CONIFER DIVERSITY IN THE MIDDLE TRIASSIC: NEW DATA FROM THE FOSSILLAGERSTÄTTE KÜHWIESENKOPF/MONTE PRÀ DELLA VACCA (PELSONIAN, ANISIAN) IN THE DOLOMITES (NORTHEASTERN ITALY)

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Guest Editor: Patricia E. Ryberg

Premise of research.   The Triassic is considered a pivotal time for the radiation of modern conifer families. In this article, we describe the conifers from the Fossillagerstätte Kühwiesenkopf/Monte Prà della Vacca, emending already known taxa and proposing a new species (*Voltzia edithae* sp. nov.). Moreover, we provide a picture of the chronostratigraphic and geographic distribution of the Middle Triassic conifer shoots of Europe.

Methodology.   The macromorphology and cuticles of the vegetative conifer organs are described, and the stratigraphic and geographic distribution pattern of the Middle Triassic conifer shoots in European is evidenced.

Pivotal results.   Six different conifer species are identified among the conifer shoots of the Kühwiesenkopf flora. Morphological analyses of our material of *Albertia* cf. *latifolia* show that the previously described species *A. latifolia*, *A. elliptica*, *A. braunii*, and *A. speciosa* probably fall within the natural variability of one species, but this has to be validated by the revision of the original specimens. The occurrence of *V. heterophylla* in the Kühwiesenkopf flora extends its geographic range to the Alpine Realm. An emended diagnosis is proposed for *V. walchiaeformis* based on well-preserved specimens, including cuticle fragments. The new species *V. edithae* sp. nov. shows significant morphological similarities to the late Permian *Majonica alpina* and the Middle–Late Triassic *V. foetterlei*.

Conclusions.   The conifers of the Kühwiesenkopf flora are unique for the Middle Triassic of Europe in their richness and diversity. The conifers are a mixture of typical Early–Middle Triassic taxa (*Pelourdea vogesiaca*, *V. heterophylla*, *V. recubariensis*), Anisian taxa (*V. walchiaeformis*), and a new species (*V. edithae* sp. nov.) that is seen as a transitional form sharing morphological characters with both late Permian and Middle–Late Triassic conifers.

Keywords: *Albertia* cf. *latifolia*, *Pelourdea vogesiaca*, *Voltzia edithae*, cuticle, conifer diversity.

Online enhancements: supplemental tables.

Introduction

The Triassic was characterized by greenhouse conditions but experienced major environmental changes linked to several short but severe climate shifts (e.g., Parrish 1993, 1998; Berner 2006; Royer 2006; Breecker et al. 2010; Preto et al. 2010). It was in this climatic scenario that a vegetation turnover took place with the appearance and radiation of modern plant families (e.g., Looy et al. 1999; Grauvogel-Stamm and Ash 2005; Hedges and Kumar 2009; Hochuli et al. 2010; Dal Corso et al. 2020) and the rapid

diversification of the gymnosperms, which became ecologically dominant for most of the Mesozoic era (e.g., Miller 1982; Anderson et al. 2007; Hedges and Kumar 2009; Kustatscher et al. 2018; Dal Corso et al. 2020). Among them, the conifers represent one of the major groups that evolved and diversified during the early Mesozoic. Between the Triassic and Early Jurassic, we have the first strong evidence of the appearance of extant conifer lineages such as Podocarpaceae, Taxaceae, Araucariaceae, Cupressaceae, and Pinaceae (e.g., Farjon 2005, 2008; Axsmith et al. 2008; Eckenwalder 2009; Rothwell et al. 2012; Escapa and Catalano 2013; Contreras et al. 2019), although lately it has been suggested that the Podocarpaceae and Araucariaceae had already originated during the Permian (e.g., DiMichele et al. 2001; Blomenkemper et al. 2018). The voltzian conifers or voltzian Voltziales (sensu Rothwell et al. 2005), which appeared in the Pennsylvanian, are considered stem lineages of several extant conifer families and the Cheirolepidiaceae (e.g., Miller 1999; Taylor et al. 2009;

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Looy and Duijnstee 2020) and have been hypothesized to be morphologically intermediate between the Late Paleozoic–early Mesozoic conifers and the modern descendants (e.g., Grauvogel-Stamm 1978; Clement-Westerhof 1987, 1988; Mapes and Rothwell 1991; Axsmith and Taylor 1997; Meyen 1997; Axsmith et al. 1998; Hernández-Castillo 2005; Rothwell et al. 2005, 2011; Escapa et al. 2010; Herrera et al. 2015). For this reason, they are also informally known as "transitional conifers" (e.g., Miller 1999; Escapa et al. 2010; Herrera et al. 2015; Looy and Duijnstee 2020).

Although several recent articles focus on the voltzian conifers (e.g., Escapa et al. 2010; Rothwell et al. 2011), their patterns of diversification and evolution remain obscure (Rothwell et al. 2005; Taylor et al. 2009). This uncertainty may be due to the incompleteness of their (Early–Middle) Triassic fossil record. A first conifer radiation seems to have taken place during the Middle Triassic (e.g., Miller 1982; Anderson et al. 2007; Hedges and Kumar 2009; Williams 2009). Voltzian conifers, mainly confined to Euramerica during the late Paleozoic, spread out to northern latitudes and the Southern Hemisphere during the early Mesozoic (e.g., Escapa et al. 2010, 2011), giving origin to a wide range of *Voltzia* species as well as several taxa with broader parallel-veined leaves, such as *Aethophyllum* Brongniart, 1828, *Albertia* Schimper in Voltz, 1837, *Heidiphyllum* Retallack, 1981, and *Pelourdea* (Seward) Ash, 1987. The discovery and description of new voltzian conifer species and the revision of well-known taxa thanks to well-preserved specimens with cuticles allow us to improve our understanding of the history of these plants that dominated the Mesozoic for the next 200 Myr.

One piece of this puzzle is represented by the conifers of the Anisian Fossillagerstätte Kühwiesenkopf/Monte Prà della Vacca, which yielded an exceptional association of marine and terrestrial biota living close to the equator some 245 million years ago (e.g., Tintori et al. 2001, 2016; Broglio Loriga et al. 2002; Posenato et al. 2004; Kustatscher et al. 2006, 2007, 2010a, 2010b; Van Konijnenburg-van Cittert et al. 2006), including what is so far the oldest squamate (Renesto and Posenato 2002; Renesto and Bernardi 2014; Simões et al. 2018). The diverse plant assemblage, representing the acme of the biotic recovery after the end-Permian mass extinction (e.g., Gall et al. 1998; Grauvogel-Stamm and Ash 2005), has been studied in detail over the past 20 years, with a particular focus on lycophytes, sphenophytes, ferns, and seed ferns, and has been used, in combination with palynological data, to reconstruct the paleoenvironment and paleoecology of the region (e.g., Kustatscher et al. 2006, 2007, 2010a, 2010b; Van Konijnenburg-van Cittert et al. 2006). Here we describe the conifer shoots from Kühwiesenkopf/Monte Prà della Vacca and compare them with other Permian and (Middle) Triassic taxa from Europe with the perspective of improving our knowledge about conifer diversity during the Middle Triassic.

Material and Methods

Geological Setting and Localities

The Anisian Fossillagerstätte Kühwiesenkopf (in Italian, Monte Prà della Vacca; hereafter, Kühwiesenkopf) is part of the northern Dolomites of the UNESCO World Heritage Dolomites in the Bolzano Province (northeastern Italy; fig. 1). The first report of

plant fossils from the northern slope of this mountain was published by Bechstädt and Brandner (1970). In 1999, a fossiliferous level rich in plant remains was reported from the same area (e.g., Tintori et al. 2001, 2016; Broglio Loriga et al. 2002; Posenato et al. 2004; Kustatscher et al. 2006, 2007, 2010a, 2010b; Van Konijnenburg-van Cittert et al. 2006). This bed belongs to the Dont Formation and has been assigned a middle–late Pelsonian age (e.g., Fugagnoli and Posenato 2004; Kustatscher and Roghi 2006; Kustatscher et al. 2006). The Dont Formation corresponds to a hemipelagic carbonate-terrigenous succession deposited in a marginal marine environment (e.g., Delfrati et al. 2000; Tintori et al. 2001; Broglio Loriga et al. 2002). It is rich in marine fossils such as brachiopods, bivalves, fishes, and ammonoids (e.g., Tintori et al. 2001, 2016; Broglio Loriga et al. 2002; Posenato et al. 2004) but also yielded abundant terrestrial plant fossils (e.g., Kustatscher et al. 2006, 2007, 2010a, 2010b; Van Konijnenburg-van Cittert et al. 2006) and a small reptile skeleton called *Megachirella wachtleri* Renesto et Posenato, 2002, which represents the oldest known squamate (Renesto and Posenato 2002; Renesto and Bernardi 2014; Simões et al. 2018). The main fossiliferous level is ca. 1 m thick and crops out about 75 m from the base of the section, representing a rapid burial event caused by submarine flows within a marine basin triggered by heavy storm events in the terrestrial domain, but plant debris and scattered plant remains occur in other layers along the section as well (e.g., Tintori et al. 2001; Broglio Loriga et al. 2002; Kustatscher et al. 2010b).

