

Equisetites arenaceus from the Upper Triassic of Germany with evidence for reproductive strategies

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Abstract

In situ triplet groups of asymmetrical ellipsoidal strobili of *Equisetites arenaceus* in different stages of maturity, borne at the end of straight equisetalean branches, are described from the Keuper (Upper Triassic) of southern Germany. Apart from the organization of the strobili, spores in situ are also described. The strobili are compared to other equisetalean strobili with in situ spores and to extant *Equisetum* material. An additional mode of vegetative reproduction by shed twigs indicating adventitious roots is proven. In autochthonous situations, dense packages of shed twigs built up patches of newly sprouted rhizome layers. Moreover, we include *Equisetites elegans* Kräusel, 1959 in *E. arenaceus* (Jaeger) Schenk and give an emended diagnosis for the species. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Upper Triassic; Equisetales; reproductive strategies; sporae in situ; Germany

1. Introduction

Equisetites arenaceus from the Keuper (Upper Triassic) is deemed as one of the largest horsetails in the fossil record. While fragments of the axis and leaf sheaths are by far the most numerous plant organs preserved in lower Keuper and Schilfsandstein floras, isolated strobili—most of them expanded—occur only in subordinate amounts. The recent discovery of new material, including strobili in organic connection with subtending branches, provides documentation for an improved reconstruction of the fertile branches and sporae in situ.

Due to the roughly similar features of isolated fertile and sterile branches, as well as their obviously similar manner of attachment on the stem, sterile branches and their peculiar reproductive function are also described in this paper.

The purpose of this investigation has been to study: (1) the peltate sporangiophores and the configuration of the strobili on their axis; (2) the sporae in situ; (3) the fertile and virtually similar sterile branches, partly with adventitious roots, and their affiliation to *E. arenaceus*; and (4) an evaluation of the different modes of propagation.

2. Material and methods

The material under investigation forms part of the lower Keuper and Schilfsandstein floras from

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several localities in southern Germany (Fig. 1). Specimens from the lower Keuper (Ladinian, Triassic) were excavated from greenish sand- and siltstones in the top of the so-called Werksandstein (Kelber, 1990; Mader, 1990; Kelber and Hansch, 1995). The Schilfsandstein material (Carnian, Triassic) from Zeil and Rothof was excavated from sand- and siltstone intercalations.

Localities are indicated by abbreviations preceding the collection number: SCHL = Werksandstein quarry west of Schleierieth; GNO = Werksandstein quarry northeast of Gnodstadt; OCH = road construction B19 near the St. Wolfgang chapel, south of Ochsenfurt (Kelber, 1987); Z = abandoned Schilfsandstein quarry at Schleifberg northeast of Zeil am Main; ROT = abandoned Schilfsandstein quarry east of Rothof near Oberlauringen (Schröder, 1970). The reinvestigated specimen nr. 12 552 (Frentzen, 1933) originated from the Schilfsandstein near Bönningheim.

All material is stored in the private collection of Kelber, Würzburg, except the strobilus from

Bönningheim (nr. 12 552) which is kept at the Staatliches Museum für Naturkunde, Stuttgart. Preparations of the sporae in situ are housed in the Laboratory of Palaeobotany and Palynology, University of Utrecht.

The plants were studied as hand specimens. Spores in situ were recovered by selecting a single (if possible) sporangium, macerating it in Schulze's reagent (after cleaning in HF if necessary), and neutralizing with 5% ammonia. Preparations were then mounted in glycerine-jelly and sealed with paraffin wax. The spores were studied using a Leitz Ortholux microscope.

3. Reproductive organs

3.1. Detached strobili and sporangiophore heads

Division SPHENOPHYTA

Order EQUISETALES

Family EQUISETACEAE

Genus *Equisetites* Sternberg, 1838

In accordance with Watson and Batten (1990) the genus *Equisetites* Sternberg is used for fossil plant remains which cannot positively be assigned to the living genus *Equisetum*. In *Equisetites*, all the leaves of a whorl are typically fused into a leaf sheath with free leaf teeth. Characters of the family Equisetaceae are specified by Hauke (1978, 1990) and Kramer (1990).

Equisetites arenaceus (Jaeger) Schenk

Although isolated equisetalian-like strobili from the German Keuper should actually have been assigned to the organ genus *Equisetostachys*, it has traditionally been customary to attribute them to *E. arenaceus*. It is proven in this paper that these detached strobili actually agree in their gross morphology and structure to those found in organic connection. Similar isolated strobili may, therefore, be referred to *E. arenaceus*.

Basionym: *Calamites arenaceus major* Jaeger, 1827, p. 37; pl. 1, 1–5; pl. 2, 1–7. All specimens

destroyed, except rhizome in pl. 2, 1, which is the new lectotype (Csaki and Urlichs, 1985, p. 3).

Synonyms and selected references with respect to strobili:

- 1864 *Equisetites arenaceus* (Jaeger) Schenk, pp. 59, 68 (new combination; strobilus).
- 1865 *Equisetum arenaceum* Heer, p. 50; fig. 27c; pl. 3, 4 (strobilus fragment).
- 1865 *Equisetites arenaceus* Schoenlein (and Schenk), p. 11; pl. 1, 7a, 7c (strobilus fragment and dispersed sporangiophores).
- 1877 *Equisetum arenaceum* Heer, p. 75; pl. 26, 1; pl. 27, 5, 5b; pl. 33, 6; pl. 38, 10; (strobili fragments, strobilus diameter 28 mm, strobilus axis 8 mm in diameter).
- 1885 *Equisetum columnare* Quenstedt, p. 1086; pl. 89, 13 (strobilus fragment).
- 1894 *Equisetites arenaceus* Compter, p. 214; pl. 3, 1, 2 (2 strobili fragments).
- 1904 *Equisetum arenaceum* Leuthardt, p. 44 (length of sporangiophore-stalk 3 mm).
- 1922 *Equisetites arenaceus* Frentzen, p. 14 (strobilus diameter approx. 1 cm).
- 1922 *Equisetites arenaceus* Compter, p. 30; pl. 1, 16 (strobilus fragment).
- 1933 *Equisetites arenaceus* Frentzen, p. 35; fig. 2; pl. 1, 4–6; pl. 2, 1a, 1b, 2 (strobilus length 95.5 mm in pl. 1, 6).
- 1934 *Equisetites arenaceus* Frentzen, p. 151; figs. 3–5 (strobilus approx. 10 cm in length(?). Specimen from Frentzen, 1933).
- 1948 *Equisetum* Ricour, p. 261; pl. 12, 4–6 (strobilus fragment).
- 1959 ?*Equisetites arenaceus* Kräusel, p. 12; pl. 2, 4 (strobilus length more than 6 cm).
- 1968 *Equisetum* Ricour, p. 31; pl. 7, 2–5 (strobilus fragment. Specimen from Ricour, 1948).

Description (Plate I, 1–9; Plate III, 1–10): Isolated strobili are usually found as disintegrated compressions or impressions, rather scarce in cast or flattened cast preservation and then mostly recorded in an immature stage. Strobili non-apiculate or obovate, 21–35 mm in length and 17–22 mm in maximum width (flattened), consisting of 7–9 whorls of 10–12 sporangiophore heads. Specimens figured in Plate I, 1–7 resulting in a total number of 70–85 contiguous sporangiophores per strobilus. In longitudinal view a strobilus axis of 2–4 mm flattened width is visible (Plate I, 9; Plate III, 3).

Sporangiophore with stalk of about 5–6 mm in length and 0.4–0.8 mm in width (narrowest part in flattened width), terminating in a pentagonal to

circularly hexagonal peltate disc ranging in diameter from 1.5–2.5 mm, via 2.5–4 mm to 3.5–5 mm. Ridges noticeable, from penta- or hexagonal corners to central area (Plate III, 4, 6–8, 10). Sporangiophores mostly disporangiate.

Outer view of the sporangiophore head often resembling a pyramid-shaped stump (Plate I, 1–4), in contrast to some three-dimensionally preserved specimens, which reveal a more pyramid to umbrella shape, partly with a mucro (Plate III, 4, 6–8). Obviously there existed a seam of slightly thicker plant tissue at the margin of the adaxial sporangiophore head (arrows in Plate III, 9). Sporangia borne on the peltate sporangiophore or basal scars of sporangia in inner view of sporangiophore heads have not been properly observed yet in dispersed material.

Discussion: Specimens in Plate I, 1–4 (from Bönningheim), and 7 (from Zeil) might be comparable to the *E. arenaceus* sporangiophores with a more plateau-like surface and 5–6 facet edges which are reported by Heer (1877, pl. 38, 10a, 10b, in unsatisfying view in 10c), and reinvestigated by Kräusel (1959), but the facet edges in the Bönningheim and Zeil specimens are only indistinctly preserved. Sporangiophore heads of *Equisetum* from Suriauville, France, most probably of *E. mytharum*, which is probably a junior synonym of *E. arenaceus*, are figured in Ricour (1948, pl. 12, 4) Ricour (1968, pl. 7, 2, 3), showing also a truncate pyramidal shape with prominent steep facets at the edges.

Nothing is known precisely about the exact number of sporangia. Heer (1877, p. 90) suspected 6 sporangia on the underside of each peltate sporangiophore, but the reinvestigation by Kräusel (1959, p. 12) did not corroborate this fact.

3.2. Strobili attached to fertile branches of *E. arenaceus* }

Description (Plate II, 1–7): Unless previously destroyed, up to 3 strobili in different stages of maturity are terminally attached on the slender equisetalean branch (Plate II, 1, 3). The strobili of non-apiculate and obovate shape are comparable to previously described dispersed strobili in all

