Paleobotanical
Publications
Jörn Lies

# *Tempskya* —
## A reinterpretation of the growth form of the Cretaceous tree fern

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### Abstract

The contribution presents a long overdue reinterpretation of the growth form of *Temskya*. For this purpose, old and new finds were examined and conclusions were drawn from the combination of the plant morphology preserved in the fossils and the biomechanical properties of extant ferns with similar growth characteristics of individual rhizomes or main axes. A main focus is on the ratio of frond stem diameter to total frond size. Discussion approaches are offered on open questions of morphology and growth, which should contribute to further discussion of the topic.

## 1 Introduction

In the more than 400 million-year history of land plants, the concept of the upright tree with woody tissue and secondary growth has proven particularly successful. However, other tree-like structures have repeatedly evolved, for example, root-supported tree ferns like *Psaronius*, which lack secondary growth. Although these are now extinct, their distant relatives have survived to this day in extant tree fern families such as *Cyatheaceae* and *Dicksoniaceae*.

A completely different concept was that of the pseudostem, which had already evolved in the Early Carboniferous of Australia in the zygopterid ferns (*Symplocopteris wyattii*) and in the Upper Carboniferous to Permian of Brazil in the botryopterid ferns (*Botryopteris nollii*) (Rößler et al. 2004). These formed „false stems“ from the interweaving of main axes, frond stalks, and adventitious roots, which were surprisingly light yet relatively strong and resilient.

The *Tempskyaceae* are an extinct family of Mesozoic ferns represented by a single genus, *Tempskya* (Tidwell 2002). *Tempskya* broadly resembles the zygopterid ferns of the Lower Carboniferous of Australia (Galtier & Hueber 2001) and consists of a pseudostem internally composed of numerous small, branched main axils and frond stalks embedded in a network of countless fine, interlocking adventitious roots (Brown 1936), creating a typical rope- or felt-like appearance.

The genus *Tempskya* Corda was first described in 1845 by A. C. J. Corda based on specimens found in Bohemia (now the Czech Republic) and was widely distributed in Europe and North America. Later discoveries extended its range to Asia, Argentina, and Australia.

However, the systematic relationship of the family remained unclear due to the lack of associated leaves and reproductive organs (Tidwell & Ash 1994). Recently, Martınez & Olivo (2015) corrected

Fig. 1: Branching model of the *Tempskya* reconstruction with fronds and roots of one generation (PalaeoBiome/Lies)

the family *Tempskyaceae* based on exceptionally well-preserved *Tempskya*, whose reproductive organs resemble those of extant *Polypodiopsida*, suggesting that *Tempskya* indeed belongs to the *Cyatheales* (Martinez & Olivo 2015).

Anatomically, *Tempskya* differs from *Symplocopteris* and *Botryopteris* by siphonostele with phloem and C-shaped xylem strands, a combination of parenchyma and sclerenchyma bark, and diarch roots that arise directly from the main axis.

It may be somewhat surprising that, given the frequency and density of *Tempskya* species found worldwide, there are no current reconstructions for this genus of tree ferns. *Tempskya* has been recorded from the Cretaceous of Central Europe, North and South America, Asia, and Australia. Various forms and species have been described, including 12 species from North America and 8–10 species from Europe (Tidwell et al. 2003, Clifford et al. 2005).

Due to the sheer size of these mostly tree-like plants, many plant fossils are almost exclusively fragments rather than complete specimens. Accordingly, one of the most rewarding goals of paleobotany is to create reliable reconstructions to show what the complete plant might have looked like.

Fig. 2: Model of *Tempskya* reconstruction as living, juvenile, and dead specimen (PalaeoBiome / Lies)

This is no easy task, especially when considering additional problems such as the varying forms of preservation at different sites. But the results are well worth the effort, as these reconstructions can bring the plants to life in our mind‘s eye.

The last reconstructions date back over three-quarters of a century (Andrews & Kern 1947) and over a century (Kidston & Gwynne-Vaughan 1911), respectively, with two more recent models (Yang et al. 2017 and Yan et al. 2023) essentially being mere reproductions of Andrews and Kern‘s 1947 model. I therefore consider it extremely necessary and useful to reassess and illustrate the current state of research.

## 2 Questions about reconstruction and contradictions in older reconstructions

To reconstruct an extinct plant, many individual questions about the plant morphology and biomechanics must be discussed and answered in order to ultimately and ideally be integrated into a logical and as complete as possible picture or model of the plant.

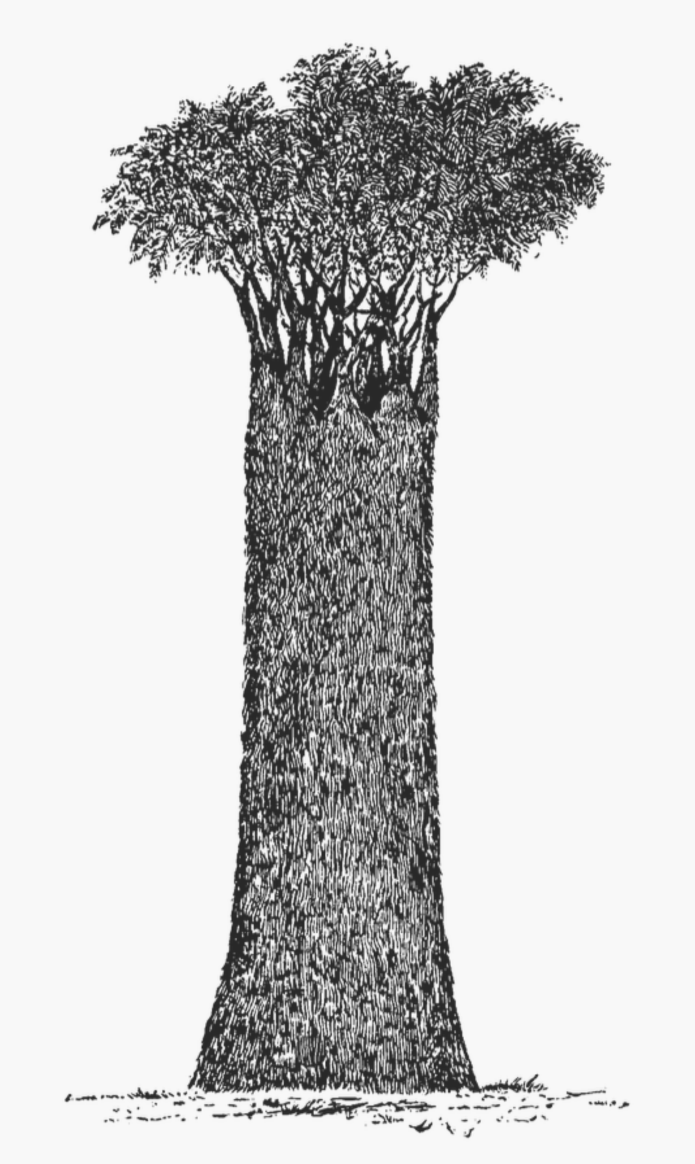


Fig. 3 & 4 (right): The two previously known reconstructions of *Tempskya* – the original model by Kidston and Gwynne-Vaughan from 1911 and that by Andrews and Kern from 1947.

How sustainable, for example, is a particular system, i.e., how large can the plant grow? How do the lack of light and the plant's ability to transport water determine its actual appearance and foliage? Each individual detailed question often raises several follow-up questions. Certainly, not all of these questions can be answered in one fell swoop. But the question itself can further sharpen the picture, even in its incompleteness.

I would therefore like to briefly summarize the prerequisites for the reconstruction and the resulting questions:

- *Tempskya* grows as a pseudostem consisting of a combination of main axes, frond stalks, and thin adventitious roots.
- The roots always have approximately the same diameter (about 1–2 mm).
- The pseudostem can reach up to 30 cm in diameter and up to 3.7 meters in height.
- At the base, the stem consists only of adventitious roots. Sometimes, in lower cross-sections, there is no main axe at all, and sometimes only a few.
- The main axes branch upwards in a forked and essentially exponential manner. Therefore, cross-sections with many main axes are more likely to be located at the top of the plant.
- The diameter of the main axes is approximately 0.5–1.5 cm
- A stele branches out every 4.5 cm
- A new frond stalk emerges every 3–5 mm
- *Tempskya*, like all ferns, is non-woody

Resulting open questions:

- How far from the tip of the main stem do the first roots emerge?
- How far do the main stems extend unrooted from the top of the pseudostem, or do they extend at all?
- Given the two previous questions, what does the actual pseudostem tip look like?
- How large are the fronds relative to the size of the plant?
- How much do the fronds weigh, and how do they behave on a freestanding main axis?
- How long are fronds photosynthetically active, and when are they shed, i.e., how many living fronds are on an active main axis, i.e., how densely leafed was a typical stem?
- Can the plant grow solitarily, and how does solitary growth affect the foliage?
- What did the typical habitat look like, and how dense was the vegetation in the habitat?
- How old do the fronds get? Do they perhaps only appear as young, light fronds at the top of the unrooted main axis, and when they are older and heavier, are they already enclosed and supported by the developing roots? For this to be the case, the main axis would have to grow slowly, while the fronds and roots would have to grow relatively quickly.
- How does water transport work? Through the main axes and roots? Or through capillary action within the root sheath? Do the older parts of the pseudostem die, or does the entire pseudostem remain alive? The answer to this question must have consequences for growth after wind damage. *Dicksonia antarctica*, for example, a leaf-root stem with a single central stele, can form new roots at the base of the stem in the substrate after a stem is severed from its base and later planted in new substrate.

Tidewell distinguishes two groups of *Tempskya*: upright pseudostems with radial symmetry and stems with a recurved or dorsiventral habitus with unidirectional leaf scars that had liana-like stems. However, he suspects that the dorsiventral habitus is actually only fragments of the characteristic radial type and that all *Tempskya* actually grew upright (Tidwell 2002). Nevertheless,

Fig. 5: *Anemia fremontii* (Knowlton 1917)

Fig. 6: *Anemia fremontii*, Reconstruction (PalaeoBiome / Lies 2025)

the question remains as to how the plant might have dealt with the opportunities for a trailing or climbing growth habit.