Fossil Plant Remains, Imaging, and Repository

More than 1200 rock slabs yielding plant remains were collected from Kühwiesenkopf. Leaves, shoots, roots, stems, dispersed seeds, and female and male fructifications belong to at least 35 taxa of lycophytes, sphenophytes, ferns, seed ferns, cycadophytes, and conifers (e.g., Kustatscher et al. 2006, 2007, 2010a, 2010b; Van Konijnenburg-van Cittert et al. 2006). The plant fossils are stored at the Museum of Nature South Tyrol (NMS) in Bozen/Bolzano, labeled with the prefix "PAL" followed by a progressive number (figs. 2–6). Specimens were photographed with a Canon EOS 550D digital camera and measured using the free software ImageJ64 (National Institutes of Health, Bethesda, MD). Cuticle samples were collected from several specimens to ascertain the botanical affinity since some of the taxa show considerable morphologic variability among the leaves. Cuticle fragments were prepared by maceration in Schulze's reagent (30% HNO_3 and a few grains of $KClO_3$) and were subsequently bleached with 10% KOH and rinsed with distilled water. The cuticles were mounted in glycerin jelly on slides and were finally sealed with paraplast (Kerp and Krings 1999; Kerp 2000). Some data relative to European Middle Triassic conifer occurrences come from unpublished material of different paleobotanical collections from the Natural History Museum of London (England), the Naturhistorische Museum Wien (Austria), the Humboldt Museum für Naturkunde Berlin, the Staatliches Museum für Naturkunde Stuttgart, the Geowissenschaftliches Museum of Göttingen University, the Bayerische Staatssammmlung für Paläontologie und Geologie (all Germany), the Naturhistoriska Riksmuseet (Sweden), the Naturalis in Leiden (Netherlands), and the paleobotanical collection Grauvogel (Straßbourg, France).
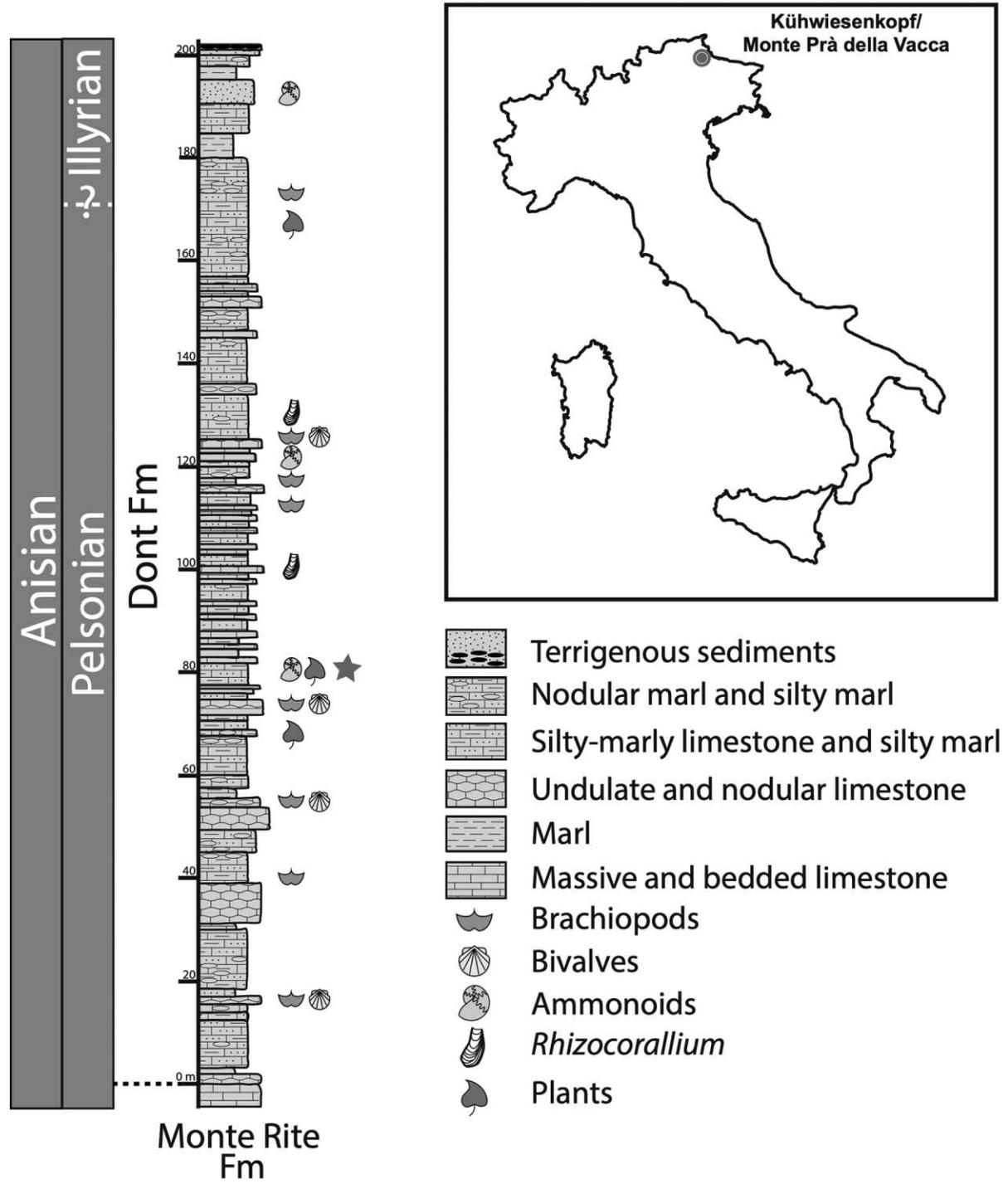
Fig. 1 Geographic location and stratigraphic section of Kühwiesenkopf/Monte Prà della Vacca. The star indicates the fossiliferous level. Fm = Formation. A color version of this figure is available online.
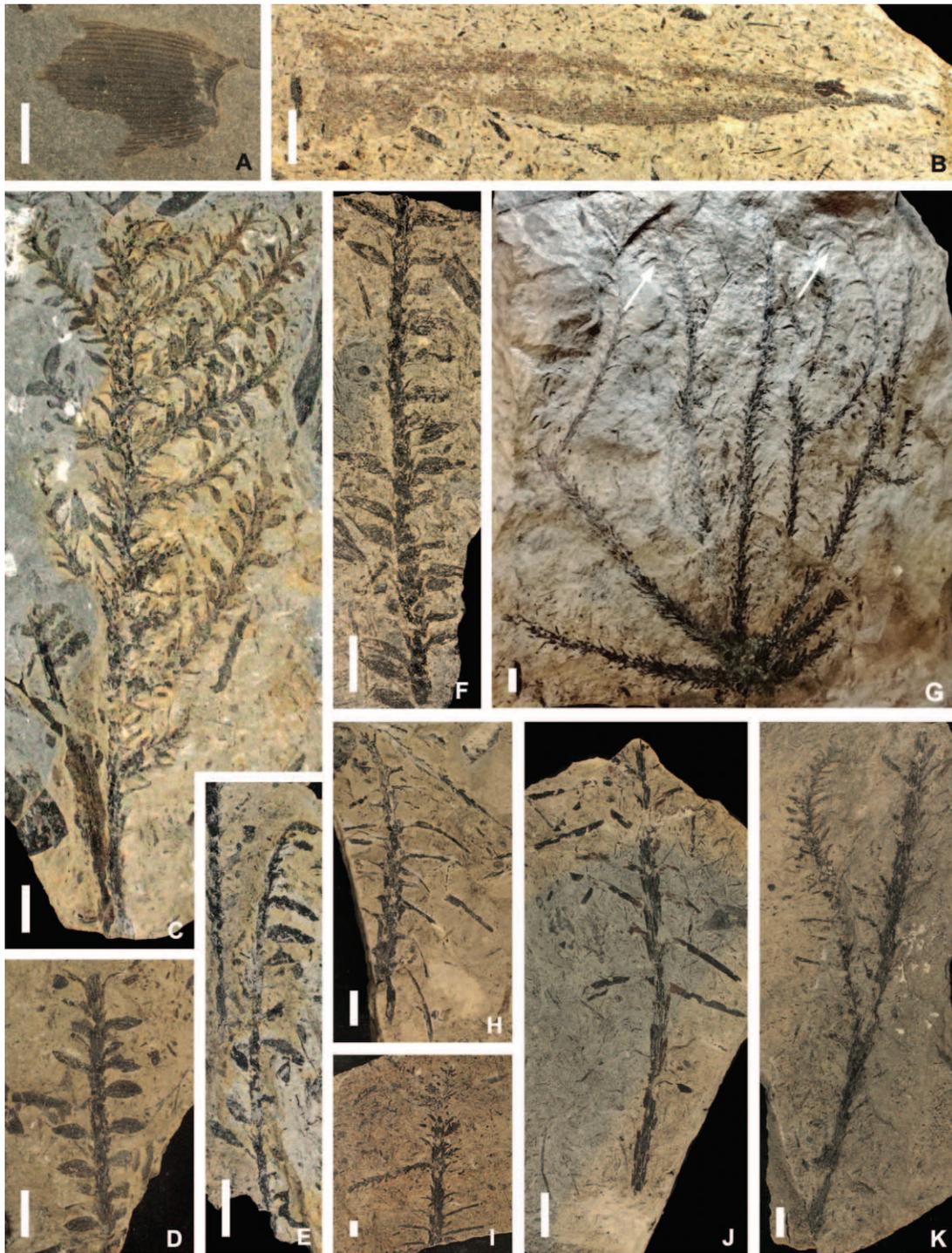
Fig. 2 Branch, shoot, and leaf fragments of *Pelourdea vogesiaca* (*A*, *B*), *Albertia* cf. *latifolia* (*C–F*), and *Voltzia heterophylla* (*G–K*) from Kühwiesenkopf/Monte Prà della Vacca. *A*, Leaf base of *P. vogesiaca* (NMS PAL577) with a thick abscission layer and parallel veins. *B*, Almost complete leaf of *P. vogesiaca* (NMS PAL578), showing the acute apex. *C*, Branch fragment of *A.* cf. *latifolia* (NMS PAL2075), showing the arrangement of the ultimate shoots. *D*, *Albertia* cf. *latifolia* ultimate shoot fragment (NMS PAL596) with leaves arising almost perpendicularly. *E*, *Albertia* cf. *latifolia* ultimate shoot fragment (NMS PAL2161) with the leaves turned almost backward as a result of a taphonomical effect. *F*, *Albertia* cf. *latifolia* ultimate shoot fragment (NMS PAL581), showing the wide range of insertion angles of the leaves. *G*, *Voltzia heterophylla* stem section with six secondary shoots spreading out, forming a whorl; two branching levels are visible, and ribbonlike leaves (leaf type 2) indicated by the arrows arise from the ultimate shoots (NMS PAL3083). *H*, Ultimate shoot of *V. heterophylla* characterized by very long linear leaves turned downward for taphonomic reasons (NMS PAL653). *I*, Penultimate shoot fragment of *V. heterophylla* characterized by the presence of two leaf types on the same shoot (NMS PAL751). *J*, Ultimate shoot fragment of *V. heterophylla* characterized by the presence of very long linear leaves (NMS PAL689). *K*, Apically branched shoot of *V. heterophylla* showing basally long leaves and apically shorter leaves (NMS PAL711). All scale bars = 1 cm.
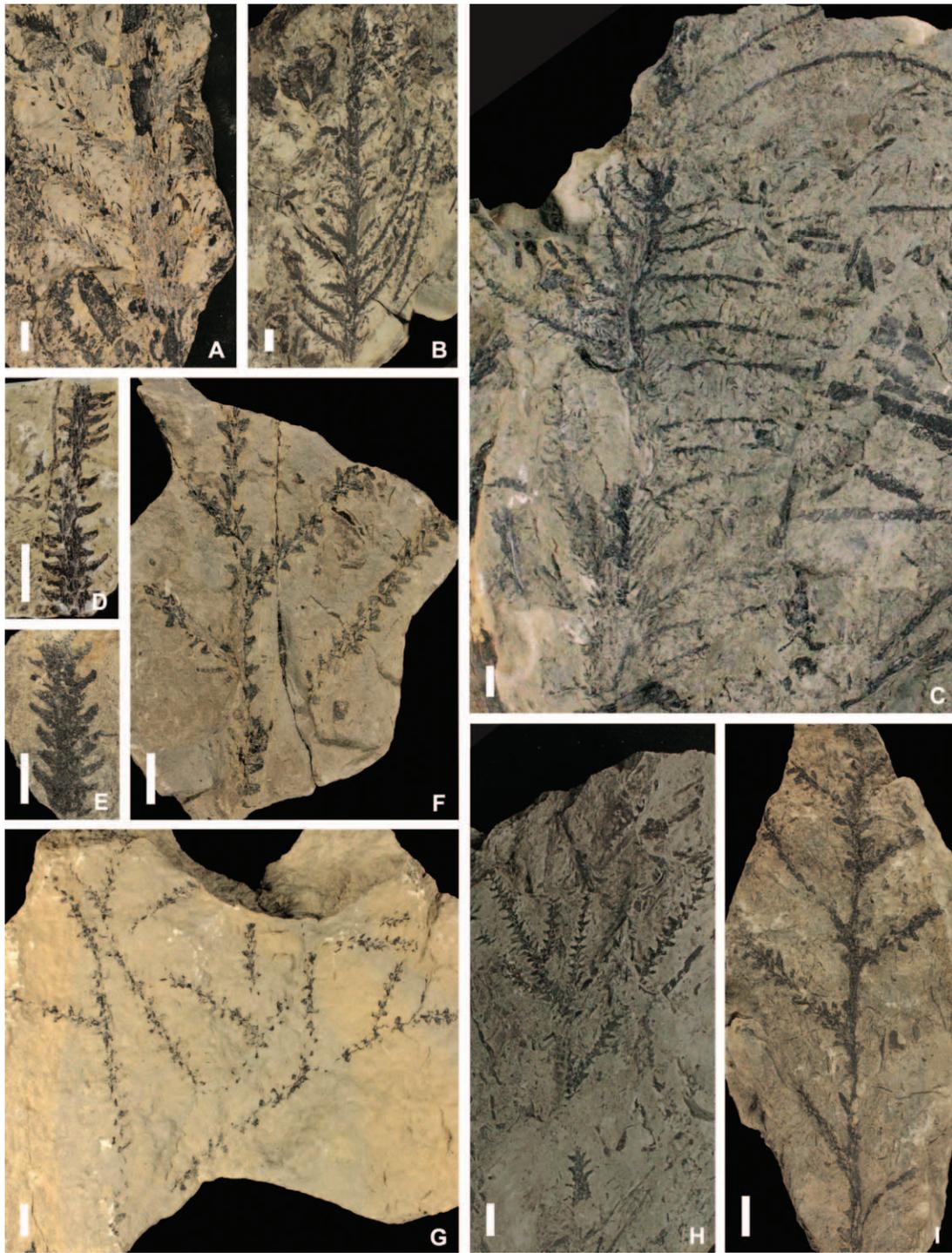
