



Conifer diversity in the Kungurian of Europe—Evidence from dwarf-shoot morphology



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ABSTRACT

A major global change, the transition from an icehouse to a greenhouse world, took place during the Permian. In the equatorial Euramerican floral realm this resulted in stepwise changes from sub-humid climates in the early Cisuralian to semi-arid/arid climate by the late Cisuralian. During the same time interval we see a change from spore plant-dominated lowland floras, to increasingly drought-tolerant floras dominated by conifers and other seed plants. A recently discovered Kungurian (late Cisuralian) flora from the “Le Fraine” section near the village of Tregiovo (Trento Province, NE-Italy), is characterized by several types of conifers, callipterids, spenopterids, and spenopsids. The conifer fossils included both vegetative and reproductive organs. Five different ovuliferous dwarf shoot types were found, ranging from forms with many scales and interspersed sporophylls, that typically resemble late Pennsylvanian and early Permian walcchian conifers, to stalked forms with largely fused sterile scales and sporophylls, comparable to early and late Permian voltzian conifers. One of the voltzian-type dwarf shoots belongs to the genus *Dolomitia*, extending the range of this genus back to the late Cisuralian. Another form strongly resembles those of the voltzian conifer *Pseudovoltzia*. The other three dwarf shoot types show a wide morphological variation, but cannot be assigned to any known genus due to the imperfect preservation. In western Euramerica, the transition from walcchian- to voltzian-conifer-dominated floras took place during the late Cisuralian. This study shows that this change occurred across the entire equatorial Euramerican realm. The well-dated Tregiovo flora is one of the very few late Cisuralian floras of Euramerica. As such, this flora documents an important step in the evolution of Permian terrestrial biotas.

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1. Introduction

The Permian (299–252 million years ago) witnessed one of the most extreme climate transitions of the Phanerozoic, from deep icehouse conditions in the Cisuralian (early Permian), to a greenhouse state in the Lopingian (late Permian, e.g., Montañez and Poulsen, 2013). The Cisuralian is an important interval as it marks the deglaciation of the Southern Hemisphere and increasing aridification in the

palaeoequatorial regions, resulting in stepwise changes from sub-humid climates (sensu Cecil and Dulong, 2003) in the early Cisuralian to semi-arid to arid climates by the late Cisuralian (e.g., Montañez et al., 2007; DiMichele et al., 2008, 2009; Tabor and Montañez, 2004; Peyser and Poulsen, 2008; Tabor and Poulsen, 2008; Horton et al., 2012; Montañez and Poulsen, 2013; Michel et al., 2015). In the equatorial Euramerican floral realm this process is reflected by a step-wise change from pteridophyte-dominated lowland floras to ones dominated by increasingly drought-tolerant seed plants (e.g., DiMichele et al., 2006). Conifers were prominent members of the more drought-tolerant Pennsylvanian and Cisuralian communities.

The earliest fossil conifers are the so-called walcchian conifers (walcchian Voltziales), a paraphyletic group of trees with plagiotropic branching patterns. The walcchian conifers originated during the middle

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Pennsylvanian in extrabasinal, relatively dry habitats (e.g., [Hernandez-Castillo et al., 2003](#)) in which the preservation potential is limited (e.g., [Looy et al., 2014](#)). The increasing aridity during the early Cisuralian resulted in the migration of the walcian conifers and other seed plants into the basinal Euramerican lowlands (see e.g., [DiMichele et al., 2008](#); [Looy et al., 2014](#)). In western equatorial Euramerica, these floras are replaced by even more drought-tolerant floras around Kungurian (late Cisuralian) times. These floras are characterized by voltzian conifers (voltzian Voltziales), more derived conifers characterized by irregular branching systems, and bifacial ovate to linear leaves ([Rothwell et al., 2005](#)), and by a different suite of seed-plants (e.g., [DiMichele et al., 2001, 2004](#)) such as peltasperms, cycads and ginkgos. In eastern Euramerica, late Cisuralian and Guadalupian sequences are rare and incomplete, and generally do not contain plant remains. Until now, evidence for the timing of the transition from walcian- to voltzian-dominated floras has been lacking.