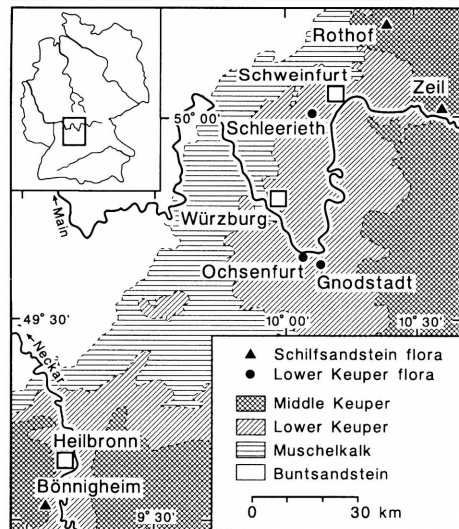
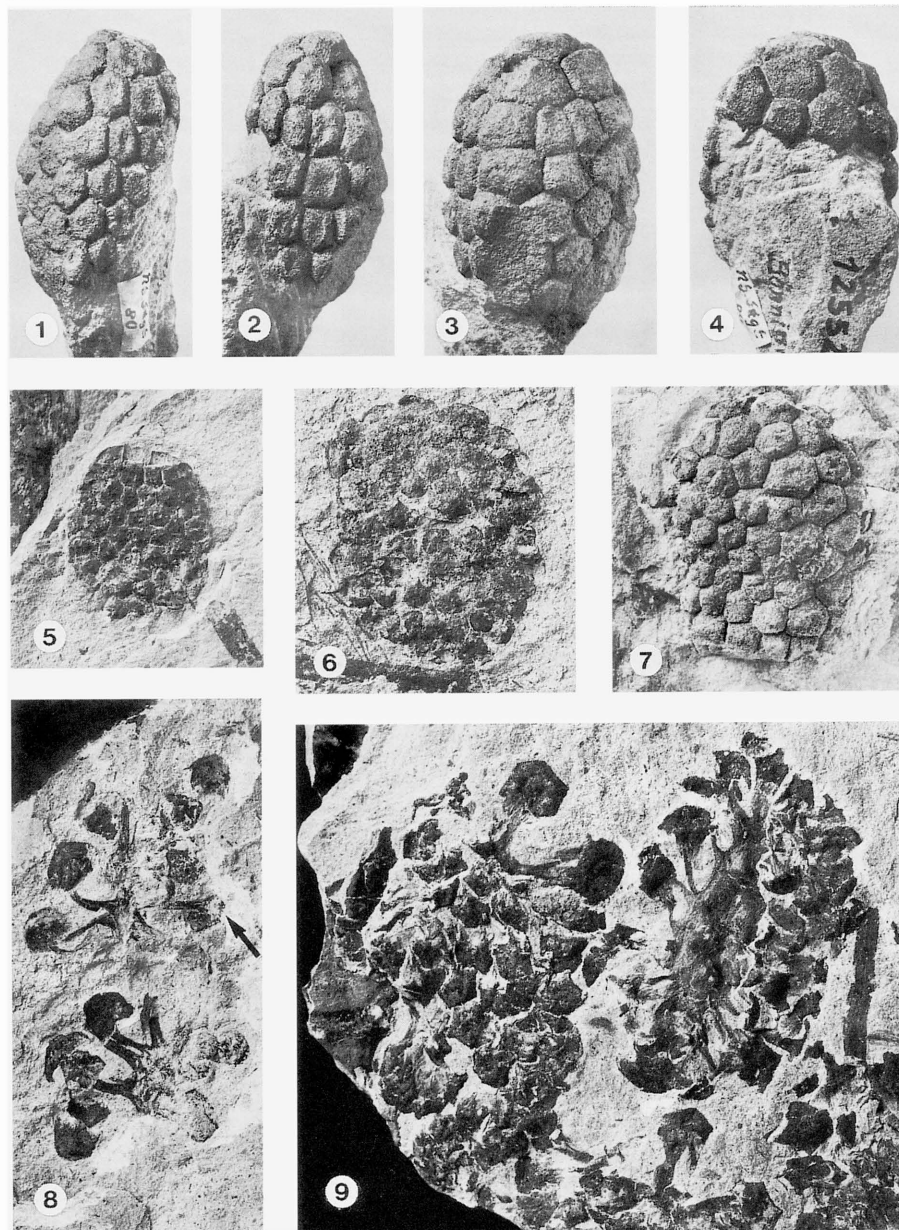


Fig. 1. Simplified geological map indicating the location of the lower Keuper (Triassic, Ladinian) and Schilfsandstein (Triassic, Carnian) localities in Germany.

PLATE I



their morphological characters and size proportions. In Plate II, 1 the left strobilus is of 16 mm maximum flattened width with sporangioophore discs of 2.5–3.5 mm in diameter. Two of the three attached strobili in Plate II, 3 are 24 and 23 mm long and 16 and 19 mm in flattened width bearing sporangioophore discs of 2–3 mm in diameter, whereas the immature strobilus in the middle shows a maximum flattened width of 8 mm and sporangioophore discs of only 1–1.5 mm in diameter. The strobilus in Plate II, 7 is 26 mm long and 19 mm wide; sporangioophore discs 2.5–3.5 mm in diameter.

The fertile branch is organized into equisetoid internodes and nodes with a flattened width of 6–7 mm. In Plate II, 3 internode length in the basal part is approx. 20–24 mm, slightly decreasing towards its distal end. All basal sheath parts are appressed to the stem, but the uppermost leaf sheath is slightly swollen and funnel shaped (Plate II, 1–7). Leaf sheaths consist of 12–14 leaf segments, 7.5–9 mm long and 0.6 mm wide near the base. The free leaf teeth are 3–4 mm long, gradually tapering into an acuminate apex. In Plate II, 6 the leaf segment of the uppermost leaf sheath is 1.4 mm wide, the free leaf teeth are 4–4.5 mm long. The commissural furrows, with a strongly sculptured surface, reach almost to the node.

Discussion: A conspicuous feature in all fertile axes in Plate II is the slight oversize and wedge-shaped arrangement of the terminal leaf sheath, in which all basal strobilus parts are sunken. There is no evidence for a thickened bulb-like distal end of the fertile branch as suggested by Frentzen (1933),

nor for circles of specialized sterile leaves (Compter, 1911, p. 103, figs. 31, 32). The latter has been a misinterpretation of ochrole structures connected to a diaphragm in transectional preservation, comparable to our Plate VI, 2.

An annulus, which is a specialized layer of cells involved in sporangioophore dehiscence forming a collar at the strobilus base (Page, 1972), comparable to those of modern *Equisetum* species, has not been recognized hitherto. This structure might be hidden by the uppermost funnel shaped leaf sheath of the fertile branch or may not have been present.

The specimen in Plate II, 3 affords additional evidence concerning the preservation of the complete triplet of strobili. A small sized immature strobilus is attached between two larger ones. The other specimens in Plate II are imperfect and document just one or two strobili connected to a branch, or display as shown in Plate II, 4 the distal portion without any strobilus. In Plate II, 6 an immature strobilus, associated with a larger crushed one (on the right) is also connected to a branch. In Plate II, 5 an obviously immature group of strobili on top of a branch is closely embraced by its terminal leaf sheath.

Sexual reproduction in *E. arenaceus* may have depended on substrate conditions suitable for prothallium growth, and fertilization. In order to prolong the period of spore dispersal, different moments of strobilus maturity may have been a successful reproductive strategy.

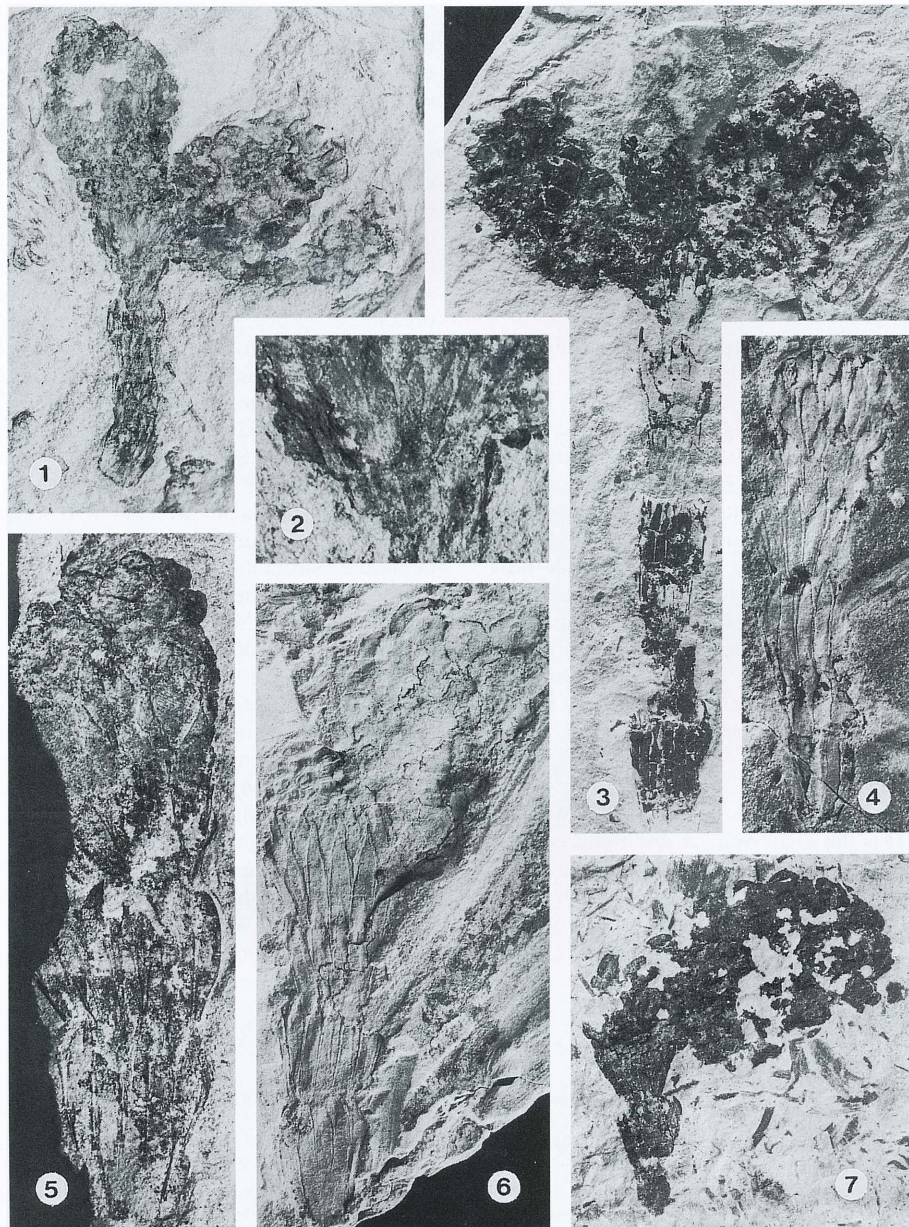
Isolated strobilus remains of *E. arenaceus* are not uncommon in the lower Keuper plant deposits, but inflorescences showing the strobili in organic connection with branches are very rare. In the

PLATE I

Isolated strobili of *Equisetites arenaceus*.

- 1–4. Different views of an immature strobilus in cast preservation, refigured from Frentzen (1933, pl. 2, a, b); Staatl. Mus. f. Naturk. Stuttgart Nr. 12 552. $\times 1.5$.
5. Small immature strobilus, compression. SCHL-047a. $\times 1.5$.
6. Immature strobilus, compression. SCHL-245. $\times 1.5$.
7. Immature strobilus, flattened cast preservation, sporangioophore heads with sunken mucros. Z-011. $\times 1.5$.
8. Fragment of strobilus axis and displaced sporangioophores. Arrow points to the underside of a sporangioophore head in organic connection with the stalk. GNO-083. $\times 2$.
9. Two isolated, expanded strobili in longitudinal view. Specimen on the right is split longitudinally to reveal strobilus axis. SCHL-062a. $\times 2$.

PLATE II



Schleerieth locality (the richest of the localities), 4 specimens are in organic connection with their branch among 102 mostly crushed strobili and only one specimen (SCHL-784a) shows the complete triplet group of strobili. This unbalanced ratio probably reveals a principle of shedding or disintegration on predetermined breaking points of the fertile branch.

