

CONIFER CONE AND DWARF SHOOT DIVERSITY IN THE ANISIAN (MIDDLE TRIASSIC) OF KÜHWIESENKOPF/MONTE PRÀ DELLA VACCA (DOLOMITES, NORTHEASTERN ITALY)

Giuseppa Forte,^{1,*} Evelyn Kustatscher,^{2,*†} Hendrik Nowak,^{3,*} and Johanna H.A. Van Konijnenburg-van Cittert^{4,‡}

*Museum of Nature South Tyrol, Bindergasse/Via Bottai 1, 39100 Bozen/Bolzano, Italy; †Paleontology and Geobiology, Department of Earth and Environmental Sciences, Ludwig-Maximilians-Universität München, Richard-Wagner-Straße 10, 80333 München, Germany, and Bayerische Staatssammlung für Paläontologie und Geologie, Staatliche Naturwissenschaftliche Sammlungen Bayerns, Richard-Wagner-Straße 10, 80333 München, Germany; and ‡Laboratory of Palaeobotany and Palynology, Vening Meinesz Building A, Princetonlaan 8A, 3584 CB Utrecht, The Netherlands, and Naturalis Biodiversity Center, PO Box 9517, 2300 RA Leiden, The Netherlands

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Premise of research. The diversity of conifers from Kühwiesenkopf/Monte Prà della Vacca has been inferred previously on the basis of foliate branches/shoots and epidermal morphology. In this article we provide the description of the reproductive organs, which reveal a variety of forms, new morphologies and new taxa, and a comparison with other Permian–Triassic taxa, improving the knowledge of Triassic conifers.

Methodology. The macromorphology, cuticles, and in situ pollen of the reproductive organs are described, and the macromorphological features are compared with those of other Permian–Triassic taxa.

Pivotal results. The macro- and micromorphological analyses of the conifer reproductive organs of Kühwiesenkopf/Monte Prà della Vacca allow us to emend previously known taxa (i.e., *Voltzia heterophylla*, *V. walchiaeformis*, *V. recubariensis*, *Pseudovoltzia edithae*) and to describe new ones (i.e., cf. *Voltzia* sp. 1, *Sidashia tridentata*), providing in some cases almost complete whole-plant reconstructions. The macromorphological comparison of the Kühwiesenkopf/Monte Prà della Vacca taxa with other Permian–Triassic ones highlights the transitional character of some of them, especially *P. edithae*. The finding of amber anatomically connected to a *V. walchiaeformis* seed cone evidences the diversity of the botanical origins of the Anisian amber.

Conclusions. The reproductive organs of the conifers of Kühwiesenkopf/Monte Prà della Vacca show in their morphology a mixture of characters typical of the early Permian to the Late Triassic Voltziales. Their study improves our knowledge of the reproductive biology of Anisian conifers and confirms the pivotal role of the “transitional” Triassic Voltziales that gave rise to modern groups of conifers.

Keywords: seed cones, polliferous cones, fertile organs, in situ pollen, amber.

Introduction

The long history of conifers started more than 300 million years ago in the late Carboniferous (e.g., Rothwell et al. 1997; Falcon-Lang et al. 2009; Plotnick et al. 2009; Taylor et al. 2009). From the Permian onward, they became one of the most diverse and important groups of seed plants (e.g., Miller 1982; Anderson et al. 2007; Hedges and Kumar 2009), although it appears that the early Mesozoic represents the most crucial time in the evolutionary history of conifers. Some authors argue that

the extant conifer lineage of Podocarpaceae originated before the end-Permian mass extinction (e.g., Blumenkemper et al. 2018). The major radiation started during the Triassic, with the origination of several families such as Araucariaceae, Taxaceae, Taxodiaceae, Cupressaceae, and Pinaceae (e.g., Miller 1982; Archibald 1995; Farjon 2005, 2008; Rothwell et al. 2005, 2012; Stockey et al. 2005; Anderson et al. 2007; Axsmith et al. 2008; Eckenwalder 2009; Escapa 2009; Hedges and Kumar 2009; Williams 2009; Escapa et al. 2010, 2011; Escapa and Catalano 2013; Contreras et al. 2019).

One of the challenges regarding the origin of modern conifer clades is to clarify the diversity and relationships of early Mesozoic conifers such as the Triassic voltzian conifers, which have been considered a transitional group and morphologically intermediate between the Paleozoic conifers and their modern descendants (e.g., Miller 1977, 1999; Grauvogel-Stamm 1978; Vischer et al. 1986; Clement-Westerhof 1987, 1988; Mapes and Rothwell 1991; Axsmith and Taylor 1997; Axsmith et al.

¹ Author for correspondence; email: giusy.forte@naturmuseum.it.

² Email: evelyn.kustatscher@naturmuseum.it.

³ Email: hendrik.nowak@naturmuseum.it.

⁴ Email: j.h.a.vankonijnenburg@uu.nl.

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1998; Rothwell et al. 2005, 2011; Escapa et al. 2010; Herrera et al. 2015). During the Triassic voltzian conifers were an important and dominant group (Escapa et al. 2010, 2011), although their fossil record is still rather incomplete, especially during the Early–Middle Triassic. This fossil record consists predominantly of vegetative foliate shoots and dispersed reproductive organs (e.g., Grauvogel-Stamm 1969, 1978; Forte et al. 2021 and references therein), which are not sufficient to reconstruct the systematic relationships of different taxa.

The flora of Kühwiesenkopf/Monte Prà della Vacca (Dolomites, northeastern Italy) is one of the best-preserved and well-documented Pelsonian (Anisian, Middle Triassic) floras (Broglia Loriga et al. 2002; Kustatscher 2004; Posenato et al. 2004; Kustatscher and Roghi 2006; Kustatscher et al. 2006, 2007, 2010a, 2010b; Van Konijnenburg-van Cittert et al. 2006; Forte et al. 2021, 2022). Recent studies of vegetative shoot fragments (i.e., foliate branches, shoots, stems, and well-preserved cuticles) revealed remarkable conifer richness and diversity, with the presence of a mixture of typically Anisian (i.e., *Voltzia walchiaeformis* and *V. recubariensis*) and Early–Middle Triassic (i.e., *Pelourdea vogesiaca*, *Albertia* cf. *latifolia*, and *V. heterophylla*) taxa, as well as a transitional form (*V. edithae*) with morphological characters common to both early Permian and Middle–Late Triassic taxa (Forte et al. 2021). Moreover, amber was found both as dispersed droplets and associated with *V. recubariensis*, the latter representing the primary resin-producing plant during the Anisian in the area of the southern Alps (Forte et al. 2022).

The aim of this article is to increase our understanding of the morphology and biology of Anisian conifers from Kühwiesenkopf/Monte Prà della Vacca and provide a further step toward whole-plant reconstructions of the various Middle Triassic voltzian conifer species. This is possible thanks to a detailed macro- and micromorphological study of the reproductive organs (i.e., seed and polliniferous cones, dwarf shoot cuticles, and in situ pollen). A comparison of the reproductive organs from Kühwiesenkopf/Monte Prà della Vacca with other early Permian to Middle–Late Triassic taxa not only fills a gap in the Middle Triassic fossil conifer record but also permits us to obtain a more complete picture of the evolution of the voltzian reproductive organs during the Early–Middle Triassic, an important time interval in the evolution of this group.

Material and Methods

The first discovery of plant fossils reported from the Anisian fossil locality of Kühwiesenkopf/Monte Prà della Vacca (fig. 1), in the Dolomites, dates to the second half of the twentieth century (Bechstädt and Brandner 1970). The rich fossiliferous level is part of the middle–late Pelsonian hemipelagic carbonate-terrigenous sediments of the Dont Formation, deposited in a marginal marine environment (e.g., Tintori et al. 2001, 2016; Broglia Loriga et al. 2002; Fugagnoli and Posenato 2004; Posenato et al. 2004; Kustatscher and Roghi 2006; Kustatscher et al. 2006, 2007, 2010a, 2010b; Van Konijnenburg-van Cittert et al. 2006). In the terrestrial domain, heavy storm events triggered submarine flows within the marine basin, causing the rapid burial of terrestrial and marine organisms such as brachiopods, bivalves, fish, ammonoids, a small terrestrial reptile, and abundant plant remains (e.g., Tintori et al. 2001, 2016; Broglia Loriga et al. 2002; Renesto and Posenato 2002; Posenato

et al. 2004; Kustatscher et al. 2006, 2007, 2010a, 2010b; Van Konijnenburg-van Cittert et al. 2006; Renesto and Bernardi 2014; Simões et al. 2018a, 2018b). The fossiliferous level is ca. 1 m thick and crops out about 75 m above the base of the Dont Formation (e.g., Tintori et al. 2001; Broglia Loriga et al. 2002; Kustatscher et al. 2010a; fig. 1). Twenty-nine taxa of lycophytes (4 taxa), sphenophytes (3 taxa), ferns (12 taxa), seed ferns (4 taxa), and cycadophytes (6 taxa) have been described so far in the plant fossil assemblage (e.g., Kustatscher et al. 2006, 2007, 2010a, 2010b; Van Konijnenburg-van Cittert et al. 2006; Forte et al. 2021). The conifers are one of the most abundant and diverse groups, with at least six taxa of conifer vegetative shoots such as *Pelourdea vogesiaca*, *Albertia* cf. *latifolia*, *Voltzia walchiaeformis*, *V. heterophylla*, *V. recubariensis*, and *V. edithae* (Forte et al. 2021).

More than 60 rock slabs with fertile conifer remains were collected from the Kühwiesenkopf/Monte Prà della Vacca. The specimens are stored at the Museum of Nature South Tyrol (NMS) in Bozen/Bolzano and labeled with the prefix “PAL” followed by successive numbers. The plant fossils consist of compressions/impressions, with cuticles and in situ pollen often preserved. Conifer cones, cone fragments, and dispersed dwarf shoots were identified both dispersed in the sediment and anatomically connected to conifer shoot fragments. More than 20 dispersed pollen cones and more than 50 seed cones were identified.

Cuticles were picked from most specimens using a dissecting stereomicroscope (Olympus SZ40) and prepared with maceration in Schulze’s reagent (30% HNO₃ and a few grains of KClO₃), bleached with 10% KOH, and then rinsed with distilled water. In situ pollen samples were collected from the pollen cones, equally macerated with Schulze’s reagent, and bleached with 5% KOH. Cuticles and pollen were mounted on slides with glycerin jelly and sealed with paraplast (Kerp and Krings 1999; Kerp 2000). The amber traces found on one seed cone (NMS PAL 748) were identified and photographed under UV light with a digital camera (Sony A7r III) at the Department of Geosciences of the University of Padova. Cuticles and pollen samples were studied under a LEICA DM2500 LED microscope and photographed with a LEICA DMC4500 camera. The photographs were adjusted with the LAS4.12 software. All specimens were photographed with a Canon EOS 550D digital camera and measured using the free software ImageJ64 (National Institutes of Health, Bethesda, MD).

Results

Seed Cones

Voltzia heterophylla Brongniart, 1828 *Emended Here* Forte, Kustatscher et Van Konijnenburg-van Cittert (Figs. 2A, 3A, 3B)

Specimen. NMS PAL 767.

Emended diagnosis. Conifer with robust stem and branches. Secondary shoots arising sometimes at an angle of 90° from the primary axis, forming a whorl. Ultimate shoots arising alternately. Densely and spirally arranged leaves dimorphic. Leaf type 1 short, needlelike, with a rounded and curved apex, leaf type 2 elongate, ribbonlike, with flat lamina and rounded apex revealing plastochrons of periodic growth. Elongate seed cones with bract–dwarf shoot complexes helically arranged, arising

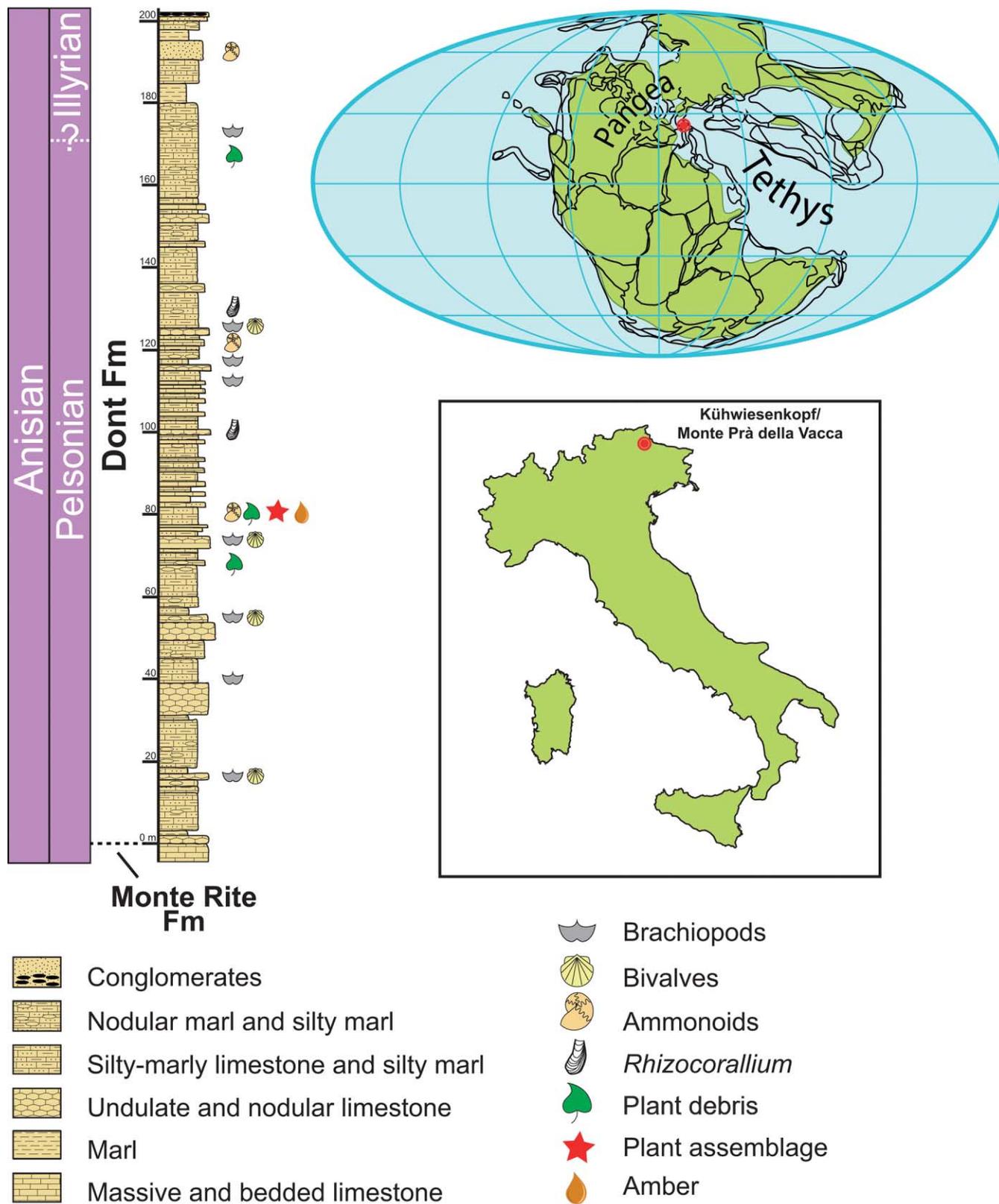


Fig. 1 Stratigraphic section and geographic position of the Kühwiesenkopf/Monte Prà della Vacca and its paleogeographic location during the Middle Triassic.

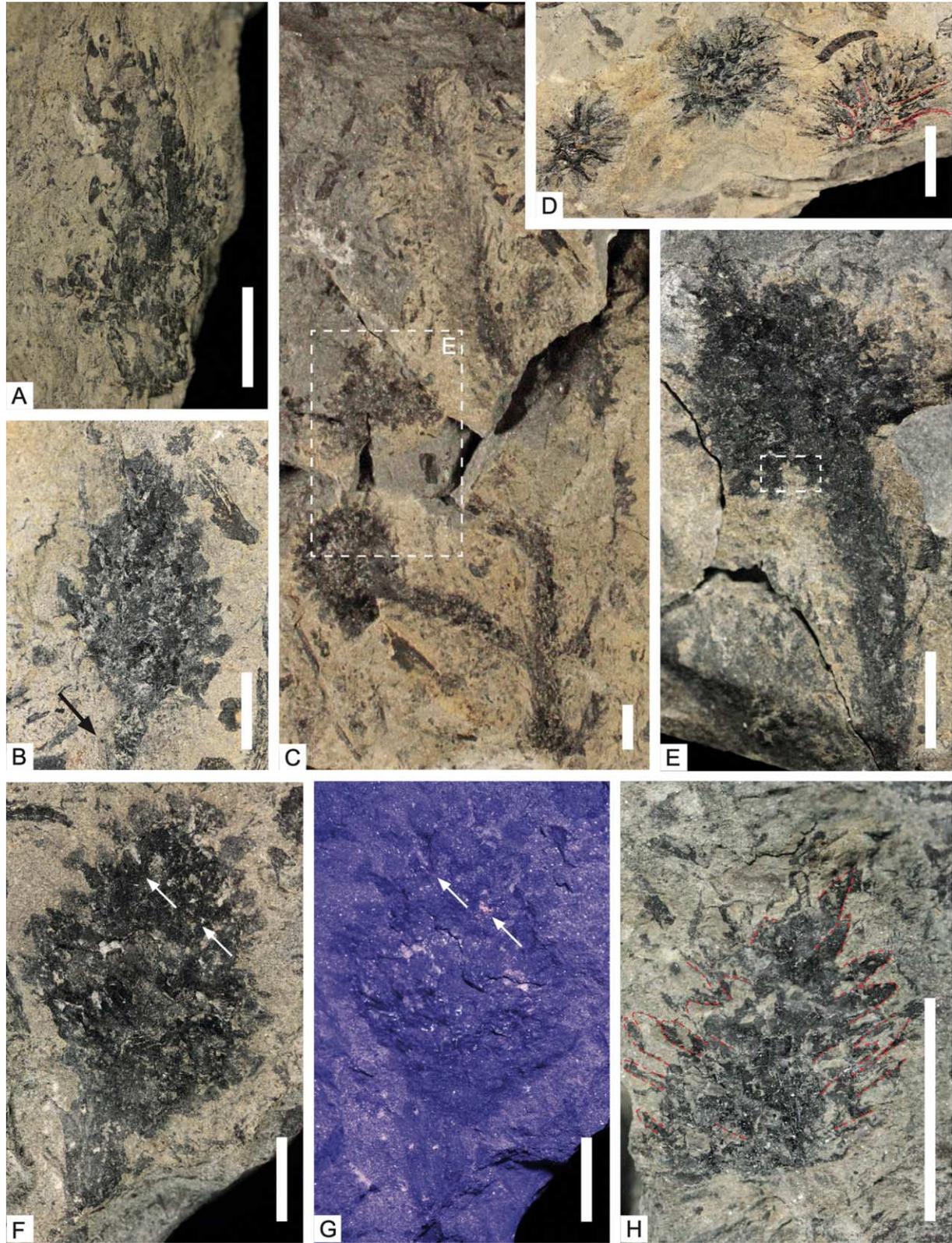


Fig. 2 Dispersed and connected seed cones of *Voltzia heterophylla* and *V. walchiaeformis*. A, Seed cone fragment of *V. heterophylla* (NMS PAL 767). B, Coalified cone of *V. walchiaeformis* connected to a shoot fragment with partly preserved triangular leaves close to the base of the cone (arrow; NMS PAL 2171). C, Roundish cones apically connected to the ultimate shoots of a large branch of *V. walchiaeformis* (NMS PAL 741). D, Three dispersed cones of *V. walchiaeformis* preserved in axial and subaxial views; dashed lines highlight the outline of the cone axis

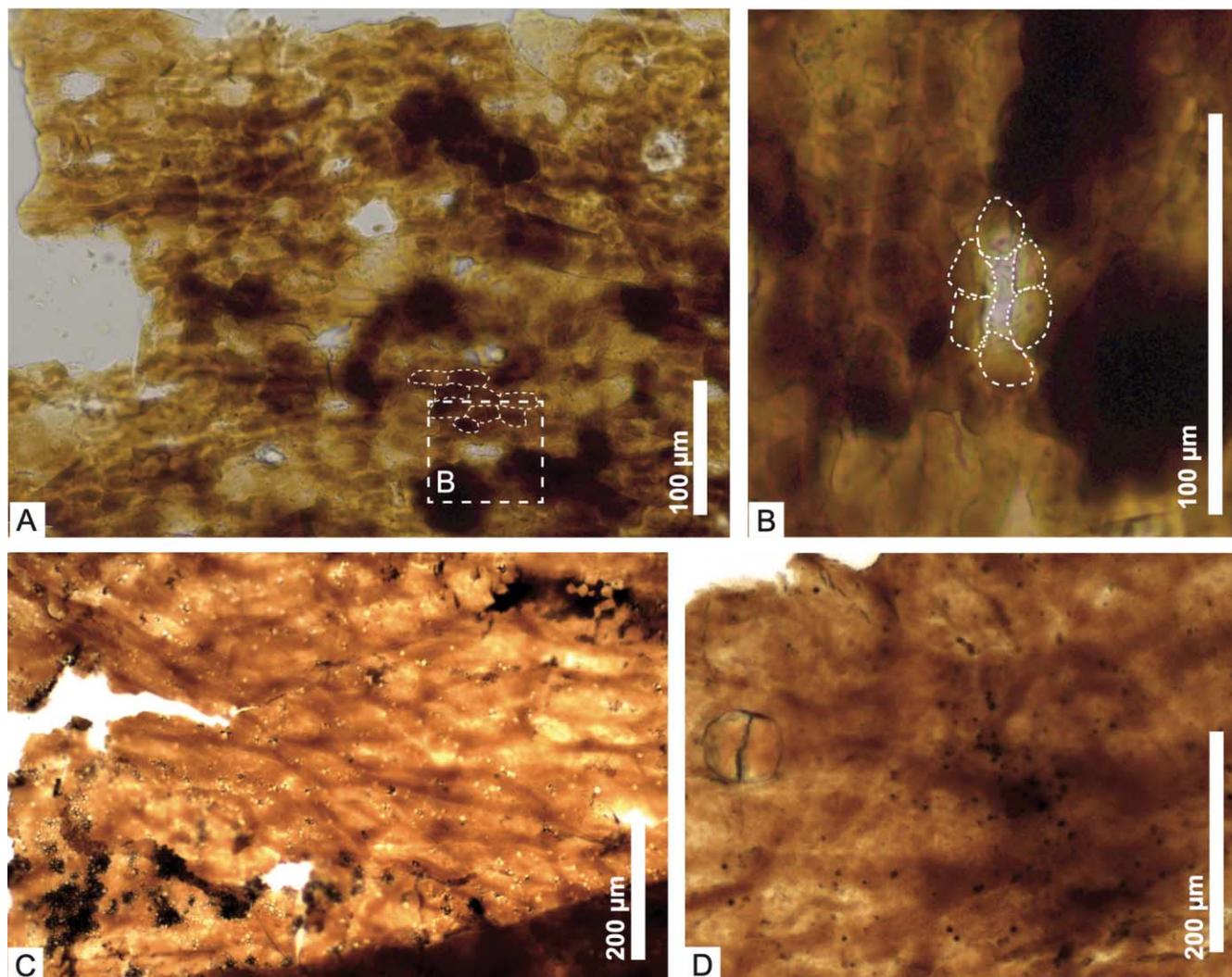


Fig. 3 Cuticles of seed cones of *Voltzia heterophylla* and *V. walchiaeformis*. *A*, Cuticle fragment of *V. heterophylla* with elongate to isodiametric epidermal cells and thick cell walls (NMS PAL 767). *B*, Magnification of the monocyclic stomata figured in *A*, with subsidiary cells (dashed lines) provided by well-developed papillae covering the stomatal aperture (NMS PAL 767). *C*, Cuticle of *V. walchiaeformis* with elongated epidermal cells characterized by thick cell walls (NMS PAL 742). *D*, Cuticle of *V. walchiaeformis* that shows the high alteration degree, which essentially obliterated the outline of the epidermal cells (NMS PAL 748).

from the cone axis at an angle of 15°–25° and curving distally toward the axes. Bract–dwarf shoot complexes narrowed in the distal part, with an acute apex. Dwarf shoots enlarged upward and divided into five lobes. Amphistomatic leaves with isodiametric to elongate epidermal cells longitudinally oriented, characterized by thick cell walls. Roundish to slightly elongate monocyclic stomata, longitudinally oriented and arranged in short, interrupted rows. Five to seven (commonly six) subsidiary cells, each bearing well-developed papillae almost completely covering the stomatal aperture. Thick dwarf shoot cuticle with

regular, isodiametric to elongate epidermal cells characterized by thick cell walls and occasionally papillae. Stomatal complexes slightly elongate, monocyclic, sunken, longitudinally oriented, and arranged in interrupted rows, stomata sometimes sharing one subsidiary cell. Six or seven papillate subsidiary cells and stomatal aperture often completely covered by papillae.