Fig. 3 Branch and shoot fragments of *Voltzia walchiaeformis* (*A–C*) and *Voltzia recubariensis* (*D–I*). *A*, Old basal branch fragment of *V. walchiaeformis*, showing the needlelike, sometimes S-shaped leaves (NMS PAL716). *B*, Branch fragment of *V. walchiaeformis* with typically stiff ultimate shoots (NMS PAL694). *C*, Branch fragment of *V. walchiaeformis* with ultimate shoots occasionally bending downward as a result of preservation (NMS PAL2118). *D*, *Voltzia recubariensis* ultimate shoot fragment with leaves preserved in frontal view; leaves are attached at an angle of ca. 90° (NMS PAL603). *E*, Ultimate shoot fragment of *V. recubariensis*, with leaves attached at an angle of ca. 45° (NMS PAL604). *F*, Branch fragment of *V. recubariensis* (NMS PAL888) with leaves preserved in profile view, showing the characteristic upper and lower leaf insertion angles. *G*, *H*, Penultimate shoot fragments of *V. recubariensis*, showing two branching levels (NMS PAL624, 722). *I*, Branch of *V. recubariensis* (NMS PAL884) with the typical organization of the ultimate shoots. All scale bars = 1 cm.
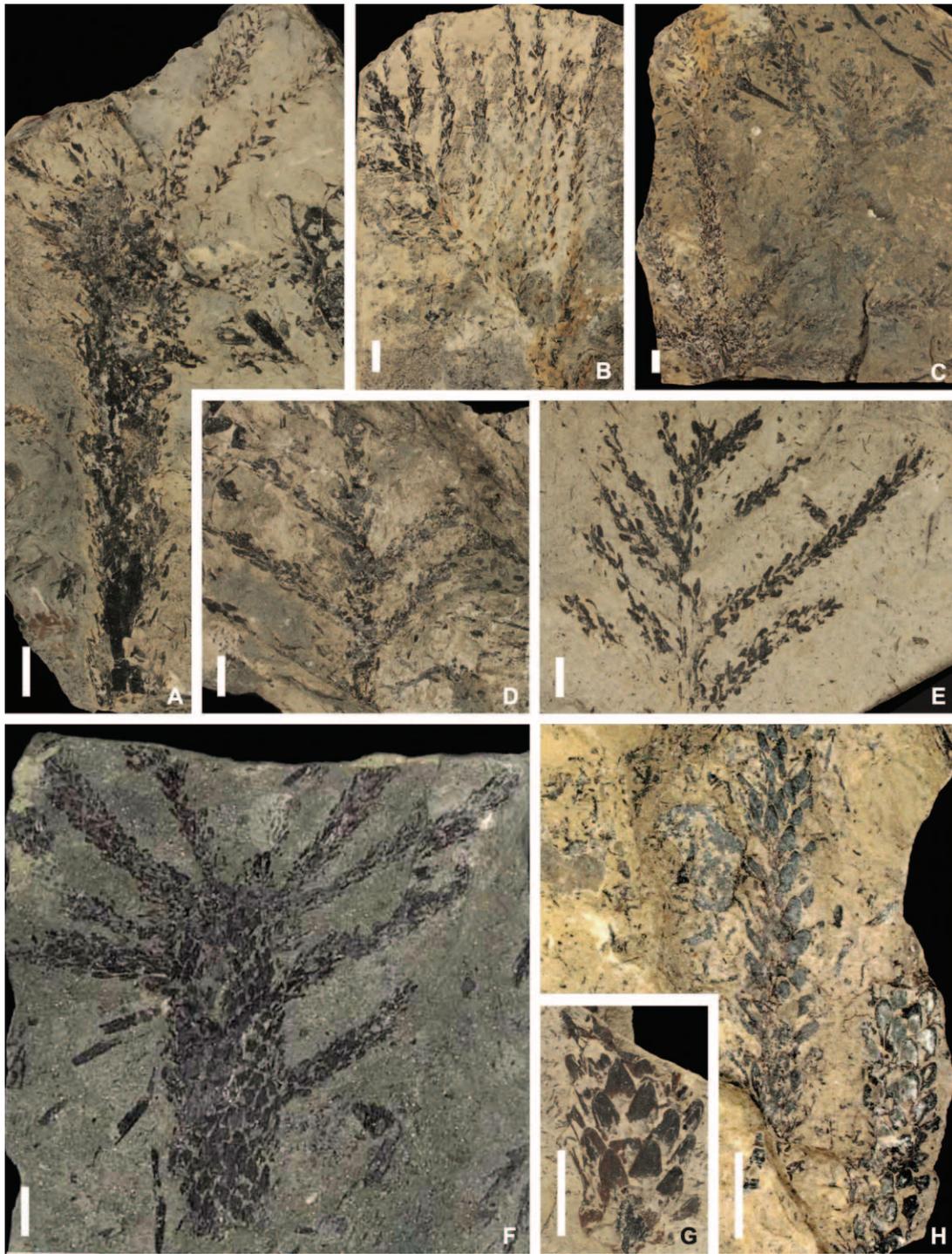
Fig. 4 Stem, branch, and shoot fragments of *Voltzia edithae* sp. nov. *A*, Stem fragment of *V. edithae* sp. nov. with six shoot bases arising radially and forming a whorl, interpreted as seasonal growth (NMS PAL676). *B*, Paratype of *V. edithae* sp. nov., a penultimate shoot fragment with helically arranged ultimate shoots and triangular leaves attached in a dense helix (NMS PAL685). *C*, Paratype representing a stem fragment with an apical whorl of shoots (NMS PAL667). *D*, Branch of *V. edithae* sp. nov., showing the helical attachment of the ultimate shoots and the leaf shape in lateral view (NMS PAL679). *E*, Paratype of *V. edithae* sp. nov., apical fragment of a branch with spirally arranged ultimate shoots (NMS PAL671). *F*, Holotype of *V. edithae* sp. nov. (NMS PAL733). *G*, Ultimate shoot fragment with well-preserved spirally arranged leaves showing the leaf shape (NMS PAL658). *H*, Well-preserved shoot fragments with spirally arranged leaves (NMS PAL683). All scale bars = 1 cm.
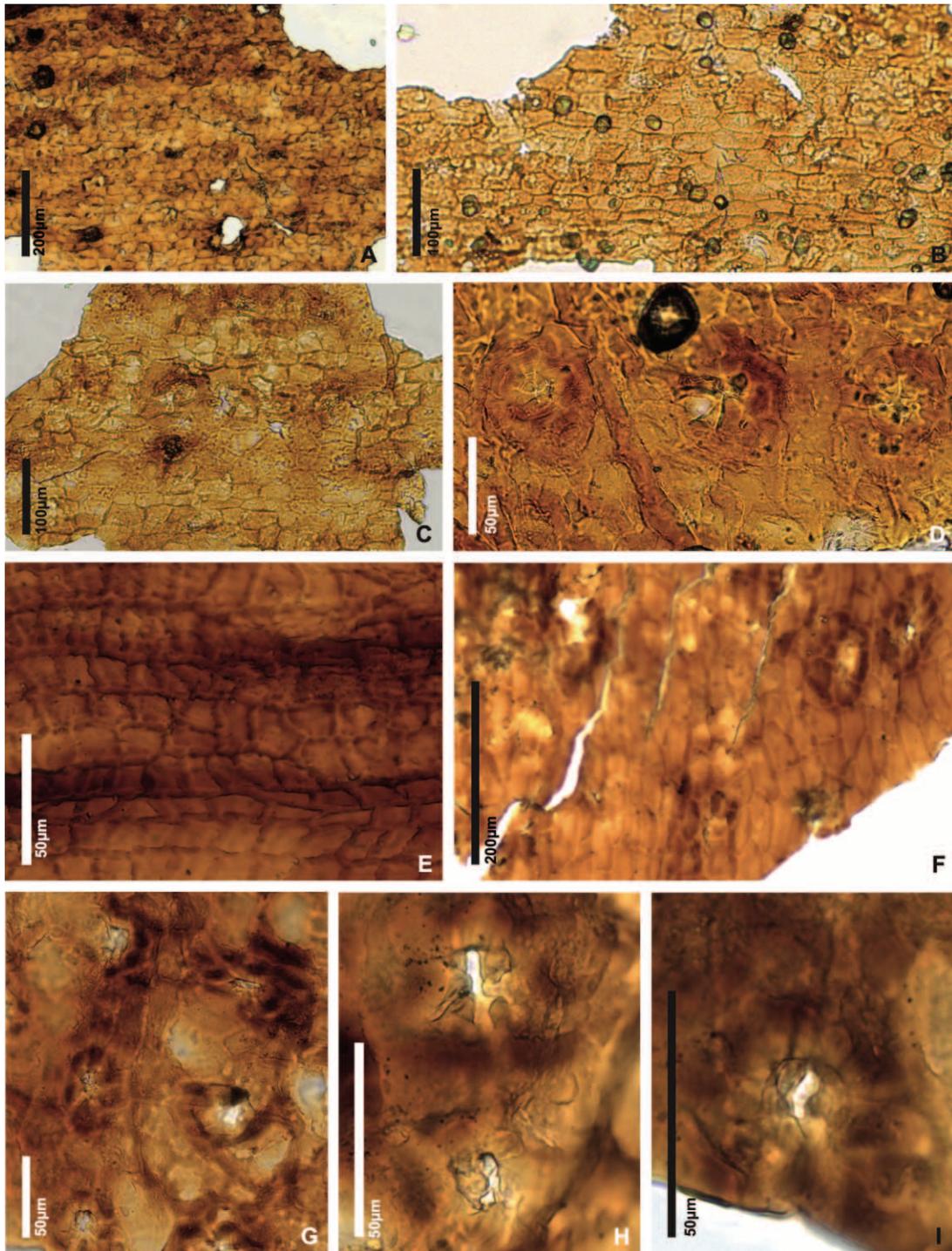
Fig. 5   Cuticle fragments of *Voltzia heterophylla* and *Voltzia walchiaeformis*. *A–D*, Cuticle fragments of *V. heterophylla* (NMS PAL258). *A*, Elongate to isodiametric epidermal cells of *V. heterophylla* and stomata arranged in longitudinal rows. *B*, Elongate and irregular epidermal cells with thick walls. *C*, Elongate epidermal cells and stomata arranged in rows; subsidiary cells are cutinized and bear papilla. *D*, Detail of the stomata that shows cutinized subsidiary cells and well-developed papillae that cover the stomatal aperture. *E–I*, Cuticle fragments of *V. walchiaeformis* (NMS PAL292). *E*, Detail of an upper cuticle with isodiametric cells, well cutinized and with thick walls. *F*, Detail of a lower cuticle with irregularly arranged stomata. *G*, Detail of monocyclic stomata with cutinized and roundish subsidiary cells bearing papillae. *H, I*, Details of monocyclic stomata, showing the papillae on subsidiary cells almost completely closing the stomatal aperture.
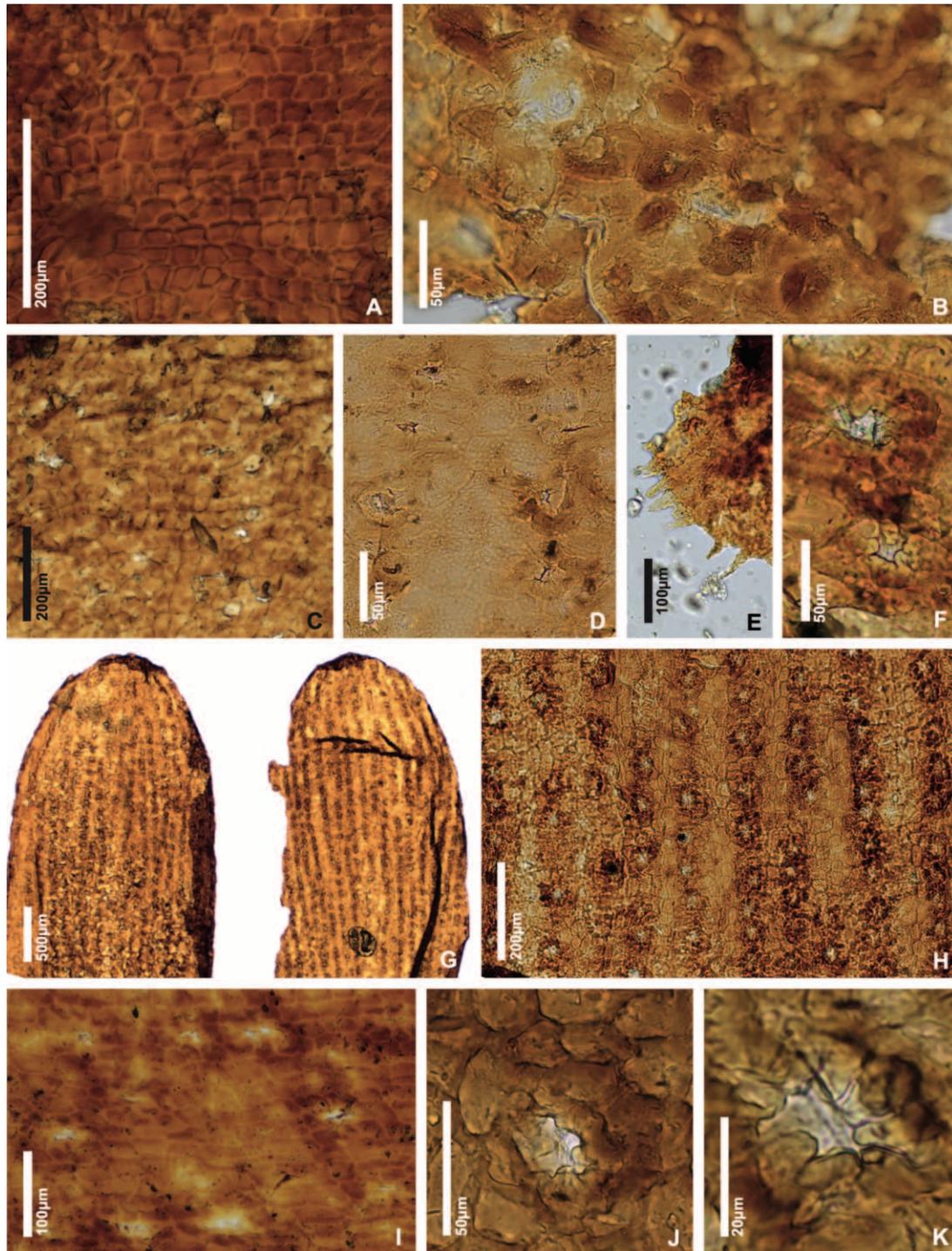
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Fig. 6 Cuticle fragments of *Voltzia recubariensis* and *Voltzia edithae* sp. nov. *A*, Upper cuticle fragment of *V. recubariensis*, showing isodiametric epidermal cells with thick walls. *B*, *C*, Epidermal cells of *V. recubariensis* with well-developed papillae (NMS PAL709). *D*, Stomata of *V. recubariensis* arranged in rows (NMS PAL728). *E*, Detail of papillae/spines on a cuticle fragment of *V. recubariensis* (NMS PAL704). *F*, Detail of *V. recubariensis* stomata with subsidiary cells provided by the papillae (NMS PAL633). *G*, Amphistomatic leaf of *V. edithae* sp. nov. with stomata arranged in long rows (NMS PAL1771). *H*, Detail of *G* (NMS PAL1771). *I*, Upper cuticle fragment of *V. edithae* sp. nov., showing more scattered stomata characterized by cutinized subsidiary cells (NMS PAL542). *J*, *K*, Details of stomata of *V. edithae* sp. nov. with cutinized subsidiary cells bearing well-developed papillae (NMS PAL1140).