Kerp (1984) pointed out that a different shedding pattern probably existed in Lower Permian *Calamites* strobili. While in *C. tuberculata* the mature strobili usually become detached, most strobili of *C. dumasii* have been found still attached to their axes. After its reproductive function, the dissporangiated strobilus may have served as an assimilation organ. The same applies for some recent *Equisetum* species: most fertile branches are colourless, unbranched and have a single strobilus at the apex. Usually they grow and shed their spores before vegetative branches appear. Other species (e.g. *E. palustre*), however, have green, branched fertile shoots with a strobilus at the apex of most lateral branches. These fertile shoots persist after shedding of the spores, and function as vegetative organs afterwards.

3.3. Sporangia with sporae in situ

Description (Plate III, 5; Plate IV, 1–7): Sporangiphore heads bearing a circle of sporangia on their lower surface; sporangia elongated, ca. 3 mm long, 1 mm wide. Spores globose, often folded; alete or with a small triradiate scar; exospore ca. 1 μ m thick, surface faintly scabrate to microrugulate; ?perispore (or epispor as it is sometimes called) smooth, ca. 0.5 μ m thick. Spores usually 50–60 μ m in diameter.

Discussion: Most specimens with attached or separate strobili or strobilus fragments appeared to be empty or yielded masses of very immature spores. Only a few specimens yielded a reasonable number of more or less mature spores (SCHL-076A, -268, -1065) and only one specimen (SCHL-1066a) yielded a number of sporangia that were filled with a large number of almost mature spores. Almost all spores were folded and proved to be of rather variable size. Most seemingly mature spores were between 50 and 60 μ m in diameter (Plate IV, 1, 2, 4), but quite a few spores were smaller (Plate IV, 5) and often rather heavily folded. Additionally presumably abortive spores occurred (Plate IV, 3), usually attached to normal spores. This feature has e.g. also been recorded by Gould (1968) from *Equisetum laterale* spores. Most of the spores were alete (Plate IV, 2) but in ca. 30% of the spores a small triradiate scar could be observed (Plate IV, 1, 3). The exospore is ca. 1 μ m thick, often appears to be either faintly scabrate (Plate IV, 4) or sometimes microrugulate (Plate IV, 5). In ca. 40% of the spores (and in none of the abortive, or heavily folded immature spores) a possible thin perispore (or epispor) was observed (Plate IV, 2, 6).

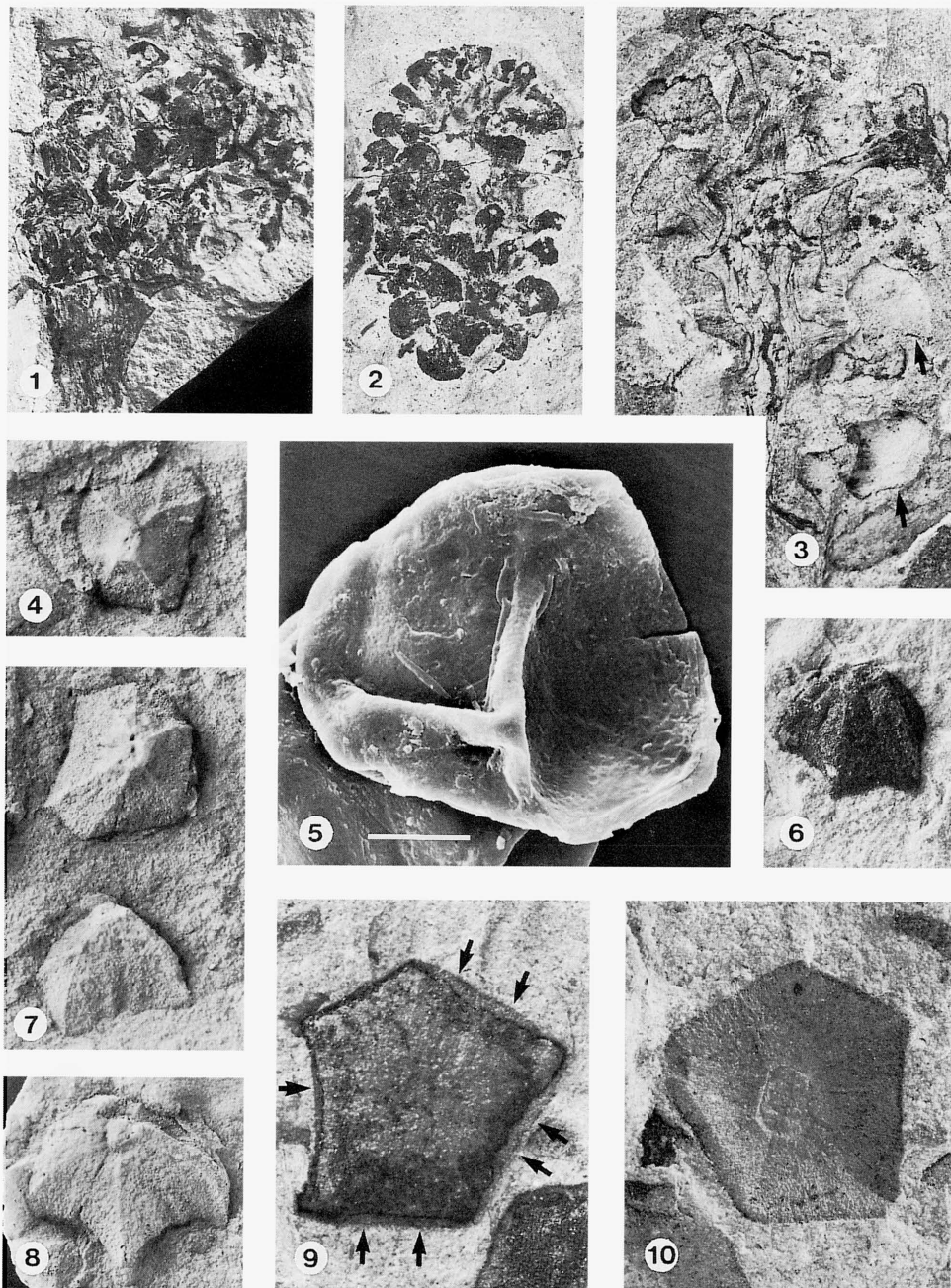
Extant *Equisetum* spores are characterized by the presence of elaters. None of the spores recovered from the fossil material described here showed any attached elaters. Only in one case has a possible indication of elaters been found (Plate IV, 7). It is possible, however, that this structure has nothing to do with elaters. It might be that no elaters were present in the spores described here just as in most Mesozoic in situ equisetalean spores described so far. It is also possible that elaters have been present but disap-

PLATE II

Strobili of *Equisetites arenaceus* in organic connection.

1. Two strobili born on an equisetalian branch. GNO-081b, $\times 1.5$.
2. Detail from Fig. 1, showing the terminate leaf sheath of the branch. GNO-08, $\times 4$.
3. A triplet group of strobili in organic connection with an equisetalian branch. Two more developed strobili on the left and right and one small immature strobilus between. SCHL-784a, $\times 1.5$.
4. Distal portion of a fertile branch. SCHL-845, $\times 4$.
5. Distal portion of a fertile branch in an early immature state. GNO-081a, $\times 4$.
6. Disintegrated strobili remains of at least two strobili in different states of maturity, termination an equisetalian branch. SCHL-310, $\times 2.5$.
7. One preserved strobilus organically connected on an equisetalian branch tip. SCHL-1078, $\times 1.5$.

PLATE III



peared during either fossilization or during spore preparation, although the latter was very cautiously carried out. Halle (1908) carried out a few experiments concerning the treatment of extant *Equisetum* spores with Schulze's reagent: the elaters disappeared after a short time; after a longer treatment effects on the exospores were also visible. In this respect a paper by Kedves et al. (1991) on high temperature effects on extant *Equisetum arvense* spores is also of relevance. They indicate that after an exposure of ca. 10 hours at 200°C, elaters separate completely from the spores. This may have happened during fossilization (since this temperature is never reached in preparation), but one would expect that at least separate elaters to be found inside the spore masses in the sporangia. Apart from the one possible indication (Plate IV, 7), this was never the case. Thus, the possibility that there were no elaters in these spores to start with, is greater than the possibility that they were lost during fossilization and/or preparation.

3.4. Other Mesozoic equisetalean strobili with in situ spores

Considering the large number of equisetalean remains known from Mesozoic sediments, relatively few strobili have been described that may have belonged to these species. Most of the records come from Jurassic floras, a few from Late Triassic and some others from Early Cretaceous floras. The majority of the species described so far belong to *Equisetum* or *Equisetites* material. These strobili, when found dispersed, have been attributed to the genus *Equisetostachys*. All have the same basic

morphology of a strobilus consisting of whorls of sporangiophores; the sporangiophore heads carry a whorl of sporangia. Their main differences lie in the shape and sizes. Quite a few strobili have been described without many details and/or their spores being known (e.g. *Equisetites iwamuroensis* Kimura from the Lower Jurassic of Japan; see Kimura and Tsujii, 1980). Of the strobili that are better known, the spores have often been described as well. These spores are comparable to the spores described here from *E. arenaceus* in so far as they are usually globose in outline, alete or with a small triradiate scar and do not possess elaters; the latter feature with one exception, *Equisetum columnare* from the Middle Jurassic of Yorkshire (Harris, 1978) which has been recorded with elaters. Another species that might have had elaters is *Equisetites platyodon* (= *E. conicus*). Compter (1911) described strobilus fragments which probably belong to this species, and some in situ spores with a possible indication of elaters. The figures are rather poor, however, and no conclusions can be drawn either from the description or from the figures. The main differences between the various better-known in situ spores are in the exospore sculpture. A few of the well-known Mesozoic equisetalean strobili are discussed in detail below and compared in Table 1.

First of all, some records of strobili not being attributed to *Equisetum* or *Equisetites* but to *Schizoneura*, e.g. the strobilus of *Schizoneura harrisii* Ash from the Upper Triassic of the USA (Ash, 1985). This strobilus differs from the strobili that have been described here in that it is at least 30 mm long (base unknown) and only 8 mm wide throughout. The arrangement of the sporangia in

PLATE III

Equisetites arenaceus: Isolated strobili, sporangiophore heads and a spore.

1. Slightly disintegrated strobilus yielding spores. SCHL-1088a. $\times 1.7$.
2. Specimen yielding spores. SCHL-268. $\times 1.7$.
3. Longitudinal view, showing strobilus axis and sporangiophore heads (arrow) and sporangiophore axes. SCHL-271. $\times 4$.
4. Three-dimensional preservation of an isolated sporangiophore head. OCH-313b, latex-cast. $\times 8$.
5. Spore from the specimen SCHL-1066a, SEM-microphotograph. Scale 10 μm .
6. Three-dimensional preservation of an isolated sporangiophore head. OCH-313a. $\times 8$.
7. Three-dimensional preservation of two isolated sporangiophore heads. OCH-313b, latex-cast. $\times 8$.
8. Three-dimensional preservation of an isolated sporangiophore head. OCH-313b, latex-cast. $\times 8$.
9. Sporangiophore head, impression of the adaxial view. An epidermal impression zone is indicated by arrows. OCH-091a. $\times 10$.
10. Sporangiophore head, impression of the abaxial view. Inner surface showing the scar of the central stalk. OCH-091b. $\times 10$.

