

Sphenophytes from the Carnian (Upper Triassic) of Lunz am See (Lower Austria)

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3 Text-Figures, 4 Plates

Niederösterreich
Nördliche Kalkalpen
Trias
Lunzer Flora
Sphenophyten
Systematik

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Sphenophyten aus dem Karn (Obertrias) von Lunz am See (Niederösterreich)

Zusammenfassung

Die Sphenophyten aus der obertriassischen Flora von Lunz werden revidiert und zum ersten Mal sowohl deskriptiv als auch fotografisch dokumentiert. Drei Taxa lassen sich unterscheiden: *Equisetites arenaceus*, *E. conicus* und *Neocalamites merianii*. *Equisetites arenaceus* und *N. merianii* sind recht häufige Vertreter innerhalb der Flora, während von *E. conicus* nur einige wenige Handstücke vorliegen. Fertile Organe (Strobili), die vermutlich zu *E. arenaceus* und *N. merianii* gehören, werden ebenfalls dokumentiert. Während die Gymnospermen (Cycadophyten-Laub und Reproduktionsorgane) von Lunz in den letzten Jahren eingehender untersucht worden sind, wurden die Pteridophyten dieser Flora seit jeher vernachlässigt. Eine detaillierte Kenntnis der Farne und Schachtelhalmgewächse stellt jedoch eine wichtige Komponente bei der Dokumentation der Komplexität des obertriassischen Paläoökosystems der Gegend um Lunz dar. Das Vorkommen dreier, in der oberen Trias weit verbreiteter Sphenophyten-Taxa komplettiert die Ansicht, dass die Lunzer Pflanzen in einer eher feuchten Umgebung wuchsen; eine Flora mit vergleichbarer Zusammensetzung ist zum Beispiel aus dem süd-deutschen Schilfsandstein bekannt. Hier lassen die sedimentologischen Befunde auf ein mäandrierendes Flusssystem schließen, welches viele feuchte Standorte und Biotope für die Pflanzen schuf.

Abstract

The sphenophytes in the Late Triassic flora of Lunz (Lower Austria) are revised and illustrated for the first time. Three taxa have been identified, i.e. *Equisetites arenaceus*, *E. conicus* and *Neocalamites merianii*. *Equisetites arenaceus* and *N. merianii* represent abundant elements of the flora, while *E. conicus* is relatively rare. Putative fertile organs assignable to two of the species (i.e. *E. arenaceus* and *N. merianii*) are also documented. The gymnosperms, especially cycadophyte reproductive structures and foliage, have received considerable scholarly attention during the last few years, while the pteridophyte component of the Lunz flora remains understudied to date. However, detailed knowledge about the ferns and sphenophytes represents a critical component in fully documenting the vegetational and ecological complexity of the Lunz palaeoecosystem. The presence of three widespread sphenophyte taxa at Lunz suggests that the Lunz flora grew in rather humid environmental conditions. This interpretation is corroborated by data from a Schilfsandstein flora from southern Germany, which is comparable to Lunz with regard to composition. Sedimentological analyses of the plant-bearing deposits have shown that this Schilfsandstein flora grew in a meandering and braided river system, in which ample moist habitats existed.

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1. Introduction

The Carnian (Late Triassic) flora from Lunz am See in the Northern Calcareous Alps is one of the most diverse and palaeobotanically significant floras of the Alpine Triassic. The flora largely consists of compression fossils, but impressions and pith casts may also occur. It includes cycadalean and bennettitalean foliage and reproductive structures, (putative) conifer and ginkgophyte leaves, sterile and fertile fern foliage, and a variety of sphenophytes. While the gymnosperms, especially the cycadophyte reproductive structures and foliage, have received considerable scholarly attention (e.g., STUR, 1885; KRASSER, 1909, 1917, 1919; KRÄUSEL, 1949; DOBRUSKINA, 1998; POTT & KRINGS, 2007; POTT et al., 2007a–e), the pteridophytic component of the Lunz flora remains understudied. This is commiserable since detailed knowledge about the ferns and sphenophytes represents a critical component in fully documenting the vegetational and ecological complexity of the Lunz palaeoecosystem.

There are a few descriptions of ferns from Lunz (e.g., *Asterotheca merianii*, *Coniopteris lunzenis*, *Speirocarpus neuberi*, *S. auriculatus*, *Oligocarpia distans*, *O. bullatus*, *Bernoullia lunzensis*, see KRASSER, 1909; in situ spores of *A. merianii*, see BHARDWAJ & SINGH, 1957), but the sphenophytes have attracted next to no attention to date, although one of the first ever illus-

trated Lunz fossils was a sphenophyte (VON ETTINGSHAUSEN, 1851; refigured in Text-Fig. 1). Only a single paper has been published that considers sphenophyte fossils from Lunz, i.e. KRASSER (1909). This paper, however, merely represents a brief commentary on the assignment of various forms either to *Equisetites* or *Equisetum*.

In the oldest known inventory of the Lunz flora, STUR (1885) lists ten sphenophyte taxa, seven of which he introduced as new to science. However, none of the new taxa was correctly typified, and neither illustrations nor descriptions were provided. As a result, the names introduced by STUR are nomina nuda. Also the remaining three sphenophyte taxa were neither illustrated nor described. Here we present a critical evaluation and detailed illustration of the sphenophytes from Lunz.

2. Material, Geological Setting and Methods

The Lunz fossils were collected in the late 19th and early 20th centuries from active coalmines in the area around Lunz am See in the Northern Calcareous Alps of Lower Austria, approximately 100 km west of Vienna. For details on the location of the coalmines and historical collection sites, see POTT et al. (2008b, fig. 1). With more than 5,000 specimens, the Lunz flora is one of the richest Late Triassic megafloras of the Northern Hemisphere. Moreover, with more than 50 taxa recorded to date (STUR, 1885; DOBRUSKINA, 1998; POTT et al., 2007a–e) the Lunz flora also represents one of the most diverse Late Triassic floras worldwide.

The fossils come from the so-called “Lunzer Sandstein”, which is part of the Lunz beds. The Lunz Formation (= Lunzer Schichten) consists of (in ascending order) sandstones, marine marls that gradually grade upwards into terrestrial sands, shales and coal. The intercalated coal-bearing part of the sequence is overlain by marls. A sandstone bed at the top completes the sequence. The plant fossils occur in the shales directly overlying the coal beds. Exact dating of the Lunz Formation continues to be problematic because adequate index fossils (e.g. ammonoids and conodonts) are absent. Recent studies, including regional correlations of biostratigraphically well-established sections within the Hallstatt and Reifling Intraplatform Basins (HORNUNG & BRANDNER, 2005), suggest that the Lunz Formation has to be placed in the upper part of the Reingraben Formation. Consequently, the Lunz Formation is proposed to be late Julian (Julian 2/II) in age. Palynological studies (DUNAY & FISHER, 1978; ROGHI pers. comm., 2006) support a Julian age of the Lunz formation. The upper subunit of the Lunzer Schichten, the Opponitzer Limestone, has been dated as Tuvanian by DUNAY & FISHER (1978).



Text-Fig. 1.
This specimen of a shoot of *Equisetites gamingianus* is one of the first ever illustrated fossils from the flora of Lunz (reproduced from VON ETTINGSHAUSEN, 1851; pl. 8, fig. 2).

The specimens considered in this study are stored in the palaeobotanical collections of the following institutions: Geological Survey of Austria, Vienna, Austria (GBAW); Museum of Natural History, Vienna, Austria (NHMW) and Swedish Museum of Natural History, Stockholm, Sweden (NRHM). Hand specimens were photographed with a Nikon D100 digital camera; in order to increase contrast, cross-polarisation (i.e. polarised light sources together with a polarising filter over the camera lens) was used (SCHAARSCHMIDT, 1973). Strongly inclined and incident illumination was used to visualise raised and depressed (micro-)structures.