Lectotype. Brongniart (1828a, pl. 15).

Emended description. The dispersed seed cone, poorly preserved and partially covered by the sediment, is elongate, 38 mm long and 16 mm wide. Bract–dwarf shoot complexes are densely

and the lower side of the bracts (NMS PAL 2157). *E*, Counterpart of the seed cone connected to the shoot of *V. walchiaeformis* figured in *C* (NMS PAL 742); the dashed rectangle indicates the cuticle sampling area. *F*, Cone attached to a short shoot fragment of *V. walchiaeformis* with traces of amber (arrows; NMS PAL 748). *G*, Cone represented in *F* photographed under UV light to show the photoluminescence of the amber (arrows; NMS PAL 748). *H*, Small immature cone of *V. walchiaeformis* with dwarf shoot lobes (highlighted in red) protruding from the outline of the cone (NMS PAL 1310). Scale bars = 1 cm.

and helically arranged on the cone axis, arising at an angle of 15°–25° (fig. 2A). Bracts and dwarf shoots are macromorphologically not easily distinguishable from each other. However, the bract–dwarf shoot complexes are curved toward the axis in lateral view and have narrow pointed apices in front view (fig. 2A). The compact appearance of the cone suggests its putative immature stage.

The cuticles are thick, with regular, isodiametric to elongate epidermal cells, 40–80 μm long and 7–30 μm wide, sometimes bearing papillae and characterized by thick cell walls (fig. 3A). Stomatal complexes are 30–70 μm long and 20–50 μm wide, slightly elongate, monocyclic, sunken, arranged in interrupted rows, sometimes doubled, sharing one subsidiary cell, and longitudinally oriented (fig. 3A, 3B). Subsidiary cells are papillate and six or seven in number (fig. 3B). Stomatal apertures are often completely covered by the papillae on subsidiary cells (fig. 3B).

Discussion. A seed cone of *V. heterophylla* was figured by Brongniart (1828a, pl. 16, fig. 1) and described by Schimper and Mougeot (1844, pl. 14, fig. 2) as oblong to cylindrical and loosely imbricated, with enlarged five-lobed dwarf shoots (Brongniart 1828a; Schimper and Mougeot 1844; Grauvogel-Stamm 1978). The cone is terminally attached to an ultimate shoot, and dwarf shoots have remarkably fused lobes (Brongniart 1828a, 1828b; Schimper and Mougeot 1844). Unfortunately, a macromorphological comparison between the latter specimen and the cone of *V. heterophylla* from Kühwiesenkopf/Monte Prà della Vacca is not possible because of the poor preservation of our specimen (fig. 2A). However, the finding of well-preserved cuticle fragments distinctively resembling those of the foliate *V. heterophylla* shoots from Kühwiesenkopf/Monte Prà della Vacca (Forte et al. 2021) justifies assigning the specimen confidently to *V. heterophylla*. This has also resulted in an emended diagnosis.

The species was erected by Brongniart (1828a) on the basis of vegetative organs and was later emended by Schimper and Mougeot (1844). *Voltzia heterophylla* had a wide distribution in Europe during the Anisian (e.g., Grauvogel-Stamm 1978; Broglio Loriga et al. 2002; Kustatscher et al. 2019; Forte et al. 2021 and references therein); in Italy it was restricted to the Dolomites (Forte et al. 2021). Epidermal characteristics of its leaves are known from the Anisian of the Grès à *Voltzia* of France (Gall et al. 2006) and Kühwiesenkopf/Monte Prà della Vacca (Forte et al. 2021), putative pollen cones from the Anisian of England (Wills 1910), and seed cones from the Anisian of France (Brongniart 1828a, 1828b; Schimper and Mougeot 1844). The cuticle patterns of the seed-bearing organs of *V. heterophylla* are here described for the first time both macro- and micromorphologically. The epidermis of the leaves and bract/dwarf shoots of *V. heterophylla* from Kühwiesenkopf/Monte Prà della Vacca shows the same characteristics, except for the elongate epidermal cells, which are slightly smaller on the seed cones than on the leaves (Forte et al. 2021; fig. 3A).

Voltzia walchiaiformis Fliche, 1908 Emended Here Forte,
Kustatscher et Van Konijnenburg-van Cittert
(Figs. 2B–2H, 3C, 3D)

Specimens. NMS PAL 741+742, 747, 748, 1310, 2136+2171, 2157, 2160.

Emended diagnosis. Conifer with pinnately branched lateral shoot systems. Penultimate axes densely covered by needle-

like, helically arranged leaves with recurved apices. Stiff ultimate shoots situated in one plane, attached (sub)oppositely to the axis; needlelike, S-shaped leaves helically arranged. Leaves hypostomatic with fewer stomata on the upper cuticle. Epidermal cells isodiametric to elongate, stomata arranged in irregular rows. Stomatal complexes monocyclic, consisting of four to seven subsidiary cells, commonly papillate and more cutinized than the epidermal cells. Papillae on subsidiary cells often completely covering the large stomatal pit.

Seed cone apically attached to ultimate shoot, rounded and compact in immature specimens and elongate to rhomboidal in shape in mature ones. Bract–dwarf shoot complexes tightly and spirally arranged on the cone axes. Coriaceous bracts triangular in axial view. Dwarf shoots at least three lobate. Cuticle covering bract–dwarf shoot complexes thick; epidermal cells elongate, with thick walls but without papillae.

Holotype. Fliche (1908, pl. 21).

Emended description. Seven specimens are assigned to *V. walchiaiformis*, including both dispersed and seed cones connected to shoot fragments (e.g., NMS PAL 741 and its counterpart, 742; 748; 1310; 2171; 2157; fig. 2B–2H). Two cones are attached to a large branch fragment (149.3 mm long and 75 mm wide) of *V. walchiaiformis* (NMS PAL 741 and its counterpart, 742; fig. 2C, 2E), with ultimate shoots arising at an angle of 45°–60° from the axis (NMS PAL 742; fig. 2E). The penultimate axis is 6.4–7.4 mm in diameter, densely covered by spirally arranged leaves 4.5–15 mm long and 1.6–2 mm wide, obovate to lanceolate, with a rounded to acute apex, arising at an angle of 25°–45°. Three ultimate shoots are 4.3–4.6 mm thick, arranged in a loose helix around the penultimate axes, arising at an angle of 40°–60° (NMS PAL 741; fig. 2C). Leaves on the ultimate shoots are 6–7.5 mm long and 1.3–1.4 mm wide, helically arranged, with a rounded to acute apex sometimes curved toward the axis, arising at an angle of 40°–65°. Two ovulate cones occur on ultimate shoots (NMS PAL 741 and its counterpart, 742; fig. 2C, 2E). The cones are ca. 19–20 mm long and 17–19 mm wide, compact, roundish, covered by triangular bracts/dwarf shoots (8–2.7 mm \times 2.9–5.5 mm), with an acute apex that spreads out radially (NMS PAL 741 and its counterpart, 742; fig. 2C, 2E). Two more seed cones were found connected to short conifer shoot fragments (NMS PAL 2136 and its counterpart, 2171; 748; fig. 2B, 2F, 2G). The shoot fragment connected to the first cone is ca. 60 mm long and 3 mm wide, with few attached lanceolate leaves (NMS PAL 2171; fig. 2B), 5–7 mm long and up to 2 mm wide, curved in lateral view. The cone is 35 mm long and 25 mm wide, almost rhomboidal in shape, and restricted at the base. The bract–dwarf shoot complexes are heavily coalified and merged with one another, and the whole cone appears very compact, with just a few bract/scale lobes that arise from the outline of the cone (NMS PAL 2171; fig. 2B). The second cone (NMS PAL 748; fig. 2F, 2G) is attached to a short shoot fragment, about 6.5 mm thick, with helically arranged leaves, up to 6 mm long, triangular in lateral view, that protrude from the axis at an angle of 70°–80° (NMS PAL 748; fig. 2F, 2G). The cone is 54 mm long and 26 mm wide, rhomboidal in shape, compact, with bract–dwarf shoot complexes tightly organized and spirally attached on the cone axis (NMS PAL 748; fig. 2F, 2G). Dwarf shoots protruding laterally and apically from the outline of the cone (NMS PAL 748; fig. 2F, 2G) are characterized by triangular to obovate lobes, up to 4 mm

long and 1.8–3.8 mm wide, with a rounded apex and preserved in both lateral and frontal views (NMS PAL 748; fig. 2F, 2G). Traces of amber were identified in several parts of the cone (NMS PAL 748; fig. 2F, 2G). A small amber drop, 1.4 mm long and 0.7 mm wide, occurs close to the cone apex (NMS PAL 748; fig. 2F, 2G). Amber is also spread over other parts of the cone surface (NMS PAL 748; fig. 2F, 2G). Dispersed cones assigned to *V. walchiaeformis* are preserved both in lateral and in axial to subaxial views (e.g., NMS PAL 1310, 2157; fig. 2D, 2H). Cones preserved laterally are ca. 15 mm long and 13 mm wide, roundish in shape, with 4–5-mm-long bract/dwarf shoots that arise from the central axis at an angle of 45°–70°, which narrows toward the cone apex (e.g., NMS PAL 1310; fig. 2H). Cones preserved in axial and subaxial views have a diameter of ca. 20 mm, with a central axis about 5 mm thick. Bracts are 5–6 mm long and up to 2 mm wide and triangular. Dwarf shoots are fragmented, ca. 9 mm long and up to 4 mm wide, and characterized by at least three narrowed lobes (NMS PAL 2157; fig. 2D).

Thick cuticle fragments were obtained from one of the specimens (NMS PAL 742, 748; fig. 3C, 3D). Epidermal cells are elongate, 51–140 μm long and 15–50 μm wide, longitudinally oriented, and characterized by thick cell walls (NMS PAL 742; fig. 3C). No papillae occur on epidermal cells, and no well-preserved stomata were observed on the cuticle fragments (NMS PAL 742, 748; fig. 3C, 3D).

Discussion. The connection of the seed cones to the branch fragments and the epidermal features allow us to assign the specimens to *V. walchiaeformis*. This species, reported from the Anisian of France (e.g., Fliche 1908; Grauvogel-Stamm 1978; Gall and Grauvogel-Stamm 2000, 2005) and Italy (Broglia Loriga et al. 2002; Kustatscher 2004; Kustatscher et al. 2012; Forte et al. 2021), was erected by Fliche (1908) and was recently emended after the finding of well-preserved branch and shoot fragments (e.g., NMS PAL 741+742; fig. 2C, 2E), as well as cuticles from Kühwiesenkopf/Monte Prà della Vacca (Forte et al. 2021). The cuticles from shoots and seed cones of *V. walchiaeformis* show both the marked cutinization of epidermal cells and the absence of papillae. The seed cone epidermal cells are longer than those of the leaves (fig. 3C, 3D). The absence of stomata on the seed cone cuticles would suggest that they are fragments of the upper cuticle since the leaf cuticle of *V. walchiaeformis* is hypostomatic or has very few stomata on the upper cuticle (Forte et al. 2021). The general shape of the seed *V. walchiaeformis* cones does not resemble that of any other Permian–Triassic conifer seed cone. The very compact nature of the *V. walchiaeformis* cones from Kühwiesenkopf/Monte Prà della Vacca and the fact that no dispersed dwarf shoots have been found so far do not allow us to describe the macromorphological features of this taxon in detail and to make a thorough comparison with other conifer seed cones. However, the finding of amber traces on one of the *V. walchiaeformis* cones represents an important piece in the puzzle of the origin and fossil record of Triassic amber (see the general discussion).

Voltzia recubariensis (Massalongo ex De Zigno, 1862)
Schenk, 1868 (Figs. 4A–4F, 6A–6E)

Specimens. NMS PAL 749, 756, 771, 776, 1275, 1291, 1783.

Description. Seven seed cones are assigned to *V. recubariensis*. Two of these cones are connected to branch fragments

of *V. recubariensis* (NMS PAL 749, 771; fig. 4A–4C). The first cone is 39.5 mm long and 28.6 mm wide, connected to a short shoot fragment (14.8 mm long and 6 mm wide), with triangular leaves (3–6.5 mm long and 2 mm wide), helically attached close to the cone base, arising from the axis, forming a lower angle of 25°–35° and an upper one of 60°–80° (NMS PAL 771; fig. 4C). The second cone is connected to a branch (NMS PAL 749; fig. 4A) that is 110 mm long and 75 mm wide, with the penultimate axis up to 5.5 mm thick, covered by coriaceous leaves that are helically arranged and falcate to triangular in shape (NMS PAL 749; fig. 4A). Ultimate shoots are 1.9–2.5 mm thick and arise from the axis at an angle of 45°–55°. The leaves are 4.5–7.5 mm long and 2 mm wide, falcate, triangular in lateral view with the apex sometimes curved toward the axis, and arranged in a loose helix, forming two attachment angles, the lower (40°–45°, measured between the abaxial leaf side and the axis) and the upper (65°–97°, measured between the adaxial leaf side and the axis) ones, typical for *V. recubariensis* (NMS PAL 749; fig. 4A). The seed cone is 23 mm long and 12 mm wide, terminally attached to the ultimate shoot (NMS PAL 749; fig. 4A, 4B). Dwarf shoots and bracts are spirally arranged and very tightly organized. Dwarf shoot lobes arising from the upper part of the cone are up to 1.7–2.7 mm wide, elongate, with a coriaceous appearance and acute to rounded apex (NMS PAL 749; fig. 4B).

Five dispersed cones found in the Kühwiesenkopf/Monte Prà della Vacca plant assemblage represent different maturation stages (e.g., NMS PAL 756, 776, 1291; fig. 4D–4F). The cones, 29–64 mm long and 14–25 mm wide, are characterized by a loose organization (e.g., NMS PAL 756; fig. 4E), with bract–dwarf shoot complexes loosely arranged around a stout axis (2.5–5 mm in diameter), forming a loose helix with an interspiral distance of 5–8 mm (e.g., NMS PAL 756, 776; fig. 4E, 4F). The bract–dwarf shoot complexes arise from the central axis at an angle of 30°–60°. The bracts are 6.7–9.5 mm long and 3.5–3.8 mm wide, flattened, coriaceous, and restricted at the base, and a triangular apex is curved toward the cone axis (NMS PAL 756; fig. 4E). On some specimens, the dwarf shoots are still attached to the bracts (e.g., NMS PAL 756; figs. 4E, 5A). Dwarf shoots (8–12 mm long and 7.5–10 mm wide) are flattened and bilaterally symmetrical, with at least five partially fused lobes, one broad central lobe (2.5–5 mm wide) with a pointed apex and four lateral ones (4.2–5 mm \times 1.5–2.3 mm) with a rounded apex, curved toward the cone axis (NMS PAL 756, 776; table 1; figs. 4E, 4F, 5A). The dwarf shoot base is stalklike, about 3.3 mm long and 2.3 mm wide, and partially fused to the bract in the basal part for ca. 30%–40% of its length (e.g., NMS PAL 756, 1291; table 1; figs. 4D, 4E, 5A).

Some thick and well-preserved cuticle fragments were obtained from dispersed cone fragments assigned to *V. recubariensis* (e.g., NMS PAL 776; figs. 4F, 6A, 6B). Epidermal cells are 15–71 μm long and 10–45 μm wide, isodiametric to elongate, longitudinally oriented, characterized by thick cell walls (NMS PAL 776; fig. 6A, 6B) and bearing large, thick, central papillae (e.g., NMS PAL 1291; fig. 6C, 6D). Trichomes are also present (e.g., NMS PAL 1291; fig. 6C). Stomata are 35–60 μm long and 28–40 μm wide, arranged in rows, monocyclic to incompletely dicyclic, and roundish to elongate, with six to nine roundish subsidiary cells, heavily cutinized and characterized by thick cell walls (e.g., NMS PAL 1291; fig. 6D, 6E). Some

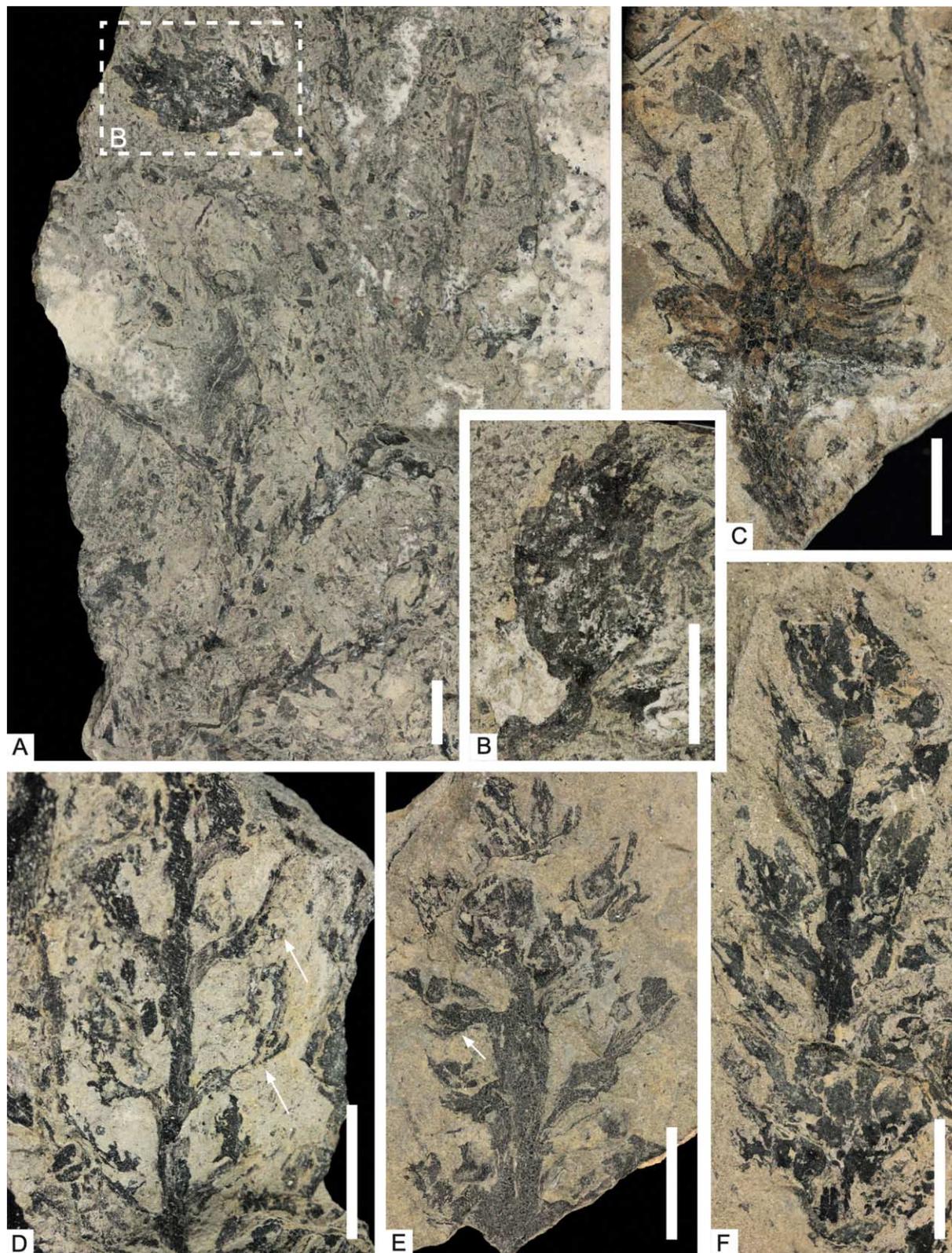


Fig. 4 Dispersed and connected seed cones of *Voltzia recubariensis*. *A*, Branch fragment of *V. recubariensis* and immature seed cone terminally attached (NMS PAL 749). *B*, Detail of the immature cone of *V. recubariensis* represented in *A* (NMS PAL 749). *C*, Empty seed cone attached to a shoot fragment of *V. recubariensis* (NMS PAL 771). *D*, Mature dispersed cone with bracts and dwarf shoots helically arranged on the thick axis; the arrows indicate dwarf shoots still attached to the bracts (NMS PAL 1291). *E*, Well-preserved seed cone with stout central axis, coriaceous bracts, and dwarf shoots with five pointed lobes; the bract and dwarf shoot are still attached to the cone axis, indicated by the arrow (NMS PAL 756). *F*, Mature cone with partly preserved dwarf shoots helically arranged on the thick central axes (NMS PAL 776). Scale bars = 1 cm.

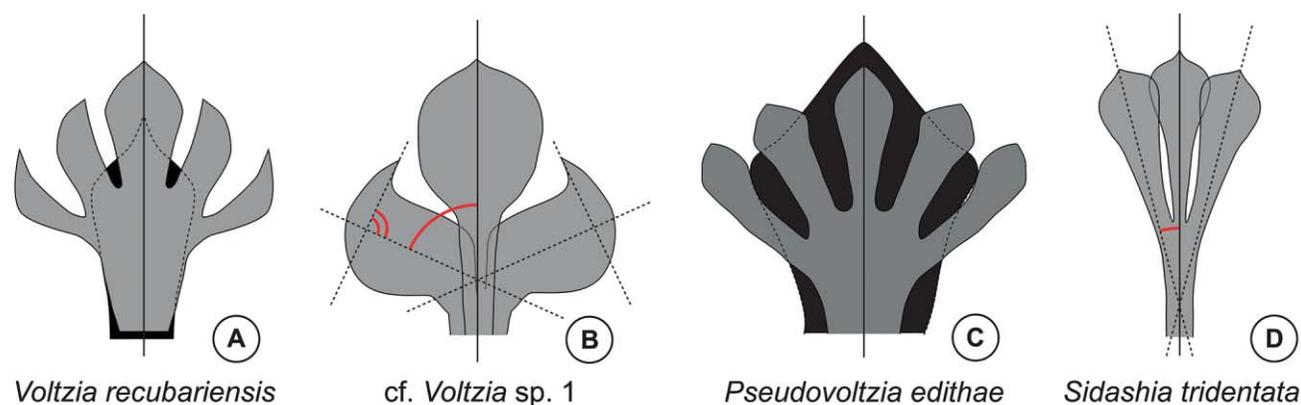


Fig. 5 Comparison of the dwarf shoots of Kühwiesenkopf/Monte Prà della Vacca. The sketches represent the dwarf shoots in adaxial view (in gray) and bracts (in black). In *cf. Voltzia* sp. 1 (B) and *Sidashia tridentata* (D), the different angles at which the two lateral lobes arise from the dwarf-shoot axis (single red arches in B and D) and the curving angle of the lateral lobe apex (double red arch in B) are highlighted.

stomata are larger than others, with large stomatal apertures and no observed papillae on subsidiary cells (e.g., NMS PAL 1291; fig. 6D, 6E).