In my opinion, the common depictions of *Tempskya* must be considered outdated or incomplete, as both lack important characteristics of the plant that significantly determine its growth form and external appearance: the countless adventitious roots, which are extremely important for the growth form; the foliage, which in both cases is unrealistic due to different interpretations; and the inaccurately depicted reversal of the thickness ratios in the pseudostems. A combination of the models from 1911 and 1947, with the addition of an adventitious root mantle that thins outward, appears more realistic.

## 3 Reconstruction

Finds of pseudostems of the genus *Tempskya* are characteristic of Cretaceous sediments on several continents and are also very common in the Pecínov Cretaceous Basin, Czech Republic. The mineralized xylitol tissues of *Tempskya* are typically found in fluvial to tidal sandstones (Mikuláš et al. 2003). This implies that repeatedly flooded river floodplains, lagoon margins, and floodplain forest swamps or lowlands with particularly high groundwater levels are preferred habitats for *Tempskya*.

Due to its modular structure and ability to regenerate vegetatively through shoot-borne axils and adventitious roots, *Tempskya* is interpreted as a possible pioneer organism in disturbed wetland habitats. Its branched growth habit and compact root sheath likely enabled rapid growth and effective anchorage in unstable substrates, such as those found along river banks, temporary sandbanks, or former landslides. Studies suggest that *Tempskya* preferentially colonized such dynamic, ecologically unstable zones, such as along active river courses, where recurring disturbances opened new colonization niches (Kvaček 2000, Martínez & Olivo 2015).

For pioneer plants, such as ferns on lava blankets in Hawaii, this lifestyle would be quite plausible to this day. But from the Late Cretaceous onward, the ferns increasingly faced competition from angiosperms. Perhaps the angiosperms were more competitive and adaptable – at least in the repeatedly disturbed wetland habitats – which may have contributed to the extinction of *Tempskya*.

Fig. 7: Central part of a *Tempskya* pseudostem with well-depicted external impressions of dichotomizing rhizomes growing up on or within the pseudostem (Sender et al. 2018), image width approx. 80 mm

## 3.1 Fronds and foliage

The composition and structure of entire fronds within the genus *Tempskya* have not yet been clarified. Associated or in situ finds of entire fronds do not appear to have existed or have not yet been published, and finds of the foliage appear to have been extremely rare. One of the few early finds of imprint fossils of the presumed foliage of *Tempskya* (*Anemia fremontii*) was collected and first described by Knowlton, but was not assigned to *Tempskya* at that time (Knowlton 1917). However, he already suggested that it was an Eocene species very closely related to, or even identical to, a European *Anemia*.

Later, fertile leaflets of *Anemia fremontii* with spores present in situ were found and described as *Anemia fremontii forma fertilis* Andrews (Andrews & Pearsall 1941). The same species was recorded for Europe from the Cenomanian of the Czech Republic (Knobloch 1999).

In only one case, Tidwell describes a discovery of upright, autochthonous *Tempskya* pseudostems

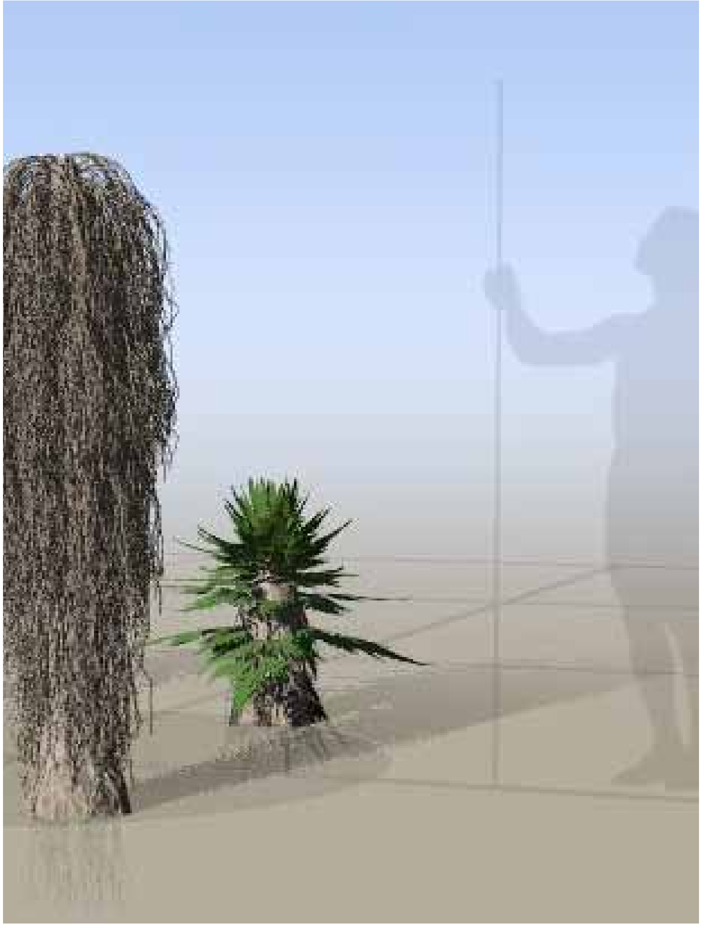


Fig. 8: Model of the *Tempskya* reconstruction in size comparison to humans with a height of approximately 1.80 m, some Tempskya could reach up to 3 meters in height (PalaeoBiome/Lies)

Fig. 9: Trunk exterior of *Dicksonia antarctica* with numerous short adventitious roots that do not form a root network, but show a conceivable surface of a living *Tempskya*, image width approx. 28 cm

from Utah in their original growth position (Tidwell et al. 1992), under which fronds of *Anemia fremontii* were found as fossil imprints. These were embedded in the carbonaceous sediments surrounding the in situ pseudostems. Since these imprints regularly occurred under *Tempskya* pseudostems at this site, this discovery suggests that *Anemia fremontii* could be the fronds of *Tempskya*.

Currently unanswered questions regarding foliage:
- How long were the frond stems?
- What was the specific gravity of the fronds, and how must they have behaved on the steles?
- How far down the stems were the steles covered in foliage?
- How long do the fronds remain alive at the shoot tips, i.e., how many living fronds are on an active main axis?

The increase in active main axes upwards due to the dichotomous growth must also have led to stronger foliage in the upper part of the pseudostem. *Tempskya* were presumably mostly or only leafy in the upper third, while in the lower areas, a lack of light and space may have played a role, which would have put the lower fronds at a clear disadvantage compared to the upper fronds. However, it cannot be ruled out that isolated or smaller fronds were also present in the lower areas.

Fig. 10: Branching model of a single *Tempskya* main axis, which divides approximately every 4.5 cm; a new frond stem emerges approximately every 3 mm, reconstruction (PalaeoBiome / Lies 2025)

Fig. 11: Partially decomposed and secondarily quartzed main axis with at least two frond stalks and several associated adventitious roots and surrounding, partially secondarily quartzed adventitious roots

Reactivation or new growth of older main axes in the outer pseudostem area and overgrowth from below up the trunk are also morphologically possible.

Earlier reconstructions have shown relatively small fronds due to the relatively small cross-sections of the stalks (see Figs. 3 and 4). This could be a misconception, as demonstrated by the fronds of *Davallia denticulata*, a modern fern with comparable growth characteristics of the rhizome. Despite an average stalk diameter at the base of only approximately 5–6 mm, they nevertheless reach a length of well over 100 cm and a width of over 50 cm. The stalk (rhachis) accounts for about half of the total length. The dimensions of various *Davallia* species are shown below:

| Species | Rhizome diameter | Frond length/width | Frond stem diameter |
|---|---|---|---|
| *D. denticulata* | ca. 1,1–1,7 cm | ca. 90–120/60–80 cm | ca. 5–6 mm |
| *D. canariensis* | ca. 1,9–2,3 cm | ca. 50–80/50–60 cm | ca. 3–5 mm |
| *D. bullata* | ca. 0,6–0,7 cm | ca. 17–22/8–10 cm | ca. 1,3 mm |

Several taphonomic and ecological reasons have been discussed for the lack of fronds directly as-

Fig. 12: Branching model with fronds of one generation, reconstruction (PalaeoBiome/Lies 2025)

sociated with *Tempskya*. Firstly, it is assumed that the fronds were relatively delicately constructed, comparable to modern tropical ferns. Such a morphological characteristic favors rapid decomposition after death and significantly reduces the chance of fossilization. Secondly, hydrodynamic

Fig. 13: Two epiphytic rhizomes of *Davallia denticulata*, a recent fern whose rhizomes are relatively close to the individual main axes of *Tempskya*

Fig. 14: A vital distal rhizome of *Davallia denticulata* with a branching frond stalk

processes in the flood-prone habitat may have caused the fronds to detach from the pseudostem, so that they were deposited in a spatially displaced manner or were not preserved at all.

Additionally, it is suspected that the foliage was shed seasonally or periodically, for example, before flooding events, which would also have contributed to its lack of preservation. The typical growth form consisting of main axes and adventitious roots, and the presumed foliage only in the upper part, would have further complicated its preservation in relation to the rest of the plant body.

While plausible classifications and attempts at functional reconstruction exist, anatomical and diagnostic fossil finds are lacking. The reason for this deficit in knowledge is most likely a combination of the plant‘s biological characteristics and the taphonomic conditions of its preferred habitat: delicate, rapidly decomposing fronds, unfavorable depositional conditions, hydrodynamic separation, and possible seasonal leaf shedding are considered the main reasons for the absence of fossil leaves.

