.N., 2018. Origin of *Equisetum*: evolution of horsetails (Equisetales) within the major euphyllophyte clade Sphenopsida. Am. J. Bot. 105 (8), 1286–1303.
Frentzen, K., 1915. II. Die Flora des Buntsandsteins Badens. Mitteilungen der Grossherzöglichen Badischen Geologischen Landesanstalt 8 (1), 63–162.
Gall, J.C., Grauvogel-Stamm, L., 1999. Paläoökologie des Oberen Buntsandsteins am Westrand des Germanischen Beckens: Der Voltziensandstein im nordöstlichen Frankreich als deltaische Bildung. Eine ganz andere Welt. München, Verlag Friedrich Pfeil, Trias, pp. 283–298.
Gothan, W., 1937. Über eine Buntsandsteinflorula von Üdingen bei Düren (Rheinland). Jahrb. Preuss. Geol. Landesanst. 58, 352–360.
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.

Grauvogel-Stamm, L., Kustatscher, E., 2021. Makrofloren der Germanischen Trias: Buntsandstein und Muschelkalk. Trias–Aufbruch in das Erdmittelalter, Pfeil, Munich, pp. 218–227.
Halle, T.G., 1908. Zur Kenntnis der Mesozoischen Equisetales Schwedens. Kungliga Svenska Vetenskapsakademiens Handlingar 41 (1), 1–40.
Harris, T.M., 1961. The Yorkshire Jurassic Flora. I Thallophyta-Pteriodphyta. Trustees of the British Museum (Natural History), London.
Holzapfel, E., 1910. Geologische Spezialkarte von Preussen und den Thüringischen Staaten und Nachfolgewerke; [Neue Nr. 5204]. Lendersdorf; Gradabteilung 66 Blatt 13. Kraatz, Berlin. https://doi.org/10.23689/fidgeo-2101.
Jux, U., Pflug, H.D., 1958. Alter und Entstehung der Triasablagerungen und ihrer Erzvorkommen am Rheinischen Schiefergebirge, neue Wirbeltierreste und das Chirotheriumproblem. Abhandlungen des Hessischen Landesamtes für Bodenforschung 27, 7–49.
Kelber, K.-P., 2015. 5. Die Makroflora des Lettenkeupers. In: Der Lettenkeuper - Ein Fenster in die Zeit vor den Dinosauriern. In: Hagdorn, H., Schoch, R., Schweigert, G. (Eds.), Palaeodiversity Supplement. Staatliches Museum für Naturkunde Stuttgart, Stuttgart, pp. 51–100.
Kustatscher, E., Van Konijnenburg-van Cittert, J.H.A., 2008. Lycophytes and horsetails from the Triassic Flora of Thale (Germany). Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen 250 (1), 65–77.
Kustatscher, E., Wachtler, M., Van Konijnenburg-van Cittert, J.H.A., 2007. Horsetails and seedferns from the Anisian locality Kühwiesenkopf (Dolomites, Northern Italy). Palaeontology 50, 1277–1298.
Labandeira, C.C., Kustatscher, E., Wappler, T., 2016. Floral assemblages and patterns of insect herbivory during the Permian to Triassic of Northeastern Italy. PloS One 11 (11), e0165205.
Mader, D., 1983. Evolution of fluvial sedimentation in the Buntsandstein (Lower Triassic) of the Eifel (Germany). Sediment. Geol. 37 (1–2), 1–84.
Pott, C., Kerp, H., Krings, M., 2008. Sphenophytes from the Carnian (Upper Triassic) of Lunz am See (Lower Austria). Jahrb. Geol. Bundesanst. 148 (2), 183–199.
Schimper, W.P., Mougeot, A., 1844. Monographie des Plantes fossiles du Grès Bigarré de la Chaine des Vosges. G. Engelmann, Leipzig, pp. 1–83.
Schenk, A. in Schönlein, J.L., 1865. Abbildungen von fossilen Pflanzen aus dem Keuper Frankens. CW Kreidel's Verlag, Wiesbaden, pp. 1–22.
Schweitzer, H.-J., 1986. The land flora of the English and German Zechstein sequences. Geol. Soc. Lond. Spec. Publ. 22 (1), 31–54.
Shen, G., 1990. *Neocalamites rugosus* Sze and *Equisetites asperrimus* Franke are synonymum. Sci. Geol. Sin. 7 (33), 302–305.
Van Konijnenburg-van Cittert, J.H.A., Schmeißner, S., Dütsch, G., Kustatscher, E., Pott, C., 2021. Plant macrofossils from the Rhaetian of Einberg near Coburg (Bavaria, Germany). Part 1. Ferns, fern allies and seed ferns. Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen 302 (3), 331–353.
Wills, L.J., 1910. On the fossiliferous Lower Keuper Rocks of Worcestershire: with descriptions of some of the plants and animals discovered therein. Proc. Geol. Assoc. 21 (5), 249–331.