Discussion. *Voltzia recubariensis* is a typical element of the Anisian floras of northern Italy (e.g., Broglio Loriga et al. 2002; Kustatscher 2004; Todesco et al. 2008; Kustatscher et al. 2011, 2012, 2019; Brack and Kustatscher 2013; Roghi et al. 2017). The species was erected by De Zigno (1862) as *Araucarites recubariensis* to identify some conifer shoots from the Recoaro “*Voltzia* beds” and was later moved to *Voltzia* by Schenk (1868). Recently, Forte et al. (2021) provided the description of the leaf epidermal characteristics of *V. recubariensis* from the flora of Kühwiesenkopf/Monte Prà della Vacca. The macromorphology and micromorphology of the seed cones of *V. recubariensis* are here described for the first time. The general loose organization of the seed cone of *V. recubariensis*, with bract–dwarf shoot complexes loosely and helically arranged around a central stout axis, resembles that of Majonicaceae such as the Permian taxa *Lebowskia grandifolia* Looy, 2007, *V. hexagona* (Bischoff) Geinitz, 1861 (e.g., Schweitzer 1996; Brandt 2010), and *Pseudovoltzia liebeana* (Geinitz) Florin, 1927 (e.g., Schweitzer 1996). However, some of these Permian taxa were characterized by the presence of not only terminal cones but also fertile zones (e.g., Schweitzer 1996; Looy 2007; Looy and Duijnste 2020; table 1), which have not been observed in *V. recubariensis* (table 1). Further Triassic seed cones characterized by a loose organization but also with different bract–dwarf shoot morphologies are, for example, *Aethophyllum stipulare* Brongniart, 1828, *Compsostrobus neotericus* Delevoryas and Hope, 1973, and *Florinostrobus andrewsii* Delevoryas and Hope, 1973 (e.g., Delevoryas and Hope 1975, 1987; Grauvogel-Stamm 1978; Rothwell et al. 2000). The other conifers from the Kühwiesenkopf/Monte Prà della Vacca flora are characterized by a loose arrangement of bract–dwarf shoot complexes as well (i.e., *Pseudovoltzia edithae*, *Sidashia tridentata*, and *cf. Voltzia* sp. 1, described and discussed below), except for *V. walchiaeformis* (NMS PAL 741+742, 748, 1310, 2157, 2171; fig. 2B–2H), which shows a more compact organization that might be due to the immature stage of the specimens (table 1; fig. 5A).

cf. Voltzia sp. 1 (Fig. 7A–7C)

Specimen. NMS PAL 762.

Description. One dispersed cone fragment, 36 mm long and 20 mm wide, was found with seven well-preserved dwarf shoots (NMS PAL 762; figs. 5B, 7A–7C). The dwarf shoots, visible only in abaxial view, are 7–11 mm long and 9 mm wide, flattened to concave, bilaterally symmetrical, and spirally arranged around the cone axis. Each dwarf shoot is characterized by three separate lobes and restricted at the base (NMS PAL 762; figs. 5B, 7B, 7C). The lobes have a very restricted base and are rounded in the distal part, ending with a pointed apex (NMS PAL 762; figs. 5B, 7B, 7C). The central lobe (6–9.8 mm × 4.1–4.7 mm) is longer than the lateral lobes (NMS PAL 762; table 1; figs. 5B, 7B, 7C). The latter are 6–7 mm long and 2.5–3.4 mm wide, arising from the dwarf shoot central axis at an angle of 40°–50° (NMS PAL 762; figs. 5B, 7B, 7C). The pointed apex curves toward the central lobe at an angle of 80°–90° from the lobe axis (NMS PAL 762; figs. 5B, 7B, 7C). No bracts are visible (NMS PAL 762; figs. 5B, 7A–7C).

Discussion. Since the cuticle was not preserved, information on epidermal characteristics is not available for *cf. Voltzia* sp. 1, making its attribution at the species level difficult. The general shape of the dwarf shoots, the low degree of fusion of the three large dwarf shoot lobes, and their shape slightly resemble the sporophylls of *V. hexagona* (Geinitz 1861; Schweitzer 1996). However, in *cf. Voltzia* sp. 1, lobes are wider, and the two lateral ones arise from the axis of symmetry at a wider angle than in *V. hexagona* (fig. 5B). The dwarf shoot morphology of *cf. Voltzia* sp. 1 slightly resembles that of *P. liebeana*. However, *Pseudovoltzia* is characterized by a higher degree of fusion of the lobes than observed in *cf. Voltzia* sp. 1 and other *Voltzia* species (e.g., Geinitz 1861; Clement-Westerhof 1987, 1988; Schweitzer 1996; Meyen 1997; Looy 2007; Looy and Duijnste 2020). Moreover, in both *V. hexagona* and *P. liebeana* dwarf shoots, two vegetative scales occur between the three sporophylls, resulting in a five-lobed dwarf shoot. In addition, the diverging angle of the two lateral lobes from the central one (e.g., NMS PAL 762; figs. 5B, 7B, 7C) measured in *cf.*

Table 1
Ovuliferous Organ Characters of Selected Permian and Early–Middle Triassic Conifer Taxa

Taxon	Ovuliferous structure	Bract–dwarf shoot complex	Dwarf shoot size (length × width; mm)	Dwarf shoot base	No. of scales	No. of fertile scales	Ovules produced	Ovule extension
<i>Lebouskia grandifolia</i>	Cone	Fused	10–13.5 × 8–10	Stalklike	5	2(3)	Laterally (adaxially)	Absent
<i>Manifera talaris</i>	...	(Free)	12–20 × 10–18	Stalklike	5	3	Laterally, adaxially	Present
<i>Wantus acaulis</i>	...	Free or fused	16–26 × 12–19	Not stalklike	5	5	Adaxially	Absent
<i>Pseudovoltzia sapfloreensis</i>	Cone	Fused	9.1–9.4 × 9.5–9.8	Stalklike	5	3	Adaxially	Absent
<i>Pseudovoltzia liebeana</i>	Cone, fertile zone	Fused	17–21.5 × 15–19	Stalklike	5	3	Adaxially	Absent
<i>Dolomitia cittertia</i>	Cone	Fused	Maximum, 14–20	Stalklike	16	3	Adaxially	...
<i>Majonica alpina</i>	Cone	Fused	Maximum, 10 × 6	Stalklike	1–7	2	Laterally	Present
<i>Ullmannia frumentaria</i>	Cone	Fused	12–15 × 13–14	Stalklike	5–7	1	Adaxially	Absent
<i>Ortiseia leonardii</i>	Cone	Free	Maximum, 11–15 × 10–11	Not stalklike	>25	1	Adaxially	Present
<i>Voltzia hexagona</i>	Fertile zone	Free	25–31 × 21–28	Stalklike	5	3	Adaxially	Absent
<i>Aethophyllum stipulare</i>	Cone	Free	14.5 × 9	Stalklike	5	5	Adaxially	Absent
<i>Telemachus elongatus</i>	Cone	Fused	11 × 5–7	Stalklike	5	5	Adaxially	Present
<i>Tricranolepis frischmannii</i>	Cone	Fused	Up to 17 × 4	Stalklike	3	3	Adaxially	Absent
<i>Cycadocarpidium pilosum</i>	Cone	Fused	9.5–17.5 × 2.5–3.5	Stalklike	3	3	Adaxially	Present
<i>Swedenborgia junior</i>	Cone	?	10 × 6–7	Stalklike	3	3?	Adaxially	?
<i>Swedenborgia megasperma</i>	?	?	13–17 × 5–7	Stalklike	3	3	Adaxially	?
<i>Swedenborgia tyttosperma</i>	?	?	4–5 × 2–2.5	Stalklike	3	3	Adaxially	Absent
<i>V. recubariensis</i>	Cone	Fused	8–12 × 7–10	Stalklike	5
<i>Pseudovoltzia edithae</i>	Cone	Partly fused	8.5–13 × 9.8–10	Stalklike	5
<i>Sidashia tridentata</i>	(Cone)	Partly fused	10–13 × 5.5–7	Stalklike	3
cf. <i>Voltzia</i> sp. 1	Cone	Fused	7–11 × 9	(Stalklike)	3

Sources. *Lebouskia grandifolia* (Looy 2007); *M. talaris* (according to Looy and Stevenson 2015); *W. acaulis* and *P. sapfloreensis* (according to Looy and Duijnste 2020); *P. liebeana* (according to Schweitzer 1962, 1963; Ullrich 1964; Clement-Westerhof 1987; Uhl and Kerp 2002; Uhl and Brandt 2004); *D. cittertia* and *M. alpina* (according to Clement-Westerhof 1987); *U. frumentaria* (Florin 1944; Schweitzer 1962); *O. leonardii* (according to Florin 1964; Clement-Westerhof 1984); *V. hexagona* (according to Schweitzer 1996; Hernandez-Castillo et al. 2001); *A. stipulare* (according to Grauvogel-Stamm 1978; Escapa et al. 2010; Herrera et al. 2015); *T. elongatus* (according to Anderson 1978; Retallack 1981; Escapa et al. 2010; Bomflour et al. 2013; Herrera et al. 2015); *T. frischmannii* (according to Roselt 1958); *C. pilosum* (according to Grauvogel-Stamm 1978); *S. junior* (according to Krassilov 1982a); *S. megasperma* and *S. tyttosperma* (according to Stanislavsky 1976). Underlined taxa are according to this article.

Note. Comparison of seed cone characteristics of selected early Permian–Middle Triassic conifers from Europe and North America. Table modified from Looy (2007).

Voltzia sp. 1 is peculiar when compared with other taxa (fig. 5B). Therefore, cf. *Voltzia* sp. 1 is different from other dwarf shoots assigned to *Voltzia* and might represent a new species. Because of the fragmentary nature of the specimens and the lack of preserved cuticles, we refrain from the erection of a new species, and we favor its temporary assignment to cf. *Voltzia* sp. 1.

Pseudovoltzia edithae nov. comb. Forte,
 Kustatscher et Van Konijnenburg-van Cittert
 (Figs. 7D–7H, 8A–8G)

Specimens. NMS PAL 630, 743, 745+746, 764, 1173.

Basionym. *Voltzia edithae* Forte, Kustatscher et Van Konijnenburg, 2021 (p. 456, fig. 4F).

Plant Fossil Names Registry number. PFN002989 for a new combination.

Type locality. Kühwiesenkopf/Monte Prà della Vacca, Bozen/Bolzano Province, northern Dolomites, northern Italy.

Type horizon and age. Middle part of the Dont Formation, middle Pelsonian, late Anisian, Middle Triassic.

Emended diagnosis. Conifer with spirally arranged, broad, obovate to lanceolate, slightly coriaceous leaves arising in a dense helix from the axis. Branches densely covered by leaves adpressed to the axis and overlapping one another. Ultimate shoots helically arranged from the penultimate shoots. Up to six shoots commonly arising from the stem, almost forming a whorl. Leaves amphistomatic with isodiametric to occasionally elongate, papillate, and relatively small epidermal cells. Stomata monocyclic to rarely incompletely dicyclic, longitudinally oriented, arranged in long rows,

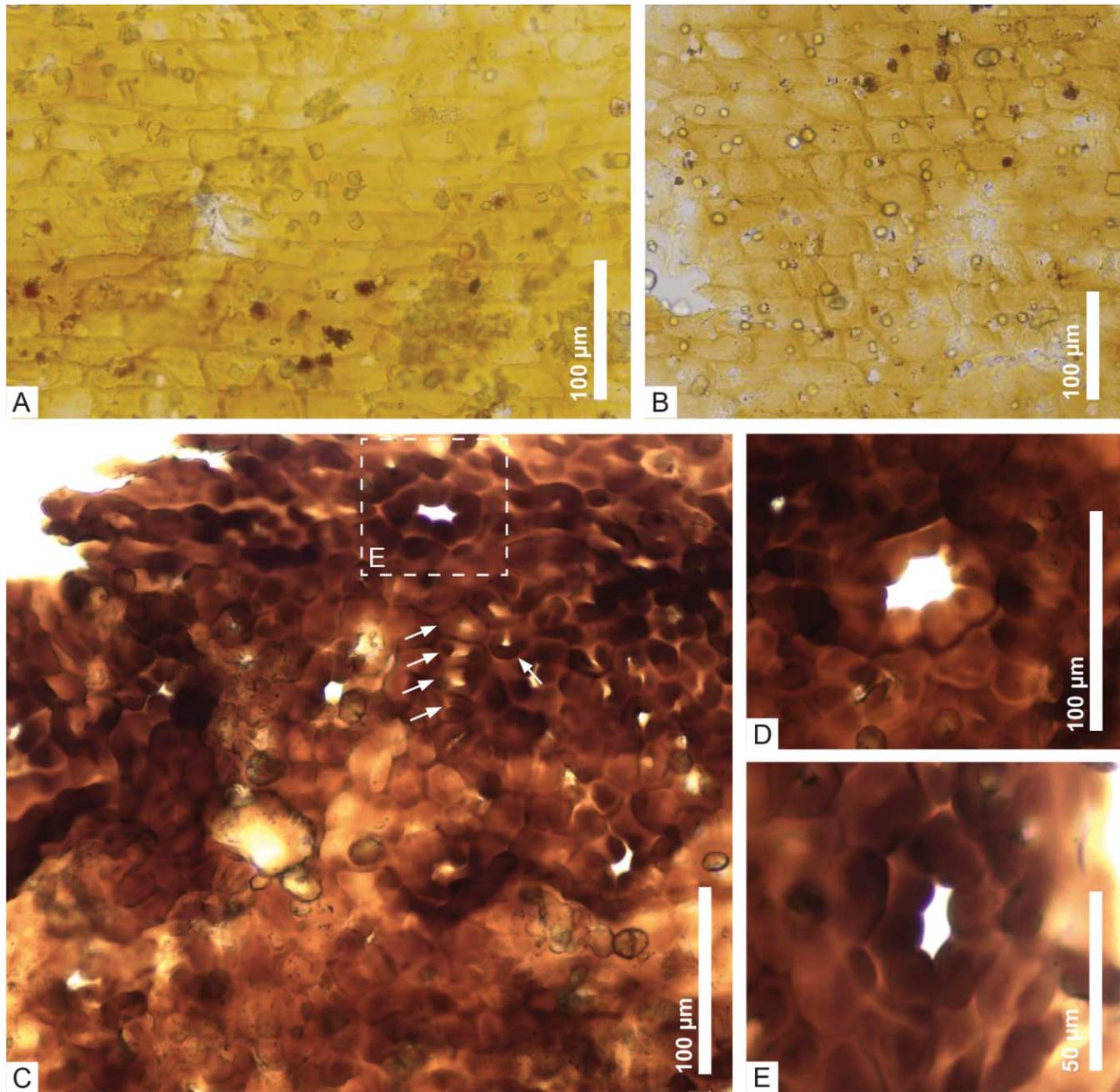


Fig. 6 Cuticle fragments of *Voltzia recubariensis* seed cones. *A, B*, Elongated to isodiametric epidermal cells of *V. recubariensis* with thick cell walls (NMS PAL 776). *C*, Cuticle fragment with heavily papillate epidermal cells, with stomata arranged in rows and trichome bases, some indicated by the arrows (NMS PAL 1291). *D*, Monocyclic stoma with thick subsidiary cells and a large stomatal aperture (NMS PAL 1291). *E*, Large, incompletely dicyclic stoma with heavily cutinized subsidiary cells (NMS PAL 1291).

occasionally double stomata within a row. Stomata on upper cuticle sometimes scattered, anticlinal walls of stomatal rows more cutinized than in epidermal cells. Six or seven subsidiary cells per stomatal complex, occasionally 5–10, trapezoid to rounded in shape, bearing papillae overhanging the stomal aperture.

Seed cones characterized by helically arranged bract-ovuliferous complexes. Coriaceous spatulate to triangular bracts

with pointed apices arise from the central axes at an angle of 40°–60° and curve distally toward the axes. Dwarf shoots flattened, bilaterally symmetrical, with stalklike base and five partially fused lobes, attached to the bract in a subaxillary position. Central lobe larger, with an obtuse apex, narrow lateral lobes characterized by a pointed apex. Cuticle covering bract–dwarf shoot complexes thick. Isodiametric epidermal cells with thick

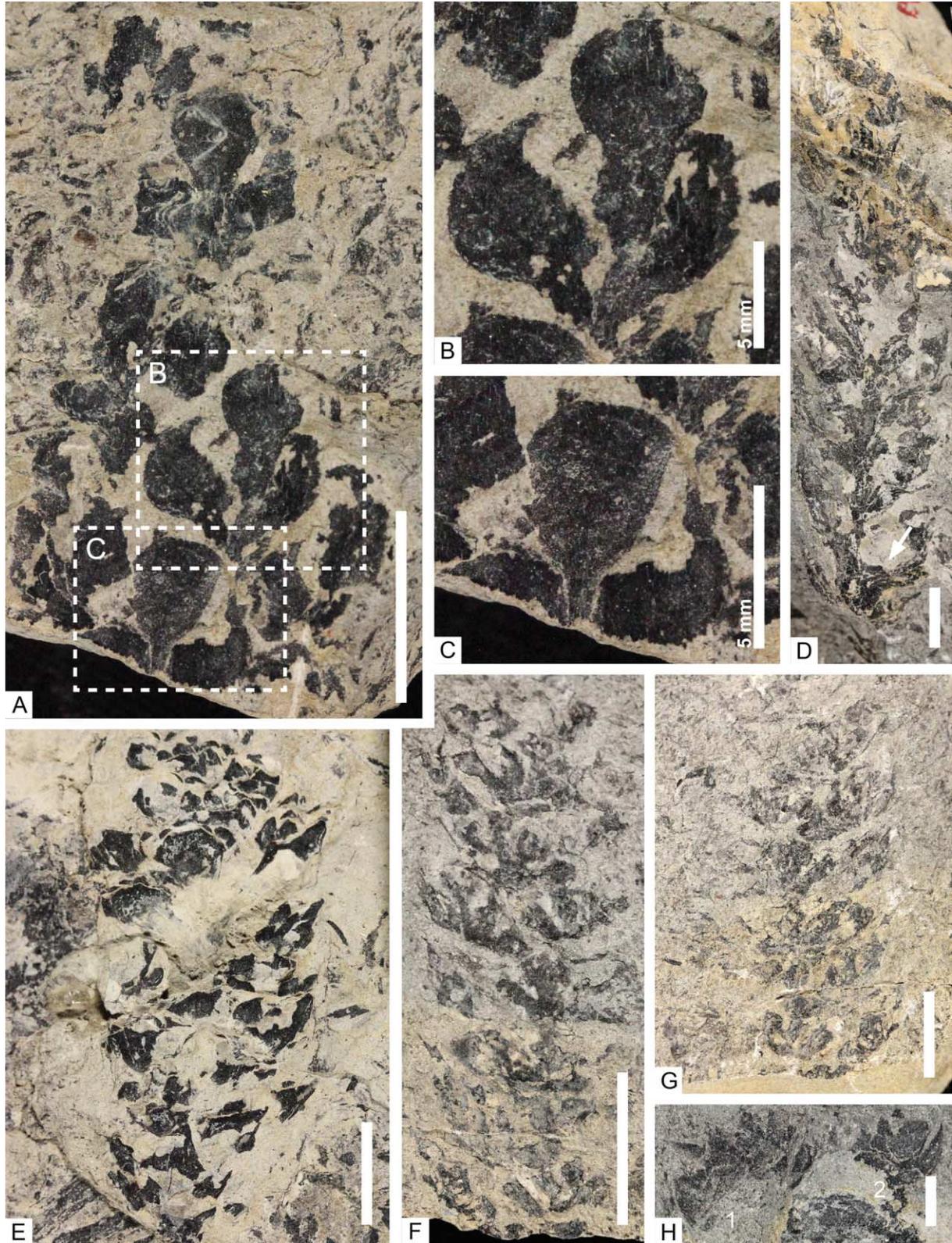


Fig. 7 Dispersed seed cones, cone fragments, and dwarf shoots of cf. *Voltzia* sp. 1 and *Pseudovoltzia edithae* comb. nov. *A*, Cone fragments of cf. *Voltzia* sp. 1 with helically arranged dwarf shoots (NMS PAL 762). *B*, *C*, Magnifications of well-preserved dwarf shoots represented in *A*, characterized by three club-shaped lobes with pointed apices (NMS PAL 762). *D*, Cone of *P. edithae* characterized by coriaceous bracts helically arranged around the axis; the arrow indicates the attachment point of a dwarf shoot in a subaxillary position (NMS PAL 743). *E*, Mature cone of *P. edithae* with attached bracts and a few partly preserved dwarf shoots (NMS PAL 764). *F*, *G*, Part and counterpart of a cone of *P. edithae* with connected dwarf shoots characterized by five lobes with pointed apices (NMS PAL 745, 746 part and counterpart). *H*, Dispersed dwarf shoots 1 and 2 assigned to *P. edithae* (NMS PAL 1173). Scale bars = 1 cm unless otherwise indicated.

anticlinal walls bearing one large central papilla. Monocyclic to incompletely dicyclic stomata, roundish to elongate and longitudinally oriented, arranged in rows, sometimes doubled, sharing one subsidiary cell. Roundish to polygonal subsidiary cells, 6–9 (6–13) per stomata complex, more cutinized than epidermal cells, bearing long papillae entirely covering the stomatal aperture.

Holotype. NMS PAL 733 (Forte et al. 2021, fig. 4F).

Emended description. Six cones and cone fragments are assigned to *P. edithae* nov. comb. Forte, Kustatscher et Van Konijnenburg-van Cittert (e.g., NMS PAL 743, 745+746, 764, 1173; fig. 7D–7H). The cones are 50–70 mm long and 20–24 mm wide (e.g., NMS PAL 745 and counterpart 746, 764; fig. 7D, 7F, 7G), with the central axes 2–3.5 mm in diameter. Bract-ovuliferous complexes are helically arranged around the axes, with an interspiral distance of 3–5.5 mm (e.g., NMS PAL 764; fig. 7D). Bracts are very coriaceous, up to 4–6 mm wide, spatulate to triangular with a pointed apex, and they arise from the central axes at an angle of 40°–60°, with the distal part curved toward the axes (e.g., NMS PAL 743, 764; fig. 7D, 7E). Anatomically connected dwarf shoots are partly preserved, with at least five pointed lobes (e.g., NMS PAL 745 and counterpart 746, 764; fig. 7D, 7F, 7G), and are attached to the bract in a subaxillary position, a few millimeters above the attachment point of the bract to the cone central axis (e.g., NMS PAL 764; fig. 7D). Two further dispersed dwarf shoots occurring a few millimeters from each other on the same rock slab are assigned to *P. edithae* (NMS PAL 1173; fig. 7H). These dwarf shoots 1 and 2 are partially preserved. The basal part is missing from dwarf shoot 1 (NMS PAL 1173; fig. 7H). The preserved part is ca. 10 mm long and 13 mm wide, with at least five partially fused lobes, 1.9–2.9 mm wide, with pointed apexes (dwarf shoot 1; NMS PAL 1173; fig. 7H). Dwarf shoot 2 is 9.8 mm long and 8.7 mm wide, with at least four partially fused lobes (NMS PAL 1173; fig. 7H). One of the lobes is 3.1 mm wide and characterized by a rounded apex (NMS PAL 1173; fig. 7H). The other three lobes are 1.6–2 mm wide and have pointed apexes (NMS PAL 1173; fig. 7H). The basal part of dwarf shoot 2, only partially preserved, is stalklike and at least 2 mm long (NMS PAL 1173; figs. 5C, 7H).