A key question regarding the fronds of *Tempskya* is whether or not they had a separating tissue along their main axis. If so, they would have fallen to the ground and fossilized more easily. If not,

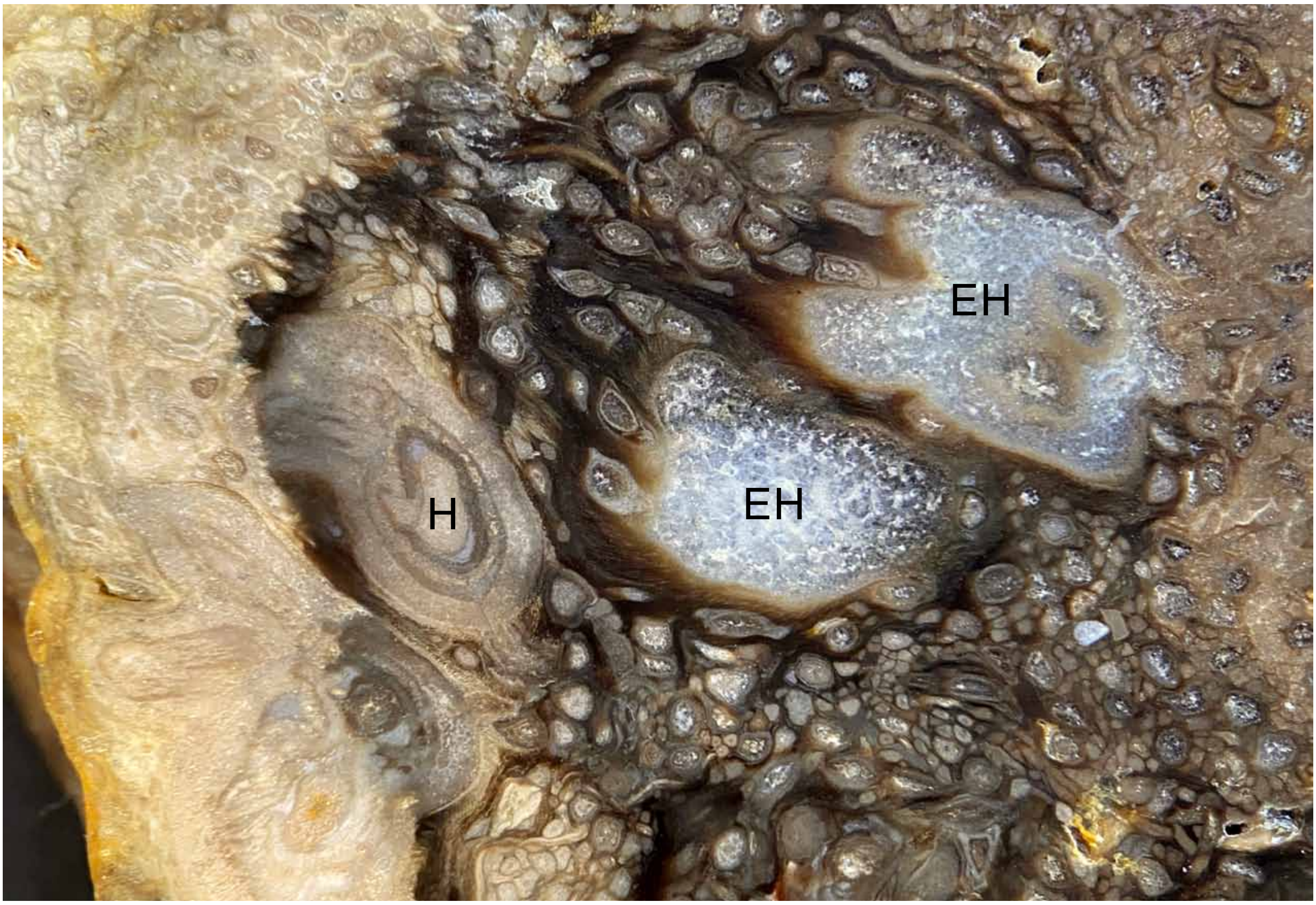


Fig. 15: Secondarily silicified (quartzed) cavities of former or already largely decomposed main axes and roots (**EH**) and permineralized main axis with outgoing roots and frond stem (**H**), image width approx. 35 mm, Georg Schiecke Collection, Collection No. 1296

they would have likely dried out on the stem and only become embedded in the surrounding sediment and fossilized during periods of severe weather. (See also Chapter 4.3).

## 3.2 Pseudo-trunk, growth and death of *Tempskya*

In general, the growth habit of pseudostem-forming ferns was probably very similar. The pseudostems consist of many small, dichotomously branching main axes embedded in a dense, rope-like mass of adventitious roots, petioles, and petiole bases. The individual main axes of *Tempskya* form small, amphiphloic-exarchous siphonostele, which produce thin frond stalks made up of C-shaped phloem/xylem strands. The bark, which is usually three-layered, consists of parenchyma and sclerenchyma.

The leaf marks sometimes develop in radial symmetry and sometimes in two rows on only one side of the stem. The diarch roots, whose bark consists of parenchyma and sclerenchyma fibers, arise directly from the main axis at short intervals of several millimeters, usually opposite the leaf mark

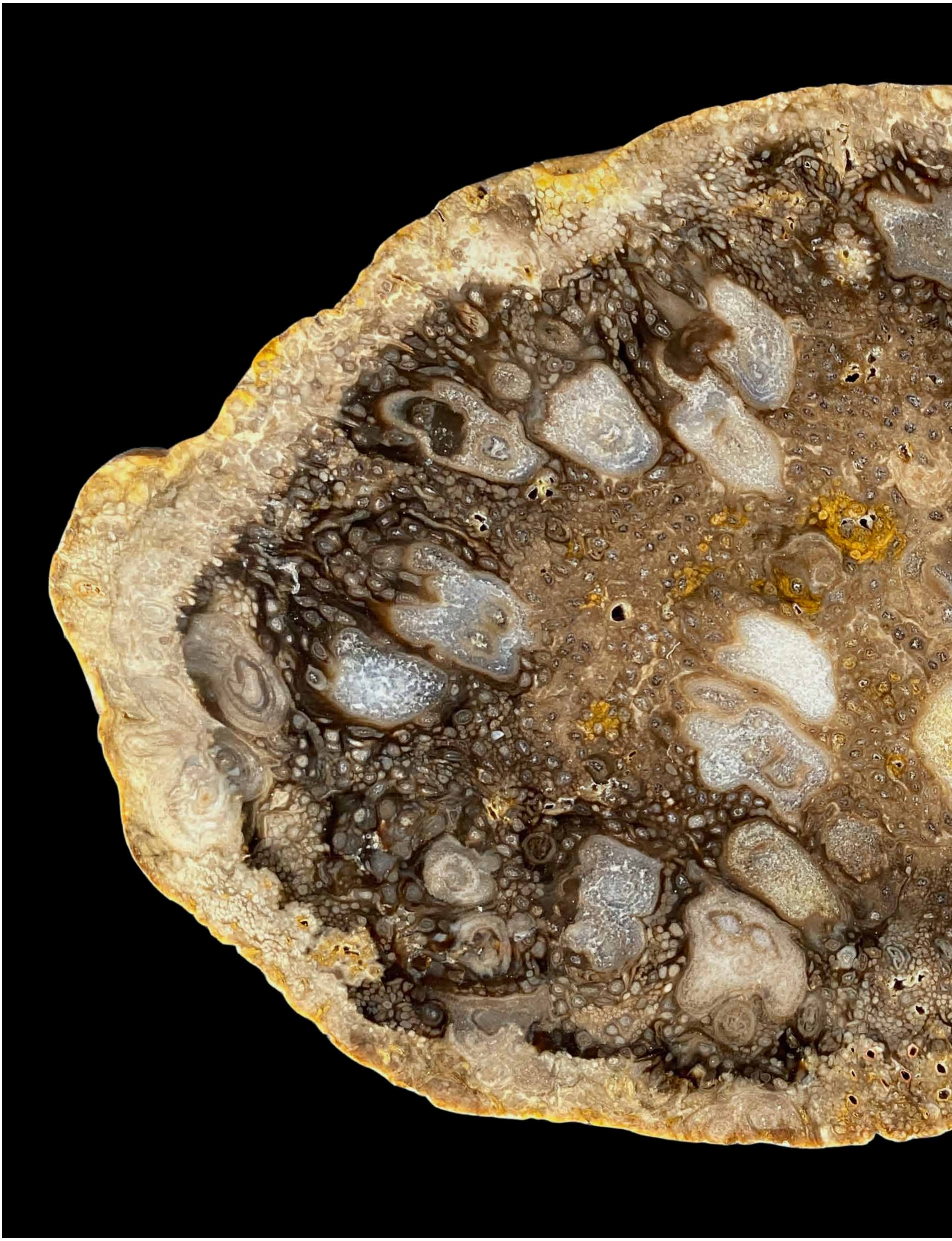
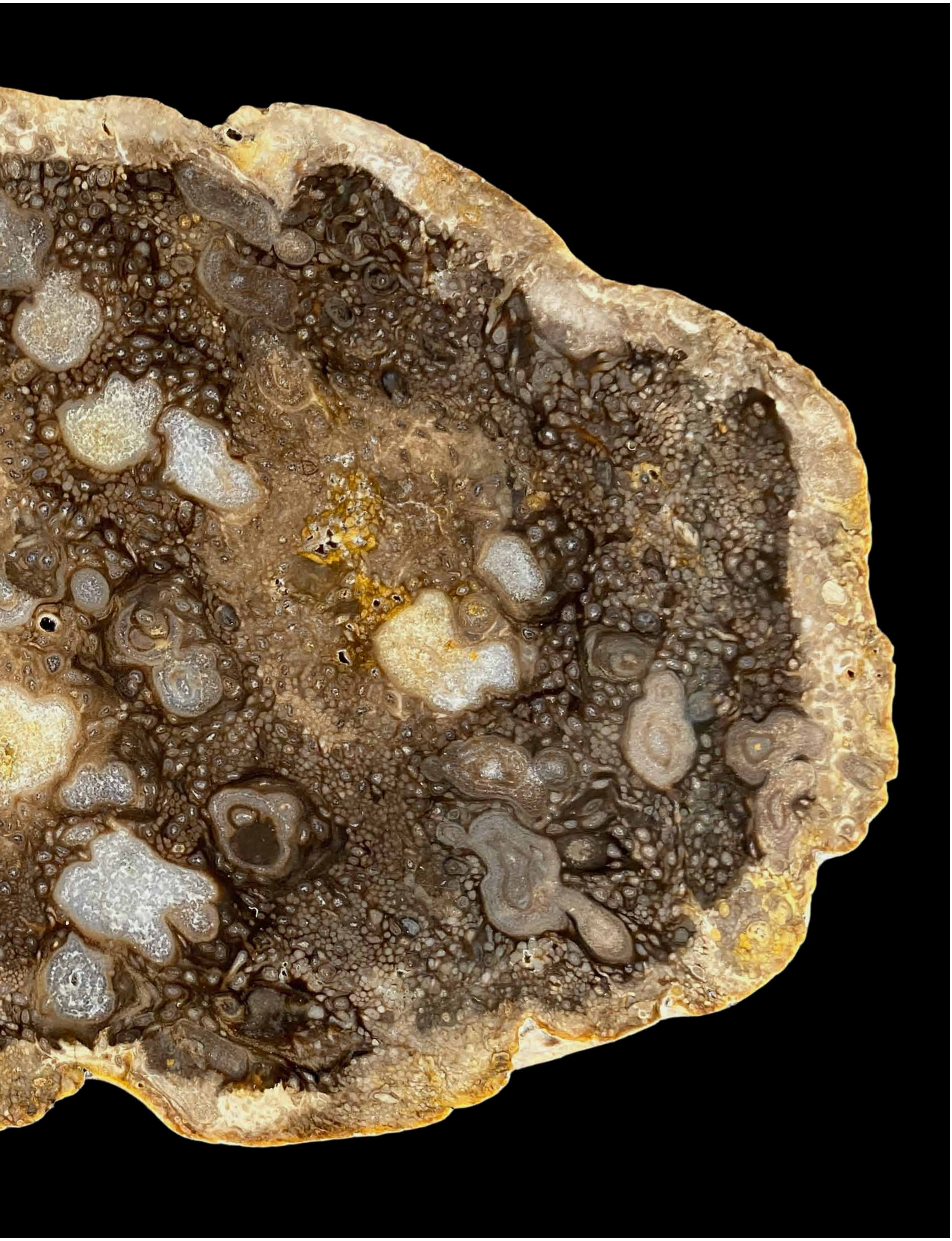