A recently discovered Kungurian (Cisuralian) flora, from the “Le Fraine” section near Tregiovo (Trento Province, NE-Italy) revealed a diverse flora with abundant conifers and several sphenopterids, callipterids, and sphenopsids as accessory elements ([Marchetti et al., 2015](#)). Apart from conifer shoots attributed to *Hermitia geinitzii* (Florin, 1939) [Visscher et al., 1986](#), *Hermitia* sp., the broad-leaved *Feysia* sp. and *Quadrocladus* sp., several ovuliferous cones and isolated dispersed ovuliferous dwarf shoots (female reproductive structures) were found. The compressions of the cones hardly show any details of the dwarf-shoot morphology. In contrast, the isolated dwarf shoots, although only preserved as coaly compressions without cuticle, show a remarkable diversity. They range from forms with a large number of sterile free scales and interspersed sporophylls, comparable to those known from the late Pennsylvanian and early Permian walcian conifers (e.g., [Rothwell et al., 2005](#)), to stalked forms with largely fused sterile scales and sporophylls, typical for the early to late Permian voltzian taxa (e.g., [Clement-Westerhof, 1987](#); [Schweitzer, 1996](#); [Looy and Stevenson, 2014](#)). Not all types can be assigned to existing taxa, but one of the forms is strongly reminiscent of *Dolomitia* [Clement-Westerhof, 1987](#), a genus so far only known from Lopingian sediments of the Dolomites. Even though the preservation is far from ideal, these finds fill a gap in our knowledge of the evolution of Palaeozoic conifers.

2. Material and methods

The material described in this paper originates from the recently discovered section “Le Fraine” near the village of Tregiovo (Trento Province, NE-Italy; more details in [Marchetti et al., 2015](#)). The fossil-bearing Tregiovo Formation is middle Kungurian in age. It is intercalated between the volcanic Gargazzone and Ora formations, of which U/Pb datings of zircon crystals gave ages of respectively 276.5 ± 1.1 Ma and 274.1 ± 1.6 Ma ([Avanzini et al., 2007](#); [Marocchi et al., 2008](#)). The new section yields a rich and diverse plant assemblage together with invertebrate and vertebrate tracks; plant-animal interactions have also been documented ([Marchetti et al., 2015](#)). Although this section is new, fossils from the Tregiovo area have been known since the late 19th century, including plant fossils, palynomorphs, vertebrate footprints and conchostracans (e.g., [Vacek, 1882, 1894](#); [Vacek and Hammer, 1911](#); [Remy and Remy, 1978](#); [Kozur, 1980](#); [Neri et al., 1999](#); [Cassinis and Doubinger, 1991, 1992](#); [Visscher et al., 2001](#)).

The Tregiovo Formation exposed in the “Le Fraine” section consists of c. 130 m of sediments ([Fig. 1](#)). The lower part (80 m) mainly consists of fine-grained, very dark, very finely laminated siltstones and claystones, whereas the upper part comprises laminated marly limestone and sandstones ([Marchetti et al., 2015](#)). The sediments were interpreted as deposited in a lacustrine environment subjected to periodic changes in the lake level. These laminated sediments are very rich in organic matter, and several plant remains show traces of pyritization ([Marchetti et al., 2015](#)) indicating sub- to anoxic conditions at the bottom of the lake. Plant fossils were found at approximately 46 m and

105 m above the base of the section, in the finely laminated levels. [Marchetti et al. \(2015\)](#) gave a preliminary description of the lower assemblage; the material here described originates also from the more recently discovered upper assemblage.

Both “Le Fraine” assemblages are dominated by conifers, e.g., *Hermitia*, *Feysia*, and *Quadrocladus*, but differ in composition. Additional elements in the lower assemblage are ginkgophytes (*Sphenobaiera*), pteridophylls (*Sphenopteris*), callipterid peltasperm foliage (*Lodevia*) and ovuliferous structures (*Peltaspermum*), two morphotypes of *Taeniopteris*, and sphenopsids (*Annularia*) ([Marchetti et al., 2015](#)). The most common forms in upper Tregiovo assemblage, apart from conifers, are at least five species of sphenopterids, including large, almost complete fronds, together with callipterids and sphenopsids as accessory elements. The sphenopterids include at least two species thus far only known from the Zechstein (Lopingian), i.e. *Sphenopteris kukukiana* and *S. patens* ([Forte et al., in prep.](#)).

The plant fossils are highly coalified, often poorly preserved, and specimens usually show little contrast with the dark sediment. Some specimens seem to be covered by a thin layer of mud. More than 1000 slabs bearing fossils were collected in the two levels of “Le Fraine” section, including 42 ovuliferous dwarf shoots of conifers; 16 in the lower and 26 in the upper assemblage. The material was collected by Mr. Ferruccio Valentini (Tuenno), a local collector who discovered the site some years ago and kindly made it available for further investigation. The rock slabs with ovuliferous dwarf shoots are partly temporary deposited at MUSE—Museo delle Scienze di Trento, where they are labelled with the prefix MUSE PAG followed by consecutive numbers (from 7089 to 7429). Some more recently collected specimens have provisional numbers (e.g., TREG followed by consecutive numbers; collezione Valentini). The specimens were studied using a dissecting stereomicroscope (SZ-ST Olympus) and photographed with a Canon EOS 550D camera. Some specimens were measured using a calliper, but most measurements were taken from digital photographs using ImageJ64® (National Institutes of Health, Bethesda, MD).