Although some of the macromorphological characteristics remain partially indistinct, the well-preserved cuticle shows the same epidermal characteristics and thus allows the cones to be assigned to *P. edithae*. Cuticles are thick and heavily papillate, with isodiametric epidermal cells, 9–91 μm long and 7–47 μm wide, with thick cell walls, bearing one large central papilla (e.g., NMS PAL 630; fig. 8A). Stomata are 32–84 μm long and 19–82 μm wide, monocyclic to incompletely dicyclic, roundish to elongate and longitudinally oriented, arranged in rows spaced about 40–200 μm apart, and sometimes doubled and sharing one subsidiary cell (e.g., NMS PAL 630; fig. 8A–8D). There are six to nine (six to eight) subsidiary cells, roundish to polygonal in shape, more cutinized than epidermal cells and bearing long papillae that entirely cover the stomatal aperture (e.g., NMS PAL 630, 743; fig. 8B–8G).

Discussion. The species *V. edithae* previously erected by Forte et al. (2021) is here emended to include the macromorphological characters of the seed organs. Although the macromorphology of *P. edithae* foliate shoots resembles at first glance that of other species belonging to the genus *Voltzia*, the dwarf shoots (fig. 5C) reveal more affinities with the genus *Pseudo-*

voltzia. On the basis of the greater similarities with *P. liebeana* and other Permian taxa, the species is emended, and the new combination, *P. edithae* nov. comb., is proposed. The partial fusion of the fertile/sterile scales (less than one-third of the scale length) is a common characteristic in Permian species such as *L. grandifolia*, *Majonica alpina*, *P. liebeana*, and *Pseudovoltzia sapplorensis* (e.g., Geinitz 1880; Florin 1927; Clement-Westerhof 1987, 1988; Uhl and Brandt 2004; Looy 2007; Looy and Duijnste 2020). A remarkable degree of fusion between fertile and sterile scales is present in Middle–Late Triassic species such as *V. coburgensis* (e.g., von Schauroth 1852; Mägdefrau 1953; Kelber 1990, 1998; Schweitzer 1996). The previous analysis of the vegetative remains of *P. edithae* already showed some similarities with the Permian conifer *M. alpina* and the Middle–Late Triassic species *V. foetterlei* (e.g., Stur 1868; Forte et al. 2021), here supported by the seed organs of *P. edithae*, confirming the transitional nature of this species (see more in Forte et al. 2021).

Genus—*Sidashia* Forte, Kustatscher et Van Konijnenburg-van Cittert, 2022 gen. nov.

Type—*Sidashia tridentata* Forte, Kustatscher et Van Konijnenburg-van Cittert gen. et sp. nov.

Generic diagnosis. Ovuliferous cone characterized by a tight organization, stout central axis with bract–dwarf shoot complexes helically arranged. Bracts arising straight in lateral view and curved beside the subaxillary attachment point of the dwarf shoot. Dwarf shoot flattened and bilaterally symmetrical, concave in lateral view, characterized by three deep lobes with pointed apexes.

Plant Fossil Names Registry number. PFN002990 for a new genus.

Etymology. The genus is named after the late paleobotanist Sidney Ash, professor at the University of New Mexico, famous for his studies of the Late Triassic Petrified Forest.

Species—*Sidashia tridentata* Forte, Kustatscher et Van Konijnenburg-van Cittert gen. et sp. nov.

Species diagnosis. Ovuliferous cone with bract–dwarf shoot complexes tightly organized around a thick axis. Bracts relatively long, curved in lateral view. Flattened and bilaterally symmetrical dwarf shoots attached to the bract in a subaxillary position, characterized by a stalklike base and three deep and elongate lobes, restricted at the base, widening distally, and narrowing again toward the pointed apex.

Plant Fossil Names Registry number. PFN002991 for a new species.

Holotype. NMS PAL 803, cone fragment with well-preserved bract–dwarf shoot complexes helically arranged around the axis (fig. 9A–9D, here designated).

Other studied specimens. NMS PAL 770, 797, 799, 800, 802, 803, 806, 807 (fig. 9A–9E).

Repository. Paleobotanical collection, Museum of Nature South Tyrol, Bozen/Bolzano, Italy.

Locality. Kühwiesenkopf/Monta Prà della Vacca, Bozen/Bolzano Province, northern Dolomites, northern Italy.

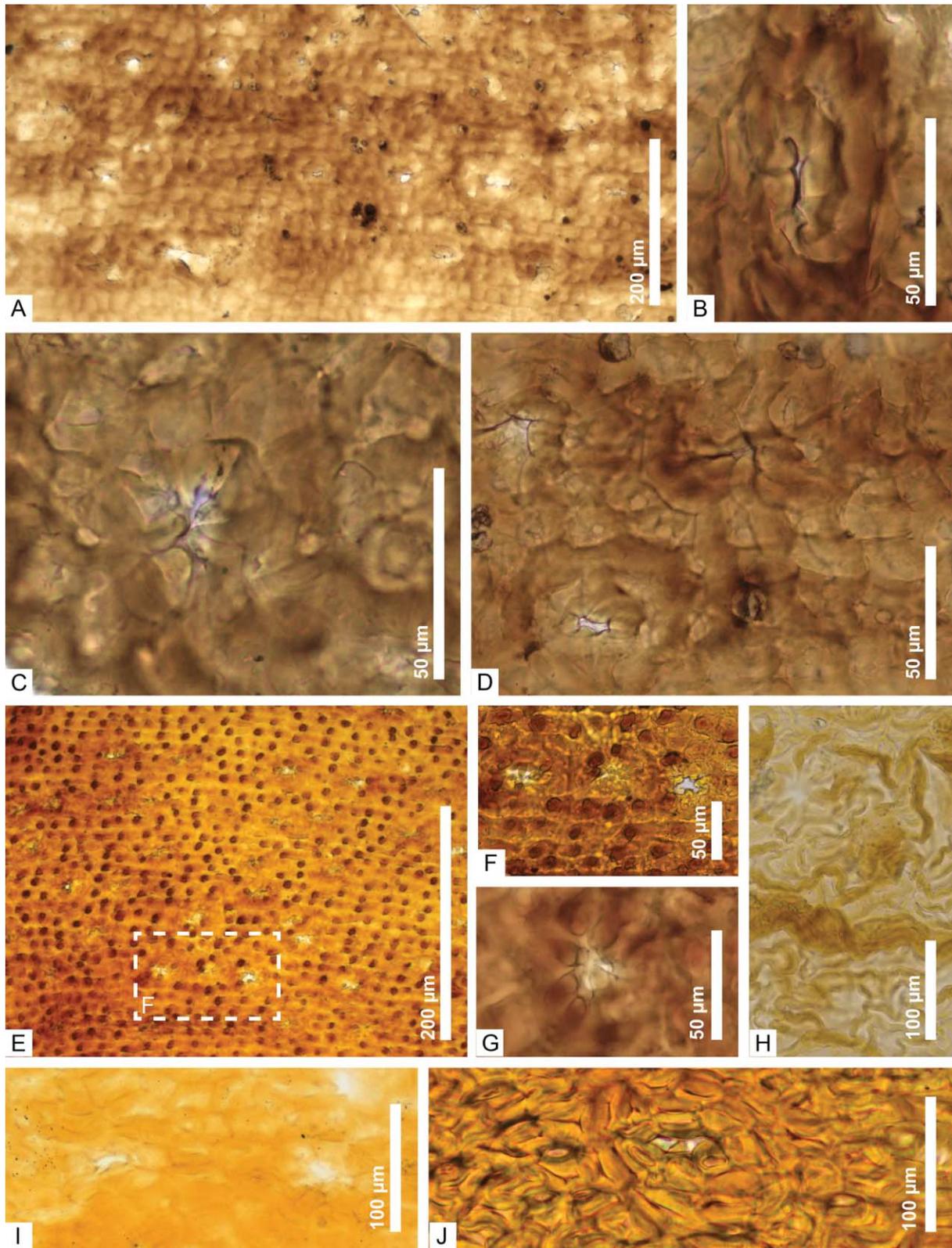


Fig. 8 Cuticle fragments of seed cones of *Pseudovoltzia edithae* comb. nov. and one undetermined dispersed cone. *A*, Cuticle fragments with elongated to isodiametric epidermal cells with thick cell walls and stomata aligned in rows (NMS PAL 630). *B*, Detail of an incompletely dicyclic stoma with cutinized subsidiary cells and well-developed papillae that close the stomatal aperture (NMS PAL 630). *C*, Epidermal cells with well-developed papillae and monocyclic stoma, with stomatal aperture almost completely closed by papillae on subsidiary cells (NMS PAL 630). *D*, Well-developed papillae

Stratigraphic horizon. Middle part of the Dont Formation, middle Pelsonian, upper Anisian, Middle Triassic.

Etymology. The specific epithet refers to the dwarf shoot shape, which resembles the symbolic trident of Poseidon, the god of the sea represented in ancient Greek mythology.

Description. Eight ovuliferous cone and dwarf shoot fragments are assigned to *S. tridentata* (e.g., NMS PAL 797, 803, 806, 807; table 1; fig. 9A–9D). The cone fragments are 19.5–70 mm long and 13–27.5 mm wide, characterized by a tight organization, with a central axis 3.5–5.4 mm thick (e.g., NMS PAL 806; fig. 9A). The bract–dwarf shoot complexes are helically arranged around the cone axes (e.g., NMS PAL 806; fig. 9A), arising at an angle of 40°–70°, which becomes narrower toward the apex (e.g., NMS PAL 803; fig. 9B). In lateral view, the bract is incurved after the attachment point of the dwarf shoots (e.g., NMS PAL 803; table 1; fig. 9B). The bracts are straight in lateral view and curved beyond the arising point of the dwarf shoot, which is in a subaxillary position (e.g., NMS PAL 797, 803; table 1; fig. 9B, 9C). The dwarf shoots are 10–13 mm long and 5.5–7 mm wide, flattened and bilaterally symmetrical, concave in lateral view, with three deep lobes, which represent sterile and/or fertile scales, without clearly visible seed attachment areas (e.g., NMS PAL 803, 806; table 1; fig. 9A, 9B). The lobes are elongate and restricted at the base, widen distally, and narrow again toward the pointed apex (e.g., NMS PAL 803, 806; fig. 9A, 9B), with the central scale (7.5–8 mm long and 1.2–2.3 mm wide) longer than the lateral ones (5–7 mm long and 1.5–2.2 mm wide). The latter arise from the dwarf shoot axis at an angle of ca. 20° (e.g., NMS PAL 806; fig. 9A). The dwarf shoot base is stalklike, up to 4.6 mm long and 0.8–1.6 mm wide, and partially fused to the bract (e.g., NMS PAL 806; table 1; fig. 9A). Epidermal characteristics of the *S. tridentata* cone are still unknown since no cuticles were obtained from the specimens.

Discussion. *Sidashia tridentata* is a conifer cone characterized by a loose arrangement of bract–dwarf shoot complexes around the axes and a typical dwarf shoot with deeply separated and elongate lobes. The loose arrangement is a common characteristic in other taxa from Kühwiesenkopf/Monte Prà della Vacca, such as *P. edithae* and cf. *Voltzia* sp. 1, but also in many other Permian–Triassic conifers, such as *L. grandifolia*, *P. liebeana*, *V. hexagona*, *A. stipulare*, *C. neotericus*, and *F. andrewsii* (e.g., Brongniart 1828a; Geinitz 1861; Delevoryas and Hope 1973, 1975, 1987; Grauvogel-Stamm 1978; Schweitzer 1996; Rothwell et al. 2000; Looy 2007; Looy and Duijnste 2020; table 1). Like *S. tridentata*, cf. *Voltzia* sp. 1 is characterized by the presence of three-lobed dwarf shoots (table 1; fig. 5C, 5D). However, in the latter, lobes are wider than in *S. tridentata*, and the two lateral ones arise at a wider angle from the axis of symmetry of the dwarf shoot (fig. 5C, 5D).

Other Middle–Late Triassic and Cretaceous taxa that are characterized by three-lobed dwarf shoots are *Tricranolepis* (Roselt 1958), *Cycadocarpidium* (Grauvogel-Stamm 1978), and several species of *Swedenborgia*, such as *Swedenborgia junior* Krassilov, 1982, *Swedenborgia megasperma* Stanislavsky, 1976,

and *Swedenborgia tyttosperma* Stanislavsky, 1976 (Krassilov 1982a). Among these taxa, dwarf shoot lobes are often not deeply incised, except for those of *S. tyttosperma*, which are narrower and deeply incised (Stanislavsky 1976; Krassilov 1982a), resembling those of *S. tridentata* more closely. However, in *S. tyttosperma*, lobes are more spaced from one another and more triangular in the distal part. In all these Middle–Late Triassic taxa with three-lobed and stalk-based dwarf shoots, each lobe represents one sporophyll, commonly bearing one seed each (e.g., Roselt 1958; Stanislavsky 1976; Grauvogel-Stamm 1978; Krassilov 1982a). It is likely that the three lobes of *S. tridentata* could all be sporophylls as well, but it is not possible to observe seed scars on any specimens because the latter are all unfortunately preserved in adaxial view.

Empty Cones

Specimens. NMS PAL 284, 300, 619, 766, 772, 773, 774, 775, 777, 779, 781, 2077, 2148, 2150, 2158 (figs. 8H, 9E–9H).

Description. Sixteen dispersed and disarticulated seed cones, preserved in both lateral and axial/subaxial views, are preserved in the assemblage (e.g., NMS PAL 619, 774, 779, 781; fig. 9E–9H). The cones preserved in section view are 27.9–94.6 mm long and 11.9–29.7 mm wide, characterized by a very loose organization and thick axes, ca. 2–7 mm in diameter (e.g., NMS PAL 774, 779; fig. 9F, 9G). In these specimens, no dwarf shoots are preserved or are only partly preserved; thus, their macromorphology is not clear. However, on some specimens it is possible to observe their attachment point in a subaxillary position (e.g., NMS PAL 774; fig. 9G). Bracts are helically arranged on the axis, with an interspiral distance of 2.2–9 mm (e.g., NMS PAL 619, 774, 779; fig. 9E–9G). They are 4.4–16 mm long and up to 3–8 mm wide and coriaceous. In lateral view, bracts are recurved toward the apex, arising from the central axis at an angle of 20°–80°, which becomes narrower (up to 20°) toward the apex of the cone (e.g., NMS PAL 774; fig. 9G).

A small cone (NMS PAL 619; fig. 9E) is anatomically connected to a shoot fragment (63 mm long and 2 mm wide), with a few badly preserved leaves (up to 4 mm long and 1 mm wide) still helically arranged on the axis of the cone (NMS PAL 619; fig. 9E). The cone is poorly preserved, 28.1 mm long and 10 mm wide, with 5.4–6.4-mm-long bracts that arise spirally from the axis at an angle of 40°–60°, narrowing toward the top of the cone and with an interspiral distance of ca. 2 mm (NMS PAL 619; fig. 9E).

Two further cones are preserved in axial and subaxial views (NMS PAL 781; fig. 9H). Cone A, 15.3 mm long and 9.5 mm wide, is preserved in subaxial view, with triangular bracts (4.4–5.7 mm × 2.9–3.9 mm) that arise from the central axis, which is ca. 2 mm in diameter (NMS PAL 781; fig. 9H). Cone B, preserved in axial view, is more radially symmetric (13.5 mm × 11.1 mm), characterized by larger triangular bracts (5.7–7.5 mm × 3.4–5 mm) that radially arise from the central axis (1.5 mm in diameter) and look slightly bilobed and thicker in the distal part (NMS PAL 781; fig. 9H).

on epidermal and subsidiary cells (NMS PAL 630). E, Heavily papillate cuticle with stomata arranged in rows, sometimes doubled and sharing the subsidiary cells (NMS PAL 743). F, Detail of E with close stomata sharing subsidiary cells (NMS PAL 743). G, Monocyclic stoma with long papillae on subsidiary cells that completely close the stomatal aperture (NMS PAL 743). H, Poorly preserved cuticle fragment of a dispersed empty seed cone (NMS PAL 777). I, Epidermal cells of polliniferous cone type 3 characterized by thick cell walls (NMS PAL 877). J, Heavily papillate cuticle with incompletely dicyclic stoma from polliniferous cone type 3 (NMS PAL 877).

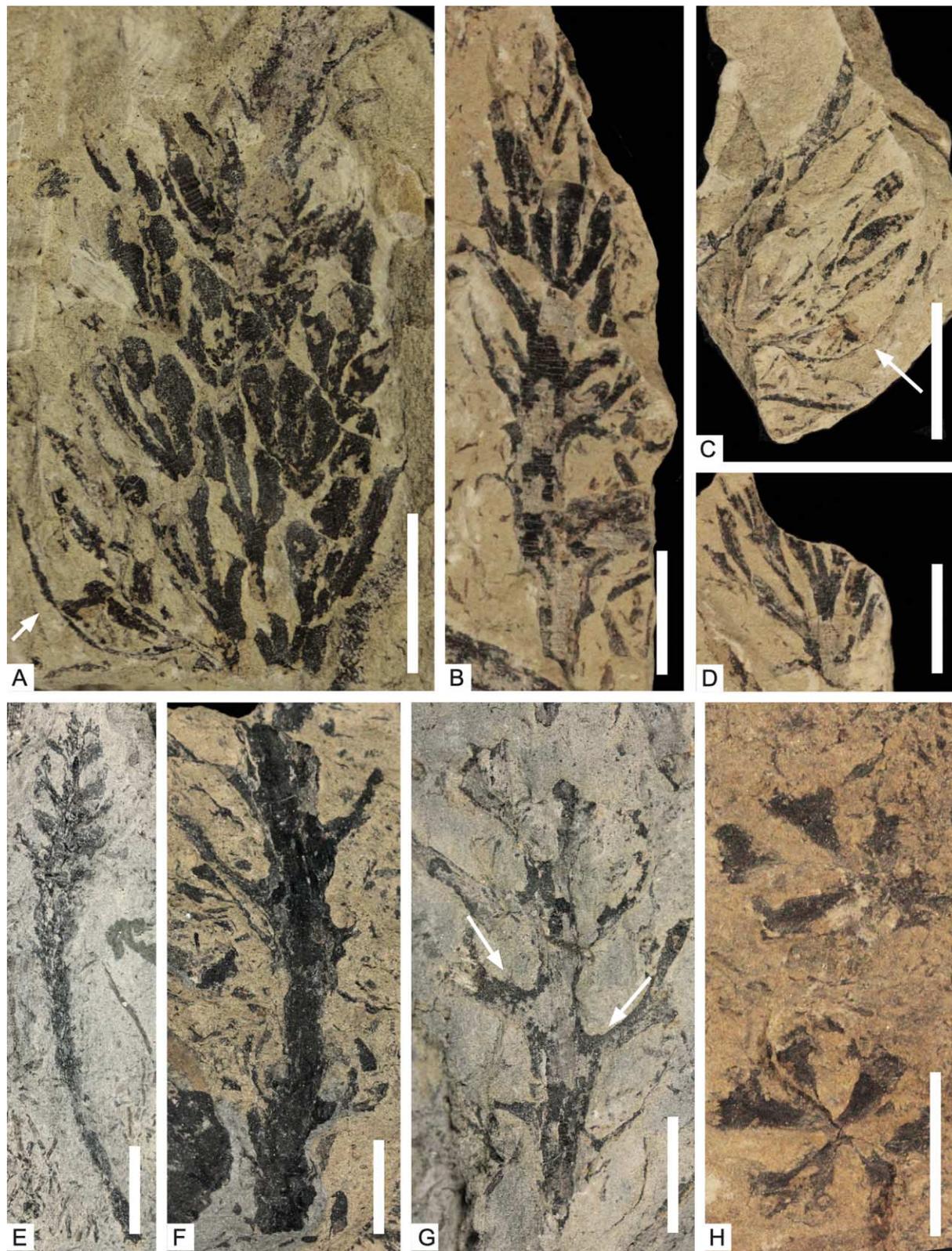


Fig. 9 Dispersed seed cone fragments of *Sidashia tridentata* gen. nov. sp. nov. Forte, Kustatscher et Van Konijnenburg-van Cittert, 2022 and empty seed cones. *A*, Holotype of *S. tridentata* representing one cone fragment with helically arranged dwarf shoots characterized by three deep and narrow lobes with pointed apices, long recurved bracts in profile view (arrow), and a thick central axis (NMS PAL 806). *B*, Cone fragment of *S. tridentata* with partly preserved dwarf shoots attached to the bracts in a subaxillary position (NMS PAL 803). *C*, Dwarf shoot fragments of

Badly preserved cuticles were obtained from one specimen (NMS PAL 777; fig. 8H). Stomata are unfortunately not well preserved, and cuticle fragments are strongly altered, with corrugated cell walls.

Discussion. The loose organization of the disarticulated empty cones resembles that of some cones described as *V. recubariensis* or some majonicacean cones (e.g., Clement-Westerhof 1987, 1988; Looy 2007; Looy and Duijnste 2020). The bract–dwarf shoot complexes are arranged in a loose helix around the axis and characterized by an interspiral distance of 3–9 mm, which is comparable to the values measured on the *V. recubariensis* cones (4.9–8 mm). Although the macromorphological comparison evidences some similarities between *V. recubariensis* and the empty cones, the missing cuticles or the bad cuticle preservation in one case (e.g., NMS PAL 777; fig. 8H) does not allow us to observe the epidermal characteristics of the empty cones and to assign them to any taxon.

Pollen Cones

Voltzia recubariensis (Massalongo ex De Zigno 1862) Schenk, 1868 Emended Here Forte, Kustatscher et Van Konijnenburg-van Cittert (Figs. 10A–10E, 12A–12D)

Specimens. NMS PAL 467, 569, 575, 783, 784, 786, 787, 788, 789, 790, 2100.

Emended diagnosis. Robust conifer with large branches and widely spaced shoots covered by falcate to triangular coriaceous leaves arranged in a loose helix around the axis. Lower and upper leaf attachment angles to the axis typically different, 45° and 70°, respectively, on average. Leaves almost hypostomatic with heavily papillate, elongate epidermal cells, longitudinally oriented, sometimes bearing hairs and trichomes. Stomata arranged in rows or scattered with six to eight roundish to polygonal subsidiary cells. Anticlinal cells thick, more cutinized than in the epidermal cells, bearing well-developed papillae. Seed cones elongate, attached apically on ultimate shoots. Bract–dwarf shoot complexes arranged in loose helix around the thick axis. Dwarf shoots coriaceous, flattened, bilaterally symmetrical, composed by five elongate lobes, partially fused. Central lobe broad, lateral lobes narrower, all with acute apices. Epidermal cells of seed cone isodiametric to elongate, oriented longitudinally, characterized by thick anticlinal walls and bearing a central, well-developed papilla. Roundish to elongate stomata, arranged in rows, monocyclic to incompletely dicyclic with six to nine subsidiary cells. Pollen cones elongate with rounded apex and stout central axis. Microsporophylls spirally arranged, with a distal head, rhomboidal in front view, with a rounded apex. Pollen sacs elongate, attached to the lower side of the microsporophyll head, parallel to the microsporophyll stalk. Pollen bisaccate, haploxytonoid. Central body circular or longitudinally elongated, with two or four taeniae. Sacci short, about as wide as the corpus.

Lectotype. De Zigno (1862, pl. 5, fig. 1).