3. Mesozoic sphenophytes

The Mesozoic sphenophytes include four major morpho-genera, i.e. *Equisetites*, *Neocalamites*, *Schizoneura*, and *Phyllothea*. The fossil record of *Schizoneura* and *Phyllothea* can be traced to the Carboniferous of the Southern Hemisphere, but the taxa were most widespread (almost cosmopolitan) and diverse during the Jurassic and Early Cretaceous (WING & SUES, 1992; STEWART & ROTHWELL, 1993). The oldest *Neocalamites* fossils are known from the Upper Permian (e.g. BANERJI et al., 1987; NAUGOLNYKH, 2004; ESCAPA & CUNEO, 2006), whereas the youngest representatives have been recorded for the Lower Jurassic; the genus was probably most widespread during the Late Triassic (KELBER & HANSCH, 1995). With regard to growth habit, the *Neocalamites* plant probably resembled a small calamite (STEWART & ROTHWELL, 1993). The fourth genus, *Equisetites*, first occurred in the Carboniferous. *Equisetites* was probably similar in overall morphology to present day *Equisetum*. However, many representatives of *Equisetites* were considerably larger than extant *Equisetum*, and some scholars have suggested that at least some of the largest forms may have produced secondary wood (e.g., SCHWEITZER et al., 1997). Based on their distinct ecological requirements, sphenophytes may provide valuable information with regard to considerations about the structure and ecology of fossil ecosystems.

Division: Sphenophyta
Order: Equisetales
Family: Equisetaceae
Genus: *Equisetites* STERNBERG, 1833

4. Systematic Palaeontology

The morphogenus *Equisetites* was originally established by STERNBERG (1833) to include casts, impressions, and compressions of stems that are similar in overall morphology to modern *Equisetum* (horsetails), but the name is today also used for the entire plant. The genus *Equisetum* encompasses a small and highly distinctive group of vascular plants that is easily recognised in the field and has a sub-cosmopolitan distribution (DES MARAIS et al., 2003). It is widely believed today that the modern horsetails diverged from *Equisetites* by anagenesis during the Cenozoic (DES MARAIS et al., 2003). However, the exact relationship between *Equisetites* and *Equisetum* remains elusive. The fossil record of *Equisetites* can be traced to the Middle Permian (e.g., SEMAKA & GEORGESCU, 1967; STEWART & ROTHWELL, 1993), perhaps even the Pennsylvanian (KIDSTON, 1892; TAYLOR et al., 2009). Some scholars have historically placed fossils that are indistinguishable from modern horsetails in *Equisetum*, whereas *Equisetites* has been used for Mesozoic fossils that could not be positively allied with extant species (KELBER & VAN KONIJNENBURG-VAN CITTERT, 1998). An extensive overview of the fossil and nomenclatorial history of *Equisetites* and its species can be found in WEBER (2005).

If *Equisetites* actually is *Equisetum*, the genus *Equisetum* has existed at least since the Permian (e.g., KIDSTON, 1892; SEMAKA & GEORGESCU, 1967; STEWART & ROTHWELL, 1993; TAYLOR et al., 2009), and thus probably represents one of the oldest extant vascular plant genera (HAUKE, 1963). However, several Triassic and Jurassic representatives of *Equisetites* were significantly larger than present day *Equisetum* (STEWART & ROTHWELL, 1993; KELBER & HANSCH, 1995). For example, the Late Triassic *Equisetites arenaceus* (one of the largest known species in the genus; see KELBER & VAN KONIJNENBURG-VAN CITTERT, 1998) had stems up to 25 cm in diameter, and plants probably grew up to 2.5–3.5 m tall. STEWART & ROTHWELL (1993), and SCHWEITZER et al. (1997) speculate that large *Equisetites* plants may have produced secondary xylem, but state that there is no direct evidence for this at present.

Type species: *Equisetites muensteri* (MÜNSTER) STERNBERG in STERNBERG, K.M. (1833): Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt, II (5–6), p. 43; pl. 16, figs 1–5.

Equisetites arenaceus (JAEGER, 1827) SCHENK, 1864

Plate 1, figs 1–5, plate 2, figs 1, 3

Basionym: *Calamites arenaceus* major, JAEGER, 1827, p. 37, pl. 1, 1–5, pl. 2, 1–7.

Selected references:

- 1827 *Calamites arenaceus* major – JAEGER, p. 37; pl. 1, 1–5; pl. 2, 1–7.
 - 1864 *Equisetites arenaceus* – SCHENK, p. 9; pl. 7, fig. 2.
 - 1877 *Equisetum arenaceum* – HEER, p. 74–75; pl. 26, figs 1–3; pl. 27, figs 1–5; pl. 28; p. 90; pl. 33, fig. 6; pl. 38, figs 10–11.
 - 1885 *Equisetum arenaceum* – STUR, p. 98 [6]
 - 1909 *Equisetites arenaceus* – KRASSER, p. 104 [4]
 - 1922 *Equisetites arenaceum* – FRENTZEN, p. 8; pl. 1, figs 1–6, 8–11
 - 1934 *Equisetites arenaceus* – FRENTZEN, p. 31; pl. 1, figs 1–6; pl. 2, figs 1–2; text-figs 1–3
 - 1959 *Equisetites arenaceus* – KRÄUSEL & LESCHIK, p. 8–12; text-fig. 2; pl. 2, figs 16–21; pl. 3, figs 22–29; pl. 4, fig. 30; pl. 5, fig. 37
 - 1995 *Equisetites arenaceus* – KELBER & HANSCH, p. 31–44; text-figs 33–82; p. 91; text-figs 186–188, 191, 193
 - 1998 *Equisetites arenaceus* – KELBER & VAN KONIJNENBURG-VAN CITTERT, p. 2–26; pl. 1–7, text-figs 2–11
- A more detailed synonymy can be found in KRÄUSEL (1958) and KELBER & VAN KONIJNENBURG-VAN CITTERT (1998).

Description: Specimens are preserved as compressions or pith casts (steinkerns). Shoots/stems are cylindrical and 4.4–11.8 cm wide. All specimens are incomplete; the longest has a length of ~54 cm. Shoots/stems are articulate, i.e. regularly subdivided into nodes and internodes (Pl. 1, fig. 1; pl. 2, fig. 1); the nodes are slightly widened, whereas the internodes are elongate and usually between 2 and 6 cm long. However, in a few specimens, the internodes are up to 14.5 cm long. The length of the internodes decreases towards the apex. At the tip of the shoot, segments are telescoped to form a dome-shaped apex (Pl. 1, fig. 5). The *Equisetites arenaceus* specimens from Lunz do not show direct evidence for the existence of lateral branches in the form of branch scars on primary shoots. However, some of the more slender specimens may represent isolated lateral branches. Reproductive structures in organic connection and ochreoles have not been observed.

The surface of compressed internodes is smooth (Pl. 1, fig. 4); short segments are completely covered by the leaf sheaths (Pl. 1, fig. 1), while longer segments (Pl. 2, fig. 1) are covered only in the lower part, close to the

lower node. The number of microphylls (leaves) per node probably exceeds 90–100. The proximal portions of the microphylls appear to have been connate (i.e. interconnected or fused) at their lateral margins (Pl. 1, figs 2–3). The connate portions of the microphylls forming the sheath are up to 3.4 mm wide and 36.0 mm long, and are characterised by a prominent central longitudinal strand (i.e. the vascular bundle) that extends into the free distal portion of the microphyll (Pl. 1, fig. 2–3). The interface between two connate microphylls is characterised by a slender, inverse-triangular and distinctly bordered depression, the so-called commissural furrow (Pl. 1, figs 2–3), which is v-shaped in cross-section. The commissural furrow extends down into the internode, is reduced in width basipetally, and eventually terminates immediately before the next lower node (Pl. 1, figs 1, 4). The free distal portion of the microphylls (Pl. 1, fig. 2) is up to 12.0 mm long, spine-like, and resembles the microphyll tips described by KELBER (1993), KELBER & HANSCH (1995), and KELBER & VAN KONIJNENBURG-VAN CITTERT (1998). Isolated distal microphyll portions occur on some of the slabs. It has been suggested that these parts are shed by the plant (KELBER & HANSCH, 1995), and thus are not preserved in some of the specimens (e.g. NHMW 2006B0008/0009, 2006B0008/0045; GBAW 1909/003/0287, 1909/003/0297, 1909/003/0324).

Only a single specimen (GBAW 1909/003/0651) in the Lunz collections displays a reproductive structure that we interpret as belonging to *Equisetites arenaceus* (Pl. 2, fig. 3) based on structural correspondences with *E. arenaceus* reproductive structures (strobili) from the Keuper of Germany (KELBER & HANSCH, 1995; KELBER & VAN KONIJNENBURG-VAN CITTERT, 1998). This specimen consists of an incomplete strobilus (18.6 × 26.9 mm) constructed of hexagonal sporangiophore heads (up to 5.3 mm in diameter) that are closely arranged around a central axis; the whole strobilus was probably ovoid in outline. Unfortunately, organic material is not preserved, and thus it is not possible to extract spores.

