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In situ pollen of voltzialean conifers from the Middle Triassic in Central Europe

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ABSTRACT

Conifers of the order Voltziales were important components of Triassic floras. Their pollen is likewise abundant in microfloras from this period. Voltzialean pollen grains are known to have a considerable range of morphologies, but taxonomic distinctions based on these differences require thorough descriptions of in situ pollen from well-preserved male cones. We studied the pollen grains extracted from male cones from the palaeofloras of the Dont Formation in Italy, the Grès à Voltzia in France (both Anisian, lower Middle Triassic), and the Erfurt Formation in Germany (Ladinian, upper Middle Triassic). Pollen cones from the Dont Formation contain taeniate bisaccate pollen that are otherwise known only from Paleozoic conifers, as well as in one case multi-taeniate pollen grains resembling those commonly associated with seed ferns. By contrast, in situ pollen grains from the Grès à Voltzia and the Erfurt Formation are mostly comparable to *Illinites*, *Angustisulcites* or alete forms such as *Voltziaceaesporites*, *Alisporites*, and *Klausipollenites*. Malformations are usually rare, but notable are recurring patterns of smaller or larger than normal corpus sizes, which could lead to different taxonomic assignments if found dispersed. Overall, pollen grain sizes in general can vary considerably within a sample and even more between samples from different specimens of the same species. By contrast, size ranges of different species are overlapping significantly.

1. Introduction

Conifers are the most diverse and widespread group of living gymnosperms, comprising more than 600 species with a global distribution (Farjon, 2010; Farjon and Filer, 2013; Leslie et al., 2018) and have one of the longest and best-known fossil records of any seed plant group (e.g., Brodribb and Hill, 1999; Taylor et al., 2009). They play a crucial role in various terrestrial ecosystems, serving as a major component of woody biomass in many temperate and boreal forests in the Northern Hemisphere and tropical montane forests (Enright and Hill, 1995; Eckenwalder, 2009). Evidence from the fossil record indicates that the evolution of the conifers began over 300 million years ago during the late Carboniferous (e.g., Rothwell et al., 1997; Hernandez-Castillo et al., 2001; Falcon-Lang et al., 2009; Plotnick et al., 2009; Taylor et al., 2009). From the Permian onwards, they underwent significant radiation and became one of the most diverse and important groups of seed plants (e.g., Miller, 1982; Anderson et al., 2007; Hedges and Kumar, 2009). The early Mesozoic was the most crucial time in the evolutionary history of conifers, with seven extant conifer families being already well established in the flora at the beginning of the Jurassic (e.g., Miller, 1982; Stockey et al., 2005; Farjon, 2005, 2008; Anderson et al., 2007; Axsmith et al., 2008; Escapa, 2009; Eckenwalder, 2009; Hedges and Kumar, 2009; Williams, 2009; Escapa et al., 2010, 2011; Rothwell et al., 2005, 2012; Escapa and Catalano, 2013; Contreras, 2018; Leslie et al., 2018; Contreras et al., 2019).

Despite this knowledge, the evolutionary history of conifers still

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holds uncertainties, particularly regarding the relationship and divergence points of various conifer families. Some authors suggest that the extant conifer lineages of Podocarpaceae and Araucariaceae evolved already before the end-Permian mass extinction (e.g., DiMichele et al., 2001; Blomenkemper et al., 2018), whereas other authors support a major radiation during the Carnian (late Triassic; Dal Corso et al., 2020; Roghi et al., 2022). One of the challenges regarding the origin of modern conifers is to clarify the diversity and relationship of early Mesozoic conifers such as the Triassic voltzian conifers or voltzian Voltziales (sensu Rothwell et al., 2005), a transitional group that was morphologically intermediate between the Paleozoic and modern conifers (e.g., Miller, 1977, 1999; Grauvogel-Stamm, 1978; Visscher et al., 1986; Clement-Westerhof, 1987, 1988; Mapes and Rothwell, 1991; Axsmith and Taylor, 1997; Axsmith et al., 1998; Rothwell et al., 2005, 2011; Escapa et al., 2010; Herrera et al., 2015). Unfortunately, the fossil record of the Triassic voltzian conifers is still rather incomplete, especially during the Early–Middle Triassic, and consists predominantly of vegetative foliate shoots and dispersed reproductive organs (e.g., Grauvogel-Stamm, 1969a, 1978; Escapa et al., 2010, 2011; Forte et al., 2021, 2022).

Conifers, primarily of the order Voltziales, were important components of Middle Triassic floras in Europe (Forte et al., 2022 and references therein). Similarly, coniferous pollen is common in palynofloras from this epoch (e.g., Looy et al., 1999). However, in situ pollen from voltzialean cones have rarely been studied in detail, with a notable exception being those from the Grès à Voltzia in France (Grauvogel et al., 1967; Grauvogel-Stamm, 1969a; Grauvogel-Stamm and Grauvogel, 1975). Recently, in situ pollen from the roughly coeval (Anisian, early Middle Triassic) flora of the Kühwiesenkopf/Monte Prà della Vacca in Italy has been described, which showed a notable difference in being consistently taeniate, a trait otherwise associated with the pollen of Paleozoic conifers or seed ferns (Forte et al., 2022). This shows that the morphological range of Triassic voltzialean pollen is still severely understudied. In addition, it is known that bisaccate pollen can vary in appearance to the point that grains from the same pollen sac can correspond to different genera of dispersed pollen (for an example from glossopterids, see Lindström et al., 1997). Hence, more detailed information on the morphological variability of bisaccate pollen grains will enhance the interpretability of palynofloras in terms of biodiversity and for the purposes of palaeoenvironmental/palaeoclimatic studies. Here, we report on in situ pollen extracted from male cones assigned to the Voltziales of the Anisian in France and Italy and the Ladinian in Germany. This study is part of a project aiming to explore the morphological variability of in situ sporomorphs from the European Triassic, with previous results having been published on the spores of leptosporangiate and marattialean ferns, as well as lycophytes of the Kühwiesenkopf/Monte Prà della Vacca flora (Nowak et al., 2022a, 2022b, 2023).

2. Materials and methods

For this study, samples were taken from male voltzialean cones (see Table 1) in organic preservation from the Anisian Dont Formation at the Kühwiesenkopf/Monte Prà della Vacca locality in Italy (close to the village Olang/Valdaora; e.g., Kustatscher and Roghi, 2006; Kustatscher et al., 2006, 2010; Forte et al., 2021, 2022), the Anisian Grès à Voltzia at Hangviller, France (e.g., Grauvogel et al., 1967; Grauvogel-Stamm, 1969a; Grauvogel-Stamm and Grauvogel, 1975; Gall and Grauvogel-Stamm, 2005), and the Ladinian Erfurt Formation ("Lettenkeuper"; see e.g., Kustatscher et al., 2012; Heunisch, 2015; Kelber, 2015) at multiple localities in Germany: Thale, Bedheim (town of Römhild), Rielingshausen (town of Marbach am Neckar), Weiler zum Stein (town of Leutenbach), Zwingelhausen (town of Kirchberg an der Murr), and Rockhausen. The cones are part of the collections of the Museum of Nature South Tyrol in Bozen/Bolzano, Italy (NMS), the Museum für Naturkunde in Berlin, Germany (MfN), and the State Museum of Natural History Stuttgart, Germany (SMNS).

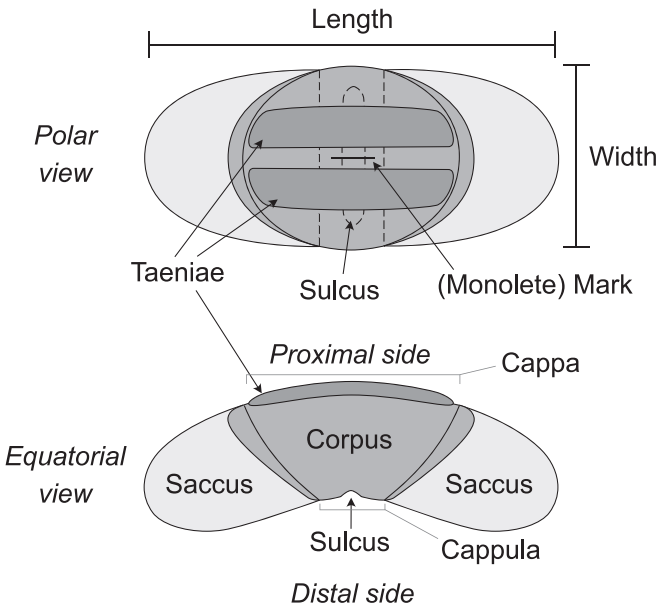

Fig. 1. Basic features and measurements of a bisaccate pollen grain.

Table 1
Studied male conifer cones and their in situ pollen grains. KWK/MpdV = Kühwiesenkopf/Monte Prà della Vacca.

Cone taxon	Collection no.	Locality	Collection
Willsiostrobus acuminatus	SMNS-P-118442a	Hangviller	SMNS
Willsiostrobus cf. *acuminatus*	MB.Pb.2000/252e	Thale	MfN
	MB.Pb.1983/424	Thale	MfN
	MB.Pb.2000/252b	Thale	MfN
	MB.Pb.2000/471	Bedheim	MfN
Willsiostrobus cf. *cordiformis*	MB.Pb.2000/484	Bedheim	MfN
	SMNS-P-115730b	Hangviller	SMNS
Willsiostrobus ligulatus	SMNS-P-115774b	Hangviller	SMNS
	SMNS-P-P001487/26	Weiler zum Stein	SMNS
Willsiostrobus rhomboidalis	SMNS-P-P001487/101	Weiler zum Stein	SMNS
	MB.Pb.2019/273	Rockhausen	MfN
	MB.Pb.2019/274	Rockhausen	MfN
	MB.Pb.1983/422a	Bedheim	MfN
Willsiostrobus willsii	SMNS-P-P001487/88	Weiler zum Stein	SMNS
Willsiostrobus cf. *willsii*	SMNS-P-110024	Rielingshausen	SMNS
Willsiostrobus sp. 1	MB.Pb.2008/210	Bedheim	MfN
Willsiostrobus sp. 2	MB.Pb.2000/780	Rockhausen	MfN
Willsiostrobus sp. sensu Forte et al., 2022	PAL 794	KWK/MPdV	NMS
Ruehleostachys sp. 1	SMNS-P-P001481-1	Zwingelhausen	SMNS
Ruehleostachys sp. 2	SMNS-P-P001481-2	Zwingelhausen	SMNS
	PAL 2100	KWK/MPdV	NMS
	PAL 467	KWK/MPdV	NMS
	PAL 569	KWK/MPdV	NMS
	PAL 575	KWK/MPdV	NMS
	PAL 783	KWK/MPdV	NMS
	PAL 784	KWK/MPdV	NMS
	PAL 786	KWK/MPdV	NMS
	PAL 787	KWK/MPdV	NMS
	PAL 788	KWK/MPdV	NMS
Voltzia recubariensis	PAL 790	KWK/MPdV	NMS

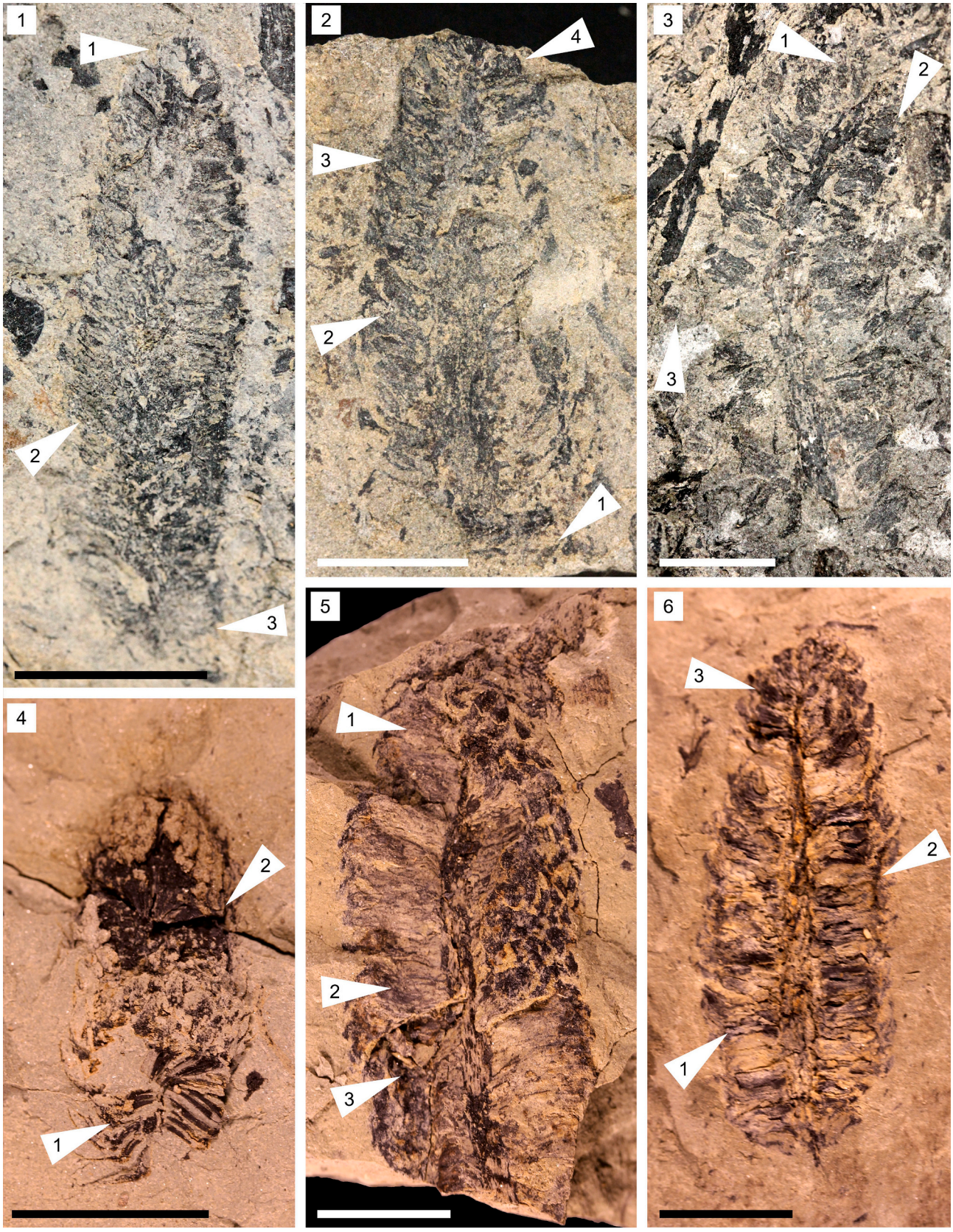

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Plate I. Sampled male (polliniferous) cone macrofossils from the Anisian Dont Formation and Grès à Voltzia. White chevrons indicate sampling positions. Scale bars = 10 mm.
1–2. *Voltzia recubariensis* (Massalongo ex De Zigno, 1862) Schenk, 1868 emend. Forte, Kustatscher et Van Konijnenburg-van Cittert, 2022, Kühwiesenkopf/Monte Prà della Vacca.
1. PAL 786.
2. PAL 784.
3. *Willsiostrobus* sp., Kühwiesenkopf/Monte Prà della Vacca, PAL 794.
4. *Willsiostrobus acuminatus* (Grauvogel-Stamm et Grauvogel) Grauvogel-Stamm et Schaarschmidt, 1978, Hangviller, SMNS-P-118442a.
5. *Willsiostrobus ligulatus* (Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978, Hangviller, SMNS-P-115774b.
6. *Willsiostrobus ligulatus* (Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978, Hangviller, SMNS-P-115730b.

The samples were taken manually with a needle and subsequently macerated using the Schulze reagent (HNO_3 + $KClO_3$) and potassium hydroxide (KOH) according to the protocol described by Nowak et al. (2022a, 2023). In situ pollen grains and masses were then picked from the macerated residues, mounted on glass slides with glycerin jelly as the mounting medium, and imaged with a Leica DMC4500 mounted camera on a Leica DM 2500 LED microscope or with a Moticam 1080 camera on a Leitz Laborlux S microscope. Fluorescence images were taken on the former using Leica TX2 and I3 filter cubes. Most images from the latter assembly were flatfield corrected for dust in the lightpath. Measurements (see Supplementary Data) of the pollen grains were taken using Fiji (ImageJ version 1.54f; Schindelin et al., 2012) and plotted using R (version 4.3.0; R Core team, 2023) with the packages ggplot2 (version 3.4.1; Wickham, 2016), ggridges (version 0.5.4; Wilke, 2021), and viridisLite (version 0.4.2; Garnier et al., 2023). For an illustration of the referenced and measured characters, see Fig. 1. Slides are housed at the NMS

3. Systematic palaeobotany

Order: Voltziales Andreanszky, 1954
Family: Voltziaceae Arnold, 1947
Genus: **Willsiostrobus** Grauvogel-Stamm et Schaarschmidt, 1978
Type species: Willsiostrobus willsii (Townrow) Grauvogel-Stamm et Schaarschmidt, 1978
Remarks on Willsiostrobus *Grauvogel-Stamm et Schaarschmidt, 1978:*
Seward (1911, p. 686) created the new genus *Masculostrobus* Seward, 1911 for male conifer cones that could not be assigned, based on the presence of pollen or by their overall structure, to any particular conifer or cycad genus (and neither to the fossil-genus *Conites* Sternberg, 1823 for fructifications that bore seeds). The type species from the Jurassic of Sutherland consisted of a shoot with anatomically attached cones with broader (triangular) sporophyll heads yielding roundish pollen. Barnard (1968) redefined the genus providing a detailed diagnosis for *Masculostrobus*, indicating that the pollen sacs were attached to the head or stalk or both, and as a major distinguishing character that the pollen grains were non-saccate. He distinguished *Masculostrobus* from the genera *Androstrobus* Schimper, 1870 (cycad male cones) and *Pityanthus* (Nathorst) Seward, 1919 considering the latter for male cones with bisaccate pollen of the *Pityosporites* type and having an affinity to abietinous genera. Léa Grauvogel-Stamm originally used the genus *Masculostrobus* to describe male conifer cones from the Middle Triassic of France (Grauvogel-Stamm, 1969a,b; Grauvogel-Stamm and Grauvogel, 1973) and England (Grauvogel-Stamm, 1972). Grauvogel-Stamm and Schaarschmidt (1978, 1979) proposed to create the new genus *Willsiostrobus* Grauvogel-Stamm et Schaarschmidt, 1978 for male voltzialean conifer cones with peltate microsporophylls bearing numerous free pollen sacs and yielding bisaccate pollen of various types, because the cones of the type species *Masculostrobus zeilleri* Seward, 1911 yielded non-saccate pollen and had bisporangiate microsporophylls.