Results

Systematics

Division—Coniferophyta

Class—Coniferopsida

Order and Family—Incertae Sedis

Genus—Pelourdea *Seward, 1917 emend. Ash, 1987*

Species—Pelourdea vogesiaca *(Schimper et Mougeot) Seward, 1917*

Basionym. *Yuccites vogesiacus* Schimper et Mougeot (1844, p. 42, pl. XXI).

Synonymies. *Yuccites vogesiacus* Schimper et Mougeot, 1844, *Noeggerathia vogesiaca* (Schimper et Mougeot) Bronn, 1858, *Zamites grandis* Arber, 1907, *Pelourdea keuperiana* (Compter) Seward, 1917.

Description. Six specimens are assigned to *P. vogesiaca*. The leaf fragments are up to 117 mm long and 18 mm wide, characterized by entire margins and clearly distinct parallel, longitudinal veins departing from the leaf base and ending in the lateral margins and apex (e.g., NMS PAL577; fig. 2A, 2B). The leaf base (e.g., NMS PAL577; fig. 2A) is crescent shaped with a thick abscission layer (ca. 1.5 mm thick). The acute leaf apex is preserved only on one specimen (NMS PAL578; fig. 2B).

Discussion. *Pelourdea vogesiaca* is a plant characterized by an erect, unbranched stem. The sessile, lanceolate to linear leaves are helically arranged on the stem and are characterized by entire margins, a crescent-shaped base, and an acute apex. Veins are distinct and run parallel from the leaf base to the lateral margins and apex (Ash 1987). The species was described for the first time by Schimper and Mougeot (1844) as *Y. vogesiacus* Schimper et Mougeot, 1844. Arber (1907) described similar leaves from the lower Keuper of England (Worcestershire; now considered late Anisian in age) as *Z. grandis* Arber, 1907, later ascribed by Wills (1910), who considered it related to *Cordaites*, to *Y. vogesiacus*.

However, the generic name *Yuccites* Schimper et Mougeot, 1844 is illegitimate according to the International Code of Botanical Nomenclature (Turland et al. 2018), as *Yuccites* Martius, 1822 has priority. Seward (1917) created the genus *Pelourdea* Seward, 1917 to replace *Yuccites* Schimper et Mougeot, 1844 for leaves of the *Yuccites* type, which in form, venation, and phyllotaxis agree with *Cordaites* leaves but cannot be assigned to the latter or even to the order Cordaitales. *Pelourdea vogesiaca* (Schimper et Mougeot) Seward, 1917 became the type species of the new genus.

Distribution. *Pelourdea vogesiaca* is a well-known species from the Triassic of Europe. Leaves have been found from the Olenekian of Germany (e.g., Schlüter and Schmidt 1927; Kustatscher et al. 2014b); the Anisian of France (Vosges; Grauvogel-Stamm 1978; Gall and Grauvogel-Stamm 2000), Italy (Dolomites; e.g., Broglio Loriga et al. 2002; Kustatscher et al. 2010b), Spain (e.g., Müller 1969; Díez et al. 1996; Díez 2000; Borruel-Abadía et al. 2014), Switzerland (Monte San Giorgio; Stockar and Kustatscher 2010), and England (e.g., Arber 1907; Wills 1910; Seyfullah et al. 2013); and the Ladinian of Italy (Dolomites;

e.g., Wachtler and Van Konijnenburg-van Cittert 2000; Kustatscher et al. 2004, 2019a) and Germany (e.g., Kustatscher et al. 2012b). Confident records of this species from the Carnian of Europe come from the Bergamasc Alps in Italy (e.g., Passoni and Van Konijnenburg-van Cittert 2003), whereas similar specimens from Raibl in the Carnic Alps (e.g., Schenk 1866–1867; Dobruskina 2001) and from the Julian Alps (e.g., Dobruskina 2001) need to be reinvestigated.

A slightly similar Triassic species is *Desmiophyllum imhoffii* (Heer) Florin, 1936, recorded from Neue Welt (near Basel) and Germany (Kelber 1990; Kelber and Hansch 1995). These leaves are also lanceolate to linear with an acute apex, but no base has ever been recorded. They are characterized by a typical preservation mode with a pattern of interconnected interstitial veins (see Kelber and Hansch 1995, fig. 158). Hence, it is not certain whether this species can be included in the genus *Pelourdea*, and we keep it in *Desmiophyllum*.

Genus—Albertia *Schimper in Voltz, 1837*

Species—Albertia *cf.* latifolia *Schimper in Voltz, 1837*

Possible synonymies (see below). *Albertia rhomboidea* Schimper in Voltz, 1837, *A. elliptica* Schimper in Voltz, 1837, *A. braunii* Schimper in Voltz, 1837, *A. secunda* Schimper in Voltz, 1837, *A. speciosa* Schimper in Voltz, 1837, *Haidingera schaurothiana* Massalongo ex De Zigno, 1862.

Description. Twenty-nine shoot fragments of various orders were assigned to *A.* cf. *latifolia*. Penultimate shoot fragments are up to 160 mm long and 70 mm wide (e.g., NMS PAL2075; fig. 2C). Ultimate shoots arise alternately from the penultimate axis at 40°–60°. Leaves are arranged in a loose spiral on the axis. They are 6–17 mm long and 2–6 mm wide, ovate to lanceolate in shape with a restricted base and an obtuse apex (tables A1, A2; tables A1–A4 are available online). Some specimens show fine longitudinal striations on the leaf lamina (e.g., NMS PAL581, 596, 2161; fig. 2D–2F). In lateral view, leaves spread from the axis at an angle of 40°–80° (table A1); occasionally, the apex bends toward the axis (e.g., NMS PAL2161; fig. 2E). Unfortunately, cuticles of *A. latifolia* were not preserved in the studied specimens.

Discussion. The genus *Albertia* was erected by Schimper (in Voltz 1837b) for broad-leaved conifer shoots characterized by spirally arranged, obovate to ovate, elongate leaves that are constricted at their base, finely striated, and slightly decurrent. The species erected by Schimper (in Voltz 1837b), *A. latifolia*, *A. rhomboidea*, *A. elliptica*, *A. braunii*, *A. secunda*, and *A. speciosa*, were initially briefly described but not figured in Voltz (1837a; Grauvogel-Stamm 1978) and are distinguished by their different leaf shapes (table A1). Schimper and Mougeot (1844) provided a more detailed description of the genus (branching system, leaves, female and male reproductive organs) and reduced the number to only four species, *A. latifolia*, *A. elliptica*, *A. braunii*, and *A. speciosa*.

Comparing our specimens to the four species identified by Schimper and Mougeot (1844), it becomes evident that the shape and dimension range of our specimens resemble those of all four species (table A1). The main differences, the observed shape of the leaves, the attachment angle, and the apex, appear to be linked to the preservation of the shoots, the position of the

leaves on the shoot, and the arrangement of the leaves in the sediment. Thus, we suggest that the morphologic variability between *A. latifolia*, *A. braunii*, *A. elliptica*, and *A. speciosa* falls within the natural variability of one single natural species (table A1). Therefore, these four taxa might be conspecific, in which case they should be named *A. latifolia* due to reasons of priority. However, before we can do this, the genus *Albertia* needs a thorough revision based on the original specimens and/or specimens collected from the type area. For that reason, we determine our specimens only as *A.* cf. *latifolia*. Seward (1919) already discussed that branches of *A. elliptica* and *A. latifolia* are not clearly distinguishable by any marked feature, that those of *A. braunii* are slightly larger, and that those of *A. speciosa* are more linear. The shoot fragments figured by De Zigno (1862) as *H. schaurothiana* Massalongo ex De Zigno, 1862 probably also belong to this species. The shoot fragment identified by Grauvogel-Stamm (1978) as *Albertia* sp. consists of a foliate branch with obovate to spatulate leaves with rounded apexes and a constricted basis (table A1) and closely resembles our specimens. The specimens that Kustatscher et al. (2011) and Feng et al. (2018) described and figured might also belong to *A. latifolia*.

Male reproductive organs ascribed by Schimper and Mougeot (1844) to the genus *Albertia* were reexamined and assigned later to two other taxa, *Darneya peltata* (Schaarschmidt and Maubeuge 1969) and *Voltziostrobus schimperi* (Grauvogel-Stamm 1969), the latter later synonymized with *D. peltata* (Grauvogel-Stamm and Galtier 1998). Moreover, Schenk (1891), according to Florin (1944), had assigned leafy twigs bearing the male cone to *Voltzia rigida* (e.g., Grauvogel-Stamm 1978). There exist several male and female conifer cones in the plant fossil assemblage from Kühwiesenkopf whose study might solve the botanical affinity of *Albertia*; the study of these was, however, beyond the scope of this article.

Comparison with some Permian conifers. Some similarities in gross morphology can be observed between *Albertia* and the late Permian conifer genus *Ortiseia* Florin, 1964 (type species, *Ortiseia leonardii* Florin, 1964). The latter has been described from a number of localities, such as Cuecenes/Val Gardena (Italy; type locality; Florin 1964; Clement-Westerhof 1984), Bletterbach Gorge (Italy; Clement-Westerhof 1984; Visscher et al. 2001; Kustatscher et al. 2017*b*), Vicentinian Alps (Italy; Clement-Westerhof 1984), and Gera (German Zechstein; Bödige 2007). *Ortiseia* is characterized by pinnately branched lateral shoot systems with more or less alternating ultimate branches in one plane. Bifacial leaves are helically arranged, not or slightly overlapping. This is in contrast to the *Albertia* specimens, in which the leaves are not densely placed and are never overlapping. The leaf shape in *Ortiseia* is mainly oblong or ovate (table A2) with an acute to slightly acute apex. Leaf bases in *Ortiseia* are only slightly contracted (Clement-Westerhof 1984; Visscher et al. 2001; Kustatscher et al. 2017*b*), in contrast to *Albertia*, in which the leaf bases are strongly contracted (see fig. 2*C*–2*F*). The leafy shoots of the genus *Majonica* Clement-Westerhof, 1987, also known from the late Permian of the Dolomites, differ in their strongly overlapping bifacial leaves with decurrent bases (Clement-Westerhof 1987).

Distribution. *Albertia* is a typical Middle Triassic genus in Europe with records also in China (Feng et al. 2018). In the Southern Alps, representatives of this genus and putatively of the species *A. latifolia* have been described from the Anisian (e.g., Recoaro,

Kühwiesenkopf, Agordo; Broglio Loriga et al. 2002; Kustatscher et al. 2006, 2010*b*, 2011, 2019*b*) and perhaps from the Ladinian (Dierico, Udine Province; Kustatscher et al. 2019*b*). It also occurred in the Anisian of Spain (e.g., Díez et al. 1996, 2010; Díez 2000; Borruel-Abadía et al. 2014), France (e.g., Schimper in Voltz 1837*b*; Schimper and Mougeot 1844; Alberti 1864; Grauvogel-Stamm 1978; Gall and Grauvogel-Stamm 2000), and Germany (e.g., Alberti 1864). The report from the Norian of Italy has to be validated (Rio Seazza, Udine Province; Kustatscher et al. 2019*b*).

Order—Voltziales

Family—Voltziaceae

Genus—Voltzia *Brongniart, 1828*

Species—Voltzia heterophylla *(Brongniart) Schimper et Mougeot, 1844*

Synonymies. *Voltzia brevifolia* Brongniart, 1828, *V. rigida* Brongniart, 1828, *V. elegans* Brongniart, 1828, *V. acutifolia* Brongniart, 1828.

Description. Twenty-nine specimens, including large branch and shoot fragments, are assigned to *V. heterophylla* (Brongniart) Schimper et Mougeot, 1844. The branch fragments are up to 230 mm long and 190 mm wide (NMS PAL3083; fig. 2*G*). Main axes are up to 5.5–9 mm thick and are densely covered by needlelike leaves, 7–14 mm long and 1.5–3 mm wide. In one specimen (i.e., NMS PAL3083; fig. 2*G*), secondary shoots spread out from the stem, forming a whorl with lateral shoots that arise at about 90°. This is interpreted here as a possible sign of seasonal growth. In another specimen (e.g., NMS PAL711; fig. 2*K*), ultimate shoots arise at an angle of ca. 20°, but this may be affected by taphonomy. In fact, ultimate shoots are often bent (e.g., NMS PAL751; fig. 2*I*). Heterophylly is clearly present. The leaves, helically arranged on the axis, are of two types characterized by different shapes, sizes, and leaf angles. Leaf type 1 is needlelike, up to 10 mm long and 1.8 mm wide, with a rounded, recurved apex. The leaves arise from the axis at an angle of 20°–40° (e.g., NMS PAL711, 751, 3083; fig. 2*G*, 2*I*, 2*K*; table A2). Leaf type 2 is ribbonlike to lanceolate in shape, up to 40 mm long and 4 mm wide, with a flat lamina and a rounded apex. They arise from the axis at an angle of up to 85° (e.g., NMS PAL689, 751; fig. 2*I*, 2*J*; table A2). Leaves of leaf type 2 are turned backward, but this can be a taphonomical effect considering the very wide angles at which the leaves arise (e.g., NMS PAL653, 689; fig. 2*H*, 2*J*). Ribbonlike leaves occur both on penultimate shoots, just below the attachment base of the ultimate shoots (e.g., NMS PAL751; fig. 2*I*) close to the base (e.g., NMS PAL711; fig. 2*K*), and on the tops of ultimate shoots (e.g., NMS PAL3083; fig. 2*G*). Shorter leaves (type 1) are more densely inserted on the axis than the longer ones (type 2; e.g., NMS PAL711, 751, 3083; fig. 2*G*, 2*I*, 2*K*). No midrib has been observed.

The *V. heterophylla* cuticles are amphistomatic and have isodiametric (up to 40 μm × 40 μm) to elongated epidermal (15–60 μm × 38–70 μm) cells (table A3), longitudinally oriented and characterized by thick walls (e.g., NMS PAL258; fig. 5*A*–5*C*). Papillae on epidermal cells may occur (table A3). Stomatal complexes (38–50 μm × 55–65 μm) are roundish to slightly elongated, longitudinally oriented, monocyclic, and arranged in short interrupted

rows (e.g., NMS PAL258; fig. 5A; table A3) at about a 38–50-µm distance. Subsidiary cells range from five to seven, but in most cases there are six (e.g., NMS PAL695; fig. 5D). They are more cutinized than the epidermal cells, with thick walls and each bearing well-developed papillae that almost completely close the stomatal aperture (e.g., NMS PAL695; fig. 5D; table A3). No shared subsidiary cells between adjacent stomata have been observed.