In a few of the stem specimens internodes are exceptionally long (GBAW 1909/003/0325; NHRM S148248, S148254; internodes up to 14.5 cm). These specimens perhaps represent parts of the horizontal rhizomatous system. However, adventitious roots have not been observed in any of the specimens.

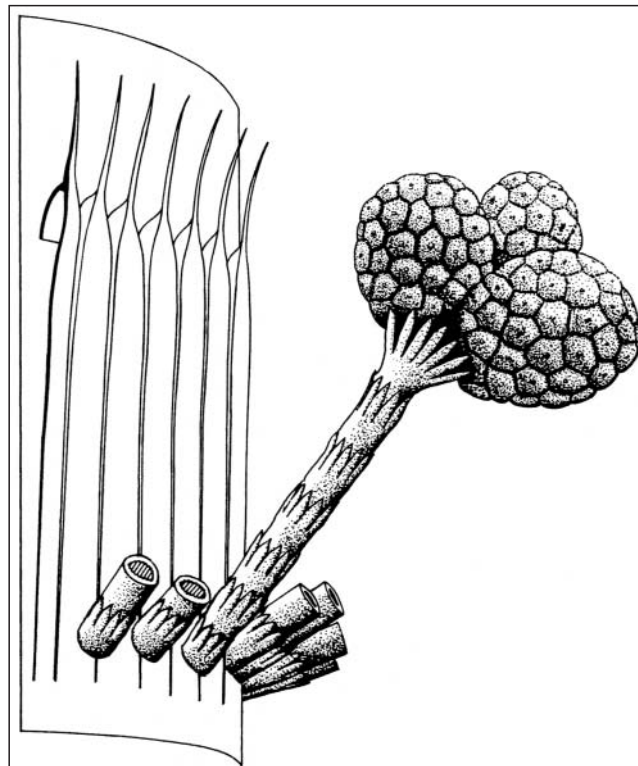
Remarks: *Equisetites arenaceus* is by far the most common sphenophyte in the Lunz flora. The species is believed to have been one of the largest horsetails ever (KELBER & VAN KONIJNENBURG-VAN CITTERT, 1998). It was widely distributed and common in Late Triassic floras from southern Germany, Switzerland and Austria (e.g. HEER, 1877; FRENTZEN, 1934; KELBER & HANSCH, 1995; KRÄUSEL, 1958; KRÄUSEL & LESCHIK, 1959), but has comparatively rarely been reported from regions outside Europe (e.g., Siberia, Turkestan; JONGMANS, 1922).

The first description was presented by JAEGER (1827) based on material from the Jurassic of southern Germany; the fossils were originally assigned to the genus *Calamites*. This assignment was retained until the form was eventually transferred to *Equisetites* by SCHENK (1864). Several authors have variously suggested assignment of *Equisetites arenaceus* to *Equisetum*. However, it has been demonstrated that the morphology of the spores of *E. arenaceus* differs from that seen in *Equisetum* spores. *Equisetites arenaceus* spores do apparently not possess elaters, which are a characteristic feature of the spores of all extant members of *Equisetum* (KELBER & VAN KONIJNENBURG-VAN CITTERT, 1998).

There are several detailed historical theories about the morphology and growth habit of the *Equisetites are-*

naceus (HEER, 1865, 1877; FRENTZEN, 1922; KRÄUSEL, 1958; KRÄUSEL & LESCHIK, 1959). Moreover, excellently preserved specimens from various sites in Germany have more recently revealed additional features, including leaf anatomy and reproductive structures (strobili, lateral branches with adventitious roots). As a result, the macromorphology and reproductive biology of this taxon are well understood today (see KELBER, 1993; KELBER & HANSCH, 1995; KELBER & VAN KONIJNENBURG-VAN CITTERT, 1998). Stems of *E. arenaceus* arose from a horizontal rhizome. The aerial shoots (primary shoots) were upright and may have reached diameters of up to 25 cm and a maximum height of 2.5–3.5 m; some authors suggest a height of up to 5 m (KELBER & HANSCH, 1995). The aerial shoots are hollow and composed of nodes and internodes throughout. The internal anatomy is constructed of a cortex layer and vascular bundles that are arranged in a ring surrounding a central medullary cavity. In the area of the nodes, the medullary cavity is interrupted by nodal diaphragms. The tip of the primary shoot is characterised by telescopically interleaved internodes (Pl. 1, fig. 5). The diameter of the shoots is consistent from base to tip. Near the tip, however, the diameter rapidly decreases to form a dome-shaped apex. Microphylls are produced in whorls in the distalmost portion of each internode. The proximally connate microphylls surround the stem like a wristband in the lower part of the next internode. Individual microphylls are characterised by a prominent longitudinal depression. Each microphyll terminates in a spiny outgrowth, which is usually ephemeral and shed from the plant relatively soon.

Reproductive structures (strobili) are produced on short lateral branches in the upper part of the primary shoots (KELBER & VAN KONIJNENBURG-VAN CITTERT, 1998; text-fig. 2). Strobili usually occur in triplets, and consist of several densely spaced whorls of umbrella-like (peltate) sporangiophores. Sporangia are attached to the lower



Text-Fig. 2.
Reproductive structures (strobili) of *Equisetites arenaceus* are produced on short lateral branches in the upper part of the primary shoots (reproduced from KELBER & VAN KONIJNENBURG-VAN CITTERT, 1998; with permission of Elsevier B.V., Amsterdam).

side of the hexa- to polygonal sporangiophore heads. The strobili resemble those seen in extant *Equisetum*, but the spores of *E. arenaceus* apparently lack elaters. On the other hand, *E. arenaceus* appears to have reproduced vegetatively as well. There are several specimens of detached narrow lateral branches with adventitious roots in organic connection. KELBER & HANSCH (1995) hypothesise that the lateral branches broke off easily, fell onto the swampy substrate, and eventually grew into new plants.

Remarks on STUR's names: STUR (1885) mentions several *Equisetum* species in his inventory of the Lunz flora, most of which he interpreted as new species. However, this author did neither describe nor illustrate the fossils that formed the basis for these new species, and thus most of the names are nomina nuda. KRASSER (1909) suggested that STUR's specimens labelled *Equisetites columnaris*, *E. gamingianus*, *E. constrictum* and *E. lunzense* in fact represent parts of the *E. arenaceus* plant, and hence are assignable to *E. arenaceus*. We confirm the conspecificity of these specimens based on comparison of the external macromorphology and measurements of STUR's specimens with bona fide *E. arenaceus* fossils.

Several authors have included *Equisetites columnaris* in *E. arenaceus* (e.g. VON ETTINGSHAUSEN, 1851; ROSELT, 1954); others, however, regard both forms as separate species (SCHWEITZER et al., 1997; WEBER, 2005). According to HARRIS (1961), SCHWEITZER et al. (1997) and WEBER (2005), both species are distinguished based principally on the diameter of the stems. However, this feature alone is unreliable with regard to the separation of species. SCHWEITZER et al. (1997) and VAN KONIJNENBURG-VAN CITTERT & MORGANS (1999) figured *E. columnaris* specimens that differ from *E. arenaceus* in that the microphylls are broader and the commissural furrows longer. HARRIS (1961) described *E. columnaris* from the Middle Jurassic of Yorkshire, but without comparing his fossils to *E. arenaceus*, while WEBER (2005) related both species without considering SCHWEITZER et al. (1997). Based on the illustrations and descriptions in the papers by HARRIS (1961), SCHWEITZER et al. (1997), VAN KONIJNENBURG-VAN CITTERT & MORGANS (1999) and WEBER (2005), both taxa appear to represent separate species. Nevertheless, *E. columnaris* has not been mentioned in the Lunz inventory by STUR (1885). On the other hand, a few specimens have been found in the old collections that are labelled *E. columnaris*. It remains unclear, however, whether these labels were placed on the slabs by STUR or someone else.

Equisetites gamingianus was originally described by VON ETTINGSHAUSEN (1851), along with a short diagnosis and an illustration. The diagnosis does not suffice to discriminate *E. gamingianus* from *E. columnaris* or *E. arenaceus*, which were regarded as synonymous by this author. The specimens from Lunz labelled *E. gamingianus* cannot be distinguished from specimens labelled *E. arenaceus*. Therefore, *E. gamingianus* from Lunz is rejected, and the specimens are included in *E. arenaceus*. *Equisetites constrictum* and *E. lunzense* are nomina nuda introduced by STUR (1885) (JONGMANS, 1922).