Arndt (2002) suggested the genus *Willsiostrobus* to be a junior synonym of *Ruehleostachys* Roselt, 1955-56, emending the diagnosis of the latter genus as follows: "Male conifer cones with spirally arranged petiolate, peltate microsporangiophores. The peltate part bears in the lower adaxial region numerous microsporangia which are nearly as long as the shaft of the microsporangiophore." The emended diagnosis of Arndt (2002) includes indeed the diagnosis of *Willsiostrobus* and is also taken as valid by several later authors (e.g., Hermsen et al., 2007). However, after looking both at the holotype of the genus *Ruehleostachys* and the original description of Roselt (1955-56) a major difference is observed: the microsporophylls of the male cone are clearly attached at an acute angle of about 40–50° to the axis whereas the attachment of the microsporophylls is perpendicular in all species of *Willsiostrobus*. Since we consider this attachment angle not a taphonomic effect but as Roselt (1955-56) a primary character of the genus, we consider the genus *Ruehleostachys* as distinct from *Willsiostrobus* and keep both genera apart.

Willsiostrobus acuminatus (Grauvogel-Stamm et Grauvogel) Grauvogel-Stamm et Schaarschmidt, 1978
Plate I, 4, Plate IV, 15–16.
Localities: Hangviller, France.
Stratigraphic horizons: Grès à Voltzia, Aegean, early Anisian.
Studied material: SMNS: SMNS-P-118442a.
Description of macroremains: The single studied pollen-bearing cone is about 20 mm long and 8 mm wide, preserved partly showing the outside and partly in section. The sporophylls are arranged helically around the central axis. Each microsporophyll can be divided into a stalk (shank sensu Rothwell et al., 2005), attached perpendicularly to the central axis, and an expanded laminar peltate portion (head), attached perpendicularly to the pedicel. The head has a rhomboidal shape with a rounded base and an elongated, acuminate apex. The extension of the acuminate apex is up to 2 mm long, which is impressive considering that the overall shape of the microphyll head (without acuminate tip) measures about 1.5 mm in length and 0.5–1 mm in width. The microsporangia are attached in a group on the lower side of the pedicel and are oriented parallel to the pedicel. In general, they appear as long as the pedicel, being 2–3 mm long and 0.2–0.5 mm wide.
Description of in situ *pollen:* In situ pollen is poorly preserved and fragile, possibly immature. Several pollen sacs were sampled and macerated, but individual pollen grains could not be isolated without damage (Plate IV, 15–16). They are bisaccate, thin-walled, with a circular to oval corpus, without a discernable aperture or proximal ornamentation. One grain (Plate IV, 15) could be measured at 79 μm total length, corpus length 48 μm.
Discussion: The assignment of this cone to *Willsiostrobus acuminatus* is based on the acuminate heads of the microsporophylls as well as the small and slender cone shape. Grauvogel-Stamm and Grauvogel (1973) described the 35 mm long and 10 mm wide holotype (with a range of 30–55 × 11 mm given for the species) yielding pollen that would belong to the dispersed pollen species *Illinites kosankei* Klaus, 1964. These pollen grains were described as eusaccate, in contrast to other known voltzialean in situ pollen (Grauvogel-Stamm and Grauvogel, 1973; Grauvogel-Stamm, 1978; Hermsen et al., 2007). The here described in situ pollen is, however, not assignable the *Illinites* because of the absence of a discernable aperture and proximal ornamentation, although this may be due to immaturity of the pollen. For the same reason, it is not clear if they were eusaccate or protosaccate.

Willsiostrobus cf. *acuminatus* (Grauvogel-Stamm et Grauvogel)

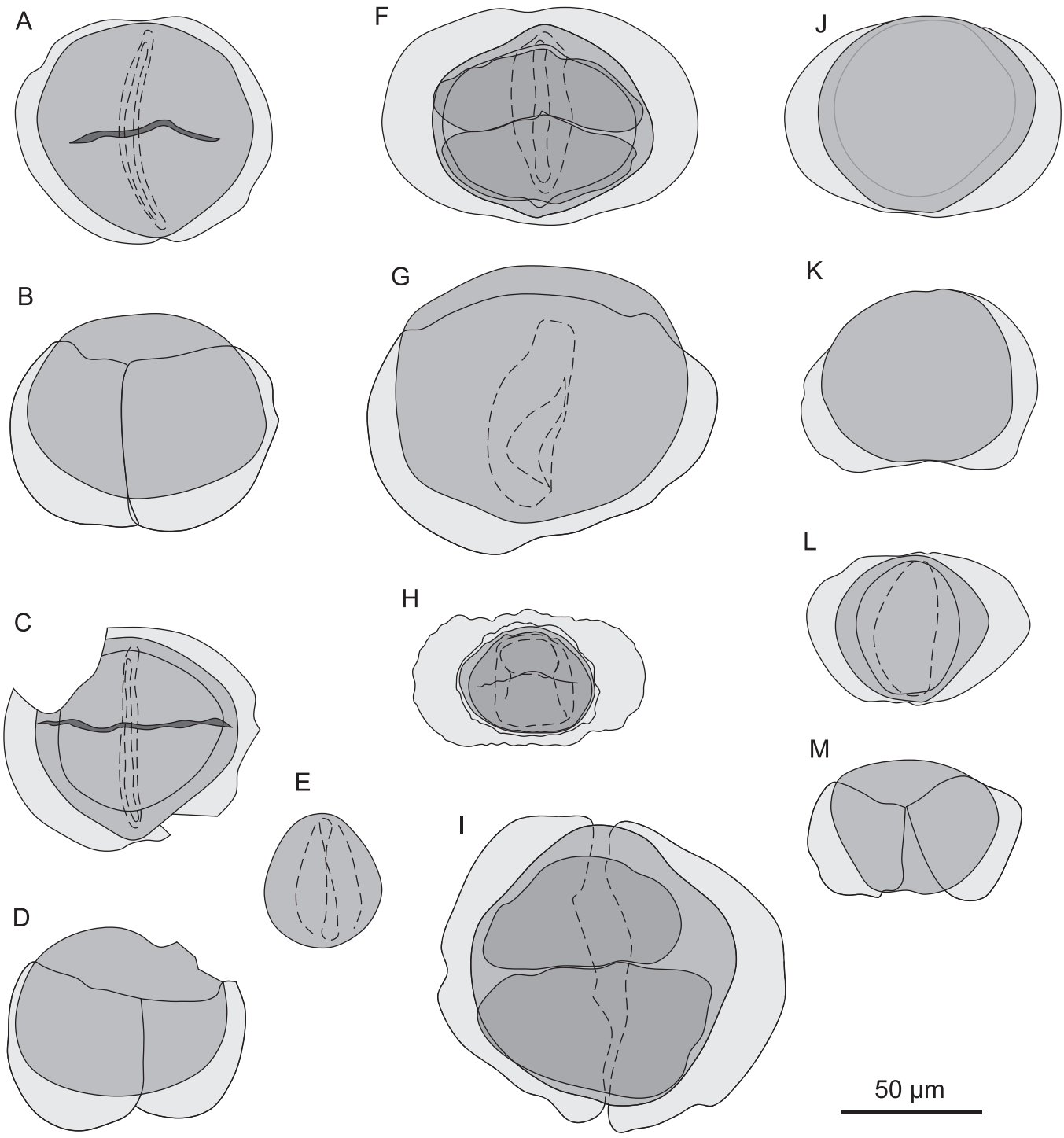

Fig. 2. Simplified interpretative line drawings of selected in situ pollen grains.
A–B. *Willsiostrobus willsii*, MB.Pb.2019/273. A. Pollen grain in polar view, sample 3, see Plate V, 4. B. Lateral-equatorial view, sample 1, see Plate V, 3.
C–E. *Willsiostrobus* sp. 2, C. Polar view, see Plate V, 8, Plate IX, 15–16. D. Polar view, see Plate V, 6–7. E. Diminutive corpus, see Plate V, 5.
F–H. *Willsiostrobus* cf. *cordiformis*. F. Regular pollen grain, MB.Pb.1983/424, sample 3, see Plate VIII, 10. G. Large pollen grain, MB.Pb.1983/424, sample 3, see Plate VIII, 14. H. Diminuitive pollen grain, MB.Pb.2000/471, sample 1, see Plate VI, 10.
I. *Willsiostrobus* cf. *acuminatus*, polar view, MB.Pb.2000/252e, sample 2, see Plate VIII, 1–3.
J–K. *Willsiostrobus* sp. 1, MB.Pb.2008/210, sample 1. J. Polar view, see Plate VI, 13. K. Lateral-equatorial view, see Plate VI, 15.
L–M. *Willsiostrobus* cf. *willsii*, SMNS-P-110024. L. Polar view, sample 6, see Plate VII, 2. M. Lateral-equatorial view, sample 7, see Plate VII, 2, 6.

Grauvogel-Stamm et Schaarschmidt, 1978
Fig. 2I, Plate II, 1, Plate VIII, 1–6
Localities: Thale, Germany.
Stratigraphic horizons: Erfurt Formation, Longobardian, late Ladinian.
Studied material: MfN: MB.Pb.2000/252e.

Description of macroremains: The cone fragment is about 45 mm long and 12.5 mm wide, preserved partly as an external impression. The sporophyll heads appear to be arranged helically. They have a rhomboidal shape (3 × 3 mm) with a central thickening and an elongated apex. No further details are visible on the cone.

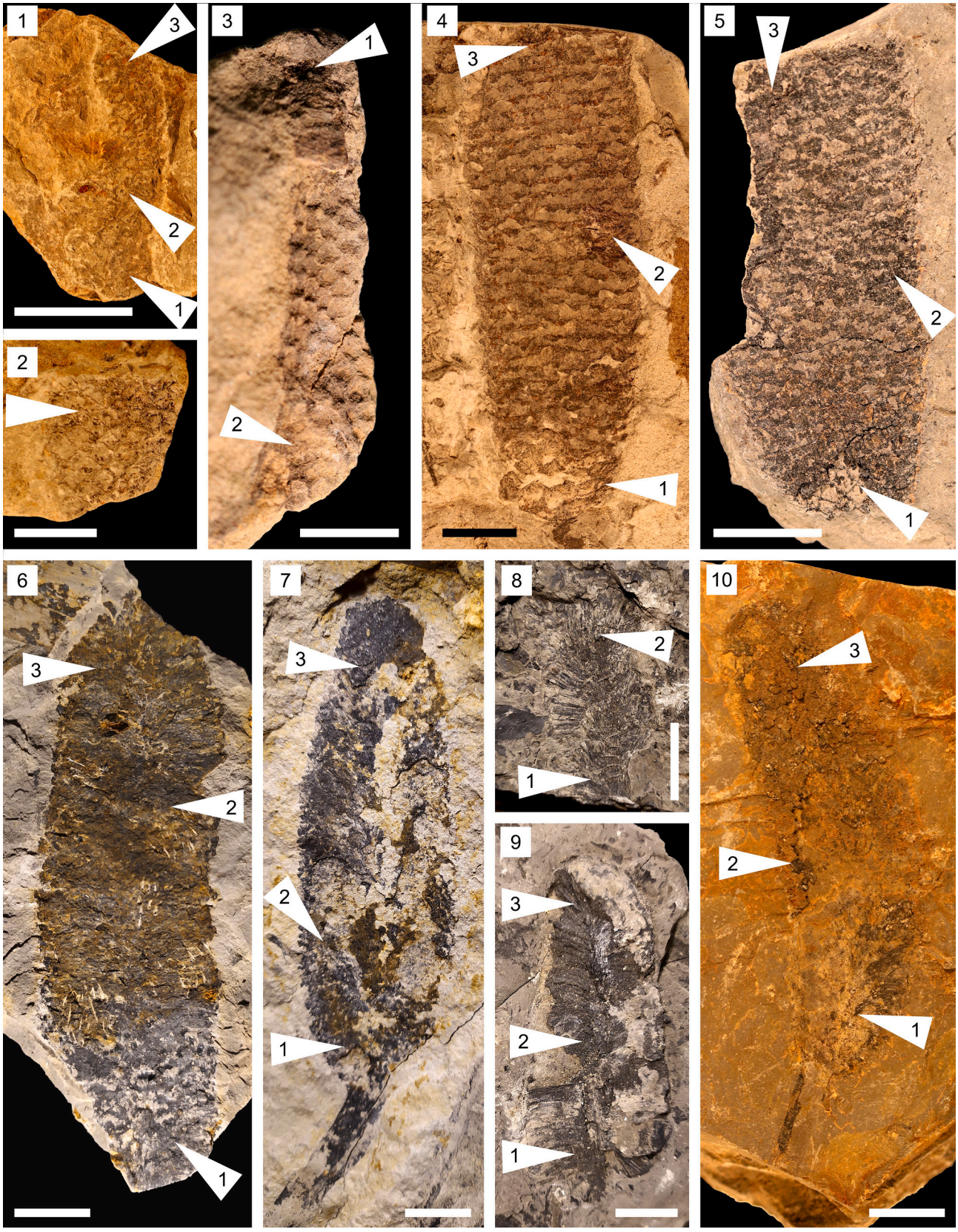

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Plate II. Sampled male (polliniferous) cone macrofossils from the Ladinian Erfurt Formation. White chevrons indicate sampling positions. Scale bars = 10 mm.
1. *Willsiostrobus* cf. *acuminatus* (Grauvogel-Stamm et Grauvogel) Grauvogel-Stamm et Schaarschmidt, 1978, Thale, MB.Pb.2000/252e.
2–5. *Willsiostrobus* cf. *cordiformis* (Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978.
2. Thale, MB.Pb.2000/252b.
3. Bedheim, MB.Pb.2000/484.
4. Thale, MB.Pb.1983/424.
5. Bedheim, MB.Pb.2000/471.
6–7. *Willsiostrobus rhomboidalis* (Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978, Weiler zum Stein.
6. SMNS-P-P001487/26.
7. SMNS-P-P001487/101.
8. *Ruehleostachys* sp. 1, Zwingelhausen, SMNS-P-P001481–1.
9. *Ruehleostachys* sp. 2, Zwingelhausen, SMNS-P-P001481–2.
10. *Willsiostrobus* sp.1, Bedheim, MB.Pb.2008/210.

Description of in situ *pollen:* Only a few pollen grains were extracted (Plate VIII, 1–6). These are haploxylonoid bisaccate pollen grains with an elongate oval outline. The sacci are equatorially connected. The corpus is approximately circular to oval (longer than wide), proximally strongly thickened, punctate/reticulate, and marked by a straight to wavy furrow running its entire length, thereby creating two taeniae. Only one grain could be measured, which is 122 μm long, the corpus measuring 92 μm × 97 μm, sacci up to 108 μm wide.

Discussion: The shape of the small and slender cone that falls within the variability of the *Willsiostrobus acuminatus* and the presence of apical extensions of the microsporophyll heads, visible in lateral view support an assignment to this species. The missing details of the microsporophyll heads and the cone structure make a confidential assignment impossible.

The pollen overall resembles *Illinites chitonoides* Klaus, 1964, but in cases with a straighter proximal furrow (Plate VIII, 1–3; comp. Plate VIII, 4–6), the grains approach the bitaeniate pollen type *Lueckisporites* Potonié et Klaus, 1954 emend. Klaus, 1963.

Willsiostrobus cf. *cordiformis* (Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978

Fig. 2F–H, Plate II, 2–5, Plate VI, 1–12, Plate VIII, 7–16, Plate IX, 5

Localities: Bedheim and Thale, Germany.

Stratigraphic horizons: Erfurt Formation, Longobardian, late Ladinian.

Studied material: MfN: MB.Pb.1983/424, MB.Pb.2000/252b, MB.Pb.2000/471, MB.Pb.2000/484.

Description of macroremains: None of the cones are complete, but the cone fragments are up to 75 mm long and up to 26 mm wide in the middle part of the cone, whereas in the lower part of the cone (preserved with outer surface in MB.Pb.1983/424) is 18 mm wide. The sporophylls are arranged in a very low helix, almost seemingly in a circle, and are heavily imbricated. The shape of the sporophyll head is distinguishable only in the lowermost part of cone MB.Pb.1983/424. The sporophyll head is very broad and rhomboidal in shape, with an extension of the base. It is ca. 5 mm wide and 5 mm high.