Fig. 16: A *Tempskya* in absolutely outstanding preservation from the Zeithain gravel pit. Not only the finest details in the roots and main axes are preserved, but also a secondary quartzification of the cavities of former and already decomposed main axes,



awhich differs significantly from the primary permineralization and is extremely rare in this rich contrast. Size approx. 80 × 140 mm, Georg Schiecke Collection, Collection No. 1269

Fig. 17: Stem of a *Tempskya*, embedded in a root mat of adventitious roots, hairs (trichomes) and scales (paleae), image width approx. 6 mm, Georg Schiecke Collection, Collection No. 1296

formation, forming an extremely dense and felt-like root network downwards that supports and carries the plants, giving them their typically delicate appearance (Rößler et al. 2004).

The surface or outer surface of most silicified pseudostems most likely does not show the actual peripheral areas of the plant, but rather a mechanically ground or biologically degenerated version of the peripheral area. Since the entire pseudostem consisted of a dense network of thin adventitious roots, which presumably thinned outwards only slowly, the outermost, lighter areas of the roots were probably not silicified and therefore not preserved. This assumption could be indirectly supported by the numerous „open-pored“ outer surfaces of silicified *Tempskya*, each of which displays numerous severed adventitious roots and sometimes also severed main axes. Taking into account the fact that fossil *Tempskya* pseudostems exist in which no single main axis can be found, but which nevertheless display natural weathering surfaces all around and are therefore referred to as pseudostems, one comes to the conclusion that these pieces can only show partial sections of a formerly complete pseudostem cross-section. Although there is currently no direct evidence for this, it could be found in silicifications of epiphytic settlements in the outskirts of *Tempskya* specimens.

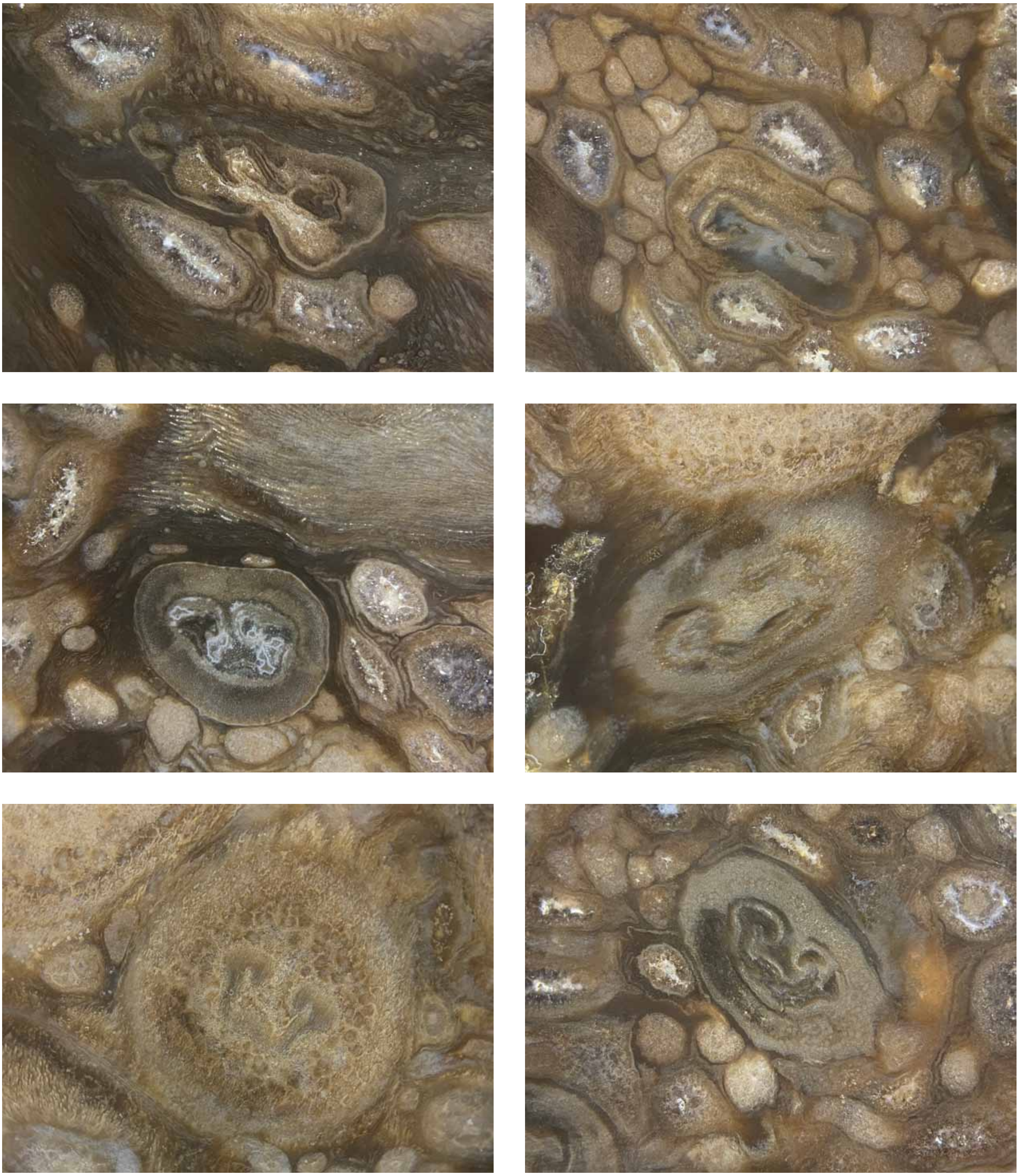


Fig. 18–23: Various examples of cross-sections of frond stems of a *Tempskya*, embedded in adventitious roots and indeterminate plant tissue, image widths approx. 6 mm each, Georg Schiecke Collection, Collection No. 1296

The extent to which frond stalks and main axes played a decisive role in the upright growth and, in particular, the stability of the structure is unfortunately difficult to determine. On the one hand, the main axes wedge themselves among themselves through the ancient dichotomy and the later