***Equisetites conicus* STERNBERG, 1833**

Plate 2, figs 2, 4–5

Type: *Equisetites conicus*, STERNBERG, 1833, p. 44, pl. 16, fig. 8.

Selected synonymy:

1833 *Equisetites conicus* – STERNBERG, p. 44; pl. 16, fig. 8.

1885 *Equisetum majus* – STUR, p. 98 [6].

1909 *Equisetites platyodon* – KRASSER, p. 105 [5].

1922 *Equisetites platyodon* – FRENTZEN, p. 16; pl. 1, fig. 7; pl. 2, fig. 1.

1959 *Equisetites conicus* – KRÄUSEL & LESCHIK, p. 12; pl. 4, figs 31–36; pl. 5, fig. 38; pl. 6, figs 39–40; text-fig. 3.

1995 *Equisetites conicus* – KELBER & HANSCH, p. 48; text-fig. 93; p. 91; text-figs 189, 192.

Description: *Equisetites conicus* is far less common in the Lunz flora than *E. arenaceus*. All specimens are preserved as compressions. Stems are cylindrical and typically 3.5–5.2 cm wide. A single, ill-preserved axis is ~7.7 cm wide. All specimens are incomplete, most consist of only a single segment; the largest specimen is approximately 24 cm long. Stems are subdivided into nodes and internodes (Pl. 2, fig. 4); the internodes are typically 3.8–4.6 cm long. Internode length decreases towards the tip. The near-apical segments are telescoped to form an acuminate apex (Pl. 2, fig. 5). Branching and reproductive structures have not been observed.

The surface of compressed internodes is smooth (Pl. 2, fig. 4); leaf sheaths cover the lower portion of the internode (Pl. 2, fig. 4), immediately above the lower node (1/4–1/5 of the internode). The individual microphylls appear to have been connate (Pl. 2, fig. 2). The number of microphylls per node varies between <25 and 30. The proximal microphyll portions that form the sheath are typically 5.7–6.1 mm wide and 26.8–29.1 mm long, but they may occasionally reach up to 8.7 mm wide and 43.2 mm long. The microphylls are characterised by a central longitudinal depression (the expression of the vascular bundle) that extends into the microphyll tip (Pl. 2, fig. 2). The commissural furrow occurs in the form of a slender, inversely triangular and distinctly bordered depression. In cross-section, this depression is broadly v-shaped. It extends down into the internode, is reduced in width basipetally, and terminates before the next lower node. The existence of free distal microphyll portions cannot be documented based on the fossils at hand, but it is likely that spiny, tooth-like outgrowths similar to those seen in *Equisetites arenaceus* were present.

Remarks: The specimens from Lunz are assigned to *Equisetites conicus* with some degree of confidence based on correspondences in macromorphology with bona fide specimens of *E. conicus* described and illustrated by KRÄUSEL & Z LESCHIK (1959). Shoots of *E. conicus* are easily distinguished from *E. arenaceus* by their broader leaf sheaths with expanded commissural furrows. Moreover, KRÄUSEL & Z LESCHIK (1959) used the consistent absence of free distal microphyll portions in *E. conicus* as an additional character to separate the two species. Another distinguishing feature is overall size. *Equisetites conicus* primary shoots are distinctly narrower than primary shoots of *E. arenaceus*, and have fewer microphylls per node. KRASSER (1909) was the first to suggest that the specimens from Lunz might belong to *E. conicus* based on a comparison of the material with *E. platyodon* (= *E. conicus*; see below).

Remarks on STUR's names: The fossils from Lunz that have been identified as *Equisetites conicus* in this study were originally labelled *Equisetum aequale*, *E. haidingeri*, *E. majus*, and *E. neubergeri* by STUR (1885). Moreover, a few specimens were labelled *Equisetites ungeri*. *Equisetum aequale*, *E. haidingeri* and *E. neubergeri* are illegitimate because they lack a formal diagnosis, description and typification. In addition, no specimens have been illustrated in the original publication (cf. JONGMANS, 1922). *Equisetum majus* is believed to be conspecific with *Equisetites platyodon* (HALLE, 1908; KRASSER, 1909; JONGMANS, 1922), which is today regarded as a junior synonym of *E. conicus* (WEBER, 2005). *Equisetites ungeri* has been published validly by VON ETTINGSHAUSEN (1851) based on material from the Liassic of Waidhofen (Austria; a city located close to

Lunz am See). However, the specimens from Lunz labelled *E. ungeri* ETT. are indistinguishable from the material assigned to *Equisetum aequale*, *E. haidingeri*, *E. majus*, and *E. neuberi* by STUR (see above). Moreover, one of the slabs has an additional label that reads *E. aequale* STUR. Therefore, *E. ungeri* from Lunz is here referred to *Equisetites conicus*. In addition, it is impossible to discriminate *E. ungeri* from Lunz from *E. conicus* based on the original diagnosis for *E. ungeri* (VON ETTINGSHAUSEN, 1851).

Equisetites conicus was introduced by STERNBERG (1833: 44) based on fossils from the Keuper of Abschwind (Austria). KRÄUSEL & LESCHIK (1959) regarded *Equisetum/Equisetites platyodon* HEER, 1877 as conspecific with *Equisetites conicus*, but they did not compile a detailed synonymy for *E. conicus*. Rather, these authors state that it is impossible to resolve the complicated synonymy. It is generally accepted today that *E. platyodon* and *E. conicus* are conspecific (KELBER & HANSCH, 1995; KELBER, 2005; WEBER, 2005).

Equisetites conicus has been reported from several Keuper floras of southern Germany (KELBER & HANSCH, 1995) and from the Carnian of Neuwelt/Switzerland (KRÄUSEL & LESCHIK, 1959). The stratigraphic range and geographic distribution of the taxon appears to be largely restricted to the Keuper (Middle Carnian) of southern Germany, Northern Switzerland and Northern Austria (SCHENK, 1864; HEER, 1877; JONGMANS, 1922; KRÄUSEL & LESCHIK, 1959; KELBER & HANSCH, 1995). We are not aware of any record for *E. conicus* from outside this area.

***Equisetum aratum* STUR nom. nud.**

Remark: We have not been able to locate any specimen that is labelled *Equisetum aratum*, a name introduced by STUR (1885). This form was never formally described and illustrated (STUR, 1885; JONGMANS, 1922), and the name therefore is illegitimate.

Genus: *Neocalamites* HALLE, 1908

The genus *Neocalamites* was introduced by HALLE (1908) for fossils that were formerly classified in *Schizoneura* ex parte, but differ from the actual *Schizoneura*. HALLE (1908) excludes the "*Schizoneura*" fossils with "entirely separate leaves" ('leaf sheaths', KRÄUSEL & LESCHIK, 1959) from *Schizoneura*, and established a new genus for which he introduced the name *Neocalamites*. According to the original diagnosis, *Neocalamites* consists of articulate, hollow stems with a smooth outer and striate inner surface and foliage consisting of whorls of narrow, lanceolate and entirely free microphylls (similar to the calamite foliage types *Annularia* and *Asterophyllites*) that are vascularised by a single bundle (HALLE, 1908, p. 6).

Type species: *Neocalamites hoerensis* (SCHIMPER) HALLE in HALLE, T. G., 1908, Zur Kenntnis der mesozoischen Equisetales Schwedens, Kungliga Svenska Vetenskaps-akademiens Handlingar, **43**, 1, 1–40.

***Neocalamites merianii* (BRONGNIART, 1828)**

HALLE, 1908

Plate 3–4

Type: *Equisetum merianii* BRONGNIART, 1828, p. 115, pl. 12, fig. 13.

Selected references:

- 1828 *Equisetum merianii* – BRONGNIART, p. 115; pl. 12, fig. 13.
- 1833 *Equisetites merianii* – STERNBERG, p. 46.
- 1864 *Calamites merianii* – SCHENK, p. 71; pl. 7, fig. 3.
- 1877 *Schizoneura merianii* – HEER, p. 78; pl. 30, fig. 1.
- 1885 *Calamites merianii* – STUR, p. 98 [6].
- 1908 *Neocalamites merianii* – HALLE, p. 6.