Description of in situ *pollen:* The pollen grains found in this group of cones are bisaccate with fused sacci or monosaccate, with a circular to oval amb and a circular to oval corpus. The sacci show a narrow offlap from the corpus and enclose a more or less narrow cappula with a long, fusiform sulcus. The reticulum is mostly coarse, distinctly finer towards the sides. Distal folds are often present. The cappa is strongly thickened with clear lateral delimitations and a central longitudinal, irregularly wavy furrow, often with a central bend. Total pollen length is 57–(94.9)–129 μm (n = 59), the corpus measuring 37–(64.3)–106 μm (n = 55) × 32–(53.1)–91 μm (n = 35), saccus width 40–(62.8)–97 μm (n = 37).

Two distinct types of pollen grains can be distinguished: One conforming mostly to *Illinites* Kosanke, 1950 – but including examples of monosaccates (Plates VI, 5–9, VIII, 9–10) –, and one with a smaller size, darker corpus, and sometimes slightly diploxylonoid appearance (Plates VI, 9–12, VIII, 7, 8, 11–13, 15–16). In these grains, the cappa is marked by coarse ornamentation, as well as a longitudinal furrow equivalent to the one seen in larger grains. Both samples from the most productive sampled cone MB.Pb.2000/471 contained these two types in abundance, with approximately equal frequency or with the smaller type being the majority (ca. 3/4 in sample 1, ca. 1/2 in sample 2). The two types occur together in the same clusters. Samples from other cone specimens yielded lower numbers of pollen grains, yet with similar ratios. Pollen grains with an even larger than normal corpus were observed in low numbers as well (Plate VIII, 14).

Discussion: The strongly imbricating microsporophyll heads, and the few details visible of the lower, very broad, slightly heart-shaped part of the microsporophyll head make a confidential assignment of the cones difficult; thus, we keep the assignment at putative level.

The smaller grains are interpreted as malformations, but it is unclear if they were abortive (=unviable), considering they are seemingly well-developed. In dispersed assemblages, the larger and smaller grains would certainly be identified as different morphospecies at least. See further discussion below (4.2).

Willsiostrobus ligulatus (Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978

Fig. 3L–M, Plate I, 5–6, Plate IV, 17–20

Selected references

1969 *Masculostrobus ligulatus* Grauvogel-Stamm, p. 98, pl. 1, fig. 3.

1978 *Willsiostrobus ligulatus*, Grauvogel-Stamm and Schaarschmidt, p. 17

Localities: Hangviller, France

Stratigraphic horizons: Grès à Voltzia, Aegean, early Anisian

Studied material: SMNS: SMNS-P-115730b, SMNS-P-115774b.

Description of macroremains: The cone fragments (including one almost complete cone, SMNS-P-115730b) are lanceolate with a rounded apex, about 40 mm long and 13–18 mm wide, partly preserved from the outside, partly in section. The sporophylls are arranged helically around a central axis of 1–2 mm width. Each microsporophyll consists of a stalk (shank *sensu* Rothwell et al., 2005), attached perpendicularly to the central axis, and an expanded peltate portion (head), attached perpendicularly to the pedicel. The head has a rhomboidal shape with a rounded base and a distinct, prolonged apex. The microphyll head measures about 2.5–3.5 mm in length and 1–1.5 mm in width. The microsporangia are attached to the lower side of the stalk and are oriented parallel to the stalk. In general, they appear to be as long as the pedicel, being 3–4.5 mm long and 0.5 mm wide. Apically, the dimensions of the heads and length of the stalk of the microsporophylls reduces noticeably.

Description of in situ *pollen:* Only a few, poorly preserved pollen grains were obtained from specimen SMNS-P-115774b. These appear to be bisaccate (Plate IV, 17). Cone SMNS-P-115730b yielded entire pollen sacs with abundant pollen grains, which are extremely thin-walled and do not show many clear features, due to preservation or immaturity, or both (Plate IV, 17). They appear to be bisaccate, usually diploxylonoid, with an oval (wider than long) corpus and sacci that are as big or bigger than the corpus (Plate IV, 18, 19) or with laterally and possibly proximally connected sacci (Plate IV, 20). Total length 46–(59.5)–79 μm (n = 6), saccus width 44–(58)–72 μm (n = 2).

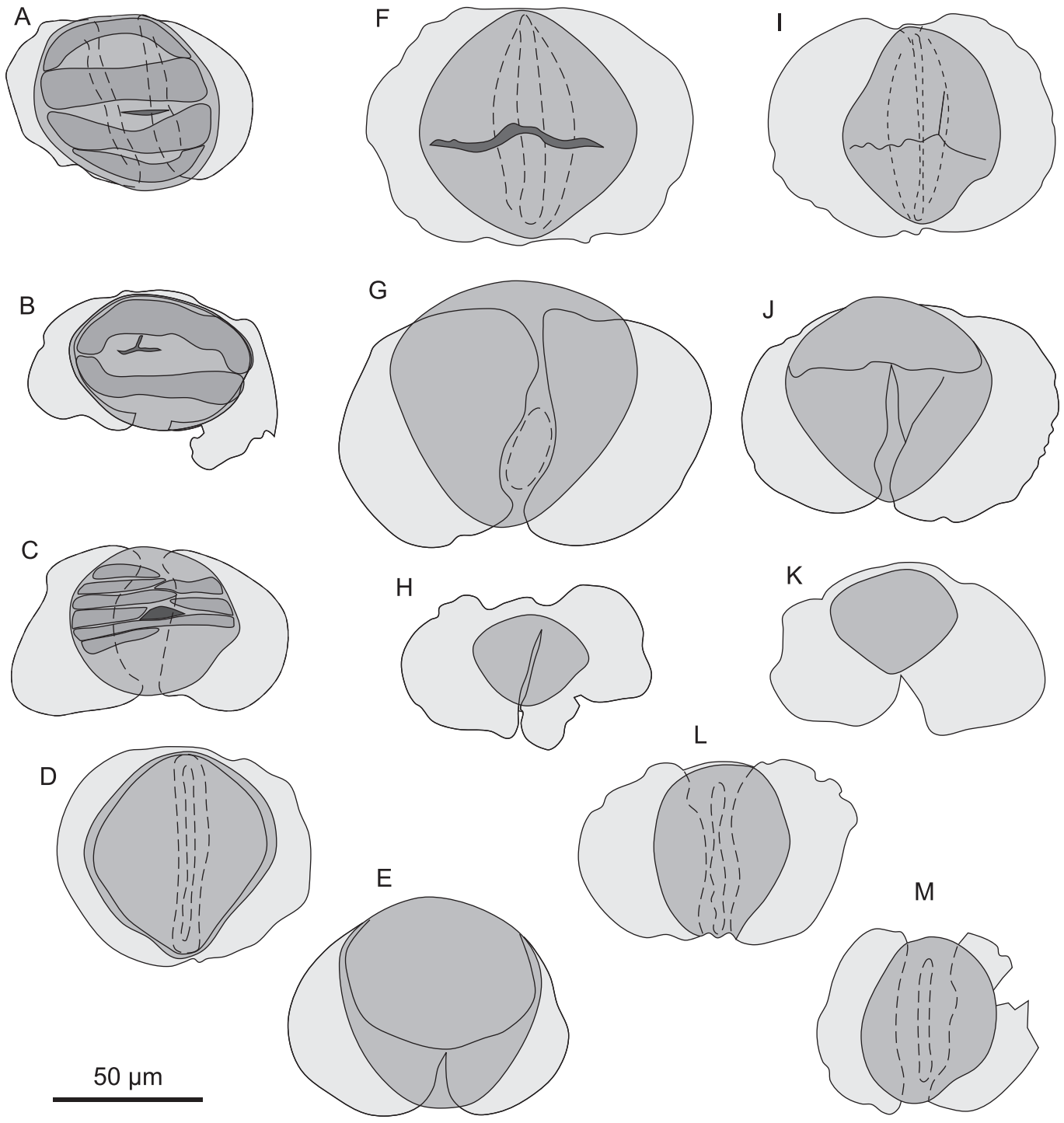

Fig. 3. Simplified interpretative line drawings of selected in situ pollen grains. A–B. *Voltzia recubariensis*. A. Pollen grain with four taeniae and monolete mark, PAL 786, sample 2, see Plate IV, 1. B. Pollen grain with two visible taeniae and apparent trilete mark, PAL 569, sample 2, see Plate IV, 6.
C. *Willsiostrobus* sp. sensu Forte et al., 2022, pollen grain in polar view, PAL 794, sample 1, see Plate IX, 4.
D–E. *Willsiostrobus rhomboidalis*, SMNS-P-P001487/26, sample 2. G. Polar view, see Plate V, 15–16. H. Lateral-equatorial view, see Plate V, 12.
F–H. *Ruehleostachys* sp. 1, SMNS-P-P001481–1, sample 2. D. Polar view, see Plate VII, 11, Plate IX, 6. E. Lateral-equatorial view, see Plate VII, 13, Plate IX, 7. F. Platysaccoid pollen grain, see Plate VII, 14.
I–K. *Ruehleostachys* sp. 2, SMNS-P-P001481–2, sample 1. I. Polar view, see Plate VII, 15–16. J. Lateral-equatorial view, see Plate VII, 17. K. Platysaccoid pollen grain, see Plate VII, 18.
L–M. *Willsiostrobus ligulatus*, SMNS-P-115730b, sample 1. L. See Plate IV, 18. M. See Plate IV, 19.

Discussion: The assignment of these specimens to *Willsiostrobus ligulatus* is supported by the ligulate microsporophyll head. The dimensions of the cones are slightly smaller than the holotype of *W. ligulatus*, but the overall proportions and shape of the cones correspond to the type specimen. In situ pollen of *Masculostrobus* (=*Willsiostrobus*) *ligulatus* was described by Grauvogel-Stamm (1969a, 1972) as indistinguishable from that of *Masculostrobus* (=*Willsiostrobus*) *rhomboidalis*, which in turn has been compared to the dispersed taxa

Table 2
Overview of voltzialean conifer species from the Triassic with previously reported in situ pollen.

Taxon	Sacci	Corpus	Length/ Diameter [μm]	Comparable dispersed taxa	References
Compsostrobus neotericus Delevoryas et Hope, 1973	Bisaccate	Nearly spherical	75	*Alisporites*	Delevoryas and Hope, 1973; Grauvogel-Stamm and Schaarschmidt, 1979
Darneya dentata Grauvogel-Stamm, 1978	Asaccate/ monosaccate/ bisaccate(?)	Irregularly ornamented, trilete?		Immature *Triadispora*?	Taylor and Grauvogel-Stamm, 1995
Darneya peltata Schaarschmidt et Mauberge, 1969	Bisaccate, haploxylonoid to slightly diploxylonoid	Trilete, leptomate	30-(45)-58 [1]; 65–80 [2]	*Triadispora* [immature, asaccate forms: *Inaperturopollenites*]	Schaarschmidt and Maubeuge, 1969 [1]; Grauvogel-Stamm, 1969a, 1978 [2]; Balme, 1995
Leastrobus fallae Hermsen et al., 2007	Bisaccate, slightly constricted at attachment	Finely reticulate, sulcate	42–73	*Alisporites*	Hermsen et al., 2007; Bomfleur et al., 2013
Rissikia media (Tenison-Woods) Townrow, 1967	Bisaccate, haploxylonoid	Multitaeniate (3–10), leptomate	ca. 50 μm	*Lunatisporites*	Townrow, 1967a; Balme, 1995; Taylor et al., 2009
Ruehleostachys pseudarticulatus Roselt, 1955–1956	Bisaccate, haploxylonoid, sometimes monosaccate	Oval, scarcely reticulate, sulcoid	78–83 [1]; ca. 85 [2]; 70–80 [3]	*Alisporites* / *Rimaesporites* (?)	Roselt, 1955-56 [1]; Townrow, 1962 [2]; Potonié, 1962, 1967; Balme, 1995; Arndt, 2002 [3]
Ruehleostachys sp. 1	Bisaccate, haploxylonoid to diploxylonoid	Rounded rhombic, triletoid/dilete, granulate, furrowed	87–(102.8)–122	*Angustisulcites*	This work
Ruehleostachys sp. 2	Bisaccate, haploxylonoid to diploxylonoid	Rounded rhombic, triletoid/dilete, granulate, furrowed	84–(99)–126	*Angustisulcites*	This work
Sertostrobus laxus Grauvogel-Stamm, 1969	Bisaccate, haploxylonoid to slightly diploxylonoid	Subcircular, leptomate	30–65 [1]; 35–55 [2]	*Klausipollenites*	Grauvogel-Stamm, 1969a [1], 1978; Grauvogel-Stamm and Schaarschmidt, 1979; Balme, 1995; Taylor and Grauvogel-Stamm, 1995 [2]
Switzianthus sensu Bomfleur et al., 2011	Bisaccate	Circular to narrow-elliptic, non-taeniate, prominent distal aperture	60–100	*Alisporites*	Bomfleur et al., 2011, 2013
Voltzia recubariensis (Massalongo ex De Zigno) Schenk, 1868	Bisaccate, haploxylonoid	Circular to oval (longer than wide), monolete (/triletoid), 2 or 4 taeaniae	50–(79.3)–125	*Lunatisporites*, *Lueckisporites*	This work
Voltzia sp. sensu Potonié, 1970	Bisaccate	Monolete, two transversal folds		*Sahnisporites*	Grauvogel et al., 1967; Potonié, 1970
Willsiostrobus acuminatus (Grauvogel-Stamm et Grauvogel) Grauvogel-Stamm et Schaarschmidt, 1978	Bisaccate Bisaccate, slightly diploxylonoid	Circular to oval, alete(?) Subcircular, monolete/ dilete, distal aperture with perpendicular equatorial to subequatorial tenuitates	79 70–130	indet. *Illinites kosankei* Klaus, 1964, *I. chitonoides* Klaus, 1964, *Parillinites*	This work Grauvogel-Stamm and Grauvogel, 1973; Grauvogel-Stamm, 1978; Grauvogel-Stamm and Schaarschmidt, 1978, 1979; Balme, 1995; Rothwell et al., 2000; Hermsen et al., 2007; Taylor et al., 2009
Willsiostrobus cf. *acuminatus* (Grauvogel-Stamm et Grauvogel) Grauvogel-Stamm et Schaarschmidt, 1978	Bisaccate, haploxylonoid	Oval (longer than wide), proximally thickened, punctate/reticulate, furrowed/bitaeniate	122	*Illinites chitonoides* Klaus, 1964, cf. *Lueckisporites*	This work
Willsiostrobus bromsgrovensis (Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978	Bisaccate (rarely trisaccate), haploxylonoid	Circular to oval (broader than long), granular sculpture	65–(75)–92 [1]; 46–93 [2]	*Voltziaceaesporites*/*Alisporites* (s. l.)	Wills, 1910; Couper, 1958 [1]; Potonié, 1962; Townrow, 1962; Grauvogel-Stamm, 1972, 1978; Balme, 1995 [2]
Willsiostrobus cordiformis (Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978	Bisaccate, haploxylonoid to slightly diploxylonoid	Circular to oval, leptomate	58–128 [1], 50–128 [2]	*Voltziaceaesporites*/*Alisporites* (s. l.) [*Alisporites cordiformis* in Grauvogel-Stamm, 1978]	Grauvogel-Stamm, 1969a [1], 1972, 1978; Balme, 1995; Taylor and Grauvogel-Stamm, 1995 [2]
Willsiostrobus cf. *cordiformis* (Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978	Bisaccate (confluent), haploxylonoid to monosaccate	Circular to oval, trilete with rudimentary third ray, proximally thickened, furrowed	57–(94.9)–129	*Illinites* spp., *Angustisulcites*	This work
Willsiostrobus denticulatus (Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978	Bisaccate, diploxylonoid	Subcircular, leptomate	46–85	*Alisporites* (s.l.) [*A. circulicorpus* Clarke 1965 acc. To Grauvogel-Stamm, 1978]	Grauvogel-Stamm, 1969a, 1978; Balme, 1995; Taylor and Grauvogel-Stamm, 1995
Willsiostrobus hexasacciphorus Grauvogel-Stamm et Álvarez-Ramis, 1996	Hexasaccate	Circular		*Stellapollenites thiergartii* (Mädler) Clement-Westerhof et al.,1974 / *Hexasaccites muelleri* Reinhardt in Reinhardt et Schmitz, 1965	Grauvogel-Stamm and Álvarez Ramis, 1996

(*continued on next page*)

Table 2 (*continued*)