Comparison with V. heterophylla *cuticle from Vosges.* The cuticle of a *V. heterophylla* leaf from the Grès à *Voltzia* Formation (Upper Buntsandstein, early Middle Triassic) was figured but not described in Gall et al. (2006, p. 64). The figured cuticle (Gall et al. 2006, p. 64) shows isodiametric to elongate epidermal cells (65–152 µm × 42–100 µm; table A3). Stomata (84–132 µm × 43–81 µm) are arranged in interrupted rows, monocyclic, randomly oriented, with sunken guard cells (the fig. shows the cuticle from the inside, displaying the guard cells prominently) and probably five to seven subsidiary cells (table A3). Guard cells are 68–118 µm long and 18–35 µm wide, and the presence of papillae on epidermal or subsidiary cells could not be observed because the figured cuticle is seen from the inside. Although the cuticle fragment from the Grès à *Voltzia* Formation is well preserved and is so far the only cuticle description of *V. heterophylla* from the Vosges (Gall et al. 2006), the lack of reference to the specimen of provenance, the inside view of the cuticle, and the missing other (adaxial or abaxial) cuticle do not allow us to compare it in detail with the cuticles and macroremains of *V. heterophylla* from Kühwiesenkopf.

Discussion. *Voltzia heterophylla* was erected by Brongniart (1828) for branches with more or less long leaves of various shapes attached helically to the axis. However, because of the great variation in the shapes and dimensions observed, Brongniart (1828) also created four more species: *V. acutifolia*, *V. brevifolia*, *V. rigida*, and *V. elegans*. Despite the fact that Brongniart (1828) described *V. brevifolia* as the first species and the only one with an attached female cone (which could suggest that it is the type species of the genus *Voltzia*), Schimper and Mougeot (1844) recognized the wide morphological variability of *V. heterophylla*, emended its original diagnosis, and moved *V. rigida*, *V. elegans*, and *V. brevifolia* as synonyms into *V. heterophylla* (e.g., Schimper and Mougeot 1844; Wills 1910; Grauvogel-Stamm 1978). *Voltzia acutifolia* remained the only other distinguished species but was added by Fliche (1910) to *V. heterophylla* as well. Later, Schlüter and Schmidt (1927) indicated that *V. heterophylla* was the "genotype" (lectotype) of the genus *Voltzia*. The specimens described and figured as *Taxites massalongii* De Zigno, 1862, *Taxites vicentinus* Massalongo ex De Zigno, 1862, and *Taxodites saxolympiae* Massalongo ex De Zigno, 1862 from the Anisian of Recoaro could also belong to this species. The specimens are, however, too fragmentary and badly preserved to permit a confident assignment to any species.

Distribution. *Voltzia heterophylla* has a European distribution. It is typical for the Anisian of France (e.g., Brongniart 1828; Schimper and Mougeot 1844; Blanckenhorn 1886; Grauvogel-Stamm 1978; Dobruskina 1994; Gall and Grauvogel-Stamm 2000, 2005), Germany (e.g., Blanckenhorn 1886; Compter 1894; Engel 1896; Sander and Gee 1994), and Spain (e.g., Almera 1909; Calzada 1987; Díez et al. 1996; Díez 2000; Borruel-Abadía et al. 2014). In the Anisian of northern Italy, it is described only from Kühwiesenkopf (Dolomites; e.g., Broglio Loriga et al. 2002; Kustatscher et al. 2019a), although some historical occurrences from

Recoaro could perhaps also belong to this species. Putative male cones of *V. heterophylla* are known from the Anisian of England (Wills 1910).

*Species—*Voltzia walchiaeformis *Fliche emend. Forte, Kustatscher et Van Konijnenburg-van Cittert*

Diagnosis (emended). Conifer with pinnately branched lateral shoot systems. Penultimate axes densely covered by needlelike, helically arranged leaves, arising at 45°–60°, with a recurved apex. Stiff ultimate shoots situated in one plane, attached (sub)oppositely to the axis at an angle of 30°–75°, covered by helically arranged needlelike S-shaped leaves arising at an angle of 15°–90°. Leaves hypostomatic, with far fewer stomata on the upper cuticle. Epidermal cells isodiametric to elongated, 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 closing the large stomatal pit.

Description. Thirty specimens represented by big branches and shoot fragments are assigned to *V. walchiaeformis*. The biggest branch in the collection is 350 mm long and 210 mm wide, with a main axis of up to 11.5 mm in diameter (NMS PAL2118; fig. 3C). Leaves on the main axis are 7–11 mm long and about 1 mm wide, with a pointed apex, and arise straight at a narrow angle of 30°–35°. Ultimate shoots are stiff, 1.2–2.2 mm thick, suboppositely inserted, arising from the axis at a distance of 5.5–9 mm and at an angle of 60°–75° (NMS PAL2118; fig. 3C). Other penultimate branches are pinnate, with subopposite to alternately inserted ultimate shoots that arise in one plane from the penultimate axis at a distance of 10–20 mm. Ultimate axes are stiff, up to 15 mm in diameter, and covered by spirally arranged leaves (e.g., NMS PAL716; fig. 3A). Leaves are needlelike, S-shaped in lateral view, helically arranged, and particularly long (up to 5–15 mm long and 1–2 mm wide) toward the base of the branch. They arise at an angle of about 45°–60°, with the apex occasionally curved toward the axis or occasionally bending downward (e.g., NMS PAL716; fig. 3A). In the apical fragments (e.g., NMS PAL694; fig. 3B), ultimate axes arise at a narrower angle of 30°–40°, recurving toward the penultimate axis at a distance of 5.5–10 mm, whereas closer to the basal part, ultimate axes are more spaced and arise at an angle of 40°–70°. Leaves on the ultimate axis are 2–11 mm long and 1–2 mm wide, triangular in shape in lateral view (table A2), falcate, and arising at an angle of 40°–60°.

Cuticle samples obtained from the *V. walchiaeformis* remains are unfortunately few. They are commonly hypostomatic or with very few stomata on the upper cuticle. Epidermal cells are well cutinized and isodiametric (21–43 µm × 16–46 µm) to elongated (18–30 µm × 38–75 µm; e.g., NMS PAL292; fig. 5E, 5F). On the lower cuticle, stomata are arranged in irregular rows (e.g., NMS PAL292; fig. 5F; table A3) that are some 45–70 µm apart. Stomatal complexes (50–70 µm × 90–110 µm) are monocyclic, roundish, consisting of four to seven subsidiary cells (e.g., NMS PAL292; fig. 5G–5I; table A3), commonly papillate, and more cutinized than the epidermal cells (e.g., NMS PAL292; fig. 5F, 5G; table A3). Papillae on subsidiary cells often completely close the large stomatal pit (e.g., NMS PAL292; fig. 5H, 5I).

Discussion. The genus *Voltzia* was erected by Brongniart (1828; see above) based on foliate shoots with needlelike elongated leaves of various shapes arranged helically on the axis

(Brongniart 1828). The high variety in leaf morphology led to a large number of species (e.g., Brongniart 1828; Schimper and Mougeot 1844; Fliche 1910; Grauvogel-Stamm 1978). Fliche (1910) erected the species *V. walchiaeformis* for vegetative conifer shoots characterized by a *Walchia*-like branching pattern, with lateral branches arising in one plane from the axis at 40° and with elliptical, short, broad, and slightly adpressed leaves. Fliche (1910) distinguished *V. walchiaeformis* from *V. heterophylla* because of the stiff branches of the first species, which arise from the axis at a relatively narrow angle. No further details about the leaf morphology were mentioned, and the figure of the type specimen does not show them well. The ample collection of specimens of *V. walchiaeformis* from Kühwiesenkopf shows the shape and general structure of the branches and leaves (i.e., attachment angle, leaf shape, and dimension) in detail and the difference between leaves on penultimate and ultimate shoots. Thus, we propose here an emendation of the original species diagnosis (see above).

The wide range of the attachment angles between penultimate and ultimate axes observed in our specimens could be a taphonomical artifact. Indeed, very long ultimate shoots are more often slightly bent (e.g., NMS PAL2118; fig. 3C). But it might also be due to the age of the conifer shoots (old vs. young shoots).

Distribution. *Voltzia walchiaeformis* has been described from the Anisian of France (Vosges; e.g., Fliche 1910; Grauvogel-Stamm 1978; Gall and Grauvogel-Stamm 2000, 2005) and Italy (Kühwiesenkopf, northeastern Italy; Broglio Loriga et al. 2002; Kustatscher 2004; Kustatscher et al. 2012a). The specimens from Spain assigned to this species (e.g., Díez et al. 1996; Díez 2000; Borruel-Abadía et al. 2014) are too fragmentary and poorly preserved to permit a confident assessment.

Species—Voltzia recubariensis *(Massalongo ex De Zigno) Schenk, 1868*

Synonymies. *Lycopodiolithes arboreus* Fuchs, 1844, *V. brevifolia* Catullo, 1846, *V. elegans* Catullo, 1846, *Araucarites agordicus* Unger, 1850, *Araucarites recubariensis* Massalongo ex De Zigno, 1862.

Description. About 110 specimens, including big branches and shoot fragments, are attributed to *V. recubariensis*. Branch fragments are up to 300 mm long and 14 mm wide, with at least two branching levels (e.g., NMS PAL624, 722; fig. 3G, 3H). Penultimate branches are 1.7–5.8 mm wide, covered by helically arranged falcate to triangular leaves (4.4–9 mm long, preserved in lateral view) characterized by a lower attachment angle of 17°–70° and an upper one of up to 90°. Ultimate shoots arise alternately from the axis at an angle of 30°–70° (e.g., NMS PAL884, 888; fig. 3F, 3I; table A2). The coriaceous leaves are arranged in a loose helix, falcate to triangular in shape (2–10 mm long and 1.5–3 mm wide), with acute apexes curved toward the axis (e.g., NMS PAL603, 604, 888; fig. 3D–3F). The leaves on the ultimate shoots can be 2–3 mm shorter than the ones on the penultimate shoot; however, no consistent differences between the leaf angles on axes of different orders have been observed (e.g., NMS PAL624; fig. 3G). The difference between the lower and upper attachment angle is typical for *V. recubariensis* and makes the species easily recognizable. The lower attachment angle of the leaf (i.e., angle between the distal leaf margin and the axis from a lateral view) ranges between 15° and 70°, with an average of about 45°, and is always narrower than the distal leaf angle (table A2). The latter (i.e., angle

between the upper leaf margin and the axis from a lateral view), indeed, ranges between 35° and 90°, with an average of 70° (e.g., NMS PAL603, 604; fig. 3D, 3E; table A2).

Voltzia recubariensis is almost hypostomatic, with far fewer stomata on the upper than on the lower cuticle (e.g., NMS PAL1140; fig. 6A). Epidermal cells (15–55 μm × 17–70 μm) are elongate (between stomata rows) to irregular/isodiametric (within stomatal rows) with thick walls.

Epidermal cells are heavily papillate (NMS PAL709; fig. 6B, 6C), sometimes also bearing hairs or trichomes (e.g., NMS PAL704; fig. 6E). Stomata can be either arranged in short rows or scattered (e.g., NMS PAL728; fig. 6C, 6D; table A3). In the former case, epidermal cells are often elongated, and rows are 70–100 μm away from each other. Stomatal complexes (25–47 μm × 40–92 μm) have six (to eight) subsidiary cells (e.g., NMS PAL633, 728; fig. 6D, 6F). Subsidiary cells are roundish to polygonal in shape (e.g., NMS PAL633, 728; fig. 6D, 6F; table A3), more cutinized than the epidermal ones, with thicker inner walls and bearing papillae (e.g., NMS PAL633, 728; fig. 6D, 6F; table A3).

Discussion. *Voltzia recubariensis* is the most common conifer in the Kühwiesenkopf flora and is a typical element of the Anisian of the Southern Alps (e.g., Broglio Loriga et al. 2002; Kustatscher 2004; Todesco et al. 2008; Kustatscher et al. 2011, 2012a, 2019a; Brack and Kustatscher 2013; Roghi et al. 2017). It is a characteristic taxon, easily distinguished from other conifers (table A2) by the attachment mode of the leaves to the axis, with a lower angle of about 45° and a larger upper one (>70°). The species was erected as *A. recubariensis* Massalongo ex De Zigno, 1862 for conifer shoots from the "*Voltzia* beds" of Recoaro and was later transferred by Schenk (1868) to the genus *Voltzia* Brongniart, 1828. There exist older records of this species under different names (Catullo 1846; Unger 1850; von Hauer 1850), but all those names are nomina nuda (no descriptions) or misidentifications (see also the discussion in Brack and Kustatscher 2013).

A specimen of *V. recubariensis* collected by Massalongo (1824–1860) has been recently restudied because of its association with fossil resin, strongly suggesting that *V. recubariensis* was a producer of amber (Roghi et al. 2017). We found traces of amber attached to one shoot fragment of *V. recubariensis* from Kühwiesenkopf.

Distribution. *Voltzia recubariensis* is so far restricted to the Anisian of the Southern Alps, where it is widely distributed. It was reported from Recoaro (Massalongo 1857; De Zigno 1862; Schenk 1868; Roghi et al. 2017) and Vallarsa Valley (Selli 1938) and later on also from Kühwiesenkopf (e.g., Broglio Loriga et al. 2002; Kustatscher 2004; Kustatscher et al. 2010a, 2019a; Kustatscher and Roghi 2016), Piz da Peres (e.g., Todesco et al. 2008; Kustatscher et al. 2019a), San Lucano Valley (e.g., Kustatscher et al. 2011), Non Valley (e.g., Kustatscher et al. 2012a), and Bagolino (Brack and Kustatscher 2013). Its wide distribution in this restricted geographical area supports a certain uniform vegetation of the entire Southern Alps even though the landscape at that time consisted of a tropical sea interrupted by several islands (Brack and Kustatscher 2013).