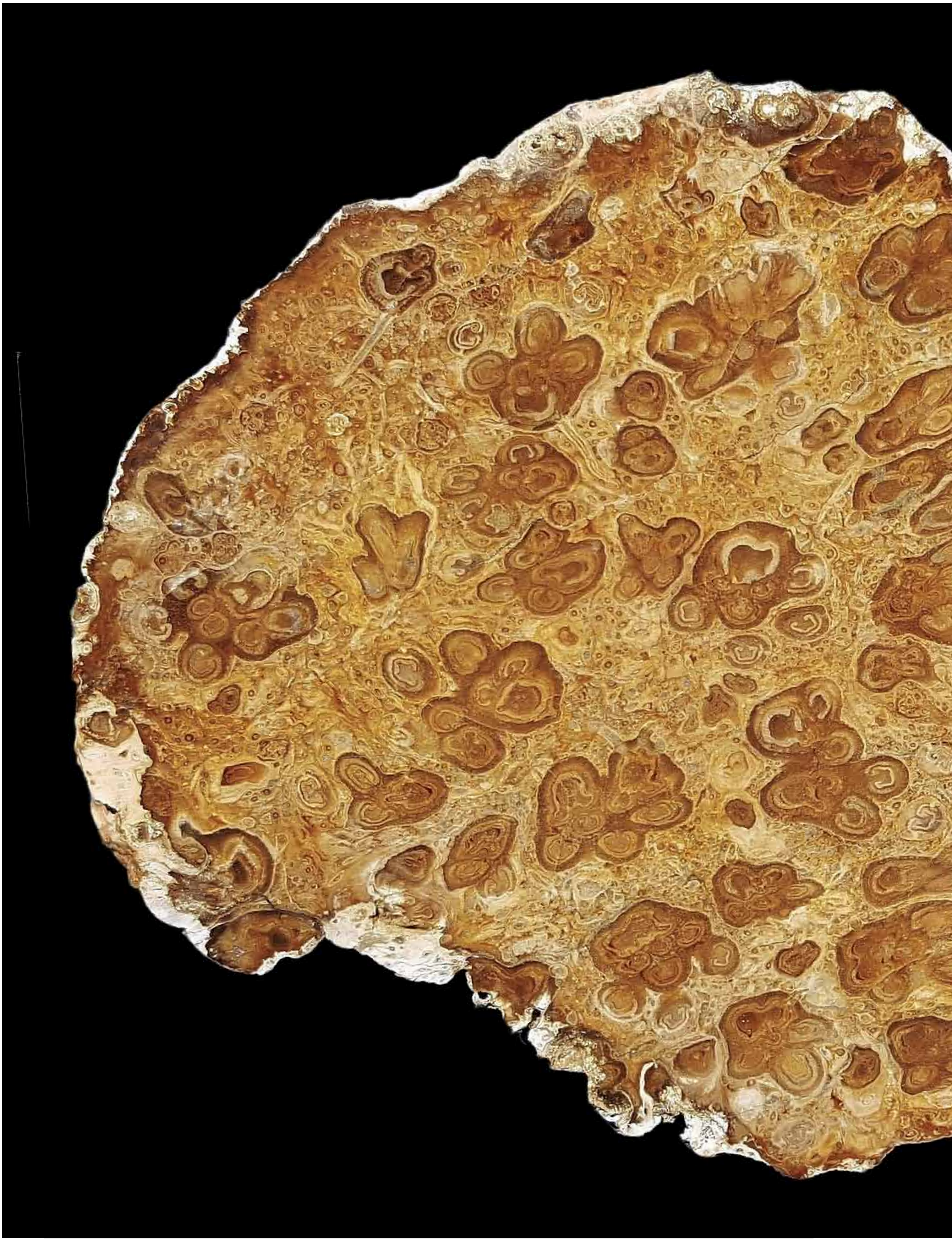
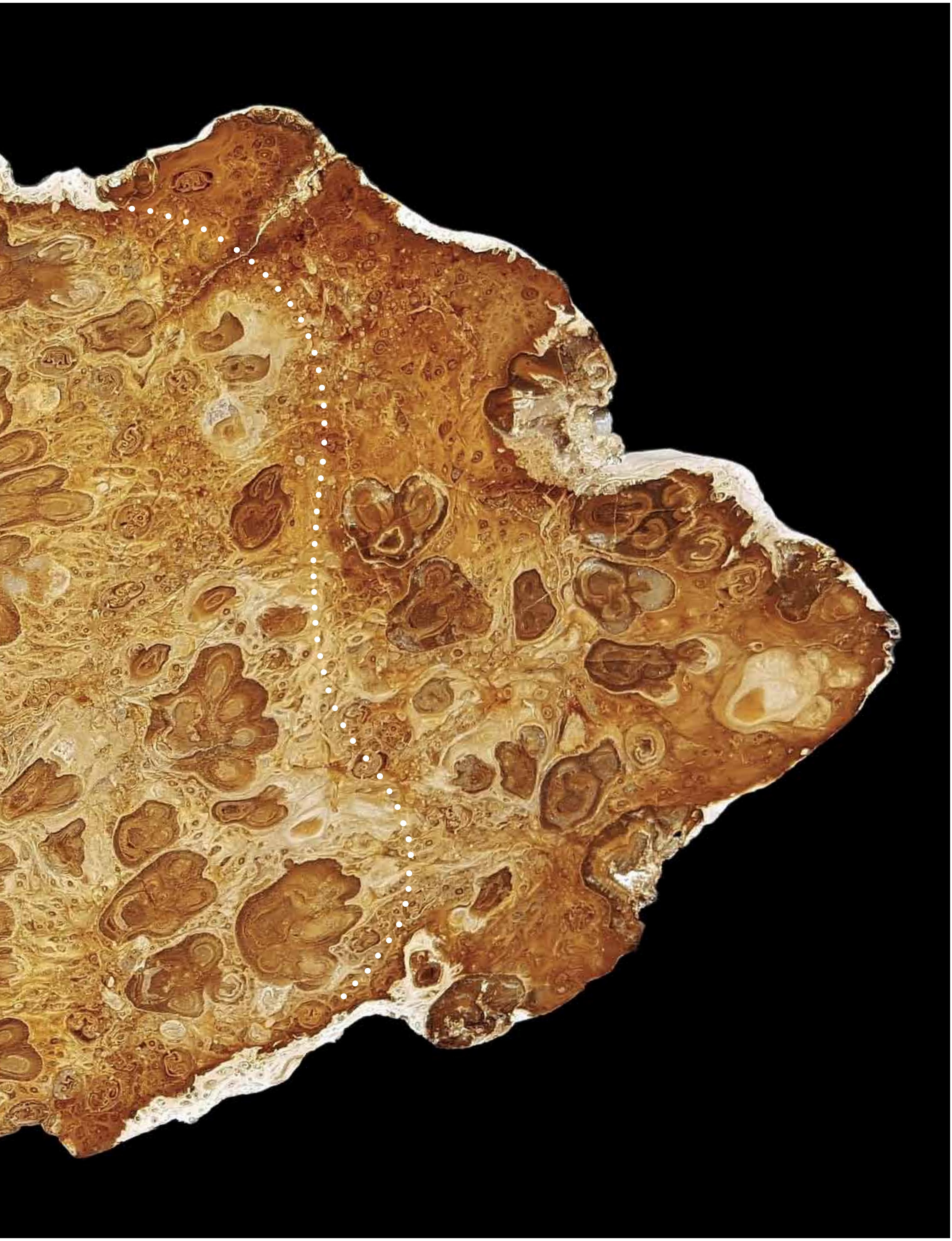


Fig. 24: This specimen appears to exhibit a clearly visible directional preference after approximately 2 p.m., as numerous fronds to the left of the dotted line point in this direction. To the right of the dotted line and at a later point in the plant's lifespan, different



growth conditions appear to have prevailed. The specimen is from Sumter County, South Carolina. Size approximately 16.5 × 10.2 cm, Douglas Moore Collection (USA)

Fig. 25: *Tempskya* reconstruction of a dead and a vital pseudostem (PalaeoBiome / Lies)

Still unanswered questions:

– How far from the tip of a main stem do the first roots emerge?
– How far do the main stems extend unrooted from the top of the pseudostem?
– How and why does the plant die?
– What happens if it collapses? Can the vital upper parts simply continue to grow?

## 4 Discussion

### 4.1 General growth

Hans Steur notes an approximately 1 mm-thick area on the outside of the stem within which the main axes can develop complete frond stalks (Steur 2022). This means that only if a new frond shoot receives rapid light exposure does it have a chance of further development. If it is located further inside the pseudostem, this is not the case; it receives no light and is likely to atrophy. This phenomenon would explain the scarring of loose leaf stalks inside *Tempskya* cross-sections. This would be entirely understandable for relatively thick pseudostems, but it would probably not be expected for other, significantly thinner pseudostems.

If fronds can only form in a relatively thin, outer vital area, this could potentially have far-reaching consequences for growth form: If frond stems grow only outward and atrophy toward the inside, outer main axes are favored over inner main axes, and a growth direction should also be preferential toward the outside and toward stronger light incidence. This is precisely what two specimens shown here appear to demonstrate (Figs. 16 and 24).

In one of the cases, one could also speculate about altered growth conditions during growth, which could be reflected in the specimen. The directional preference of the frond shoots changes significantly toward the outside in the right outer half of the specimen (see Fig. 24). Several slices of this specimen exist, all of which exhibit a similar directional prevalence.

One might even speculate about secondary growth, as outer lower main axes might grow upwards from below along the already formed pseudostem, renewing and thickening it from below. In *Davallia denticulata*, both renewed growth of a new rhizome over its own old rhizome and renewed frond growth from very old rhizome sections were observed (Fig. 13).

Abb. 26: Querschnitt einer *Tempskya* aus Nové Strašecí, Tschechien, die neben einer fehlenden Hauptachse und zugehöriger Wedelstiele (vergl. Abb. 32) vermutlich auch viele wiederbewurzelte Hohlräume ehemaliger Hauptachsen zeigt, Größe ca. 10 × 11 cm, Sammlungs-Nr. #0604

## 4.2 Different states of preservation of main axes

Dead main axes appear to regularly decompose within the pseudo-trunks, leaving cavities behind; this phenomenon has been directly observed in at least two specimens so far (Fig. 7, Sender et al. 2018 and Fig. 26); in several other specimens, the varying coloration of individual main axes and secondary quartzification of cavities could support this. This is because, especially in existing Saxon finds, main axes are repeatedly found in completely different states of preservation (cf. Figs. 15, 16, 40–42): rather brownish-colored, excellently permineralized main axes showing organ anatomy, and rather colorless, presumably secondarily quartzified, former cavities of main axes, which sometimes also still show heavily decomposed remains of plant anatomy, but otherwise

Fig. 27–28: Secondarily silicified (quartzed) cavities of former or already decomposed main axes and roots (left) and permineralized main axis with partially quartzed frond stem (right), image widths approx. 6 mm each, Georg Schiecke Collection, Collection No. 1296

only coarsely crystalline quartz. This phenomenon is also generally found in adventitious roots (Figs. 11 and 27) and strongly suggests that active and dead main axes coexisted in the pseudostems and thus that in some cases far fewer main axes could have been active in a pseudostem than the cross-sections of main axes show.