Taxon	Sacci	Corpus	Length/ Diameter [µm]	Comparable dispersed taxa	References
Willsiostrobus ligulatus (Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978	Bisaccate, diploxylonoid, partly monosaccate	Oval, alete(?)	46–(59.5)–79	*Voltziaceaesporites*	This work
	Bisaccate	Wide distal aperture	60–99		Taylor and Grauvogel-Stamm, 1995
Willsiostrobus rhomboidalis (Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978	Bisaccate, haploxylonoid	Circular to oval (longer than wide) or rounded rhombic, faint monolete mark, proximally granulate, sulcate	71–(87.9)–101	cf. *Alisporites/Illinites*	This work
	Bisaccate, slightly diploxylonoid, nexinal folds	Circular to oval, sulcate	43–100 [1]; 46–101 [2]	*Voltziaceaesporites heteromorphus* Klaus, 1964 / *Scopulisporites toralis* Leschik, 1955	Grauvogel-Stamm, 1969a [1], 1978; Balme, 1995; Grauvogel-Stamm and Álvarez Ramis, 1996; Taylor and Grauvogel-Stamm, 1995 [2]
Willsiostrobus willsii (Townrow) Grauvogel-Stamm et Schaarschmidt, 1978	Bisaccate, haploxylonoid	Oval (longer than wide), proximally thickened, granulate, furrowed	86–(97.8)–117	*Illinites*, *Voltziaceaesporites/ Alisporites*	This work
	Bisaccate, diploxylonoid	Circular, alete, sulcate	75 [1]; 55–100 [2]	*Voltziaceaesporites/Alisporites* (s. l.)	Wills, 1910; Couper, 1958; Potonié, 1962; Townrow, 1962 [1]; Grauvogel-Stamm, 1972 [2], 1978; Balme, 1995; Taylor and Grauvogel-Stamm, 1995
Willsiostrobus cf. *willsii* (Townrow) Grauvogel-Stamm et Schaarschmidt, 1978	Bisaccate, haploxylonoid	Circular to slightly elongated oval, sulcate	49–(64)–77	cf. *Alisporites*	This work
Willsiostrobus cf. *willsii* sensu Grauvogel-Stamm, 1978	Bisaccate, diploxylonoid to haploxylonoid, sometimes platysaccoid	Oval to circular, alete	51–(70.7)–90	*Alisporites*?	Grauvogel-Stamm, 1972, 1978
Willsiostrobus sp. 1	Bisaccate, haploxylonoid	Oval, alete	59–(82.1)–93	*Klausipollenites*	This work
Willsiostrobus sp. 2	Bisaccate, haploxylonoid	Rounded rhombic, monolete/triletoid, furrowed, sulcate	85–(92.5)–101	*Illinites*	This work
Willsiostrobus sp. sensu Forte et al., 2022	Bisaccate, diploxylonoid	Oval, multitaeniate, monolete	68–(84.5)–99	*Striatoabieites*	This work
Pollen cone 1 sensu Forte et al., 2022	Bisaccate, haploxylonoid to diploxylonoid	Circular or longitudinally elongated, two or four taeniae, monolete	55–96	*Lueckisporites*, *Lunatisporites*	Forte et al., 2022
Pollen cone 2 sensu Forte et al., 2022	Bisaccate, haploxylonoid	Circular or longitudinally elongated, two or four taeniae, monolete	63–95	*Lueckisporites*, *Lunatisporites*	Forte et al., 2022

Voltziaceaesporites heteromorpha Klaus and *Scopulisporites toralis* Leschik (Grauvogel-Stamm, 1969b) or *Voltziaeeaesporites/Alisporites* (s.l.; Balme, 1995). The in situ pollen grains at least partially resemble *Voltziaceaesporites* Klaus, 1964, as the sacci appear to grade into a proximal thickening (Plate IV, 20). This pollen type has been reported from other species of *Willsiostrobus* (see Table 2) as well.

Willsiostrobus rhomboidalis (Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978

Fig. 3D–E, Plate II, 6–7, Plate V, 9–16

Selected references

1969a *Masculostrobus rhomboidalis* Grauvogel-Stamm, p. 96, pl. 1, figs. 2, 8–9, text-fig. 2.

1969b *Masculostrobus rhomboidalis* Grauvogel-Stamm, p. 355.

1978 *Willsiostrobus rhomboidalis,* Grauvogel-Stamm and Schaarschmidt, p. 17.

Localities: Weiler zum Stein and Zwingelhausen, Germany

Stratigraphic horizons: Erfurt Formation, Longobardian, late Ladinian

Studied material: SMNS: SMNS-P-P001487/101, SMNS-P-P001487/26

Description of macroremains: The cones are lanceolate in shape, about 70–85 mm long and 25 mm wide. Cone SMNS-P-P001487/101 is complete and attached to a 4 mm wide and 25 mm long axis. The sporophylls are arranged in a low helix around the central axis. The sporophyll heads are rhomboidal to subtriangular in shape, about 1.5 mm in length and 1–1.5 mm in width. The microsporangia are attached parallel to the stalk on the lower side of the microsporophyll. In general, they appear as long as the stalk, being up to 10 mm long and 1 mm wide.

Description of in situ *pollen:* Pollen grains are bisaccate, haploxylonoid, oval (usually longer than wide) with finely reticulated sacci not extending far from the corpus and possibly in some cases laterally fused into a narrow bridge. The corpus is circular to elongated oval (sometimes tending towards rounded rhombic) in polar view, proximally granulate, sometimes with a faint transversal, nearly straight mark, distally showing a long and narrow sulcus in a slightly wider cappula. Distal folds can sometimes be seen. Total length 71–(87.9)–101 µm (n = 15), corpus 46–(62.1)–73 µm (n = 14) × 46–(62)–79 µm (n = 8), saccus width 54–(70.6)–84 µm (n = 7).

Discussion: The in situ pollen grains share many features with those of *Ruehleostachys pseudarticulatus* Roselt, 1956, but are on average larger than the reported size range for that species (70–85 µm total length, see Roselt, 1955-56; Townrow, 1962; Arndt, 2002). In the absence of distinct proximal ornamentation and given the presence of a sulcus, most of the pollen grains are best compared with *Alisporites*. However, this may in part be a preservational effect, as a faint mark can be seen in some cases. The better-preserved grains are reminiscent of *Illinites* in their overall appearance.

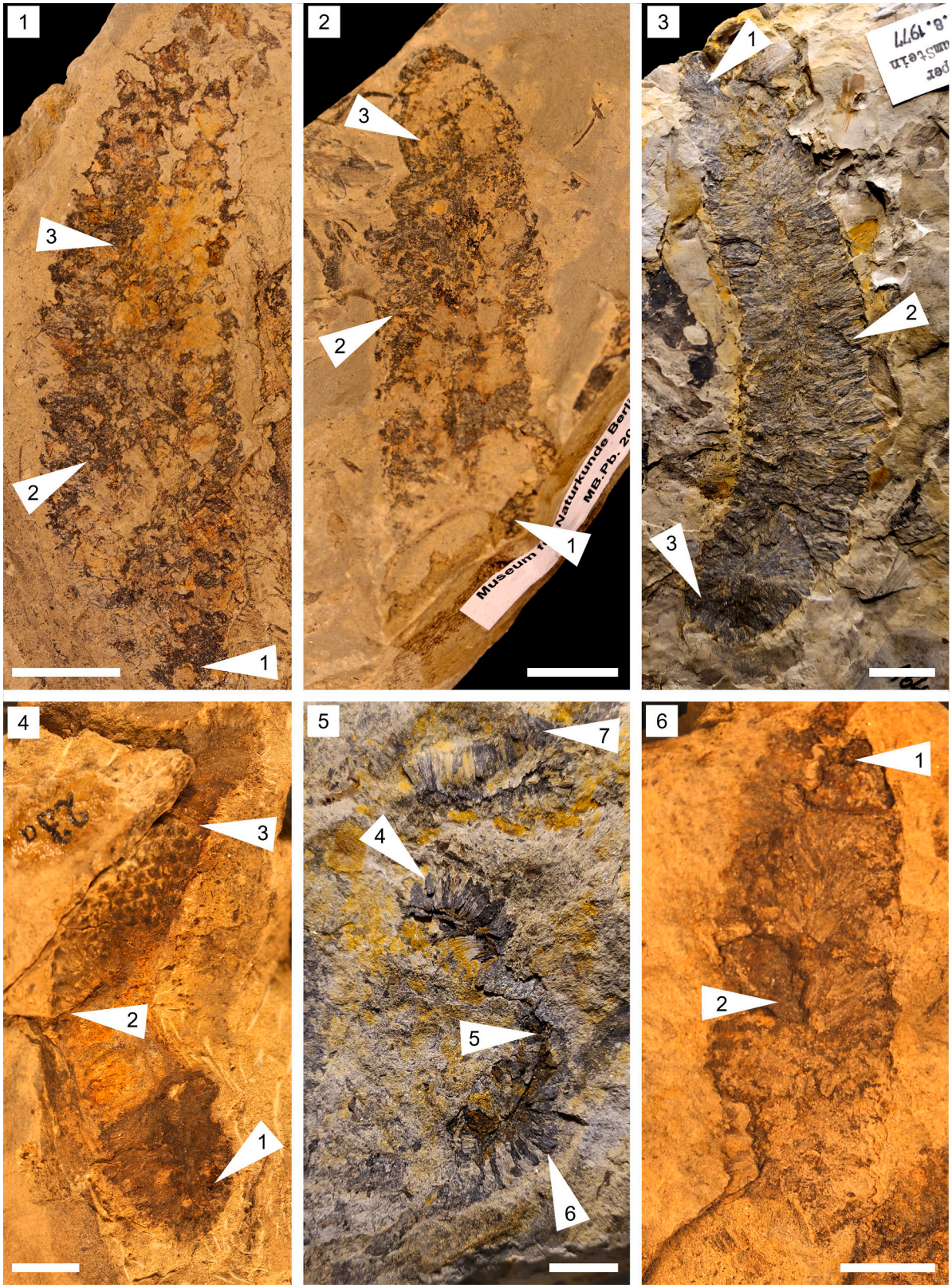

Plate III. Sampled male (polliniferous) cone macrofossils from the Ladinian Erfurt Formation. White chevrons indicate sampling positions. Scale bars = 10 mm.
1–2. *Willsiostrobus willsii* (Townrow) Grauvogel-Stamm et Schaarschmidt, 1978, Rockhausen.
1. MB.Pb.2019/273.
2. MB.Pb.2019/274.
3. *W. willsii* (Townrow) Grauvogel-Stamm et Schaarschmidt, 1978, Weiler zum Stein, SMNS-P-P001487/88.
4. *W. willsii* (Townrow) Grauvogel-Stamm et Schaarschmidt, 1978, Bedheim, MB.Pb.1983/422a.
5. *Willsiostrobus* cf. *willsii* (Townrow) Grauvogel-Stamm et Schaarschmidt, 1978, Rielingshausen, SMNS-P-110024.
6. *Willsiostrobus* sp. 2, Rockhausen, MB.Pb.2000/780.

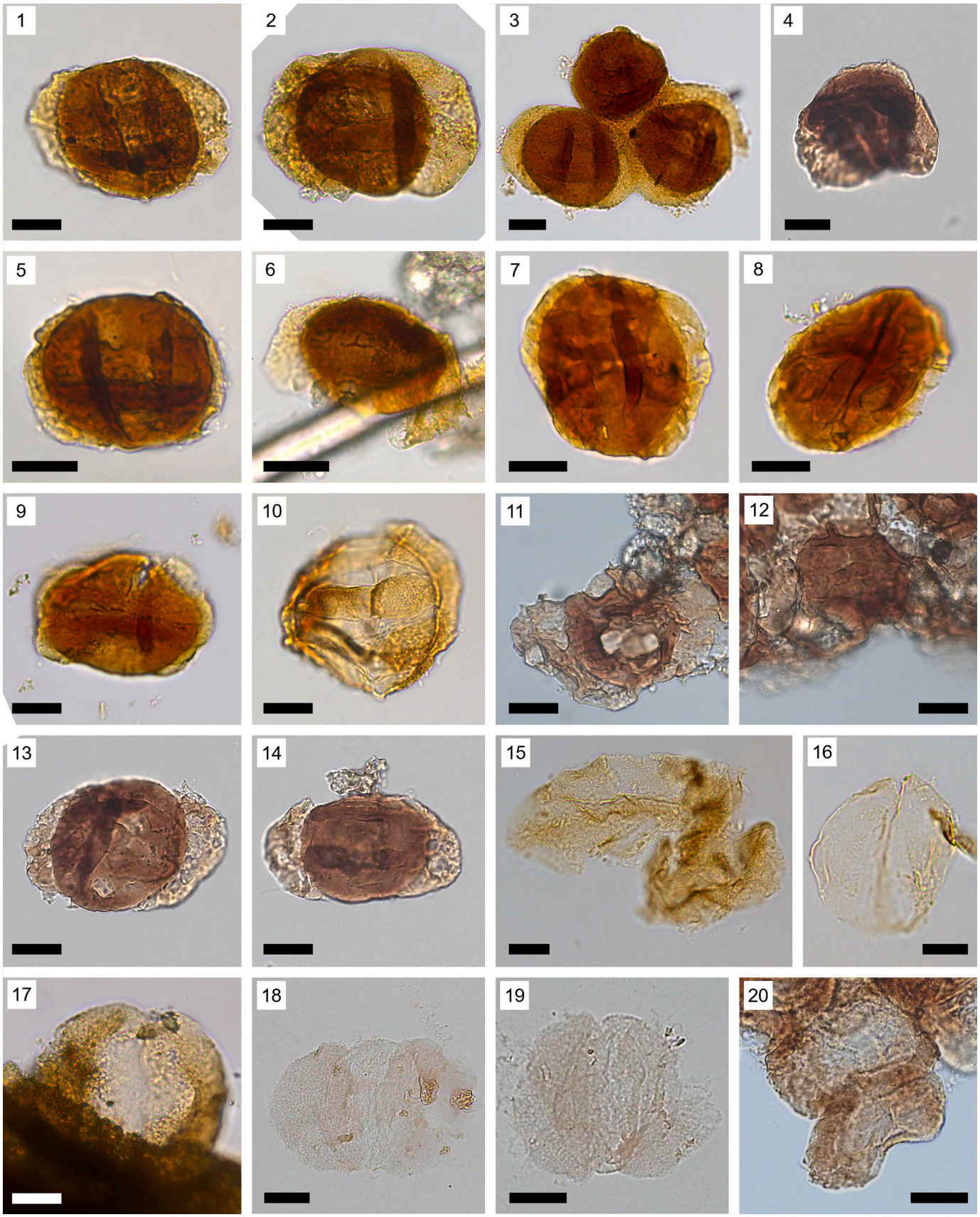

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Plate IV. In situ pollen from the Anisian floras of the Dont Formation at the Kühwiesenkopf/Monte Prà della Vaccca locality in Italy and the Grès à Voltzia at Hangviller, France. Scale bars = 20 μm.
1–10. Pollen grains of *Voltzia recubariensis* (Massalongo ex De Zigno, 1862) Schenk, 1868 emend. Forte, Kustatscher et Van Konijnenburg-van Cittert, 2022, Kühwiesenkopf/Monte Prà della Vacca.
1–4. PAL 786.
1. Sample 2, slide 1.
2–3. sample 3, slide 1.
4. Trisaccate pollen grain, sample 2+, slide 1.
5–6. PAL 569, sample 2, slide 1.
6. Pollen grain with apparent trilete mark.
7–8. PAL 2100, sample 2, slide 1.
8. Pollen grain shown with fluorescence in Plate IX, 1–2.
9. PAL 784, sample 4, slide 1.
10. PAL 787, sample 2, slide 1.
11–14. *Willsiostrobus* sp. sensu Forte et al., 2022, Kühwiesenkopf/Monte Prà della Vacca, PAL 794.
11–12. Multitaeniate (or -striate) pollen grains, sample 1, slide 2.
13–14. Probably foreign pollen grains; note differences with pollen shown in figs. 11, 12 and similarities with pollen of *V. recubariensis* (Massalongo ex De Zigno, 1862) Schenk, 1868 emend. Forte, Kustatscher et Van Konijnenburg-van Cittert, 2022, e.g., figs. 1, 2, sample 3, slide 1.
15–16. Poorly preserved pollen of *Willsiostrobus acuminatus* (Grauvogel-Stamm et Grauvogel) Grauvogel-Stamm et Schaarschmidt, 1978, Hangviller, SMNS-P-118442a.
15. Pollen grain in lateral view, sample 2, slide 4.
16. Isolated corpus(?), sample 2, slide 3.
17–20. *Willsiostrobus ligulatus* (Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978, Hangviller.
17. Pollen grain with missing or faint corpus, SMNS-P-115774b, sample 3, slide 1.
18–20. SMNS-P-115730b.
18–19. Poorly preserved (flattened, thinned, and damaged) pollen grains, sample 1, slide 2.
20. Pollen grains at the edge of a pollen sac, sample 3, slide 3.

Willsiostrobus willsii (Townrow) Grauvogel-Stamm et Schaarschmidt, 1978

Fig. 2A–B, Plate III, 1–4, Plate V, 1–4, Plate VI, 16

Selected references

1962 *Masculostrobus willsii* Townrow, p. 25, text-fig. 4a, c, e, h, pl. 1, figs. e, h, pl. 2, fig. i.

1978 *Willsiostrobus willsii* Grauvogel-Stamm and Schaarschmidt, p. 15.

Localities: Rockhausen, Weiler zum Stein, and Bedheim, Germany

Stratigraphic horizon: Erfurt Formation, Longobardian, late Ladinian

Studied material: MfN: MB.Pb.1983/422a, MB.Pb.2019/273, MB.Pb.2019/274

SMNS: SMNS-P-P001487/88

Description of macroremains: In general, the cones are broadly lanceolate in shape and commonly slightly curved; they are 60–115 mm long and 17–25 mm wide. The cones are sometimes attached to a pedicel. The axis of the cone is 2 mm wide, with perpendicularly attached microsporophylls with a 9 mm long stalk and 2–3 mm long, subtriangular sporophyll heads. The microsporangia are attached to the lower side of the stalk and up to 10–12 mm long and 0.5 mm wide. The microsporophyll heads are subtriangular and 2–3 mm long and wide.