- 1909 *Neocalamites merianii* – KRASSER, p. 104 [4].
 - 1922 *Neocalamites merianii* – FRENTZEN, p. 18; pl. 1, fig. 12, pl. 2, fig. 2.
 - 1934 *Neocalamites merianii* – FRENTZEN, p. 151; text-figs 6–7.
 - 1954 *Neocalamites merianii* – ROSELT, p. 619; pl. 2, fig. 2; pl. 3–9.
 - 1958 *Neocalamites merianii* – KRÄUSEL, p. 82; pl. 6, fig. 36; pl. 7, figs 38–41; pl. 8, figs 42–43.
 - 1959 *Neocalamites merianii* – KRÄUSEL & LESCHIK, p. 6; text-fig. 1; pl. 1, figs 1–7; pl. 2, figs 8–14.
 - 1995 *Neocalamites merianii* – KELBER & HANSCH, p. 48; text-figs 94, 96, 98–107.
- For an extensive list of synonyms, see KRÄUSEL (1958) and KRÄUSEL & LESCHIK (1959).

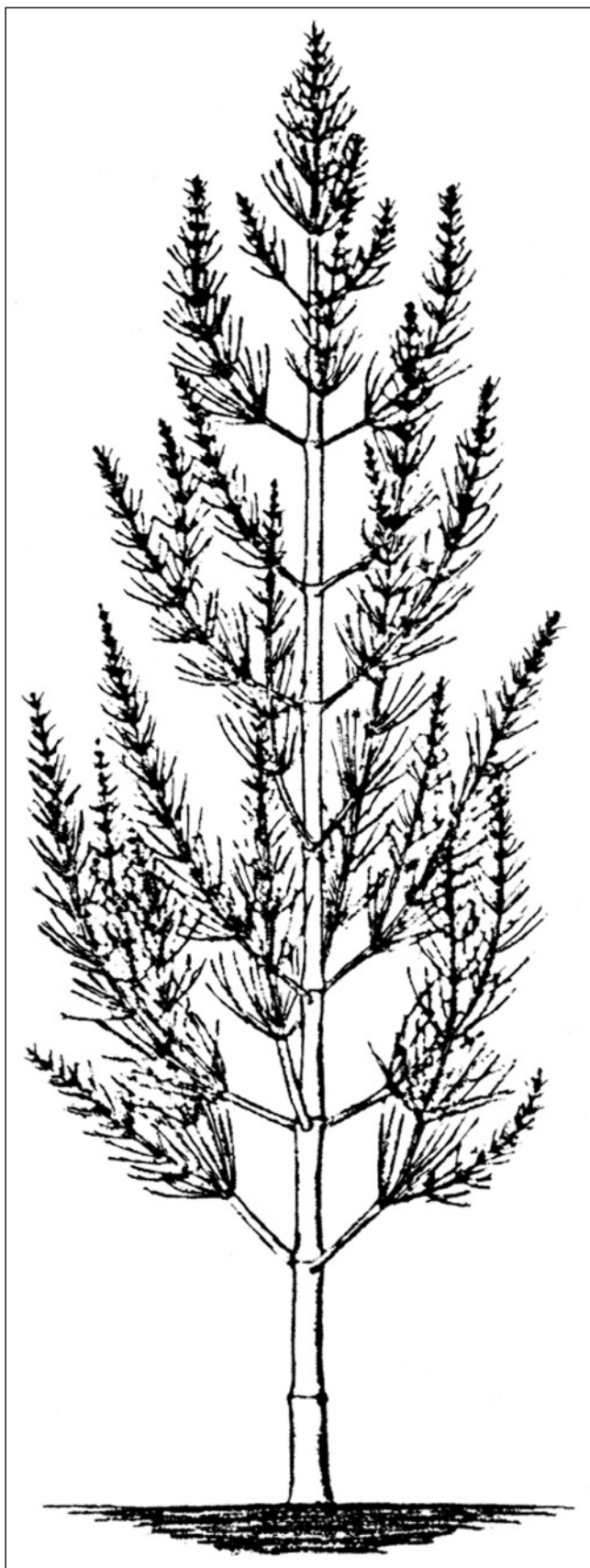
Description: *Neocalamites merianii* is a common element in the Lunz flora. Fossils are preserved as compressions or pith casts (steinkerns). All specimens are incomplete; the largest shoot portion is ~48 cm long. Shoots of *N. merianii* are cylindrical and regularly subdivided into nodes and internodes (Pl. 3, figs 1–2, 4; pl. 4, figs 1–2). Two distinct size categories of shoots occur: (1) shoots that are between 12.5 and 29.7 mm wide (Pl. 3, figs 1, 4; pl. 4, figs 1–2), and (2) other shoots that are 38.5–45.6 mm wide in the middle of the internodes (Pl. 3, fig. 2). All shoots are usually slightly wider at the nodes. The narrower shoots (secondary shoots) probably represent lateral branches that were given off by the wider (primary) shoots (Pl. 4, fig. 3). Internodes are typically 36.1–59.1 mm long and somewhat concave laterally. Some specimens have internodes exceeding 70 mm in length and are up to 114.3 mm long. Only a single specimen displays the apical region of the primary shoot; the exact form of the apex, however, remains elusive because the apex is covered by one of the four slender branches that extend from the shoot laterally at approximately 45 mm below the tip (Pl. 4, fig. 3). In the area of the nodes, the medullary cavity is interrupted by nodal diaphragms (Pl. 3, fig. 3).

The outer surface of the internodes is smooth or characterised by broad longitudinal striae (Pl. 3, fig. 2), while the inner surface is marked by densely arranged prominent longitudinal striae (depicting the massive vascular bundles; Pl. 4, figs 1–2, 3). A whorl of fine antrorse to horizontally arranged, linear microphylls is born slightly above each node (Pl. 3, figs 1, 4; pl. 4, figs 1–2). The exact number of microphylls per whorl cannot be determined, but there were probably at least 54–60 per whorl. Microphylls appear to have been restricted to the narrower shoots (secondary shoots). The preserved (incomplete) microphyll remains are up to 94.1 mm long and 1.3–2.1 mm wide and demonstrate that the microphylls were entirely free from base to tip, and reminiscent in appearance to calamite foliage of the *Annularia*- or *Asterophyllites*-type (Pl. 4, figs 1–2). Microphylls are vascularised by a single bundle (Pl. 4, fig. 1), and are believed to have been quite robust based on the absence of evidence for bending and other forms of distortion. Shedding or braking off of the microphylls usually leaves a punctual scar on the shoot surface (Pl. 4, fig. 4). Shoots belonging to the second type (primary shoots with diameters exceeding 30 mm) do not show any evidence for the presence of microphylls (Pl. 3, fig. 2; pl. 4, fig. 3).

A fragment of a strobilus probably belonging to *Neocalamites merianii* (see below) is ovoid in outline, 91 mm long and up to 26 mm wide (Pl. 4, fig. 5). Sporangio-phores are hexa- to polygonal in outline, peltate, and up to 6 mm in diameter. A spiny appendix, similar to that described by KRÄUSEL & LESCHIK (1959), is recognisable on the outer surface of some of the sporangio-phore heads.

Remarks: *Neocalamites merianii* is a common element of several Late Triassic and Early Jurassic floras from cen-

tral Europe (e.g. HEER, 1877; HALLE, 1908; COMPTON, 1912; FRENTZEN, 1934; KELBER & HANSCH, 1995; KRÄUSEL, 1958; KRÄUSEL & LESCHIK, 1959). The species was



Text-Fig. 3.
Classic reconstruction of the habit of a *Neocalamites merianii* plant (reproduced from FRENTZEN, 1934).

originally described based on material from the Keuper of Neuwelt near Basel, Switzerland, and was named *Equisetum merianii* (BRONGNIART, 1828). STERNBERG (1833: 46) later transferred the species to *Equisetites*. HEER (1877) substantiated the foliar (*Annularia*-/*Asterophyllites*-like) character of the microphylls, which had earlier been interpreted as 'articulate twigs' (BRONGNIART, 1828). However, HEER (1877) assigned the species to *Schizoneura*. The genus *Schizoneura* is characterised by connate leaf groups (KRÄUSEL, 1958) or large, linear leaves with a single vascular bundle and flattened lateral laminae (KELBER & HANSCH, 1995). Based on the narrow and entirely free microphylls (KRÄUSEL & LESCHIK, 1959), *Equisetites*/*Schizoneura merianii* was eventually re-interpreted as a member of the genus *Neocalamites* (HALLE, 1908). This classification is retained to date (KELBER & HANSCH, 1995).