PLATE IV

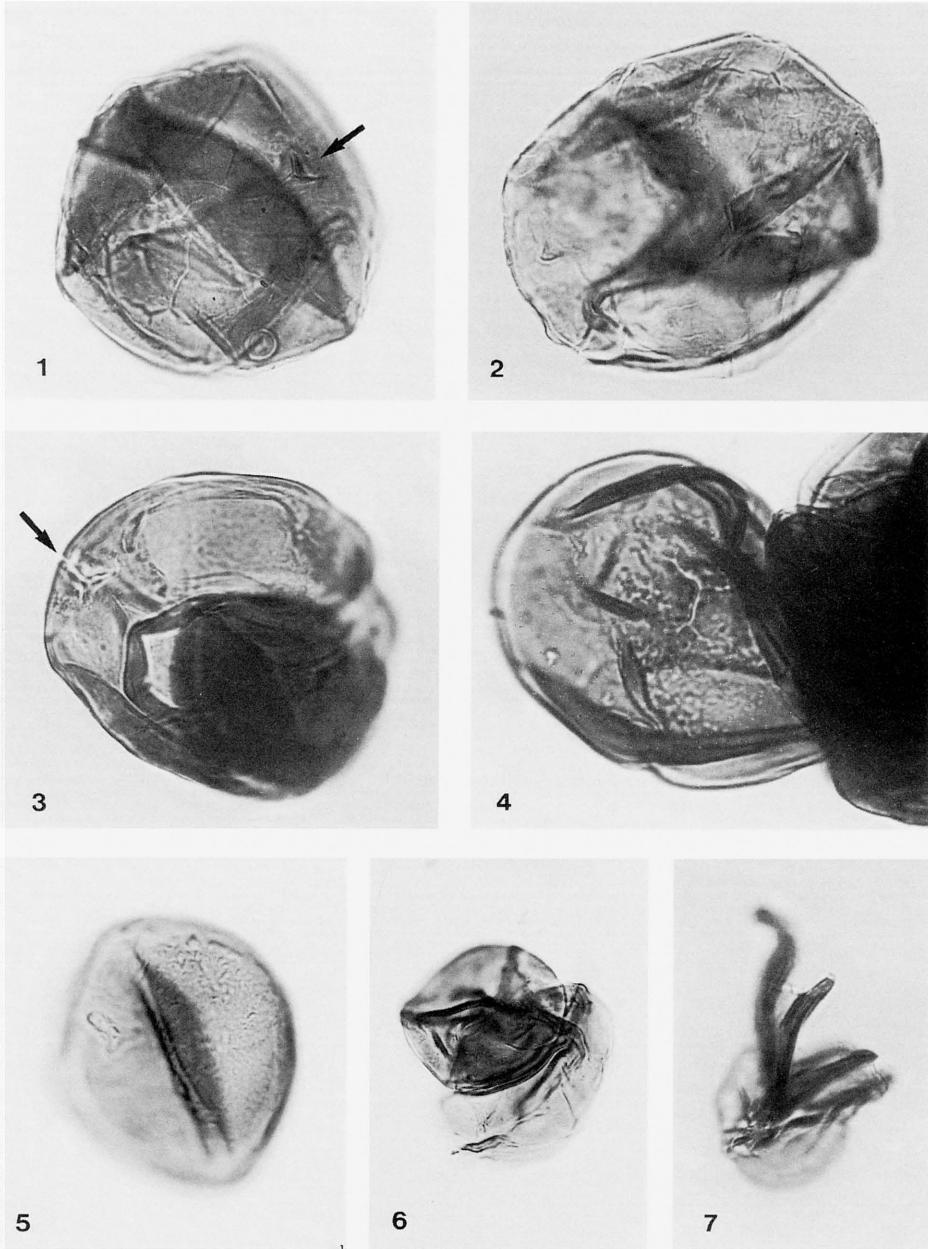


Table 1
Comparison between various Mesozoic *Equisetum*, *Equisetites* and *Equisetostachys* strobili and their spores

	Length of cone (mm)	Width of cone (mm)	Diameter spor. head (mm)	Length of stalk (mm)	Spore diameter (µm)	Alete or trilete	Exine sculpture	Elaters
<i>E. arenaceus</i>	21–35	17–24	3–5	5	50–60	alete or trilete	scarbrate to micro-rugulate	–
<i>E. verticillate</i>	15–30	5–10	1.5–2.5	1.5–3	41–49	trilete	?smooth or scabrate	–
<i>E. boureaui</i>	?	7	?	?	30	?	smooth	–
<i>E. nathorstii</i>	>20	10	1–1.6	?	35–40	trilete	smooth	–
<i>E. suecicus</i>	>20	20	2–3	2	40–50	alete	smooth	–
<i>E. muensteri</i>	>40	20	2.5	2	40–50	alete	smooth	–
<i>E. laterale</i>	10	5	0.8–0.9	?	24–41	alete	scabrate to micro-rugulate	–
<i>E. columnare</i>	>25	~20	3	3–4	40–50	alete	scabrate	+
<i>E. lyellii</i>	?	?	1.2	?	28–48	alete	smooth or scabrate	–

this strobilus is unknown. The spores from the American strobilus are globose, presumably alete, smooth with a thin spore wall (1 mm) and 25–30 µm in diameter. Long, narrow strobili like this one are also known from other Triassic sediments; they are usually placed in the formgenus *Echinostachys*. They have often been attributed to *Neocalamites* or *Schizoneura* species (Grauvogel-Stamm, 1978; Ash, 1985). Better known are the strobili *Echinostachys paradoxa*, attributed to *Schizoneura paradoxa* from the Upper Triassic of France (Grauvogel-Stamm, 1978). These strobili differ from all strobili attributed to *Equisetum* or *Equisetites* in the arrangement of the sporangia. In *Equisetum* (or *Equisetites*) the sporangia are attached in one whorl on the sporangiophore head, while in the *Schizoneura paradoxa* strobili the sporangia are attached in several whorls on the sporangiophore stalk. These strobili have been found attached to leafy plant parts, apically situated on small axillary, unbranched shoots. Another difference with the material described here, and also with other *Equisetum* strobili, is that the

sporangiophore heads show a central thickening which can vary in size. There is also a slight differentiation between strobili with miospores and strobili with macrospores. The strobili with miospores and the strobili with macrospores are rather similar, showing only small differences in size and shape of the sporangiophores. The mio- and macrospores recovered from these strobili are also extremely alike, differing only in size. Both types are globose in outline, always heavily folded and carry a small triradiate scar. The exospore sculpture is granulate. The mean diameter of the miospores is 42 µm (range 32–52 µm), while that of the macrospores is 53 µm (range 41–80 µm). Grauvogel-Stamm (1978) described *Equisetostachys verticillata* strobili from the same Upper Triassic beds in France, that she attributed to *Equisetites* on the base of their similarity to strobili of extant *Equisetum* species (like the strobili of *E. arenaceus* described here). These strobili are 15–30 mm long, 5–10 mm wide and show at their base a whorl of *Equisetum* leaves. The 1.5–3 mm wide axis is surrounded by whorls of peltate spo-

PLATE IV
Equisetites arenaceus—spores. 1–4, 6, 7 from SCHL-1066a; 5 from SCHL-268.

- 1. Spore showing trilete mark (arrow). × 1000.
- 2. Alete spore showing exospore and a possible, thin perispore. × 1000.
- 3. Normal and abortive spore sticking together; normal spore shows trilete mark (arrow). × 1000.
- 4. Mature spore on the edge of a spore mass, note forked trilete mark. × 1000.
- 5. Small spore showing surface structure. × 1000.
- 6. Two spores or possibly an exospore and a perispore that originally belonged to the same spore. × 500.
- 7. The only possible indication of the presence of elaters. × 1000.

rangioophores. The sporangioophores consist of a stalk 1.5–3 mm long and 0.2 mm wide, and a usually hexagonal sporangioophore head (1.5–2.5 mm in diameter) bearing a whorl of 1–1.5 mm long and 0.3 mm wide sporangia at their lower side. These strobili are extremely like the strobili of *Equisetites arenaceus*, except that larger strobili may occur in the latter. The spores of *Equisetostachys verticillata* are similar to those of *Equisetites arenaceus*, except that they always bear a trilete scar. Their size is slightly smaller than in *E. arenaceus* (41–49 µm versus 50–60 µm). *E. verticillata* has been attributed to *Equisetites mougeotii* (Grauvogel-Stamm, 1978).

Another, not so well-known Upper Triassic equisetalean strobilus is *Equisetum boureauui* described from Cambodia (Vozenin-Serra and Laroche, 1976). This strobilus is ca. 7 mm wide (length unknown) and differs from the general type of fossil and extant *Equisetum*-like strobili in the presence of only 4 sporangia (2 groups of 2 sporangia) per sporangioophore. The spores are globose, ca. 30 µm in diameter and heavily folded. They are probably immature as they stuck together and had to be separated before study.

Halle (1908) described two very similar *Equisetostachys* species from the Rhaeto-Liassic floras of Sweden: *E. nathorstii* and *E. suecicus*. The first species (only the holotype is known) is a strobilus at least 2 cm long and 1 cm wide with rather small sporangioophores: the hexagonal sporangioophores are only 1–1.6 mm in diameter. *E. suecicus* is larger: the strobili are at least 4 cm long and 2 cm wide with sporangioophores 2–3 mm in diameter. The sporangioophores were often found separately, just as is the case in *E. arenaceus*. It is of course possible that *E. nathorstii* is a young form of *E. suecicus*, but this seems unlikely as the spores from both species appear to be (almost) mature and are slightly different. Both spore types are globose and usually folded, with a thin exine. *E. nathorstii* spores are 35–40 µm in diameter and always show a short, clear triradiate scar. They are extremely like those of *E. verticillata*, their slightly smaller size being the only difference. *E. suecicus* spores are slightly larger (40–50 µm), probably aleate and smooth. They were, however,

too badly preserved to see many details. Halle (1908) did not give any possible attribution to an *Equisetum* species for these strobili.

Barnard (1967) described strobili belonging to *Equisetum muensteri* from the Liassic of Iran. The strobili which were not figured are at least 4 cm long and 2 cm wide. The strobilus axis is 5–10 mm in diameter with 14–16 sporangioophores in each whorl. The peltate sporangioophores have a 2 mm long stalk and a hexagonal head 2.5 mm in diameter. The spores are round, smooth and thin-walled like all fossil *Equisetum*-like spores and 40–50 µm in diameter. In fact, this strobilus description fits *Equisetostachys suecicus* so well, that they may be identical. It is possible that *Equisetostachys suecicus* might have belonged to *E. muensteri*. However, as the stem associated with this Iranian material was determined as belonging to *E. leavis* (Schweitzer et al., 1997), these strobili may well have belonged to *E. leavis*, a species which also occurs in the Liassic of Sweden (Halle, 1908).

Gould (1968) described the strobilus of *Equisetum laterale* from the lower Middle Jurassic of Australia. This strobilus is borne terminally on a normal vegetative stem and is subtended by a segmented collar which is possibly a modified leaf sheath. The oval strobilus is ca. 10 mm long and 5 mm wide (only 2 specimens). This is the smallest strobilus size found so far. The sporangioophores are peltate with polygonal heads (0.8–0.9 mm in diameter). The sporangial walls are not well preserved, but the strobili contain numerous, apparently almost mature spores. These spores are (sub)globose, with a mean diameter of ca. 35 µm (extremes 24–41 µm) and only some of the spores are folded. The exine is rather thick, 1–3 µm, with a scabrate to microrugulate sculpture. Abnormal (abortive) spores have sometimes been found, exactly as in *E. arenaceus*.