Description of in situ *pollen:* Pollen grains are bisaccate, haploxylonoid. Sacci are semicircular to crescentic in outline, attached proximally in the equatorial region, and overlapping the corpus distally. Only a very narrow cappula is present. A sulcus might be present but obscured by the sacci regularly folding over the cappula. Saccus reticulum is moderately coarse. The corpus is oval (longer than wide) and proximally thickened, with a granulate surface and a bent furrow running along its length. Total length 86–(97.8)–117 μm (n = 13), corpus 61–(69.1)–76 μm (n = 11) × 55–(64.7)–71 μm (n = 3), saccus width 73–(74.7)–76 μm (n = 3).

Discussion: One of the main features of the cones is the curved axis, which hampers precise measurements of cone length.

The pollen grains principally correspond to *Illinites*, but the characteristic mark/furrow is not always recognizable. Those pollen grains rather resemble *Alisporites* or *Voltziaceaesporites*, to which the pollen of *Willsiostrobus willsii* from France have previously been compared (Grauvogel-Stamm and Schaarschmidt, 1979). Cone SMNS-P-P001487/88 only yielded immature pollen, which are therefore not further described.

Willsiostrobus cf. *willsii* (Townrow) Grauvogel-Stamm et Schaarschmidt, 1978

Fig. 2L–M, Plate III, 5, Plate VII, 1–8, Plate IX, 9–10

Localities: Rielingshausen, Germany.

Stratigraphic horizons: Erfurt Formation, Longobardian, late Ladinian.

Studied material: SMNS: SMNS-P-110024.

Description of macroremains: The cone fragment is strongly curved, twisted, and up to 15 mm wide. The axis is 1.2 mm wide, with perpendicularly attached microsporophylls bearing 8 mm long and 1–2 mm wide microsporangia. The sporophyll heads cannot be observed.

Description of in situ *pollen:* Abundant pollen was obtained from entire pollen sacs, but individual grains are for the most part not easily separated and fragile, as they are relatively thin walled. They appear to be slightly immature. Pollen grains are bisaccate, haploxylonoid, without mark or distinct proximal ornamentation. The corpus is approximately circular to slightly elongated oval. The finely reticulated sacci have a narrow offlap from the corpus, are inclined distally and closely attached equatorially. They overlap large parts of the corpus, leaving a narrow cappula, on which a long and narrow lanceolate sulcus can often be seen. Total length 49–(64)–77 μm (n = 16), corpus 38–(50.7)–60 μm (n = 13) × 42–(45)–49 μm (n = 3), saccus width 46–(48.4)–53 μm (n = 5).

Discussion: The cone fragment is not just slightly curved as is typical for *Willsiostrobus willsii*; the cone seems almost to twist on its own axis making measurements of the size impossible. Moreover, the microsporophyll heads cannot be observed in detail even if the microsporangia are preserved very nicely. The width and arrangement of the sporophylls is typical of *W. willsii*, but since some important features are missing such as the microsporophyll heads, a definite assignment is impossible.

The in situ pollen is overall similar to that of *W. rhomboidalis* as described above, as well as *Ruehleostachys pseudarticulatus*, but smaller than both, with few exceptions. It is likewise of the *Alisporites*-type.

Willsiostrobus sp. 1

Fig. 2J–K, Plate II, 10, Plate VI, 13–15

Localities: Bedheim, Germany.

Stratigraphic horizons: Erfurt Formation, Longobardian, late Ladinian.

Studied material: MB.Pb.2008/210.

Description of macroremains: The single poorly preserved cone is about 70 mm long and 15 mm wide with a slightly curved axis. The axis is 15 mm long and 4 mm wide. The sporophylls seem to be arranged helically around the central axis. Each microsporophyll is up to 7 mm long.

Description of in situ *pollen:* Pollen grains are bisaccate, haploxylonoid. Sacci are semi-circular to crescentic in outline, slightly distally inclined, and having a moderately coarse reticulum. Saccus bases are indistinct. The corpus is (sub)circular to elongated oval, with no clear aperture and apparently no taeniae. Total length 59–(82.1)–93 μm (n = 24), corpus 35–(63.8)–76 μm (n = 22) × 49–(61.1)–73 μm (n = 8), saccus width 57–(67)–80 μm (n = 9).

Discussion: The cone is attached to a short axis and has spirally arranged microsporophylls visible by the arrangement of the microsporangia. However, the compression is badly preserved not permitting to understand any details of the microsporophyll arrangement and the cone structure. Thus, only an assignment to the genus *Willsiostrobus* is possible but none at species level. Macromorphologically, it differs from *Willsiostrobus* sp. 2 (see below) because of its reduced cone width and slightly curved shape. We cannot attribute the cone to *Willsiostrobus willsii* because apart from the slightly curved axis, relevant information on the macromorphology of the cone and its microsporophylls cannot be retrieved. The in situ pollen resembles *Klausipollenites* Jansonius, 1962 in sharing the characteristics of being alete and non-taeniate, with the distally inclined sacci not being clearly delimited from the corpus.

Willsiostrobus sp. 2

Fig. 2C–E, Plate III, 6, Plate V, 5–8, Plate IX, 13–16

Localities: Rockhausen, Germany.

Stratigraphic horizons: Erfurt Formation, Longobardian, late Ladinian.

Studied material: MB.Pb.2000/780.

Description of macroremains: The single poorly preserved cone is 62 mm long and 21 mm wide. The axis is 1.5 mm wide. The sporophylls seem arranged helically around the central axis. Each microsporophyll is up to 10 mm long.

Description of in situ *pollen:* In situ pollen grains are abundant, but poorly preserved; almost all obtained pollen grains are damaged (corroded), fragile, or clustered, which hinders observations on individual grains. Nonetheless, it can be observed that the in situ pollen grains are bisaccate, haploxylonoid, with distally inclined and laterally touching (or almost touching) sacci, leaving a narrow cappula with a long and narrow sulcus. The corpus is often faint to invisible, but in some cases well-defined. In the latter case, the corpus looks smooth and conspicuously sulcate, with a rounded rhombic amb and a slightly wavy proximal furrow extending along its length. A secondary ray extends approximately perpendicularly from the longitudinal furrow and has a variable length, reaching up to the equator. Total length 85–(92.5)–101 μm (n = 10), corpus 30–(53.8)–76 μm (n = 14) × 34–(48.6)–71 μm (n = 9), saccus width 70–(77.3)–82 μm (n = 3).

Discussion: The cone fragment is small, and the shape and dimensions of the microsporophyll heads is not visible. Thus, we decided to assign the specimens to the genus *Willsiostrobus* only. The slightly curved axis would support a tentative assignment to the species *Willsiostrobus willsii*. The in situ pollen is comparable to *Illinites*.

Willsiostrobus sp. sensu Forte et al., 2022

Fig. 3C, Plate I, 3, Plate IV, 11–14, Plate IX, 4

Reference: Forte et al., 2022, figs. 10I, 12E, 12F

Localities: Kühwiesenkopf/Monte Prà della Vacca, Italy.

Stratigraphic horizons: Dont Formation, Pelsonian, late Anisian.

Studied material: NMS: PAL 794.

Description of macroremains: The dispersed cone is elongate and slightly curved, 85 mm long and 18 mm wide. The axis is 1.4–2.3 mm wide. The microsporophylls are arranged in a loose helix with a perpendicular attachment angle. The stalk of the microsporophyll is 7–7.5 mm long, the head is rhomboidal with a long, pointed apex, about 3 mm long and up to 3 mm wide. Microsporangia are elongate, attached to the lower side of the microsporophyll stalk, 3–4.5 mm long and 0.5 mm wide.

Description of in situ *pollen: Willsiostrobus* sp. yielded bisaccate, diploxylonoid, multitaeniate (9+ partially discontinuous taeniae) pollen grains, 68–(84.5)–99 μm (n = 17) long, with an oval corpus (41–(55)–69 μm (n = 17) long and 38–(48.9)–60 μm (n = 9) wide), a short monolete aperture, and sacci which are approximately semi-circular in outline and 44–(50.4)–58 μm (n = 9) wide.

Discussion: The cone is an open cone with microsporophylls that do not overlap, differently from all other *Willsiostrobus* cones encountered so far. However, the perpendicular attachment of the microsporophylls, the shape and dimension of the microsporophyll heads agree with the general diagnosis of the genus *Willsiostrobus*. Although the head of the microsporophylls is rhomboidal in shape with a long, pointed apex it cannot be assigned to *Willsiostrobus acuminatus* because assignment to this species would require a smaller cone width and a long, acuminate apex of the microsporophyll heads. *Willsiostrobus ligulatus* also has a smaller cone width, but the sporophyll heads are very similar to those of our specimen. The loose spacing of the microsporophylls makes an assignment to either of the two species impossible.

In situ pollen grains have been previously described from the same material (Forte et al., 2022). The new measurements are extending the size range from earlier reported lengths of 67–89 μm. The appearance of the pollen resembles *Striatoabieites* Sedova, 1956. *Striatoabieites* ex gr. *aytugii* Visscher, 1966 emend. Scheuring, 1970 is known to be present in the dispersed sporomorph assemblages of the Dont Formation (Kustatscher and Roghi, 2006) and may be related to this cone type. Similar multitaeniate (or multistriate) bisaccate pollen grains are commonly associated with seed ferns (e.g., Balme, 1995).

Genus: **Ruehleostachys** Roselt, 1956

Type species: Ruehleostachys pseudarticulatus Roselt, 1956

Ruehleostachys sp. 1

Fig. 3F–H, Plate II, 8, Plate VII, 9–14, Plate IX, 6–8

Localities: Zwingelhausen, Germany.

Stratigraphic horizons: Erfurt Formation, Longobardian, late Ladinian.

Studied material: SMNS: SMNS-P-P001481–1.

Description of macroremains: The dispersed cone is subtriangular, 28 mm long and 18–25 mm wide. The microsporophylls are attached helically in an acute, slightly curved angle. They arise from the axis with an angle of 20–30°, then curve outwards to obtain an angle of about 50°. The axis is 1.5–3 mm wide. The microsporangia are elongate, 6–7 mm long and 0.8–1 mm wide.

Description of in situ *pollen:* Pollen grains are bisaccate, haploxylonoid to slightly diploxylonoid (rarely strongly diploxylonoid/platysaccoid, see Plate VII, 14, Fig. 3H). Sacci are semicircular in outline with a rather coarse, imperfect reticulum. They are distally inclined and may touch laterally. The cappula is narrow and sulcate. Distal folds are present. The corpus is rounded rhombic in polar view and rounded kite-like or diamond-shaped in equatorial view. The proximal side is marked by a granulate surface and a usually wavy (rarely straight) furrow with a central bend. Total length is 87–(102.8)–122 μm (n = 12), corpus 44–(65.4)–78 μm (n = 12) × 42–(69)–81 μm (n = 5), saccus width 61–(76.6)–87 μm (n = 5).

Discussion: The microsporophylls of this specimen are clearly attached at an acute angle and not perpendicularly as is typical for *Willsiostrobus*. The so far only known Triassic male conifer cone characterized by such an attachment of the microsporophylls is *Ruehleostachys*. Unfortunately, the cone fragment is too badly preserved to assign the specimen to any species. The type species *Ruehleostachys pseudarticulatus* has much longer and slender cones. *Ruehleostachys* sp. 1 resembles *Ruehleostachys* sp. 2 in the acute angle of attachment of the microsporophylls, but the cone assigned to the former is more open, shorter and wider than the latter.

Table 3
Overview of discussed dispersed pollen morphogenera that are comparable to voltzialean in situ pollen.

Taxon	Sacci	Corpus	Cappa	Aperture	References
Alisporites Daugherty, 1941 emend. Jansonius 1971	Bisaccate, haploxylonoid	Elongated oval to circular	Not thinkened, distinct from sacci, non-taeniate	Alete	Jansonius and Hills, 1976
Angustisulcites Freudenthal, 1964	Bisaccate, haploxylonoid to diploxylonoid	Circular	Non-taeniate, sometimes punctate or fine reticulate radially	Reduced trilete mark	Freudenthal, 1964
Illinites Kosanke, 1950	Bisaccate, haploxylonoid	Circular to oval	Granulate, non-taeniate	Reduced trilete mark	Klaus, 1964
Klausipollenites Jansonius, 1962	Bisaccate, haploxylonoid, not clearly delimited	Circular to oval	Smooth	Alete	Jansonius and Hills, 1976
Jugasporites Leschik, 1956	Bisaccate, haploxylonoid	Circular to triangular or oval	Smooth around the mark	Monolete, dilete or trilete reduced	Leschik, 1956
Lueckisporites Potonié et Klaus, 1954 emend. Klaus,1963	Bisaccate, diploxylonoid	Circular to oval	Taeniate (at least 2 taeniae)	Monolete	Potonié and Klaus, 1954; Jansonius and Hills, 1976
Lunatisporites Leschik in Kräusel et Leschik, 1955 emend. Bharadwaj, 1962	Bisaccate, diploxylonoid	Oval	Taeniate (at least 4 taeniae)	Monolete	Leschik, 1956; Jansonius and Hills, 1976
Ovalipollis Krutzsch, 1955 emend. Scheuring, 1980	Bisaccate, haploxylonoid, to diploxylonoid, reduced	Elongate oval	Lateral oval tenuitates	Monolete or dilete/ rudimentary trilete	Jansonius and Hills, 1976
Parillinites Scheuring, 1970	Bisaccate, haploxylonoid to diploxylonoid, distal	Circular to oval	Granulate, non-taeniate	Monolete	Scheuring, 1970
*Pityosporites (*Seward, 1914) Potonié et Klaus, 1954	Bisaccate, haploxylonoid	Circular	Smooth	Alete	Potonié and Klaus, 1954
Platysaccus Potonié et Klaus, 1954	Bisaccate, diploxylonoid, large	Subcircular/oval	Non-taeniate	Alete	Potonié and Klaus, 1954
Rimaesporites Leschik, 1956	Bisaccate, haploxylonoid, not clearly delimited	Circular to elongate oval	Smooth, non-taeniate, indistinct	Monolete?	Leschik, 1956
Sahnisporites Bharadwaj, 1954	Bisaccate, diploxylonoid	Elliptical	Smooth	Alete	Bharadwaj, 1954
Staurosaccites Dolby in Dolby et Balme, 1976	Bisaccate, haploxylonoid	Circular to slightly oval	Polar cleft	?	Dolby and Balme, 1976
Striatoabieites Sedova, 1956	Bisaccate, diploxylonoid	Circular to oval	Taeniate (more than 6 taeniae, fine-striated)	Alete	Jansonius and Hills, 1976
Triadispora Klaus, 1964	Bisaccate, haploxylonoid	Circular to rectangular	Smooth	Trilete	Klaus, 1964
Voltziaceaesporites Klaus, 1964	Bisaccate, haploxylonoid	Circular to oval	Thickening, continuous with sacci	Alete	Klaus, 1964

The in situ pollen of *Ruehleostachys* sp. 1 can be attributed to the dispersed genus *Angustisulcites* Freudenthal, 1964 (see Table 2 and discussion under *Ruehleostachys* sp. 2).

Ruehleostachys sp. 2
Fig. 3I–K, Plate II, 9, Plate VII, 15–20, Plate IX, 11–12
Localities: Zwingelhausen, Germany.
Stratigraphic horizons: Erfurt Formation, Longobardian, late Ladinian.
Studied material: SMNS: SMNS-P-P001481-2.

Description of macroremains: The dispersed cone is 56 mm long and 15 mm wide. The microsporophylls are attached helically in an acute angle. They arise at an angle of 30 ° and then curve outward reaching the margin with an angle of 50–60°. They have a slightly spateolate shape and are 3.5–4.6 mm long and 1.5–2 mm wide. The head of the microsporophyll is not clearly visible. Microsporangia are elongate, 3 mm long and 0.3–0.5 mm wide.

Description of in situ *pollen:* Pollen grains are bisaccate, haploxylonoid to slightly diploxylonoid (rarely strongly diploxylonoid/platysaccoid, see Plate VII, 18, Fig. 3K), 84–(99)–126 μm (n = 12) long. Sacci offlap clearly from the corpus, are distally inclined, laterally close, and are 72–(75.6)–83 μm (n = 5) wide. Distal folds are present. The reticulum seems to be moderately coarse but is regularly obscured by crystal imprints. The corpus is rounded rhombic in polar view, measuring 43–(62.9)–77 μm (n = 12) × 58–(64)–71 μm (n = 5), and rounded kite-like or diamond-shaped in equatorial view. The proximal side is marked by a granulate surface and a more or less straight longitudinal furrow with a not always conspicuous perpendicular secondary ray.

Discussion: The assignment to this genus is based on the acute angle of attachment of the microsporophylls. However, an assignment to the type species *Ruehleostachys pseudarticulatus* is impossible since the present cone is much shorter and broader. It resembles *Ruehleostachys* sp. 1 in the acute attachment angle of the microsporophylls, but the sporophylls are arranged more densely. This would be suggestive of an immature cone, in contrast to the fairly developed pollen.

The pollen is referrable to *Angustisulcites*, similar to the in situ pollen of *Ruehleostachys* sp. 1 (SMNS-P-P001481-1) and some diminutive pollen grains from *Willsiostrobus* cf. *cordiformis*. Pollen grains are more diploxylonoid compared to those found in *Willsiostrobus* cf. *cordiformis*, with more distally inclined sacci, and rather triletoid than dilete as in *Ruehleostachys* sp. 1. To some degree, these differences may have been caused by stage of maturity or by preservation.