Because the terms used to describe elements of ovuliferous structures of early conifers deviates from those applied to modern species, some terms used here are explained below (see [Hernandez-Castillo et al., 2001](#); [Rothwell et al., 2005](#)). Bracts are foliar appendages of the axis of ovuliferous cones or fertile zones, which are interpreted as modified leaves. Ovuliferous dwarf shoots (or dwarf-shoots) are lateral branches of limited growth, which arise in the bract axils. Sterile scales are foliar appendages of the dwarf shoots, and sporophylls are (potentially) seed-bearing appendages. Important criteria used to assign the dwarf shoots to a particular taxon are the number of sterile scales and sporophylls per dwarf shoot, the differentiation between these two types of appendages and their degree of fusion.

3. Results

Based on their morphology five different types of dwarf shoots can be recognized. One type is attributable to the genus *Dolomitia* [Clement-Westerhof, 1987](#). Other specimens show a distinctly different morphology but cannot be attributed to existing nor to new genera due to the lack of information on the shape and number of sterile scales, sporophylls and ovules. Due to their imperfect preservation these are informally described as *Pseudovoltzia*-like and as types A–C.

3.1. *Dolomitia* sp.

Description: Seven specimens are assigned to the genus *Dolomitia*. These are flattened and bilaterally symmetrical, with more than 20 partially fused elements, and a stalk-like base (e.g., MUSE PAG 7315; [Plate 1, 1](#)). The dwarf shoots are up to 13.3–20.4 mm long and 13–19.8 mm wide. There are three large ovate elements with obtuse apices (interpreted as ovuliferous scales), two of these are positioned on the lateral sides of the dwarf shoot, and one in a median position on the