Harris (1978) is the only author (apart from Compter, 1911; see above) who described in situ *Equisetum* spores with attached elaters. The strobili of *E. columnare* from the Middle Jurassic of Yorkshire, which have never been found attached, and never complete, are at least 2.5 cm long and 2 cm wide. The strobilus fragments were rather decayed, and the rock matrix among the sporangioophore heads (ca. 3 mm in diameter) showed a

large number of globose spores which seemed to bear fine threads resembling recent *Equisetum* elaters. Harris did not describe the spores in detail, but judging from his figures they are aleate, about 40–50 µm in diameter and with a thin scabrate exine. The presumed elaters are too short to cover the whole spore.

Watson (1983) and Watson and Batten (1990) described dispersed sporangioophores probably belonging to *Equisetites lyellii* from the Wealden of England. These sporangioophores are peltate but differ from all other sporangioophores in their circular heads with about 24 surface ribs radiating from the centre. The sporangia are rounded rather than elongated as in all other species where the sporangia are known, and yielded spores in large masses. The spores are globose, aleate, often slightly folded, with a smooth or scabrate 1.5 µm thick exine. The mean diameter is ca. 37 µm (extremes 28–48 µm). In the dispersed spore species *Pilasporites allenii* Batten, 1968 which probably represents the dispersed spores of *Equisetites lyellii*, a thin (less than 0.5 µm) smooth perispore was observed, just as in some of the *E. arenaceus* spores. No traces of elaters were found, although Watson and Batten (1990) record an intensive search for elaters in the spore masses, including unmacerated material. The various *Equisetum* or *Equisetites* strobili and spores discussed above, are compared in Table 1.

3.5. Comparison with recent spores

The spores found in *E. arenaceus* strobili, and indeed most spores found in situ in Mesozoic equisetalean fructifications, differ from those of extant *Equisetum* species primarily in the absence of elaters, with the possible exception of *E. columnare* (see Harris, 1978). This has already been discussed in the spore description. A second difference is the aperture: extant *Equisetum* spores have long been regarded as inaperturate (alete). Recent SEM and TEM work (see Tryon and Lugardon, 1991) revealed, however, that they possess a very small, circular to oval aperture; this is totally different from the mono- or trilete spores that are common in the ferns. The Mesozoic equisetalean spores that have been described so far are either trilete with a distinct, short triradiate scar on the

proximal surface, or they are aleate (inaperturate). As most of the work done on these in situ spores has mainly been carried out by light microscope only, a tiny circular to oval aperture could easily have been missed as was the case in the extant spores. The trilete spore type is, however, certainly different from the extant one.

The exospore in extant *Equisetum* spores is smooth, the perispore (or episporium as it is sometimes called) is granulate with scattered spherules (orbicules) and fused with the exospore and the elaters near the aperture (Tryon and Lugardon, 1991). The size of the various recent *Equisetum* spores varies between 35 and 65 µm. This is in accordance with the sizes recorded from the fossil spores. Furthermore, the globose shape and the exine sculpture of the mesozoic spores agree more or less with the extant ones. As stated above, the main difference is the absence of elaters and the presence of a triradiate mark in some species.

Extant *Equisetum* is considered to have isosporous; thus, no mio- and macrosporous have been distinguished. This is in contrast to *Schizoneura* (*Echinostachys*) where mio- and macrosporous have been recorded, with small differences only (Grauvogel-Stamm, 1978). So far, all fossil *Equisetites* species have been recorded with isosporous.

It should be mentioned that spores attributed to the extinct group of the Calamites have been recorded from the Carboniferous, which possess three elaters. Recent *Equisetum* is probably related to the Calamites based on similarities of stems, leaves and strobili. Work on one of these Carboniferous spores (*Elaterites triferens*) by Kurmann and Taylor (1984) revealed that they differ from extant *Equisetum* spores in a generally thinner exospore, a thicker perispore and the presence of three elaters; the usual number in extant *Equisetum* being two. A further difference is that, while the elaters in extant *Equisetum* envelop the spores, the elaters in *Elaterites* do not do so but each elater is rather short and coiled. These spores show a distinct triradiate scar on the proximal surface of the exospore while the perispore often shows a circular opening over this suture. The elaters are attached on the distal surface of the spores (Kurmann and Taylor, 1984). The aperture

region and thus the place of attachment of the elaters are considered to be on the proximal surface in extant *Equisetum* spores (Uehara and Kurita, 1989). Therefore, the number of elaters, their shape and their place of attachment in the Carboniferous *Elatrites* spores differs from the extant spores. It is a pity that no intermediate spore forms have been found to date in the Mesozoic.

3.6. Comparison with dispersed spores

The spores of *Equisetites arenaceus*, when found dispersed, would certainly fall in the dispersed species *Calamospora keuperiana* Mädlar. This species has been recorded from several European Late Triassic sediments (Brugman et al., 1994), including the surroundings of Würzburg where the fossil material has also been found (Heunisch, 1986). Other equisetalean in situ spores have usually been attributed to either this species or other species of *Calamospora* (Grauvogel-Stamm, 1978; Mangerud, 1994). Batten (1968) attributed the spores found in *E. lyelli* to *Pilasporites allenii*. *Pilasporites* is a late Palaeozoic (mainly Permian) genus for inaperturate spores, while *Calamospora* is a genus for Palaeozoic or Mesozoic spores that are sometimes inaperturate or usually possess a small triradiate mark (e.g. *C. mesozoica*). Therefore, Mesozoic in situ equisetalean spores fall either in *Calamospora* when they are trilete or sometimes alete (as the spores of *E. arenaceus*) or

in *Pilasporites* when they are completely inaperturate.

4. Isolated slender branches of *Equisetites arenaceus*

Description (Figs. 8–10; Plate V, 1–11; Plate VI, 1; Plate VII, 1, 4, 5): Slender articulate branch fragments almost uniform in flattened width of 4.5–6 mm, occasionally with various ramifying shoots of equal diameter (Fig. 8; Plate V, 6). Internode with smooth surface, sometimes slightly longitudinal ridges visible (Plate V, 6, 8). Length of internodes varying, largest 32 mm long, gradually decreasing towards its distal part, branch apex rounded (Plate V, 3, 4).

Leaf sheath of slender branches 3.5–5 mm long, composed of 12–15 raised leaf segments. Leaf segments 0.7–1.2 mm wide, free leaf teeth diverging from gradually tapering into acuminate apex (Plate V, 1, 3, 4), triangular in form (Plate V, 8, 9) or slightly blunt (Plate V, 7; Plate VI, 5). Commisural furrows often indistinctly preserved (Plate VII, 1). Several specimens carry monopodial root structures born on the nodes (Figs. 8 and 9; Plate V, 2, 5, 7; Plate VII, 5).

Nodal diaphragms of branches often isolated (Plate V, 5, 10) or showing oblique displacement due to rotating by compression, but usually not displaced upwards or downwards (Plate V, 8, 9). All diaphragms circular in front view and more or

PLATE V

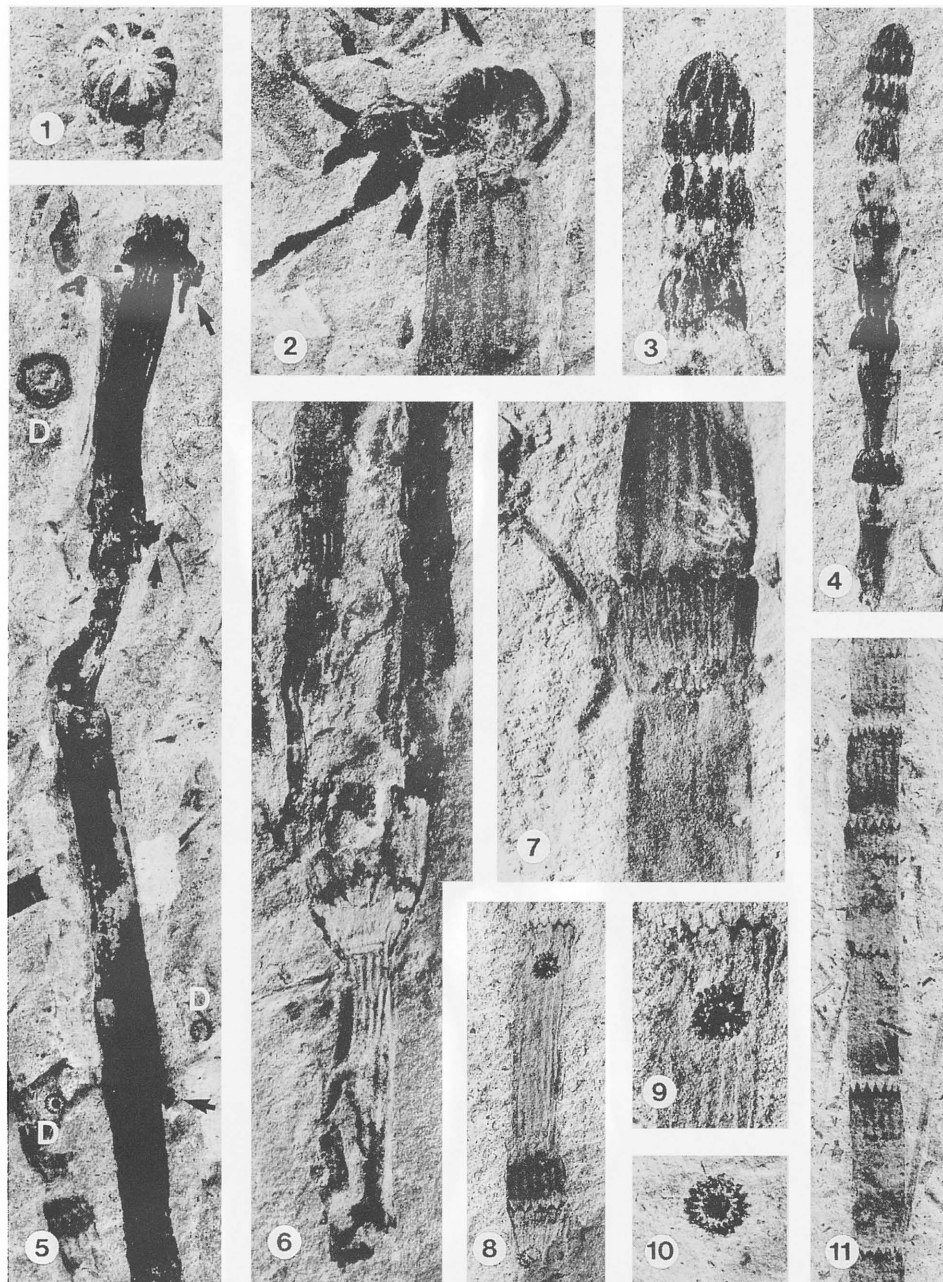
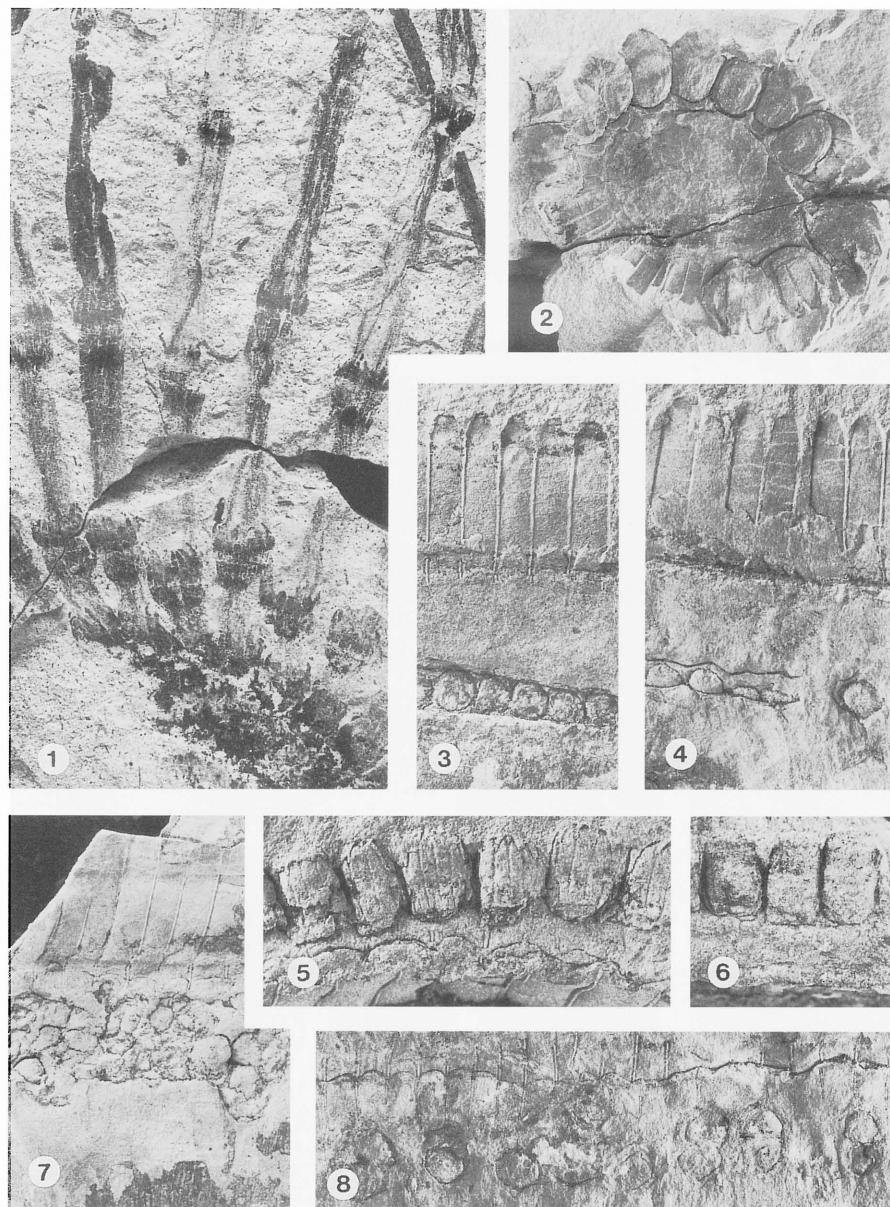