Genus: **Voltzia** Brongniart, 1828
Type species: Voltzia heterophylla Brongniart, 1828.
Voltzia recubariensis (Massalongo ex De Zigno, 1862) Schenk, 1868 emend. Forte, Kustatscher et Van Konijnenburg-van Cittert, 2022
Fig. 3A–B, Plate I, 1–2, Plate IV, 1–14, Plate IX, 1–3
Selected references
1862 *Araucarites recubariensis* Massalongo ex De Zigno, 1862, p. 21, pl. 6, figs. 1–5.
1868 *Voltzia recubariensis* Massalongo, Schenk, p. 86.
2022 *Voltzia recubariensis* (Massalongo ex De Zigno, 1862) Schenk, 1868, Forte et al., p. 735, figs. 4A–F, 6A–E
Localities: Kühwiesenkopf/Monte Prà della Vacca, Italy
Stratigraphic horizons: Dont Formation, Aegean, early Anisian
Studied material: NMS: PAL 2100, PAL 467, PAL 569, PAL 575, PAL 783, PAL 784, PAL 786, PAL 787, PAL 788, PAL 790

Description of macroremains: The pollen cones are found both dispersed and attached to branches of *Voltzia recubariensis*. The cones are lanceolate, 20–38.5 mm long and 9.5–17 mm wide. The axis is 1.6–4 mm in diameter. Microsporophylls are spirally arranged, and almost perpendicularly attached, although apically the angle of attachment decreases. They are 3.2–6.5 mm long and 2–5.3 mm wide, with a thick distal head, almost rhomboidal in front view with a rounded apex, and

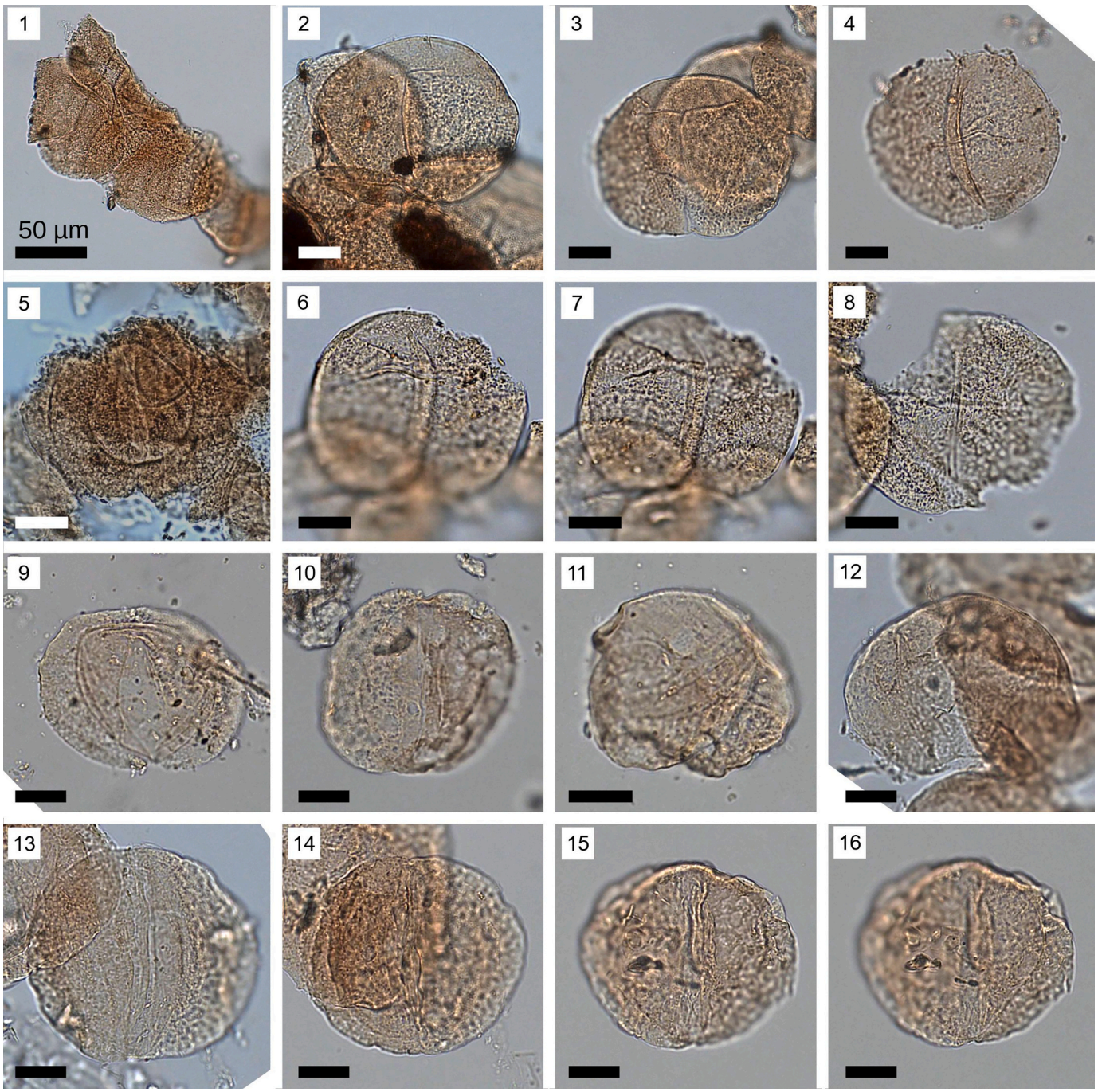

Plate V. In situ pollen from the Ladinian flora of the Erfurt Formation at Rockhausen and Weiler zum Stein in Germany. Scale bars = 20 µm unless otherwise indicated.

1–4. *Willsiostrobus willsii* (Townrow) Grauvogel-Stamm et Schaarschmidt, 1978, Rockhausen.

1. A few unseparated but large pollen grains, MB.Pb.2019/274, sample 1, slide 1.

2–4. MB.Pb.2019/273.

2–3. Pollen grains in equatorial (2, 3) and polar (4) views showing the distally extensive and extremely narrowly arranged sacci. Note also reticulation of the proximal surface (2) and bent mark (4), sample 1, slide 1.

4. Pollen grain in polar view showing a bent mark, sample 3, slide 1.

5–8. Pollen grains of *Willsiostrobus* sp. 2 in polar (5, 8) and equatorial (6, 7) views, Rockhausen, MB.Pb.2000/780, sample 2, slide 1. Note small and clearly delimited corpus in fig. 5 compared to large and indistinct corpus in figs. 6–8. Note as well distally extensive and narrowly arranged sacci in figs. 6–8, and relatively straight mark (8). Grain in fig. 8 is also shown with fluorescence in Plate IX, 13–16.

9–16. Pollen grains of *Willsiostrobus rhomboidalis* (Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978 in polar (9, 10, 13–16) and equatorial (11, 12) views, Weiler zum Stein.

9–11. SMNS-P-P001487/101, sample 3, slide 1.

12–16. SMNS-P-P001487/26, sample 2, slide 1. Note long and narrow sulcus in figs. 13–16.

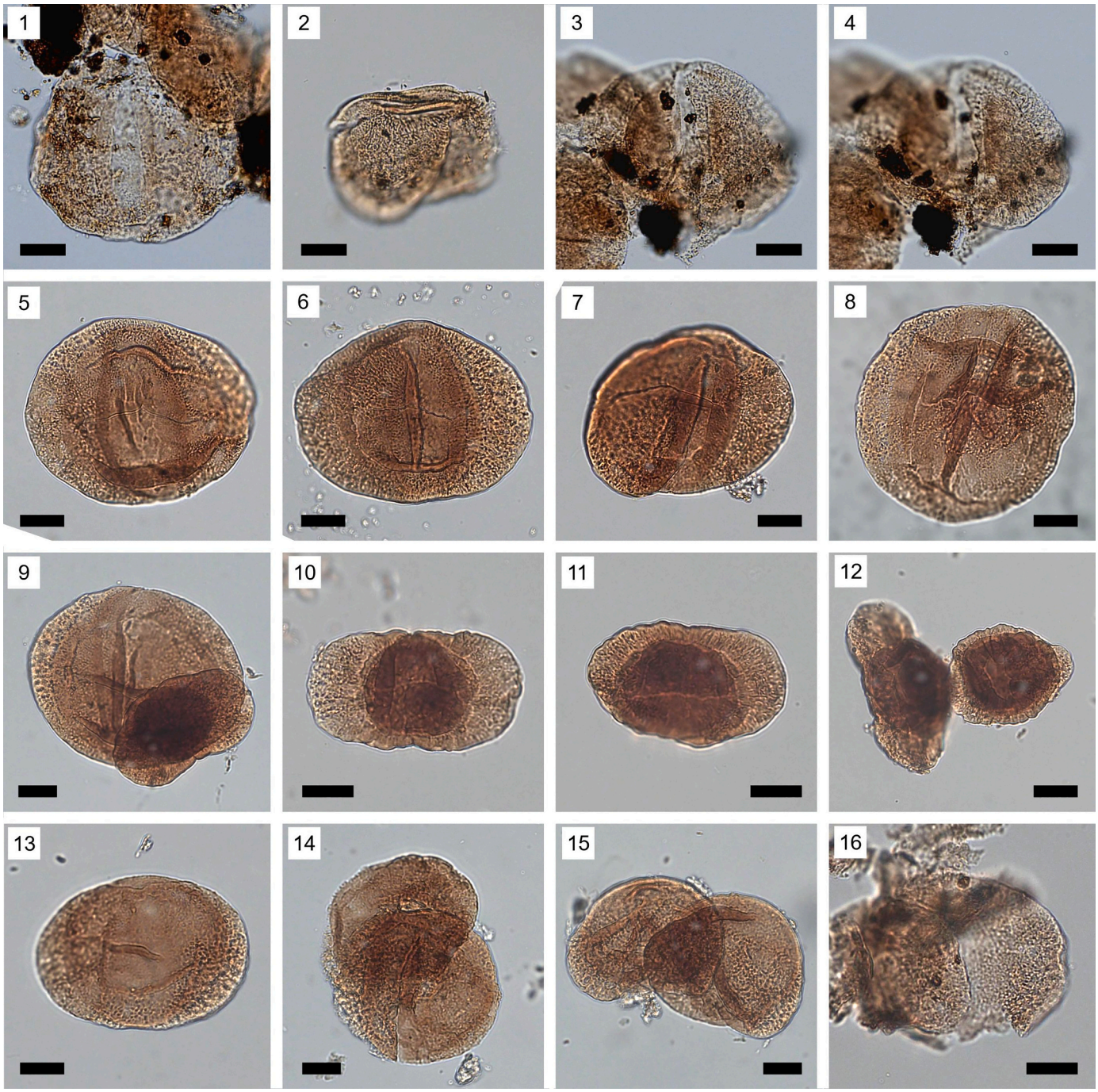

Plate VI. In situ pollen from the Ladinian flora of the Erfurt Formation at Bedheim, Germany. Scale bars = 20 μm.
1–12. Pollen grains of *Willsiostrobus* cf. *cordiformis* (Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978 in polar (1, 3–12) and equatorial (2) views. Note differences in size, color of the corpus, and outline between grains in figs. 1–8 and 10–12, with fig. 9 showing large and small types together.
1–4. MB.Pb.2000/484, sample 2, slide 2. Grain in 3–4 is also shown with fluorescence in Plate IX, 5.
5–12. MB.Pb.2000/471.
5–6, 10, 12. sample 1, slide 1.
7,9, 11. sample 1, slide 2.
8. Sample 3, slide 2.
13–15. Pollen grains of *Willsiostrobus* sp. 1 in Polar (13, 14) and equatorial (15) views, MB.Pb.2008/210, sample 1, slide 2.
16. Imperfectly preserved pollen grain of *Willsiostrobus willsii* (Townrow) Grauvogel-Stamm et Schaarschmidt, 1978, MB.Pb.1983/422a, sample 2, slide 1.

triangular in lateral view with two lobes. Microsporangia are elongate, attached to the lower side of the stalk.

Description of in situ *pollen:* The more well-preserved pollen grains are bisaccate (rarely aberrantly trisaccate in PAL 786, Plate VI, 4), haploxylonoid, and 55–97 μm long, with a circular or oval (longer than wide) central body and two or four taeniae (e.g., NMS PAL 569, 786; figs. 10E, 12A–12D). The sacci have a narrow offlap from and are about as wide as the corpus. A short monolete or triletoid mark is sometimes visible (e.g., NMS PAL 569; fig. 12C). Some pollen grains seem to lack clearly defined taeniae in transmitted light but do show them under fluorescence. In

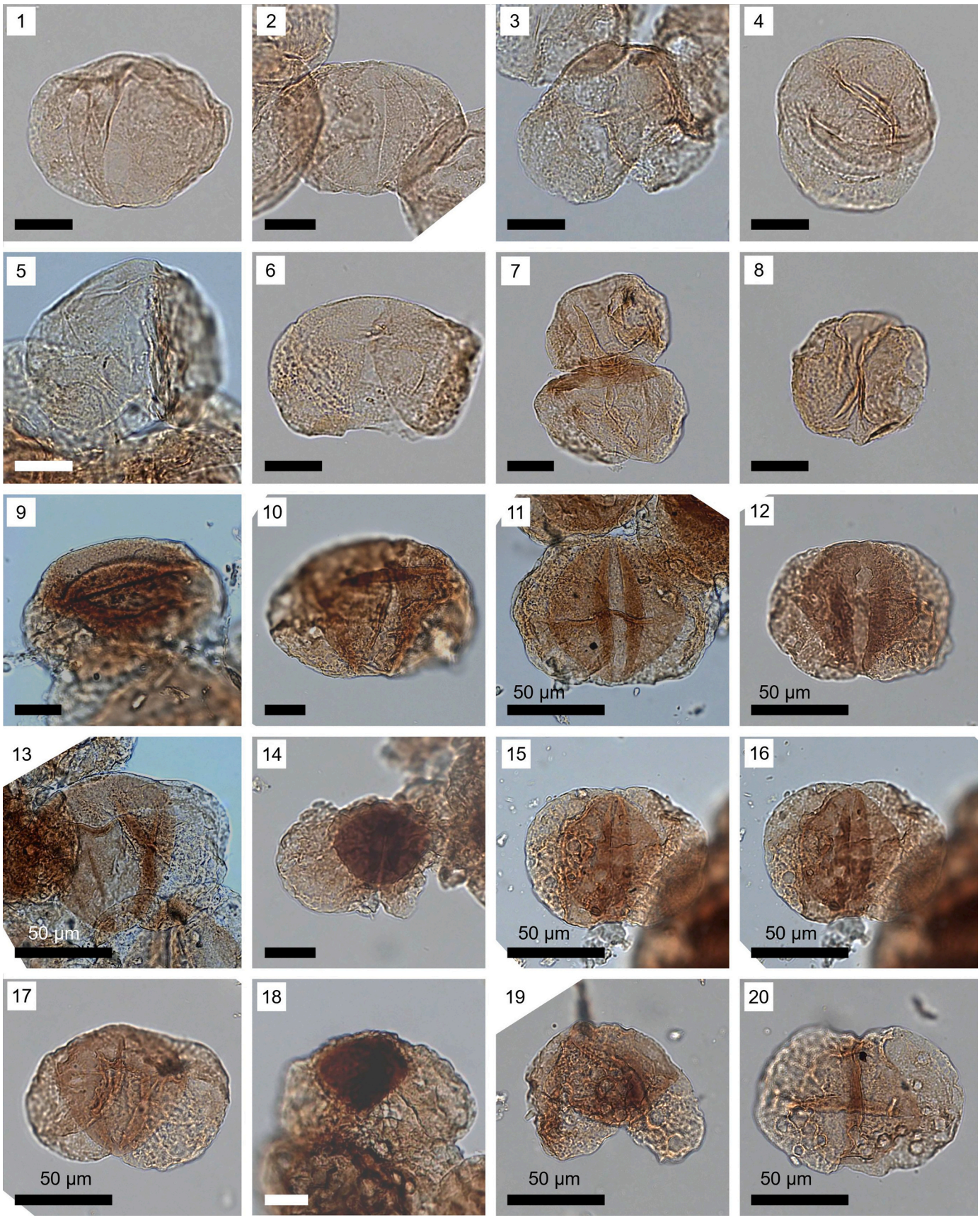

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Plate VII. In situ pollen from the Ladinian flora of the Erfurt Formation at Rielingshausen and Zwingelhausen in Germany. Scale bars = 20 μm unless otherwise indicated.
1–8. Pollen grains of *Willsiostrobus* cf. *willsii* (Townrow) Grauvogel-Stamm et Schaarschmidt, 1978 in polar (1, 2, 8) and equatorial (3–7) views, Rielingshausen, SMNS-P-110024.
1–3. sample 6, slide 2.
4–5. sample 6, slide 1.
6–8. sample 7, slide 4. Grains in figs. 6 and 7 are also shown with fluorescence in Plate IX, 9 and 10, respectively.
9–14. Pollen grains of *Ruehleostachys* sp. 1 in equatorial (9, 13, 14), oblique (10), and polar (11, 12) and equatorial (17–19) views, Zwingelhausen, SMNS-P-P001481–1, sample 2, slide 1.
14. Malformed (platysaccoid) grain with small and dark corpus.
15–20. Pollen grains of *Ruehleostachys* sp. 2 in polar (15, 16, 20) and equatorial (17–19) views, Zwingelhausen, SMNS-P-P001481–2, sample 1, slide 1.
18. Malformed (platysaccoid) grain with small and dark corpus.

specimens with four taeniae, the outer ones are often faint, while in those with two taeniae, these are narrow and usually located centrally, like the central taeniae in grains with four taeniae.