The hypothesis that the main axes decompose during the lifetime of an individual, leaving cavities, could also be supported by our own experiments, in which vital, ananatomically comparable rhizomes of *Phlebodium aureum* decomposed almost completely within a few weeks. These rhizomes remained on moist substrate for approximately 4–8 weeks, completely collapsed, and reduced their circumference by approximately one-third. This process left an empty shell of the rhizomes, and the cavities inside the rhizomes were clearly visible (Fig. 29). These observations, especially considering the humid and poorly ventilated microclimate in the root felt of the pseudostems, could indicate a regular decomposition of already dead main axes within a vital *Tempskya* pseudostem and explain the varying states of preservation of individual mineralized main axes. In the above-mentioned attempt to explain the penetrating silica, the cavities of the main axes created during decomposition did not provide an "accumulation surface" for permineralization.

Fig. 29: View of a decomposed rhizome of *Phlebodium aureum* with a clearly visible cavity within the rhizome, image width approx. 5.5 cm

It is likely that the decaying main axes of *Tempskya* were re-penetrated by adventitious roots during their lifetime. This is suggested by Tidwell's findings, in which rooted parts of already decomposed lianas were found. The ex-

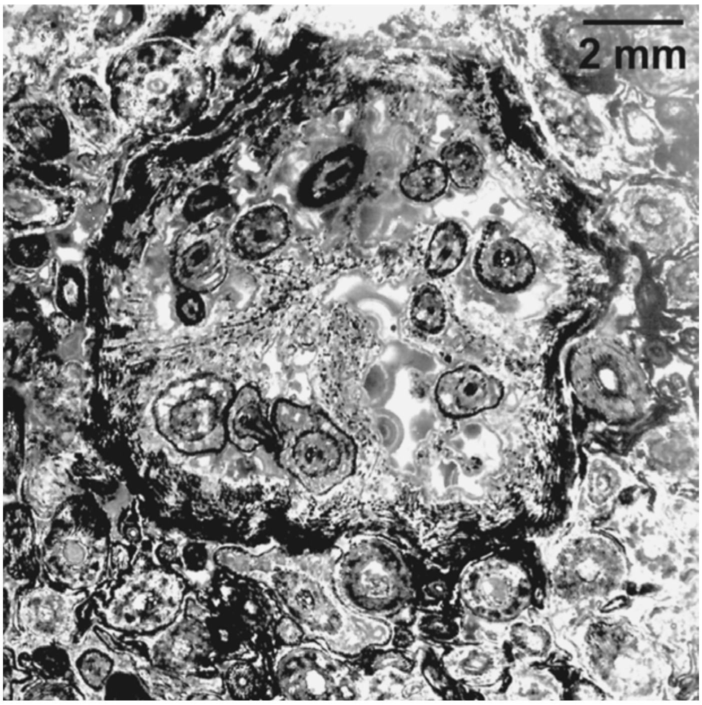


Fig. 30: Close-up of a decomposed vine with *Tempskya* roots, from Tidwell et al. 2010

Abb. 31: Detail from Fig. 26, hollow space of a main axis and two associated frond stems, image width approx. 1.8 cm

traneous shoots were partially destroyed or significantly altered (Fig. 30, Tidwell et al. 2010). A rooted frond stem in a specimen from Saxony (Fig. 32) and a rooted main axis in a specimen from Czech Republic (Fig. 33) also demonstrate this.

Indications for the filling of rotted main axes by fresh adventitious roots are also the regular absence of main axes in the lower areas of the pseudo-trunks and repeated defective spots in the silicification on the outer sides of the pseudo-trunks and in the interior of lower cross-sections, where former main axes can or must be assumed at the relevant locations due to the distribution of these spots within the cross-sections and which presumably show former cavities of main axes that are incompletely filled with roots.

An example of this is a specimen from the Bohemian Cretaceous Basin (Figs. 26, 31 and 33), which shows preserved main axes only at the edges. Inside the specimen, only former (presumably rerooted) cavities of main axes are visible. In the upper area, even the cavity of a main axe with its associated frond stems is preserved in its typical outlines (Fig. 26).

That these are indeed former main axes, however, can only be assumed based on a chain of circumstantial evidence: It can be assumed that main axes were present inside at an earlier stage of growth. Main axes can rot during life, as the specimen (and several others) itself demonstrates. „Poorly preserved areas" are distributed throughout the specimen in a similar rhythm to those known for main axes. Furthermore, many large-diameter cross-sections from the lower regions of pseudo-trunks are known, which show no main axes at all, but only roots. It can therefore be as-

Fig. 32: Decomposed and disintegrated frond stem in the specimen from Fig. 16, showing an adventitious root within, Image width approx. 6 mm, Georg Schiecke Collection, Collection No. 1296

sumed that the „poorly preserved areas“ are – at least in part – former cavities of rotted main axes. Frond stalks are also missing in the lower parts of the plant. Since rhizomes (and fronds) only grow on the outer parts of the plant (Andrews & Kern 1947), they must have decomposed and the former cavities filled with adventitious roots. The adventitious roots thus appear to be the plant‘s longest-lasting organs.

From this point of view, the amorphous roots, which can be seen in Fig. 33 and which are also documented in numerous pieces from Lusatia, could be of particular importance with regard to the stability of the pseudo-trunks, since on the one hand they are more voluminous than the round roots of Tempskya and on the other hand they “squeeze” into cavities and thus additionally ensure stronger tension within the “root felt” of the pseudo-trunks and thus inevitably increase their stability.

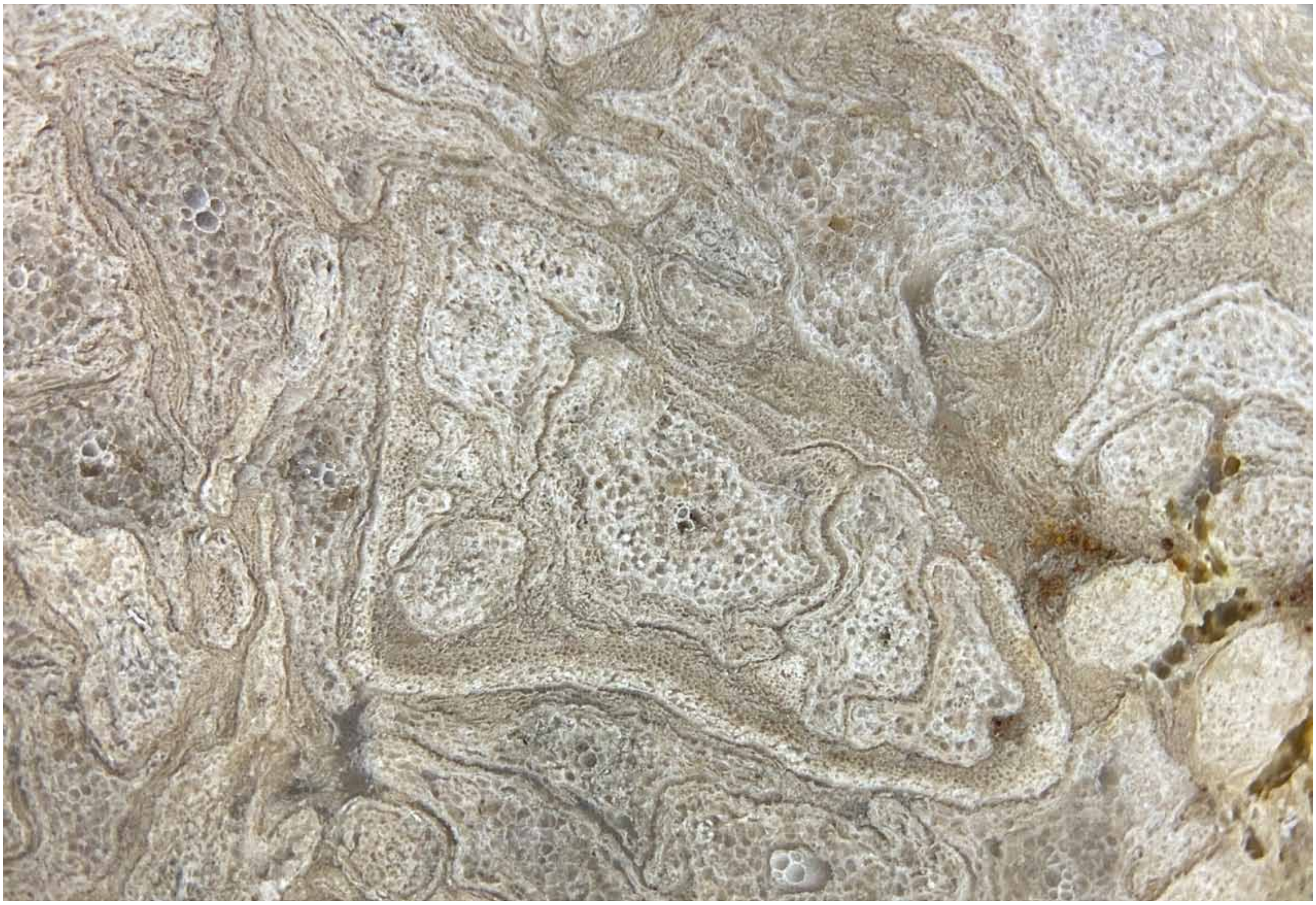


Fig. 33: *Tempskya* roots, presumably completely filling the cavity of a former main axis, image width approx. 6 mm, Collection No. #0604

## 4.3 Foliage

Presumably, fluvial-palustrine, and in the Bohemian Cretaceous Basin also tidal flood zones, where *Tempskya* preferentially grew, prevented the preservation of the fronds. *Tempskya* fronds were probably thin and poorly sclerified, i.e., delicately constructed – similar to modern tropical ferns. Such leaf structures decomposed rapidly, especially in the warm, moist, microbially active soils of the Cretaceous climate.

Previous studies attempted to reconstruct the size of *Tempskya*'s foliage based on comparisons with modern tree ferns. The relatively small rachis diameter in *Tempskya* was used to infer very small fronds with a maximum length of 30 cm (Andrews & Kern 1947). This argument has a significant weakness: modern tree ferns such as *Dicksonia* or *Cyathea* are not suitable for comparison with ferns with creeping rhizomes due to their completely different morphology and plant physics, and the ratios of frond stem thickness to frond size cannot simply be extrapolated from these extant tree ferns to *Tempskya*. It would be more realistic to use species with creeping rhizomes, such as *Davallia*, for comparison.