Species—Voltzia edithae *sp. nov. Forte, Kustatscher et Van Konijnenburg-van Cittert*

Diagnosis. Conifer with spirally arranged, broad, obovate to lanceolate, slightly coriaceous leaves arising in a dense helix

from the axis at an angle of 30°–40°. Branches densely covered by leaves adpressed to the axis and overlapping each other. Ultimate shoots arise helically arranged from the penultimate shoots at angles of 30°–70°. Up to six shoots commonly arising from the stem almost form 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, occasionally double stomata within a row. On upper cuticle, stomata sometimes scattered. Stomatal rows more cutinized than epidermal cells. Six or seven or occasionally 5–10 subsidiary cells per stomatal complex, trapezoid to rounded in shape, bearing papillae overhanging the stomal aperture.

Holotype.   NMS PAL733, figure 4*F*, here designated.

Paratypes.   NMS PAL685, figure 4*B* (most complete penultimate shoot, showing not only the spiral arrangement of the ultimate shoots but also the imbricated arrangement of the leaves and their shape in frontal view), PAL667, figure 4*C* (stem fragment with six shoots arising radially, forming a whorl interpreted as seasonal growth), PAL679, figure 4*D* (spiral attachment of the ultimate shoots and the leaf shape in lateral view), PAL1771, figure 6*G*, 6*H* (most complete and well-preserved cuticle) here designated.

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

Locus typicus.   Kühwiesenkopf/Monta Prà della Vacca, northern Dolomites, northern Italy.

Stratum typicum.   Middle part of the Dont Formation, middle Pelsonian, upper Anisian, Middle Triassic.

Etymology.   The species is in honor of Professor Edith Taylor for her outstanding contributions in the field of paleobotany.

Description.   Fifty-eight specimens include stem, branch, and shoot fragments of up to 200 mm in length and 170 mm in width. Stem fragments (e.g., NMS PAL676, 667, 733; fig. 4*A*, 4*C*, 4*F*) are 15–22 mm in diameter and densely covered by helically arranged coriaceous leaves. The leaves are lanceolate (e.g., NMS PAL658, 671, 683, 733; fig. 4*E*–4*H*) and up to 15 mm long and 5 mm wide in frontal view, with a slightly restricted basis. They arise at a narrow angle (about 20°–30°) from the stem and partially imbricate (e.g., NMS PAL667, 658; fig. 4*C*, 4*G*). Up to six penultimate shoots arise in a whorl from the stem fragments. Branch fragments are up to 160 mm long and 100 mm wide (e.g., NMS PAL667, 671, 676, 733; fig. 4*A*, 4*C*, 4*E*, 4*F*) and are characterized by at least two branching levels (e.g., NMS PAL667; fig. 4*C*). Ultimate shoots arise helically at an angle of 30°–70° from the penultimate axis (e.g., NMS PAL671, 685; fig. 4*C*). Penultimate shoots are up to 150 mm long and 4–5.5 mm wide (e.g., NMS PAL667, 676, 733; fig. 4*A*, 4*C*, 4*F*). They are densely covered by broad to lanceolate, slightly coriaceous leaves (3.5–12 mm long and 1.5–4.5 mm wide, with a rounded apex) arising at 15°–60° from the axis and commonly overlapping each other (e.g., NMS PAL658; fig. 4*G*). Leaves of ultimate shoots are 3.5–10 mm long and 1–4.5 mm wide, lanceolate, helically arranged, arising from the axis at an angle of 10°–60°.

Leaves of *V. edithae* are amphistomatic (e.g., NMS PAL1771; fig. 6*C*) with some elongate (7–31 μm × 23–70 μm; between stomatal rows) to mainly small isodiametric (10–30 μm) epidermal cells (e.g., NMS PAL542, 1140, 1771; fig. 6*G*–6*K*), sometimes

heavily papillate. Stomata (31–60 μm × 35–108 μm) are monocyclic to rarely incompletely dicyclic (table A3). Stomata are longitudinally oriented (e.g., NMS PAL542; fig. 6*I*), arranged in long rows (NMS PAL1771; fig. 6*G*, 6*H*), occasionally with double stomata within a row (e.g., NMS PAL1771; fig. 6*H*; table A3), or are sometimes scattered, mainly on the upper cuticle (e.g., NMS PAL542; fig. 6*I*). Stomatal rows are 40–110 μm distant, with subsidiary cells more cutinized than the epidermal ones (e.g., NMS PAL1771; fig. 6*I*). There are commonly six or seven subsidiary cells per stomatal complex, but they can occasionally range between 5 and 10 cells, trapezoidal to rounded in shape, although polar ones can also be elongated (e.g., NMS PAL1140; fig. 6*J*, 6*K*). All subsidiary cells bear papillae overhanging the stomatal aperture (table A3).

Comparisons.   Stem and branch fragments of *V. edithae* sp. nov. differ noticeably from all other *Voltzia* species in the assemblage (table A2) because of the spatial arrangement of the shoots and the shape and dimensions of the leaves; thus, we assign them to a new species. The other *Voltzia* species occurring in the same flora, *V. walchiaeformis*, *V. recubariensis*, and *V. heterophylla*, differ from *V. edithae* remarkably, especially in leaf morphology and attachment angle (table A2), the three-dimensional arrangement of the ultimate shoots, and the attachment of the penultimate shoots in whorls. In *V. walchiaeformis*, the ultimate shoots arise pinnately on one plane from the axis of the penultimate shoots. Moreover, they are very stiff and oppositely inserted, and the leaves are more needlelike and arise at a much wider angle (table A2). *Voltzia recubariensis* differs from *V. edithae* because of the particular leaf attachment, with leaves arising from the axis in two very characteristic lower and upper angles (e.g., Brack and Kustatscher 2013; table A2). *Voltzia heterophylla* shares with *V. edithae* the fact that they both show seasonal growth signs. In *V. heterophylla*, this is mainly shown by two types of leaves, needlelike ones that arise at a narrower angle from the axis and long ribbonlike leaves (table A2) observed in the various ranges of the shoots. In *V. edithae*, the leaves vary only slightly in size and shape, but the seasonal growth is shown by the penultimate shoots arising from the stem forming a whorl (e.g., NMS PAL667, 676, 733; fig. 4*A*, 4*C*, 4*F*).

Pelourdea vogesiaca and *A. latifolia* are very typical broad-leaved conifers that are completely different from *V. edithae*. *Albertia latifolia* is slightly similar to *V. edithae* in its leaf shape but differs in its longer and wider leaves, which are attached in a loose spiral and at a much wider angle than the leaves of *V. edithae*. Moreover, the leaf apex of *A. latifolia* can occasionally turn down toward the axis, which was never observed in *V. edithae* (table A2).

Other Triassic Voltzia *species in Europe.*   Among the other Triassic European *Voltzia* species, *V. foetterlei* Stur, 1868, originally from the Carnian of Italy and Austria (Bronn 1858; Schenk 1866–1867; Stur 1868; Schütze 1901) but lately also putatively described from the late Anisian of Germany (Kustatscher et al. 2019*b*), resembles *V. edithae* in its general leaf shape and size (table A2) as well as its leaf arrangement in a close helix. *Voltzia foetterlei* differs, however, because the shoots often bifurcate or branch irregularly and terminate in small shoots or cones. Moreover, the leaves of *V. edithae* have a rounded apex, whereas the apex of *V. foetterlei* leaves is generally acute. The Anisian *V. weissmannii* Schimper, 1870 is also characterized by spirally arranged lanceolate to falcate leaves with a rounded apex (table A2) slightly resembling those of *V. edithae*. However, leaves are wider

in the former and arise from the axes in a loose helix and at a wider angle than in *V. edithae* (table A2). Moreover, *V. weiss-mannii* is characterized by a distinct central vein not observed in *V. edithae*. Broad lanceolate leaves also occur in *V. e-fraasii* Schütze, 1901, in which, however, heterophylly is present and possibly four different types of leaves, from triangular and falcate to lanceolate and elongate, are recognized (e.g., Schütze 1901; Kustatscher et al. 2019*b*; table A2). *Voltzia koenenii* Schütze, 1901 is another taxon originally described from the Anisian of Germany. Leaf morphology and arrangement in *V. koenenii* are very different from in *V. edithae*, as the latter is characterized by very needlelike leaves adpressed to the stem (table A2). Three *Voltzia* taxa were described from the Ladinian of the northern Dolomites, *V. dolomitica* Wachtler et Van Konijnenburg-van Cittert, 2000, *V. ladinica* Wachtler et Van Konijnenburg-van Cittert, 2000, and *V. pragsensis* Wachtler et Van Konijnenburg-van Cittert, 2000. These conifers are characterized by triangular, falcate leaves with acute apexes that are attached to the stem in a close helix (Wachtler and Van Konijnenburg-van Cittert 2000). They are thus quite different from the broader leaves of *V. edithae* (table A2). Moreover, *V. ladinica* is slightly heterophyllous in leaf size. Slightly similar in general leaf shape are the fragments figured by De Zigno (1862) as *Araucarites pachyphyllus* De Zigno, 1862. However, the fragments are too small to show the spatial arrangement of the shoots, and the original material has not yet been found, making it impossible to say whether these two species actually belong to our new species. Since the species is assigned to a more modern genus, we refrain from using its distribution for the stratigraphic and geographic range of vegetative conifer shoots in Europe (figs. 7, 8).

Comparison with some Permian conifers. Conifers with linear to lanceolate leaves from the Dolomites are also reported from the late Permian flora of Bletterbach (e.g., Clement-Westerhof 1987, 1988; Visscher et al. 2001; Kustatscher et al. 2012*c*, 2017*a*). *Majonica alpina* Clement-Westerhof, 1987, the type species of the Permian family Majonicaceae (e.g., Clement-Westerhof 1987, 1988; Looy 2007; Looy and Stevenson 2014), resembles *V. edithae* in having shoots covered by helically arranged and slightly overlapping bifacial leaves with a rounded apex (e.g., Clement-Westerhof 1987, pl. 1, figs. 1–2). In *Majonica*, heterophylly may occur, and Clement-Westerhof (1987) distinguished three leaf types: leaves with a narrow-subtriangular shape and acute apex, up to 35 mm long and 6 mm wide (type 1), leaves with an ovate shape and obtuse apex, up to 10 mm long and 4 mm wide (type 2), and lanceolate leaves with an obtuse (to acute) apex, up to 30 mm long and 3 mm wide (type 3). Both leaf types 1 and 2 are adpressed, completely covering the axes. The leaves of *V. edithae* are also closely adpressed to the stem and resemble leaf type 2 of *M. alpina* in shape and size (i.e., ovate shape, obtuse apex, observed dimension of up to 10 mm long and 4 mm wide; table A2).

Discussion. *Voltzia edithae* resembles both late Permian taxa such as *M. alpina* and Middle to early Late Triassic conifers (e.g., *V. foetterlei*) in its morphological features. This may suggest that it represents a transitional form. However, as long as we do not have female reproductive organs assigned confidently to this species, this hypothesis cannot be evaluated.

Distribution. *Voltzia edithae* is so far known only from the Anisian (Middle Triassic) Dont Formation of Kühwiesenkopf (northeastern Italy).

Discussion

Relevance of the Fossillagerstätte Kühwiesenkopf for Our Understanding of Biotic Recovery in the Paleotropics

There is an ongoing debate on the effect and extent of the end-Permian mass extinction for plant communities and diversity (e.g., Fielding et al. 2019; Nowak et al. 2019; Vajda et al. 2020 and references therein) as well as the dynamics with the transition from the Permian to Triassic floras. Frederiksen (1972) suggested that the Mesophytic started in the late Permian with the more derived gymnosperms migrating from the uplands/hinterlands into the depositional environments, showing that the stratigraphic boundary between Paleophytic and Mesophytic (terminology introduced by Potonié 1899; Gothan 1912) is based on migration rather than on sudden evolution and extinction and, thus, is diachronous throughout the world. Dobruskina (1987, 1994) still assigned the Early Triassic and early Middle Triassic floras to the Paleophytic but showed evidence of a major floral turnover taking place with the onset of the "real" Mesophytic at the Ladinian-Carnian boundary. Kerp (2000) showed evidence of a general replacement trend of predominantly hydro- to hygrophilous plants by more meso- to xerophilous floras as an expression of climate change and paleogeographic evolution. Some authors (e.g., Gall et al. 1998; Looy et al. 1999; Grauvogel-Stamm and Ash 2005) supported a catastrophic end-Permian mass extinction event with an Early Triassic survival interval extending over 5 Myr and the complete recovery or repopulation process taking up to 14 Myr. This extended period was explained by the considerable time required by the plants to rediversify and adapt to the new environments and harsh conditions of the Triassic. Finally, DiMichele et al. (2008) suggested abandoning the terms "Paleophytic" and "Mesophytic" because of their confusing and misleading use and the nonexistence of a global "Paleophytic" or "Mesophytic" vegetation, considering the plants to be organized in complex global vegetation types reflecting climate change at many geographic and stratigraphic levels.