Discussion: The cones resemble those of *Willsiostrobus rhomboidalis* in shape and dimension of the microsporophylls although the cones are distinctly smaller than those of all conifer taxa from the Anisian of France.

The in situ pollen grains with four taeniae belong to *Lunatisporites* Leschik in Kräusel et Leschik, 1955 emend. Bharadwaj, 1962, while those with two taeniae could be referred to *Lueckisporites*. However, *Lueckisporites* normally has broader taeniae, and the specimens in question clearly form a spectrum with examples of *Lunatisporites* with weakly developed outer taeniae. The sometimes observed triletoid mark does not fit the description of these genera but may conceivably be derived from tearing to the side of an originally monolete mark. Where taeniae are not clearly observable, this may be due to immaturity or preservational effect. Both *Lueckisporites* and *Lunatisporites* have been reported from dispersed sporomorph assemblages of the Dont Formation at the Kühwiesenkopf/Monte Prà della Vacca (Kustatscher and Roghi, 2006). At the same locality, similarly taeniate pollen was found in situ in two types of unnamed male cones (Forte et al., 2022). Otherwise, these types of taeniate bisaccate pollen grains are known in situ from the Permian (Clement-Westerhof, 1974). Pollen grains from *Willsiostrobus willsii* and *Rissikia media* (Tenison Woods) Townrow, 1967 have also been compared to *Lunatisporites* (Townrow, 1962, 1967a; Balme, 1995; Traverse, 2007).

4. Results and discussion

4.1. Basic morphotypes

The studied pollen grains (for an overview, see Table 2) are commonly bisaccate, with only a few monosaccate or monosaccoid and rare trisaccate (aberrant grains in *Voltzia recubariensis*, cone PAL 786; Plate IV, 4; see also Section 4.2) variants. They tend to be haploxylonoid or weakly diploxylonoid. All observed variants are protosaccate.

Conifer pollen of the Permian and Triassic can broadly be divided into taeniate and non-taeniate forms, with taeniate ones having distinctly strip-like longitudinal thickenings (= taeniae) on the proximal surface of the corpus. Table 3 lists dispersed pollen genera that are potentially of voltzialean affinity. Most of the pollen in our samples from *Willsiostrobus*-type cones has some degree of proximal thickening, but not usually in the form of distinct taeniae, while pollen with "proper" taeniae were only found in material from the Kühwiesenkopf/Monte Prà della Vacca assemblage (Plate IV, 1–14) and as a rare variant in *Willsiostrobus* cf. *acuminatus* (MB.Pb.2000/252e, Plate VIII, 1–3). Even though pollen of this type is common in dispersed assemblages from the Triassic, in situ findings are otherwise limited to the Permian (Forte et al., 2022).

Most of the taeniate in situ pollen can be compared to *Lunatisporites* (e.g., Plate IX, 1–2). The same type of pollen is also often referred to *Taeniaesporites* Leschik, 1956. Both names are commonly treated as synonymous, with *Lunatisporites* having priority (Bharadwaj, 1962). *Lunatisporites* has typically four taeniae, but occasionally these are partially or completely subdivided. Pollen with only two taeniae are commonly assigned to *Lueckisporites*. *Lueckisporites*-type pollen does occur in our material but appears to be merely a variant of the *Lunatisporites*-type (Plate IX, 3) where the outer taeniae are not developed or of the *Illinites*-type with a straight mark and a proximal thickening with unusually clear delimitations (Plate VIII, 1–3).

Multitaeniate (or multistriate) pollen grains in *Willsiostrobus* sp. sensu Forte et al., 2022 might be derived from *Lunatisporites*-type pollen as well, considering that the latter can have taeniae with subdividing grooves, which can also be seen in some specimens of *Voltzia recubariensis* from the same assemblage of the Kühwiesenkopf/Monte Prà della Vacca. The pollen grains from *Willsiostrobus* sp. sensu Forte, 2022 however do not show the central gap between taeniae that is characteristic of *Lunatisporites*, which may be due in part to imperfect preservation. They superficially resemble *Protohaploxypinus* Samoilovitch, 1953, *Striatites* Pant, 1955, or *Striatoabieites* Sedova, 1956 – forms that are more commonly associated with seed ferns instead of conifers (e.g, Balme, 1995), but a few specimens were also reported attached to *Voltziopsis wolganensis* Townrow, 1967b (Townrow, 1967b). The presence of a monolete mark, which is most clearly seen using fluorescence (Plate IX, 4) fits with *Striatoabieites*.

Well-defined, but highly variably (see 4.2) pollen corresponding to *Illinites* were found in *Willsiostrobus* cf. *cordiformis* (Plates VI, 5–12, VIII). The pollen of *Willsiostrobus willsii* in our study also for the most part aligns with *Illinites*, but often appears alete (possibly due to poor preservation), which corresponds to previous descriptions (e.g., Grauvogel-Stamm and Schaarschmidt, 1979). Similarly, pollen of *W. rhomboidalis* usually appears to be alete, but a faint mark has been observed occasionally (Plate V, 10, 16). Pollen of *W. ligulatus* and *W. acuminatus* may belong to this category as well, but in our samples were too poorly preserved for certainty. Previously, pollen of *W. acuminatus* has been described as belonging to *Illinites* or *Parillinites* Scheuring, 1970 (e.g., Grauvogel-Stamm and Grauvogel, 1973; Balme, 1995), while descriptions of *W. ligulatus* were inconclusive (Taylor and Grauvogel-Stamm, 1995). *Parillinites* differs from *Illinites* in having distally displaced (subequatorial) saccus attachments, which has not been observed in our material. Specimens of the *Illinites*-type with a straighter furrow in *Willsiostrobus* cf. *cordiformis* (e.g., Plate VI, 9) and *Willsiostrobus* sp. 2 (Plate V, 8) can also superficially resemble *Ovalipollis* Krutzsch, 1955 emend. Scheuring, 1980 or *Staurosaccites* Dolby in Dolby et Balme, 1976. *Ovalipollis* is marked by two oval, proximal tenuitates, whereas in *Staurosaccites* both the cappa and saccus exine are characteristically columellate. Apart from *W. willsii* and *W. rhomboidalis pro parte*, non-taeniate alete pollen that are tentatively comparable to *Alisporites* were observed in *Willsiostrobus* cf. *willsii* and *W. acuminatus*, while at least some of the pollen of *W. ligulatus* (Plate IV, 20) resembles *Voltziaceaesporites*, and those of *Willsiostrobus* sp. 1 are more aligned with *Klausipollenites*. Among these three types, *Alisporites* has a distinct separation of corpus and sacci, while in *Klausipollenites* the saccus attachment is not clearly delimited, and in *Voltziaceaesporites* the sacci extend into a thickening across the cappa.

Ruehleostachys sp. 1 and *Ruehleostachys* sp. 2 yielded *Angustisulcites*-

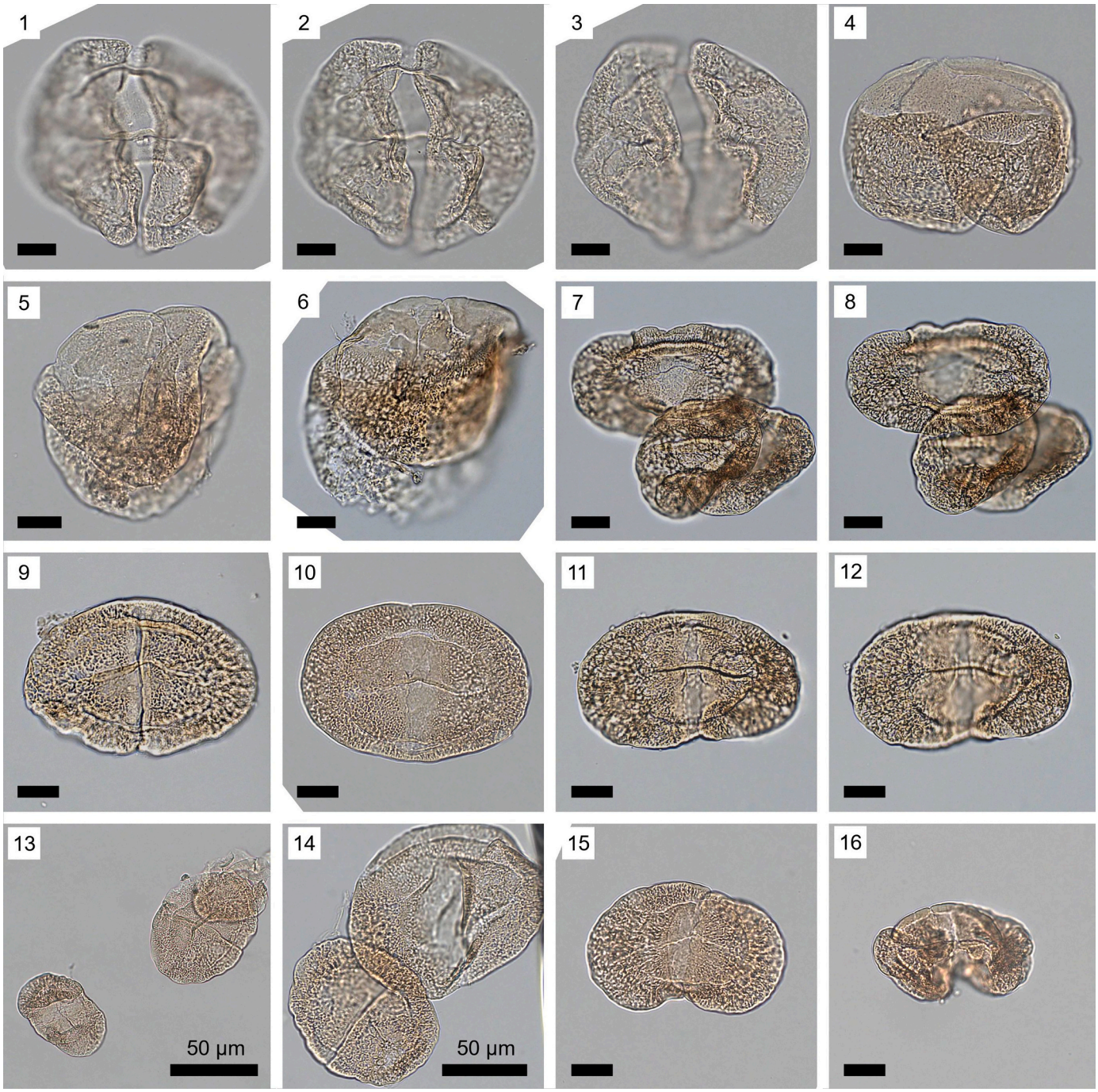

Plate VIII. In situ pollen from the Ladinian flora of the Erfurt Formation at Thale in Germany. Scale bars = 20 µm unless otherwise indicated.
1–6. Pollen grains of *Willsiostrobus* cf. *acuminatus* (Grauvogel-Stamm et Grauvogel) Grauvogel-Stamm et Schaarschmidt, 1978 in polar (1–3) and equatorial (4–6) views, MB.Pb.2000/252e.
1–3. *Lueckisporites*-type pollen grain with two distinct taeniae, sample 2, slide 1.
4–6. Pollen grains showing the pronounced proximal thickening and longitudinal furrow, sample 1, slide 1.
7–16. Pollen grains of *Willsiostrobus* cf. *cordiformis* (Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978. Note differences in total size, as well as relative sizes of sacci and corpus, with fig. 13 showing a relatively small grain next to a regular one, while fig. 14 shows a regular grain next to an unusually large one.
7–8. MB.Pb.2000/252b, sample 1, slide 1.
9–16. MB.Pb.1983/424.
9, 11–12. sample 1, slide 1.
10. Sample 3, slide 1.
13. Sample 2, slide 1.
14–16. sample 3, slide 2.
15–16. Pollen grains with small corpus and aberrant saccus development.

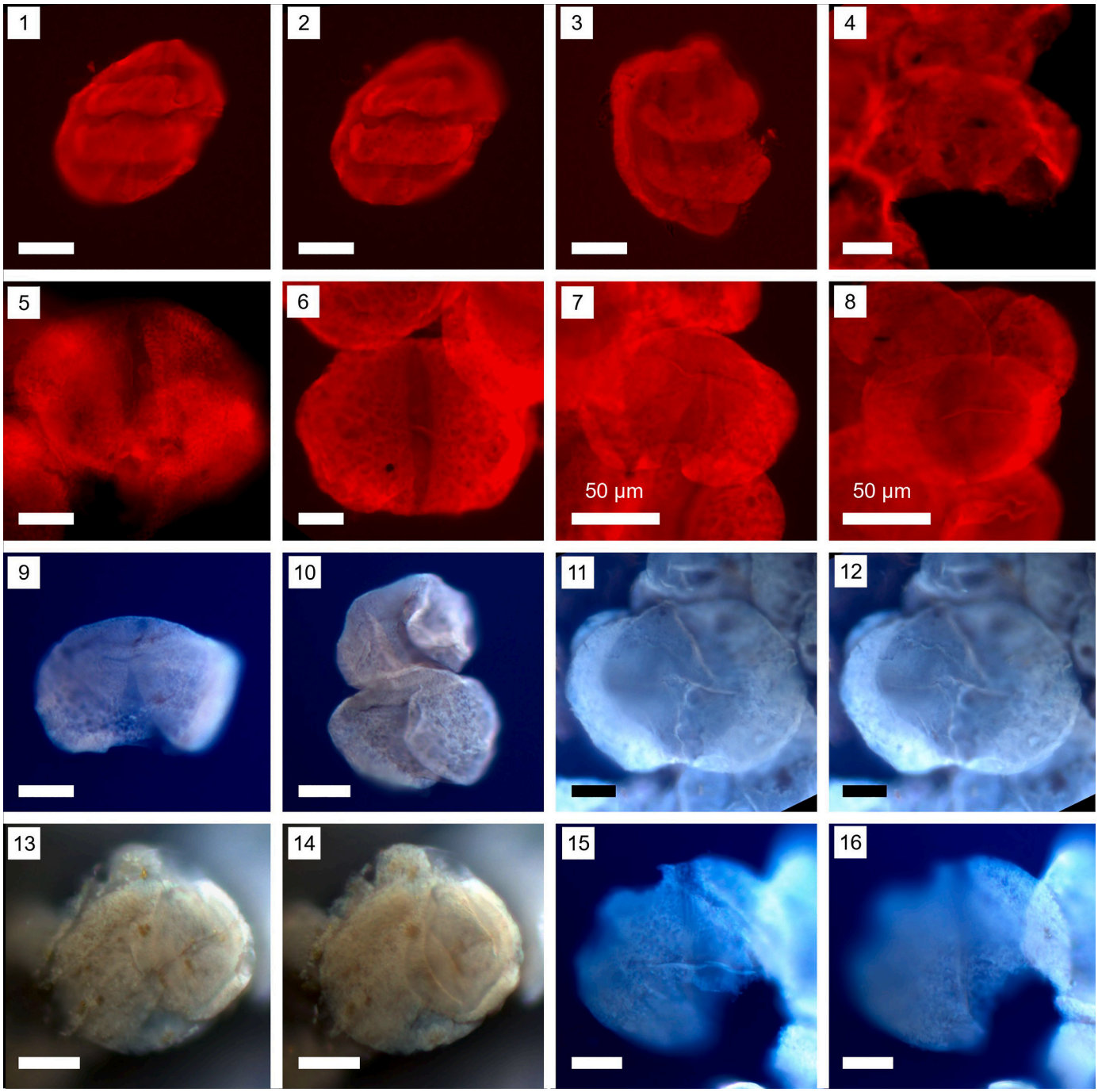

Plate IX. Fluorescence images of in situ conifer pollen. Images were taken with Leica TX2 (figs. 1–8) and I3 (figs. 9–16) filter cubes. Scale bars = 20 µm unless otherwise indicated.

1–3. *Voltzia recubariensis* (Massalongo ex De Zigno, 1862) Schenk, 1868 emend. Forte, Kustatscher et Van Konijnenburg-van Cittert, 2022, Kühwiesenkopf/Monte Prà della Vacca, PAL 2100, sample 2, slide 1.

1–2. Pollen grain with four taeniae, same grain as in Plate IV, 8.

3. Very narrow pollen grain with two taeniae.

4. Multitaeniate pollen grain of *Willsiostrobus* sp. sensu Forte et al., 2022, note proximal aperture, Kühwiesenkopf/Monte Prà della Vacca, PAL 794, sample 1, slide 2.

5. Pollen grain of *Willsiostrobus* cf. *cordiformis* (Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978 showing a prominent sulcus, same grain as in Plate VI, 3–4, Bedheim, MB.Pb.2000/484, sample 2, slide 2.

6–8. Pollen grains of *Ruehleostachys* sp. 1 in distal (6), equatorial (7), and proximal (8) views, Zwingelhausen, SMNS-P-P001481–1, sample 2, slide 1.

9–10. Pollen grains of *Willsiostrobus* cf. *willsii* (Townrow) Grauvogel-Stamm et Schaarschmidt, 1978 in equatorial view, same grains as in Plate VII, 6 and 7, respectively, Rielingshausen, SMNS-P-110024, sample 7, slide 4.