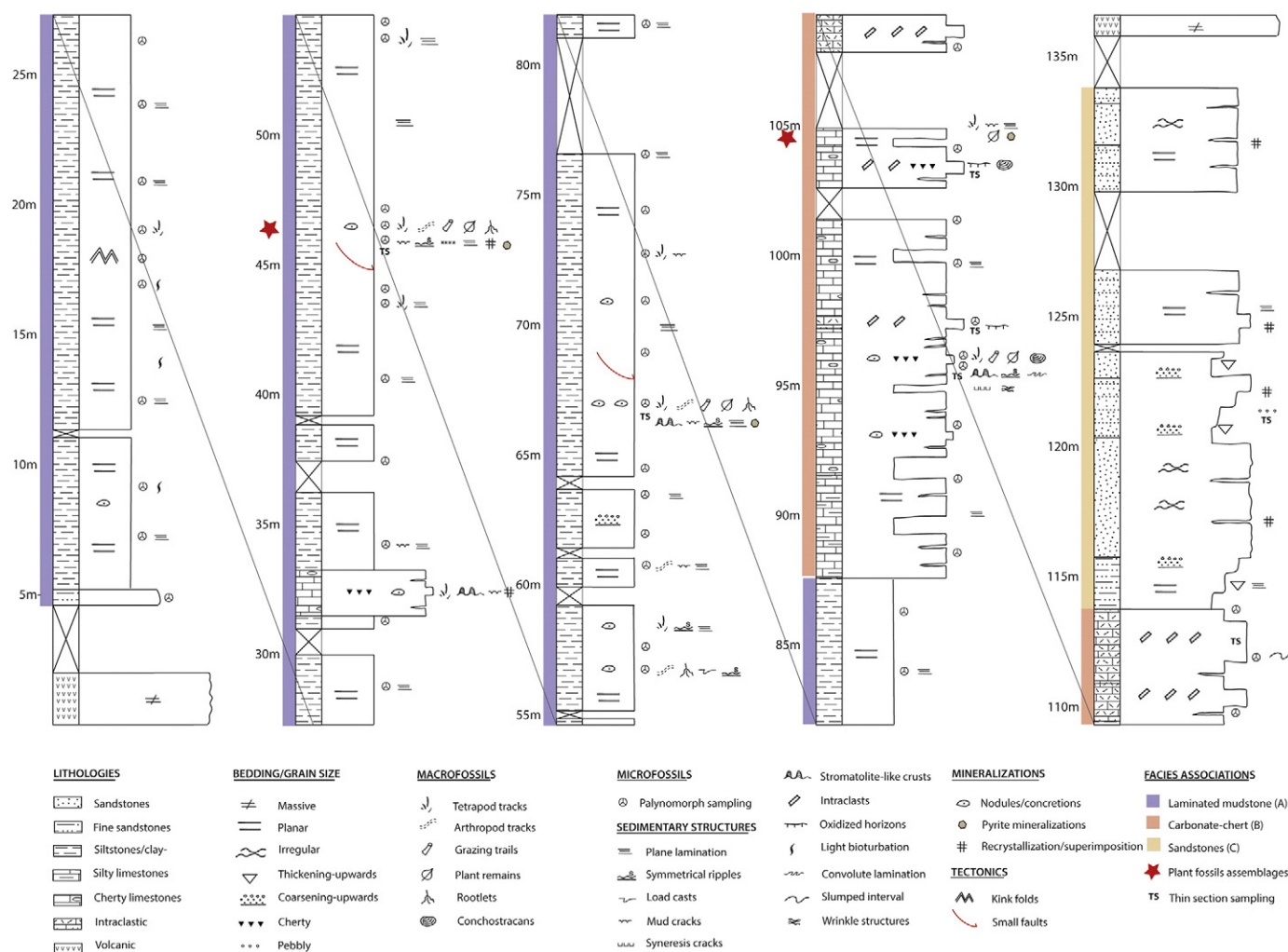


Fig. 1. Stratigraphic section of "Le Fraine", from Marchetti et al. (2015) (modified).

adaxial side. Ovule attachment areas or ovules cannot be discerned. Positioned between each of the two lateral and median sporophylls are two triangular sterile scales with pointed apices. At least 14 other sterile triangular scales are positioned behind the sporophyll-sterile scale row, and originate from the abaxial surface of the dwarf shoot (Fig. 2). The stalk-like base, measured from the maximum curvature point of the upper portion down (e.g., MUSE PAG 7315; Plate I, 1; Fig. 3), is up to 6.8–11.7 mm long and 1.2–2.5 mm wide. This basal part represents 42–47% of the whole dwarf shoot length. On some specimens it is difficult to distinguish if the dwarf shoot is preserved from the adaxial or abaxial side, since only the general outline is preserved (Plate I, 1).

Remarks: Specimens assignable to the genus *Dolomitia* occur in both the lower and upper assemblage and are the most abundant dwarf shoots from Tregiovo. There are no significant morphological differences between the dwarf shoots of this type from the two different levels.

Comparison: The monotypic voltzian conifer genus *Dolomitia* was established by Clement-Westerhof (1987) for material from the Gröden/Val Gardena Sandstone of the Butterloch locality (Wuchiapingian, late Permian) near Aldein/Aldino in the Southern Alps (NE Italy). The description of the dwarf shoots was based on one complete specimen and several dwarf shoot fragments. The complete *Dolomitia cittertia* Clement-Westerhof, 1987 dwarf shoot is flattened, bilaterally symmetrical, with numerous fused elements and a short stalk-like base. The dwarf shoots have three ovate sporophylls with a rounded apex, two in lateral position and one in median position on

the adaxial side of the dwarf shoot. The approximately thirteen sterile scales are triangular with acuminate apices. Two of the sterile scales are positioned between the central and lateral sporophylls; the others arise from the abaxial side. The basal part of the dwarf shoot is stalk-like and relatively short (~3.5 mm), indicating a partial fusion with the bract (Clement-Westerhof, 1987). The whole dwarf shoot is ~14 mm long and 20 mm wide. The specimens from Tregiovo look very similar to *D. cittertia* in having two lateral sporophylls, one median sporophyll on the adaxial side of the dwarf shoot, and a large number of small sterile scales. However, they differ in having more sterile scales (18 or more) than *D. cittertia*, and a longer stalk. Although they show the same basic organization, they likely represent a different species. Because of the imperfect preservation of the Tregiovo specimens, in which seed attachments cannot be discerned, we refrain from formally describing a new species and provisionally identify these specimens as *Dolomitia* sp.

3.2. Pseudovoltzia-like dwarf shoot

Description: Three specimens of this type were found (Plate I, 2, 3). The dwarf shoots are flattened, bilaterally symmetrical, with five fused elements and a stalk-like base. They have one central and two lateral broadly rounded elements, probably sporophylls, and two intermediate narrow triangular sterile scales. The dwarf shoots are up to 17.9 mm long and 12.6 mm wide, with well-developed stalks of up to 6.7 mm length and 2.8 mm width. The individual scales are fused up to at least



Plate 1. 1. Dwarf shoot of *Dolomitia* sp. (MUSE PAG 7315); 2. *Pseudovoltzia*-like dwarf shoot (TREG P1600859), from the upper flora; 3. *Pseudovoltzia*-like dwarf shoot laterally folded (MUSE PAG 7389), from the lower flora; the arrow indicates ovoid coaly structure that may be attribute to an ovule or a seed; 4. Type A dwarf shoot (TREG 526), abaxial side, with several sterile scales and a well-defined stalk-like base; the arrow indicates a putative sporophyll; 5. Type B dwarf shoot (TREG 0078), showing a small number of almost free scales; 6. Type C dwarf shoot (TREG 0038) with a well-defined stalk-like base, lanceolate scales free down to their base; scale bar 1 cm.