There are still many uncertainties and questions, especially for the late Permian to Middle Triassic time interval compared with, for example, the Carboniferous and Late Triassic–Jurassic, because of the low preservation potential of the plant fossils (both qualitatively and quantitatively) as a result of the dominance of dry environments with a reduced sedimentation rate. In Europe, only a scattered plant fossil record exists, restricted to a few stratigraphic sequences such as the middle-upper Wuchiapingian Zechstein and the Gröden/Val Gardena Formation (e.g., Kustatscher et al. 2012*c*, 2014*b*, 2017*b*; Labandeira et al. 2016), the Olenekian Solling Formation (e.g., Kustatscher et al. 2014*c*), the lower Anisian Grès à *Voltzia* (e.g., Grauvogel-Stamm 1969, 1978; Gall and Grauvogel-Stamm 2000; Gall et al. 2006), the upper Anisian Dont Formation and its time equivalents (e.g., Kustatscher 2004; Kustatscher and Roghi 2006; Van Konijnenburg-van Cittert et al. 2006; Kustatscher et al. 2010*a*, 2010*b*, 2014*b*, 2017*b*, 2019*a*), and the upper Ladinian "Lettenkeuper" (now the Erfurt Formation; Kelber and Hansch 1995; Hagdorn et al. 2015; Nitsch 2015) and Wengen/La Valle Group (Wachtler and Van Konijnenburg-van Cittert 2000; Kustatscher and Van Konijnenburg-van Cittert 2005; Kustatscher et al. 2019*a*). The late Anisian plant assemblage of Kühwiesenkopf grew, thus, during a very important
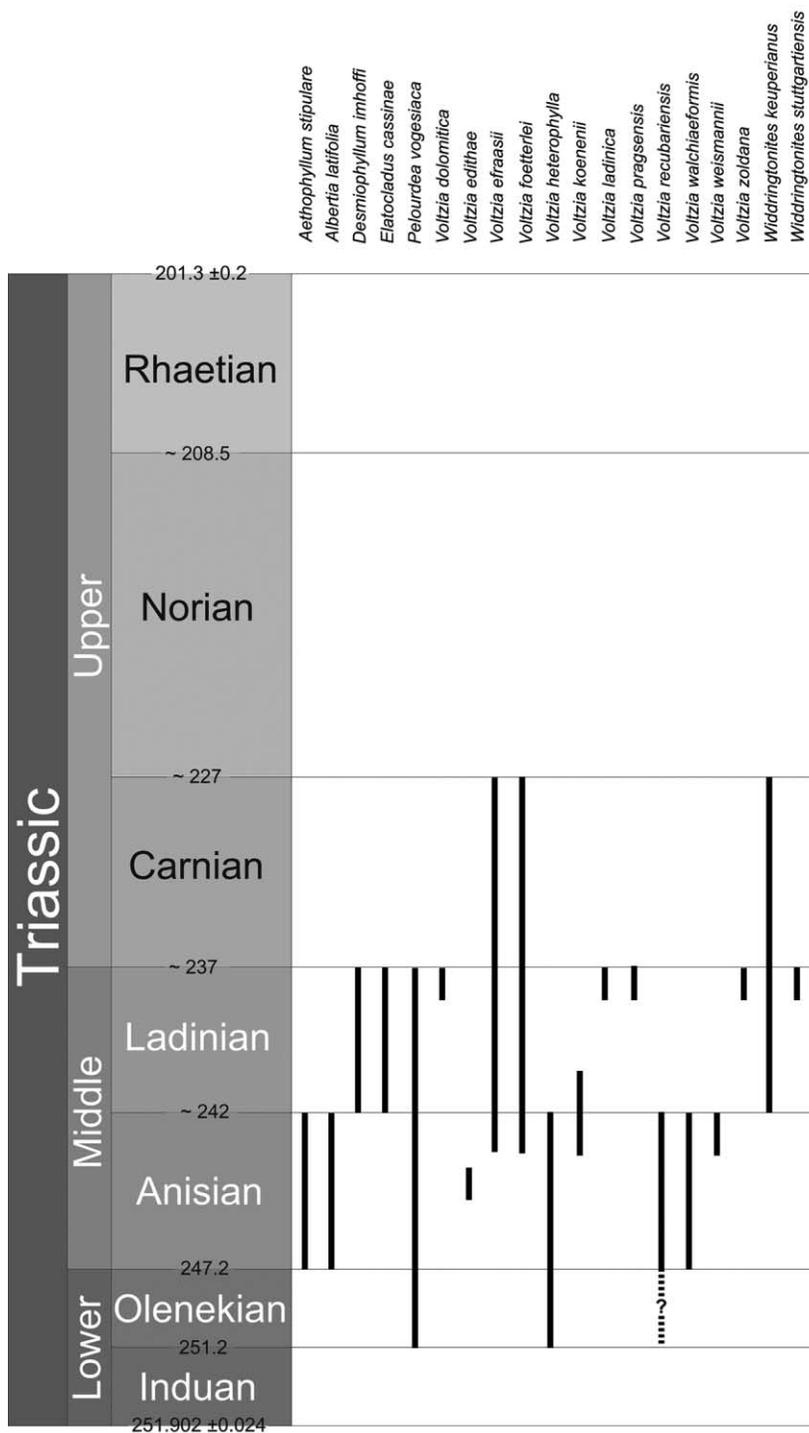
Fig. 7 Chronostratigraphic range of conifers present in the Middle Triassic of Europe. Some occurrence data come from unpublished material that is in European paleobotanical collections. Additional information is listed in table A4 (tables A1–A4 are available online). A color version of this figure is available online.

time for our understanding of the transition from the Permian to the Triassic floras.

During the late Permian, there existed two main paleogeographic realms of plants in central Europe (central and western Europe sensu Grauvogel-Stamm and Ash 2005): the Alpine Realm and the Zechstein Basin. The middle Wuchiapingian Gröden/Val Gardena Formation of the Southern Alps and the more or less coeval Kupferschiefer flora of the Zechstein Basin are dominated by conifers with exceptional preservation (Schweitzer 1968; Visscher et al. 2001; Bödige 2007; Kustatscher et al. 2017a and references
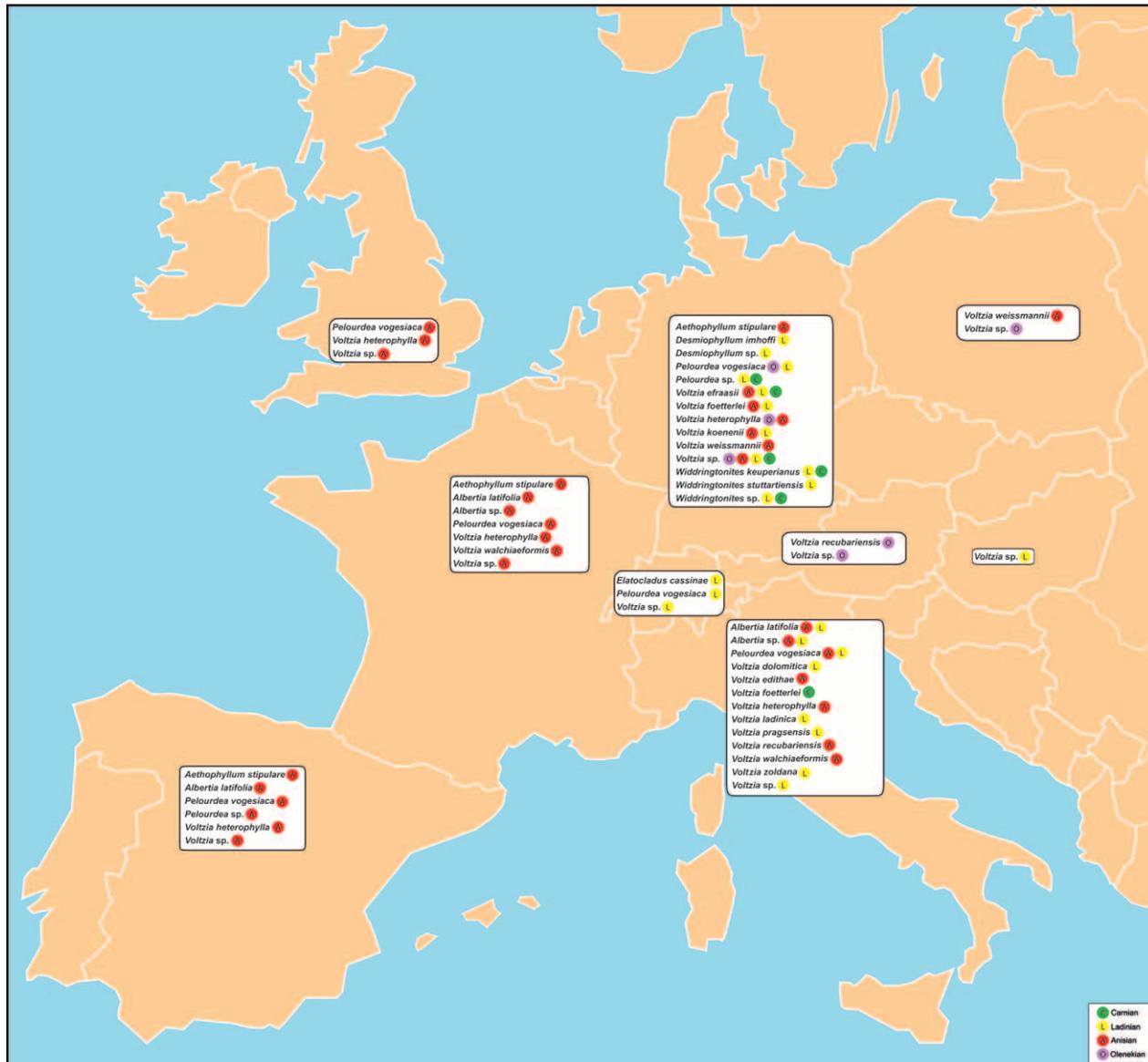
Fig. 8 Geographic distribution of Triassic conifer shoot taxa of Europe. Species and genera based only on wood or reproductive organs are not considered. Species are grouped by country. See additional information in table A4 (tables A1–A4 are available online) and appendix A5 (available online) for localities and references.

therein). The conifers are the most diverse group, with the voltzialean families Utrechtiaceae (*Ortiseia* Florin, 1964, *Ullmannia* Göppert, 1850, and *Culmitzschia* Ullrich, 1964), Majonicaceae (*Majonica* Clement-Westerhof, 1987, *Dolomitia* Clement-Westerhof, 1987, and *Pseudovoltzia* Florin, 1927), and *Quadrocladus* Mädler, 1957 so far not assigned to any family (Schweitzer 1968, 1986; Kerp 2000; Bödige 2007; Kustatscher et al. 2012c, 2017a and references therein). Ginkgophytes are generally rare but locally abundant (Bauer et al. 2014; Kustatscher et al. 2017a). Seed ferns (including the order Peltaspermales), ferns, sphenophytes, putative cycadophytes, and Czekanowskiales are rare in the plant assemblages (Schweitzer 1968, 1986; Kustatscher et al. 2017a).

The Induan has not yielded any plant remains so far. The oldest Triassic plant remains come from the Karlstal Formation in Germany, which is early Olenekian in age. The low-diversity flora is dominated by lycophytes of the order Pleuromeiales (Fuchs et al. 1991; Grauvogel-Stamm and Kustatscher, forthcoming). The late Olenekian to earliest Anisian Solling flora is more diverse. In addition to the characteristic lycophyte genus *Pleuromeia* Stiehler, 1859, the sphenophytes (Equisetales) and ferns (Osmundales) are common in the flora. The conifers are rare and are represented by the genera *Voltzia* and *Pelourdea* (Kustatscher et al. 2014c; Grauvogel-Stamm and Kustatscher, forthcoming). The early Anisian Grès à *Voltzia* flora is rich in hygrophytic elements such as lycophytes, sphenophytes (Equisetales), ferns (Osmundales),

ginkgophytes, and putative cycadophytes. The conifers are represented by, for example, *Aethophyllum stipulare*, *Albertia latifolia*, *Pelourdea vogesiaca*, and *V. heterophylla* (e.g., Grauvogel-Stamm 1978; Gall and Grauvogel-Stamm 2000, 2005; Rothwell et al. 2000; Gall et al. 2006).

The Pelsonian (late Anisian) plant fossil assemblage of Kühwiesenkopf (northeast Dolomites, north Italy) represents a very rich and diverse flora. Lycophytes are represented by at least four herbaceous and subarborescent forms (Selaginellales and Isoetales; Kustatscher 2004; Kustatscher et al. 2010a, 2010b) and sphenophytes, the least abundant group of the flora, by three taxa (Equisetales; Kustatscher et al. 2007). Ferns, the most diverse group with 12 taxa, include mainly Osmundales and Marattiales (Van Konijnenburg-van Cittert et al. 2006). Seed ferns are represented by fronds and female reproductive organs attributed to four taxa (Peltaspermales, Caytoniales; Kustatscher et al. 2007). Cycadophytes consist of subarboreous plants with entire or strap-like leaves and female fructifications assigned to at least seven different taxa (Broglio Loriga et al. 2002; Kustatscher et al. 2010b). Conifers are also diverse. About 285 plant remains were assigned to six different conifer taxa, *P. vogesiaca*, *A.* cf. *latifolia*, *V. heterophylla*, *V. walchiaeformis*, *V. recubariensis*, and the new species, *V. edithae*.