Emended description. Ten pollen cones, both dispersed and attached to branches of *V. recubariensis*, were found at Küh-

wiesenkopf/Monte Prà della Vacca (e.g., NMS PAL 783, 788, 789; fig. 10A–10C). Only one pollen cone was found anatomically connected to a shoot fragment of *V. recubariensis* (NMS PAL 787/788 part and counterpart; fig. 10A). The shoot fragment is 46 mm long and 14.5 mm wide, with a 4.3-mm-thick axis (NMS PAL 788; fig. 10A), from which falcate, helically arranged, triangular leaves (6–7 mm long and 2 mm wide) depart, with an acute apex and characterized by upper and lower angles of 65°–100° and 45°–60°, respectively. The cone, 28 mm long and 9.2 mm wide, is terminally attached to the shoot. The other dispersed cones are 20.7–38.5 mm long and 9.5–17 mm wide, with a rounded apex and base. The central axis is stout (ca. 1.6–4 mm in diameter; e.g., NMS PAL 789; table 2; fig. 10B). Microsporophylls are spirally arranged, with an interspiral distance of 0.7–1.1 mm and arising from the thick axis at angles of 20°–100°, which become narrower toward the top of the cone (e.g., NMS PAL 784, 788, 789, 790; table 2; fig. 10A–10D). 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 triangular in lateral view with two lobes (e.g., NMS PAL 569, 789; table 2; figs. 10B, 10E, 11A, 11B). Pollen sacs are elongate, attached to the lower side of the microsporophyll head, parallel to the microsporophyll stalk (e.g., NMS PAL 789; table 2; figs. 10B, 11A, 11B).

In situ pollen. In situ pollen with varying qualities of preservation was obtained from several cones of *V. recubariensis* (e.g., NMS PAL 569, 786; table 2; figs. 10E, 12A–12D). The better-preserved pollen grains are bisaccate, haploxytonoid, and 55–97 µm in length, with a circular or longitudinally elongated central body and two or four taeniae (e.g., NMS PAL 569, 786; figs. 10E, 12A–12D). The sacci are short and about as wide as the corpus. A short monolete or triletole mark is sometimes visible (e.g., NMS PAL 569; fig. 12C). Some pollen grains do not clearly show taeniae. In cases with four taeniae, the outer ones are often faint, while in cases with two taeniae, these are narrow and usually located centrally, like the central taeniae in grains with four taeniae.

Discussion. Several well-preserved pollen cones attached to big branch fragments of *V. recubariensis* or dispersed in the sediment were already described from the Anisian “*Voltzia* beds” (e.g., Massalongo 1857; De Zigno 1862; Schenk 1868; Kustatscher et al. 2012; Kustatscher and Roghi 2016) of Recoaro (Vicenza, northern Italy). The latter were compared to the pollen cones assigned to *Willsiostrobus* sp. from the Anisian of France (Grauvogel-Stamm 1978; Kustatscher et al. 2012). Bisaccate in situ pollen was also obtained from these *V. recubariensis* cones (G. Roghi, personal observation) but was never described and discussed in detail.

The main morphological differences between *V. recubariensis* and other Triassic pollen cones are the reduced microsporophyll length and the variable axis-microsporophyll angle (table 2). In gross morphology, pollen cones of *V. recubariensis* resemble those of some species of *Willsiostrobus* Grauvogel-Stamm et Schaarschmidt, 1978, such as *Willsiostrobus ligulatus*, *Willsiostrobus acuminatus*, and *Willsiostrobus rhomboidalis* (e.g., Grauvogel-Stamm 1969, 1978; Grauvogel-Stamm and Grauvogel

S. tridentata with visible deep and elongated lobes and one bract in side view, indicated by the arrow (NMS PAL 797). *D*, Fragments of dwarf shoots of *S. tridentata* with visible stalklike basal parts and a bract in profile view (NMS PAL 807). *E*, Empty cone attached to a poorly preserved shoot fragment (NMS PAL 619). *F*, Empty seed cone characterized by thick axes (NMS PAL 779). *G*, Empty seed cone with fragmented bracts and two visible points of attachment for dwarf shoots (arrows; NMS PAL 774). *H*, Two dispersed cones preserved in axial and subaxial views, with triangular and coriaceous bracts (NMS PAL 781). Scale bars = 1 cm.

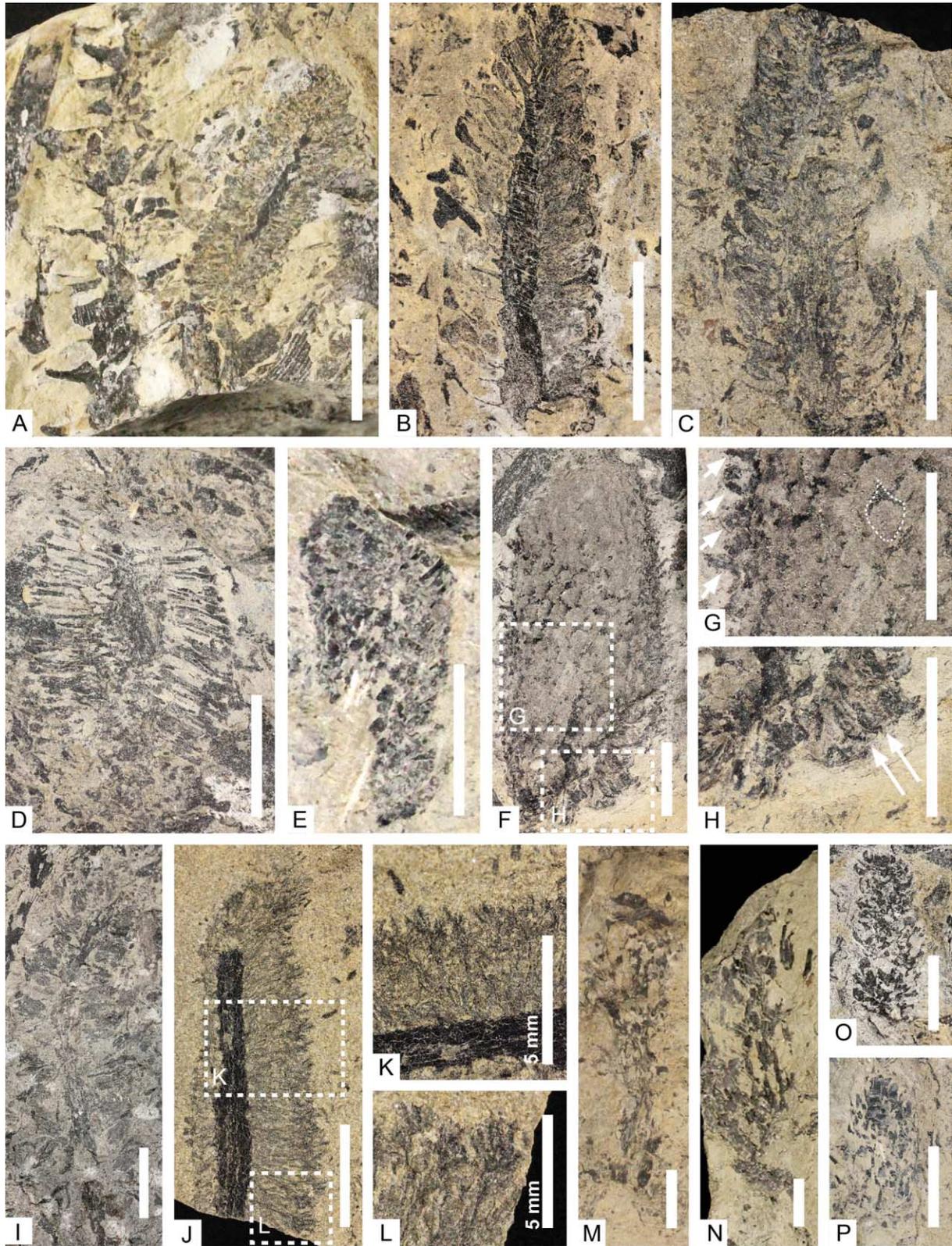


Fig. 10 Polliniferous cones of *Voltzia recubariensis*, *Willsiostrobus* cf. *rhomboidalis*, and *Willsiostrobus* sp., type 1 and type 2. A, Cones of *V. recubariensis* connected to a shoot fragment (NMS PAL 788). B, Dispersed cone of *V. recubariensis* with pollen sacs attached to the microsporophyll axes (NMS PAL 789). C, Cone of *V. recubariensis* with well-preserved microsporophylls in side view (NMS PAL 784). D, Cone of *V. recubariensis* with a thick central axis (NMS PAL 790). E, Dispersed cone fragment of *V. recubariensis* with microsporophyll shields preserved

1975; Grauvogel-Stamm and Schaarschmidt 1978, 1979; table 2). *Willisostrobos acuminatus* and *V. recubariensis* have comparable microsporophyll lengths but differ in their axis-microsporophyll angles (much more variable in *V. recubariensis* and ca. 90° in *W. acuminatus*; table 2) and in the dimension and shape of the microsporophyll heads, which are subtriangular and characterized by a pointed apex in *W. acuminatus* (e.g., Grauvogel-Stamm 1978; Grauvogel-Stamm and Schaarschmidt 1978; table 2). *Willisostrobos ligulatus* differs because its microsporophyll head has expanded bases and a narrow, elongated apex (table 2). *Voltzia recubariensis* and *W. rhomboidalis* are similar in having a rhomboidal microsporophyll head. However, the microsporophyll head is more rounded in *V. recubariensis* than in *W. rhomboidalis*, and the cones of the former species are smaller and more elongate (table 2; fig. 11A, 11B). Moreover, the latter species is characterized by longer microsporophylls (e.g., Grauvogel-Stamm 1978; Grauvogel-Stamm and Schaarschmidt 1978; table 2; fig. 11A, 11B). The pollen cone *Sertostrobus laxus* has microsporophyll lengths comparable to those of *V. recubariensis* (table 2). However, *S. laxus* differs from *V. recubariensis* in having microsporophylls arranged in a loose spiral, a mucronate apex and expanded base of the microsporophyll head, and pollen sacs arranged into clusters (Grauvogel-Stamm 1969, 1978; Grauvogel-Stamm and Schaarschmidt 1979; Taylor and Grauvogel-Stamm 1995; table 2).

The in situ pollen grains of *V. recubariensis* (NMS PAL 569, 786; fig. 12A–12D) are comparable to those of the genera *Lueckisporites* (in cases with two taeniae) or *Lunatisporites* (with four taeniae). However, a triletoid mark is unusual for both genera. Grains without clear taeniae may be immature or affected by poor preservation. Several forms of *Lueckisporites* and *Lunatisporites* are known from the dispersed sporomorph assemblages of the Dont Formation in the Kühwiesenkopf/Monte Prà della Vacca section (Kustatscher and Roghi 2006). Similar forms are known in situ from late Permian voltzialean conifers (Clement-Westerhof 1974). Pollen grains from the Triassic conifers *Masculostrobus* (= *Willisostrobos*) *willsii* and *Rissikia media* described by Townrow (1962, 1967a) have also been compared to *Lunatisporites* (Balme 1995; Traverse 2007).

Willisostrobos cf. rhomboidalis (Grauvogel-Stamm)
Grauvogel-Stamm et Schaarschmidt, 1978 (Fig. 10F–10H)

Specimen. NMS PAL 757.

Description. The large, dispersed cone is 52.8 mm long and 23 mm wide (NMS PAL 757; fig. 10F–10H). The cone is elongate, with a rounded apex, compact appearance, and thick central axis (5.8 mm in diameter; NMS PAL 757; table 2; fig. 10F–10H). Microsporophylls are 5.7–5.9 mm long, becoming shorter near the cone apex and arising almost perpendicularly from the

axis. The microsporophyll heads are 3.1–3.9 mm long and 2.5–3 mm wide, almost rhomboidal and symmetrical in face view (NMS PAL 757; table 2; figs. 10F–10H, 11C, 11D). In lateral view, two curved, pointed parts (2.1–2.9 mm long) are visible arising from the upper and lower parts of the microsporophyll axis, with the upper one longer than the lower one (NMS PAL 757; table 2; figs. 10F–10H, 11C, 11D). Pollen sacs (1–1.5 mm long) are attached to the lower part of the microsporophyll head, parallel to the microsporophyll axis and protected by the lower part of the microsporophyll head (fig. 11C). Unfortunately, only fragments of possible poorly preserved pollen were obtained from specimen PAL 757, which does not allow a detailed description.

Discussion. The putative assignment to *W. rhomboidalis* is based on macromorphological features. *Willisostrobos rhomboidalis* was originally described as *Masculostrobus rhomboidalis* from the Anisian of France (e.g., Seward 1911; Grauvogel-Stamm 1969, 1978; Grauvogel-Stamm and Schaarschmidt 1978, 1979). The microsporophyll heads are similarly rhomboidal in shape and size (table 2), but the microsporophylls from Kühwiesenkopf/Monte Prà della Vacca are slightly smaller and more perpendicularly inserted than the type material from France (Grauvogel-Stamm 1969, 1978; table 2; figs. 10G, 11C, 11D). Moreover, in *W. cf. rhomboidalis*, the sporophyll head shape is characterized by two curved “spines” (figs. 10G, 11C, 11D), which are not evident in *W. rhomboidalis*. The in situ pollen of the original specimens was assigned to the dispersed pollen species *Voltziaceasporites heteromorpha* Klaus (Grauvogel-Stamm 1969, 1978; table 2). Furthermore, fragments of *W. rhomboidalis* cones with subtriangular to rhomboidal microsporophyll heads were described from the Anisian of Majorca (Spain; Grauvogel-Stamm and Álvarez Ramis 1996). The Spanish cones also yielded in situ pollen of the *V. heteromorpha* type (Grauvogel-Stamm and Álvarez Ramis 1996). While this pollen taxon is well represented in the palynoassemblage of Kühwiesenkopf/Monte Prà della Vacca (Kustatscher and Roghi 2006; Kustatscher et al. 2006, 2010a), the *W. cf. rhomboidalis* described here has so far not yielded any identifiable in situ pollen.

Willisostrobos sp. (Figs. 10I, 12E, 12F)

Specimen. NMS PAL 794.

Description. The single dispersed cone is elongate, 85 mm long and 18 mm wide (NMS PAL 794; table 2; fig. 10I), with a 1.4–2.3-mm-wide axis and helically arranged microsporophylls with an interspiral distance of 2.3–2.8 mm (table 2; fig. 10I). Microsporophylls arise from the axis at ca. 90°. They have a 7–7.3-mm-long stalk and terminate distally, with a head preserved only in lateral view (NMS PAL 794; table 2; fig. 10I). Microsporangia are elongate and attached to the lower part of

in front view (NMS PAL 569). F, Polliniferous cone of *W. cf. rhomboidalis* (NMS PAL 757). G, Detail of F, where the dashed line highlights the shape of a microsporophyll head in front view (NMS PAL 757). H, Detail of F, with the arrows indicating microsporophylls and pollen sacs in side view (NMS PAL 757). I, Dispersed cone of *Willisostrobos* sp. with spirally arranged microsporophylls and parallel pollen sacs (NMS PAL 794). J, Dispersed cone of ?*Darneya* sp. with thick central axes and microsporophylls preserved in side view (NMS PAL 2139). K, Detail of J, showing microsporophylls in side view (NMS PAL 2139). L, Detail of J, showing visible hand-shaped microsporophyll heads and stalked pollen sacs arranged in clusters, attached on the microsporophyll axes. M, Polliniferous cone assigned to type 1 (NMS PAL 890). N, Polliniferous cone assigned to type 2 (NMS PAL 1253). O, Polliniferous cone type 3 (NMS PAL 793). P, Polliniferous cone type 3 (NMS PAL 877). Scale bars = 1 cm unless otherwise indicated.

Table 2
Morphological Characteristics of Polliniferous Organs from Kühwiesenkopf/Monte Prà della Vacca and Selected Anisian Localities

Taxon	Microsporophyll arrangement	Microsporophyll length (mm)	Axis-microsporophyll angle	Microsporophyll head (length × width; mm)	Microsporophyll head shape	Microsporangia arrangement	Pollen
<u><i>Voltzia recubariensis</i></u>	Spiral	2–4	20°–100°	3.2–6.5 × 2–5.3	Rhomboidal	Parallel	? <i>Lueckisporites</i> ? <i>Lunatisporites</i>
<u><i>Willsiostrobus cf. rhomboidalis</i></u>	Spiral	5.5–5.9	ca. 90°	3.1–3.9 × 2.5–3	Rhomboidal	Parallel	...
<u><i>Willsiostrobus sp.</i></u>	Spiral	7–7.3	ca. 90°	Parallel	<i>Striatites/Striatoabieites</i>
<u>?<i>Darneya sp.</i></u>	Spiral	5.1–7.9	60°–120°	2.9 × 2.5	Hand shaped		...
<i>Darneya dentata</i>	Spiral	5–6	...	12–20 × 5–7	Subtriangular, indented, mucronate	Stalked, clusters	?
<i>Darneya mougeotii</i>	Spiral	16	...	13–26.5 × 8–12.5	Elongated, mucronate	Stalked, clusters	<i>Triadispora falcata</i> (<i>Inaperturopollenites</i> sp. = immature form)
<i>Darneya peltata</i>	Spiral	10–19	ca. 90°	5.8–16 × 6–15	Mucronate	Stalked, clusters	<i>T. falcata</i> (<i>Inaperturopollenites</i> sp. = immature form)
<i>Sertostrobus laxus</i>	Loose spiral	2–4	...	3–12 × 2.5–6	Expanded basis and apically mucronate	Stalked, clusters	<i>Triadispora staplinii</i>
<i>Willsiostrobus acuminatus</i>	Spiral	5	ca. 90°	2–3 × 4–7	Subtriangular with narrow, elongated apex	Parallel	<i>Illinites kosankei</i>
<i>Willsiostrobus bromsgrovensis</i>	Spiral, imbricate	9	90°	4.5 × 3.5	Triangular	Parallel	<i>Alisporites grauvogelii</i>
<i>Willsiostrobus cordiformis</i>	Spiral, imbricate	11.5	90°–100°	5–6 × 4–4.7	Mucronate	Parallel	<i>Alisporites cordiformis</i>
<i>Willsiostrobus denticulatus</i>	Spiral, imbricate	1.5–3.5	ca. 90°	2–4 × 2.2–3.2	Indented, mucronate	Parallel	<i>Alisporites circulicarpus</i>
<i>Willsiostrobus ligulatus</i>	Spiral	10–11	30°–90°	5 × 3	Expanded basis with narrow, elongated apex	Parallel	<i>Voltziaceasporites heteromorpha</i>
<i>Willsiostrobus rhomboidalis</i>	Spiral, imbricate	9	60°	4.5 × 3	Lozenge, expanded basis	Parallel	<i>V. heteromorpha</i>
<i>Willsiostrobus willsii</i>	Spiral, imbricate	6	ca. 90°	3.5 × 2	Triangular	Parallel	<i>Alisporites willsii</i> <i>Voltziaceasporites</i>

Sources. *Darneya dentata*, *D. mougeotii*, and *D. peltata* (according to Grauvogel-Stamm 1978); *S. laxus* (according to Grauvogel-Stamm 1969); *W. acuminatus*, *W. bromsgrovensis*, *W. cordiformis*, *W. denticulatus*, *W. ligulatus*, *W. rhomboidalis*, and *W. willsii* (according to Grauvogel-Stamm 1969, 1978).

Note. Comparison of morphological characteristics of polliniferous cones from Kühwiesenkopf/Monte Prà della Vacca (underlined) and other Anisian taxa.

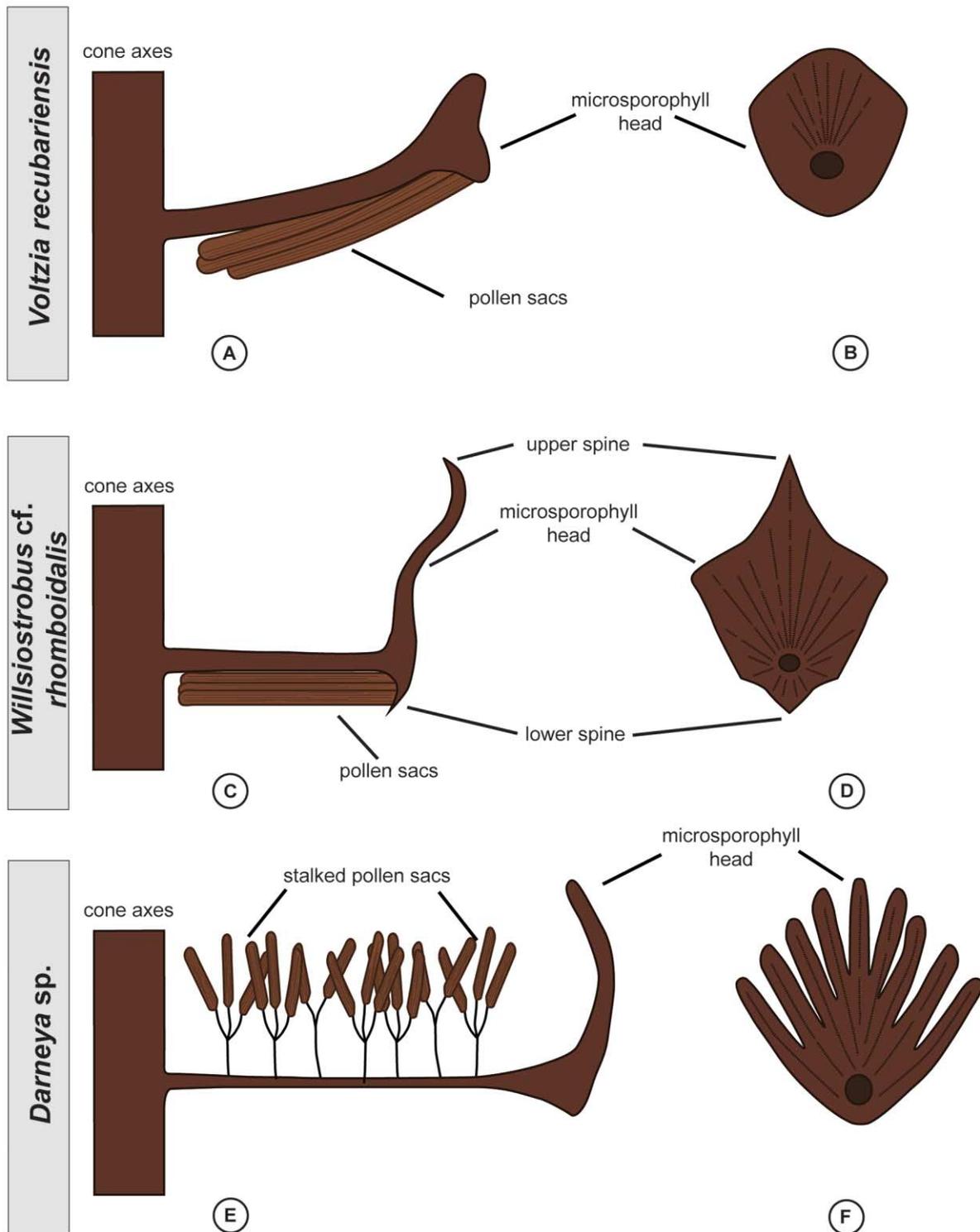


Fig. 11 Sketches representing microsporophylls and microsporangia of *Voltzia recubariensis* (A, B), *Willsiostrobus cf. rhomboidalis* (C, D), and *?Darneya sp.* (E, F) polliniferous cones.