The fronds of *Davallia denticulata*, although over 100 centimeters long and physically similar to the fronds of *Dicksonia* or *Cyathea* in their vital state, are comparatively delicate and wafer-thin when withered. While the individual pinnules of *Dicksonia* and *Cyathea* curl and become hard and brittle after drying out, the pinnules of *Davallia denticulata* largely remain in their original shape, with only the frond curling or collapsing slightly. It stands to reason that the delicate fronds would decompose quickly and be easily transported away in a permanently moist environment, which is the assumption behind the lack of *Tempskya* fronds.

The complete frond of a recent *Davallia denticulata*, perhaps most comparable in construction and design to *Anemia fremontii*, weighs only about 55 grams (dried, about 7–15 grams) at approximately 121 cm long and 105 cm wide (Fig. 34). *Davallia denticulata* has very delicate pinnae for its size and surprisingly strong, almost wire-like, tough frond stalks. With a relatively high estimate of 50 fronds, a larger pseudostem would only have to support 2–3 kilograms of frond mass. However, since the fronds of *Tempskya* were very likely much smaller than those of *Davallia denticulata*, the assumed total mass would also be significantly reduced.

From these considerations, the following possible frond dimensions for *Tempskya* result, as an example and hypothetically, based on an average rachis diameter of 3 millimeters (measured on the ground specimen by G. Schiecke, collection no. 1296) based on the ratios of:

| | | | |
|---|---|---|---|
| A: *D. denticulata* | (100 x 70 x 5,5 cm) | – | 54 x 38 cm |
| B: *D. canariensis* | (70 x 55 x 4 cm) | – | 53 x 41 cm |
| C: *D. bullata* | (20 x 9 x 1,3 cm) | – | 46 x 21 cm |

A key question regarding *Tempskya* foliage is the presence or absence of a separating tissue between the frond base and the main axis, where the fronds are regularly shed seasonally or when they decompose. Since the frond stems are part of the overall *Tempskya* structure, they should ideally have no separating tissue between the main axes, as otherwise the overall structure would be weakened by loose frond stems inside the structure and there would probably be more *Tempskya* fronds left standing. A more realistic option would be the absence of a separating tissue, which would increase the strength of the overall structure through tighter bracing. However, fronds that do not fall off could also be ecologically detrimental. Old fronds, for example, increase the load and provide a surface for wind attack.

On the other hand, the presence of separating tissue could have been an additional piece of the puzzle regarding selective disadvantages. For now, however, this question must remain unanswered and left to future researchers. It should at least be noted that many modern representatives of creeping and climbing ferns (*Davallia* and *Phlebodia*) exhibit separating tissue.

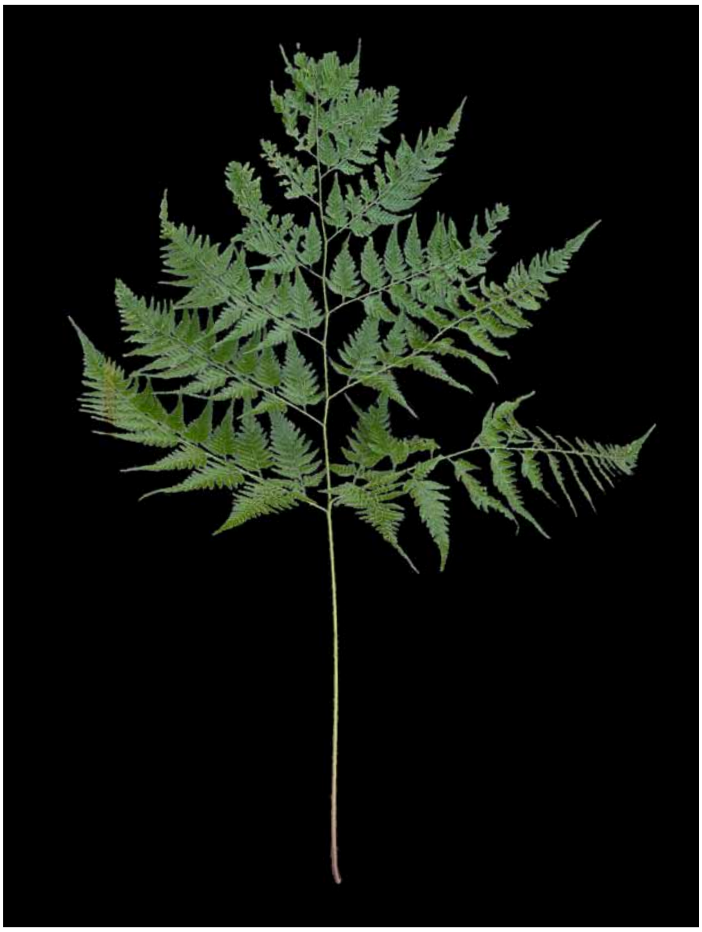


Fig. 34: Complete frond of a *Davallia denticulata* (121 x 105 cm), a recent fern, whose fronds are likely to be relatively similar to the fronds of Tempskya in their basic structure

It is striking that there are virtually no longitudinal sections through the frond stems in cross-sections through the pseudostems. If this observation is correct, this would have several implications for the general appearance of the plant, as the fronds would then tend to grow only upwards within the pseudostem and would only have sunk slightly outside of the pseudostem. Overall, this construction would support a growth habit more in the direction of the „tuft model."

Furthermore, the frond cross-sections within the pseudostems lack any beginnings of pinnae, which would require a long and leafless rachis, which would only exhibit pinnae or blades outside the pseudostem. This would be entirely understandable for the pseudostem structure of *Tempskya*, as a long rachis helps the plant reach the light quickly and efficiently. This is not an insignificant aspect for plants that not only functioned as pioneer plants but also competed with much larger plants as understory.

## 4.4 Top-heavy growth form

The pseudostems were demonstrably top-heavy, or at least that is what many known specimens suggest, and their club-like appearance clearly demonstrates this (Fig. 37). Perhaps this top-heavy nature was the selective disadvantage that repeatedly caused this type of pseudostem to become extinct, even after multiple evolutionary developments? After heavy rain, and especially in connection with storms, the top-heavy growth habit could have become a fatal trap for *Tempskya*: Since the stems do not lignify, thicken towards the top, and are able to store enormous amounts of water due to the mass of fine, water-absorbing tissue, a tipping point in the system could have been reached at some point during persistent rain, especially in conjunction with simultaneous wind. This is especially true given that the pseudostem had to bear only low mechanical stress under normal conditions. This would, incidentally, be expected not only with the well-known club-like growth habit, but also in older and thus taller specimens of *Tempskya*.

Kvaček proposes partial decomposition of the pseudo-trunks in the lower part of the trunk during

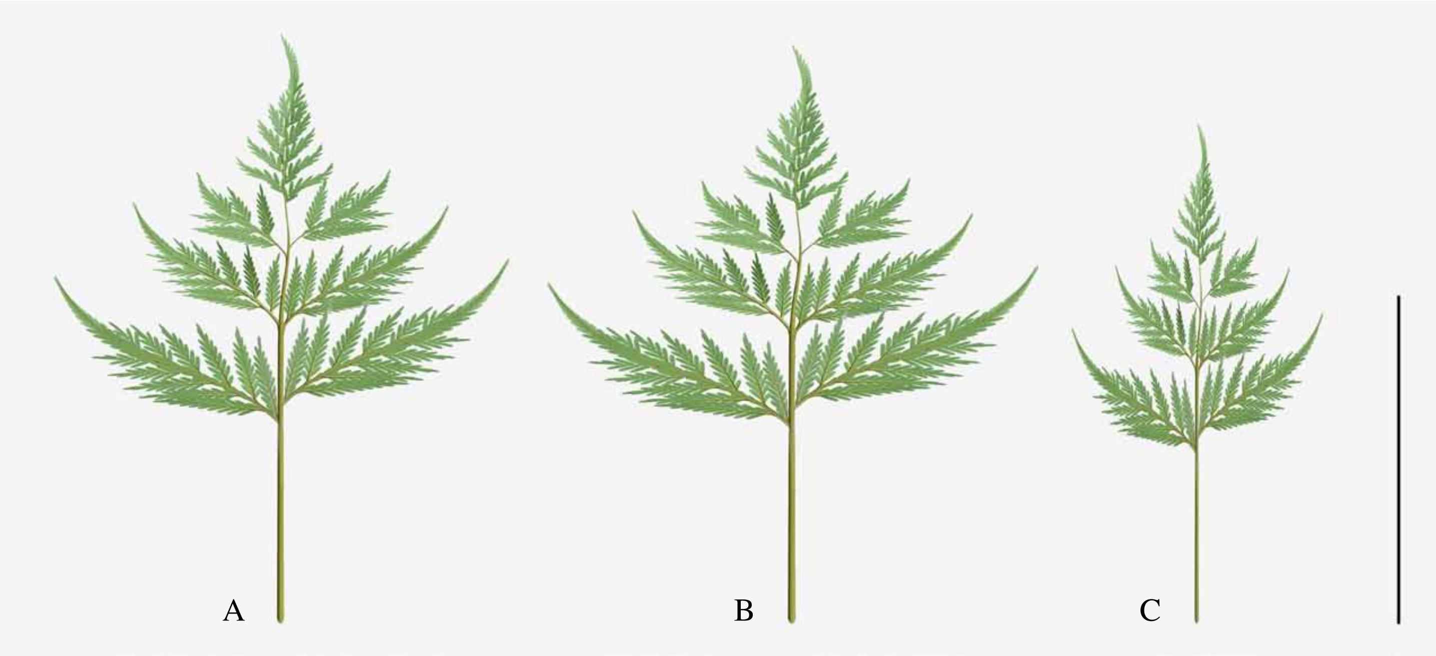


Fig. 35: Size comparison of hypothetically possible *Tempskya* fronds based on the ratios of the frond dimensions of *D. denticulata* (**A**), *D. canariensis* (**B**) and *D. bullata* (**C**), bar length 30 cm

the individual‘s lifetime, which could result in the downwardly tapered and pointed conical shape of the pseudo-trunks (Kvaček 2000). This should not be questioned as a possible explanation for the top-heavy nature of the preserved fossils. However, the increase in the diameter of the pseudo-trunks towards the top due to the dichotomous growth form of the main stems may have played at least an additional and supporting role.