The transitional character of this flora is evidenced by several plant orders that were already well known from the Paleozoic (Isoetales, Selaginellales, Osmundales, Marattiales, Peltaspermales) in combination with the first appearance of typical Mesozoic groups such as the Caytoniales and the genus *Ptilozamites* Nathorst, 1878 among the seed ferns and the genus *Bjuvia* Florin 1933 among the Cycadales. Among the conifers, *V. edithae* is of special interest. A comparison with other broad-leaved conifers similar in age and/or geographic area highlights the similarities in leaf shape and cuticular characters to the Permian family Majonicaceae (*Majonica alpina*; see table A3), including in *Majonica* leaves (especially types 1 and 2) being appressed to the rachis, imbricating, and showing an obtuse apex (Clement-Westerhof 1987, p. 380). These characters, common in late Permian conifers (Clement-Westerhof 1984, 1987), are unusual in Early and Middle Triassic conifers except, to a lesser degree, for the genus *Albertia* (this article). Moreover, the thick amphistomatic leaves of *V. edithae*, with their relatively small epidermal cells, long, closely spaced stomatal rows, and stomata with a high number of subsidiary cells, are more common in Permian conifers such as *M. alpina* (Clement-Westerhof 1984, 1987) than in Middle Triassic ones. These similarities might suggest a certain affinity of *V. edithae* to the Majonicaceae (or other late Permian conifers) and indicate that some characters, such as amphistomatic leaves with long, crowded stomatal rows and a high number of subsidiary cells, common in Permian conifer taxa were still present during the Anisian. This would make *V. edithae* a transitional form that passed across the Permian-Triassic crisis and persisted during the Early Triassic. Of course, to confirm this hypothesis, we need the female cone of *V. edithae*, but there seems to be a good candidate for this that indeed shows some Permian conifer cone features (G. Forte, E. Kustatscher, and J. H. A. Van Konijnenburg-van Cittert, unpublished data). The transitional character of Anisian conifers has already been observed before. Some authors mentioned the resemblance between the Permian genera *Ullmannia* and *Culmitzschia* and the Anisian forms *Darneya* and *Albertia* (Grauvogel-Stamm and Ash 2005). Mapes and Rothwell

(1998) discussed the similarities between the Upper Pennsylvanian (Stephanian) walchian conifers and the Triassic conifer reproductive organs *Darneya*, *Voltziostrobus*, and *Sertostrobus*, which also bear adaxial pollen sacs (Grauvogel-Stamm 1969, 1978; Schaarschmidt and Maubeuge 1969; Grauvogel-Stamm and Galtier 1998). Similarly, Grauvogel-Stamm and Ash (2005) commented on similarities between Permian and Early to Middle Triassic conifers, including the compound pollen cones of the Anisian *Darneya* and Permian conifers from Germany (Kerp et al. 1990; Schweitzer 1996).

During the late Ladinian, more typical Mesozoic groups, such as the Dipteridaceae and Matoniaceae among the ferns (Kustatscher et al. 2012b, 2014a), in combination with already well-established orders such as Isoetales (lycophytes), Equisetales (sphenophytes), Marattiales, Osmundales (ferns), Cycadales, Peltaspermales, Caytoniales (seed ferns), and Voltziales (conifers), appeared. Some of the cycad remains have cuticles with aberrant stomata almost resembling syndetocheilic ones (e.g., *Bjuvia thalensis*; Kustatscher et al. 2010a), which might suggest some affinities with the Bennettitales or a common ancestor. In the Carnian, undisputed Bennettitales (cycadophytes) and Cheirolepidiaceae (conifers) appeared in Europe (e.g., Kustatscher et al. 2018). In general, in the Late Triassic, Gnetales and the extant conifer families Pinaceae, Taxodiaceae, and Araucariaceae, as well as enigmatic plants putatively related to the angiosperms, appeared (e.g., Kustatscher et al. 2018). Then the typical Mesozoic flora that would also dominate the Jurassic and Cretaceous was well established.

Conifers in the Kühwiesenkopf Flora

Voltzia is the dominant conifer genus in the Kühwiesenkopf flora, with *V. recubariensis* as the most common species, representing up to 40% of the conifers (fig. 9). *Voltzia edithae* is common, representing about 20% of the conifers (fig. 9). *Albertia* cf. *latifolia*, *V. walchiaeformis*, and *V. heterophylla* are equally abundant in the flora (~10%; fig. 9), whereas *P. vogesiaca* is rare (2%; fig. 9). Moreover, several specimens (24) could not be assigned to any species because of their fragmentary nature and bad preservation (fig. 9).

All *Voltzia* species in the Kühwiesenkopf flora were probably parts of trees, corroborated by the presence of fragments of large branches and stems with branch attachments. These trees would have grown mostly on drier areas of the hill slopes and/or in better-drained soils of the lowland (Kustatscher et al. 2010b), as suggested by the thick cuticles and the protected stomata.

The lanceolate leaves of *P. vogesiaca* were inserted spirally on a 1–1.5-m-high erected, unbranched stem (Schimper and Mougeot 1844; Ash 1987; Kustatscher et al. 2014c). Remains of *P. vogesiaca* have been found in levee-crevasse sediments and were interpreted as having lived in riparian environments (Kustatscher et al. 2014c). The shoot fragments of *A.* cf. *latifolia* could belong to small, up to 1 m high, shrublike plants with multiple branched shoots (Gall and Grauvogel-Stamm 2000). In the Anisian of the Vosges (France; Grauvogel-Stamm 1978), fragments of *Pelourdea* and *Albertia* have been found in lacustrine sediments, suggesting an adaptation to wetter environments.

The fossiliferous horizon yielding plant fossils at Kühwiesenkopf represents a "very rapid burial event caused by gravity flows within a marine basin in connection with heavy storms in the terrestrial domain" (Broglio Loriga et al. 2002, p. 382; see also
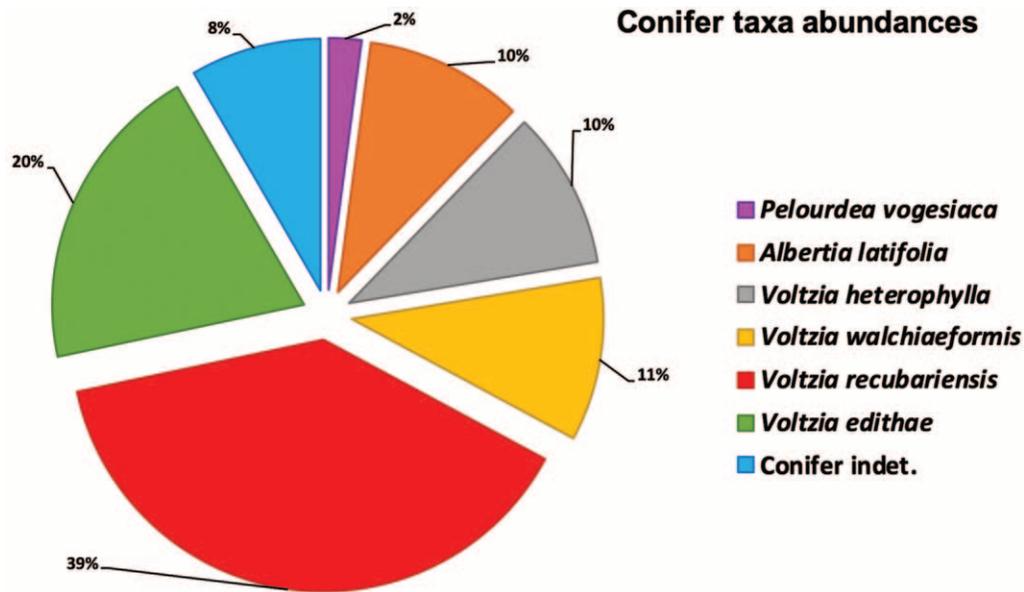
Fig. 9   Relative abundance of the various conifer species in the Kühwiesenkopf/Monte Prà della Vacca plant fossil assemblage. indet. = indeterminate.

Tintori et al. 2001). This way of the simultaneous deposition of plant remains coming from different environments of a restricted geographic area and subjected to a similar taphonomic bias makes it a unique flora for this time period and helps to reconstruct the paleoenvironment and paleoclimate conditions of the early Middle Triassic (Kustatscher et al. 2010*b*).

Spatial and Chronostratigraphic Distribution of the Middle Triassic Conifers

The conifers are among the most diverse and common plant fossils in the Middle Triassic floras of the Alpine Realm. From the Anisian, seven taxa (from three genera) are represented in the Southern Alps, whereas from the Ladinian, nine taxa (from four genera) are distinguished (table A4; fig. 8). *Voltzia recubariensis* is the dominant species from the Anisian of the Southern Alps and the most common taxon, particularly in Pelsonian and Illyrian plant localities (e.g., Recoaro, Piz da Peres; Massalongo 1857; De Zigno 1862; Schenk 1868; Todesco et al. 2008; Kustatscher et al. 2011, 2012*a*, 2019*a*; Brack and Kustatscher 2013; Roghi et al. 2017). This led to the hypothesis that the vegetation growing on different islands on the northwestern margin of the Tethys was rather uniform (Brack and Kustatscher 2013). *Pelourdea vogesiaca* and *V. recubariensis* are well known and widely distributed in the Southern Alps (e.g., Kustatscher et al. 2006, 2010*b*, 2011, 2019*a*; Roghi et al. 2017), whereas *V. walchiaeformis* and *V. heterophylla* are so far known only from Kühwiesenkopf in the Alpine Realm (e.g., Kustatscher et al. 2010*b*). *Albertia* cf. *latifolia* and *V. edithae* sp. nov. are here recorded for the first time from the Southern Alps, although De Zigno (1862) described some conifer shoot fragments as *Haidingera schaurothiana* from the Anisian of Recoaro that could belong to *A.* cf. *latifolia* as well.

The various areas of the Central European Basin show an interesting range of conifers. In the Buntsandstein of Spain, six taxa

were identified (from four genera; Díez et al. 2010; Borruel-Abadía et al. 2014; fig. 8), in France, seven taxa were identified (four genera; e.g., Brongniart 1828; Schimper and Mougeot 1844; Grauvogel-Stamm 1978; Gall and Grauvogel-Stamm 2005; fig. 8), and in Germany, seven taxa were identified (two genera; fig. 8). The Anisian of England yielded at least three taxa (one genus) and Poland one taxon (fig. 8). During the Ladinian, the conifers became more diverse in Germany, with 11 taxa (four genera). It is the only country of the former Central European Basin yielding Anisian and Ladinian conifers (fig. 8; table A4). The most diverse conifer genus is *Voltzia*, present with at least one taxon in all plant assemblages. Several Middle Triassic conifers were originally (or also) described from the Carnian. This includes, for example, *V. foetterlei* Stur, 1868, originally described from the Carnian of Raibl (Cave del Prezzo, Italy; Stur 1868) and lately also found in the Middle Triassic of Germany (e.g., Kustatscher et al. 2019*b*; fig. 8).

Considering the stratigraphic distribution of the conifers, it is interesting to observe (fig. 7) that several of the Middle Triassic conifers are restricted to the Anisian, such as, for example, *A. stipulare*, *A. latifolia*, *V. edithae* sp. nov., *V. walchiaeformis*, and *V. weissmannii*. At least two taxa had already appeared during the Olenekian (fig. 8), one extending up to the Ladinian (*P. vogesiaca*), whereas the other (*V. heterophylla*) disappeared from the fossil record at the end of the Anisian. *Voltzia recubariensis* might have appeared during the Olenekian and disappeared at the end of the Anisian, but the Olenekian occurrence is questionable (Brack and Kustatscher 2013). *Voltzia e-fraasii* and *V. foetterlei* appeared during the late Anisian and extended up to the Carnian (Kustatscher et al. 2019*b*), whereas *V. koenenii* appeared during the late Anisian but disappeared during the early Ladinian (fig. 7). *Elatocladus cassinae* is so far restricted to the Ladinian, and *Desmiophyllum imhoffi*, *V. ladinica*, *V. dolomitica*, *V. pragsensis*, *V. zoldana*, and *Widdringtonites stuttgartiensis* have so far been found only from the late Ladinian (Wachtler and Van

Konijnenburg-van Cittert 2000). *Widdringtonites keuperianus* is restricted to the Ladinian-Carnian of Germany (Kelber and Hansch 1995).

Thus, at the European level, the conifer species from Kühwiesenkopf have a stratigraphic range from the Olenekian to the Carnian (fig. 7) and a geographic distribution in several European countries (fig. 8). They have been described under various names that are often conspecific and that were here all put into synonymies for clearness (table A4). This shows how the Kühwiesenkopf flora not only includes transitional forms from the Permian to the Triassic but also represents a mixed flora that includes elements typical for the "Germanic Basin" and the Alpine Realm (fig. 8; table A4). Moreover, the conifers are unique for this time interval in their richness and diversity (figs. 7, 8), especially with the wide range of leaf shapes and spatial organizations of the shoot within the voltzian Voltziales group.

Conclusions

The morphological and cuticular study of the conifers enables us to distinguish six different conifer taxa in the Kühwiesenkopf flora, one more than originally indicated by Kustatscher et al. (2010*b*). *Pelourdea vogesiaca* is a well-known taxon from the Middle Triassic of Europe, and *Voltzia recubariensis* is the most characteristic conifer of the Anisian of the Southern Alps. The detailed morphological analysis of the *Albertia*-type shoots evidences that the four *Albertia* species distinguished by Schimper and Mougeot (1844), *A. latifolia*, *A. elliptica*, *A. braunii*, and *A. speciosa*, could correspond to a single species, *A. latifolia*, but this needs detailed study and a revision of the genus. Since our specimens show some characters present in all four abovementioned taxa, we assign our specimens putatively for the moment to the type species *A.* cf. *latifolia*. *Voltzia walchiaeformis*, so far poorly described from the Anisian of France, is emended thanks to better-preserved specimens, and the diagnosis now includes details on the structure of the branches, the leaves, the differences between penultimate and ultimate shoots, and the cuticle. The geographical range of *V. heterophylla*, a typical element of the Buntsandstein of the Central European Basin, is now confidently extended to the Alpine Realm.

Last but not least, a new species, *V. edithae*, which resembles in some morphological characters both the late Permian *Majonica alpina* and the Middle–Late Triassic *V. foetterlei*, is proposed. This indicates that some characters common in early and late Permian conifer taxa might still have been present during the Anisian and suggests *V. edithae* as a transitional form in the voltzialean lineage that survived the end-Permian crisis and persisted until the Middle Triassic. As pointed out by some authors (e.g., Looy and Duijnstee 2020), our knowledge about the evolution of Mesozoic conifers is still scarce, and there is still more to investigate, with special attention to the Anisian to Carnian conifers.

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