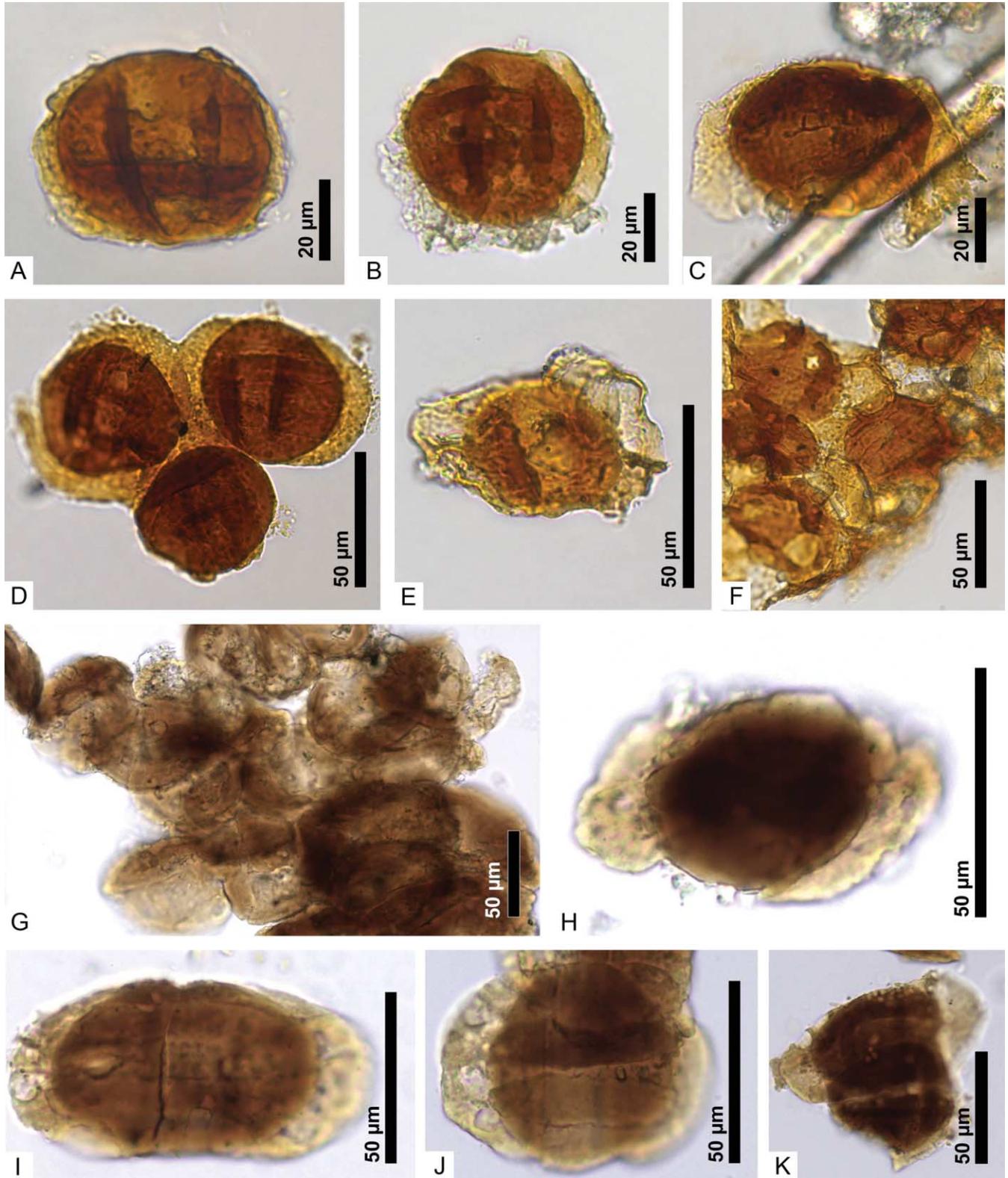


Fig. 12 In situ pollen from *Voltzia recubariensis* and *Willsiostrobus* sp. type 1 and type 2 polliniferous cones. A, B, Taeniate bisaccate pollen grains from a *V. recubariensis* cone comparable to *Lueckisporites/Lunatisporites* (NMS PAL 569). C, Taeniate bisaccate pollen grain from *V. recubariensis* with a trilete marker (NMS PAL 569). D, *Lueckisporites/Lunatisporites* pollen grains from a *V. recubariensis* cone (NMS PAL 786). E, Bisaccate, haploxytonoid, multitaeniate pollen from *Willsiostrobus* sp. assigned to *Striatites/Striatoabieites* grain (NMS PAL 794). F, Cluster of *Striatites/Striatoabieites* pollen grains (NMS PAL 794). G, Cluster of taeniate pollen grains from a type 1 cone (NMS PAL 890). H, Taeniate bisaccate pollen grain from a type 1 cone (NMS PAL 890). I, J, Taeniate bisaccate pollen grains from a type 2 cone (NMS PAL 1253). K, Taeniate bisaccate pollen grain fragment from a type 2 polliniferous cone (NMS PAL 1253).

the microsporophyll head, where they run parallel to its axis (NMS PAL 794; table 2; fig. 10I).

In situ pollen. *Willsiostrobus* sp. yielded bisaccate, haploxyloxyloid to slightly diploxyloxyloid, multitaeniate pollen grains, 67–89 μm in length, with an oval corpus, approximately semi-spherical sacci, and no visible proximal aperture. It is assigned to *Striatites*/*Striatoabieites* (NMS PAL 794; table 2; fig. 12E, 12F).

Discussion. The assignment to the genus *Willsiostrobus* is based on the arrangement of the pollen sacs, which are parallel and attached on the lower side of the microsporophyll head (table 2). The microsporophylls of *Willsiostrobus* sp. are arranged in a loose spiral, forming an open structure that is usually more compact in the other *Willsiostrobus* species (e.g., Grauvogel-Stamm 1969, 1978; Grauvogel-Stamm and Schaarschmidt 1978, 1979; Grauvogel-Stamm and Álvarez Ramis 1996). The microsporophyll length of *Willsiostrobus* sp. is comparable to that of *W. rhomboidalis* and *W. willsii* (e.g., Grauvogel-Stamm 1978; Grauvogel-Stamm and Schaarschmidt 1978, 1979; table 2). However, in *Willsiostrobus* sp. the microsporophylls are always preserved in lateral view; thus, the microsporophyll head shape and dimension are not known in detail. This makes a comparison to other *Willsiostrobus* species and an assignment to the species level difficult (table 2).

The in situ pollen grains are comparable to those of *Striatoabieites* or *Striatites*. *Striatoabieites* ex gr. *ayugii* 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.

Multitaeniate (or multistriate) bisaccate pollen grains are known mostly from seed ferns (e.g., Balme 1995). Townrow (1967b) reported small groups of pollen grains with multiple striae attached to the cuticle of *Voltziopsis wolganensis* Townrow, 1967b from Australia that may have been ex situ and were compared to *Protobaploxylinus microcorpus* by Balme (1995). The spores of *M.* (= *W.*) *willsii* from the Lower Keuper in England were first described by Townrow (1962, p. 26) as having a thickened proximal exine “pierced by numerous sometimes anastomosing light lines,” suggesting a (multi)taeniate condition, but this feature is not clear from the illustrations. In a later study, in situ pollen from the type specimen was figured and described as nontaeniate (Grauvogel-Stamm 1972, 1978).

?*Darneya* sp. (Fig. 10J–10L)

Specimen. NMS PAL 2139.

Description. The dispersed pollen cone is elongate and 39 mm long and 13 mm wide (table 2; fig. 10J–10L) and has a stout central axis, up to 3.7 mm thick (table 2; fig. 10J–10L). In lateral view the microsporophylls are 5.1–7.9 mm long, with a 4–4.5-mm-long stalk. The distal part forms a symmetrical head, up to 2.9 mm long and 2.5 mm wide, which is hand shaped with up to nine lobes (table 2; figs. 10J–10L, 11E, 11F). Microsporophylls are tightly arranged, arising spirally from the axes at angles of 60°–120°, narrowing toward the cone apex (table 2). Pollen sacs are elongate, stalked, and arranged in clusters attached to the microsporophyll stalk (table 2; figs. 10J–10L, 11E, 11F). In situ pollen grains are not preserved.

Discussion. The putative assignment to the Anisian genus *Darneya* is mainly due to the presence of stalked pollen sacs ar-

ranged in clusters attached to the microsporophyll stalk, which is common among other species of *Darneya*, such as *Darneya dentata*, *Darneya peltata*, and *Darneya mougeotii* (e.g., Schaarschmidt and Maubeuge 1969; Grauvogel-Stamm 1978; Taylor and Grauvogel-Stamm 1995; Gall and Grauvogel-Stamm 2005; table 2; figs. 10J–10L, 11E, 11F). The same arrangement of pollen sacs is observed in *S. latus*. However, in the latter species microsporophylls are arranged in a loose helix (table 2), whereas the spiral organization in ?*Darneya* sp. is more tight, resembling the one in *Darneya* cones (e.g., Grauvogel-Stamm 1978). The main macromorphological differences among various *Darneya* species are the microsporophyll length and shape of the head (e.g., Grauvogel-Stamm 1978; table 2). *Darneya mougeotii* and *D. peltata* have longer microsporophylls than *D. dentata*; in turn, *D. peltata* has smaller microsporophyll heads than *D. mougeotii* (table 2). While the microsporophyll lengths of ?*Darneya* sp. and *D. dentata* are comparable (table 2), ?*Darneya* sp. also shows remarkable differences in the shape and dimension of the microsporophyll heads (table 2; figs. 10J–10L, 11E, 11F). Microsporophyll heads of ?*Darneya* sp. are smaller and shorter than in the other *Darneya* species and have a characteristic hand shape, with up to nine lobes (table 2; fig. 11E, 11F). These significant morphological differences observed in ?*Darneya* sp. do not allow us to assign it confidently to any species of *Darneya*.

Pollen Cone Type 1

Specimen. NMS PAL 890 (figs. 10M, 12G, 12H).

Description. One dispersed specimen is described as “pollen cone type 1,” as no further assignment was possible (fig. 10M). The cone is disarticulated, 56 mm long and 20 mm wide, with a central axis ca. 4.1 mm thick. Microsporophylls are helically arranged around the axis and very fragmented. Thus, their dimensions and shape remain unclear so far. Similarly, unfortunately no information is available for the pollen sacs because of the poor preservation of the specimen (fig. 10M).

In situ pollen. Despite the poor preservation of the cone, abundant and well-preserved in situ taeniate bisaccate pollen was found in this cone (figs. 10M, 12G, 12H). Pollen grains are grouped in little masses (fig. 12G), diploxyloxyloid or haploxyloxyloid, 55–96 μm in length, with a circular or longitudinally elongated corpus, two or four taeniae, and in some cases a faint monolete mark. The sacci are short, sometimes as wide as the central body but often narrower.

Discussion. The in situ pollen grains are generally like those of *V. recubariensis* described above, except that the sacci are often reduced and a trilete mark has not been observed (fig. 12G, 12H). They are likewise assignable to *Lueckisporites* or *Lumatisporites* depending on the number of taeniae (fig. 12G, 12H).

Pollen Cone Type 2

Specimen. NMS PAL 1253 (figs. 10N, 12I–12K).

Description. This poorly preserved pollen cone is 54.3 mm long and 20.1 mm wide (NMS PAL 1253; fig. 10N). Microsporophylls are helically arranged around the axis (fig. 10N); they have a stalk and an elongate, narrow, leaf-shaped head, ca. 4–7.5 mm long and 2–2.4 mm wide, terminating in a pointed apex (fig. 10N). The specimen is partly disarticulated; thus, no further

details are available about the cone structure, arrangement, dimensions, and shape of the microsporophylls and pollen sacs (fig. 10N).

In situ pollen. The in situ pollen grains are bisaccate, generally haploxylonoid, 63–95 μm in length, with a circular to elongated oval corpus and two or four translateral taeniae, the outer taeniae being less conspicuous (fig. 12I–12K). Between the taeniae, a strip of unthickened exine may or may not be present, as well as an often inconspicuous monolete aperture. The sacchi are about semispherical, as wide as the corpus, with a fine and imperfect reticulum.

Discussion. The in situ pollen grains are comparable to those of *Lueckisporites* (two taeniae) or *Lunatisporites* (four taeniae). They partly resemble the taeniolate pollen extracted from other conifer cones in the assemblage, but in many cases, the taeniae of this type are broader and have only narrow gaps between them. Some of the grains are similar to those of *Lueckisporites* sp. figured in Kustatscher and Roghi (2006, pl. 4, fig. 5), but the latter has larger sacchi.

Pollen Cone Type 3

Specimens. NMS PAL 707, 793, 877 (fig. 10O, 10P).

Description. Three structures between 18 and 23 mm long and 6 and 15 mm wide are assigned to pollen cone type 3 (e.g., NMS PAL 793, 877; fig. 10O, 10P). The cones are compact and elongated, narrowing in the upper part and partially covered by the sediment. Microsporophylls are helically arranged, with a rhomboidal head, 1.35–1.83 mm long and 1.16–1.21 mm wide.

Thick cuticle fragments were obtained from one specimen (NMS PAL 877; fig. 8I, 8J). The epidermal cells are isodiametric to elongate, 10–45 μm long and 10–31 μm wide, with large papillae and thick cell walls. Stomata, ca. 55–130 μm long and 25–43 μm wide, are longitudinally oriented, monocyclic to incompletely dicyclic (NMS PAL 877; fig. 8I, 8J), with up to 11 (6 or 7) roundish to polygonal subsidiary cells, bearing one large papilla and having thick cell walls (NMS PAL 877; fig. 8I, 8J). Unfortunately, no in situ pollen was obtained.

Discussion. The epidermal features observed in one of the pollen cone fragments (NMS PAL 877; fig. 8I, 8J) show some similarities to the ones observed on both the seed organs and leaves of *P. edithae* (Forte et al. 2021), such as the thick and heavily papillate epidermal cells, the thick cell walls, the similar shape, and the presence of monocyclic to incompletely dicyclic stomata. However, the number of subsidiary cells is different, and the epidermal cells of pollen cone type 3 are smaller than the ones of *P. edithae* (fig. 8A–8G). Pollen cones assigned to type 3 also differ from the other pollen cones of Kühwiesenkopf/Monte Prà della Vacca, which are generally big, typical for other Mesozoic pollen cones. The pollen cone type 3 shows a rather reduced size, like the Paleozoic forms. The preservation of the specimens did not allow us to analyze in detail microsporophyll head shape, pollen sac arrangement, and the presence of in situ pollen. For this reason, until new material is found, we refrain from assigning these pollen cones to any species.

Discussion

The early stages of the evolution from the early Voltziales to more derived families of modern conifers are still poorly docu-

mented and understood. A significant hiatus affects, for instance, the middle Permian, for which little information is available (e.g., Lippolt and Hess 1989; Menning and German Stratigraphic Commission 2002; Looy 2007; figs. 14, 15). The Triassic is another important time interval in the evolutionary history of conifers; during the Triassic, the radiation and diversification of several lineages started, leading to the origin of the modern conifers (e.g., Niklas et al. 1983; Knoll 1986; Williams 2009). In fact, both morphological and molecular analyses suggest that most of the extant families originated during the Triassic–Jurassic (Townrow 1967a; Leslie et al. 2012, 2018), although recent findings suggest that the Podocarpaceae originated earlier, during the Paleozoic (Blomenkemper et al. 2018).

It is widely accepted that voltzian Voltziales represent a “transitional” group between the most ancient conifers and the extant conifer families because they are morphologically and stratigraphically intermediate between the walchian Voltziales and living conifer families. However, more precise phylogenetic relationships between these groups are not clearly understood (e.g., Florin 1951; Miller 1977, 1982, 1988, 1999; Grauvogel-Stamm 1978; Stockey 1981; 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; Serbet et al. 2010; Herrera et al. 2015; Contreras et al. 2017). This is mainly caused by a lack of information related to the natural incompleteness of the fossil record and the preservation of the fossil conifer remains, especially the reproductive organs. New data on the reproductive organs of Triassic Voltziales are thus fundamental for linking the Paleozoic forms to the living ones and reconstructing the origins of the modern conifer families (e.g., Rothwell et al. 2009, 2011).

Seed Cones

Reproductive organs reveal systematically important morphological characters that are fundamental to reconstructing patterns of relationships (e.g., Hernandez-Castillo et al. 2001; Rothwell et al. 2005, 2009, 2013; Escapa et al. 2010; Serbet et al. 2010; Herrera et al. 2015). Seed cones are especially useful for reconstructing conifer phylogeny (e.g., Mapes et al. 2007, 2008; Rothwell et al. 2009, 2011; Escapa et al. 2010; Herrera et al. 2015). The preference given to seed cones in the phylogenetic investigations is due to a larger morphological diversity compared with what is observed among pollen cones, which are characterized by low variations in morphology (Leslie 2011). In fact, unlike among seed cones, no major change in pollen cone morphology is associated with the radiation of conifers (e.g., Leslie 2011). It is widely accepted that this is linked to the only function of conifer pollen cones: to disperse pollen by wind. Since the morphology of the Paleozoic conifer cones was already adequate in this regard during that time, no significant selective pressure was exercised through time (e.g., Leslie 2011). By contrast, seed cones experience more varied interactions with the environment and other organisms and have several functional roles. They are the sites for pollen capture, enclose and protect ovules/seeds from predators, and facilitate the dispersal of mature seeds (e.g., Tomlison et al. 1991; Chandler and Owens 2004; Leslie 2011). The main evolutionary changes in the seed-bearing organs of voltzian Voltziales are related to the bract–dwarf shoot complex, ovule/seed morphology and arrangement, and the whole structural

organization, which can consist of fertile zones or distinct seed cones that evolved from much more open to compact forms (e.g., Leslie 2011; Herrera et al. 2015; Klymiuk et al. 2015). Paleozoic seed cones/fertile zones are characterized by lax structures composed of numerous loosely imbricated units, whereas this complexity is reduced in modern conifers. Structurally, Triassic seed cones resemble those of Paleozoic conifers, characterized by bract–dwarf shoot complexes loosely arranged around the central axis, but the sterile scales are simple, reduced, and not abundant as in the early conifers (e.g., *Ortiseia leonardii*, *Ortiseia jonkeri*, *Ortiseia visscheri*, *Dolomitia cittertae*; e.g., Florin 1964; Clement-Westerhof 1984, 1987, 1988; Looy 2007; Forte et al. 2017; table 2; fig. 13G, 13J–13L). The simplified organization consists of a bract subtending the flattened and lobed dwarf shoot bearing seeds (e.g., Clement-Westerhof 1984, 1987, 1988;

Looy 2007; Leslie 2011; Looy and Duijnste 2020). The relatively open structure of Paleozoic voltzian conifer cones/fertile zones during maturation (e.g., Schweitzer 1963, 1996; Looy 2007; Leslie 2011; Looy and Stevenson 2014) has been explained by the limited presence of seed predator arthropods (e.g., Labandeira 2002). However, with the advent of new animal feeding strategies, new adaptations by the voltzian conifers were necessary (e.g., more compact cones, imbrication and interlocking of bract–dwarf shoot complexes, presence of spines) for the protection of ovules/seeds (e.g., Escapa et al. 2010; Herrera et al. 2015; Klymiuk et al. 2015).

The seed cones of *Voltzia recubariensis*, cf. *Voltzia* sp. 1, *Pseudovoltzia edithae*, and *Sidashia tridentata* are characterized by loosely organized structures with helically arranged bract–dwarf shoot complexes that resemble those of the Permian

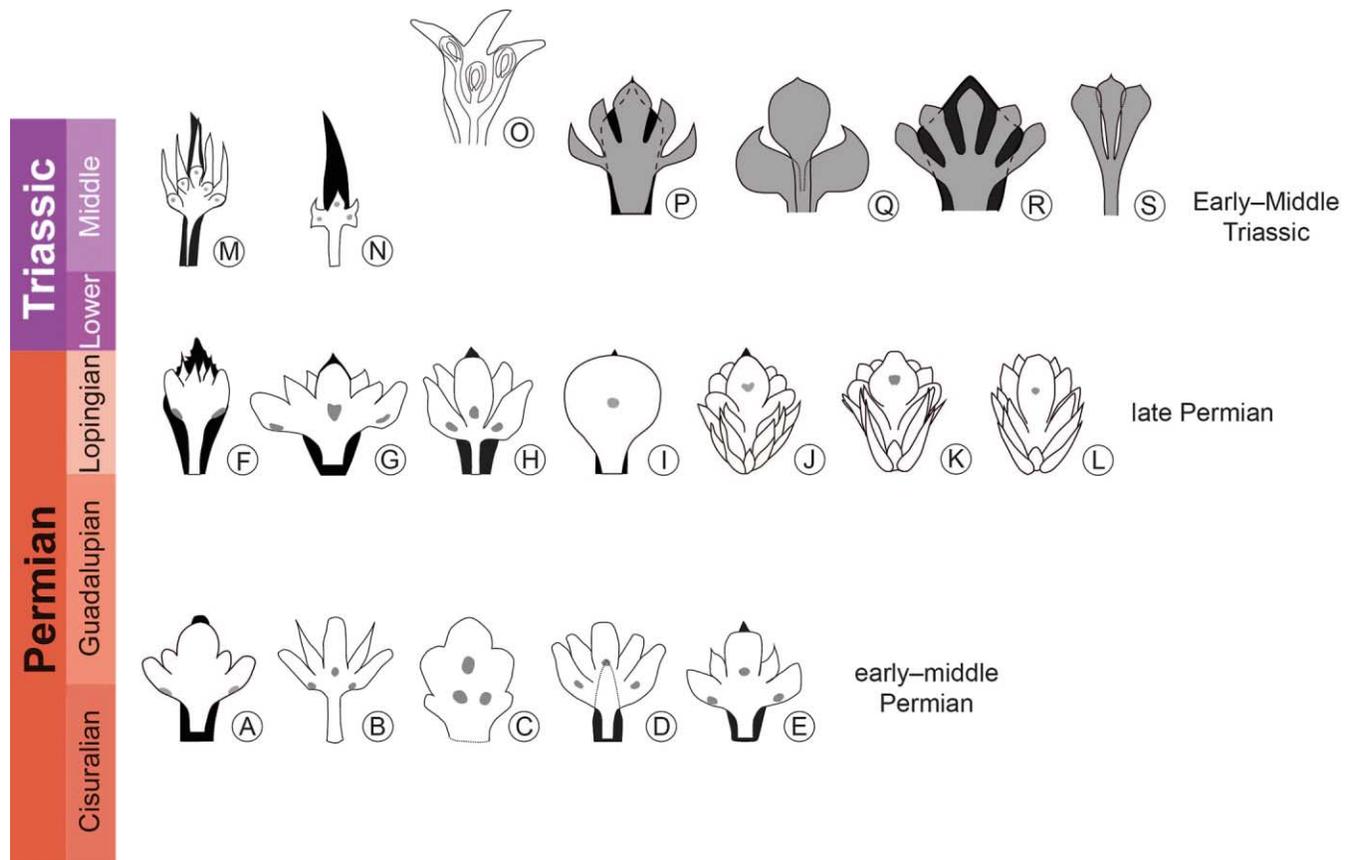


Fig. 13 Ovuliferous bract–dwarf shoot complexes of selected conifers from the early Permian to Middle Triassic. Bracts are colored in black and outlined by dashed lines when they are covered by the scales. Dwarf shoots from Kühwiesenkopf/Monte Prà della Vacca are colored in gray. A, *Lebowskia grandifolia* modified after Looy (2007). B, *Manifera taralis* modified after Looy and Stevenson (2014). C, *Wantus acaulis* modified after Looy and Duijnste (2020). D, *Pseudovoltzia sapfloreensis* modified after Looy and Duijnste (2020). E, *Pseudovoltzia liebeana* modified after Schweitzer (1963) and Clement-Westerhof (1988). F, *Majonica alpina* modified after Clement-Westerhof (1987). G, *Dolomitia cittertae* modified after Clement-Westerhof (1987). H, *Voltzia hexagona* modified after Schweitzer (1996). I, *Ullmannia frumentaria* modified after Schweitzer (1963). J, *Ortiseia leonardii* modified after Clement-Westerhof (1984). K, *Ortiseia jonkeri* modified after Clement-Westerhof (1984). L, *Ortiseia visscheri* modified after Clement-Westerhof (1984). M, *Aethophyllum stipulare* modified after Grauvogel-Stamm (1978). N, *Cycadocarpidium pilosum* modified after Grauvogel-Stamm (1978). O, *Tricranolepis frischmannii* modified after Roselt (1958). P, *Voltzia recubariensis*. Q, cf. *Voltzia* sp. 1. R, *Pseudovoltzia edithae* comb. nov. Forte, Kustatscher et Van Konijnenburg-van Cittert, 2022. S, *Sidashia tridentata* gen. nov. sp. nov. Forte, Kustatscher et Van Konijnenburg-van Cittert, 2022.