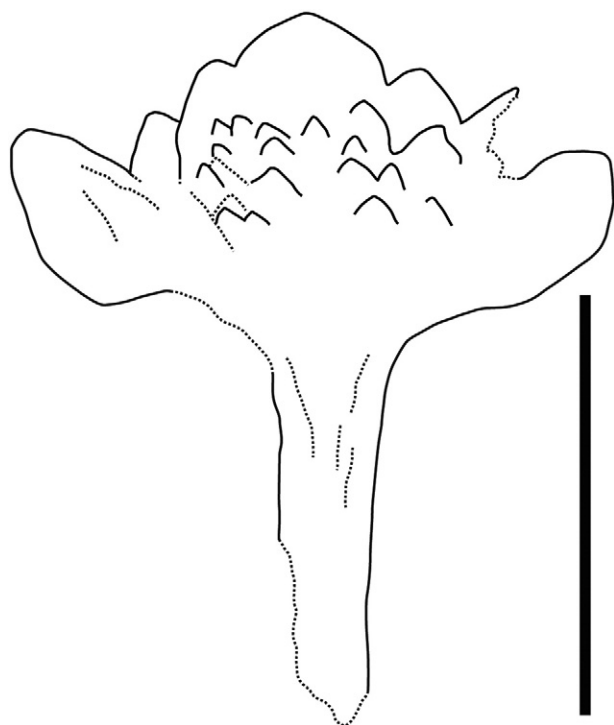


Fig. 2. Reconstruction of dwarf shoot of *Dolomitia* sp. (MUSE PAG 7315), showing several acute sterile scales (17–19) and three main rounded fertile scales; scale bar 1 cm.

half of their length. The larger scales are up to 4.6 mm long and 4.1 mm wide. On one specimen (TREG P1600859; Plate I, 2), some bundles are visible on the central scale and along the stalk. One of the specimens (MUSE PAG 7389; Plate I, 3), appears laterally folded and shows ovoid coaly structures (2.8 mm long and 1.6 wide) near the base of the lateral scales.

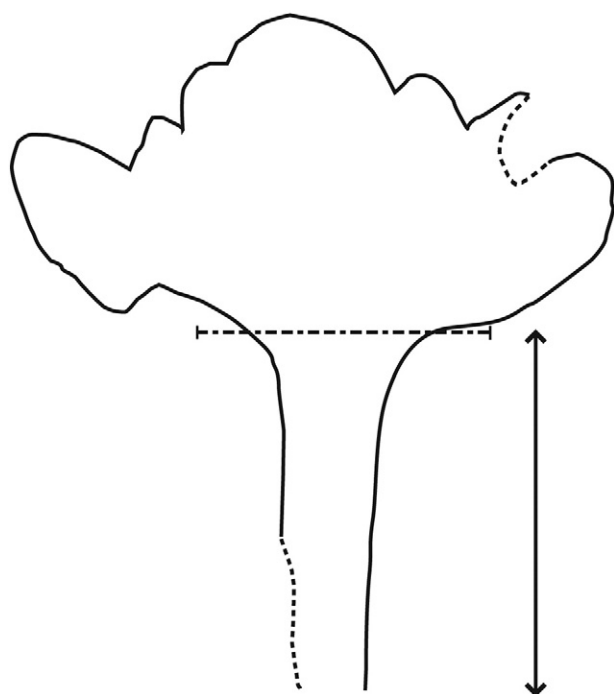


Fig. 3. Indication of the length of *Dolomitia* sp. stalk-like base; the dotted line links the two maximum curvature point of the upper portion down.

Remarks: *Pseudovoltzia*-like dwarf shoots are found in both Tregiovo assemblages (two in the lower and one in the upper). On the narrower, putatively slightly laterally compressed specimens, the two smaller scales are not easily visible, although in general, the dwarf shoots are entirely preserved, stalk included. One of them shows the adaxial side (Plate I, 2).

Comparison: Although the preservation is not optimal, these dwarf shoots are reminiscent of those of *Pseudovoltzia* Florin, 1927, a voltzian conifer genus known from the upper Permian of Germany and Italy (see Clement-Westerhof, 1987; Schweitzer, 1963). However, the fertile nature of the central and lateral elements cannot be ascertained due to the poor preservation, although the ovoid bodies of one of the dwarf shoots might represent ovules (Plate I, 3). Therefore, we refrain from a formal identification.

3.3. Dwarf shoot Type A

Description: A single specimen from the upper assemblage, here designated as Type A, is characterized by a large number of elements that are hardly fused, with a stalk-like base (Plate I, 4). The dwarf shoot is 24 mm long and 19.5 mm wide. Scales on the abaxial side seem to be attached in at least three successive rows (Fig. 4). The scales in the basal row (6.5–7.5 mm long) are smaller than those in the third row (2.5–3 mm width), but within a particular row there is no clear distinction with regard to shape or size of the scales. Scales in the central part of the dwarf shoot seem wider than the lateral ones, which are laterally compressed. Several more centrally positioned scales have obtuse tips. The stalk-like base is 1 mm long and 4.5 mm wide, and bears small, helically arranged, up to 4.5 mm long sterile scales.