PLATE V

Lateral branches of *E. arenaceus*.

1. Showing hollow branch with sharply pointed leaf-tips in oblique transverse section. SCHL-834. $\times 4$.
2. Node with adventitious roots. SCHL-875. $\times 4$.
3. Sterile branch apex, part of 4. SCHL-844a. $\times 4$.
4. Distal part of a sterile branch with apex, showing the gradual decrease of the internode length. SCHL-844a. $\times 2$.
5. Branch showing adventitious roots on the nodes (arrows); together with isolated branch diaphragms (indicated with D). SCHL-884. $\times 2$.
6. Ramification of a branch. SCHL-841a. $\times 2$.
7. Nodal zone of a branch showing adventitious roots and a whorl of leaves with blunt tips. SCHL-796. $\times 4$.
8. Portion of an isolated branch showing two rotated diaphragms at the nodes. SCHL-848. $\times 2$.
9. Detail from 8 showing acicular leaf tips. SCHL-848. $\times 4$.
10. Isolated branch diaphragm. SCHL-835. $\times 4$.
11. Distal part of a branch, showing the decreasing internode length towards the apex. SCHL-864. $\times 2$.

PLATE VI



less constant in size, about 2–2.5 mm in diameter, showing a central granular area surrounded by a ring of zigzag spokes (Plate V, 10).

Comparison: Schoenlein and Schenk, 1865, p. 11; pl. 1, 8; pl. 6, 3) and Heer (1865, p. 50; fig. 27g) were the first to depict dispersed slender equisetalean shoots which were regarded as branches from *E. arenaceus*, just as the narrow axis in Heer (1877, p. 75; pl. 28, 5). Kräusel (1959), however, reinterpreted these specimens together with a small isolated leaf sheath in Schoenlein and Schenk (1865, pl. 1, 7a, b), as belonging to his newly established species *E. elegans*.

All these specimens fit the here described *E. arenaceus* branches in terms of size and leaf sheath variation. Also the known features of *E. elegans* in Kräusel (1959) with encompassed roots on some nodes, suggest very strongly that one is dealing with branches of the larger *E. arenaceus* instead of it being a species of its own. Therefore, we include *E. elegans* in *E. arenaceus* and give the following emended diagnosis.

Equisetites arenaceus – emended diagnosis: Rhizome horizontal with short internodes bearing erect stems and long, vertical roots. Erect vegetative stems large. Internode length gradually decreasing towards basal and apical regions; in the middle region slightly longer than wide. Outer surface of internode smooth. Nodal diaphragm large, continuous with a finely granular surface. Nodes usually with a large number of leaves (>100), basally united into a leaf sheath, with commissural furrows continuing below leaf sheath.

Distal leaf parts folded forming an adaxial cuff (4–6 mm high, ca. 4 mm wide). Raised pyramidal and thick-textured leaf apices terminating abruptly in spine-like teeth.

Erect stems occasionally with whorls of slender branches, almost uniform in flattened width (4–6 mm). Branch internode smooth, varying in length, gradually decreasing distally and proximally. Leaf sheaths of slender branches usually 3.5–5 mm long, composed of 12–15 raised leaf segments. Leaf segments ca. 1 mm wide; free leaf teeth diverging from gradually tapering into acuminate apex. Commissural furrows often indistinct. Nodal diaphragm circular, 2–2.5 mm in diameter, showing a central granular area surrounded by a ring of zigzag spokes.

Up to three strobili terminally attached on a slender branch, in different stages of maturity. Strobili non-apiculate or obovate (largest 35 mm long, 22 mm wide) consisting of up to 9 whorls of sporangiophores. Sporangioophores with a stalk terminating in a penta- to heptagonal peltate head (up to 3.5 mm in diameter) bearing a circle of elongated sporangia on its lower surface. Spores usually 50–60 µm in diameter, globose, often folded; aleate or with a small triradiate scar. Exospore c. 1 µm thick, faintly scabrate to micro-rugulate; ?perispore smooth, 0.5 µm thick.

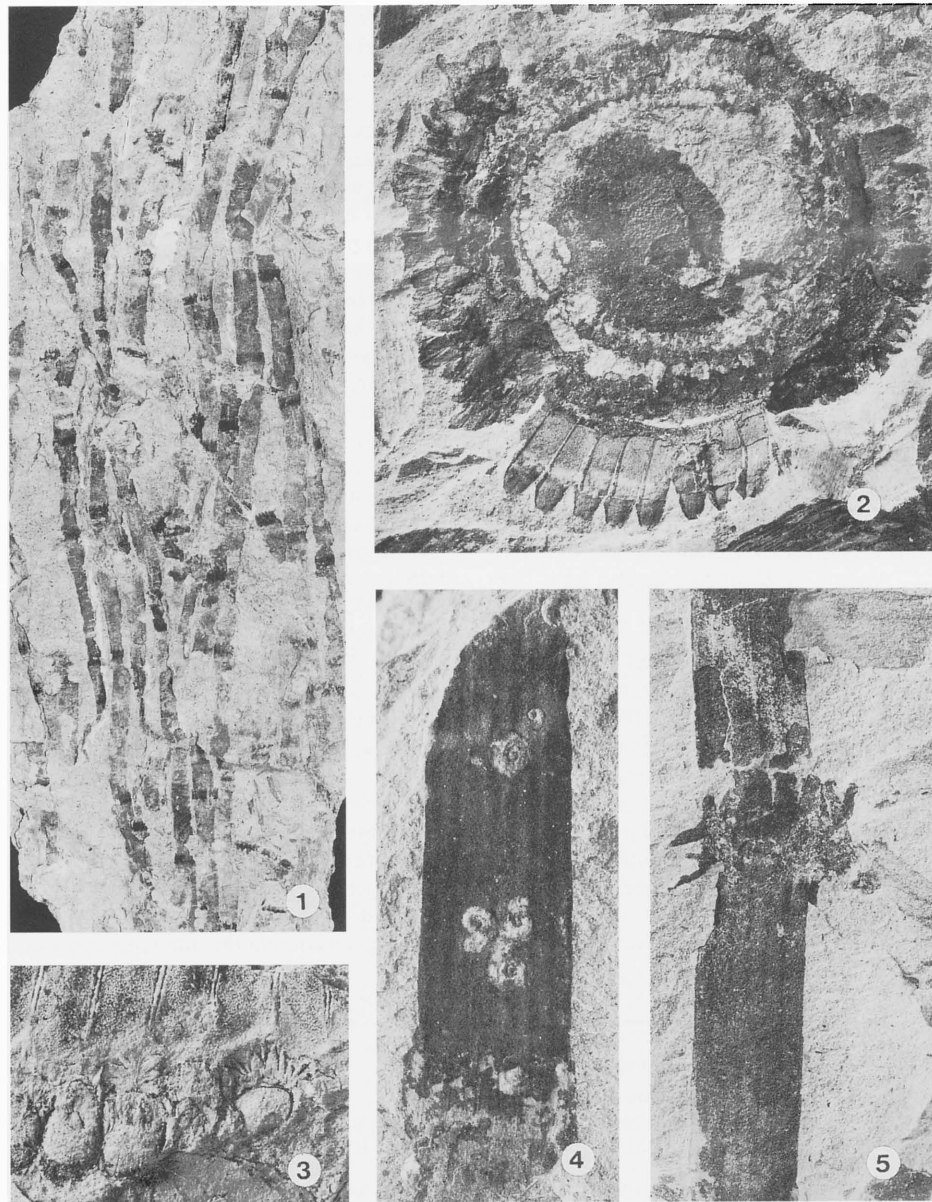
Discussion: A certain designation of sterile or fertile branches is only enabled by the presence of their complete distal parts, either showing the telescope-like vegetative branch apex (Plate V, 3,4) or the attached strobili, but those finds are extremely rare. In considering the differences and similarities

PLATE VI

Junction of *Equisetites arenaceus* sterile and fertile branches.