The specimens from Lunz were initially identified as *Calamites merianii* by STUR (1885), but KRASSER (1909) transferred the material to *Neocalamites merianii*, referring directly to the new genus introduced by HALLE (1908). The fossils from Lunz closely resemble *N. merianii* from coeval sites elsewhere (i.e. Neuwelt, Switzerland; Bamberg, Germany; Höör, Sweden). Features supporting the systematic affinities of the Lunz fossils include the articulate nature of all shoots, the striate inner surface of the hollow stems, narrow, entirely free microphylls arranged in whorls, as well as correspondences in size to *N. merianii* specimens from elsewhere. The Lunz specimens cannot be included in *Schizoneura* based on the morphology of the microphyll whorls, which is different from the configuration seen in *Schizoneura*. Moreover, the material from Lunz cannot be included in *Equisetites* because the microphylls do not form sheaths.

The material from Lunz generally concurs with the classic reconstruction of *Neocalamites merianii* by FRENTZEN (1934: fig. 7; refigured in text-fig. 3). However, the Lunz specimens provide a few new details: Discovery of a branched apical shoot segment adds support to the suggestion that the *N. merianii* plant was dumose. A whorl of four branches, which are less than half as thick as the main shoot, extends from a single node. This indicates that the primary shoots may have been considerably wider than the secondary shoots or branches. It may therefore be possible to distinguish primary shoots from secondary shoots/branches based on width alone. Moreover, the thinner secondary shoots/branches typically have whorls of elongate microphylls slightly above the nodes (Pl. 3, figs 1, 4; pl. 4, figs 1–2), whereas the wider primary shoots are consistently leafless (Pl. 3, fig. 2; pl. 4, fig. 3). Axis portions with very long internodes may represent segments of the rhizome system. However, other features indicative of the rhizomatous nature of these specimens (i.e. adventitious roots, cataphylls) have not been observed.

Reproductive structures of *Neocalamites merianii* are virtually unknown to date (FRENTZEN, 1922; KRÄUSEL & LESCHIK, 1959; KELBER & HANSCH, 1995). KRÄUSEL & LESCHIK (1959: Pl. 2, fig. 15) described a strobilus fragment from Neuwelt as belonging to *N. merianii*, but the authors remained uncertain with regard to the affinities of this fossil. ESCAPA & CUNEO (2006) described a reproductive structure assigned to *Neocalamites* from the Permian of Patagonia; another record of a fertile organ assigned to *Neocalamites* aff. *carrerei* comes from the Middle Triassic (Keuper) of Chelyabinsk (Russia) (VLADIMIROV, 1958). Moreover, vegetative remains of *N. hoerensis* from the Keuper (Triassic) of Madygen, Middle Asia, are associated with elongate cones, up to 8 cm long, that have tentatively been assigned to the morphogenus *Neocalamostachys* (DOBROUSKINA, 1985). Based on these records, the strobilus found in the Lunz collec-

tions may perhaps belong to *N. merianii* (Pl. 4, fig. 5). Although the specimen is not organically connected to a vegetative shoot, it is quite similar to the strobili assigned to *Neocalamites* by ESCAPA & CUNÉO (2006). The specimen from Lunz is approximately three times larger than the strobilus from Patagonia. However, the *Neocalamites* sp. fossils from Patagonia appear to have been generally smaller than the European forms.

5. Discussion

Sphenophytes were important elements of many Late Triassic–Early Jurassic ecosystems in south-central Europe based on their abundance and diversity in several local floras (e.g. KELBER & HANSCH, 1995). *Equisetites arenaceus* and *Neocalamites merianii* are probably the most common taxa, followed by *E. conicus*, *E. macrocoleon*, *N. schoenleinii* and *Schizoneura paradoxa*. The composition of the sphenophyte flora from Lunz is similar to that seen in several central European Keuper floras (e.g., the Neuwelt flora, Basel, Switzerland, and several early Keuper and Schilfsandstein floras from the vicinity of Würzburg, Germany; see HEER, 1877; KRÄUSEL & LESCHIK, 1959; KELBER & HANSCH, 1995). Unfortunately, only a few of the studies that have been published on these floras include data about the proportional abundance of the various sphenophyte taxa recorded. *Equisetites arenaceus* undoubtedly is the most common sphenophyte in most of the Early Keuper (Ladinian) and Schilfsandstein (Carnian) floras of southern Germany (KELBER & HANSCH, 1995), as well as the middle Carnian floras of Switzerland (HEER, 1877; KRÄUSEL & LESCHIK, 1959), while *E. conicus* and *N. merianii* appear to have played a rather subordinate role.

Detailed knowledge about the exact spatial and temporal distribution of the sphenophytes from Lunz would certainly contribute considerably to a more accurate reconstruction of the Carnian palaeobiomes in which these plants lived. Unfortunately, we are not able to determine as to whether sphenophytes were restricted to certain horizons of the stratigraphic succession or ‘regions’ of the palaeoecosystem, and thus we are unable to fully assess the role(s) that these plants played in the Lunz ecosystem. All specimens were collected in underground coalmines, and the information about the collection sites is mostly restricted to the name of the mine from where the specimens had been recovered. Thus, hypotheses relating to the habitat and palaeoecology of the Lunz sphenophytes must be formulated solely based on information available on the (palaeo-)ecology of other fossil and extant sphenophytes.

Most late Palaeozoic sphenophytes are known to have grown in (relatively) humid environments. Some of the the arborescent Carboniferous forms (calamites) were part of the peat-forming vegetation; others grew along the banks of lakes and rivers, or in disturbed areas (DIMICHELE & HOOK, 1992). Extant sphenophytes thrive a broad spectrum of habitats, ranging from humid to dry. However, most *Equisetum* species today prefer humid habitats or areas in which sufficient groundwater is available (SITTE et al. 1998). *Equisetum arvense* and *E. ramosissimum* sometimes appear to grow in xeric conditions, but even in these superficially dry places the extensive rhizome system reaches down to water-saturated soils. It is therefore reasonable to conclude that the sphenophytes from Lunz (and Mesozoic sphenophytes in general) probably grew in the more humid ecotopes. Since most sphenophytes are clonal, they may have formed more or less extensive (monotypic) stands along the margins of bodies of water. In these environments, clonal plants are often especially successful. The rhizomes are effective in sustaining the plants during periods of flooding, erosion, or sediment accumulation. Moreover, the resources stored in the rhizomatous system facilitate aerial shoot regeneration if the aerial parts of the plant are destroyed. Vegetative reproduction by means of fragmentation, as has been suggested for *Equisetites arenaceus*, may have been advantageous under these conditions. The fragments (narrow branches) may have been transported by water, and ultimately started new clones in other areas.

The presence of three widespread sphenophyte taxa in the Lunz flora adds support to the hypothesis that the Lunz flora grew in a rather humid environment (POTT et al., 2008a). Similar habitat preferences with regard to moisture availability can also be supposed for several of the herbaceous ferns (e.g. *Oligocarpia robustior*, *O. lunzensis*, *Clathropteris reticulata*) and tree-ferns (e.g. *Asterotheca merianii*, *Coniopteris lunzensis*, *Speirocarpus auriculatus*, *Bernoullia lunzensis*) from Lunz. In addition, the majority of gymnosperms (bennettitaleans, cycads and ginkgophytes) in the Lunz assemblages display morphological features that are suggestive of humidity-affected environments (POTT et al., 2007b–e, 2008a,b). A nearly coeval flora that is very similar to Lunz with regard to floral composition occurs in the Schilfsandstein of southern Germany. This flora contains ferns (*Bernoullia helvetica*, *Sphenopteris schoenleiniana*, *Clathropteris meniscoides*) and bennettitaleans (*Pterophyllum filicoides*), as well as many sphenophytes (i.e. *Equisetites arenaceus*, *E. conicus*, *E. macrocoleon* and *Neocalamites merianii*). The sedimentology of the plant-bearing Schilfsandstein deposits indicates that the flora grew in a meandering and braided river system where no doubt numerous moist and wet habitats were created by the water (KELBER & HANSCH, 1995).

Plate 1

Equisetites arenaceus (JAEGER, 1827) SCHENK, 1864

- Fig. 1: Shoot fragment with short internodes.
Specimen NHMW 2006B0008/0045 in the collection of the Natural History Museum, Vienna.
- Figs. 2,3: Detail of leaf sheaths and spiny distal microphyll portions; note commissural furrows interconnecting the individual microphylls laterally, and central vascular bundles.
Specimen GBAW 1909/003/0235 in the collection of the Geological Survey of Austria, Vienna (Fig. 2).
Specimen NHMW 2006B0008/0009 in the collection of the Natural History Museum, Vienna (Fig. 3).
- Fig. 4: Compressed internode portion with leaf sheaths and smooth surface.
Specimen GBAW 1909/003/0242 in the collection of the Geological Survey of Austria, Vienna.
- Fig. 5: Apical portion of a large primary shoot, showing the telescoped distal segments.
Specimen NHRM S148251 in the collection of the Swedish Museum of Natural History, Stockholm.