The threatening top-heaviness, which is reflected in the typical club-like shape of many of the fossils, could, however, also simply result from decomposition of the lower outer regions of the adventitious root mantle during the plant‘s lifetime and have nothing to do with the actual growth characteristics of the plant. Especially when one considers the swampy, damp locations in which *Tempskya* at least partially grew..

Fig. 36: Size ratios of the hypothetical *Tempskya* fronds on a dummy trunk with a height of 2 meters

Fig. 37: A particularly top-heavy preserved example of a *Tempskya* from West Bohemia, height of the piece 22 cm, Copyright: Marian Timpe

## 4.5 Liana-like growth of *Tempskya*

Tidwell describes pseudostems of Tempskya (Tidewell et al. 2010) with lianas (Munzingoxylon delevoryasii and Rodoxylon scheetzii) growing through them. The lianas are said to have climbed young Tempskya stems and later integrated into the pseudostems. However, evidence of specialized climbing organs such as tendrils, hooks, or adhesive discs is lacking. Presumably, the lianas used the surface of young Tempskya stems to climb upwards, and as the pseudostems continued to grow thicker, their shoots were then encircled and preserved by the fern's adventitious roots. The encircling and enclosing of foreign plant axes is a frequently observed occurrence in tree ferns (Rößler 2000), and most recently, numerous fossil ferns in Brazil were described and illustrated in Rößler et al. (2024).

From Saxony, there is evidence (Figs. 42 and 42a) of a gymnosperm as an epiphyte. While an epiphytic colonization seems plausible here, the question still arises whether it might not have been the other way around: Did Tempskya orient itself, when possible, on the growth patterns of other plants and then later incorporate them into the pseudostem?

## 4.6 Regeneration

*Tempskya* presumably grew as a pioneer plant in tidal and fluvial floodplains, thus repeatedly exposed to flooding and possibly even heavy rainfall events. In particular, the tendency of its growth form to be top-heavy may have repeatedly led to *Tempskya* plants being bent and washed away. However, since the vital parts of the plant can repeatedly resprout and establish roots as long as sufficient water and sediment are available, this at least suggests the possibility of continued growth of bent or transported pseudostems at the same or even new locations.

Fig. 38: *Tempskya* cross-section from Greenhorn Mountain, Oregon, USA, ca. 13 × 15 cm, showing a rare example of „horizontal" growth of the main axes, which may indicate the flexion of the pseudostem, Rod Miller Collection (USA)

Continued growth after a bend due to weather events should, in principle, also be reflected in certain fossil stem forms. Relatively strong bends of 45 to 90 degrees within a pseudostem would be expected. However, such *Tempskya* pseudostems have not yet been found, which of course does not necessarily mean that they do not exist or have existed. A first indication to confirm the theory of regeneration after a bend could be a *Tempskya* cross-section from North America (Fig. 38), which shows several multiply branched main axes that grew in a completely unusual „horizontal" plane through the entire cross-section. It cannot be ruled out that this directional growth represents a reaction to the pseudostem bending, and that individual, still vital main axes sought their way through the root mat after the pseudostem had fallen to its knees in order to revitalize the plant.

The highly directional growth of several adjacent main axes in a specific direction, as can be observed repeatedly in individual specimens, could also be related to the bending of the pseudos-

Fig. 39: Reconstruction of a Cretaceous habitat with numerous *Tempskys* (PalaeoBiome / Lies)

tems. However, it could also simply be a reaction of the plant to changing light conditions in its original location.

## 4.7 Reconstruction of the habitat of *Tempskya* in the late Mesozoic

*Tempskya* exhibits unique morphological features that suggest adaptation to permanently moist environments. The species was characterized by modular growth as a pseudostem, with numerous shoot-borne main axes and countless frond stalks clustered within a dense sheath of adventitious roots. This structure enabled both stability in soft substrates and presumably a high regenerative capacity (Taylor et al. 2009).

Fossil finds from Europe, North America, and South America demonstrate a preference for wetland-like sites in subtropical to tropical climates. The stratigraphic contexts indicate floodplains, lagoon margins, and swampy lowlands, where *Tempskya* presumably occurred as a pioneer plant in open, periodically flooded areas (Tidwell, W.D. 2002, Kvaček 2000, Martínez & Olivo 2015). The absence of xeromorphic adaptations and the associated flora – consisting of other ferns, early angiosperms, and conifers – suggest a humid microclimate with high air humidity and low seasonal fluctuations. This is consistent with the sea level highstand that created widespread and large bodies of water in Central Europe during the Late Cretaceous.

Particularly in coastal lowland regions with high groundwater levels, the nutrient-rich floodplain sediments provided ideal conditions for the growth of *Tempskya*. These backwater floodplains, or riparian forest swamps, had a relatively poor understory of herbaceous lycophytes and ferns and were likely the original habitat of *Tempskya*. The plants likely occurred in loose stands, with their dense root mass likely contributing to the stabilization of dynamic substrates such as alluvial sand or silt. These paleoenvironments could most easily be compared to the present-day *Taxodium* swamps in Florida (Kvaček 2017).

Furthermore, a specimen found in Argentina with aerenchymatous tissue around the adventitious roots suggests that *Tempskya* also grew in true swampy areas, at least there (Martínez & Olivo 2015). Aerechyma, a special plant tissue permeated by large intercellular spaces (air chambers), generally suggests plants adapted to swampy environments.

The ecological niche of Tempskya can be described as that of a moisture-loving tree fern in repeatedly disturbed but consistently moist habitats – a habitus type that no longer has an exact equivalent in today‘s flora.

## 4.8 Summary of selection disadvantages

It was probably a multitude of possible small selective disadvantages that, in conjunction with and especially in combination with the advantages possessed by angiosperms from the Late Cretaceous onwards, led to the extinction of *Tempskya*. Of particular note here is the tendency toward a top-heavy growth form, which results in dyarchic growth and can create disastrous physics, especially in the context of extreme weather events such as rain and wind.

A significant selective advantage for angiosperms from the Late Cretaceous onwards may also have come into play, placing the ferns under fierce competition. Presumably, the angiosperms were better and more adaptable – at least in these habitats. In any case, they had a distinct advantage in the fight for light: their woody growth allowed them to grow much taller than the ferns. And with the fall in sea level and the progressive silting, they probably had a clear advantage in colonizing the newly emerging habitats, which, in terms of weather and environmental conditions, were much more stable.

The fact that, as a pioneer plant, it is dependent on rather sandy soils repeatedly affected by flooding events may also have been a decisive selective disadvantage. This is especially true in conjunction with the tropical and subtropical habitat requirements and the retreat of sea levels, combined with the continental drift of the ancestral habitats to colder climates northward.

Finally, the length of *Tempskya*'s rachis, which has not yet been documented, may also have played a role in the selective disadvantage. A presumed short rachis would lead to the plant emerging slowly, which could have become a selective disadvantage, especially in competition with the much taller angiosperms from the Late Cretaceous onwards.

## 5. Outlook

Based on recent and older *Tempskya* finds, a reinterpretation of the growth habit of *Tempskya* was undertaken. Particular attention was paid to adventitious roots, which had been neglected in previous reconstructions, and a morphologically predictable foliage was reconstructed from the growth characteristics of recent ferns.

One disappointment remains the persistent lack of definitive in situ evidence of *Tempskya* foliage. The discovery of complete *Tempskya* fronds and their fertile remains directly attached to the pseudostems would be scientifically significant and could contribute to the clarification of many open questions.

Fig. 40: Original size illustration, 80 × 140 mm, collection Georg Schiecke, collection no.. 1269

Fig. 41: Original size illustration, 91 × 116 mm, collection no.. #0527

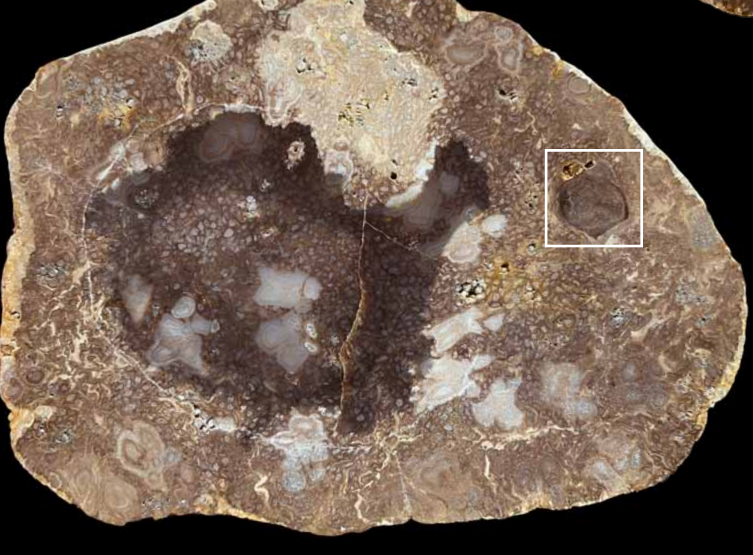


Fig. 42: Original size illustration, 75 × 100 mm

Fig. 42a: Gymnosperm axis

Fig. 40–42a: *Tempskya* from the Zeithain gravel pit, Saxony; *Tempskya* from the Mühlberg gravel pit, Brandenburg; and *Tempskya* from the Mühlberg gravel pit, Brandenburg with epiphyte from the Werner Gehlert collection

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## Notes and thanks:

The numbers following the image numbers are collection numbers from my private collection, i.e., all items marked like this (#0371) come from my own collection. All items marked differently come from other collections and are each marked with the name and, if applicable, the collection number of the owner or finder.

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Please send comments, criticism and additions to info@joernlies.com - thank you very much!