Majonicaeae, such as *Dolomitia*, *Majonica*, and *Lebouskia* (e.g., Clement-Westerhof 1987; Schweitzer 1996; Looy 2007; Looy and Stevenson 2014; table 1; fig. 14), and some Middle Triassic conifers, such as *Aethophyllum stipulare*, *Compsostrobus neotericus*, and *Florinostrobus andrewsii* (e.g., Delevoryas and Hope 1975, 1987; Grauvogel-Stamm 1978; Rothwell et al. 2000; tables 1, 3; fig. 14). The seed cones of *V. heterophylla* and *V. walchiaeformis*, on the other hand, are compact, with densely arranged bract–dwarf shoot complexes around the axis. The dispersed empty cones with bracts still attached to the axes highlight the loose organization of some seed cones of Kühwiesenkopf/Monte Prà della Vacca (fig. 9E–9G) and support the hypothesis that these cones were likely deciduous, disarticulating after maturation, similar to many extant conifer genera (e.g., *Araucaria*, *Agathis*, *Abies*, *Cedrus*, and *Pseudolarix*; e.g., Eckenwalder 2009). The thick central axes of the empty cones might suggest that they belong to *V. recubariensis* and/or *P. edithae*. However, the interspiral distance of the bracts around the axis is more comparable to that of *V. recubariensis*. This is not surprising since *V. recubariensis* is the most common conifer species in the Kühwiesenkopf/Monte Prà della Vacca flora (Forte et al. 2021). Only in the case of *P. edithae* (fig. 7H) have isolated dwarf shoots and seeds been found, similar to some of the Majonicaeae (e.g., *Majonica alpina*, *Manifera talaris*), suggesting that they probably abscised close to seed maturation (e.g., Clement-Westerhof 1987; Looy and Stevenson 2014).

Moreover, the presence of stomata on the dwarf shoots (figs. 6, 8A–8G) suggests that they photosynthesized until abscission from the plant (e.g., Clement-Westerhof 1987; Looy 2007; Looy and Stevenson 2014).

Concerning general dwarf shoot morphology, the seed cones of Kühwiesenkopf/Monte Prà della Vacca are characterized by flattened, bilaterally symmetrical, lobed dwarf shoots attached to the bract in a subaxillary position (table 1; fig. 5). The dwarf shoots are characterized by diverse morphologies (table 1; fig. 5) and show several similarities to both late Paleozoic and Mesozoic taxa (table 1; fig. 13). The conifers of Kühwiesenkopf/Monte Prà della Vacca are characterized by three-lobed (i.e., cf. *Voltzia* sp. 1 and *S. tridentata*; table 1; figs. 5B, 5D, 13Q, 13S) to five-lobed (i.e., *V. recubariensis* and *P. edithae*; table 1; figs. 5A, 5C, 13P, 13R) dwarf shoots. The three-lobed dwarf shoots of cf. *Voltzia* sp. 1 and *S. tridentata* are remarkably different in both lobe shape and orientation (fig. 5B, 5D). The lobes of cf. *Voltzia* sp. 1 are expanded and more projected toward the sides, whereas in *S. tridentata*, they are elongated, about parallel to the apex of the dwarf shoots (fig. 5B, 5D). So far, no three-lobed conifer dwarf shoots have been reported from the Permian. Therefore, this character seems to have evolved in the Triassic since other three-lobed conifer dwarf shoots, such as *Tricranolepis frischmannii*, *Cycadocarpidium pilosum*, *Swedenborgia junior*, *Swedenborgia megasperma*, and *Swedenborgia tyttosperma*, are known from the Middle Triassic–Cretaceous (e.g., Roselt 1958;

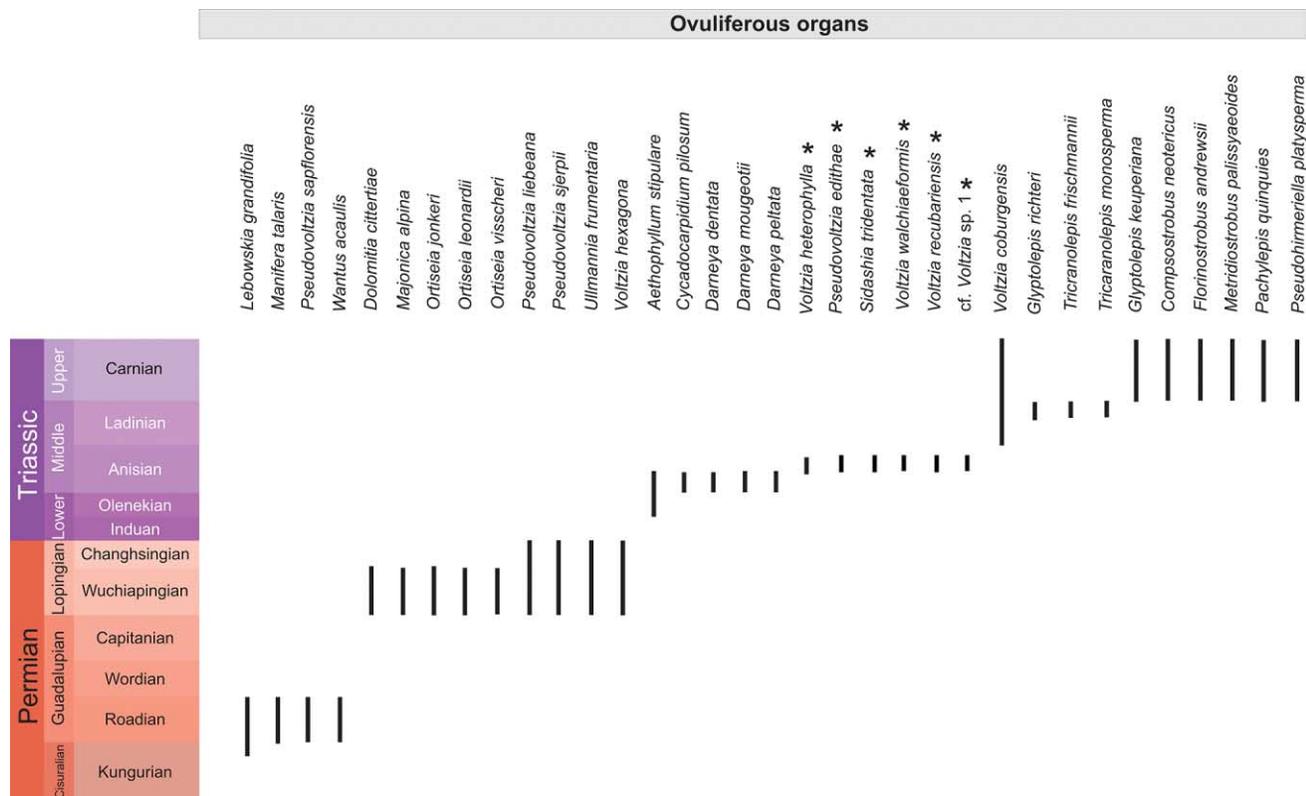


Fig. 14 Stratigraphic ranges of selected early Permian–Middle Triassic conifer taxa referred to seed reproductive organs from Europe and North America. Taxa from Kühwiesenkopf/Monte Prà della Vacca discussed in this article are indicated with an asterisk.

Table 3

Selected Permian and Mesozoic Conifer Ovuliferous Organ Taxa from Europe and North America

Taxon	Author(s)	Reference(s)	Age	Locality
<i>Aethophyllum:</i> <i>Aethophyllum stipulare</i>	Brongniart, 1828a (Brongniart) Grauvogel-Stamm, 1978	Brongniart 1828a; von Alberti 1834; Schimper and Mougeot 1844; Bronn 1851–1852; Frentzen 1931; Grauvogel-Stamm and Grauvogel 1975; Grauvogel-Stamm 1978; Miller 1982; Rothwell et al. 2000; Gall and Grauvogel-Stamm 2005; Díez et al. 2010; Escapa et al. 2010; Herrera et al. 2015; Pacyna et al. 2017	Olenekian–early Anisian	Soultz-les-Bains, Arzviller, Bust, Hangviller, Wald- hambach, Vosges du Nord, Vogesen, France
<i>Compsostrobus:</i> <i>Compsostrobus neotericus</i>	Delevoryas et Hope, 1973 Delevoryas et Hope, 1987	Delevoryas and Hope 1987; Pacyna et al. 2017	Carnian	North Carolina
<i>Conewagia:</i> <i>Conewagia longiloba</i>	Axsmith, Taylor et Taylor, 1998 Axsmith, Taylor et Taylor, 1998	Axsmith et al. 1998; Pacyna et al. 2017	Late Triassic	Pennsylvania
<i>Cycadocarpidium:</i> <i>Cycadocarpidium pilosum</i>	Nathorst, 1902 Grauvogel-Stamm, 1978	Nathorst 1902 Nathorst 1902; Grauvogel- Stamm 1978	Anisian	Vosges, France
<i>Dolomitia:</i> <i>Dolomitia cittertae</i>	Clement-Westerhof, 1987 Clement-Westerhof, 1987	Clement-Westerhof 1987, 1988; Forte et al. 2017	Wuchiapingian	Bletterbach, Italy
<i>Florinostrobus:</i> <i>Florinostrobus andrewsii</i>	Delevoryas et Hope, 1987 Delevoryas et Hope, 1987	Delevoryas and Hope 1975, 1987; Pacyna et al. 2017	Carnian	North Carolina
<i>Glyptolepis:</i> <i>Glyptolepis keuperiana</i>	Schimper, 1870 Schimper, 1870	Schimper 1870–1872; Sandberger 1882; Arndt 2002	Carnian	Sachsen-Anhalt, Coburg, Hassfurt, Stuttgart, Germany
<i>Glyptolepis richteri</i>	Axsmith et Taylor, 1997	Axsmith and Taylor 1997	Late Ladinian	Thale, Germany
<i>Lebowskia:</i> <i>Lebowskia grandifolia</i>	Looy, 2007 Looy, 2007	Looy 2007	Early–middle Permian	Texas
<i>Majonica:</i> <i>Majonica alpina</i>	Clement-Westerhof, 1987 Clement-Westerhof, 1987	Clement-Westerhof 1987	Wuchiapingian	Bletterbach, Italy
<i>Manifera:</i> <i>Manifera talaris</i>	Looy et Stevenson, 2014 Looy et Stevenson, 2014	Looy and Stevenson 2014	Early–middle Permian	Texas
<i>Metridiostrobus:</i> <i>Metridiostrobus palissyaoides</i>	Delevoryas et Hope, 1981 Delevoryas et Hope, 1981	Delevoryas and Hope 1981	Carnian–Jurassic	North Carolina
<i>Ortiseia:</i> <i>Ortiseia jonkeri</i>	Florin, 1964 Clement-Westerhof, 1984	Clement-Westerhof 1984	Wuchiapingian	Cortiana, Bletterbach, Italy
<i>Ortiseia leonardii</i>	Florin, 1964	Florin 1964; Clement-Westerhof 1984, 1987, 1988; Kustatscher et al. 2012	Wuchiapingian	Cuecenes/Val Gardena, Bletterbach, Vicentinian Alps, Italy
<i>Ortiseia visscheri</i>	Clement-Westerhof, 1984	Clement-Westerhof 1984	Wuchiapingian	Bletterbach, Italy

Table 3 (Continued)

Taxon	Author(s)	Reference(s)	Age	Locality
<i>Pachylepis:</i> <i>Pachylepis quinquies</i>	Kräusel, 1952 (Linck) Kräusel, 1952	Linck 1950; Kräusel 1952 Linck 1950; Kräusel 1952; Grauvogel-Stamm 1978; Kelber and Hansch 1995; Axsmith and Taylor 1997	Late Ladinian–Carnian	Thale, Jägerhaus, Heilbronn, Odenheim bei Tiefenbach, Eberstadt-Buchhorn, Mergelgrube, Stuttgart, Burgholzof, Germany
<i>Patokaea:</i> <i>Patokaea silesica</i>	Pacyna, Barbacka et Zdebska, 2017 Pacyna, Barbacka et Zdebska, 2017	Pacyna et al. 2017	Norian	Silesia, Poland
<i>Pseudobirmerella:</i> <i>Pseudobirmerella platysperma:</i> <i>Glyptolepis platysperma</i>	Arndt, 2002 (Mägdefrau) Arndt, 2002 Mägdefrau, 1963	Kräusel 1939; Mägdefrau 1956, 1963; Arndt 2002; Pacyna et al. 2017 Mägdefrau 1963; Cornet 1977; Axsmith and Taylor 1997	Carnian Carnian	Coburg, Hassfurt, Germany
<i>Pseudovoltzia:</i> <i>Pseudovoltzia liebeana</i>	Florin, 1927 (Geinitz) Florin, 1927	Florin 1927; Schweitzer 1962, 1963; Ullrich 1964; Clement-Westerhof 1987; Uhl and Kerp 2002; Uhl and Brandt 2004	Late Permian	Rossenray, Hoerstgen, Germany; Butterloch, Scocchi, Italy
<i>Pseudovoltzia sapfloreensis</i>	Looy et Duijnste, 2020	Looy and Duijnste 2020	Roadian	Texas
<i>Pseudovoltzia sjerpii</i>	Clement-Westerhof, 1987	Clement-Westerhof 1987	Wuchiapingian	Vicentinian Alps, Bletterbach, Italy
<i>Swedenborgia:</i> <i>Swedenborgia junior</i> <i>Swedenborgia megasperma</i> <i>Swedenborgia tyttosperma</i>	Nathorst, 1876 Krassilov, 1982a Stanislavsky, 1976 Stanislavsky, 1976	Krassilov 1982a Stanislavsky 1976; Krassilov 1982a Stanislavsky 1976; Krassilov 1982a	Early Cretaceous Early Cretaceous Early Cretaceous	Mongolia, Russia Donet, Ukraine Donet, Ukraine
<i>Telemachus:</i> <i>Telemachus elongatus</i>	Anderson, 1978 (Anderson) Yao, Taylor et Taylor, 1993	Anderson 1978; Yao et al. 1993; Escapa et al. 2010	Middle–early Late Triassic	Central Transantarctic Mountains, Antarctica; Mendoza Province, Argentina
<i>Tricranolepis:</i> <i>Tricranolepis frischmanii</i> <i>Tricranolepis monosperma</i> <i>Tricranolepis</i> sp.	Roselt, 1958 Roselt, 1958 Roselt, 1958	Roselt 1958 Roselt 1958; Grauvogel-Stamm 1978; Pacyna et al. 2017 Kelber 2015	Late Ladinian Late Ladinian Late Ladinian	Bedheim, Germany Bedheim, Philippsgarten, Turnplatz, Germany Thüringen, Germany
<i>Ullmannia:</i> <i>Ullmannia frumentaria</i>	Göppert, 1850 (Schlotheim) Göppert, 1850	Göppert 1850; Florin 1944; Schweitzer 1962	Late Permian	Gera, Germany
<i>Voltzia:</i> <i>V. coburgensis</i>	Brongniart, 1828a von Schauroth, 1852	Compter 1883, 1894, 1911; Frentzen 1922, 1930–1931; Kirchner 1928; Mägdefrau 1953; Freyberg 1965; Kelber 1990, 1998; Kelber and Hansch 1995; Arndt 2002; Silvestro et al. 2015	Ladinian–Carnian	Franken, Baden-Württemberg, Thüringen, Germany; Udine, Italy; Basel, Switzerland
<i>V. heterophylla</i>	Brongniart, 1828a	Brongniart 1828a; Grauvogel-Stamm 1978; Grauvogel-Stamm and Grauvogel 1975; Arndt 2002; Kustatscher et al. 2014	Olenekian–Anisian	Soultz-les-Bains, Vogesen, France; Fürstenberg, Germany
<i>V. hexagona</i>	(Bischoff) Geinitz 1861	Schweitzer 1963, 1996; Hernandez-Castillo et al. 2001; Pacyna et al. 2017	Late Permian	Altenmittlau, Huckelhem, Hofstädten, Germany
<i>Wantus:</i> <i>Wantus acaulis</i>	Looy et Duijnste, 2020 Looy et Duijnste, 2020	Looy and Duijnste 2020	Guadalupian	Texas

Note. List of European Middle Triassic conifer seed organ species. Authors, references, ages, and localities are indicated for each taxon. *Glyptolepis platysperma* is a synonymy of *P. platysperma*.

Stanislavsky 1976; Grauvogel-Stamm 1978; Krassilov 1982a; Herrera et al. 2015; tables 1, 3; figs. 13N, 13O, 14). In these taxa, all lobes are sporophylls characterized by different degrees of fusion, and no vegetative scales are present. The three lobes in cf. *Voltzia* sp. 1 and *S. tridentata* dwarf shoots likely represent sporophylls. However, this hypothesis cannot be confirmed until specimens are found preserved in adaxial view and traces of the attachments of the ovules/seeds are described. Five-lobed dwarf shoots, such as in *Lebouskia*, *Pseudovoltzia*, *Voltzia*, *Wantus*, *Manifera*, and *Aethophyllum* (table 1; figs. 13A–13E, 13H, 13M, 14), are commonly known from the early Permian to the Middle Triassic. These Permian–Triassic taxa are characterized by markedly separated (e.g., *V. hexagona*, *M. talaris*), partially fused (e.g., *Lebouskia grandifolia*, *Pseudovoltzia sapfloreensis*, *Pseudovoltzia liebeana*), or almost completely fused (e.g., *Wantus acaulis*, *A. stipulare*; Schweitzer 1963, 1996; Grauvogel-Stamm 1978; Looy 2007; Looy and Stevenson 2014; Looy and Duijnste 2020; table 1; figs. 13C, 13M, 14) lobes. They are generally composed of three sporophylls (one central and two lateral ones) and two vegetative scales (e.g., Looy 2007; Looy and Duijnste 2020; fig. 13A, 13B, 13D, 13E, 13H), where the sporophylls are usually prominent and larger than the vegetative scales. The five-lobed dwarf shoots of *V. recubariensis* and *P. edithae* of Kühwiesenkopf/Monte Prà della Vacca are characterized by same-sized pointed lobes (figs. 5A, 5C, 13P, 13R), and the preservation in abaxial view does not allow us to observe the presence of ovule/seed attachment points. Therefore, it is not possible to distinguish between vegetative and ovuliferous scales. The newly proposed combination *P. edithae* is based on the reduced fusion of the sporophylls (compared with that in the Triassic taxa of *Voltzia*) and vegetative scales observed in other *Pseudovoltzia* dwarf shoots (e.g., Florin 1927; Schweitzer 1963, 1996; Clement-Westerhof 1987; Looy and Duijnste 2020). The presence of *P. edithae* in the Anisian Kühwiesenkopf/Monte Prà della Vacca flora extends the genus *Pseudovoltzia* from the Permian up to the Middle Triassic. Nonetheless, the past contradicting interpretations of the *Voltzia/Pseudovoltzia* complex, which have generated and still continue to generate confusion and misidentifications, and a formal revision of the *Voltzia/Pseudovoltzia* complex genera would be needed (for details, see Looy and Duijnste 2020). This is, however, beyond the aims of this article.

Pollen Cones

The Triassic conifer pollen cones were diversified and included several simple but also some compound forms (e.g., Grauvogel-Stamm 1969, 1978; Schaarschmidt and Maubeuge 1969; Grauvogel-Stamm and Grauvogel 1973; Meyen 1976; Grauvogel-Stamm and Schaarschmidt 1979; Taylor and Grauvogel-Stamm 1995; Grauvogel-Stamm and Galtier 1998). One of the characteristics of the Triassic voltzialean pollen cones (e.g., *Aethophyllum*, *Darneya*, *Hercynostrobus*, *Ruehleostachys*, *Sertostrobus*, *Willsiostrobus*; e.g., Roselt 1956; Schaarschmidt and Maubeuge 1969; Grauvogel-Stamm 1978; Grauvogel-Stamm and Schaarschmidt 1979; Arndt 2002; table 4; fig. 15) compared with other younger conifer forms (e.g., *Classostrobus*, *Hirmeriella*, *Kobalostrobus*; e.g., Serlin et al. 1981; Krassilov 1982b; Clement-Westerhof and Van Konijnenburg-van Cittert 1991; Barbacka et al. 2007; Rothwell et al. 2007; Hieger et al. 2015; Pacyna et al. 2017) is their larger size. The size of polliniferous

cones was gradually reduced from the most ancient to the younger forms, with some exceptions in the Upper Triassic and Lower Cretaceous (e.g., *Patokaea*, *Tomaxellia*; Archangelsky and Gamberro 1967; Archangelsky 1968; Pacyna et al. 2017). The pollen cones of Kühwiesenkopf/Monte Prà della Vacca are relatively large, with sizes comparable to those of most of the other Triassic taxa, ranging from 40 to 85 mm long and 15 to 23 mm wide.

Another characteristic that distinguishes the Triassic Voltziales from most recent conifers is their large number of pollen sacs (e.g., Grauvogel-Stamm 1969, 1972; Grauvogel-Stamm and Álvarez Ramis 1996; Grauvogel-Stamm and Galtier 1998; Pacyna et al. 2017). Unfortunately, the number is difficult to interpret in the Kühwiesenkopf/Monte Prà della Vacca specimens because of their preservation. However, it was possible to identify their arrangement in some of the taxa (i.e., *V. recubariensis*, *Willsiostrobus* cf. *rhomboidalis*, *Willsiostrobus* sp., ?*Darneya* sp.). Characterizing the late Paleozoic and Mesozoic conifer pollen cones, Meyen (1997) proposed three different groups based on the arrangement of pollen sacs: (i) cones with pollen sacs attached to the microsporophyll head (perisporangiate peltate forms), such as *Willsiostrobus* and *Ruehleostachys* (e.g., Roselt 1956; Grauvogel-Stamm 1978; Arndt 2002; tables 2, 4), which have pollen sacs that are parallel and attached to the abaxial side of the sporophyll head; (ii) those with pollen sacs directly attached to the microsporophyll stalk; and (iii) those with stalked microsporangia attached to the microsporophyll stalk and arranged in clusters (episperangiate peltate forms), such as *Darneya* and *Sertostrobus* (e.g., Grauvogel-Stamm 1978; Grauvogel-Stamm and Schaarschmidt 1979; Taylor and Grauvogel-Stamm 1995; Meyen 1997; tables 2, 4). The occurrence of pollen sacs attached to the microsporophyll stalk is considered a primitive characteristic present in Permian and Triassic Voltziales (Pacyna et al. 2017).