Scale bars: 5 mm.

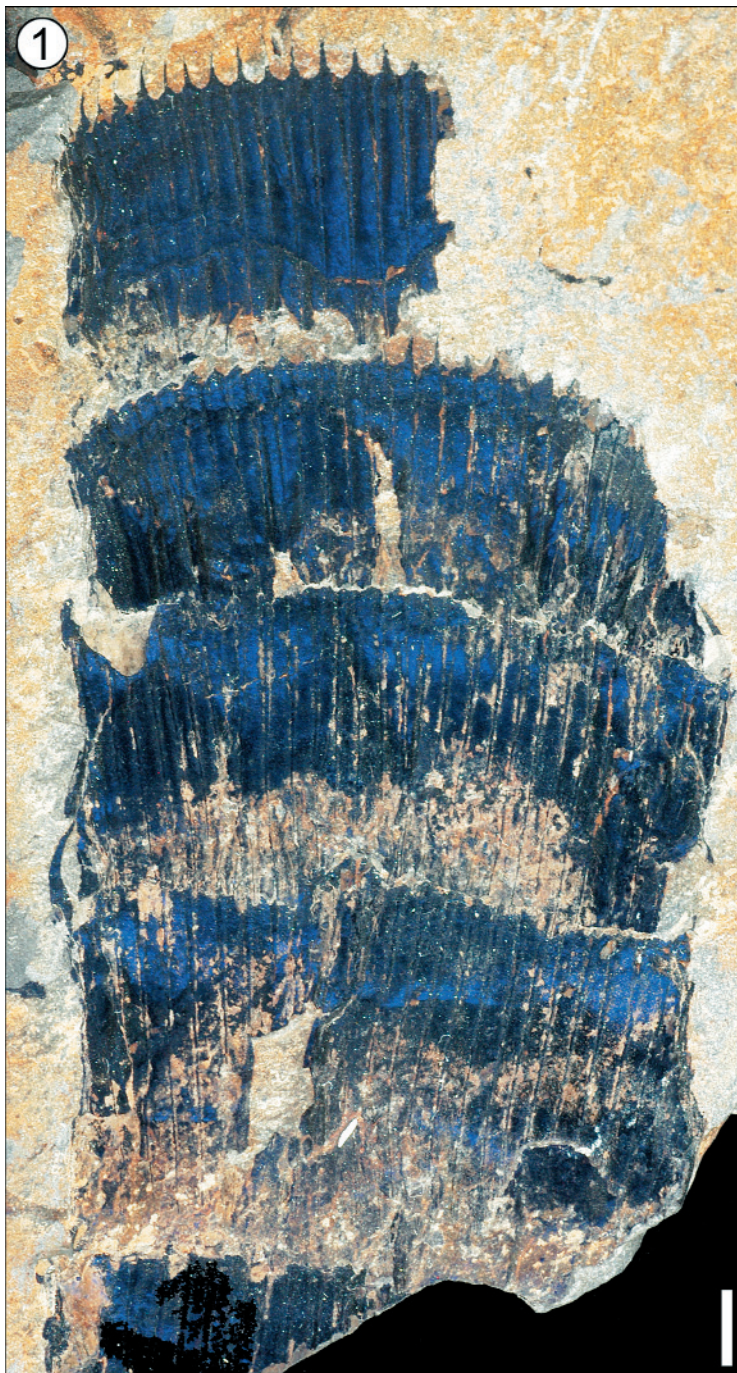


Plate 2

Equisetites arenaceus (JAEGER, 1827) SCHENK, 1864 and *Equisetites conicus* STERNBERG, 1833

- Fig. 1: Large decayed primary shoot of *E. arenaceus* showing wristband-like arrangement of leaf sheaths.
Specimen NHMW 1885/D/3862 in the collection of the Natural History Museum, Vienna.
- Fig. 2: Leaf sheaths of *E. conicus* showing the commissural furrows.
Specimen NHMW 2006B0008/0019 in the collection of the Natural History Museum, Vienna.
- Fig. 3: Strobilus (possibly belonging to *E. arenaceus*) with hexagonal sporangiophore heads.
Specimen GBAW 1909/003/0651 in the collection of the Geological Survey of Austria, Vienna.
- Fig. 4: Shoot of *E. conicus* with alternating nodes and internodes, the latter partly covered by leaf sheaths.
Specimen NHRM S148253 in the collection of the Swedish Museum of Natural History, Stockholm.
- Fig. 5: Apical portion of a shoot of *E. conicus*, showing the telescoped apical segments.
Specimen GBAW 1909/003/0344 in the collection of the Geological Survey of Austria, Vienna.

Scale bars: 10 mm.

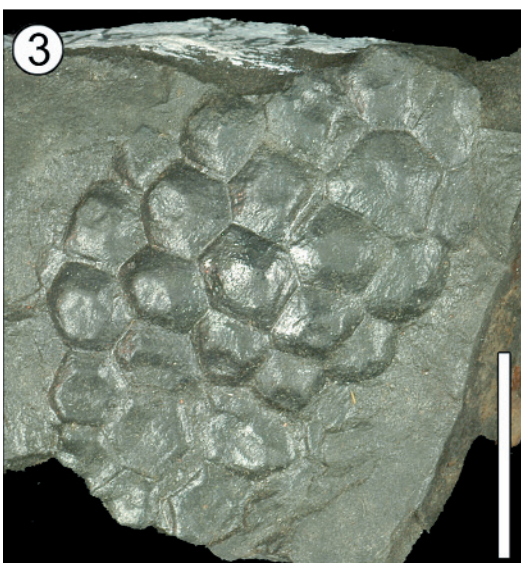
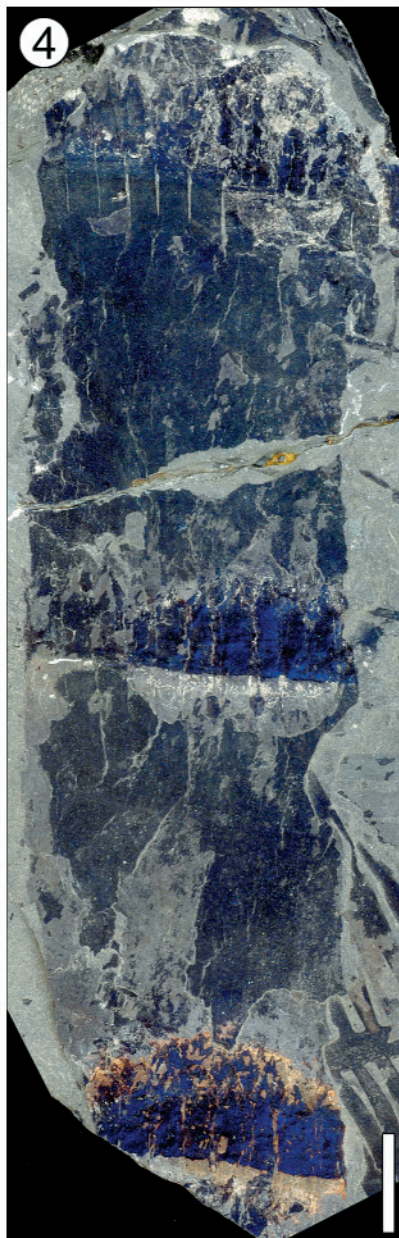
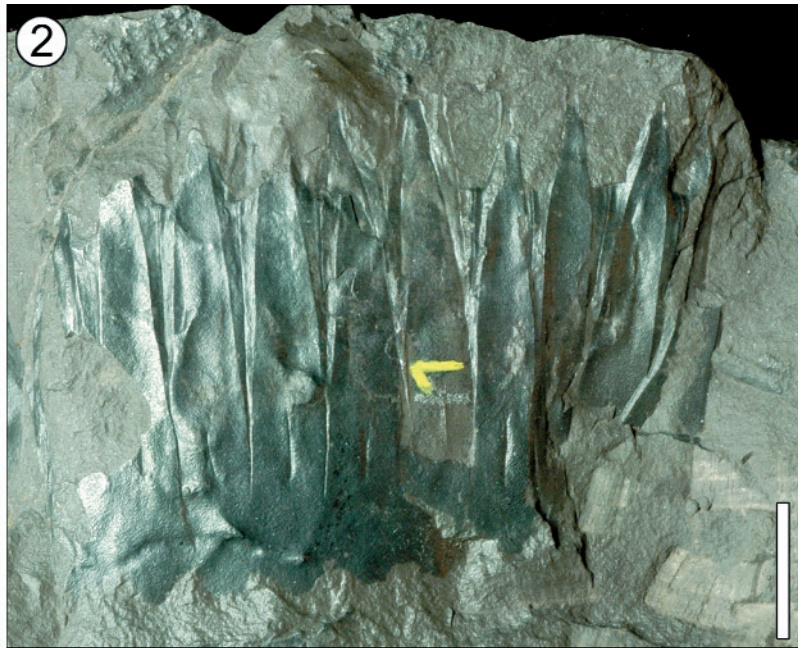
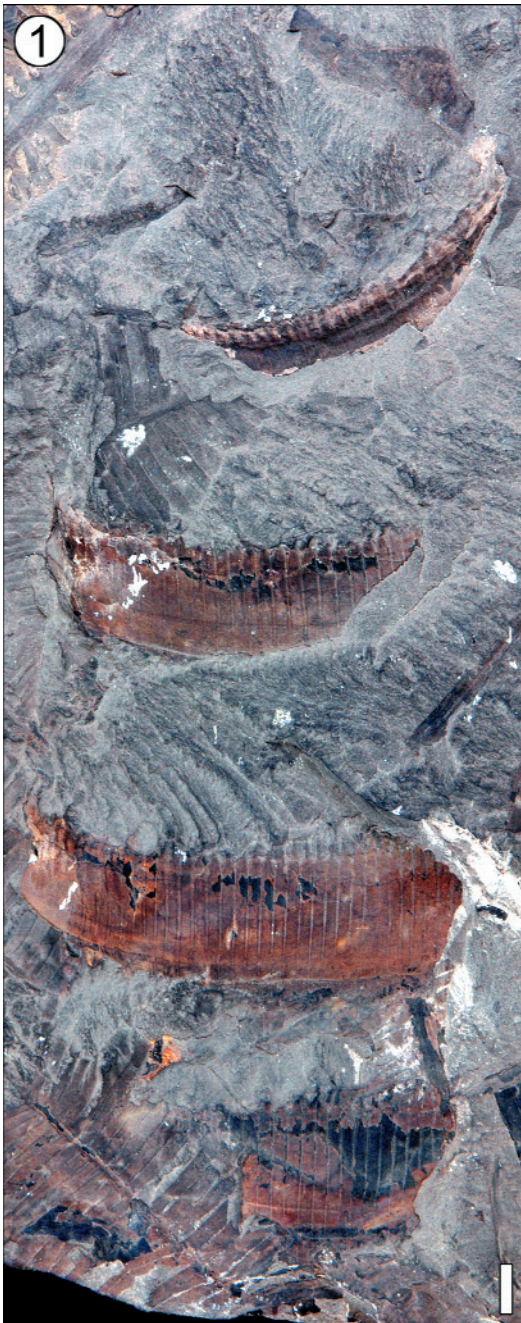