Remarks: Even though uncertainties exist regarding morphological details, this type is easily recognizable and differs from all other dwarf shoots from Tregiovo in having a larger number of scales per dwarf shoot than any of the other types.

Comparison: One of the main characteristics of the dwarf shoot Type A that shows the abaxial side, is the large number of individual elements, which are free for most of their length. There is no obvious

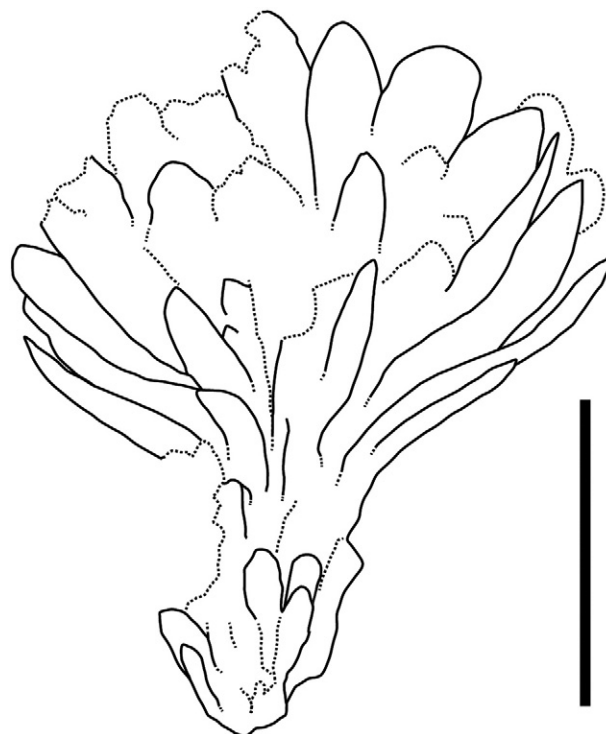


Fig. 4. Reconstruction of Type A dwarf shoot (TRE 526), showing several rows of scales that also cover the stalk-like base; scale bar 1 cm.

differentiation between the sterile scales and the sporophylls, and it is unclear how many appendages there are. The appendage with a slightly heart-shaped apex (arrow in Plate I, 4), might either be a sporophyll or, more unlikely, an ovule. Walchian conifers with high number of largely free scales are *Emporia lockardii* Mapes et Rothwell, 2003 from the uppermost Pennsylvanian of Kansas, *Otovicia hypnoides* (Brongniart) Kerp et al., 1990 from the uppermost Pennsylvanian and lower Permian of Euramerica, and *Ortiseia* Clement-Westerhof, 1984 from the upper Permian of the Southern Alps. Type A from Tregiovo differs from all these taxa in having more appendages and a well-developed stalk. In *E. lockardii* and *O. hypnoides* the upper row of sterile scales has pointed tips, whereas they are broader and rounded in Type A. Apart from the lack of a clear stalk, the arrangement and shape of the sterile scales is reminiscent of that of *Ortiseia jonkeri* as reconstructed by Clement-Westerhof (1984, fig. 13b).

3.4. Dwarf shoot Type B

Description: Only one specimen of dwarf shoot Type B was found in the “Le Fraine” section (TREG 0078). Dwarf shoot Type B is flattened, bilaterally symmetrical with 8–9 narrow elements that are fused at the base. The complete dwarf shoot is 17 mm long and 18 mm wide. The larger central element is narrow ovoid, 8 mm long and 3 mm wide. The lateral elements are narrow triangular, up to 4 mm long and 1 mm wide, with obtuse apices (Plate I, 5).

Remarks: The type B dwarf shoot has been found only in the upper flora. Because of the preservation many details about the scales and the complete morphology are not visible. Nonetheless, this type of dwarf shoot clearly differs from the other dwarf shoots at this section.

Comparison: The type B is different from the other dwarf shoots in having a rather small number of elements that are free almost to their base, forming a remarkably loosely arranged structure. The imperfect preservation does not allow distinguishing sterile scales from sporophylls, although the larger size of the central scale suggests that it was fertile. This dwarf shoot lacks a stalk but it is not clear whether it was either fused with the bract at the base, or had a stalk that was broken off or preserved at a different angle in the sediment. Other dwarf shoots with a limited number of elements similar to Type B are *Thuringiostrobus meyenii* Kerp and Clement-Westerhof, 1991 from the Rotliegend (lower Permian) of Germany and *Manifera talaris* Looy and Stevenson, 2014 from the uppermost lower Permian of Texas. *Thuringiostrobus meyenii* has four connate sporophylls and several smaller sterile scales (Kerp and Clement-Westerhof, 1991). *Manifera talaris* has three partly fused ovate sporophylls and two narrow triangular sterile scales with acute apices. On some *M. talaris* specimens, other scale-like structures were found preserved on a different level in the matrix, therefore; they might represent another rank of sterile scales or part of bract-like structures. (see for more details Looy and Stevenson, 2014).