11–12. Pollen grain of *Ruehleostachys* sp. 2 in proximal view, Zwingelhausen, SMNS-P-P001481–2, sample 2, slide 1.

13–16. *Willsiostrobus* sp. 2, Rockhausen, MB.Pb.2000/780, sample 2, slide 1.

13–14. Pollen grain with small and conspicuous corpus in oblique view.

15–16. Pollen grain with large and faint corpus, which is nevertheless indicated by a visible longitudinal furrow or mark (15). Same grain as in Plate V, 8.

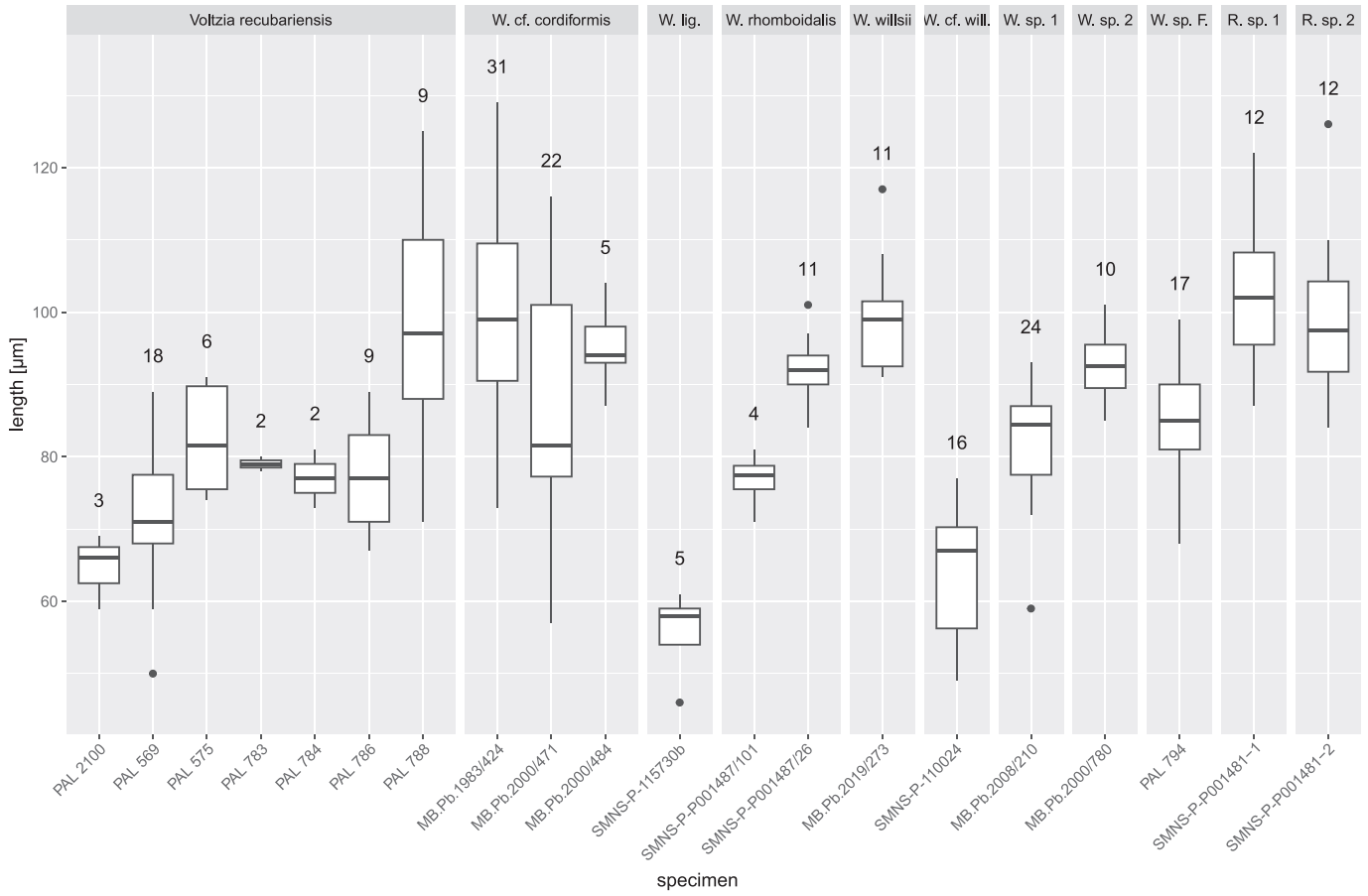

Fig. 4. Size distribution (total length) of in situ pollen grains per specimen. Specimens with only one measured pollen grain are excluded. W. = *Willsiostrobus*, lig. = *ligulatus*, will. = *willsii*, F. = sensu Forte et al., 2022, R. = *Ruehleostachys*.

type pollen, which share some similarity with *Illinites*, but is distinctly diploxylonoid. Some forms with a diminutive corpus and oversized sacci (Plate VII, 14, 18) even approach *Platysaccus*.

A pollen type that is known from several taxa of the Voltziales in the Grès à Voltzia but was not observed in our samples is *Triadispora* Klaus, 1964 (see Grauvogel-Stamm, 1978). This type consists of non-taeniate bisaccates with a (short) trilete mark. Cones of the macrofossil taxa in question were sampled but unfortunately did not yield identifiable pollen material.

Willsiostrobus hexasacciphorus Grauvogel-Stamm et Álvarez-Ramis, 1996 is unusual for having hexasaccate pollen corresponding to *Stellapollenites thiergartii* (Mädler) Clement-Westerhof et al., 1974 or *Hexasaccites muelleri* Reinhardt in Reinhardt et Schmitz, 1965 (Grauvogel-Stamm and Álvarez-Ramis, 1996). This is in fact diagnostic (and eponymous) for the taxon and was not observed in any of the cones studied here.

4.2. Malformations

Common deviations from the usual morphologies observed in the pollen grains relate to reduced sizes of the corpus or the sacci. A common occurrence is also a slight to considerable asymmetry between the sacci. To some degree this overlaps with normal variation, but when sacci are strongly unequal in the same grain, this is considered a malformation (see Plate VIII, 15). Due to the fact that the grains are often obliquely compressed, it is not always apparent whether the sacci are equal or unequal. It is known that bisaccate conifer pollen can have other saccus-related malformations, such as trisaccate and tetrasaccate conditions or fused sacci (Benca et al., 2018), but apart from a few trisaccate grains (Plate IV, 4) in one cone of *Voltzia recubariensis* these were not observed in our samples. Malformed grains are presumably rare in the studied assemblages because the environmental settings were relatively undisturbed, but they could also be hidden in pollen sac contents that did not separate well during maceration. Permanently unseparated pollen grains in the form of dyads, triads or tetrads are another category of malformations known from dispersed assemblages and extant plants (Benca et al., 2018), but fossilized examples would be particularly difficult to identify in situ, due to the fact that in situ pollen grains were rarely at the dispersal stage before burial and thus natural separation would not have occurred.

An especially noteworthy type of malformation that is present in some cones from the Ladinian Erfurt Formation are pollen grains with a diminutive corpus (Plates VI, 9–12, VII, 14, 18). These can appear perfectly well-developed, unless compared to other grains from the same cone or from the same age. This is most obvious in cone MB.Pb.2000/471 (assigned to *Willsiostrobus* cf. *cordiformis*), which produced both normal pollen grains and those with a diminutive corpus (and consequently an overall smaller size) in high numbers, with the latter being dominant. At first glance, they have very different appearances; one type is relatively large and haploxylonoid with a relatively narrow saccus offlap, with a broad and transparent corpus, the other small, with a comparatively large saccus offlap, sometimes slightly diploxylonoid, with a compact and dark corpus. However, both types occur in clumps with each other, showing that they do in fact belong together. Similar cases are observed in other cones, but much more rarely and often less pronounced. Cones with high amounts of diminutive grains are all assigned to *Willsiostrobus* cf. *cordiformis*. Two cones of *Ruehleostachys* yielded rare but conspicuous grains with a diminutive corpus and oversized sacci (Plate VII, 14, 18) that appear comparable to the genus *Platysaccus*. The differences between the larger and smaller pollen grains

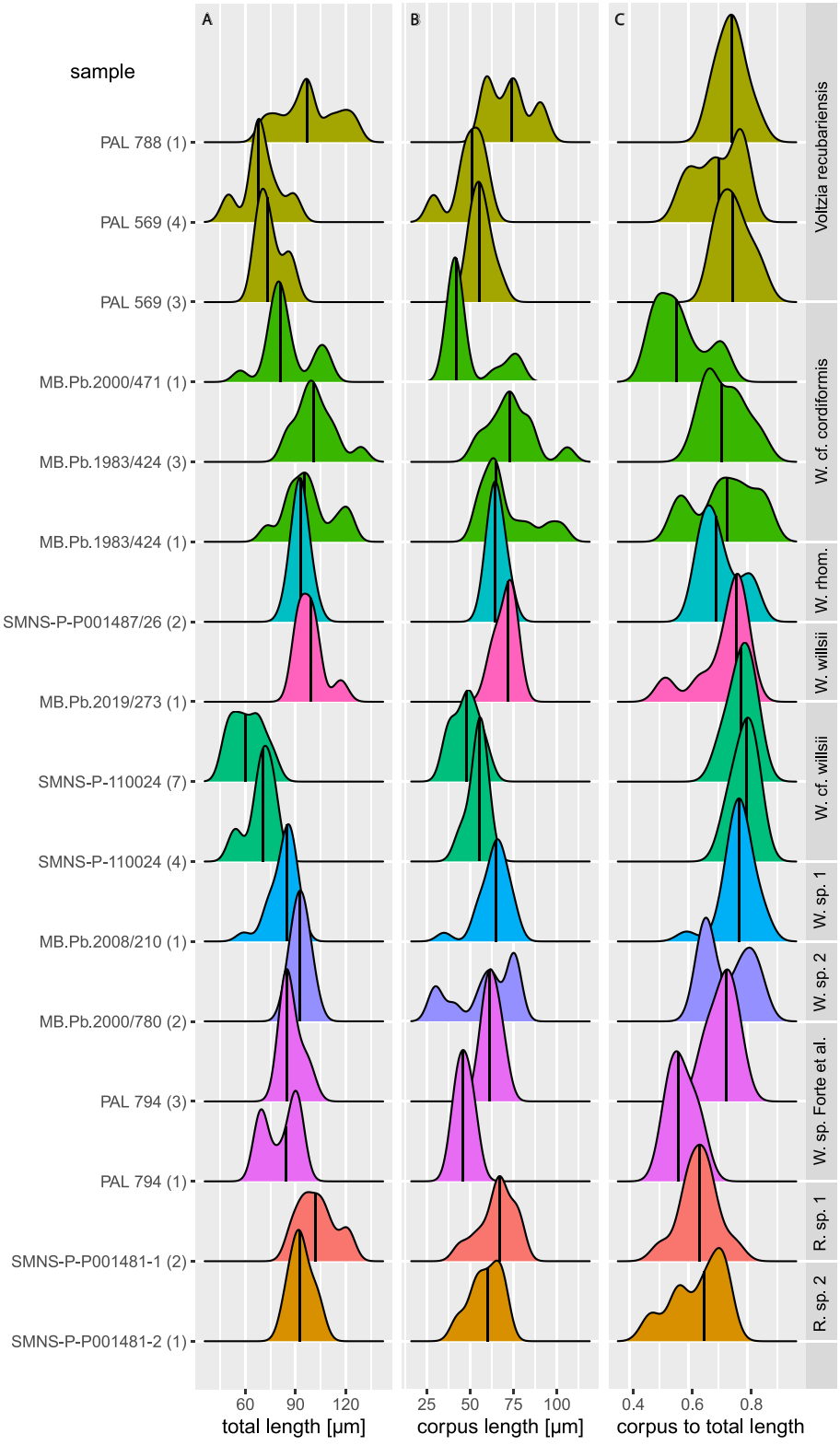

Fig. 5. Size distribution (total length) of in situ pollen grains per sample. Only samples with six or more measured grains are shown. A. Total length in µm. B. Corpus length in µm. C. Corpus length to total length ratio. W. = *Willsiostrobus*, rhom. = *rhomboidalis*, R. = *Ruehleostachys*.

all but assure that they would be identified differently in dispersed assemblages. When Klaus (1964) erected *Illinites kosankei* Klaus, 1964 and *I. melanocorpus* Klaus, 1964, he speculated that the latter might be a *Platysaccus* stage of the former. The main difference between the two species is that *I. melanocorpus* has a smaller and darker corpus, like what we observed in our material, which supports Klaus' conjecture. It is not clear whether the small grains were viable. As mentioned, they appear well-developed, and in fact, in their sizes and the constitution of the corpus, they appear similar to the more „primitive"conifer pollen types of the Permian and Anisian (such as in the Dont Formation, see Plate IV, 1–14). They could thus be considered atavistic. The co-occurrence of larger *Illinites*-type pollen and high numbers of grains with a diminutive

corpus was also observed in one specific cone of *Masculostrobus* (= *Willsiostrobus*) *willsii* by Grauvogel-Stamm (1972). She cited Van Campo-Duplan (1950) for the theory that this phenomenon could indicate hybridisation.

In addition to pollen grains with a diminutive corpus, the opposite has also been observed, although more rarely; pollen grains with an unusually large corpus (Plate VIII, 14) even occur alongside those with an unusually small one, indicating that the cause may be a general disturbance of the corpus growth regulation. Pollen grain size in general is often assumed to be related to ploidy levels. In this context, different sizes can appear together in one plant due to meiotic errors causing the production of gametes with unreduced genomes and consequently developing into unusually large pollen grains. This has been demonstrated to occur in extant conifers (Pichot and El Maâtaoui, 2000) and has been proposed as an explanation for unequal sizes in *Classopollis* at the Triassic–Jurassic boundary (Kürschner et al., 2013). Pollen with ploidy-related size differences could furthermore be the product of plants with odd ploidy levels due to gametes having partly odd and even ploidy levels – e.g., a triploid plant producing haploid and diploid pollen. However, experimental data from angiosperms on such cases are not conclusive (Sanders, 2021).

Conifer pollen evidently show various kinds of malformations, but the range of variations seen in any single macrofossil specimen is more limited. It is conceivable that the specific mix can indicate different causes, such as hybridisation or environmental stress. Experimental results regarding malformations in modern conifer pollen also suggest the existence of such a signal (Benca et al., 2022).

4.3. Pollen sizes

The studied pollen grains range between 46 μm and 129 μm in length (total length), with a mean of 87 μm. The variation can be almost equally large within a species (e.g., *Voltzia recubariensis*, see Fig. 4). Individual samples tend to yield grains with a more constraint size range, but a considerable variation has been observed in several cases. These involve especially deviations of the corpus size. As mentioned above, relatively common are the co-occurrences of pollen grains with smaller and larger corpi, respectively, and a correspondingly different ratio of corpus length to total length, as the sacci are often not proportional to the size of the corpus. A bimodal or multimodal distribution can be seen in corpus length, total length, and corpus to total length ratio in some samples (Fig. 5), evidencing that these are not simple outliers. If found ex situ, such rather consistently distinct proportions would reasonably support a taxonomic distinction.

Other potentially informative allometric ratios are total length to total width and saccus width to corpus width, but width measurements were often affected by slight rotations of the pollen grains and consequently less well documented in our data. Grauvogel-Stamm (1969a) found total length and the corpus length to total length ratio to be the most informative for the separation of populations. In our material, the overlap in distributions on the one hand and the spread of values within samples and species suggest that separations based on these values can only be tentative.

Our values are comparable to most previously published sizes for voltzialean in situ pollen. However, smaller forms have been reported as well, with some of the pollen of *Darneya peltata* Schaarschmidt et Maubeuge, 1969 and *Sertostrobus laxus* Grauvogel-Stamm, 1969a being as small as 30 μm (Grauvogel-Stamm, 1969a; Schaarschmidt and Maubeuge, 1969). These may not be representative, as the reported sizes can vary significantly between publications (comp. Schaarschmidt and Maubeuge, 1969 and Grauvogel-Stamm, 1978 for *Darneya peltata*). Our findings confirm that individual samples rarely capture the size variance of a species (Fig. 4).

5. Conclusions

The in situ pollen from male cones of Voltziales from the Middle and Upper Triassic of Europe display a remarkable variety. The morphological spectrum ranges from taeniate forms reminiscent of Permian conifers to those marked by conspicuous apertures like in *Illinites* and *Angustisulcites* and extending to alete forms resembling *Alisporites*, *Voltziaceaesporites*, or *Klausipollenites*. The specific pollen morphologies are not clearly linked to specific macrofossil taxa. The genus *Willsiostrobus* encompasses cones that yielded almost the entire range of pollen morphologies documented herein. Even on the level of cone species, we occasionally found in situ pollen that differs from previous descriptions.

To some degree, these differences can be attributed to poor preservation or immaturity, but our findings confirm that intraspecific variability needs to be taken into account, both for the description of in situ pollen and for the comparison with dispersed material. Individual samples rarely show the range of possible variations adequately. Thus, a broad sampling strategy is recommended.

Malformations in particular appear to be normally rare, but when present these are characterized by morphologically distinct pollen populations that would warrant separate species or even genus assignments in disperse assemblages. These patterns, evident in a bimodal distribution of corpus size, among others, might even be useful for tracking the causes of the malformations and consequently provide information on hybridisation events or environmental disturbances not only through their frequency.

Declaration of competing interest

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

Data availability

Measurements of the studied pollen grains are available as supplementary data.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2024.105077.

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