The pollen cones of Kühwiesenkopf/Monte Prà della Vacca can be included in at least two of these groups, the perisporangiate peltate and episperangiate peltate ones (fig. 11). The former group includes, in our case, the taxa *V. recubariensis*, *W. cf. rhomboidalis*, and *Willsiostrobus* sp. (table 2; figs. 10A–10I, 11A–11D). In the case of *V. recubariensis*, a pollen cone was even found anatomically connected to the branch (NMS PAL 787/788; fig. 10A). *Voltzia recubariensis* cones resemble some *Willsiostrobus* species (e.g., Grauvogel-Stamm 1969, 1978; Grauvogel-Stamm and Grauvogel 1975; Grauvogel-Stamm and Schaarschmidt 1978, 1979; table 2; figs. 10A–10I, 11A–11D), especially in the tight and spiral arrangement of the microsporophylls around the axis and the pollen sacs attached to the microsporophyll head (fig. 11). The taeniate bisaccate in situ pollen grains of *V. recubariensis* cones are comparable to *Lueckisporites/Lunatisporites*, differing from other *Willsiostrobus*-type cones, from which only nontaeniate *Alisporites*-, *Illinites*-, or *Voltziaceasporites*-type pollen grains have so far been described (e.g., Grauvogel-Stamm 1978; table 2). Pollen cone type 1 and type 2 (NMS PAL 890, 1253; figs. 10M, 10N, 12G–12K) are characterized by poor preservation of the macroremains, which unfortunately do not allow us to provide a complete macromorphological description. Both of the cones, however, yielded pollen grains assignable to the dispersed pollen genera *Lueckisporites* or *Lunatisporites*, which may suggest that they belong to *V. recubariensis* or closely related *Voltzia* species. On the basis of currently available information regarding in situ pollen, the presence

Table 4

Selected Permian–Triassic Polliniferous Organ Conifer Taxa from Europe and North America

Taxon	Author(s)	Reference(s)	Age	Locality
<i>Darneya:</i>	Schaarschmidt et Maubeuge, 1969			
<i>Darneya dentata</i>	Grauvogel-Stamm, 1978	Grauvogel-Stamm 1978; Gall and Grauvogel-Stamm 2005	Early Anisian	Vilsberg, France
<i>Darneya mougeotii:</i>	Grauvogel-Stamm, 1978	Grauvogel-Stamm 1978; Gall and Grauvogel-Stamm 2005	Early Anisian	Bust, Oeting, Vilsberg, France
<i>Voltziostrobus mougeotii</i>	Grauvogel-Stamm, 1969	Grauvogel-Stamm 1969	Early Anisian	Bust, Oeting, Vilsberg, Carrière Dietsch, France
<i>Darneya peltata:</i>	(Schaarschmidt et Maubeuge) Grauvogel-Stamm, 1978	Schaarschmidt and Maubeuge 1969; Grauvogel-Stamm 1978; Grauvogel-Stamm and Schaarschmidt 1979; Grauvogel-Stamm and Galtier 1998; Díez et al. 2010	Early Anisian	Vosges, Darney, Vilsberg, Petersbach, Oeting, Hangviller, Gottenhouse, Bust, Arzwiller, Adamsviller, Bust, Carrière Schneider G., Carrière Dietsch, Sultz-les-Bains, France; Rodanas-Tabuena, Spain
<i>Voltziostrobus schimperi</i>	Grauvogel-Stamm, 1969	Grauvogel-Stamm 1969	Early Anisian	Vosges, France
<i>Darneya</i> sp.		Díez et al. 1996, 2010; Borrueal-Abadía et al. 2014	Bithinian–Pelsonian, Anisian	Rodanas, Rodanas-Tabuena, Maya del Baztán, Spain; Sultz-les-Bains, France
<i>Hercynostrobus:</i>	Arndt, 2002			
<i>Hercynostrobus digitatus</i>	Arndt, 2002	Arndt 2002	Late Ladinian	Bedheim Irmelshausen, Thale, Germany
<i>Majonica:</i>	Clement-Westerhof, 1987			
<i>Majonica alpina</i>	Clement-Westerhof, 1987	Clement-Westerhof 1987	Wuchiapingian	Bletterbach, Italy
<i>Millerostrobus:</i>	Taylor, Delevoryas et Hope, 1987			
<i>Millerostrobus pekimensis</i>	Taylor, Delevoryas et Hope, 1987	Taylor et al. 1987; Axsmith and Ash 2006	Late Triassic	North Carolina
<i>Ortiseia:</i>	Florin, 1964			
<i>Ortiseia jonkeri</i>	Clement-Westerhof, 1984	Clement-Westerhof 1984	Wuchiapingian	Cortiana, Bletterbach, Italy
<i>Ortiseia leonardii</i>	Florin, 1964	Florin 1964; Clement-Westerhof 1984, 1987, 1988; Kustatscher et al. 2012	Wuchiapingian	Cuecenes/Val Gardena, Bletterbach, Vicentinian Alps, Gera, Italy
<i>Ortiseia visscheri</i>	Clement-Westerhof, 1984	Clement-Westerhof 1984	Wuchiapingian	Bletterbach, Italy
<i>Rhenania:</i>	Schweitzer, 1962			
<i>Rhenania reichelti</i>	Schweitzer, 1962	Schweitzer 1962; Schaarschmidt and Maubeuge 1969	Late Permian	Hoerstgen, Germany
<i>Ruehleostachys:</i>	Roselt, 1956			
<i>Ruehleostachys pseudarticulatus</i>	(Roselt) Arndt, 2002	Roselt 1956; Arndt 2002	Late Ladinian	Bedheim, Germany
<i>Ruehleostachys</i> sp.		Kelber 2015		Rockhausen bei Arnstadt/Erfurt, Germany
<i>Sertostrobus:</i>	Grauvogel-Stamm, 1969			
<i>Sertostrobus laxus</i>	Grauvogel-Stamm, 1969	Grauvogel-Stamm 1969, 1978; Grauvogel-Stamm and Schaarschmidt 1979; Taylor and Grauvogel-Stamm 1995	Early Anisian	Adamsviller, Arzwiller, Carrière Bopp et Dintzner, Bust, Gottenhouse, Oeting, Schoenbourg, Vilsberg, Wasselonne, France
<i>Sertostrobus</i> sp.			Late Ladinian	Alter Turnplatz, Dedheim, Thüringen, Philippsgarten, Germany

Table 4 (Continued)

Taxon	Author(s)	Reference(s)	Age	Locality
<i>Ullmannia</i> :				
<i>Ullmannia frumentaria</i>	Geinitz, 1880	Geinitz 1880; Schweitzer 1962, 1996	Late Permian	Hoerstgen, Rossenray, Germany
<i>Uralostrobos</i> :	Naugolnykh, 2014			
<i>Uralostrobos voltzioides</i>	Naugolnykh, 2014	Naugolnykh 2014	Kungurian	Chekarda, Russia
<i>Voltzia</i> :	Brongniart, 1828a			
<i>Voltzia hexagona</i>	(Bischoff) Geinitz, 1861	Schweitzer 1963, 1996	Early Permian	Altenmittlau, Huckelhem, Hofstädten, Germany
<i>Voltzia recubariensis</i>	(De Zigno) Schenk emend. Forte, Kustatscher et Van Konijnenburg-van Cittert, 2022	This article	Pelsonian	Kühwiesenkopf/Monte Prà della Vacca, Italy
<i>Willsiostrobos</i> :	Grauvogel-Stamm et Schaarschmidt, 1978			
<i>Willsiostrobos acuminatus</i> :	Grauvogel-Stamm et Schaarschmidt, 1978	Brongniart 1828a; von Alberti 1834; Schimper and Mougeot 1844; Bronn 1851–1852; Frentzen 1931; Grauvogel-Stamm and Grauvogel 1975; Grauvogel-Stamm and Schaarschmidt 1978, 1979; Grauvogel-Stamm 1987; Rothwell et al. 2000; Gall and Grauvogel-Stamm 2005; Díez et al. 2010; Escapa et al. 2010; Herrera et al. 2015	Early–Middle Triassic	Bust, Gottenhouse, Sultz-les-Bains, Vilsberg, Arzviller, Hangviller, Waldhambach, Vosges du Nord, France; Lower Saxony, Germany; Majorca, Spain
<i>Masculostrobos acuminatus</i>	Grauvogel-Stamm, 1978	Grauvogel-Stamm 1978	Early Anisian	Alsace, Vosges, France
<i>Aethophyllum stipulare</i>	(Brongniart) Grauvogel-Stamm, 1978	Grauvogel-Stamm and Grauvogel 1973, 1975; Grauvogel-Stamm 1978; Grauvogel-Stamm and Schaarschmidt 1978; Gall and Grauvogel-Stamm 2005	Early Anisian	Vosges, France
<i>Willsiostrobos bromsgrovensis</i> :	Grauvogel-Stamm et Schaarschmidt, 1978	Grauvogel-Stamm 1978; Grauvogel-Stamm and Schaarschmidt 1978, 1979; Kustatscher et al. 2014	Anisian	Worcestershire, England
<i>Masculostrobos bromsgrovensis</i>	Grauvogel-Stamm, 1972	Grauvogel-Stamm 1972		
<i>Willsiostrobos cordiformis</i> :	Grauvogel-Stamm et Schaarschmidt, 1978	Grauvogel-Stamm 1978; Grauvogel-Stamm and Schaarschmidt 1978, 1979; Kustatscher et al. 2014	Late Olenekian, early Anisian	Vosges du Nord, France
<i>Masculostrobos cordiformis</i>	Grauvogel-Stamm, 1969	Grauvogel-Stamm 1969		
<i>Willsiostrobos denticulatus</i> :	Grauvogel-Stamm et Schaarschmidt, 1978	Grauvogel-Stamm 1978; Grauvogel-Stamm and Schaarschmidt 1978, 1979	Early Anisian	Bust, Hangviller, Vilsber, France
<i>Masculostrobos denticulatus</i>	Grauvogel-Stamm, 1969	Grauvogel-Stamm 1969		
<i>Willsiostrobos hexasaccisphorus</i>	Grauvogel-Stamm et Alvarez Ramis, 1996	Grauvogel-Stamm and Alvarez Ramis 1996	Middle Anisian	Majorca, Spain
<i>Willsiostrobos ligulatus</i> :	(Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978	Grauvogel-Stamm 1969; Grauvogel-Stamm and Schaarschmidt 1978, 1979	Early Anisian	Vosges, France
<i>Masculostrobos ligulatus</i>	Grauvogel-Stamm, 1969	Grauvogel-Stamm 1969		
<i>Willsiostrobos rhomboidalis</i> :	(Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt, 1978	Grauvogel-Stamm 1969; Grauvogel-Stamm and Schaarschmidt 1978, 1979; Kustatscher et al. 2014	Late Olenekian–early Anisian	Bremke, Fürstenberg, Germany
<i>Masculostrobos rhomboidalis</i>	Grauvogel-Stamm, 1969	Grauvogel-Stamm 1969	Anisian	Adamsviller, Arzviller, Bust, Hangviller, Oeting, Petersbach, Vilsberg, France

Table 4 (Continued)

Taxon	Author(s)	Reference(s)	Age	Locality
<i>Willsiostrobus willsii</i> :	(Townrow) Grauvogel-Stamm et Schaarschmidt, 1978	Grauvogel-Stamm 1978; Grauvogel-Stamm and Schaarschmidt 1978, 1979; Seyfullah et al. 2013	Anisian	Vosges, France; Bromsgrove, Worcester, England
<i>Masculostrobus willsii</i>	Grauvogel-Stamm, 1969	Grauvogel-Stamm 1969, 1972	Anisian	Worcestershire, England
<i>Willsiostrobus</i> sp.		Kelber 1990; Kelber and Hansch 1995; Díez et al. 1996, 2010; Kelber and Nitsch 2005; Kelber 2015	Late Olenekian–Carnian	Maya del Baztán, Rodanas, Rodanas-Tabuena, Majorca, Spain; Thale a. Harz, Alter Steinbruch, Homannsküche bei Bremke, Bedheim, Philippsgarten, Turnplatz, Rockhausen bei Arnstadt/Erfurt, Werksandsteinbruch Schleiereth, Simsheim, Schmollenmühle, Ilsfeld, Steinbruch Gläser, Zwingelshausen, Steinbruch Schönbühlhof bei Markgröningen, Str. Klöpfer, Rielingshausen, Weiler zu Stein, Germany

Note. List of European Middle Triassic polliferous conifer organ species. Authors, references, ages, and localities are indicated for each taxon. Synonymies are listed beneath related species.

of taeniate pollen is unusual in Triassic conifers, but comparable forms are known from late Permian Voltziales (see Clement-Westerhof 1974), suggesting a close relationship. *Willsiostrobus* cf. *rhomboidalis* of Kühwiesenkopf/Monte Prà della Vacca (table 2; figs. 10F–10H, 11C, 11D) resembles in general morphology the type specimens described from France (Grauvogel-Stamm 1969, 1978), especially in the shape of the microsporophyll head, but differs in the presence of two curved spines in the sporophyll head, never observed in the original material. Moreover, no in situ pollen was obtained from *W.* cf. *rhomboidalis*. The pollen sac arrangement of the cone assigned to *Willsiostrobus* sp. (NMS PAL 794; fig. 10I) resembles that of other *Willsiostrobus* species. The arrangement of microsporophylls is lax, similar to that of *Sertostrobus laxus*, which, however, is characterized by a different arrangement of the pollen sacs. The latter are attached to the sporophyll head in *Willsiostrobus* and to the sporophyll stalk in *Sertostrobus* (e.g., Grauvogel-Stamm 1969; Grauvogel-Stamm and Schaarschmidt 1979). Moreover, *Willsiostrobus* sp. yielded bisaccate pollen assigned to *Striatites/Striatoabieites* (table 2; fig. 12E, 12F). So far, this pollen has never been reported in *Willsiostrobus* species (e.g., Grauvogel-Stamm 1969, 1978; Grauvogel-Stamm and Schaarschmidt 1978, 1979; Grauvogel-Stamm and Álvarez Ramis 1996; table 2). Therefore, we refrain from an assignment at the species level. The cone assigned to ?*Darneya* sp. is one of the most peculiar in the Kühwiesenkopf/Monte Prà della Vacca flora. The presence of stalked pollen sacs arranged in clusters and attached to the microsporophyll stalk represents a more primitive condition and signifies that it belongs to the episorangiate peltate group (Meyen 1997; Pacyna et al. 2017). Among the forms included in this group, the compact arrange-

ment of the microsporophylls suggests a greater affinity with *Darneya* (e.g., Schaarschmidt and Maubeuge 1969; Grauvogel-Stamm 1978; Taylor and Grauvogel-Stamm 1995; Gall and Grauvogel-Stamm 2005; tables 2, 4; figs. 10J–10L, 11E, 11F) than *Sertostrobus*, which, conversely, is characterized by a more compact arrangement of the microsporophylls (e.g., Grauvogel-Stamm 1969; Taylor and Grauvogel-Stamm 1995; tables 2, 4). Concerning the microsporophyll head shape of this type of pollen cone, the distal head is often characterized by a triangular to rhomboidal shape, mucronate or with an indented outline (e.g., Grauvogel-Stamm 1969, 1978; Schaarschmidt and Maubeuge 1969; Taylor and Grauvogel-Stamm 1995; Gall and Grauvogel-Stamm 2005; table 2). The hand-shaped microsporophyll heads of ?*Darneya* sp. are different (table 2; figs. 10J–10L, 11E, 11F) and might suggest that it belongs to a new species. However, since only one specimen was found and it was not possible to obtain in situ pollen, we refrain for now from the erection of a new taxon.

Amber

The dispersed amber droplets in the Kühwiesenkopf/Monte Prà della Vacca specimens and anatomically connected to conifer shoots of *V. recubariensis* represent one of the oldest worldwide occurrences of amber (Forte et al. 2021, 2022). The finding of amber in two different points of a seed cone of *V. walchiaiformis* (NMS PAL 748; fig. 2F, 2G) suggests that, together with *V. recubariensis*, this species was also a resin producer and partly contributed to the production of the amber droplets found dispersed in the sediments of Kühwiesenkopf/Monte Prà della

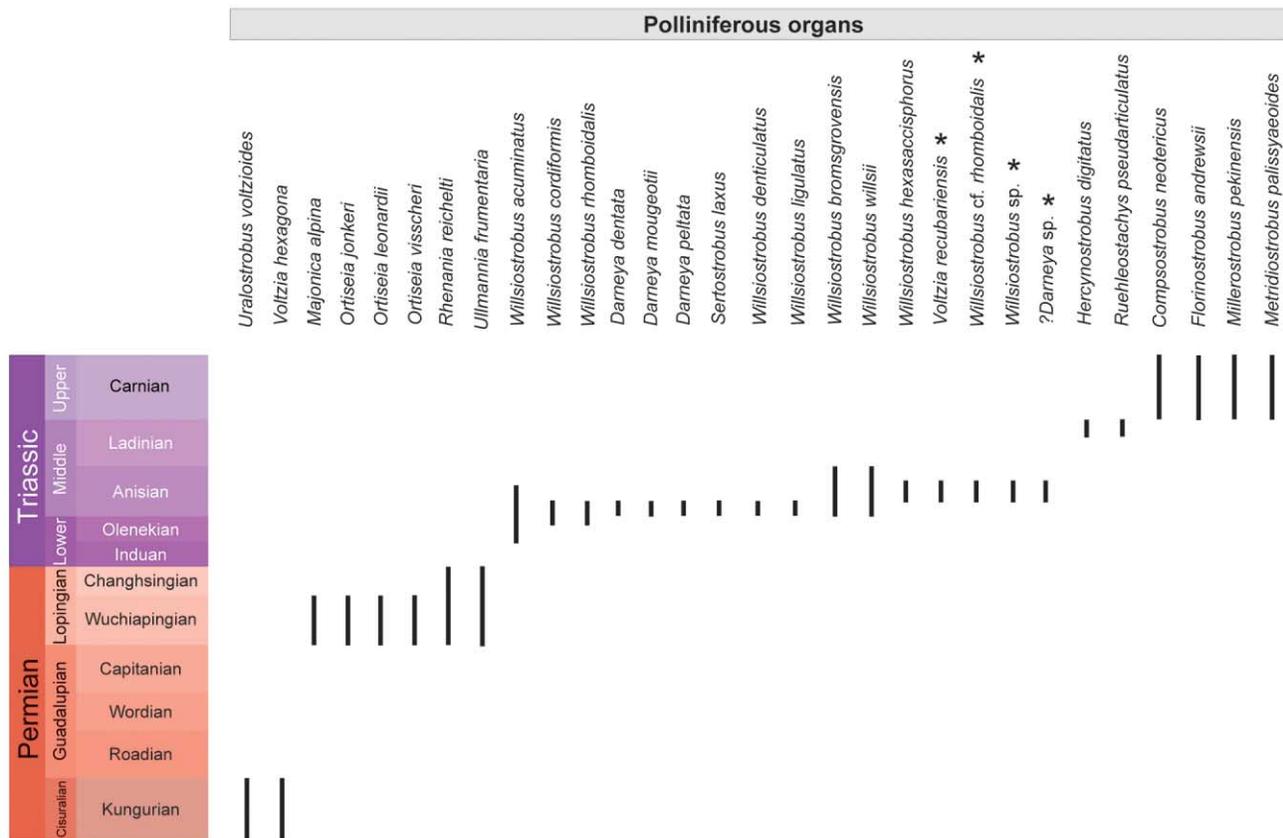


Fig. 15 Stratigraphic ranges of selected early Permian–Middle Triassic conifer taxa referred to polliniferous cones from Europe and North America. Taxa from Kühwiesenkopf/Monte Prà della Vacca discussed in this article are indicated with an asterisk.

Vacca (Forte et al. 2021, 2022). The presence of amber was reported in different localities from the Triassic and was related to stress/environmental conditions triggered by paleoclimatic events (e.g., Gianolla et al. 1998; Schmidt et al. 2006, 2012; Dal Corso et al. 2011, 2018, 2020; Roghi et al. 2017; Seyfullah et al. 2018; Forte et al. 2022). The Anisian amber of northeastern Italy was found in different localities (i.e., Recoaro, Piz da Peres, Kühwiesenkopf/Monte Prà della Vacca) and was related to paleoclimatic events and particular environmental conditions (i.e., humid episodes; e.g., Kustatscher et al. 2010a; Stefani et al. 2010; Roghi et al. 2017; Forte et al. 2022 and references therein) that occurred in the area, causing a rise in the production rate of resin and favoring its accumulation and the formation of amber (Roghi et al. 2017; Forte et al. 2022). Similar conditions occurred during the Ladinian, during which amber was found in association with *V. ladinica* (Roghi et al. 2017). The presence of amber anatomically connected to *V. recubariensis* not only is important for knowing the botanical origin of the Anisian amber of Kühwiesenkopf/Monte Prà della Vacca (Forte et al. 2021, 2022) but also confirms the important contribution of the family Voltziaceae (i.e., *V. recubariensis*, *V. walchiaeformis*, *V. ladinica*)

to the production of amber during the Anisian–Ladinian (Roghi et al. 2017; Forte et al. 2021, 2022).

Conclusions

To address questions about conifer evolution, phylogeny, and the origin of modern lineages, the characterization of Triassic conifer reproductive organs, especially seed cones, is fundamental. This study of the reproductive organs of the conifers from Kühwiesenkopf/Monte Prà della Vacca represents a further contribution to our understanding of the morphology and biology of the Triassic conifers. The presence of seed and pollen conifer cones attached to branch/shoot fragments and the preservation of cuticles in both the vegetative and reproductive organs allow us to provide more complete whole-plant reconstructions of some of the most iconic Anisian conifer taxa and to describe new morphological structures so far unknown among Triassic conifers (e.g., cf. *Voltzia* sp. 1, *Sidashia tridentata*).

The description of seed cones and their comparison with other well-known late Paleozoic–early Mesozoic species show that the Anisian conifers of Kühwiesenkopf/Monte Prà della Vacca have

similarities to late Permian–Middle Triassic species, confirming the transitional character of the voltzian Voltziales. The description of *Pseudovoltzia edithae* nov. comb. confirms its close affinity with Permian taxa and extends the fossil record of the genus *Pseudovoltzia* to the Triassic. However, it also emphasizes the urgent need for a formal revision of the *Voltzia/Pseudovoltzia* complex. The presence of empty cones with bracts still attached to the axis, resembling *V. recubariensis* cones, suggests that dwarf shoots abscised with the maturation of the seeds, whereas the presence of stomata on the dwarf shoot cuticles evidences that they were photosynthetic until their detachment from the plant, like in other Majonicaceae species.

The high morphological diversity of the Kühwiesenkopf/Monte Prà della Vacca conifers is supported by their dwarf shoot morphology, with the presence of three-lobed (i.e., *S. tridentata* and cf. *Voltzia* sp. 1) and five-lobed (i.e., *V. recubariensis* and *P. edithae*) forms. Three-lobed dwarf shoots occur in conifers only from the Triassic onward, but the dwarf shoots of Kühwiesenkopf/Monte Prà della Vacca differ remarkably from other Middle–Late Triassic taxa in morphology.

Pollen cones of Kühwiesenkopf/Monte Prà della Vacca are diverse and reflect the general diversity that characterized the Voltziales during the Triassic. Their large size is a characteristic in common with the early Permian–Triassic Voltziales. With respect to microsporophyll and pollen sac arrangements, two groups have been distinguished: the episporangiate peltate (i.e., ?*Darneya* sp.) and the perisporangiate peltate (i.e., *V. recubariensis*, *Willsiostrobus* cf. *rhomboidalis*, *Willsiostrobus* sp.) forms.

In the Kühwiesenkopf/Monte Prà della Vacca plant assemblage, pollen cones are generally dispersed. Only in the case of *V. recubariensis* have they been found anatomically connected to vegetative shoots and yielded the *Lueckisporites/Lunatisporites* type of pollen. These pollen types are otherwise known from late Permian conifers and therefore represent another transitional characteristic. ?*Darneya* sp. represents one of the most primitive and peculiar pollen cones of Kühwiesenkopf/Monte Prà della Vacca, with a noteworthy microsporophyll head shape that has never been reported in other Triassic pollen cones so far and that could represent a new taxon.

Finally, the discovery of fossil resin anatomically connected to a seed cone of *V. walchiaeformis* suggests that this species was a resin producer and that it, together with *V. recubariensis*, con-

tributed to the production of the amber found in the sediment of Kühwiesenkopf/Monte Prà della Vacca. This also supports the hypothesis that particular paleoclimatic/paleoenvironmental conditions that occurred in the southern Alps during the Anisian induced stress among the plants, causing them to increase the production of resin. Moreover, this finding confirms the contribution of Voltziaceae to the production of amber during the Anisian–Ladinian of the southern Alps.

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