3.5. Dwarf shoot Type C

Description: The only specimen of Type C (TREG 0038) is a 17 mm long and 16 mm wide dwarf shoot with an 8 mm long and 3 mm wide stalk vaguely showing what could be vascular bundles. It has at least 5–6 non-connate lanceolate elements, 1.9–2 mm wide and at least 7 mm long, with an acute apex, and a constricted base. They are free down to the base. The lateral ones that are laterally compressed show a recurved apex, pointing toward the central scale, but there are no clear differences between individual scales (Plate I, 6).

Remarks: The only specimen assigned to Type C was found in the upper assemblage. The specimen is incomplete; the more distal parts of the elements are not preserved on this slab.

Comparison: Like in Type A and B the elements of Type C are only fused at their bases. Type C, however, has fewer elements than type A,

and they are broader than in both other types. The elements of type B come in two shapes, whereas those of Type C are all very similar.

4. Discussion

Conifer shoots described from Tregiovo represent the genera *Hermitia*, *Feysia* and *Quadrocladus* (Marchetti et al., 2015). *Hermitia* is a fossil-genus established by Visscher et al. (1986) to accommodate many species previously assigned to the genus *Walchia*, that can be diagnosed mainly by leaf morphology (Visscher et al., 1986). *Feysia* is a genus with a plagiotropic branching pattern and rather broad, non-decurrent leaves (Broutin and Kerp, 1994). Although it has been described from the lower Permian, this type of foliage is very rare. *Feysia* is somewhat reminiscent of *Ortiseia* Florin, 1964, an upper Permian conifer with bifacial spirally arranged leaves, originally described by Florin, from the Gröden/Val Gardena Sandstone (Dolomites, N-Italy) as a fossil-genus, and then established as a natural genus by Clement-Westerhof (1984). *Quadrocladus* Mädlar, 1957 is a genus for conifer shoots with linear bifacial leaves with a round apex, and scattered stomata. Originally the genus was described from the upper Permian Zechstein (Mädlar, 1957), but it was also reported from a mixed “Rotliegend-Zechstein” assemblage from northern Germany (Mädlar, 1992). The reproductive organs of *Quadrocladus* are not known, but the leaves are similar to two other voltzian conifers taxa (Looy, 2007). However, it should be noted that the identification of late Palaeozoic conifers based on leaves alone is difficult if cuticles are not preserved. Therefore, dwarf shoots are of great importance, because they, more than any other part of the plant, show the true diversity within this group.

The number of elements per dwarf shoot, the morphological differentiation between sterile scales and sporophylls, the degree of fusion of the individual elements and the number of ovules per dwarf shoot are the essential features on which to classify late Palaeozoic conifers. The dispersed dwarf shoots from Tregiovo show a rather wide morphological variety, ranging from forms with a large number of hardly fused elements (Type A), to forms with fewer hardly fused elements (Type B–C), to forms with partly fused elements (*Pseudovoltzia*-like and *Dolomitia*). Even though the *Dolomitia* sp. and *Pseudovoltzia*-like dwarf shoots cannot be identified at species level, both types seem to fit the diagnosis of the Majonicaeae. The ovuliferous dwarf shoot members of this family are bilaterally symmetrical and flattened, have partially fused sporophylls and sterile scales, have lateral to adaxial ovule attachments, and stalk-like bases (Clement-Westerhof, 1987). The family was described based on cutinized dwarf shoots, shoots, leaves from the Southern Alps (Bletterbach Gorge, NE Italy), and originally encompassed the genera *Majonica*, *Dolomitia* and *Pseudovoltzia*. Since then members of the Majonicaeae have been documented from the upper Permian Zechstein Basin, Germany (*Voltzia hexagona*; Schweitzer, 1996), and the Kungurian of North America (*Lebowskia* and *Manifera*; Looy, 2007, Looy and Stevenson, 2014).

The most common type of dwarf shoot was identified as *Dolomitia* sp. This monospecific genus of the Majonicaeae, was so far only known from the late Permian of the Southern Alps. *Dolomitia cittertia* Clement-Westerhof, 1987 was described based on a few leafy twigs, one complete and several fragmented ovuliferous dwarf shoots. *Dolomitia* differs from the other members of the Majonicaeae by having a relatively high number of small sterile scales positioned on the abaxial side of the dwarf shoot. The longer stalk and the larger number of sterile scales as seen in the Tregiovo material were hypothesized by Clement-Westerhof (1988) as typical for a stage being intermediate between the walchian conifers and the Majonicaeae (Stage H of Fig. 7.13). Interestingly, the taxa that have longer stalk-like bases (*Majonica* and *Manifera*) are considered to be more derived and have large wings at the chalazal end of the seeds (Looy and Stevenson, 2014).