1. Branches radially emanating in situ from the node. SCHL-793. × 2.
2. A small nodal stem diaphragm in backside view, surrounded by the underneath stem leaf sheath (visible left) as well as some proximal nodes of the branch showing branch diaphragms (in the top) and branch leaf sheaths (right below). OCH-312a. × 2.5.
3. Detail of a stem leaf sheath with single lined branch scars. SCHL-898. × 2.
4. Detail of Fig. 5. Portion of a stem leaf sheath showing single line of branch scars with a gap. SCHL-828a. × 2.
5. Detail of Fig. 4. Proximal branch internodes in cast preservation showing the branch leaf sheath. SCHL-811. × 4.
6. Detail of Fig. 6. Proximal branch internodes in cast preservation. ROT-021b. × 4.
7. Detail of Fig. 2. Portion of a stem leaf sheath showing branch scars in several lines. SCHL-826a. × 2.
8. Detail of Fig. 3. Irregular branch scars, partly in longitudinal pairs and impressions of the commissural grooves (below). SCHL-821. × 2.

PLATE VII



it becomes obvious that sterile and fertile branch portions, with the exception of their distal parts, are not significantly different. Both fall within the same size range of branch diameter, and the arrangement of the leaf sheath is virtually similar in both, except for the more prominent leaf segment configuration on the repeated ramifying branch zone (Plate V, 6) and the uppermost leaf sheaths on the fertile branch, respectively (Plate II, 1, 5–7).

Rotated diaphragms as shown in Plate V, 8, 9, are also apparent in other fossil slender horsetail axes, e.g. in *E. iwamurensis* (Kimura and Tsujii, 1980, p. 346; fig. 1e, j), *E. gracilis* (Halle, 1908, pl. 3, 12, 13, 15, 16), and *E. muensteri* (Harris, 1931, pl. 2, 7, 10).

The branches repeat the morphology of the stem except for the three dimensional leaf tip architecture of the primary stem (Kelber, 1993). The tissue of the branch seems to have been rather unsubstantial. In some specimens the impressions of the internodes are weaker (e.g. in Plate VI, 1; Plate VII, 1), then only the carbonaceous substance of the leaf sheaths remains a good deal thicker. Similar preservation patterns on narrow *Equisetites* axes have been reported from *E. gracilis* (Halle, 1908) and *Equisetites* sp. 'a' (Douglas, 1973).

This phytotaphonomic feature may have been caused by processes of fossil diagenesis. On the other hand, evidence exists for a surprising durability of *E. arenaceus* branches: Impressions of adult dwelling tubes of the polychaete *Spirorbis* sp. on these branches (Fig. 10; Plate VII, 4) suggest that they lasted in a submersed stage at least 6 months or more. The pseudoplanctically living worm requires this time span for its adult growth, with

a constant oxygen concentration in the water. The settled plant tissue has apparently been resistant to microbiological destruction (Kelber, 1987).

5. Affiliation of sterile and fertile branches to *E. arenaceus*

One of the aims of this paper is the piecing together of disarticulated fertile or sterile slender branches with the aerial primary stem. Owing to the lack of in situ fossils it has been necessary to testify the linkage by suitable branch scars as well as connected basal branch portions and ochreoles on the *E. arenaceus* stem. *E. arenaceus* is mainly taxonomically based on the limited characters of its leaf segments, which are connate to a leaf sheath. In Keuper macrofloras, *E. arenaceus* can be easily confused with *E. conicus* which has been frequently designated as *E. platyodon* in the past (Kräusel, 1959). Species assignment has been clarified by Frentzen (1933) and Kräusel (1959). In comparison, *E. conicus* shows much broader leaf segments. The most salient morphological character that distinguishes *E. arenaceus* stem leaf sheaths from those of *E. conicus* is nevertheless the organization of the leaf tips. In *E. conicus* the leaf tips terminate wedge-shaped or bluntly toothed without a spine, whereas in *E. arenaceus* the multishaped variety of leaf tips are consistently characterized by spines attached to an abscission layer. Recent study on well preserved leaf sheaths from Schleierth and Ochsenfurt (Kelber, 1993) has shown that all distal leaf parts in *E. arenaceus* are folded forming an adaxial cuff. Spines occasionally broke off leaving their thickened squari-

PLATE VII

Lateral branches of *Equisetites arenaceus*.

1. Cluster of subparallel detached *Equisetites arenaceus* branches. GNO-033. $\times 0.7$.
2. Stem diaphragm in upside-down view, radially surrounded by proximal leaf sheaths of branches. An upper layer (basal part of the photograph) shows the partly preserved stem leaf sheath in organic connection. SCHL-812a. $\times 2.5$.
3. Branch scars with impressions of the proximal branch leaf sheaths (right) and two first branch internodes in cast preservation (left). In the upper part the impression of the stem leaf sheath with their commissural furrows. SCHL-918. $\times 4$.
4. Detail from Fig. 10. Isolated branch settled by dwelling tubes of *Spirorbis* sp. OCH-008a. $\times 4$.
5. Portion of an isolated branch showing the node with adventitious roots. SCHL-846. $\times 4$.

form or trapezoid abscission layer at the end of the dome shaped leaf apex.

A comparison between the lower preserved parts of the fertile branch in Plate II, 3 and the sterile branch in Plate V, 4 shows no significant differences. The slightly varying leaf segment morphology is within the variability of isolated branch portions (Plate V, 1–9, 11) which are also comparable to or might even be fertile ones. Only the distal branch parts exhibit a certain difference: flattened fertile branches show a more triangular leaf sheath outline with prominent and elongated leaf teeth. The uppermost 2–3 leaf sheaths gradually increase in width (Plate II, 1–7; Plate III, 1). In contrast, the sterile branch tips maintain their constant diameter (Plate V, 4, 11). In both fertile and sterile distal branch parts the internode length gradually diminishes. This implies that branch portions without their terminal zones cannot be unequivocally determined as fertile or sterile. The same uncertainty applies to basal branch portions or branch traces on the stem.

It should be mentioned that *E. arenaceus* stems are additionally ramified by thick branches indicated by large branch scars, e.g. Frentzen (1922, pl. 1, 14). The following descriptions concentrate on branch scars in main stem leaf sheath which fit perfectly the separated sterile or fertile branches and on small basal branches or branch ochreoles organically connected with the stem.

5.1. Branch scars

Description (Figs. 2, 3 and 5; Plate VI, 3, 4, 7, 8): Stem fragments showing branch scars on the node in uniform diameter of about 3 mm, which are composed in a regular whorl (Plate VI, 3), occasionally interrupted or additionally arranged in longitudinal pairs (Figs. 3 and 5; Plate VI, 4, 8) or even in multiple lines (Fig. 2; Plate VI, 7). Stem leaf segments of 3–3.5 mm width, fused into nodal sheath which is born beneath the node; impressions of the more contracted internode partly preserved (Figs. 2, 3 and 5).

Comparison: Small branch traces on leaf sheaths in lateral preservation have been described from *E. conicus* [*E. platyodon*] (Heer, 1877, p. 76; pl.

28, 8) and from *E. conf. beanii* and *E. scanicus* (Halle, 1908, pl. 5, 1, 2; pl. 6, 7). Similar single lined branch scars occurring between commissural grooves have also been reported from *E. richmondensis* (Bock, 1969, p. 82, figs. 139, 140).

5.2. Ochreoles in transectional preservation

Description (Figs. 4, 6 and 7; Plate VI, 2, 5, 6; Plate VII, 2, 3): *Equisetites* stem nodal diaphragms up to 90 mm in diameter, organically connected with a whorl of branch internodes, uniform in size, 3–4 mm (Figs. 6 and 7; Plate VI, 6), as well as fragments of the species indicating leaf sheaths of the main stem of *Equisetites arenaceus* (Fig. 4; Plate VI, 2, 5, Plate VII, 2, 3). Branch nodal diaphragm 2.5–3.5 mm in diameter (Plate VI, 2), branch leaf sheath composed of 10–12 leaf segments of 0.8–1.0 mm.

In Plate VI, 1 attached branches on a diaphragm fragment reveal the rapid internode increase of branch internode length. So far as recognizable, the first 2 proximal internodes are very short, followed by third internode of 40 mm length and 4th internode of 44 mm length. Emanating from the main stem, all branch nodes are more or less in the same radial distance level.

Comparison: Schenk (1864, p. 66) already mentioned branches on *E. arenaceus*, displaying concentric leaf sheaths. Beyond this, preserved proximal branch remains (ochreole-structures) on *E. arenaceus* stems have been misinterpreted in previous works and with the exception of the photograph in Kräusel (1959, pl. 4, 36), indistinctly figured. The radial appendices have been considered in the past as roots (Jaeger, 1827, pp. 19, 37; pl. 4, 5), a rim of vallecular canals (Heer, 1877, p. 75; pl. 26, 2), scales of a strobilus (Compter, 1911, p. 101; figs. 31, 32), sclerenchymatic tissue (Frentzen, 1933, p. 32; pl. 1, 2) and remains of the leaf sheath (Kräusel, 1959, p. 14; pl. 4, 36). The latter specimen was erroneously determined as *E. conicus*.

Up to our present knowledge, a proper taxonomic assignment is only possible by the leaf sheath of the main axis with its clearly defined

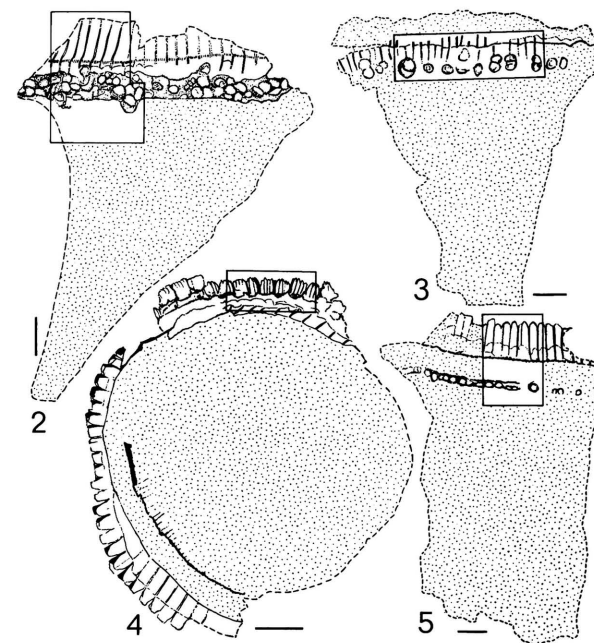


Fig. 2. Figs. 2–5: Overall view of branch scars and ochreoles on *Equisetites arenaceus*. Scale: 1 cm.

Fig. 2. Branch scars in several lines. See Plate VI, 7; SCHL-826a.

Fig. 3. Irregular branch scars, partly in longitudinal pairs. See Plate VI, 8; SCHL-821.

Fig. 4. Nodal stem diaphragm, partly surrounded by leaf sheath remains (left) and ochreole structures (above) in cast preservation. See Plate VI, 5; SCHL-811.