Plate 3

Neocalamites merianii (BRONGNIART, 1828) HALLE, 1908

- Fig. 1: Shoot fragment (secondary shoot) with several microphylls produced close to the nodes.
Specimen GBAW 1909/003/0005 in the collection of the Geological Survey of Austria, Vienna.
- Fig. 2: Primary shoot fragment, showing smooth outer surface and distinctly striate inner surface.
Specimen NHRM S148605 in the collection of the Swedish Museum of Natural History, Stockholm.
- Fig. 3: Nodal diaphragm.
Specimen NHMW 2006B0008/0024 in the collection of the Natural History Museum, Vienna.
- Fig. 4: Secondary shoot fragment with several linear microphylls.
Specimen GBAW 1909/003/0012 in the collection of the Geological Survey of Austria, Vienna.

Scale bars: 10 mm.

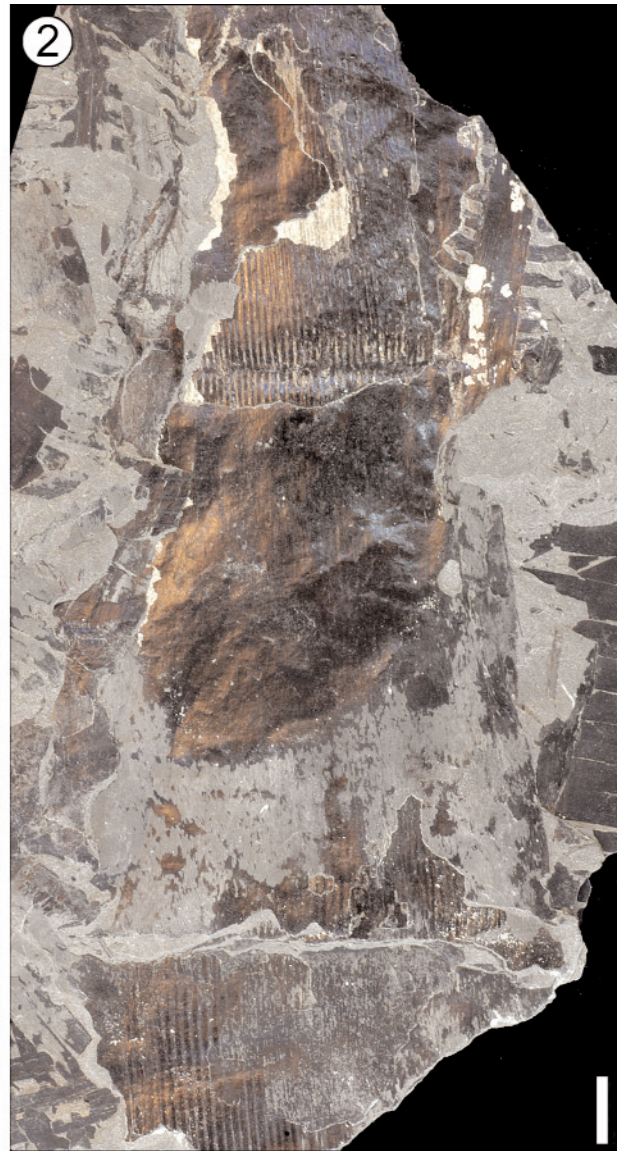
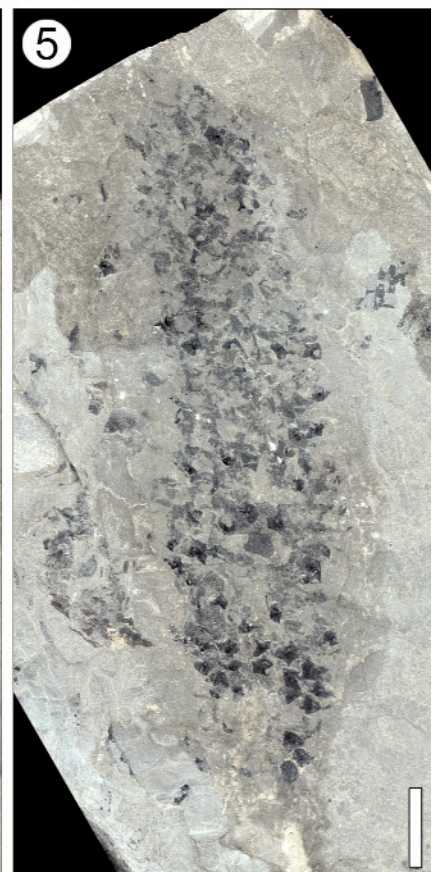


Plate 4

Neocalamites merianii (BRONGNIART, 1828) HALLE, 1908

- Fig. 1: Secondary shoot fragment with linear microphylls.
Specimen NHRM S148335 in the collection of the Swedish Museum of Natural History, Stockholm.
- Fig. 2: Secondary shoot fragment with very long microphylls.
Specimen GBAW 1909/003/0004 in the collection of the Geological Survey of Austria, Vienna.
- Fig. 3: Primary shoot giving off four secondary shoots (branches).
Specimen GBAW 1909/003/0062 in the collection of the Geological Survey of Austria, Vienna.
- Fig. 4: Secondary shoot, showing punctual scars (leaf scars) near the internodes.
Specimen GBAW 1909/003/0049 in the collection of the Geological Survey of Austria, Vienna.
- Fig. 5: Strobilus (possibly belonging to *N. merianii*) with near-hexagonal sporangiophore heads.
Specimen GBAW 1909/003/0019 in the collection of the Geological Survey of Austria, Vienna.

Scale bars: 10 mm.



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