Another member of the Majonicaeae is *Pseudovoltzia*. This genus is characterized by three large sporophylls (a truncated central one plus

two lateral ones) and two small obovate sterile scales that are fused with the sporophylls for at least half of their length. The three ovules are positioned near the base and mid-region of the sporophyll (Schweitzer, 1963), and the upper part of the dwarf shoot is supported by a short stalk-like base. The type species, *P. liebeana*, is a common element in the European Zechstein and is found as far East as North China (Wang and Wang, 1986). One of the dwarf shoot types from Tregiovo seems to look similar to *Pseudovoltzia*, but not many details including the position of the ovule attachment can be discerned. Even though a formal generic identification is not possible, these specimens were clearly produced by a voltzian conifer.

In Tregiovo's Types B and C fewer dwarf shoot elements are visible, not more than eight, which are free for most of their length. Type B looks somewhat similar to *Manifera*, but it has more scales and does not show a stalk-like base; there is no clear differentiation between the sporophylls and sterile scales. The same can be said about Type C, which has at least elements of the same shape and size.

Type A has many elements, arranged in three rows; these elements become larger upwards and the upper row consists of broader and more rounded ones. Type A superficially resembles *Ortiseia*, especially *O. jonkeri* in which there are many sterile scales (24–28), which have variable shapes, from lanceolate to obovate, toward the apical part of the dwarf shoot (Clement-Westerhof, 1984). Unfortunately, the preservation does not permit identification of any sporophylls, and the presence of a stalk-like shaped base differs from the known *Ortiseia* dwarf shoots. Nonetheless the occurrence of a large number of free elements is a characteristic of other walthian conifers like *Emporia*, *Otovicia* and *Ortiseia* too. This may suggest a close walthian affinity for the Type A dwarf shoot.

The Tregiovo material fills a gap in our knowledge with regard to the evolution of late Cisuralian and Guadalupian lowland floras from equatorial Euramerica. The only two other floras of comparable age are the western Euramerican Lower Pease River (DiMichele et al., 2001; Looy, 2007; Looy and Stevenson, 2014) and South Ash Pasture floras (DiMichele et al., 2004). These floras are from North-Central Texas and of respectively Kungurian to Wordian (Guadalupian) age (Wardlaw, 2005). Like the Tregiovo Flora, the Lower Pease River Flora is dominated by conifers, and the floral assemblage also shows a mixture of forms known from the lower Permian and taxa that were previously only known from the upper Permian or Mesozoic (DiMichele et al., 2001). Two conifer genera have been described from the Lower Pease River Flora so far, i.e. *Lebowskia* and *Manifera* (Majonicaeace, Looy, 2007; Looy and Stevenson, 2014). The South Ash Pasture assemblage is dominated by gymnosperms, including *Pseudovoltzia*-like ovuliferous cones and dwarf shoots, with five fused rounded elements.

The Tregiovo floras are the earliest deposit in eastern Euramerica that includes dwarf shoots and branch systems that are characteristic for both walthian and voltzian taxa. Originally established for the late Permian taxa in Europe, the Majonicaeace have been documented also from the Kungurian of North America (Looy, 2007; Looy and Stevenson, 2014). The occurrence of *Dolomitia* in Tregiovo is the oldest well-dated record of the genus, the range of which now extends down to the Kungurian. Four members of the Majonicaeace can now be traced back to the latest early Permian, i.e. *Manifera* and *Lebowskia* from North-Central Texas, and *Dolomitia* and cf. *Pseudovoltzia* from the Southern Alps.

The coeval nature of the Texan and Tregiovo floras provides strong evidence that the transition from walthian to voltzian conifer dominated floras may have happened roughly at the same time across the entire Euramerican region. It is not clear, whether the vegetational change in the Tregiovo region was one within ecosystems, or a shift in biomes. Paleoclimatological data from western Euramerica (the Midland Basin) indicate a change from seasonally dry to non-seasonal climates from the latest Kungurian to early Wordian times. (e.g., Montañez et al., 2007). It is not unlikely that, just like in the Midland Basin, shifts in the amount of precipitation, the degree of seasonality, and temperature caused the floral transition in the Tregiovo Basin.

At present, the geographic region and the timing of the origin of the more derived voltzian conifers is still unknown. Evidence so far suggests that this group evolved in seasonally-dry habitats in extrabasin areas in Euramerica where chances on being preserved were very small (Looy et al., 2014). The precocious glimpses of voltzian conifers in Tregiovo, and recently discovered voltzian-like conifers from a dry coastal setting of Asselian age (early Cisalurian) in New Mexico (Falcon-Lang et al., 2015), show that voltzian conifers were present in the landscape much earlier than previously thought.

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