Fig. 5. Stem leaf sheath, displaying interrupted single line of branch scars. See Plate VI, 4; SCHL-828a.

distal leaf teeth, organically connected with the ochreole structure or the basal branch portion.

Discussion: The absence of any root scar on the branch scar bearing stem leaf sheath and partly preserved internode indicates that the plant fragment is part of a subareal stem.

Narrow aerial branches developed regularly or irregularly in a single or multiple whorl from a primary stem node. Whereas the isolated branches are randomly broken in portions of one to several internodes, the leaf sheath of the first basal branch node/internode remained on the stem. This situation is particularly recognizable in transectional

preservation (Figs. 4, 6 and 7; Plate VI, 5, 6; Plate VII, 3). On the basis of this evidence, it is clear that the durable part in organic insertion on the primary axis is an ochreole, comparable to such plant organs in modern *Equisetum* species.

An ochreole or basal sheath is considered to be a protective structure for the branch bud, analogous to the bud scales of phanerogams. Many extant *Equisetum* species show a basal collar formed by the outer tissues of the nodal sheath through which the branch has erupted. The branch bud is originally enclosed by the leaf sheath and must grow out through its base. Where it emerges, a fringe of scarious and brownish sheath tissue is left around the branch base. In its gross morphol-

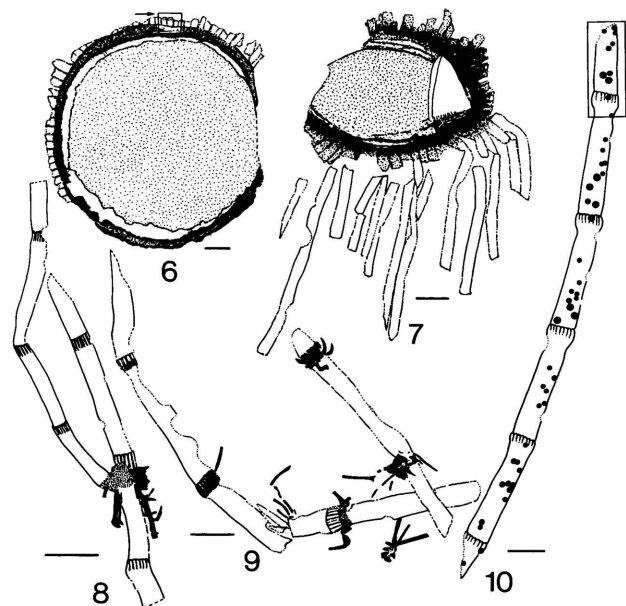


Fig. 6. Figs. 6–10: Overall view of *Equisetites arenaceus* nodal diaphragms and isolated branches, partly with adventitious roots. Scale: 1 cm.

Fig. 6. Stem nodal diaphragm 9 cm in diameter, partly surrounded by ochreole structures. See Plate VI, 6; ROT-021a.

Fig. 7. Oblique view of a stem nodal diaphragm with partly attached branches. SCHL-895.

Fig. 8. Forked isolated branch, showing adventitious roots. SCHL-883a.

Fig. 9. Assemblage of branches bearing adventitious roots. SCHL-842

Fig. 10. Branch bearing spiral tests of the aquatic encrusting annelid *Spirorbis* sp. See Plate VII, 4; OCH-008a.

ogy, it is similar to a regular branch leaf sheath or in some cases slightly reduced (Hauke, 1987; Sharma, 1992).

6. A new reconstruction of the strobili-bearing axis

6.1. Previous work

The first reconstruction of a triplet strobilus group terminating a slightly curved, short, thick leafless articulated branch was given by Frentzen (1933) and repeated in Frentzen (1934). Two allegedly fertile branches figured in Frentzen (1933) are stored in Stuttgart. Reinvestigation shows two axes in cast preservation, 103 and

61 mm in length, respectively. Both are 27 mm in diameter near the branch base. There is no evidence of any detached or connected strobilus. A polygonal pattern at the branch base belonging to the primary stem might erroneously be interpreted as impressions of strobili. We suggest that these might be leaf scars in a clearly defined area around the branch base on the stem. Axes of these proportions are not comparable to fertile branches of *E. arenaceus*.

Coloured plaster replicas from Frentzen (1933) deposited in the Naturhistorisches Museum in Heilbronn show no recognisable contact between strobili and axes, and have no evidential value. We suspect that some confusion arose as a result of the overprint of two strobili.

The few photos in Frentzen (1933) document neither a proper view of the natural arrangement of the strobili in triplet groups nor the manner of strobili attachment on the branch or its insertion on the stem. Despite these deficiencies, Frentzen's reconstruction given in 1933 (fig. 3) fits perfectly in its basic principles. Architecture, shape and proportion of the strobiliferous branch and its insertion requires modification, however.

6.2. Suggested reconstruction

Although Frentzen developed concepts of triplet strobili groups on fertile branches, the chain of evidence for these relevant fossil plant organs in their natural connection is only provided in this paper. The improved suggested reconstruction (Fig. 11) is chiefly based on a combination of specimens with strobili bearing branches (Plate II, 3) and the insertion of similar branch portions on the primary stem of *E. arenaceus*.

The asymmetrically ellipsoid strobili are situated in triplet groups of different maturity at the ends of fertile branches. A strobilus consists of whorls of peltate sporangiophores carrying sporangia and attached via a stalk to the central axis. The shape of the sporangiophores is more or less irregularly polygonal, and the size depends on their organic position and stage of maturity.

The fertile branches, probably together with similar sterile branches, arise in single or multiple whorls from the primary stem node. The basal part of the stem leaf sheath would be penetrated forming an ochreole structure. There is a gradual decrease in internode length along the distal direction and, assuming that certain proximal branch portions are fertile, also in the proximal direction.

6.3. Discussion

The position of sterile and/or fertile branch radiation on the primary stem is still unknown. Examination of leafy terminal portions of *E. arenaceus* primary stems in the collection of Kelber, Würzburg, gave no evidence of branch scars on these axes which have been preserved for a length approx. 30 cm from the stem apex downwards. A massive bulk of fertile lateral branches in the upper part of the stem near the apex, as suggested

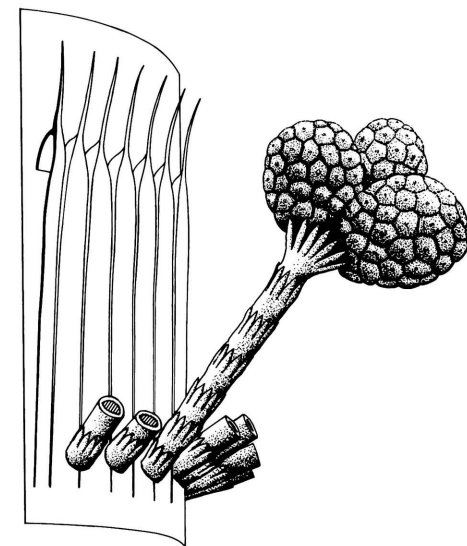


Fig. 11. Suggested reconstruction of the strobili bearing branches of *Equisetites arenaceus*. Three-dimensional architecture of leaf tips after Kelber (1993).

by Frentzen (1934) seems, therefore, rather improbable.

There is no conclusive evidence hitherto of the basal portions of the fertile branch that can only be properly indicated by its conspicuous distal leaf sheaths and by attached strobili, respectively, as well as the overall branch length. It is also unknown whether fertile branches alternate with sterile at the same node or not.

It seems that evolutionary tendencies are corroborative in two living *Equisetum* species. *E. palustre* forma *polystachum* and *E. myriochaetum* are considered to be more primitive species because the lateral branches terminate in a strobilus (Sporne, 1975; Dostal, 1984). This arrangement was regarded as such on the basis that it involves the least specialization (Foster and Gifford, 1974).

7. Reproductive strategies

Equisetites arenaceus is deemed as the most prolific floral element in the Germanic Triassic

Keuper flora. Besides these dominant macroplant remains, trunks in the vertical position of growth have been observed in the lower Keuper of Leonberg, Baden-Württemberg (Kelber and Hansch, 1995, fig. 42). Numerous hydromorphic palaeosols in the lower Keuper (Ladinian) as well as in middle Keuper (Carnian and Norian) are indicated by the typifying *Equisetites* root horizons (Linck, 1943; Mader, 1990, table 61), which belonged in all likelihood to *E. arenaceus*. Extensive populations occurred in marginal strips along the anastomosing river system and dense *E. arenaceus* reeds also invaded the levee belt as well as every hygromorphic environment surrounding standing waterbodies in the flood plain (Mader, 1990, 1997).

The extraordinary dominance of *E. arenaceus* may occur because of its three intrinsic modes of propagation:

(1) In *E. arenaceus* sexual reproduction and therefore a gametophyte generation can be inferred by the documented spore-bearing sporangiophores (Plate III, 1, 2) and their organization in strobili attached on fertile branches (Plate II).

(2) On the assumption of modern horsetails and proven by fossils of certain *E. arenaceus* rhizomes (Kelber, 1990, fig. 27; Kelber and Hansch, 1995, figs. 33, 36) we assume the vegetative reproduction of the sporophyte.

In extant *Equisetum* the shallow to deep-seated rhizome gives rise to both upright aerial shoots and, in some species, to tuberous storage organs. The rhizome may become separated either by being broken or by older parts dying, and thus beginning an independent existence. A number of *Equisetum* species are found growing along exposed banks of streams where fragmented rhizomes are washed out and carried downstream to initiate new colonies (Bierhorst, 1971).

(3) Supplementary *E. arenaceus* has been reproducing itself prolifically by means of branches with adventitious roots. After their shedding they become independent plants in the soil.

There is no evidence hitherto whether adventitious roots are born on a branch organically connected to the stem or were developed in a second stage after shedding. Rapid growing, even of adventitious roots, may have been stimulated

by the hygromorphic environment. In modern *Equisetum* from Norway, it has been demonstrated that roots are longer and more densely spaced in aquatic habitats than on dry land (Bockelie, 1994).

8. Conclusions

Sexual reproduction in *Equisetites arenaceus* is proven by triplets of strobili on small fertile branches. An extended period of spore dispersal may have been obtained by the different stages of maturity.

In situ spores of *E. arenaceus* are similar to the general type in Mesozoic equisetalean strobili; partly alete, partly with a small triradiate scar, exospore faintly scabrate, perispore smooth; no elaters have been found. The last feature is in contrast with extant *Equisetum* spores.

Size and morphological comparison suggest that both slender fertile and sterile branch portions are in complete agreement apart for their ultimate distal parts.

The paucity of branches on aerial stems as well as strobili on fertile branches might mean that a principle of shedding on predetermined breaking points is significant in *E. arenaceus*.

Because of the similarity in terms of proportion, size and leaf sheath variation, we include *E. elegans* Kräusel in *E. arenaceus* (Jaeger) Schenk.

Implied by comparison with extant *Equisetum* species and proven by fossil rhizomes, *E. arenaceus* could propagate itself by growth of its rhizome. An additional mode of vegetative reproduction is testified by adventitious roots borne at the nodes of slender lateral branches.

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